

Spawning Site Selection and the Influence of Incubation Environment on Larval Success in Interior Fraser Coho

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ABSTRACT

Habitat features have been shown to influence salmonid spawning site selection as well as the survival and growth of larval fish throughout incubation. Most studies have been conducted in coastal watersheds, however, and little is known regarding habitat features associated with spawning sites for interior populations of salmon. My study examined factors affecting spawning site selection and incubation success for a population of interior Fraser coho salmon (IFC) (*Oncorhynchus kisutch*), in McKinley Creek watershed, British Columbia. Ground surveys coupled with radio telemetry were used to identify spawning site locations. An information theoretic approach was used to examine the probability of spawning site use based on habitat features. Incubation of larval fish within in-stream artificial redds allowed for the assessment of survival and growth in different incubation environments. The spawning habitat use of IFC throughout the McKinley Creek watershed was more extensive than previously realized. Hyporheic conductivity, dissolved oxygen, temperature and specific discharge were the best indicators of spawning site selection. Despite significant differences in habitat variables between used and unused spawning sites, survival and growth of larval IFC did not differ between sites; maternal effects were greater than incubation habitat features. This study has provided critical information about spawning site selection and the incubation environment of IFC, and has contributed to the understanding of the influence of habitat features on salmonids in interior watersheds.

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CHAPTER 1

General Introduction

Coho salmon (*Oncorhynchus kisutch*) are indigenous to the Pacific coasts and rivers of Asia and North America (McPhail, 2007). Coho salmon are anadromous and semelparous, and typically spend their first year in freshwater and the next eighteen months in the ocean before returning to their natal streams to spawn (Sandercock, 1991). In British Columbia most coho salmon spawn within 250 km of the ocean, with the exception of populations that migrate considerable distances upstream to spawn in the Skeena River and Fraser River watersheds (McPhail, 2007). The Fraser River is the longest river in British Columbia (COSEWIC, 2002) and drains an area of 231 510 km² (Encyclopedia of British Columbia, 2000). Commonly, the Fraser River is divided into two sections; the *lower Fraser River* south of the Fraser Canyon, and the *interior Fraser River* north of the Fraser Canyon. A population of coho salmon is known to spawn exclusively in the Fraser River watershed north of the Fraser Canyon and is generally referred to as Interior Fraser coho (IFC).

IFC are reproductively isolated from lower Fraser River coho (Irvine, 2004) and because of this are genetically distinct from coho in the lower Fraser (Small et al., 1998). There are five sub-populations of IFC: North Thompson, South Thompson, Lower Thompson/Nicola, Fraser Canyon, and Upper Fraser (DFO, 2002). To date most research on IFC has been conducted on fish from the North and South Thompson River sub-populations. Escapement data from the North and South Thompson River watersheds indicated an average decline of 60% in IFC from 1990-2000 (Irvine, 2002). Furthermore, Bradford (1998) found that IFC were no longer present in 32% of the streams that were inhabited a decade earlier in the Thompson River watershed. Based on this declining trend, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) concluded “that there is a serious risk of extinction of Interior Fraser coho” (COSEWIC, 2002, p.iii), and thus designated IFC as an

endangered species in 2002. With this designation IFC were considered for legal protection under the Species at Risk Act (SARA), however, based on uncertainties in the marine environment and potential socio-economic impacts, listing under SARA was denied (Canada Gazette, 2006).

COSEWIC (2002) attributed over-fishing, changing marine conditions, and freshwater habitat perturbations to the decline of IFC. In 1996, fishery exploitation of IFC was estimated to be approximately 68%; a number dramatically reduced in 1998 with the introduction of strict fisheries regulations (DFO, 2002). These regulations included no directed fisheries on coho, as well as a mandatory non-retention and non-possession of coho in all areas, with the exception of some terminal fisheries (DFO, 2001). Irvine and Bradford (2000) suggest that these fishery changes were the most significant changes ever implemented in Pacific Canada. In 2006 the estimate for IFC mortality in fisheries was 2.1% in Canadian waters, and approximately 12% when United States fisheries were included (R. Bailey, Fisheries & Oceans Canada, personal communication).

Even with substantial changes to fisheries practices and an increased awareness of the impacts of freshwater habitat perturbations, the short-term forecast for IFC remains poor (Simpson et al., 2001). Increased escapements have been noted in the Thompson River watershed recently, although these numbers remain approximately half of what was recorded in 1991 (DFO, 2005). Conservation efforts may be hindered by a narrow scope of understanding founded upon a limited knowledge of the freshwater habitat requirements of IFC. Studies on the habitat requirements of lower Fraser River and coastal coho populations are relatively abundant, but may not be applicable to IFC populations. It is likely that IFC life history strategies differ from coastal coho populations as interior populations evolved

with substantially different hydrological regimes; interior watershed runoff is primarily snow-dominated, while coastal watershed runoff is rain-dominated.

Information on freshwater habitat requirements for IFC is scarce for sub-populations residing outside of the Thompson River watershed, particularly for the most northerly sub-population – the Upper Fraser River IFC. The Upper Fraser River sub-population is defined as IFC that spawn upstream of the confluence of the Thompson and Fraser Rivers. IFC, like all Pacific salmon, utilize freshwater habitats during three stages of their life history: spawning, incubation, and rearing. There is a paucity of information on habitat requirements that influence IFC spawning site selection, as well as larval survival and growth throughout incubation. Suitable site selection is crucial because the highest rates of mortality over the life of a fish generally occur during the incubation period (Quinn, 2005). The bulk of mortality that occurs during this time is directly related to characteristics of the site that the female selected (Quinn, 2005).

Identification of positive and negative attributes of spawning site characteristics can provide vital information for conservation and management initiatives, and moreover add to the understanding of species-specific habitat needs. A considerable amount of work has been conducted to determine factors that influence spawning site selection in salmonids. These factors include substrate size (Kondolf and Wolman 1993; Shepherd et al., 1986), stream slope (Montgomery et al., 1999), stream scouring (DeVries, 1997; Tripp and Poulin, 1986), stream velocity (Quinn, 2005), fine sediment (Bradford and Irvine, 2000; Scrivener and Brownlee, 1989), dissolved oxygen (Chapman, 1988; Alderdice et al., 1958, Einum et al., 2002), and cover features, such as overhanging vegetation, woody debris, undercut banks, or small tributaries (Quinn, 2005).

Spawning site selection influences incubation success of larval fish. For example, dissolved oxygen has a strong influence on salmonid survival and growth during incubation (Shumway et al., 1964). The concentration of dissolved oxygen that flows through the intragravel environment is closely linked to stream velocity and the amount of fine sediment in the system. Incubation success can be decreased in low velocity environments if there is not adequate flow for dissolved oxygen exchange or the dispersal of metabolic waste materials (Chapman, 1988). Fine sediment can fill or partially block intragravel spaces resulting in insufficient dissolved oxygen levels for larval fish. The amount of fine sediment in a system can be augmented by human activities such as agriculture and road construction (Bradford and Irvine, 2000) as well as logging (Scrivener and Brownlee, 1989).

Temperature is another important factor for incubation success. Rombough (1997) indicated that each species has a specific range of temperature tolerance, at which extreme temperatures have lethal effects upon the fish. This 'zone of thermal tolerance' is much narrower during embryonic development than in later life stages. Murray and McPhail (1988) demonstrated that incubation temperature is also directly related to the rate of embryonic development. Additionally, timing of spawning is influenced primarily by temperature. Salmonids have evolved specific life history strategies, such that spawning occurs at a time that will maximize the incubation and emergence survival of their offspring (Brannon, 1987). Coho tend to spawn later in the fall than other species of salmon, principally in October and November and at water temperatures below 5°C (Shepherd et al., 1986), but some populations are known to spawn as late as January. Much of the information specific to coho salmon, however, is limited to coastal populations. The late season and low

temperatures when interior populations of coho spawn likely contribute to the lack of information in the literature for these populations.

In regions where winter temperatures drop below freezing, salmonids generally select spawning sites associated with groundwater upwelling (Leman, 1993; Geist and Dauble, 1998; Cunjak et al., 1986; Baxter and McPhail, 1999). Although the term “groundwater” indicates a single form, it is important to differentiate between the terms that are commonly used to describe groundwater; phreatic groundwater and hyporheic water. Phreatic water is devoid of oxygen and originates deep in the sub-surface (Freeze and Cherry, 1979), and provides a toxic environment for fish. Conversely, hyporheic water is found in the intragravel region of a stream where mixing of groundwater and surface water occurs (Valett et al., 1993). Hyporheic zones have a relatively constant temperature throughout the year and tend to be warmer than stream water in the winter, but have lower concentrations of dissolved oxygen (Quinn, 2005). Hyporheic zones can provide thermal stability for fish throughout the incubation period, which is especially important in systems where anchor ice is prevalent (Power et al., 1999).

My research was conducted in McKinley Creek watershed from 2006-2008 to investigate the spawning and incubation habitat requirements of the Upper Fraser River sub-population of IFC. The objectives of my study were to (1) determine locations within the McKinley Creek watershed where IFC spawn, (2) characterize the physical and chemical features of specific spawning sites, and (3) investigate the influence of habitat features on survival and growth of larval fish throughout incubation. Stream surveys and radio telemetry were used to identify the location of spawning grounds in McKinley Creek watershed (Chapter 2). The physical and chemical features of spawning sites and sites not used for

spawning were measured and an information theoretic approach was used to assess models and determine the probability of site use based on habitat features (Chapter 3). The survival and growth of larval IFC in artificial redds located within McKinley Creek were used to investigate the influence of incubation environment habitat features on incubation success (Chapter 4). Lastly, general conclusions and recommendations generated from this study are presented (Chapter 5).

The aim of this work was to develop a better understanding of the spawning and incubation habitat requirements of IFC in a northern interior watershed, McKinley Creek. McKinley Creek is proposed as an indicator watershed as it is one of the few systems where IFC have been documented to spawn and a long-term enumeration of spawners has been conducted. McKinley Creek is in central British Columbia near the town of Horsefly. Findings from my study will play a key role in understanding the freshwater life history of IFC and contribute significantly to the identification of critical habitats and their basin-wide distribution.

CHAPTER 2

Spawning Site Locations for a Proposed Indicator Stock
of Interior Fraser Coho in McKinley Creek, British
Columbia

ABSTRACT

Interior Fraser Coho (IFC) salmon (*Oncorhynchus kisutch*) are an endangered sub-species of coho that spawn exclusively in the interior Fraser River watershed. McKinley Creek is a proposed indicator stream for the most northerly population of IFC. Prior to this study the locations and extent of spawning habitat use by IFC have not been quantified in McKinley Creek watershed. Stream surveys and radio telemetry were used to determine the locations of IFC spawning sites throughout the 2006 and 2007 spawning period. Radio telemetry indicated that two thirds of tagged fish remained in the lower 12km of McKinley Creek and one third migrated into the upper portion of the watershed. There was no significant size difference between the individuals that utilized spawning habitat in the lower portion of the watershed compared to the upper portion. Findings of this study show that the extent and distribution of IFC throughout McKinley Creek watershed is larger than previously expected. Further investigation and identification of spawning habitats locations within the McKinley Creek watershed is recommended for the recovery and conservation of this sub-species.

INTRODUCTION

Pacific salmon are anadromous species that migrate upstream to spawn in their natal streams (McPhail, 2007). Although some straying occurs, the rate of return to natal streams has been reported to be high, and approximately 95-99% of salmonids home to their natal stream (Quinn, 2005). Homing precision has resulted in both the isolation of spawning populations and development of stream-specific adaptations (Dittman and Quinn, 1996; Groot and Margolis, 1991). There are various mechanisms that salmon use to successfully return “home”, but olfaction is the primary mechanism responsible for their upstream homing migrations (Wisby and Hasler, 1954; Dittman et al., 1996; Hasler and Scholz, 1983). Previous work has demonstrated that odours associated with the natal stream are imprinted during the juvenile out-migration (Donaldson and Allen, 1957; Hasler and Scholz, 1983), and have been linked to thyroxine levels which surge during the parr-smolt transformation and may allow key freshwater landmarks to be learned during downstream migration (Dittman and Quinn, 1996).

High levels of spawning site fidelity coupled with some straying have been successful for the propagation and distribution of Pacific salmon throughout western North America. Specifically, straying has allowed these species to successfully invade new habitats when they have become available. Natural disturbances and anthropogenic changes to the environment, however, often lead to rapid changes in freshwater watersheds that can disrupt spawning habitats. Identification of specific spawning grounds within natal streams has implications for conservation and protection of salmon, particularly because perturbations to the freshwater environment are frequently cited as a reason for declining fish populations

(Anderson, 1993; Bradford and Irvine, 2000; COSEWIC, 2002; Phillipow and Williamson 2004).

This study focused on identifying specific spawning habitat locations for Interior Fraser coho (IFC) in McKinley Creek watershed. The spawning habitat locations and requirements of the upper Fraser River sub-population of IFC have not been studied in detail. This knowledge could be critical for conservation purposes and would contribute to the general understanding of this understudied sub-population. To date, the principle focus of research in McKinley Creek watershed has been on enumeration. Previous research verified, by visual surveys, that the lower 12km of the watershed are actively used for spawning, but enumeration of redds has only been undertaken in a region measuring approximately 200m in length. The objective of this study was to identify the locations of specific spawning grounds in McKinley Creek watershed to gain an understanding of the extent and distribution of watershed use by spawning IFC.

MATERIALS AND METHODS

Study Site

McKinley Creek is a tributary to the Horsefly River, and is located in central British Columbia near the town of Horsefly (Figure 2-1). The Horsefly River flows into Quesnel Lake. The Quesnel River flows out of Quesnel Lake and into the Fraser River near the town of Quesnel. The major human impacts in the McKinley Creek watershed are recreation activities and logging. Active logging is ongoing, but does not occur directly adjacent to the creek. There is an active logging road that runs in close proximity to the creek and crosses over McKinley Creek with bridges at two locations.

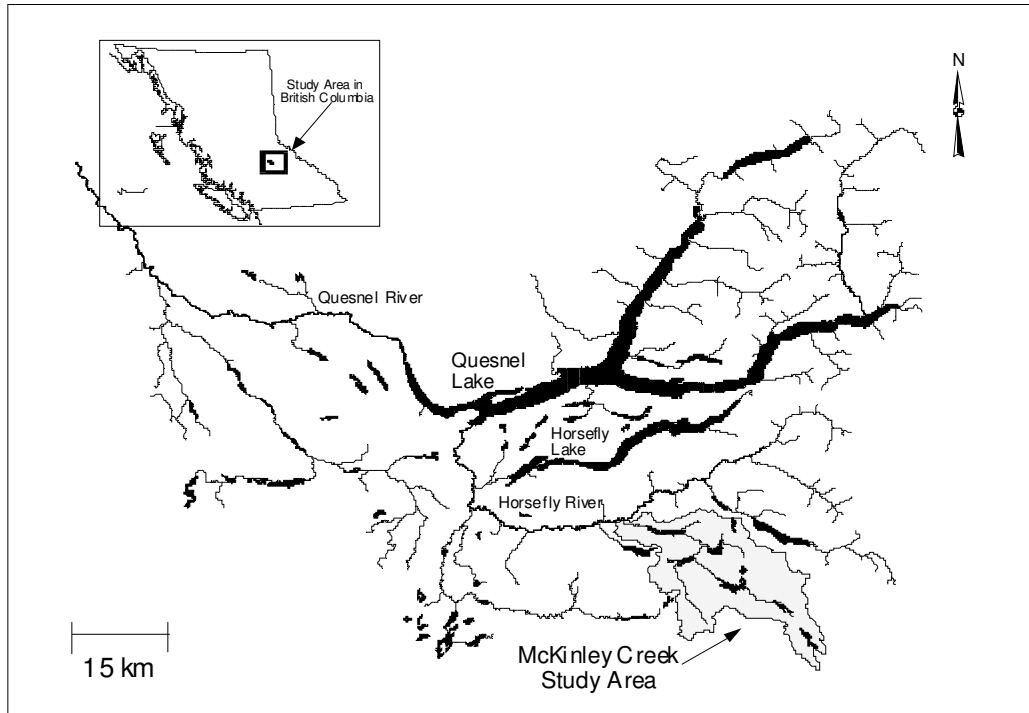


Figure 2-1: Map showing the McKinley Creek watershed within the Horsefly River watershed. Map produced by Mike Chamberlain, Fisheries and Oceans Canada based on a coverage map produced by GeoBC (<http://geobc.gov.ca>).

Two prominent features on McKinley Creek are an enumeration fence and a temperature control structure. The enumeration fence is located approximately 200m upstream of the confluence of McKinley Creek and the Horsefly River. The enumeration fence is installed annually in July and removed at the end of the IFC spawning period, which is usually at the end of November. The Northern Shuswap Tribal council operates the enumeration fence in conjunction with Fisheries and Oceans Canada.

The McKinley Lake temperature control structure is a dam at the outlet of McKinley Lake, which is approximately 12km upstream of the confluence of McKinley Creek and the Horsefly River. The dam was constructed in 1969 to control myxobacterium (*Chondrococcus columnaris*), which was associated with prespawning mortality of sockeye

salmon (*Oncorhynchus nerka*) (Williams, 1973). A siphon draws cold water from the bottom of the lake to the dam where it mixes in a chamber with surface water, and is then released into McKinley Creek. This dam is currently operated to maintain water temperatures below 58°F (approximately 14°C) during the sockeye spawning period in August and September.

2006 Spawning Period

Stream Surveys

Typically, salmonid spawning sites are located either by aerial observation flights or stream surveys conducted on foot. Irvine and Bradford (2000) observed that spawning IFC do not generally occur in high densities and that their cryptic colouration makes them difficult to see. Based upon this observation, coupled with the relatively small size of the 2006 McKinley Creek study area (12 km), stream surveys on foot were selected as an appropriate means of identifying spawning site locations. In 2006, weekly on-foot stream surveys were completed from mid-September until the end of November to locate IFC spawning sites known as redds. A redd is characterized by an oval shaped depression in the gravel that has no, or very little, periphyton growth. At the downstream end of a redd a mound of gravel is formed, known as the tailspin, which is where the female buries her eggs (DeVries, 1997). Stream surveys focused on the lower 12km of the McKinley Creek watershed based on sampling logistics coupled with regional knowledge of the watershed provided by Fisheries and Oceans Canada and the Northern Shuswap Tribal Council.

The sockeye spawner run in McKinley Creek precedes the IFC spawner run. From mid-September to mid-October, stream surveys were conducted to locate and mark sockeye redds to reduce the probability of sockeye spawning sites being mistakenly identified as IFC

sites. After the first coho passed the counting fence, IFC redd sites identified were referenced by GPS co-ordinates and identified with numbered flagging tape attached to rebar pounded into the gravel at the upstream end of the redd.

2007 Spawning Period

Radio Tagging

Twenty-nine IFC were captured and radio tagged during the 2007 spawning period to determine regions of the McKinley Creek watershed where fish migrated to potentially spawn. Females were principally tagged because they defend redds after spawning and have longer redd residence time than males (Quinn, 2005; Fleming and Gross, 1989). Twenty-three females and six males were tagged between October 12th-25th. Fish were caught with a dip net as they approached or passed through the enumeration fence on McKinley Creek. Additionally, some fish that entered the enumeration fence live box were also tagged.

After capture, fish were held in-stream in black zippered float tubes with circular meshed ends until they were tagged. Fish were placed in a v-shaped trough fitted with a battery powered bilge pump to provide a flow of stream water over the gills during tagging. Fork length and girth were measured. Coded Radio Transmitters (LOTEK: MCFT-3EM series, 11 x 49mm), which emit a unique code on one of two frequencies (149.230 and 149.680), were used to enable the identification of individual fish. Transmitters were externally mounted through the adipose tissue below the dorsal fin using a modified version of the methodology described by Winter (1996). Petersen tag pins were used to attach the transmitter. Two pins were inserted into the holes of the transmitter and pushed through the fish, and then through the holes of a plastic plate on the opposite side. The pins were tied into

a Petersen knot to ensure that the transmitter remained securely in place. Neoprene pads were put under the transmitter and the plastic plate to reduce abrasion. Prior to release, a hole punch was used to mark the operculum of each fish (2 holes for females; one hole for males) to ensure that if the fish was recovered without a transmitter it would be evident that the transmitter had been lost. Upon completion of tagging, fish were placed in the creek and held by the caudal peduncle until handling was actively resisted and the fish swam away freely. Fish were not anesthetized during tagging. External radio transmitters were used in this study because they are faster and easier to attach than surgical implantations, and have been successfully used elsewhere on spawning populations. Negative attributes of external radio transmitters include induced balance and drag problems, as well as abrasion and an increased potential for snagging on objects (Winter, 1996). These limitations were mitigated by using a transmitter size that was <2% of the fish's body weight (Winter, 1996), and by mounting the transmitter as symmetrically as possible below the dorsal fin.

Fish Tracking

Movement of tagged fish was monitored using receivers located at three fixed stations in the McKinley Creek watershed and by three aerial tracking flights. LOTEK (SRX 400) receivers were set to scan both study frequencies for five-second cycles at each fixed stations and during the helicopter flights.

Fixed stations were located immediately upstream of the McKinley Lake dam, approximately 10m upstream of the mouth of Offset Creek, and approximately 15m upstream of the upper McKinley Creek confluence (Figure 2-4). Fixed stations were installed at these locations to test whether or not IFC were (1) passing upstream of the McKinley Lake dam, and (2) utilizing habitats upstream of McKinley Lake for spawning. The receiver at each

fixed station was placed in a metal box that was mounted onto a large tree in the area. Receivers were powered by a car battery that was charged by solar panels. Three four-element Yagi antennas were attached to neighboring trees at the dam fixed station. Three-element Yagi antennas were located at the Offset Creek (one antenna) and Upper McKinley Creek fixed stations (three antennas). Fixed stations were operational from October 12th-October 26th, and were taken down when temperatures began to drop below 0°C.

Helicopter flights were conducted on November 1st, 7th, and 15th. I conducted the tracking during the first flight, and Fisheries & Oceans Canada personnel undertook the tracking during the second and third flights. For each flight a two-element antenna was attached to the helicopter to receive transmitter signals, and a continuously logging GPS unit was used to mark the location where transmitter signals were received. A power reading was associated with the reception of each transmitter signal and the highest power reading recorded for each fish indicated the most accurate tracking location. The GPS co-ordinates associated with the highest power reading for each fish were used to create a map of fish movement throughout the spawning period using OziExplorer (version 3.90) and Corel Draw (version 8).

DATA ANALYSIS

Analysis of variance (ANOVA) was used to compare the size of fish that migrated upstream of the McKinley Lake dam and those that remained downstream. Residual plots were examined to ensure that the assumptions of normality and equal variance were met.

RESULTS

2006 Spawning Period

The total 2006 IFC escapement in the McKinley Creek watershed, as enumerated by the Northern Shuswap Tribal Council, was 273. This is relatively low compared to historical IFC enumeration data for McKinley Creek (Figure 2-2). Stream surveys located six redds upstream of the McKinley Creek enumeration fence and twenty-four downstream of the fence during the 2006 spawning period. Figure 2-3 shows a map of the redd locations identified in McKinley Creek. Due to redd clustering, the GPS co-ordinates for the downstream redds were recorded for only eight of the twenty-four redds. The six upstream redds were located within approximately 5km of the enumeration fence. These six redds likely only represent a small proportion of the spawning site locations for the 273 individuals that passed through the enumeration fence. The majority of the 2006 spawning site locations upstream of the enumeration fence remain unknown.

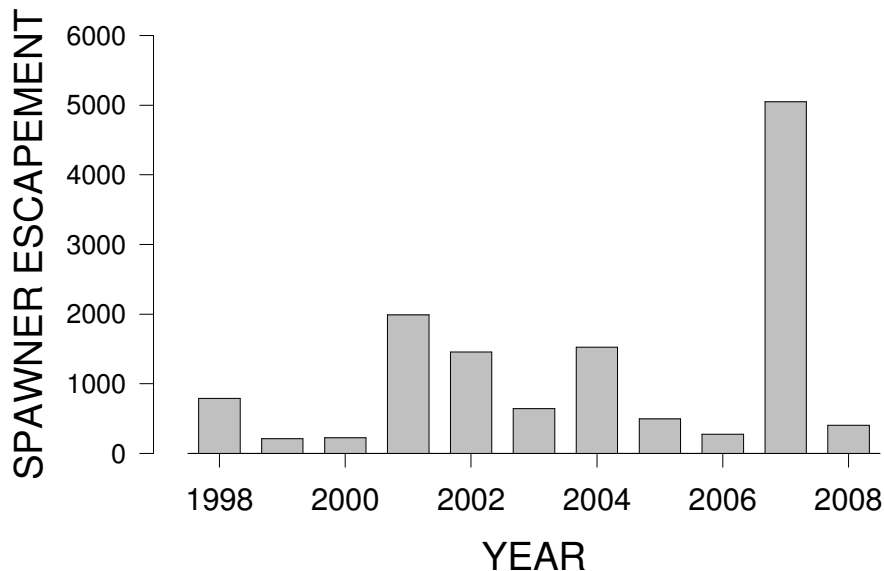


Figure 2-2: Enumeration of interior Fraser coho spawners in McKinley Creek watershed from 1998-2008. Data were collected by the Northern Shuswap Tribal Council.

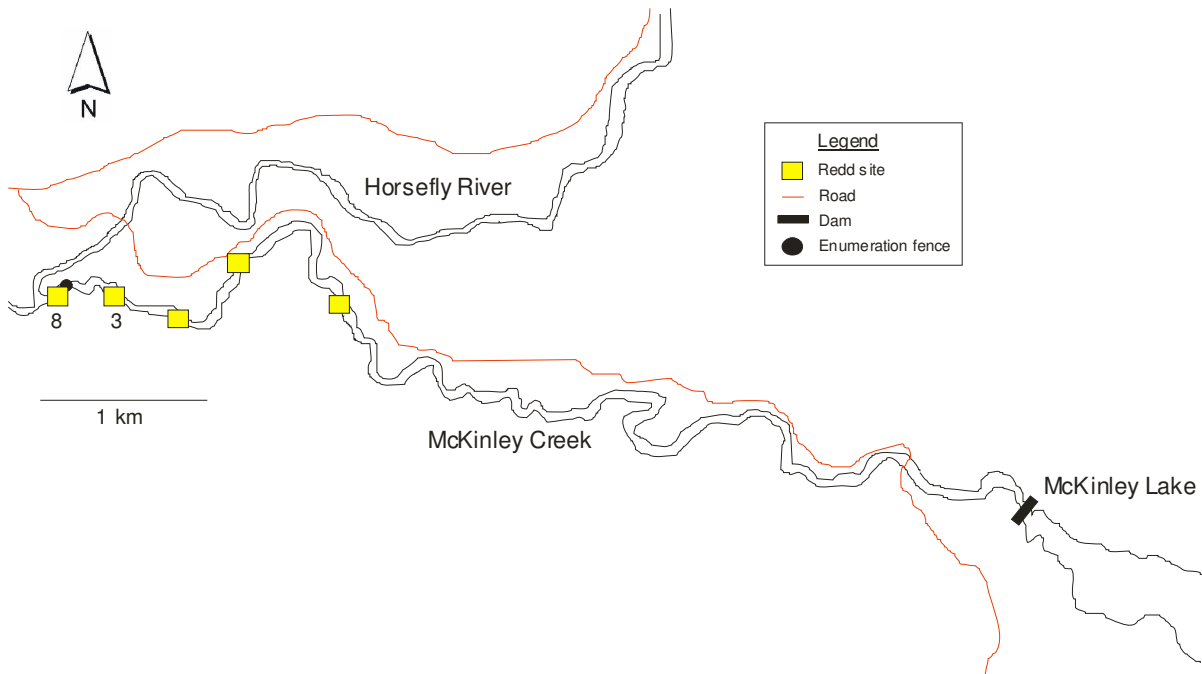


Figure 2-3: Locations of interior Fraser coho redds during the 2006 spawning period in McKinley Creek watershed. Number adjacent to symbol represents the number of redds at that location.

2007 Spawning Period

The total 2007 IFC escapement in the McKinley Creek watershed, as enumerated by the Northern Shuswap Tribal Council, was 5050. This is relatively high compared to historical IFC enumeration data for McKinley Creek (Figure 2-2). Fixed station and tracking flight data indicated that approximately two thirds of the tagged fish did not move above the dam at the outlet of McKinley Lake; twenty of the tagged fish, five males and fifteen females remained in the lower 12km of McKinley Creek. Almost one-third of the tagged fish, however, passed upstream of McKinley Lake dam; nine fish in total, one male and eight females. Figure 2-4 shows the location of tagged fish during the three helicopter tracking flights. The first flight (November 1st) identified the locations of twenty-two tagged fish. All of the fish tracked during the first flight were located in the lower 12 km of McKinley Creek

watershed. The upper portion of McKinley Creek watershed was flown extensively during the first flight but no tagged fish were located. The second (November 7th) and third flights (November 15th) focused exclusively on the upper portion of the McKinley Creek watershed. The second flight located six of the tagged fish, and the third flight located eight of the tagged fish. During the second flight, fish were found in upper McKinley Creek between Elbow Lake and Bosk Lake (n=3) and in Molybdenite Creek (n=3). Throughout the third flight fish were located in upper McKinley Creek between McKinley Lake and Elbow Lake (n=3), in upper McKinley Creek between Elbow Lake and Bosk Lake (n=3; one of which was found in a meadow), in upper McKinley Creek between Bosk Lake and Gotchen Lake (n=1), and in Molybdenite Creek (n=1).

Analysis of Variance indicated that there was no significant difference in fork length ($p=0.210$, $F=1.651$, $df=1$) or girth ($p=0.400$, $F=0.733$, $df=1$) between tagged fish that migrated upstream of McKinley Lake dam and fish that remained in lower McKinley Creek (Figure 2-5).

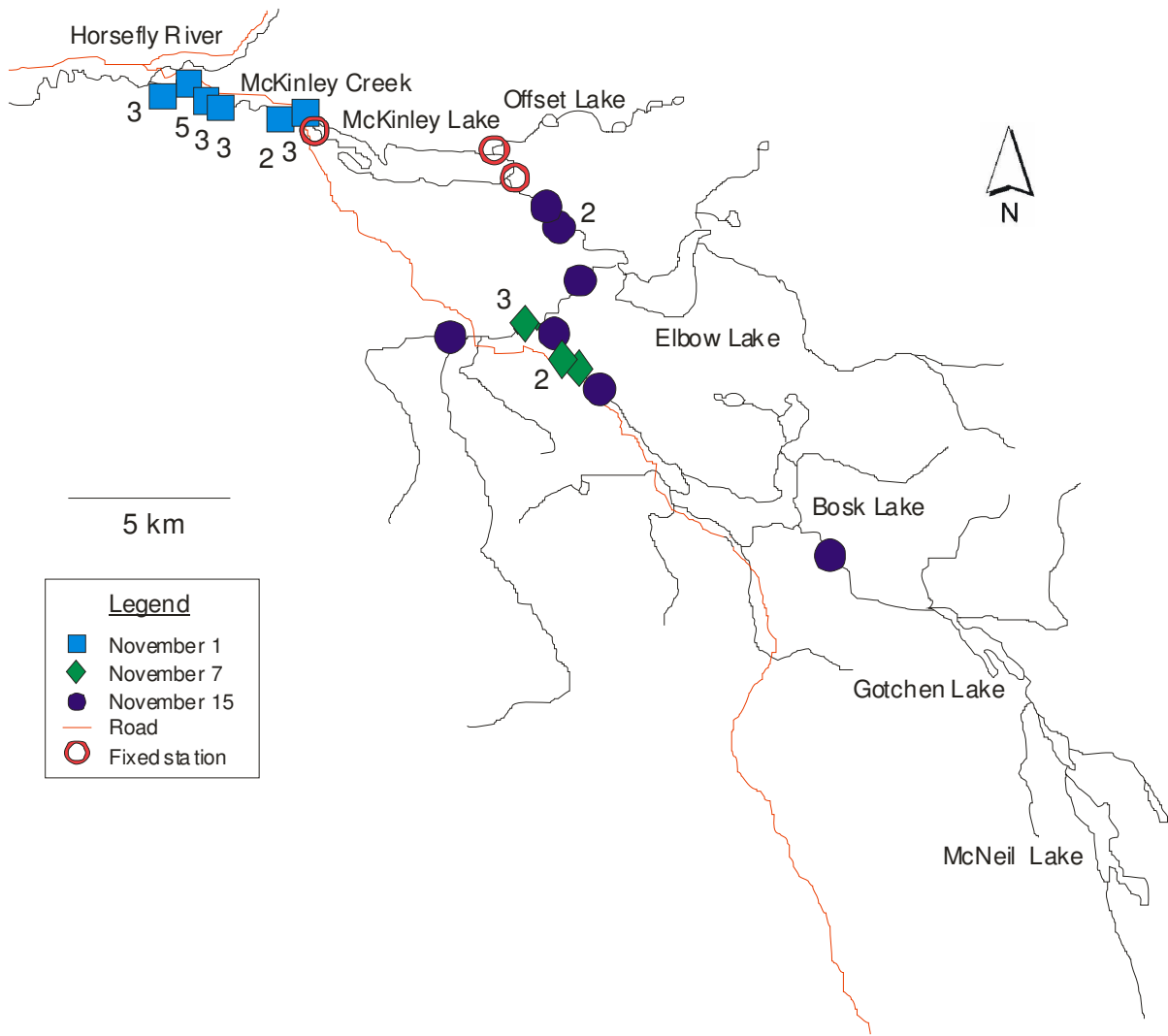


Figure 2-4: Locations of tagged interior Fraser coho spawners tracked in the fall of 2007 during three flights in McKinley Creek watershed. Number adjacent to symbol represents the number of observations bounded by the symbol.

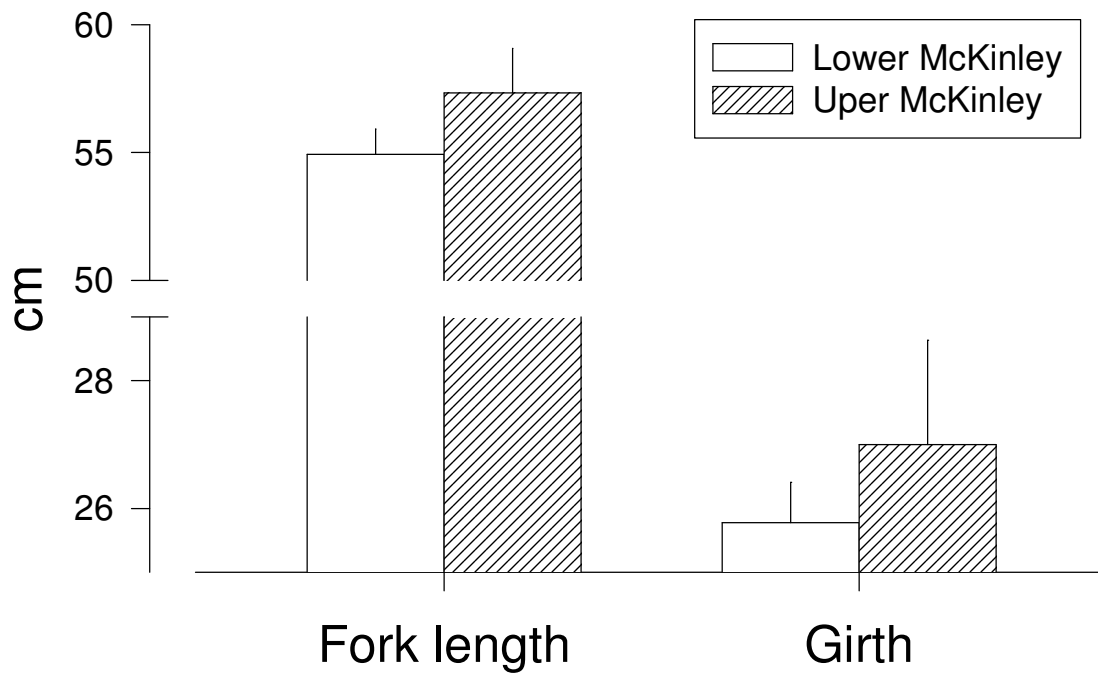


Figure 2-5: *Size comparison of interior Fraser coho that migrated upstream of the McKinley Lake dam (n=9) compared to those that remained in lower McKinley Creek watershed (n=20). Error bars represent standard error.*

DISCUSSION

The goal of this study was to determine the locations of IFC redds in McKinley Creek watershed. Results indicate that IFC migrated extensively throughout the watershed during the 2006 and 2007 spawning periods. The scarcity of redd sites identified downstream of the McKinley Lake dam in 2006 (despite 273 spawners being enumerated) coupled with radio telemetry tracking results in 2007, provide evidence for substantial IFC migration into the upper McKinley Creek watershed. Stream surveys used to identify specific spawning sites (redds) in McKinley Creek were unsuccessful in upper McKinley Creek due to logistical constraints, however, redds were located in the lower 12km of McKinley Creek in both 2006 and 2007. An abundance of redds were located downstream of the enumeration fence, suggesting that upstream migration for spawning may be impeded or delayed by the enumeration fence.

The total number of fish that migrated upstream of the enumeration fence in 2006 was 273, but weekly on-foot stream surveys only found 6 redds. Possible explanations for this disparity are: (1) stream surveys were unable to effectively locate redds; (2) there was a high proportion of prespawning mortality because of predation; or (3) IFC migrated upstream of the McKinley Lake dam out of the predetermined 2006 study area boundaries to spawn. Based on the small IFC run size, it is possible that weekly on-foot surveys missed redds, but I am relatively confident that these surveys were effective due to the thorough examination of McKinley Creek that was undertaken. There was some evidence of eagle and bear predation on IFC in McKinley Creek, but the influence of predation was not quantified. The migration of IFC into the upper portion of McKinley Creek watershed was not previously known. The McKinley Lake dam is equipped with a fish ladder, and the dam openings also present a

relatively simple opportunity for passage through this obstacle. The potential migration of IFC upstream of the McKinley Lake dam was hypothesized to be the most likely explanation for the small number of redds located in 2006. As a result of these findings radio telemetry was used to locate IFC spawning sites in 2007.

Fixed stations and helicopter flights tracked the movement of twenty-nine radio tagged IFC throughout the 2007 spawning period. The last known tracking location of each tagged fish indicated that twenty of the fish remained in the lower 12km of McKinley Creek watershed and nine migrated upstream of McKinley Lake dam. The findings of this study highlight the importance of both the upper and lower portions of McKinley Creek watershed for IFC spawners. A large number of redds were observed during on-foot stream surveys in lower McKinley Creek in 2007 confirming its use for IFC spawning. Ground-truthing in the upper portion of McKinley Creek watershed was attempted, but high flow and water levels impeded efforts. As a result no redds were physically observed in the upper portion of the watershed during the spawning period, but juveniles were identified in the spring approximately 5km upstream of the inflow of upper McKinley Creek into McKinley Lake (K. Warren, University of Northern British Columbia, personal communication.). Since juvenile coho have the capacity for both upstream and downstream movement, it could be argued that IFC may have incubated in lower McKinley Creek and then migrated into upper McKinley Creek upon emergence. Although, it seems unlikely that newly emerged IFC in lower McKinley Creek would swim such a distance upstream through a variety of challenging environments. This would necessitate passing through McKinley Lake dam, navigating through McKinley Lake, and then traveling a further 5km upstream into upper McKinley Creek. Bolton et al. (2002) conducted a study investigating the movement of

young-of-the-year coho salmon and found that the maximum distance traveled upstream was 500m. The presence of juveniles in upper McKinley Creek watershed is thus regarded as support for the occurrence of spawning habitat use in this part of the watershed.

Prior to this study only the lower portion of McKinley Creek watershed was considered IFC spawning habitat. This was likely based on the relative abundance of spawning habitat in the lower 12km of McKinley Creek. Perhaps it was thought that IFC would use the more easily accessible lower McKinley Creek habitat rather than proceeding much further upstream where a variety of obstacles would be encountered (McKinley Lake dam, McKinley Lake, beaver dams, and log jams). In contrast, there are a number of possible reasons for spawning habitat use in upper McKinley Creek watershed. Firstly, IFC migrate approximately 900 km from the Pacific Ocean to reach McKinley Creek, and along the way they pass through a variety of challenging environments successfully, including the Fraser Canyon. It is unlikely that a population that undergoes such a tremendous migration would be deterred by the relatively mild challenges presented in the McKinley Creek watershed. Another explanation could be that fish that arrive earlier to their natal stream tend to proceed further upstream than those that migrate later in the spawning run (Briggs, 1953). Although, based on our radio telemetry tracking, early arriving and later arriving fish were equally as likely to migrate into upper McKinley Creek watershed as they were to remain in lower McKinley Creek. Alternatively, some IFC may proceed to spawning grounds in upper McKinley Creek to minimize the chance of redd superimposition in the relatively densely populated spawning grounds in lower McKinley Creek. This would allow females to expend less energy competing for, and defending, redd locations.

In this study it was hypothesized that the fish size may also influence the distance traveled upstream. Spawning fish size is variable and can depend on a number of factors including sex, age, and arrival timing at the natal stream (Sandercock, 1991). Larger fish may have the ability to swim further upstream and navigate more effectively through high flow areas, such as an outflow of a dam. Conversely, small fish may be more capable of passing through complex obstacles such as beaver dams, and furthermore may be less likely to be detected by predators. ANOVA results indicated that there was no significant difference in fork length or girth of the fish that migrated into upper McKinley Creek watershed compared to those that remained in the lower 12km. Based on these results the specific reason that some IFC migrate further upstream than others remains unclear. Although, it is clear that a relatively substantial proportion of tagged IFC utilized the upper portion of McKinley Creek watershed, meriting future attention and investigation into the potential importance of this habitat.

Spawning sites located in 2006 indicated a high number of redds downstream of the enumeration fence (n=24) compared to a lower number of redds located upstream of the enumeration fence (n=6). This distribution of redds suggests that the enumeration fence may have been a potential barrier to migration of IFC throughout McKinley Creek watershed. There are no studies published, to the best of my knowledge, that specifically focus on the effect of enumeration fences upon spawning salmonids, but there is a general consensus that enumeration fences have the potential to delay salmon runs as well as impose stress upon migrating salmon (Irvine et al., 1991; Reddin et al., 1992). A possible response to a migration barrier is backtracking to alternate downstream habitats. This may result in the selection of sub-optimal spawning habitat that does not encompass ideal species-specific

features. Furthermore, if a migration barrier results in backtracking, individuals may be confined to a relatively small area for spawning, which increases the likelihood of redd superimposition. Redd superimposition is considered to be a substantial source of egg mortality in salmonids (Quinn, 2005; Fleming and Gross, 1989; McNeil, 1964). Alternative means of enumeration that have been shown to be successful for adult salmonids include mark and recapture estimations (Miyakoshi and Kudo, 1999), infrared sensors (Shardlow and Hyatt, 2004), underwater photo-enumeration (Shardlow, 2001) mean count visual surveys (Holt and Cox, 2008), and resistivity counters (Reddin et al., 1992). Such devices may have less influence on migration behaviour for McKinley Creek IFC.

Conclusion

This study confirmed the use of lower McKinley Creek as IFC spawning habitat and also found that IFC migrated into the upper portion of the watershed to spawn. These results suggest that spawning habitat locations in McKinley Creek watershed are more extensive than previously expected. Fish size did not provide an explanation for the migration of some fish into the upper watershed and the remainder of others in the lower portion of the McKinley Creek. Alternative explanations may be related to density of fish in the lower watershed and the possibility of two distinct populations of IFC in McKinley Creek.

CHAPTER 3

Factors influencing Interior Fraser Coho Spawning Site
Selection in McKinley Creek, British Columbia

ABSTRACT

Considerable research effort has focused on examining the influence of habitat features on spawning site selection in salmonids. Traditionally, habitat features used to predict spawning site selection included stream velocity, depth, and a measure of substrate particle size. Recent evidence indicates that habitat selection likely encompasses a wider range of habitat features. The present study aimed to examine the relative influence of a variety of habitat features on spawning site selection in interior Fraser coho (*Oncorhynchus kisutch*) during the 2006 and 2007 spawning periods in McKinley Creek watershed, British Columbia. The objectives of this study were: (1) to compare the physical and chemical features of sites used for spawning with sites not used for spawning, and (2) to develop a logistic regression model to predict the probability of spawning site selection based on habitat features. An information theoretic approach was used to assess candidate models and jackknife internal validation was used to determine predictive ability. The traditional habitat features model, which included stream velocity, depth, and the percentage of gravel within the substrate, ranked low and had poor predictive ability. Physical and chemical features of the intragravel environment dominated the top ranked models in this study. Habitat features in the top four models included hyporheic conductivity, dissolved oxygen, temperature, and specific discharge. Each of the top model variables had a positive influence on spawning site selection with the exception of hyporheic conductivity, which had a negative influence. The model with the highest predictive ability (ROC value = 0.91) was comprised of hyporheic conductivity and specific discharge as habitat variables. Intragravel habitat features may play a more prominent role in spawning site selection than previously described.

INTRODUCTION

There is a considerable amount of research that has focused on determining factors that influence spawning site selection in salmonids. The selection of a specific spawning habitat can influence the reproductive success of adult salmon. Selection of a suitable site is critical because the highest rate of mortality in salmonids generally occurs during the incubation period, and this mortality is closely related to the features of the spawning/incubation site (Quinn, 2005). Traditionally, studies of spawning habitat selection have focused on stream depth, velocity and a physical property of the channel, such as substrate particle size (Milhous, 1979; Stalnaker, 1979; Bovee, 1982; Orth and Maughan, 1982; Milhous, 1999). Although, recently it has become evident that traditional habitat features may not provide the most effective means of assessing spawning habitat suitability (Mathur et al., 1985; Mull and Wilzback, 2007; Geist and Dauble, 1998; McHugh and Budy, 2004). Rather, the complexity of spawning site selection may encompass a wider range of habitat features. Furthermore, changes in habitat features may be deleterious to larval development and survival. In fact, perturbation of freshwater habitat is frequently cited as a reason for declines in salmonid populations (Nehlsen et al., 1991; NRC, 1996; COSEWIC, 2002). As such, the evaluation of specific spawning site features may provide vital information for conservation and management initiatives, and moreover add to the understanding of species-specific habitat needs.

Surface features not included in the traditional models such as slope and the associated potential for streambed scouring (Montgomery et al., 1999; DeVries, 1997; Tripp and Poulin, 1986) have also been shown to influence spawning site selection. Habitat features such as overhanging vegetation, woody debris, undercut banks, or small tributaries

have also been found to influence spawning site selection (McMahon et al., 1996). Cover features have the potential to provide protection from predators as well as adverse stream conditions, such as high stream velocity. In addition to habitat features, there may be a behavioral component to spawning site selection. Essington et al. (1998) found that brown trout (*Salmo trutta*) and bull trout (*Salvelinus confluentus*) females demonstrated a behavioral preference for spawning on existing redds even when suitable spawning habitat was not limited. Other studies suggest that spawning clusters and redd superimposition may more effectively be explained by the influence of site-specific hyporheic flow (Vronskly and Lemen, 1991; Geist et al., 2002).

In addition to stream habitat features, the potential influence of groundwater-stream water interactions may play a key role in salmonid spawning site selection. Groundwater is more appropriately referred to as phreatic water and is devoid of oxygen and originates deep in the subsurface (Freeze and Cherry, 1979). The subsurface region where phreatic water mixes with stream surface water is referred to as the hyporheic zone (Valett et al., 1993). The physical and chemical similarities of hyporheic water compared to either phreatic water or stream water is mainly a function of the penetration depth and residence time of the hyporheic flow pathway (Cooler and Boulton, 1993). Hyporheic flow pathways embody a dynamic relationship in which stream water infiltrates the streambed (downwelling), flows through the subsurface, and later emerges (upwelling) back into the stream (Boulton, 1993). Conversely, phreatic water flow pathways enter or leave the stream at specific regions with little horizontal movement through the streambed (Jones and Mulholland, 2000). On a small-scale, upwelling and downwelling is primarily governed by stream discharge, streambed permeability, and channel morphology (Vaux, 1962; Boulton, 1993; Brunke and Gonsler,

1997; Geist and Dauble, 1998). Conversely, large-scale upwelling and downwelling is principally determined by the geology of the watershed (Brunke and Gonser, 1997).

Previous studies have examined the influence of hyporheic flow on spawning site selection. Species that have been found to select spawning sites associated with upwelling include brook trout (*Salvelinus fontinalis*) (Curry and Noakes, 1995), sockeye salmon (*Oncorhynchus nerka*) (Lorenz and Eiler, 1989), chum salmon (*Oncorhynchus keta*) (Leman, 1993), Chinook salmon (*Oncorhynchus tshawytscha*) (Geist, 2000), rainbow trout (*Oncorhynchus mykiss*) (Sowden and Power, 1985), and Arctic char (*Salvelinus alpinus*) (Cunjak et al., 1986). Other studies have found spawning sites specifically associated with downwelling regions (Atlantic salmon (*Salmo salar*); Mills, 1989). Studies on bull trout (*Salvelinus confluentus*) indicate selection of spawning sites associated with upwelling at a stream-reach spatial scale (Baxter and McPhail, 1999; Baxter and Hauer, 2000; Williamson, 2006) and downwelling at redd sites (Baxter and Hauer, 2000). Spawning sites have not been linked to upwelling or downwelling, however, in all species studied. Brown trout (*Salmo trutta*) have been found to select spawning sites with and without upwelling to approximately the same extent (Hansen, 1975).

Describing spawning site selection solely in terms of upwelling and downwelling may provide some insight into habitat selection cues, but this likely summarizes the driving forces behind site selection too simplistically. It is important to examine additional physical and chemical features of hyporheic water to understand the potential cues affecting spawning site selection. Water in the hyporheic zone differs from surface water primarily in terms of temperature and dissolved oxygen content (Baxter and Hauer, 2000). In temperate regions, hyporheic water tends to be cooler than stream water in summer and warmer in winter

(Cunjak and Power, 1986; Nielson et al., 1994). Water in the hyporheic zone has very little diurnal and seasonal variation compared to stream water (Schmidt et al., 2006), and as such can provide a refuge for fish during temperature extremes (Power et al., 1999; Quinn, 2005). This moderating temperature can be especially advantageous for incubating larval fish in regions where anchor ice is prevalent (Benson, 1955; Williamson, 2006). The moderate and relatively stable temperature regime of the hyporheic zone is typically coupled with lower dissolved oxygen concentration than stream water. Therefore, a spawning site associated with upwelling hyporheic water must be coupled with an appropriate combination of stream and intragravel flow to provide a favourable incubation environment. Incubation success can be compromised in low velocity environments if there is not enough stream flow for appropriate dissolved oxygen exchange or removal of metabolic waste materials (Chapman, 1988). As larval fish develop they require more dissolved oxygen, particularly prior to hatching, (Alderdice et al., 1958), thus an adequate flow of oxygen-rich stream water is essential for successful development. Fine sediment can fill or partially block gravel interstitial spaces resulting in a reduced delivery of dissolved oxygen. Increases in fine sediment have been attributed to a number of human activities such as agriculture and road construction (Bradford and Irvine, 2000), as well as logging (Scrivener and Brownlee, 1989). Other features of hyporheic water chemistry, such as conductivity and pH, have not been examined in much detail in the literature but may also play a role in spawning site selection.

My study examined habitat features that may influence spawning site selection of interior Fraser coho (IFC) salmon. The majority of research that has been conducted on coho salmon spawning site selection, and Pacific salmon in general, has been undertaken in coastal regions with rain-dominated hydrological regimes, while few studies have exclusively

examined the spawning habitat features of interior watersheds with snow-dominated hydrological regimes. The relative importance of habitat features for spawning site selection may differ dramatically between interior and coastal watersheds.

There are numerous features that have the potential to influence spawning site selection. The relative importance of these features, however, likely differs among species and even geographic locations within a taxonomic species. Therefore, it is prudent to closely examine the influence of these features in a site and species-specific context. The goal of this research was to contribute to a better understanding of the habitat features associated with IFC spawning site selection and to provide site-specific information to aid in the conservation and protection of this ‘endangered’ population of coho salmon. The objectives of this study were to (1) compare the physical and chemical features of sites used for spawning with sites not used for spawning by IFC in McKinley Creek watershed during the 2006 and 2007 spawning periods, and (2) to develop a logistic regression model to predict the probability of spawning site selection based on habitat features.

MATERIALS AND METHODS

Location of Study Sites

Stream surveys and radio telemetry were used to identify IFC spawning sites in the McKinley Creek watershed (see Chapter 2). Specific spawning sites, hereafter referred to as *used* sites, were defined by the presence of a redd. A redd is characterized by an oval shaped depression in the gravel that has no, or very little, periphyton growth and by a downstream mound of gravel, known as the tailspin (DeVries, 1997). Sites where no spawning occurred, hereafter referred to as *unused* sites, were chosen purposefully as locations that, based on

qualitative visual cues of substrate size, stream velocity, and depth, seemed appropriate for spawning but where no spawning was observed. Unused sites were determined to be qualitatively appropriate for spawning based on observations of habitat features at redd sites in McKinley Creek. The GPS coordinates of used and unused sites were recorded, and each study site location was marked with rebar flagged with the site number. The rebar was pounded into the substrate at the upstream end of the used sites to ensure that egg pockets were not disturbed. The selection of study sites for this project was based upon a cluster sampling approach (Brown and Austen, 1996) that was directed by logistical constraints of stream access, although every effort was made to sample as broad a range of reaches within McKinley Creek as possible and provide a well-balanced study design.

Spawning Habitat Assessment

Surface Habitat Features

A variety of physical and chemical surface habitat features were measured during the 2006 and 2007 IFC spawning periods (October-December). A Swoffer flow meter (Model 2100) was used to measure stream velocity at 15cm above the streambed. This depth was selected because it represents the approximate depth a spawning fish would hold in the stream flow. Dimensions of the wetted stream channel were assessed by measuring width, slope, and depth. Depth at used sites was measured immediately to the left upstream side of the redd to represent the original stream depth that would have been encountered prior to redd construction. Stream slope was measured over a 6m distance which was centered over the redd (at used sites) using a clinometer. Visual surveys were conducted to estimate the percentage of boulder, cobble, gravel, and fine sediment at each used and unused site. Visual

surveys were also undertaken immediately to the left upstream side of the redd to mitigate for the disturbed substrate within the redd itself. Definitions of substrate size were based on a simplified version of the modified Wentworth classification as described by Cummins (1962); categories of substrate were defined as follows: boulder > 256mm, cobble 32-256mm, gravel 4-32mm, and fines <4mm.

Surface water chemistry measurements included: dissolved oxygen, conductivity and pH. Dissolved oxygen was measured using a YSI 550A handheld dissolved oxygen and temperature system in 2007, and a WTW Multi-metre (Model 340i) in 2006. Conductivity and pH were measured using a HANNA pH/EC Combo meter in 2007 and a WTW Multi-metre (Model 340i) in 2006.

The presence or absence of cover features, such as undercut banks, overhanging vegetation, and woody debris were recorded at each study site. Presence or absence of existing redds was also recorded. Redds that were within 10m of the study site were counted as present. Models in this study did not include a 'presence/absence of other redds' variable as other studies have (Mull and Wilzback, 2007) because it was reasoned that the inclusion of this parameter presents a risk of variable pseudo-replication. Without the inclusion of an intensive spawning behavior study it is not possible to differentiate whether the presence/absence of other redds is a function of habitat features, or alternatively a behavioral selection parameter.

All habitat features of unused sites were measured towards the end of the spawning period to ensure that the potential influence of sampling did not affect spawning site selection. Conductivity and pH values were automatically temperature compensated during

measurement, and dissolved oxygen values were converted from mg/L to percent saturation (Colt, 1984) to mitigate for temporal temperature variation.

Intragravel Features

Mini-piezometers were used to measure temperature, dissolved oxygen, conductivity, pH, vertical hydraulic gradient, and hydraulic conductivity of the intragravel environment at each study site. Mini-piezometers were constructed based on the design described by Lee and Cherry (1978). Mini-piezometers were constructed from a 1m section of polyvinyl chloride (PVC) tubing attached to 15cm of perforated polyethylene (PE) tubing. The PVC tubing was secured to PE tubing with glue. Ten perforations (1.5mm in diameter) were made through the PE tubing to allow for the movement of water into the mini-piezometer. The perforated tubing was wrapped in 14x11cm of 250 micron Nitek screen to restrict the introduction of fine sediment into the mini-piezometer.

Mini-piezometers were inserted into the substrate at depths of 30 and 60cm at each study site as per the procedures outlined by Lee and Cherry (1978). A lag bolt was inserted into the bottom end of a steel pipe that was pounded into the substrate to desired depths using a sledgehammer. Once the 30 or 60cm depth was achieved the mini-piezometer was fed into the top of the pipe and gently pushed to the bottom of the pipe with a piece of rebar. The rebar was then used to hold the mini-piezometer in place while the steel pipe was slowly removed from the substrate. Mini-piezometers were inserted into the substrate at the upstream end of redds at used sites to prevent disturbance to the downstream egg pockets.

A modified syringe was used to draw water up from the mini-piezometers so that temperature, dissolved oxygen, conductivity, and pH of the hyporheic water could be

measured. A barb-splicer was attached to the tip of a graduated 60ml syringe, which enabled a seal to be formed when the syringe was inserted to the exposed end of the mini-piezometer. Dissolved oxygen was calculated as percent saturation for the intragravel measurements. Phreatic water is devoid of oxygen, whereas surface water is usually fully saturated. Percent saturation, therefore, not only provided a measure of oxygen content, but also an indication of the groundwater contribution to the hyporheic zone.

Two measures of hyporheic flow within the intragravel environment were measured; vertical hydraulic gradient and hydraulic conductivity. Vertical hydraulic gradient is a unitless measurement that is positive for upwelling and negative for downwelling (Freeze and Cherry, 1979, Geist et al., 2002). A manometer, based upon the design by Lee and Cherry (1978) and modifications by Williamson (2006), was used to measure the head differential that is necessary for calculating vertical hydraulic gradient. The manometer was made by attaching two pieces of PVC tubing to a compressible bulb that was mounted on half an aluminum metre stick. The equation for calculating vertical hydraulic gradient (VHG) is:

$$\text{VHG} = \Delta h / \Delta L$$

where Δh is the water surface elevation inside the piezometer minus the water surface elevation of the river, and ΔL is the distance below the streambed to the first perforation in the piezometer (Freeze and Cherry, 1979).

Hydraulic conductivity refers to the ease at which a porous medium can transmit a fluid (Sanders, 1998). Hydraulic conductivity differs from permeability, although these two terms are sometimes used interchangeably. Permeability is a function of just the porous medium, whereas hydraulic conductivity is a function of both the porous medium and the fluid that is being transmitted (Freeze and Cherry, 1979; Sanders 1998). A falling-head slug

test (Freeze and Cherry, 1979; Sanders, 1998; Baxter et al., 2003) was used to measure hydraulic conductivity at each study site. A known volume of water was added to the mini-piezometer and the rate at which the water level returned to its initial level in the mini-piezometer was timed. Slug tests are relatively simple to undertake, but are site specific and do not indicate the hydraulic conductivity at a large scale (Sanders, 1998). The slug test was conducted by adding 10ml of stream water to the mini-piezometer and measuring the rate of change in water level. An estimate of hydraulic conductivity (K_h) (cm/second) was calculated using an equation derived by Baxter et al., (2003) that was designed to be used specifically when measurement of time lag is not practical. The equation is:

$$K_h = \left[\frac{(0.2501) (d)}{\Delta t} \right] \left[\log_e \frac{h_0}{h} \right]$$

where d is the diameter of the mini-piezometer, t = time, h_0 = water level at time zero, and h = water level at time t . This equation assumes isotropic flow such that the vertical and horizontal components of hydraulic conductivity are equal. Lastly, measurements of vertical hydraulic gradient and hydraulic conductivity were used to calculate specific discharge (v) at each study site using the equation (Baxter et al., 2003):

$$v = K_h * VHG$$

DATA ANALYSIS

Logistic regression models were created to predict the probability of selection of spawning sites based on stream and intragravel features. Logistic regression allows for the analysis of a wide range of independent variables (discrete, continuous, or a mix) to determine a dependent outcome (Menard, 2001; Tabachnick and Fidell, 1996). An

information theoretic approach (Burnham and Anderson, 1998) was used to assess candidate models that were built using data from the 2007 spawning period in McKinley Creek watershed. Candidate models can be grouped into four categories; models that included (1) surface variables, (2) physical and chemical variables of the intragravel environment, (3) surface and intragravel flow variables, and (4) a combination of physical, chemical, and flow variables. Akaike's information criterion (AIC) was used to compare and rank candidate models and furthermore to select the 'best approximating model'. The model with the lowest AIC value is "estimated to be the 'closest' to the truth and is the best approximation for the information in the data" (Burnham and Anderson, 1998, p.47). Models that have a difference <2 AIC values from the 'top' model are also considered to have substantial support and should be taken into account when making inferences. For small sample sizes AIC may perform poorly (Sakamoto et al., 1986), and a corrected AIC (AICc) should be used. Model building for this study was based on a data set from 40 sites, therefore AICc was used to rank models. AICc is calculated using the formula:

$$AICc = AIC + \frac{[2K(K+1)]}{n-K-1}$$

where K is the number of model parameters (including the intercept), and n is sample size (Burnham and Anderson, 1998). AIC weight (w_i) was also calculated for each model (i) using the following formula (where R is the number of models):

$$w_i = \frac{\exp(-1/2 \Delta AIC_i)}{\sum_{r=1}^R \exp(-1/2 \Delta AIC_r)}$$

AIC weight indicates the probability that the model would be ranked as the 'best model if the data were to be collected again under identical circumstances (Whittingham et al., 2006), and

as such gives an indication of the whether or not model ranking indicates a clear top model or rather a variety of relatively good models.

Before conducting the logistic regression analysis the data were examined for non-linearity, overdispersion, and multicollinearity. Linearity was examined by developing a model with one habitat variable, and then running the same model with the addition of the quadratic form of the original habitat variable. The AICc values of these two models were compared and a habitat variable was determined to be non-linear if the AICc value for the model with the additional quadratic variable had a lower AICc score by more than or equal to two. The data were checked for overdispersion by examining the dispersion parameters of three 'full' models; 'full' models were examined rather than the global model due to the high number of habitat variables measured in this study. To check for multicollinearity, plotted data were inspected and the correlation (r) of each habitat variable was calculated.

According to Menard (2001) the cut off for multicollinearity in logistic regression modeling is $r=0.8$, but due to the variability associated with ecological data it is unlikely that this would ever occur. Therefore variance inflation factors (VIF) were examined for each of the candidate models to determine if independent parameters were involved in multicollinearity. Any parameter with a VIF greater than 10 was considered to have a high degree of multicollinearity (Freund and Wilson, 1998) and as a result was not used in a model with other highly collinear parameters.

Full reality can never be modeled based on a finite number of observations, and as such inference based on any model should only be undertaken after a model has been shown to adequately fit relevant empirical data (Burnham and Anderson, 1998; Pearce and Ferrier, 2000). To assess the predictive performance of a model Pearce and Ferrier (2000) suggest

that evaluation is best undertaken by assessing the predictive ability of a model based on independent data not included in the model building process. Unfortunately, equipment malfunction prevented the use of 2006 data as a means of externally validating the models built with 2007 data. As a result internal model validation was undertaken using a jackknife approach. Jackknifing has been found to produce relatively unbiased estimates of model performance (Olden and Jackson, 2000; Olden et al., 2002).

A logit function was used to calculate the probability of spawning site selection for each observation in the top candidate models using the equation:

$$p(Y) = \frac{\exp(\beta_0 + \beta_1 x_1 + \dots + \beta_i x_i)}{1 + \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_i x_i)}$$

Where β_0 is the intercept term, and β_i is the coefficient for each covariate in the model, and x_i is the value of the covariate. Probability values from top candidate models were validated using the area under a relative operating characteristic (ROC) curve, which relates relative proportions of correctly and incorrectly classified predictions (Pearce and Ferrier, 2000). The area under the ROC curve index ranges from 0.5 indicating models with no discrimination ability, to 1 which indicates models with perfect discrimination ability (Swets, 1986). In general the predictive ability of a model based on the area under the ROC curve index can be classified as poor from 0.5-0.7, reasonable to good from 0.7-0.9, and very good >0.9 (Swets, 1988).

Guthery et al. (2005) presented a critical assessment of the prevalent use of information theoretic approach and AIC, in which they concluded by urging researchers to employ alternative analytical techniques for data analysis. Based on this criticism, descriptive statistics for each habitat parameter were calculated for used and unused sites to

provide a complimentary alternative to the information theoretic approach used in this study. All statistical analyses were completed using R (version 2.51).

RESULTS

Identification of Study Sites

In 2006 weekly ground surveys located fourteen used sites, and five unused sites were also sampled (Figure 3-1). The relatively small number of used sites identified in 2006 was related to the low escapement (McKinley Creek enumeration was 273), and the fact that only the lower 12km of McKinley Creek was surveyed. In 2007 radio telemetry coupled with ground surveys identified thirty-four used and twenty unused sites that were sampled (Figure 3-2). IFC escapement in 2007 was the highest ever recorded, totaling 5050 individuals. Many more sites were located than could be sampled, and as a result a clustered sampling approach was used to focus on selected reaches that were most accessible. An effort was made to include a broad range of reaches, but high flow prevented sampling in the middle section of McKinley Creek.

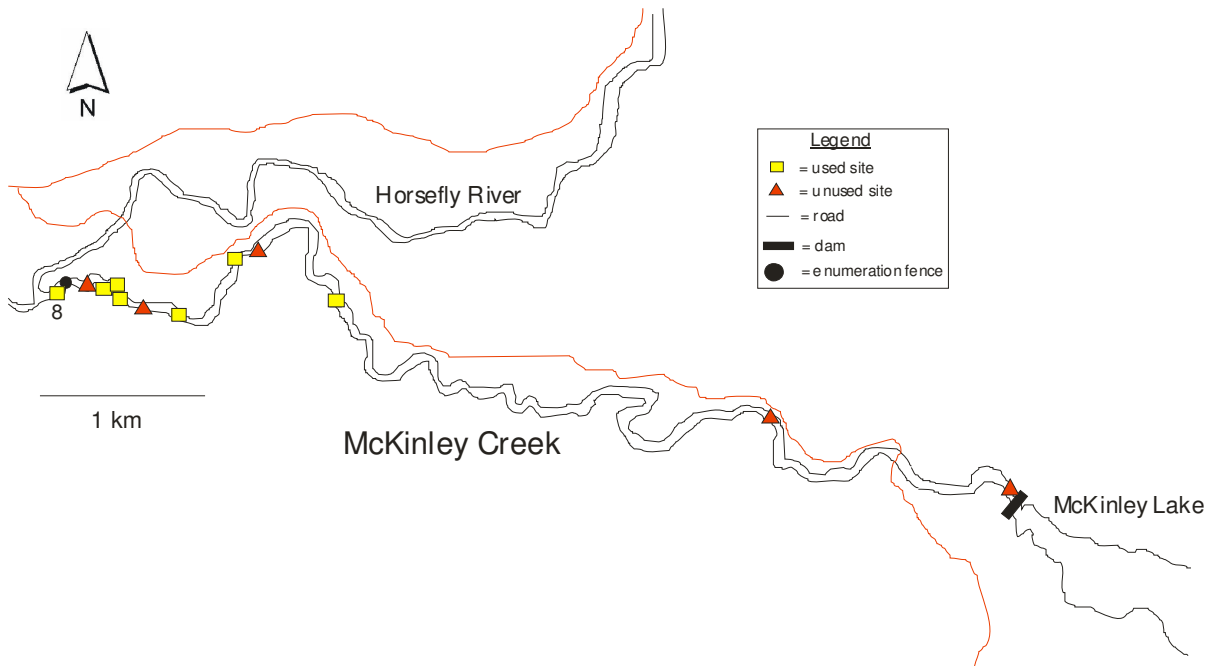


Figure 3-1: Map of 2006 used and unused study sites. The McKinley Creek enumeration fence and McKinley Lake Dam are shown on the figure. Number adjacent to symbol represents the number of spawning redds sampled that are within the area bounded by the symbol.

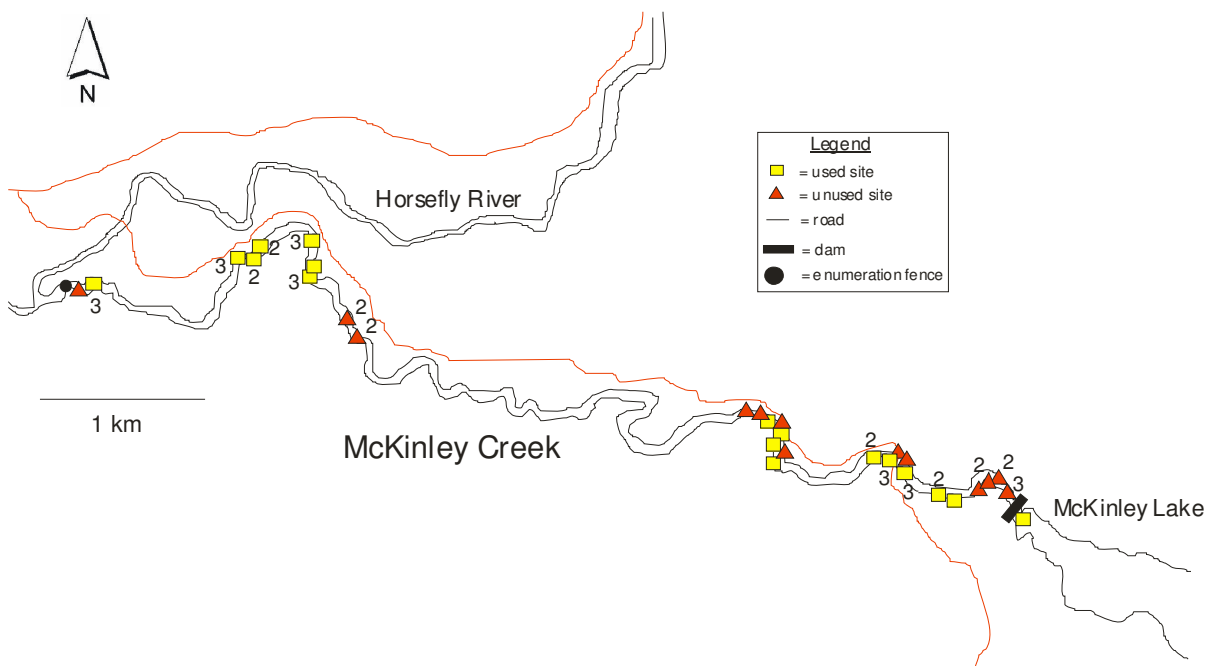


Figure 3-2: Map of 2007 used and unused study sites. The McKinley Creek enumeration fence and McKinley Lake Dam are shown on the figure. Number adjacent to symbol represents the number of spawning redds sampled that are within the area bounded by the symbol.

Spawning Habitat Assessment

Habitat Use Models

Combinations of twenty-two habitat variables (Table 3-1) were used to build twenty candidate models (Table 3-2). Examination of linearity indicated that stream conductivity, stream velocity, hydraulic conductivity at depths of 30 and 60cm, as well as temperature and vertical hydraulic gradient at the 60cm depth were non-linear. When a quadratic was used in a model the linear form of the same variable was also included. An examination of dispersion parameters and VIFs indicated that multicollinearity and overdispersion were not evident. Logistic regression models were built with the inclusion of a random effect for study site location. McKinley Creek was divided into two location categories; *upper* and *lower* sections of the 12km study site. This was used to mitigate for potential differences that may have arisen based on the spatial gap between the upper and lower study sites in McKinley Creek.

Table 3-1: Summary of spawning habitat variables used for logistic regression modeling of spawning site selection of interior Fraser coho in McKinley Creek watershed during the 2007 spawning period. 'Location' was included as a random effect in each model to account for potential differences between the upper and lower sections of the 12km study site.

Physical Stream Variables	Stream velocity ($\text{m}\cdot\text{s}^{-1}$)
	Stream depth (m)
	Stream width (m)
	Stream slope
	Gravel (% of substrate composition)
	Location
Chemical Stream Variables	Dissolved oxygen (% saturation)
	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)
	pH
Intragravel Flow Variables (at depths of 30cm and 60cm)	Vertical Hydraulic Gradient
	Hydraulic Conductivity ($\text{cm}\cdot\text{s}^{-1}$)
	Specific Discharge ($\text{cm}\cdot\text{s}^{-1}$)
Intragravel Physiochemical Variables (at depths of 30cm and 60cm)	Dissolved oxygen (% saturation)
	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)
	pH
	Temperature ($^{\circ}\text{C}$)

Table 3-2: Summary of logistic regression candidate models for interior Fraser coho spawning site selection in McKinley Creek watershed in 2007 (used n=28, unused n=12). DO= dissolved oxygen, COND= conductivity, TEMP= temperature, VHGH= vertical hydraulic gradient, Kh=Hydraulic conductivity, v=specific discharge. S, 30, or 60 represents where measurements were taken from: the stream surface, or the intergraded environment at depths of either 30cm or 60cm respectively. 'Location' was included as a random effect in each model to account for potential differences between the upper and lower sections of the 12km study site.

Model Variables	
Surface variables	depth + velocity + velocity ² + Pgravel + location width + depth + slope + location SDO + SCOND +SCOND ² + SpH + location
Intergravel physiochemical Variables	30DO + 30COND + 30pH + location 60DO + 60COND +60pH + location 30DO + 30COND + location 60DO + 30COND + location 60COND + 60TEMP +60TEMP ² + location 30COND + 30TEMP + location 30DO + 60COND + location
Flow variables (hyporheic and/or surface flow)	30VHG + 30Kh +30Kh ² + location 60VHG + 60VHG ² + 60Kh +60Kh ² + location 30v + velocity + velocity ² + location 60v + velocity + velocity ² + location
Combination of intergravel physiochemical and flow variables	30DO + 30v + location 60DO + 60v + location 30COND + 30v + location 60COND + 60v + location 60COND + 30v + location 30COND + 60v + location

Table 3-3 shows a summary of AICc ranking, and indicates that there were four top models. Habitat variables in the top four models included conductivity at the 60cm depth (Figure 3-3), dissolved oxygen at the 30cm depth (Figure 3-4), temperature at the 60cm depth (Figure 3-5), and specific discharge at 30 and 60cm depth (Figure 3-6). Table 3-4 presents

the β coefficient, standard error, Z and P values, odds ratio, and confidence interval for each variable in the top models. Conductivity at the 60cm depth was included in each of the top four models and β coefficients indicated that this variable had a negative effect, such that the probability of site use decreased with increased conductivity. In contrast, β coefficients of other variables included in the top models (dissolved oxygen at the 30cm depth, and specific discharge at 30cm and 60cm depth) showed a positive effect on site use. Temperature at the 60cm depth was found to have a positive and negative effect on site use for its linear and quadratic term respectively. This indicates that increases in temperature at the 60cm depth will have a positive effect on spawning site selection until a certain threshold is reached, and thereafter increases in temperature will have a negative effect on spawning site selection.

AICc ranking results demonstrated that the traditional habitat model, with the habitat variables of depth, velocity, and a measure of substrate size (% gravel composition of the substrate), scored relatively poorly with a rank of sixteenth out of twenty candidate models. In addition, models comprised of only physical and chemical surface variables were ranked poorly. Models with solely flow variables (vertical hydraulic gradient, hydraulic conductivity, and stream velocity) also scored poorly unless coupled with an intragravel physical or chemical variable. Physical and chemical variables of the intragravel environment alone, or in combination with an intragravel flow variable, exclusively dominated the top twelve models.

AIC weights indicted that there were three top models that fit the data reasonably well. These top three models included hyporheic conductivity and hyporheic dissolved oxygen ($w_i = 0.283$), hyporheic conductivity and hyporheic temperature ($w_i = 0.265$), and hyporheic conductivity and specific discharge ($w_i = 0.221$).

Table 3-3: Summary of AICc ranking of candidate models for interior Fraser coho spawning site selection in McKinley Creek watershed during the 2007 spawning period (used n=28, unused n=12). Model type abbreviations indicate: I= Intragravel model, IF= Combination of intragravel and flow model, F= flow model, and S= surface model. K indicates the number of model parameters (including the intercept). DO= dissolved oxygen, COND= conductivity, TEMP= temperature, VHVG= vertical hydraulic gradient, Kh=Hydraulic conductivity, v=specific discharge. The notation of S, 30, or 60 represents where measurements were taken from: the stream surface, or the intragravel environment at depths of either 30cm or 60cm respectively.

Model Rank	Model Type	Model Parameters	K	AICc	$\Delta AICc$	w_i
1	I	DO30 + 60COND + location	4	25.69	0	0.283
2	I	60COND + 60TEMP + 60TEMP ² + location	5	25.82	0.13	0.265
3	IF	60COND + 30v + location	4	26.18	0.49	0.221
4	IF	60COND + 60v + location	4	27.11	1.42	0.139
5	I	60DO + 60COND + 60PH + location	6	28.35	2.66	0.075
6	I	30DO + 30COND + location	4	33.5	7.81	0.006
7	I	30DO + 30COND + 30PH + location	5	33.73	8.04	0.005
8	IF	30DO + 30v + location	4	35.44	9.75	0.002
9	IF	30COND + 60v + location	4	36.71	11.02	0.001
10	I	30COND + 30TEMP + location	4	37.88	12.19	0.001
11	I	60DO + 30COND + location	4	37.93	12.24	0.001
12	IF	30COND + 30v + location	4	39.03	13.34	<0.001
13	S	SDO + SCOND + SCOND ² + SPH + location	6	39.05	13.36	<0.001
14	F	60v + velocity + velocity ² + location	5	39.44	13.75	<0.001
15	F	30v + velocity + velocity ² + location	5	39.5	13.81	<0.001
16	S	depth + velocity + velocity ² + gravel + location	6	40.21	14.52	<0.001
17	IF	60DO + 60v + location	4	41.65	15.96	<0.001
18	F	60VHG + 60VHG ² + 60Kh + 60Kh ² + location	6	44.81	19.12	<0.001
19	S	width + depth + slope + location	5	45.96	20.27	<0.001
20	F	30VHG + 30Kh + 30Kh ² + location	5	46.73	21.04	<0.001

Table 3-4: Summary of the model output for the top ranked models for spawning site selection in interior Fraser coho in McKinley Creek watershed (used n=28, unused n=12).

Model Rank	Parameter	B	Standard Error	Z	P	Odds Ratio	β 95% CI	
							Lower	Upper
1	30DO	0.0721	0.0389	1.8517	0.0641	1.07	-0.0041	0.1483
	60COND	-0.0363	0.0140	-2.5830	0.0098	0.97	-0.0637	-0.0089
2	60TEMP	3.2452	1.9436	1.6700	0.0950	1.18	-0.5643	7.0547
	60TEMP ²	-0.4669	0.3617	-1.2910	0.1967	0.95	-1.1758	0.2420
	60COND	-0.0435	0.0169	-2.5711	0.0101	0.96	-0.0766	-0.0104
3	30v	2.0593	1.1039	1.8650	0.0621	7.84	-0.1043	4.2229
	60COND	-0.0566	0.0180	-3.1390	0.0017	0.94	-0.0919	-0.0213
4	60v	3.1885	1.9179	1.6630	0.0964	24.25	-0.5706	6.9476
	60COND	-0.0498	0.0159	-3.1320	0.0017	0.95	-0.0810	-0.0186

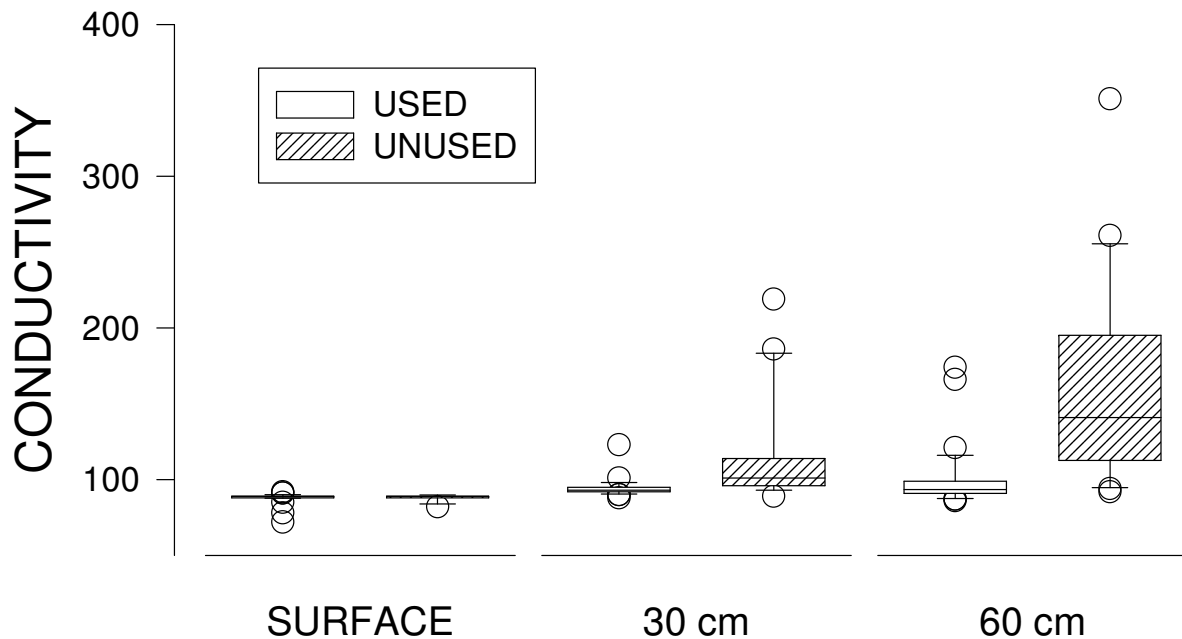


Figure 3-3: Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) measured at used and unused study sites in McKinley Creek watershed during the 2007 interior Fraser coho spawning period (used n=34, unused n=20); measurements taken from surface water and hyporheic water at depths of 30cm and 60cm. Line inside box marks the value of 50th percentile, the box extends to the 25th and 75th percentiles. Capped bars indicate the 10th and 90th percentiles and open circles represent all data outside the 10th and 90th percentiles.

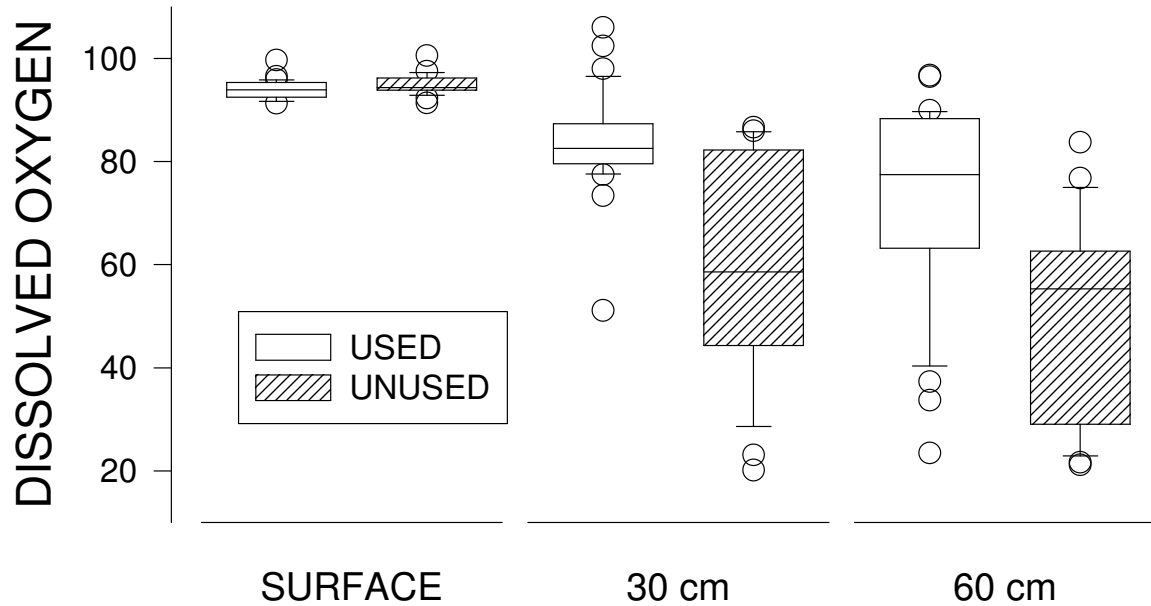


Figure 3-4: Percent Saturation of dissolved oxygen measured at used and unused study sites in McKinley Creek watershed during the 2007 interior Fraser coho spawning period (used $n=34$, unused $n=20$); measurements taken from surface water and hyporheic water at depths of 30cm and 60cm. Line inside box marks the value of 50th percentile, the box extends to the 25th and 75th percentiles. Capped bars indicate the 10th and 90th percentiles and open circles represent all data outside the 10th and 90th percentiles.

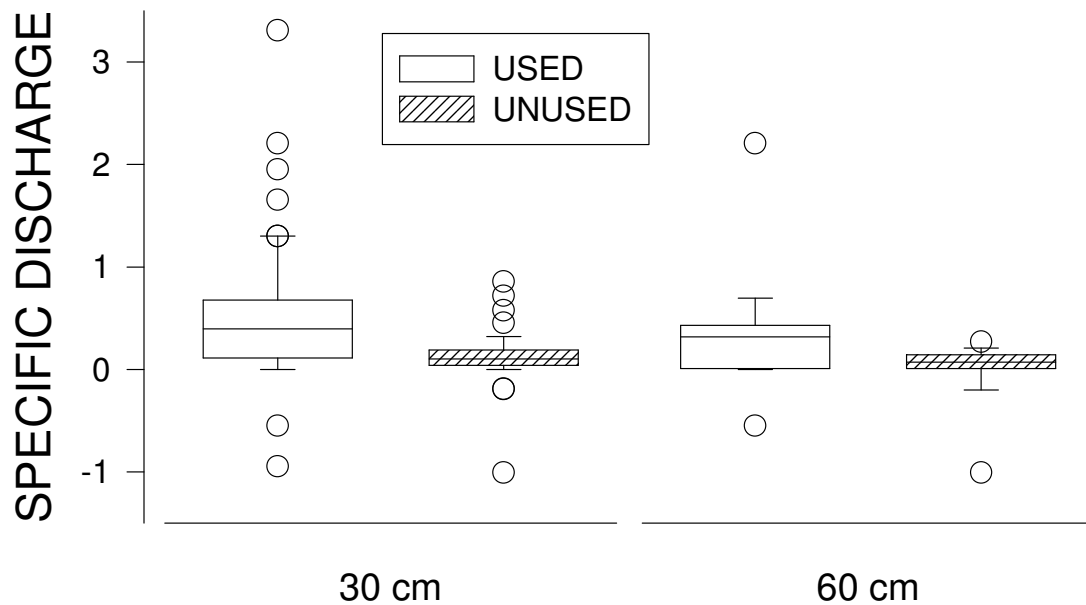


Figure 3-5: Specific discharge ($cm \cdot s^{-1}$) measured at used and unused study sites in McKinley Creek watershed during the 2007 interior Fraser coho spawning period (used $n=34$, unused $n=20$); measurements taken from surface water and hyporheic water at depths of 30cm and 60cm. Line inside box marks the value of 50th percentile, the box extends to the 25th and 75th percentiles. Capped bars indicate the 10th and 90th percentiles and open circles represent all data outside the 10th and 90th percentiles.

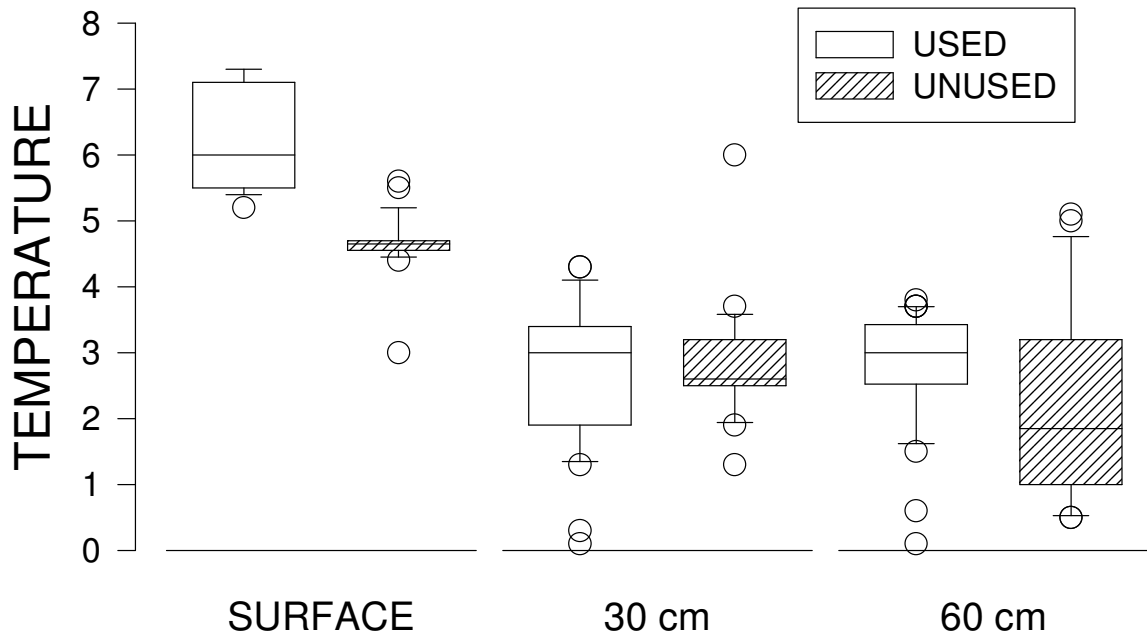


Figure 3-6: Temperature ($^{\circ}\text{C}$) measured at used and unused study sites in McKinley Creek watershed during the 2007 interior Fraser coho spawning period (used $n=34$, unused $n=20$); measurements taken from surface water and hyporheic water at depths of 30cm and 60cm. Line inside box marks the value of 50th percentile, the box extends to the 25th and 75th percentiles. Capped bars indicate the 10th and 90th percentiles and open circles represent all data outside the 10th and 90th percentiles.

Model Validation

The area under the ROC curve analysis indicated that the 3rd ranked model, with habitat parameters of conductivity at the 60cm depth and specific discharge at the 30cm depth, had the highest ROC value of 0.91 which indicates that the model has a very good predictive ability. Table 3-5 shows the area under the ROC curve values for the top four candidate models as well as the poorest AICc ranked model and the traditional habitat model for comparison. The remaining top candidate models had area under the ROC curve values ranging from 0.78 to 0.84, indicating reasonable to good predictive ability. The area under

the ROC curve values for the traditional and last ranked candidate model were 0.72 and 0.55 respectively, indicating reasonable to poor predictive ability.

Table 3-5: Summary of area under the ROC curve values for top candidate models, the traditional model, and the last ranked AICc model for interior Fraser coho spawning site selection in McKinley Creek watershed during the 2007 spawning period (used n=28, unused n=12). DO= dissolved oxygen, COND= conductivity, TEMP= temperature, VHG= vertical hydraulic gradient, Kh=Hydraulic conductivity, v=specific discharge. The notation of 30, or 60 represents where measurements were taken from the intragravel environment at depths of either 30cm of 60cm respectively.

Model Rank	Model Parameters	AICc value	ROC value
1	30DO + 60COND	25.69	0.84
2	60COND + 60TEMP +60TEMP ²	25.82	0.78
3	60COND + 30v	26.18	0.91
4	60COND + 60v	27.11	0.81
16 (Traditional Model)	depth + velocity + velocity ² + Pgravel	40.21	0.72
20 (Ranked Last)	30VHG + 30Kh +30Kh ²	46.73	0.55

Descriptive Statistics

A summary of the means and standard error of all model variables are shown in Table 3-6 for used and unused sites. Table 3-7 provides a summary of the presence/absence of cover at used and unused sites. Figure 3-7 compares the percentage of substrate type observed at used and unused sites.

Table 3-6: Summary of habitat variable means and standard errors for used and unused sites for interior Fraser coho during the 2007 spawning period in McKinley Creek watershed (used n=34, unused n=20).

	Habitat Variable	Mean (\pm standard error)	
		Used	Unused
Surface physiochemical variable	Stream velocity ($\text{m}\cdot\text{s}^{-1}$)	0.63 \pm 0.03	0.44 \pm 0.06
	Stream depth (m)	0.55 \pm 0.03	0.47 \pm 0.02
	Stream width (m)	18.89 \pm 1.40	24.54 \pm 2.11
	Stream slope	-0.17 \pm 0.26	0.09 \pm 0.34
	Dissolved oxygen (% saturation)	93.96 \pm 0.31	94.88 \pm 0.45
	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	88.09 \pm 0.62	88.05 \pm 0.49
	pH	8.03 \pm 0.01	7.98 \pm 0.04
Intragravel physical/chemical variable (at 30cm)	Dissolved oxygen (% saturation)	83.73 \pm 1.77	61.36 \pm 5.04
	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	94.33 \pm 1.10	118.44 \pm 8.72
	pH	7.57 \pm 0.04	7.42 \pm 0.07
	Temperature ($^{\circ}\text{C}$)	2.64 \pm 0.20	2.86 \pm 0.22
	Vertical Hydraulic Gradient	0.12 \pm 0.02	0.08 \pm 0.03
	Hydraulic Conductivity ($\text{cm}\cdot\text{s}^{-1}$)	5.70 \pm 0.49	4.32 \pm 0.69
	Specific Discharge ($\text{cm}\cdot\text{s}^{-1}$)	0.66 \pm 0.14	0.32 \pm 0.12
Intragravel physical/chemical variable (at 60cm)	Dissolved oxygen (% saturation)	72.53 \pm 3.58	50.30 \pm 4.56
	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	100.10 \pm 3.73	163.76 \pm 16.28
	pH	7.53 \pm 0.04	7.39 \pm 0.06
	Temperature ($^{\circ}\text{C}$)	2.81 \pm 0.17	2.27 \pm 0.36
	Vertical Hydraulic Gradient	0.04 \pm 0.01	0.03 \pm 0.16
	Hydraulic Conductivity ($\text{cm}\cdot\text{s}^{-1}$)	5.02 \pm 0.64	3.94 \pm 1.03
	Specific Discharge ($\text{cm}\cdot\text{s}^{-1}$)	0.17 \pm 0.04	0.01 \pm 0.08

Table 3-7: Percentage of cover features located at used and unused sites for interior Fraser coho during the 2007 spawning period in McKinley Creek watershed (used n=34, unused n=20).

	Overhanging Vegetation	Woody Debris	Undercut Bank	No obvious cover
Used Sites	97	97	50	0.03
Unused Sites	80	80	20	15

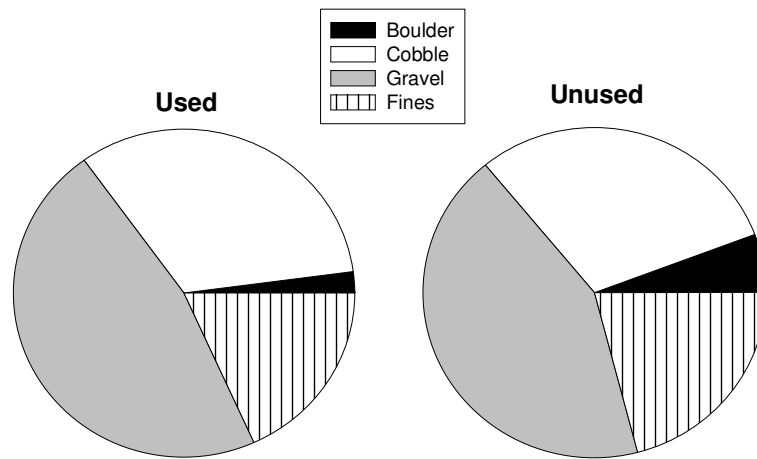


Figure 3-7: *Percent of substrate composition at used and unused study sites in McKinley Creek during the 2007 interior Fraser coho spawning period in McKinley Creek watershed (used n=34, unused n=20).*

DISCUSSION

Spawning Habitat Features

This study aimed to identify specific habitat features that affect IFC spawning site selection in McKinley Creek watershed. An information theoretic approach coupled with jackknifing internal model validation was used to determine which (if any) habitat features effectively predicted spawning habitat use. Results indicated four top models with good predictive ability. The habitat features identified in each of the top models will be discussed in terms of their biological significance.

Conductivity

Conductivity of the intragravel environment at unused sites was on average higher than used sites at both the 30 and 60cm depths. AIC ranking demonstrated that conductivity at the 60cm depth was present in each of the top four models. ROC values for these models ranged from 0.78 to 0.91, indicating reasonable to very good predictive ability. In each model β coefficients and odds ratios indicated that conductivity had a negative effect on spawning site selection, as such it is suggested that high intragravel conductivity may be used as an indication of unsuitable habitat. The confidence intervals for conductivity at 60cm depth did not overlap with zero and had a relatively narrow range which is indicative of further support for the use of conductivity as a means of IFC spawning site selection. Similar studies have shown that Chinook salmon and brown trout have also been found to avoid spawning in regions associated with high conductivity levels (Hansen, 1975; Baxter and Hauer, 2000). High conductivity levels are common in areas that are strongly influenced by upwelling groundwater that has had minimal interaction with hyporheic or surface water

(Curry and Noakes, 1995). The findings of my study suggest that IFC may be avoiding spawning in areas with relatively concentrated groundwater associated with high conductivities.

An alternative explanation is that high conductivities in some regions of McKinley Creek are a result of human disturbances. The majority of unused sites that were associated with high conductivity values were typically in close proximity to either the gravel road that runs adjacent to portions of McKinley Creek, or within 100m of the McKinley Lake dam. The potential influence of human disturbance was not specifically included in the scope of my study, but findings suggest that this may merit further investigation.

Dissolved oxygen

Many studies have examined the influence of dissolved oxygen concentration on fish. One branch of research has focused on examining how reduced dissolved oxygen levels can induce behavioral and physiological responses. These responses range from a reduction in activity level, changes in cardiac function, increased use of alternatives for gas exchange, to changes in habitat use (Kramer and McClure, 1982; Magnuson et al., 1985; Bejda et al., 1987; Kramer, 1987; Barton and Taylor, 1996). These responses highlight the ability of a fish to detect and respond to low dissolved oxygen concentrations. If these responses are not successful, however, low dissolved oxygen concentrations reduce the survival and growth of larval fish (Alderdice et al., 1958; Shumway et al., 1964; Witzel and MacCrimmon, 1983; Chapman, 1988; Bjornn and Reiser, 1991; Einum et al., 2002). Due to the adverse effects associated with low dissolved oxygen on incubating larval fish, it is not surprising that dissolved oxygen has been linked to spawning site selection (Hansen, 1975; Geist et al., 2002; Quinn, 2005). To ensure reproductive success, female salmon should select spawning

sites that maximize the survival and growth potential for their offspring. A relatively abundant supply of dissolved oxygen may indicate to the spawning female that a particular site is appropriate for larval incubation.

Results of my study showed that dissolved oxygen of stream water was similar for all sites, but that on average hyporheic water dissolved oxygen levels at unused sites were lower than used sites at depths of both 30 and 60cm. At greater depth in the hyporheic zone there is less interaction with the stream water and the influence of phreatic water is greater (Triska et al., 1993). Dissolved oxygen at the 30cm depth was found to have a positive effect on spawning site selection, as indicated by a positive β coefficient and an odds ratio > 1 . Dissolved oxygen at the 30cm depth was included in the top ranked model (with conductivity at 60cm depth) and had an area under the ROC curve value of 0.84 indicating good predictive ability. Confidence intervals for dissolved oxygen, however, overlapped with zero and indicated that there was considerable variability in this measurement. Females may be able to detect dissolved oxygen concentrations at a depth of 30cm while digging a redd, and thus use this habitat feature to determine whether a spawning site is suitable.

Temperature

Temperature is one of the most influential abiotic features affecting fish throughout their lives. Salmonids have evolved temperature specific life history strategies to ensure that spawning occurs at a time that will maximize the incubation and emergence survival of their offspring (Murray and McPhail, 1988; Quinn, 2005). The influence of temperature has been extensively studied, and findings show that temperature can control the timing of upstream migration (Shepherd et al., 1986; Hodgson and Quinn, 2002) and affects the growth rate and development of larval fish (Heming, 1982; Tang et al., 1987; Beecham and Murray, 1990;

Leman, 1993; Killeen et al., 1999; Ojangurgen et al., 1999). In general, mature salmonids in temperate regions can tolerate a wide range of temperatures, but this tolerance is reduced for larval fish during incubation (Humpesch, 1985). The temperature sensitivity of larval fish emphasizes the need to select spawning habitat with a temperature regime conducive to successful incubation.

An additional challenge to salmonid incubation is cold winter temperatures that are associated with interior regions. These environments have winter air temperatures that drop well below freezing and as a result many streams form surface and anchor ice. Anchor ice can be especially detrimental to incubating larval fish, either directly by freezing them, or indirectly by displacing portions of the substrate during intermittent warm temperatures associated with anchor ice movement (Power et al., 1999). To mitigate for this some species select spawning sites associated with warmer water, typically from upwelling groundwater. Hansen (1975) found that brown trout redds associated with groundwater upwelling had higher and less variable hyporheic water temperatures, which resulted in earlier hatching compared to incubation at cooler temperatures. Leman (1993) found that redds influenced by groundwater did not freeze during winter incubation. Baxter and Hauer (2000) found that areas influenced by groundwater upwelling had more stable temperature regimes and had less surface ice and no anchor ice formation. These studies illustrate that there is a benefit to spawning in areas associated with warmer waters, but it should be noted that these sites are also typically associated with lower dissolved oxygen levels. Therefore, a balance must be reached between reducing the chance of ice formation and ensuring appropriate levels of dissolved oxygen for incubating larval fish. The means by which a spawning fish assesses

this balance is unclear, but this study has revealed that temperature appears to be a cue for spawning site selection.

Results of my study show that the linear term for temperature at the 60cm depth had a positive effect on spawning site selection, as indicated by a positive β coefficient and an odds ratio > 1 . The model including temperature at a depth of 60cm in combination with conductivity at 60cm had an ROC value of 0.78 which is indicative of reasonable predictive ability. Confidence intervals for temperature at the 60cm depth, however, did overlap with zero indicating considerable variation of this variable among used and unused sites.

Specific Discharge

Hyporheic flow is typically examined in terms of vertical hydraulic gradient and hydraulic conductivity. Specific discharge provides a means of examining the interacting influence of these two measurements of hyporheic flow. There have been conflicting conclusions drawn in the literature regarding the potential influence of specific discharge on spawning site selection. While substantial evidence outlines the linkage between warmer intragravel temperatures and upwelling flow (Velson, 1987; Beacham and Murray, 1990; Power et al., 1999), the precise effect of flow itself is less clear. Curry and Noakes (1995) conducted a study in a variety of lakes and streams on the Canadian Shield and found that specific discharge did not differ significantly between used and unused brook trout spawning sites, but that in general the unused sites had somewhat lower specific discharge. A study by Baxter and McPhail (1999) on bull trout in the Chowade River watershed (northeastern British Columbia) found that on average unused spawning sites were associated with negative specific discharge and used sites had positive specific discharge. A study by Mull and Wilzbach (2007) examined only vertical hydraulic gradient as a measure of hyporheic

flow and found no significant difference between used and unused sites for coastal coho salmon. It is interesting that the studies conducted in colder snow-dominated regions showed differences in specific discharge between used and unused sites; this may indicate that higher levels of specific discharge are more pertinent to species that spawn in cold regions. This is further supported by higher specific discharge levels at sites used by IFC as opposed to unused sites in McKinley Creek watershed. The ability and mechanism for spawning fish to detect specific discharge are not known; however, it is possible that other physical and chemical features (temperature, dissolved oxygen, and conductivity) of the intragravel environment are used to indirectly access specific discharge.

Specific discharge was found to have a positive effect on IFC spawning site selection as indicated by positive β coefficients and odds ratios >1 . Relatively wide confidence intervals associated with specific discharge in the 3rd and 4th ranked models indicate substantial variability in measurements of this variable. The influence of specific discharge on spawning site selection is supported by the rather high ROC values for models that included specific discharge in combination with conductivity at 60cm depth; ROC values of 0.91 and 0.81 (Table 3-4). The relatively high ROC values and good AIC ranking of models that include specific discharge provide support that this habitat parameter plays a key role in spawning site selection.

Habitat Features in Poorly Ranked Models

Top candidate models were dominated by physical and chemical intragravel features, whereas surface and flow features alone ranked poorly. A possible reason that surface features scored poorly is partially due to the way unused sites were determined in this study. An unused site was chosen based upon its qualitative similarity to used sites. It was reasoned

that purposely selecting unused sites that were outside of typical coho spawning criteria (Groot and Margolis, 1991) would only lead to a superficial assessment of spawning site selection. Rather, this study aimed to examine sites that seemed suitable for spawning and then explored the reasons why some sites were selected while others were not. The means of allocating unused sites may have slightly skewed the results in favour of non-surface variables, but it should be noted that no quantitative measurements were taken prior to selecting an unused site and the only means of ensuring a site was similar to a used sites was based on a coarse qualitative assessment. Used sites on average had slightly negative slopes, higher velocities and were deeper and narrower than unused sites, whereas surface water chemistry was similar for used and unused sites. It is critical to recognize that apparent differences in habitat features between used and unused sites do not necessitate that these features are cues for habitat selection. It is reasoned that only some habitat features are used to differentiate between high and low quality spawning sites, while other features are potentially perceived merely as noise.

Models containing only flow features (vertical hydraulic gradient, hydraulic conductivity, specific discharge, and velocity) ranked poorly in this study unless coupled with a physical or chemical intragravel habitat feature. This suggests that IFC may not use flow as a habitat selection cue, or that IFC are unable to detect specific changes in flow. Alternatively, IFC may use intragravel water chemistry and temperature as an indirect means of accessing hyporheic flow.

Traditional Habitat Model Parameters

Traditional habitat features used to predict spawning site selection (depth, velocity, and a measure of substrate size) have been widely criticized for misclassification of sites, and

more broadly for failing to account for the complexity of habitat selection (Shirvell, 1989; McHugh and Budy, 2004; Mull and Wilzbach, 2007). The traditional model had both a poor AIC ranking (16th out of 20 models), and was at the low end of reasonable predicative ability (ROC value=0.72). These results demonstrate that perhaps the traditional habitat features are not nearly as indicative of suitable habitat as previously thought. Traditional habitat features are likely more a function of logistically simple measurements as opposed to a reflection of critical habitat features.

Results of this study found that on average used sites were at greater depths than unused sites. Although, it is suggested that depth is more a function of fish size (Bjornn and Reiser, 1991; Groot and Margolis, 1991) than an indication of habitat suitability. While it is recognized that a shallow depth would likely result in poor spawning habitat due to the increased risk of freezing or drying up, the modeling results of this study do not indicate that depth is a primary cue for spawning site selection.

Stream velocity at used sites was on average higher than at unused sites, and it was somewhat surprising that the results of this study did not determine this parameter to be a spawning site selection cue. Velocity has traditionally been linked to dissolved oxygen concentrations and the efficiency at which fine sediment and metabolic waste is removed from the incubation environment. While velocity may play an important role in these processes, IFC do not appear to be utilizing this habitat feature as a spawning site selection cue. In a study on steelhead trout (*Salmo gairdneri*) embryos, Coble (1961) found that when velocity varied but oxygen concentrations remain constant there was no survival difference during incubation. Dissolved oxygen, rather than velocity, may be used as a habitat selection

cue. Alternatively, stream velocity at spawning sites may be reflective of fish size and their ability to hold in fast water, rather than an indicator of suitable spawning habitat.

There was little difference in substrate size composition between used and unused sites, and this is likely the main reason that this habitat feature was not identified as a spawning site selection cue for IFC. Substrate size has typically been regarded as an important feature for spawning site selection, but this may not hold true in groundwater fed environments. Sowden and Power (1985) found that the survival of rainbow trout was not related to substrate size in a groundwater-fed stream but rather was primarily influenced by dissolved oxygen concentrations and velocity. Based on these results they suggested that substrate size may not provide a proper indication of the quality of a spawning habitat. Furthermore, studies on brook trout have shown that preferential spawning occurred at silty sites coupled with upwelling rather than at gravel sites without upwelling (Carline, 1980; Witzel and MacCrimmon, 1983).

Traditional habitat features likely contribute to the overall quality of the habitat, but these features have not been identified as cues for IFC. Models with intragravel habitat features had much higher probabilities of being the 'best' model for the prediction of spawning site use. The combined AIC weights of each of the habitat variables showed that conductivity at 60cm had a probability of 0.983 which was higher than any of the other variables. Hyporheic dissolved oxygen (30cm depth), hyporheic temperature, and specific discharge (at depths of 30 and 60cm) had probabilities of 0.296, 0.265, 0.223, and 0.14, respectively. Probabilities for all other habitat features were less than 0.1. My study highlights the need for species and site-specific habitat selection models that provide a more realistic assessment of the influence of habitat features on spawning site selection.

Habitat Selection or Homing?

In the literature it has been proposed that fish actively select specific spawning sites based on habitat characteristics. The findings of this study supports this proposition by outlining apparent differences in IFC used and unused spawning sites. Furthermore, the internal validation of logistic regression models indicated good predictive ability based on habitat features. In contrast to selection based on habitat features, one could argue that spawning site selection can be explained by homing to a microhabitat scale. The spatial scale at which salmon imprint, and at which they home, is largely unknown, but this factor will determine the finest scale at which their populations can be structured. Quinn et al. (2006) present evidence of very fine scale homing in sockeye salmon. Genetic evidence has shown that masu salmon (*Oncorhynchus masou*) have clear genetic structure at the microgeographical scale (21 km) due to precise homing behaviour (Kitanishi et al., 2009). Fine scale homing, however, fails to explain the ability of fish to successfully exploit new habitats (straying). Although fine-scale homing to natal sites has been shown, genetic analysis has often revealed little evidence for restricted gene flow among sites (Stewart et al., 2003). Recently, Walter et al. (2009) suggest that low straying levels may have evolved to favor local adaptation, but low levels of gene flow are important for maintaining genetic variability. Additionally, straying may occur because of habitat perturbations in natal streams. The ability of straying fish to be successful in new habitats, therefore, must be linked to an assessment of habitat suitability, where habitats with specific features are preferentially used. Consequently, habitat selection provides a more comprehensive explanation of spawning site use than homing to a microhabitat scale.

Applicability of study findings

Due to the commonly held notion that “all models are wrong, but some are useful” (Box and Draper, 1987, p.424), it is crucial to recognize that model validation is an ongoing process that requires monitoring and re-adjustment over time. Furthermore, it is essential to realize that modeling is site- and species-specific and extrapolation should not be undertaken outside the range of data for which the model was built. Since model building in this study was undertaken on a relatively small data set and over only one season of data collection, it is advised that results be interpreted as plausible explanations for spawning site selection, rather than a static and definitive identification of critical features. The results from this study may be used as a foundation for further research whereby external data could be used to validate top models to test the applicability of these models more realistically.

Conclusion

This study has revealed that IFC spawning site selection appears to be directly linked to the physical and chemical features of the intragravel environment. Examining the types of disturbances and natural changes that may influence the intragravel environment may provide some insight into possible reproductive success limitations. Various types of resource development have been found to impact groundwater hydrology and chemistry (Barton et al., 1985; Hartman and Scrivener 1990; Curry et al., 1994). The most evident resource activity in the McKinley Creek watershed is forestry. It is recommended that the impacts of current and future forestry resource development be evaluated and thoughtfully considered in the McKinley Creek watershed. In conclusion, it is recommended that research in McKinley Creek continue and further, that habitat assessment studies be conducted on

other populations of IFC to gain a better understanding of the cues associated with spawning site selection.

CHAPTER 4

The Effect of Incubation Environment on Survival and
Growth of Larval Interior Fraser Coho: McKinley
Creek, British Columbia

ABSTRACT

Incubation success of larval fish has been closely linked to incubation habitat features. Specifically, dissolved oxygen, temperature, and intragravel flow can affect survival and growth of larval incubating fish. This study examined interior Fraser coho (*Oncorhynchus kisutch*) in McKinley Creek watershed, British Columbia, to investigate the effect of incubation environment features on survival and growth of larval fish. The objectives were: (1) to compare the physical and chemical features of the incubation environment at used and unused spawning sites, and (2) to compare the survival and growth of larval fish incubated in artificial redds in close proximity to IFC redds, to the survival and growth of larval fish incubated in artificial redds located in areas where no natural spawning had occurred. Stream and hyporheic water chemistry and vertical hydraulic gradient measurements were taken at three time points throughout winter incubation (February, April, and May of 2008). Larval fish, incubating within in-stream artificial redds, were sampled at the same three times throughout incubation to measure survival and growth. Measures of hyporheic temperature, dissolved oxygen, and conductivity consistently differed between used and unused sites throughout the incubation period. Despite differences between used and unused incubation environments the survival and growth of larval fish did not differ between used and unused artificial redds, although survival and growth differed significantly among families of artificially spawned fish. The findings of this study suggest that although some types of incubation environments appear to be selected preferentially over others, this selection does not have a significant influence on the incubation success of larval IFC in McKinley Creek.

INTRODUCTION

Incubation success is of paramount importance to the viability of healthy fish populations because the highest rates of mortality occur during this life stage (Quinn, 2005). Although the importance of this life stage is widely recognized in fisheries research, the specific factors that influence incubation success remain poorly understood. Interior watersheds in British Columbia are a good example: there has been a limited focus on incubation research compared to coastal watersheds (example of coastal bias shown in a review by Richter and Kolmes, 2005), with the exceptions of Cope (1996) and Williamson (2006). In addition, studies that have examined incubation habitat features in relation to larval salmonid success have typically done so in a laboratory or hatchery setting, rather than in-stream environments (Shumway et al., 1964; Murray and McPhail, 1988). While it is recognized that these laboratory studies are useful, it is questionable whether or not their results can provide a realistic evaluation of the factors that affect incubation success within a stream environment.

A variety of habitat features have been linked to the survival and growth of larval salmonids during incubation. Low dissolved oxygen levels reduce survival and growth (Alderdice et al., 1958; Shumway et al., 1964; Davis, 1975; Bjornn and Reiser, 1991; Barton and Taylor, 1996; Malcolm et al., 2003) and have been shown to alter fish morphology (Brannon, 1965). Temperature is closely related to dissolved oxygen levels, such that as temperature increases the percent saturation of dissolved oxygen decreases (Colt, 1984). Temperature also affects larval fish size, growth rate, duration of incubation, and timing of hatch (Alderdice and Velsen, 1978; Heming, 1982; Humpesch, 1985; Tang, 1987; Beacham and Murray, 1990; Rombough, 1997; Ojanguren et al., 1999). Furthermore incubation

temperature tolerances and adaptations have been shown to differ among species of Pacific salmon (Combs, 1965; Murray and McPhail, 1988). Coho salmon, for example, have been found to have the fastest developmental rate (Beacham and Murray, 1990), and the highest survival at low incubation temperatures of Pacific salmon (Murray and McPhail, 1988). Incubation temperature is of particular importance in cold interior watersheds due to the potential formation of anchor ice, which can be especially detrimental to survival and growth of larval fish (Power et al, 1999). Intragravel flow of water in the incubation environment has also been linked to incubation success because sufficient flow is necessary for the transport of oxygen to larval fish and also for the dispersion of metabolic wastes (Silver et al., 1963; Sowden and Power, 1985; Chapman, 1988).

Habitat features that have been found to influence dissolved oxygen, temperature, and intragravel flow include percentage of substrate fines, stream velocity, and amount of riparian cover (Chapman, 1988; Bjornn and Reiser, 1991). Anthropogenic disturbances can also affect these variables. For example, logging activities have been linked to reductions in intragravel flow and dissolved oxygen concentrations and increases in stream and intragravel temperatures (Ringler and Hall, 1975; Platts et al., 1989; Curry et al., 2002). Habitat features that are commonly not included in incubation habitat studies include intragravel pH and conductivity. pH levels outside of species-specific tolerance ranges have been found to interfere with respiration (Haines, 1981), ion regulation (Randall et al., 1982), and have induced mortality in embryos (Daye and Garside, 1980). The effects of intragravel conductivity on larval survival and growth have not been clearly addressed and remain relatively poorly understood.

To better understand the factors influencing incubation success in an interior watershed, the present study examined incubation habitat features and survival and growth of larval interior Fraser Coho (IFC) in McKinley Creek watershed, British Columbia. Fertilized IFC eggs were placed within in-stream artificial redds located in areas that were representative of typical spawning sites (used sites), and sites that were representative of seemingly suitable sites but where no natural spawning had occurred (unused sites). The objectives of this study were to (1) compare the physical and chemical features of the incubation environment at used and unused sites; and (2) compare the survival and growth of larval fish that incubated in ‘used’ and ‘unused’ artificial redds. This study will contribute to a more comprehensive understanding of factors that influence the success of IFC populations, and furthermore provide insight into in-stream growth and development of larval fish in interior watersheds.

MATERIALS AND METHODS

Incubation Environment Measurements

Monitoring over the 2007 and 2008 incubation periods was undertaken at the used and unused sites identified in Chapter 3. Dissolved oxygen, pH, conductivity, and temperature of the stream and hyporheic water (at both 30 and 60cm depth) as well as vertical hydraulic gradient were measured at three time points throughout the incubation period (January, Early March, Late March in 2007; February, April, and May 2008) using the same equipment and methodology as described in Chapter 3. To obtain a relatively continuous measure of hyporheic water temperature, data loggers (HOBO U22 Pro. v2) were buried at a depth of approximately 25cm at used and unused sites. These loggers measured

the temperature of the hyporheic water hourly throughout the incubation period. Hourly temperature data are only available for the sites identified in the fall of 2007.

Survival and Growth of Larval Fish in Artificial Redds

In the fall of 2007 survival and growth of IFC throughout the incubation period was determined using a field incubation experiment. Six sites in McKinley Creek were chosen to represent used and unused IFC spawning sites. Three sites were defined as *used* because they were close (<2m) to IFC redds. The remaining three sites were defined as *unused* because they appeared suitable for spawning but lacked any evidence of IFC redds in close proximity (>20m). Each artificial redd was purposefully constructed to provide an incubation environment that would be similar to a natural redd and also meet logistical sampling needs. To meet this goal each artificial redd had two egg pockets (25cm depth) that were approximately half a metre apart, and a downstream tailspin region.

Five mature IFC were intercepted at the McKinley Creek enumeration fence and transported to the Quesnel River Research Centre in Likely, British Columbia, where they were placed in circular tanks and monitored until the females were ripe (approximately one week). When the females were determined to be ripe, two males and three females were sacrificed and their gametes were extracted and stored separately in clean containers. The approximate number of eggs from each female was calculated based on the weight of a sample of 10ml of eggs from each individual (Fecundities: Female 1= 2783, Female 2=1277, and Female 3= 932). Individual egg weights from each female were 0.19 mg (Female 1), 0.14 mg (Female 2), and 0.17 mg (Female 3). Gametes were transported to McKinley Creek where eggs and milt were combined by hand to make three separate families; *Family 1*:

Female 1 x Male 2; *Family 2*: Female 2 x Male 1; and *Family 3*: Female 3 x Male 1. After approximately two minutes, stream water was added to the fertilized eggs and the containers were left undisturbed for one hour. Then approximately 30 fertilized eggs from each family were placed in capsules that were partially filled with gravel from McKinley Creek. The capsules were cylindrical in shape and made of perforated extruded food-grade polyethylene tubing with perforated polyethylene caps (T-series CAPLUG®). Capsules used in this study followed the design described by Williamson (2006).

Six capsules from each family were buried at a depth of approximately 25cm in all of the artificial redds within three hours of fertilization. The number of capsules used in this study (total = 36 capsules) enabled collection of two capsules from each family per artificial redd at three time points throughout incubation. In each artificial redd, the capsules were clustered into six groups (three in each egg pocket) and contained a capsule from each family. A coloured wire attached to each capsule was tied to a piece of rebar that was inserted into the streambed upstream of each group. This allowed for a simple and relatively low disturbance sampling procedure whereby two pieces of rebar (and their associated capsules) were pulled out of the substrate from each artificial redd during each collection period.

Capsules were collected in February, April, and May of 2008. After each capsule collection period, the larval fish were removed from the capsules and placed individually into plastic centrifuge tubes and frozen on dry ice for transportation to the University of Northern British Columbia. Survival and hatch were enumerated for each capsule. Standard length and weight of the somatic tissue and yolk were measured in the laboratory for a subset of larval fish from each capsule. The subset individuals (a maximum of ten larval fish per

capsule; mean eggs/capsule for each family were: Family 1 = 8.7, Family 2 = 6.7, Family 3 = 5.6) were chosen haphazardly by removing larval fish tubes one at a time from a bag containing all individuals from that capsule. Low subset values for family 2 and 3 were due to low survival of larval fish in these families. The standard length of each larval fish was measured with digital calipers (Mitutoyo Absolute IP66) using a dissection microscope. The somatic tissue was removed from the yolk material and each tissue was weighed separately. After wet weights were determined, somatic tissue and yolk were placed in a drying oven at 60°C for 24 hours, after which the samples were measured again to determine dry weight.

DATA ANALYSIS

A linear mixed effect model with a random effect for location was used to test for difference between the physical and chemical features of used and unused study sites during the 2008 incubation period. Location refers to where a site was situated in the lower 6kms or upper 6kms of McKinley Creek study area (see Figure 3-2); this factor was included as a random effect because temperature differed between these portions of the Creek. Residual plots were examined to ensure that the assumptions of normality and equal variance were met. No statistical analysis was performed on the 2007 incubation data due to small sample sizes, but these data have been graphically presented for comparison to the 2008 data. The accumulated thermal units (ATUs) for used and unused study sites were calculated by cumulatively adding an average daily temperature for used and unused sites respectively over the course of the 2008 incubation period. ATUs and daily mean temperatures were calculated for all study sites as well as artificial redds from December 1st-April 30th. The end date for this time period was purposefully selected before freshet to prevent loss of loggers

during high flows. A linear mixed effect model with a random effect for location was also used to test for difference in ATUs and daily mean temperatures between used and unused sites.

A linear mixed effect model with a random effect for family was used to test for differences in survival percentage, hatch percentage, standard length, somatic tissue dry weight, and yolk dry weight of larval fish at used and unused sites. Analysis of Variance (ANOVA) was used to test for differences in survival percentage, hatch percentage, standard length, somatic tissue dry weight, and yolk dry weight among families of artificially spawned fish. Residual plots were examined to ensure that the assumptions of normality and equal variance were met. Tukey tests were used to test for differences among individual families when ANOVA results indicated a significant difference in family for a given survival or growth parameter. Descriptive statistics of the habitat features monitored at artificial redds were presented to examine trends and to compare these trends to habitat features of used and unused study sites.

RESULTS

Incubation Environment Measurements

Used and Unused Study Sites

Habitat features at used and unused sites measured throughout the 2007 and 2008 incubation periods are shown in Figure 4-1 (dissolved oxygen), Figure 4-2 (temperature), Figure 4-3 (vertical hydraulic gradient), Figure 4-4 (conductivity), and Figure 4-5 (pH). Only 12 incubation sites were monitored in 2007 (8 used and 4 unused). In general, the unused sites in 2007 were associated with lower hyporheic dissolved oxygen, higher surface

and hyporheic temperatures, lower vertical hydraulic gradient (with the exception of the late March collection), higher hyporheic conductivity, and lower pH (with the exception of the January collection) than used sites.

A more robust examination of habitat features throughout the incubation period was possible with a larger sample size in 2008. The sample sizes were 27 (16 used; 11 unused), 37 (23 used; 14 unused), and 42 (26 used; 16 unused) for collections in February, April, and May respectively. The variability in the sample size throughout these collections was dependent on logistical constraints due to the abundance of surface ice cover. The first data collection in February found that used sites had higher stream dissolved oxygen ($p < 0.001$, $F = 19.262$, $df = 1, 26$), higher hyporheic dissolved oxygen at 30cm depth ($p = 0.038$, $F = 4.800$, $df = 1, 26$) (Figure 4-1), and lower hyporheic conductivity at 30cm depth ($p = 0.015$, $F = 6.866$, $df = 1, 26$) (Figure 4-4) than unused sites. The second data collection in April found that used sites had lower hyporheic conductivity at 30cm ($p = 0.021$, $F = 5.869$, $df = 1, 36$) and 60cm ($p < 0.001$, $F = 20.579$, $df = 1, 36$) depths than unused sites (Figure 4-4). The final data collection in May was conducted immediately prior to freshet, and found a number of differences between used and unused sites. Results from the May collection indicate that prior to emergence used sites had higher levels of dissolved oxygen (surface: $p = 0.013$, $F = 6.796$, $df = 1, 41$; 30cm depth: $p < 0.001$, $F = 13.636$, $df = 1, 41$; 60cm depth: $p = 0.004$, $F = 9.425$, $df = 1, 41$), lower levels of hyporheic conductivity (30cm: $p < 0.001$, $F = 18.792$, $df = 1, 41$; 60cm: $p < 0.001$, $F = 25.842$, $df = 1, 41$), cooler hyporheic temperature at 60cm depth ($p = 0.012$, $F = 6.880$, $df = 1, 41$) (Figure 4-2), and higher hyporheic pH at the 30cm depth ($p = 0.010$, $F = 7.415$, $df = 1, 41$) (Figure 4-5) than unused sites. Vertical hydraulic gradient did not differ between used and unused sites during any sampling collections (Figure 4-3).

Accumulated thermal units and mean daily temperatures for used and unused sites were calculated from December 1st-April 30th 2008 (Figure 4-6; Figure 4-7). Mean daily hyporheic temperatures at unused sites were significantly higher than used sites ($p=0.011$, 6.411 , $df=1, 23$). Accumulated thermal units (ATUs) for used and unused sites also demonstrated that unused sites were significantly warmer ($p<0.001$, $F=23.982$, $df=1, 23$). The mean total ATUs for used and unused were $158\text{ }^{\circ}\text{C}$ and $201\text{ }^{\circ}\text{C}$ respectively on April 30th.

DISSOLVED OXYGEN

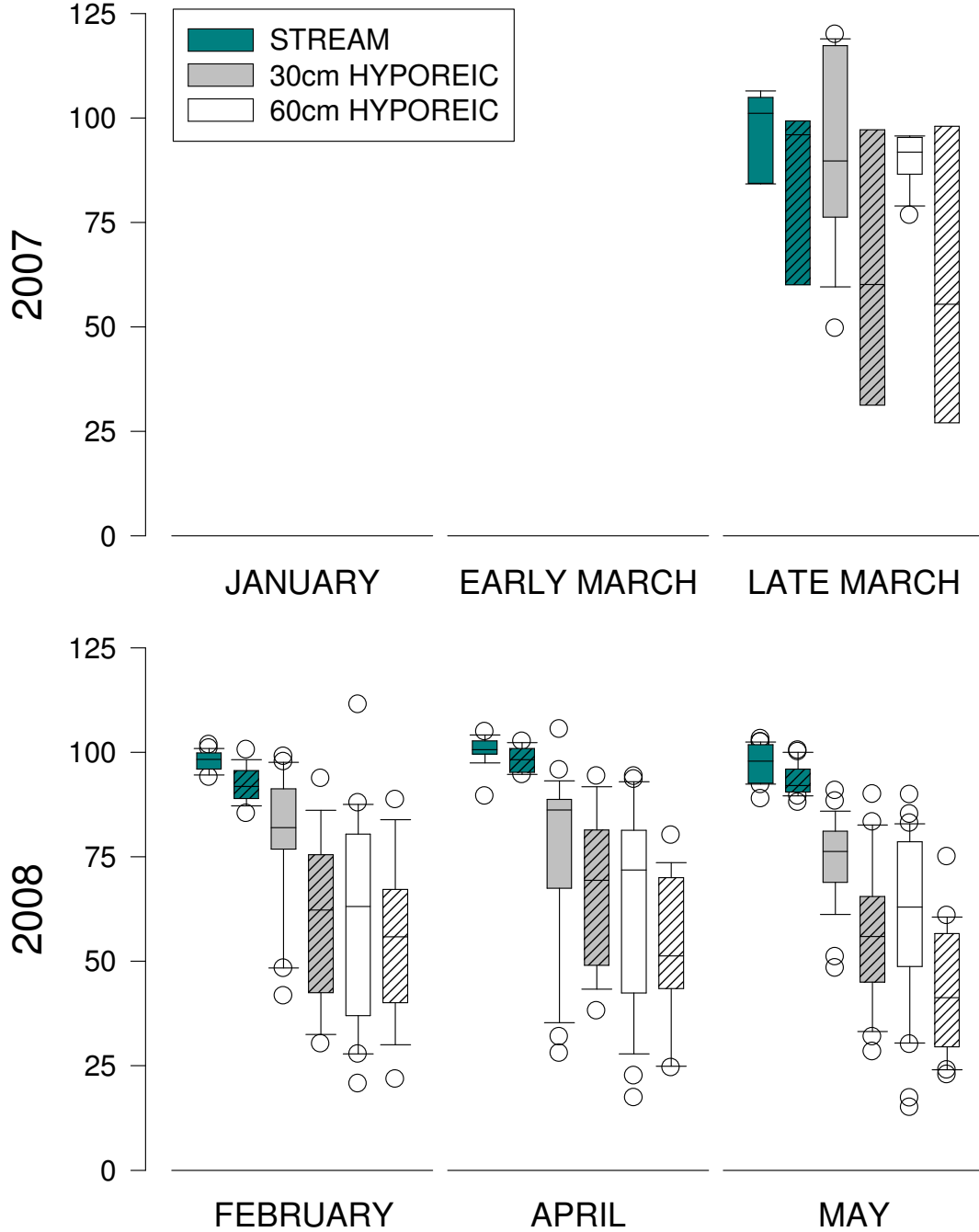


Figure 4-1: Comparison of dissolved oxygen (% saturation) measured at used and unused sites throughout the 2007 and 2008 incubation periods for interior Fraser coho in McKinley Creek watershed. Used sites are represented by the clear boxes and unused sites are represented by the dashed boxes (February: used n=16, unused n=11; April used n=23, unused n=14; May used n=26, unused n=16).

TEMPERATURE

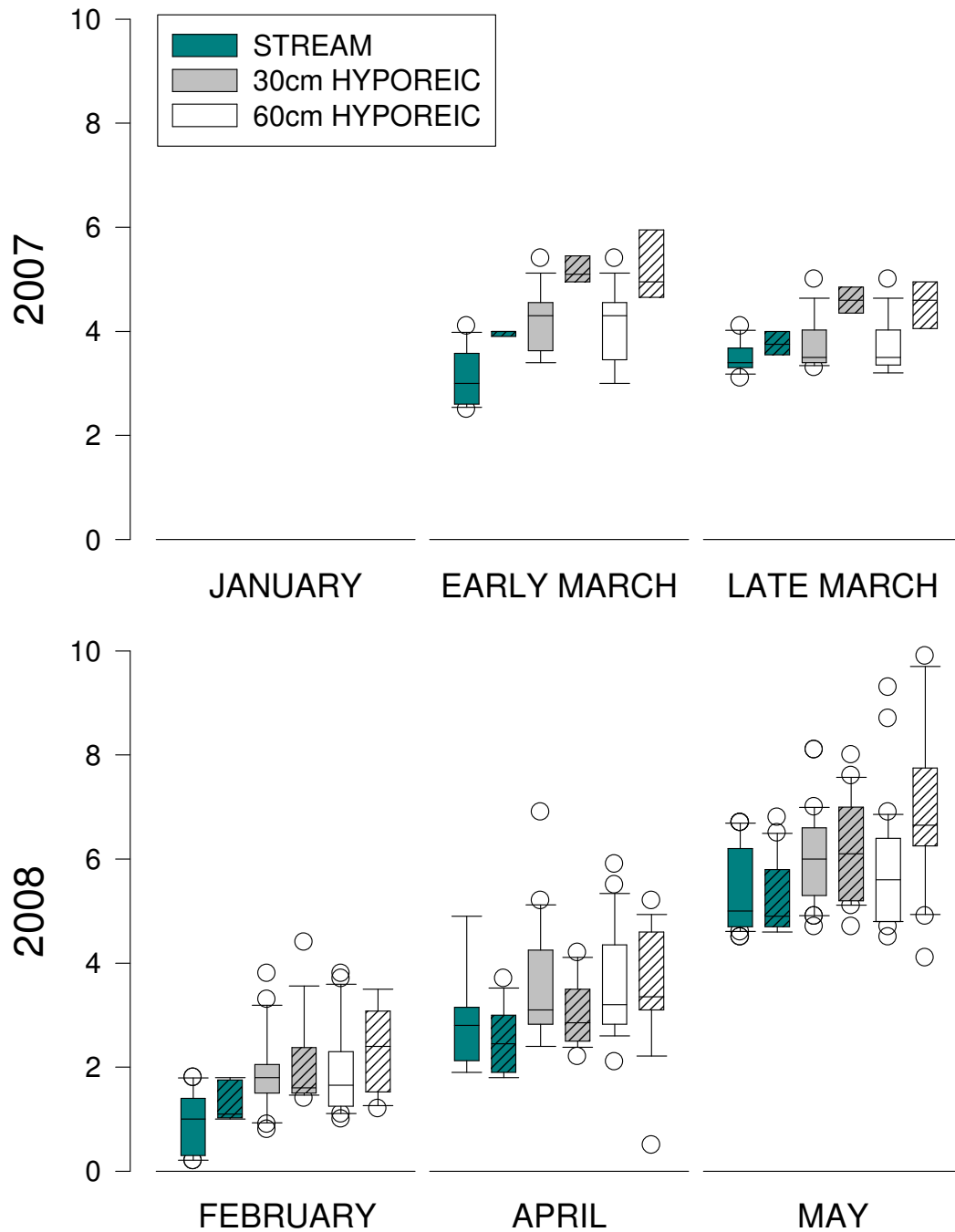


Figure 4-2: Comparison of stream and hyporheic temperature ($^{\circ}\text{C}$) measured at used and unused sites throughout the 2007 and 2008 incubation periods for interior Fraser coho in McKinley Creek watershed. Used sites are represented by the clear boxes and unused sites are represented by the dashed boxes (February: used $n=16$, unused $n=11$; April used $n=23$, unused $n=14$; May used $n=26$, unused $n=16$).

VERTICAL HYDRAULIC GRADIENT

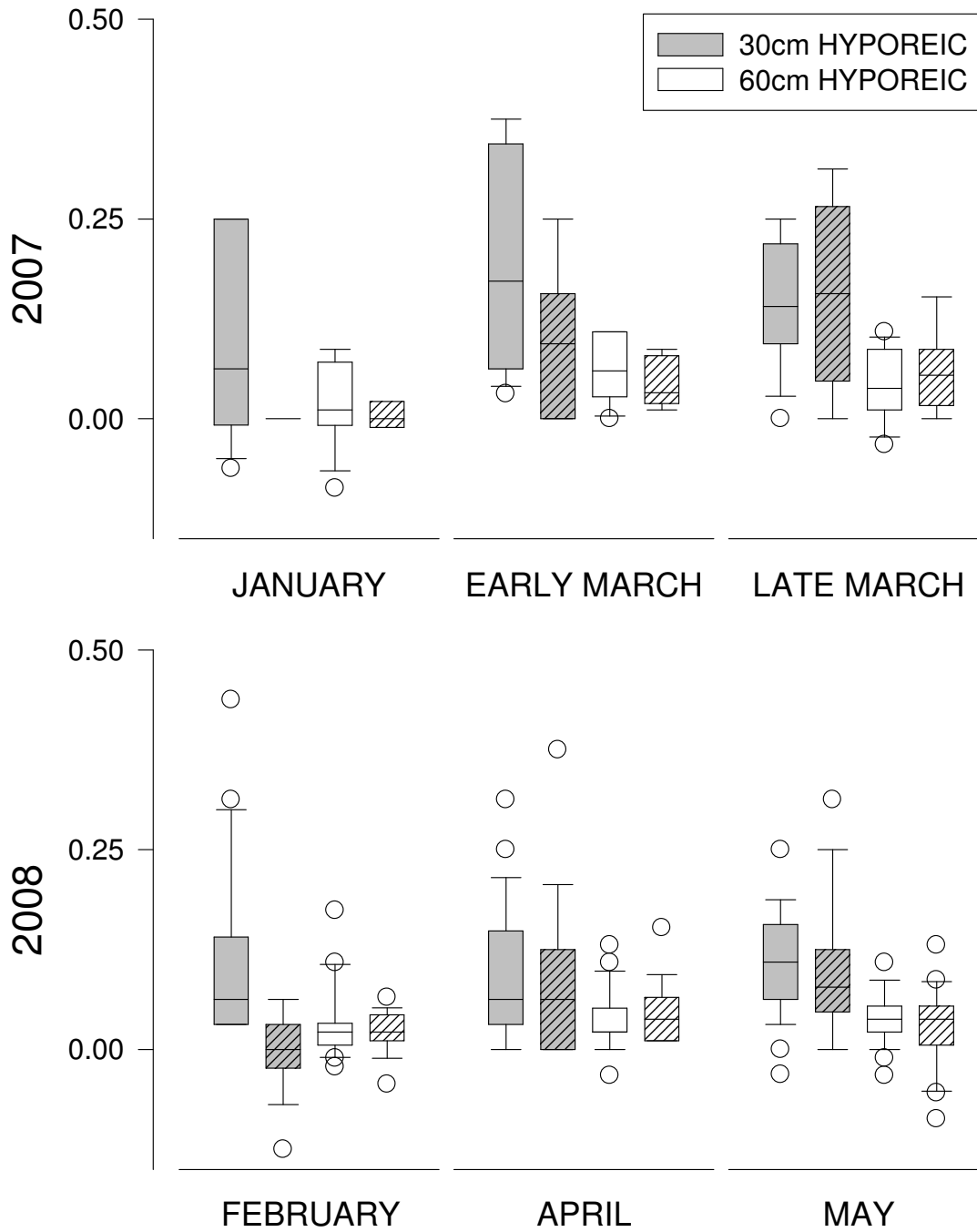


Figure 4-3: Comparison of vertical hydraulic gradient measured at used and unused sites throughout the 2007 and 2008 incubation periods for interior Fraser coho in McKinley Creek watershed. Used sites are represented by the clear boxes and unused sites are represented by the dashed boxes (February: used n=16, unused n=11; April used n=23, unused n=14; May used n=26, unused n=16).

CONDUCTIVITY

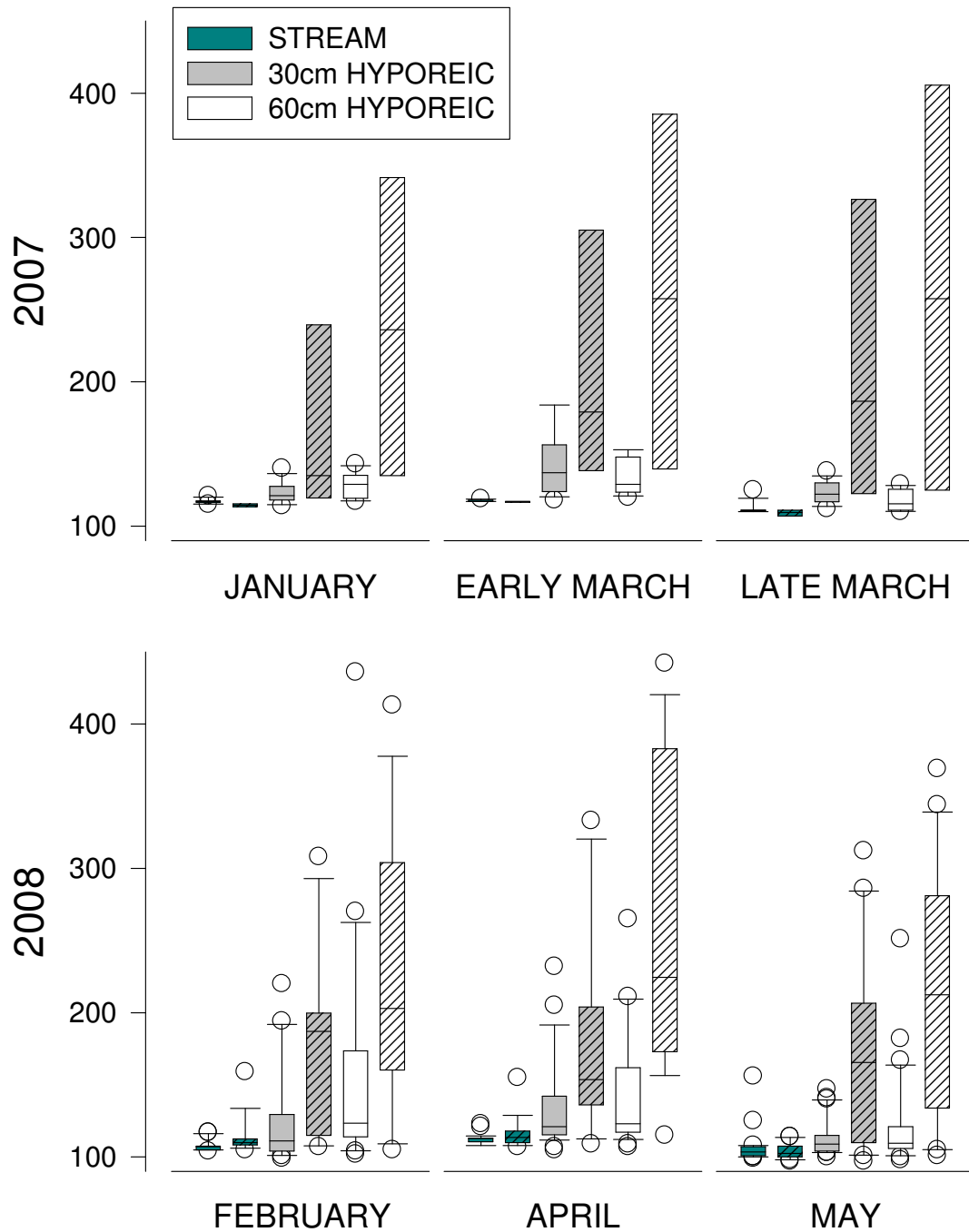


Figure 4-4: Comparison of conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) measured at used and unused sites throughout the 2007 and 2008 incubation periods for interior Fraser coho in McKinley Creek watershed. Used sites are represented by the clear boxes and unused sites are represented by the dashed boxes (February: used $n=16$, unused $n=11$; April used $n=23$, unused $n=14$; May used $n=26$, unused $n=16$).

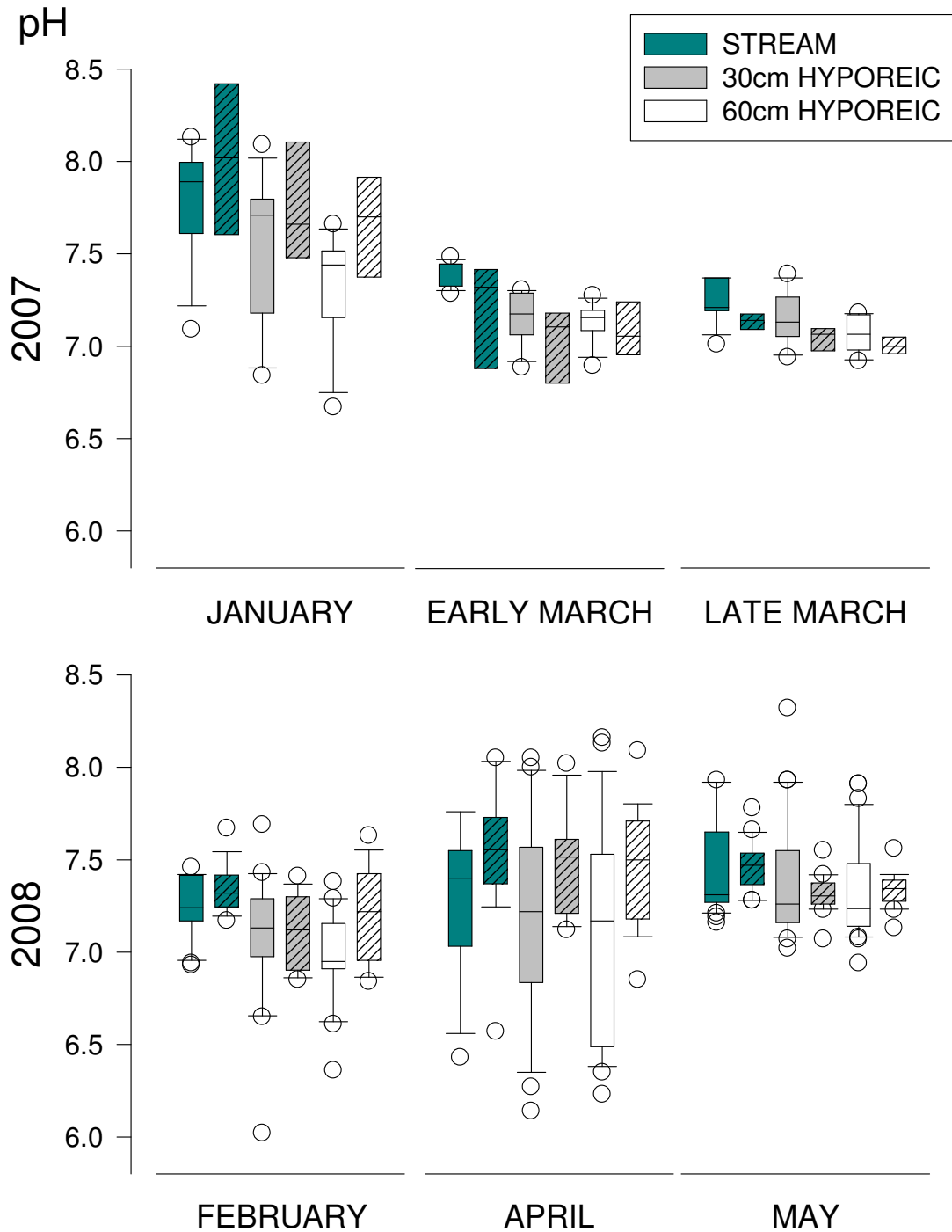


Figure 4-5: Comparison of pH measured at used and unused sites throughout the 2007 and 2008 incubation periods for interior Fraser coho in McKinley Creek watershed. Used sites are represented by the clear boxes and unused sites are represented by the dashed boxes (February: used $n=16$, unused $n=11$; April used $n=23$, unused $n=14$; May used $n=26$, unused $n=16$).

TEMPERATURE

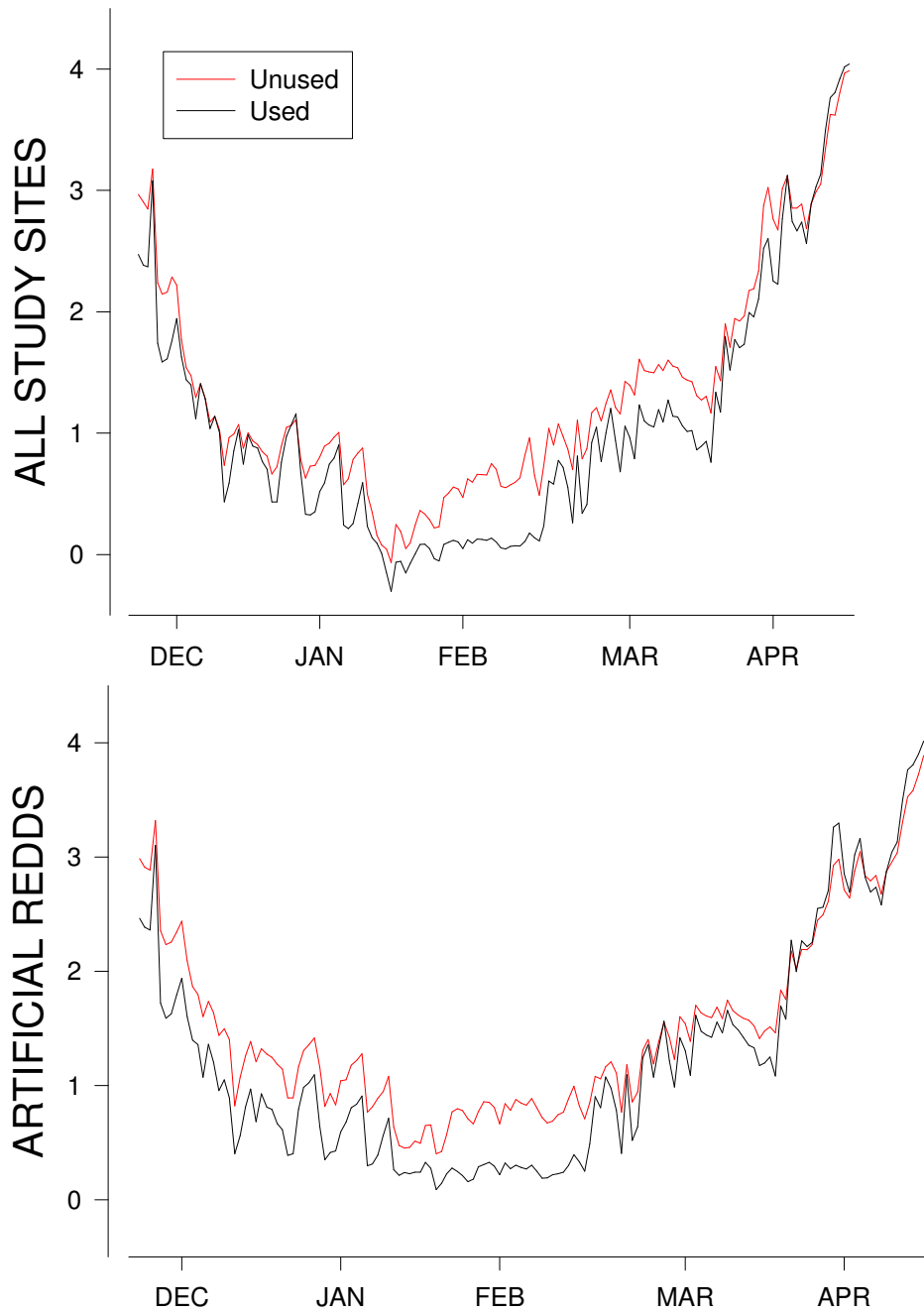


Figure 4-6: Mean daily temperatures ($^{\circ}\text{C}$) at used ($n=13$) and unused ($n=11$) study sites compared to used ($n=3$) and unused ($n=3$) artificial redd sites measured throughout the incubation period for interior Fraser coho in McKinley Creek watershed (December 1- April 30, 2008).

TEMPERATURE

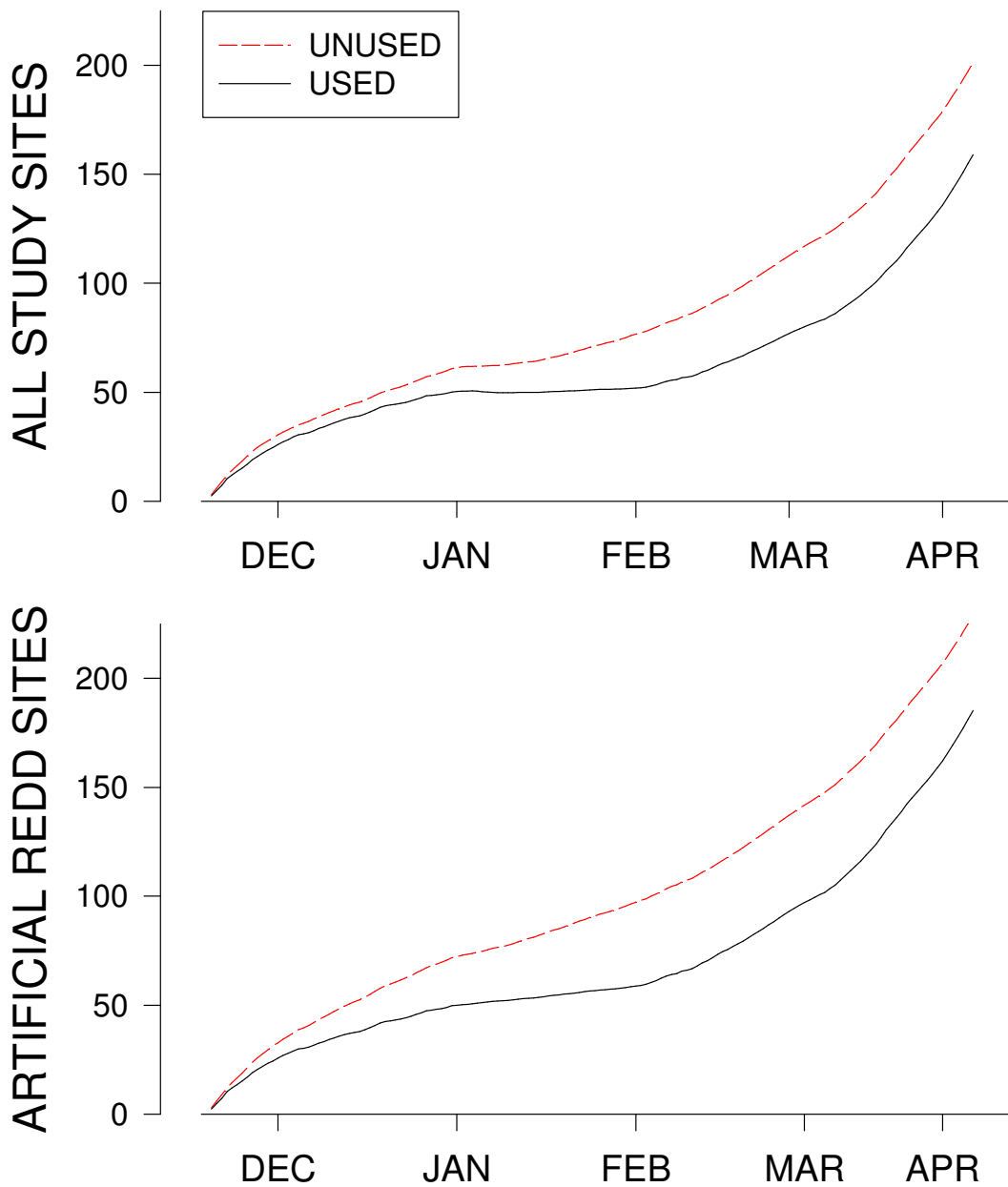


Figure 4-7: Accumulated thermal units ($^{\circ}\text{C}$) at used ($n=13$) and unused ($n=11$) study sites compared to used ($n=3$) and unused ($n=3$) artificial redd sites measured throughout the incubation period for interior Fraser coho in McKinley Creek watershed (December 1- April 30, 2008).

Artificial Redds

A summary of the habitat features measured at artificial redds compared to all used and unused study sites is presented in Table 4-1. These data indicate that, with the exception of hyporheic conductivity at the 30cm depth, trends over the incubation period were similar for artificial redds and used and unused study sites. In general the artificial redds were representative of conditions for used and unused sites in McKinley Creek. No statistical analysis was performed on the habitat monitoring data, with the exception of temperature, for artificial redds due to the small sample size. Mean daily hyporheic temperatures were significantly warmer at unused artificial redds compared to used artificial redds ($p=0.0067$, $F=7.443$, $df=1, 5$) (Figure 4-6). Accumulated thermal units at unused artificial redds were also significantly greater than used artificial redds ($p<0.0001$, $F=31.469$, $df=1, 5$) (Figure 4-7). The mean total ATUs for used and unused artificial redds were 185°C and 229°C respectively on April 30th.

Survival and Growth of Larval Fish in Artificial Redds

The survival and growth of larval fish were compared between used and unused artificial redd sites as well as among families of artificially spawned fish. Percentage survival (Figure 4-8), percentage hatch (Figure 4-9), standard length (Figure 4-10), dry somatic tissue weight (Figure 4-11), and dry yolk weight (Figure 4-12) are presented for each collection period. No significant differences were found between used and unused sites for any variable. Table 4-2 summarizes the means and standard error of each survival and growth variable for used and unused sites throughout the incubation period.

Significant differences were found between families for percentage survival (February: $p < 0.001$, $F = 10.159$, $df = 2, 312$; April: $p = 0.001$, $F = 8.357$, $df = 2, 267$; May: $p = 0.003$, $F = 6.907$, $df = 2, 185$), somatic weight (February: $p = 0.001$, $F = 6.868$, $df = 2, 312$; April: $p = 0.001$, $F = 7.000$, $df = 2, 267$; May: $p < 0.001$, $F = 14.050$, $df = 2, 185$), yolk weight (February: $p < 0.001$, $F = 338.21$, $df = 2, 312$; April: $p < 0.001$, $F = 178.57$, $df = 2, 267$; May: $p < 0.001$, $F = 105.87$, $df = 2, 185$), and standard length (February: $p < 0.001$, $F = 15.018$, $df = 2, 312$; May: $p < 0.001$, $F = 24.672$, $df = 2, 185$). No significant differences were found between families for hatch percentage. Table 4-3 summarizes survival and growth parameters throughout the incubation period for each family. Results of Tukey tests (Table 4-4) indicated that the survival and growth for Families 2 and 3 were rarely significantly different from one another; whereas these families typically differed significantly from Family 1.

SURVIVAL

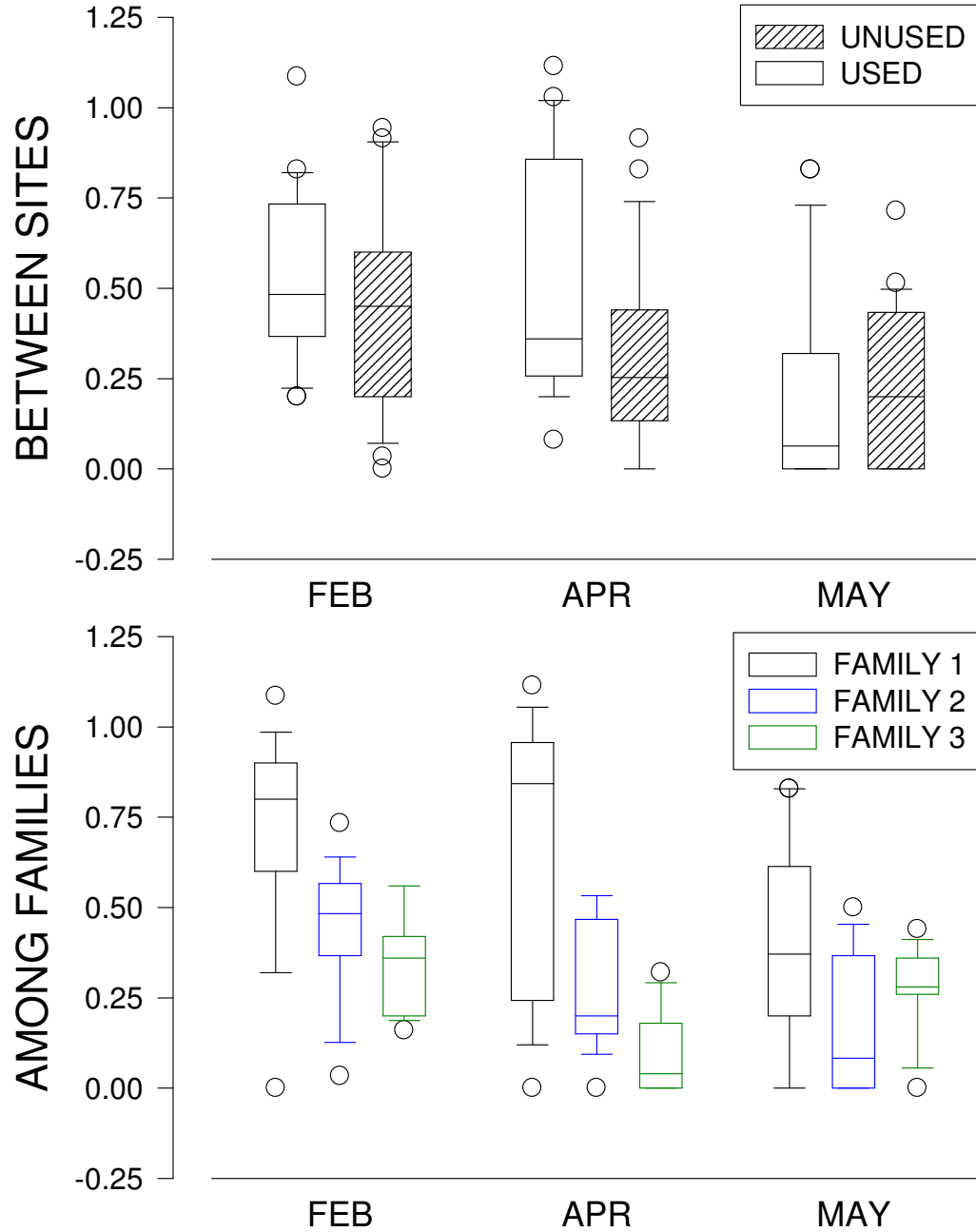


Figure 4-8: Percentage survival for larval interior Fraser coho collected from artificial redds in McKinley Creek watershed; comparison between used and unused sites (top), and comparison among families (bottom).

PERCENTAGE HATCH

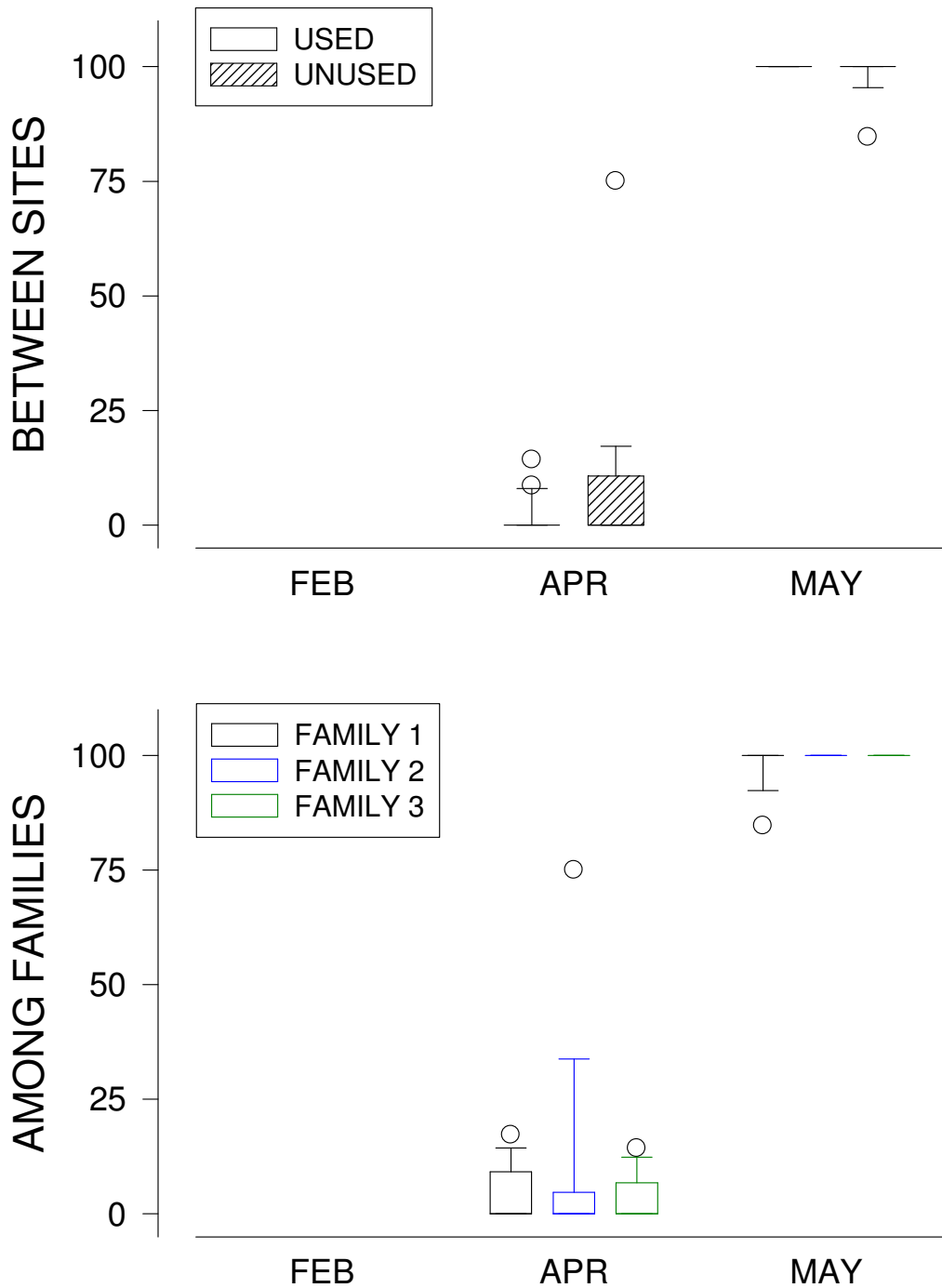


Figure 4-9: Percentage hatch of larval interior Fraser coho collected from artificial redds in McKinley Creek watershed; comparison between used and unused sites (top), and comparison among families (bottom). (April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family 3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family 3 n=32).

STANDARD LENGTH

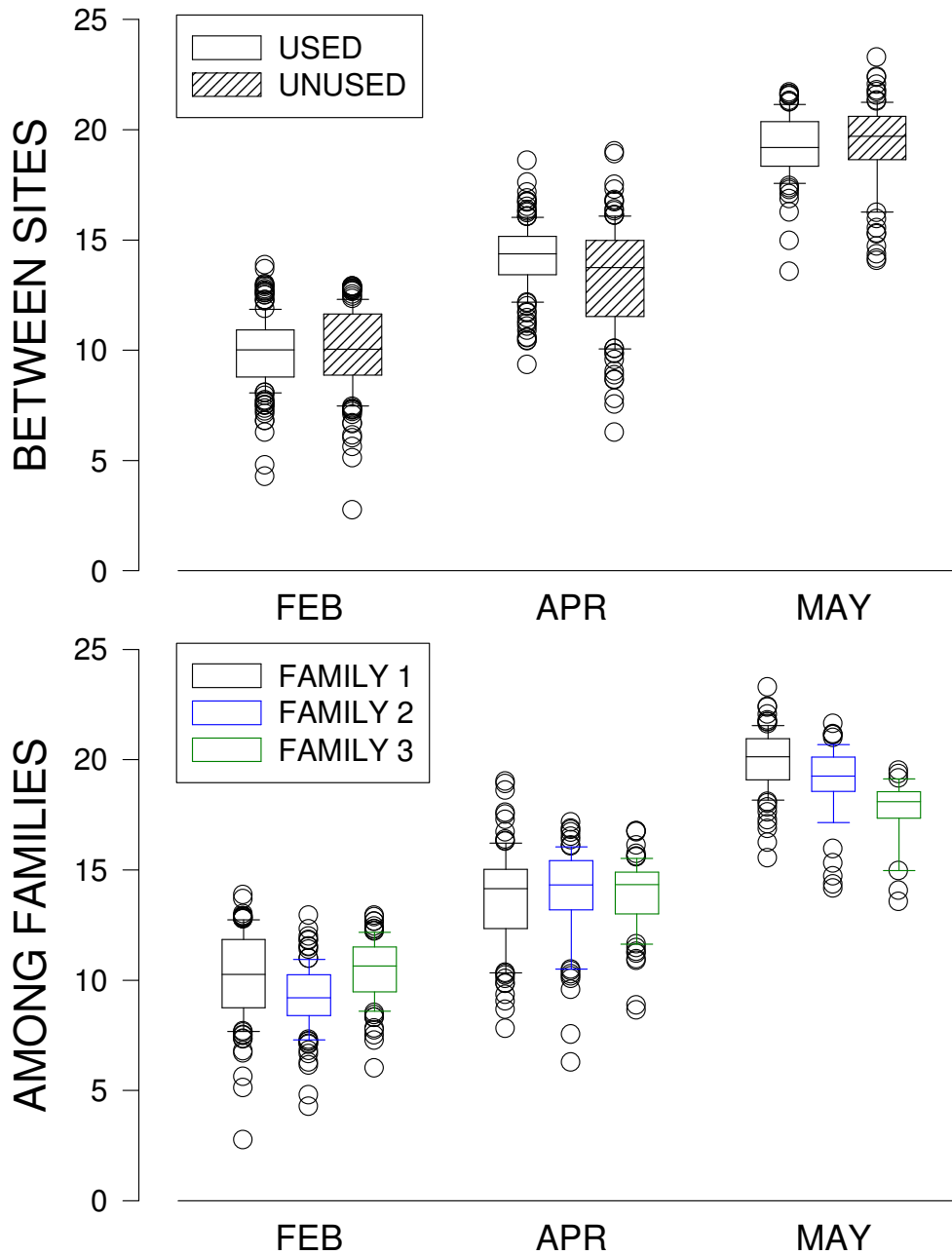


Figure 4-10: Standard lengths (mm) for larval interior Fraser coho collected from artificial redds in McKinley Creek watershed; comparison between used and unused sites (top), and comparison among families (bottom). (February: used n=145, unused n=167, Family1 n=112, Family2 n=106, Family 3 n=94; April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family 3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family 3 n=32).

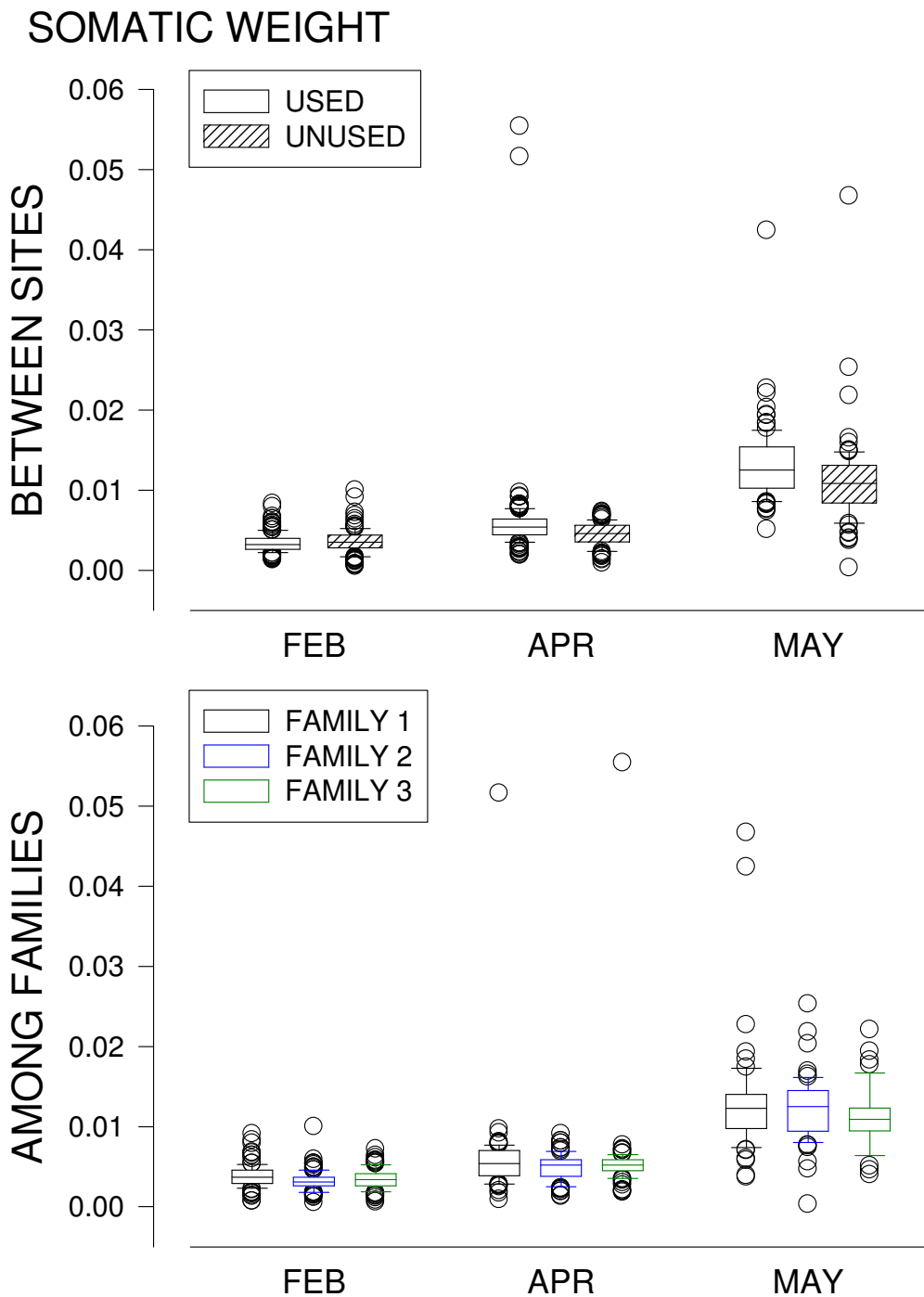


Figure 4-11: Dry somatic weight (g) for larval interior Fraser coho collected from artificial redds in McKinley Creek watershed; comparison between used and unused sites (top), and comparison among families (bottom). (February: used n=145, unused n=167, Family1 n=112, Family2 n=106, Family 3 n=94; April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family 3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family 3 n=32).

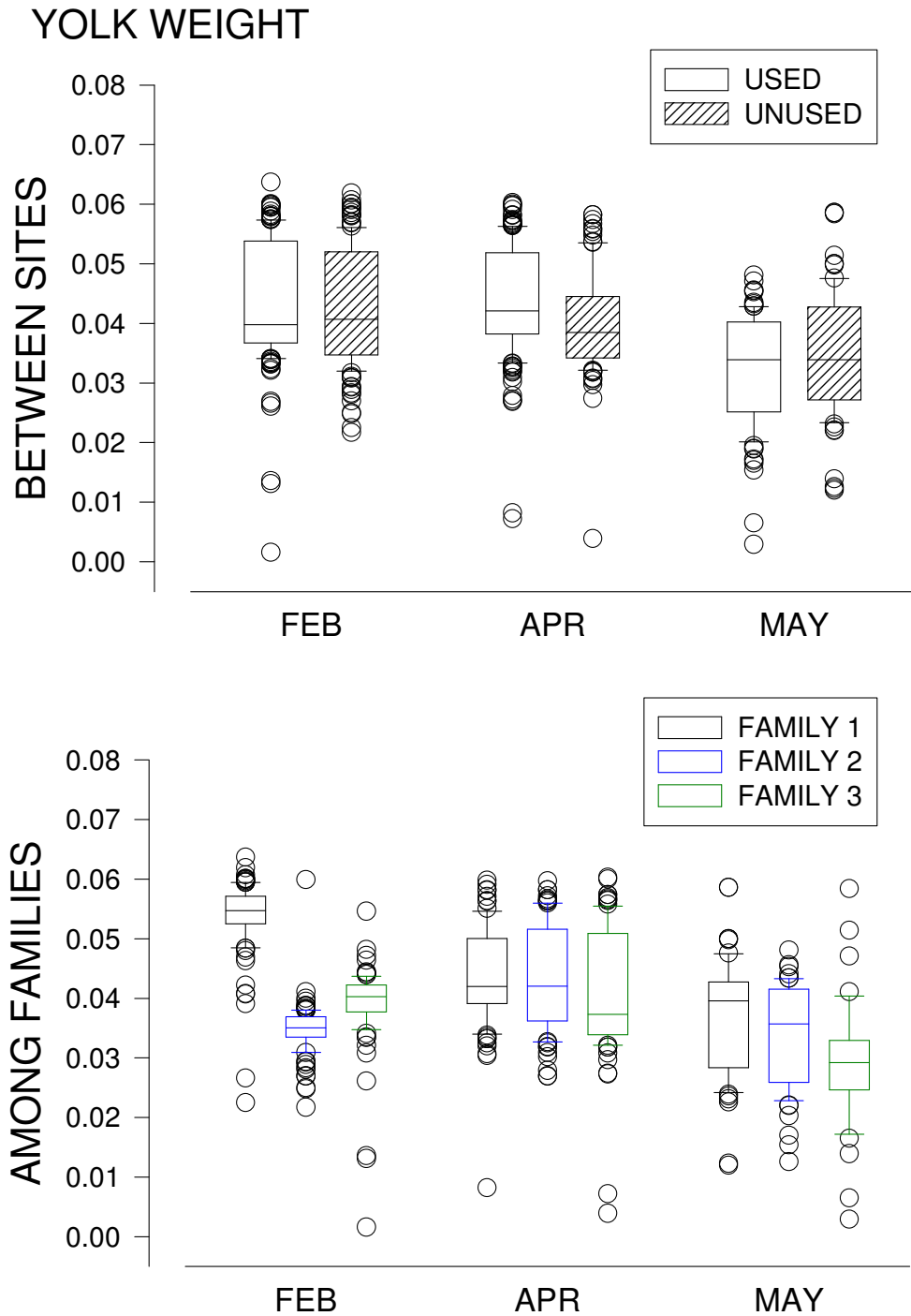


Figure 4-12: Dry yolk weight (g) for larval interior Fraser coho collected from artificial redds in McKinley Creek watershed; comparison between used and unused sites (top), and comparison among families (bottom). (February: used n=145, unused n=167, Family1 n=112, Family2 n=106, Family 3 n=94; April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family 3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family 3 n=32).

Table 4-1: Means and standard errors of habitat features at used and unused sites (normal font) compared to artificial redds (in parentheses, bold font) (February: used n=16, unused n=11; April used n=23, unused n=14; May used n=26, unused n=16).

	Collection 1 (February)		Collection 2 (April)		Collection 3 (May)	
	Used	Unused	Used	Unused	Used	Unused
Dissolved Oxygen (stream)	97.8 ± 0.7 (97.8 ± 1.6)	93.0 ± 1.4 (96.9 ± 1.2)	100 ± 0.7 (100 ± 1.7)	98.8 ± 0.9 (99.8 ± 1.1)	97.8 ± 0.9 (98.7 ± 3.1)	94.1 ± 1.0 (95.7 ± 3.2)
Dissolved Oxygen (30cm)	78.9 ± 4.4 (78.0 ± 23.0)	62.0 ± 6.2 (61.6 ± 12.1)	76.4 ± 4.4 (74.6 ± 18.2)	65.8 ± 5.6 (59.1 ± 13.8)	73.1 ± 2.3 (70.8 ± 7.8)	55.7 ± 4.8 (48.5 ± 5.5)
Dissolved Oxygen (60cm)	59.9 ± 6.4 (93.1 ± 10.5)	56.0 ± 7.1 (41.5 ± 14.8)	62.5 ± 5.0 (75.5 ± 17.3)	53.8 ± 4.8 (48.2 ± 19.6)	59.2 ± 4.1 (64.0 ± 7.2)	42.5 ± 3.8 (38.3 ± 13.0)
Temperature (stream)	0.9 ± 0.15 (0.43 ± 0.23)	1.3 ± 0.13 (1.3 ± 0.40)	2.9 ± 0.23 (2.2 ± 0.30)	2.4 ± 0.17 (2.6 ± 0.32)	5.5 ± 0.16 (5.3 ± 0.60)	5.3 ± 0.19 (5.2 ± 0.38)
Temperature (30cm)	1.9 ± 0.22 (1.5 ± 0.07)	2.0 ± 0.27 (1.3 ± 0.52)	3.6 ± 0.24 (3.9 ± 1.50)	3.0 ± 0.17 (2.8 ± 0.37)	6.0 ± 0.18 (5.9 ± 0.29)	6.2 ± 0.24 (5.7 ± 0.16)
Temperature (60cm)	0.9 ± 0.15 (1.6 ± 0.42)	2.2 ± 0.25 (1.3 ± 0.45)	3.6 ± 0.23 (2.8 ± 0.27)	3.5 ± 0.33 (3.9 ± 1.39)	5.8 ± 0.22 (5.4 ± 0.26)	7.0 ± 0.43 (5.4 ± 0.38)
Conductivity (stream)	107 ± 0.95 (107 ± 0)	114 ± 4.34 (108 ± 0.58)	112 ± 0.71 (112 ± 0.35)	118 ± 3.77 (115 ± 5.02)	106 ± 2.10 (104 ± 1.85)	104 ± 1.20 (104 ± 1.44)
Conductivity (30cm)	127 ± 9.08 (150 ± 20.96)	171 ± 20.14 (111 ± 1.21)	137 ± 7.15 (168 ± 22.57)	178 ± 22.16 (116 ± 3.87)	113 ± 2.57 (115 ± 3.87)	164 ± 16.83 (130 ± 10.16)
Conductivity (60cm)	161 ± 21.38 (119 ± 6.64)	234 ± 31.27 (175 ± 39.61)	142 ± 8.22 (174 ± 27.08)	269 ± 31.03 (192 ± 4.62)	120 ± 6.10 (122 ± 5.60)	216 ± 21.58 (176 ± 41.40)
pH (stream)	7.26 ± 0.04 (7.35 ± 0.12)	7.34 ± 0.04 (7.16 ± 0.07)	7.27 ± 8.13 (7.30 ± 0.02)	7.53 ± 0.09 (7.31 ± 0.16)	7.44 ± 0.05 (7.49 ± 0.21)	7.48 ± 0.04 (7.68 ± 0.24)
pH (30cm)	7.07 ± 0.10 (6.90 ± 0.32)	7.09 ± 0.06 (6.96 ± 0.14)	7.18 ± 0.12 (7.12 ± 0.45)	7.44 ± 0.07 (7.00 ± 0.27)	7.40 ± 0.06 (7.28 ± 0.14)	7.33 ± 0.03 (7.50 ± 0.22)
pH (60cm)	6.97 ± 0.07 (7.03 ± 0.33)	7.19 ± 0.08 (6.96 ± 0.17)	7.11 ± 0.12 (6.91 ± 0.32)	7.48 ± 0.09 (6.97 ± 0.28)	7.31 ± 0.05 (7.42 ± 0.23)	7.34 ± 0.02 (7.47 ± 0.15)
Vertical Hydraulic Gradient (30cm)	0.094 ± 0.037 (0.104 ± 0.038)	0.017 ± 0.020 (0.115 ± 0.021)	0.093 ± 0.018 (0.150 ± 0.055)	0.077 ± 0.029 (0.041 ± 0.021)	0.098 ± 0.014 (0.093 ± 0.018)	0.098 ± 0.030 (0.041 ± 0.055)
Vertical Hydraulic Gradient (60cm)	0.033 ± 0.013 (0.083 ± 0.036)	0.017 ± 0.009 (0 ± 0.017)	0.035 ± 0.008 (0.025 ± 0.013)	0.043 ± 0.011 (0.032 ± 0.013)	0.039 ± 0.008 (0.043 ± 0)	0.026 ± 0.013 (0.033 ± 0.058)

Table 4-2: Summary of the means and standard errors of survival and growth measurements for interior Fraser coho collected throughout winter incubation for used and unused artificial redds in McKinley Creek watershed. (February: used n=145, unused n=167, Family1 n=112, Family2 n=106, Family3 n=94; April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family3 n=32).

	Collection 1 (February)		Collection 2 (April)		Collection 3 (May)	
	Used	Unused	Used	Unused	Used	Unused
Percent Survival	53.3 ± 1.4	46.9 ± 1.7	49.2 ± 2.5	30.9 ± 1.5	21.8 ± 2.4	22.6 ± 2.0
Percent Hatch	—	—	2.0 ± 0.3	9.37 ± 1.1	100 ± 0	98.7 ± 0.4
Standard Length (mm)	9.91 ± 0.12	9.98 ± 0.16	14.20 ± 0.13	13.33 ± 0.22	19.21 ± 0.16	19.39 ± 0.19
Somatic Weight (g)	0.0034 ± 0.000008	0.0036 ± 0.0001	0.0060 ± 0.0004	0.0048 ± 0.0001	0.0131 ± 0.0005	0.0112 ± 0.0005
Yolk Weight (g)	0.0433 ± 0.0008	0.0423 ± 0.0008	0.0439 ± 0.0008	0.0402 ± 0.0008	0.0323 ± 0.001	0.0349 ± 0.001

Table 4-3: Summary of the means and standard errors of survival and growth measurements for interior Fraser coho collected throughout winter incubation for each family of artificially spawned fish in McKinley Creek watershed. (February: used n=145, unused n=167, Family1 n=112, Family2 n=106, Family3 n=94; April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family3 n=32).

	Collection 1 (February)			Collection 2 (April)			Collection 3 (May)		
	Family 1	Family 2	Family 3	Family 1	Family 2	Family 3	Family 1	Family 2	Family 3
Percent Survival	72.1 ± 1.6	43.9 ± 1.5	34.3 ± 1.4	65.0 ± 2.4	27.5 ± 1.8	27.6 ± 1.4	40.5 ± 2.2	18.1 ± 2.5	9.0 ± 2.3
Percent Hatch	—	—	—	4.3 ± 0.3	1.4 ± 0.3	1.0 ± 0.2	98.5 ± 0.4	100 ± 0	100 ± 0
Standard Length (mm)	10.54 ± 0.16	9.77 ± 0.13	9.42 ± 0.20	14.32 ± 0.21	13.64 ± 0.18	13.32 ± 0.24	19.92 ± 0.14	19.03 ± 0.22	17.63 ± 0.28
Somatic Weight (g)	0.0038 ± 0.0001	0.0032 ± 0.0001	0.0034 ± 0.0001	0.0062 ± 0.0006	0.0050 ± 0.0001	0.0043 ± 0.0001	0.0140 ± 0.0006	0.0100 ± 0.0003	0.0102 ± 0.0004
Yolk Weight (g)	0.0538 ± 0.0006	0.0349 ± 0.0004	0.0390 ± 0.0007	0.0507 ± 0.0008	0.0339 ± 0.0004	0.0407 ± 0.0002	0.0401 ± 0.0007	0.0245 ± 0.0007	0.0280 ± 0.0009

Table 4-4: Summary of p-values for Tukey test comparisons among families for survival and growth of interior Fraser coho incubated in artificial redds in McKinley Creek watershed. (February: used n=145, unused n=167, Family1 n=112, Family2 n=106, Family 3 n=94; April: used n=119, unused n=148, Family1 n=104, Family2 n=80, Family 3 n=83; May used n=97, unused n=88, Family1 n=95, Family2 n=58, Family 3 n=32).

Collection Period	Family Comparison	Survival	Length	Somatic weight	Yolk weight
February	1 vs. 2	0.002	0.009	<0.001	<0.001
	1 vs. 3	<0.001	<0.001	0.080	<0.001
	2 vs. 3	<0.001	0.176	0.351	<0.001
April	1 vs. 2	0.382	0.006	<0.001	<0.001
	1 vs. 3	0.997	0.005	<0.001	<0.001
	2 vs. 3	0.382	0.979	0.179	<0.001
May	1 vs. 2	0.002	0.037	<0.001	<0.001
	1 vs. 3	<0.001	0.002	0.001	<0.001
	2 vs. 3	<0.001	0.191	0.988	0.071

DISCUSSION

This study has characterized habitat features associated with the incubation environment and examined the effect of habitat features on larval survival and growth. It is one of the first studies to examine incubation sites for an anadromous salmonid from an interior watershed. Environmental conditions within the intragravel habitat of incubation sites remained relatively consistent throughout the incubation period, despite the below freezing air temperatures and marked reductions in surface flow. The importance of a stable environment for successful incubation of larval fish has been repeatedly cited, but has been seldom tested in an interior watershed due to the logistic difficulties associated with winter fieldwork. There was also little relationship between habitat features and the incubation success of larval IFC despite significant differences in incubation environment. Variation among families, however, was much greater and accounted for all the survival and growth differences measured.

Stability of the intragravel environment

Sites used for spawning by IFC differed significantly from unused sites; daily mean temperatures, ATUs, and hyporheic conductivity were significantly higher at unused sites throughout the incubation period. Hyporheic dissolved oxygen levels differed initially and prior to emergence between used and unused sites during incubation, but did not differ significantly during the middle of the incubation period. Hyporheic dissolved oxygen levels were higher at used sites relatively early in incubation (February), and were once again significantly higher late in incubation (May). Artificial redd habitat features followed trends similar to that of used and unused study sites throughout the incubation period. Mean daily

hyporheic temperatures and ATUs at artificial redds were consistent with the findings for used and unused sites.

Perhaps more importantly, habitat features at study sites and artificial redds remained relatively consistent throughout the incubation period. This stability is critical for both the selection of high-quality spawning sites and incubation environments. Habitat stability throughout the spawning and incubation periods ensures that spawning site selection is indicative of the habitat features of the incubation environment. In the absence of the relative consistency of habitat features females may select spawning sites that become unsuitable for the incubation of larval fish. The stability of spawning and incubation sites is especially important for salmonids due to specific incubation and emergence life history strategies that have evolved to maximize survival of larval fish (Brannon, 1987).

Incubation Environment and Growth

Habitat feature differences between used and unused sites generally have an effect on larval coho development. Higher hyporheic temperatures were measured at unused compared to used sites (Figure 4-2; Figure 4-6; Figure 4-7). An increase in temperature results in a remarkably consistent increase in physiological reactions, and as such a small change in ambient temperature can have profound effects on developing fish due to the cumulative effect of temperature. It was surprising, therefore, that no significant differences in larval fish survival or growth were measured between used and unused artificial redds. One explanation for this result is that interactions between habitat features may have counteracted the typical influence of individual habitat features on larval fish. Specifically, the higher growth potential of hyporheic temperatures at unused sites may have been

inhibited or impeded by low dissolved oxygen levels at these sites. Silver et al. (1963) found that length of larval Chinook salmon was positively related to dissolved oxygen concentrations in the incubation environment, and further found that although survival was possible at low dissolved oxygen levels (2.5mg/L at 11°C; approximately 23% saturation), there was an associated decrease in growth and developmental rates as a result. Additionally, higher hyporheic conductivity at unused sites may have affected the growth of larval fish, but there has been little research on the effect of conductivity on larval fish and the potential of a relationship remains unclear. Differences in pH levels (at 60cm depth) may have also contributed to the lack of observable differences in larval growth between used and unused sites, but it is unlikely that relatively small differences in pH at the 60cm depth had an influence on larval fish incubating at a depth of approximately 25cm.

The lack of growth differences between used and unused sites could alternatively be explained by the temporal limitations of this study. Specifically, the logistics of sampling egg capsules late in incubation, at the onset of freshet, was problematic and not undertaken. It is possible that significant differences in growth may have been observed had the duration of the study been extended and another collection been attempted immediately prior to emergence (June). A factor that may have accentuated differences later in incubation is a decrease in solubility of dissolved oxygen with warming temperatures; consequently dissolved oxygen levels at unused sites may become insufficient. Warmer temperatures for fish at unused sites may also exhaust yolk material at a faster rate late in incubation and force fish to emerge to seek food prematurely.

Incubation Environment and Survival

In contrast to growth and development, the lack of difference in survival between used and unused sites is likely not a result of habitat feature interactions, but rather due to the general resilience of larval fish. Survival has generally been shown to reduce significantly only when critical species-specific habitat tolerance limits are surpassed (Shumway et al., 1964; Silver et al., 1963; Einum, et al., 2002; Williamson, 2006). The lack of differences between used and unused sites, therefore, could be associated with a broad range of incubation habitats that meet the requirements for larval IFC survival and growth. Incubation habitat requirements for salmonids have been almost exclusively defined by hatchery or coastal population requirements, and the specific requirements for IFC populations have not been previously investigated. Furthermore, the data published regarding specific upper and lower habitat limits are variable among species and even among populations.

Sigma (1983) stated that the minimum dissolved oxygen requirements for incubating salmonids in a cold-water hatchery setting (2.5 °C) is 8.5 mg/L (approximately 60% saturation). Minimum dissolved oxygen levels, measured at the 30cm depth, at used and unused study sites throughout incubation were 3.77 mg/L and 3.41mg/L, respectfully. Only mean dissolved oxygen levels in artificial redds at the 30cm depth as a percentage of saturation were lower than the suggested hatchery minimum levels at unused sites (used mean range: 70.8-78.0%; unused mean range: 48.5-61.6%). Mortality has been reported when dissolved oxygen is below 6 mg/L for coastal coho (Koski, 1966), 4 mg/L for sockeye salmon (Cope 1996), and 2.5 mg/L for Chinook salmon (Silver et al. 1963) which represent fairly low percent saturation of oxygen. Direct comparison to these values is difficult due to the differences in temperature, but temperature of the incubation environment in McKinley

Creek was low resulting in greater oxygen solubility. Consequently, dissolved oxygen levels in the intragravel environment in McKinley Creek were sufficient for survival of larval IFC at the temperatures recorded throughout the winter. Dissolved oxygen levels measured in used and unused artificial redds, therefore, were within the range acceptable for salmonid survival.

Temperature minimum and maximum incubation limits for coho have been defined as $<1.6-13^{\circ}\text{C}$ (Sigma, 1983). The mean daily temperatures for used and unused artificial redds in McKinley Creek were 1.2°C (range: $0.1 - 4.0^{\circ}\text{C}$) and 1.5°C (range: $0.4-3.9^{\circ}\text{C}$), respectively. The mean and range of temperatures at both used and unused sites are low compared to the standard set by Sigma (1983), but this report explicitly indicates the lack of data available to determine exact minimum temperature cut-offs below 1.6°C . There have been a number of recent investigations that found successful incubation at temperatures well below 1°C (Humpesch, 1985; Curry et al., 2002; Williamson, 2006). Additionally, coho have been found to be the most tolerant of cold incubation temperatures of the Pacific salmon (Murray and McPhail, 1988), and their minimum incubation temperatures are likely much lower than what has been previously defined, particularly for interior populations. Furthermore, the lack of survival differences between used and unused sites shows that although temperature differences were observed they were not large enough to adversely affect survival of IFC.

Trends in hyporheic conductivity levels in artificial redds were variable at the 30cm depth; measurements in February and April were higher at used sites, and in May conductivity was higher at unused sites. In contrast, conductivity at the 60cm depth in artificial redds was consistently higher at unused sites compared to used sites. Unfortunately,

the mean hyporheic conductivity levels at the 60cm depth in unused artificial redds was less ($175\text{-}192\ \mu\text{S}\cdot\text{cm}^{-1}$) than found at the unused study sites ($216\text{-}269\ \mu\text{S}\cdot\text{cm}^{-1}$) and did not represent the full range of values measured at unused study sites. The effect of conductivity on salmonid development and survival in the incubation environment is unclear. A study by Malcolm et al. (2003) utilized artificial redds to compare the incubation environments of a degraded agricultural catchment and a relatively pristine stream and found that the degraded stream hyporheic conductivity levels were much higher ($279\text{-}310\ \mu\text{S}\cdot\text{cm}^{-1}$) than the pristine stream ($54\ \mu\text{S}\cdot\text{cm}^{-1}$). In contrast, Williamson (2006) found a mean hyporheic conductivity of $271\ \mu\text{S}$ for a relatively pristine river in the Peace/Williston watershed. Although, comparisons of conductivity levels between watersheds is akin to comparing apples and oranges due to the differences in geology and stream productivity. Therefore in the absence of clear baseline data for comparison, the relationship between intragravel conductivity and larval survival and growth remains uncertain and moreover highlights a gap to be filled in incubation research.

Few studies have examined pH requirements in the incubation environment. Sigma (1983) stated that hatchery pH levels should be maintained from 6.5 - 8.5. Mean pH levels in artificial redds at the 30cm depth ranged from 6.90-7.28 for used sites, and 6.96-7.50 for unused sites. These ranges suggest that both used and unused sites are within the acceptable pH requirement range, even based on relatively conservative hatchery requirements. More specifically, Rombough (1982) ranked coho as the least sensitive to low pH levels of all Pacific salmon and determined that the minimum acceptable pH for coho was 6.0.

Family Effect and Incubation Success

Significant differences in survival and growth were found among families of artificially spawned fish. Results showed that in general Family 1 had significantly higher survival and growth than other families. Since paternal effects are generally uncommon (Heath et al., 1999), a probable explanation for these differences is related to maternal effects and the egg weight differences between females. Female 1 had larger eggs than females 2 and 3. Incubation success and growth for larval fish has been shown to increase with egg size (Shumway et al., 1964; Beacham and Murray, 1990; Einum et al., 2002).

The differences in survival and growth among families observed in this study, particularly in light of the lack of differences in survival and growth based on habitat features, merits further investigation. Perhaps the factor that is limiting the success of IFC populations is not related to a perturbation or scarcity of good-quality habitat, but rather to the quantity and quality of female gametes. The differences in survival among families may be of particular concern for the viability of IFC in McKinley Creek if Families 2 and 3 are representative of the majority. The survival percentages prior to emergence for Family 2 (18.1%) and Family 3 (9.0%) were lower than the normal range for coho (23-27%; Chapman, 1965; Koski, 1966), and additionally were much lower than Family 1 (40.5%).

Furthermore, based on 2007 data, the fork lengths of the females associated with Family 2 (55.0 cm) and Family 3 (52.0 cm) were much closer to the average female fork length of 56.7cm (n=239; Northern Shuswap Tribal Council, 2007) in McKinley Creek, than the female associated with Family 1 (66.0cm). Since fecundity has been closely linked to

female size (Drucker, 1972; Bjornn and Reiser, 1991) this suggests that the fecundity of females is on average more similar to the relatively lower fecundities of Female 2 and 3.

The examination of female size in relation to incubation success and to the overall sustainability of the IFC population in McKinley Creek, was not a specific objective of this study. Although the differences observed between family incubation success suggests that research directed at identifying and categorizing female gamete quality and quantity may be critical to the comprehensive understanding of factors that influence the success of IFC.

Conclusion

The findings of this study highlight the complexity of understanding the relationship between incubation environments in relation to incubation success. Many factors influence the survival and growth of larval fish and the potential and magnitude of each factors' influence likely depend on the interaction between environmental features as well as the heritability of traits from parents. Results of this study support the preferential selection of spawning habitats (Chapter 3) by demonstrating differences between used and unused incubation sites, but also indicate that there may not be a shortage of good quality habitat in McKinley Creek based on the lack of differences in survival and growth between used and unused artificial redds.

CHAPTER 5

General Discussion

The paucity of information on freshwater habitat requirements for interior Fraser coho (IFC) limits management and conservation initiatives, as well as the general understanding of the life history strategies of salmonids in interior watersheds. This study aimed to fill this knowledge gap by evaluating the habitat features associated with spawning site selection and incubation success. The productivity of a population can be limited by both spawning and incubation success; determining the influence of habitat features during these stages, therefore, is critical. This is particularly relevant for IFC due to the submission by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) that recent declines are potentially a result of habitat perturbations. My thesis aimed to determine locations within McKinley Creek watershed where IFC spawn (Chapter 2), characterize the physical and chemical features of specific spawning sites (Chapter 3), and investigate the influence of habitat features on survival and growth of larval fish throughout incubation.

Chapter 2 utilized a combination of ground surveys and radio telemetry to identify regions used for spawning by IFC in McKinley Creek watershed. Findings reaffirmed that the 12km region downstream of McKinley Lake was used for spawning, but also showed that IFC migrated to reaches upstream of McKinley Lake. Logistic constraints prevented the identification and sampling of specific redds upstream of McKinley Lake, but it is likely that this region was used for spawning. This suggests that IFC are using much more of the watershed than had previously been thought. It is recommended that further research be undertaken upstream of McKinley Lake to determine the extent and distribution of spawning sites and furthermore to determine the proportion of IFC that utilize this habitat.

Specifically, future research could (1) enumerate IFC that migrate into the upper portion of McKinley Creek watershed; (2) locate and characterize specific IFC spawning sites in upper

McKinley Creek watershed, (3) determine the extent of watershed used by IFC, and (4) examine the potential influence of the forest industry on IFC habitat in upper McKinley Creek watershed. An additional observation that arose during the identification of spawning sites, especially in 2006, was the abundance of redds located in the 200m section downstream of the McKinley Creek enumeration fence. IFC appear to backtrack to this habitat, which may or may not provide good quality habitat, due to the obstacle presented by the enumeration fence. It is recommended that the suitability and effectiveness of a resistivity counter (or other alternatives means of enumerating) as a potential replacement for the McKinley Creek enumeration fence be investigated.

Chapter 3 utilized logistic regression to examine the relationship between habitat features and the probability of spawning site use by IFC. An information theoretic approach was used to assess a set of candidate models that were founded on previously determined biologically significant habitat features. Results showed that intragravel habitat features dominated the top models; furthermore the models demonstrated good predictive ability based on internal validation. Whereas, the traditional model for spawning site selection ranked poorly. These results support other recent studies which indicate that traditional habitat features may not effectively account for the complexity of spawning site selection in salmonids.

Hyporheic conductivity was present in each of the top ranked models, and was shown to have a negative effect on spawning site selection. Hyporheic conductivity is not commonly identified as a key spawning site selection cue, but study results suggest that IFC may be using this variable (directly or indirectly) as an indication of sub-optimal spawning habitat. Whether or not IFC can actually detect changes in conductivity has not been studied,

but previous research does indicate that high conductivity levels, as well as reduced dissolved oxygen levels, are associated with regions influenced by relatively undiluted groundwater which have been shown to be both preferentially selected or avoided by different species of salmonids. Based on the logistic regression results as well as descriptive statistics for used and unused sites (which indicated higher hyporheic conductivity and lower dissolved oxygen at unused sites) it is suggested that IFC are preferentially selecting sites that are not associated with relatively undiluted groundwater influence. Gaining a better understanding of groundwater influence in McKinley Creek would be useful. Presently, the Northern Shuswap Tribal Council is conducting a study to identify the locations of groundwater seepage in McKinley Creek. These findings could be used as a foundation to determine the location and extent of relatively undiluted groundwater in the watershed, which may provide insight into the amount of suitable IFC spawning habitat. Further, it is recommended that future spawning site selection models incorporate intragravel habitat features to provide a more robust examination of spawning sites selection.

Chapter 4 investigated the influence of habitat features on the incubation success of larval fish. Incubation habitat monitoring showed that habitat features remained relatively consistent throughout incubation. This demonstrates the important linkage between spawning site selection and the incubation environment. Female salmon are presented with the difficult task of selecting a spawning site that will result in the successful incubation of their offspring based on habitat features encountered throughout the spawning period. This study reveals that the habitat features encountered by females in the fall are generally representative of incubation habitat features throughout the winter.

Prominent and significant differences found between the used and unused study sites included intragravel dissolved oxygen, temperature, and conductivity. Unused sites were associated with higher hyporheic temperature, conductivity and lower dissolved oxygen. This supports the findings of Chapter 3, indicating that IFC are preferentially selecting sites with minimal influence of undiluted groundwater. Vertical hydraulic gradient did not differ significantly throughout the incubation period, however, specific discharge was among the top models for spawning site selection (Chapter 3). Intragravel flow may be used to assess the quality spawning sites during the fall, but due to a general decrease in flow throughout the winter this influence is likely reduced.

Despite habitat differences between used and unused incubation environments no significant differences in survival and growth of larval fish were found. The relatively good quality habitat provided in McKinley Creek watershed could account for the lack of differences in survival. However, it was surprising that no growth differences were observed particularly based on temperature differences between sites. These findings highlight the need for more research to examine the interactions between habitat features and their influence on larval fish in an in-stream environment, rather than solely focusing on individual habitat features in a controlled laboratory setting.

Differences between families in terms of survival and growth are likely a reflection of variable of marine success of returning IFC spawners. Changing marine conditions was also proposed as a reason for IFC decline by COSEWIC. Small egg size and low fecundity of female spawners can result in poor survival and growth of larval fish and may be having a substantial impact on the productivity of IFC populations. Therefore it is recommended that

studies aimed at assessing the quantity and quality of adult gametes be undertaken in McKinley Creek watershed.

Although there are a number of significant findings presented in my thesis, I believe that it is important to recognize some of the limitations. The primary limitation is the duration of the project. The majority of findings in this study are based on data collected in the 2007-2008 field season. Data collected in the 2006-2007 field season were presented, but only descriptive statistical analyses were performed due to a smaller sample size and the lack of some data due to intermittent equipment malfunction. Further, both the 2006 and the 2007 spawning periods were somewhat unusual. The 2006 spawning period had relatively poor return of spawners, whereas the 2007 spawning period had relatively high return of spawners. Replication of this study over more years would have provided a more robust assessment of IFC habitat use and the influence of habitat features on incubation success. Additionally, the assessment of model predictive ability would have been improved if an external data set was used to validate top models rather than the internal jackknife validation. Lastly, further replication of the artificial redd incubation study (both in terms of additional redds, and additional years of investigation) would have potentially provided more definitive results regarding the influence of habitat features on IFC incubation success. Despite these limitations, I think that the findings of my study have contributed important information required to understand basic biology of IFC.

In summary, there is a general shortage of fisheries research that focuses on interior watersheds, particularly throughout the winter months. Conducting spawning and incubation research in interior environments presents many logistical challenges, but can also provide critical information about the life history strategies of under-studied species. I have outlined

practical methodologies that can be used to further investigate spawning site selection and the influence of incubation environment habitat features on larval fish. It is my hope that further research can build upon my findings to develop and expand our understanding of the freshwater habitat requirements of salmonids in interior watersheds in general, and more specifically, contribute to the future viability of IFC.

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