FACTORS INFLUENCING HABITAT USE BY
JUVENILE INTERIOR FRASER COHO

by

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Abstract

The influence of physical and biological factors on juvenile interior Fraser coho (*Oncorhynchus kisutch*) habitat use was examined within the Horsefly River watershed using three approaches. Otolith microchemistry was used to assess potential movement of juveniles throughout the watershed. This analysis showed evidence of an average of 3.5 movements to different habitats within the Horsefly watershed during juvenile lifestage. It was not possible to track the location and timing of most of those migrations, but some appear to be the result of a movement into small tributaries in late summer and winter. A microhabitat model was used to determine physical characteristics of habitats where juvenile coho were captured. Low velocity, small stream width, a greater proportion of gravel as substrate, and high instream and overhead cover were strongly related to the presence and abundance of juvenile coho within the streams examined. A behavioural study in an artificial stream channel assessed the type of interactions that occur among juvenile coho. Juvenile interior Fraser coho exhibited little evidence of territoriality, contrasting with published reports of highly territorial juvenile coho behaviour in coastal systems. The lack of territoriality of the interior Fraser coho studied, their frequent migrations, and their strong association with cover, all suggest interior Fraser coho exhibit different habitat use patterns than coho in coastal streams. The difference in habitat use and requirements may influence the effectiveness of current management strategies, many of which are based solely on criteria from coastal coho research studies.

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Prologue

Given that habitat destruction is the most common cause of species extinction in the world today (Pimm and Raven, 2000), the difficult task of determining the connection between organisms and their environment is of vital importance. Yet, for most species, the effects of genetic background and population-level differences are unknown and create additional uncertainty when making species-wide generalizations regarding their ecology.

Coho salmon (*Oncorhynchus kisutch*) are found in small streams along the Pacific coast of North America and Asia, but some fish spawn hundreds of kilometres from the ocean; for example the Interior Fraser River coho from central BC. Genetic analysis indicates that coho found in the interior of BC are genetically distinct from coastal coho and have been genetically isolated for at least 10,000 to 15,000 years (Small *et al.*, 1998). Recent reports have indicated an alarming population decline of 60% over three generations, and have suggested that freshwater habitat destruction may be a factor in the decline (DFO, 2002; Interior Fraser Coho Recovery Team, 2006). Current conservation strategy documents urge the identification and preservation or restoration of critical habitat for interior Fraser coho salmon (Interior Fraser Coho Recovery Team, 2006). This conservation mandate is complicated by the lack of information regarding interior Fraser coho habitat requirements, and the growing evidence that it is inappropriate to assume geographically separated populations have identical habitat use patterns (Mäki-Petays *et al.*, 2002; Guay *et al.*, 2003; Interior Fraser Coho Recovery Team, 2006).

My thesis focused on identifying factors that may contribute to population-level differences in interior Fraser coho freshwater habitat use with an emphasis on management and conservation. As juvenile coho spend up to two years rearing in freshwater, identifying

habitat use patterns in this portion of the life cycle is a top priority. My first study utilized the emerging methodology of otolith microchemistry to characterize broad habitat use patterns within a watershed. The second study determined the physical factors influencing juvenile interior Fraser coho microhabitat use. Models relating habitat variables to juvenile coho presence and abundance were evaluated for explanatory power and the results used to look for evidence of local adaptation. The third study approached the role of intraspecific interactions in juvenile coho behaviour from the perspective of habitat use: it examined the possibility of territorial behaviours as an influence on distribution.

All three studies were conducted with juvenile coho located in the Horsefly-McKinley watershed. This system, near the town of Horsefly, supports the largest known number of interior Fraser coho spawners upstream of the Thompson River system. Given the focus on Thompson River coho in the existing interior Fraser coho literature, a study outside this river system will increase the knowledge and understanding of the interior Fraser coho population.

Chapter 1: Using Otolith Microchemistry to Track Migrations of Juvenile Interior Fraser Coho

ABSTRACT

Traditional tagging methods are difficult to use, especially on juvenile fish. The use of natural tagging methods such as otolith microchemistry show promise in tracking migrations of juvenile fish, as otoliths grow in layers with each layer reflecting the elemental composition of the surrounding water. This paper explores their possible use in tracking juvenile interior Fraser coho in the Horsefly watershed to aid in conservation. Water samples were taken from areas within the watershed and their water chemistry compared using discriminant function analysis. Laser Ablation Inductively-Coupled Mass Spectrometry (LA ICP-MS) was used to analyze the microchemistry of the layers of otolith tissue in otoliths from adult coho to determine the elemental composition of the water at many points during their juvenile period. The elemental ratios of many of the waterbodies in the Horsefly system were similar, preventing the assignation of the otoliths to specific areas. There was, however, enough variation to detect changes in otolith ratios through breakpoint analysis. This analysis indicated that juvenile interior Fraser coho move an average of 3.5 times during the juvenile lifestage. Several of the latter sections of otoliths were attributed to a tributary with a distinct elemental signature where spawning has not been observed, indicating that interior Fraser coho may leave the area in which they hatched to rear in tributaries later in the season. Otolith microchemistry has limited use as a conservation tool in this region, but was sufficient to indicate surprisingly frequent movements and the use of tributaries by juveniles of this population.

INTRODUCTION

Tracking juvenile salmonid movements has proved to be problematic due to drawbacks such as size limitations, cost, tag loss, and inability to distinguish individuals (Roussell *et al.* 2000; Thorrold *et al.*, 2002). "Natural tags" using the physiological life processes of the fish to trace movements, are an emerging alternative (Campana, 1999; Campana and Thorrold, 2001; Thorrold *et al.*, 2002; Elsdon *et al.*, 2008). Otoliths are a calcified structure commonly used as natural tags (Elsdon and Gillanders, 2003). Otoliths grow by the addition of layers of aragonite containing trace elements in concentrations controlled by environmental factors. Analyzing these layers allows researchers to estimate the water conditions surrounding a fish during a given period and use that information to identify likely areas of residence (Radtke *et al.*, 1990; Chesney *et al.*, 1998; Campana and Thorrold, 2001; Elsdon and Gillanders, 2003; Wells *et al.*, 2003; Martin *et al.*, 2004; Clarke *et al.*, 2007).

Life histories of coho salmon have previously been described as highly variable, ranging from "nomad" individuals that migrate to estuaries almost immediately after emerging to male "jacks" that spend very little of their life in the ocean (Quinn, 2005; Koski, 2009). Given the breadth of possibilities and the commonality of multiple life histories within a single population, density monitoring or mark-recapture alone may be ineffective at gauging large-scale movement, while acoustic and transmitter tags cannot be used on very small fish and are not appropriate for studying early rearing patterns. Therefore, despite uncertainties in the influence of environmental factors (Swearer *et al.*, 1999; Secor and Rooker, 2000; Elsdon and Gillanders, 2002; Wells *et al.*, 2003; Elsdon *et al.*, 2008), otolith tags are the most appropriate method of examining fish movement for very young juvenile fish.

Interior Fraser coho may utilize multiple types of habitats during their first year of rearing, but the extent of movements is not known (Interior Fraser Coho Recovery Team, 2006). My study had two primary objectives: to evaluate the feasibility of using otolith signatures to track juvenile coho movements and to characterize the scale and patterns of the movements as recommended in the Interior Fraser Coho Recovery Plan.

METHODS

Study Site

The Horsefly River is approximately 98km long and flows into the Fraser River by way of the Quesnel River and Quesnel Lake (Barr, 1923; British Columbia Ministry of Environment, 2006). Its main tributaries include McKinley Creek, Moffat Creek, Little Horsefly River and Crooked River (Barr, 1923). A 10m waterfall creates a barrier to upstream fish migration and effectively excludes migratory fish from moving into the upper half of the Horsefly River: my study focused on the Horsefly below this point to the townsite, the McKinley River below Elbow Lake, and the tributaries in this section (British Columbia Ministry of Environment, 2006).

Water Sample Collection and Analysis

Water sampling methods were based on the methods of Shiller (2003) as modified by Clarke *et al.* (2007). High-density polyethylene bottles were rinsed with deionized water and then filled with 600μL of 2% high-purity HNO_3 to acidify the water samples. Polyethylene syringes were likewise soaked and rinsed, then air-dried in a fume hood before use. Water samples were taken from the sites identified in Figure 1.1 from August to September, 2006.
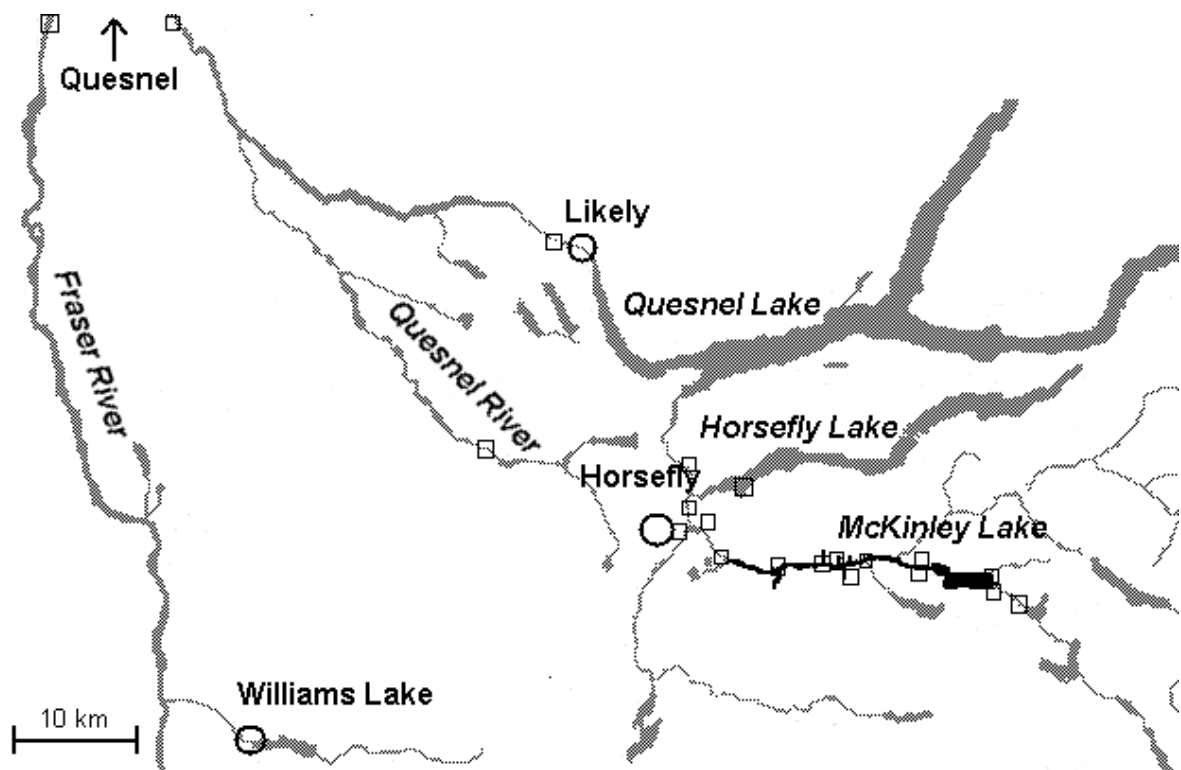
Figure 1.1*: The study area (in black), and the approximate location of the water samples (squares) and townsites (circles).*

Water samples from tributaries were taken in a single location and mainstem streams were sampled above and below their confluences with tributaries. At each sampling location, a syringe was rinsed with river water, and then filled with 40mL of water for the sample. A clean 0.45μm filter was placed on the syringe, and approximately 10mL of water expelled to rinse the filter. The remaining 30mL was filtered into the bottle containing the HNO_3 and the acidified sample stored away from light until analysis. A second replicate was taken at the same time, using the same syringe and filter but a different sample of river water.

The acidified water samples were analyzed at the University of Northern British Columbia using a PS1000-UV Inductively-Coupled-Plasma-Atomic-Emission-Spectrometer (ICP-AES) (Leeman Labs). Each sample, including two laboratory blanks run every 30 samples, was measured for Ba, Ca, Li, Mg, Mn, Sr, and Zn.

Otolith Collection and Analysis

Juvenile coho salmon were collected by minnow trap from the mouth of McKinley Creek, the Horsefly River downstream of the McKinley confluence, Patenaude Creek, and Woodjam Creek; euthanized with clove oil, and their otoliths removed. Juvenile otolith collection occurred in the months of June and August in 2007. Otoliths were removed from four juveniles from each sampling area and used to determine the relationship between the measured water elemental ratios and the corresponding ratios in the otoliths. The following fall, otoliths were collected from carcasses of 52 post-spawned returning adults. Forty otoliths were used for determining freshwater movement patterns: due to the status of interior Fraser coho populations, it was considered less harmful to use posthumously sampled adult otoliths than to remove this number of living juveniles from the population.

Otoliths were embedded, sectioned and analyzed at the University of Victoria (Aqueous Geochemistry/ICP-MS Lab), using the standard procedure developed by the School of Earth and Ocean Sciences for analyzing otolith microchemistry. The otoliths were cleaned using deionized water, forceps, and gentle abrasion as needed, dried and then embedded in epoxy (Buehler Epoxy-Cure Resin). The discs were then sectioned close to the core area with an isomet saw (Buehler). The sectioned otolith was embedded in a larger piece of epoxy and cured for 8 hours. Embedded otoliths were polished to reveal the core section. Lapping papers with grit sizes of 320, 600, and 1200 were wetted with deionized water and used to hand-polish the otoliths until the core was reached. The sectioned samples were rinsed and sonicated in deionized water for three minutes to remove any loose particles. A final polishing with 0.2µm diamond suspension spray (Buehler, Metadi Supreme) on 2500 grit polishing pads (Buehler, Texmet) ensured a smooth surface. The samples were rinsed and sonicated again, then analyzed.

Laser ablation inductively-coupled mass spectrometry was used to determine elemental chemistry of the otoliths. Samples were run through a laser ablation system (UP-213 Laser Ablation System, New Wave Research) coupled to a mass spectrometer (X Series II ICP-MS, Thermo Electron Corporation), and the data collected using the associated software (PlasmaLab ver. 2.5.3.280, Thermo Electron 2003). Three standards (NIST standard glasses 615, 613, and 611) were run at the beginning of the analysis to create a calibration curve, and were run every 10 samples for quality control purposes. Otolith analyses were conducted by tracking a line scan across the widest axis of the embedded otolith, through the core. The line scans measured Ba, Ca, Li, Mg, Mn, Sr, and Zn and were conducted at 5.0µm/s at a frequency of 20Hz. As otoliths are composed of an aragonite (calcium carbonate) matrix, calcium is generally used as an internal standard in the otolith chemistry

analysis, and the concentration of elements in the water expressed as a ratio of the calcium concentration (Campana and Thorrold, 2001).

Statistical Analysis

All statistical procedures were undertaken using the statistical program R (R 2.6.0, The R Foundation for Statistical Computing, 2007). Discriminant Function Analysis (DFA) was used to examine the water chemistry from the sampled areas for differences that may result in distinct signatures in the otolith microchemistry of the resident fish. The DFA was run using Ba, Mn, and Sr. Zn , Li, and Mg were removed from further analyses due to contamination of blanks, lack of variation, and high background noise, respectively.

To determine a relationship between water chemistry and otolith chemistry, a reduced major axis regression analysis (RMA) compared the chemistry of the juvenile otoliths from each the four representative areas with the chemistry of the water samples taken in the same area. The elemental ratios of the outermost otolith layers were averaged within each area then plotted against the elemental ratios of the water from that area. The slope of the line created by the RMA regression provided the relationship between the elemental ratio in the water and the elemental ratio in the otolith and formed the "water-to-otolith" equations for each element.

Increases in Sr provide the standard method of pinpointing seaward migration (Campana and Thorrold, 2001), and allowed the otolith to be separated into the "maternal signature" at the core, the juvenile period, and the adult period (Figure 1.2). Laser ablation
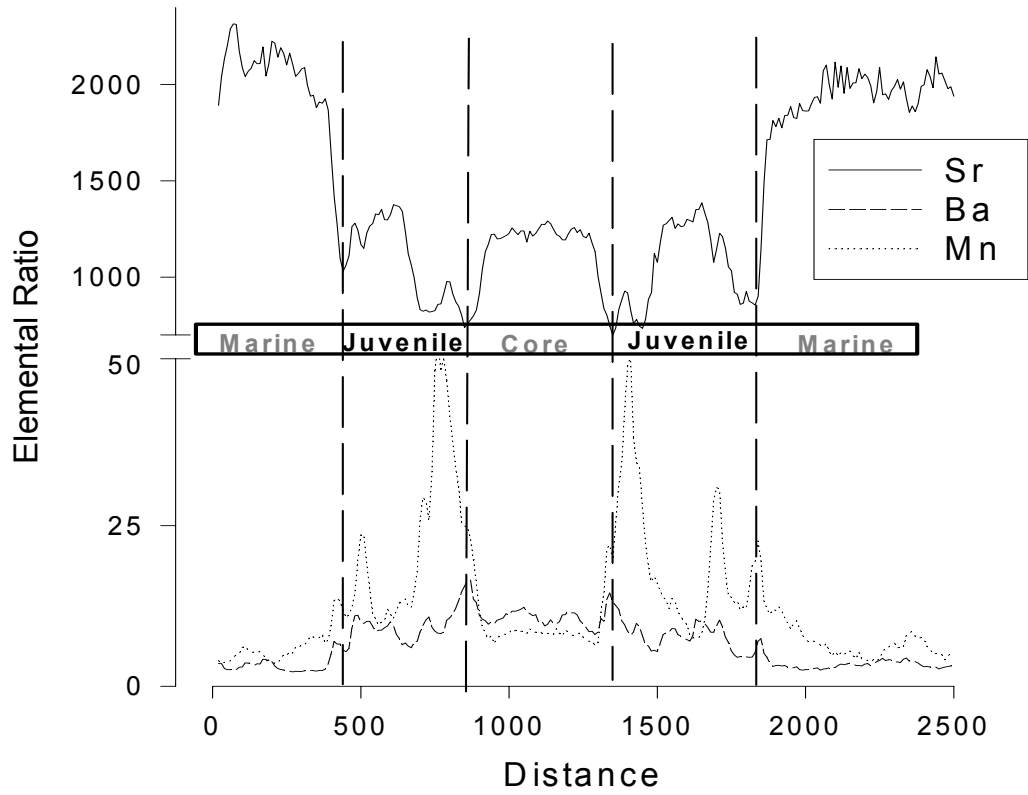
Figure 1.2: *Linescan of a representative otolith from adult coho Q2 with dashed vertical lines marking the sections of the otolith.*

line scans crossed the entire otolith; the outer edge represents the spawning adult and the core is the larval signature. Otoliths do not always show equal deposition on all sides, so the longer axis was used to provide the best resolution. One otolith was removed from analysis because its linescan did not cross the core, and therefore may not have captured the chemistry of the layers laid down at the beginning of the fish's life. Another otolith was removed from analysis because background levels of some elements were unusually high in the mass spectrometer.

The water-to-otolith equations provided by the RMA regression were used to convert the otolith elemental ratios from the juvenile portion of the lifecycle to the predicted elemental ratios of the water where the fish putatively resided. The calculated water chemistries were then compared against the water samples used in the DFA to identify likely areas of residence.

The number of changes in the elemental levels was used as a measure of the motility of fish in this watershed. Each detected shift was considered evidence of a migration to a new area. To incorporate the weighted influence of all three elements into a single variable, water chemistries of each point on the line scans were predicted using the equations created in the DFA previously used for the water samples. The DFA was used to allow for comparison between water and otolith ratios to assign the otolith chemistries to possible locations. The first linear discriminant (LD1) was used as a surrogate for the three elements, allowing a breakpoint analysis to detect changes in any of the three elements simultaneously. Breakpoint analysis is a test for structural change in a linear regression and estimates a number of shifts (m) dividing the regression into segments ($m+1$) by testing for inconsistent regression coefficients (Zeileis *et al.*, 2003). As it does not require prior identification of the number or placement of the shifts, and is relatively robust to autocorrelation and unequal variance

between segments, it was deemed the most appropriate measure of structural change for these data (Bai and Perron, 1998). The "breakpoint" procedure from the "strucchange" package in R was chosen as it has shown strong performance in comparison with other breakpoint methods (Zeileis and Kleiber, 2005). The formula used for this analysis compared the time series of LD1 against a constant to test for deviation from the plateau that would indicate a stable environment due to residence in a single area. The trimming factor was increased to 0.20 as suggested by Bai and Perron (1998) to reduce the impact of autocorrelation on the detection of breakpoints. The resulting output gave the residual sum of squares (RSS) and Bayesian Information Criteria (BIC) for each probable number of breakpoints. The fit with the lowest BIC was selected as the most probable number of breakpoints. If the BIC for two possible fits were within one unit of each other, the fit with the lowest RSS was chosen.

Fifteen of the otoliths were randomly chosen for analysis of movement patterns in fresh water. This analysis was only run on the subsample of fifteen for ease of interpretation. The calculated water chemistries within each segment were averaged so that each otolith was associated with an average Ba, Mn, and Sr ratio for each segment. A hierarchal cluster analysis using complete linkage was run on the segment averages to look for patterns in the segments indicating commonalities in the movement patterns of the fish.

RESULTS

Water Samples

The DFA of the water samples had limited ability to discriminate between the sample sites. Water samples from McKinley Creek and Horsefly River loosely clustered, but there was considerable overlap between these two rivers (Figure 1.3). Differences in water chemistry for the smaller tributaries to the Horsefly, however, did separate by DF1. DF2,

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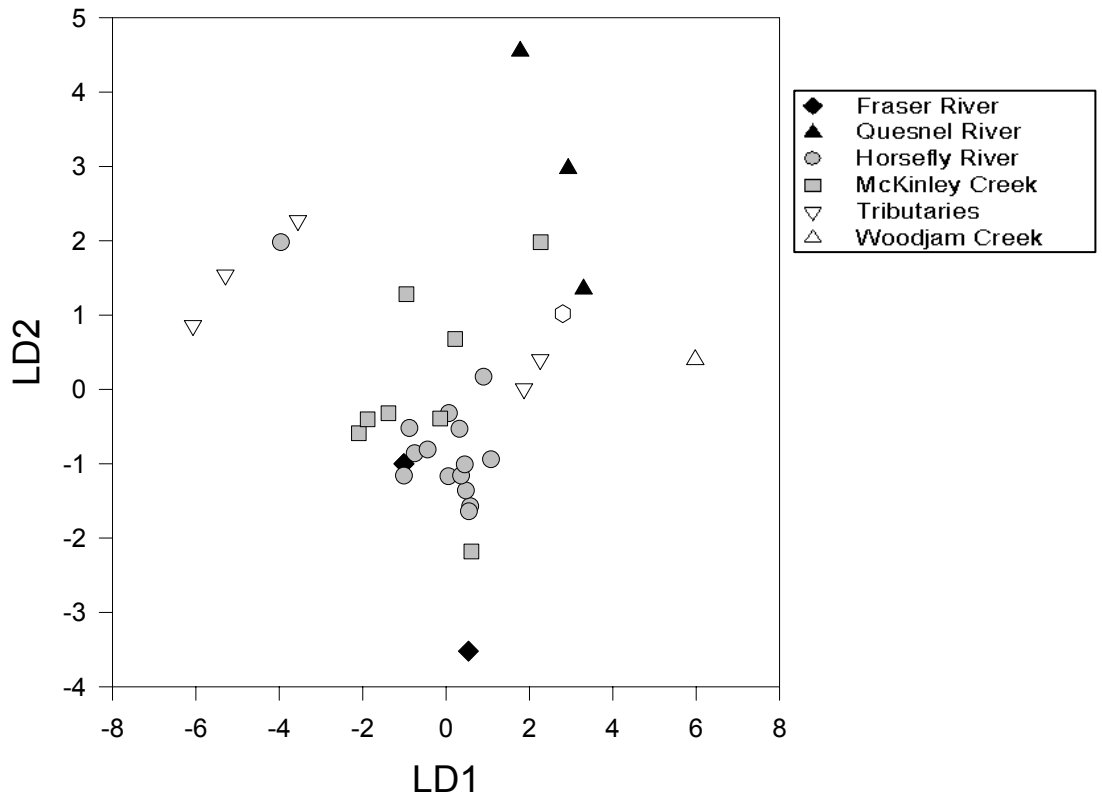
Figure 1.3: *LD1 and LD2 from the Discriminant Function Analysis of the water chemistry samples. Light grey fill signifies sites within the Horsefly River watershed including the Horsefly itself (grey circles), McKinley Creek (grey squares) and associated tributaries (white). Samples outside the Horsefly watershed are in black triangles (Quesnel River) and black diamonds (Fraser River)*

and to a lesser extend LD3, seemed to distinguish among sites within the watershed (the Horsefly River, McKinley River, Little Horsefly River, and associated tributaries) and the Fraser River and Quesnel River.

The relationship between otolith elemental ratios and the water elemental ratios, as determined through the juvenile otoliths (Figure 1.4) were highly significant (Ba: $R^2 = 0.58$, b = 10.7, $p < 0.001$; Mn: $R^2 = 0.71$, b = 36.3, $p < 0.001$; Sr: $R^2 = 0.77$, b = 184.9, $p < 0.001$).

Otoliths

All otoliths had between 1 and 4 breakpoints, indicating 2-5 segments. The median number of segments was 4 (3 breakpoints), with a mean of 3.5. Examples of representative line scans are shown in Figures 1.5. All three elements appeared to change over time, and showed distinct peaks and dips. For the subset of 15 otoliths selected for further analysis there was a total of 51 segments; cluster analysis of the 51 segments indicated four major groups (Figure 1.6). Otoliths segments from an individual sometimes appeared in more than one group. Groups 1 and 2 contained segments assigned to the Fraser River, the Quesnel River, and the Horsefly watershed. All but one of the segments assigned to Groups 3 and 4 were assigned to Woodjam Creek. All but one of the otoliths in this group were also from the second, third, or fourth segments of their respective otoliths. This indicates that the majority of the fish in this system did not originate there, but migrated to the area later in life.

DISCUSSION

Suitability of Otolith Analysis

There are many conditions that must be met for the appropriate use of otoliths as natural tags. The extents to which these conditions are met dictate the possible uses of the
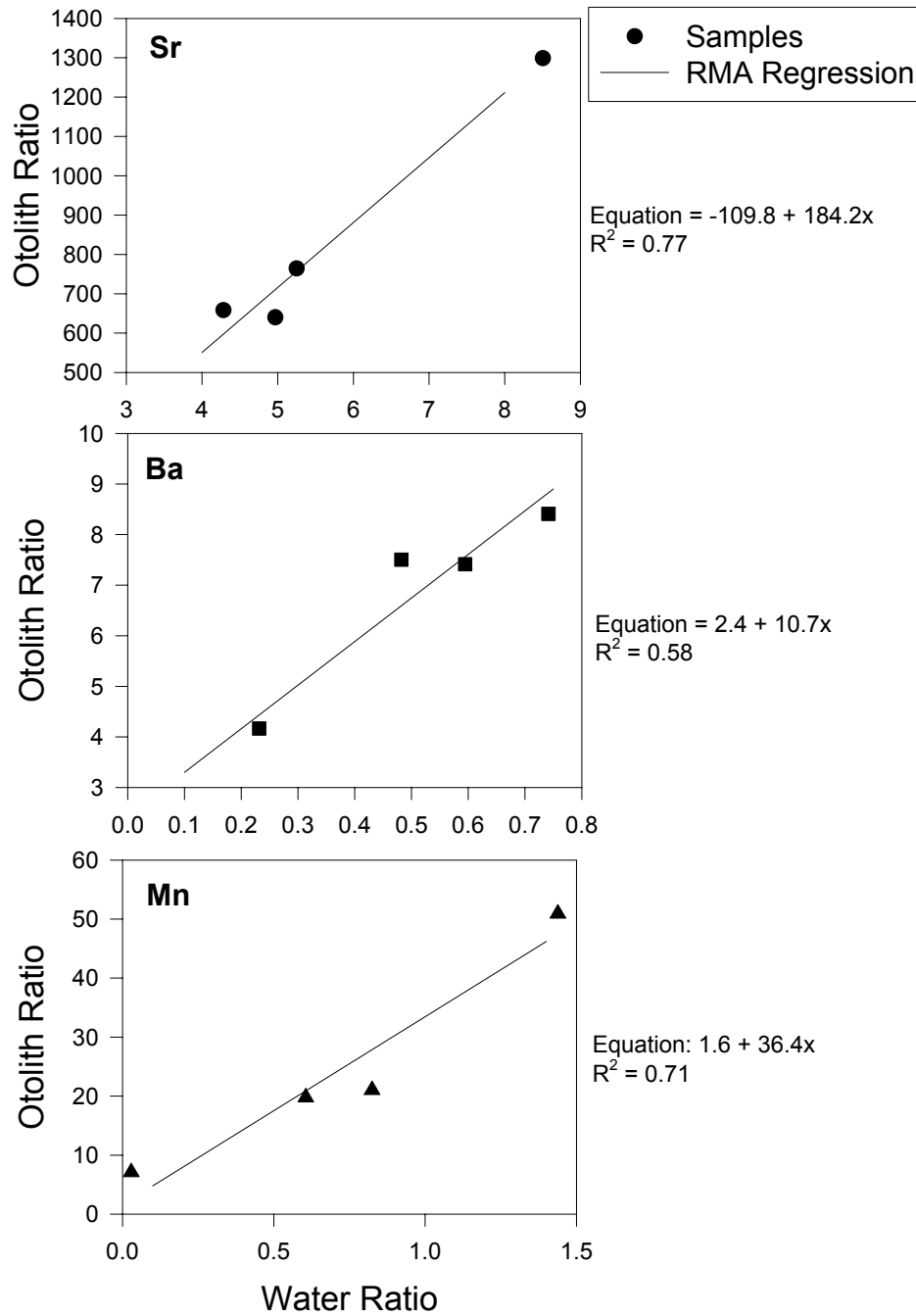
Figure 1.4: *The relationship between the elemental ratios of the representative juvenile otoliths and associated water ratios for strontium (Sr), barium (Ba) and manganese (Mn) as calculated by RMA regression. Regression equation and R^2 value are shown.*
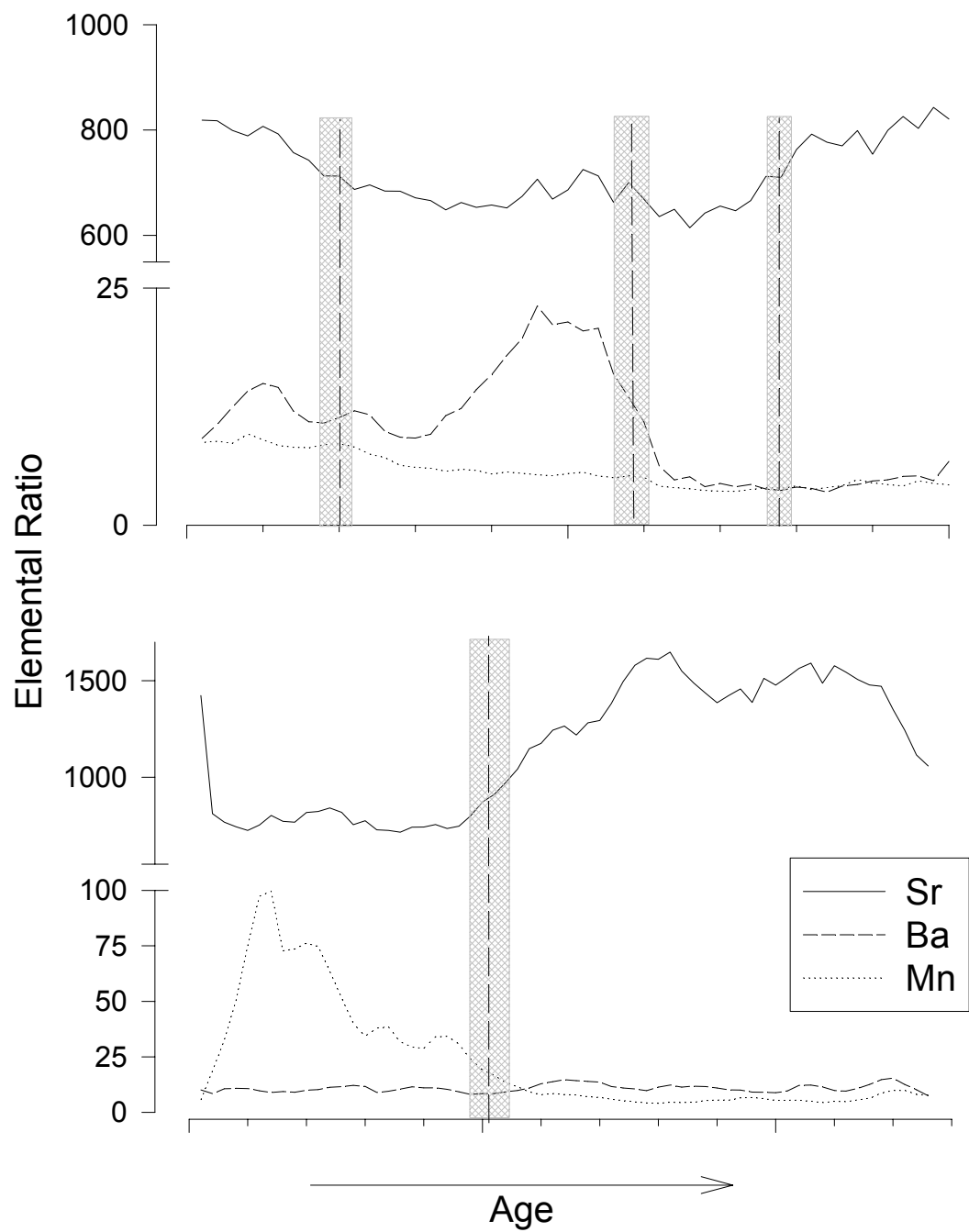
Figure 1.5: *Linescans from representative otoliths (coho Q25, top; coho Q4, bottom). The vertical dashed lines mark suggested breakpoints, and the grey boxes indicate the 95% confidence interval for the location of the breakpoints.*
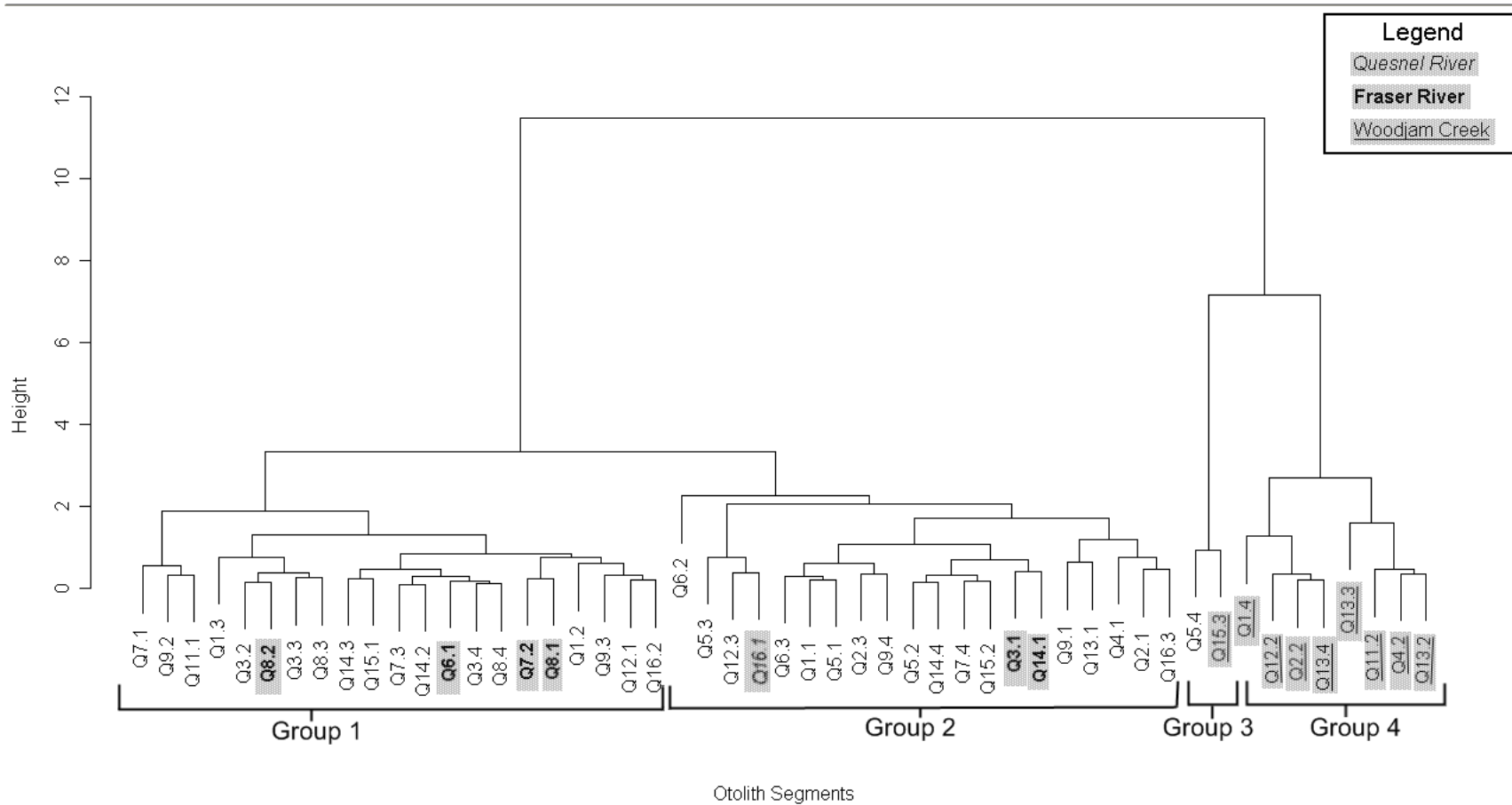
Figure 1.6: *Cluster analysis of otolith segments. The first number before the decimal refers to the otolith number, the number after the decimal refers to the segment of the otolith (e.g. Q13.2 is the second segment of Q13). The cluster analysis indicated four major groups, which are marked. The segments attributed to the Quesnel River (italics), the Fraser River (bolded), and Woodjam Creek (underlined) are highlighted.*

otolith data. While several of these conditions were met, others were not, which limits the usefulness of otolith microchemistry tags in investigating this system.

The relationship between environmental water chemistry and otolith chemistry was supported by this study and confirms earlier findings by Chesney *et al.* (1998), Wells *et al.* (2003), and Clarke *et al.* (2004; 2007). Although the relationship was strong, the elemental ratios of the most recent layers of the juvenile otoliths showed variation that was not explained by the elemental ratios of the surrounding water. Variation has been shown to be influenced by temperature (Campana, 1999), salinity (Fowler *et al.*, 1995) or exposure delay (Elsdon and Gillanders, 2005). Nevertheless, the significant relationship derived for each elemental ratio allowed the otolith chemistry to be used to predict the elemental chemistry of the area in which the otolith layer was deposited. Given that otolith microchemistry was driven by water elemental signatures, changes in the linescans indicated movement of juvenile coho. Although the otolith linescans show considerable noise and autocorrelation, the breakpoint analysis (BPA) was sufficiently flexible to detect breakpoints in the line scans. The validity of the breakpoints would ideally be tested by the use of conventional tags on the same fish, but conventional tags cannot be used with fish of the size targeted by this study.

Interpreting the breakpoints in the data, unfortunately, was hampered by the limited differentiation between the waterbodies revealed by the DFA. While there were differences among some of the Horsefly tributaries, there was considerable variation within and overlap among the groups which made predicting location based on water chemistry unreliable. The variation within a waterbody means that changes in otolith microchemistry may result from movement to a different section of the waterbody, and not necessarily from movement between waterbodies. As a result, it is unlikely that movements between most of waterbodies of this watershed can be mapped through otolith microchemistry. Although the DFA could

not differentiate between areas within the watershed, it indicated relatively good differentiation between the Horsefly watershed and the Quesnel and Fraser River systems; even if movements within the Horsefly system cannot be characterized, it may be possible to determine if juveniles spawned in McKinley Creek use the Horsefly system to rear or if they quickly travel downstream to rear in other areas.

The possibility that microchemistry changes are due to environmental changes and not emigration, cannot be ruled out (Elsdon *et al.*, 2008). Temporal variation in water elemental ratios is a possible source of error in the use of otoliths for tracking purposes (Elsdon *et al.*, 2008). While it appears evident that marine and estuarine waters show strong temporal variation (see Elsdon *et al.* (2008) for review), most freshwater studies found temporal variation to prove no barrier to identifying locations from otolith chemistry (Thorrold *et al.*, 1998; Wells *et al.*, 2003; Clarke *et al.,* 2004; Limburg and Siegel, 2006). Therefore, changes in otolith signatures in the Horsefly system are unlikely to be due to changing water chemistry around a stationary fish, although budgetary constraints prohibited testing of this hypothesis.

Habitat Use in the Horsefly Watershed

While, with some exceptions, it was not possible to trace movements to individual waterbodies, the use of otoliths as natural tags provided insight into habitat use for interior Fraser coho in the Horsefly watershed. Despite the lack of distinct signatures for many of the sampled areas, the breakpoint analysis (BPA) indicated that fish moved between areas that differed in chemical signature. The BPA suggests McKinley Creek juvenile coho use an average of three habitats before final seaward migration. Previous work has indicated that coastal coho are fairly stationary during the juvenile life stage (Bell *et al.,* 2001; Roni and

Quinn, 2001b) and it is often assumed that deviations from strict site-fidelity in juvenile coho are caused by forced migration (Chapman, 1962; Bell *et al.,* 2001; Roni and Quinn, 2001b; Minakawa and Kraft, 2005). The results of my study indicate that emigration may be a normal characteristic of interior Fraser coho life history. Juvenile coho that emigrate have sometimes been found to have higher growth and survival rates than stationary juveniles (Tschaplinski, 1982; Swales and Levings, 1989; Kahler *et al.,* 2001). A positive effect on growth rate and survival suggests that movement carries few penalties and confers benefits to individuals. The benefit of emigration to salmonids has been explained as a consequence of "egg-fry conflict" in which the cold, low production streams which benefit incubating eggs are ill-suited for rearing juveniles (Quinn, 2005; Koski, 2009). Emigrating from natal areas may allow juvenile coho to find more suitable habitat.

McKinley Creek coho appear to spend most of their rearing period within the Horsefly watershed and do not move downstream until late in the freshwater life stage. While some segments were identified as a Fraser River signature, they were almost all the earliest segment, suggesting the possible influence of the maternal signature rather than previously-unheard of extensive upstream migration. Once this is taken into account, it would appear that the Quesnel River and the Fraser River are likely only used as a migration corridor by coho from McKinley Creek, and do not have an appreciable contribution to rearing habitat for coho in the Horsefly watershed.

The cluster analysis indicated the presence of two groups attributed to Woodjam Creek (Figure 1.6). Group 3, however, was very different from Group 4 and may be the result of residence in an unknown location not included in the water sampling. None of the individuals that reared in Woodjam Creek were likely hatched in that area, as no spawning was observed in Woodjam Creek during two spawning seasons. Juvenile coho have been

reported to use non-natal tributaries as rearing habitat, especially in the fall (Bramblett *et al.*, 2002; Anderson *et al.,* 2008; Koski, 2009), and interior Fraser coho have been suggested to follow this pattern as well (Shepherd *et al.*, 1986). The cluster analysis supports this hypothesis, provided other tributaries are used in the same manner as Woodjam Creek.

Relevance

The results of this study provide some indication that the life history of interior Fraser coho in McKinley Creek may involve substantial movement between areas, and that tributaries may provide important rearing habitat. Most rearing seems to take place within the Horsefly watershed, but juvenile coho move frequently within the watershed. Salmonid habitat requirements are often examined with the assumption juvenile salmonids are stationary, and therefore usually refer to a single natal reach or stream (Bovee, 1978; McMahon, 1983; Nickelson, 1998). The current Recovery Plan for interior Fraser coho seems to follow this assumption, identifying only sections of mainstem rivers for conservation with little recommendations for the preservation of associated tributaries (Interior Fraser Coho Recovery Team, 2006). The evidence gathered from the otoliths of McKinley spawning coho suggests that a new approach is needed, where larger watersheds are considered, with more emphasis on tributaries, and additional research to indicate emigration patterns. Unfortunately, identifying patterns of movements may be hampered by the limitations of otolith microchemistry as a natural tag. While microchemistry may be useful in other regions, it has limited use in the Horsefly watershed.

Chapter 2: Microhabitat Characteristics Influencing Juvenile Interior Fraser Coho Habitat Use

ABSTRACT

Interior Fraser coho provide an excellent model group for the study of population-level adaptations to novel environments. Severe recent population declines that may be due to habitat destruction also necessitate habitat assessments. This study examined the characteristics associated with habitat use by interior Fraser coho juveniles in interior British Columbia, allowing a contrast of their habitat use patterns against those observed in coastal coho populations. Juvenile interior Fraser coho presence and abundance in microhabitats were measured by minnow trapping, and the characteristics of each microhabitat assessed. Candidate explanatory models were created based on biological relevancy and Akaike's Information Criteria was used to select the model that best explained the observed patterns of presence and abundance. Stream width had a negative effect on coho presence and also abundance, while instream cover, overhead cover, and gravel substrate showed a positive association. Water velocity had a negative effect on coho presence and a positive effect on abundance. Instream cover, overhead cover, and stream width appear to influence juvenile interior Fraser coho habitat use patterns differently from the effects reported on coastal juvenile coho habitat use. These findings cast doubt on the current practice of assuming that habitat requirements are transferrable between spatially disparate populations. The models may also have value for future management practices in the region by informing policy makers on which habitat characteristics are of highest priority when attempting to preserve or restore habitat for juvenile interior Fraser coho salmon.

INTRODUCTION

Studies of habitat selection are common in fish ecology research, where the results of

such studies are often used to provide direction for conservation efforts (McMahon, 1983;

Knowler *et al.*, 2003). Consequently, examining habitat selection is a popular approach for

regulatory bodies (McMahon, 1983; Shepherd *et al.*, 1986), as it has implications for the

management, conservation, and restoration of habitats (McMahon, 1983; Gore *et al.*, 2001;

Knowler *et al.*, 2003; Morris, 2003). Implicit in the use of habitat selection information is the

assumption that the information is applicable in the situation in which it is to be used. The

destruction of freshwater habitat through anthropogenic means is considered one of the

greatest threats to salmonid populations (Nehlsen *et al.,* 1991; Frissell *et al.*, 1986). Current

declines in many salmon populations on the west coast of North America have resulted in

widespread concern for their future viability (Nehlsen *et al.*, 1991). Managing salmonid

populations requires accurate, scientific information identifying habitat requirements in order

to address the sources of the decline.

Like other species of salmon, many coho salmon (*Oncorhynchus kisutch*) stocks have

been identified as "at risk", likely due at least in part to the destruction of their freshwater

habitat (Nehlsen *et al.*, 1991). Efforts have been made to combine a number of studies of

juvenile coho habitat to create an overarching description of juvenile coho habitat

requirements. McMahon (1983) found that food and cover were the most important factors

identified by previous studies, and pools and riffles with abundant cover both on the bank

and in the stream, little fine sediment, and water between 10 ºC – 15 ºC and dissolved oxygen

near saturation provided the optimum habitat for rearing coho parr. Shepherd *et al.* (1986)

used data from 16 bioreconnaissance studies undertaken by the Salmonid Enhancement

Program in British Columbia, Canada to evaluate the importance of habitat variables in

juvenile coho habitat use. They concluded that habitat type and velocity were the most important variables, resulting in areas of "slow" water velocity being the most commonly used habitat by juvenile coho. Keeley and Slaney (1996) surveyed existing literature to develop a picture of the "average" habitat used by juvenile coho. When the findings of the studies in their survey were compiled, the mean water depth of a habitat in which juvenile coho were found was 20cm, the mean water velocity 11cm/s, and the mean substrate size was 5 on a scale of 1-10.

Previous work emphasized coho from coastal streams, but in accordance with the assumption of full transferability, data from different areas were combined with no acknowledgement given to the different geographical sources included. There is growing scepticism over this approach, and an increasing body of evidence suggests that habitat preferences do not have full transferability among populations and that generalizations should be treated cautiously (Leftwich *et al.*, 1997; Mäki-Petays *et al.*, 2002; Guay *et al.*, 2003). It is likely that some preference variables are fairly universal among different populations of the same species, while others vary considerably (Beecher *et al.*, 2002; Guay *et al.*, 2003). Shepherd *et al.* (1986) noted that while velocity and habitat type showed relatively consistent trends among studies, all other measured habitat characteristics, namely depth, substrate, and in some cases cover, were characterized by so wide a range of preferences as to impede attempts to generalize. This may point towards several juvenile coho habitat selection strategies in action in the different populations of coho included in the previous studies.

In British Columbia, several distinct stocks of coho salmon have been identified. Even within the Fraser River there appears to be multiple distinct groups with little genetic exchange. The coho salmon found spawning near the mouth of the Fraser River are closely

related to coho found in other nearby coastal areas, while genetic analysis indicates coho spawning above Hell's Gate Canyon, interior Fraser coho, are a distinctly different stock, and have been for at least 10,000 years (Small *et al.*, 1998). Despite recent reports of an alarming 60% population decline between 1990 and 2000, much about interior Fraser coho is still unknown, including the exact sources of the decline (DFO, 2001). As it seems likely that freshwater habitat destruction may play a part in these declines, the Interior Fraser Coho Recovery Team's three year strategy included the recommendation that critical habitat for interior Fraser coho should be identified and preserved or restored to maintain healthy populations (Interior Fraser Coho Recovery Team, 2006).

The objective of this study was to determine physical and biological factors influencing habitat use by juvenile interior Fraser coho on a microhabitat scale. The Horsefly-McKinley watershed is an area which contains one of the few substantial populations of interior Fraser coho known to exist outside of the Thompson River. Microhabitats ($1m^2$ in scale) in this watershed were assessed in the summer of 2007. All major stream types available were sampled: mainstem, offchannel areas, and tributaries of multiple sizes. In addition to measuring the presence or absence of juvenile coho in each microhabitat and the number of juvenile coho captured, stream characteristics, water characteristics, measurements of cover, and biological characteristics were recorded. A literature review indicated the variables most likely to be important, from which candidate models were built. Logistic regression models were built to explain coho presence/absence based on habitat characteristics, and the distribution of the catch data necessitated the use of Zero-Inflated Poisson (ZIP) models to examine catch data. The candidate models were evaluated through the use of Akaike's Information Criteria (AIC), and validated against habitat assessments made the next year to test their predictive strength.

METHODS

Study Area

The Horsefly-McKinley system consists of the Horsefly River, a fifth-order watercourse, a large creek called McKinley Creek that runs from Elbow Lake through McKinley Lake (which divides it into Upper and Lower McKinley) to the Horsefly, as well as numerous small tributaries (Figure 2.1). Most juvenile coho can be found in the Horsefly between the small tributary of Patenaude Creek and the McKinley confluence, as well as within the McKinley itself (Shepherd *et al.*, 1986; Andrew Meshue, Northern Shushwap Tribal Council, personal communication). Above the McKinley confluence on the Horsefly River is an impassable 30m waterfall. The present study focused on McKinley Creek downstream from McKinley Lake, and the Horsefly from the McKinley confluence to Woodjam Creek (Figure 2.1). To gain a fuller understanding of the possible patterns of habitat use in the Horsefly system, and because there is some evidence that juvenile coho may prefer smaller streams (<5m width) (Bendock and Bingham, 1988; Rosenfeld *et al.*, 2000), smaller tributaries, including Woodjam Creek and Patenaude Creek, were also surveyed.

The Horsefly is composed of moderately paced areas with cobble substrate, and slow-moving sections with a substrate of almost entirely mud. The McKinley Creek is composed of mostly riffles and glide sections with the occasional pool, and contains a temperature control structure at the outlet of McKinley Lake. Most of the tributaries to the Horsefly River are small, fed from springs or small ponds, and relatively free of fine sediments. McKinley Creek has no substantial permanent tributaries.

Figure 2.1: *The areas included in the study site (black), including Woodjam Creek, Patenaude Creek, McKinley Creek and parts of Horsefly River from the McKinley confluence to Woodjam Creek.*

McKinley Creek is surrounded by forested land, although a substantial portion of its watershed has been logged. The upper portion of the Horsefly River is in a similar state, although shortly after its confluence with the McKinley it enters an agricultural area in which most of the forest has been cleared. It is in this section that most of the tributaries enter the Horsefly River, and many run through pastureland, paddocks, or fields before entering the Horsefly River. There has been some restoration work on sections of the Horsefly, including planting, access restoration, cattle exclusion, and bank protection. Likewise, several of the tributaries, especially Woodjam Creek and Patenaude Creek, have been the focus of restoration efforts, including replanting the riparian zone and excluding cattle from some areas. Most of the agricultural land is the property of small-scale farmers, although a section adjacent to Patenaude Creek is owned by the Land Conservancy.

Habitat Sites and Assessment

From June-August, 2007, 87 microhabitat sites were assessed in the watershed, 79 of which were used in the final analysis, after 8 were removed due to missing data or equipment malfunction. The final 79 included 22 sites from Horsefly River, 32 from McKinley Creek, 13 from Patenaude Creek, 15 from Woodjam Creek, 2 from Black Creek, and 3 from Wilmot Creek.

Microhabitats were selected to sample as many available habitat types as possible from the study area. All available habitat types were not represented in proportion to their prevalence in the study area, however, as there was an emphasis on areas that appeared superficially to provide acceptable habitat as indicated in the available literature. This is a violation of the assumption that the habitat characteristics measured accurately reflect available habitat in the stream (Keating and Cherry, 2004). Due to time constraints and the

relative rarity of selected habitats relative to unselected habitats, however, unequal sampling was deemed to be necessary to ensure an adequate sample of selected habitats. This emphasis allows habitat variables to be examined at a finer resolution than a more general sampling design would allow and has been used in other studies (Rosenfeld *et al.*, 2000; Apps *et al.*, 2004; Hanrahan *et al.*, 2004). As a result, this study is not a measurement of habitat selection, but rather the characteristics that most accurately separate a site in which coho were present from one in which they were not. Sites were placed at least 8m apart from one another to avoid the possibility of interactions between sites.

Coho juvenile presence and abundance was measured by using minnow traps baited with preserved salmon roe. Minnow traps were chosen as a sampling method because they accurately determine basic patterns of abundance while preventing injury, mortality, and stress that may be caused by more invasive sampling methods (Shepherd *et al.*, 1986; He and Lodge, 1990; Bryant, 2000). In light of the population declines and the uncertain population status of interior Fraser coho, the reduced potential for injury and mortality with minnow traps was viewed as an important feature for sampling.

Minnow traps were set for approximately 3 hours. Most traps were set in the morning and removed in the afternoon or set in the afternoon and removed in the evening. In sites where fish were observed when setting the minnow trap, however, the trap was set in the afternoon and left until the next morning to ensure that the fish would be caught so their species could be identified. The exception to this method was Wilmot Creek, which had such high population densities that overnight trapping would likely result in overcrowding of the trap. After the sampling period, the traps were removed and all fish in the trap identified and enumerated. Identifications was aided by the use of 30mg/L clove oil in a 1:10 clove oil:ethanol ratio as an anesthetic where necessary. The anesthetized fish were then transferred

to a bucket of clean water, allowed to recover and released. Observations of trap efficacy during the raceway study in Chapter 3 indicated that traps rarely caught all the fish in an area, nor did fish appear to move from other areas in response to the trap, so the risk of "false positives" due to the long trapping period appeared low, while overnight sampling reduced the likelihood of "false negatives" due to catching no fish in an area where fish were present. The data was examined during the statistical modeling to test for bias created by the unequal sampling (see Statistical Analysis section for details).

Twenty one characteristics comprising the physical, chemical, and biological habitat of the area were assessed in the $1m^2$ area surrounding the trap location (Table 2.1). The stream itself was described by measurements of wetted width and water depth. The presence or absence and depth of the overhang on the nearest bank were recorded. Bank condition was estimated on two indices by ranking the extent of bank vegetation and bare rock or soil on scales of 1-4, with 1 indicated little or none of the evaluated component, and 4 indicating that the bank was entirely composed of that groundcover. The percentage of substrate comprised of fine sediment, gravel, cobble, and boulder was estimated as suggested by Bain and Stevenson (1999) and developed by Cummins (1962). The embeddedness of the substrate was also visually estimated on a scale of 1-3 as suggested by Bain and Stevenson (1999).

Basic chemical measurements of water were taken at each site: dissolved oxygen was measured on a YSI 550A Handheld Dissolved Oxygen Instrument, and a Hanna Instruments Model HI98129 meter was used to measure water pH, temperature, and conductivity. The presence or absence of water turbulence or turbidity sufficient to obscure the substrate was noted. Water velocity at 60% depth was measured with as described in Bain and Stevenson (1999) using a Swoffer Model 2100 Velocity Meter. Although velocity at 60% depth is a

Table 2.1: *Variables measured in habitat analysis*

Characteristic Category	Variable	Unit	Measured as
Stream	WIDTH	m	Distance from bank to bank of stream or offchannel
	DEPTH	m	Water depth at trap
	OVERHANG	cm	Distance from outer edge of overhang to deepest undercut
	VEGETATION	1-3	Amount of vegetation on bank: 1 = <80%; 2 = 80%-95%; 95%<vegetated
	ROCK	%	Amount of bank covered by rock: 1 = <5%; 2 = 5% - 10%; 3 = 10%
	FINES	%	Percentage of substrate composed of fines
	GRAVEL	%	Percentage of substrate composed of gravel
	COBBLE	%	Percentage of substrate composed of cobble
	BOULDER	%	Percentage of substrate composed of boulders
	EMBEDDEDNESS	1-3	Substrate embedded in fines: 1 = little or none; 2 = moderate; 3 = most
Water	TEMP	ºC	Water temperature
	DO	mg/L	Dissolved oxygen
	PH	pH	Water pH
	CONDUCTIVITY	µS	Conductivity
	VELOCITY	m/s	Velocity at 60% of depth at trap
	TURBIDITY	0/1	Do water characteristics obscure substrate?: 1 = yes; 0 = no
Cover	INSTREAM	1-9	Overall density of instream cover: 1= none to 9=heavy
	WOOD	1-3	Amount of woody instream cover: 1 = little or no; 2 = moderate; 3 = heavy
	EMERGENT	1-3	Amount of emergent vegetation: 1=little or no; 2=moderate; 3=heavy
	SUBMERGENT	1-3	Amount of submerged vegetation: 1=little or no; 2=moderate; 3=heavy
	OVERHEAD	%	Percentage overhanging cover

debatable measurement for fish habitat, Beecher *et al.* (2002) found it was sufficient to determine coho juvenile distribution within a stream.

Measurements of cover were made within $1m^2$ of the trapping location and involved several factors which were evaluated separately. Overhead cover due to overhanging rocks, bushes, or trees was measured using a modification of the densitometer method described in Bain and Stevenson (1999). In this modified version, photographs were taken of the canopy directly above the site, and then overlaid with a 36 point grid. By counting the number of grid intersections that fall on some form of overhead cover versus the number that do not, the density of the overhead cover was estimated. Visual estimates were made of the amount of instream cover resulting from woody debris, emergent vegetation, and submerged vegetation. These estimates were ranked on a scale from 1-3, with a rank of 1 indicating little instream cover, 2 indicating moderate instream cover, and 3 indicating high levels of instream cover. As woody debris, emergent vegetation, and submerged vegetation were not the only sources of instream cover, the overall amount of instream cover was also visually estimated on a scale of 1-9, which was developed for this study. This ranking included cover due to woody debris, vegetation, and other sources of instream cover such as boulders or other debris. Increasing rankings indicated increasing amounts of cover and instream complexity.

Statistical Analysis

All statistical calculations were carried out using the statistical program R (R 2.6.0, The R Foundation for Statistical Computing, 2007). The function utilized for generalized linear mixed models was "lmer" from the "lme4" package. ZIP modeling utilized the "zeroinfl" function.

Presence/Absence Model

The relationship between the presence (1) or absence (0) of coho at a site and the measured characteristics was described through a series of candidate logistic regression mixed effects models as described by Bates (2005). These models used coho presence or absence from the site as a binomial response variable and evaluated the explanatory value of the measured habitat variables through a process of marginal fitting. The stream in which the site was located was included as a random effect in order to reduce the impact of random inter-stream differences (Raudenbush and Liu, 2000). The variables for which the existing literature suggested the possibility of a non-linear relationship (velocity, instream cover, and temperature) were examined by fitting a single-variable model with that variable as either a linear or a parabolic variable. The Akaike's Information Criteria (AIC) scores of a model describing linear relationship and a model describing a parabolic relationship between the variable and coho presence were compared to determine which relationship was the most appropriate fit to the data, which in all cases was linear. Two variables, the percentage of substrate composed of boulders and the concentration of dissolved oxygen in the water, were removed before the analysis due to rarity of non-zero values and missing data due to equipment malfunction, respectively.

Twenty two candidate models were created using variables chosen based on existing literature and biological relevancy. An information-theoretic approach as outlined in Burnham and Anderson (1998) was followed in the selection of the most appropriate model. In accordance to this approach, the candidate models were compared using Akaike's Information Criteria corrected for small sample size (AIC_c) scores, as well as the AIC weight (w_i) to further compare the relative strength of the models. The candidate models focused on the environmental variables noted in previous studies as important for juvenile coho and

other salmonids, namely, stream width, stream depth, water velocity, measures of cover, water temperature, and substrate composition (models listed in the Results section). A null model with the intercept as the only variable was included to test for relevance of the others, and a model with the trapping time was included to check for biases based on the sampling regime. The model was also run with and without trapping time as a variable. The addition of trapping time had little effect on the AIC_c score and no effect on the inclusion of other variables. The global model was tested to determine that there was no evidence of non-linear relationships, as measured by Variance Inflation Factors and that the dispersion factor indicated normal dispersion.

Catch Model

A second model, the "catch model", was created to identify the variables correlated with the total number of fish caught in each site. A Zero-Inflated Poisson (ZIP) model was chosen to best describe the data, as the number of sites in which no fish were caught caused a deviation from the otherwise Poisson distribution through overdispersion, necessitating the use of a zero-inflated model to compensate (Chin and Quddus, 2003). The ZIP distribution accounts for the overrepresentation of zeros by use of a dual-state process in which sites are either in a zero, or perfect, state (in which the habitat is unsuitable, and there are no fish) or a non-zero, imperfect, state (1+ fish, in which the habitat is suitable and there is likely fish present) (Chin and Quddus, 2003). The process of moving from a zero to a non-zero state (i.e., the variables determining the suitability of a site for at least one fish) was examined through binomial generalized linear regression, while the non-zero state (i.e. the variables that control the worth of a suitable site by influencing the number of fish present) was examined by generalized linear regression with a Poisson distribution (Chin and Quddus,

2003). Consequently, the factors influencing both whether or not a site had fish and number

of fish in areas that were suitable to fish are examined separately by the model and the two

resulting equations combined to make a single predictive model encompassing both states.

As the zero-state analysis was similar to the presence/absence model created above, the

variables from the presence/absence model were used for the zero-state equation on all

candidate models: the only variation was in the non-zero state equation. A limitation of ZIP

models is that they are designed for use with count data, and therefore can only be used with

integers. Due to this limitation, "total fish captured" at a site was used as the dependent

variable instead of the more commonly used variable of catch-per-unit-effort; a variable

derived through calculations which result in non-integer data. As with the presence/absence

model, one of the candidate models used trapping time as the sole variable to test for bias

introduced through unit effort. The candidate models were evaluated through the information

theoretic approach as described for the presence/absence model above.

Model Validation Data Collection

During the period of July 18th-July 22nd, 2008, new habitat sites were assessed to use

as a validation set for the habitat assessment models generated from the previous year's data.

Minnow traps baited with salmon roe were set in Moffat Creek, Barker Creek, Upper

McKinley Creek, and areas of McKinley Creek, Black Creek, and Horsefly River that had

not been trapped the previous summer. All traps were left overnight. The next day, the fish

within were identified and released. A total of 48 sites were sampled. Coho were caught at 24

sites and the remaining 24 sites were designated "uninhabited". These sites were assessed

using a subset of the original habitat assessment procedure. Only the factors identified as

significant by the models were examined. This shortened habitat assessment included stream

width, stream depth, water velocity, overhead cover, instream cover, fines, gravel, and water temperature. The characteristics were measured using the protocol developed for the original habitat assessment as described above.

The presence/absence model was used to predict the probability of finding coho in each site. At sites where the calculated probability was greater than 0.5, the model was designated as predicting the presence of coho, while a probability of less than 0.5 predicted the absence of coho. Sites at which the model correctly predicted the presence or absence of coho were assigned a value of 1, while sites in which the prediction was incorrect were assigned a value of 0. A one-sample t-test compared the rate of correct prediction to the 50% rate of correct prediction that would result from a random assignation of coho presence or absence. A receiver operating characteristic (ROC) curve (Hanley and McNeil, 1982; Pearce and Ferrier, 2000) was also created and the area under the curve used to validate the predictive value of the model. This method compares the sensitivity and false positive fraction of the model's predictions to determine the ability of the model to differentiate correctly between a used and an unused site.

The model developed to explain the catch number also used the validation set to generate predictions using the "predict" function in R. These predictions were compared to the actual catch numbers by ordinary least squares regression. Olden and Jackson (2000) have shown that while this method of validation had a slight tendency to underestimate predictive value, the relationship between predicted and observed results give a fairly valid measure of accuracy. Both predicted and observed data were transformed using a log+1 transformation to achieve normalcy before the regression was calculated.

RESULTS

Presence/Absence Model

Of the 87 sites sampled, 36 were found to have coho present, while at 51 sites no coho were observed. There were three models with AIC_c values less than two apart. The top three presence/absence models identified stream width, water velocity, the amount of overhead cover, and the amount of instream cover as important variables, two identified percent gravel substrate, and one identified temperature (Table 2.2). The AIC_c weight of the top model was 0.464, with the second and third model weighted 0.268 and 0.247 respectively indicating some uncertainty regarding the inclusion of gravel substrate and temperature.

A summary of the regression coefficients and odds ratios for the variables in the top ranked model is shown in Table 2.3. Water velocity had a strong negative effect on the presence of juvenile coho salmon (Figure 2.2). Stream width was found to negatively influence the probability of the presence of coho (Figure 2.3). Overhead cover appeared to have a positive impact (Figure 2.4), and a similarly positive effect was found with instream cover (Figure 2.5). The percentage of substrate that was composed of gravel was also positively associated with the probability of presence (Figure 2.6)

Presence/Absence Validation

The top presence/absence model generated correct predictions at 30 of 48 sites sampled in 2008. The top presence/absence model had significantly more predictive ability than would be expected from a randomly generated set of predictions, which would be expected to be correct 50% of the time (t_{47} = -4.03, p < 0.001).

Table 2.2: *The 22 candidate models explaining the presence or absence of juvenile coho using habitat variables. Models are reported with the number of variables (k), their AIC$_c$ value, the difference between their AIC$_c$ value and the best candidate model, and the AIC$_c$ weight (*w$_i$*). For parameter descriptions, see Table 2.1.*

Ranking	Parameters	k	AIC$_c$	ΔAIC$_c$	*w$_i$*
1	Instream + Velocity + Width + Gravel + Overhead	5	76.6	0	0.464
2	Instream + Velocity + Width + Gravel + Overhead + Temperature	6	77.6	1.0	0.268
3	Instream + Velocity + Width + Overhead	4	77.9	1.3	0.247
Global	Instream + Velocity + Width + Depth + Overhead + Temperature + Wood + Gravel + Fines	9	83.5	4.8	0.03
4	Instream + Velocity + Width + Gravel	4	84.8	8.4	0.07
5	Velocity + Width + Gravel	3	85.2	9.0	0.01
6	Instream + Velocity+ Width	3	86.0	9.8	0.00
7	Velocity + Width + Fines	3	86.3	10.2	0.00
8	Velocity + Width	2	86.9	10.9	0.00
9	Velocity + Width + Wood	3	88.6	12.5	0.00
10	Width + Overhead	2	94.1	18.1	0.00
11	Instream + Width + Temperature	3	96.1	20.0	0.00
12	Instream + Width	2	98.3	22.3	0.00
13	Instream + Velocity	2	98.4	22.4	0.00
14	Instream + Width + Gravel	3	98.8	22.6	0.00
15	Instream + Overhead	2	99.1	23.0	0.00
16	Velocity + Temperature	2	99.8	23.8	0.00
17	Velocity	1	101.9	26.0	0.00
18	Width	1	102.4	26.5	0.00
19	Width + Temperature	2	106.1	30.1	0.00
20	Instream	1	108.8	32.9	0.00
21	Time	1	114.9	38.3	0.00
22	Intercept	0	119.1	42.5	0.00

Table 2.3: *Summary of variables in the top model of coho juvenile presence and absence based on physical characteristics. Each variable is reported with its regression coefficient and standard error in parentheses, along with the odds ratio. For parameter descriptions, see Table 2.1.*

Model	Intercept	Width (m)	Velocity (m/s)	Overhead Cover (%)	Instream	Gravel (%)
Presence/Absence	-1.02 (1.1)	-0.06 (0.04)	-16.3 (5.9)	0.03 (0.01)	0.15 (0.15)	0.02 (0.01)
Odds Ratio		0.91	8.0×10^{-8}	1.03	1.16	1.02
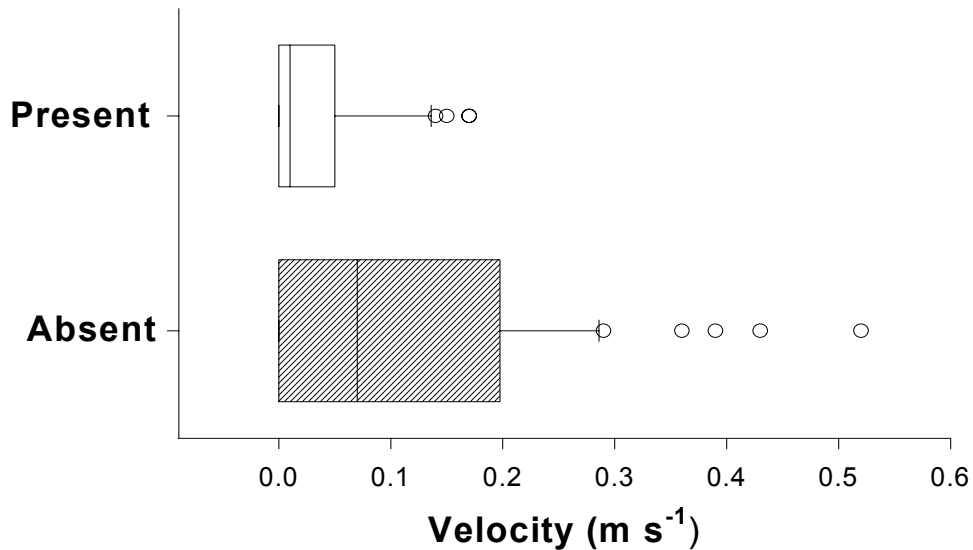
Figure 2.2: *Average velocity (middle bar), quartiles (box) with 10 and 90% percentiles (whiskers) and outliers at sites where juvenile coho were present and absent.*
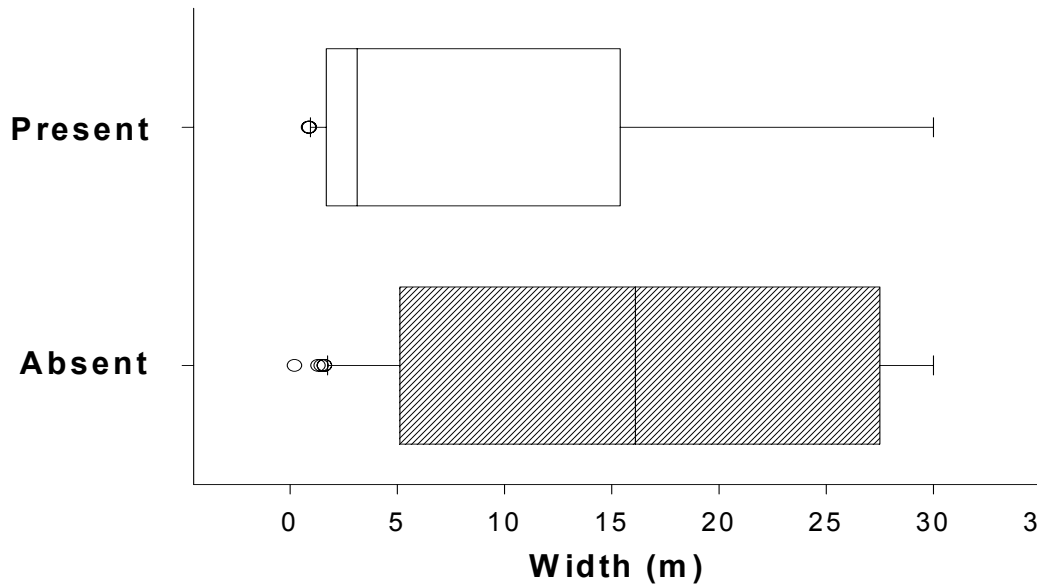
Figure 2.3: *Average stream width (middle bar), quartiles (box) with 10 and 90% percentiles (whiskers) and outliers at sites where juvenile coho were present and absent.*
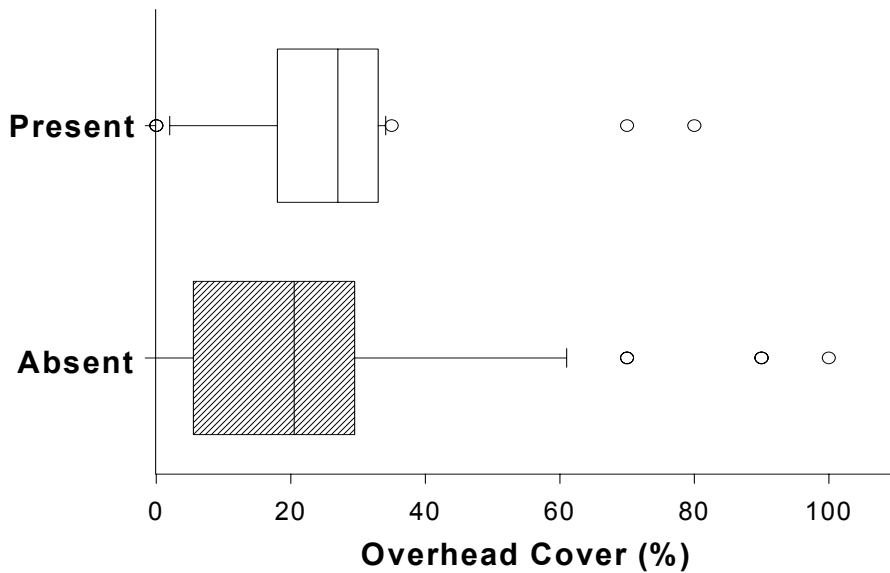
Figure 2.4: *Average overhead cover (middle bar), quartiles (box) with 10 and 90% percentiles (whiskers) and outliers at sites where coho juveniles were present and absent.*
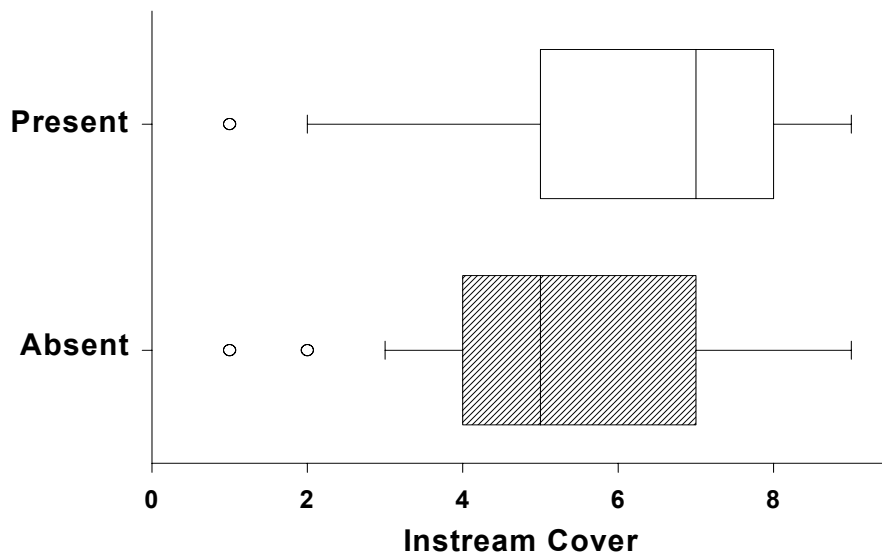
Figure 2.5: Average instream cover (middle bar), quartiles (box) with 10 and 90% percentiles (whiskers) and outliers at sites where juvenile coho were present and absent.
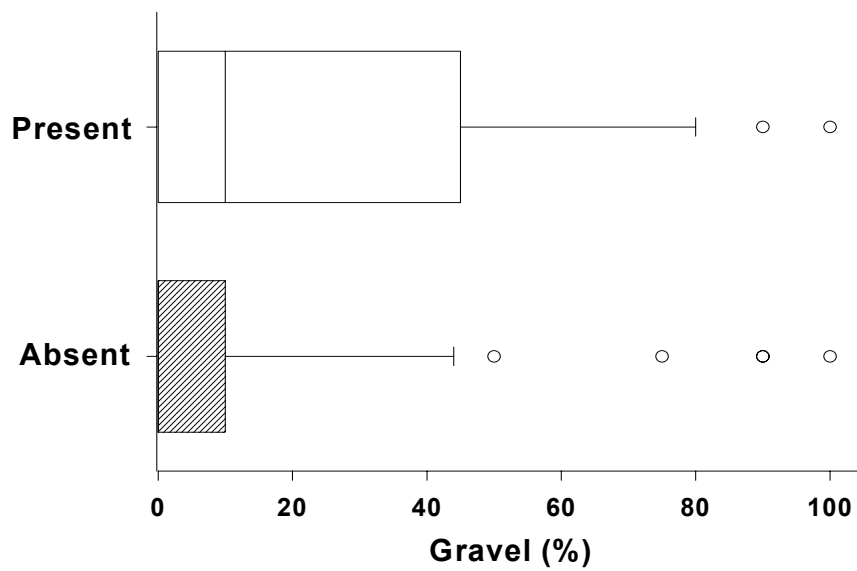
Figure 2.6: Average percentage of substrate composed of gravel (middle bar), quartiles (box) with 10 and 90% percentiles (whiskers) and outliers at sites where juvenile coho were present and absent.

The model had high refinement as defined by Pearce and Ferrier (2000) as the predicted probabilities ranged from 0.00 to 0.95, encompassing almost the full range of possible probabilities. The area under the ROC curve was 0.693. This suggests that the presence/absence model had a 69.3% chance of distinguishing properly between two sites: one with coho and one without coho (Hanley and McNeil, 1982). Using the suggestions by Pearce and Ferrier (2000) this model's area under the ROC curve is 0.007 short of the definition of a model "reasonable discrimination", and falls under the category of "poor discrimination".

Catch Model

The variables in the top model explaining the number of fish caught were width, water velocity, gravel substrate, overhead cover, and cover (Table 2.4). Increased width was negatively associated with catch. Both overhead cover and instream cover were positively associated with the number of fish caught. In contrast, velocity and gravel were both associated with an increased number of fish (Table 2.5). The AIC_c weight of the top model was 0.91, indicating that it was very likely to be the best of the models.

Catch Model Validation

The catch model showed significant predictive value when compared with the 2008 sites in the validation set ($R^2 = 0.17$, $p = 0.004$; Figure 2.7).

Table 2.4: *Candidate models to explain number of juvenile coho. Models are reported with the number of variables included (k), their AIC_c value, the difference between their AIC_c value and the best candidate model, and the AIC_c weight (*w_i*).*

Ranking	Parameters	K	AIC_c	Δ AIC_c	w_i
1	Instream + Velocity + Width + Gravel + Overhead	5	270.7	0.0	0.91
2	Instream + Velocity + Width + Cobble + Overhead	5	277.9	7.2	0.03
3	Instream + Velocity + Width	3	277.9	7.2	0.02
4	Velocity + Fines	2	278.3	7.6	0.02
GLOBAL	Instream + Velocity + Width + Gravel + Overhead + Depth + Temp + Fines + Emergent + Cobble + Wood	11	279.3	8.6	0.01
5	Velocity	1	280.0	9.3	0.01
6	Velocity + Width + Depth + Cobble	4	280.5	9.7	0.01
7	Instream + Velocity	2	281.1	10.4	0.00
8	Instream + Velocity + Cobble	3	282.3	11.5	0.00
9	Instream + Width	2	286.1	15.4	0.00
10	Instream + Overhead	2	287.1	16.4	0.00
11	Instream	1	288.0	17.3	0.00
12	Temp + Fines + Emergent	3	288.5	17.7	0.00
13	Intercept	0	289.2	18.5	0.00
14	Width	1	289.8	19.1	0.00
15	Wood + Emergent	2	292.7	22.0	0.00
16	Width + Wood + Emergent	3	293.1	22.3	0.00
17	Time	1	299.9	29.2	0.00
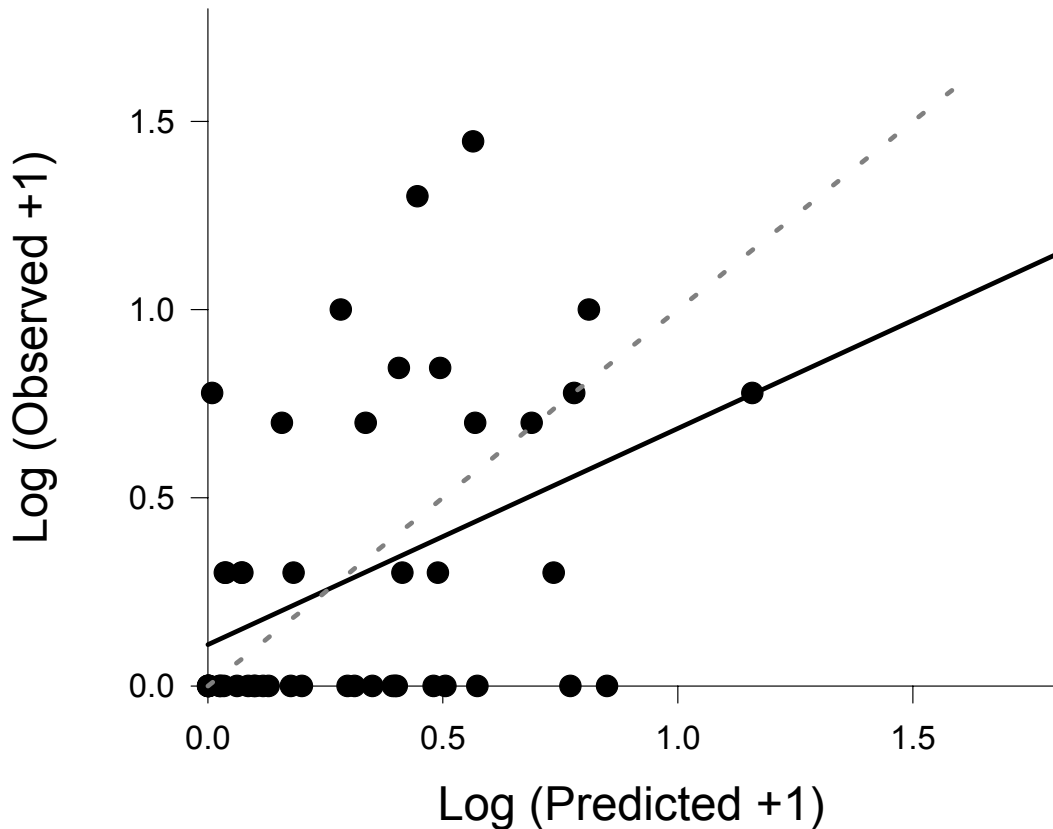
Figure 2.7: *Transformed values of predicted fish catch (Predicted) and the observed catch (Observed) for model validation sites collected in 2008. Regression lines indicate the line of best fit for the observed vs. predicted relationship (in black) and the line that would result from a perfect correlation (1:1 ratio) between the two values (grey dashed).*

Table 2.5: *Summary of variables chosen for model of juvenile coho catch rates. Variables that affect the perfect state (zero-catch) and non-perfect state (1+ catch) are reported separately. Each variable is reported with its estimate and standard error in parentheses. Note that the Zero-Catch State model indicates the probability of a site belonging to the Zero-Catch group.*

State	Intercept	Width (m)	Velocity (m/s)	Overhead (%)	Gravel (%)	Instream
Zero-Catch	2.23 (1.5)	0.08 (0.04)	19.9 (9.5)	-0.02 (0.02)	0.05 (0.03)	-0.23 (0.18)
1+ Catch	1.81 (0.44)	-0.06 (0.01)	2.33 (2.7)	0.007 (0.00)	0.02 (0.01)	0.03 (0.04)

DISCUSSION

The results presented in this study represent the first examination of habitat requirements for juvenile interior Fraser coho. Sampling methods were designed to assess use at the micro-habitat scale and the sampling approach directly assessed variables associated with stream characteristics, water characteristics, cover availability, and presence of other fish species. Both the presence/absence model and the catch model identified the same group of variables in the preferred candidate model: water velocity, stream width, gravel substrate, overhead cover, and instream cover.

Water Characteristics

The top models for both presence and abundance suggested a strong correlation between velocity and habitat use by coho salmon. Greater velocity was associated with the absence of coho in the top presence/absence model, but paradoxically, the top catch model also indicated that higher water velocity was also associated with increased numbers of coho. While the results appear contradictory where water velocity is concerned, they are explained if one considers the role of velocity in habitat use as the result of a cost-benefit trade-off. High velocity water provides a greater abundance of instream vertebrates due to drift, but holding in high velocity areas is energetically costly (Mundie, 1969; Hill and Grossman, 1993). While slow water may be attractive to juvenile coho for energetic reasons, explaining the association between low velocity and higher probability of coho presence, the low food input may prevent juvenile coho from aggregating in these areas.

Stream Characteristics

Width is not commonly measured as a habitat variable in studies of salmonid habitat, but was found to be negatively correlated with catch numbers in this study. Many studies treat width as a constant throughout their study area (Giannico, 2000; Bramblett *et al.*, 2002; Ebersole *et al.*, 2003) and when width is included as a habitat variable for salmonids, there is no agreement as to its significance even within the same species (Eklöv *et al.*, 1999; Myrvold, 2006). The association of coho with small tributaries, however, is well established (Dolloff, 1987; Nickelson *et al.*, 1992a; Nielsen, 1992; Bramblett *et al.*, 2002). Rosenfeld *et al.* (2000) found the highest densities of coho in streams that were narrower than 5m, indicating that coastal coho may also prefer narrow channels. This association is not ubiquitous in coho salmon research. Beecher *et al.* (2002) found that coho in the Washington streams they studied preferred deeper water, which is more likely in larger streams. Smaller streams have many advantages, including lower velocity and high structural complexity (Rosenfeld *et al.*, 2000), energetic advantages (Mundie, 1969), increased pool formation (Rosenfeld and Huato, 2003), and predator protection (Harvey, 1991).

Juvenile coho were found in association with an increased percentage of gravel as substrate. This preference for gravel was also noted in Sheppard and Johnson (1985) and Rosenfeld *et al.* (2000). A preference for gravel may be beneficial as gravel may provide protection as a source of cover (Gries and Juanes, 1998; Bradford and Higgins, 2001), or through aiding crypsis (Donnelly and Dill, 1984). Gravel may also provide better hunting grounds with more available aquatic invertebrates (Suttle *et al.*, 2004).

Cover Characteristics

Cover appeared to be a major influence on habitat use for juvenile coho. Juvenile coho were found to be positively associated with instream cover and to be present more often in areas with more overhead cover. The connection between salmonid juveniles and instream cover is well-established in the literature (Taylor, 1988; Nickelson *et al.*, 1992b; Giannico, 2000; Roni and Quinn, 2001a) and identified as important by both models in this study. Surprisingly, some studies show juvenile coho to have no preference or even a negative association with instream cover. Roni and Quinn (2001b) found that woody debris content within a pool had no effect on the densities of coho observed there. Likewise, some studies found woody debris to be a poor predictor of coho abundance and distribution (Fausch, 1993; Cederholm *et al.*, 1997; Rosenfeld *et al.*, 2000). The inconsistent findings suggest possible population-associated variability regarding the preference for instream cover. Variable preference for cover was noted by Taylor (1988) where 79%-89% wild-caught coho associated with cover objects in an artificial setting compared to 17%-36% hatchery-reared coho in a similar set-up. The association between coho and instream cover may be a characteristic of the population.

Overhead cover was also positively but weakly correlated with both the presence of coho in a site and the number of individuals at that site. While preference for overhead cover definitely varies among salmonids (Heggenes and Traaen, 1988), there has been some evidence to suggest that overhead cover is not an important factor for juvenile coho salmon (Glova, 1986). Overhead cover is generally associated with fish in two ways: as an influence on food intake and as a form of protection from avian predation and damage from UV radiation (Gotceitas and Godin, 1991; Kelly and Bothwell, 2002). The connection between overhead cover and food is unclear. Some studies have shown an increase in the input of

terrestrial insects with increased canopy cover (Wipfli, 1997). In contrast, greater abundance of food and more complex fish communities have also been found in the absence of overhead cover, suggesting overhead cover effects food supplies by preventing wind and rain from knocking canopy-dwelling terrestrial insects into streams (Growns *et al.*, 2003; Romaniszyn *et al.*, 2007). The discrepancies could be due to interactions between insect input and vegetation type (Mason and MacDonald, 1982; Wipfli, 1997; Romaniszyn *et al.*, 2007). My study would imply that the Horsefly River and possibly other streams supporting interior Fraser coho, are of the former category and increased overhead cover provides benefits for juvenile interior Fraser coho. It would appear that forest composition, a factor not often noted in aquatic habitat studies, may have a significant impact on the transferability of habitat factors between areas.

Synthesis

When all habitat characteristics are considered together, the findings of this thesis give insight into the habitat use patterns of juvenile Interior Fraser coho and the environmental pressures that may influence habitat choices. Stream width, velocity, and gravel substrate have all been shown to be important to coastal populations as well as interior Fraser coho (McMahon, 1983; Sheppard and Johnson, 1985; Dolloff, 1987; Bramblett *et al.*, 2002). This indicates that to some extent, both populations face similar challenges with regard to mortality or reduced fitness from high-flow events and insufficient food. The other variables identified by my study as important – instream cover and overhead vegetation – have limited evidence as to their importance in coastal coho juvenile habitat (Glova, 1986; Taylor, 1988; Fausch, 1993; Cedarholm *et al.*, 1997; Rosenfeld *et al.*, 2000; Roni and Quinn, 2001b).

Model Predictive Value

Both models created to explain coho habitat use showed significant predictive value. Given how close the ROC area value of 69.3% from the presence/absence model is to 70%, and that it was generated by comparison with a test set removed both physically and temporally from the model-building set, I do not believe that falling 0.7% short of the cutoff is cause for discarding the model. While the 0.7% deficiency suggests caution when using the model for predictive purposes, it does not invalidate the findings with regards to general trends in habitat use by juvenile interior Fraser coho, as the model was able to predict coho presence with some degree of accuracy. Like the presence/absence model, the catch model describing the number of coho per site showed fair discriminative ability but also exhibited weaknesses in predictive power. In both cases the models predicted appropriately for a majority of sites, and therefore likely captured at least a portion of important relationships between juvenile interior Fraser coho and their habitat.

Relevance

The moderate-to-weak predictive strengths of the models created by this study would indicate that while they are useful in some contexts, they should not be used as a definitive description of coho habitat in all conditions. These models were created using a relatively small number of sites from a single watershed and likely do not encompass the full range of habitats available to interior Fraser coho throughout their range in interior British Columbia. This limits their potential as a predictor of coho production in streams across the region. I would not suggest that they be used as the sole measure of habitat suitability in other

locations, as they do not describe the majority of the variation in the number of juvenile coho at each site.

Instead of being used to calculate exact production numbers and probabilities, I would suggest that these models identify habitat characteristics that should be conserved at an appropriate state or for their return to an appropriate state after perturbation. The inclusion of three categories of habitat variables in both models emphasizes the need for a holistic, whole-stream approach to habitat management, as many seemingly unconnected habitat characteristics have the potential to influence coho habitat use.

The results of this study are in some areas contradictory to the results of previous habitat studies on coastal populations; several of the habitat variables suggested by the model as being important indicators of habitat use by interior Fraser coho do not have the same effect on coastal juvenile coho. These results highlight the dangers of assuming full transferability of habitat preferences between interior and coastal populations. It is evident that coho in interior areas interact differently with their environment when compared to coastal coho. The implications for fisheries management, both with this species and likely with other salmonids, are clear: where there are large differences in the hydrology or habitat composition between areas, the habitat requirements of populations must be studied separately.

Chapter 3: The Effect of Territorial Behaviour as a Factor in Juvenile Interior Fraser Coho Habitat Use

ABSTRACT

The influence of territorial behaviour in increasing food acquisition, maintaining population densities, and encouraging migration has often been noted in juvenile salmonids. Such behaviour may vary among populations in response to local environmental factors. Coho salmon (*Oncorhynchus kisutch*) are found throughout British Columbia, but environmental conditions differ between coastal and interior regions which may select for different life history traits. This study examined the behaviour of juvenile coho salmon found in the interior of British Columbia and compared it to territorial behavioural patterns reported in juvenile coastal coho. Habitat features were created in a concrete raceway to monitor spatial distribution and individual interactions. Juvenile coho were found to aggregate early in the season, then conform to a random distribution later in the summer. Interactions were overwhelmingly positive, with little aggressive behaviour. Interactions were stable throughout the diel cycle, but variation in type and extent of positive and aggregating behaviour was seen within and among individual trials. While territorial behaviour is difficult to quantify, there was little or no evidence of territoriality. Instead, coho exhibited slight schooling behaviour early in the season. This may indicate that the environmental conditions experienced by interior Fraser coho result in decreased benefits or increased costs for expressing territorial behaviour when compared to coastal populations. A similar effect may be found in other populations of coho or other salmonids that inhabit environments exhibiting a wide diversity of habitats, and indicate that behaviour within a species cannot be assumed to be static among populations.

INTRODUCTION

Behaviour of fishes has implications for management, conservation, population estimation, and survival, and has been the topic of much study (for example Grant *et al.*, 1998; Armstrong and Griffiths, 2001; Leis, 2002). Territoriality in salmonids is a behaviour that can affect salmonid abundance (Grant *et al.*, 1998), is a commonly studied topic, and yet it is not well understood. Simple questions ranging from the functions of fights between individuals (Stamps and Krishnan, 1997) to the actual size of the territories in question (Grant *et al.*, 1998) remain more in the domain of theory than evidence.

There are two major obstacles for researching territorial behaviour: the absence of a common definition of "territoriality" and the lack of a direct, quantifiable measurement of territorial behaviour (Weckerly, 1992; Maher and Lott, 1995). The most common definition is the establishment of a ***defended area***. Other definitions using multiple criteria are also common and Maher and Lott (1995) suggested that the ***defended area*** definition is overly simplistic and instead recommended the use of the ***maintenance of an exclusive area that is defended***, which includes a second criterion of exclusivity. Weckerly (1992) explored the difficulties inherent in measuring territoriality and identified two major research pathways, each corresponding to one of Maher and Lott's (1995) criteria: the indirect but quantifiable measurement of dispersal indicating the establishment ***exclusive areas***, and direct measurement of aggression, a behaviour difficult to accurately quantify but one associated with the ***defense*** of an area.

Without a common definition and method of measurement, the study of population-level variations in territorial behaviour in salmonids has remained haphazard. Aggressive behaviour in salmonids is highly plastic (Grant, 1991), but there is some evidence it has a genetic basis as well. Taylor (1990) found that juvenile Chinook salmon (*Oncorhynchus*

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tshawytscha) in populations with dissimilar life history patterns showed different levels of agonistic behaviour, even when reared in identical conditions. In the same vein, juvenile coho salmon (*O. kisutch*) from separate streams appeared to show small differences in the occurrence of aggression, and those differences appeared to persist in their laboratory-bred and reared progeny (Rosenau and McPhail, 1987).

Coho salmon are generally considered to be territorial in their juvenile stage (Chapman, 1962; Rosenau and McPhail, 1987; Dolloff and Reeves, 1990; Vøllestad and Quinn, 2003), but all evidence for this behaviour comes from individuals from coastal stocks. Interior Fraser coho salmon are found hundreds of kilometers up the Fraser River in the heart of British Columbia, Canada. As inhabitants of an interior, northern region, they experience very different environmental pressures and patterns than their conspecifics found in the coastal Pacific Northwest. Interior Fraser coho are also genetically distinct from their coastal relatives and have been shaped by a different environmental history for at least 10,000 years (Small *et al.*, 1998).

The objective of this study was to examine the behaviour of juvenile interior Fraser coho for evidence of territoriality through an experiment designed to assess both territorial criteria. Distribution was assessed through observations of fish throughout an artificial channel, while cameras in the same channel were used to monitor interactions in select areas to determine levels of aggression. Fish were examined in groups of approximately 30 individuals to create a population density similar to densities found in the Horsefly watershed during the sampling in Chapter 2 to increase the applicability of the findings to natural habitats and to decrease the impact of the study set-up on behaviour. While some studies have tested behavioural interactions in pairs to allow better control of extraneous variables (e.g. Johnsson and Carlsson, 2000), the realism created by multiple fish in an area was

considered more important for the purposes of this experiment. Several territorial

alternatives, such as schooling or hierarchies, are facilitated by a larger number of

individuals.

METHODS

General Methods

All experiments were carried out at the Quesnel River Research Center in Likely

(QRRC), British Columbia. The first trial (Trial 1) was observed between July 9th – July 24th,

Trial 2 from July 25th – August 8th, and Trial 3 from August 9th – August 25th. A 5.5m x 2m

concrete raceway was used for the experiments and modified to mimic a natural stream. A

steady flow of 8 ºC well water was pumped through the channel. A layer of river gravel was

laid on the bottom of the channel. This layer was shaped to create heterogeneous depth

within the channel and to form different sections (Figure 3.1a). A deeper area, with a depth of

approximately 0.25m, was created at the upstream end, bounded by a metal barrier that raised

the water level and channeled most of the water into a narrow gap at one side and increased

the flow at this spot (Figure 3.1b). The downstream side of the barrier had more gravel to

form a riffle area with a depth of approximately 0.05m, which led into the bottom section:

another pool created by an indentation in the gravel and the screen marking the end of the

channel to a maximum depth of 0.17m. Habitat complexity in the upper pool was created by

a well-weathered block of wood (approximately 1m x 0.2m x 0.2m) held underwater using

rocks. Cedar sticks were wedged under the block and woven together to create brushy cover.

In addition, three large rocks were placed in the upper pool. A small structure was formed in

the riffle area using three rocks: two holding up a horizontal third rock to form overhead

cover. The lower pool had a second block of wood held diagonally by the channel wall. Two
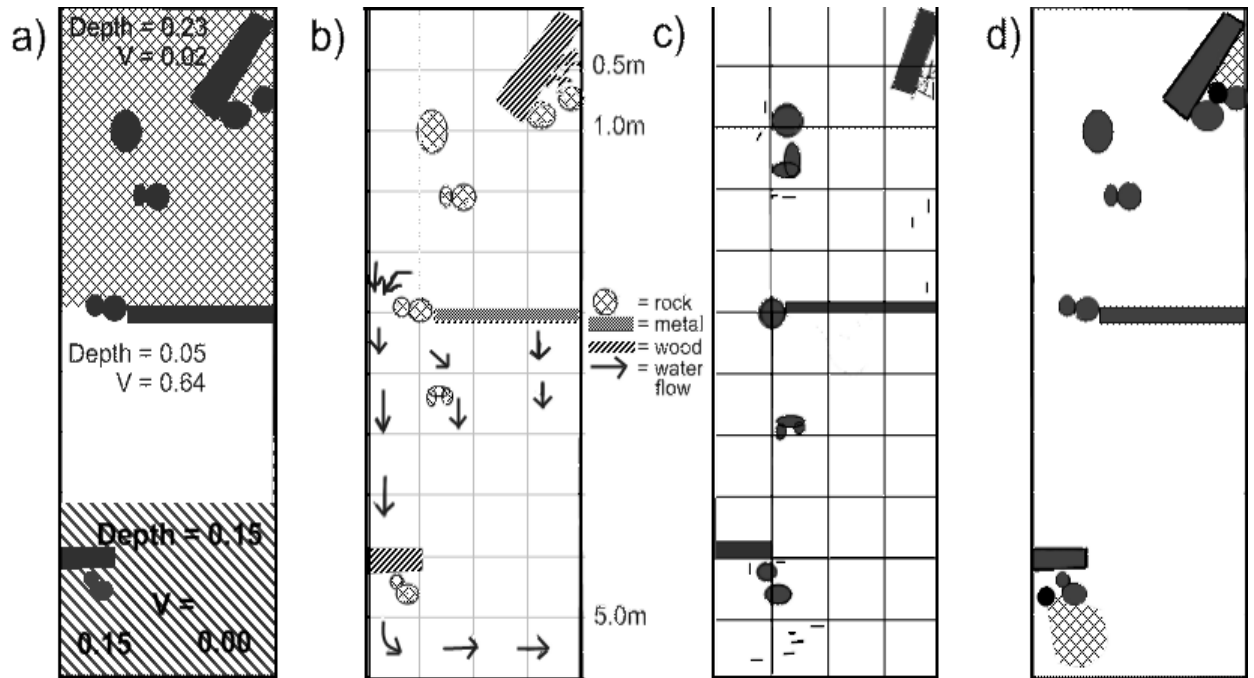
Figure 3.1: a) Upper pool (crosshatch), riffle (no fill), and lower pool (diagonal fill) areas of the channel with depth (Depth) and velocity (V) measurements from each area; b) diagram of channel set-up channel features (fills), and water flow (arrows) marked; c) example of positional diagram with channel features (shaded). Fish positions are marked as dashes; d) positions of cameras (black) in the channel with approximate fields-of-view (cross hatch)

rocks were placed adjacent to the wood. Markings every 0.5m on the edge of the channel provided reference points for distances during visual observations.

The day before the beginning of a trial, minnow traps were set in areas of the McKinley and Horsefly watersheds (described in Chapter 2). Approximately 25 young-of-the-year coho were used for each trial (29 for Trial #1, 20 for Trial #2, and 25 for Trial #3). Differences in the number of fish per trial were dictated by the number of fish caught in the traps that day. Once the fish had been collected, they were transported to the QRRC where they were acclimatized to the channel temperature, weighed and measured, and released in the top pool. This was considered Day 1 of the experiment. Fish were fed once a day in the morning, at amounts of approximately 0.5g per fish. Frozen bloodworms (mosquito larvae) were thawed and sprinkled across the channel. More were added to the upstream end of the upstream pool to simulate invertebrate drift. The raceway was also uncovered and situated underneath several trees, which were observed to provide periodic inputs of fallen terrestrial insects throughout the day. The fish were observed feeding on the provided blood worms at feeding time and on terrestrial invertebrate inputs throughout the day. After the final observation period of the trial, the fish were removed and returned to the Horsefly watershed. All fish were accounted for and there were no mortalities during the course of the experiment.

Positional Observations

Observations for fish position began on day 8 to allow fish a week to explore the channel and establish positions. For each observation day the channel was observed for 10 minutes at the beginning of each hour from 8:00 to 20:00. During each observation period, the position of all visible individuals was recorded as accurately as possible on a scale

drawing of the channel (Figure 3.1c). All possible care was taken to avoid creating a startle response from the fish in the channel. For each trial, there were three observation days: every second day for a week. During the third trial, Observation Day 2 and Observation Day 3 were not separated by a non-observation day as timing was dictated by nearby activities unrelated to the project which may have had an effect on the test subject's behaviour.

Interaction Observations

Territorial behaviour in juvenile salmonids is usually expressed through aggressive displays and contests (Chapman, 1962). Displays are mostly carried out through body and fin position, while contests can consist of nipping, charging, and chasing (Chapman, 1962; Martel, 1996; Cutts *et al.*, 1998; Johnsson and Carlsson, 2000). For the purposes of this study, three forms of aggression commonly used as indicators of territoriality were selected: displaying, nipping, and chasing. While most studies of salmonid territoriality involve an *a priori* assumption of its presence based on previous observations, common knowledge, or personal experience, this study makes no such assumptions. Therefore, a corresponding list of three behaviours that would indicate a lack of territoriality was also created. As this step is not often taken in examinations of territoriality, no previous studies were available from which to create this list. Three behaviours were chosen as possible alternatives to defense: the tolerance of other individuals at close range without aggressive response, the alignment of an individual to parallel another individual, and grouping of fish and formation of schools.

For the entire duration of the experiment, two underwater cameras (National Bullet C/IR) were present in the channels. They were set up prior to the addition of fish in the channel, and in approximately the same position for all three trials (Figure 3.1d). The cameras recorded six hours each day. There was an effort to represent dusk, dawn, night, and

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day in the recorded periods. Due to the changing photoperiod throughout the study, the recorded times for the dusk period was moved to ensure the capture of the period near sunset and sunrise. After the first week of observation, it was noted that very little interaction occurred during the night, so the night recording period was removed and more focus placed on the dawn and dusk periods. The final recording schedule included two hours at dawn, one at noon, and three hours at dusk. Early in the season, dawn observations were recorded from 5:00-7:00 and dusk from 20:00-21:00, while later in the season it was switched to 5:00-7:00 and 18:00-20:00.

During the third trial, an equipment malfunction resulted in the loss of much of the latter period of the trial. As a result, only the first three and last two days were available for analysis, and the third trial was removed from further analysis of video interactions, but not for positional data.

Analysis

Positional

The positional records were used to generate approximate nearest-neighbour distances for all visible individuals. The difficulty inherent in determining the exact positions of individuals in a heterogeneous habitat without disturbing the fish made all positions approximate. Therefore, distances were only expressed to the nearest 0.5m to avoid inappropriate conclusions based on the resolution of the data.

The nearest neighbour distances for each observation period were compared using the formula from Griffith and Amrhein (1991):

$$R = \frac{\sum NND}{0.5\sqrt{\frac{a}{n}}}$$

where R is an estimate of dispersion; NND is the distance to the nearest neighbour, a is area, and n is the number of individuals. This equation results in an R score which represents the spread of the data points (in this case, the fish). R scores are between 0 and 2.15, with numbers less than 1 indicating hyperdispersion, and numbers greater than 1 indicating aggregation as specified by Griffith and Amrhein (1991).

At no time were all individuals visible as fish sheltered beneath objects and in the interstitial spaces of the gravel. Each observation was ranked by the number of visible individuals, and the lowest quartile (less than 8 visible fish) was removed from further analysis to reduce overestimation of dispersion. ANOVAs compared differences between scores by hour of the day, day of the trial, and by trial. As the ANOVAs indicated a significant effect due to trial, the effects of day and hour were examined separately for each trial. Significant differences ($p < 0.05$) were further examined by Tukey's multiple contrast comparisons. Single sample t-tests were used to compare the R values from each trial to 1 to test for significant dispersion or aggregation. All ANOVAs and t-tests were carried out using R (v 2.6.0, the R Foundation for Statistical Computing).

Interactions

All video was recorded onto a National NL-DVR-374 4 DVR at 25 images/second. The video was then watched and all interactions were recorded. An "interaction" was defined as any instance in which two fish were within 5 body lengths of one another. Body length was used as a substitute for actual distance as it was easier to estimate in the context of the

video recordings, and allowed the definition to take into account the increasing size of the fish throughout the three trials. Interactions were categorized on a six point, two directional scale. The scale ranged from -3 to +3: the negative numbers described aggressive or "negative" interactions, while the positive numbers described non-aggressive or "positive" interactions. A score of +1 was given any time two fish were within 5 body lengths of each other and did not exhibit any aggressive behaviour ("tolerating"). A score of +2 described any instance where two fish approached within two body lengths of one another and aligned their bodies in parallel, indicating both a willingness to allow an individual to approach closely and an acknowledgement of the presence of the other individual ("alignment"). When the fish took this further, approaching within two body lengths, aligning their bodies, and travelling in parallel as in a school, a score of +3 was given ("schooling").

Scores of -1 were given when a fish responded to another with an aggressive display, characterized by raised fins ("displaying"). A score of -2 was given for instances of "nipping" when a fish moved rapidly towards another fish. Since it was often difficult to tell if an actual nip had occurred, if the attacking fish came within half a body length of another it was considered a nip. A score of -3 was given if the attacking fish not only came within half a body length, but continued to pursue the attacked fish after it retreated ("chasing").

A two-sample t-test using the first nine hours of recorded interactions found that there was no significant differences in the proportion of interactions attributed to each scoring level when the entire hour was watched and when 20% of the hour's footage was watched ($t_8 = -0.13$, $p = 0.89$). Therefore, only the first 12 minutes of each hour was analyzed as a representative subset of the entire hour.

A two-sample t-test was used to compare the positive, negative and the negative subtracted from the positive ("total") scores in Trials 1 and 2. As these t-tests and the

positional data gathered earlier suggested the possibility of a difference between behaviour in the two trials, all future analysis of the scores separated the two trials. ANOVAs with log transformations compared the average and total scores by hour of the day. The non-normal distribution of the total negative scores in Trial 1 necessitated the use of a nonparametric Kruskal-Wallis rank sum test instead of an ANOVA to compare hours of the day. Tukey's multiple contrast comparisons were used to determine which time periods were significantly different. With the exception of the change-point analysis discussed below, all statistical tests were carried out using R (v 2.6.0, The R Foundation for Statistical Computing).

To test for possible changes in behaviour over time within a trial, a change-point analysis was run on all observation periods, using order as the independent factor. The analysis itself and all assumption tests of these data were carried out using Change-Point Analyzer (v 2.3, Taylor Enterprises). The Change-Point Analyzer uses cumulative sums and bootstrapping with 1000 replicates to locate the point at which the changes, if any occurred.

RESULTS

Positional

With the exception of Trial 1 (t_{80} = -5.09, p<0.01) the average R score did not differ significantly from 1, which signifies random dispersion. The mean R score was 0.83 (SE = 0.06), and the trials were not statistically different from each other ($F_{2,78}$ = 2.64, p = 0.07). The average nearest-neighbour distance was 0.42m, but Trial 1 had a significantly smaller nearest distance than Trial 2 and Trial 3 (t_{34} = 2.91, p = 0.012; t_{34} = 3.02, p = 0.009) (Figure 3.2).

Neither R score nor the average nearest-neighbour distance was affected by the hour of the day, and remained steady throughout the experiment (all p-values > 0.12). The number
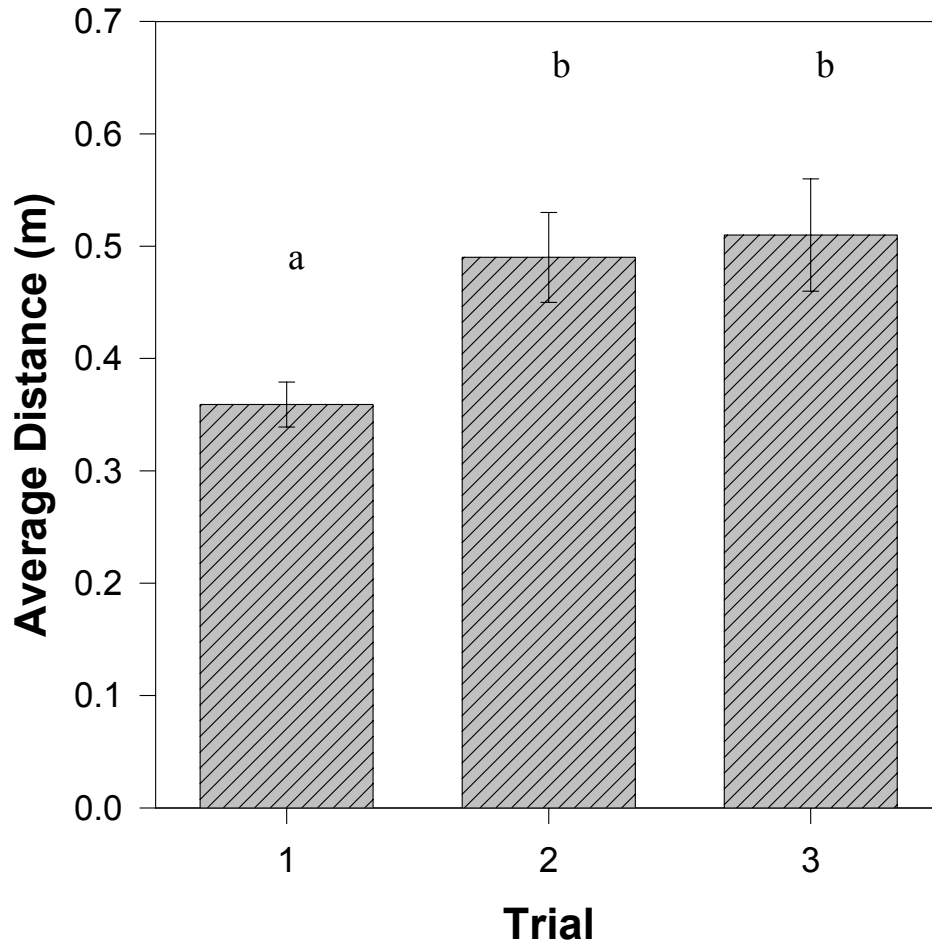
Figure 3.2: *Average distance between nearest neighbours (± SE) in the three trials. Values with a common letter do not differ significantly*

of fish seen during the observation period also had no effect on R score ($R^2 < 0.01$, $F_{1,79} = 0.05$, p = 0.82) or nearest-neighbour distance ($R^2 = 0.04$, $F_{1,79} = 3.20$, p = 0.08).

Interactions

Trial showed an effect on the total score for each observation period (Figure 3.3). The total number of negative scores in Trial 2 was greater than in Trial 1 ($t_{167} = -9.28$, p < 0.001), but the total number of positive scores and overall total score did not differ between Trial 1 and Trial 2 ($t_{167} = 0.62$, p = 0.54; $t_{167} = 1.18$, p = 0.24). It also appeared that both positive and negative scores increased for Trial 3, although data loss prevented further analysis. Average scores for the first two trials did not differ.

Positive interactions scores outweighed negative interaction scores ($t_{185} = 14.41$, p < 0.001). In fact, there were only two hour-long periods in which observed negative interactions scored higher than observed positive interactions among all three trials. Generally, average scores were consistent throughout the experiment. Additionally, average total, average positive, and average negative scores were not affected by either the day of the experiment, the time of the day, nor the trial number (p > 0.05). The one exception occurred during Trial 2 (Figure 3.4), in which the average positive score for 18:00 was significantly lower than the average positive score at 5:00 and 12:00 (Tukey's Contrasts: t = -3.46, p = 0.011; t = -3.57, p = 0.008, respectively).

Hour of day showed no significant effect on total positive (Trial 1: $F_{7,80} = 1.01$, p = 0.42; Trial 2: $F_{5,75} = 2.16$, p = 0.07), total (Trial 1: $F_{7,80} = 0.64$, p = 0.72; Trial 2: $F_{5,75} = 1.12$, p = 0.36) or negative scores (Trial 1: $H_{15} = 24.8$, p = 0.053; Trial 2: $F_{5,75} = 1.93$, p = 0.10). The day of the experiment, however, showed a significant effect on total positive score (Trial 1:
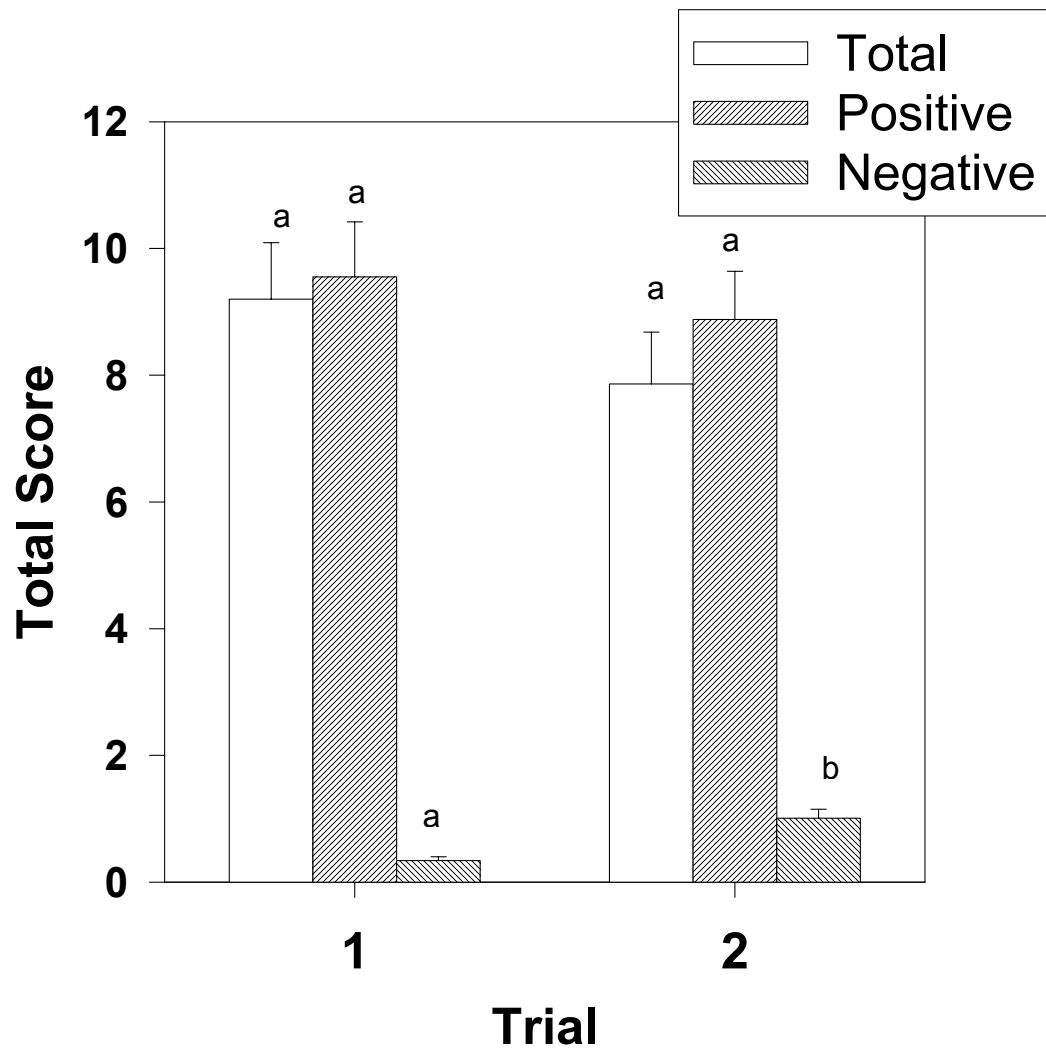
Figure 3.3: *Total score (open bar), total positive score (right hatch bar), and total negative score (left hatch bar) by Trial with standard error. Significant differences marked where p<0.05. Values with a common letter do not differ significantly.*
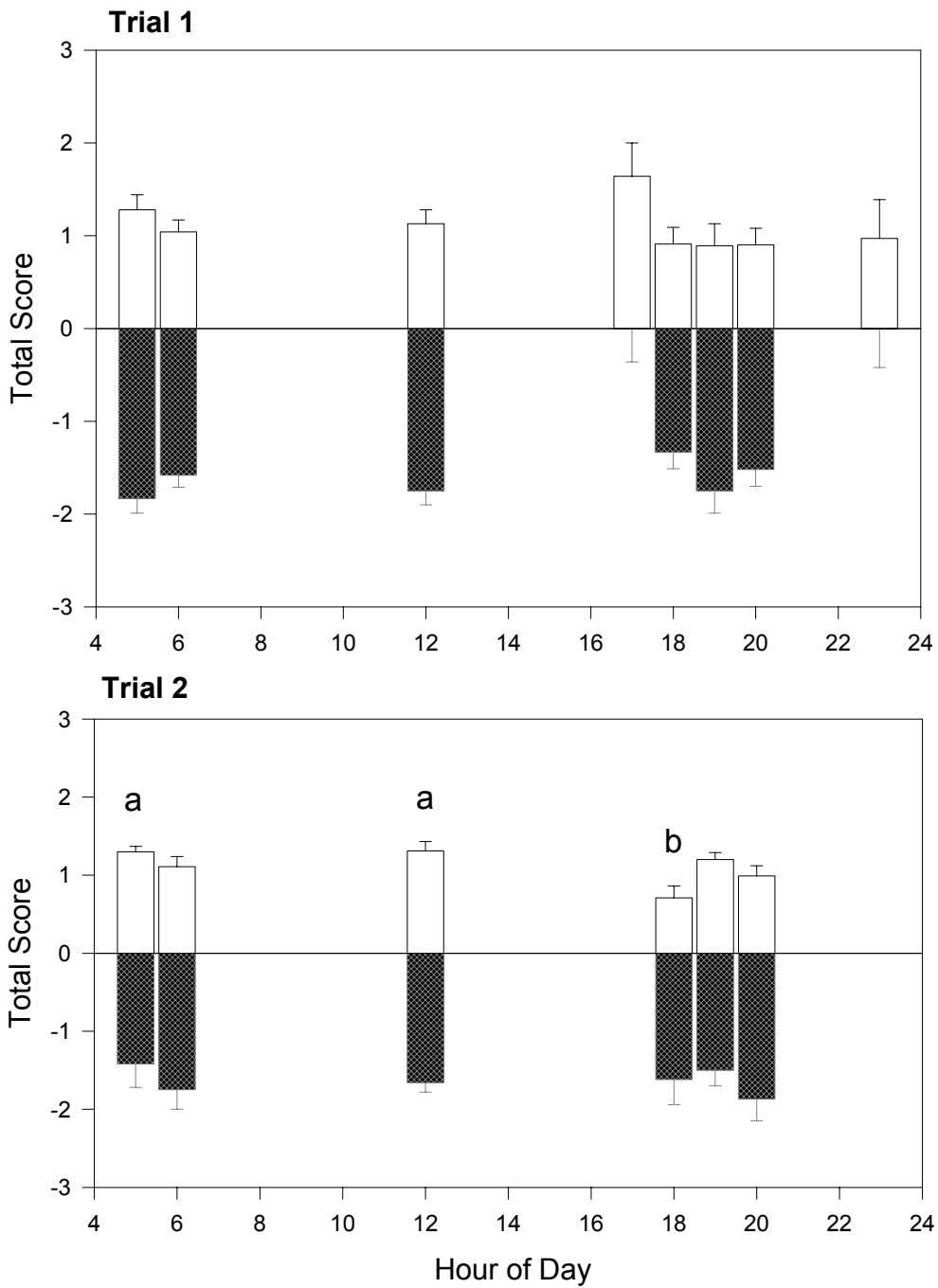
Figure 3.4: *The average total (positive – negative), positive, and negative scores by hour of the day. Significance, denoted by a different letter, at p<0.05. Absence of a letter denotes no significant differences from any other bar.*

$F_{15,72} = 6.22$, p <0.001; Trial 2: $F_{13,67} = 6.09$, p < 0.001) and total negative score (Trial 1: $F_{15,72} = 1.90$, p = 0.04; Trial 2: $F_{13,67} = 2.69$, p = 0.004).

The timing for changes in score differed between trials as assessed by the change-point analysis. The change-point analysis for Trial 1 indicated a change in total positive score at 20:00 on the second day (Figure 3.5) (p = 0.03). A second change in the positive score in Trial 1 was noted on the eleventh day at 20:00 (p < 0.001). Negative scores indicated only one change on the tenth day (p < 0.001). The analysis of total positive score for Trial 2 also indicated a single change point at 5:00 on the fifth day (p = 0.01). Total negative scores in Trial 2 were characterized by two change points: the first on the second day (p = 0.001), and the second on the sixth day (p = 0.04). When the two scores were combined into a total score, Trial 1 indicated a change at 20:00 on the eleventh day (p < 0.001) (Figure 3.6). Trial 2 indicated a change at 5:00 on the fifth day (p < 0.001).

DISCUSSION

My results represent the first examination of behavioural interactions for juvenile interior Fraser coho. Interactions were assessed with an artificial channel experiment designed to assess social interactions (positive and negative) and spatial distribution. Nearest neighbour analysis determined that fish aggregated within the channel and direct observations revealed a greater number of positive interactions than negative aggressive interactions between the fish. Interior Fraser coho, therefore, appear to show a high level of tolerance for one another. This finding is discussed in relation to other populations of coho salmon and other species of salmonids in general.
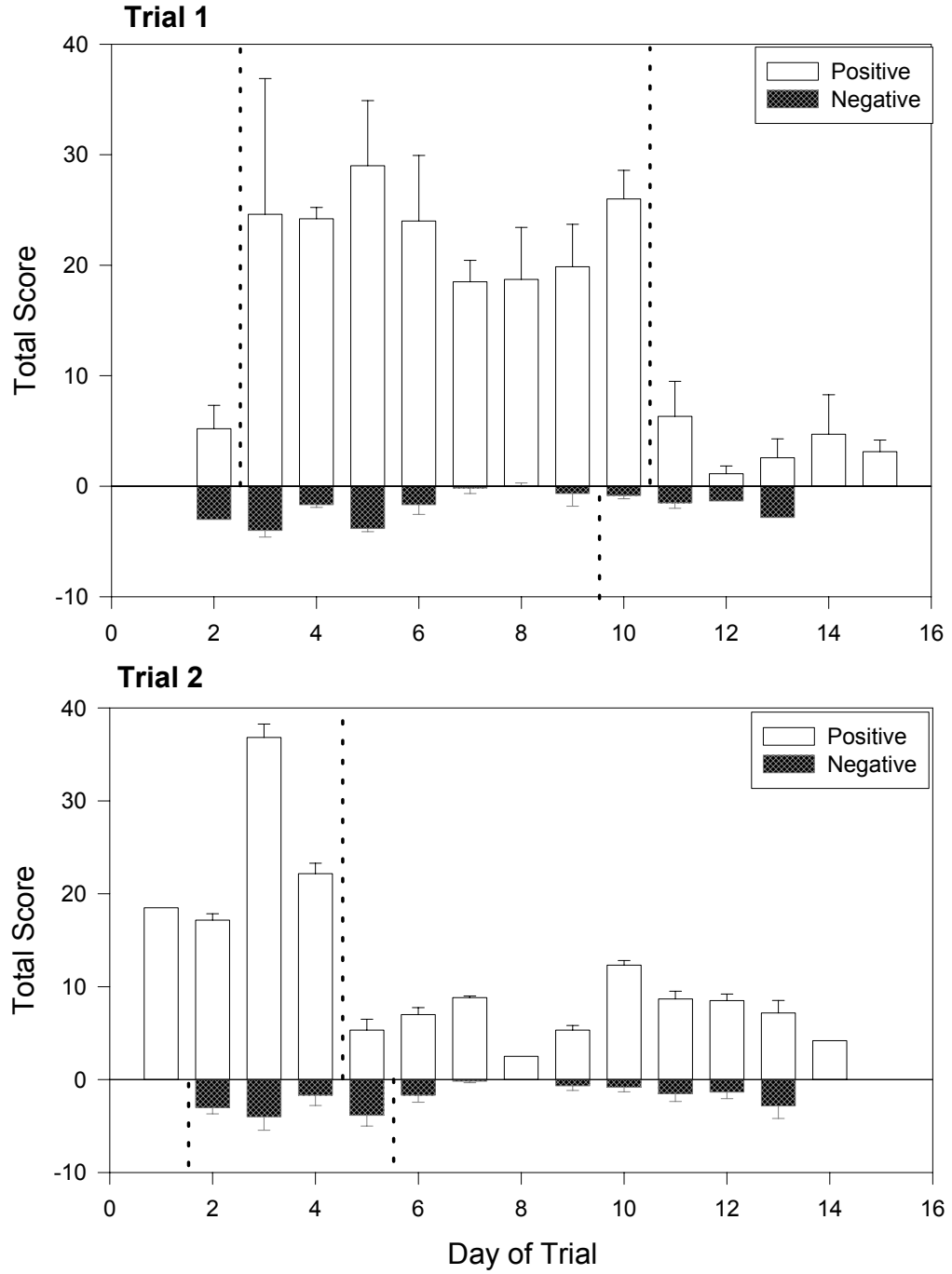
Figure 3.5*: Total positive and total negative scores by day since the beginning of the trial. Dotted lines mark the change points.*
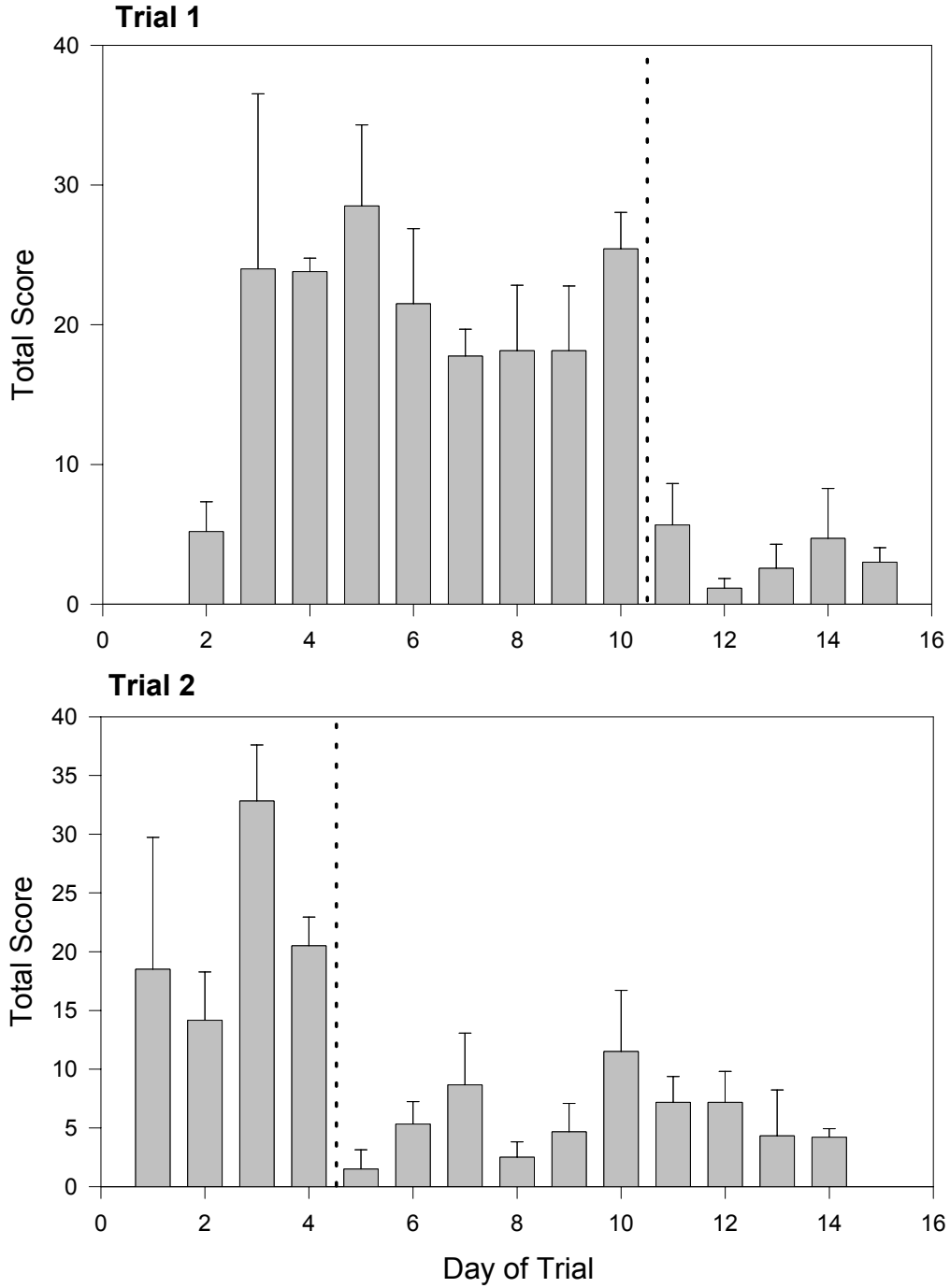
Figure 3.6*: Total scores (Positive score – Negative score) by day since the beginning of the trial (± SE). Dotted line marks change points.*

Positional

The pattern of aggregation and significantly shorter distance between individuals in Trial 1 compared to the other two trials suggests that juvenile coho may form schools during the early part of the summer, but are less likely to do so later in the season. A similar seasonal influence on spatial partitioning has been previously documented in other salmonids. Mäki-Petäys *et al.* (2004) found that juvenile Atlantic salmon (*Salmo salar*) exhibited a pattern of aggregation towards others of their size class most strongly during the summer, but less so in other seasons.

Interactions

Juvenile coho monitored by underwater cameras enabled me to characterize interactions among individuals. The average sum of the positive scores outweighed the sum of the negative scores for all time periods and days. While mostly stable throughout the day, behaviour seemed to show changes between days, with the change-point analysis indicating changes in behaviour of both positive and negative types, as well as in the total score. The changes, however, did not seem tied to time-since-introduction, since little pattern was noted. Behaviour exhibited on the first and second day was observed to differ from later behaviour, with no feeding activities and little movement noted, although that was not always reflected in the change-point analysis. By the third day, activity increased. Each trial showed changes in positive and negative behaviour later on in the trial. Interactions, both positive and negative, appear to show periods of high and low activity.

Many behavioural experiments include a habituation period to allow for initial changes in behaviour due to introduction to a new area (Glova, 1986; Grand, 1997; Sabo and Pauley, 1997; Rhodes and Quinn, 1998; Kelly and Bothwell, 2002) but these periods range

from overnight (Rhodes and Quinn, 1998; Kelly and Bothwell, 2002) to a week (Sabo and

Pauley, 1997). Trial 1 positive interactions, Trial 2 negative interactions, and qualitative

observation of behaviour throughout this study suggests that two days may be a reasonable

habituation period for this population.

The behaviour during the first few days may be indicative of the types of behaviours

exhibited by individuals when they enter a new area. Juvenile coho likely explore new areas

several times during their freshwater rearing period. Mass movements due to flooding events

have been observed (Bell *et al.*, 2001) and fish have been observed to voluntarily move up to

200m up or downstream throughout the rest of the summer (Bolton *et al.*, 2002). Otolith

elemental chemistry (Chapter 1) indicated that juvenile interior Fraser coho move often

during their rearing stage. Additionally, trapping (Chapter 2) found juvenile coho in areas in

which no spawning was observed, suggesting migration to those areas. Therefore, it seems

likely that juvenile interior Fraser coho regularly migrate to new areas, and may have

developed behaviours that confer benefits during these periods.

In contrast to many territorial species that exhibit a period of heightened aggression

during the establishment of territories (Stamps and Krishnan, 1997), juvenile interior Fraser

coho appear to show a period in which both positive and negative interactions are heightened,

and in which the increase in positive interactions outweighs the increase in negative

interactions. Positive social interaction may be beneficial to juvenile coho entering a novel

area by facilitating social learning. Social learning occurs when fish with less knowledge of a

situation or area copy others who may have more experience, and has been found to provide

benefits by providing orientation in a novel habitat and by enhancing foraging efficiency

(Brown and Leland, 2003). While none of the individuals in the experiment had prior

knowledge of the raceway, the schooling instinct may still control behaviour.

In addition to the initial acclimatization period, behaviour changed within the trial. Given the limited sample size, it is difficult to draw conclusions regarding the prevalence or cause of these changes. Given the possibility of behavioural variation from day to day, it may be prudent for future behavioural studies of juvenile coho to monitor for several days, as data gathered in a shorter time period may not give an accurate picture of their behaviour.

Behavioural differences between the two trials were noted. The first trial, beginning in early July, was characterized by lower total negative scores than the second trial, but showed no difference in positive scores, either total or average. The available evidence from the first three days and the last day of the third trial indicates that negative scores may have continued to increase, and that positive scores were higher than Trial 1 and 2.

Weaknesses in the measurement of behaviour, both due to the methods utilized and weaknesses inherent in quantifying complex behaviour, suggest a certain amount of caution in the interpretation of these results. The observations in my study are limited to interactions that occurred in the area monitored by the cameras during the periods in which the cameras were running, and given the placement of the cameras in areas of favourable habitat, aggression may be overestimated (Gabor and Jaeger, 1995; Johnsson and Carlsson, 2000). Drawing conclusions from these data is further hampered by the loss of much of the video recorded during Trial 3, effectively reducing the number of trials to two. Despite these weaknesses, a picture of juvenile interior Fraser coho behaviour emerges and allows for a reasonably confident description of intraspecific interactions in this population. In general, aggression levels appear to be low in the observed fish, and their tolerance for conspecifics appears to be high.

Synthesis

While it can be advantageous for territorial species to aggregate in response to resource aggregation, the individuals then usually show heightened aggression either through increased frequency or intensity of displays and other aggressive interactions (Greenfield *et al.*, 1987; Sánchez-Prieto *et al.*, 2004). In contrast, aggressive behaviour was uncommon in all three trials, despite the high density of individuals. Using the territorial paradigm outlined in the introduction, the hypothesis of territoriality in this population is not supported. The observed behaviour does not match the descriptions of coastal juvenile coho behaviour available, and suggests behavioural differences among coho populations may exist.

Whether or not the observations are an appropriate basis for making conclusions about behaviour also relies on the experimental conditions accurately reflecting natural conditions, as the extent and even presence of territoriality can be affected by external factors. Velocity (Wankowski and Thorpe, 1979), food availability (Mason, 1976; Dill, 1978; Giannico, 2000), and fish density (Grant, 1991) may influence dispersion or aggression by modifying the energetic costs and benefits of territoriality. Attempts to mimic natural streams in the area with regard to the range of depths, velocities, and cover types; the availability of food; and the fish density were considered necessary to maximize the likelihood of the observed behaviour accurately reflecting natural behaviour.

While behaviour seemed relatively stable throughout a given day, differences were seen on a longer temporal scale when the individual trials were compared. Early on, individuals were more aggregated than individuals monitored later in the summer. At the same time, negative scores increased steadily throughout the season. In a study of juvenile Chinook salmon in Idaho, a species that exhibits territoriality, aggression was also observed to increase between May and July (Peery and Bjornn, 2004).

Relevance

Territory size, and consequently territorial behaviour itself, is often viewed as the result of an energetic cost-benefit analysis (Rubenstein, 1981; Martel, 1996; Vøllestad and Quinn, 2003). The forming of territories is energetically more costly than refraining from their formation, but can result in the acquisition of larger amounts, or a higher quality, of resources (Grant, 1991; Vøllestad and Quinn, 2003). Whether or not territorial behaviour results in an increase in energetic intake sufficient to counteract its costs is debatable, as several studies have found that dominant territorial individuals do not see much benefit in the form of increased food (Rubenstein, 1981; Vøllestad and Quinn, 2003), although others have found otherwise (Martel, 1996). Territorial behaviour also carries with it a predation risk (Martel and Dill, 1993). If interior Fraser coho have abandoned territoriality for alternate types of behaviour, it may indicate that conditions of the interior Fraser region have altered the costs or benefits of territoriality to the point where it is no longer profitable.

Although the extent to which salmonid territorial behaviour is dependent on external factors is unknown, there is some evidence that it also has a genetic component (Rosenau and McPhail, 1987; Taylor, 1990; Tiira *et al.*, 2003). Some have even suggested that morphological differences between populations may be partly attributable to behavioural variation between populations. Taylor and McPhail (1985) found that interior juvenile coho salmon from the Coldwater and upper Columbia rivers had significantly smaller median fins than coastal coho from the lower portion of the Fraser River and creeks on Vancouver Island, which they attributed to longer migration distance to the ocean. Swain and Holtby (1989) found similar difference in fin size in a comparison of lake-dwelling and river-dwelling coho from a single watershed, and additionally found a corresponding difference in behaviour with

large-finned river-dwelling coho showing territoriality while the lake fish with small fins

seemed to school. Their suggestion of behaviour as an alternate cause for the findings of

Taylor and McPhail (1985) is supported by this study, where low aggression and territoriality

accompanies the small median fins of interior Fraser coho in the study. While the link

between fin size and behaviour is not firmly established, it does at least suggest that fin size

is an accurate predictor of aggressive behaviour. If this is true, the results of Taylor

and McPhail (1985) would suggest that low levels of aggression characterize juvenile Interior

Fraser coho throughout their range, not just the Horsefly River system, and the lack of

territoriality found in this study is not an artifact of the study design.

Epilogue

This work expands the current knowledge of interior Fraser coho ecology by contributing information on juvenile habitat use. Emigration patterns and behavioural interactions were studied and the results compared to published information from coastal coho populations. Analysis suggests that interior Fraser coho differ considerably from coastal coho and caution should be taken when extrapolating among populations from the two locations.

The high mobility of the interior Fraser coho population, combined with the lack of observed territorial interactions, challenges the common assumption that intraspecific aggression is the primary driver of movement in juvenile coho (Chapman, 1962; Anderson *et al.,* 2008; Koski, 2009). The juvenile interior Fraser coho studied did not exhibit territoriality and seemed to migrate more often than their territorial coastal relatives. Territorial behaviour may penalize emigration due to the costs of establishing new territory or avoiding dominant individuals in a new location. Without territoriality, interior Fraser coho may be able to avoid some of the cots of emigration, allowing them to emigrate more often.

A population of highly mobile individuals can also react to a changing environment by moving to a new location. Several of the habitat characteristics identified in Chapter 2, such as velocity, cover, or even stream width, fluctuate in a given site over the course of a year. The high number of migrations seen in interior Fraser coho in Chapter 1 may be a response to the high seasonal variations in water flow and temperature of the interior environment. Observations during the trapping portion of Chapter 2 suggested a mass emigration from McKinley Creek during mid-to-late summer, and a corresponding increase in catch rates in smaller tributaries: this supports the conclusion that tributaries provide late-season habitat for juvenile interior Fraser coho as found in Chapter 1.

Both Chapter 1 and Chapter 2 highlighted the possible importance of small tributaries to the juvenile lifestage of interior Fraser coho. Habitat in small tributaries is easily degraded by surrounding land use, which is often managed by private owners. Small, low-order streams are often devalued in watershed management, as their contribution to ecological processes is overlooked and their conservation appears less efficient compared to larger rivers. Smaller-order streams usually support less complex fish assemblages than higher-order streams (Gorman and Karr, 1978; Beecher *et al.,* 1988); they are often discounted in favour of larger streams with more diverse communities. Fish assemblages in small streams, however, may include species not found in higher-order streams and rivers (Beecher *et al.,* 1988) and my findings suggest that they also provide necessary habitat for economically important species on a seasonal basis.

Small streams such as the Horsefly River tributaries are vulnerable to impacts from surrounding land use (Beschta and Platts, 1986) and due to their small size may be more sensitive than larger streams (Lowe and Likens, 2005). Agriculture, deforestation, and pastured livestock are some of the greatest threats to the integrity of small streams (Schlosser, 1991). The impacts of agriculture, logging, and livestock husbandry are removal of woody debris, channelization, removal of streamside vegetation, introduction of contaminants, increased nutrient loading, and sedimentation (Schlosser, 1991; Fausch and Northcote, 1992; Liess *et al.,* 1999; Riley *et al.,* 2003). Some land use activities impinge directly on the habitat characteristics identified in Chapter 2. Woody debris removal during logging decreases instream cover (Fausch and Northcote, 1992). Vegetation removal through logging or the preparation of land for agriculture decreases overhead cover (Riley *et al.,* 2003). Channelization through all three land use activities can result in increased velocity as well as causing erosion that can lead to increased stream width (Emerson, 1971). Contamination with

pesticides or sediment due to agriculture and livestock may impact aquatic invertebrate populations (Liess *et al.* 1999). All three threats are present in the Horsefly watershed. Historically, logging has taken place in much of the watershed and is still ongoing in the area surrounding McKinley Creek. Many of the small tributaries included in the study run through former or current agricultural or pastureland, including Horsefly River, Woodjam Creek, Barker Creek, Patenaude Creek, Black Creek, and Moffat Creek. It seems likely that the entire watershed is currently affected, and may be further affected in the future, by threats from the surrounding land use.

The impact of land use on small tributaries can be lessened through preventative measures. One mitigation strategy is the maintenance of riparian buffer strips: areas of forest or other vegetation along the sides of the stream. The vegetation in the strips maintains overhead cover, filters contaminants or nutrients from run-off, and stabilizes the bank to reduce sediment load (Osborne and Kovacic, 1993). The use of buffer strips shows promise for mitigating harvesting and agriculture on small streams (Osborne and Kovacic, 1993; Brosofske *et al.,* 1997; Moore and Palmer, 2005). Forestry and rangeland regulations often require buffer strips or zones surrounding watercourses. Unfortunately, BC timber harvesting regulations do not require a buffer zone to protect streams less than 1.5m in width (Forest Range and Practices Act, 2002), which includes many of the tributaries containing juvenile coho in the Horsefly watershed.

In much of BC, the Fish Protection Act requires a 30m strip of no harvesting or development surrounding any stream or watercourse, regardless of size (Riparian Areas Regulation, 2004). The Riparian Areas Regulation, however, does not pertain to much of interior BC, including the Horsefly River watershed. Several of the tributaries included in the study showed evidence of degradation from development and agricultural practices.

Protection for these smaller tributaries may contribute to a healthier and more stable population of interior Fraser coho.

Protection of interior Fraser coho tributary habitat is additionally complicated by private land owners. Much of the Horsefly watershed, and especially the land surrounding the tributaries, is owned by small-scale farmers. Applying a top-down approach to stream protection for very small streams over a large area may be ineffective (Calhoun *et al.*, 2005). Local conservation alternatives with a focus on participation from landowners, communities, and local governments have shown promise as a method of conserving small ecosystems (Selman, 2004; Calhoun *et al.,* 2005; Oscarson and Calhoun, 2007). Throughout this project the local community has shown interest in conservation of coho in the watershed and local landowners have indicated a willingness to become involved. Most landowners I communicated with, however, were unaware of the presence of juvenile coho on their property and lacked the information necessary to minimize their impact on the tributary habitats. Capitalizing on private interest through community outreach, participation, and incentives may prevent the loss of these important tributary habitats and strengthen the coho population.

The decline of interior Fraser coho populations is so rapid as to require immediate response. The importance of habitat conservation in reversing the population decline seems certain, and therefore takes on great urgency. I hope that the findings of these studies will help to guide further research and conservation efforts.

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