

Seasonal Distribution and Habitat Associations of Salmonids with Extended Juvenile Freshwater Rearing in Different Precipitation Zones of the Skagit River, WA January, 2020

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Introduction

Anadromous salmonids (Salmonidae spp.) experience a variety of freshwater and marine habitats through the completion of their life cycle. Certain life stages and habitats have been associated with critical periods of growth or survival, wherein the growth performance achieved within the critical period is highly and positively correlated to survival through subsequent life stages. Alternatively, disproportionately high or variable mortality might be associated with these periods, but the variability in mortality is strongly mediated by growth or environmental conditions (Beamish and Mahnken 2001). The timing and location of these critical periods can vary considerably among species, populations, among years within populations, and could operate on the growth performance achieved in either freshwater (e.g., Steelhead, Ward et al. 1989; Ward 2000; spring Chinook, Zabel and Williams 2002) or marine habitats (Coho, Beamish et al. 2004; pink salmon Moss et al. 2005 and Cross et al. 2009; ocean-type Chinook, Duffy and Beauchamp 2011; yearling spring Chinook Tomaro et al. 2012). Life history diversity and migrations can stabilize the magnitude of inter-annual population variability by buffering the impact of catastrophic events that negatively affect some life history types, while other life history types might benefit from anomalous conditions (portfolio effect; Hilborn et al. 2003; Schindler et al. 2010). Two common life-histories are expressed in stream-rearing salmonid populations: 1) ocean-type characterized by a sub-yearling ocean migration within 0-6 months of becoming a free swimming juvenile; and 2) stream-type characterized

a freshwater rearing period lasting more than one year (Quinn 2005, SRSC and WDFW 2005).

As climate change progresses, the timing and magnitude of hydrologic cycles are expected to shift significantly, and these changes could dramatically affect the overall capacity of watersheds to support anadromous salmonids as well as the spatial-temporal distribution of habitats that support the positive growth trajectories that improve the survival of these fishes (Battin et al. 2007; Schindler et al. 2008). Pacific salmonids, *Oncorhynchus* and *Salvelinus* spp., that rely on extended freshwater rearing like steelhead *O. mykiss*, spring, summer, and fall Chinook salmon *O. tshawytscha*, Coho salmon *O. kisutch*, Sockeye salmon *O. nerka*, and Bull Trout *S. confluentus* are likely to be more vulnerable to climatic shifts in hydrology and thermal regime than species that exhibit ocean-type freshwater rearing strategies like Pink *O. gorbuscha*, Chum *O. keta*, and most fall Chinook salmon.

The Puget Sound/Salish sea region contains many populations of Pacific salmon and trout (*Oncorhynchus* spp.), and char (*Salvelinus* spp.). The primary freshwater life-history for salmon in this region, besides Coho salmon and steelhead, is an ocean-type migrant. Some Puget Sound rivers also have stream-type Chinook salmon, but little is known about habitat associations of these southern latitude populations in the warmer, wetter watersheds on the west side of the Cascade Mountain Range. The Skagit River in northwest Washington State is the largest tributary to Puget Sound and contains one of the largest populations of Bull Trout *Salvelinus confluentus* and Chinook

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salmon *Oncorhynchus tshawytscha* in the Puget Sound region and a regionally large population of steelhead; all three species are listed as threatened under the Endangered Species Act (ESA). The Skagit River also contains among the largest populations of Pink and Chum salmon in the lower 48 states (Connor and Pflug 2004).

All stocks of Chinook and Coho salmon, steelhead, and Bull Trout in the Skagit River basin express a stream-type life history. Steelhead and Bull Trout are more plastic in their life history strategies but exhibit ontogenetic trajectories similar to the stream-type life history observed in Pacific salmon. Of the data gaps identified in individual recovery plans; habitat use, production estimates, and identification of limiting factors for all three listed species have been highlighted as a priority for recovery and require comprehensive investigations to meet recovery objectives. Currently fishery managers are at different stages of recovery planning based on their scientific understanding of both the biological and ecological requirements of these species. Currently little is known about habitat use by stream-type juveniles of all three listed species within the Puget Sound/Salish Sea basin. Habitat occupation and seasonal distribution by fishes will vary due to behavioral, environmental, and ecological factors. By linking our understanding of these species to the location of habitat types, we gain a spatial and temporal perspective of the freshwater rearing period of each of the listed species in the Skagit River basin.

The Skagit Chinook Recovery Plan (SRSC and WDFW 2005) identified habitat use by the stream type life history as a data gap and research priority. SRSC and WDFW (2005) called for a detailed investigation of seasonal habitat use and distribution of this life-history across the Skagit watershed. Information on habitat use could then inform additional modelling efforts to predict productivity and survival for future recovery actions, adaptive management plan updates, and design criteria for habitat restoration. In the Skagit River, stream type life history smolts have consistently contributed to the spawning escapement of the six independent Chinook populations, with spring stocks having a higher proportion than the other summer and fall stocks

(SRSC and WDFW 2005). Stream type life history expression in Chinook stocks has been observed at the WDFW Skagit Mainstem juvenile trap and has been observed in otolith and scale samples from returning adults (Beamer et al. 2005b). Currently information on outmigration estimates confound recovery actions for this life history strategy in all six Skagit populations due to bias in trapping efficiency for these individuals (Seiler et al. 1998, Kinsel et al. 2008).

The long-term goal of Chinook salmon recovery is to achieve self-sustaining populations of Skagit and Puget Sound Chinook salmon in terms of abundance, productivity, spatial distribution, and diversity conceptually recognized as viable salmonid populations (McElhany et al. 2000). The stream type life history strategy is an example of life history diversity expressed by Puget Sound Chinook salmon. The timing and spatial diversity of adult spawning was also used to measure uniqueness of populations across Puget Sound. McElhany et al. (2000) recommended the use of the viable salmonid population approach across Puget Sound to identify de-listing criteria. The occurrence of the stream type life history is an example of a diversity indicator, highlighting the importance of this strategy as a rare and diminishing component of Puget Sound Chinook populations.

This project will help managers and researchers identify ontogenetically mediated behaviors such as habitat selection, distribution, and rearing location from the basin to the stream or habitat reach scale. Most research on stream-type Chinook salmon, Bull Trout, and steelhead in Washington State has been conducted in the Columbia River basin, rather than Puget Sound, where all three species, but not the same life histories, are commonly found in sympatry. Currently no research focuses on the interaction of these species/life history types since they are uniquely sympatric in the Puget Sound/Salish Sea region. The Skagit River is an opportune location to study these fishes in this manner since this is the only river system where population levels are large enough to provide sufficient opportunities for detailed observations.

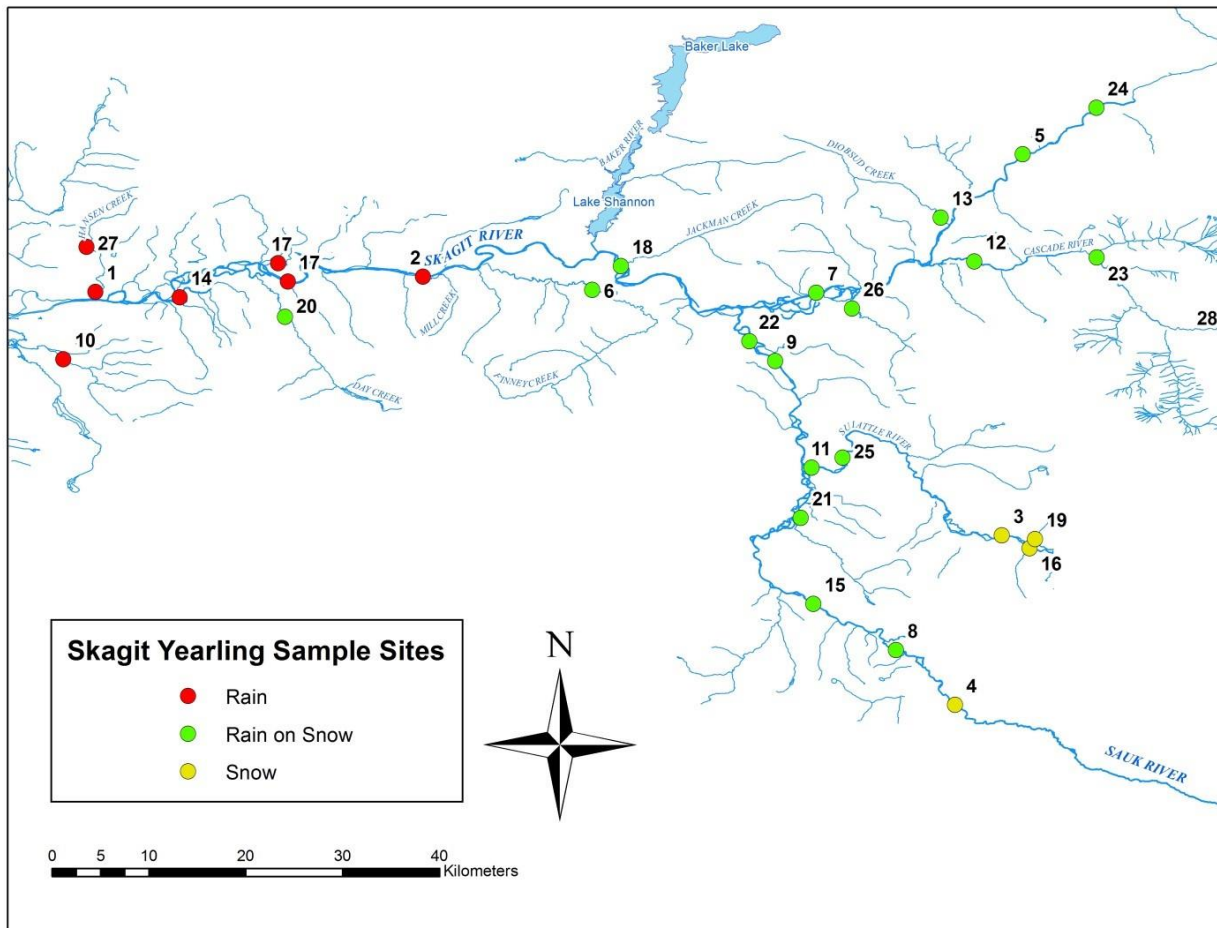
Goals and Objectives

This investigation was designed to describe the spatial-temporal distribution of the stream-type life history expressed by anadromous salmonids in the Skagit River, WA. The results of this investigation are intended to fill data gaps necessary for effective recovery planning of Chinook salmon, steelhead, and Bull Trout in the Skagit River basin, and to inform similar efforts in other watersheds in the Puget Sound region. The specific objectives of this investigation are to; 1) describe the spatial distribution of stream-type juvenile Chinook and Coho salmon, steelhead, and Bull Trout among sub-basins and precipitation zones within the Skagit river system on a seasonal basis and 2) identify which physiographic variables, aquatic habitat variables, and channel types are associated with seasonal fish use.

Study Area

The Skagit River is the largest tributary to Puget Sound draining an approximate 8,100 km², from the mountainous regions of the Western Cascades in Washington state and Southern British Columbia, and the northern Puget Sound lowlands (Figure 1). Flow regimes and upland precipitation are characterized by three major hydrological regions within the basin, which include snowmelt, mixed snow and rain, and rain (Beechie 1992, Beechie et al. 2006). In general, stream flows and upland precipitation in high elevation drainages are influenced by snow and glaciers, streams and uplands at intermediate elevations are characterized by mixed snow and rain hydrology types, and streams in low elevation drainages are primarily influenced by rain. The hydrographs of larger mainstems can be influenced by the flow regimes in

Figure 1. Location of the study area and sample sites by hydro-regions within the Skagit River basin.



their respective upper watersheds. Permanent sources of flow management within the river system due to the presence of hydroelectric projects can also have an influence of the shape of the annual hydrograph. Two hydro-electric projects are located within the Skagit River basin. The Gorge Powerhouse, owned and operated by the public utility Seattle City Light, is located at the terminus of Chinook salmon spawning at river km 96.5 on the mainstem Skagit River in Whatcom County, WA. The other project, owned and operated by the private utility Puget Sound Energy, is located 2km upstream of the mouth of the Baker River whose confluence with the mainstem Skagit is located at river km 56.5 in Skagit County, WA. The spatial extent of this investigation was defined as the known Chinook salmon spawning distribution in the Skagit River system, including the mainstem Skagit beginning at river km 11 and Sauk Rivers, and tributaries in these basins (Figure 1). The fish community in the Skagit River system includes Dace *Rhinichthys* spp., Three-spine Stickleback *Gasterosteus aculeatus*, Sucker *Catostomus* spp., lamprey *Lampetra* spp., sculpin *Cottus* spp., Mountain Whitefish *Prosopium williamsoni*, Pacific salmon and trout *Oncorhynchus* spp.: stream and ocean-type Chinook salmon *O. tshawytscha*, stream and ocean-type Coho salmon *O. kisutch*, ocean-type Chum salmon *O. keta*, ocean-type Pink salmon *O. gorbuscha*, stream and ocean-type Sockeye salmon *O. nerka*, Rainbow Trout and anadromous steelhead *O. mykiss*, resident and anadromous Cutthroat Trout *O. clarki*, and resident, fluvial, adfluvial, and anadromous Bull Trout *Salvelinus confluentus*.

Six recognized populations of Chinook salmon occur in the Skagit River (Beamer et al. 2005a and Ruckelshaus 2006): Upper Skagit Summers (mixed hydro-region), Lower Skagit Falls (mixed and rain hydro-regions), Lower Sauk Summers (mixed hydro-region), Upper Sauk Springs (primarily snow hydro-region), Suiattle Springs (primarily snow hydro-region), and Upper Cascade Springs (primarily snow-hydro-region). Each stock is designated by location and timing of spawning. Upper Skagit Summers spawn from September through early October in the mainstem Skagit and tributaries upstream of the confluence with the Sauk River. Lower Skagit Falls

spawn in October in the mainstem Skagit River and tributaries downstream of the confluence with the Sauk River. Lower Sauk Summers spawn from September through early October in the mainstem Sauk River and tributaries downstream of the Darrington Bridge at river km 34.1. Upper Sauk Springs spawn from late July through early September in the mainstem Sauk River and tributaries upstream of the Darrington Bridge at river km 34.1 and primarily upstream of the confluence with the White Chuck River. Suiattle Springs spawn from late July through early September in the Suiattle mainstem and tributaries. Upper Cascade Springs spawn in the Cascade river mainstem and tributaries upstream of the canyon starting at river km 12.6. All Skagit River stocks express ocean-type and stream-type life histories as evidenced from scales collected during spawning surveys (Beamer et al. 2005b).

Ocean-type migrants are divided into three categories in the Skagit River: fry migrants, delta rearing migrants, and parr migrants. Fry migrants emigrate to the marine nearshore soon after emerging during February and March. Delta rearing migrants emigrate during the same period as fry migrants and rear in delta habitat until migrating to marine habitats in May-June. Parr migrants rear in the Skagit River until out-migrating to the marine environment in May-June. Stream-type Chinook salmon remain in the Skagit River for one-two years prior to emigrating to the marine environment in late March-May. Of these four migrant types, only Stream-type and parr migrants include extended freshwater rearing as a component of their expressed life-histories (Beamer et al. 2005b).

O. mykiss express two primary life-histories; anadromous (steelhead) and resident. Genetic analysis has found no difference between resident and anadromous *O. mykiss* in the regions of the Skagit River basin accessible to anadromous fishes (Pflug et al. 2013) so we will use "*O. mykiss*" when reporting on this species in this paper. *O. mykiss* spawn from February-mid June and rear in freshwater from one-three years prior to ocean immigration, most migrants are age two or three.

Coho salmon are found in every major drainage and hydro-region in the Skagit River where spawning

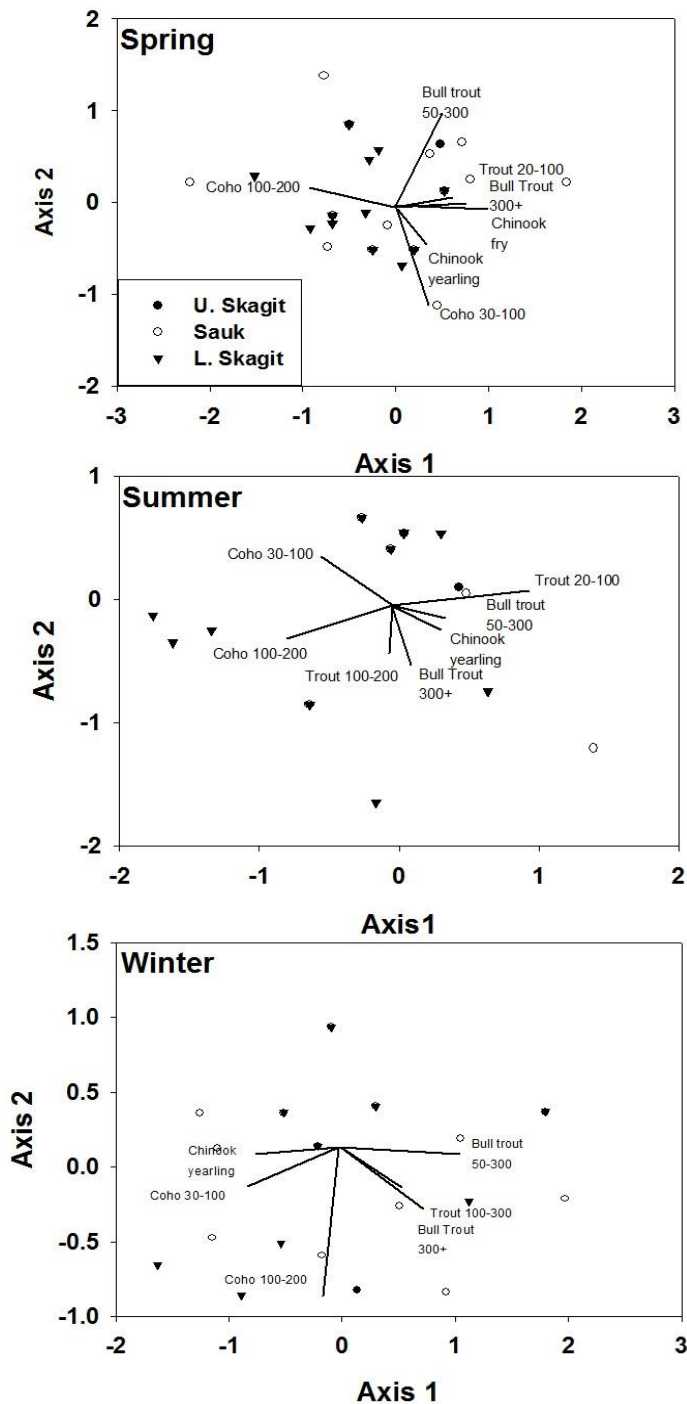


Figure 2. Ordination of seasonal nonmetric multidimensional scaling (NMS) analysis of species assemblage composition in the Skagit River basin. Shapes are coded by river basin. The joint plot overlay represents the species most correlated with each axis and depicts the orientation and magnitude of those correlations to each axis.

occurs from October through February. Most Coho salmon express a stream-type life history and immigrate to saltwater after one or two years in freshwater. Some individuals express an ocean-type fry life-history. The presence of an ocean-type life-history in the Skagit River is consistent with other Coho salmon populations in the region. Typically, this life-history is associated with a seaward migration in autumn prior to their first winter (Roni et al. 2012).

Bull Trout are found in most major drainages of the Skagit River. Their primary spawning habitats are in smaller mainstems and tributaries. Spawning occurs from September-mid October. Bull Trout express four life histories in the Skagit River: resident, fluvial, adfluvial, and anadromous. Marine and estuary migrations begin at age 3 and are completed by all subsequent age classes of Bull Trout in the Skagit River. Bull Trout are the only fish predator in the Skagit system where their effects on prey populations have been investigated. Lowery (2009 and 2015) concluded that Bull Trout are abundant enough to potentially regulate prey populations, including Pacific salmon, in the Skagit River.

Methods

Spatial-temporal analysis of juvenile salmonid distribution was stratified by season and regions with similar annual upland precipitation and hydrographs (hydro-regions), and secondarily by stream channel types (Montgomery et al. 1999, Beechie et al. 1999). Initial analysis of species assemblage from our surveys using Nonmetric Multidimensional Scaling (NMS), a non-parametric multivariate ordination technique, indicated that fish communities stratified by hydro-regions were more distinct than those grouped by sub-basins and therefore stratification by sub-basin was removed from this analysis (Figure 2).

Analysis of stream-type salmonid distributional patterns was based on observations from nighttime snorkeling. Supplemental sampling with electrofishing in a subset of locations provided higher resolution data on size structure, species identification, and biological samples for scale pattern analysis of stage specific size and growth for Chinook salmon and *O. mykiss*. Physical and biological samples were collected at each site during

spring (May-June) and summer (August-September) of 2011, and winter (January-March) and spring (April-May) of 2012.

Directed seasonal field sampling of physical and biological variables was conducted in stream reaches at spatially balanced locations within the Chinook salmon spawning distribution, analyzed with multivariate ordination methods, occupancy modeling, recursive partitioning, and graphical assessments to characterize the habitat use and

structure observations characterized seasonal distribution and habitat use by target species.

Site Selection

a population of randomly selected and spatially balanced points within the known Chinook salmon spawning distribution was selected using the Generalized Random Tessellation Stratified (GRTS) algorithm in the R package SPSURVEY (v2.10) (Stevens and Olsen 2004). Power analysis from a pilot study determined that a minimum of 24 sample

Primary Hydrological Region	Secondary Reach Type	Tertiary Channel Type	Sample Length (m)	Habitat Unit	Data Collected From Each Channel
Rain	Large Mainstem	Mainstem Edge	400	Bank, Bar, Backwater Pool	Measurements: Visibility, Wetted Width, Bankfull Width, Unit Length, Depth, and Velocity
Mix	Tributary	Tributary, Secondary Channel, Floodplain Channel	300 200 75	Riffle, Glide, Pool, Pond	Estimates: % Cover; Wood, Substrate, Velocity, Pool, Vegetation, and Undercut Bank, and Dominant and Sub-Dominant Substrate Types
Snow		Large Wood Jam	Varied	Wetted Edge	

Table 1. Table illustrating the nested hierarchical structure of the study design.

distribution of salmonids exhibiting a stream-type life history in the Skagit River basin. Habitat data collected from selected stream channels included direct measurements and visually estimated cover, large woody debris (LWD) counts, and substrate composition. Fish species identification and size structure was estimated by direct observation during nighttime snorkeling. The seasonal analysis characterized dominant gradients within habitat space by hydrology and stream channel types, and species composition with respect to hydrology. Occupancy modeling, recursive partitioning, and size

points for stream-type Chinook salmon, and 10 for *O. mykiss* would adequately reduce the chance of false negative observations during snorkel surveys (Beamer et al. 2010). Twenty-four oversample points were included to account for impediments to access, safety, and water clarity at the initial 24 sites. For a site to be included in the study, year-round access was required. Site suitability was ground-truthed for access, safety, and water clarity prior to the start of field sampling and sites were substituted as needed from the oversample as described in Stevens and Olsen (2004) (Figure 1).

A hierarchical structure was used a priori to stratify sample sites (Table 1). The primary stratum was the hydrological regime at each of the 24 selected sites (snow, mixed, or rain), defined by the shape of the annual hydrograph and dominant type of upland precipitation which was modified from Beechie (1992) and Beechie et al. (2006) (hereafter referred to as hydro-region) (Figure 1). The secondary stratum was major channel types at each sample site categorized as mainstem edge or tributary. Mainstems were generally large (>50m wetted width) streams and tributaries were streams primarily <50m. The tertiary stratum was defined as ancillary channel types present at each site i.e. secondary channel, floodplain channel, and large wood jam (Table 1). Secondary channels were defined as any section of river >200m in length containing less than 50% of the total mainstem flow through that site. The head and mouth of secondary channels were always directly connected to the mainstem. Flood plain channels were any low flow

channel in the floodplain of larger mainstems or tributaries. Floodplains could be connected at either the head (river flow dominated), mouth (ground water flow), could originate as a wall base channel, or small groundwater tributary. A large wood jam was any concentration of wood with a continuous wetted edge of a minimum of 100 linear meters. Sample sites were a composite of channels and not every sample site contained each channel type. For example, most tributary sample sites contained only the tributary channel type, whereas many mainstem sample sites were more diverse and could contain mainstem edge, secondary, large wood jam, and floodplain channel types.

Sampling Periodicity

Temporal strata for sampling events were selected based on ecologically significant life stages of the stream-type life histories expressed by target species (Table 2). Due to logistical constraints we selected a subset of these periods *a priori* that were assumed to represent periods of local residency subsequent

Spring	(May/early June)	End of smolt migration, ocean type fish have migrated. Parr and Stream-type fish remain in river.
End of summer	(Aug/early Sep)	Peak of the growing season with low flow and higher water temperatures.
Fall	(Oct)	Transition to higher flows and/or lower temperature that has redistributed stream-type fish.
End of Fall	(Nov/Dec)	End of growing season. Abundant adult salmon spawners present in system (abundant food).
Late winter	(Feb/early Mar)	End of salmon spawning, low flow, and scarce food.
Smolt Migration	(April)	Stream type smolts migrate to saltwater.

Table 2. Temporal strata for sampling periods based on ecologically significant life stages/seasonal benchmarks of the stream-type life histories expressed by target salmonid species.

and prior to periods of migration and emigration. Of the six periods identified in Table 2, we selected the descending limb of the spring smolt migration, summer low flow, and winter low flow. This resulted in a sampling cycle oriented to both Chinook salmon and *O. mykiss* stream-type individuals. The sampling cycle driven by a stream-type Chinook salmon life history began May/early June 2011 and concluded late April/May of 2012. Sampling in the summer after ocean-type (fry) Chinook salmon juveniles migrated (May/early June) resulted in only ocean-type parr and potential stream-type individuals in the study area. Data on species composition and outmigration timing from smolt trapping downstream of the study area suggested that most ocean type Chinook salmon fry have out-migrated by May (Zimmerman et al. draft manuscript). Chinook salmon that remained in river after this time were presumed to be ocean-type parr or stream-type juveniles. *O. mykiss* fry emerge in late summer and generally migrate as smolts at age 2 by May (Kinsel et al. 2008). *O. mykiss* young of the year (YOY) that remained in-river after January 1 were presumed to be age-1 and included both juvenile steelhead or non-anadromous residents. The *O. mykiss*-oriented sampling cycle began in April/early May 2011 while 2- and 3-year old *O. mykiss* smolts were out-migrating and concluded the following April. This resulted in observations of the 2009 brood year (age-2), 2010 brood year (age-1) and the 2011 brood year (age-0) individuals.

Habitat

Habitat measurements were collected during sample periods in each channel type per site. Mainstem edges and tributary habitat units were delineated following Beechie et al. (2005) and (Snider et al. 1992). Data were collected at the scale of habitat units within a given channel type (see Table 1 and appendix 2 for more detail). A handheld GPS (Garmin GPSmap 60CSx) was used to demarcate habitat units and the position of each measurement within units. Wetted widths, bank full widths, and unit lengths were measured with a handheld laser range finder (Bushnell Sport 850). Bank-full width was defined as the greatest elevation along the stream margin with evidence of hydraulic action, determined by the lack of shrubby vegetation. If the

river was too wide to effectively measure bank-full width in the field, bank-full width was measured in a GIS program (ESRI v.10.0 build 2414) from aerial photographs. Depth and flow velocities were measured using a Swiffer flow meter (Model 2100). We visually estimated percent cover by type, large woody debris (LWD) counts, and dominant and subdominant substrates within each unit. Substrate sizes were categorized following Kauffman et al. (1999), 6 categories were used to characterize substrates: 1) fines <0.06mm, 2) sand 0.06-2mm, 3) gravel (fine) 2-16mm, 4) gravel (course) 16-64mm, 5) cobbles 64-250mm, and 6) boulders 250-4000mm. Water temperatures in each channel type were measured at 20-minute intervals with archival temperature loggers (Onset U22-001 HOBO Water Temp Pro v2). All habitat measurements were collected during the day a minimum of 4 hours and a maximum of 8 hours prior to snorkel surveys to reduce the effects of short-term variability on fine scale hydraulic effects on habitat and lessen fish disturbance.

Fish Observations

Seasonal species composition, relative density, and size structure were estimated using upstream nighttime snorkeling along channel margins. All snorkelers were trained in species identification and size estimation techniques with refresher training prior to each sampling period. Snorkel surveys were conducted at each site along a longitudinal strip transect parallel to shore within each channel delineated during daytime habitat surveys. Surveys commenced one hour after sunset and consisted of one snorkeler with a handheld underwater LED dive light and one data recorder on shore. Surveys were conducted upstream beginning at the lowermost boundary of the channel. Visibility was measured in each channel type using a 100-mm fish shaped

Hydro-Region	Rain				Mixed				Snow			
	Spring '11	Summer '11	Winter '12	Spring '12	Spring '11	Summer '11	Winter '12	Spring '12	Spring '11	Summer '11	Winter '12	Spring '12
Total Sites Surveyed	6	6	6	3	15	15	15	5	3	5	4	2
Total Channels Surveyed	11	10	12	6	27	19	26	8	5	6	5	3
Total Channel Length (m)	2,758	2,351	2,646	1,316	6,873	5,666	7,377	2,247	1,137	1,813	1,469	873
Mean Elevation (m)	24	25	25	27	119	133	113	107	317	281	322	326
(min,max)	(12, 44)	(12, 44)	(12, 44)	(12, 35)	(57, 294)	(54, 294)	(57, 294)	(71, 286)	(281, 349)	(161, 406)	(281, 349)	(281, 349)
Mean Constraintment	0.18	0.2	0.17	0.17	0.11	0.16	0.15	0.13	0	0.5	0.2	0
(min,max)	(1,0)	(1,0)	(1,0)	(1,0)	(1,0)	(1,0)	(1,0)	(1,0)	(0,0)	(1,0)	(1,0)	(0,0)
Mean Distance from the Skagit Delta (km)	56	57	57	61	122	125	119	121	162	152	162	165
(min,max)	(40, 72)	(40, 72)	(40, 72)	(40, 72)	(86, 161)	(79, 161)	(86, 161)	(93, 161)	(156, 169)	(138, 169)	(156, 169)	(156, 169)
Mean distance from River Mouth (km)	1	2	1	1	11	14	9	8	36	21	36	50
(min,max)	(0, 7)	(0, 7)	(0, 7)	(0, 6)	(0, 53)	(0, 53)	(0, 53)	(0, 53)	(1, 62)	(1, 62)	(1, 62)	(27, 62)
Mean Solar Radiation (Wh/m ²) (min,max)	1,005,533 (975,317, 1,039,718)	1,004,687 (975,317, 1,039,718)	1,003,015 (975,317, 1,039,718)	988,933 (975,317, 1,027,864)	986,769 (718,973, 1,018,248)	972,091 (718,973, 1,018,248)	981,040 (718,973, 1,018,248)	979,823 (877,167, 1,015,908)	1,020,457 (1,002,703, 1,036,068)	983,225 (928,369, 1,036,068)	1,016,105 (1,002,703, 1,036,068)	1,011,937 (1,002,703, 1,030,405)
Mean Basin Area (km ²) (min,max)	33,919 (1,229, 48,947)	32,416 (1,229, 48,947)	34,786 (1,229, 48,947)	30,088 (1,229, 44,318)	9,802 (745, 18,241)	7,837 (745, 18,241)	9,236 (745, 18,241)	10,985 (1,035, 18,241)	6,955 (955, 9,596)	4,334 (955, 9,596)	6,955 (955, 9,596)	8,074 (7,314, 9,596)
Mean Maximum Temperature (°C) (min,max)	15.8 (14, 18.4)	15.7 (14, 18.4)	15.7 (14, 18.4)	15.7 (14.5, 18.4)	14.7 (11, 21.4)	14.3 (11, 19.2)	14.8 (11, 21.4)	13.5 (11, 19.2)	17 (12.8, 20.3)	14.3 (11.5, 18.4)	16.6 (12.8, 20.3)	17.3 (13.1, 20.3)

Table 3. Summary of sampling effort and physiographic variables collected from each site.

object (FSO) with simulated parr marks. Visibility was defined as the maximum distance the snorkeler could distinguish parr marks on the FSO. The width of each strip transect was defined as twice the visibility. As recommended by Thurow (1994) a minimum visibility criterion was established for these surveys, if visibility was less than 0.6m (1.2m survey track width) no surveys were conducted. Fish species identification, counts, and total lengths (TL) were estimated within one strip transect per channel type. Fish total length was estimated in 10-mm increments up to 100 mm, and by 50-mm increments above 100 mm. No fish outside the strip transects were counted. This resulted in an estimate of fish density and modal sizes associated specifically with the strip transect rather than to the entire wetted channel area.

Fish Collection

Stream-type Chinook salmon and juvenile *O. mykiss* were collected from 15 mainstem, 12 tributary, and two floodplain channels using single pass upstream electrofishing without block nets (Smith Root Model 12-B, 400-1000 v, standard pulse 80 Hz, 500µs). Sampling occurred in or near a subset of the selected sample sites during summer (July 1–October 5, 2011), autumn (October 6–December 31, 2011), winter (January 1–March 31, 2012), and spring (April 1–June 30, 2012). Fish were captured within stream

margin transects up to 400 m in length. Stunned fish were netted and placed in a bucket of water, anesthetized with MS-222, measured (fork length mm), and weighed (0.1 g). Scales were removed from the preferred area above the lateral line and below the posterior end of the dorsal fin. Processed fish were allowed to regain equilibrium in a recovery bath and released when able to swim freely. Fish handling protocols were approved under the auspices of the University of Washington Office of Animal Welfare IACUC #3286-20 and #3286-21.

Data Analysis

All habitat and fish use data were analyzed at the channel type scale rather than at the habitat unit scale. This was necessary to reduce the effects of pseudo-replication (Hurlbert 1984) and autocorrelation between adjacent habitat units (Heffner et al. 1996).

Graphical Assessments of Spatial-Temporal Length Frequency Patterns

Length frequency histograms were used to identify the size structure of each target species populations by season and hydro-region. Size modes in target populations were identified visually and used to characterize the general growth performance and age structure of salmonid populations within hydro-regions. Where applicable, we tested for differences in mean modal lengths of *O. mykiss*, Chinook

salmon, and Coho salmon between hydro-regions and the electro-fished samples and snorkel observations in summer and winter using ANOVA and Tukey's HSD post-hoc test. Size-at-age of Chinook salmon and *O. mykiss* from scale measurements were compared to modal size structure to describe the age and size structure of target populations. These life stages were combined with relative mean densities obtained from snorkel surveys within channel types to identify stage specific seasonal patterns of habitat use.

Graphical Assessments of Mean Relative Densities
 Mean densities of all target species were calculated within each stream section surveyed. Sample area was defined as:

$$A = 2V * L$$

Where *A* is the sample area, *V* is the measured visibility, and *L* is the transect length. Stage specific

mean density relative to the area sampled for all target species/life stages within the study area.

Habitat

Dominant seasonal gradients in habitat space were identified using principal component analysis (PCA) with a correlation matrix (PC-Ord v. 6). Habitat variables were separated into two groups: physiographic variables that were invariant by season (Table 3), and aquatic habitat variables that varied by season (Table 4). Physiographic variables were measured and analyzed by sample site, whereas aquatic habitat variables were measured and analyzed seasonally for the various channel types within sample sites. Measurements from subunits of varying lengths within each channel type were normalized by total channel length (weighted mean by length) in terms of the percentage of the channel each subunit covered to produce one value

Hydro Region	Rain			Mixed			Snow					
	Spring '11	Summer '11	Winter '12	Spring '12	Spring '11	Summer '11	Winter '12	Spring '12	Spring '11	Summer '11	Winter '12	Spring '12
Mean Wetted Width (m) (min,max)	51 (3, 202)	54 (3, 214)	50 (2, 209)	46 (4, 127)	41 (1, 125)	36 (2, 97)	41 (2, 116)	46 (20, 101)	27 (2, 61)	26 (3, 44)	25 (2, 50)	28 (1, 52)
Mean Bankfull Width (m) (min,max)	82 (5, 252)	72 (9, 241)	76 (9, 226)	71 (11, 200)	100 (5, 442)	95 (13, 314)	74 (5, 184)	69 (34, 128)	64 (4, 151)	77 (24, 114)	80 (7, 157)	62 (3, 118)
Mean Depth (m) (min,max)	0.42 (0.18, 1)	0.38 (0.16, 0.60)	0.37 (0, 0.70)	0.23 (0, 0.46)	0.41 (0.12, 1.28)	0.38 (0.13, 0.95)	0.52 (0.17, 2.19)	0.37 (0, 0.95)	0.25 (0.1, 0.33)	0.31 (0.12, 0.39)	0.37 (0.19, 0.46)	0.25 (0.19, 0.3)
Mean Velocity (m/s) (min,max)	0.25 (0, 0.65)	0.16 (0, 0.35)	0.25 (0, 0.66)	0.27 (0.05, 0.56)	0.29 (0, 0.69)	0.29 (0.03, 0.64)	0.25 (0, 0.56)	0.27 (0.07, 0.46)	0.36 (0.17, 0.59)	0.32 (0.17, 0.41)	0.34 (0.23, 0.52)	0.35 (0.26, 0.41)
Mean Wood Cover (%)	5 (0, 18)	24 (2, 100)	6 (0, 29)	23 (0, 83)	14 (0, 90)	20 (0, 90)	15 (0, 40)	25 (1, 95)	8 (0, 27)	3 (0, 10)	13 (0, 44)	33 (0, 88)
Mean Substrate Cover (%)	1 (0, 9)	15 (0, 75)	3 (0, 16)	9 (0, 35)	12 (0, 85)	21 (0, 75)	29 (0, 92)	41 (0, 85)	38 (0, 69)	57 (13, 85)	65 (1, 89)	55 (0, 85)
Mean Velocity Cover (%)	11 (0, 38)	15 (0, 50)	7 (0, 39)	8 (0, 25)	21 (0, 72)	34 (0, 85)	11 (0, 51)	13 (0, 44)	13 (1, 33)	34 (5, 88)	12 (0, 45)	9 (8, 10)
Mean Pool Cover (%)	21 (0, 100)	35 (5, 100)	40 (4, 100)	14 (0, 34)	16 (0, 51)	24 (0, 59)	32 (0, 100)	27 (0, 81)	28 (5, 57)	30 (5, 67)	31 (10, 52)	28 (25, 33)
Mean Vegetation Cover (%)	49 (0, 91)	44 (0, 96)	33 (0, 90)	30 (0, 81)	37 (0, 100)	31 (0, 100)	20 (0, 71)	25 (3, 47)	36 (0, 100)	24 (0, 84)	30 (0, 84)	30 (5, 71)
Mean Undercut Bank (%)	4 (0, 20)	10 (0, 37)	15 (0, 58)	7 (0, 25)	4 (0, 35)	6 (0, 35)	10 (0, 40)	16 (0, 70)	1 (0, 2)	4 (1, 7)	5 (1, 13)	5 (2, 9)
Mean Dominate Substrate (1-6) (min,max)	2.52 (2, 3.9)	3.22 (2, 5.4)	2.88 (2, 4)	3.18 (2, 4)	3.39 (2, 6)	3.78 (2, 6)	3.63 (2, 5.6)	3.55 (2, 5.3)	4.82 (3.1, 6)	5.15 (4.5, 5.7)	4.66 (2.8, 5.8)	4.38 (3, 5.2)
Mean Subdominate Substrate (1-6) (min,max)	3 (2, 4.6)	2.78 (2, 4.2)	2.82 (2, 4)	2.87 (2, 4)	3.41 (2, 6)	4.07 (2, 5.5)	3.75 (1.3, 5.9)	4.54 (2.5, 5.7)	4.78 (2.9, 5.9)	4.63 (2.8, 5.9)	4.31 (2.4, 5)	3.82 (2, 5)
Mean LWD Count (min, max)	391 (0, 4000)	84 (5, 600)	29 (0, 185)	172 (3, 1000)	190 (0, 1038)	102 (0, 300)	402 (0, 5200)	84 (3, 500)	112 (2, 226)	92 (0, 196)	358 (0, 1535)	23 (0, 54)

Table 4. Summary of aquatic habitat variables collected from each site.

seasonal densities of target species within each stream channel were averaged within each hydro-region. This resulted in a seasonal measurement of

for each aquatic habitat variable at each channel type per site (Table 4).

Species Assemblage

Seasonal shifts in life stage specific species assemblages between hydro-regions were analyzed using nonmetric multidimensional scaling (NMS) ordination (PC-Ord v.6). NMS arranges samples in ordination space using rank dissimilarity values and is recommended for most species community data (Minchin 1987, Clarke 1993). Stress values, a measurement of dissimilarity between original data and data in ordination space, were used to determine the best solution (number of dimensions) for the ordination (McCune and Grace, 2002). Data were transformed using the Beal's smoothing (Beal 1984, McCune 1994) function in PC-Ord (V. 6) For each season, we used Bray-Curtis (Sørensen) distance measures with random starting configurations, a maximum of 500 iterations, and 250 runs with real data. We ran a Monte Carlo simulation of 250 runs with randomized data to determine if a random solution reduced stress more effectively than a solution based on real data. A maximum mean stress of 0.20 was used to determine the appropriate dimensionality of the final ordination (Clarke 1993, McCune and Grace 2002). The ordination was then re-run using the recommended starting configuration and number of dimensions to produce the final ordination.

Occupancy

We characterized the seasonal/spatial distribution of species with low detection rates (bull trout and Chinook salmon) using occupancy modeling (MackKenzie 2006). Bull trout were modeled as single taxa by pooling all life stages. Chinook salmon were modeled as two distinct taxa by size class to represent ocean and stream type individuals; 20-80mm and 80+mm. Channel-specific surveys at each site were used to generate a family of surveys within each hydro-region during spring 2011, summer 2011, and winter 2012. Each channel was split into one, two, or three longitudinal sections depending on survey day, logistical constraints, and experience of the field crew. This resulted in surveys with one, two, or three sample units at each channel. These surveys were then pooled by season and hydro-region to calculate the probability of detection, probability of occupancy, and an estimate of the standard error of probability of occupancy for

the target taxa. Probability of occupancy and detection probabilities were calculated using the single group with constant detection probability model in Presence software v. 4.0 (Hines 2006). For this analysis the single groups were a species specific size group within a hydro-region within a season.

Classification modeling

We examined the factors associated with the presence and absence of ocean and stream-type Chinook salmon and bull trout sub-adults using a recursive partitioning algorithm known as a classification and regression tree model (CART). A classification tree uses recursive partitioning of nominal data (i.e. presence/absence or 0, 1, 2, etc.) to classify the presence of a species with respect to explanatory variables (Olden et al. 2008). We used the package rpart in R (v 2.14) for this analysis. Explanatory variables used in this analysis included season, hydro-region, and the physiographic and aquatic habitat variables. Final tree size was determined by use of the cross-validation rule algorithm in the rpart package. The largest tree that accounted for the greatest reduction in the relative error associated with the explanatory variable was chosen as the final tree. This analysis produces a decision tree that predicts the presence/absence of a species based on threshold values calculated from the range of values for each explanatory variable, and the number of correct assignments/predictions associated with those values. Attempts to predict densities of *O. mykiss* and Coho salmon were unsuccessful with this method likely due to their wide distribution across all levels of the sample hierarchies in time and space.

Age and Growth

Juvenile *O. mykiss* and yearling Chinook salmon scale samples were mounted on gum cards, pressed into acetate tiles, and age was assigned to each fish based on the presence of annular checks (annuli) (Carlander 1987). Scale acetate impressions were read using a microscope-mounted camera and digital microscopic photography software (ImagePro® v.4.5.1.22). On each scale, radius to focus, annuli, and scale margin were measured at an angle 20° off-axis. Regenerated scales, or those with an unclear focus (i.e., focus >0.04 mm dia.) were removed from analysis. Juvenile scale images were

taken using a 1x eyepiece and 1x objective, and magnification was set to 4.0. Age determination was based on the presence of annuli and date of capture. This resulted in an estimate of seasonal size-at-age by hydro-region for juvenile *O. mykiss* and stream-type Chinook salmon.

Results

Seasonal Fish and Habitat Surveys

We met our sampling goals for every hydro-region and season of this investigation. In spring 2011 we surveyed 24 sites containing 43 stream channels which totaled 10.7km of stream. In summer 2011 we surveyed 26 sites containing 35 stream channels which totaled 9.8km of stream. In winter 2012 we surveyed 25 sites containing 43 stream channels which totaled 11.5km of stream. In spring 2012 we surveyed 10 sites

region during winter. Coho salmon were found in most habitats and hydro-regions except their habitat use was more limited in the snow hydro-region.

Size structure, age and growth

The observed size structure for the different

Chinook Salmon Season	Age	Snow		Mixed		Rain	
		n	FL(SE)	n	FL(SE)	n	FL(SE)
Summer	0			19	58(1.0)		
	1			23	72(1.7)	5	81(2.9)
Autumn	0			1	36		
	1	7	89(4.0)	35	83(1.5)	1	98
	2					2	128(7.5)
Winter	0			69	40(0.6)	32	40(0.3)
	1	8	87(2.1)	49	81(1.3)	4	81(3.2)

Table 6. Scale ages of Chinook salmon.

salmonid species varied by season, hydro-region and sampling method. The estimated size modes from snorkel surveys for the six salmonid groups: bull trout sub-adults and adults, Chinook juveniles 30-160mm, *O. mykiss* 20-100mm and 100-300mm, and Coho salmon 30-100mm and 100-200mm are reported below by hydro-regions from upper watershed to lower watershed: snow, mixed, and rain; and by season: spring, summer, and winter. Size structures were compared between electrofishing and snorkeling for samples from both summer and winter.

Chinook salmon stream-type juveniles were present in all hydro regions and seasons (Figure 3). Chinook salmon showed a single size mode at 70mm which spanned 50-100mm during spring in all hydro-regions. During summer in the snow hydro-region a single mode was observed at 90mm with a mean length of 83mm (se=2.59). The modal size in the mixed and rain hydro-regions was 70mm with mean lengths of 79mm (se=0.51) and 75mm (se=0.38). This corresponds with the estimated length of age 1 individuals from scale aging (Table 6). The lower tails of the distributions varied amongst hydro-regions

Hydro-Region	Season	Total channels surveyed						Total channel length (m) surveyed					
		Total Sites	Tributary	Mainstem	Side Channel	Flood Plain Channel	Large Log Jam	Tributary	Mainstem	Side Channel	Flood Plain Channel	Large Log Jam	
Rain	Spring '11	6	4	2	2	2	1	1188	924	403	152	91	
	Summer '11	6	3	2	2	2	1	905	800	401	172	73	
	Winter '12	6	4	2	2	3	1	1115	800	397	225	109	
	Spring '12	3	2	1	1	1	1	600	368	198	75	75	
Mixed	Spring '11	15	5	11	2	7	2	1489	4277	401	520	186	
	Summer '11	15	6	9	1	2	1	1820	3437	189	150	70	
	Winter '12	15	5	11	2	6	2	1531	4797	396	482	171	
	Spring '12	5	1	4	1	1	1	300	1576	198	73	100	
Snow	Spring '11	3	1	2	-	2	-	191	796	-	150	-	
	Summer '11	5	2	3	-	1	-	551	1187	-	75	-	
	Winter '12	4	1	3	-	1	-	288	1105	-	76	-	
	Spring '12	2	-	2	-	1	-	-	798	-	75	-	

Table 5. Summary of sampling effort.

containing 17 channels which totaled 4.4km of stream (Table 5). With few exceptions *O. mykiss* were found in every season, hydro-region, and channel type. Chinook salmon were found in every season and hydro-region but their distribution and use of channel type was patchier and occurred in lower densities compared to other salmonids. Chinook salmon (stream-type and fry) had a low detection rate during winter using snorkeling when compared to electro-fishing which limited the breadth of our analysis during that season. Bull trout used habitats generally similar to Chinook salmon except they were not detected in the rain hydro-

(40mm-60mm). The upper tails of the distributions from all hydro-regions extended to 105mm. Significant differences in mean modal lengths were detected among hydro-region and between method (Figure 4) (snorkeling vs. electrofishing) in summer ($F=17.13$, $df=4$, $p<0.001$). Mean modal lengths differed significantly between snow (mean=83, $se=2.59$) and rain (mean=75, $se=0.38$) ($p=0.001$) and rain (mean=75, $se=0.38$) and mixed (mean=79, $se=0.51$) ($p<0.001$) hydro-region snorkel observations. Significant differences among electro-fished mean modal lengths were detected between populations in the rain (mean=87, $se=3.74$) and mixed (mean=71, $se=1.59$) hydro-regions ($p=0.009$). During winter in the snow hydro-region a mode

representing one individual was observed at 125mm. In the mixed (mean=131, $se=4.72$) and rain hydro-regions the mode was observed at 145mm (figure 3). The size structure of the electro-fished populations was similar to the snorkel observations in summer (Figure 4). In winter the snorkel observations appeared to capture only the upper tail of the size distribution with mean modal lengths greater than the electro-fished samples in all instances (figures 3 and 4). Results from scale aging suggest that some larger individuals could be age-2 stream-type Chinook salmon (Table 6). In the snow hydro-region during winter the electro-fished size structure exhibited a single mode at 90mm which corresponds to age one individuals from scale aging.

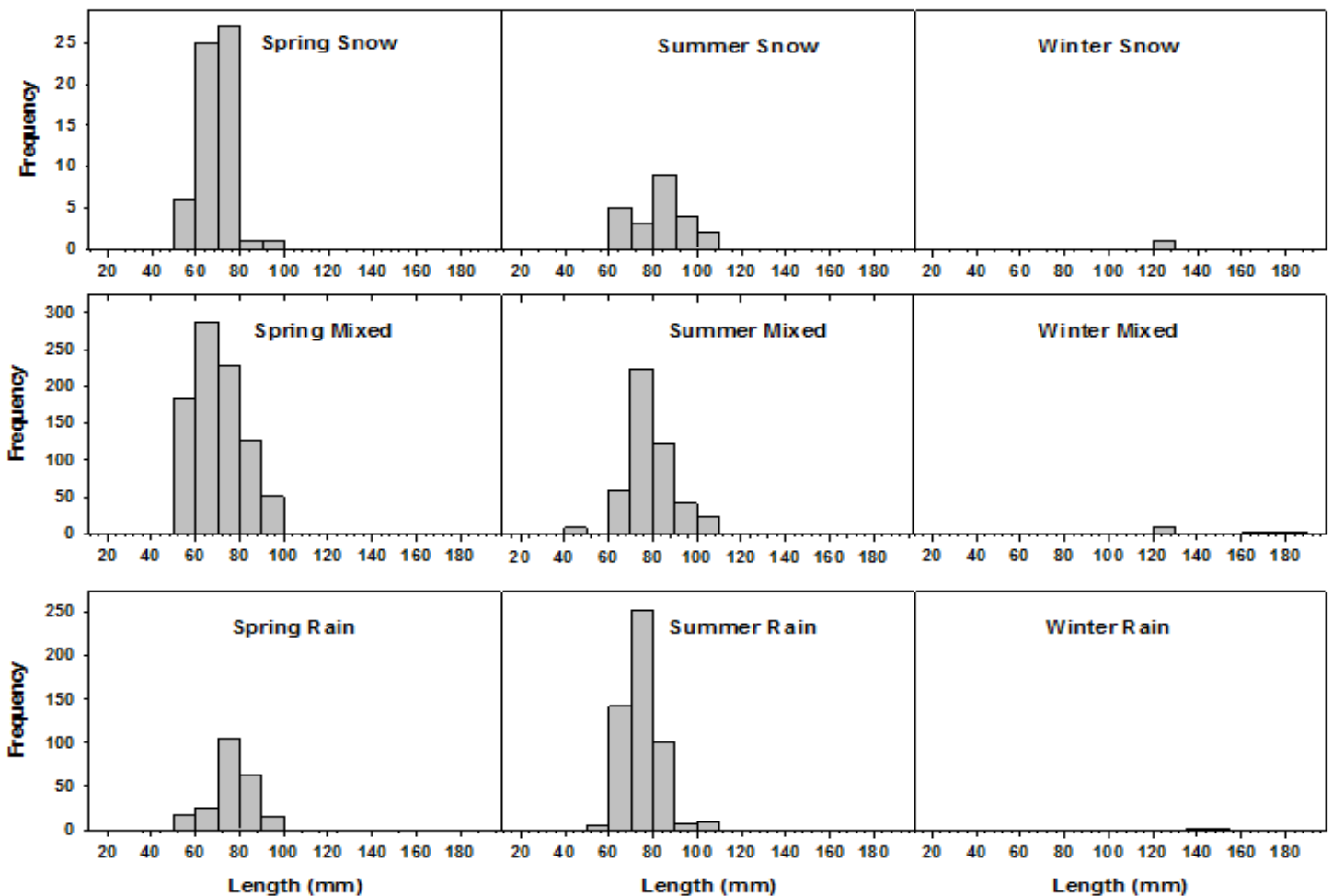
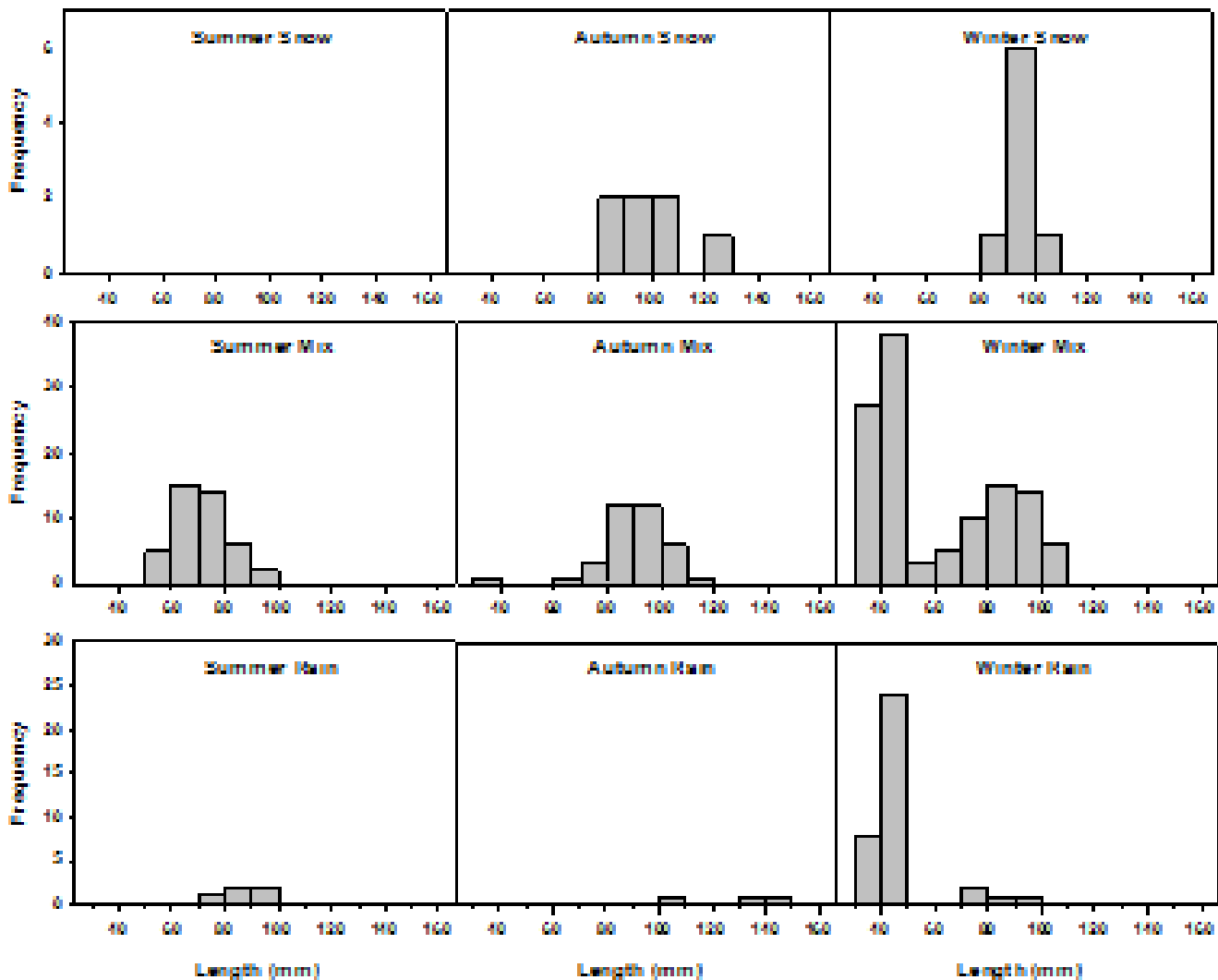


Figure 3. Observed seasonal size structure of Chinook salmon, by hydro-region, from snorkel surveys in the Skagit River during spring and summer 2011 and winter 2012.

In the mixed and rain hydro-regions a bimodal distribution was observed in the electro-fished population with peaks at 50mm (mixed mean =41mm, se=0.69, rain mean=43mm, se=0.78) and 90mm (mixed mean=86mm, se=1.66, rain mean=83mm, se=4.79) (figure 4). No significant difference in the mixed and rain hydro-regions was detected between mean lengths within the first mode ($F=0.821$, $df=1$, $p=0.376$). Within the second mode, significant differences ($F=45.09$, $df=3$, $p<0.001$) in mean modal length were detected between the electro-fished (mean=86, se=1.66) and snorkeled (mean=131, se=4.72) populations in the mixed hydro-region ($p<0.001$). Scale aging indicates

corresponded to age 0, 40mm (se=0.6) in the mixed and 40mm (se=0.3) in the rain hydro-regions, or age 1, 81mm (se=1.3) in mixed and 81mm (se=3.2) in rain hydro-regions. The modal sizes from electrofishing are larger than the estimated length at age from the scale ages (table 6).

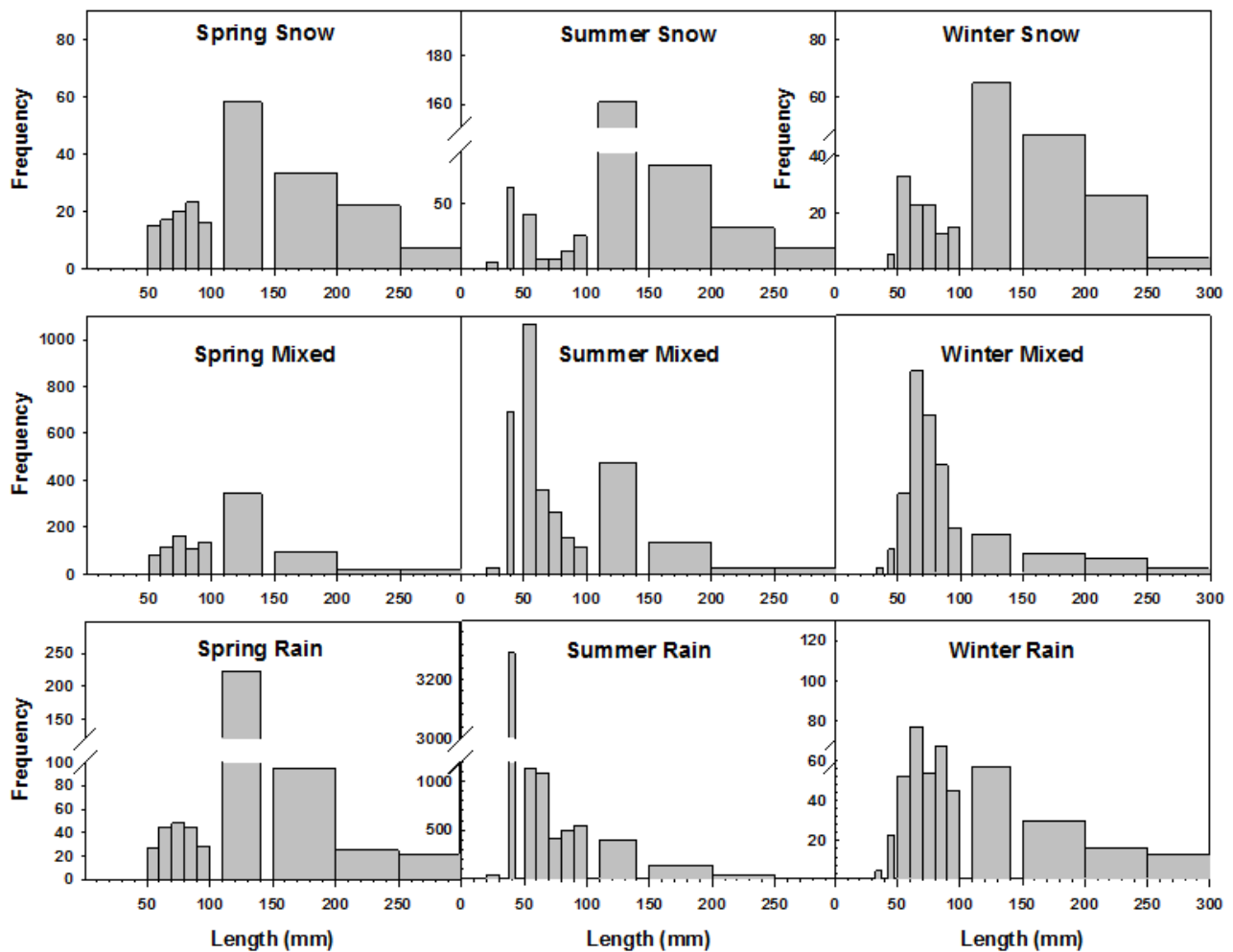
O. mykiss were observed in all hydro-regions during all seasons (Figure 5). Observed seasonal size structure from snorkel observations of *O. mykiss* was similar regardless of hydro-region. In spring, modes were observed at 75mm, 125mm, 175mm, and >200mm. In summer the size structure was similar to spring with an additional mode at 40mm corresponding with the emergence of that year's



that these peaks *Figure 4. Observed seasonal size structure of Chinook salmon, by hydro-region, from electrofishing surveys in the Skagit River during summer and autumn 2011 and winter 2012.*

YOY. Significant differences in mean length were detected within the first ($F=65.69$, $df=4$, $p<0.001$) and second ($F=54.63$, $df=4$, $p<0.001$) size modes in summer. Significant differences were detected within the first size mode of the electro-fished population between the rain (mean=53, se=1.62) and mixed (mean=43, se=0.69) hydro-regions ($p<0.001$) and the snow (mean=42, se=0.72) and rain (mean=53, se=1.62) hydro-regions ($p<0.001$). Differences were also detected between the snorkel and electro-fished populations in the mixed (snorkel mean=39, se=0.11, electro-fish mean =43, se=0.69) ($p<0.001$) and snow hydro-regions (snorkel mean=39, se=0.51, electro-fish mean =42, se=0.72) ($p=0.005$). Within the second mode differences

significant between the snow (72, se=1.74) and mixed (mean=64, se=0.28) hydro-region snorkel populations ($p<0.001$) and the snorkel (mean=64, se=0.28) and electro-fished (mean=89, se =1.28) populations in the mixed hydro-region ($p<0.001$). Estimates from scale aging in summer suggest that length-at-age is similar in all three hydro regions for age zero 40-50mm, one 90-100mm, and two 118-144mm which generally correspond with the observed size modes from snorkeling and electro-fishing (Table 7). In winter the size modes from snorkeling and electro-fishing were visually similar to spring (Figure 6) but the estimated size at age increased in spring for age-0 55-60mm, age-1 103-114mm, and age-2 148-160mm individuals. The



were most

Figure 5. Observed seasonal size structure of *O. mykiss*, by hydro-region, from snorkel surveys in the Skagit River during spring and summer 2011 and winter 2012.

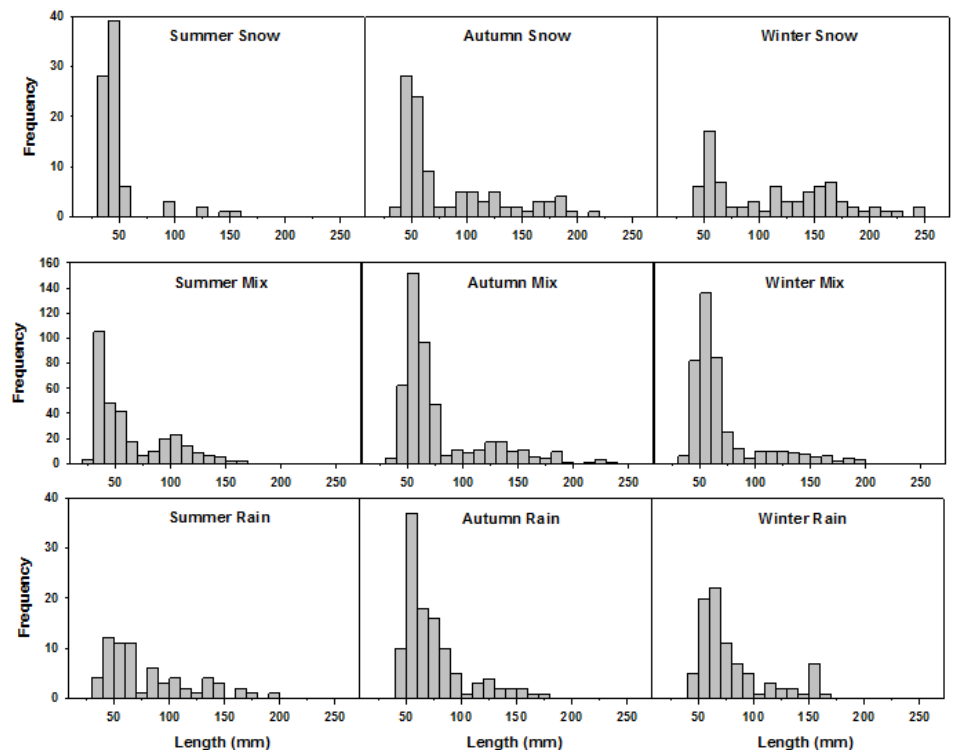
<i>O. mykiss</i>		Snow		Mixed		Rain	
Season	Age	n	FL(SE)	n	FL(SE)	n	FL(SE)
Summer	0	73	40(0.6)	215	42(0.6)	39	50(1.4)
	1	5	100(6.8)	66	96(1.6)	15	90(2.9)
	2	2	144(6.5)	24	118(4.2)	10	134(4.1)
	3			4	136(2.6)	2	171(16.5)
Fall	0	65	51(1.0)	363	56(0.5)	92	61(1.2)
	1	19	101(0.7)	46	100(2.2)	11	105(3.6)
	2	17	156(4.7)	60	141(2.5)	9	137(5.9)
	3	1	201	7	197(8.8)		
Winter	0	32	55(1.2)	341	55(0.5)	60	60(1.1)
	1	22	111(3.8)	55	114(2.5)	19	103(4.2)
	2	20	155(2.8)	15	160(4.3)	6	148(1.2)
	3	2	194(3.0)	3	181(3.8)	2	161(5.5)
	4	4	220(8.1)				

Table 7. Scale ages of *O. mykiss*.

observed modes differed between the snorkel observations and the electrofishing data (Figures 5 and 6) but the size structure, based on the location of modes, in the electro-fished population was visually similar to the snorkel observations. Mean modal length differed among hydro-regions and collection methods ($F=85.77$, $df=5$, $p<0.001$) for the first mode. The only significant difference in mean modal length detected between snorkeling (mean=109, se=0.78) and electro-fishing (mean=117, se=2.01) was in the mixed hydro-region ($p<0.001$). Significant differences in mean modal length from snorkeling were found between the rain (mean=89, se=0.47) and mixed (mean=109, se=0.78) ($p<0.001$) and snow (mean=90, se=0.96) and mixed (mean=109, se=0.78) ($p<0.001$) hydro-regions. In the electro-fished populations significant differences were detected between the snow (mean=108, se=3.61) and rain (mean=66, se=1.59) ($p<0.001$) and snow (mean=108, se=3.61) and mixed (mean=117, se=2.01) ($p<0.001$) hydro-regions. In the second mode significant differences ($F=56.93$, $df=5$, $p<0.001$) in

mean modal length were found between snorkeling and electro-fishing in the snow (snorkel mean=90, se=0.96, electro-fish mean=107, se=3.66) ($p<0.001$), mixed (snorkel mean=109, se=0.78, electro-fish mean=117, se=2.01) ($p=0.002$), and rain (snorkel mean=89, se=0.47, electro-fish mean=121, se=3.75) ($p<0.001$) hydro-regions. No differences in mean modal length were detected between hydro-regions in the electro-fished populations. Mean modal lengths from snorkeling were significantly smaller for rain (mean=89, se=0.47) than mixed (mean=109, se=0.78) ($p<0.001$) and for snow (mean=107, se=3.66) than mixed (mean=109, se=0.78) ($p<0.001$) hydro-regions).

Figure 6. Observed seasonal size structure of *O. mykiss*, by hydro-region, from electrofishing surveys in the Skagit River during summer and autumn 2011 and winter 2012.



We observed Coho salmon in all hydro-regions during all seasons (Figure 7). The seasonal size structure for Coho salmon was more dynamic than Chinook salmon and *O. mykiss*. In the snow hydro-region during spring, two size modes were observed at 50mm and 80mm. In summer those modes shifted to 70mm and 90mm. This bimodal distribution was also observed in the electro-fished populations in the snow hydro-region during summer (Figure 8). In winter, those modes increased again to 90mm and 125mm. In the mixed and rain hydro-regions a similar pattern was observed with one mode moving from 50mm to 70mm to 90mm in spring, summer, and winter. The size distribution was broader in these hydro-regions with tails accounting for larger and smaller individuals than in the snow hydro-region. A second size mode at 125mm was also observed in most seasons in the mixed and rain hydro-regions (Figure 8). The electro-fishing data suggested that the observations from the mixed and rain hydro-regions incorrectly identified two size modes which were actually part of a unimodal distribution. However in autumn, the electro-fished population contained an individual which was larger (140mm) than the modal size (90mm) and separate from the upper tail of the distribution by 30mm (Not visible but present in Figure 8). Significant differences among hydro-regions and sampling methods in mean modal length were detected in the first ($F=40.41$, $df=5$, $p<0.001$) and second ($F=88.11$, $df=1$, $p<0.001$) modes in summer. In the first mode for electro-fished samples, mean modal lengths were significantly larger in the rain (mean=80, $se=1.28$) than the mixed (mean=65, $se=0.71$) hydro-regions ($p<0.001$), smaller in the snow (mean=51, $se=1.09$) than in the mixed (mean=65, $se=0.71$) hydro-regions ($p<0.001$), and smaller in the snow

Figure 7. Observed seasonal size structure of coho salmon, by hydro-region, from snorkel surveys in the Skagit River during spring and summer 2011 and winter 2012.

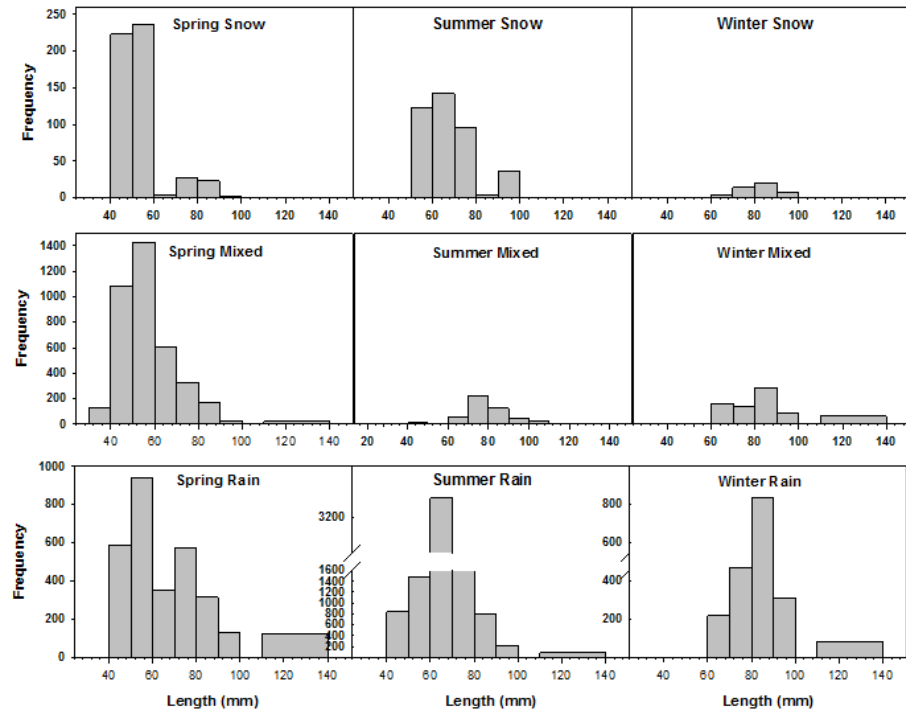
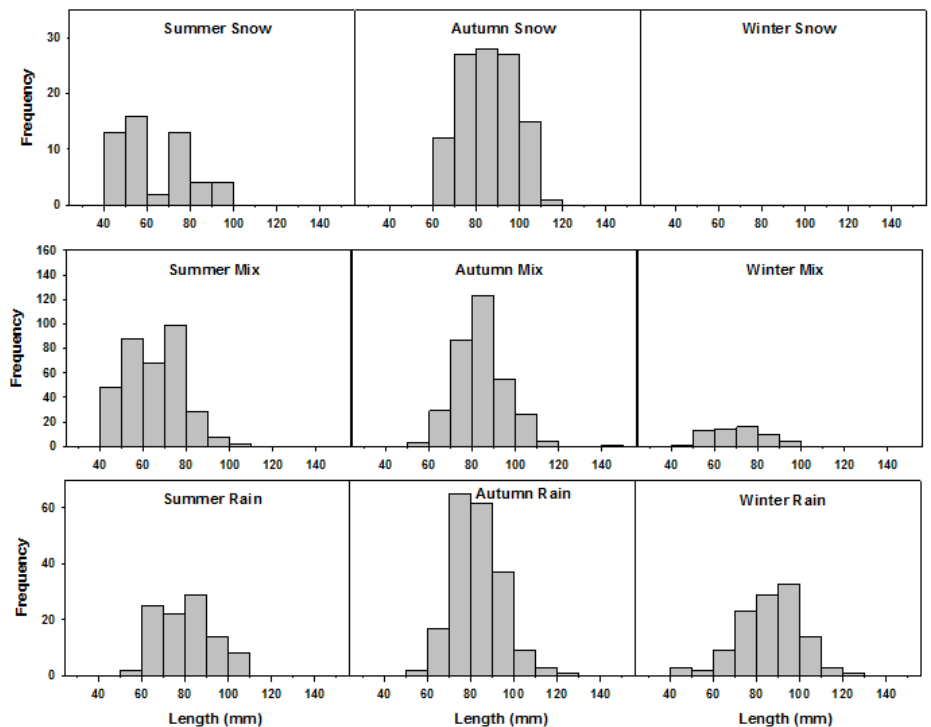


Figure 8. Observed seasonal size structure of coho salmon, by hydro-region, from electrofishing surveys in the Skagit River during summer and autumn 2011 and winter 2012.



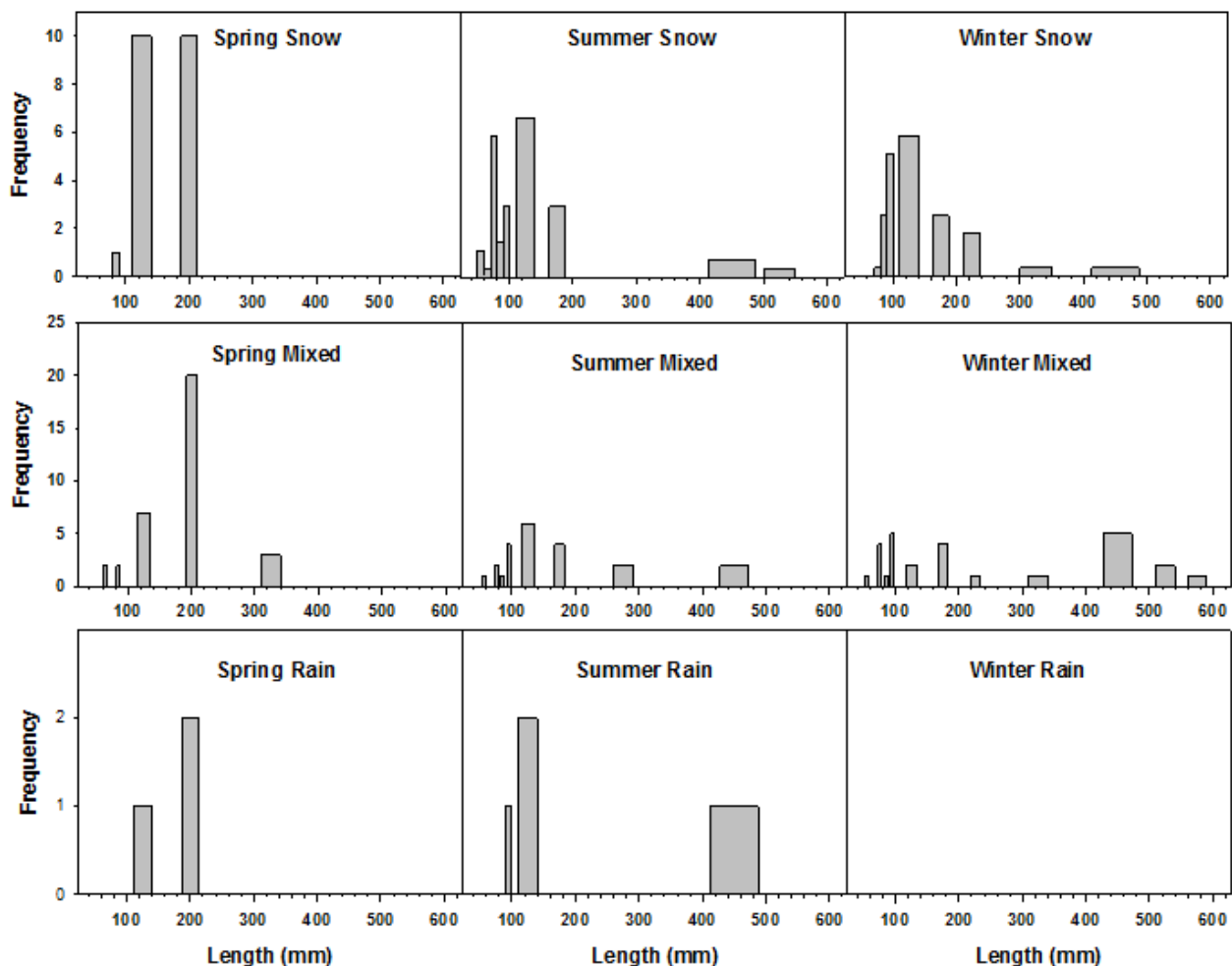


Figure 9. Observed seasonal size structure of bull trout, by hydro-region, from snorkel surveys in the Skagit River during spring and summer 2011 and winter 2012.

(mean=51, se=1.09) than in the rain (mean=80, se=1.28) hydro-regions ($p < 0.001$). In the snorkel samples the first mode was significantly smaller in the snow (mean=64, se=0.41) compared to the mixed (mean=67, se=0.15) hydro-regions ($p < 0.001$) and the snow (mean=64, se=0.41) compared to the rain (mean=67, se=0.13) hydro-regions ($p < 0.001$). Significant differences in mean modal length between collection methods were detected in the rain (snorkel mean=67, se=0.13, electro-fish mean=80, se=1.28) ($p < 0.001$) and snow (snorkel mean=64, se=0.41, electro-fish, mean=51, se=1.09) ($p < 0.001$) hydro regions. The second mode was only observed in the snow hydro-region and mean modal length was significantly larger in the snorkel (mean=94, se=0.47) observations compared to the electrofishing samples (mean=81, se=1.77)

($p < 0.001$). In winter significant differences in mean modal lengths were detected ($F=14.44$, $df=4$, $p < 0.001$) between snorkeling (mean=83, se=0.59) and electrofishing (mean=71, se=1.65) ($p < 0.001$) in the mixed hydro-region and between electro-fished populations in the rain (mean=86, se=1.37) and mixed (mean=71, se=1.65) hydro-regions.

We observed a similar seasonal size structure in bull trout populations in all hydro-regions with some exceptions (Figure 9). During spring, size modes appeared at 80mm, 125mm, and 200mm in all hydro-regions. In the mixed hydro-region we observed an additional mode at 325mm, and in the rain hydro-region we did not observe the mode at 80mm. In summer, size structure was more complex due to the emergence of the new age-0 cohort. In

the snow and mixed hydro-regions modes were observed at 70mm, 90mm, 125mm, 175mm, and 450mm. Additionally in the snow hydro-region a mode was observed at 525mm, in the mixed hydro-region an additional mode was observed at 275mm. In the rain hydro-region the size structure was less complex with observed size modes only at 90mm, 125mm, and 450mm. In winter the snow and mixed hydro-regions were similar again with observed modes at 90mm, 125mm, 175mm, 225mm, 325mm, and 450mm. The mixed hydro-region had additional modes at 75mm and 550mm. No bull trout were observed during winter in the rain hydro-region. Patterns of Mean Relative Densities

Stream-type Chinook salmon juveniles were observed in lower densities in the snow hydro-region compared to the mixed and rain hydro-regions. In general Chinook stream-type juveniles were associated with channel types adjacent with larger mainstems like mainstems, large log jams, and

flood plain channels (Figure 10). Chinook salmon fry densities were greatest in mainstem channels during spring in all hydro-regions. Springtime densities of stream-type Chinook salmon in the snow hydro-region were greatest in flood plain channels, while in summer, densities were greatest in mainstems. Detections were too low during winter in the snow hydro-region for an accurate assessment. In the mixed hydro-region during spring and summer, stream-type Chinook salmon densities were similar in all channel types. In winter, densities were greatest in flood plain channels. In the rain hydro-region, densities were greater in mainstems and large log jams. In summer, greater densities were observed in large log jams and flood plain channels. In winter greater densities were observed in flood plain channels (Figure 10).

O. mykiss densities were greater in the mixed and rain hydro regions with a relatively lower density in the snow hydro-region. Densities in the snow and

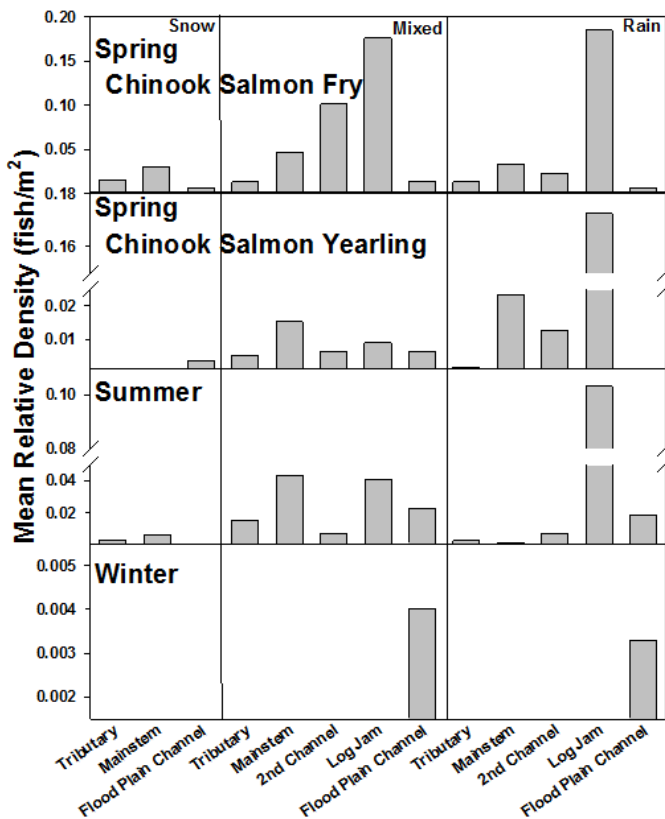


Figure 10. Mean relative density of Chinook salmon, fry and stream-type, by season and channel type from snorkel surveys in the Skagit River.

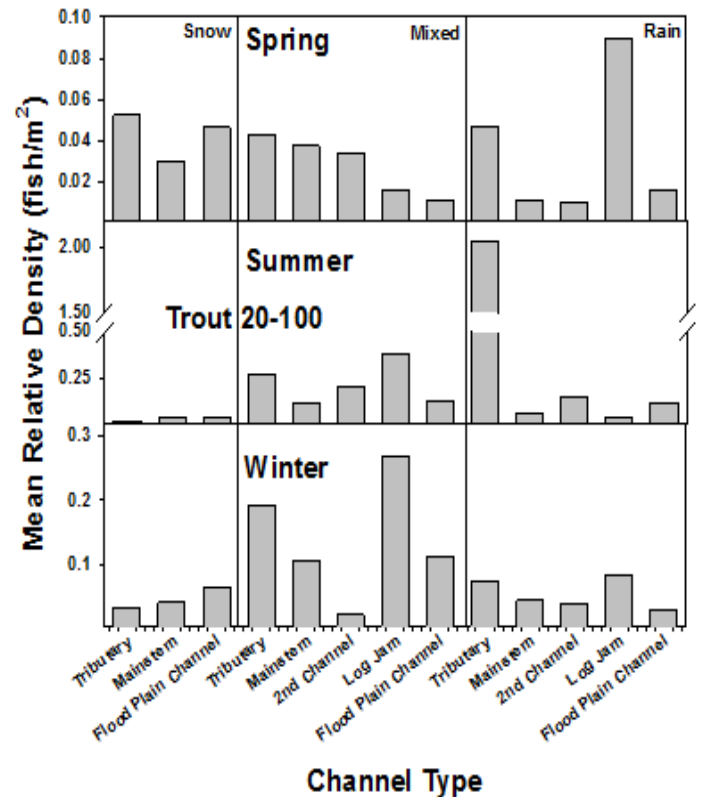


Figure 11. Mean relative density of Trout 20-100mm by season and channel type from snorkel surveys in the Skagit River.

mixed hydro-regions were similar in all channel types with a tendency to increase in habitats associated with larger mainstems (Figure 11). Lower in the watershed, *O. mykiss* densities were greater in tributaries relative to other channel types. Densities of *O. mykiss* 20-100mm in the snow hydro-region were generally high in all habitats and use was similar in all habitats and all seasons. In the mixed hydro-region, densities were generally high in all habitat types through spring and summer. In winter, greater densities were observed in tributaries and large log jams. In the rain hydro-region, springtime densities were greatest in tributaries, in summer high densities were observed in tributaries and large log jams, and in winter generally high densities were observed in all channel types (Figure 11). Springtime densities of *O. mykiss* 100-300mm in the snow hydro-region were greater in tributaries and mainstems (Figure 12). In summer and winter densities were generally high in tributaries, mainstems, and flood plain channels. In the mixed hydro-region densities were greater in tributaries and large log jams all seasons and similarly high in

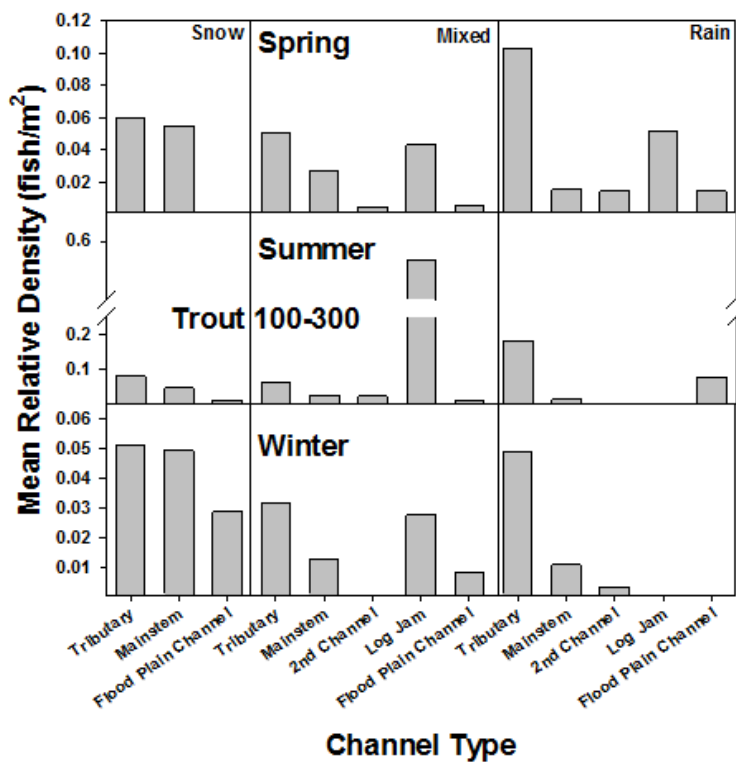


Figure 12. Mean relative density of Trout 100-300mm by season and channel type from snorkel surveys in the Skagit River.

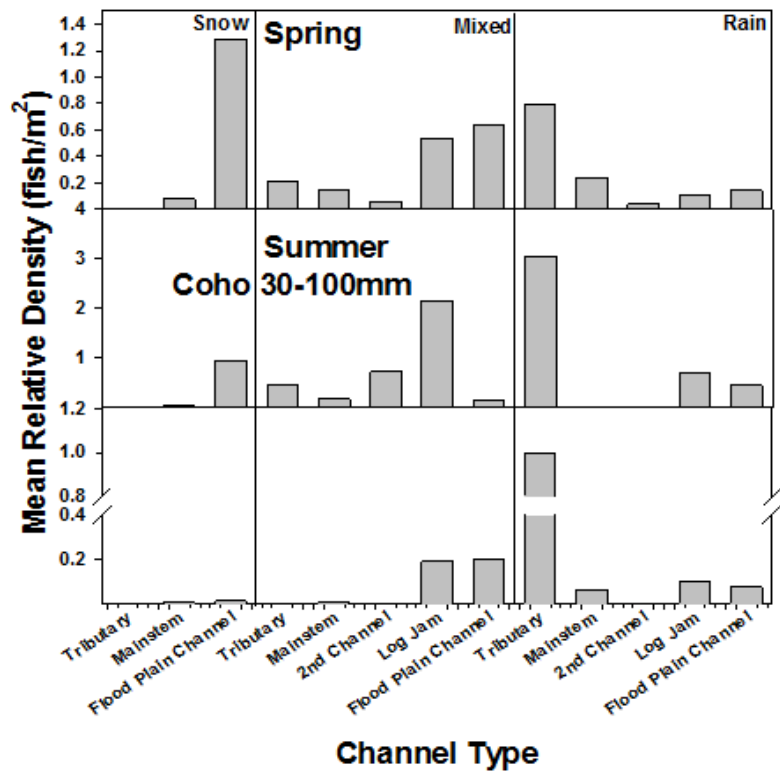


Figure 13. Mean relative density of coho salmon 30-100mm by season and channel type from snorkel surveys in the Skagit River.

mainstems during spring. In the rain hydro-region densities were greatest in the tributary channels all seasons. In addition to tributaries, spring densities were also high in large log jams, in summer greater densities were observed in flood plain channels, and in winter densities were higher in mainstems (Figure 12).

Coho salmon densities were greater in floodplain channels in the snow and mixed hydro-regions and transitioned to an increase in densities in tributary channels in the rain hydro-region (Figure 13). Densities of Coho salmon 30-100mm in the snow hydro-region were greater in flood plain channels all seasons. In the mixed hydro-region densities were greatest in large log jams all seasons. In addition, densities were high in flood plain channels in spring and winter and in secondary channels in summer. In the rain hydro-region densities were greater in mainstems during spring. In summer and winter higher densities were observed in tributaries, large log jams, and flood plain channels. Observed densities of Coho salmon 100-200mm were too low

to make an assessment in the snow-hydro region. In the mixed hydro-region springtime densities were greatest in large log jams. The summer assessment was inconclusive due to low observations, and in winter densities were highest in flood plain channels. In the rain hydro-region densities were greatest in tributaries all seasons with higher densities in flood plain channels during summer as well (Figure 13). Bull trout sub-adult densities in the snow hydro-region were greatest in mainstem channels during all seasons and increased in flood plain channels during spring and winter (Figure 14). In the mixed hydro-region, largest densities were found in flood plain channels during spring, secondary channels and large log jams in summer, and large log jams in winter. In the rain hydro region, densities were greatest in large log jams in spring and in flood plain channels during summer. No bull trout were detected in the rain hydro-region during winter (Figure 14).

See appendix tables A4, A8, A12, A13, A14, A15, and A16 for additional detail concerning observed densities.

Physical Habitat and Fish Assemblage Structure

Results from the PCA of physiographic variables indicated a strong gradient by hydro-region along the first axis (40.03% of the variance). Basin area was positively associated with the rain hydro-region and negatively associated with elevation, distance from the Skagit river delta, and distance from the river/stream mouth where the surveys occurred (Figure 15). The rain hydro-region was more distinct and the snow and mixed hydro-regions exhibited some overlap along the first axis. For more detail see appendix.

In all seasons NMS showed a strong gradient in species composition along the first axis exhibiting a distinction between the rain and snow hydro-regions. Greater first axis scores were associated with the snow hydro-region and the rain hydro region was associated with lower axis 1 scores (Figure 16 a, b, and c). The mixed hydro region did not show a distinct cluster, rather in spring and summer the rain and mixed hydro-region overlapped and in winter the snow and mixed hydro-regions overlapped. The gradient in species

composition along the second axis showed less distinction among hydro-regions than along the first. In spring, rain and snow hydro-regions were centrally clustered in the plot. The mixed hydro-region points also clustered centrally encompassing the rain and snow points and spreading further in both positively and negatively along the second axis. In summer, rain and snow exhibited some separation compared to spring with the rain hydro-region spanning the origin, the snow hydro-region clustering below zero, and the mixed hydro-region spanning the origin at greater magnitudes than the

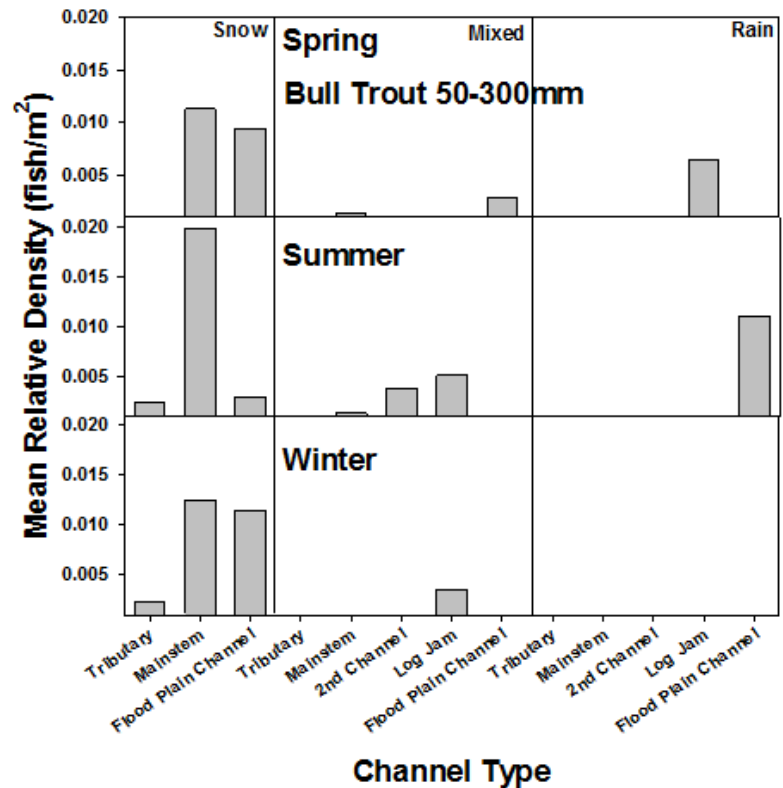


Figure 14. Mean relative density of bull trout sub-adults by season and channel type from snorkel surveys in the Skagit River.

rain or snow hydro-regions. In winter, snow and rain hydro-regions occupied a similar position along the second axis with the mixed hydro-region again spanning the origin in similar magnitudes as in summer.

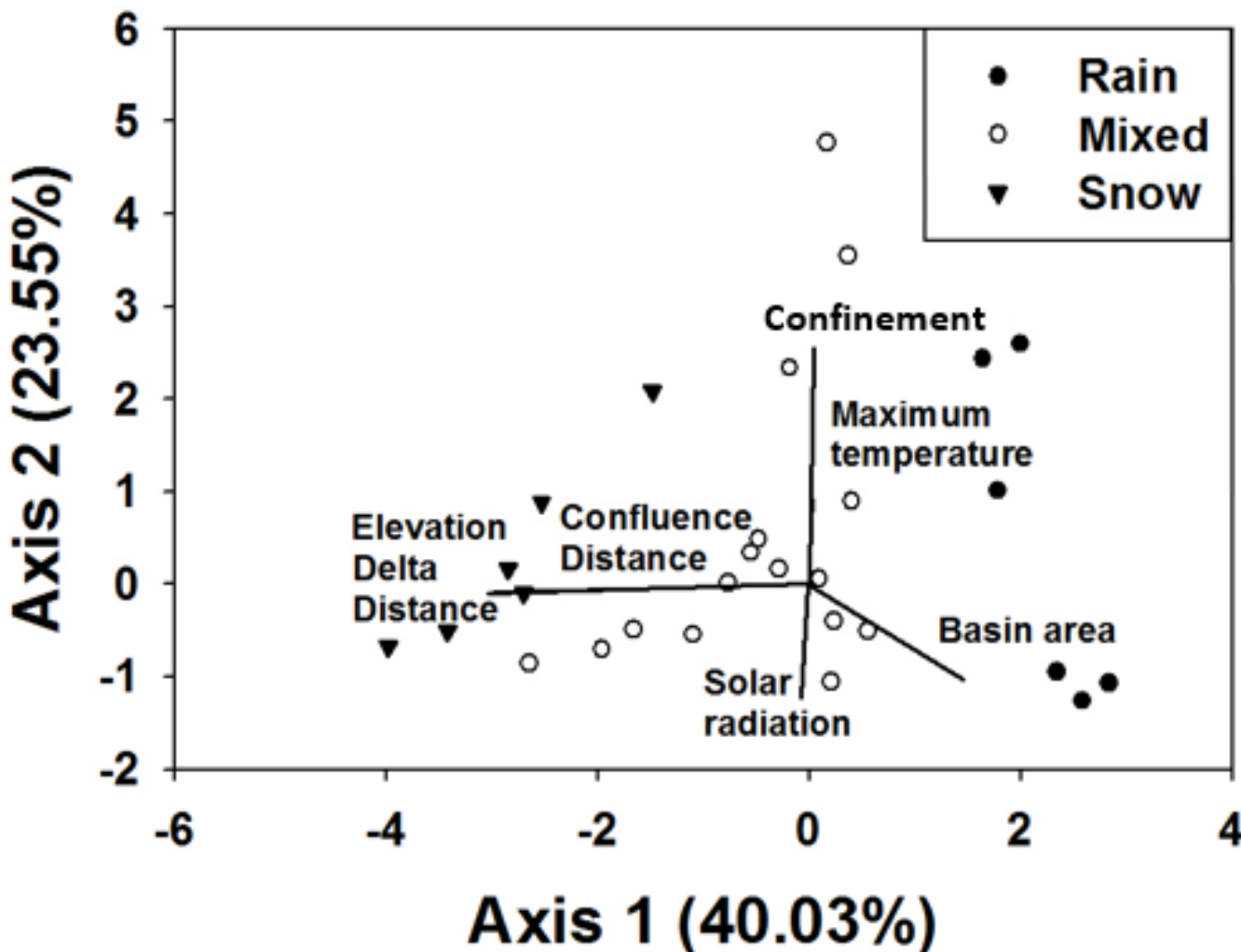
Springtime gradients in species composition along the first axis were structured by 100-200mm Coho salmon associated with the rain and mixed hydro-region and 20-100mm *O. mykiss*, Chinook salmon

fry, and 300+mm bull trout associated with the snow hydro-region. Bull trout sub-adults were associated with the snow and mixed hydro-regions (higher axis-2 scores) and stream-type Chinook salmon and 30-100mm Coho salmon were associated with the mixed hydro-region (lower axis 2 scores) (Figure 16 a). In summer, large and small Coho salmon were associated with the rain and mixed hydro-regions (lower axis 1 scores) with small *O. mykiss*, bull trout sub-adults, and stream-type Chinook salmon associated with the mixed and snow hydro-regions (larger axis 1 scores). Small Coho salmon associated with the rain and mixed hydro-regions (higher axis 2 scores) and large bull trout and large trout were associated with the snow and mixed hydro-regions (lower axis 2 scores) (Figure 16 b). In winter stream-

type Chinook salmon and small Coho salmon were associated with the rain and mixed hydro-regions (lower axis 1 scores) and 300+mm and sub-adult bull trout and 100-200mm *O. mykiss* were associated with the snow and mixed hydro-regions (higher axis 1 scores). Coho salmon 100-200mm trended towards an association with the rain and mixed hydro-regions. Bull trout 300+mm, and 100-200mm *O. mykiss* trended towards the snow and mixed hydro-regions. All three taxa had low axis 2 scores and no species associated with higher axis 2 scores (Figure 16 c).

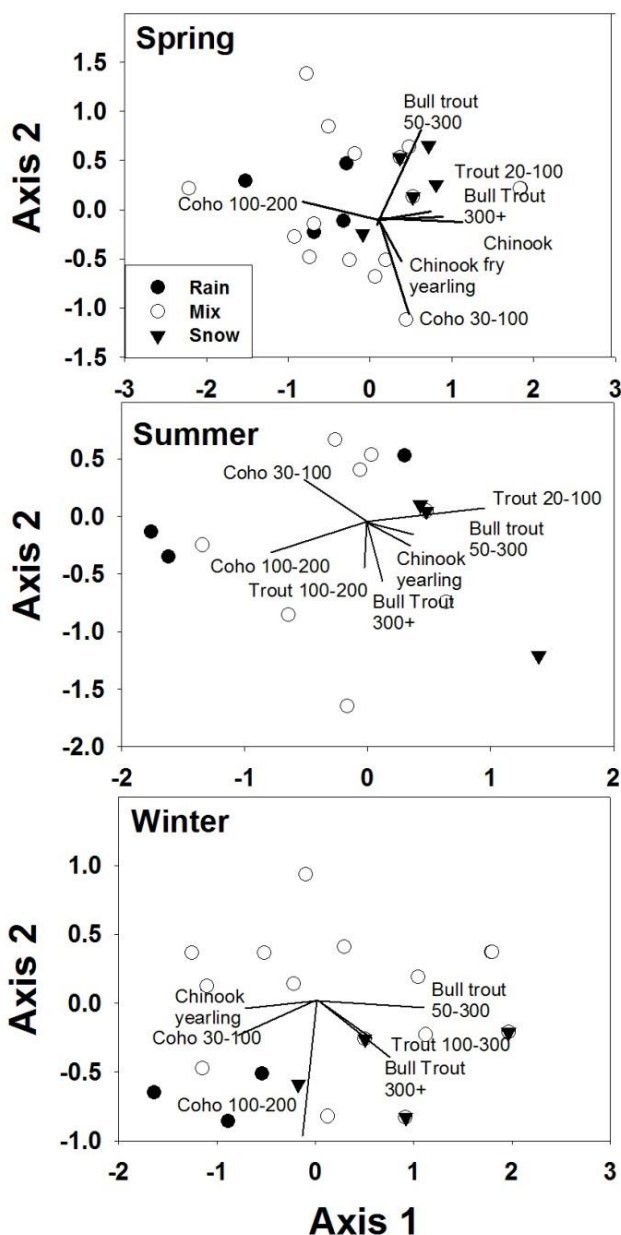
Seasonal associations between hydro-regions and species were variable. In Spring 100-200mm Coho salmon were associated with rain and mixed hydro regions, 50-300mm and 300+mm bull trout, *O.*

Figure 15. Principal component analysis (PCA) of physiographic habitat variables in the Skagit River basin. Points within the ordination, coded by shape, represent sample locations within three hydro-regimes of the Skagit river basin. The joint plot overlay represents the habitat variables correlated with each axis and depicts the orientation and magnitude of those correlations to each axis.



mykiss 20-100mm, and Chinook salmon fry were associated with the snow hydro-region, and stream-type Chinook salmon and 50-100mm Coho salmon were associated with the snow and mixed hydro-regions (Figure 16 a). Summertime patterns indicate that 30-100mm Coho salmon are associated with the

Figure 16 Ordination of seasonal nonmetric multidimensional scaling (NMS) analysis of species assemblage composition in the Skagit River basin. Shapes are coded by hydro-regime. The joint plot overlay represents the species most correlated with each axis and depicts the orientation and magnitude of those correlations to each axis.



rain and mixed hydro-regions, 100-200mm Coho salmon associated with the mixed hydro-region, and *O. mykiss* 20-100mm and 100-200mm, bull trout sub-adults and 300+mm, and stream-type Chinook salmon were associated with the snow and mixed hydro-regions (Figure 16 b). In winter 30-100mm Coho salmon and stream-type Chinook salmon were associated with the mixed and rain hydro-regions, Coho salmon 100-200mm, *O. mykiss* 100-200mm, and 300+mm bull trout were associated with all 3 hydro-regions, and 50-300mm bull trout were associated with the snow and mixed hydro-regions (Figure 16 c).

Occupancy Modeling

Seasonal probability of occupancy (Ψ) (SE) by hydro-region, was successfully calculated for stream-type Chinook salmon, Chinook salmon fry, and bull trout (all life stages pooled). Bull trout Ψ in the snow dominated hydro-region for every season was $\Psi=1(0.0)$, but Ψ varied by season in the mixed hydro region: spring $\Psi= 0.51(0.22)$, summer $\Psi= 0.73(0.33)$, and winter $\Psi= 0.44(0.14)$. In the Rain hydro region, $\Psi= 1.0(0.0)$ in spring, $\Psi= 0.61(0.43)$ in summer, but bull trout were not detected in winter.

We detected a trend in Chinook salmon occupancy in all hydro-regions towards larger body size as spring and summer transitioned to winter. Chinook salmon 20-80mm were detected only in spring and summer within all hydro-regions. In the snow hydro-region, $\Psi= 1.0(0.0)$ during spring and $\Psi= 0.75(0.22)$ in summer. In the mixed hydro-region $\Psi= 1.0(0.0)$ during spring and $\Psi= 0.94(0.07)$ in summer. In the rain hydro-region $\Psi= 0.75(0.24)$ in spring and $\Psi= 0.95(0.15)$ in summer. Chinook salmon 80+mm were detected all seasons within all hydro-regions. In the snow hydro-region, $\Psi= 1.0(0.0)$ during spring, $\Psi= 0.78(0.23)$ in summer, and $\Psi= 0.26$ in winter (sample size was too small to calculate SE). In the mixed hydro-region $\Psi= 0.93(0.12)$ in spring, $\Psi= 1.0(0.0)$ in summer, and $\Psi= 0.55(0.43)$ in winter. In the rain hydro-region $\Psi= 0.75(0.24)$ in spring, $\Psi= 1.0(0.0)$ in summer, and $\Psi= 0.15$ in winter (sample size was too small to calculate SE) (Table 8).

Classification Modeling

Bull trout sub-adult presence within the project area was estimated using a five node tree (Figure 17). The explanatory variables that effectively classified bull

Table 8. Occupancy model results.

Season	Hydro-Region	Species	PAO	se
Spring	Snow	Bull Trout 30-300mm	1.00	0.0
Spring	Mixed	Bull Trout 30-300mm	0.51	0.22
Spring	Rain	Bull Trout 30-300mm	1.00	0.0
Summer	Snow	Bull Trout 30-300mm	1.00	0.0
Summer	Mixed	Bull Trout 30-300mm	0.73	0.33
Summer	Rain	Bull Trout 30-300mm	0.61	0.43
Winter	Snow	Bull Trout 30-300mm	1.00	0.0
Winter	Mixed	Bull Trout 30-300mm	0.44	0.14
Winter	Rain	Bull Trout 30-300mm	0.00	0.0
Spring	Snow	Chinook 30-80mm	1.00	0.0
Spring	Mixed	Chinook 30-80mm	0.93	0.12
Spring	Rain	Chinook 30-80mm	0.75	0.24
Spring	Snow	Chinook 80-160mm	1.00	0.0
Spring	Mixed	Chinook 80-160mm	1.00	0.0
Spring	Rain	Chinook 80-160mm	0.75	0.24
Summer	Snow	Chinook 30-80mm	0.78	0.23
Summer	Mixed	Chinook 30-80mm	1.00	0.0
Summer	Rain	Chinook 30-80mm	1.00	0.0
Summer	Snow	Chinook 80-160mm	0.75	0.22
Summer	Mixed	Chinook 80-160mm	0.94	0.07
Summer	Rain	Chinook 80-160mm	0.95	0.15
Winter	Snow	Chinook 80-160mm	0.26	xx
Winter	Mixed	Chinook 80-160mm	0.55	0.43
Winter	Rain	Chinook 80-160mm	0.15	xx

trout presence were distance from the Skagit delta, hydro-region, basin area, season, and depth. The tree predicted that few or no bull trout are found less than 114 river km from the Skagit delta. In habitats greater than 114 km from the delta and in the snow hydro-region, bull trout were present in all channel types. In habitats greater than 114 km from the delta and in the mixed hydro-region bull trout were found in basins less than 585km². This includes the upper Skagit River, lower Cascade River, Diobsud creek, and Illabot creek. In basins located in the mixed hydro-region and larger than 585km² bull trout were not likely to be present in winter. These areas included the portion of the lower Skagit greater than 114km from the delta, the lower Sauk River, and the lower Suiattle River. In these areas during spring and summer bull trout were present and more common in velocities greater than 0.49m/s.

Chinook salmon fry were classified with a three node tree. The explanatory variables that best described Chinook fry presence were season and depth. If the season was not spring no Chinook salmon fry were present. During spring, Chinook salmon fry were found in water greater than 0.24m (Figure 18).

Stream-type Chinook salmon presence was best classified using a 5 node tree (Figure 19). The explanatory variables used in the best fit tree were season, distance upstream from the river mouth, wetted width, wood cover, and vegetation cover. The tree predicted that Chinook salmon yearlings were not common (or detection rates were low) in winter unless they were greater than 21km from a river mouth. During spring and summer stream-type Chinook salmon were more common in wetted channels greater than 7.3m in width with less than 58% vegetation cover. In channels less than 7.3m wide stream-type Chinook salmon were less common but when present were found in places with greater than 17% wood cover (Figure 19).

We were unable to find a tree that met the cross-validation rule for Coho salmon and *O. mykiss* likely due to their widespread distribution and apparent generalist habitat use. Therefore we graphically assessed the mean relative densities of all salmonid taxa with regards to season, hydro-region, and channel type in previous sections.

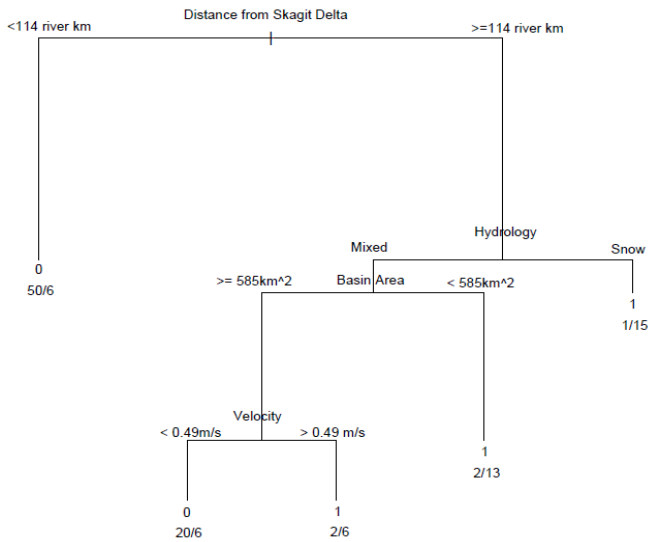


Figure 17. Classification tree of bull trout sub-adult presence/absence in the Skagit River, WA. Explanatory variables associated with a split are located centrally. The threshold values or categories defining a split are located on the top of the right and left branches. Branches to the left denote absences, to the right presences. Values at terminal nodes first define a presence (1) or absence (0), followed by a pair of numbers separated by a slash (n/k) which is defined as the number of absences/presences assigned by the model to the terminal node(s).

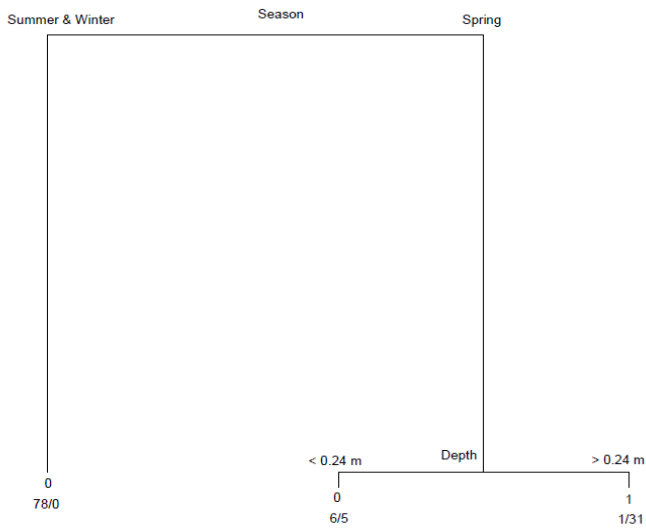


Figure 18. Classification tree of Chinook salmon fry presence/absence in the Skagit River, WA. Explanatory variables associated with a split are located centrally. The threshold values or categories defining a split are located on the top of the right and left branches. Branches to the left denote absences, to the right presences. Values at terminal nodes first define a presence (1) or absence (0), followed by a pair of numbers separated by a slash (n/k) which is defined as the number of absences/presences assigned by the model to the terminal node(s).

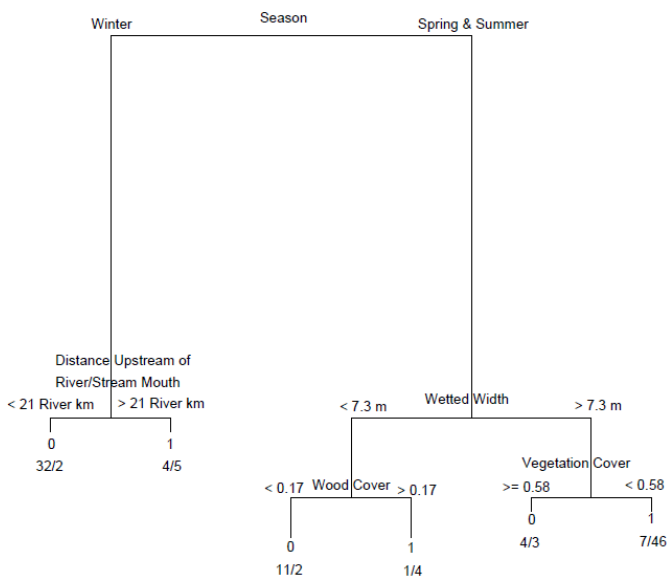


Figure 19. Classification tree of stream-type Chinook salmon presence/absence in the Skagit River, WA. Explanatory variables associated with a split are located centrally. The threshold values or categories defining a split are located on the top of the right and left branches. Branches to the left denote absences, to the right presences. Values at terminal nodes first define a presence (1) or absence (0), followed by a pair of numbers separated by a slash (n/k) which is defined as the number of absences/presences assigned by the model to the terminal node(s).

Life History Summaries

Chinook Salmon

In the snow hydro-region in spring, stream-type Chinook salmon occupied flood plain channels with moderate to low wood cover. In summer, stream-type Chinook salmon were found primarily in mainstem edges and tributaries with moderate vegetation cover. In winter greater relative densities of stream-type Chinook salmon were observed in mainstem edges which represented habitat with relatively less vegetation cover and greater substrate and velocity cover compared to tributaries and flood plain channels in this hydro-region. Mainstems were negatively, and tributaries were positively, associated with vegetation cover which accounted for a strong gradient in habitat space during this investigation. Stream-type Chinook salmon had low detection rates in winter in the snow hydro-region. When observed they were greater than 21km from the mouth of the mainstem edge they were observed in. Eight age 1 and no age 0 individuals were collected via electrofishing from mainstem edges in the snow hydro-region during winter which corroborates our observations from snorkel surveys. In the mixed hydro-region during the spring outmigration period stream-type Chinook salmon used channel types associated with larger mainstems with the greatest densities found in mainstem edges, secondary channels and large log jams. In spring, the dominant gradient in the environmental variables associated with these channel types indicated that large jams were associated with greater wood and undercut bank cover types and greater overall depth. Mainstem edges were associated with greater substrate cover, greater dominant and subdominant substrates and higher relative velocities. The secondary channels were intermediate in aquatic habitat variable space to the log jams and mainstem edges. All three channel types were positively associated with greater bankfull and wetted widths and greater overall LWD counts. During summer, stream-type Chinook salmon were found in all channel types with greater densities in mainstem edges with moderate to low vegetation cover, large log jams, and flood plain channels with moderate to high wood cover. These channel types encompass the extent of the

observed gradients in habitat space indicating a generalist habitat use during summer and loose associations to specific aquatic habitat variables beyond those already discussed for spring. In winter, stream-type Chinook salmon were found in flood plain channels and were associated with Coho salmon 30-100mm. Aquatic habitat variables associated with the flood plain channel type were wood, vegetation, undercut bank, pool, and depth cover types.

In the rain hydro-region during spring, age-0 stream-type Chinook salmon fry were associated with mainstem edges, large log jams, and secondary channels. As in the mixed hydro-region these channel types were positively associated with greater bankfull and wetted widths and greater LWD counts. In summer, stream-type Chinook salmon were found primarily in large log jams. Which were associated with greater pool, wood, and undercut bank cover types, increased depth, and greater LWD counts. In winter, stream-type Chinook salmon were found only in flood plain channels just as in the mixed hydro-region.

O. mykiss

In the snow hydro-region in spring, *O. mykiss* 20-100mm occupied floodplain channels, mainstems, and tributaries. The major gradients in aquatic habitat variable space are encompassed by these channel types indicating that *O. mykiss* are associated with vegetation, pool, and substrate cover types, larger sized dominant and subdominant substrate types, greater LWD counts, and greater velocities. They were also somewhat negatively associated with wood and undercut bank cover types and greater depths. *O. mykiss* 100-300mm were only found in mainstem edges and tributaries, which associates these larger individuals with similar aquatic habitat variables as the smaller size class of *O. mykiss*. In summer, *O. mykiss* 20-100mm and 100-300mm occupied similar habitats to stream-type Chinook salmon, mainstem edges and tributaries with moderate vegetation cover. Our analysis did not find a strong association with any physiographic or aquatic habitat variables; however, the channel types associated with greater densities of *O. mykiss* were similar to those for stream-type Chinook salmon.

During spring in the mixed hydro-region, patterns of mean densities and channel use for both size classes of *O. mykiss* were highly homogenous. In general, during this season most species used channel types associated with mainstem edges and tributaries. These channel types were associated with greater pool and substrate cover types, larger dominant and subdominant substrate, and greater velocities. Mainstem edge habitats were more strongly associated with greater LWD counts and greater wetted and bankfull widths. Tributary channels were more strongly associated with greater vegetation cover. *O. mykiss* 20-100mm were highly generalist in their use of habitat and stream channels throughout the mixed hydro-region in summer. Larger *O. mykiss* tended to occupy large log jams and tributary streams. *O. mykiss* 20-100mm were associated with bull trout sub-adults and stream-type Chinook salmon. Our investigation observed stream-type Chinook salmon occupying every channel type, but in much lower densities than all other stream-type salmonids. This is indicative of a generalist habitat use pattern for all target species during summer in the mixed-hydro-region. In winter in the mixed hydro-region both size classes of *O. mykiss* were found primarily within tributaries and large log jams and secondarily within mainstem edges and flood plain channels. This suggests a generalist habitat use in winter as in the other seasons.

In the rain hydro-region during spring and summer, both size classes of *O. mykiss* were primarily associated with tributary streams which were characterized by greater vegetation cover. In winter, *O. mykiss* were found in similar densities in all channel types which again suggests a generalist use of available habitat.

Coho Salmon

In the snow hydro-region in spring, Coho salmon 30-100mm occurred primarily in flood plain channels. Which were characterized by greater depth, and greater vegetation, wood, and undercut bank cover types. In summer Coho salmon 30-100mm were only found in flood plain channels, which had similar positions in aquatic habitat space as in spring. In winter, Coho salmon 30-100mm were observed in similar densities in floodplain channels and

mainstem edges. Only in winter were Coho salmon observed using most channel types that we investigated. In general, Coho salmon in the snow hydro-region were primarily flood plain channel specialists.

In the mixed hydro-region in spring, Coho salmon 30-100mm were found primarily in flood plain channels and large log jams. Both habitats were associated with wood and undercut bank cover types, and greater depth. Flood plain channels and large log jams represented both extremes of the secondary gradient within aquatic habitat variable space. This suggests that in addition to the aquatic habitat variables listed above, Coho salmon 30-100mm were also associated with greater vegetation cover, greater bankfull and wetted widths, and greater LWD counts. During summer they were associated with large log jams, secondary channels, and tributaries. In this season, the aquatic habitat variables associated with Coho salmon 30-100mm are similar to spring. In winter, Coho salmon 30-100mm were associated with large log jams and flood plain channels, Coho salmon 100-200mm were also observed in flood plain channels during this time. The aquatic habitat variables associated with these channels are greater wood, pool, vegetation, and undercut bank cover types, greater depth, and greater wetted and bankfull widths.

In the rain hydro-region during summer, winter, and spring, densities of Coho salmon 30-100mm and Coho salmon 100-200mm were greatest in tributaries. This associates both size classes of Coho salmon with greater vegetation and substrate cover types, greater velocities, and larger dominant and subdominant substrate types in the rain hydro-region.

Bull Trout

In the snow hydro-region in spring, bull trout sub-adults occupied floodplain channels, mainstem edges, and tributaries. In summer, bull trout sub-adults and adults were found in greater densities in mainstem edges and were observed in lower densities in flood plain channels and tributaries during this period. In winter bull trout sub-adults and adults were observed in mainstem edges,

tributaries, and flood plain channels. During all seasons in the snow hydro-region, the channel types used by bull trout were associated with the two dominant gradients in aquatic habitat variable space. This suggests that bull trout are generalist in their use of channel types and occupy the majority of habitats available to them in the snow hydro-region. In the mixed hydro-region in spring bull trout sub-adults were associated with mainstem edges and flood plain channels. In summer, bull trout sub-adults and adults were associated with stream-type Chinook salmon and found in large log jams, secondary channels, and mainstem edges. In winter, both age classes of bull trout were observed in large log jams. In this hydro-region bull trout/habitat associations trended from generalist in spring to more specific in winter. Most bull trout observed were associated with larger mainstem edges.

In the rain hydro-region in spring bull trout sub-adults were found in large log jams and in summer sub-adults and adults were found in flood plain channels. We did not observe any bull trout in the rain hydro-region in winter. In all habitats in the rain hydro-region that we observed bull trout, they were associated with greater depths and wood or vegetation cover.

During our investigation bull trout were primarily associated with the snow hydro-region. Analysis of our snorkel surveys from the mixed and rain hydro-regions indicated that bull trout were present but less frequent. Our surveys were limited to the mainstem edge and were not designed to comprehensively survey all available bull trout habitat in tributaries and mainstems.

Discussion

The results from this investigation suggest that the interaction between hydro-region (physiographic variables), channel type (aquatic habitat variables), and season best describe the spatiotemporal distribution patterns of stream-type Pacific salmon, *O. mykiss*, and bull trout. These interactions can be highly specific, as in Coho salmon use of floodplain channels in the snow hydro-region, or general, as in the broad habitat use by *O. mykiss* in all hydro-regions.

The observed distribution of stream-type salmonids at the end of the smolt migration period represents the establishment of rearing territories that will be used by individuals during their initial growing season (Jonsson and Jonsson 1993). Our temperature data suggests that a general growing season for stream-type salmonids in the Skagit River begins in late spring and extends through the anadromous salmonid spawning season in late autumn. Habitat use and species composition of juvenile salmonids during the end of the spring outmigration was less distinct than during summer and winter low flow periods. This is likely due to the presence of stream-type inter-river migrants establishing rearing territories and late migrating smolts. After ocean-type fry have emigrated in spring, individuals of all species with the potential to express the stream-type life-history inhabited different channel types depending on hydro-region. In summer in the snow hydro-region, stream-type Chinook salmon were found primarily in the margins of mainstems and tributaries with moderate vegetation cover. Greater mean relative densities of stream-type Chinook salmon were observed in mainstems which represented habitat with relatively less vegetation cover and increased LWD counts compared to tributaries and flood plain channels in this hydro-region. This accounted for a strong gradient in habitat space during this investigation. *O. mykiss* 20-100mm and 100-300mm occupied similar habitats to stream-type Chinook salmon but were not strongly associated with any habitat variables. Bull Trout sub-adults were found in greater densities in mainstems which could pose a predation risk to stream-type Chinook salmon and particularly *O. mykiss* (Lowery 2009, Lowery 2011, and Lowery 2015).

Bull Trout were strongly associated with the snow hydro-region and represent a potential predation risk for most stream-type salmonids. Overlaps were observed between Bull Trout and stream-type salmonids in species composition analysis and in channel specific mean relative densities in the snow hydro-region during spring and summer. In summer, greater daily temperatures and reduced flows in mainstems and tributaries versus lower temperatures and stable flows in flood plain

channels likely provide greater growth potential in tributary and mainstem habitats (Mesa et al. 2013). The increased risk of predation by Bull Trout and other predators in larger tributary and mainstem habitats could be reduced if the energetic potential in these habitats is great enough for stream-type salmonids to out-grow the gape of local predators (Reimchen 1991, Higham 2007). Coho salmon were the only habitat specialist observed in the snow hydro-region, occupying almost exclusively flood plain channels during all periods of observation. Coho salmon growth and behavior could be limited by temperature in the snow-hydro region and may remain in flood plain channels to reduce exposure to predation and occupy a niche not fully exploited by other stream-type salmonids in these habitats. Coho salmon in the Skagit and other systems will use ponded portions of streams and flood plain channels more regularly than other stream-type salmonids (Taylor 1990). In general, Coho salmon production will decrease with increasing gradient and increase with increasing pool and pond habitat types (Sharma and Hilborn 2001). Previous observations of Coho salmon suggest that size at the end of summer or end of autumn can be a determining factor influencing in-stream movements. Roni et al. (2012) found that Coho salmon tagged in upper portions of a watershed tend to delay migrations compared to conspecifics in lower portions of the same stream. Additionally, larger individuals tended to be more mobile and more able to take advantage of other habitats not available to smaller con-specifics (Roni et al 2012).

In the mixed hydro-region during summer stream-type Chinook salmon were found in all channel types with greater densities in mainstem edges with moderate to low vegetation cover, large log jams, and flood plain channels with moderate to high wood cover. *O. mykiss* 20-100mm and Bull Trout sub-adults were associated with stream-type Chinook salmon. This association, as in the snow hydro-region, could pose a predation risk to *O. mykiss* and stream-type Chinook salmon. Our investigation observed stream-type Chinook salmon occupying every channel type but in much lower densities than all other stream-type salmonids. The primary behavior of this life history type was to

occupy habitats with moderate depth, cover, and structure. This generalist behavior allows stream-type Chinook salmon to take advantage of habitats that meet their growth and anti-predation needs. A diversified behavior should buffer this life history from localized negative impacts and allow it to take advantage of under exploited niches not fully used by more specialized salmonids such as Coho salmon which primarily occupied large log jams, tributaries, and secondary channels. A pattern of delayed migration is typical for stream-type individuals (Everest and Chapman 1972). Chinook salmon parr production is the precursor to the stream-type life history and is hypothesized to be independent of fry (ocean-type) production. Fry production is hypothesized to be a density dependent process (Zimmerman et al. 2010) while parr production appears to be driven by a combination of density and habitat dependent processes where individuals will establish rearing territories and emigrate approximately 90 days after most fry. Taylor (1990) determined that phenotypic expression of fry/parr/stream-type life histories is partially driven by inherited traits and represents, in part, an adaptive divergence within and between Chinook salmon populations.

Bull Trout sub-adults were associated with smaller basins in the mixed hydro-region including the Upper Skagit River, Lower Cascade River, Diobsud creek, and Illabot creek but were also observed in other tributaries closer to the Skagit delta. In most of these areas Bull Trout sub-adults tended to occupy deeper portions of the stream margins which were associated with lower local velocities. Bull Trout were not present in greater relative densities in other channel types that tended to be occupied by stream-type Coho salmon, Chinook salmon, and *O. mykiss*. Experimental work with Coho and Chinook salmon suggests that juvenile Coho are more likely to occupy areas of greater depth and lower velocity, while Chinook salmon are found in portions of streams with less relative depth and greater velocities (Taylor 1988). This behavior could reduce the exposure of stream-type Chinook salmon to predation by Bull Trout. The summer low flow period marks the beginning of the spawning period for Bull Trout and most adult Bull Trout individuals

are likely staging or migrating to spawning habitats out of the mixed hydro-region. Diet analysis of Skagit River Bull Trout during the summer period in the mixed hydro-region indicates that their primary prey are resident fishes such as Sculpin spp., Dace spp., and Mountain Whitefish, but *O. mykiss* 20-100mm can be locally vulnerable to Bull Trout predation (Lowery 2009 & 2011).

In the mixed hydro-region *O. mykiss* 20-100mm had a similar distribution to stream-type Chinook salmon but occurred in much higher relative densities. Both of these species were highly generalist in their use of habitat and stream channels throughout the mixed hydro-region in summer. Larger *O. mykiss* tended to occupy large log jams and tributary streams. The opportunity to migrate from the mixed and rain hydro-region appears to be greater than in the snow hydro-region based on patterns of relative mean densities and observed size structure. In the snow and rain hydro-regions larger *O. mykiss* occurred in greater densities and appear to trend towards a tributary specialist habit. This observation supports hypotheses suggesting that colder environments found in snow dominated systems tend to delay growth and migration (McMillan et al. 2011).

In winter, stream-type Chinook salmon were associated with Coho salmon 30-100mm and flood plain channels. Coho salmon 100-200mm were also observed in flood plain channels during this time. Use of off channel habitat by stream-type Coho and Chinook salmon is widely documented (Bell et al. 2001, Sommer et al. 2001) during periods of high and low flows. In high flows during warmer months Chinook salmon can take advantage of increased production and temperatures in flood plain channels to maximize their growth potential. In cooler months flood plain channels tend to maintain higher temperatures and stable flows relative to adjacent mainstems which could allow them to take advantage of this relatively stable environment to more efficiently regulate metabolic processes (Pecquerie et al. 2011). These habitats can also serve as a refuge from high flow and turbidity during storm events.

During spring in the mixed hydro-region patterns of mean densities and channel use for all species were highly homogenous with most species using channel

types associated with larger mainstems and tributaries. Coho salmon 30-100mm were the only exception to this behavior where they were found primarily in flood plain channels and large log jams. In general stream-type salmonids were observed in greater densities and exhibited generalist habitat use in middle to lower portions of the river.

Stream-type juvenile salmonids in the Skagit River appear to use non-natal habitats on a seasonal basis, which has been observed in other systems with similar species. In the Yukon River in the USA and Canada, stream-type Chinook salmon juveniles will make extensive use of non-natal habitats for rearing. Daum and Flannery (2012) observed up to 100% of Chinook salmon fry rearing in Alaskan portions of the Yukon River were from stocks originating in Canadian portions of the Yukon River up to 1,300km from the sample sites. The absolute extent to which individuals and populations in the Skagit River system exhibit these inter-river migrations is uncertain, but we did identify this behavior in all hydro-regions and seasons.

This study identified the seasonal and spatial distribution of stream-type salmonids in the Skagit River basin. Seasonal use of different channel types and habitats within and between hydro-regions varied by species and represented the result of successful; fry to parr and parr to smolt rearing behavior of the average anadromous salmonid individual exhibiting a stream-type life history in the Skagit River. Habitat use is a manifestation of behaviors that helps mitigate density dependent mortality (Rose et al. 2001, Brio et al. 2003) and density dependent body growth (Walters and Post 1993, Vicenzi et al. 2012), support optimized growth trajectories, reduces negative interactions with other species and conspecifics, and reduces predation risk (Abrahams and Healey 1993).

The Chinook Recovery Plan for the Skagit River (WDFW and SRSC 2005) identified juvenile rearing habitat as a limiting factor for stream type Chinook salmon. Zimmerman et. al (2015) demonstrated evidence of limitations for Chinook salmon parr migrants but were unable to demonstrate a conclusive result for yearling migrants. As such, there remains uncertainty in our understanding of population dynamics that contribute to these

carrying capacity limitations for the yearling life history.

Potential piscine predators of salmonid fry and older conspecifics that are less vulnerable to gape limited predators typically occupy deeper portions of streams away from stream margins while juvenile salmonids generally occupy stream margins during their initial growth stages (Beechie et al. 2005, Cattaneo et al. 2002). To maximize growth during early life stages, individuals must initially reduce the potential for intra-cohort competition (Vicenzi et al. 2012). After this point, individuals must reach a growth stage that reduces inter-cohort competition for populations with protracted spawning periods or populations with multiple year class smolts (Nordwall et al. 2001) such as *O. mykiss* and some Coho and Chinook salmon. Intra-specific interactions that can reduce growth or increase predation risk must also be reduced. A stage specific migration is usually associated with an attempt to reduce negative inter- and intra- cohort, and interspecific interactions. These behaviors result in a more generalist habitat use which can involve smolting and direct emigration from freshwater or a more indirect pattern of using multiple habitats within freshwater prior to ocean migration (Satterthwaite et al. 2012). A focus on these behaviors in terms of species recovery is appropriate as managers move forward in developing and implementing recovery strategies. Most population monitoring programs in the Puget Sound/Salish Sea region rely on smolt trapping at the river mouth and are primarily focused on estimating basin wide production. This approach is effective at broad scale monitoring but it is not designed to investigate specific limiting factors in freshwater which are needed for a diversified recovery strategy that accounts for the various life-history strategies discussed here. Further investigations into the physical mechanisms that drive rearing and migratory behaviors are necessary to effectively achieve conservation and recovery goals for endangered salmon populations.

Relevance to Species Recovery

A primary goal of this investigation was to describe the spatial distribution and patterns of habitat use by stream-type Chinook Salmon in the Skagit River. The Skagit River Chinook Salmon Recovery Plan (SRSC and WDFW 2005) (hereafter "*the plan*") identified rearing habitat in freshwater as a limiting factor for juvenile Chinook salmon with extended freshwater rearing strategies, primarily individuals that rear for a year or more in freshwater (i.e. yearlings). Specifically *the plan* called for studies that identify the: life stages of yearling Chinook within the one plus year they spend in freshwater, habitats used (and not used) by yearlings for each life stage, and capacity and survival associated with each habitat type for each life stage. We designed this investigation to determine the spatial distribution of stream-type salmonids, across the known Chinook salmon spawning distribution in order to support recovery efforts within the Skagit Basin in particular, and in Puget Sound in general. Our results support the conclusions of *the plan* which indicated that stream-type Chinook salmon are found within all drainages where Chinook salmon spawn. Another objective of this study was to identify seasonal differences in habitat use by these fish. While fine scale habitat use was not an objective of this investigation, our findings suggest that there are seasonal differences in habitat use by Stream-Type Chinook salmon by hydrological regime at the reach scale. *The plan* concluded that there was evidence of freshwater rearing habitat for stream type Chinook salmon juveniles reaching capacity and was subsequently supported by Zimmerman et al. (2015) for parr migrants. Their results for Yearling migrants was inconclusive. As such, there remains uncertainty in specific habitat features that contribute to these carrying capacity limitations for the yearling life history. Our findings determined that Stream type Chinook salmon use river channels greater than 7.3m in wetted width, with moderate, <0.58, overhead vegetation cover, in mainstems, log jams and floodplain channels. But specific physical attributes that could be used to design built habitats was not determined and was beyond the scope of this investigation.

The current study was the second phase of an effort to develop a mechanistic understanding of how stream-type Chinook salmon are using habitats throughout the Skagit basin. Phase one, Beamer et al. (2010), focused primarily on detectability and the feasibility of using snorkeling to observe and quantify habitat use and distribution. This phase of the project was designed to determine the spatial distribution, relative abundance, and habitat use of stream-type Chinook salmon (and other stream type salmonids encountered) at the reach scale.

In order to meet the goals of *the plan* and move this population towards recovery, additional effort must be made to determine the specific habitat use requirements of stream-type Chinook salmon at a spatial scale relevant to individuals. With the objective of developing design criteria for habitat restoration projects that specifically address this known limiting factor.

Future phases of this effort should focus on portions of the river that contain habitats exhibiting the physical attributes associated with stream-type Chinook salmon which were identified in the current study. Locations should be selected where the spawning population is sufficiently large

enough to fully seed all available habitats. With the two objectives of quantifying habitat use on a fine scale (objective one) which leads to the development of design criteria (objective two) for habitat restoration projects, mitigation measures, and similar activities in support of species recovery. Without science-based criteria to design and evaluate these types of projects, their utility will be difficult to quantify and their contribution to species recovery will be uncertain.

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Appendix

Multivariate Analysis of Habitat Features

Results from the PCA of physiographic variables indicated a strong gradient by hydro-region along the first axis (40.03% of the variance). Basin area was positively associated with the rain hydro-region and negatively associated with elevation, distance from the Skagit river delta, and distance from the river/stream mouth where the surveys occurred (Figure 15). The rain hydro-region was more distinct and the snow and mixed hydro-regions exhibited some overlap along the first axis. Channel confinement and maximum temperature were associated with positive second axis scores and were negatively associated with solar radiation along the second axis (23.55% of the variance). Most sites clustered near the origin along the second axis with some exceptions. Sites 1 at Lower Hansen creek, 10 Lower East Fork Nookachamps creek, 6 Upper Finney creek, 26 Illabott creek, and 5 Skagit River at Damnation Creek had axis scores higher than 1 indicating a positive association with higher maximum summer temperatures and more confinement of the active channel. In contrast sites 14 Ross Island Slough, 7 Skagit at Illabott, and 17 Skagit at Cockerham Island were positively associated with solar radiation and negatively associated with channel confinement and higher maximum summer temperature. Both of the extremes in second axis scores were sites in the rain and mixed hydro-regions.

Dominant gradients along the first two axes from the PCA of aquatic habitat variables varied by season (Figure A a, b, and c). Channel types rather than hydro-regions showed distinct patterns in habitat variables at this level of the hierarchy. In general, large log jams were distinct from other channel types, forming their own cluster. Floodplain channels and secondary channels formed a second cluster and tributaries and mainstems formed a third cluster in the ordination along the first axis. Along the second axis, large log jams, mainstems, and secondary channels formed one cluster with tributaries and floodplain channels forming a second.

Along the first axis (27.9% of the variance) in spring 2011 larger dominant and sub-dominant substrates and higher velocities were associated with lower axis one scores and were negatively associated with greater wood cover, undercut bank cover, and depth which had larger axis one scores (Figure Aa). Large wood jams, secondary channels, and most flood plain channels had higher scores along the first axis and were more associated with greater wood cover, undercut bank cover, and depth (i.e. lower velocity). Tributary and mainstem channels had lower axis one scores and were associated with larger substrates and higher velocities. Along the second axis (18.8% of the variance) in spring 2011, higher axis scores were associated with tributary and floodplain channels which were described by greater vegetation cover. Mainstems, secondary channels, and large log jams exhibited lower axis two scores and were associated with greater bankfull widths, wetted widths, and LWD counts. In summer 2011, the dominant gradients along the first axis (28.3% of the variance) were described by larger dominant and sub-dominant substrates and higher velocities having lower axis scores which described most mainstems, tributaries, and secondary channels. Higher axis one scores were associated with wood cover, pool cover, and undercut bank cover which described large log jams and most floodplain channels (figure Ab). Along the second axis (21.7% of the variance) higher scores were associated with greater depths, LWD counts, bankfull widths, and wetted widths which described large log jams and mainstems. Lower axis 2 scores were associated with greater vegetation cover and described most tributaries and floodplain channels. Secondary channels clustered near the origin so were intermediate during the summer surveys. In winter 2012 lower scores along the first axis (29.7% of the variance) were described by greater dominant substrate, sub-dominant substrate, velocity, and substrate cover and were associated with mainstems and tributaries (figure Ac). Lower axis one scores were associated with greater depth, undercut bank

cover, and pool cover and described large log jams and floodplain channels. Secondary channels were clustered near the origin, similar to summer, and intermediate to other channel types. Higher second axis (18.4% of the variance) scores were associated with wood cover and vegetation cover and described most floodplain channels and tributaries. Lower second axis scores were associated with greater bankfull width, wetted width, and velocity cover and described mainstems, secondary channels, and large log jams.

Discussion

Analysis of the physiographic variables identified a distinction between hydro-regions within the first level of our landscape hierarchy. The dominant primary gradient in physiographic variable space was characterized as basin area negatively associated with elevation, the distance to the nearest confluence, and the distance to the Skagit delta. These four physiographic variables were adequate in describing differences between hydro-regions with the rain hydro-region more distinct from the snow and mixed hydro-regions. Along the secondary gradient in physiographic variable space we identified that maximum temperature and channel confinement were positively associated with each other and negatively associated with solar radiation. It is counterintuitive that maximum temperature would be negatively associated with solar radiation but it is the interaction between channel confinement and maximum temperature that is negatively associated with total annual solar radiation suggesting that geomorphological processes beyond just solar radiation are acting to increase temperature in the few locations at one extreme of the secondary gradient (characterized by increased channel confinement) in physiographic variable space, which included sites in all hydro-regions. The maximum temperatures measured in these confined channels fell within the range of temperatures for optimal growth, depending on food availability, for salmonids and other fishes present in these areas (Reference). Although these were the highest temperatures recorded during our investigation they do not pose a thermal limitation to the local fish community and likely provide a growth benefit if the food supply is adequate.

We found that channel types, the second level in our defined hierarchy, were best defined by aquatic habitat variables and were qualitatively independent from the physiographic variables measured during this investigation. This suggests that channel types are independent of hydro-region and adequately describe the current channel habitat used by stream-type anadromous salmon and other fish with prolonged freshwater rearing.

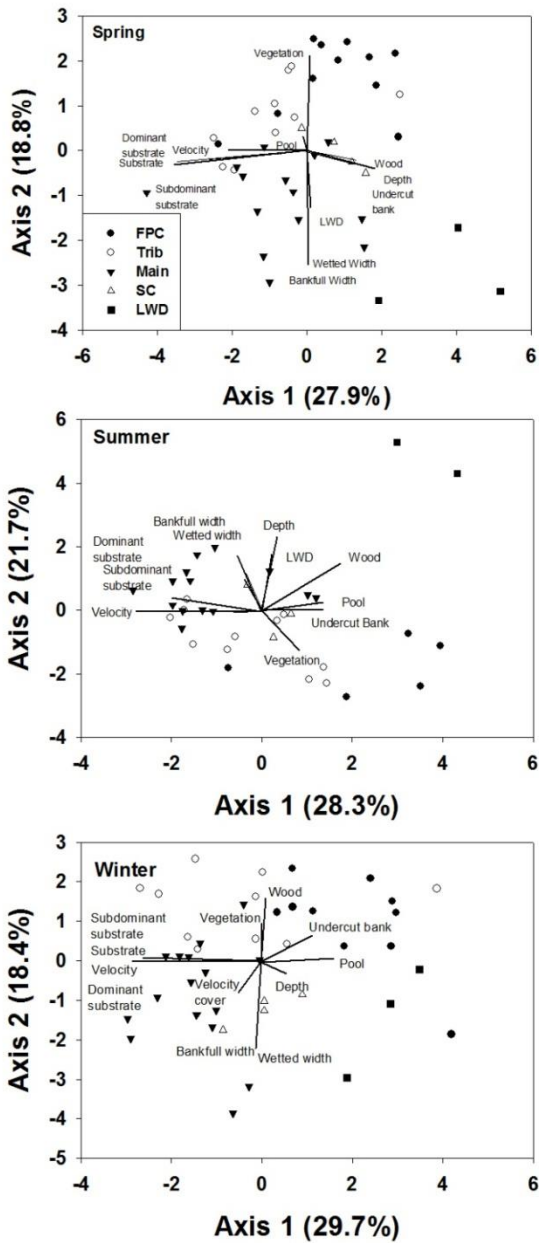


Figure A1 a, b, and c. Principal component analysis (PCA) of aquatic habitat variables in the Skagit River basin. Points within the ordination, coded by shape, represent the five stream channel types surveyed in the Skagit river basin. The joint plot overlay represents the habitat variables correlated with each axis and depicts the orientation and magnitude of those correlations to each axis.