Brook trout (*Salvelinus fontinalis*) spawning habitat in a Boreal stream: the effects of groundwater, hyporheic flow and fine sediment loadings on reproductive success

Jan Franssen

Department of Geography, McGill University, Montreal

Submitted October 2011

A thesis submitted to McGill University in partial fulfillment
of the requirements of the degree of Doctor of Philosophy

Abstract

The reproductive success of brook trout (*Salvelinus fontinalis*) populations, like those of other salmonid species, is dependent on the availability and quality of spawning/incubation habitats. For brook trout in particular substrate composition and groundwater-hyporheic flow characteristics are key abiotic factors influencing both the suitability of lotic spawning habitats and the survival of embryos nested within these habitats. Egg-to-emergence survival has been shown to be negatively related to substrate fine sediment concentrations and positively related to interstitial flow velocity. Both substrate composition (through filtering effects) and interstitial flow are also thought to influence the susceptibility of egg pockets to fine sediment infiltration. The objectives of this doctoral study are to clarify the roles of groundwater and hyporheic flow in brook trout redd site selection; as well as the effect of substrate composition and interstitial flow on the survival of embryos to emergence. A complementary objective is to determine how local hyporheic flow and substrate composition influence fine sediment accumulation within reproductive habitat. To test various hypotheses, we conducted field studies in brook trout spawning streams situated within a boreal forest system in Quebec, Canada. We complemented these field studies using laboratory and field experiments. Our field studies indicated that in these boreal forest streams, brook trout did not exhibit a systematic preference for spawning in microhabitats dominated by upwelling groundwater. Redds were located in sites with both upwelling groundwater and downwelling surface water and we observed that the origin of the water resulted in distinct thermal regimes and incubation rates within the reproductive habitat, suggestive of possible alternate life history strategies within the population. The results of our laboratory experimentation revealed that high embryo mortality in fines-rich-substrates could not be mitigated by increased flow velocity/oxygen flux through the egg pocket. Furthermore, CT Scans of laboratory incubation substrates support entombment effects, as mortality was related to the density of 3-4 mm pore spaces suitable for emergence. Field experiments suggested that the ingress of fine sediments into redds is primarily a gravity driven process influenced by the size of the infiltrating fine sediments and the size of the substrate pore spaces as controlled by filter fraction content. This infiltration process was not influence by the intensity of vertical or horizontal hydraulic gradients, at least over the range of gradients that were observed in the brook trout reproductive habitats studied here.

Resume

Le succès de la reproduction de l'omble de fontaine (*Salvelinus fontinalis*), comme ceux d’autres espèces salmonidés, est dépendant de la disponibilité et la qualité des l'habitat de fraye/incubation. Pour l'omble de fontaine, en particulier, la composition du substrat et l’écoulement des eaux souterraines et hyporhéiques sont des facteurs clés qui influencent à la fois la convenance d’habitat lotiques et la survie des embryons imbriqués dans ces habitats. La survie à l'émergence été démontrée être négativement liée à la concentration des sédiments fins dans les substrat et positivement liée à la vitesse d'écoulement interstitiel. La composition du substrat (par des effets de filtrage) et le flux interstitiel sont suggérés dans la litérature comme influencant la susceptibilité des poches d'œufs à l'infiltration de sédiments fins. Les objectifs de cette étude de doctorat sont à clarifier les rôles des ressurgences souteraines ou de l’écoulement hyporhéique dans la selection des nids par l'omble de fontaine; et l'effet de la composition du substrat et l'écoulement hyporhéique sur la survie des embryons à l'émergence. Un objectif complémentaire est de déterminer comment l'écoulement hyporhéique et la composition du substrat influencent l'accumulation de sédiments fins dans l'habitat de reproduction. Pour tester différentes hypothèses liées, nous avons mené des études de terrain dans les ruisseaux d’un ecosystème de forêt boréale dans la Réserve Faunique des Laurentides au Québec, Canada où nous avons observé les frayères de l'omble de fontaine. Nous avons complété ces études de terrain à l'aide d’experiences en laboratoire et sur le terrain. Nos études sur le terrain a indiqué que dans ces ruisseaux, l'omble de fontaine n'a pas démontré une préférence systématique pour les microhabitats de fraye sous l'influence des ressurgences d’eaux souterraines. Les nids étaient situés a la fois dans des sites de ressurgence et dans des endroits ou les eaux de surface pénètrent dans le lit. Nous avons observé que l'origine de l'eau était liée à des régimes thermiques distincts dans l'habitat de reproduction. Les résultats de nos incubations en laboratoire ont révélé que les taux élevés de mortalité ne pouvaient pas être atténués par une augmentation d'écoulement d’eau/ l'oxygène a travers le nid. Par ailleurs, les données sur la structure des substrat d’incubation collectées en trois dimensions (3-D) par tomodensitométrie assistée par ordinateur (TAO) ont confirmée un effet de ‘mise au tombeau’, indiquée par le lien entre la mortalité des embryons et la densité des ‘megapores’ de 2-3 mm qui sont appropriés pour l'émergence. Les expériences de terrain ont suggéré que la pénétration des nids par les sédiments fins est un processus influencé par la taille des sédiments fins en movement par rapport a la taille de l’espace interstitiel. Ce processus d'infiltration n'etait pas influencé par l'intensité des gradients hydrauliques verticaux ou horizontaux, au moins pour la gamme de gradients observées dans les habitats de reproduction omble de fontaine étudiés ici.

Table of Contents

CHAPTER 4 THE ROLE OF HYPORHEIC FLOW IN BROOK TROUT SPAWNING SITE SELECTION AND ITS EFFECT ON INCUBATION MICROHABITATS IN A BOREAL FOREST STREAM

CHAPTER 5 FIELD STUDY TO ASSESS THE ROLE OF FILTER FRACTION AND UPWELLING-DOWNWELLING FLOW IN CONTROLLING THE RE-INFILTRATION OF FINE SEDIMENT INTO SALMONID REDDS

List of Tables

List of Figures

Acknowledgements

This document is the outcome of an academic journey that began in the autumn of 2005. Along the way I have had the good fortune to be accompanied by two extraordinary mentors in Michel Lapointe and Pierre Magnan. Thank you for providing me with this opportunity and for your generous guidance and support. Thank you to Jeff McKenzie, Normand Bergeron, Wayne Pollard, and Andrea Bertolo whose advice and support is also very much appreciated. Thank you to Ian McKenzie of the University of Waterloo who helped foster my interest in geoscience.

If the manuscript chapters in this thesis were to include acknowledgement sections each would begin with the following two words: Yves Paradis. Without your intelligence, grace and good humour this research would not have been as successful or as much fun. Thank you my friend. I thank Marc Pepino whose similar journey has enriched my own.

While it stood, the “Maison du Nord” was the temporary home/workshop to a fantastic group of students whose efforts made this research possible. I thank: Julien Saint-Laurent, Véronique Boily, Chantal Fournier, Sylvain Thélème, Simon Beaulac, Leonora King, Gabriel Pépin, Jean-Daniel Trottier, Annie Larose, Geneviève Pelletier, Mr. Praxair, and the extraordinary contributions made by Catherine Blais and Patrice Leroux. Merci a les bricoleur superbes Robert Drolet et Gilles Saint-Arnaud de la Université du Québec à Trois-Rivières et Francis Bérube et Marc-Andre Pouliot de Aquartis.

I thank my family: Mom, Dad & Ida, Shannon & Matt, Jeff & Christine, Maya and Elise. Your support was essential. To my dearest Laura, your selfless encouragement shall never be forgotten. Thank you for your understanding, patience and love. Thank you to Helen & Casey for your encouragement. To my

friends I thank you for your support and most of all your patience. There is much catching up to do.

Most of this thesis was written at La Grande Bibliothèque de Montreal. Thank you to the staff, builders, architects, and citizens of Québec ‘pour créer un tel espace merveilleux’ where one can go to learn, think and create. The ethos represented in this building is a reason I’m pleased to call Montréal and Québec my home. Thank you to John Richards and KEXP for providing the soundtrack.

The research presented in this thesis was supported by funds provided from the Ministère des Transports du Québec (MTQ) and grants from the Natural Sciences and Engineering Research Council of Canada to my co-supervisors Michel Lapointe and Pierre Magnan. A final, but no less sincere, thank you to Martin Lafrance, Yves Bedard, and the MTQ advisory committee for their interest in this research. There is more to come!

Contribution of Authors

Chapters 3 to 5 have been written as manuscripts in a format suitable for publication in peer-reviewed journals. These three chapters are co-authored by my supervisors Michel Lapointe and Pierre Magnan. Both aided in the planning of this research, the refining of the arguments presented, the editing of manuscripts, and the provision of laboratory resources and financial support.

The formulation of objectives and hypothesis, the implementation of research plans, and the analysis and interpretation of the results are my own contributions. However, these actions were not carried out in isolation and I have benefited greatly from many fruitful discussions with Michel Lapointe, and my other coauthors whose specific contributions are detailed below.

Chapter 3. “Asphyxiation and entombment mechanisms in fines rich spawning substrates: experimental evidence with brook trout embryos” by Jan Franssen, Catherine Blais, Michel Lapointe, Francis Berube, Normand Bergeron, Pierre Magnan (To be published early in 2012 in the Canadian Journal of Fisheries and Aquatic Sciences). Catherine Blais conducted the laboratory incubation experiment in the freshwater ecology laboratory at the Université du Québec à Trois-Rivières managed by Pierre Magnan. Francis Berube and Norman Bergeron assisted with incubator design and construction. Francis Berube performed the image analysis of the experimental redds using a medical CT scanner. Norman Bergeron provided editing of the manuscript. Michel Lapointe and Pierre Magnan provided discussions and editing of the manuscript. Comments provided by two anonymous reviewers and an associate editor of CJFAS improved the clarity and completeness of this paper.

Chapter 4. “The role of hyporheic flow in brook charr spawning site selection and its effect on incubation microhabitats in a boreal forest stream” by Jan Franssen, Marc Pepino, Michel Lapointe, Pierre Magnan (to be submitted). Marc Pepino conducted the brook charr spawning site surveys. Michel Lapointe and Pierre Magnan provided discussions and editing of the manuscript.

Chapter 5. “Field study to assess the role of filter fraction and upwelling-downwelling flow in controlling the re-infiltration of fine sediment into salmonid redds” by Jan Franssen, Michel Lapointe, Pierre Magnan (to be submitted).

Chapter 1 Introduction and objectives

1.1 Thesis structure

This thesis is comprised of three distinct manuscripts (chapters three through five) written in a format suitable for submission and eventual publication in peer-reviewed journals. The three manuscripts are presented as stand alone documents with the exception that: i) all references are provided at the end of the thesis; and ii) each manuscript chapter includes a preface section explaining how the detailed hypothesis tested in each of these studies/experiments relate to those in the other two manuscript chapters. The thesis includes an introductory chapter (chapter one) which outlines the main objectives of this work and briefly summarizes the key findings of this doctoral research. A description of the field study sites is also provided along with a selection of site photographs. A literature review is provided in chapter 2.

1.2 Introduction

Stream morphology is determined by a dynamic interaction between hydrologic, geomorphic and biological processes (Leopold et al 1964, Thorne 1997). This dynamic interaction continually shapes and structures stream channels, thereby creating an evolving mosaic of habitat types; which in turn influences the distribution, abundance and diversity of stream organisms (Frissell et al 1986; Montgomery 1999). This close association between habitat availability and the structure of stream biotic communities is representative of stream organisms from algae to fish (Bunn and Arthington 2002). Disturbances that alter the quantity or quality of required habitats have been shown to alter species abundances (Schlosser 1999).

Disturbance has been defined as a relatively discrete event in time that disrupts ecosystem, community, or population, and that changes resources, availability of substratum, or the physical environment (Resh et al. 1988).

Disturbances may be natural events such as fire, drought, or flood. Alternatively, they may be anthropogenic activities such as: agriculture, urbanization, or logging. These types of anthropogenic disturbance tend to be particularly disruptive to lotic ecosystems because they increase the intensity of landscape erosional processes, which can dramatically increase the quantity of sediment being transported into nearby streams. Increased sediment concentrations can negatively impact aquatic species by causing respiratory impairment, reduced feeding and growth (Waters 1995, Wheeler et al 2005), and may be particularly disruptive to fish reproductive success where fine sediments clog streambed spawning/incubation habitats. Elevated concentrations of fine sediment in incubation substrates may increase embryo mortality by interrupting the vital flow of interstitial water thus reducing the oxygen flux to developing embryos (Chapman 1988).

The viability of brook charr populations, and those of other salmonid species, is dependent on the availability and quality of spawning/incubation habitats. Substrate composition is a key abiotic factor influencing both the suitability of lotic habitats for spawning and the survival of embryos nested within these habitats. Redd excavation and embryo burial reduces the proportion of fine sediment within the incubation microhabitat as fines mobilized by the spawner’s digging are subsequently flushed downstream (Everest et al. 1987; Kondolf 2000). This process is thought to improve the quality of the incubation environment. However, during the period of embryo incubation (which may last 8 months in some northern habitats) fine sediment may re-infiltrate into the redd. Numerous studies have demonstrated a negative relationship between salmonid embryo survival and the proportion of fine sediment within the incubation environment. Landscape disturbances which increase fine sediment loading to streams may therefore degrade downstream spawning/incubation habitats and threaten the existence of local salmonid populations (Turnpenny and Williams 1980).

The primary objective of this doctoral study is to improve our understanding of the mechanisms by which increased sediment loading to streams may influence the reproductive success of brook trout. The processes controlling stream sediment loadings and those influencing reproductive success occur at distinct spatial scales. Stream discharge, geology, topography, vegetation types, and land uses influence the supply of fine sediment within the catchment and within the specific segments of the channel network (i.e., the largest spatial scales within the stream system hierarchy; sensu Frissell et al. 1986). However, the effects of fine sediment on an embryo survival occurs at the scale of the substrate interstices within redd microhabitats (i.e., the smallest spatial scale within the channel network). How physical habitat factors influence salmonid redd site selection and early life cycle fitness remains a complex topic that is not fully understood (Guillemette et al. 2011; Lapointe, In press). This doctoral study thus focuses on improving our understanding of the microhabitat conditions (e.g., local bed morphology, hyporheic conditions) in brook trout spawning sites, as the process occurring at this spatial scale may affect egg pocket fines infiltration, the thermal regime experienced by developing embryos, and embryo mortality. Knowledge gained from studying microhabitats scale processes will help to clarify the link between the spatially disparate processes of watershed scale fine sediment transport and the reproductive success of brook charr.

1.3 Thesis objectives and key findings

Clarifying the linkage between watershed scale fine sediment transport and reproductive success requires a detailed understanding of the physical characteristics of spawning habitats (the focus of Chapter 4); the processes controlling fines infiltration into incubation substrates at these sites (the focus of Chapter 5); and the complex mechanisms by which infiltrating fine sediment interacts with interstitial flow velocity to influence embryo mortality (the focus of Chapter 3). To advance our understanding of these topics we conducted a series of observational studies and field/laboratory experiments, and tested specific hypotheses concerning each of these topics. Specific hypothesis are detailed in the concluding paragraph of the introduction section in each of the manuscripts (Chapters three through five). The subsections below state the specific research objective addressed in each of these chapters. I also provide a brief rational for pursuing each of the stated objectives and present the key findings that resulted from this research.

1.3.1 Research Objective #1: Characterization of brook trout spawning microhabitats in a boreal system (Chapter 4)

While freshly created salmonid redds are relatively winnowed of fines, fines infiltration during the winter long incubation period is a key process driving embryo mortality (Chapman 1988; Lisle 1989; Lapointe et al. 2004). The physical characteristics at spawning microhabitats (e.g., upstream fines supply, flow hydraulics, coarse sand-granule filter fraction content in the substrate, upwelling and downwelling flow) may influence the infiltration of fine sediments into incubation microhabitats. These characteristics are investigated in Chapter 4. Although the complete causal mechanism(s) of brook trout redd site selection have yet to be determined, it is hypothesized that site selection is a behavioral response to environmental cues that ensure the female has positioned the redd in a microhabitat that will provide optimal conditions for embryonic development (Bjornn and Reiser, 1991). A strong association between brook trout redd-site selection and the presence of upwelling groundwater has frequently been reported (see review in Guillemette 2011; Van Grinsven et al. in press). Groundwater is thought to provide more stable thermal regimes throughout the incubation period (Baxter and McPhail 1999). Brook trout are an ideal species with which to evaluate the potential of upwelling groundwater to hinder the infiltration of fine sediment into gravel bed substrates (Schalchli 1992; Curry and MacNeill 2004). A key finding presented in Chapter 4, are field observations suggesting the existence of distinct reproductive strategies within a brook trout population that spawn within a single boreal forest stream. Redds were located at sites with contrasting thermal regimes that would appear to significantly influence the phenology of hatching and emergence.

1.3.2 Research Objective #2: Improve understanding of the physical processes controlling fines infiltration into incubation substrates (Chapter 5)

Early flume experiments conducted by Einstein (1968) and Beschta and Jackson (1979) indicated that a predominant factor affecting fines infiltration into gravel bed substrates was the size ratio between the diameter of the infiltrating sediments and the diameter of the particles comprising the bed. This finding was confirmed by more recent laboratory experiments (see review by Gibson et al. 2009). Although numerous laboratory studies have characterized the grain size controls affecting the infiltration of fine sediment into gravel bed substrates, few field studies have investigated fines infiltration into actual spawning/incubation microhabitats. In natural channels substrate composition is more varied and fines infiltration may be influenced by other factors such as the presence of upwelling (or downwelling) flow through the bed. It has been argued that upwelling interstitial flow may hinder downward percolation of fine sediment, while downwelling flows may increase the local, downward flux of infiltrating particles (Schalchli 1992; Curry and MacNeill 2004). Chapter 5 provides original data and analysis regarding fines infiltration into spawning substrates situated across multiple streams. We show in a field setting that upwelling flow did not significantly influence the infiltration of fine sediment (<0.5 mm) into gravel bed substrates. Our results also indicate that fines infiltration is negatively related to the proportion of filter sized particles (0.5 - 4 mm) within gravel bed substrates, and that bed surface mobilization may enhance the deeper infiltration of fines.

1.3.3 Research Objective #3: Investigate the mechanisms by which infiltrating fine sediment interacts with interstitial flow velocity to influence embryo mortality (Chapter 3)

The two key mechanisms by which fine sediment is thought to induce embryo mortality are asphyxiation and entombment (Kondolf 2000, Jensen et al.

2009). Asphyxiation is related to oxygen flux to the developing embryos which is a function of interstitial flow velocity and oxygen content. Entombment refers to mortality caused by the prevention of emergence. The egress of hatched embryos from gravel bed substrates is related to the availability of large diameter macropores or loose substrates. The effect of these two mortality-inducing mechanisms may occur at distinct stages of embryo life and may not be similarly affected by the physical characteristics of selected redd sites. Egg-to-Emergence (EtE) survival has repeatedly been related to substrate composition and interstitial flow velocity (see reviews by Chapman 1988; Bjornn and Reiser 1991; Guillemette et al. 2011). However, in natural sediments these variables are correlated through permeability effects and thus, in previous studies, asphyxiation and entombment are generally confounded as mortality inducing mechanisms. The incubation experiments presented in Chapter 3 were designed to directly examine the relationship between interstitial flow velocity and survival at fixed substrate composition, which is necessary to decouple the effects of entombment and asphyxiation. The key finding in Chapter 3 is the demonstration, using medical imaging technology, of a positive relationship between egg-to-emergence survival and the density of substrate macropores large enough to permit larvae emergence. To our knowledge this is the first study to show direct a relationship between survival and the size and density of interstitial pore spaces.

1.4 Study site

Field work was carried out in the Réserve Faunique des Laurentides (RFL), a 7,861 km^2 wildlife reserve situated north of Quebec City, Canada (47^{0}35’N, 71^{0}13’W). Study sites were accessed via Hwy 175 which traverses the RFL from north to south linking the Ville du Québec with the Ville de Chicoutimi (Figure 1.1). The highway passes through a dissected plateau landscape with elevations culminating at over 1000 m above sea level. The RFL nature reserve was established for the conservation and management of natural resources in this area. There is an abundance of lakes, streams and wildlife in the reserve, which is intensely utilized by sport hunters and fishers, as well as cross-country skiers and

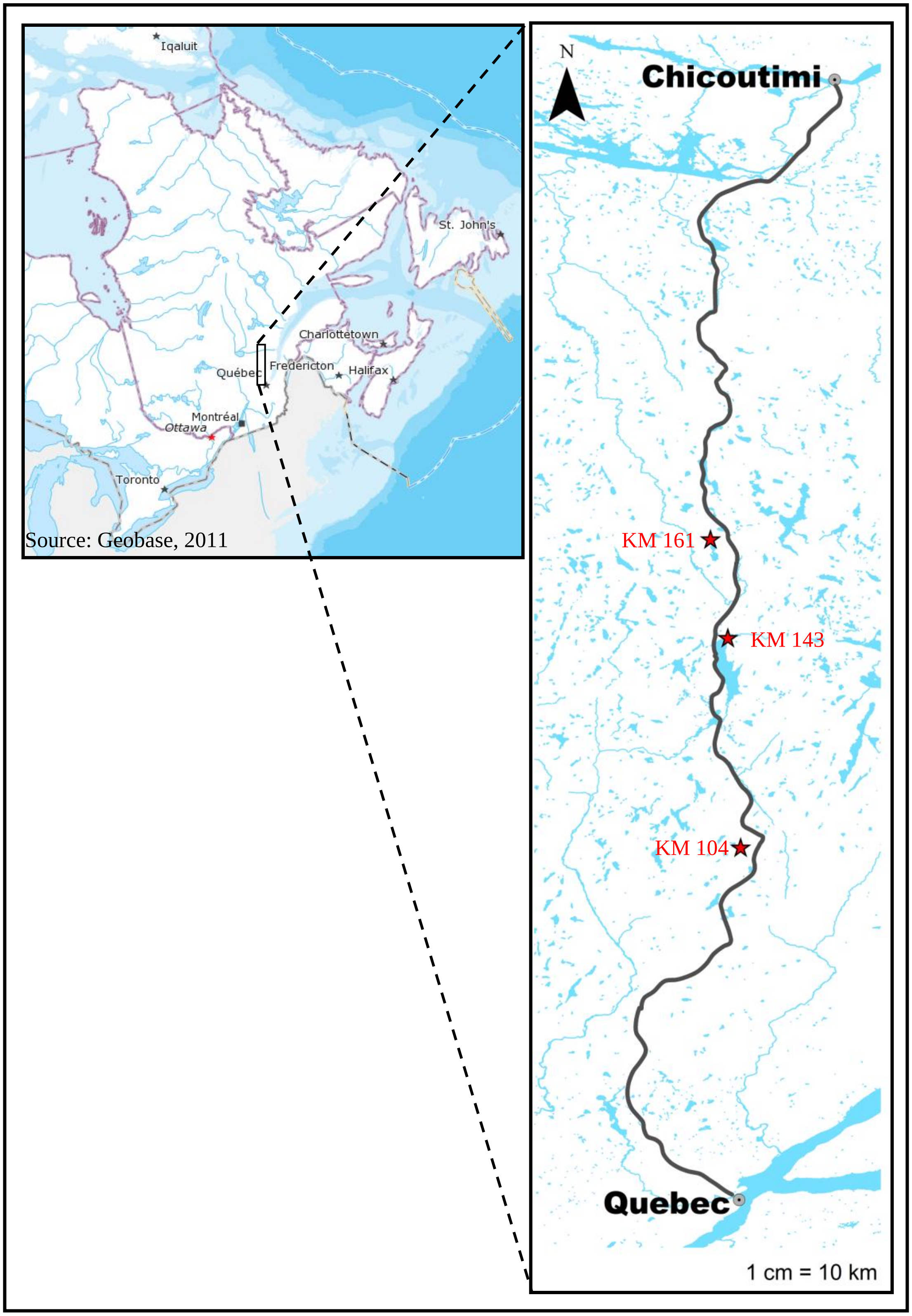


Figure 1.1. Location of field study sites (red symbols). Right map shows the route of highway 175 (grey line) between Quebec City and Chicoutimi, Quebec.

outdoor enthusiasts.

The RFL is situated in a relatively high precipitation (for Southern Quebec) continental mountain climate, with an annual precipitation of 1589 mm, abundant winter snowpak (mean snow depth at February month-end is 86 cm), and an average annual air temperature of 0.3ºC (Environment Canada 2007). The annual average soil temperature 5.2ºC (depth of 3 m below surface), as measured at the Foret Montmorency, situated approximately 40 km south of the main study area (Environment Canada 2007). The highest average monthly temperature occurs in June (14.8°C) and the lowest in January (-15.3°C; Environment Canada 2007). Spring melt usually occurs within the month of May and that the elevated discharge associated with the spring melt is generally sustained for approximately one month. Flood flows of a similar (or greater) magnitude can occur between June and November but are of a much shorter duration (Figure 1.2).

In 2006, construction began on a Hwy 175 expansion project undertaken to expand the existing 2-lane highway within the RFL into a 4-lane divided highway. There was considerable concern from stakeholders that the earthworks associated with the highway construction activities would dramatically increase stream sediment loads. An Environmental Impact Assessment of the project (Genivar-Tecsult 2003) identified over 300 watercourses (including lakes, streams and drainage channels) that may be impacted (i.e., those located either adjacent to or traversed by the highway). Fieldwork conducted in the autumn of 2005, and during the summer and autumn of 2006, indicated that the majority of these watercourses are drainage channels that were likely to remain dry throughout the year and therefore are not suitable brook charr habitat. Detailed field evaluation of the watercourses along the existing highway indicated that there were 57 permanent streams, 66 intermittent streams, with a total of 34 streams, ranging in widths from 1 m to 15 m, that are known or potential brook charr habitat. Field studies described in this thesis were conducted at stream sites that had not yet been subjected to construction impacts.

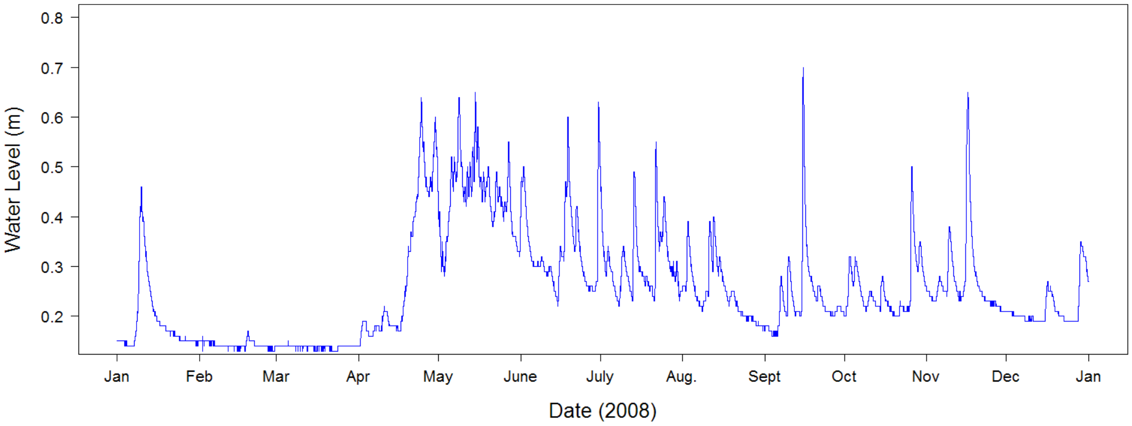


Figure 1.2. Stream hydrograph for the year 2008 (water level in meters above datum) recorded at stream study site KM 143. Note the initiation of the spring snowmelt flood in mid-April following the typical prolonged period of winter baseflow conditions.

The Environmental Impact Assessment that preceded the initiation of the Hwy 175 expansion project (Genivar-Tecsult 2003) identified Brook Charr (*Salvelinus fontinalis*) as the aquatic species most likely to be affected by construction activities. Brook charr are indigenous to eastern North America and are one of the most popular game fishes in eastern Canada (Scott and Crossman 1998). The species is often referred to as a trout due to its resemblance to the European Trout (*Salmo trutta*) (Power 1980). Other common names include: speckled trout, brookie, coaster and speckled charr. The RFL is home to one of the largest allopatric populations of brook charr in North America; with the annual catch from the RFL representing more then 50% of the brook charr caught within Quebec's extensive network of nature reserves (Boivin et al. 1995). Brook charr are also the dominant fish is the RFL representing 98% of the 2002 catch (Gouvernement du Quebec 2003). Brook charr spawn in autumn (when temperatures and daylight are decreasing) in headwater streams or on the shoals of lakes (Power 1980, Scott and Crossman 1998). Egg incubation in redds buried in substrate proceeds over the winter. The incubation period is directly related to water temperature with incubation times ranging from 100 days (at 5°C) to 50 days (10.0°C) (Scott and Crossman 1998). When the eggs hatch the brook charr alevins remain in the gravel until their yolk sac is absorbed after which the brook charr must emerge to begin feeding. Population studies indicate high mortalities during the first months of life, with brook charr seldom living longer than 5 years (Power 1980, Scott and Crossman 1998).

Chapter 2 Literature Review

2.1 Introduction

Since early investigations into the reproductive behavior of salmonids (White 1930; Belding 1934), much knowledge has been gained regarding the factors likely to influence spawning site selection and embryo survival to emergence. The following subsections provide a brief summary of extant literature and findings on the topics of: i) salmonid redd site selection; ii) the effect of fine sediment in salmonid spawning/incubation microhabitats; iii) processes controlling infiltration of fine sediment into gravel bed substrates. More detailed treatment of each of these topics is provided in the Introduction of each of the following three chapters. Much of the literature reviewed pertains to processes applicable to the various species of the family Salmonidae (salmon, trout, charr, whitefishes, and graylings). However, on the topic of redd site selection the focus is on the reproductive traits/characteristics of brook charr (*Salvelinus fontinalis*).

2.2 Redd site selection

Typical salmonid spawning habitats are found in the well oxygenated waters of a gravel bed stream, although certain species may also spawn in gravelly shoals and littoral zones of lakes (e.g., sockeye salmon, brook trout). All salmonid species have the common reproductive behavior of egg deposition within interstices of substrate sediments. Females excavate a pit within the selected spawning substrate in which they lay their eggs, they then backfill the resultant egg pocket thus creating a redd. Embryo burial is a reproductive trait that decreases the probability of embryo mortality due to predation and scour (DeVries 1997; Blanchfield and Ridgway 1999). Depending on size and fecundity, individual females may lay more then 10,000 eggs in a single spawning season (Klemetsen et al. 2003). Such high egg yields are necessary to sustain populations as field studies indicate that salmonid embryo survival to emergence is generally low (i.e., < 30%; Quinn 2005; Blanchfield and Ridgway 2005). It is hypothesized that females can assess the quality of available habitats and select specific spawning microhabitats which have a suite of physical characteristics that will ensure the maximum survival and fitness of their progeny (Fretwell and Lucas 1970; Fleming and Reynolds 2004). Factors cited as influencing habitat quality or as cues in redd site selection include: substrate composition; water depth; water velocity; instream cover; interstitial flow velocity, and the physiochemical properties of hyporheic flow (e.g., temperature, dissolved oxygen concentration). Numerous researchers have sought to establish the specific environmental determinants involved in spawning site selection (see summaries in Bjornn and Reiser 1991; Armstrong et al. 2003; and Guillemette et al. 2011) and this research has provided a broad understanding of spawning habitat preferences. However, many of the physical habitat variables identified are confounded as factors that may influence redd site selection or habitat quality. Thus, controlled experiments are required to disentangle, for example, the effect of dissolved oxygen flux from that of interstitial flow velocity (see discussion in Guillemette et al. 2011).

Previous investigations suggest that the environmental determinants of spawning site selection vary between species (Witzel and MacCrimmon 1983; Geist et al 2002); and among isolated populations of a species due to adaptation to local environmental conditions (Hendry et al. 1998). However, reproductive success for all populations is dependent on the selection of redd sites that will ensure: i) a sufficient flux of dissolved oxygen (DO) to the developing embryos; and ii) a low probability of entombment of hatched embryos. Oxygen flux through the redd is a function of interstitial flow velocity and DO concentration in local hyporheic water. Thus interstitial flow velocity, or correlated environmental cues such as substrate permeability and local water surface slope (i.e., as reflected in water column velocity) are likely to be associated with the process of spawning site selection. The redd locations of some species, such as Atlantic salmon (*Salmo salar*) and Chinook salmon (*Oncorhynchus tshawytscha*), have been associated with proximity to stream morphological features such as point bars, island bars, and pool-riffle transitions where variations in longitudinal water gradients may induce the downward flow of surface water into the streambed (Coulombe-Pontbriand and Lapointe 2004; Giest and Dauble 1998; Moir and Pasternack 2008). Other species, such as brook charr, have been shown to exhibit a preference for sites with upwelling groundwater (Guillemette et al. 2011, Blanchfield and Ridgway 1997). The use of these distinct reproductive strategies is assumed to be a response to local environmental factors that influence embryo survival and fitness. It has been hypothesized that spawning site selection may also involve cues at multiple spatial scales (Baxter and Hauer 2000). However, this hypothesis has not yet been tested across the microhabitat and reach scales.

Early observational studies noted the presence of upwelling groundwater at brook charr spawning sites (White 1930; Hazzard 1932). Almost all subsequent investigations confirmed an association between brook charr redd site selection and the presence of upwelling flow observed either at the scale of the redd or the reach (see discussion in Guillemette et al. 2011). Brook charr's range in eastern North America extends from the mid-Atlantic (40^0N) to northern Quebec (60^0N; Scott and Crossman 1998). Yet, most redd site selection studies have occurred in the southern half of brook charr's range (e.g., Curry et al. 1995; Essington et al. 1998). To our knowledge the study by Curry et al. (2002) discusses the northernmost site (48^0N) at which brook charr spawning/incubation habitats have been characterized. At these sites, redds were not located at groundwater upwellings but rather situated in zones of downwelling surface water. It is unknown if this reproductive strategy is unique to this specific population and stream ecosystem, or if this study suggests that redd site selection in more northern populations is unrelated to upwelling groundwater. The field study presented in Chapter 4 pursues this general question, and tests a number of specific hypotheses related to this topic. At northern latitudes, the temperature of upwelling groundwater through brook charr incubation habitats may be several degrees warmer then that of the surface water. As temperature is the dominant factor controlling rates of embryonic development (Kamler 2002) the thermal regime in the redd is likely to affect the phenology of emergence; with warmer redd temperatures leading to accelerated development rates and thus early hatching (Crisp 1981). Fry mortality in the weeks following emergence is high and presumably exerts a strong selective pressure, thus habitat selection for emergence timing and fry condition at emergence is expected to be strong (Milner et al., 2003).

2.3 The effect of fine sediment on embryo survival to emergence

There is a large body of work associating embryo mortality with the proportion of fine sediment within salmonid incubation microhabitats. Early observational studies indicated that embryo survival was reduced in redds with elevated concentrations of fine sediment (Harrison 1923; Hobbs 1937). Chapman (1988) provided a seminal review of extant studies (see also reviews by Everest et al. 1987; and NCASI 1984) and this synopsis showed that survival to emergence was negatively related to substrate fines content and positively related to associated substrate metrics (e.g., geometric mean grain size; permeability), and also positively related to dissolved oxygen concentrations and interstitial flow velocity within the incubation environment. In much of this early work, embryo survival was modeled in relation to these physical habitat variables using single factor linear regression analyses (e.g., Koski 1966, Cooper 1961)

Recent conceptual models provided by Kondolf (2000) and Greig et al. (2005) show how multiple physical habitat factors (e.g., amount of fine sediment, oxygen concentration, size of framework gravels) are likely to affect the probability of embryo survival through to emergence. These models indicate that fines content can induce mortality through reductions in substrate permeability which reduces interstitial flow velocity/oxygen flux to the developing embryos. As explained by Darcy’s law, substrate fines content (thus permeability) and flow velocity (thus oxygen flux) are correlated as factors influencing embryo mortality. At equal hydraulic gradients, fines rich substrates induce weaker interstitial velocities. Independent of flow velocity, fine sediments may also affect embryo mortality through the physical entombment of hatched embryos. Lapointe et al. (2004) sought to disentangle the effects of substrate fines content from that of interstitial flow velocity/oxygen flux by subjecting substrate mixtures to various hydraulic gradients, creating a range of interstitial flow velocities at fixed substrate compositions. Their results indicated that the effect of flow velocity is nonlinear; beyond a minimal flow rate increased flow velocity did not completely mitigate the mortality of Atlantic salmon (*Salmo salar*) embryos. Thus, contradicting the notion that in all incubation environments increased fines content can be mitigated by elevated gradients maintaining sufficient flow velocity/oxygen flux. It was suggested that mortalities in fines rich substrates with medium to high interstitial velocities may have been due to embryo entombment but this hypothesis was not directly tested.

Entombment effects are related to the size and density of the pore spaces large enough to allow the egress of hatched embryos. Laboratory experiments in glass aquaria have shown that the mobility of hatched embryos is dependent on the size of pore spaces between gravel particles (Dill and Northcote 1970; Rubin 1998). To date there are no known methods to directly measure the size and density of interstitial spaces within actual redds. Instead researchers have relied upon indices such as geometric mean grain size or the Fredle Index (Lotspeich and Everest, 1981) to provide an index for the amount of interstitial pore space. Haschenburger and Roest (2009) suggest that these common substrate indices are imperfect indicators of interstitial pore space. Recently, medical imaging technology (e.g., CT scanner) has been used to provide direct measurements of the interstitial structure of sediment deposits (Montety et al. 2003; Kleinhans et al. 2008). In Chapter 3, we describe how these techniques were applied in the testing of a set of specific hypotheses concerning the mechanisms effecting salmonid embryo survival.

2.4 Fines infiltration into spawning gravels

Whether a particle of silt or fine sand is filtered by, or can percolate through, a gravel bed is determined by the size of the pore openings between the particles that comprise the bed. The complexity in the packing and filling or pore spaces in alluvial mixtures has not been sufficiently investigated (Haschenburger and Roest 2009). Early investigations into the process of fines infiltration into gravel bed substrates were motivated by a desire of researchers to understand how this physical process affected the reproductive success of salmonids (Einstein 1968; Beschta and Jackson 1978). These investigations indicated that the predominant factor affecting the infiltration processes is the ratio between the diameter of the infiltrating fine sediment (d_{load}) and the diameter of the substrate granules (D_{sub}). In a bed of uniform spheres the size of substrate pore constrictions scales with the diameters of the particles comprising the bed (i.e., the framework particles), and is influenced by how tightly these framework particles are packed together (Friggs et al. 2008). Einstein's (1968) experiments showed that that silt sized particles (d_{load} = 0.03 mm) easily percolated through a gravel bed with constituent particles as small as 6 mm (D_{sub} = 6 mm; D_{sub}/d_{load} = 200). Silt particles percolated downward until they reached the base of the flume (i.e., impermeable layer) and thus began to fill the pore spaces from the bottom up. Beschta and Jackson's (1979) experiments showed that infiltrating particles of medium sand (0.5 mm) became trapped in the upper 10 cm of a gravel bed with a median grain size of 15 mm (D_{sub}/d_{load} = 30). This filtration process, where infiltrating fine sediment is retained in the upper layers of a gravel bed, did not occur in runs using fine grained sand (0.2 mm; D_{sub}/d_{load} = 75). Fine grained sand percolated through to the base of the flume and began infilling pore spaces from the bottom up, thus indicating the existence of a process threshold (filtration vs percolation) related to the $D_{sub}:d_{load}$ ratio. Subsequent laboratory investigations confirmed that the $D_{sub}:d_{load}$ ratio influenced whether or not fines percolated through or were filtered by bed sediments (see review of extant studies in Gibson et al. 2009). Using flume experiments researchers also argued that: i) the amount of fines deposition is positively related to the concentration of material in transport across the bed (Carling 1984; Diplas and Parker 1985); ii) that bed mobilization removes fine sediment accumulations from the mobilized layer (Diplas 1991; Schalchli 1992); and iii) that upwelling flow may reduce fines accumulation through an upward drag on settling fines (Schalchli 1992).

There have been few investigations investing the process of fines accumulation in natural channels. Exceptions include Lisle's (1989) investigations using buckets filled with streambed gravels, and Frostick's et al. (1984) more elaborate fine sediment traps installed along a tributary of the River Lee, England. Both of these field experiments revealed that fines sediments tended to accumulate near the top of the streambed thus forming a sand seal. Meyer et al. (2005) also showed that the formation of sand seals may increase the probability of embryo survival by preventing the percolation of fine sediment to the depth of the egg pocket. Lisle (1989) noted in natural channels that the sand fractions in transport are already present in the bed, whereas in flume experiments there is generally little overlap in the grain size distributions of the material comprising the bed and the sediment in motion across it. This suggests that filtration processes (i.e., clogging of the upper layers) are likely to be important in natural channels. However, field researchers have yet to examine the processes of fines infiltration into gravel bed substrates that are representative of actual spawning substrates (i.e., that include at least some proportion of medium and coarse sands < 2 mm). Nor have hydraulic gradients been measured at field sites to examine the potential for interstitial flows to affect the process of fines infiltration. Results of such experiments are presented in Chapter 5.

2.5 Summary thesis outline

The results presented in the following three chapters improve on our knowledge of the physical factors affecting: the early life cycle survival of brook charr; brook charr redd site selection; and the infiltration of fine sediment into brook charr spawning microhabitats. The results presented in Chapter 3 further our understanding of the two key mechanisms (asphyxiation and entombment) thought to induce mortality during salmonid embryonic development. Chapter 4 describes the results of various field investigations into the role of hyporheic flow in brook charr redd site selection and its effect on redd thermal regimes. Our field investigation examining factors controlling fines infiltration into spawning microhabitats is presented in Chapter 5. This chapter focuses on the role of filter fractions and local interstitial flow in modulating the infiltration of fine sediment into spawning microhabitats. Each of the aforementioned chapters has been written and formatted in a style suitable for eventual publication in a peer-reviewed journal. Each chapter includes a preface which describes the status of the manuscript and list of its authours, and presents the context of the manuscript chapter within the overall thesis.

Chapter 3

Asphyxiation and entombment mechanisms in fines rich spawning substrates: experimental evidence with brook trout embryos

3.1 Preface

3.1.1 Manuscript details

This manuscript is authored by Jan Franssen, Catherine Blais, Michel Lapointe, Francis Berube, Normand Bergeron, Pierre Magnan. It has been accepted for publication in the Canadian Journal of Fisheries and Aquatic Sciences and will appear in print in early 2012.

3.1.2 Context within thesis

In the following manuscript we detail the results of a laboratory experiment designed to investigate the distinct physical controls influencing the egg-to-emergence survival of salmonid embryos. Previous work has related embryo survival to various physical habitat factors (e.g., fines content, interstitial velocity), however many of these physical factors are correlated. In this manuscript we focus on the two key mechanisms, asphyxiation and entombment, thought to induce embryo mortality. The results presented in the following chapter link to the topic of redd site selection (Chapter 4) by improving our understanding of how the physical characteristics of selected spawning/incubation habitats affect survival during embryonic development, and the fitness of larvae emerging from redds. These results also link to the topic of fines infiltration into spawning gravels (Chapter 5) by substantiating key thresholds in various substrate metrics (e.g., percent fine sediment under 0.5 mm; substrate permeability) that are likely to distinguish high survival from low survival substrates.

3.1.3 Abstract

We investigated the distinct physical controls causing entombment and asphyxiation, the two key mechanisms influencing salmonid Egg-to-Emergence (EtE) survival. Entombment occurs when sediment blocks the interstitial pathways (macropores) that larvae use to emerge from the streambed while asphyxiation is related to oxygen flux, a function of interstitial flow velocity. EtE survival has already been related to substrate composition and flow velocity. However, in streambed sediments these variables are correlated and few studies have examined the sensitivity of EtE survival to changes in velocity and oxygen flux at fixed substrate composition, and EtE survival has not yet been directly related to the size and density of substrate macropores. We incubated brook charr (*Salvelinus fontinalis*) embryos in artificial redds with a range of sediment compositions and hydraulic gradients to examine independently the effects of substrate composition, macropore geometry and flow velocity on EtE survival, emergence timing and fry condition. In situ measurements of macropore size were obtained from images generated by a medical CT scanner. Despite high water oxygen concentrations we observed that entombment or blockage effects caused high embryo mortality in fines rich substrates with few large macropores, and triggered early emergence of rare survivors. These outcomes could not be mitigated by increased flow velocity and oxygen flux to the egg pocket.

3.2 Introduction

Assessing the quality of salmonid incubation habitats requires an understanding of the controlling factors and mechanisms that influence both the survival rates and the fitness of individuals emerging from these microhabitats. Two of the primary mechanisms causing reductions in salmonid Egg-to-Emergence (EtE) survival are: i) asphyxiation, and ii) entombment (Kondolf 2000, Wu 2000, Greig et al. 2007). Entombment occurs when the macropores that larvae (sensu Balon 1975) use to emerge from the streambed are too small or have been clogged with fine sediment. Asphyxiation is related to oxygen flux through the incubation microhabitat which is a function of both dissolved oxygen concentration and interstitial flow velocity. EtE survival has been shown to be both negatively related to substrate fines content and positively related to flow velocity (see reviews by Chapman 1988; Bjornn and Reiser 1991; Guillemette et al. 2011). In streambed sediments flow velocity and fines content are correlated as bed permeability is negatively related to fines content. Thus asphyxiation and entombment are confounded as mechanisms leading to early life cycle mortality.

These two mortality-inducing mechanisms may occur at distinct stages of embryo life and may not be similarly affected by the physical characteristics of selected redd sites. The effects of entombment occur post hatching. Asphyxiation may occur at any stage when oxygen flux drops below critical thresholds for survival. Low oxygen flux may be related to low interstitial water velocities or low oxygen concentrations, or to the effect of silt and clay sized particles enveloping the embryo and reducing oxygen exchanges across the embryo membrane (Greig et al. 2005; Finn 2007). Moderate reductions in streambed permeability due to higher fines content can in theory be mitigated by the selection of redd sites with stronger hydraulic gradients (stronger upwelling or downwelling zones, steeper bar complexes) that increase flow velocity and thereby oxygen flux through the egg pocket (Storey et al. 2003; Coulombe-Pontbriand and Lapointe 2004; Tonina and Buffington 2007). While sufficient oxygen flow may allow embryos to survive to the later stages of embryonic development, entombment may occur due to the post-spawning deposition of finer grained sediments within the gravel interstices. In contrast to asphyxiation, entombment may not be mitigated through site selection for stronger hydraulic gradients.

Although fines content affects both macropore availability (thus entombment) and interstitial flow/oxygen flux (thus asphyxiation) few experiments have directly examined the relationship between interstitial flow velocity and survival at fixed substrate composition, which is necessary to decouple the effects of entombment and asphyxiation. Interstitial flow velocities were measured in several laboratory experiments examining the effect of substrate composition on EtE survival (Reiser and White 1988, Bennett et al. 2003). However, because the hydraulic gradients were constant across treatments, the reported flow velocities were directly related to changes in substrate composition and permeability. The results obtained in a field experiment (Curry and MacNeill 2004) suggest that increased flow velocity does improve survival to emergence in substrates of broadly similar composition. However, in the laboratory incubations of Lapointe et al. (2004) where controlled hydraulic gradients allowed flow velocities to vary independently of substrate composition, results indicated that in fines rich incubation substrates, increased flow velocity (beyond a minimal flow rate) does not completely mitigate the mortality of Atlantic salmon (Salmo salar) embryos, contradicting the notion that survival is positively related to flow velocity and oxygen flux in all incubation environments. The authors suggested that this velocity independent mortality may be due to an embryo entombment effect but did not directly test this hypothesis.

Although entombment effects should be related to the size and connectivity of the largest interstices within the streambed, these structural factors have not yet been directly investigated. The pore size in compact assemblages of equally sized grains is directly proportional to the diameter of the grains (Frings et al. 2008). EtE survival experiments conducted with treatments of clean, uniform gravels (i.e., same diameter gravel with no sand or silt; Witzel and MacCrimmon 1983; Sternecker and Giest 2010) show that macropore size, in itself, has a strong influence on EtE survival thus confirming that entombment is a distinct process from asphyxiation. However, entombment effects are not as easily distinguished in most incubation experiments which use treatments consisting of heterogeneous mixtures that include sand and silt sized fractions (<2 mm) which are more representative of conditions observed in actual incubation microhabitats and in which mortality may be caused by asphyxiation.

Increased fines content has also been observed to affect the timing of larval emergence. Researchers have observed that elevated fines content delays emergence (Hausle and Coble 1976) presumably by impeding the egress of larvae. However, others researchers have observed the opposite effect of premature larvae emergence in fines rich substrates with prematurely emergents exhibiting physical characteristics indicating that they are at an earlier stage of development (i.e., shorter in length, larger yolk sacs; Witzel and MacCrimmon 1983). It is uncertain whether premature emergence is a response triggered by: i) insufficient oxygen flux, or ii) a lack of sufficient macropore space within the incubation environment.

This study presents experimental evidence clarifying which physical factors affect these two mortality-inducing mechanisms. To better disentangle the effects of substrate composition, macropore sizes, and interstitial flow intensity on salmonid EtE survival we incubated brook charr (*Salvelinus fontinalis*) embryos in artificial redds with a range of fine sediment compositions across a range of hydraulic gradients. The timing of emergence and morphological indicators of larvae development were also measured. EtE survival has generally been related to a variety of compositional metrics (e.g., median grain size (D_{50}), geometric grain size (Dg), percentage finer than 0.85 mm) that can only serve as surrogates for the actual structure of the interstitial space. Three-dimensional images of the artificial redds were generated using a medical CT scanner that allowed direct in situ measurements of macropore volume and structure.

This study aims to test the following specific hypotheses: i) increases (from medium to high) in hydraulic gradient and flow velocity do not improve EtE survival in incubation microhabitats in which there are elevated proportions of sand and silt; ii) EtE survival is positively related to the size and density of substrate macropores large enough to allow larvae emergence; iii) the reduction in large pore spaces associated with increasing proportions of fine sediment induces the premature emergence of larvae; and iv) the physical characteristics of incubation microhabitats influence the morphological characteristics of larvae at the time of emergence; prematurely emerging larvae have shorter body lengths and larger yolk sacs than larvae emerging after a complete incubation period .

3.3 Materials and Methods

We manipulated interstitial flow velocity and substrate composition by crossing a hydraulic gradient treatment (3 levels) with a sediment treatment (16 levels) that was nested within each of the hydraulic gradient treatments. The experiment was conducted between November 2007 and March 2008 at the freshwater ecology laboratory at the Université du Québec à Trois-Rivières. Brook charr (*Salvelinus fontinalis*) embryos were incubated in sediment mixtures contained in one of 47 cylindrical incubators (dia. = 15 cm, height = 30 cm). The incubators were open at the top and connected to one of six flow-through cylinders. Each incubation array consisted of 8 incubators nested around each flow-through cylinder (Figure 3.1; one incubator was found to be defective and removed from the experiment). Six incubation arrays were situated in one of two large rectangular basins. A static water level was maintained in each of the large rectangular basins which submerged all incubators but not the flow-through cylinders. Water levels in each of the flow-through cylinders were maintained at a lower level than that of the rectangular basins by means of an internal adjustable overflow pipe (Figure 3.1). The resulting hydraulic gradient induced the downward flow of water through the incubators. For the purpose of statistical analysis (see below) the incubators are considered subsamples of the incubation array to which the same vertical hydraulic gradient (VHG) treatment was applied. A pair of incubation arrays were subject to one of three VHGs, calculated as the change in hydraulic head (Δh) over the distance (ΔL) between the top of the

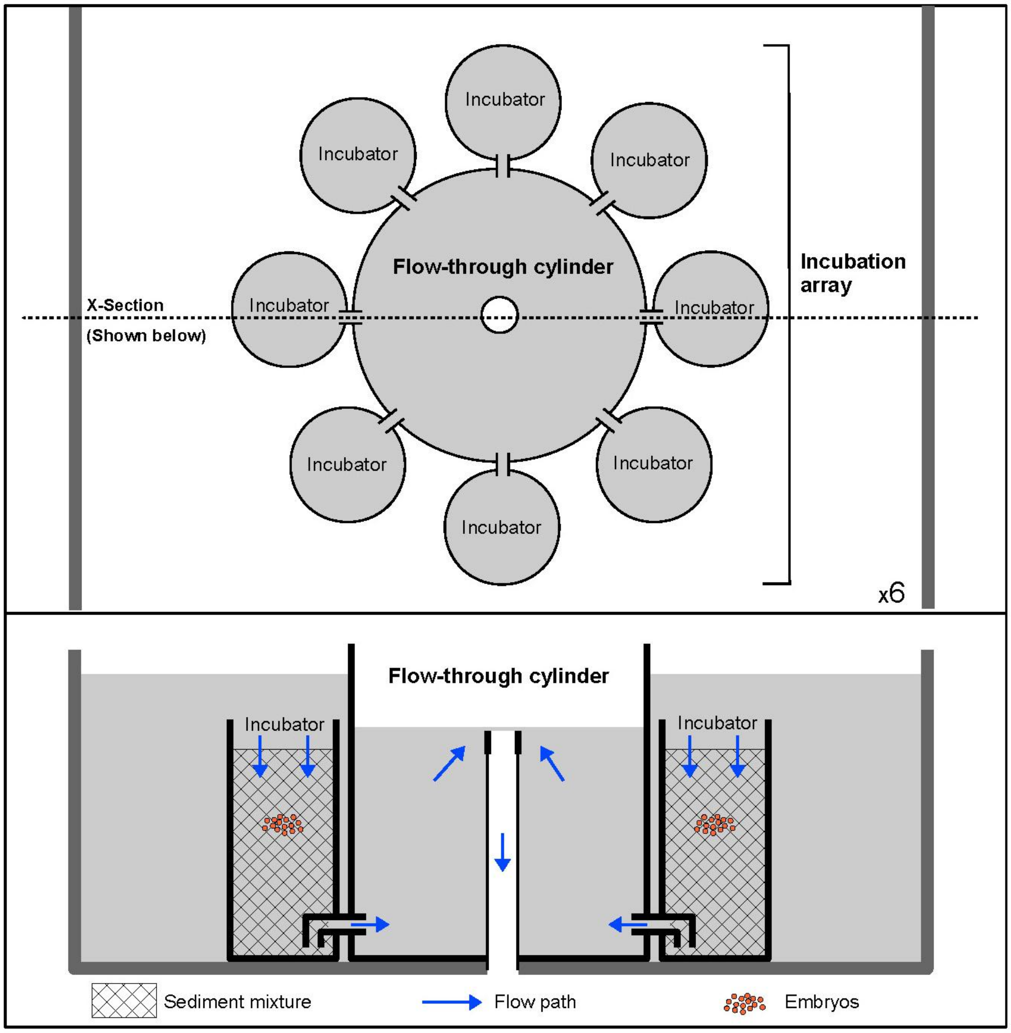


Figure 3.1. Diagram showing: i) aerial perspective of an incubation array (n=6) consisting of eight incubators connected to a flow-through cylinder situated within a larger rectangular basin; and ii) cross section showing flow paths and position of embryos within incubators.

sediment mixture and the outlet in each of the incubators ($\Delta h/\Delta L = 0.009, 0.048, 0.143$). These hydraulic gradients were chosen to span the range of VHG measured with piezometers at brook charr spawning sites within the Réserve Faunique des Laurentides (RFL; a 7861 km² wildlife reserve situated north of Québec City, Québec, Canada). To ensure removal of water borne pathogens, water flowing through the system was passed through a cartridge filter, biological filter and a UV lamp. The water circulation system was equipped with refrigeration units which maintained a constant water temperature of 7°C (± 1°C). Water temperature, water level, dissolved oxygen concentration; pH and conductivity were continuously monitored to ensure that these physical parameters were held constant throughout the experiment. A 12:12 photoperiod was maintained in the laboratory during the experiment.

Sediment mixtures were prepared with sand and gravel extracted from a point bar located along a brook charr spawning tributary of Lake Jacques-Cartier, RFL. Grain sizes larger than 32 mm were removed from the source sediment and the remaining sediment was dry sieved at the following size boundaries: 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, 0.09, 0.063 mm, and silt (<0.063 mm). Sixteen distinct mixtures were then prepared to be representative of the complete grain size distributions previously measured at known brook charr spawning sites in the RFL. The percent of fine sand and silt were augmented in some of the mixtures to simulate an increase in substrate fine sediment concentration that could result from increased anthropogenic sediment loading into spawning microhabitats. Mixtures contained one of four concentrations of silt (under 0.063mm: 0.2, 1.4, 2.6 and 3.8% by weight) and one of four concentrations of river bed sands (0.063-2mm: 10, 20, 30, 40% by weight). The sand fraction was comprised of the following size classes: 0.065–0.09 mm (0.5%), 0.09–0.13 mm (1.5%), 0.13-0.25 mm (9%), 0.25-0.50 mm (23%), 0.5-1.0 mm (33%), 1-2 mm (33%). The four gravel size fractions were mixed in the following percentages: 2-4 mm (15%), 4-8 mm (20%), 8-16 mm (35%), 16-32 mm (30%). The gravel component in each mixture was adjusted relative to the percentage of silt and sand so that the %silt +

%sand + %gravel = 100. One of each of the 16 mixtures was randomly assigned to each of the 16 incubators, in each of the three VHG treatment groupings. Details of the grain size distributions were used to calculate the following common substrate metrics: median grain size (D_{50}), geometric mean grain size (Dg), D_{25}, D_{75}, and Fredle Index (Lotspeich and Everest 1981).

Brook charr embryos were provided by the Pisciculture de la Jacques-Cartier (Cap-Santé, Québec) from broodstock taken from Lac Saint-Michel, Québec (Canada). The embryos were transferred to the Université du Québec à Trois-Rivières in one sealed water filled jar that was transported in an insulated container. Prior to their incubation, the embryos were acclimated to the water temperature of the experimental apparatus at a rate of not more than 1°C per hour. The incubators were prepared by layering moistened homogenized subsets of each treatment mixture to a depth of 13 cm above the base of the incubator, 100 embryos were randomly selected and then carefully deposited on top of the sediment and delicately covered with layers of the sediment mixture to a depth of 10 cm (above the embryos). During this process, water levels in each incubator were raised incrementally to prevent damage to embryos and stratification of sediment as it was added to incubator. Each incubator was then fitted with a mesh screen to contain emergent larvae.

The expected hatching date was calculated using equation 1b from Crisp (1981) at a temperature of 7°C. Each incubator was inspected daily for emergent larvae. Emergent larvae were captured with an aquarium net, sacrificed with an overdose of eugenol (anesthetic) and then preserved in a solution of 75% alcohol. Daily enumeration and preservation of emergent larvae continued through the emergence period which was determined to have ended 142 days post fertilization (day of last emerging larvae) after 5 consecutive days of observation revealed no further emergence of larvae.

Prior to the experiment, the porosity (p) of each sediment mixture was estimated using the following calculation: $p = V_v/V_t$; where V_v is the volume of water needed to saturate the total volume (V_t) of the sediment mixture in the incubator. During the experiment, the bulk flow velocity (flow velocity; cm·s) through each of the 47 incubators was estimated by using a seepage bag to measure the discharge ($cm^3 \cdot sec$) from each incubator. The seepage bag was prefilled with a known volume of water and a minimum of three discharge measurements were made per incubator. Flow velocity was calculated by dividing mean discharge by the cross-sectional surface area (cm^2) of the incubator. The hydraulic conductivity (K) of each incubator was then estimated using the Darcy equation: $V = -K \cdot (VHG)$; where V is the measured flow velocity and VHG is the vertical hydraulic gradient ($\Delta h/\Delta L$) through each incubator (Fetter 2001). Interstitial flow velocity was calculated by dividing flow velocity by porosity. The permeability (k; cm^2) of each mixture was calculated using: $k = K(\mu/\rho \cdot g)$; where μ and ρ are the dynamic viscosity and water density at 7°C respectively, and g is acceleration due to gravity (Fetter 2001).

Following the completion of the experiment, a series of morphological measurements were made on each emerged larvae (n=995); total weight (0.0001g), total length (TL), tip of the snout to the tip of the longer lobe of the caudal fin, and the length (L) and height (H) of larval yolk sacs (if present) with digital caliper (0.01 mm) and the aid of a 10x microscope. Yolk sac volume (Vy) was calculated as follows: $Vy = (\pi/6) \cdot L \cdot H$ (Vollestad & Lillehammer, 2000). We did not directly measure the width of each larvae but were able to estimate larvae width using the length (measured) to width ratios taken from a selection of reference photographs.

To obtain images of the internal pore structure of the incubation substrates, a selection of incubators (n=16) were submitted for scanning using a medical CT scanner (Siemens SOMATOM Sensation 64). Cross-sectional images (thickness = 0.6 mm) were made perpendicular to the vertical axis of the incubator (n=516). Each image slice was digitized (pixel resolution = 0.5 mm) and a Moore-Neighbor tracing algorithm (Gonzales et al. 2004) was used to estimate the size of the larger individual pores (macropores) for each cross sectional image of the incubator. We define macropores here as any individual pore space greater than the 0.5 mm pixel size, the smallest individual pore size detectable from the image. We defined “megapores” as all the macropores with a cross-sectional area greater than >9.6 mm^2 (equivalent to a diameter of 3.5 mm), a threshold size chosen to reflect the width of the larvae which emerged during this experiment (i.e., 3-4 mm). For each cross-sectional image we calculated the size (mm^2), number and density of megapores.

The relationship between the response variable Egg-to-Emergence (EtE) survival and our experiments fixed effect variables (i.e., % Sand, % Silt, VHG) was assessed using a linear mixed model to account for the nested structure of our experimental design (i.e., incubators nested within experimental units to which the VHG treatments were applied). Selection of the optimal model was based on the top-down protocol described in Zuur et al. (2009) in which the selection process begins with a beyond optimal model containing all the fixed effects, the fixed effect interactions, and the random effect of incubators nested within experimental units. The significance of the random effect and then the fixed effects were determined using a likelihood ratio test with the least significant of the non-significant terms (p-value > 0.05) sequentially removed from the beyond optimal model until only significant terms remained (i.e., optimal model). Data exploration revealed a nonlinear effect of sand on EtE survival and therefore sand was modeled as a nominal variable. For the mixed model analysis, the response variable EtE survival (percentage of emergent larvae per incubator as proportion of the number of embryos placed in each incubator) was arcsine transformed and the analysis was completed using the nlme package (Pinheiro et al. 2010) for the statistical software R 2.9.2 (R Development Core Team 2009).

To assess the relationship between EtE survival and various metrics describing substrate composition and flow velocity, we used regression tree analysis (especially useful for the detection of threshold effects) using the RPART package (Atkinson and Therneau, 2000) for the statistical software R 2.9.2 (R Development Core Team 2009). RPART uses a stepwise splitting algorithm to find the value of the explanatory variable that provides the smallest sum of the squared deviations around the mean for the cluster of points on either side of an identified threshold (i.e., split point). We used the cross-validation technique described in De'ath and Fabricius (2000) to select the optimal size of the regression trees. Regression tree analysis provides a goodness-of-fit statistic known as the Proportion of Reduction in Error (PRE) that is equivalent to R^2 from the linear least squares regression method that can be used as an indication of the relative importance of exploratory variables (Zuur et al. 2007). The relationship between larvae morphological features and Emergence Day were analyzed using Generalized Additive Modeling (GAM; Zuur et al. 2009) as data exploration revealed potentially significant nonlinear relationships between the response and explanatory variables. Generalized Additive Mixed Modeling (GAMM; Zuur et al. 2009) was used for modeling the relationship between Emergence Day and substrate metrics to account for both a nonlinear effect between the response and explanatory variables and the random effects of incubators nested within experimental units (described above) and the effect of embryos nested within each incubator. GAM and GAMM analysis were performed using the mgcv package (Wood 2010) for the R software program.

3.4 Results

3.4.1 Effect of sand, silt, and VHG treatments on EtE survival

Overall mean survival across all treatments was 21.3% (SD ±16.3%; range: 0-55%; n=47). The selection of an optimal linear mixed effects model for the response variable EtE survival from the experiments fixed (Sand, Silt, VHG) and random effects (Experimental Unit and Incubator nested within Experimental

Unit) resulted in a model that included the fixed effects Sand (0.063-2 mm; p-value <0.00001), Silt (<0.063 mm; p-value 0.0002) and the random effects of Experimental Unit and Incubator nested within Experimental Unit (p-value 0.0024). Over the range of gradients tested, Vertical Hydraulic Gradient (VHG) did not have a significant effect on EtE survival nor did any of the fixed effect interaction terms which were excluded from the optimal model:

$$\text{EtE survival}_{ij} = \alpha + \beta_1 \text{ x SAND}_{ij} + \beta_2 \text{ x SILT}_{\mathrm{ij}} + a_j + a_{i|j} + \varepsilon_{ij}$$

Where: ij = the i^{th} incubator in the j^{th} experimental unit, $a_j \sim N(0,\sigma_{\text{experimental unit}}^2)$, $a_{i|j} \sim N(0,\sigma_{\text{incubator}}^2)$, $\varepsilon_{ij} \sim N(0,\sigma^2)$; parameter estimates, standard errors, and p-values for the model are provided in Table 3.1. EtE survival was negatively related to both Sand and Silt concentrations and the interaction between Sand and Silt was not significant (p-value > 0.05).

3.4.2 Can flow rate mitigate mortality in fines rich substrates?

Low flow velocities and substrates with a higher proportion of fine sediment were both associated with low EtE survival while high velocities and coarser substrates were associated with higher rates of survival (Figure 3.2a). From first principles (Darcy’s law), flow velocity depends both on: i) applied hydraulic gradient, and ii) on substrate fines content as it determines permeability. Thus inevitably, flow velocity and fines content were correlated across incubators (Pearson correlation coefficient = 0.77; t = 8.33, df = 45, p-value <0.0001). By varying the applied hydraulic gradient (i.e., VHG) across substrate treatments, the results of our linear mixed model (Table 3.1) disentangle these two effects and show that at any given substrate composition increased flow velocity (associated with increasing VHG) did not significantly improve survival. Multiple VHG treatments created similar flow velocities (0.03 to 0.07 mm·s) over a subset of incubators (n=13) spanning the full range of sediment treatments (horizontal band in Figure 3.2a). For this subset, subjected to similar flow velocities and thus

Table 3.1. Linear mixed effects model predicting egg-to-emergence survival as a function of the experiments fixed (sand, silt, and VHG) and random effects.

Model term	Estimate	SE	p-value
Fixed Effects			
Intercept	49.32	3.69	<0.00001
sand	-0.71	0.09	<0.00001
silt	-2.96	0.72	0.0002
Random Effects			
σ	2.53	--	--
$\sigma_{\text{incubator}}$	5.97	--	0.0024
$\sigma_{\text{experimental unit}}$	5.79	--	0.0024

Note: The fixed effect VHG was found not to be significant and was dropped from the model. The random effect of incubator nested with experimental unit was found to be statistically significant using a likelihood ratio test (L-Ratio=10.65, df=2, p-value=0.0024) and was retained in the model.

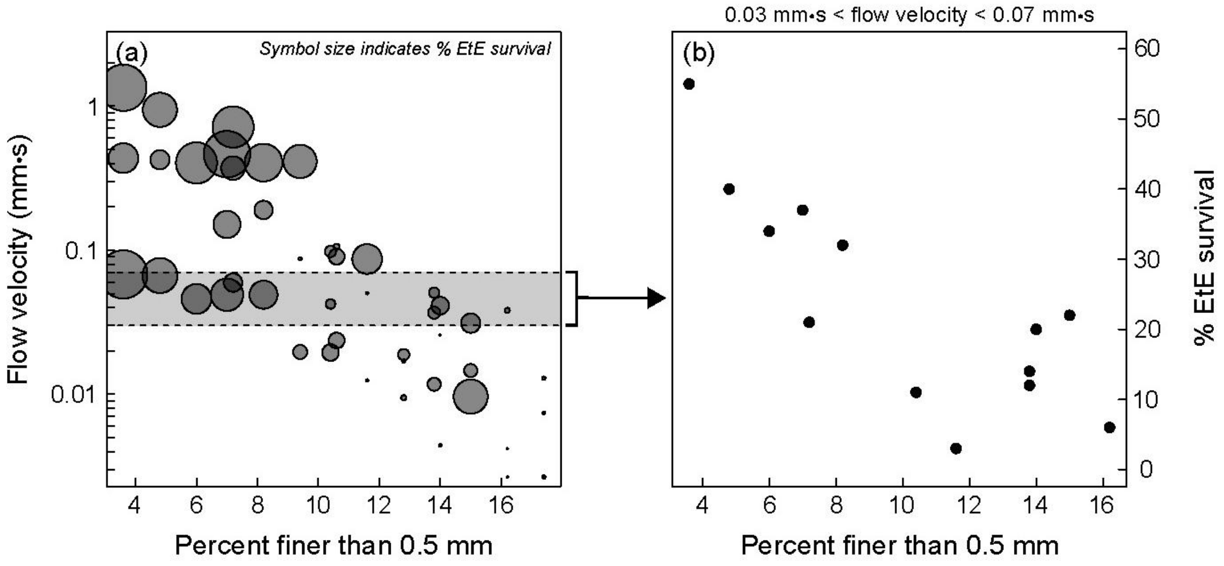


Figure 3.2 (a) Size of symbols indicates % Egg-to-Emergence (EtE) survival (smallest diameter circles indicate < 5% survival and the diameter of the largest circle 55% survival). Low EtE survival associated with both finer substrates (e.g., % finer than 0.5 mm) and lower flow velocities. Flow velocity and substrate composition are correlated. At any given substrate composition increased flow did not improve EtE survival. Multiple vertical hydraulic gradient treatments created similar flow velocities over the full range of sediment treatments (highlighted). (b) Negative relationship between EtE survival and % finer than 0.5 mm for subset of incubators with similar flow velocities.

oxygen fluxes, EtE survival ranged from 3% to 55% (the maximum percentage measured) with increased mortality associated with higher fines content (Figure 3.2b). These higher mortalities cannot be caused by insufficient oxygen flow through the egg pocket.

3.4.3 Threshold conditions for survival

Regression tree analysis of the entire dataset (47 incubators) identified statistically significant thresholds between high and low EtE survival involving both substrate size metrics and substrate permeability (k; permeability) (Table 3.2). Permeability was the explanatory variable that accounted for the greatest proportion of variance in EtE survival (PRE 0.62); significantly higher EtE survival (Welsh's t-test; t=8.38 p-value <0.0001) occurred in substrates with $k > 3.8 \times 10^{-6}$ cm^2 (mean survival = 37.5%) than in substrates with $k < 3.8 \times 10^{-6}$ cm^2 (mean survival = 11.3%). A step function response of survival to permeability is apparent in Figure 3.3. For the model subsets (i.e., High Survival and Low Survival) on either side of the $k = 3.8 \times 10^{-6}$ cm^2 threshold there were no statistically significant linear relationships (p-value < 0.05) between EtE survival (arcsine transformed) and k (log transformed). Regression tree models of various substrate metrics were all single split (i.e., two branches) models: Percent finer than 0.5 mm, Porosity, Geometric mean grain size, Percent finer than 2.0 mm, Percent finer than 1.0 mm, D_{50}, D_{75}, and D_{25} (Table 3.2). These size metrics explained more of the variance in EtE survival (PRE=0.57) than did the more complex regression tree model of flow velocity (PRE=0.52) that included a secondary split (i.e., three branches). The regression tree model of EtE survival as a function of silt (<0.063 mm) although statistically significant (p-value = 0.006) explained the least amount of variance amongst the individual substrate metrics tested (Table 3.2).

3.4.4 Macroporosity and EtE survival

Survival was higher in sediment mixtures with a greater density of large diameter pores (diameter > 3.5mm; defined here as megapores) above the egg

Table 3.2. Summary of regression tree analysis for the relationship between egg-to-emergence survival and each of the selected explanatory variables. The Proportional Reduction in Error (PRE; equivalent to R2 from linear regression analysis), split points (threshold values), sample size (n), mean survival, standard deviation (SD) of the subsets of data on either side of the threshold are shown along with the t-value (t), degrees of freedom (df) and p-value results from two sample t-tests for model subsets (i.e., high and low survival).

Explanatory Variable	PRE	Threshold Values	n	Mean Survival	SD	t	d.f.	p-value
Permeability	0.62	$> 3.8\mathrm{x}10^{-6}\ \mathrm{cm}^2$	18	37.5	10.84	8.38	32.9	<0.0001
		$< 3.8\mathrm{x}10^{-6}\ \mathrm{cm}^2$	29	11.3	9.62			
Percent finer	0.57	< 8.8 %	17	37.4	11.18			
than 0.5 mm		> 8.8 %	30	12.2	10.65	7.56	40.0	<0.0001
Sand	0.43	<25	23	32.0	14.44			
		>25	24	11.0	10.23	- 5.73	40.0	<0.0001
Silt	0.15	< 2.0%	24	27.5	15.49			
		> 2.0 %	23	14.9	14.74	- 2.86	45.0	0.0063
Flow Velocity	0.52	>0.039 cm·s	9	41.8	9.88	6.40	16.0	<0.0001
	(0.38)	<0.039 cm·s	38	16.5	13.49			
Flow Velocity								
(<0.039 cm·s)	(0.14)	>0.004 cm·s	16	24.3	14.50	3.26	24.1	0.003
		<0.004 cm·s	22	10.8	9.46			

Note: All models are single split point (i.e., double branch) models with the exception of egg-to-emergence survival as a function of flow velocity which has a single secondary split point (i.e., three branch model) where the PRE attributed to full model with 2 splits (3 branches) equals 0.52, PRE attributed in primary split equals 0.38 and to secondary split 0.14. Regression Tree models for explanatory variables that are not shown here but which have PRE values equal to that of the 'Percent finer than 0.5 mm' model include (thresholds in brackets): Dg (5.47 mm); Porosity (0.21); Percent finer than 2.0 mm (22%); Percent finer than 1.0 mm (15.4); D50 (8.4 mm); D25 (2.46 mm); D75 (15.33); Fredle Index (2.19).

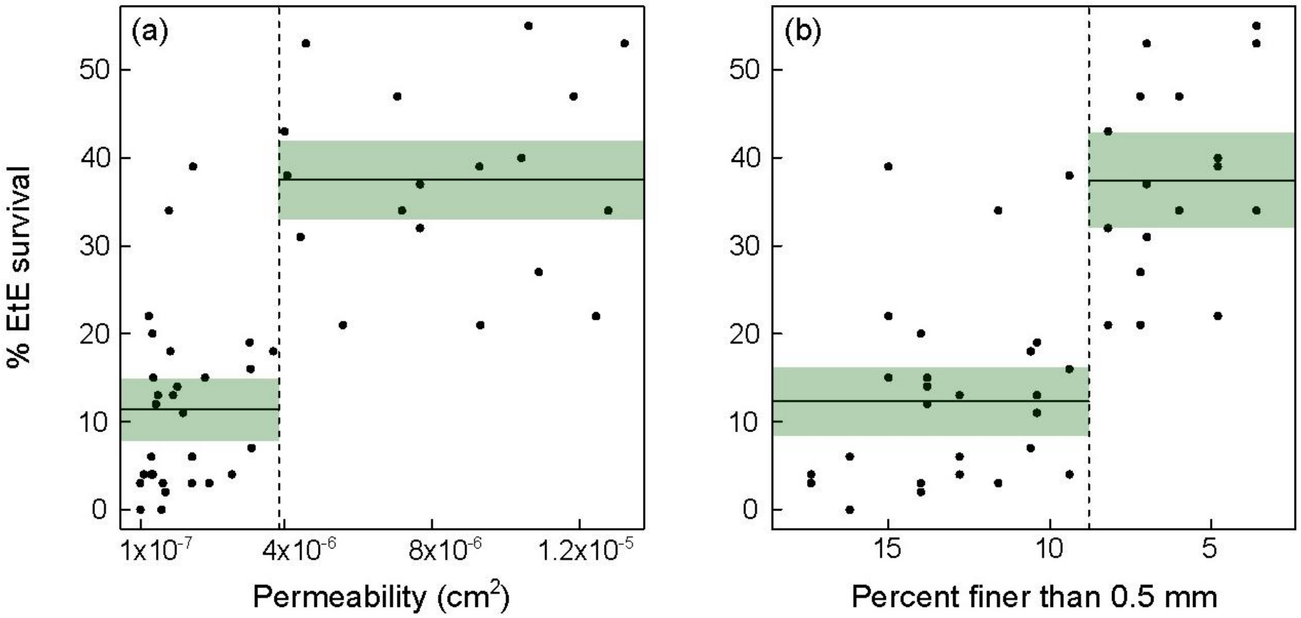


Figure 3.3. Step function response of Egg-to-Emergence (EtE) survival to substrate permeability (k) and substrate composition (e.g., % finer than 0.5 mm). Hatched lines show the split/threshold values (k = 3.8x10^{-6} cm^2, % finer than 0.5 mm = 8.8%) obtained from regression tree analysis; the Proportion of Reduction in Error (PRE) values for k and % finer than 0.5 mm models are 0.62 and 0.57 respectively (see text for details). The horizontal lines on either side of the thresholds mark the estimate of the mean EtE survival for each subset (i.e., high or low survival). Highlighted areas extend to two times the standard error of the estimate of the means.

pocket (Figure 3.4). Megapores were presumed ample enough to allow the relatively unrestricted movement of 3-4 mm wide larvae. A regression tree model of EtE survival as a function of the mean density of megapores in all slices between the depth of embryo burial and the top of the sediment mixture (i.e., emergence zone), indicated that survival was significantly higher (PRE 0.68) in substrates with a megapore density greater than 3.6 pores per 10 cm^2 (mean survival = 41.0%, sd = 8.19, n = 7) than in substrates where the density was less than 3.6 pores per 10 cm^2 (mean survival = 12.0%, sd = 12.13, n = 8). CT scan images revealed the existence of larger, more interconnected macropores in incubators with higher EtE survival relative to incubators with low EtE survival (Figure 3.4). There was a strong positive correlation between the density of megapores and the following common indices of substrate composition: geometric mean, D_{75}, D_{50}, fredle index, D_{25}, porosity, permeability (Table 3.3). Megapore density was negatively correlated with the percentage of sediment finer than (PFT) 2 mm, and PFT 0.5 mm. There was no correlation between megapore density and the proportion of silt within the substrate mixtures.

3.4.5 Emergence timing and larvae condition at emergence

The emergence period spanned 76 days with the first larvae emerging 66 days post fertilization (from fines rich sediments) and the last larvae emerging 142 days post fertilization (Figure 3.5*a*). Median emergence was 115 days post fertilization with a peak of emergence between 105 and 125 days post fertilization, which accounted for 72% of emerging larvae. Larval emergence dates were not normally distributed (Shapiro-Wilk Test, $p<0.001$) and were skewed toward early emergence with the first larvae exiting the incubation sediments 49 days prior to the median day of emergence, and six days after the predicted day of hatching (i.e., 72 days post fertilization).

We observed a statistically significant threshold type effect of substrate composition on the timing of emergence (Figure 3.6). Results from the GAMM

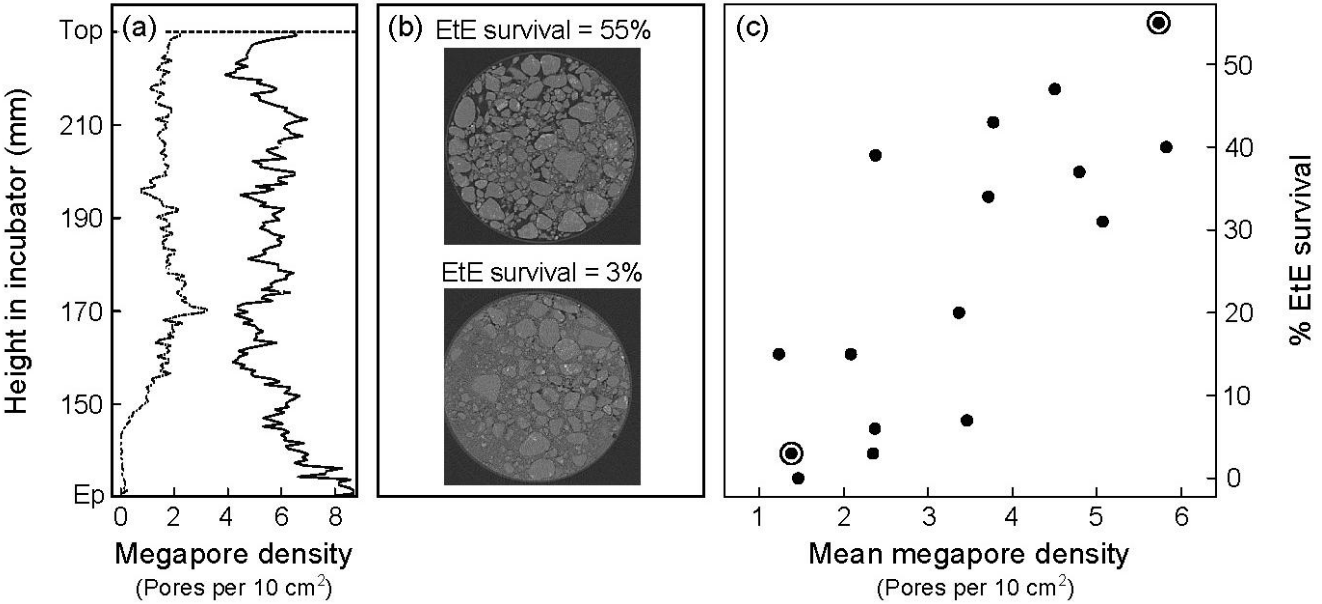


Figure 3.4. (a) Vertical profiles of megapore density in the emergence zone, egg pocket depth (Ep = 130 mm) to top of sediment mixture (Top = 230 mm; horizontal hatched line), for a cylinder with low Egg-to-Emergence (EtE) survival (3%; dotted line), and with high EtE survival (55%; solid line). Megapores are individual pores large enough to allow passage of larvae (i.e., pores with diameters > 3.5 mm). Plotted values are mean megapore densities (pores per 10 cm2) for each horizontal cross section (n=167) within the emergence zone. EtE survival is positively related to the density of megapores in the emergence zone. See Figure 3.4c. (b) Cross sectional CT scanner image from within the emergence zone for an incubation cylinder with high (55%) and a cylinder with low (3%) EtE survival (cylinder diameter = 15 cm). Note the more open pore structure in the high survival incubator relative to the low survival incubator. (c) Positive relationship between percent EtE survival and the mean density of megapores within the emergence zone of each of the scanned incubators. Highlighted points correspond to the CT scanner images shown in (b).

Table 3.3. Pearson correlation coefficients (r) and p values for the relationship between the density of large macropores (diameter >3.5 mm) and common indices of substrate composition.

Substrate Indices	r	p-value
Geometric Mean	0.94	<0.00001
D_{75}	0.94	<0.00001
D_{50}	0.93	<0.00001
Fredle Index	0.92	<0.00001
D_{25}	0.91	<0.00001
Porosity	0.90	<0.00001
Permeability	0.84	0.00006
% Finer than 2 mm	-0.94	<0.00001
% Finer than 0.5 mm	-0.94	<0.00001
Silt	-0.39	0.13

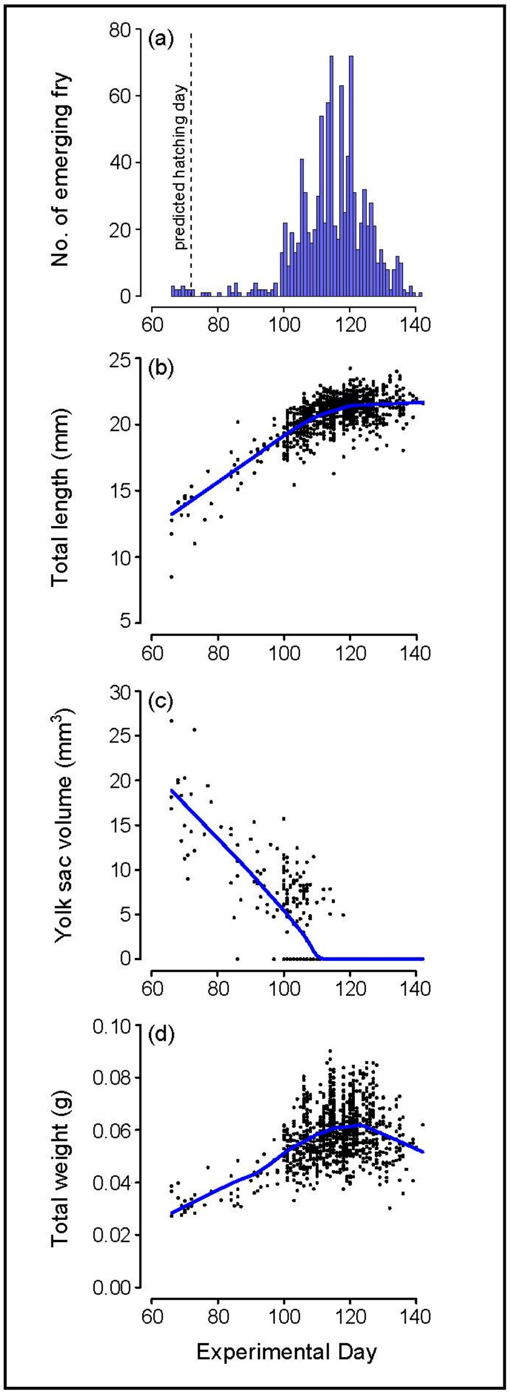


Figure 3.5. (a) Histogram of total daily larval emergence from all incubators (n = 47) for the duration of the emergence period. The vertical hatched line in (a) indicates predicted hatching day. Plots (b), (c), and (d) show trends in morphological features over the same period.

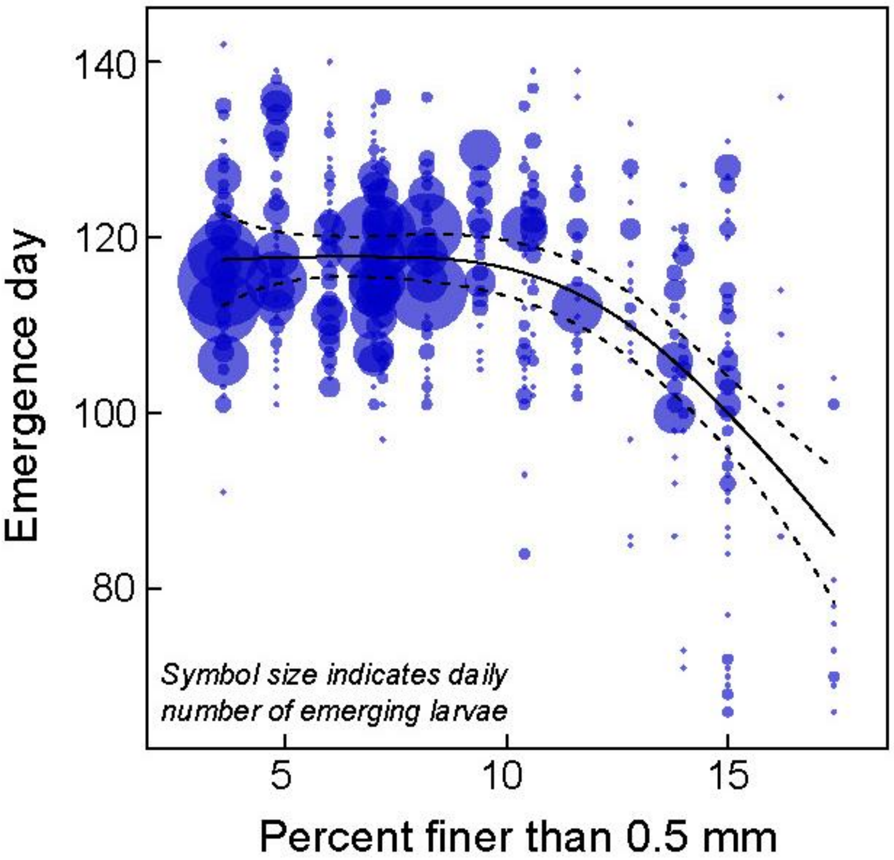


Figure 3.6. Premature emergence and high mortality in finer substrates (e.g., % finer than 0.5 mm). The smallest diameter circle indicates the emergence of a single larvae and the diameter of the largest circle 18 individuals. Solid line represents the estimated smoothing term (% finer than 0.5 mm) for the additive model of emergence day as a function of percent finer than 0.5 mm. Hatched lines are 95% confidence bands.

of Emergence Day as a function of Percentage Finer Than 0.5 mm (PFT 0.5 mm; smoothing term) indicated that: i) the smoothing term was statistically significant (p-value <0.0001, estimated degrees of freedom = 2.9, F-value = 22.1); and ii) that there was a negative relationship between Emergence Day and PFT 0.5 mm when the PFT 0.5 mm was >10% and no effect when the PFT 0.5 mm was <10%.

Early emerging larvae were shorter in length, had greater yolk sac volumes, an absence of parr marks, and a lower total mass (yolk sac included) than larvae emerging during the peak emergence period (Figures 3.5*b*-3.5*d*). The range of length to width ratios obtained from photographs showed that larvae widths ranged from 3-4 mm. GAM confirmed that there was a significant nonlinear effect of the day of emergence on larval length (${}_{adj}R^2 = 0.65$, p-value < 0.0001), yolk sac volume (${}_{adj}R^2 = 0.71$, p-value < 0.0001), and total mass (${}_{adj}R^2 = 0.26$, p-value < 0.0001). Mean larval lengths increased steadily from approximately 13 mm at the initiation of emergence to approximately 21 mm by the median day of emergence and were constant thereafter; mean yolk sac volumes decreased from approximately 19 mm^3 at the beginning of emergence until approximately 112 days post fertilization, after which nearly all larvae emerged with fully absorbed yolk sacs. Mean larval mass increased from 0.03 g at the beginning of emergence to approximately 0.06 g at median day of emergence and then began to decrease following the peak emergence period.

3.5 Discussion

3.5.1 Can flow rate mitigate mortality in fines rich substrates?

Our results support the hypothesis that, for substrates with elevated proportions of sand and silt, increased flow velocity and oxygen flux through gravel bed incubation microhabitats does not improve EtE survival. By varying both VHG and substrate composition we were able to demonstrate that increases in EtE survival were associated with coarsening of the substrate rather than increases in hydraulic gradient and flow velocities. This result is consistent with the findings of Lapointe et al. (2004) who also showed that there is a reduction in EtE survival associated with an increasing proportion of sand and silt within a gravel substrate, even where moderately strong flow velocities are maintained (by varying gradients).

Of course, one should not conclude from these data (collected over a range of non-zero interstitial velocities) that interstitial flow is wholly irrelevant to EtE survival. Our experiment did not include a zero gradient treatment to test EtE survival in the absence of flow, as salmonids have been shown to situate redds in microhabitats where there is interstitial flow (Blanchfield and Ridgway 1997; Giest 2002; Guillemette et al. 2011). As it is interstitial flow that transports oxygen into the egg pocket, at least a minimal flow rate is required to avoid embryo asphyxiation (Greig et al. 2005). During our experiment, the oxygen concentration in water flowing through the incubation cylinders exceeded 10 mg·L (80% saturation at 7^0C), and interstitial flow velocities (mean: 248 cm·h; range: 5-1832 cm·h) were an order of magnitude above the oxygen-related threshold interstitial flow velocity (15 cm·h) associated with high (75%) salmon embryo survival (Greig et al 2007). Although lack of flow and oxygen will lead to asphyxiation, low oxygen flux through the egg pocket did not occur in any incubator cell here and so was not responsible for the observed mortalities in conditions tested. Instead, our results showed that EtE survival was determined by substrate composition and that the negative effect of increasing fine sediment on EtE survival could not be mitigated by increasing the flow velocity/oxygen flux through the incubation habitat.

We are aware of only one field study (Curry and MacNeill 2004) in which emerging larvae were captured (using emergence traps) and where EtE survival was related to both substrate composition and flow velocity. The results of Curry and MacNeill (2004) indicate that high rates of EtE survival were associated with both coarser substrates and higher flow velocities, with the authors suggesting that increased mortality in finer grain substrates may have been associated with a reduction in oxygen flux associated with reduced flow velocities. As neither oxygen concentrations nor the percentage of entombed larvae were reported in the results of this field study, one cannot determine whether the observed mortalities were likely to have been caused by asphyxiation or entombment. Proposed asphyxiation related thresholds for incubation habitat quality (Greig et al. 2007) suggest that where interstitial water is sufficiently oxygenated (i.e., > 6 mg·L) asphyxiation is unlikely to be associated with velocity unless flow rates are extremely low (i.e., < 1 cm·h); moreover because dissolved oxygen concentration and flow velocity combine to determine oxygen flux the threshold velocity for asphyxiation likely increases as oxygen concentration declines. In effect, our laboratory incubations reproduced field conditions with both well oxygenated water (> 10 mg·L) and moderate to strong gradients, thus explaining the lack of a velocity effect in our study.

3.5.2 Fine sediment and embryo mortality

We detected a threshold effect of substrate composition on EtE survival. Low survival (mean = 12%) occurred in substrates where the proportion (by weight) of sediment under 0.5 mm was greater than 9%, or equivalently when the proportion of sediment under 2 mm (all fractions finer than coarse sand) was greater than 22%. This result is consistent with the conclusions of a recent meta-analysis of studies of pacific salmon species (Jensen et al. 2009) that identified a threshold effect on EtE survival when the proportion (by weight) of fine sediment under 0.85 mm constitutes more than 10% of the incubation substrate. In gravel bed substrates, the threshold value (22%) for fractions finer than 2 mm is consistent with the beginning of the transition zone between a gravel bed (<20% sand) to a sand bed river (>40% sand) in which the interstitial spaces between the gravel particles become filled with sand (Wilcock 1997). A threshold effect is consistent with the proposed mechanism of entombment which suggests the increased mortality occurs once the larger interstitial pore spaces between gravel particles become clogged with fine sediment thereby inhibiting larval emergence. However, despite high oxygen fluxes we cannot exclude the potential role of fine sediment in causing embryo asphyxiation which might have occurred if an impervious layer of very fine sediment (< 0.063mm; clays and silts) enveloped the embryo and prevented interstitial flow/oxygen flux from reaching the surface of the embryo. Our experiment was not designed to test such an effect. However, our results do indicate that coarser sediment (i.e., sand), not associated with such a membrane level asphyxiation mechanism, had a stronger effect on EtE survival than did the finer fractions (i.e., silt). Our results demonstrate that even if asphyxiation results from embryo envelopment by very fine sediment, such an effect on survival cannot be mitigated by increasing oxygen flux through the incubation habitat.

3.5.3 Relationship between EtE survival and available macroporosity

The probability of survival to emergence was positively related to the density of large diameter macropores (pores > 3.5mm in diameter) which we describe here as “megapores”. In this experiment with width of emerging larvae ranged from 3-4 mm and thus, such megapores were presumably large enough to allow the unrestricted movement of larvae. Our results showed that the mean density of megapores in the sediment layers above the egg pocket was strongly correlated to common substrate metrics indicating that greater percentages of sand size particles (0.063 - 2 mm) reduced the availability of the larger intergravel spaces within our mixtures. The highest EtE survival was associated with mean megapore densities above 4 megapores per 10 cm2 in the sediment layers above the egg pocket. This density theoretically corresponds to a mean lateral spacing between such megapores of approximately 2 cm, in an average horizontal cross-section through the emergence zone. In such conditions (megapore density above 4 per 10 cm2 and associated PFT 0.5 mm under approx. 10%), successful larvae apparently located emergence pathways, with limited tunneling into loosely packed sands at obstructions.

In gravel bed substrates, the availability of megapores is critical given the difficulty of larvae in displacing larger interlocking gravel particles that form the framework of the streambed. The role observed here of a 3-4 mm ‘megapore” threshold in facilitating emergence in gravel mixtures is also consistent with results obtained in several published incubation experiments where sediment treatments consisted of clean uniform gravels (i.e., gravel particles all same size and no sand and silt; Sternecker and Giest 2010, Witzel and MacCrimmon 1983). For an assemblage of homogenously sized spherical gravel particles, macropore size is directly proportional to grain size diameter. Very loosely packed clean spheres of diameter D have a mean pore size of 0.414D (Frings et al. 2008). Experiments conducted on brown trout and Danube salmon (Sternecker and Giest, 2010) and brown trout and brook charr (Witzel and MacCrimmon 1983) show that the gravel size diameter of 9 mm (thus maximum pore size=3.7 mm) demarks a clear threshold between high (>75%; >9 mm) and low rates of survival (<15%; <9 mm) under clean gravels conditions, where embryo mortality would not have been caused by asphyxiation. The size of the interstitial spaces between grains that are <9 mm in diameter appear to be too small to allow the unrestricted movement of larvae (Witzel and MacCrimmon 1983). In glass aquaria, Rubin (1998) observed that sea trout larvae could not emerge through a gravel layer composed of 8-15 mm sized particles (thus maximum pore sizes 3.3-6.2 mm), whereas Dill and Northcote (1970) observed that coho larvae could freely disperse within a substrate composed of 19-32 mm gravel (thus maximum pore sizes 7.9-13.2 mm). In heterogeneous mixtures, as in our experiments, macropore size is a more complex function related to proportion, and arrangement of the various grain sizes and therefore, not easily discerned.

The relatively small gravel sizes used in our experiment (reflecting our target brook trout streams) may explain the narrower than expected range in EtE survival observed here (0-55%) relative to the range of EtE survivals (0-97%) reported in Lapointe et al. (2004) in coarser Atlantic salmon (Salmo salar) spawning substrate, or to the expected rates of embryo survival (>75%) for incubation habitats with sufficiently strong oxygen fluxes (Grieg et al. 2007). The geometric mean grain size of our gravel mixtures was only slightly larger than the

9 mm size threshold between high (75%) and low (15%) EtE survival discussed above (Witzel and MacCrimmon 1983). This suggests that some of the mortality in our experiment may have been due to larvae entombment related specifically to the narrower interstitial spaces created by the gravel particle sizes that were the base (Dg = 10 mm; range: 2-32mm; 60-90% by weight) of our sediment mixtures. In Lapointe et al. (2004), gravel particles constituted 71-93% (by weight) of the sediment mixtures, however, the larger size of the constituent particles (Dg = 19 mm; range: 2-55mm) would have resulted in larger interstitial spaces between the framework gravels, thereby reducing the probability of larval entombment.

3.5.4 Premature emergence and larval condition at emergence

Our results support the hypothesis that increased concentrations of fine sediment and associated dearth of megapore pathways induce both the premature emergence of some larvae and high mortality of others. We also observed that early emerging larvae have physical characteristics that confirm they are at a much earlier development stage than later emerging larvae. Our results are consistent with the findings of Witzel and MacCrimmon (1983) and Fudge et al. (2008) who showed a statistically significant effect of substrate composition on the timing of emergence of brook charr and rainbow trout respectively. The observations by Witzel and MacCrimmon (1983), whose transparent incubators permitted direct observation of larvae, suggest that substrate composition did not affect the timing of hatching and that larvae in fine gravel substrates (Dg = 2.7 mm) began to die shortly after hatching while larvae in coarser substrates (Dg = 7.2 mm) either survived until emergence or were unable to emerge and died following yolk sac absorption. The authors suggested that these post-hatching mortalities were due to insufficiently large gravel interstices rather than an absence of a sufficient flux of oxygen. Presumably a minimum macropore size is required to allow for the survival and growth of hatched embryos. Our results show that in fines rich substrates (>15% PFT 0.5 mm) survival of larvae was low and that nearly all survivors emerged prematurely. We are uncertain whether premature emergence is a stress response triggered by physical pressure exerted on the hatched embryos by the surrounding substrate (Witzel and MacCrimmon 1981) or whether hatched embryos can sense the amount of interstitial space required to accommodate their growth and decide to emerge prematurely where they detect that this space is inadequate. From an evolutionary perspective, the selection of early emergence could be an adaptive developmental response associated with either the presence of elevated fines or the associated reduction in the size and density of substrate megapores. The trigger for this response could be low interstitial flow velocities or reduced macropore sizes. Recall that lower % PFT 0.5 mm implies more megapores. In substrates with slightly less fine sediment (12-15% PFT 0.5 mm) premature emergence still occurred but larvae also emerged during the period of peak of emergence suggesting that some larvae were able to locate interstitial habitats that were sufficiently large. In substrates with <12% PFT 0.5 mm, nearly all larvae emerged within 10 days of the median date of emergence.

Substrates with elevated proportions of fine sediment not only reduce EtE survival but also affect the fitness of surviving larvae. Our results showed that early emerging larvae were shorter, lighter and had large, unabsorbed yolk sacs. Under normal conditions of development, hatched embryos continue their early ontogenesis within substrate interstices until they are sufficiently developed and the yolk sac has been resorbed (Power 1980). Although early emergence of yolk sac larvae may under some conditions be advantageous for gaining superior feeding territories (Skoglund and Barlaup 2006), it is plausible that such an advantage is insignificant relative to the disadvantage of underdevelopment for predator avoidance (Fresh and Schroder 1986). A reduction in the fitness of early emergers suggests that survival rates for prematurely emerging larvae are likely to be poor and that our estimates of EtE survival from fines rich substrates overestimate the percentage of individuals that are likely to survive the initial period of exogenous, open water feeding.

3.6 Conclusion

Asphyxiation and entombment represent sequential controls on EtE survival and our results suggest that the entombment mechanism cannot be mitigated by higher velocities regardless of interstitial oxygen concentrations. Thus, reproductive success in gravel bed streams should depend on the selection of redd sites where: i) there is a minimum interstitial flow velocity (the threshold of which is dependent on oxygen levels) that ensures sufficient oxygen flux to the developing embryos to avoid embryo asphyxiation; ii) the macropores between gravel particles are sufficiently large to allow for the growth and emergence of hatched embryos; and iii) there is a low probability of the clogging of these macropores before emergence due to the infiltration of fine sediment. Combined with previous experimental studies, our results suggest that the quality of salmonid incubation microhabitats is determined by thresholds in three key abiotic factors: dissolved oxygen concentration, interstitial flow velocity, and the size and interconnectedness of substrate macropores. High quality incubation microhabitats appear to be those where dissolved oxygen concentration exceed 9 mg·L and where the interstitial flow velocity is greater than 0.04 mm·s (Greig et al. 2007) thus reducing the probability of embryo asphyxiation; and where the median grain size of the gravel particles is > 9 mm and the percentage of fine sediment (< 0.5 mm) is below 10%, thus ensuring a size and density of substrate macropores sufficient to prevent entombment.

Chapter 4

The role of hyporheic flow in brook charr spawning site selection and its effect on incubation microhabitats in a boreal forest stream

4.1 Preface

4.1.1 Manuscript details

This manuscript is authored by Jan Franssen, Michel Lapointe, and Pierre Magnan. It has not yet been submitted for publication.

4.1.2 Context within thesis

In the following manuscript we detail the results of a various field studies designed to investigate the role of hyporheic flow in brook charr redd site selection. Previous work has shown a strong association between brook charr redd site selection and hyporheic flow that is predominantly groundwater. In this manuscript we test various alternate hypotheses regarding hyporheic flow and redd site selection, and the influence of the origin of the flow (i.e., groundwater vs surface water) on the thermal regimes likely to be experience by embryos nested in the gravel bed substrates of a boreal forest stream. The results presented in the following chapter link to topic of early life cycle survival (Chapter 3) by improving our understanding of the physical characteristics of known spawning/incubation habitats. These results also link to the topic of fines infiltration into spawning gravels (Chapter 5) by defining the interstitial flow conditions within redds, as the direction and intensity of flow is thought to influence fines accumulation into gravel bed substrates

4.1.3 Abstract

Species with distributions that span a broad range of latitudes may have populations that exhibit distinct life history traits associated with environmental

gradients. Although the majority of previous studies indicate a strong association between brook trout (*Salvelinus fontinalis*) spawning site selection and the presence of upwelling groundwater, the thermal regimes at northern sites suggest that the microhabitat scale association between groundwater upwelling and redd site selection may not span the entire latitudinal range of this species. We investigated the role of hyporheic flow in brook trout redd site selection in a relatively high latitude boreal system. Hyporheic flows through streambed substrates can be groundwater or surface water dominant, and be influenced by the presence of morphological features. For autumn spawners such as brook trout, embryos situated in microhabitats where hyporheic flow in the shallow substrate is groundwater dominant (i.e., warmer in winter) are likely to experience accelerated development rates relative to embryos nested in redds that are under the influence of downwelling surface water (i.e., colder in winter). To explain observed patterns in trout redd site selection in relation to hyporheic flow patterns we measured vertical hydraulic gradients (VHG) at the microhabitat scale, and the spatial and temporal variation in upwelling/downwelling flow and thermal regimes in brook trout spawning/incubation habitats. Additionally, we noted the proximity of redd sites to stream morphological features (e.g., riffle-crests). Our results indicate that upwelling flow was not used as a decisive cue in redd site selection at the microhabitat scale (100m), as an approximately equal number of redds were situated in microhabitats with upward flow as were situated in microhabitats with downward flow. Redds adjacent to a riffle-crest or log-step bedforms were associated with downward flow, whereas redds not immediately adjacent to these morphological features were associated with upward flow. Winter streambed temperatures confirmed that both steady upwelling (i.e., warm incubation regime) and downwelling (i.e., cold incubation regime) sites were indeed selected by spawners and thus over two spawning seasons redd sites with distinct thermal regimes were selected. Our observations that spawners utilized both cold regime and warm regime sites suggests the existence of distinct reproductive tactics related to hyporheic flow patterns in this boreal system. As temperature is the dominant factor controlling rates of embryonic development, the use of spawning microhabitats with distinct thermal regimes implies substantial differences in the timing of hatching and the phenology of emergence from these habitats.

4.2 Introduction

One of the fundamental problems in biology is to understand the linkage between an organism's behaviour and its ecology (Krebs & Davies, 1997). Elucidating this relationship is important for our understanding of habitat selection theory (Kramer, Rangeley & Chapman, 1997), and is a prerequisite for the successful assessment, protection, and restoration of habitat (Maddock, 1999; Fausch et al. 2002; Beechie et al. 2008). One of the challenges in associating the behavioural trait of a species with an environmental determinant (e.g., brook trout spawn at sites where there is upwelling groundwater) is that many fish species have broad geographic distributions (Diana, 2004), and thus local populations may have distinct behaviours related to gradients in environmental factors (e.g., latitudinal/attitudinal gradients in temperature). For example, in local populations of American shad (*Alosa sapidissima*) the proportion of repeat spawners was found to increase from south to north (Legget and Carscadden, 1978). Additional examples of behavioural variation attributed to latitudinal clines include: spawning season duration in Roach (*Rutilus rutilus*; Lappalainen & Tarkan, 2007); spawning season timing in Atlantic silverside (*Menidiu menidiu*; Conover, 1992); and the timing of smolt migration in Coho salmon (*Oncorhynchus kisutch*; Spence & Hall, 2010). Conclusions based on associations between behaviour and environmental factor(s) must therefore take into account the potential for intraspecific differences in behaviour across environmental gradients.

The reproductive behaviour of brook trout (*Salvelinus fontinalis*), whose endemic range in eastern North America spans from the mid-Atlantic (40^0N) to northern Quebec (60^0N), has been closely associated with groundwater (Scott and Crossman, 1998). Brook trout have been observed to spawn almost exclusively in substrates directly under the influence of upwelling groundwater (see review in

Guillemette et al. 2011). An exception to this reproductive trait was observed in a population located on the western coast of Newfoundland, Canada (48^0N; altitude = 400m) where redds were observed to be situated in zones of downwelling surface water (Curry, Scruton, & Clark, 2002). To our knowledge, this is the northernmost location where the substrate flow characteristics at brook trout spawning/incubation microhabitats have been observed. The results of this study suggest that the microhabitat scale association between groundwater upwellings and redd site selection may not span the entire latitudinal range of this species.

In cold climates, river bed substrates that are under the influence of upwelling groundwater will be warmer in winter relative to substrates where groundwater flux is absent (Conant, 2005). As temperature is the dominant factor affecting the rate of embryonic development in salmonids (Kamler, 2002), the intensity of local groundwater inputs will thus affect the thermal regimes experienced by developing embryos and thus the phenology of hatching and emergence (Lapointe, 2012). The embryos of autumn spawners, such as brook trout, that are nested in microhabitats where hyporheic flow in the shallow substrate is groundwater dominant (i.e., warmer substrate) will experience accelerated development relative to embryos nested in redds that are under the influence of downwelling surface water (i.e., colder substrate). Thus, the positioning of redd sites in relation to the continuum of hyporheic flow conditions (i.e., from groundwater dominant to surface water dominant) implies an association between local hyporheic flow patterns and reproductive success, as emergence phenology is thought to be critically linked to a spike in the availability of food sources that coincides with the spring pulse in primary production (Wootton, 1998).

Groundwater temperature is inversely related to both latitude and altitude. Shallow groundwater temperatures are generally 1-2^0C warmer than mean annual air temperature (Todd 1980). However in northern climates with abundant snowpack, groundwater temperature may be even warmer due to the insulating effect of the deep snow cover which reduces heat loss from the ground during winter (Meisner, Rosenfeld & Regier, 1988). It may follow that, in harsher climates, spawners such as those observed in Newfoundland (Curry, Scruton, & Clark, 2002) may avoid groundwater upwellings and situate redds in microhabitats that are under the influence of surface water (i.e., colder) to moderate development rates, and thus ensure that emergence coincides with the appearance of food sources in spring. Additional observations of brook trout reproductive behaviour at sites with harsher winters (i.e., sites at higher latitudes/altitudes) are required to substantiate the possibility of a distinct reproductive traits associated with gradients in temperature and snow cover.

Substrate thermal regimes are determined by the relative contributions of surface water and groundwater flowing within the hyporheic zone. Stream morphology is a primary factor controlling hyporheic exchange. The bedform features (e.g., riffles, log-steps) typically present in the first and second order streams where brook trout spawn, have been shown to create complex hyporheic flow patterns (Tonina & Buffington, 2007), with microhabitat scale (10^0m) variation in hydraulic gradients and surface water/ground water interactions. Indeed substrate temperature, in addition to being a biologically relevant parameter has also been shown to be useful in delineating microhabitat scale variability in hyporheic exchange (Conant, 2005). Morphological features such as point bars, island bars, and pool-riffle transitions create variations in longitudinal water gradients that induce the downward flow of oxygen rich surface water into the streambed (Thibodeaux & Boyle, 1987; Karahara & Wondzell 2003; Gooseff et al., 2006). Populations of Atlantic salmon (Salmo salar) and Chinook salmon (Oncorhynchus tshawytscha) have been observed to cluster redds in close proximity to such bedforms (Coulombe-Pontbriand & Lapointe 2004; Geist & Dauble 1998). Generally, descriptions of channel bed and bar morphology have been absent from previous studies investigating the environmental determinants of brook trout redd site selection, a weakness this study also aims to remedy.

The spatial scale of any association between groundwater upwelling and redd site selection also must be considered. Although the presence of upwelling groundwater may not be a critical cue for redd site selection at microhabitat scale across brook trouts' entire range (e.g., Curry, Scruton, & Clark, 2002), in northern climates the presence of upwelling groundwater in trout spawning streams is indeed likely to be a critical habitat variable at larger spatial scales (i.e., >100m). In the northern half of brook trouts' range (the subarctic regions of eastern North America; Scott and Crossman 1998) the long cold winters are practically free of surface runoff events. In this region, groundwater inputs to spawning tributaries are required to insure sufficient mid-winter stream flow and ice free substrates. Thus, the selection of redd sites must at some spatial scale incorporate either a direct or indirect cue for groundwater to insure that developing embryos are not subjected to either desiccation or freezing due to the absence of streamflow. The thermal regimes in these northern systems suggest that redd site selection behaviour may involve cues across multiple spatial scales. Such a hypothesis was proposed for a population of bull trout (Salvelinus confluentus; Baxter & Hauer, 2000), where at the pool-riffle spatial scale bull trout redds were associated with sites where there was localized downwelling that were nested in reaches where there was groundwater discharge. These authors suggested that finer scale measures of VHG would be required to substantiate the importance of hyporheic flow in redd site selection at the microhabitat scale. To our knowledge this hypothesis has not yet been formally tested with detailed data on hyporheic flow and thermal regimes within spawning reaches, which we provide here.

The goal of the present study is to investigate the role of hyporheic flow with varying groundwater inputs as a factor in brook trout redd site selection in a relatively high latitude (47°N) and moderately high altitude (> 750m asl) boreal system, and the influence of these hyporheic flow patterns on the thermal regimes that would be experienced by developing embryos nested within these sites. We conducted a series of field observations in brook trout spawning streams where the presence of stream morphological features (e.g., pool-riffle transitions) indicated the potential presence of complex hyporheic flow patterns. Observations where designed to test the following hypotheses applicable to harsh winter environments:

i) in these boreal forest stream systems brook trout use downwelling flow as a cue for redd site selection at the microhabitat scale;

ii) in pool-riffle and step-pool channels, brook trout locate redds immediately upstream of riffle-crests and steps where the water surface gradients created by these morphological features induce the downward flow of surface water into the streambed (Gooseff et al., 2006) thus ensuring interstitial flow through the redd; and

iii) brook trout situate redds in microhabitats where there is downwelling surface water that are nested within reaches where there is upwelling groundwater (e.g. Baxter and Hauer 2000);

A secondary objective of this study was to determine if the thermal regimes observed at upwelling vs downwelling sites throughout the incubation period would affect estimates of hatching dates based on extant incubation models (Crisp 1981) for embryonic development as a function of incubation temperature. A priori, the thermal regimes associated with the selection of spawning sites have clear ecological implications for the rates of embryonic development and thus the phenology of brook trout emergence.

4.3 Materials and Methods

4.3.1 Study Area

This study was carried out in the Réserve Faunique des Laurentides (RFL), a 7,861 km2 wildlife reserve situated north of Quebec City, Canada at (47°35’N, 71°13’W). Study sites were located on the Laurentian Plateau at altitudes above 750 m. Geologically sited within in the Grenville province of the Canadian Shield, the RFL receives mean annual precipitation of 1600 mm, has abundant winter snowpack (mean snow depth at February month-end = 86 cm), and a mean annual air temperature of 0.3°C (Environment Canada 2007). January is the coldest month (mean temperature = –15.8°C) while mean monthly air temperatures remain below zero from November to April. Because of the insulation provided against cold penetration by the abundant snowpack, the annual average soil temperature at 3 m depth (5.2°C, Environment Canada 2007) is approximately 5°C warmer than the mean annual air temperature. Shallow groundwater temperatures in the region are approximately 5°C (Meisner et al. 1988). Brook trout is the dominant fish is the RFL representing 98% of the 2002 sports fishing catch (Gouvernement du Québec, 2003).

Spawning site surveys (details below) were conducted along three small, trout bearing streams within the RFL that were designated by milepost distance from south to north: KM104 (47°18’39”N, 71°10’56”W), KM143 (47°38’13”N, 71°14’22”W), and KM161 (47°47’18”N, 71°13’24”W). These alluvial streams were categorized either as “pool-riffle” (KM 143) or “log-step” (KM104 and KM161) channels. These classifications were used to describe either an undulating alluvial streambed comprised of alternating sequences of pools and riffles, or a channel with periodic drops in water surface elevation related to partially buried logs. Stream KM104 is a first order tributary to lake Petit lac à l’Épaule with an average channel width of approximately 3 m. Its streambed is composed of sand and gravel with several naturalized log-step features created by the partial burial of 0.3 m diameter logs across the width of the wetted channel. Stream KM143 is a second order tributary to lake Jacques-Cartier with a pool-riffle morphology and channel widths ranging from 6-8 m. Its streambed is composed of sand and gravel. Stream KM161 is a first order tributary to lake Jupiter with a channel width of approximately 2 m. This channel has undergone habitat enhancement including the construction of log step-pool features and gravel placement. The streambed is predominantly gravel with some sand.

4.3.2 Spawning Site Observations

To identify redd locations, spawning site observations were conducted over two consecutive years: annual surveys began on 5 September 2007 and 3 September 2008 and continued until the spawning season was completed on 10 October 2007 and 15 October 2008 respectively. The observations were completed on stream segment lengths of 290 m, 1100 m and 360 m for sites KM104, KM143, and KM161 respectively (Fig. 4.1). Redd sites were identified by the presence of an actively digging female, by male fighting for a stationary female, or by the appearance of a clearly defined redd (disturbed streambed sediments with a characteristic pit tailspill formation; Crisp & Carling 1989; Blanchfield & Ridgway, 1999). These locations were flagged with an onshore marker positioned along the bank and the exact transverse distance (± 0.1 m) of the redd axis relative to the bank was recorded. In several locations different females were observed spawning within the same channel unit (e.g., a riffle). Here we use the term SITE to refer to area occupied by these adjacent redds. A monitoring station equipped with a datalogger (Starlogger Model 6004-1, Unidata Pty Ltd., O'Connor, Australia) and water level sensor (KPSI 700, Pressure Systems Inc., Hampton, Virginia) situated along the KM143 tributary provided a continuous record of water levels (accuracy ±0.01m) during the two fall study periods.

4.3.3 Measurements of vertical hydraulic gradient at redd sites

To test the hypothesis that brook trout use downwelling flow as a cue for redd site selection in these boreal forest streams, a total of 78 piezometers of the type described in Baxter, Hauer & Woessner (2003) were installed between October 16-19, 2007 (6-10 days following the completion of spawning activity) in the three streams described above: KM104 (n=26), KM143 (n=22), and KM161 (n=30). As hyporheic conditions change with season and river stage, such observations must be made in same conditions as spawning site selection. The first of each pair of piezometers (n=39) was installed into a flagged redd location (selected); and the second at an arbitrary location within two to five meters of the

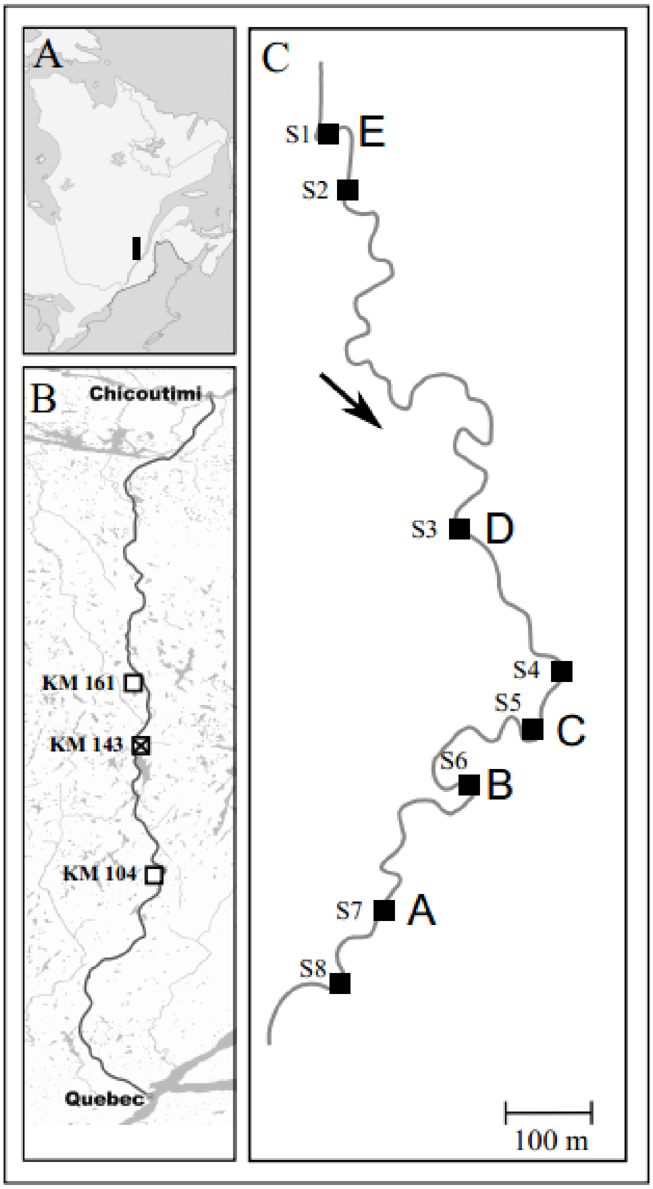


Figure 4.1 (A) Map of Québec, Canada showing the region (black rectangle) illustrated below. (B) Region north of the City of Québec where the three study streams (square symbols) are located. Site KM designation (i.e., KM143) refers to milepost distance from south to north along provincial Highway 73/175 (grey line). (C) Diagram of study area at site KM 143. Square symbols show the eight spawning site locations (S1 to S8), with letters (A to E) designating the five reaches where winter streambed temperatures were mapped. Arrow indicates direction of streamflow.

selected site where there was similar substrate, depth and velocity but at which spawning activity was not observed (non-selected). At each location, piezometers were used to obtain measurements of Vertical Hydraulic Gradient (VHG), a unitless measure of the change in total hydraulic head with distance below the substrate, where positive gradients drive upward flow of water and negative gradients downward flow. Water levels within the piezometer and attached surface water stilling well were measured to within 0.001 m with a custom made analogue water level dipper constructed using a length of steel measuring tape with 1 mm graduations. To test the hypothesis that brook trout position redds in relation to stream morphological features known to induce the downwelling of surface water into the streambed (e.g., pool-riffle and step-pool transitions), we noted the presence of morphological features such as riffle crests and log-steps and their proximity to redd locations at each site.

The relationship between the response variable VHG and the explanatory variable microhabitat TYPE (selected vs non-selected) was assessed using a linear mixed model to account for the nested structure of our observational data (i.e., selected microhabitat TYPE nested within SITE (n=22) nested within STREAM (n=3)). Selection of an optimal model was based on the top-down protocol described in Zuur et al. (2009) in which the selection process begins with a ‘beyond optimal’ model containing the fixed effect of microhabitat TYPE and the random effects of microhabitat nested within SITE and SITE nested within STREAM. The significance of the random effects was determined using a likelihood ratio test with non-significant terms (p-value > 0.05) removed from the ‘beyond optimal’ model. The mixed model analysis was completed using the nlme package (Pinheiro et al. 2010) for the statistical software R 2.9.2 (R Development Core Team 2009). We used the same protocol to test the relationship between the response variable VHG and the explanatory variable MORPHOTYPE. Here MORPHOTYPE refers to the presence/absence of a break in water surface slope associated with the presence of a riffle-crest or log-step feature within the width of the wetted channel of the redd.

4.3.4 Thermal mapping of streambed temperatures

To test the hypothesis that brook trout redds were nested within broader upwelling reaches, we mapped winter time streambed temperatures at the microhabitat scale (10^0m) across all the five reaches (10^1m) along tributary KM143 where direct observations of brook trout spawning activity were observed during the 2007 spawning season. The length of mapped reaches ranged from approximately 18-63 m. December streambed temperature measurements were taken at a depth of 25 cm below the surface of the substrate and used to determine the variable influence of upwelling (warmer) phreatic groundwater within the study reaches. Several researchers have successfully utilized streambed temperature mapping to characterize hyporheic and groundwater flow patterns (White, Elzinga & Hendricks 1987; Conant 2004). Here, water chemistry (e.g., dissolved oxygen; conductivity) was not utilized as a means of clarifying the relative contribution of groundwater vs surface water in the hyporheic flow through the spawning habitat. Instead, the origin of interstitial water is identified using the water's thermal signature (Conant, 2005). Temperature is the physiochemical parameter of primary interest due to its effect on the rate of embryonic development and therefore on the phenology of embryo hatching and larvae emergence. Interpretation of temperature patterns is easiest in winter conditions, as in this study, where phreatic groundwater temperatures are warmer than surface water temperatures, and when surface water temperatures fluctuate much less than during any other seasons.

These streambed temperature measurements were made between December 5-11, 2007 by hammering into the streambed a drive point (tapered steel rod; o.d. ¾-inch) which was inserted into an opened ended piezometer (PVC pipe; i.d. ¾-inch). The drive point/piezometer was advanced into the streambed to a depth of 0.25 m after which the exterior piezometer pipe was firmly held in place while the interior drive point was slowly removed to draw hyporheic water into the piezometer. A temperature probe (YSI Model 30, YSI Incorporated, Yellow Springs, Ohio; accuracy: ±0.1°C) was lowered to the bottom of the piezometer to record the temperature of the water at depth. Surface water temperatures were taken at each measurement point by positioning the temperature probe just above the streambed. A total station (S6, Trimble, Sunnyvale, California) was used to map the position and relative streambed elevation of each measurement point; the depth of water at each point was also measured.

4.3.5 Monitoring of hyporheic flow conditions during the incubation period

To observe hyporheic flow and thermal conditions at redd sites throughout an entire incubation period, beyond the late fall spawning period monitored above, we also installed long term temperature loggers at the streambed surface and within the substrate (depth = 20 cm) at selected redd sites. Daily temperature cycles were used to provide a relative indication of the groundwater/surface contributions within the substrate at each site. The temperature of the phreatic groundwater at our sites is approximately 5°C. A constant substrate temperature of approx. 5°C thus indicates a steady upward flux of phreatic groundwater (Constantz 2008). Stronger diurnal temperature fluctuations at depth and gravel temperatures closer to that of the surface water indicate sites where there was more downwelling surface water within the substrate. To obtain these paired temperature time series records we inserted wooden stakes (Fig. 4.2) into the streambed that were fitted with two iButton temperature loggers (Model DS1922L, Maxim Integrated Products, Sunnyvale, CA); accuracy of ±0.1°C. On October 21 2008, iButton stakes were inserted into eight brook trout redds situated in each of the eight distinct stream reaches (scale = 101 m) along tributary KM143 (selected reaches), where spawning activity was observed during the fall of 2008. The iButtons were synchronized and set to record temperatures at an interval of 86 minutes. All iButton stakes were retrieved on June 21-22, 2009.

We used the temperature times series record from each of the instrumented redd sites to infer the duration of the incubation period (i.e., fertilization to 50%

hatching) that would have occurred at each site had embryo fertilization occurred at the time of sensor installation. Estimates of days to 50% hatching were calculated as a function of redd temperature using equation 1b and parameter set given in Table 2 for brook trout in Crisp (1981). The model was not validated for the specific populations studied here. However, as temperature is the dominant factor affecting rates of embryonic development (Kamler 2002), the inferred estimates to 50% hatching provide a relative, first order estimate of the effect of redd site location, with respect to upwelling and downwelling zones and their distinct thermal regimes, on the relative duration of the incubation period at these sites.

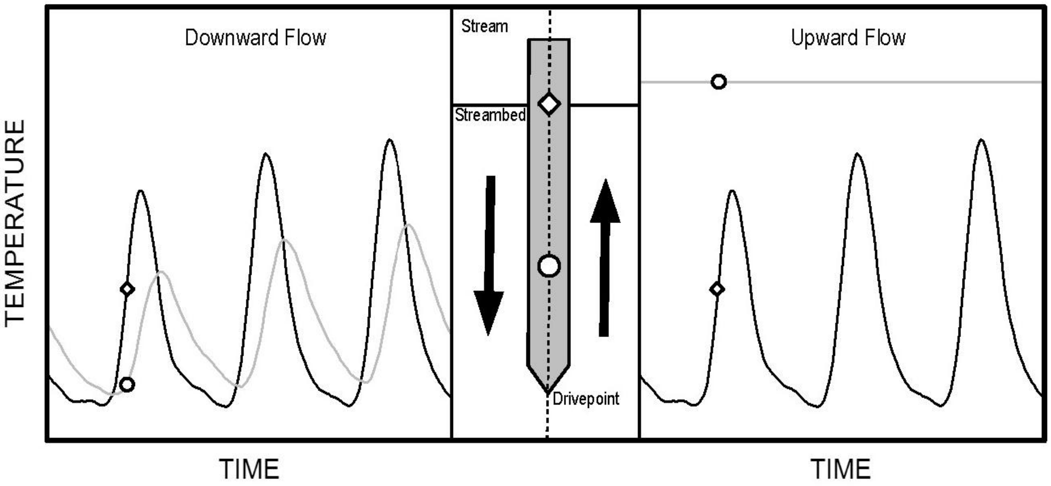


Figure 4.2. Diagram of temperature sensor installation (center) showing surface sensor (diamond), streambed sensor installed at depth of 20cm (circle), and arrows indicating direction of streambed flow. Temperature traces for surface water (black) and substrate (grey) for both downward (of left) and upward (on right) flow conditions. The absence of diurnal temperature fluctuations and higher streambed temperatures indicates a strong upward flow of groundwater.

4.4 Results

4.4.1 Upwelling flow as a cue for redd site selection at the microhabitat scale

Our data indicate that upwelling flow was not used as a decisive cue in redd site selection at the microhabitat scale. Our observations conducted a week after spawning at 39 redds distributed over 22 spawning sites, reveal that an approximately equal number of redds were situated in microhabitats with positive (upward) VHG (Vertical Hydraulic Gradient; n=18; 46% of redds) as were situated in microhabitats with negative (downward) VHG (n=16; 41%); with the remaining redds (n=5; 13%) situated in locations with near-neutral VHG. We also observed no significant difference in VHG between redd sites and adjacent non-selected sites at the microhabitat scale (Fig. 4.3), hence no local preference for stronger upwelling. The linear mixed model of the fixed effect of site type (selected vs. non-selected; n=39 pairs) and the random effect of spawning site (n=22) nested within stream (n=3) indicated that the difference in VHG between selected (median=0.00, range: -0.289 to 0.211, n=39) and non-selected sites (median=0.010, range: -0.259 to 0.430, n=39) was not statistically significant (t = -1.043, df = 55, p-value = 0.30; Fig. 2). The likelihood ratio test used to indicate the significance of the random effect of site nested within stream showed that there was no significant difference in VHG between streams (L-Ratio=1.1x10-9, p-value=1). Grouped by spawning site (n=22; 1 to 4 redds per site), we noted that there were 10 sites (45%) were the orientation of the median VHG was the same at the selected and adjacent non-select site. Of these 10 sites, seven (32% of total) had a median VHG that was positive; and three sites (14% of total) had a median VHG that was negative. There were four sites (18% of total) where the median VHG was positive at the selected sites and negative at the adjacent non-selected sites, and six sites (27% of total) where the median VHG at the selected sites was negative (i.e., downwelling) while at the adjacent non-selected sites median VHG was positive (i.e., upwelling). At the remaining two sites (9% of total) the VHG at the selected sites was near-neutral.

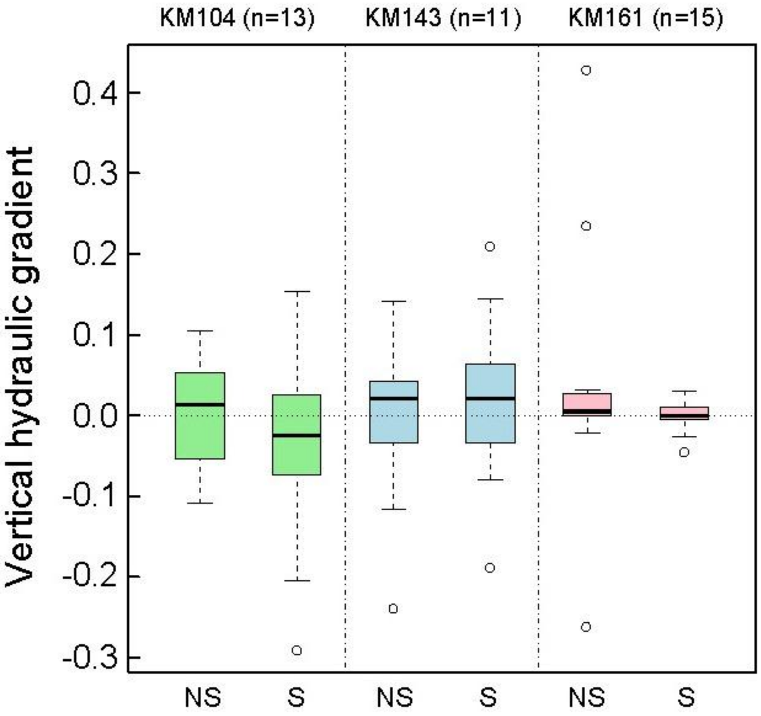


Figure 4.3. Boxplot of Vertical Hydraulic Gradients at Selected (S) and NonSelected (NS) spawning sites for each of the three stream segments surveyed in this study. Positive values indicate an upward gradient.

4.4.2 Redd site selection in relation to stream morphological features

Redds that were located in close proximity (i.e., within the distance of one width of the fall time, wetted channel) to a riffle-crest or log-step were associated with negative VHGs (i.e., downwelling; median = -0.022; range: -0.289 to 0.153; n=25), whereas redds that were not immediately adjacent to these morphological features were associated with positive VHG (i.e., upwelling; median = 0.025; -0.063 to 0.211; n=14; Fig. 4.4). Overall, the majority (63%) of the 39 redds (located in one of 22 distinct spawning sites) were situated immediately upstream of a riffle-crest or log-step. The linear mixed effect model of the fixed effect of site morphotype (i.e., presence/absence of a local slope break feature such as riffle-crest or log-step) and the random effect of redd (1 to 4) nested within site (n=22), indicated that the difference in VHG due to morphotype was statistically significant at the 5% level (t = -2.08, df = 20, p-value = 0.05).

4.4.3 Were redds situated in downwelling microhabitats nested in upwelling reaches?

Microhabitat scale (10^0m) mapping of winter streambed temperatures across five reaches of stream KM143 indicated that hyporheic flow conditions at the redd sites were similar to flow conditions at the reach scale (10^1m) in three out of five reaches (Fig. 4.5, Table 1). Over reaches A, B, and E, mean ΔT values (substrate temperature – surface water temperature) were +0.5°C or less, as were ΔT value at each of the individual redd sites located within these reaches. This indicates that there was no significant influx of groundwater at these spawning sites at either the redd microhabitat or the local reach scale. In Reach C, substrate temperatures at the redd site (ΔT value = 1.0°C indicating a surface influence) differed appreciably from the substrate temperatures measured over much of the reach (Reach C mean ΔT value = 2.5°C, indicative of significant groundwater inputs to the stream bed). Of the 5 reaches studied, Reach C was the only reach where a redd site that was clearly under the influence of downwelling surface water that was nested in a reach where there was significant influx of groundwater. Note that in Reach D, observed redds were indeed situated within a reach where substrate temperatures indicated that there was a significant upward flux of groundwater (Reach D mean ΔT value = 2.5°C), however redds were situated adjacent to a zone (i.e., within 2 meters) within the reach where ΔT values indicated that there was a localized increase in the influence of surface water (Fig. 4.5).

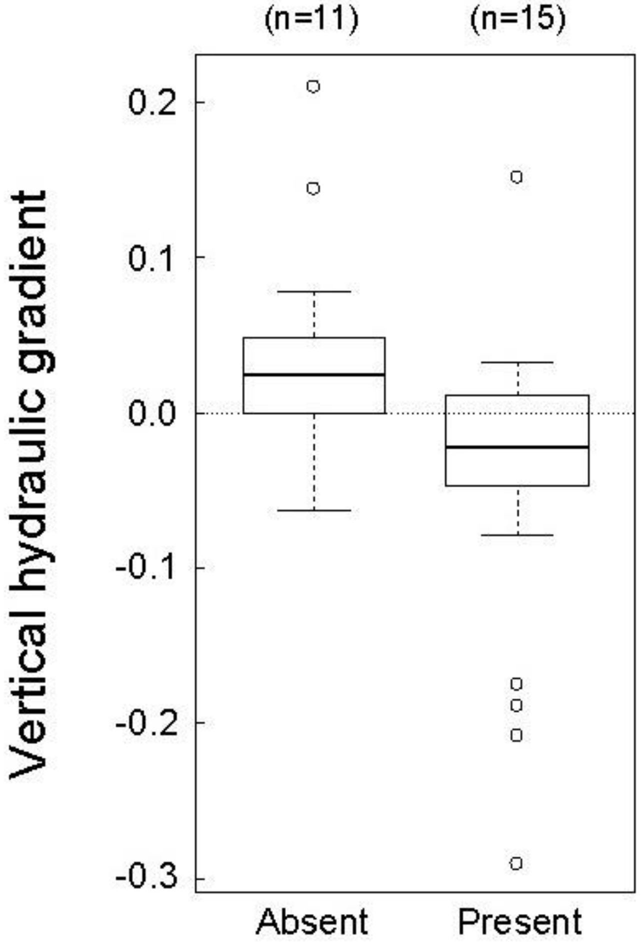


Figure 4.4. Boxplot of Vertical Hydraulic Gradients at redds situated within the width of the wetted channel of a break in water surface slope associated with a riffle crest or log step (present) and redds not situated in adjacent to either type of morphological feature (absent). Negative values indicate a downward gradient.

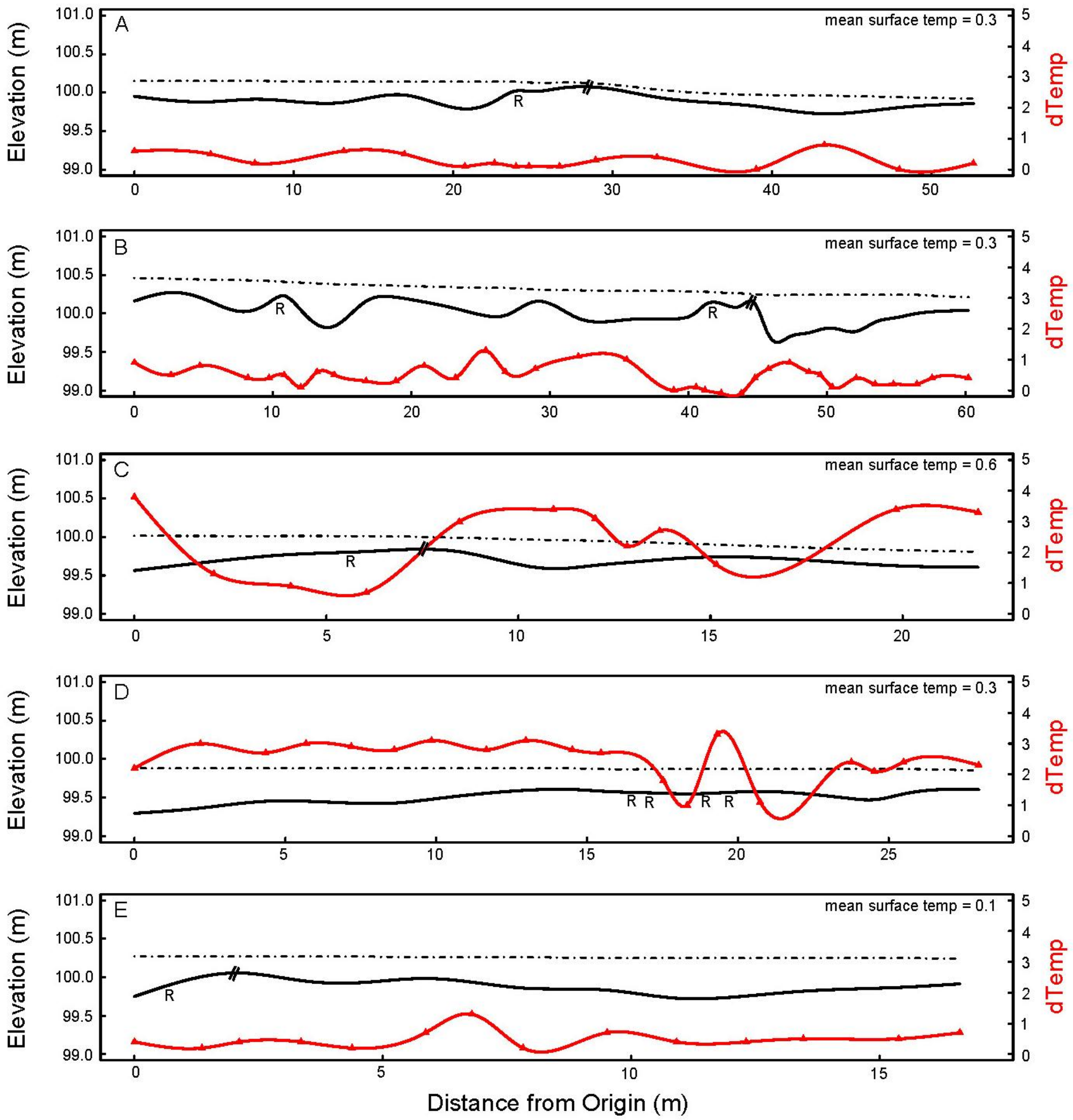


Figure 4.5. Long profile of streambed (solid black line) and water surface (dotted line) elevations through reaches where brook charr where observed to have spawned; the location of specific redd sites shown (R). Temperature difference (red line: delta T in degrees Celsius) was calculated by subtracting surface water temperature from substrate temperature; dTemp (scale at right) provides an indication of the relative influence of surface water and phreatic groundwater within the streambed. The temperature of phreatic groundwater is ~5.0°C; dTemp values greater than 4.0°C indicate strong upward flow of groundwater whereas lower dTemp indicate surface water influence. Double diagonal lines through streambed profile indicate position of riffle crests.

Table 4.1. Statistical summary: thermal mapping of spawning reaches

Reach[1]	Redds	n[2]	Mean Surface Water Temperature	Mean Substrate Temperature	Mean ΔT	Site ΔT	Water Surface Slope (%)
A (52m)	1	18	0.3 (0.2 - 0.3)	0.4 (0.1 - 1.0)	0.2 (-0.2 - 0.8)	0.1	0.44
B (60m)	2	70	0.3 (0.2 - 0.5)	0.7 (0.2 - 2.1)	0.4 (-0.1 – 1.8)	0.5 / 0.0	0.42
C (22m)	1	38	0.6 (0.5 - 0.6)	2.8 (0.9 – 4.4)	2.5 (0.6 – 4.1)	1.0	0.94
D (28m)	4	43	0.3 (0.2 - 0.4)	2.8 (1.3 – 3.8)	2.5 (1.0 – 3.5)	1.0 – 3.5	0.11
E (17m)	1	36	0.1 (0.1 - 0.2)	0.6 (0.2 – 1.4)	0.5 (0.1 - 1.3)	0.3	0.18

Notes:

[1] Length of Reach in meters

[2] Number of measurement points used in longitudinal profile

4.4.4 Hyporheic flow conditions/thermal regimes during the winter incubation period

Winter monitoring of streambed temperatures using iButtons confirmed that both steady upwelling and downwelling sites were indeed selected by spawners and thus embryos nested in these sites were exposed to distinct thermal regimes (see below). Our observations indicated that two of the eight sites (with total of five redds) were consistently under the influence of upwelling groundwater while the remaining six sites (the clear majority of sites, with 11 redds) were persistently under the influence of downwelling surface water (Fig. 4.6, Table 2). After fall and early winter runoff events, there were no significant changes in stream stage (i.e., more steady state conditions) through the mid-winter incubation period (Feb 1 – Apr 1; see Fig. 4.7 below). During these winter months, we observed three distinct thermal regimes indicative of the hyporheic flow conditions in these incubation microhabitats: i) constant substrate temperatures (depth = 20 cm) at approximately the temperature of the phreatic groundwater (~ 5°C), despite diel surface water temperature cycles, thus indicating significant upwelling flow (S3 and S4; Fig. 4.6; only S4 shown); ii) clear diurnal temperature fluctuations observed in the substrate indicating sites under the influence of surface water (S5 to S8; Fig.4.6; only S8 shown); and iii) no diurnal temperature fluctuations in the surface water but substrate temperatures nearly equal to surface water temperatures, denoting ice covered sites (S1 and S2; Fig. 4.6; only S2 shown; see Appendix Figure A.1 for mid-winter temperature traces for the five sites not shown here). Note that all these sites are within the same stream segment (1100 m in length; Fig. 1c) and thus were subjected to similar climate conditions. At upwelling sites S3 and S4, both the absence of diurnal temperature fluctuations and mean, minimum daily substrate temperatures of 5.1°C and 4.6°C respectively (Feb. 1 to Apr. 1) indicate that there was a strong upward flux of groundwater at these sites. At downwelling sites S5 to S8, the difference between the mean minimum daily surface and substrate temperatures (between Feb. 1 and Apr. 1) ranged from 0°C to only 1.2°C indicating that the sites were either entirely or predominately under the influence of downwelling surface water. In the third group (sites S1 and S2; ice covered), the low mean minimum daily substrate temperatures measured between Feb. 1 and Apr. 1 (S1: 0.3°C; S2: 0.6°C) indicated that there was an absence of upwelling groundwater at these sites. While there was also an absence of diurnal temperature cycles at these two sites between Feb. 1 and Apr. 1 (indicating ice cover), subsequent diurnal fluctuations at these sites in early spring (April-May; prior to high discharge period associated with the spring snowmelt) confirmed that the substrates at site S1 and S2 were under the influence of downwelling surface water (Fig. A.2). In summary, the paired surface water-substrate thermal records at these eight instrumented spawning sites indicate that 31% (n=5) of the observed redds were situated in areas of upwelling groundwater while 69% (n=11) of redds were situated in areas of downwelling surface water.

Table 4.2. Statistical summary: temperature time series at redd sites

Site	Redds	Mid-Winter[1] Mean Minimum Daily Temperatures			dTemp[3]	Morphotype[3]
		Surface	Substrate	Pool		
S1	3	0.3 (0.03)	0.6 (0.07)	0.6 (0.07)	0.3	P
S2	1	0.2 (0.02)	0.3 (0.01)	0.4 (0.03)	0.1	P
S3	2	1.5 (0.53)	4.6 (0.02)	4.2 (0.04)	3.1	A
S4	3	1.9 (0.25)	5.1 (0.04)	5.0 (0.06)	3.2	A
S5	3	1.1 (0.19)	2.3 (0.13)	5.3 (0.07)	1.2	P
S6	1	0.8 (0.23)	1.2 (0.12)	2.2 (0.12)	0.4	P
S7	2	0.6 (0.28)	0.8 (0.18)	0.9 (0.20)	0.2	P
S8	1	0.5 (0.29)	0.5 (0.26)	0.7 (0.26)	0.0	P

Notes:

[1] Mid Winter Period from Febuary 1 to April 1, 2009; period of stable baseflow conditions; (n.nn) = standard deviation

[2] dTemp = Substrate Temperature – Surface Temperature

[3] Morphotype = redds situated within the width of the wetted channel of a break in water surface slope associated with a riffle crest or step (P = present) or redds not adjacent to either type of morphological feature (A = absent).

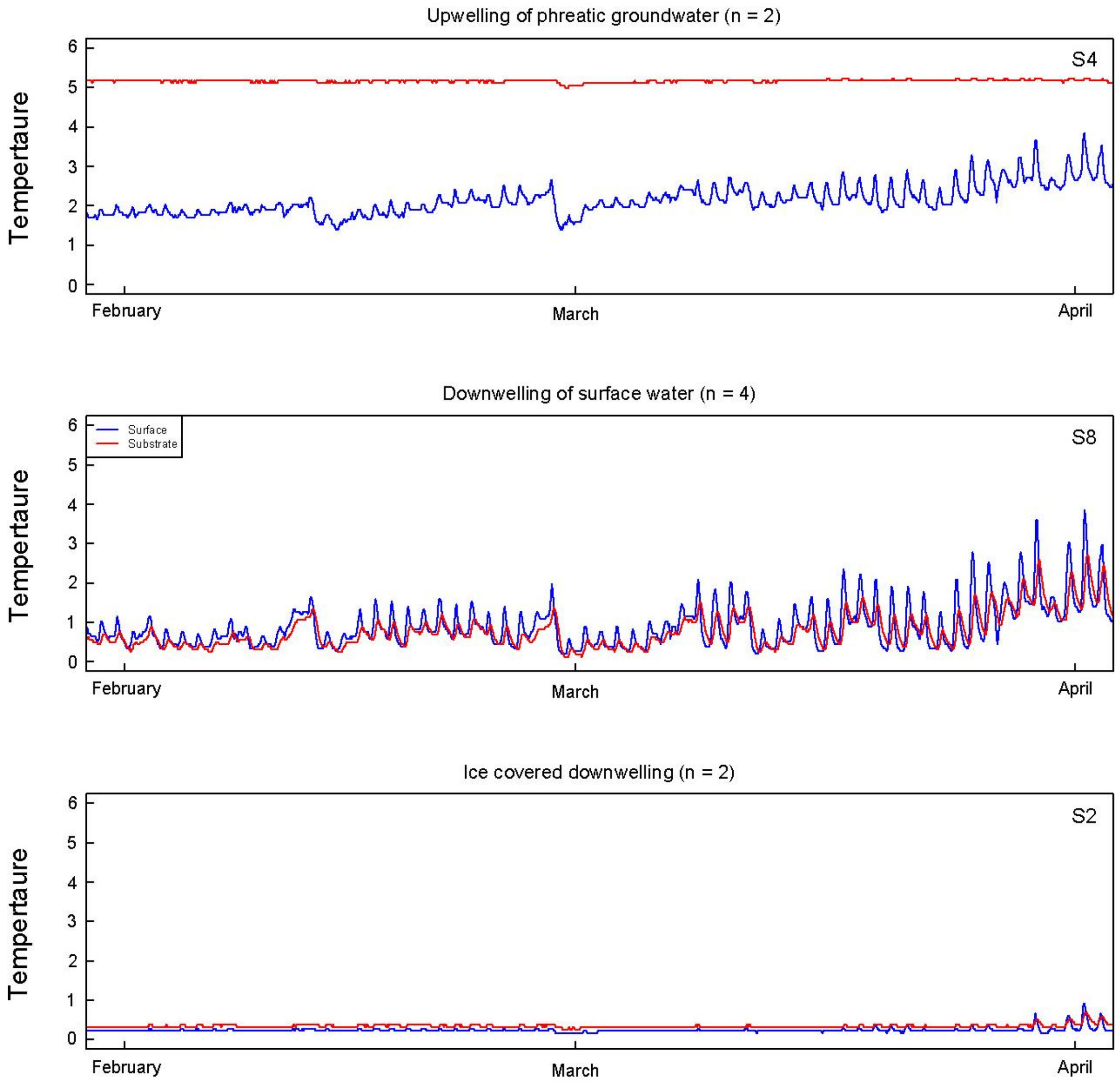


Figure 4.6. Examples of the three types of thermal regimes observed at the eight spawning sites instrumented with surface/substrate temperature sensors. Plots show surface (blue; depth = 0 cm) and streambed (red; depth = 20 cm) temperatures during the mid winter incubation period (Feb. to April 2008) when stream water levels remained at winter baseflow conditions. The vertical scale is constant to illustrate the contrasts in thermal ranges.

4.4.5 Influence of thermal regimes on inferred hatching dates

The monitoring of redd temperature throughout the incubation period indicated that redd position within reach scale groundwater and hyporheic flow nets affected incubation temperatures and therefore, in theory, inferred hatching dates. Thermal data and hatching models (Crisp 1981) indicated that embryos buried at sites S3 and S4 (upwelling sites with warmer gravel temperatures, at 4.6-5.1°C) would experience significantly accelerated rates of embryonic development relative to embryos in egg pockets at the six other sites (cooler gravel temperatures of 0.7 - 2.6°C), that were under the influence of surface water (Fig. 4.7; Table 3). We observed that Cumulative Degree Days (CDD) at spawning sites ranged from 146.8 to 1050.9 days from the date of temperature sensor installation (October 22) to the peak of the spring freshet (May 15). These CDD values correspond to a mean daily streambed temperature range of 0.7 - 5.1°C. The difference in CDD between upwelling sites (mean=992.5, n=2) and downwelling sites (mean=278.25, n=6) was highly significant (t=-8.655, df=3.319, p-value=0.002). Inferred hatching dates for downwelling sites S1 to S2 and S5 to S8 indicate that embryos buried at these colder substrate sites on October 22 would reach the 50% hatching stage at dates ranging from March 1 to April 12. Inferred hatching dates for upwelling sites S4 and S3 are January 22 and January 29, respectively (Fig. 4.7), approximately 4 to 11 weeks earlier. At upwelling, warmer gravel sites (S3 and S4) the mean duration of this development period was 96.2 days (range: 92.4 to 99.9, n=2) compared to a mean of 157.7 days (range: 130.6 to 172.3, n=6) at downwelling sites (S1, S2, S5-S8), a difference of 62 days.

4.5 Discussion

4.5.1 Upwelling flow as a cue for redd site selection at the microhabitat scale

The absence of a preference for upwelling over downwelling at redd sites as well as the observed selection in some cases of downwelling microhabitats in the presence of adjacent upwelling ones, suggests that upwelling flow was not strongly and exclusively sought as a cue in redd site selection at microhabitat scale, in these stream systems. Brook trout were observed to locate redds in upwelling and downwelling microhabitats, located either in upwelling and downwelling reaches. In contrast with previous studies investigating microhabitat scale redd site selection by brook trout (Curry and Noakes 1995; Bernier-Bourgault and Magnan 2002; Guillemette et al. 2011), we observed distinct flow directions at selected and adjacent (< 5 m) non-selected sites. At 45% of our spawning sites (n = 10 of 22), the vertical orientation of substrate flow (upwelling/downwelling) at the selected sites was opposite to that at the adjacent non-selected sites, and in this subset 60% (n = 6 of 10) of spawning sites were at downwellings. The presence of distinct vertical flow directions over short distances observed here is likely related to the presence of large pool-riffle or step-pool bedforms in our systems (see below). Published reports do not say if such bedforms were also present near redds in the trout spawning habitats investigated previously.

In the boreal stream systems studied here, the origin of the flow (within a mixing gradient, from surface water to mostly groundwater flow) has important implications for the temperatures experienced by developing embryos. Redds situated in zones of discharging phreatic groundwater may be consistently as much as 5°C warmer during the entire winter incubation period relative to those in zones of downwelling surface water (see discussion below).

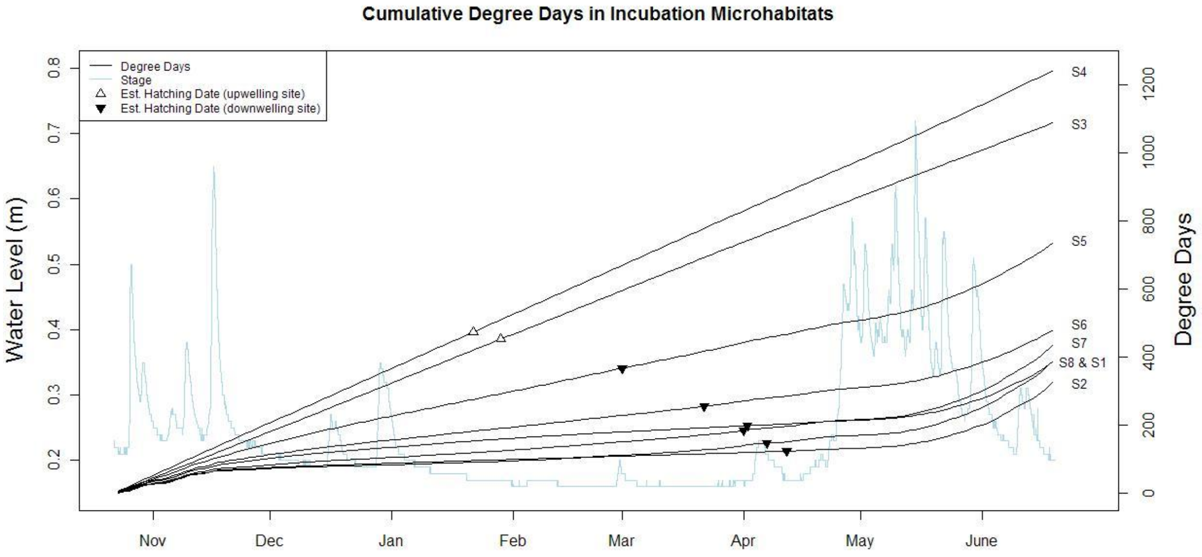


Figure 4.7. Thermal units (cumulative degree days) at selected sites over the winter incubation period; with a stream hydrograph (water level in meters above datum) recorded within the study reach over the same period. The linear and more steeply sloping lines for the two sites where there was upwelling groundwater (white triangles) are reflective of the elevated temperatures recorded at these two sites.

Table 4.3. Cumulative thermal units (Degree-Day) between Oct 22, 2008 (data logger installation) and May 15, 2009 (peak of spring freshet) at selected spawning sites.

Site	Cumulative thermal units (Degree-day)
TS-1	187.1
TS-2	234.8
TS-3	330.0
TS-4	541.4
TS-5	1050.9
TS-6	934.0
TS-7	146.8
TS-8	228.8

4.5.2 Redd site selection in relation to stream morphological features

In our study systems, a majority of redds (63%) were situated immediately upstream (within one channel width) from a bedform such as a riffle crest or a log-step. We observed no redds immediately downstream of such features where positive gradients and upwelling hyporheic flow would be expected. Our observation that downwelling sites were situated upstream and in close proximity to bedforms that cause convex upward thalweg and water surface profiles is consistent with previous work on hyporheic flow patterns (Stuart 1953, Vaux 1968, Gooseff et al. 2006; Tonina and Buffington 2009); the convex longitudinal water surface gradients created by these bedform features induce the downwelling of surface water into the streambed on the upstream side of the bedform and the upwelling of hyporheic water on the downstream side. The observed spawning pattern upstream of riffles and log-steps is also consistent with numerous previous studies on salmonid spawning behaviour showing a clustering of redds in association with substantial morphological features such as islands, channel bars, and pool-riffle transitions (Salmo salar: Coulombe-Pontbriand & Lapointe 2004; and Moir et. al. 2004; Oncorhynchus tshawytscha: Geist & Dauble 1998; Oncorhynchus tshawytscha and Oncorhynchus kisutch: Montgomery et al. 1999), which create locally stronger longitudinal gradients and more intense hyporheic flow.

Although flow velocities in gravel interstices are difficult to measure (and were not here), from first principles (Darcy's law), they are a function of: i) applied hydraulic gradient, and ii) substrate permeability (or hydraulic conductivity). Thus, in substrates that are sufficiently permeable (hydraulic conductivities > 0.02 cm/s (indicative of sand-gravel substrates; Bear 1972), local longitudinal water surface slopes in excess of 0.5% (on the order of magnitude of those observed here; cf Table 1) should be sufficient to generate bulk interstitial flow velocities of more than 4 mm/hr, which are above the critical threshold for survival that has been suggested for this species (1mm/hr; Blanchfield & Ridgway

2005; Franssen et al. 2012). Thus, at such pool-riffle or log-step sites as selected here, upwelling conditions are not required to maintain sufficient gravel flow for embryo incubation.

4.5.3 Microhabitat vs reach scale hyporheic flow conditions

Our results do not support the hypothesis that brook trout incubation microhabitats are systematically located in downwelling microhabitats that are nested within upwelling reaches (i.e., reaches with a significant influx of phreatic groundwater). In only two of the five mapped reaches did substrate temperatures indicate a significant influx of phreatic groundwater at the reach scale (cf. Table 2), and in only one of these, was the redd clearly situated within a downwelling microhabitat. In the remaining three reaches, very cold substrate temperatures indicated that the streambed (depth = 25 cm) was predominantly under the influence of downwelling surface water.

However, we cannot rule out that the upwelling of phreatic groundwater may have played a role in the selection of incubation habitats at a scale larger than the extent of the individual reaches surveyed here (20 to 60 m in length). The long cold winters that occur over much of the brook trout’s eastern North American range mean that streamflow in spawning tributaries cannot be maintained without a persistent groundwater discharge upstream. This is particularly the case at our relatively high latitude/altitude sites where mean monthly air temperatures are below 0°C from November to April. Thus, at least at the catchment scale, brook trout presumably select spawning tributaries that receive sufficient groundwater flux to avoid the freezing or dewatering of incubation microhabitats (Power 2002). Note that the relatively high precipitation (1.6 m annually) watersheds studied here have abundant gravelly sand, fluvio-glacial deposits mantling the bedrock in valleys, a context where groundwater input into streams can be expected.

Within the segment of stream studied (cf Fig. 4.1), winter flow without bottom freezing observed at spawning sites S5-S8 (located in the downstream portion of our study site) was apparently sustained by the upstream occurrence of discharging, phreatic groundwater at sites S3-S4 (centrally located with our study site, cf Fig 1). Persistent winter flow at sites S1-S2 (located at the upstream end of the study site) would have been sustained by additional reaches with significant groundwater inputs which must certainly have been present upstream of our study site. Our study was designed to investigate the cues for spawning site selection at the microhabitat/reach scale and not at the tributary or catchment scales. The role of groundwater inputs in brook trout spawning site selection at these larger, sub watershed scales has to our knowledge not yet been sufficiently clarified.

4.5.4 Contrasting thermal regimes in incubation microhabitats: distinct life history tactics?

We identified incubation microhabitats with two clearly distinct thermal regimes. A minority of the observed redd sites (25%), observed along stream KM143 during the 2008 spawning season, were under the influence of a strong upward flux of phreatic groundwater, and thus a significantly warmer egg pocket regime during winter time incubation period. Embryos nested in these redds would have been exposed to a significantly greater number (on average approximately 2.5 times) of thermal units (i.e., Cumulative Degree Days) during incubation than the majority of sites observed to be under the influence of downwelling surface water (i.e., cold regime sites). In lotic environments, the emergence of brook trout fry is thought to coincide with the arrival of the spring freshet and the onset of primary production (White 1930; Noakes 1989; Curry, Noakes & Morgan, 1995). Our inferred hatching dates indicate that fry would have emerged from the cold regime sites at approximately the same time as the spring freshet (May). In contrast, fry in the warm regime sites would have emerged in mid-winter (February-March). Although these dates were inferred with a model that was not validated for this specific system (i.e. high latitude/altitude), we presume that the relative difference in inferred hatching dates between cold and warm regimes sites is valid given that all sites were utilized by the same brook trout population (i.e., all sites are located within a single stream segment). The delayed emergence of fry from warm regime sites until after the peak of the spring freshet would thus require either: i) significantly slower rates of embryonic development per degree-day relative to embryos incubating in cold regime sites; or ii) a much extended residence period of embryos within the gravel bed at warm regime sites (hatching February/March) sites till emergence in May.

Statistically significant differences in ontogenetic rates of embryonic development have in fact been attributed to adaptive variation to local environmental conditions in isolated populations of brook trout (Baird, Krueger & Josephson, 2002) and other salmonids (Tallman 1986; Murray and Beacham 1987). However, the individuals observed spawning in distinct thermal habitats at our study site are presumably from the same population (i.e., observed to spawn in the same stream segment during the same period). Synchronization of the phenology of emergence of larvae from warm and cold regime sites (i.e., to coincide with the spring freshet) would thus require a factor other than temperature acting to moderate development rates at warm regime sites. We could find no evidence from previous experimental studies to suggest that other extrinsic (dissolved oxygen, pH) and intrinsic (egg size) factors known to have a direct influence on ontogenetic rates would delay hatching/emergence at warm regime sites (Garside 1966; Kamler 2002) , sufficiently to reconcile emergence dates across these thermal incubation regimes. As temperature is the dominant factor controlling the rate of embryonic development in salmonids, we presume that embryos nested in zones of discharging phreatic groundwater must have reached the hatching and emergence dates many weeks earlier than individuals at observed cold regime sites. Following complete yolk sac absorption, the survival of mid-winter emergents from warm regime sites would require sufficient food sources (i.e., stream or terrestrial invertebrates) to begin exogenous feeding.

Could in-stream food sources be available in mid-winter in reaches with warmer, groundwater fed substrate? During cold winter months, phreatic groundwater discharge has been shown to provide favourable conditions for the growth of stream invertebrates (Pepin and Hauer 2002; Schutz et al. 2001). In a study investigating the seasonal dynamics of macroinvertebrate communities in an stream in the Austrian Alps, with similar hydrological and thermal characteristics to our study sites, Schutz et al. (2001) found high densities of stream invertebrates (as high as 94,000 individuals per m2) during winter months (November - May) at sites that remained ice free and had slightly warmer water temperatures due the presence of discharging groundwater. It is thus possible that such favourable conditions for the winter growth of macroinvertebrates occurred at our study sites and thus that fry emerging in reaches where there was a significant influx of upwelling groundwater may have had the required food sources to sustain their growth.

The observed conspecific use of both cold (75%) and warm regime sites (25%) might thus be an example of distinct life history tactics in this boreal stream. Distinct spawning behaviours related to either the timing of spawning and or use of specific habitats which influence the duration of the incubation period have already been reported in other salmonid species (Beer and Anderson 2001; Hendry, Hensleigh, & Reisenbichler, 1998). Our observations that a significant fraction of spawners utilized both cold and warm regime sites in multiple years suggests that: i) it is unlikely that warm regime/upwelling sites are ecological traps (sensu Schlaepfer, Runge & Sherman, 2002); and ii) the existence of these distinct life history tactics suggest that the selection of cold regime/downwelling sites vs. warm regime/upwelling sites does not confer an improvement in fitness because both tactics have been maintained since brook trout colonized the Canadian Shield approximately 12K years ago. However, the co-existence of these distinct tactics may be an evolutionary advantage to population stability in rapid changing environments, as suggested for the brown trout in mountain streams (Champigneulle, Largiader & Caudron, 2003). These distinct tactics might ensure that at least a portion of individuals within a cohort survive extreme environmental events that might cause high mortality in one of the two distinct habitat types (i.e., warm regime / cold regime). For example, if in any given year, spring snowmelt floods occur earlier than normal, there may be a greater probability of high mortalities at ‘cold regime’ (later hatching) sites due to scouring away of underdeveloped embryos. During such seasons, the early emergence of larvae from warm regime sites might ensure that there was at least some survival of progeny within such a harsh environment.

Chapter 5

Field study to assess the role of filter fraction and upwelling-downwelling flow in controlling the re-infiltration of fine sediment into salmonid redds

5.1 Preface

5.1.1 Manuscript details

This manuscript is authored by Jan Franssen, Michel Lapointe, and Pierre Magnan. It has not yet been submitted for publication.

5.1.2 Context within thesis

In the following manuscript we detail the results of a field experiment investigating the role of substrate composition and upwelling/downwelling flow in controlling the re-infiltration of fine sediment into gravel bed substrates. Most the hypotheses regarding the role of these physical factors in modulating infiltration processes have been derived from laboratory investigations. Here, we test these hypotheses in experimental redds constructed in brook charr spawning microhabitats located in a gravel bed stream. The results presented in the following chapter link to the topic of early life cycle survival (Chapter 3) as they improving our understanding of the factors that control the egress of fine sediment into spawning/incubation microhabitats. These results also link to the topic of redd site selection (Chapter 4) by addressing issues regarding the specific characteristics of selected microhabitats that may, or may not, confer a resistance of these habitats to fines infiltration.

5.1.3 Abstract

We investigated the role of filter fractions and upwelling/downwelling flow in controlling the re-infiltration of fine sediment into brook charr spawning habitats. Elevated fines content is known to be detrimental to embryo survival. Laboratory investigations have determined that the predominant factor affecting the infiltration processes is the ratio between the diameter of the infiltrating fine sediment and the diameter of the interstitial pore openings in the surface and subsurface layers. Pore opening size is a fraction of, and scales with, the diameter of the particles that comprise the streambed. Thus where sufficient coarse sand and fine gravels fractions are present within the substrate they may act as a filter (i.e., filter fractions) limiting infiltrating fine sediment. Previous studies also suggest that the amount of fine sediment in transport across the bed, and the direction and intensity of interstitial flows, may also influence fines infiltration. Few field studies with natural, freshly spawned substrate, have been conducted to investigate fines infiltration. There is also an absence of field studies examining the effect of upwelling/downwelling flow on fines infiltration. Here we installed experimental redds (n=17) into known brook charr spawning microhabitats in a Boreal stream. To simulate the effect of spawning in coarsening the incubation substrates, redds were partially cleaned of coarse sand and fine gravel (i.e., filter fractions) and of all fine sediment (<0.5 mm). At the end of the 9 week, fall-time experimental period, which included a near bankfull event, experimental redds were sampled using freeze cores to completely preserve both fines content and substrate stratigraphy. In a majority of our experimental redds (76%), we observed a reduction with depth in newly infiltrated fines under 0.5mm (i.e., a filtering effect). This response was positively associated with the proportion of filter fraction (coarse sand and fine gravel) within the upper layers of the redds. Fines accumulation at egg pocket depth however was neither statistically associated with fine sediment exposure (measured in separate sedimentation cans), nor with upwelling/downwelling flow or horizontal flows through the redds.

5.2 Introduction

The interstitial spaces within the uppermost layers of gravel streambeds provide important habitats for a wide variety of macroinvertebrates and these spaces are critical to the early life cycle survival of stream spawning fish species such as salmonids (Williams and Hynes 1974, Bjornn and Reiser 1991). The availability of suitably large (i.e., biological relevant) interstices is inversely related to the proportion of finer fractions (mainly medium and fine sand and silt) within the gravel substrate (Franssen et al., In Press; Chapter 3 here). Macroinvertebrate densities and salmonid egg-to-emergence survival have both been shown to be negatively related to substrate fines content (Wood and Armitage 1997; Chapman 1988), with increased fine sediment loading to streams implicated as a cause in the degradation of these gravel bed microhabitats (Alexander 1986). However, these interstitial habitats will only suffer degradation if the fine sediment that is in transport actually infiltrates into the subsurface layers of the gravel bed, a process that can be hindered by filtering at the bed surface (Gibson et al. 2009) or by local hydraulic conditions (Schalchli 1992). Thus understanding the linkage between increased fine sediment loading to streams and habitat degradation requires an understanding of the mechanisms modulating fines infiltration.

Substrate spawners, such as salmonids, have been shown to reduce the proportions of fine sediment (<2 mm) within gravel substrates during redd excavation and embryo burial (Kondolf 2000). This removal of fines is thought to improve microhabitat quality by increasing substrate permeability and thus oxygen flux to the developing embryos. However, re-infiltration of fine sediment during the incubation period (which may span several months) may negatively impact salmonid embryo survival if the fines concentrations at egg pocket levels during incubation reach densities that would reduce oxygen flux to (or abrade) embryo membranes, or clog the interstitial spaces required for successful emergence of hatched embryos (Meyer 2005, Greig et al. 2005, Franssen et al., in press and Chapter 3 here). The process of fines infiltration into gravel bed substrates is thought to be influenced by: i) the ‘dose’ of fine sediment travelling over the surface of the bed during incubation season (Lisle 1989); ii) pore opening sizes, expressed as the size ratio between the diameter of the infiltrating fine sediment and the diameter of the interstitial spaces (Frings et al. 2008); and iii) water velocities through the gravel interstices, which are driven by vertical and horizontal gradients through/across the streambed (Schalchli 1992). It has thus been argued that fines re-infiltration into the spawning microhabitats is only likely to occur in substrates where the fines transported to the surface of the bed are smaller in diameter then the openings between the particles that comprise the bed, and where strong, upwelling flow from the bed does not hinder the downward percolation of fines.

Deep infiltration of harmful silt and fine sand fractions is inhibited by the presence of a filter layer rich in coarse sand and pea gravel near the substrate surface (Lisle 1989, Meyer 2005). Fines re-infiltration into redds may also occur through the lateral movement of fines within the substrate that are transported by horizontal interstitial flows (Carling 1984). A number of studies have investigated the details of the filtering process inhibiting fines intrusion. In a bed of uniform spheres the size of pore constrictions through which fines would travel downward: i) scales with the diameters of the particles comprising the bed (i.e., the framework particles); and ii) is influenced by how tightly these framework particles are packed together (Frings et al. 2008). In laboratory experiments, the infiltration processes has been shown to be particularly sensitive to the size ratio between infiltrating particles and the framework pore constrictions (Einstein 1968; Beschta and Jackson 1979). For uniform spheres of diameter D, pore constrictions range in size from 0.15D to 0.40D, depending on how tightly the framework particles are packed together (Frings et al. 2010). These geometric relations suggest, for example, that a 0.5 mm particle (medium sand) would not percolate through a uniformly packed framework comprised of particles < 3.1 mm in diameter. For 0.5 mm size particles, coarse sands and fine gravel would in effect act as a filter (i.e., filter classes). However, gravel bed substrates are generally comprised of a wide range of particle sizes, complicating simple geometric relations uncovered using bimodal mixtures in the laboratory. Other laboratory experiments into the infiltration of sand sized particles into frameworks comprised of a range of gravel sizes suggest that the size of the pore constrictions (Dc) scale with the relatively rare, finer framework fractions (e.g., substrate D_{15});

with $Dc = 0.20 \cdot D_{15}$ framework (Kenney et al. 1984), where D_{15} is the maximum diameter of the smallest 15% of the particles in a granular mixture.

While numerous laboratory studies have been done to characterize the grain size controls on infiltration of fine sediment into gravel bed frameworks (see summary in Gibson et al. 2009), few field studies have been conducted to characterize infiltration processes into actual spawning substrates, where framework composition is more varied while flow conditions and sediment transport patterns are likely to differ significantly from those created in laboratory flumes. A previous field study (Meyer et al. 2005) modeled the flow conditions under which effective filter layers were created and explained survival to emergence as associated to a reduction in fine sediment (<0.5 mm) at egg pocket depth with increased proportion of course sand and fine gravel in the upper layers of the gravel bed. However, Meyer et al. (2005) did not investigate the previously hypothesized effects of upwelling/downwelling on fines infiltration. Moreover, only part of study reported in Meyer et al. (2005) relies on freeze-core samples, while other parts rely on substrate sampling techniques (McNeil samples) which can lose fines at sample extraction. Here, to evaluate the role of filtering and hydraulic factors influencing the re-infiltration of fine sediment (<0.5 mm) into gravel bed spawning microhabitats, we constructed experimental redds only partially cleaned of coarse sand and fine gravel (i.e., filter fractions) and located these in microhabitats with variable substrates were brook charr (*Salvelinus fontinalis*) spawning activity had been previously observed. Redds were partially cleaned to simulate the effect of spawning in winnowing away a portion of substrate fines (Kondolf 2000). We also only relied on freeze core sampling to preserve both fines content and substrate stratigraphy. We used these installations to test the following hypotheses related to the re-infiltration of fine sediment fractions associated with increased embryo mortality (grain size <0.5 mm; Franssen et al., In Press and Chapter 3) into experimental redds constructed in known brook charr spawning habitats:

a) the reduction in re-infiltrated fine sediment (< 0.5 mm) content with depth (i.e., filtration effect) in experimental redds is positively related to the proportion of filter sized particles within the substrate; where the filter class is defined as the 0.5 to 4 mm sized particles (based on geometric relations described in Frings et al. 2010);

b) this reduction in fine sediment (<0.5 mm) content with depth is also negatively related to the effective size of the framework pore constrictions (Dc); the metric Dc is estimated as $0.20 \cdot D_{15}$ (Kenney et al. 1985);

c) re-infiltrated fine sediment (< 0.5 mm) content within experimental redds is positively related to the amount of infiltratable fine sediment in transport across the redd (i.e., the ‘exposure dose’, measured by local sedimentation buckets);

d) fine sediment (<0.5 mm) content within experimental redds are related to the strength and direction of the local vertical hydraulic gradient (VHG); with greater accumulation at sites with negative VHG (i.e., downwelling) and lesser accumulation at sites with positive VHG (i.e., upwelling); and

e) fine sediment (<0.5 mm) content within partially cleaned experimental redds are positively related to the strength of the local horizontal hydraulic gradient (HHG); higher HHG are associated with greater horizontal flow velocities which can drive lateral transport of fine sediment into the partially fines poor redd.

5.3 Material and Methods

Between August 13 and 21, 2008 we constructed 17 experimental redds along three small, trout bearing streams located in the Réserve Faunique des Laurentides (RFL), a 7,861 km2 wildlife reserve situated north of Quebec City, Canada. The three streams were designated by milepost distance from south to north along the principal highway through the RFL: KM104 (47^{0}18’39”N, 71^{0}10’56”W), KM143 (47^{0}38’13”N, 71^{0}14’22”W), and KM161 (47^{0}47’18”N,

$71^{0}13'24''$W). We installed five, ten and two redds, respectively, along streams KM104, KM143 and KM161. Stream KM104 is a first order stream with an average channel width of approximately 3 m. Its streambed is composed of sand and gravel with subsurface D_{50} and D_{84} at spawning sites in the range of 2-10 mm and 10-50 mm respectively. Study reaches containing several naturalized log-step features created by the partial burial of 0.3 m diameter logs across the width of the wetted channel. Stream KM143 is a second order tributary to lake Jacques-Cartier (RFL) with pool-riffle morphology and stream widths ranging from 7-10 m. Its streambed is composed of sand and gravel with subsurface D_{50} and D_{84} at spawning sites in the range of 5-20 mm and 20-50 mm respectively. Stream KM161 is a first order tributary to Lake Jupiter (RFL) and has a channel width of approximately 2 m within the study reach. Its streambed is composed of sand and gravel with subsurface D_{50} and D_{84} at spawning sites in the range of 4-10 mm and 10-20 mm respectively. This channel has undergone habitat enhancement including the construction of log step-pool features and gravel placement. Experimental redds were situated within 2 m of where brook trout spawning activity was observed during the 2006 and/or 2007 spawning seasons.

5.3.1 Redd construction

Redds were constructed by carefully excavating streambed sediments within a 25 cm diameter hollow cylinder that was advanced to a depth of 15-20 cm below the top of the streambed. To simulate the partial flushing of fine sediment by the action of spawning females (Montgomery et al. 1996, Kondolf 2000), excavated sediments were wet sieved onsite to remove precisely a third of coarse sand (1-2 mm) observed in the local sample, two thirds of medium sand (0.5-1 mm) and all particles finer than 0.5 mm. These ratios were arbitrarily chosen to reflecting how spawner activity induces flow winnowing of progressively less of the coarser and heavier sands. After removal of appropriate proportions of the fines, all sieved sediments were then thoroughly mixed and returned to the excavation in small, well mixed layers to avoid stratification. The enclosing excavation cylinder was then carefully removed. Typically experimental redds were situated upstream and within a distance equal to one wetted channel width of riffle crests or log-steps. Some redds were installed in runs (i.e., relatively straight section of channel with moderate depths and surface water velocities) where riffle crest/log-step features were not present. None of the experimental redds were situated in pools. Local water depths at redd sites at the time of installation ranged from 6 to 30 cm (mean: 17 cm; n=17). A photo of a typical installation is shown in Figure 5.1.

Since all fractions under 0.5 mm were removed at setup, fine sediments (<0.5 mm) measured in the any layer of the redd core at the completion of the field experiment were fines that re-infiltrated into the redd during the experiment. The initial, in-situ bulk volumetric density ($g \cdot cm^3$) of fine fractions in the substrate was estimated by dividing the mass of fines separated from the excavated sediment during redd construction, by the volume of the excavation.

5.3.2 Sediment transport measurements

The location of each redd was marked with survey pins and several larger gravel sized particles (of local surface D_{90} caliber) that were painted white and placed with the other gravel particles in the top layer of the redd as their displacement would allow for detection of full bed mobilization during the experiment period. A marker consisting of a wire mesh (1cm by 1cm openings) was placed at the base of each excavation prior to backfilling, giving us a benchmark from which to detect if there was a net increase in bed level (i.e., aggradation) during the experiment. At each site, a sediment trap was installed 50 cm downstream of the redd to provide and indication of the relative amount of finer sediments to which the experimental redds were exposed during the experiment (the ‘dose’ of infiltratable fines for the period and site). Sediment traps consisted of a 9 cm diameter by 20 cm deep plastic bucket, installed flush with the streambed surface. Five centimeters below the top of each trap, a wire mesh with 5x5 mm openings was installed to: i) support a layer of clean stones

Figure 5.1. Photograph showing typical experimental redd installation. Photo taken immediately following installation. Water flow is from left to right. White marker gravels (D_{90} caliber) denote location of the experimental redd. Sediment collection bucket is located approximately 50 cm downstream.

(D_{90} caliber) used to buffer turbulence penetration below the mesh and thereby inhibit the re-suspension of fines that had accumulated within the trap, while ii) maximizing the volume of space below the mesh available for the accumulation of fine sediment. At the end of the experimental period the traps were transported to laboratory where particles size analysis was used to determine the total mass fine sediment (< 0.5 mm) accumulation (i.e., local fine sediment dose).

5.3.3 Hyporheic gradient data at each redd

Around each redd, to quantify the direction and intensity of vertical and horizontal hydraulic gradients, we installed four minipiezometers, of the type described by Baxter et al. (2003). Surrounding the redd, they were positioned approximately 1 m from the redd (1 upstream and 1 downstream parallel to the direction of flow, and 1 each toward the left and right banks perpendicular to the direction of flow). We used the minipiezometers to measured head at a 20 cm depth within the substrate at the time of redd construction and used a total station to measure the exact position and elevation of each piezometer in relation to the experimental redd. Water levels within the minipiezometers and attached surface water stilling well were measured with an analogue water level dipper to within 0.001 m.

5.3.4 Redd core retrieval

The redds, installed in mid-late-August, were left in place for approximately 9 weeks during which time there was one large magnitude flow event (Figure 5.2). Note that the highest peak stage of the year occurred during the fall experimental period (although this flood event had a shorter duration than typical spring snowmelt events). We returned to the sites during the week of October 17-23, 2008 and sampled each redd using the freeze core technique by injecting liquid nitrogen through a copper pipe inserted precisely at redd centers. Freeze-core sampling has been used in numerous studies to assess the composition of salmonid spawning gravels (Crisp and Carling, 1989; Zimmermann et al. 2005). Freeze-coring is necessary in this study, as the

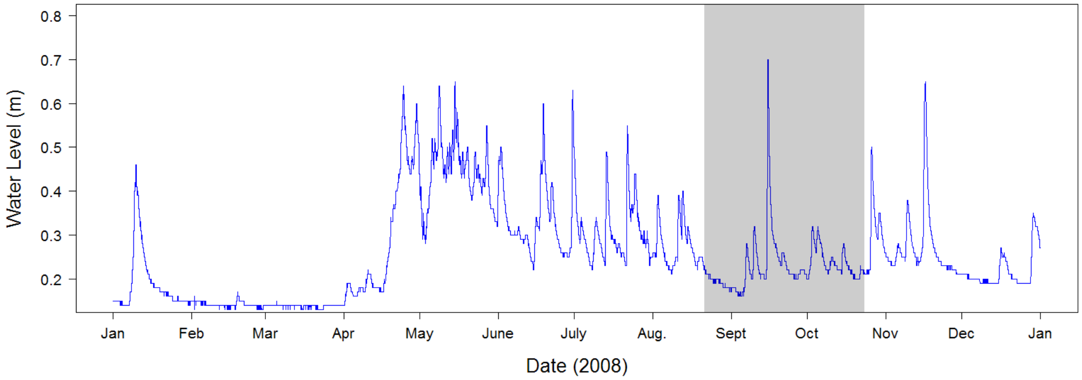


Figure 5.2. Stream hydrograph (water level in meters above datum) recorded at stream KM 143. Shaded portion of the graph indicates the period during which the experimental redds were in place; installation late August 2008 and removal late October 2008. Note that the maximum peak flow for the year occurred during the sampling period.

technique both prevents the loss of fine sediment, and also maintains the stratification of sediment within the core. These sampling traits are necessary to determining both the amount of fine sediments and their depth of penetration into the redd. Here, data on fines content per layer are analyzed as there is no a priori basis for determining fines rich layers when filtering effects are likely to be variable in response to the different substrate compositions at each individual redd site (Gibson et al. 2010). However, in gravel beds freeze-core samples have been shown to over represent larger framework gravels, as some of these adhere to the outside of the core without all of the associated matrix material (Zimmerman et al. 2005, see photo Appendix 5.A). To minimize this known bias, we truncated our freeze-core samples at the 32 mm size class (see Appendix 5.A for details). Freeze-core samples were melted onsite and partitioned into three equal segments corresponding to depth below the top of the redd (ie: 0-4 cm, 4-8 cm, 8-12 cm depth below top of streambed) and transported to laboratory of particle size analysis. Brook trout egg pockets depths were previously observed to occur atdepths of approximately 10 cm at these study sites. ‘Density’ of fines (mass of fine fraction per bulk substrate volume) in each layer in the truncated core was estimated by dividing the mass of fraction under 0.5 mm by the volume of the core layer. Here core volume was estimated as $V=\pi r^2 L$; where r = the mean radius of the core (extending only to edge of the frozen matrix), over the given 4cm stratum and L = the length of the core stratum. This volumetric density estimate ($V_{density}$) is strongly correlated with the more conventional metric of % fines by weight (PF_{mass}; $V_{density} = 0.0198(PF_{mass})+0.0002$; ${}_{adj}R^2 = 0.95$; df=15; p-value: <0.00001). However, here it is a better absolute measure of fines abundance as it is: i) not mathematically affected by simple, inter-redd and inter-layer differences in substrate packing and porosity (i.e., bulk density); and ii) importantly, it is also unaffected by uncertainties in substrate layer masses introduced when the total mass of few larger gravel particles straddling our arbitrary partitioning depths (i.e., 4, 8, 12 cm) are assigned to only one sampling stratum.

5.4 Results

5.4.1 Range of conditions across redd study sites

At the time of substrate excavation and prior to redd creation, the in-situ volumetric density of fine sediment (< 0.5 mm) in the streambed substrates ranged from 0.07 to 0.23 g·cm^3 (mean: 0.14, sd: 0.05, n:17). The equivalent percentages by mass of this fine fraction were in the range of 3 – 10%. Substrates in stream KM 104 had a higher density of fine sediment (mean: 0.17 g·cm^3, sd: 0.03, n: 5) than those in stream KM143 (mean: 0.13, sd: 0.05, n: 10) and stream KM161 (mean: 0.09, sd: 0.001, n: 2), however the variance across sites was not statistically significant (f-statistic: 3.15, df:14, p-value: 0.07). Local mean vertical hydraulic gradients measurements for the groups of four mini-piezometers installed adjacent to each redd ranged from -0.156 (downward) to 0.170 (unitless; mean across all sites: -0.012, sd: 0.08, n: 17). For reference, a gradient of 0.100 corresponds to an observed head difference of 20 mm between the substrate surface and a point inserted 20 cm below the bed surface. Here, negative gradient pushes water downward into substrate, positive upwards. In the RFL study systems, although some trout redds occurred over upwellings, many spawning sites were located at downwelling riffle zones (Franssen et al., unpublished Chapter 4)). Horizontal hydraulic gradients, measured as the slope of the potentiometric surface in the downstream direction across the experimental redds, ranged from -0.002 to 0.019 (mean: 0.006; sd: 0.01, n: 17). Mean HHG of 0.006 would equate to the gradient associated with a water surface slope of 0.6%. There was no statistically significant variance in vertical gradients (f-statistic: 1.652, df:14, p-value: 0.23) or horizontal gradients (f-statistic: 2.64, df:14, p-value: 0.11) between streams.

5.4.2 Fines infiltration into experimental redds

Freeze cores collected at the end of the experimental period revealed that the fine sediment fractions (< 0.5 mm), completely removed from redds at the start of the experiment, had re-infiltrated into all experimental redds. With the exception of one site, < 0.5 mm densities averaged over the top 12 cm of the cores remained below those initially measured in the streambed prior to redd installation (Figure 5.3). Densities at the end of the experiment ranged from 0.02 to 0.11 g·cm^3 (mean: 0.06, sd: 0.03, n: 17), corresponding to 14% to 127% (mean: 47%) of the in-situ fine sediment densities observed in the substrates prior to substrate excavation and redd installation. At two of the 17 experimental redds there was complete mobilization of the bed surface D_{90} stones (Figure 5.3; bed type = mobilized), and at one site we observed 10 cm of bed aggradation above the level of the bed level at the beginning of the experimental period.

5.4.3 Filtration effect indicated by a reduction of fines density with depth

At 13 of the 17 experimental redds, we observed (Figure 5.4) a reduction in the density of fine re-infiltrated sediment between the top layer (depth: 0–4 cm) of the experimental redd and the depth at which we would most likely expect to find trout embryos (i.e., egg pocket depth 8-12 cm below the streambed). Fine sediment densities in the top layer ranged from 0.01 to 0.12 g·cm^3 (mean: 0.06, sd: 0.04, n: 17). Fines densities were 0.13 to 4.8 times (mean: 1.7) those measured at egg pocket depth (8-12 cm). The difference in fines density between the top 4 cm and the 8-12 cm depth (i.e., Δfines = density top layer – density at egg pocket depth) was negative at only four of the 17 experimental redds, indicating more fines at the 8-12 cm depth. These four sites included the only two sites where the bed surface D_{90} stones had been mobilized.

5.4.4 Filtering effect associated with size of pore constrictions

We observed a weak but significant, positive relationship between Δfines and percentage of filter class (the 0.5 to 4 mm fraction) in the substrate above the egg pocket (Figure 5.5a; $R^2 = 0.26$, df=15, p-value = 0.02). Less filter fraction in surface layers, here expressed as a % by weight of the filter fraction in the layer (after truncation at 32 mm), is associated with lower Δfines (less stratification). We found a slightly stronger relationship between Δfines and 'pore constriction size' (Dc) above the egg pocket (Figure 5.5b; $R^2 = 0.38$, df=15, p-value = 0.005).

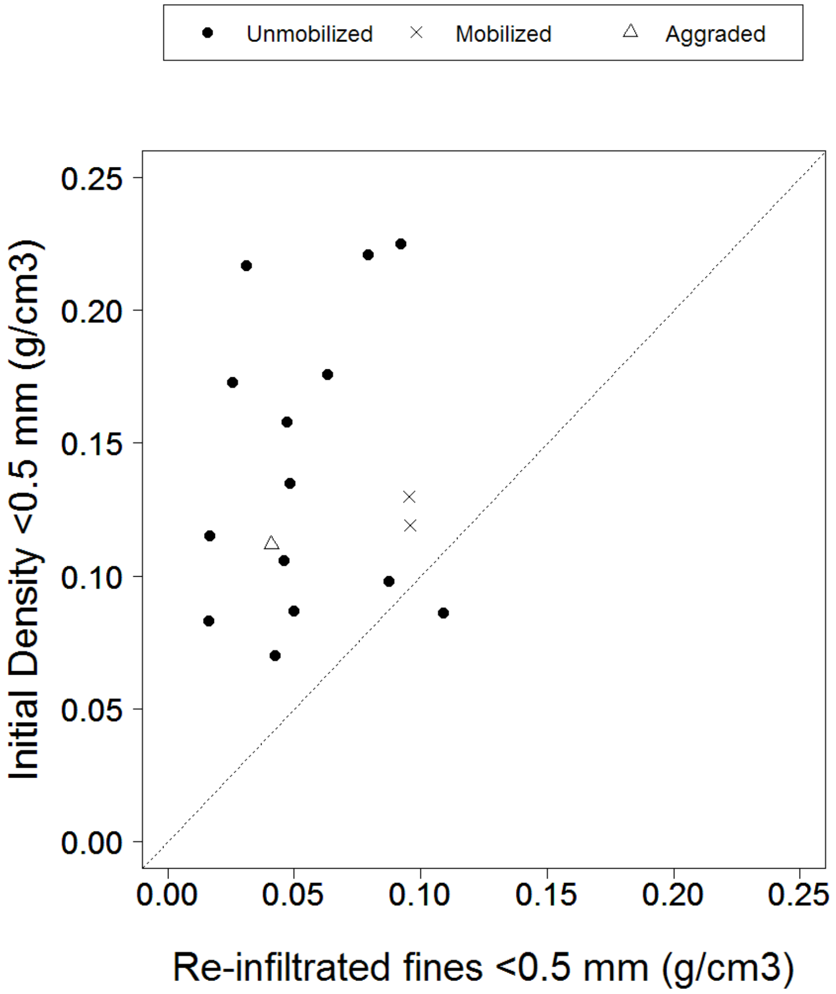


Figure 5.3. Relationship between the initial, in-situ density of fine sediment (g·cm^3) under 0.5 mm (fines) in the streambed substrates at the time of substrate excavation (August 2008) and the density of fines in freeze cores samples taken at the end of the sampling period (October 2008). The density of re-infiltrated fines at the end of the sampling period remained below initial densities at all but one site. Dashed line represents equality between values (i.e., 1:1). Symbols above the line indicate higher initial density of fines.

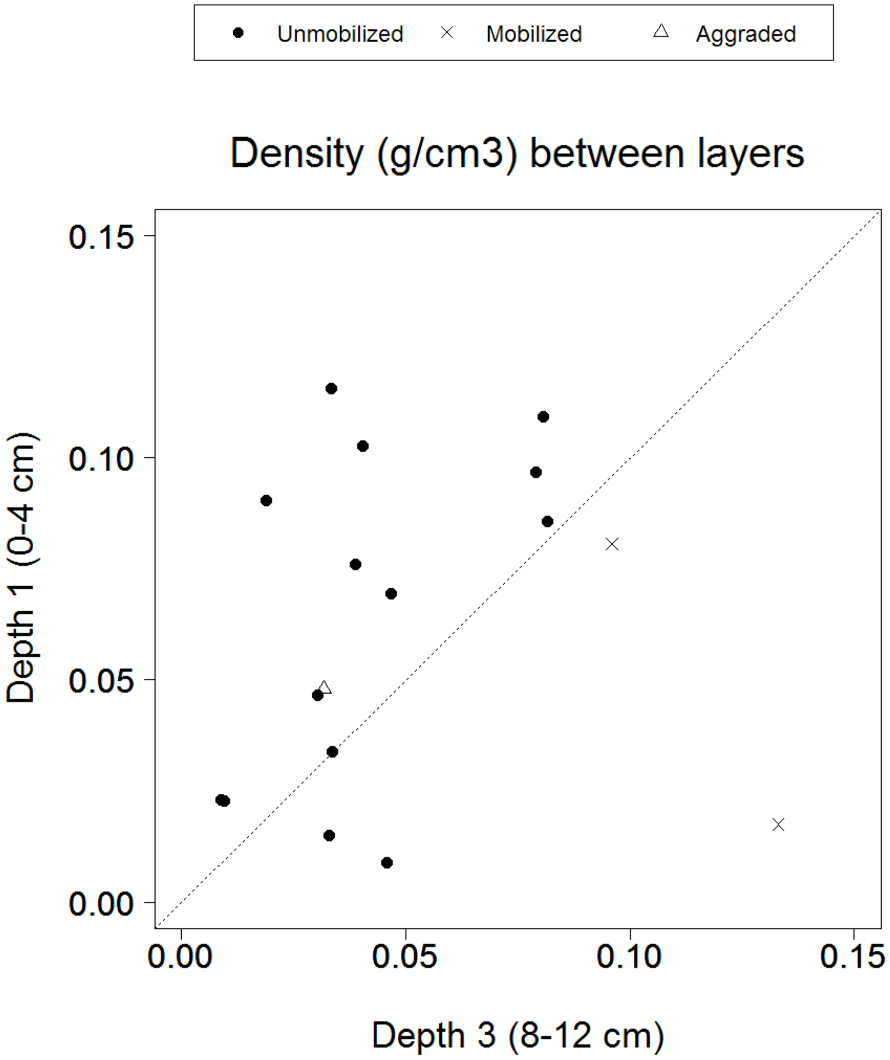


Figure 5.4. Relationship between the density of re-infiltrated fine sediment (g·cm^3) under 0.5mm between the top 4 cm of the experimental redd and egg pocket depth (8-12cm); results show a reduction in density of fines with depth at most sites. Dashed line represents equality between values (ie: 1:1). Symbols above the line indicate a decrease in density with depth.

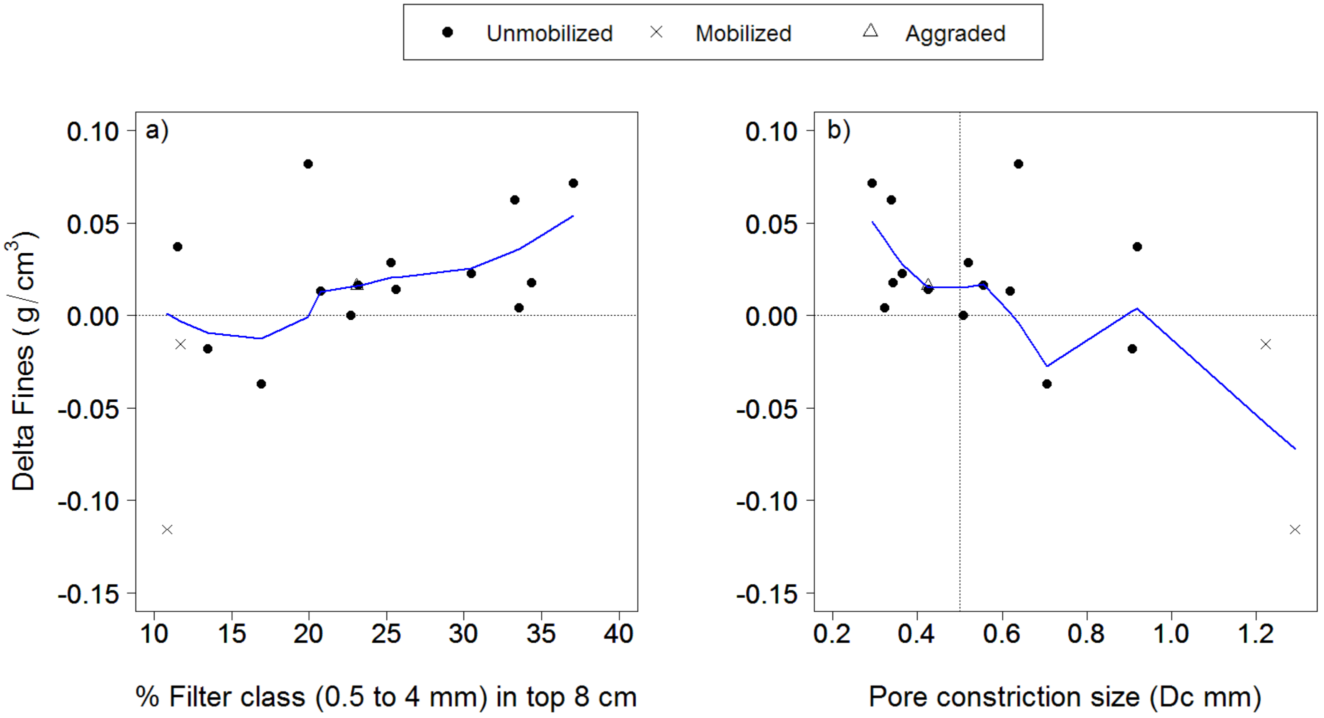


Figure 5.5. a) Results indicated a weak, positive relationship between the difference (delta fines) in density of fine sediment (< 0.5 mm) in the surface layer (0-4 cm) and the density of fine sediment at egg pocket depth (8-12 cm) as a function of the percentage of filter class (0.5 to 4 mm) in the substrate above the egg pocket (0-8 cm depth). Symbols above the dotted line indicate higher densities in the surface layer (0-4 cm); symbols below the dotted line indicate higher densities at egg pocket depth; b) a weak negative relationship between delta fines and the estimated size of the pore constrictions (Dc) above egg pocket depth (0-8 cm). Note that higher densities of fines (<0.5 mm) at egg pocket depth were only observed at sites where Dc > 0.5 (as indicated by the vertical dotted line). Solid lines in both graphs generated using a LOWESS (locally weighted scatterplot smoothing) function with a span of 0.5; where the span equals the proportion of points in the plot that influence the model estimates.

Larger ‘constrictions sizes’ are associated with lower Δfines (less stratification). Negative Δfines (i.e., more fines at egg pocket depth than top layer) only occurred in substrates where estimates of Dc were > 0.5 mm (recall that here fines were defined as particles < 0.5 mm). As expected, the alternative explanatory variables ‘filter class content’ and ‘pore constriction size’ shown in Figure 5.5 are strongly correlated (Pearson's correlation coefficient: -0.91; t = -8.48, df = 15, p-value < 0.00001).

5.4.5 Density of fine sediment at egg pocket depth unrelated to dose or hydraulic gradients

We found no statistically significant associations (at $p < 0.05$ level) between the amount of fine sediment that had infiltrated to egg pocket depth (density, g·cm3, 8-12 cm below streambed surface) and either of the following explanatory variables: i) the amount of fine sediment (<0.5 mm) in transport (dose) as measured by accumulations of fine sediment in the local sediment trap; Figure 5.6a); ii) the intensity of local vertical hydraulic gradient (VHG; Figure 5.6b); iii) the intensity of horizontal hydraulic gradient (HHG; Figure 5.6c). Similarly, we found no statistically significant association between these three explanatory variables and the density of fine sediment in either of the top two layers or on fine densities averaged over all three layers. We also found no statistically significant relationships between Δfines and either of the following explanatory variables: i) the ‘exposure dose’ or amount of fine sediment (<0.5 mm) available for infiltration into coarse, clean substrate as measured in the sediment trap; ii) the intensity of vertical hydraulic gradient; or iii) the intensity of horizontal hydraulic gradient. We found no other statistically significant associations (p-value < 0.05) between fines density (g·cm^3) measured in either of the top two layers (i.e., 0-4 cm; and 4-8cm below streambed) or the overall density (averaged over all three layers) and the explanatory variables: exposure dose, VHG, and HHG. Results did indicate a weak and possibly non-linear negative relationship between the density of fines (g·cm^3) in the top 4 cm of the redd and the exposure dose measured as fines in traps ($R^2 = 0.21$, df=14, p-value = 0.04; Figure 5.7).

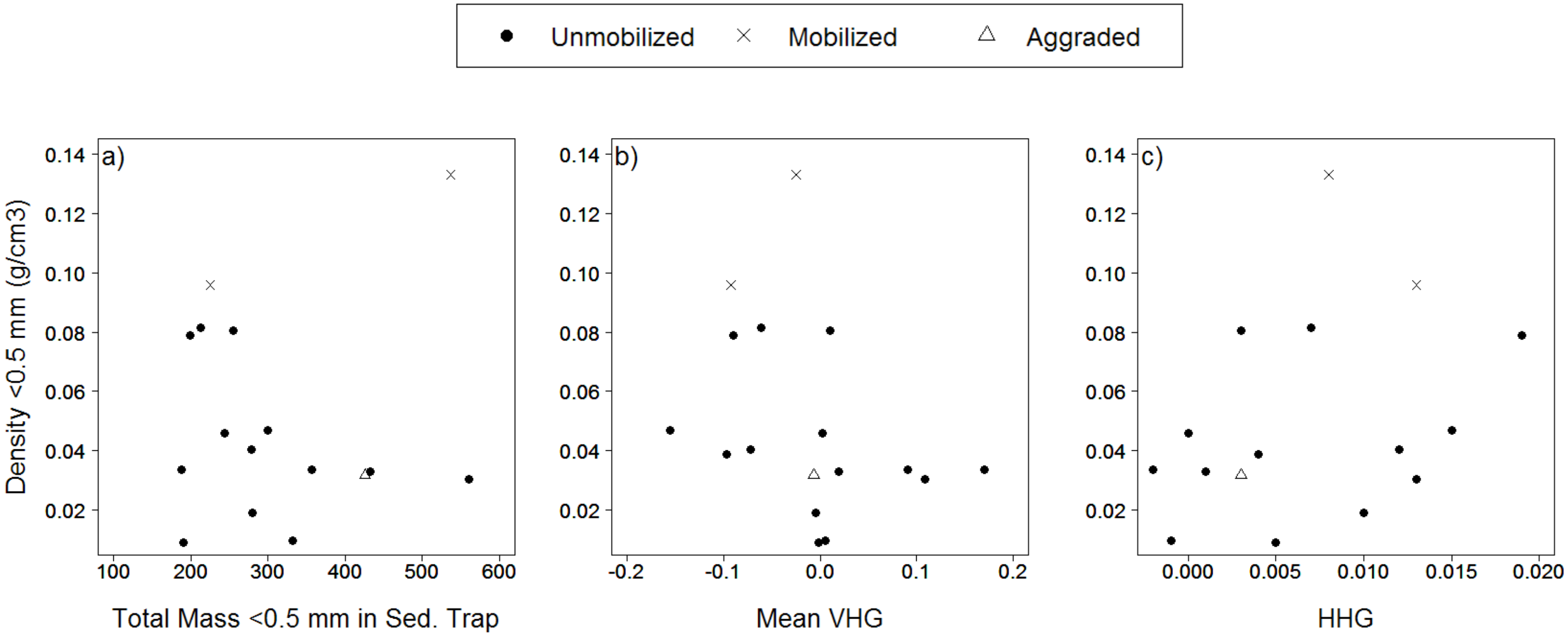


Figure 5.6. There was no significant relationship between the density of fine sediment (<0.5 mm) at egg pocket depth (8-12 cm) and either: a) the total mass of fine sediment captured in the sediment trap situated immediately downstream of the experimental redd; b) the mean vertical hydraulic gradient (positive denotes upward gradient); c) the horizontal hydraulic gradient at substrate depth of 20 cm (HHG: positive denotes downstream) as measured across the redd in the direction parallel to streambed.

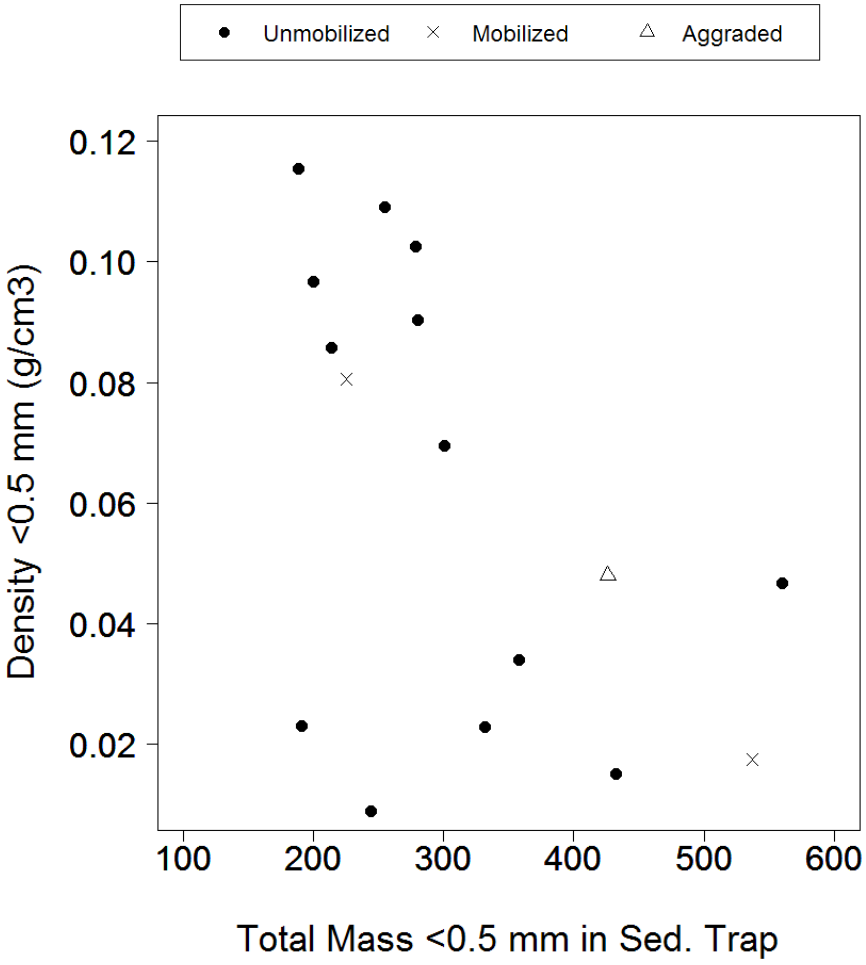


Figure 5.7. We observed a weak but statistically significant (p-value < 0.05) negative relationship between the density of fine sediment (<0.5 mm) in the top layer (0-4 cm) of the redds and the total mass of fine sediment captured in the sediment trap situated immediately downstream of the experimental redd (i.e, exposure dose).

5.5 Discussion

5.5.1 Coarse sands and fine gravel act as filters for fine sediment

Our experimental results with naturally variable field mixtures support the hypothesis that the coarse sands and fine gravel (0.5 – 4 mm; filter fractions) in spawning substrates act to filter percolating fine sediment (<0.5 mm), the fractions previously shown to increase salmonid embryo mortality (Lapointe et al. 2004; Franssen et al. In Press and Chapter 3 here). We observed the effects of this filtration process at a majority of our sites (13 of 17) as evidence by a reduction in the density of fines with depth, a reduction that was weakly correlated with greater amounts of filter fraction within the experimental redd and with smaller values of the variable 'pore constriction sizes'. We observed increases in fine densities with depth only at sites where the substrate had a lower percentage of filter fractions or where the substrate D_{90} stones had been mobilized during the experiment (more on this below). Where infiltrating particles are preferentially trapped in the uppermost layers of the streambed their entrapment reduces the mean size of pore openings. This reduction increases the trapping efficiency of these layers for subsequently infiltrating particles. Subsequent infiltration produces further increases in trapping efficiency, with a positive feedback mechanism that can lead to the clogging of the uppermost portion of the streambed, and an associated exponential reduction in the infiltration rate of fines with depth. This mechanism has been previously observed to cause the formation of sand seals in both flume (Beschta and Jackson 1979; Wooster et al. 2008) and field experiments (Lisle 1989; Frostick 1984; Meyer, 2005).In our experiments, despite this filtering effect, relatively small amounts of fine sediment were able to infiltrate to egg pocket depth (8-12 cm). However, the range of final fines accumulations under 0.5mm observed at egg pocket depth (across all 17 experimental redds) was 0.5 to 6.1% of total sediment mass (truncated at 32 mm). These observed loadings were below thresholds (9%, Franssen et al. in Press and Chapter 3 here) observed to cause significant increases in embryo mortality in laboratory incubations of trout eggs. We can conclude from our data that the sediment mobilized during a large magnitude, fall storm event was not sufficient to increase substrate fine sediment densities to levels that would have had a negative impact on EtE survival.

5.5.2 Did mobilization directly increase the density of fines at egg pocket depth?

Although data points are limited, we observed the highest fine sediment densities at egg pocket depth at the two sites where surface D_{90} stones had been mobilized. Bed mobilization may have played a role in the deeper layer accumulation of fine sediment at these sites if it resulted in the scouring away of filter particles at a period of high suspension loads. This increase in fines at depth associated with mobilization seemingly contradicts the proposed theory that fine sediments are flushed from substrate during surface mobilization (Cui et al. 2008). Based on this theory, numerous researchers have suggested flushing flows which mobilize the bed surface as a means of removing fines sediment accumulations from salmonid spawning substrates (Reiser et al. 1989; Wu 2000). As shown in Meyer (2005), the effects of various levels of flow events during incubation and egg pocket fines content are complex and includes both positive and negative links. Although flushing of excess fines in the surface layer may indeed occur and be beneficial to benthic habitat, our limited results suggest that bed mobilization may also be associated with increased density of fine sediment in the layers of spawning substrates immediately below the mobilized surface layer. However, this issue merits further field study. The two redd sites where bed mobilization occurred also had somewhat lower percentages of filter particles and higher values of pore constriction size. Thus the high densities of fines observed at these sites may have also been partly associated with a lack of filter particles rather then bed mobilization. Our results do support the view that prescription of flushing flows as a management technique for improving the quality of spawning habitats should take into account the need to retain filter sizes within the spawning substrates (Kondolf and Wilcock, 1996). As suggested by the Meyer (2005) model, managers adopting flushing flows as a management technique to mitigate fines accumulation for example below dams have the difficult task of determining discharges that will be sufficient to remove excess fine and medium sands without at the same time stripping the reach of slightly larger coarse sand and granule filter particles.

5.5.3 Filtering effect associated with size of pore constrictions

Our results indicated that the reduction of fines with depth was positively related to: i) the % of filter class in red (0.5 – 4 mm sized particles); and ii) negatively related to pore constriction size (D_c, estimated as 0.20· D15, as per filtering tests of Kenney et al. 1985). As expected, these two explanatory variables are strongly correlated as filter class particles were the finest fractions within the redd substrate (defined here as 0.5 – 32 mm) at the beginning of the experiment. $D_{15substrate}$ values ranged from 1.5 to 5.1 mm, which corresponds to a range in D_c values of 0.3 mm to 1 mm. Thus both metrics point to the role of coarse sands and fine granule gravel as filter fractions in our experiments. As predicted by filter theory (Kenney et al. 1985), the only sites where there was an increasing density of fines (<0.5 mm) with depth were those redds with Dc values > 0.5 mm.

While the bivariate linear models of Δfines as a function of Dc and of '% filter class' were both statistically significant at 5% level, both models leave a considerable amount of unexplained variance. We attribute a portion of this unexplained variance to the inherently stochastic nature of the filtration process, attributable to the random arrangement of interconnected pore spaces in a bed of mixed grain sizes. Nonetheless, the overall trend observed here suggests that filter fractions and associated smaller pore constrictions play an important role in restricting the accumulation of fine sediments into salmonid egg pockets, where elevated concentrations of fines have been shown to increase embryo mortality (Lapointe et al. 2004, Franssen et al. In Press and Chapter 3 here).

The relationship between fines ingress and filter fractions observed here is particularly relevant to salmonid habitat restoration projects that use gravel augmentation to increase the amount of suitable incubation substrates (e.g. Merz and Setka 2004), or gravel cleaning to remove accumulations of fine sediment (e.g. Meyer et al. 2008). Spawning habitat restoration projects that do not account for the crucial role of these filter fractions risk creating filter poor, spawning substrates that are susceptible to the accumulation of fine sediments (‘washload) at egg pocket depth. Even where, over time, coarse sand and fine gravel buildup are anticipated through bed load inputs, restoration sites will remain vulnerable to fines accumulation, particularly by lower magnitude discharges (which preferentially transport silt and fine sand wash fractions produced upstream) until such time that sufficient accumulation of filter particles (course sand/fine gravel) has taken place. Previous work (Franssen et al. In Press and Chapter 3 here; Sternecker and Geist 2010) also suggests that an overabundance of heavier, small gravels (i.e., 10 mm) in experimental spawning substrates may not only allow infiltration of detrimental fines under 0.5mm but also cause the entombment of larvae, given the weight of individual 1 cm gravels and the small pore sizes (3-4 mm) involved. Thus, managers should be aware of these relationships during the implementation of gravel augmentation schemes aiming to improve spawning habitats.

5.5.4 A negative relationship between fines accumulation and fines exposure

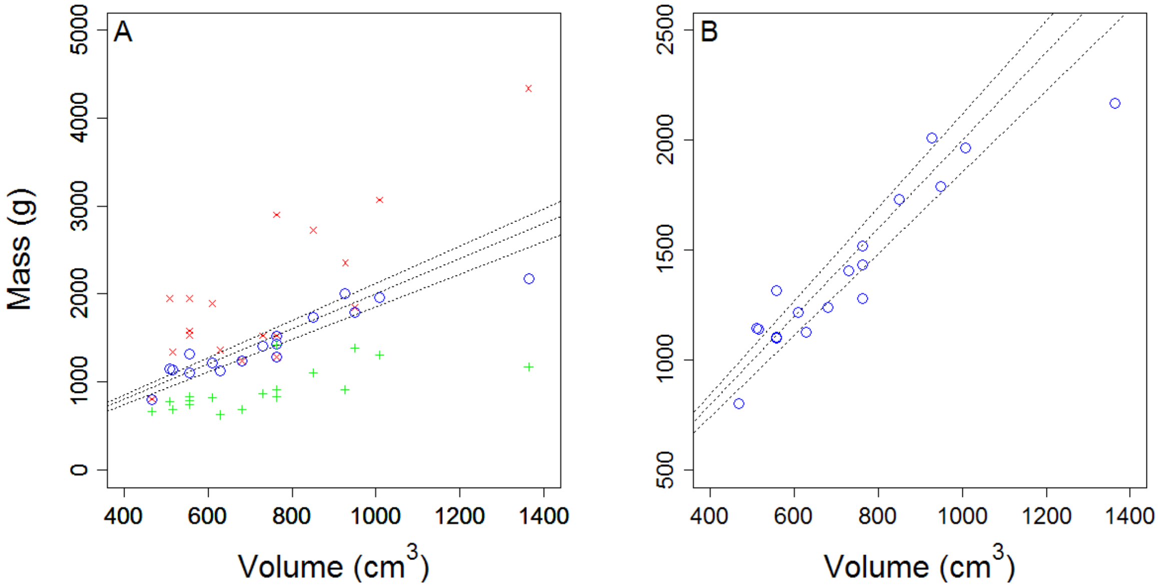
Counter intuitively, our results indicated that there was no statistically significant relationship between fines re-infiltration to egg pocket depths and the dose/exposure of fines (as measured in local sediment traps). However, we observed a weak but statistically significant negative relationship between fine density in the top layer of the redd and dose/exposure to fines (cf Fig 5.6). Although this result seems paradoxical, it concurs with several flume studies which indicate that subsurface accumulations may decrease at higher sediment loads (Gibson et al. 2009). This inverse relationship may be related to increased probability, at higher fine sediment loads, of two or more infiltrating particles entering a single pore space simultaneously thereby leading to the bridging and clogging of larger pore openings in the upper layers of the streambed. Such a bridging mechanism has been suggested by others (Wooster et al. 2008), and indicates that within gravel bed substrates, low intensity but protracted fine sediment doses may result in greater fines accumulation at depth. These results indicate that factors other than the aggregate magnitude of fine sediment loading should be considered when assessing the impact of increased fine sediment exposure on salmonid incubation microhabitats.

5.5.5 Density of fine sediment at egg pocket depth is unrelated to hydraulic gradients

Our results suggest that vertical hydraulic gradients (VHG) in the range of –0.16 (downwelling) to 0.17 (upwelling), and horizontal hydraulic gradients (HHG) as high as 0.02 did not significantly influence the accumulation of fine sediment in our experimental redds. This can be explained from first principles. Fall velocities for fine sand (0.125 mm) and medium grained sand (0.5 mm) in water at 10^0C are approximately 1 cm·s and 7 cm·s respectively (Rouse 1937). A priori, upward velocities of this order of magnitude in substrate interstices would be required to significantly inhibit the downward movement of these particles sizes within the streambed. However at the sites used for this field experiment, the maximum vertical interstitial flow velocity estimated in a related study (calculated using Darcy's Law) did not exceed 0.005 cm·s (Franssen et al., unpublished data). This maximum interstitial velocity estimate is almost 3 orders of magnitude below the 1cm·s velocities required to affect the motion of fine sand (<0.125 mm). Although even week downward flow velocities would theoretically increase the downward fluxes of infiltrating particles, our results indicated that downward flow did not increase the density of fine sediment in the experimental redds. Our results suggest that the suggested advantage of citing salmonid redds in upwelling zones because such zones limit the ingress of fine sediment (Curry and MacNeill, 2004) may only be relevant at sites with extremely high upward velocities in surface substrate (i.e, of order 0.1- 1 cm·s).

Horizontal velocities at our studies sites are also not likely to have been sufficient to mobilize fine sands. Even at sites with very high hydraulic conductivities (K = 1cm·s; gravel beds with little or no sand content) and using the maximum observed horizontal gradient (i.e., 0.02, unitless) maximum bulk interstitial velocities (calculated using Darcy's law) would be on the order of 0.02 cm·s, or about 2 orders of magnitude weaker than the fall velocity (1cm·s) of 0.125 mm sand. This suggests that the horizontal gradients measured at our sites are not likely to have influenced the motion of fine sand sized particles percolating through the streambed, although they could transport any silts and clays in substrate. Our results suggest that the ingress of fine sediments in our experimental redds was primarily a gravity driven process influenced by the size of the infiltrating fine sediment and the size of the substrate interstitial spaces.

APPENDIX 5.A



A) Relationship between the volume of the intact freeze core sample and i) total mass untruncated (x); ii) mass of sample truncated at 32 mm size class (o); and iii) sample truncated at 16 mm size class (+). The dotted lines indicate mean porosities of 0.20 (upper), 0.25 (middle), and 0.30 (lower). Porosities of these substrates expected to be approximately 0.25 based on porosity estimates made on gravel mixtures representative of the substrates sampled here (Franssen et al. in press). The lower porosities of untruncated samples (x) indicate a the well known overrepresentation of coarser clasts on the outside of core (Photo A.1) while the higher porosities of samples truncated at 16mm (+) indicate under representation of coarser clasts.

B) The relationship between mass and volume for samples truncated at 32 mm (o) indicates that most samples lie within or adjacent to the porosities expected for these substrates (i.e., approximately 0.25). In this paper metrics describing substrate composition were calculated with samples truncated at the 32 mm size class.

Photo A.1

Photo showing the field processing of a freeze-core sample. Note the overrepresentation of larger clasts on the outside of the core.

Chapter 6

Summary, conclusions and directions for future research

Our investigation of the factors effecting salmonid egg-to-emergence (EtE) survival (Chapter 3) focused on the key mechanisms thought to induce mortality during embryonic development: asphyxiation and entombment. We highlighted how these mechanisms are confounded through a correlation of substrate permeability with both: i) interstitial flow velocity (thus oxygen flux / asphyxiation); and ii) the density of large diameter macropores required by larvae for emergence from gravel bed substrate (thus entombment). By varying vertical hydraulic gradients (VHG) we exposed developing embryos to a range of flow velocities at fixed substrate compositions. We observed higher mortalities in fine rich substrates even at relatively high interstitial flow velocities (i.e., > 0.03 cm/s), where embryos would have had sufficient oxygen supply. We used medical imaging technology to determine the density of macropores large enough to allow larvae emergence (pore sizes which we referred to as megapores). To our knowledge we are the first to show a direct relationship between EtE survival and megapore density, with EtE survival positively related to the density of megapores within the incubation substrate. This result represents evidence of an entombment mechanism related to megapore availability. We utilized regression tree analysis to identify thresholds between high and low EtE survival related to substrate permeability and the proportion of fine sediment <0.5% within the incubation substrates. Both of these substrate metrics were strongly correlated with megapore density. The existence of a nonlinear relationship between EtE survival and substrate fines content has been suggested by others (Jensen et al. 2009) and such a relationship is consistent with the proposed mechanisms of entombment. Theoretically, entombment cannot occur once the size of the pore constrictions between substrate gravel particles exceeds the width of the emerging larvae. We noted that mortalities were still relatively high (i.e., maximum EtE survival = 55%) even in high flow and low fines mixtures which had the highest density of megapores. We attributed this result to the relatively small D_{50} of our gravel mixtures which presumably created an incubation substrate through which a proportion of the hatched embryos did not successfully locate an emergence pathway of sufficiently large pore spaces. We also observed premature emergence of the relatively rare survivors in fines-rich-substrates. We used a Generalized Additive Mixed Model (GAMM) to show a statistically significant nonlinear relationship between the timing of emergence and proportion of fine sediment within the gravel incubation substrates.

Chapman (1988) argues in his seminal review of the factors affecting embryo survival in salmonid redds that an improved understanding of physical conditions within the redd environment is required for researchers to adequately predict survival to emergence in natural systems. Subsequent researchers have focused on understanding the interactive effects of dissolved oxygen concentration and flow (Giest et al. 2005) and of fines content and interstitial velocity (Kondolf 2000, Lapointe et al. 2004) on embryo mortality. These studies have resulted in an improved understanding of how a suite of physical habitat factors interact to influence EtE survival. The results presented in Chapter 3 expand on this more recent work by improving our understanding of the mortality inducing mechanisms within these incubation microhabitats. Methods have not yet been developed to permit adequate in-situ physical characterization (e.g., size of interstitial pore spaces) of salmonid incubation microhabitats. It remains difficult to establish at what stage embryo mortality occurs without altering habitat variables. Nonetheless, the development and refinement of physical habitat models that predict survival to emergence in natural channels should prove useful to: i) those attempting to assess spawning habitat quality based on physical habitat criteria; and ii) those seeking to successfully restore, or construct, salmonid spawning/incubation habitats.

In Chapter 4, we presented the results of investigations into the role of hyporheic flow in brook charr redd site selection and its effect on redd thermal regimes. In contrast with many previous studies (e.g., Curry and Noakes 1995; Guillemette 2011) we found that for this population a majority of redd sites were situated in habitats where hyporheic flow was predominantly surface water. However, we also observed the selection of many redd sites, over multiple years, in microhabitats where there was a strong upward flux of groundwater. Our results indicate in these systems, upwelling groundwater was not strongly or exclusively used as a cue in redd site selection at the microhabitat scale. To test the Baxter and Hauer (2000) hypothesis that redd site selection for some charr may occur across multiple spatial scales, we also mapped winter substrate temperatures at fine scale (i.e., ~ 1 m spacing) across stream reaches where brook charr spawning was observed. During the winter groundwater temperatures in these boreal forest streams are several degrees warmer than surface water temperatures. Thus, temperature is a reliable indicator of the origin of hyporheic flow (i.e., groundwater dominant vs surface water dominant). Our substrate thermal mapping indicated that redds were not systematically located in downwelling microhabitats that are nested within upwelling reaches (i.e., reaches with a significant influx of phreatic groundwater). Instead, our results indicate that significant groundwater inputs at the reach and sub-reach scales measured here (i.e., mapped lengths of 20 – 60 m) did not appear to be an essential habitat requirement in the selection of spawning sites. Nonetheless, the long winter incubation periods in these boreal forest streams suggests that groundwater inputs, at least at larger spatial scales within the catchment, are likely an important habitat requirement as it is these upstream groundwater inputs that sustain instream flows during the many sub-freezing winter month, absent of rainfall. By monitoring substrate temperatures at redd sites throughout an entire winter incubation period we also observed that redds were situated in habitats with distinct thermal regimes. A minority of instrumented sites were situated in zones of warmer upwelling groundwater and a majority in zones of colder downwelling surface water. In these systems, embryos nested at groundwater upwellings sites would have been exposed to a significantly greater number of thermal units (i.e., cumulative degree days), which we presumed would have substantially accelerated embryonic development and thus the timing of hatching and emergence relative to sites where hyporheic flow was surface water dominant (i.e., significantly cooler incubation temperatures). We tentatively propose that the use of these thermally distinct habitats by the same population of brook charr may be an example of distinct life history strategies.

More broadly, previous work has established a strong association between brook charr spawning site selection and the presence of upwelling groundwater (see discussion in Guillemette et al. 2011). However, our results and those of Curry et al. (2002) suggest that this relationship may be more complex than originally thought. To our knowledge, our study sites (~47^{0}N) and those of Curry et al. (2002; ~48^{0}N) encompass the highest latitudes at which brook charr spawning/incubation habitats have been studied; these studies suggest that the association between local groundwater upwellings and redd site selection may not span the entire latitudinal range of this species. There is indeed an absence of studies documenting the characteristics of brook charr spawning habitats in the entire northern half of this species endemic range in eastern North America (40-60^{0}N; Scott and Crossman 1998). This lack of study on the northern habitats of brook charr represents an interesting avenue for future research. Our hypothesis of multiple life histories strategies with contrasting hatching dates in a single stream remains tentative, as we only observed temperature regimes at selected redd sites and not the actual hatching or emergence of larvae. Direct observations establishing the phenology of emergence from Boreal zone redds under the direct influence of upwelling groundwater are required to substantiate this hypothesis.

Further research is required to substantiate any linkages between groundwater, benthic macroinvertibrates, and the early life cycle of brook charr. Our hypothesis that upwelling groundwater may sustain a benthic food source for early emerging larvae (i.e., mid-winter emergence) in these boreal forest streams remains speculative. The results presented in Schutz et al. (2001), showing abundant mid-winter macroinvertebrate populations associated with groundwater inputs in a European alpine stream, provide evidence in support of this hypothesis. However, to our knowledge this phenomenon has not yet been observed in brook charr spawning habitats of northeastern North America. Our hypothesis suggesting that brook charr may exhibit distinct reproductive strategies in a single stream system merits further study particularly in the context of this species capacity to respond to anticipated changes in climate. If substantiated, plasticity in reproductive behaviours within a single population of brook charr suggests that this species may, at least during the reproductive stage of their life cycle, have a certain capacity to respond to rapid changes in climate.

Our investigation into factors controlling fines infiltration into spawning microhabitats (Chapter 5) focused on the role of filter fractions and local interstitial flow in modulating the infiltration process in natural-like redd mixtures. As mentioned above, substrate grain size composition (GSC) influences the size of interstitial pore constrictions and previous research suggests that it is the size of these pore openings which is the primary determinant of whether infiltrating fine sediment will percolate through, or be filtered by, the upper layers of the streambed. However, much of the current knowledge regarding the infiltration of fines into gravel bed substrates has been obtained from laboratory investigations and few studies have examined this process in natural channels with graded and variable GSDs. To our knowledge no one has yet conducted field studies to examine the role of upwelling/downwelling or horizontal flows in fines infiltration. Field data was obtained by constructing experimental redds in known brook charr spawning microhabitats. At the start of the experiment, fine sediments (i.e., < 0.5 mm) were completely removed from the experimental substrates. At each site we measured vertical and horizontal gradients at the time of redd installation, and estimated local fine sediment loads using sediment traps installed immediately downstream of each redd (which were removed at the end of the study period). At the end of the experiment substrate fines re-infiltration was assessed using the freeze-core technique. Our results showed a reduction in fine sediment accumulations with depth in a majority (i.e., 76%) of redds. A statistically significant positive relationship was observed between the change in fines density with depth (Δfines) and the proportion of coarse sands and fine gravel (i.e., filter fractions) within the upper layers of the redd. Our results also revealed that observed fines accumulation at egg pocket depth was significantly associated neither with fine sediment exposure-dose, upwelling/downwelling flow, or horizontal flows through the redds.

Our results concur with those of laboratory investigations which suggest that the ingress of fine sediments in gravel bed substrates is primarily influenced by the size of the infiltrating fine sediment and the size of the substrate interstitial spaces. Although our results are statistically significant there is a considerable amount of unexplained variability in these relationships. This unexplained variability may be associated with the inherently stochastic nature of the filtration process in beds of randomly arranged, mixed grain sizes. However, variability may also be introduced during substrate sampling. As yet, we do not have measurement techniques that allow accurate in-situ measurement of the amount and depth of fines infiltration into gravel bed substrates. Freeze-cores maintain substrate stratigraphy but have a known bias toward larger gravel particles. Also, any microscale structure of the core (i.e., less then 10 mm) is destroyed once the core is melted into sections of arbitrary thickness; the minimum size of which is influenced by the size of the larger gravel particles within the core. The development of improved field sampling techniques may help to resolve some to the uncertainty in the relationships described in Chapter 5. Previous researches have suggested that the filtration processes which we observed in our experimental redds, may lead to the formation of clogged surface layers, or sand seals (Lisle 1989, Meyer 2005), which prevent the subsequent infiltration of fines to egg pocket depths. Further field research is required to determine how long and under what hydraulic and geomorphic conditions these seals are likely to persist. Questions also remain as to how the clogging of the upper layers of the streambed relates the survival to emergence of salmonid embryos. Does this clogging improve survival by decreasing fines infiltration into the egg pocket, or is it likely to result in the entombment of hatched embryos? Our observations and those of others (Wooster et al. 2008) suggest that higher fine sediment doses may result in less infiltration of fines below the surface layer of the streambed. Requiring further study is the the hypothesis that lower fine sediment doses may actually result in greater accumulations of fines in salmonid egg pockets, as such a relationship has important implications for understanding how increased sediment loading to streams impacts salmonid reproductive successes.

7. References

Alexander, G.R., and Hansen, E.A. 1986. Sand bed load in a brook trout stream. North American Journal of Fisheries Management **6**: 9-23.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., and Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research **62**: 143-170.

Atkinson, E.J., Therneau, T.M., and Atkinson, B. 2010. rpart: Recursive partitioning and regression trees. In R package version 3.1-48. Available from http://cran.r-project.org/web/packages/rpart/rpart.pdf

Balon, E.K. 1975. Terminology of Intervals in Fish Development. Journal of the Fisheries Research Board of Canada **32**: 1663-1670.

Baird, H.B., Krueger, C.C., and Josephson, D.C. 2002. Differences in incubation period and survival of embryos among brook trout strains. North American Journal of Aquaculture **64**: 233-241.

Baxter, C.V., and Hauer, F.R. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences **57**: 1470-1481.

Baxter, C., Hauer, F.R., and Woessner, W.W. 2003. Measuring groundwater-stream water exchange: New techniques for installing minipiezometers and estimating hydraulic conductivity. Transactions of the American Fisheries Society **132**: 493-502.

Baxter, J.S., and McPhail, J.D. 1999. The influence of redd site selection, groundwater upwelling, and over-winter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. Canadian Journal of Zoology **77**: 1233-1239.

Beechie, T., G. Pess, P. Roni, and G. Giannico. 2008. Setting river restoration priorities: A review of approaches and a general protocol for identifying and prioritizing actions. North American Journal of Fisheries Management **28**:891-905.

Beer, W.N., and Anderson, J.J. 2001. Effect of spawning day and temperature on salmon emergence: interpretations of a growth model for Methow River chinook. Canadian Journal of Fisheries and Aquatic Sciences **58**: 943-949.

Belding, D.L. 1934. The Spawning Habits of the Atlantic Salmon. Transactions of the American Fisheries Society **64**: 211-218.

Bennett, D.H., Connor, W.P., and Eaton, C.A. 2003. Substrate composition and emergence success of fall chinook salmon in the Snake River. Northwest Science **77**: 93-99.

Bernier-Bourgault, I., and Magnan, P. 2002. Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site. Environmental Biology of Fishes **64**: 333-341.

Beschta, R.L., and Jackson, W.L. 1979. The intrusion of fine sediments into a stable gravel bed. Journal of the Fisheries Research Board of Canada **36**: 204-210.

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. *In* Influences of forest and rangeland management on salmonid fishes and their habitats. *Edited by* W.R. Meehan. American Fisheries Society Special Publication 19. pp. 83-138.

Blanchfield, P.J., and Ridgway, M.S. 2005. The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **62**: 2694-2705.

Blanchfield, P.J., and Ridgway, M.S. 1999. The cost of peripheral males in a brook trout mating system. Animal Behaviour **57**: 537-544.

Blanchfield, P.J., and Ridgway, M.S. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **54**: 747-756.

Boivin, J., Fournier, G., and Dulude, P. 1995. Proposition de programmes d'intervention sur les habitats et les populations d'omble de fontaine, Ministere de l'Environnement et de la Faune.

Bunn, S.E., and Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management **30**: 492-507.

Carling, P.A. 1984. Deposition of Fine and Coarse Sand in an Open-Work Gravel Bed. Canadian Journal of Fisheries and Aquatic Sciences **41**: 263-270.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society **117**: 1-21

Conant Jr, B. 2004. Delineating and Quantifying Ground Water Discharge Zones Using Streambed Temperatures. Ground Water **42**: 243-257.

Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. Journal of Fish Biology **41**:161-178.

Coulombe-Pontbriand, M., and Lapointe, M. 2004. Geomorphic controls, riffle substrate quality, and spawning site selection in two semi-alluvial salmon rivers in the Gaspe Peninsula, Canada. River Research and Applications **20**: 577-590.

Crisp, D.T., and Carling, P.A. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology **34**: 119-134.

Crisp, D.T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology **11.** 361-368.

Curry, R.A., and MacNeill, W.S. 2004. Population-level responses to sediment during early life in brook trout. Journal of the North American Benthological Society **23**: 140-150.

Curry, R.A., Scruton, D.A., and Clarke, K.D. 2002. The thermal regimes of brook trout incubation habitats and evidence of changes during forestry operations. Canadian Journal of Forest Research **32**: 1200-1207.

Curry, R.A., and Noakes, D.L.G. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **52**: 1733-1740.

Curry, R.A., Noakes, D.L.G., and Morgan, G.E. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **52**: 1741-1749.

De'ath, G., and Fabricius, K.E. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology **81**: 3178-3192.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences **54**: 1685-1698.

Diana, J. S. 1995. Biology and ecology of fishes. Biological Sciences Press.

Dill, L.M., and Northcote, T.G. 1970. Effects of gravel size, egg depth, and egg density on intragravel movement and emergence of coho salmon alevins. Journal of the Fisheries Research Board of Canada **27**: 1191-1199.

Diplas, P., and Parker, G. 1985. Pollution of gravel spawning grounds due to fine sediment. St. Anthony Falls Hydraulic Laboratory Project Report No. 240. University of Minneapolis.

Einstein, H.A. 1968. Deposition of suspended particles in a gravel bed. Journal of the Hydraulics Division of the American Society of Civil Engineers **94**: 1197-1205.

Essington, T.E., Sorensen, P.W., and Paron, D.G. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Canadian Journal of Fisheries and Aquatic Sciences **55**: 2310-2316.

Environment Canada. 2007. Canadian Climate Normals 1971-2000: Foret Montmorency, Quebec http://www.climate.weatheroffice.ec.gc.ca/climate_normals.

Everest, F.H., Beschta, R.L., Scrivener, J.C., Koski, K.V., Sedell, J.R., and Cederholm, C.J. 1987. Fine sediment and salmonid production: a paradox. *In* Streamside management and forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Seattle.

Fanelli, R.M., and Lautz, L.K. 2008. Patterns of water, heat, and solute flux through streambeds around small dams. Ground Water **46**: 671-687.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. BioScience **52**:483-498.

Fetter, C.W. 2001. Applied Hydrogeology. Prentice-Hall, Upper Saddle River, N.J.

Fleming, I.A., and Reynolds, J.D. 2004. Salmonid Breeding Systems. *In* Evolution Illuminated: Salmon and Their Relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford.

Finn, R.N. 2007. The physiology and toxicology of salmonid eggs and larvae in relation to water quality criteria. Aquatic Toxicology **81**: 337-354.

Fresh, K.L., and Schroder, S.L. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. Canadian Journal of Fisheries & Aquatic Sciences **44**: 236-243.

Fretwell, S.D., and Lucas, H.L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. . Acta Biotheoretica **19**: 16-36.

Frissell, C.A., Liss, W.J., Warren, C.E., and Hurley, M.D. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management **10**: 199-214.

Frostick, L.E., Lucas, P.M., and Reid, I. 1984. The infiltration of fine matrices into coarse-grained alluvial sediments and its implications for stratigraphical interpretation. Journal of the Geological Society of London **141**: 955-965.

Frings, R.M., Kleinhans, M.G., and Vollmer, S. 2008. Discriminating between pore-filling load and bed-structure load: A new porosity-based method, exemplified for the river Rhine. Sedimentology **55**: 1571-1593.

Fudge, T.S., Wautier, K.G., Evans, R.E., and Palace, V.P. 2008. Effect of different levels of fine-sediment loading on the escapement success of rainbow trout fry from artificial redds. North American Journal of Fisheries Management **28**: 758-765.

Garside, E.T. 1966. Effects of Oxygen in Relation to Temperature on the Development of Embryos of Brook Trout and Rainbow Trout. Journal of the Fisheries Research Board of Canada **23**: 1121-1134.

Geist, D.R., and Dauble, D.D. 1998. Redd site selection and spawning habitat use by fall chinook salmon: The importance of geomorphic features in large rivers. Environmental Management **22**: 655-669.

Geist, D.R., Hanrahan, T.P., Arntzen, E.V., McMichael, G.A., Murray, C.J., and Chien, Y.J. 2002. Physicochemical characteristics of the hyporheic zone affect redd site selection by chum salmon and fall chinook salmon in the Columbia River. North American Journal of Fisheries Management **22**: 1077-1085.

Genivar-Tecsult. 2003. Étude d'impact du projet d'amélioration de la route 175 à 4 voies divesées du km 84 au km 227 (143 km) dans la réserve fauniques des Laurentides et dans la Ville de Saquenay. , Rapport du Consortium Genivar-Tecsult pour le ministère des Transports du Québec et présenté au ministre de l'Environnement du Québec et au ministre des Transports du Canada.

Gibson, S., Abraham, D., Heath, R., and Schoellhamer, D. Bridging process threshold for sediment infiltrating into a coarse substrate. Journal of Geotechnical and Geoenvironmental Engineering **136**: 402-406.

Gonzalez, R. C., Woods, R. E., and Eddins, S. L. 2004. Digital Image Processing Using MATLAB. Pearson Prentice Hall, Upper Saddle River, N.J.

Gooseff, M.N., Anderson, J.K., Wondzell, S.M., LaNier, J., and Haggerty, R. 2006. A modelling study of hyporheic exchange pattern and the sequence, size, and spacing of stream bedforms in mountain stream networks, Oregon, USA. Hydrological Processes **20**: 2443-2457.

Greig, S.M., Sear, D.A., and Carling, P.A. 2007. A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. Hydrological Processes **21**: 323-334.

Greig, S.M., Sear, D.A., Smallman, D., and Carling, P.A. 2005. Impact of clay particles on the cutaneous exchange of oxygen across the chorion of Atlantic salmon eggs. Journal of Fish Biology **66**: 1681-1691.

Guillemette, F., Vallee, C., Bertolo, A., and Magnan, P. The evolution of redd site selection in brook charr in different environments: same cue, same benefit for fitness. Freshwater Biology **56**: 1017-1029.

Hall, J.L., and Wissmar, R.C. 2004. Habitat factors affecting sockeye salmon redd site selection in off-channel ponds of a river floodplain. Transactions of the American Fisheries Society **133**: 1480-1496.

Harrison, C.W. 1923. Planting eyed salmon and trout eggs. Transactions of the American Fisheries Society **52**: 191-200.

Haschenburger, J.K., and Roest, P. 2009. Substrate indices as indicators of interstitial pore space in gravel-bed channels. River Research and Applications **25**: 98-105.

Hatch, C.E., Fisher, A.T., Revenaugh, J.S., Constantz, J., and Ruehl, C. 2006. Quantifying surface water-groundwater interactions using time series analysis of streambed thermal records: Method development. Water Resources Research **42**.

Hausle, D.A., and Coble, D.W. 1976. Influence of sand in redds on survival and emergence of brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society **105**: 57–63.

Hazzard, A.S. 1932. Some Phases of the Life History of the Eastern Brook Trout, *Salvelinus Fontinalis Mitchell*. Transactions of the American Fisheries Society **62**: 344-350.

Heibo, E., Magnhagen, C., and Vallestad, L.A. 2005. Latitudinal variation in life-history traits in Eurasian perch. Ecology **86**: 3377-3386.

Hendry, A.P., Hensleigh, J.E., and Reisenbichler, R.R. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. Canadian Journal of Fisheries and Aquatic Sciences **55**: 1387-1394.

Hobbs, D.F. 1937. Natural reproduction of quinnat salmon, brown trout in certain New Zealand waters. New Zealand Marine Department of Fisheries Bulletin 6.

Jensen, D.W., Steel, E.A., Fullerton, A.H., and Pess, G.R. 2009. Impact of fine sediment on egg-to-fry survival of pacific salmon: A meta-analysis of published studies. Reviews in Fisheries Science **17**: 348-359.

Kamler, E. 2002. Ontogeny of yolk-feeding fish: An ecological perspective. Reviews in Fish Biology and Fisheries **12**: 79-103.

Kenney, T.C., Chahal, R., Chiu, E., Ofoegbu, G.I., Omange, G.N., and Ume, C.A. 1985. Controlling constriction sizes of granular filters. Canadian Geotechnical Journal **22**: 32-43.

Keery, J., Binley, A., Crook, N., and Smith, J.W.N. 2007. Temporal and spatial variability of groundwater-surface water fluxes: Development and application of an analytical method using temperature time series. Journal of Hydrology **336**: 1-16.

Kleinhans, M.G., Jeukens, C.R.L.P.N., Bakker, C.J.G., and Frings, R.M. 2008. Magnetic Resonance Imaging of coarse sediment. Sedimentary Geology **208**: 69-78.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar L*., brown trout *Salmo trutta L*. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish **12**: 1-59.

Kondolf, G.M., and Wilcock, P.R. 1996. The Flushing Flow Problem: Defining and Evaluating Objectives. Water Resour. Res. **32**: 2589-2599.

Kondolf, G.M. 2000. Assessing salmonid spawning gravel quality. Transactions of the American Fisheries Society **129**: 262-281.

Koski, K.V. 1966. The Survival of coho salmon (*Oncorhynchus kisutch*) from egg deosition to emergence in three Oregon streams. Oregon State University, Corvallis.

Kramer, D. L., R. W. Rangeley, and L. H. Chapman. 1997. Habitat selection: patterns of spatial distribution from behavioural decisions. in J. J. Godin, editor. Behavioural ecology of teleost fishes. Oxford University Press.

Krebs, J. R. and N. B. Davies. 1997. Behavioural ecology: an evolutionary approach. 4th edition. Blackwell Science.

Lapointe, M.F., Bergeron, N.E., Berube, F., Pouliot, M.A., and Johnston, P. 2004. Interactive effects of substrate sand and silt contents, redd-scale hydraulic gradients, and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **61**: 2271-2277.

Lapointe, M. In Press. River geomorphology and salmonid habitat: some examples illustrating their complex association, from redd to riverscape scales. Chapter 17 in Gravel-bed Rivers: Processes, Tool, Environments. Church, M., Biron, P. and Roy, A., editors. Chichester, John Wiley and Sons.

Lappalainen, J. and A. S. Tarkan. 2007. Latitudinal gradients in onset date, onset temperature and duration of spawning of roach. Journal of Fish Biology **70**:441-450.

Lautz, L.K., Kranes, N.T., and Siegel, D.I. 2010. Heat tracing of heterogeneous hyporheic exchange adjacent to in-stream geomorphic features. Hydrological Processes **24**: 3074-3086.

Leggett, W. C. and J. E. Carscadden. 1978. Latitudinal Variation in Reproductive Characteristics of American Shad (Alosa sapidissima): Evidence for Population Specific Life History Strategies in Fish. Journal of the Fisheries Research Board of Canada **35**:1469-1478.

Leopold, L.B., Wolman, M.G., and Miller, J.P. 1964. Fluvial Processes in Geomorphology. Dover Publications, Mineola, New York.

Lisle, T.E. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. Water Resources Research **25**: 1303-1319.

Lotspeich, F.B., Everest, F.H. 1981. A new method for reporting and interpreting textural composition of spawning gravel. U.S. Forest Service Research Note PNW-139.

Maddock, I. 1999. The importance of physical habitat assessment for evaluating river health. Freshwater Biology **41**:373-391.

Meisner, J.D., Rosenfeld, J.S., and Regier, H.A. 1988. The Role of Groundwater in the Impact of Climate Warming on Stream Salmonines. Fisheries **13**: 2-8.

Merz, J.E., and Setka, J.D. 2004. Evaluation of a Spawning Habitat Enhancement Site for Chinook Salmon in a Regulated California River. North American Journal of Fisheries Management **24**: 397-407.

Meyer, C.B., Sparkman, M.D., and Klatte, B.A. 2005. Sand seals in coho salmon redds: Do they improve egg survival? North American Journal of Fisheries Management **25**: 105-121.

Milner, N.J. Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. and Ladle, M. 2003. The natural control of salmon and trout populations in streams. Fisheries Research **62**: 111-125. doi: 10.1016/S0165-7836(02)00157-1

Moir, H.J., and Pasternack, G.B. 2008. Relationships between mesoscale morphological units, stream hydraulics and Chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat on the Lower Yuba River, California. Geomorphology **100**: 527-548.

Moir, H.J., Gibbins, C.N., Soulsby, C., and Webb, J. 2004. Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar L.*). Geomorphology **60**: 21-35.

Montety, L.d., Long, B., Desrosiers, G., Cramer, J.-F.o., Locat, J., and Stora, G. 2003. Utilisation de la scanographie pour l'etude des sediments : influence des paramatres physiques, chimiques et biologiques sur la mesure des intensites tomographiques. Canadian Journal of Earth Sciences **40**: 937-948.

Montgomery, D.R., Beamer, E.M., Pess, G.R., and Quinn, T.P. 1999. Channel type and salmonid spawning distribution and abundance. Canadian Journal of Fisheries and Aquatic Sciences **56**: 377-387.

Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Hames, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences **53**: 1061-1070.

Murray, C.B., and Beacham, T.D. 1987. The development of chinook (*Oncorhynchus tschawytscha*) and chum salmon (*Oncorhynchus keta*) embryos and alevins under varying temperature regimes. Canadian Journal of Zoology **65**: 2672-2681.

NCASI. 1984. The effects of fine sediment on salmonid spawning gravel and juvenile rearing habitat - a literature review. National Council of the Paper Industry for Air and Stream Improvement Technical Bulletin 428.

Owens, P.N., Batalla, R.J., Collins, A.J., Gomez, B., Hicks, D.M., Horowitz, A.J., Kondolf, G.M., Marden, M., Page, M.J., Peacock, D.H., Petticrew, E.L., Salomons, W., and Trustrum, N.A. 2005. Fine-grained sediment in river systems: environmental significance and management issues. River Research and Applications **21**: 693-717.

Pepin, D.M., and Hauer, F.R. 2002. Benthic responses to groundwater-surface water exchange in 2 alluvial rivers in northwestern Montana. Journal of the North American Benthological Society **21**: 370-383.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and the R Core Team. 2010. nlme: Linear and Nonlinear Mixed Effects Models. In R package version 3.1-97. Available from http://cran.r-project.org/web/packages/nlme/nlme.pdf

Power, G. 2002. Charrs, glaciations and seasonal ice. Environmental Biology of Fishes **64**: 17-35.

Power, M., Dempson, J.B., Reist, J.D., Schwarz, C.J., and Power, G. 2005. Latitudinal variation in fecundity among Arctic charr populations in eastern North America. Journal of Fish Biology **67**: 255-273.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. *In* Charrs: fishes of the genus Salvelinus. *Edited by* E.K. Balon. Dr. W. Junk, The Hague. pp. 141-203.

Quinn, T.P. 2005. The behaviour and ecology of pacific salmong and trout. University of Washington Press, Seattle.

Reiser, D.W., Ramey, M.P., Beck, S., Lambert, T.R., and Geary, R.E. 1989. Flushing flow recommendations for maintenance of salmonid spawning gravels in a steep, regulated stream. Regulated Rivers: Research & Management **3**: 267-275.

Reiser, D.W., White, R.G. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. North American Journal of Fisheries Management. 432-437.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, W.G., Reice, S.R., Sheldon, A.L., Wallace, B.J., and Wissmar, R.C. 1988. The Role of Disturbance in Stream Ecology. Journal of the North American Benthological Society **7**: 433-455.

Rubin, J.F. 1998. Survival and emergence pattern of sea trout fry in substrata of different compositions. Journal of Fish Biology **53**: 84-92.

Schalchli, U. 1992. The clogging of coarse gravel river beds by fine sediment. Hydrobiologia **235-236**: 189-197.

Scott, W.B., and Crossman, E.J. 1998. Freshwater fishes of Canada. Galt House, Oakville, Ontario.

Schlaepfer, M.A., Runge, M.C., and Sherman, P.W. 2002. Ecological and evolutionary traps. Trends in ecology & evolution **17**: 474-480.

Schlosser, I.J. 1999. Stream fish ecology: a landscape perspective. NCASI Technical Bulletin **2**: 471-472.

Schuttz, C., Wallinger, M., Burger R., and Fureder, L. 2001. Effects of snow cover on the benthic fauna in a glacier-fed stream. Freshwater Biology **46**:1691-1704.

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.

Spence, B. C. and J. D. Hall. 2010. Spatiotemporal patterns in migration timing of coho salmon (Oncorhynchus kisutch) smolts in North America. Canadian Journal of Fisheries and Aquatic Sciences **67**:1316-1334.

Sternecker, K., and Geist, J. 2010. The effects of stream substratum composition on the emergence of salmonid fry. Ecology of Freshwater Fish **19**: 537-544.

Storey, R.G., Howard, K.W.F., and Williams, D.D. 2003. Factors controlling riffle-scale hyporheic exchange flows and their seasonal changes in a gaining stream: A three-dimensional groundwater flow model. Water Resources Research **39**(2): SBH81-SBH817

Stuart, T.A. 1953. Water Currents through Permeable Gravels and their Significance to Spawning Salmonids, etc. Nature **172**: 407-408.

Tallman, R.F. 1986. Genetic differentiation among seasonally distinct spawning populations of chum salmon, Oncorhynchus keta. Aquaculture **57**: 211-217.

Thorne, C.R. 1997. Channel types and morphological classification. *In* Applied Fluvial Geomorphology for River Engineering and Management. *Edited by* C.R. Thorne, R.D. Hey and M.D. Newson. Wiley, Chichester. pp. 175-222.

Todd, D. K. 1980. Groundwater hydrology. Wiley, New York.

Tonina, D., and Buffington, J.M. 2009. A three-dimensional model for analyzing the effects of salmon redds on hyporheic exchange and egg pocket habitat. Canadian Journal of Fisheries and Aquatic Sciences **66**: 2157-2173.

The R Core Development Team. 2010. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Tonina, D., and Buffington, J.M. 2007. Hyporheic exchange in gravel bed rivers with pool-riffle morphology: Laboratory experiments and three-dimensional modeling. Water Resources Research **43**(1). W01421.

Turnpenny, A.W.H., and Williams, R. 1980. Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology **17**: 681-693.

Valett, H.M., Hakenkamp, C.C., and Boulton, A.J. 1993. Perspectives on the Hyporheic Zone: Integrating Hydrology and Biology. Introduction. Journal of the North American Benthological Society **12**: 40-43.

Van Grinsven, M., Mayer, A., and Huckins, C. In Press. Estimation of Streambed Groundwater Fluxes Associated with Coaster Brook Trout Spawning Habitat. Ground Water. http://dx.doi.org/10.1111/j.1745-6584.2011.00856.x

Vaux, W.G. 1968. Intragravel flow and interchange of water in a streambed. Fishery Bulletin, 66, pp. 479-489.

Vollestad, L.A., and Lillehammer, T. 2000. Individual variation in early life-history traits in brown trout. Ecology of Freshwater Fish **9**: 242-247.

Waters, T.F. 1995. Sediment in Streams: Sources, Biological Effects and Control. American Fisheries Society Monograph 7.

Wheeler, A.P., Angermeier, P.L., and Rosenberger, A.E. 2005. Impacts of new highways and subsequent landscape urbanization on stream habitat and biota. Reviews in Fisheries Science **13**: 141-164.

White, D.S. 1993. Perspectives on Defining and Delineating Hyporheic Zones. Journal of the North American Benthological Society **12**: 61-69.

White, D.S., Elzinga, C.H., and Hendricks, S.P. 1987. Temperature patterns within the hyporheic zone of a northern Michigan river. Journal of the North American Benthological Society **6**: 85-91.

White, H.C. 1930. Some Observations on the Eastern Brook Trout (S. Fontinalis) of Prince Edward Island. Transactions of the American Fisheries Society **60**: 101-108.

Wilcock, P.R. 1998. Two-fraction model of initial sediment motion in gravel-bed rivers. Science. 280: 410-412.

Williams, D.D., and Hynes, H.B.N. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwater Biology **4**: 233-256.

Witzel, L.D., and MacCrimmon, H.R. 1981. Role of gravel substrate on ova survival and alevin emergence of rainbow trout, *Salmo gairdneri*. Canadian Journal of Zoology **59**: 629-636.

Witzel, L.D., and MacCrimmon, H.R. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society **112**: 760-771.

Wood, P.J., and Armitage, P.D. 1997. Biological Effects of Fine Sediment in the Lotic Environment. Environmental Management **21**: 203-217.

Wood, S. 2010. mgcv: Routines for GAMs and other generalized ridge regression with multiple smoothing parameter selection. In R package version 1.7-2. Available from http://cran.r-project.org/web/packages/mgcv/mgcv.pdf

Wooster, J.K., Dusterhoff, S.R., Cui, Y., Sklar, L.S., Dietrich, W.E., and Malko, M. 2008. Sediment supply and relative size distribution effects on fine sediment infiltration into immobile gravels. Water Resour. Res. **44**: W03424.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London; New York.

Wu, F.C. 2000. Modeling embryo survival affected by sediment deposition into salmonid spawning gravels: Application to flushing flow prescriptions. Water Resources Research **36**(6): 1595-1603.

Zimmermann, A., Coulombe-Pontbriand, M., and Lapointe, M. 2005. Biases of submerged bulk and freeze-core samples. Earth Surface Processes and Landforms **30**: 1405-1417.

Zuur, A.F., Ieno, E.N., and Smith, G.M. 2007. Analysing Ecological Data. Springer, New York.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.