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THE LIFE HISTORY AND ECOLOGY OF RIVERINE SOCKEYE
SALMON (*ONCORHYNCHUS NERKA*) IN A LARGE FLOODPLAIN
RIVER

By

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B.Sc., University of Montana, Missoula, Montana, 1998

Thesis

presented in partial fulfillment of the requirements
for the degree of

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The Life History and Ecology of Riverine Sockeye Salmon (*Oncorhynchus nerka*) in a Large Floodplain River

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The productivity and life history diversity of salmonids is linked to the complexity of habitat in large floodplain rivers. Dynamic floodplain processes are driven by flow, sediment transport, cut and fill alluviation, woody plant succession, and ecosystem engineers, notably beavers, that create dynamic and biophysically complex off-channel rearing and spawning habitats. Sockeye salmon (*Oncorhynchus nerka*) display some of the most variable life history traits of all Pacific salmon, using lake and river rearing strategies throughout rivers of the northern Pacific Rim. However, sockeye management has primarily focused on the lake-type life history with minimal regard to the importance of the riverine form.

In the Kwethluk River, Alaska, we identified both the lake (lake-type) and river (riverine) driven life histories. To elucidate the importance of lateral floodplain habitats to this species, we compared lake and riverine spawning habitat attributes, determined the densities, seasonal changes in length and weight, and diet of juveniles. We also quantified the amount of off-channel habitats that were available for spawning and rearing.

We found that floodplain and lake spawning habitats had similar hydrological, physical, water chemistry attributes. Lake-type spawning occurred along the alluvial fans of the lake shoreline and in the outlet channel, whereas, riverine sockeye spawned exclusively in off-channel spring brooks and side channels. But, all spawning was located in areas dominated by upwelling ground water. We found that juvenile sockeye reared in spring brooks, beaver ponds, and backwaters of the river flood plain and that these habitats types made up over 70% of the available off-channel habitat. The average density of floodplain rearing juveniles in the fall was between .02 to .54 fish · m⁻² and a total of 165, 711 juvenile sockeye were rearing in the floodplain study reach. The mean length of flood plain rearing juveniles in the fall of 2006 ranged from 57 to 66 mm and was similar to the mean length of ocean migrating smolts (68 mm) the following spring. The diet of juveniles rearing in off-channel habitats was dominated by zooplankton, but juveniles fed on a variety of invertebrate prey, while the diet of lake-type juveniles was dominated by zooplankton.

We concluded that riverine sockeye take advantage of the complexity of large river systems and that floodplain habitats are key spawning and rearing habitats for this species. The riverine life history type may be an important part of large river systems throughout the Pacific Rim.

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I dedicate my master's thesis to the life and memory of my stepfather Scott D. McQueeney who told me to always follow my dreams.

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INTRODUCTION

The relationship between aquatic organisms and their environment has been traditionally viewed as a suite of ecosystem processes that change along a river continuum from headwaters downstream to the ocean (Vannote et al. 1980). River ecosystems, especially large floodplain rivers, are continually interacting within lateral, longitudinal, and vertical dimensions that connect habitat throughout the river corridor (e.g., Ward 1989a; Stanford 1998). Natural floodplain structure and function is driven by the temporal dynamics of flooding, sediment transport, cut and fill alluviation, wood deposition, plant succession, and ecosystem engineers, such as beaver (*Castor canadensis*) and are embedded within the geologic and geographic setting of the catchment basin. These processes are the basis of a unifying theory of river ecosystems termed the Shifting Habitat Mosaic (SHM) (Stanford et al. 2005), whereby, biota benefit from a multitude of habitats that greatly increase opportunities for life history diversity, thus increasing biodiversity at all levels of trophic organization. The complexity of floodplain sections within the catchment setting are a primary determinant of productivity and biodiversity in all rivers (Tockner and Stanford 2002).

Pacific salmon (*Oncorhynchus* spp.) populations are regarded as an important ecological aquatic resource that enhance the productivity of aquatic and terrestrial ecosystems by bringing marine-derived nutrient subsidies (MDN) into freshwater environments (Wipfli et al. 1998; Chaloner and Wipfli 2002; Helfield and Naiman 2001; Gende et al. 2002; Schindler et al. 2003; Wipfli et al. 2003). However, urbanization, flood control, habitat disconnection and degradation, over-harvest, and mismanagement practices have resulted in many stocks becoming threatened or extinct (Nehlsen et al. 1991; Gregory and Bisson 1996). The loss of floodplain connectivity has been found to be one of the key factors in the decline of the diversity and productivity of salmonids in large river systems (Beechie et al. 1994; Sommer et al. 2001; Hall and Wissmar 2004), yet fisheries managers often focus on the main channel habitats ignoring off-channel or lateral floodplain habitats.

It is well known that the life histories of riverine fishes, and in this study particularly salmonid fishes, salmon and trout (*Oncorhynchus* spp. and *Salmo* spp.) and

charr (*Salvelinus* spp.), are controlled by the dynamics of spawning and rearing habitat (e.g., Murphy et al. 1989; Schlosser 1991; Sommer et al. 2001; Fausch et al. 2002). Salmonids typically select spawning environments at a microhabitat scale which are set within a larger scale of environmental conditions (eg. Sowden and Power 1985; Lorenz and Eiler 1989; Geist and Dauble 1998; Baxter and McPhail 1999; Baxter and Hauer 2000; Geist 2000). The hydrological, physical, and chemical (water chemistry) environmental attributes of these spawning habitats have a direct influence on the survival and success of incubating embryos (cf., Quinn 2005). More specifically, surface water-groundwater interactions (e.g., Witzel and MacCrimmon 1982; Baxter and Hauer 2000; Geist et al. 2002), water depth and water velocity (e.g., Beland et al. 1982; Knapp and Preisler 1999), bed-sediment particle size (e.g., Hoopes 1972; Knapp and Vredenburg 1996), and water chemistry (dissolved oxygen, temperature, specific conductance, and pH)(e.g., Leman 1993; Geist and Dauble 1998; Geist 2000), have all been linked to redd site selection by spawning salmonids and the survival of embryos.

The selection of habitat for spawning is not only linked to embryo survival, but also the subsequent habitat conditions that rearing off-spring will be exposed to after incubation (Burgner 1991). The time of the year that salmonids spawn is typically associated with water temperature regimes that facilitate the synchronization of juvenile emergence to coincide with prey abundance and favorable environmental conditions (e.g., temperature), that provide the best opportunity for juvenile growth and survival (e.g., Brannon 1987; Burgner 1991; Quinn 2005). Furthermore, the size that anadromous salmonids attain during their first year of growth and during the freshwater portion of their life cycle (from emergence to smoltification) plays a large role in over-winter survival and juvenile-to-adult survival in saltwater (cf., Quinn 2005).

Sockeye salmon (*Oncorhynchus nerka*) display some of the most variable life history traits of all Pacific salmon and multiple freshwater life history strategies (or ecotypes) have been identified (e.g., Forester 1968; Wood et al. 1987; Burgner 1991; Wood 1995; Wood 2007). Traditionally, this species was regarded as having life history requirements linked to lacustrine ecosystems and the anadromous lake ecotype, termed “lake-type” hereafter, have long been found to spawn along the alluvial fans of lake shorelines or in fluvial channels that are connected to nursery lakes (e.g., lake outlets,

inlet streams or spring-fed tributaries) (e.g., Hanamura 1964; Ricker 1966; Foerster 1968; Burgner 1991; Leonetti 1997). The progeny of lake-type sockeye typically rear in lake environments for at least one year before migrating downstream (as smolts) to the ocean and the freshwater productivity of lake-type juveniles has been linked to the abundance of zooplankton prey populations (cf., Burgner 1991).

In some rivers throughout the Pacific Rim, populations of sockeye salmon are known to spawn in riverine habitats that are not associated with lakes (Gilbert 1918; Semko 1954; Ricker 1966; Foerster 1968; Bugaev 1984; Craig 1985; Wood et al. 1987; Sharr et al. 1988; Lorenz and Eiler 1989; Russell et al. 1989; Eiler et al. 1992; Hall and Wissmar 2004). The progeny of these river ecotype or river-type (“riverine” hereafter) spawners either rear in riverine habitats for one to two years (Wood et al. 1987; Murphy et al. 1989; Wood 1995; Wood 2007) or migrate downstream as underyearlings to estuarine or marine ecosystems (“sea-type”) after spending a short time in freshwater (Wood et al. 1987; Heifetz et al. 1989; Murphy et al. 1997; Wood 2007).

On the Kwethluk River in Alaska, we have found that floodplain spring brooks are one of the most productive habitats of the SHM and provide spawning and rearing habitats for a multitude of salmonid species (SaRON, unpublished data). Spring brooks are defined as alluvial flood channels that are predominantly fed by effluent hyporheic-groundwater (Stanford et al. 2005) and when compared to the main channel, can provide a distinctly different suite of environmental conditions for spawning and rearing.

The importance of floodplain habitats, particularly spring brooks, for spawning and rearing of sockeye, has not been thoroughly studied and most of the information on the life histories of riverine populations has been cursory (Lorenz and Eiler 1989; Murphy et al. 1989; Eiler et al. 1992) or limited to genetic stock comparisons with lake-type (Beacham et al. 2004) or sea-type (Gustafson and Winans 1999) populations. During the 2004 and 2005 field seasons, SaRON scientists observed the riverine life history type in the Kwethluk River and in other rivers around the Pacific Rim, including the Kol and Utkholok Rivers, Kamchatka, and the Taku and Kitlope Rivers, British Columbia. In all cases, spawning and rearing of sockeye appeared to be occurring in shallow spring-fed habitats available in the flood plains of these large river systems. Yet, only three

published studies have described the ecology of riverine sockeye rearing (Murphy et al. 1989) and spawning (Lorenz and Eiler 1989; Eiler et al. 1992) in the Taku River.

We hypothesized that lateral floodplain habitats are important spawning and rearing habitats for sockeye salmon in the Kwethluk River (Fig. 1) and expected that if this could be clearly documented that the results could be applicable to other rivers throughout the Pacific Rim with known riverine populations.

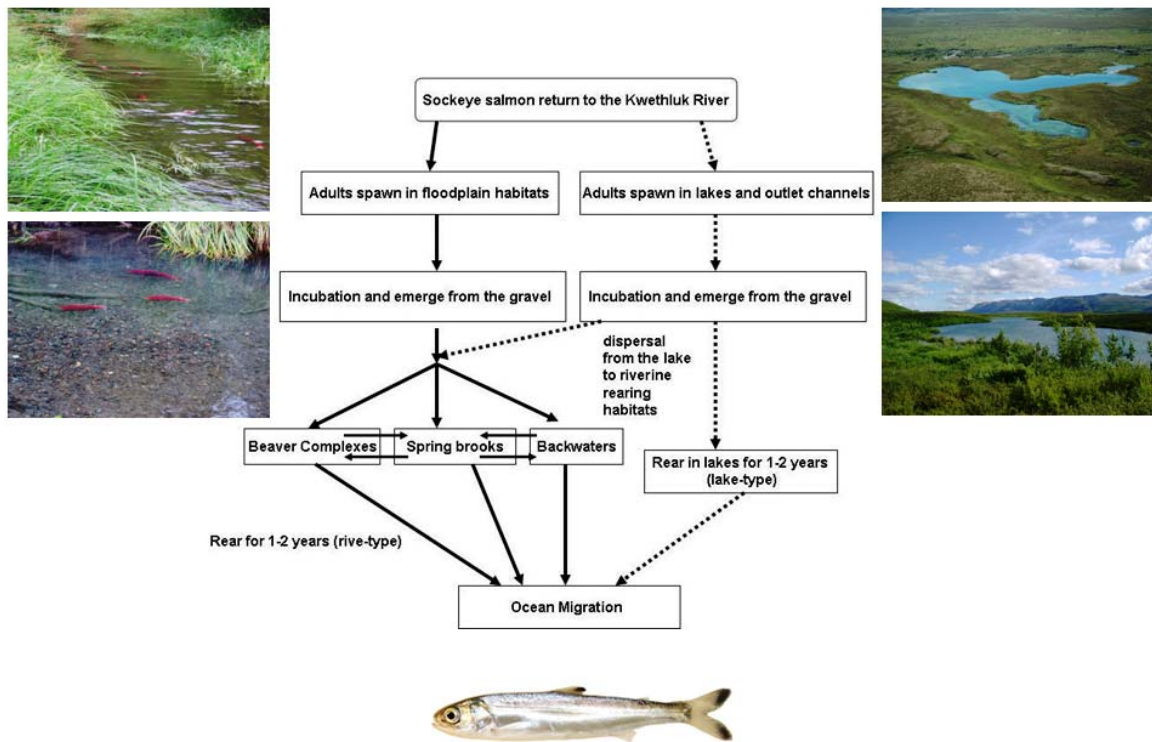


Fig. 1. The conceptual foundation for our research of the freshwater life histories of Kwethluk River sockeye salmon.

In preliminary work at the Kwethluk, we observed that sockeye salmon spawned in floodplain spring brooks ~120 km downstream from small headwater lakes that were described by local biologists as nursery lakes for lake-type sockeye (M. Rearden, USFWS, personal communication). We asked what habitat attributes are associated with spawning in spring brook habitats and was there gene flow between the lake and river types? Second, during SaRON across-site sampling events, we captured sockeye juveniles that clearly were rearing in floodplain spring brooks. Thus, we hypothesized

that once juveniles emerged from the gravels they would use floodplain habitats for rearing (e.g., spring brooks, beaver ponds, and backwaters) and that it seemed possible that the progeny of lake-type spawners might either stay and rear in the small spring-fed nursery lakes (traditional view) or disperse from these nursery lakes to rear in riverine habitats (e.g., Fig. 1). Likewise, we show elsewhere (McPhee et al. 2008, submitted) that sockeye collected in the lakes area of the upper Kwethluk, both from the spring-fed lakes and outlet channels (L in Fig. 2), are in fact genetically distinct from riverine sockeye using floodplain habitats in the lower river (R in Fig. 2).

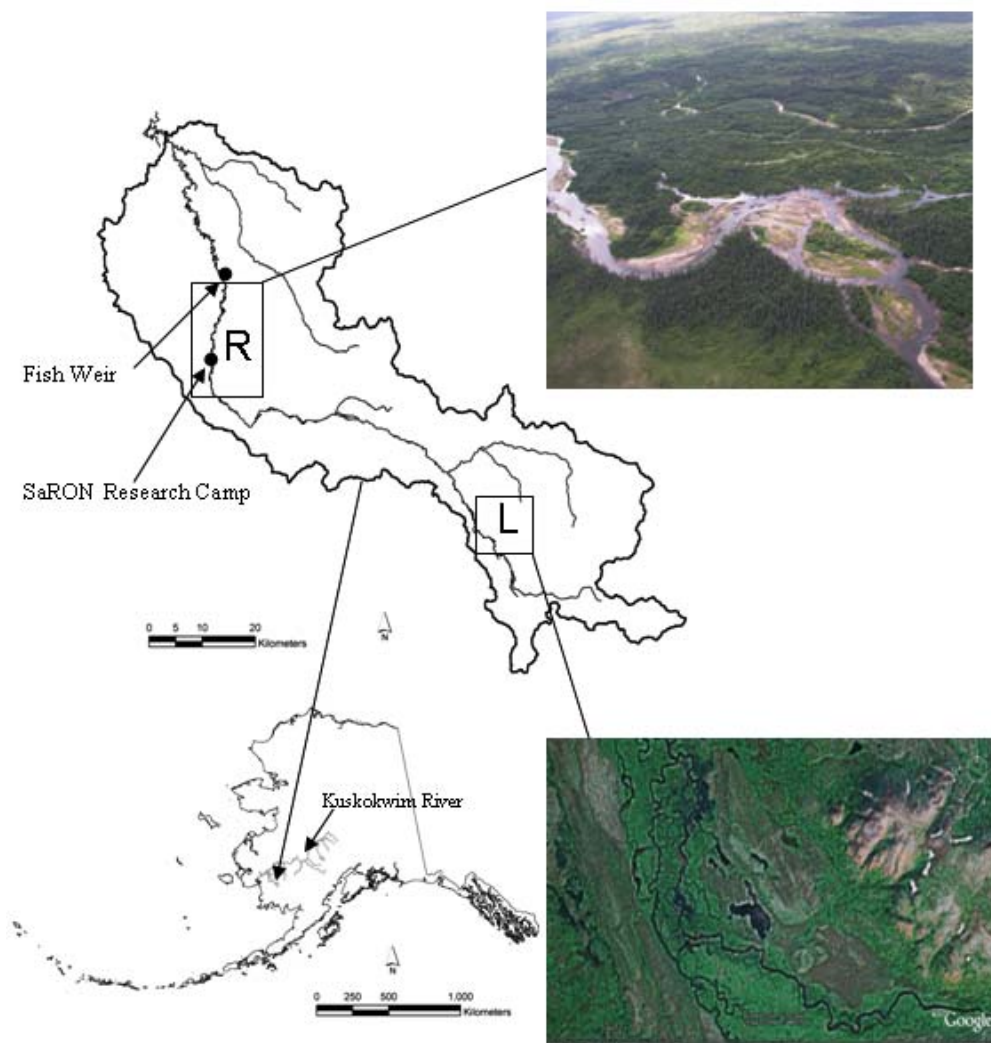


Fig. 2. Location of the Kwethluk River, a lower Kuskokwim tributary in Alaska, and the two primary study areas on the river. Riverine sockeye were studied within the reach labeled R and lake-type sockeye were studied in the Boundary Lakes area labeled L. Boundary Lakes image provided by Google Earth.

The objectives of this study were to; 1) determine what floodplain habitats are used by riverine sockeye for spawning and rearing; 2) quantify the amount of available floodplain spawning and rearing habitat using remote sensing tools; 3) describe and compare the hydrological, physical, and chemical (intergravel and surface water chemistry) attributes of spawning habitat used by lake-type and riverine sockeye and determine the size and freshwater age of adult spawners; 4) determine densities and population size of juveniles rearing in floodplain habitats; 5) compare the length, weight, and diet of juveniles rearing in lakes and floodplain habitats and the temperature patterns of floodplain rearing habitats; 6) compare the length and study reach wide population estimates of floodplain rearing juveniles in the fall to the length and number of ocean migrating smolts caught the following spring.

STUDY SITE

The Kwethluk River is one of six long-term research sites within the Salmonid Rivers Observatory Network (SaRON, www.umt.edu/flbs/Research/SaRON.html). SaRON is an international project that examines how habitat complexity, MDN, and flood plain processes drive aquatic and terrestrial productivity and biodiversity in very pristine salmon rivers around the Pacific Rim. A majority of the rivers within SaRON are large gravel-bed rivers with expansive and biophysically complex flood plains characterized by abundant off-channel aquatic habitats that are the primary rearing areas for multiple species of salmon, trout, charr, and many other resident species. SaRON is particularly interested in the positive feedback cycle of MDN that returning adults provide to their anadromous progeny and many other species that coexist in floodplain habitats. Moreover, a key goal of SaRON is to elucidate how salmonid life history diversity and productivity are linked to the complexity of lateral floodplain habitats. Thus, documenting how sockeye salmon and other species use complex floodplain environments of the Kwethluk River system for spawning and rearing is fundamental to the SaRON project.

The Kwethluk River catchment (3,787 km²) is a pristine 5th order tributary of the Lower Kuskokwim River (total catchment 118, 000 km²) and is located within the Yukon

Delta National Wildlife Refuge (YDNWR), Alaska (Fig. 3). The YDNWR is the largest refuge in North America and encompasses 19.6 million acres (Fig. 3). Nearly, 25,000 native Yup'ik Eskimos live within 42 villages spread throughout the refuge and village residents depend on the abundance of wild game (birds and mammals) and native fish species for subsistence living. The Kuskokwim River is largely pristine, being the 9th largest and one of the longest (1,165 km) free-flowing river in the United States (Richardson and Milner 2005) (Fig. 3). The human impacts within the Kuskokwim and Kwethluk River catchments are minimal. However, two gold mining operations are proposed outside the refuge boundaries on State Lands (D. Gillikin, USFWS, personal communication). The Donlin Creek mine is located in the head waters of the Kuskokwim River and the Kisaralik Lake mine is located in the headwaters of the Kisaralik River, the first tributary upstream of the Kwethluk. These proposed mines threaten the fish and wildlife populations that Kuskokwim residents depend on for survival.

Commercial logging is not allowed within the refuge boundaries and the commercial fishing industry is very small compared to other areas of Alaska. However, village residents are allowed to harvest timber to heat their homes and subsistence fishing does have an impact on anadromous and resident fish populations throughout the refuge. The Kuskokwim watershed is primarily roadless, with the exception of short paved and dirt roads that connect housing communities within the small villages and towns throughout the refuge. Although, most towns and villages are set within the refuge, they are designated as private land managed and maintained by the local communities (Fig. 3). The only modes of transportation between the villages and small towns within the refuge are by airplane, helicopter, boat, and snow machines in the winter.



Fig. 3. Map showing the locations of the Kwethluk (red box) and Kuskokwim (blue box) Rivers within the Yukon Delta National Wildlife Refuge (YDNWR) and the YDNWR boundary (outlined in green) and the private lands set within the refuge (in grey). Map provided by Dan Gillikin, USFWS.

The Kwethluk River originates in the Kilbuck Mountains (Kuskokwim Mountain Range) and flows northwesterly for ~222 km to its confluence with the lower Kuskokwim River, near the Kwethluk Village that supports ~720 residents (Miller et al. 2007) (Fig. 2 and 3). The upper river is a braided-anastomosing system with complex flood plains that can be >5 km wide. The lower 47 km of the river, from the USFWS fish counting weir described below to the confluence with the Lower Kuskokwim, is a meandering river that is influenced by tide hydrology of the lower Kuskokwim and its large estuary (Fig. 3). The annual hydrologic cycle of the Kwethluk begins with spring flooding that is dominated by snow melt, to base flow during the summer and early-fall

with periodic spikes in the hydrograph resulting from summer rains, to fall floods resulting from coastal rain storms that move inland across the refuge.

Permanent SaRON research sites are located in multiple floodplain habitat types throughout the river system, however, sockeye were most often observed in the R and L reaches shown in Fig. 2. The two small headwater lakes are spring-fed and total ~17 ha (170,000 m²). Both lake outlets are connected to the main channel of the upper Kwethluk and gain substantial flow from upwelling groundwater from the outlets downstream to the confluence with the main channel. The lakes may be receiving phreatic (deep storage groundwater) inflow from upland sources, but the outlet streams are located within the river flood plain and likely are receiving ground water from the alluvial aquifer.

The common vegetation on the Kwethluk flood plain includes alder (*Alnus crispa* and *Alnus incana*), cottonwood (*Populus balsamifera*), and willow (*Salix arbusculoides*, *Salix pulchra*, and *Salix alexensis*) forest stands. Although, birch (*Betula papyrifera*) and white spruce (*Picea glauca*) are found within the flood plain, they dominate the overstory in late-succession stands toward the floodplain boundaries. The upland is dominated by *sphagnum* tundra and low growing shrubs. The dynamic interactions between flooding, sediment flux, and wood deposition, influence the spatial arrangement and successional stage (or chronosequence) of terrestrial vegetation throughout the Kwethluk River flood plain (Mouw et al. 2008, submitted). Moreover, beavers truncate the river driven chronosequence and create a unique, diverse, and highly productive patch mosaic of vegetation within this chronosequence (J. L. Chaffin, unpublished data).

The main or primary channel is composed of run-glide-tailout-riffle habitat sequences (or hydrogeomorphic units) that are spatially arranged by dynamics of geomorphology and flow (Lorang and Hauer 2006). Over-bank flooding in the spring and fall drive erosion and deposition, and channel avulsion. Thus, the seasonal rise and fall in the hydrograph connects and disconnects off-channel habitats from main channel surface water. Once flooding recedes, some channels disconnect from surface water flows and become dominated by emergent ground water from the alluvial aquifer, resulting in a spring brook. This “spring” flow is connected at the downstream end to the main or secondary channels by the baseflow channel network of this braided-anastomosing river. Some tertiary or “side” channels also have reaches heavily influenced by groundwater

discharge. Beavers colonize both spring brooks and some side channels and dammed spring brooks and side channels create a mosaic of lentic habitats that add substantial complexity to the aquatic-terrestrial interface of the river flood plain (Fig. 2).

Floodplain spring brooks, beaver ponds and groundwater-influenced reaches of side channels and backwaters provide spawning and rearing habitats for all five North American anadromous Pacific salmon species: chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*Oncorhynchus keta*), pink salmon (*Oncorhynchus gorbuscha*), coho salmon (*Oncorhynchus kisutch*), and sockeye salmon, which near the northern limit of their range in North America (Burgner 1991). Moreover, these habitats support resident populations of rainbow trout (*Oncorhynchus mykiss*), Arctic grayling (*Thymallus arcticus*), dolly varden (*Salvelinus malma*), round whitefish (*Prosopium cylindraceum*), northern pike (*Esox lucius*), Alaska blackfish (*Dallia pectoralis*), slimy sculpin (*Cottus cognatus*), and ninespine stickleback (*Pungitius pungitius*). Salmon populations on the Kwethluk River are highly depended upon for subsistence living by members of the Organized Village of Kwethluk at the mouth of the river and other lower Kuskokwim residents.

The U.S. Fish and Wildlife Service (USFWS), Kenai Fishery Resources Office, operates a resistance board fish weir (Tobin 1994) on the Kwethluk River to enumerate annual returns of salmon. The weir is located ~88 river km upstream from the confluence with the lower Kuskokwim River (Harper and Watry 2001; Roettiger et al. 2002; 2003; 2004; 2005; Miller et al. 2007) (Fig. 2) and adult salmon spawning migrations are monitored and species biological samples are collected throughout the season. Annual escapement reports for sockeye salmon in 1992, 2000, 2002-2004, 2006, and 2007 indicate that peak spawning escapement at the Kwethluk weir occurs from the end of June to mid-July and that the returns of sockeye salmon to the Kwethluk are small compared to other species encompassing only 1%, 2.4%, 0.4%, 1.7%, 2.5%, 6.8%, and 5.5% of the total salmon escapement, respectively (Harper 1998; Harper and Watry 2001; Roettiger et al. 2003; 2004; 2005; Miller et al. 2007) (Table 1). However, returns of sockeye appear to be increasing during the time of record.

Table 1. Kwethluk weir escapement estimates and percent of the returning run by species, as well as total escapement estimates for the years of weir operation 1992, 2000, 2002-2004 and 2006-2007. Note: 2007 escapement estimates are preliminary. Weir picket spacing was increased after 1992 so pink salmon estimates are rough estimates at best

Year	Chum	%	Chinook	%	Sockeye	%	Pink	%	Coho	%	Total Escapement
1992	30,595	23.0	9,675	7.3	1,316	1.0	45,952	34.5	45,605	34.2	133,143
2000	11,691	27.0	3,547	8.2	1,049	2.4	1,407	3.2	25,610	59.2	43,304
2002	34,681	51.0	8,395	12.3	272	0.4	1,415	2.1	23,298	34.2	68,061
2003	41,812	24.8	14,474	8.6	2,928	1.7	1,885	1.1	107,789	63.8	168,888
2004	38,646	28.0	28,604	20.7	3,491	2.5	3,053	2.2	64,216	46.5	138,010
2006	47,490	47.9	17,618	17.8	6,732	6.8	1,685	1.7	25,664	25.8	99,189
2007	54,913	58.8	12,927	13.8	5,148	5.5	626	0.7	19,743	21.2	93,357

METHODS

Objectives 1 and 2: Lake and River Spawning, Floodplain Rearing, and Quantity of Spawning and Rearing Habitat Available to Sockeye Salmon

River flow

To assess the hydrologic regime that occurs during spawning migration, stage height (cm) was recorded daily using a staff gauge to calibrate hourly data obtained with a Global Water (model# WL16) pressure transducer. Using periodic flow measurements with a Sontek ADP (Acoustic Doppler Profiler) and handheld Flowtracker (ADP and Flowtracker, Sontek/YSI San Diego, California), which use Acoustic Doppler technology to determine velocities, we obtained a stage-total Q relationship that predicted river flow.

Spawning sites and adult counts in the Boundary Lakes, floodplain spring brooks, and side channels

We conducted preliminary surveys in 2005 and found riverine sockeye spawning in spring brooks and side channels that were dominated by hyporheic-groundwater flow (Table 2). We then used our 2005 observations as a guide and surveyed the entire SaRON study reach and the Boundary Lakes area for spawning adults (Table 2). Adults were counted, spawning behavior was documented, redd locations were mapped, and marked for detailed study described below (Table 3).

Table 2. Observations of floodplain spawning sockeye during the 2005 field season and system wide spawning surveys of riverine and lake-type spawning adults during the 2006 field season. Note: (-) sex of individual fish was not determined and 2005 surveys were preliminary.

Habitat Type	Sites	Males	Females	Totals	Carcass	Redds
<i>2005 Surveys</i>						
Spring brook	6	38	48	86	14	47
Side channel	1	12	10	22	1	10
Main channel	~25 km	0	0	0	0	0
<i>Total Riverine Spawners</i>	7	50	58	108	15	57
<i>2006 System Surveys</i>						
Spring brook	12	223	221	444	6	202
Side channel	9	22	38	60		37
Side channels w/o fish	29					
Spring brook w/o fish	17					
Backwater w/o fish	12					
Beaver ponds w/o fish	22	0	0	0	0	0
Main channel	~31 km	0	0	0	0	0
<i>Totals Riverine Spawners</i>	79	245	259	504	6	239
Boundary Lake (BL)		-	-	100	7	
Boundary Lake 2 (BL2)		-	-	88	0	40
Boundary Creek (BC)		-	-	379	237	~97
Boundary Spring brook (BOS)		-	-	205	371	-
Boundary Lake 2 Outlet (B2O)		-	-	15	0	10
<i>Total Lake-type Spawners</i>		-	-	787	615	~147

Table 3. Habitats selected for detailed study in 2006. Columns represent the habitat type, GPS coordinates of sites in UTM's (Zone 4), and the life history data collected. Note: (Yes) detailed research was conducted or (No) detailed research was not conducted. (NP) no adults were observed during spawning surveys and no juveniles were found during spring, summer, or fall sampling periods. GA is a smaller spring brook channel arm of GS. When individual site comparisons are made hereafter, LK_ refers to lake study sites, SB_ refers to spring brook study sites, BP_ refers to beaver pond study sites, and BW_ refers to backwater study sites.

Habitat Type	Eastings	Northing	Spawning Behavior	Juvenile Ecology
Lake and Outlet (LK_)				
Boundary Lake (BL)	444504	6659716	No	Yes
Boundary Lake 2 (BL2)	444619	6660333	Yes	Yes
Boundary Creek (BC)	444417	6659692	Yes	No
Boundary Spring brook (BOS)	444514	6659814	No	No
Boundary Lake 2 Outlet (B2O)	444624	6660412	No	No
Spring brooks (SB_)				
Elbow Spring brook (EO)	390485	6687057	NP	NP
Lost Duck Spring brook (LD)	387901	6688898	NP	NP
Merganser Spring brook (MO)	386939	6689891	NP	Yes
Bunyan Spring brook (BS)	383870	6695931	Yes	Yes
Green Acres Spring brook (GA)	383606	6695576	No	Yes
Green Acres Spring brook (GS)	383603	6697278	Yes	No
Shannon's Side Channel (SH)	383983	6700397	Yes	No
Nerka Spring brook (NS)	383556	6699517	No	Yes
Scott's Spring brook (SS)	383363	6701932	Yes	No
Mack's Spring brook (MS)	383811	6704458	Yes	No
Parafluvial Spring brook 1 (PS)	384629	6705649	No	Yes
Beaver Ponds (BP_)				
Upper Elbow Beaver Complex (UE)	392515	6686142	NP	Yes
Elbow Beaver Complex (EC)	390485	6687147	NP	Yes
<i>Salix</i> Beaver Complex (SC)	386757	6690133	NP	Yes
<i>Picea</i> Beaver Complex	387125	6689012	NP	NP
Lost Duck Beaver Complex (LB)	387898	6688940	NP	Yes
Paleo Beaver Complex (PO)	386300	6690722	NP	Yes
Camp Beaver Complex (CB)	385547	6691051	NP	Yes
Tyson's Beaver Complex (TC)	385965	6690986	NP	Yes
Green Acres Beaver Complex (GB)	383494	6695620	NP	Yes
<i>Alces</i> Beaver Complex (AC)	383746	6699555	NP	Yes
Vortex Complex (VC)	383408	6699694	NP	NP
Vortex II Beaver Complex (VW)	383389	6699726	NP	Yes

Continued on next page

Table 3. Continued

Habitat Type	Easting	Northing	Spawning Behavior	Juvenile Ecology
Backwaters (BW_)				
Elbow Backwater (EB)	390496	6687305	NP	NP
Sleepy Frisco Backwater (SF)	389152	6688485	NP	Yes
Beaver Backwater I (BB)	383969	6699479	NP	Yes
Nip Backwater (NB)	383649	6695231	NP	Yes
Beaver Backwater II (BW)	384411	6692211	NP	Yes
Beaver Backwater III (BR)	386621	6690299	NP	Yes
Lower Backwater (LW)	384408	6704989	NP	Yes
Main Channel Shallow Shoreline				
Elbow Main Channel (EM)	390492	6687300	NP	NP
Midway Main Channel (MW)	383794	6695522	NP	NP
Lower Main Channel (LS)	384594	6706029	NP	NP

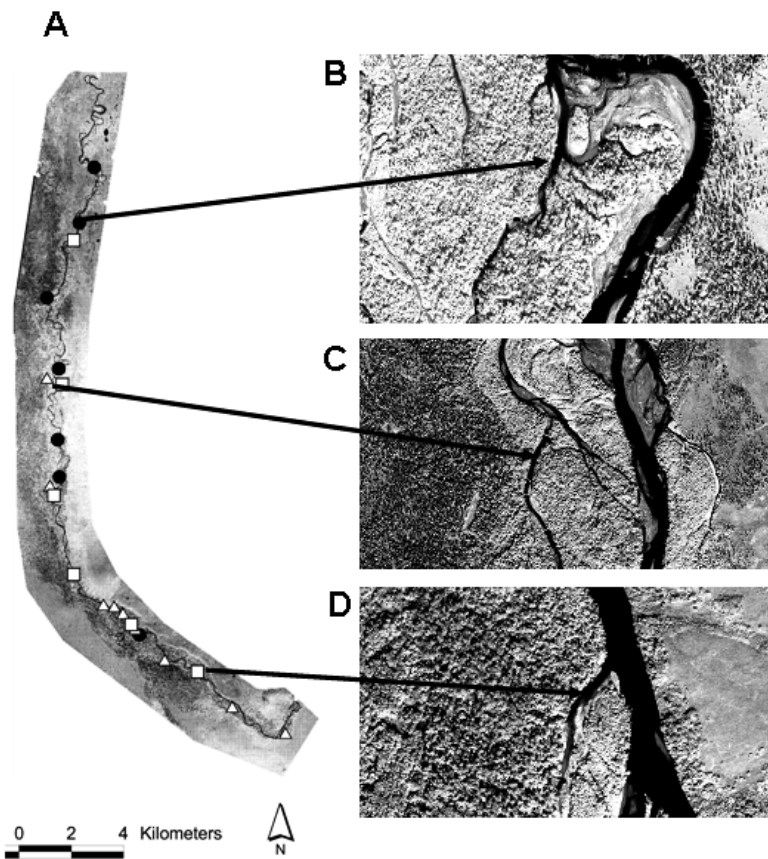


Fig. 4. Specific sites selected for study of juvenile ecology in the primary study reach (A), including spring brooks (closed circles in A, example in B), beaver ponds (triangles, C) and backwaters (squares, D). Images are from SaRON satellite imagery (Quickbird) used to quantify the areal extent of each habitat type.

Juvenile rearing sites

Juvenile sockeye were captured in 2004 and 2005 in multiple spring brook research sites and in a beaver pond in 2005. Based on these observations, in 2006 we continued investigations in the SaRON sites and added two additional spring brooks, 12 beaver ponds, and six backwater habitats for detailed study of juvenile ecology described below (Table 3; see Fig. 4 B-D for habitat examples).

Abundance of off-channel habitat

Satellite (Quickbird imagery) data consisting of four multi-spectral bands (blue - 450 to 520 nm, green – 520 to 600 nm, red -630 to 690 nm, NIR – 760 to 900 nm) at a 2.4 m spatial resolution and a panchromatic band at a 0.6 m spatial resolution were acquired for the primary floodplain study reach (R in Fig. 2). The imagery was used to determine the total amount (ha) of main channel and off-channel habitat in the Kwethluk River (D. Whited, Flathead Lake Biological Station, unpublished data).

Ground truth data (e.g., real time GPS positions, classified habitats, and measured depth and velocity) were collected in multiple habitat types (e.g., spring brooks, side channels, main channel, shallow shorelines, backwaters, and beaver ponds) and at multiple scales throughout the study reach. Using the ground truth data, a supervised classification was performed to isolate and extract water surfaces from the surrounding land areas. The extracted water was then converted from raster to vector format and discrete aquatic habitats were manually delineated (e.g., spring brooks, beaver pond, and backwater) from the water surface coverage using ArcGIS software (Arcmap v. 9.2, ESRI, Inc.). Main channel shallow shore (depth and velocity < 0.5 m) was classified using ground truth data collected with a Sontek ADP and Flowtracker. The total area (ha) was then calculated for each particular aquatic habitat.

We quantified the number of spring brook, side channel, beaver pond, and backwater habitats within the study reach and converted the area from ha to m², thus quantifying amount of available spawning and rearing habitat for riverine sockeye in the primary study reach.

Objective 3: Habitat Attributes of Lake and Floodplain Spawning and Size and Freshwater Age of Spawning Adults

Surface water-groundwater exchange

Spawning sockeye appeared to be selecting upwelling areas in the floodplain spring brooks and side channels during our preliminary 2005 surveys (Table 2). Piezometers were used to describe the surface water-groundwater exchange at specific redd locations, in areas not used by spawning adults, and to characterize the intergravel microhabitat variables that may be associated with redd placement by female sockeye in detailed study sites. Piezometers were installed in pairs, one in the redd and one outside the redd, at all flood plain and lake study sites. However, in the lake outlet study site, 17 piezometers were installed in redds and 12 were installed outside redds (12 pairs and 5 additional redds). This was due to a high concentration of spawners and no evident areas that were undisturbed.

We used a modified piezometer design after Baxter et al. (2003). A 2.1 cm diameter x 152 cm long piezometer was constructed out of clear Schedule 40 Polyvinyl Chloride (PVC) pipe (Harvel Plastics, Inc.). A perforated section of the piezometer was created by drilling 30 evenly spaced 3/32 in diameter holes over the bottom 15 cm section of the piezometer and the bottom was plugged with a cork stopper. Following Baxter et al. (2003), piezometers were installed using PVC peizometer driver. (Fig. 5A-D shows the installation method). Disrupted bed sediments around the piezometer were then tamped down to make sure that only hyporheic-groundwater is flowing into the piezometer. A Tempo® universal hand pump was then used to clear the wells of fine sediments that infiltrated the piezometer during installation and ensure its communication with hyporheic-groundwater.

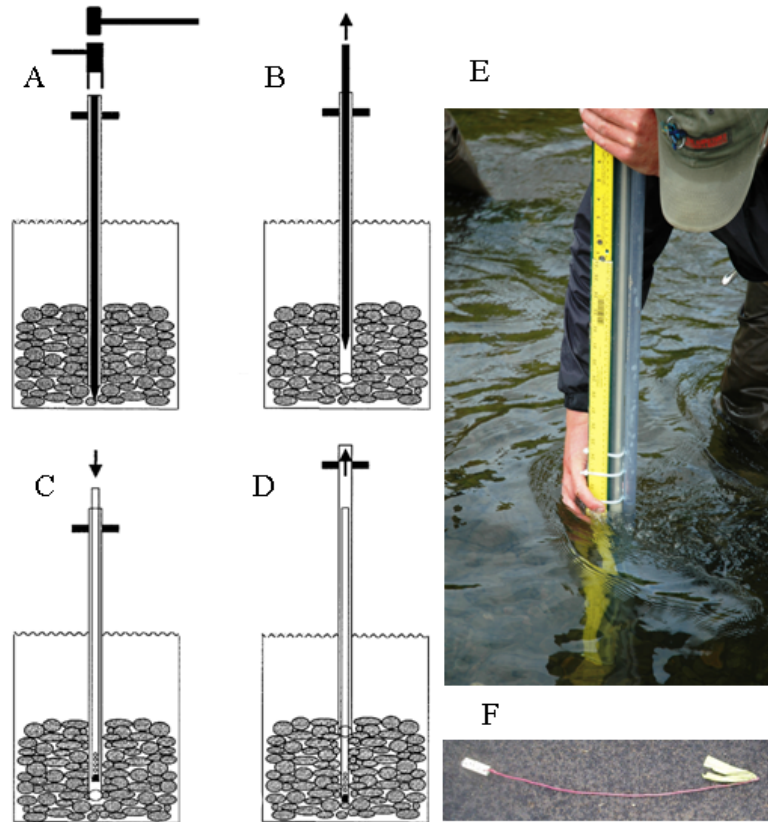


Fig. 5. (A-D) Method used for installing piezometers using the driver system (modified from Baxter et al. 2003). (A) The pounding cap is attached to the driver and driven into the streambed with a sledge hammer. (B) The steel driving rod is then removed while the imbedded sleeve is held in the bed sediments. (C) The clear PVC piezometer is then slide into the metal sleeve and (D) held in place while the metal sleeve is removed. (E) Stilling well/measuring device designed to obtain accurate measurements of the differences in head used to calculate VHG. (F) iButton capsule used to record redd temperatures.

Piezometers were used to describe the vertical movement of hyporheic-groundwater and surface water and calculate the Vertical Hydraulic Gradient (VHG). VHG is a measurement that describes a positive (upwelling or hyporheic-groundwater discharge) pressure gradient or negative (downwelling or surface water recharge) pressure gradient of hyporheic-groundwater surface water exchange (Lee and Cherry 1978; Freeze and Cherry 1979; Geist 2000; Baxter et al. 2003; Dahm et al. 2006) and is calculated using the equation:

$$(1) \quad \text{VHG} = \Delta h / \Delta l$$

where Δh is the difference in head between the water level in the piezometer and the water level of the stream (the difference in hydraulic head, recorded in cm) and Δl is the depth at which the first row of the perforations are placed into the streambed (the difference in elevation head, recorded in cm) (Baxter and Hauer 2000; Baxter et al. 2003).

We designed a modified stilling well/measuring device (after Baxter et. al. 2003), to measure the differences in piezometer and stream water levels (Fig. 5E). A meter stick was attached to the front of a 2.54 cm x 2.54 cm x 1 m long board and a clear (non-perforated) piezometer (stilling well) was attached to the side of the measuring board with zip-ties. The stilling well/measuring device was placed parallel to the installed piezometer (perpendicular to stream flow) and two sliding zip-ties were used as measurement place holders.

We estimated the horizontal hydraulic conductivity (K_h) of the streambed by using a modified falling head slug test following Baxter et al. (2003) and using the equation:

$$(2) \quad K_h = \left[\frac{(0.2501)(d_{piezometer})}{\Delta t} \right] \left[\log_e \frac{h_o}{h} \right]$$

where $d_{piezometer}$ is the inside diameter of the piezometer, Δt = the time it takes for a known volume of water to move through the stream sediments, h_o is the starting head in the piezometer at a single time (Δt), and h = the final head measurement. The falling head test was conducted by attaching a clear, graduated, pitcher that was fitted with a nylon coupler and a radiator hose that fit over the top of the piezometer. The piezometer was filled stream water and the pitcher was filled with a known volume of stream water (3.5 L). We recorded the time (S.ss) that it took for pitcher to empty. This measurement gave an estimate of the flow of water through the pore spaces of the streambed sediments or horizontal hydraulic conductivity (K_h).

We calculated the vertical hydraulic conductivity (K_v) following Anderson and Woessner (1992) and Dahm et al. (2006) using the equation:

$$(3) \quad K_v = K_h(0.10)$$

this is assuming that vertical hydrologic conductivity (K_v) values are ~10% of the K_h . Based on the K_v values, we calculated the specific discharge (q ; $\text{cm}^3 \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$ or $\text{cm} \cdot \text{s}^{-1}$) or the flux rate of upwelling hyporheic-groundwater or the downwelling of stream surface water at redd and outside redd piezometer locations, using the equation presented by Dahm et al. (2006):

$$(4) \quad q = K_v(VHG)$$

Water depth and velocity in redds

Water depth is important in rivers where freezing and desiccation can occur during the incubation period. Likewise, stream bed scour during high water events can have detrimental effects on egg survival (Montgomery et al. 1996; Devries 1997; Rennie and Millar 2000). We measured redd nose velocity ($\text{cm} \cdot \text{s}^{-1}$) (taken 10 cm upstream of the redd) and redd depth (m) at each redd at five floodplain spawning sites to determine if there was a correlation between the depth and velocity of areas that riverine sockeye build redds. Nose velocities were measured with a handheld SonTek Flowtracker.

Bedform and bed-sediment particle size

Surface water-groundwater exchange is influenced by bed slope and morphology at the reach and channel unit (run-glide-tailout-riffle) scales (Baxter and Hauer 2000). We measured channel gradient (or slope) with a laser level in channels with spawning sockeye and without, to determine if riverine spawning sockeye spawned in areas of concave or convex streambed morphology.

We conducted a modified, Wolman (1954) pebble count at each spawning location to calculate the median (D50) particle size of bed-sediments in sockeye redds and areas outside redds. Sediment samples were used as an index to determine mean D50 of bed sediments used by sockeye to construct redds and to evaluate the percentage of fine sediments in and outside of redds. We randomly selected 10 sediment samples from each redd and the area outside the redd, by blindly reaching into the water with one finger and measuring the first sediment that was touched, using a Gravelometer. The Gravelometer is a template that contains 12 square holes of common sediment sieve size classes. However, the template size classes fit a range of sizes (e.g., a particle that fit through the 5.7 mm template square, but not the 4 mm, could be any size in between those two diameters). Therefore, we calculated the average diameter between template size classes to eliminate any measurement bias and used those values to calculate the mean D50. We classified sediment sizes ≤ 4 mm as fine sediments (including sand and silt) and were expressed as a percent of the 10 rocks collected for each redd.

Surface and intergravel water chemistry

We measured the temperature ($^{\circ}\text{C}$), specific conductance ($\mu\text{S}\cdot\text{cm}^{-1}$), pH, and dissolved oxygen (DO) ($\text{mg}\cdot\text{L}^{-1}$ and % saturation), of the surface water and hyporheic-groundwater using an OAKTON® (Model #35630-02) multi-probe (temperature, specific conductance, pH) meter and an OAKTON® 300 (Model #35641) dissolved oxygen meter. Surface water samples were collected by simultaneously placing meters into the stream water and intergravel water samples were extracted from the piezometers using a MASTERFLEX® (model #7518-02) peristaltic pump that was mounted onto a rechargeable handheld drill (Woessner 2007). Water was pumped from the piezometer into a 300 ml beaker and allowed to continuously overflow until readings stabilized (Geist 2000). Water quality point measures were collected from lake study sites during a 3 day period (08/07/06 and 08/09/06) and from floodplain study sites within an 11 day period (09/3/06 to 09/14/06).

Spawning site surface water and redd temperatures and main channel versus spring brook annual temperature patterns in relation to life history

Surface water temperatures were continuously recorded every hour using Vemco (model MiniLog-T) and HOBO® (Model # U20-001-01) water level/temperature loggers placed on the bottom of the spawning channels and at a two sites in the main river. Vemco surface water temperature loggers were installed in the lake sites on 08/09/06 and 08/10/06 and recorded temperatures for a 49 to 50 day period. We installed four HOBO® temperature loggers and one Vemco temperature logger in floodplain sites from 08/03/06 to 09/12/06 and recorded temperatures for 30 to 70 days.

Intergravel temperatures were recorded every hour using Dallas Thermochron iButton temperature loggers (Model # DS1921Z-F5) that were encased in a perforated 2.54 cm dia. x 5.08 cm long PVC capsules (iButton capsule) (refer to Fig. 5F above). IButton capsules were attached to heavy-duty (8 gauge) red colored wire and installed by threading the wire into an inverted (open-end) piezometer and using the same methods for piezometer installations as above. The iButton capsule acted like a “bottle rocket” wherein, the capsule stuck out from the end of the piezometer and was inserted to a depth of 22-26 cm (within the range of the perforations) near the redd nest pocket adjacent to the piezometer. The piezometer was then wiggled out, while the capsule remained seated in the bed sediments. Ibutton capsules were installed in 10 redds in lake study sites on 08/09/06 and 08/10/06 and in five redds that were randomly selected (odd or even redds) from the 10 redds that were measured for other spawning habitat attributes in floodplain study sites from 09/03/06 to 09/14/06.

We attempted to compare mean daily temperature and mean degree days (or cumulative mean daily temperatures above 0 °C) of redds in flood plain and Boundary Lake detailed study sites over a 50 day period. However, we were not able to get a full 50 days from flood plain and the lake outlet detailed study sites. In order to compare all sites for the same amount of time (50 days), we extrapolated all floodplain sites back to 08/21/06 (observed peak spawning) and the lake outlet back a day to 08/09/06.

The temperatures in lake outlet redds during a three day period after installation did not change more than .3 °C (mean=0.1 °C, SE=0.04, range 0 to 0.3) in any of the six

redds where iButtons were recovered. Thus, in order to synchronize the date that lake and lake outlet redd iButtons began recording, we used the mean daily temperature of 08/10/06 for 08/09/06. In floodplain sites, we used the mean daily temperature from the time period of actual data collected (between 28-35 days). This is an acceptable estimation because mean daily temperatures were reasonably stable in floodplain study sites (mean change=1.2 °C, SE=.2 °C, range=0 to 3.2 °C, n=22), although the extrapolations potentially resulted in a slight underestimation of the mean daily temperature and degree days experienced by incubating riverine sockeye embryos.

We examined the general temperature patterns associated with the riverine life history (peak spawning, embryo incubation, fry emergence, and smolt migration), by comparing annual mean daily surface water temperatures of the main channel (n=1) and spring brook (n=3) from mid-august 2005 to early-September 2006 and main channel (n=2) and spring brook (n=7) surface water from early-September 2006 to mid-October 2007.

We calibrated iButton temperature loggers using temperature baths against an ASTM thermometer, with a three point calibration (0.5, 10, 20 °C). IButton temperature loggers typically overestimated temperature by 0.1 to 0.5 °C (Johnson et al. 2005). However, variation in Vemco temperature loggers were generally ≤ 0.1 °C that of the temperature bath. We calibrated a HOBO® temperature logger against a Vemco temperature logger in the field and found that differences ranged from 0.0 to ± 0.9 °C, with an average difference over a 21 day period of 0.3 °C).

Adult size and freshwater age

We collected spawning and spent adults using hook-n-line and dip-nets, to determine size of spawning riverine and lake-type, males and females and to collect scales for freshwater age analysis. Likewise, tissues samples were collected for genetic analysis used in other studies (McPhee et al. 2008, submitted). The lengths (mm) of female and male spawning riverine and lake-type sockeye were measured from the middle of the eye to the end of the hypural bone (MEHP). Scale samples were mounted onto gummed tape, which were then secured to the back of 3”x 5” acetate scale impression slides (Wildco part #112-

A27) and pressed using a heated, hydraulic scale press. A digital image of the scale impression was then made using a dissecting scope with a mounted digital camera. The freshwater and saltwater annuli were then identified to determine the years spent in freshwater, for both riverine and lake-type spawning adults.

Objective 4: Densities and Population Size of Juveniles Rearing in Floodplain Habitats

Seasonal fish densities and population estimates

Spring brooks, beaver ponds, and backwaters were selected throughout the SaRON study reach for investigation into juvenile sockeye rearing ecology (refer to Table 3 for detailed study sites and Fig. 4A for flood plain locations). We obtained population estimates and calculated densities of juvenile sockeye (fish · m⁻²) inhabiting five spring brook sites in the spring, summer, and fall (refer to Fig. 4B for an example). Ten beaver ponds (refer to Fig. 4C for an example) and three backwaters (refer to Fig. 4D for an example) were also sampled three times during the field season in late-spring, late-summer, and fall. In addition, three backwater habitats were sampled in the fall.

Lotic study sites were sampled using a Smith-Root (Model # LR-24) backpack electrofisher and a closed population 3-pass (depletion) sampling design was employed over a 25-50 m long reach. Sampling reaches were blocked at the top and bottom ends with 5 mm diameter mesh nets. To determine the density of juveniles (fish · m⁻²) we measured the channel wetted width (channel metrics) at four-six transect locations along the electrofishing reach and those measurements were used to estimate the total area (m²) of the reach. The number of juveniles captured during each electrofishing pass was entered into the program CAPTURE (www.mbrusgs.gov/software) (Pollock 1991; Lancia et al. 1996; Pine et al. 2003) which calculated population estimates on each sampling occasion and at each site.

We used closed population depletion minnow trapping to sample beaver ponds and three of the backwaters (Bryant 2000) because beaver ponds and three of the backwaters were too deep (>1.5 m) for backpack electrofishing. We placed 48-50 Gee minnow traps (Model # 125-G10) evenly throughout a blocked sampling reach and baited

each trap with salmon roe that was enclosed in perforated film canisters. Traps were operated for three, two hour trapping sessions at each study site. Trapping reaches ranged from 17 to 50 m in length and channel metrics were also measured at four-six locations along each reach.

Lake-type juvenile sockeye were collected by electrofishing the lake littoral zones of the two headwater lakes, during a single sampling session in the summer (refer to Table 3 for detailed study sites).

Objective 5: Comparisons of Length, Weight, and Diet of Lake and Floodplain Rearing Juveniles and Temperature Patterns of Floodplain Rearing Habitats

Juvenile length, weight, and diet

Juvenile sockeye fork lengths were measured to the nearest mm using a fish measuring board and weight was measured to the nearest 0.1 g using a Ohaus Scout® Pro (model # SP2001) 2000 g digital scale. Length and weight measurements were obtained from all juvenile sockeye that were captured during electrofishing and minnow trapping sessions and were used to compare the size of juvenile sockeye rearing in different habitat types throughout the season.

To assess the diet of juveniles rearing in different habitats, we quantified the stomach contents from a subsample of fishes collected as described above. Gut dissections were performed in the field, samples were preserved, and prey items were later identified to order or family. The length (mm) of each prey item was measured at 10-20x magnification using a dissecting scope and ocular micrometer. Dry mass estimates (mg) of different prey taxon were estimated using published length-dry mass regression equations (Nalepa and Quigley 1980; Rosen 1981; Sage 1982; Culver et al. 1985; Sample et al. 1993; Burgherr and Meyer 1997; Granihar 1997; Benke et al. 1999) and each prey taxon is presented as a percent of total invertebrate dry biomass.

Floodplain rearing habitat temperature patterns

We compared surface water temperature patterns from 06/21/06 to 06/01/07 to determine the thermal regime that flood plain rearing juveniles experienced during the spring, summer, fall, and winter seasons of the year in different habitats. Vemcos and HOBOS® were installed in three of the spring brooks and five of the beaver ponds that were selected for detailed study, as well as, two main channel sites (used as backwater comparisons).

Objective 6: Length Comparisons Between Floodplain Rearing Juveniles and Ocean Migrating Smolts and Fall Juvenile Density Expansions

We compared the mean lengths of floodplain rearing juveniles in the fall of 2006 to ocean migrating smolts in the following spring of 2007. These comparisons were used to assess if fall juveniles were significantly smaller than smolts, potentially leading to lower over-winter survival. We also determined if smolts had met the 50 mm size threshold limits needed for 100% to survival in saltwater (Heifetz et al. 1989) and how the size of spring smolts compared to literature values reviewed by Burgner (1991) for lake-type populations. Smolt data was obtained from The United States Geological Survey (USGS), which operated two downstream migration smolt traps from 04/26/07 to 05/31/07 at the USFWS weir site (Fig. 2).

We used fall density data and the total habitat area (m²) quantified from the remote sensing (see habitat quantification methods above), to estimate the total number of juvenile sockeye rearing within the study reach and to make some comparisons to the numbers of smolts caught during the USGS smolt trapping operation.

Statistical Analysis

The length of riverine and lake-type adults were compared using Mann-Whitney U tests because they would not meet the assumptions of t-tests. Comparisons between spawning habitat attributes in redds and areas outside redds were made with parametric paired

sample t-tests or non-parametric Wilcoxon signed ranks tests when data would not meet the assumptions of t-tests. Correlations between redd depth and velocity were analyzed using Spearman's rho bivariate correlations. Spawning habitat attributes between site comparisons, were made using either parametric one-way ANOVA's or non-parametric Kruskal-Wallis one-way ANOVA's, when data would not meet the assumptions of ANOVA. When significant differences were found between sites, Tukey or Tamhane's T2 pairwise comparisons were made. The length and weight of juveniles rearing in different habitat types were compared seasonally and to smolts (fall juveniles only) using One-way ANOVA and Tukey pairwise comparisons. All statistical tests were two-tailed and alpha was set to 0.05 for statistical significance.

RESULTS

Objectives 1 and 2: Lake and River Spawning and Quantity of Spawning and Rearing Habitat Available to Sockeye Salmon

River flow

The main channel of the Kwethluk River remained covered in ice until the end of April to Early-May (<http://aprfc.arh.noaa.gov/php/brkup>) in 2006. Spring runoff followed breakup and the hydrograph declined to base flow in early-July which lasted till early-October, when fall flooding ensued. However, periodic storm events raised the hydrograph for short time periods throughout the summer (data not shown). Sockeye salmon peak escapement at the USFWS weir (refer to Fig. 2) occurred during the week of 07/02/06 to 07/08/06 (Miller et al. 2007) and coincided with the falling limb of spring runoff. However, sockeye passed by the weir from 07/02/06 to 09/02/06 and presumably moved throughout the river system during that time period. Sockeye were routinely observed staging in backwaters at the lower ends of spring brooks and side channels where they were later observed spawning.

Spawning sites and adult counts in the Boundary Lakes, floodplain spring brooks, and side channels

Boundary Lakes Area (L in Fig. 2) - During the period of 8/06/06 to 08/10/06, we observed lake-type sockeye spawning in Boundary Lake (BL), Boundary Creek (BC) (the Boundary Lake outlet), a small spring brook (Boundary Spring brook (BOS)) that flowed into BC, Boundary Lake 2 (BL2), and the outlet of Boundary Lake 2 (B2O) (Fig. 6). We counted a total of 787 spawning adults plus 615 carcasses in the Boundary Lakes area and out of those 787 spawning adults, 100 were observed spawning in BL, 379 in BC, 205 in BOS, 88 in BL2, and 15 in B2O (refer to Table 2). Of the 608 carcasses observed in BC and BOS, 75% were obviously killed by bears (e.g., teeth punctures, claw scrapes, and partially eaten).

Kwethluk River - In 2005, we observed riverine sockeye spawning in six spring brooks and a side channel (refer to Table 2) within the SaRON study reach (R in Fig. 2). In 2006, we surveyed the entire study reach for spawning sockeye and we observed exclusive use of spring brooks or side channels in addition to the Boundary Lakes (refer to Table 2; Fig. 4B for an example of a spring brook). Even though we concentrated our flood plain studies to the SaRON study reach and the Boundary Lakes area of the catchment, we did observe riverine sockeye spawning in floodplain spring brooks during our float down from the Boundary Lakes on 08/10/06 through 08/11/06.

During our reach wide spawning surveys, we found riverine sockeye were actively spawning in 12 of the 29 spring brooks and in 9 of the 38 side channels (secondary and tertiary) that we surveyed (refer to Table 2). We also surveyed 12 backwaters where sockeye adults were staging or resting during migration, but no spawning was observed and no sockeye were observed spawning anywhere in the main channel (refer to Table 2). We documented a total of 504 adult riverine sockeye (245 males and 259 females) spawning in specific off-channel areas of the flood plain (refer to Table 2). Crews in 2007, observed spawning adults in these same habitats but the extensive survey of 2006 was not repeated.

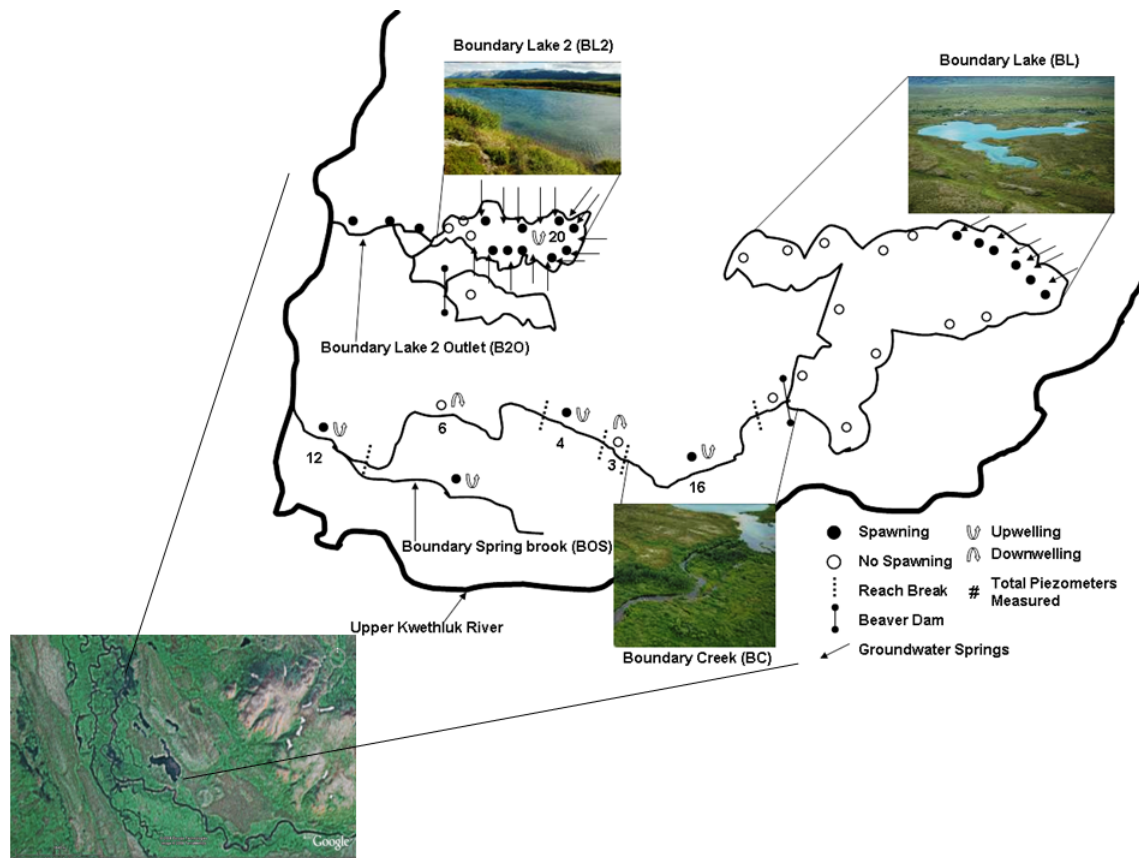


Fig. 6. Enlarged view of the Boundary Lakes area of the upper Kwethluk River. Spawning (closed circles) and non-spawning (open circles) reaches are shown. Areas where groundwater springs fed the two lakes (line arrows) and surface water-groundwater exchange (block arrows) are shown. The values represent the total number of piezometers that were measured for VHG. Note: BL has a beaver dam that is a partial barrier and the small lake adjacent to BL2 has a beaver dam that is a full barrier. BOS and B2O were not measured, but upwelling was observed. Boundary Lakes image provided by Goggle Earth.

Abundance of off-channel habitat

Based on our habitat classification methods described above, there was 1,279,070 m² of off-channel habitat available to floodplain spawning and rearing sockeye within the SaRON study reach (~30 km long-R in Fig. 2) and composed 46% of the total aquatic habitat. Spring brooks and side channels made up 26.3% (335,773 m², n=180) and 27.3% (348,677 m², n=42) of the available off-channel habitat, respectively. Beaver complexes (a series of beaver ponds) made up the highest percent of off-channel habitat (40.0%,

n=101) and provided 515,701 m² of off-channel habitat. Backwater habitats were not as prevalent as other off-channel habitats and made up only 4.0% (55,966 m², n=65) of the available off-channel habitat.

Objective 3: Habitat Attributes of Lake and Floodplain Spawning and Size and Freshwater Age of Spawning Adults

Surface water-groundwater exchange

In all cases, riverine and lake-type sockeye constructed redds in areas where ground water was upwelling (Fig. 7). We observed that in the Boundary Lake outlet (LK_BC) study site, lake-type sockeye were spawning in three distinct reaches and that redds were placed in areas that were upwelling or neutral but never in areas or reaches that were downwelling (losing) (Fig. 6). We found no significant differences comparing VHG in and areas adjacent to redds in both lake-type sockeye study sites (exact p -values=.344 and .891, Wilcoxon signed ranks test) (Fig. 7). VHG transects were conducted in two of the three non-spawning reaches (Fig. 6), and we found that these were indeed areas of downwelling surface water (Fig. 7). Likewise, VHG in riverine sockeye redds and areas adjacent to redds were not significantly different (exact p -values >.10 for all sites, Wilcoxon signed ranks test) (Fig. 7). Riverine sockeye did not spawn in areas with downwelling (losing) or neutral VHG readings, similar to what we found in the lake outlet study site (Fig. 7).

Overall, we did not see marked differences in hydraulic conductivity (K_h) or specific discharge (q). Estimates of K_h ranged from $3.55 \cdot 10^{-3} \text{ cm} \cdot \text{s}^{-1}$ to $5.65 \cdot 10^{-2} \text{ cm} \cdot \text{s}^{-1}$ (n=50) in floodplain redds, from $1.65 \cdot 10^{-2} \text{ cm} \cdot \text{s}^{-1}$ to $4.05 \cdot 10^{-2} \text{ cm} \cdot \text{s}^{-1}$ (n=10) in lake shoreline redds, and from $2.48 \cdot 10^{-2} \text{ cm} \cdot \text{s}^{-1}$ to $4.65 \cdot 10^{-2} \text{ cm} \cdot \text{s}^{-1}$ (n=16) in lake outlet redds. The K_h in riverine sockeye redds was not significantly higher than in lake-type sockeye redds (p -value>.050 for all site comparisons, ANOVA). Likewise, K_h was not significantly different in redds than areas outside redds (p -value>.100, ANOVA). The q of redds from all sites ranged from $1.0 \cdot 10^{-5} \text{ cm} \cdot \text{s}^{-1}$ to $5.55 \cdot 10^{-3} \text{ cm} \cdot \text{s}^{-1}$. However, SB_SH had significantly higher q in redds than areas outside of redds (exact p -

value=.048, Wilcoxon signed ranks test) and pairwise comparisons found that SB_SS (mean= $5.68 \cdot 10^{-4} \text{ cm} \cdot \text{s}^{-1}$) had higher q than SB_GS (mean= $9.58 \cdot 10^{-5} \text{ cm} \cdot \text{s}^{-1}$) (p -value=.026, Kruskal-Wallis ANOVA).

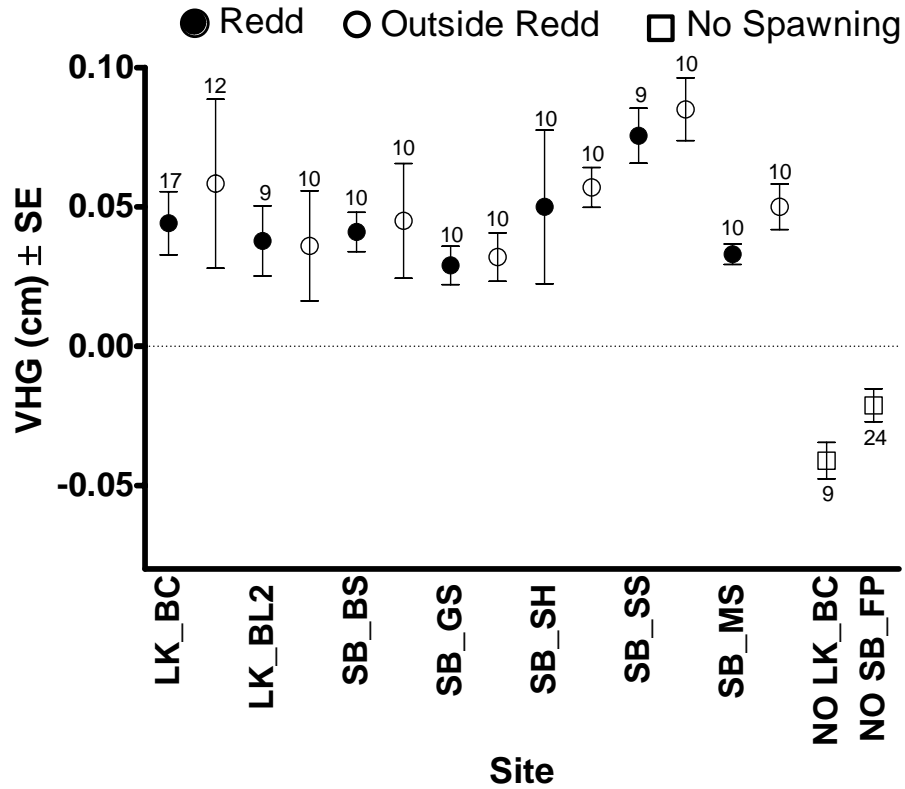


Fig. 7. Vertical Hydraulic Gradient (VHG) (cm) calculated from piezometers placed in sockeye redds, in areas outside redds, and in areas where sockeye were not spawning in Boundary Creek (NO LK_BC) (n=2) and in floodplain sites (NO SB_FP) (n=3). Note: Two sockeye redds had VHG values that were outliers (LK_BL2=1.93) and (SB_SS=.56). These redds were excluded from this graph to display the overall relationships of VHG, but were included in statistical analysis.

Water depth and velocity

We found that the water depths (m) at which riverine sockeye and lake-type sockeye placed redds ranged from .12 m to .83 m. Redd depths ranged from .20 to .83 (mean's=.28 to .55, SE=.02 to .07, n=10 at each site) in floodplain sites, from .12 m to .61 (mean=.27, SE=.03, n=10) in the lake outlet study site, and .22 m to .74 m (mean=.55, SE=.06, n=10) in lake study site. Riverine sockeye redds in SB_BS, SB_GS,

and SB_SH were constructed in deeper water than in LK_BC (p -value $<.010$ for all, ANOVA), but SB_BS, SB_GS, SB_SH, and SB_SS redds were not deeper than redds constructed in LK_BL2 (p -value $>.050$ for all, ANOVA). Redd nose velocities ($\text{cm} \cdot \text{s}^{-1}$) were not collected in the lake outlet study site, but floodplain spawning sites had nose velocities that ranged from 0 to $28.3 \text{ cm} \cdot \text{s}^{-1}$. We found no correlation between redd depth and nose velocity in floodplain spawning sites (Spearman's rho ($\rho = -.432$ to $-.104$, p -value $>.100$ for all sites)).

Bedform and bed-sediment particle size

Riverine and lake-type (lake outlet) sockeye primarily spawned within run and glide habitats of concave bedform and exclusively in areas of upwelling groundwater, as stated above. In some riffle habitats sockeye spawned along channel margins, typically near small spring channels ($<1\text{m}$ wide) or spring seeps that emerged from the stream bank. The gradient of riverine sockeye spawning reaches ranged from $.02 \text{ cm} \cdot \text{m}^{-1}$ to $.14 \text{ cm} \cdot \text{m}^{-1}$ and non-spawning reaches ranged from $.10 \text{ cm} \cdot \text{m}^{-1}$ to $.27 \text{ cm} \cdot \text{m}^{-1}$. Thus, the associated bedform was linked to the slope of the habitat and the surface water-groundwater exchange that was measured.

Sediment size classes that were measured in riverine and lake-type, lake, sockeye redds ranged from $<4\text{-}90$ mm in diameter. Median (D50) sediment size of redds and areas outside redds were compared using paired samples t-tests. Redd sediments were larger in SB_SH (p -value $=.012$) and SB_MS (p -value $=.032$) than areas outside redds (Fig. 8). ANOVA pairwise comparisons between sites revealed that SB_BS redds had significantly larger sediments than LK_BL2 (p -value $=.007$), SB_SS (p -value $=.030$), and SB_MS (p -value $=.018$) redds (Fig. 8). No data was collected for individual redds in the lake outlet due to time constraints. We found fine sediments in only 4 of the 60 redds that we sampled and fines made up between 10% and 40% (mean $=22.5\%$, SE $=8\%$) of the redd sediments. However, in areas outside redds we found fine sediments made up between 10% and 100% (mean $=45.8\%$, SE $=4.9\%$, $n=40$) of the sediments.

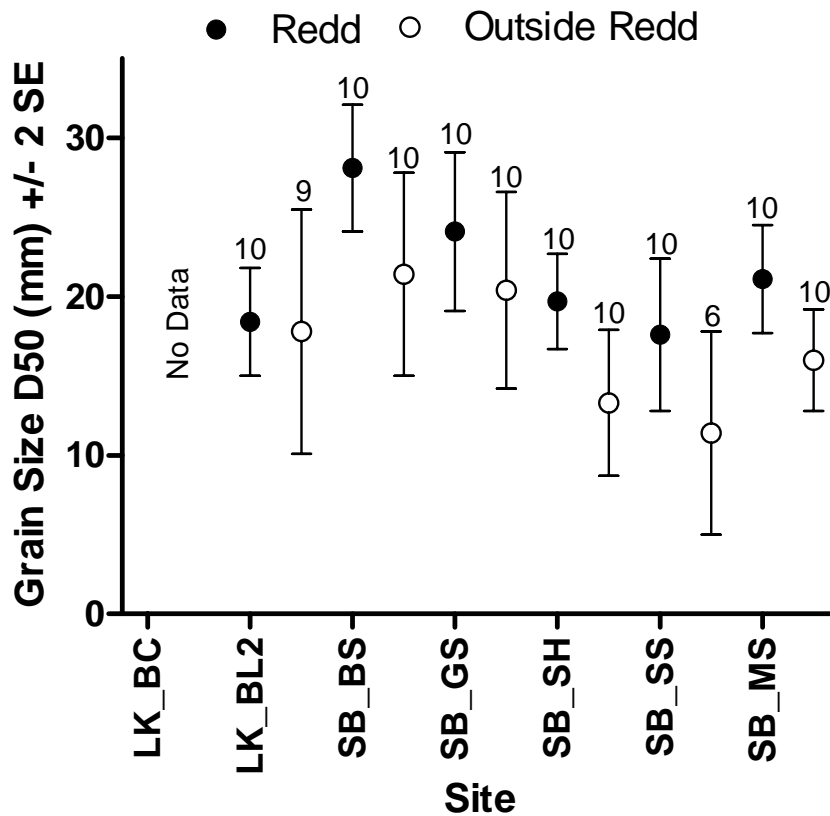


Fig. 8. Mean median sediment (grain) sizes (D50) of LK_BL2 and floodplain redds and areas outside redds. Note: Sediment sizes were not collected for individual redds or areas outside redds for LK_BC. In LK_BL2 one area outside the redd contained 90% fine sediments, so D50 could not be calculated and in SB_SS four areas outside redds had 100% fine sediments.

Surface and intergravel water chemistry

Water chemistry point measures were compared in redds, areas adjacent to redds, and to the surface water using Wilcoxon signed ranks tests. Temperatures (°C) in redds were not significantly different in areas outside redds (exact *p*-value's >.05 for all sites) and all redd temperatures were significantly colder compared to surface water (exact *p*-value's < .020 for all sites), except for SB_SS (exact *p*-value=.899) which was closer to surface water (Table 4).

Table 4. Mean water quality measures of LK_BC, LK_BL2, lake spawning sites and SB_BS, SB_GS, SB_SH, SB_SS, and SB_MS floodplain spawning sites. Measures were taken from piezometers placed in redds and outside redds as well as, the surface water surrounding those piezometers.

	Temp. °C	SE	Conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$)	SE	pH	SE	DO ($\text{mg} \cdot \text{L}^{-1}$)	SE	DO (% sat)	SE
LK_BC										
Redds	5.2	2.75	153.0	7.49	7.25	0.12	8.2	1.86	70	16.00
Outside redds	5.6	2.73	153.5	5.22	7.20	0.07	7.2	1.36	60	9.76
Surface	9.8	0.93	145.4	1.95	7.22	0.06	9.4	0.64	82	5.85
LK_BL2										
Redds	4.4	0.78	154.1	3.92	7.47	0.07	8.5	0.62	69	5.03
Outside redds	5.2	1.17	153.2	2.21	7.43	0.09	8.6	1.26	70	11.93
Surface Water	5.6	0.50	152.5	2.75	7.52	0.11	9.9	0.50	83	4.00
Floodplain Sites										
SB_BS										
Redds	6.5	0.44	112.0	0.21	6.90	0.04	6.2	0.20	55	1.96
Outside redds	6.5	0.42	112.3	0.27	6.83	0.03	6.2	0.24	53	2.38
Surface water	8.4	0.08	111.7	0.17	6.73	0.07	8.3	0.10	73	1.03
SB_GS										
Redds	7.7	0.34	108.8	0.42	7.02	0.03	5.5	0.54	50	5.00
Outside redds	7.9	0.27	108.7	0.48	6.86	0.03	5.6	0.53	50	4.73
Surface water	9.2	0.08	110.8	0.15	7.01	0.04	10.0	0.23	90	2.20
SB_SH										
Redds	6.9	0.57	110.6	1.32	7.00	0.01	5.4	0.40	47	3.47
Outside redds	6.6	0.63	110.3	1.24	6.87	0.02	5.4	0.53	46	4.22
Surface water	8.5	0.15	112.7	0.34	7.06	0.01	9.4	0.34	84	2.84
SB_SS										
Redds	5.5	0.33	105.4	0.23	6.57	0.02	2.6	0.11	23	1.23
Outside redds	5.3	0.30	105.8	0.28	6.55	0.01	2.6	0.10	22	0.83
Surface water	5.6	0.09	109.3	0.51	6.78	0.04	4.5	0.10	39	0.67
SB_MS										
Redds	5.8	0.72	103.0	1.42	6.83	0.04	7.4	0.56	66	4.87
Outside redds	5.8	0.58	102.9	1.43	6.74	0.05	7.5	0.43	64	3.21
Surface water	9.0	0.12	111.9	0.47	6.88	0.05	10.1	0.31	88	2.37

Specific conductance ($\mu\text{S} \cdot \text{cm}^{-1}$) was not different in and outside of redds (exact p -value's $> .100$, for all sites) (Table 4). Specific conductance was lower in SB_GS (p -value=.005), SB_SS (p -value=.002), and SB_MS (p -value=.002) redds than the surface water (Wilcoxon signed ranks tests) (Table 4). Specific conductance was higher in lake-type sockeye redds compared to redds in all floodplain spawning sites (p -value<.001 for both sites, Kruskal-Wallis ANOVA) (Table 4). Mean pH was significantly higher in lake-

type redds than in any of the floodplain spawning sites (p -value $<.001$ for both sites, Kruskal-Wallis ANOVA) (Table 4).

Dissolved oxygen (DO; $\text{mg} \cdot \text{L}^{-1}$) was not significantly different in floodplain or lake redds and areas outside redds (paired samples t-test, p -value $>.100$ for all sites) (Table 4). However, redds in the lake outlet had significantly higher DO than areas outside redds (paired samples t-test, p -value $=.032$) (Table 4). This was most likely caused by the high concentration of spawning adults in the outlet, creating a series of “dunes” or back to back redds that increased surface water flow through the redds. Further analysis, showed that lake redds had significantly higher DO levels compared to all floodplain sites (p -values $<.050$), except SB_MS (p -value $=.928$) and that the lake outlet redds had significantly higher DO levels than SB_GS (p -value $=.017$) and SB_SS (p -value $<.001$) (ANOVA) (Table 4). Although, SB_SS redds had the lowest DO of all sites, we conducted a spot check 30 days later and mean DO increased by $4.0 \text{ mg} \cdot \text{L}^{-1}$ (Mean $=6.6 \text{ mg} \cdot \text{L}^{-1}$, SE $=.68$, $n=10$), in fact the mean DO in all floodplain sites increased between 2.1 to $5.2 \text{ mg} \cdot \text{L}^{-1}$ when checked \geq a month later.

Spawning site surface water and redd temperatures and main channel versus spring brook annual temperature patterns in relation to life history

Surface water mean daily temperatures in the lake outlet steadily decreased from 10.2 at the time of spawning to 7.0 °C and from 6.2 to 4.5 °C in the lake (Fig. 9). Surface water mean daily temperatures in declined from 10.0 to 6.3 °C to 5.0 to 4.0 °C in flood plain detailed study sites (Fig. 9). In mid-October a large decrease in surface water temperatures was caused by fall flooding (Fig. 9) and during that time the main channel dropped to 2 °C (data not shown).

We compared the mean daily temperatures of redds using Kruskal-Wallis ANOVA and found that floodplain spring brooks had significantly warmer redd temperatures than the lake environments (p -value $=.004$, p -value $=.008$, and p -value $<.001$, respectively), although SB_GS had warmer redd temperatures than SB_SS (p -value $<.025$) (Fig. 10A). However, the 95% CI of the mean daily temperatures of the lake outlet redds encompassed the redd temperatures of all floodplain sites and the lake, and

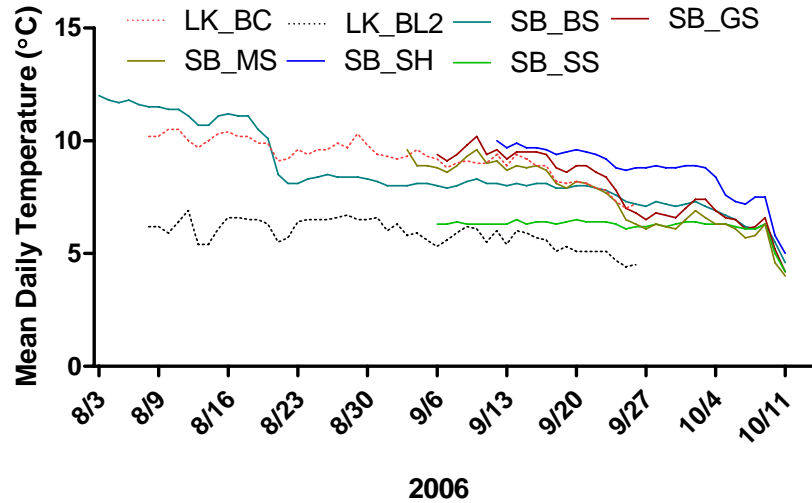


Fig. 9. Mean daily surface water temperatures of flood plain (solid color lines) and lake (dashed color lines) spawning sites that coincides with recorded redd temperatures.

had the highest variability (1.8 to 10.7 °C) (Fig. 10A). We found the same between site differences when comparing mean degree day's (Fig. 10B). In general, some riverine sockeye redds had between .9 and 6.4 °C higher redd temperatures and 100.9 and 251.1 more incubation degree days than the lake, lake-type, sockeye redds.

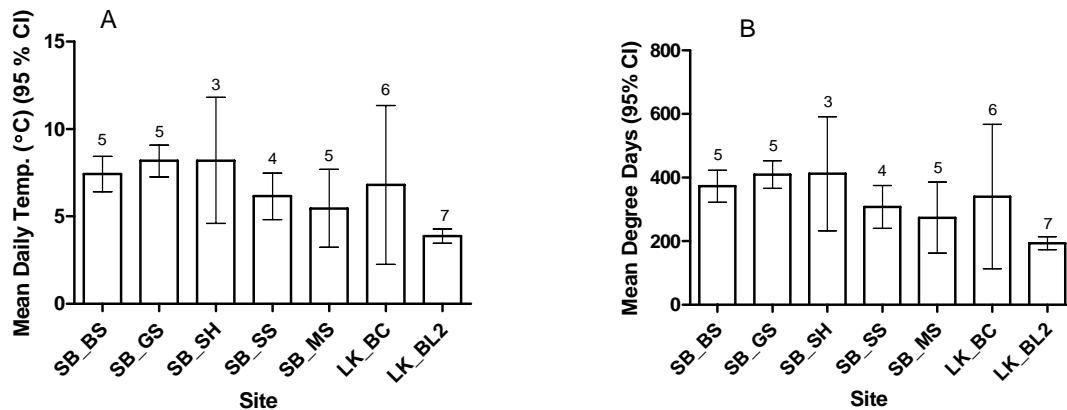


Fig. 10. (A) Means of the mean daily temperature and (B) the mean degree days that incubating riverine and lake-type sockeye embryos experienced during a 50 day period. Values above error bars represent the number of redd temperature loggers used in analysis at each site.

Annual temperature patterns showed that spring brooks were generally warmer during the winter and cooler during the summer, than main channel surface water (Fig.

11). During the winters of 2005-2006, spring brook surface water temperatures ranged from 0.0 to 6.8 °C (mean of daily means=1.1, SE=0.1, n=187 days) when the main channel was 0.0 °C and during the winter of 2006-2007, spring brook surface water temperatures ranged from 0.0 to 6.4 °C (mean of daily means=1.5, SE=0.1, n=166 days) when the main channel was between 0.0 and 0.3 °C (Fig. 11).

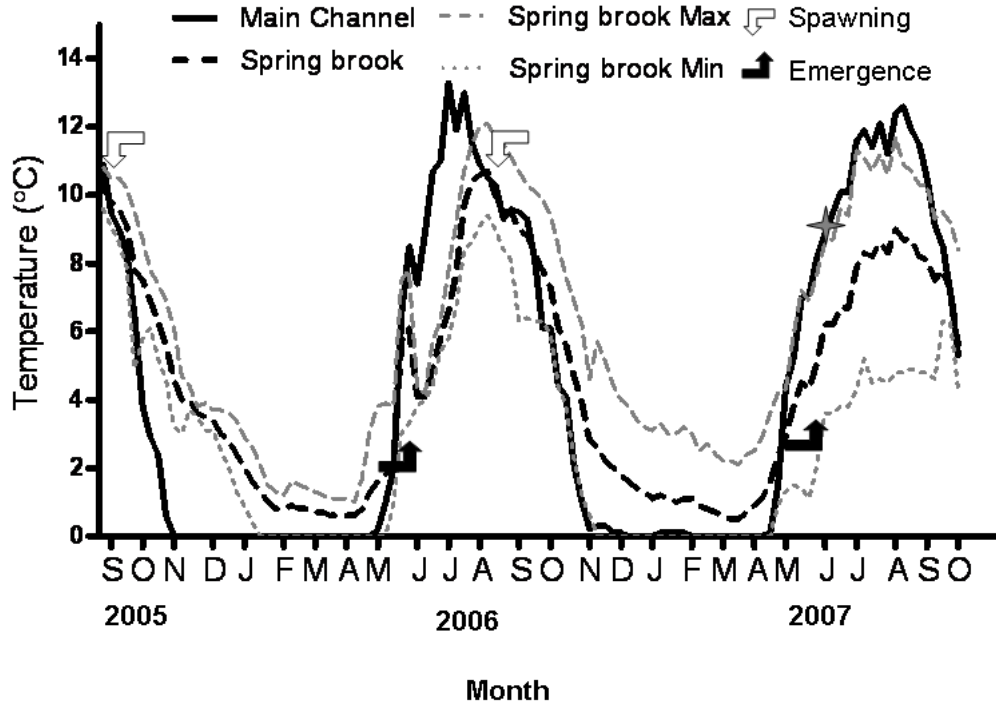


Fig. 11. Annual surface water temperature patterns in relation to riverine sockeye life history. Main channel and spring brook surface waters were compared from mid-August 2005 through October 2007 and described when peak floodplain spawning was observed (clear arrows), relative fry emergence (black arrows), and peak smolt migration (grey star) occurred in the SaRON study reach. Temperature patterns are reported as 7-day averages of the mean daily temperature. Spring brook maximums and minimums are reported as 7-day average maximums and minimums.

The surface water temperatures of some spring brooks did drop to 0.0 °C during the winter (see Fig. 11, spring brook minimums), but we were able to recover three iButton capsules that were lost during the 2006 mid-October flooding (see above). One of the iButtons recorded temperatures till mid-November and two of the iButtons continued recording temperatures until the first of December. The mean, mean daily intergravel

redd temperatures, were 4.1 to 4.2 °C warmer than the spring brook surface water at 0.0 °C (data not shown).

Peak spawning in floodplain spawning sites occurred during the same time frame in 2005 and 2006 and appeared to coincide with spring brook water becoming warmer than main channel water (Fig. 11). We estimated that riverine sockeye fry emergence occurred from late-April to early-June and that it also coincided with increasing water temperatures (Fig. 11). We based this estimate on the size of fry captured in floodplain spring brooks in the spring of 2006 (see spring length data below) and on the USGS trap catch data which also caught newly emerged sockeye juveniles (not migrating to the ocean; see adult scale analysis below) from 04/29/07 through 05/31/07, with a mean fork length of 29 mm (range 26 to 33 mm, n=98). This size range is typical range for juveniles that had recently emerged from redds (Murphy et al.1988; Heifetz et al. 1989; Burgner 1991; Quinn 2005). Sockeye smolts (migrating downstream to the ocean) were caught on 04/26/07 through 05/31/07, with the peak catch occurring on 05/18/07 (S. Burrell, USGS, Alaska Science Center, unpublished data) (Fig. 11).

Adult size and freshwater age

The average lengths of lake-type and riverine females were 485 mm (SE=4, n=44) and 481mm (SE=4, n=29), respectively. Riverine females were not significantly larger than lake-type females (exact p -value=.607). However, we did find that riverine males 519 mm (SE=5, n=26) were significantly larger in average length than lake-type males 481 mm (SE=9.42, n=43) (exact p -value=.045). Adult scale analysis confirmed that riverine (n=40) and lake-type adults (n=25) had reared in freshwater for at least one year and in some cases both riverine (n=8) and lake-type (n=8) sockeye had reared in freshwater for two years.

Objectives 1 and 4: Habitats Used by Juveniles for Floodplain Rearing and Juvenile Densities and Population Size

Juvenile rearing sites, seasonal fish densities, and population estimates

Juvenile sockeye were found rearing in five of the seven spring brooks, 10 of the 12 beaver ponds, and six of seven backwaters that were studied (refer to Table 3; refer to Fig. 4B-D for habitat examples). No juvenile sockeye were found rearing along the shallow shoreline of the main channel at any of the three sites sampled or during any of the three seasonal sampling periods, or in either of the two brown water tundra tributaries that were sampled during the same time periods. A total of 243 hours was spent trapping beaver ponds and 171 hours was spent electrofishing lotic floodplain habitats, during SaRON across site sampling. All sockeye collected were young-of-the-year (YOY) and no yearling (1+) juveniles were collected indicating that the downstream migration of sockeye smolts going to the sea, occurred early in the spring (as noted in Fig. 11).

Our study of juvenile densities and population size was focused on five floodplain spring brooks (spring, summer, and fall sampling) and in the fall, three backwaters and three beaver ponds that captured enough juveniles and could be easily reached from the research camp. There were between .05 to .51 fish · m⁻² rearing in spring brooks in the spring (two sites) and .24 to .68 fish · m⁻² in spring brooks in the summer (three sites). In the fall, there were between .27 to .54 fish · m⁻² in spring brooks (four sites), .03 to .19 fish · m⁻² in backwaters (three sites), and .02 to .07 fish · m⁻² in beaver ponds (three sites) (Fig. 12A). Our population estimates varied (Fig. 12B) for the spring brooks, backwaters, and beaver ponds, but in the fall, spring brooks had higher population size estimates than backwaters and beaver ponds.

We caught a total of 79 juvenile sockeye in beaver ponds over the course of three sampling periods (late-spring, late-summer/early-fall, and fall) and 180 hours of minnow trapping. In the three deeper backwaters that were sampled using minnow traps, during the same time periods, we caught a total of 37 juveniles, in 54 hours of minnow trapping. However, during one late-spring beaver pond trapping session we only caught two juvenile sockeye in the minnow traps, but counted 51 during snorkeling surveys.

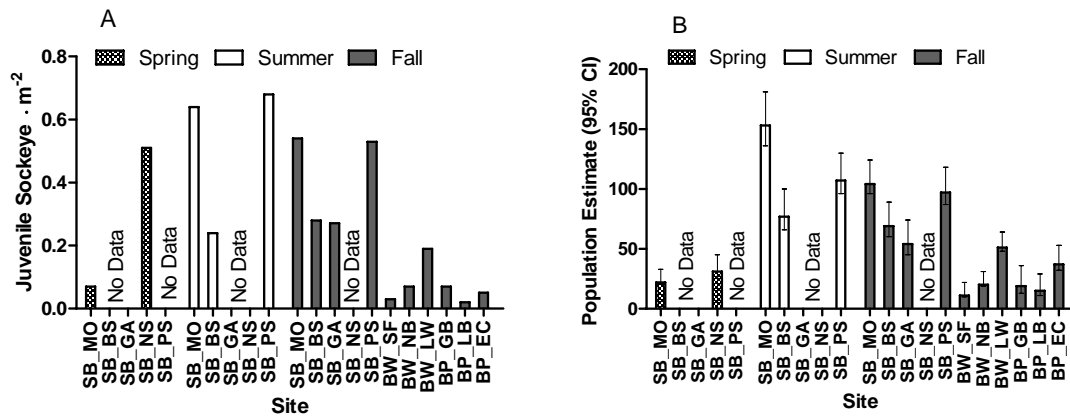


Fig. 12. (A) The density (fish · m⁻²) and (B) population estimates for riverine sockeye juveniles rearing in SB_MO (spring, summer, and fall), SB_BS (summer and fall), SB_GA (fall), SB_NS (spring), and SB_PS (summer and fall) spring brooks and BW_SF, BW_NP, and BW_LW backwaters (fall only), and BP_GB, BP_LB, BP_EC beaver ponds (fall only) floodplain habitats. Note: No Data=Flooding prevented closed population electrofishing in three of the five spring brooks in the spring and in the summer and fall too few fish were captured to estimate population size or reliable density estimates.

Likewise, during another minnow trapping session we only caught four juvenile sockeye, but counted 33 during snorkeling surveys. Thus, we concluded that juvenile sockeye were not particularly attracted to the roe in the minnow traps and this limited our ability to determine fish densities and obtain population estimates.

Objective 5: Comparisons of Length, Weight, and Diet of Lake and Floodplain Rearing Juveniles and Temperature Patterns of Floodplain Rearing Sites

Juvenile length and weight

We pooled sampling sites by rearing habitat type and season for length and weight comparisons (refer to Table 3 for detailed study sites). In early-spring, spring brook rearing juveniles were 27 to 43 mm long (mean=33, SE=.3, n=140) and weighed from .1 to .8 g (mean=0.3, SE=.01, n=140), in the summer, juveniles were 37 to 65 mm long (mean=49, SE=.3, n=264) and weighed from .5 and 2.5 g (mean=1.1, SE=.02, n=264), and in the fall juveniles were 43 to 70 mm long (mean=58, SE=.3, n=246) and weighed

from .8 to 3.1 g (mean=1.8, SE=.03, n=246) (Fig. 13A-B). Juveniles rearing in beaver ponds in late-spring were from 50 to 59 mm long (mean=54, SE=1, n=8) and weighed from 1.1 to 1.9 g (mean=1.4, SE=0.1, n=8), in late-summer/early-fall, were 60 to 77 mm long (mean=67, SE=1, n=13) and weighed from 1.9 to 4.6 g (mean=2.8, SE=.2, n=13), and in the fall, were 52 to 77 mm long (mean=66, SE=1, n=58) and weighed from 1.4 to 3.90 g (mean=2.5, SE=.1, n=58) (Fig. 13A-B). Backwater rearing juveniles in late-spring were 42 to 55 mm long (mean=49, SE=2, n=7) and weighed from 0.8 to 1.1 g (mean=1.1, SE=0.1, n=7), in late-summer/early fall, were 32 to 75 mm long (mean=54, SE=2, n=34) and weighed from .2 to 3.9 g (mean=1.6, SE=.1, n=34), and in the fall, were 32 to 72 mm long (mean=57, SE=1, n=86) and weighed from .2 to 3.6 g (mean=1.7, SE=.1, n=86) (Fig. 13A-B).

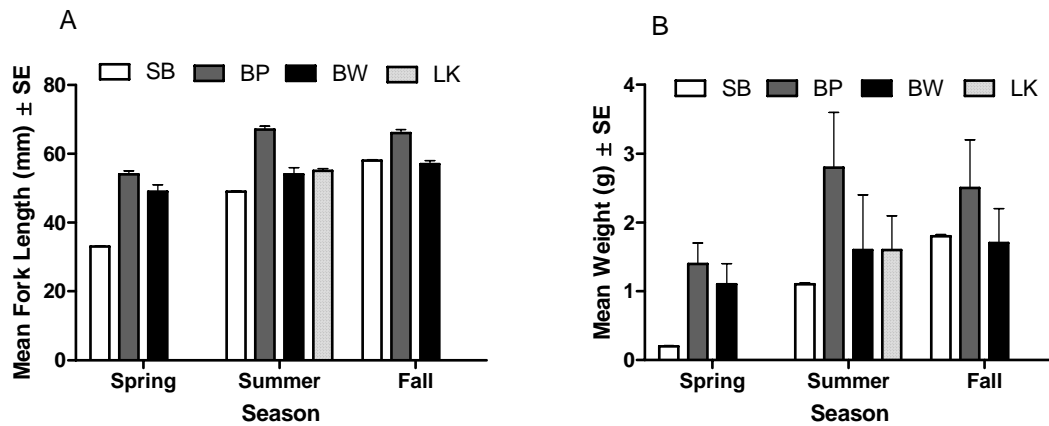


Fig. 13. (A) Mean length (mm) and (B) mean weight (g) of juveniles rearing in spring brooks (SB), beaver ponds (BP), backwaters (BW), and the Boundary Lakes (LK) by season. Note: Spring brooks were sampled in early-spring (06/19/06-06/22/06), summer (07/26/06-08/15/06), and fall (09/24/06-10/03/06). Beaver ponds were sampled in late-spring(07/05/06-07/11/06), late-summer/early-fall (09/01/06-09/14/06), and fall (10/01/06-10/08/06). Backwaters were sampled in late-spring (07/08/06-07/13/06), late-summer/early-fall (08/18/06-09/05/06), and fall (09/23/06-10/07/06). The Boundary Lakes were only sampled during the summer on 08/09/06 and 08/10/06.

During the summer sampling period, lake-type juveniles rearing in both Boundary Lakes were from 39 to 64 mm long (mean=55, SE=.7, n=45) and weighed from .6 to 2.8 g (mean=1.6, SE=.1, n=45) (Fig. 13A-B). Lake-type juveniles were significantly larger in both mean fork length and mean weight (p -value's<.020 for both comparisons, for all sites) in the summer than all floodplain spring brooks. We did not make statistical

comparisons of mean fork lengths and weights of juveniles rearing in beaver ponds and backwaters to spring brooks or lake rearing juveniles because of the differences between sampling periods in the spring and summer (some sites were >two weeks). It does appear that sockeye juveniles were larger in fork length and weight in backwaters and beaver ponds than juveniles rearing in the spring brooks in the spring and beaver pond rearing juveniles were larger in fork length and weight than spring brook, backwaters, and lake rearing juveniles in the summer (Fig. 13A-B).

Juveniles rearing in beaver ponds in the fall were significantly larger in fork length than juveniles rearing in backwaters (p -value<.001) and spring brooks (p -value<.001) and weighed significantly more compared to backwaters and spring brooks (p -value<.001 for both) (Fig. 13A-B) However, juveniles rearing in spring brooks had significantly higher mean fork lengths than those rearing in backwaters (p -value=.047), but were not significantly different in mean weight in the fall (p -value=.168) (Fig. 13B). Scale analysis confirmed that larger fish (n=20) in all habitat types were YOY and comparisons were made on the same age class.

Juvenile diet

Juvenile sockeye rearing in spring brook, beaver pond, and backwater habitats ate mostly zooplankton and various small macroinvertebrates (Fig. 14A-B). Lake-type juveniles primarily ate zooplankton (Fig. 14A-B). Interestingly, flood plain and lake rearing juveniles were both feeding on Chydorid cladocerans, but they were, *Alona* in the lakes and *Eurycerus* in floodplain habitats. We were able to determine that the floodplain cladoceran was *Eurycerus lamellatus*, but the lake cladoceran was so small and immature that species identification could not be determined. Both *Eurycerus lamellatus* and the unknown *Alona* species are known to be pond, littoral, and bottom dwelling zooplankton (Smith 2001), but have been found to inhabit groundwater and hyporheic zones (Dumont 1995; Dumont and Negrea 1996).

Juvenile feeding in floodplain spring brooks, beaver ponds, and backwaters was compared for the entire season. Zooplankton was present in 77.8%, 43.5%, and 62.5% of the stomachs sampled in spring brooks (n=90), beaver ponds (n=23), backwaters (n=40),

respectively. Spring brook rearing juveniles had a larger percent of zooplankton biomass (dry mass in mg) in their diet (50.7%, SE=4.5%), than juveniles rearing in backwaters (31.4%, SE=5.8%), and beaver ponds (28.9%, SE=8.6%) throughout the sampling season (Fig. 14A). However, spring brook rearing juveniles had a smaller percent of aquatic macroinvertebrate biomass (including Gastropods) in their diet (39.9%, SE=4.3%) compared to beaver pond (61.8%, SE=8.7%) and backwater (66.7%, SE=5.9%) rearing juveniles (Fig 14A). Winged and identified terrestrial invertebrates made up a small percent of the overall biomass in juvenile sockeye diets, but were eaten by juveniles rearing in all habitat types (Fig. 14A).

Zooplankton were present in 100% of the stomachs analyzed and made up 71.7% (SE=6.6%, n=15) and 97.7% (SE=1.8%, n=30) of the prey biomass in BL and BL2, lake rearing juveniles, respectively (Fig. 14A-B). Winged and identified terrestrial invertebrates were present in 40% of the BL juveniles and made up 25.6% (SE=6.5%, n=30) of the prey biomass (Fig. 14A-B). The prey biomass in the diet of beaver pond rearing juveniles switched from 56.2% (SE=18.5%, n=6) zooplankton in the summer to 80.2 % (SE=8.5%, n=12) aquatic invertebrates in the fall. Winged, identified terrestrial, and unknown invertebrates were fed on in the fall, but not in the spring in beaver pond rearing juveniles (Fig.14B). On the contrary, the biomass of zooplankton in the diet of spring brook rearing juveniles increased from 42.5% (SE=7.7%, n=30) in the summer to 60.0% (SE=6.3, n=46) in the fall and winged and identified terrestrial invertebrates were still part of the diet of spring brook rearing juveniles in the fall (Fig. 14B). Backwater rearing juveniles fed primarily on aquatic macroinvertebrates making up 60.0% (SE=19%, n=5) and 70.4% of the prey biomass in the summer and fall, respectively (Fig. 14B).

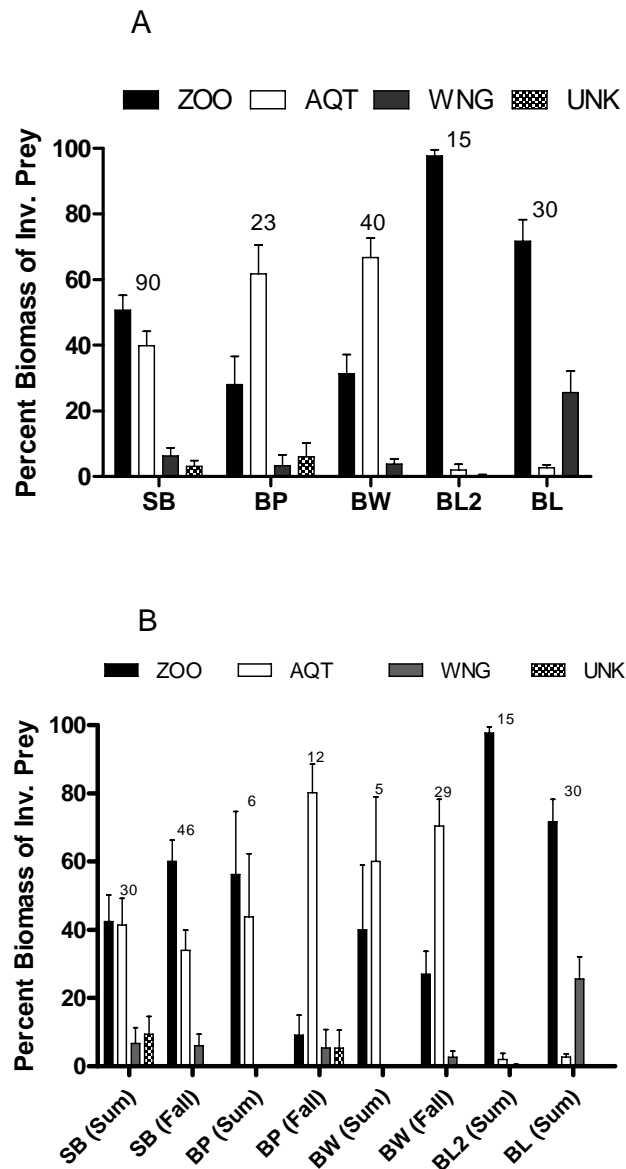


Fig. 14. (A) Percent biomass (dry mass in mg) of invertebrate prey taxon throughout the season (6/19/06 to 10/08/06) and (B) from summer to fall in the diet of sockeye rearing in spring brooks (SB), beaver ponds (BP), backwaters (BW), Boundary Lake 2 (BL2), and Boundary Lake (BL) habitats (lake's are summer only). Note: ZOO=Cladocera (*Alona* and *Eurycerus*), Ostracoda, and Copepoda, AQT=aquatic macroinvertebrates (Plecopterans (stoneflies), Trichopterans (caddisflies), Ephemeropterans (mayflies), Hydracarinids (water mites), Ceratopogonids (biting midges), Chironomids (midges), Tipulids (craneflies), and Gastropoda (aquatic snails)), WNG/TERR=winged invertebrates of either terrestrial or aquatic origin, Hymenoptera (wasps), Hemiptera (leaf hoppers), and Arachnids (spiders), UNK=Collembola (spring-tails) and Coleoptera (beetles) larvae that were not defined as aquatic or terrestrial. Values above bars represent the number of fish used for diet analysis. Bars represent \pm one standard error of the mean.

Floodplain rearing habitat temperature patterns

Temperature pattern comparisons between floodplain rearing habitats revealed that beaver pond and back water rearing juveniles experience a similar thermal regime throughout the year, where as, spring brook rearing juveniles experience a significantly different thermal regime than both beaver ponds and backwaters. The mean daily temperature that juveniles experienced in spring brooks 06/21/06 through 10/01/06 was significantly colder (mean=8.4 °C, SE=.2 °C) than those experienced in beaver ponds (mean=10.7 °C, SE=.2 °C, p -value<.001) and backwaters (mean=10.4 °C, SE=.2 °C, p -value<.001) (Fig. 15A). During the fall, winter, and into early-spring (10/01/06-06/01/07) spring brooks were significantly warmer than beaver ponds and backwaters (p -value<.001 for both) (Fig. 15A). During the same time periods, beaver ponds and backwaters had between 200 and 244 more cumulative degree days than spring brooks and between 199 and 230 less cumulative degree days than spring brook rearing juveniles (Fig. 15B).

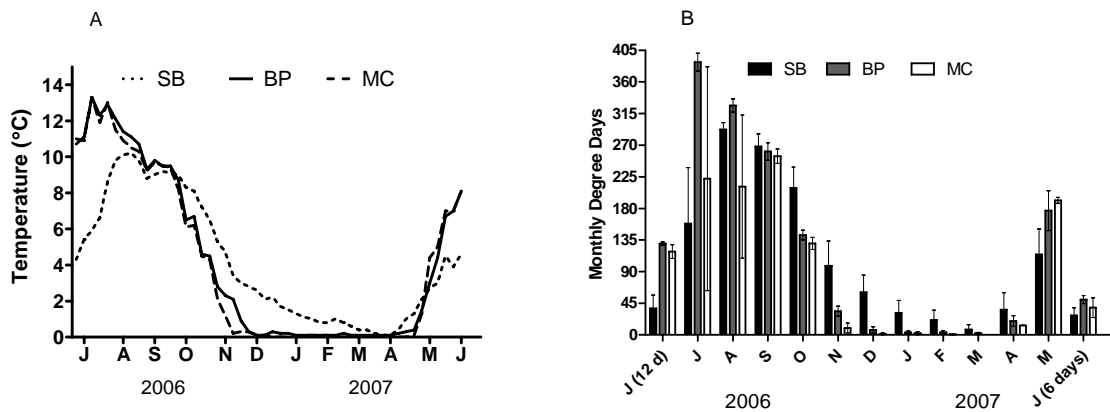


Fig. 15. (A) Monthly 7-day average of the average mean daily temperatures and (B) average monthly degree days for spring brook (SB) (n=3), beaver pond (BP) (n=5), and backwater (BW) (n=2) juvenile rearing sites. Note: Temperature loggers from the main channel were used for BW comparison to SB and BP. Error bars are \pm one standard error of the mean.

Objectives 6: Length Comparisons Between Floodplain Rearing Juveniles in the Fall and Ocean Migrating Smolts the Following Spring and Juvenile Density Expansions

Size of smolts versus fall YOY

A total of 655 smolts were caught during a 36 day period by USGS personnel operating smolt traps at the USFWS weir site. As stated above, the first smolt was caught on 04/26/07 and peak catch (104) was on 05/18/07 and 30 smolts were caught on the 05/31/07 (last day of trap operation). All smolts were 1+ year old fish with a mean fork length of 68 mm (range 55 to 84 mm, n=121) (Fig. 16), had met the 50 mm minimum size range for 100% saltwater survival (Heifetz et al. 1989), and were within the range (54-203 mm) of 1-3 year old lake-type smolts (reviewed by Burgner 1991; Koenings et al. 1993).

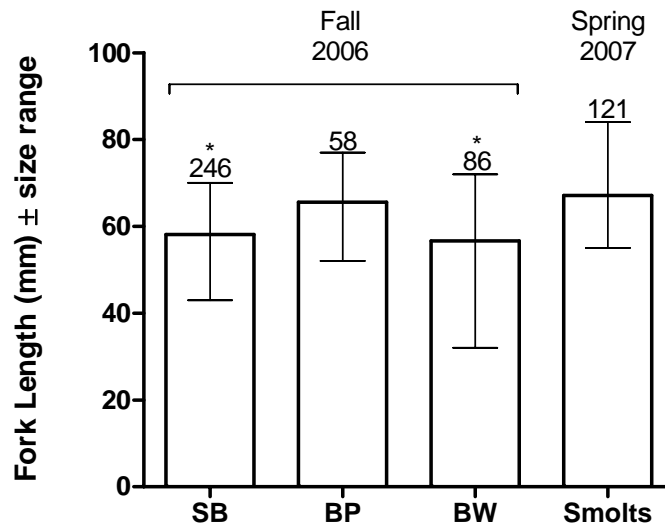


Fig. 16. Mean fork length comparisons between juvenile sockeye rearing in spring brook (SB), beaver ponds (BP), and backwaters (BW) in the fall of 2006 to smolts (1+ year old sockeye juveniles migrating downstream to the ocean) that were caught in the USGS Kwethluk River smolt traps in the spring of 2007. Note: The numbers above the size range bars represent the number of fish captured and measured in each habitat type and the number of smolts that were measured during the smolt trapping operation at the USFWS weir. Data provided by S. Burril, USGS, Alaska Science Center. Note: (*) p -value < .001.

Juveniles rearing in beaver ponds in the fall had attained smolt size (>99%) and were not significantly smaller in mean length than smolts captured the following spring, however smolts were significantly larger than spring brook and backwater rearing YOY in the fall (Fig.16). On the contrary, we compared the length frequency distributions for fall YOY spring brook and backwater rearing juveniles and 76% of spring brook and 74% of backwater rearing juveniles had reached smolt size in the fall. These results suggest that fish rearing in all floodplain rearing habitat types had relatively high over-winter survival.

Fall juvenile density expansion

By expansion of density data to total habitat area quantified from the remote sensing we estimated that there was an average of 136,466 juvenile sockeye rearing in spring brooks, 23,909 juvenile sockeye rearing in beaver ponds, and 5,336 juvenile sockeye in rearing in backwaters in the fall of 2006. Based on our age analysis of adults, juveniles rear in the Kwethluk for at least one year, thus, there were a lot more juvenile sockeye rearing in the flood plain in the fall than was caught by the smolt trapping operation in the following spring. Our estimates suggest that floodplain habitats could be responsible for a larger proportion of the total smolt production and that there were probably more smolts than what was captured.

Based on our study reach wide population estimates above and if over-winter survival was between 10% and 26%, the total estimated number of ocean migrating juveniles in 2007 from the SaRON study reach would be between 16,571 and 43,085 smolts (Koenings and Kyle 1997). Likewise, 92% of the measured smolts were at or above the size threshold of 60 mm in length which has been found to be a size threshold that has a smolt-to-adult survival rate of 13% (Koenings et al. 1993). Based on this survival rate and assuming that smolts had meet that size range, between 2,154 and 5,601 adults would return to the Kwethluk River from smolts produced in the SaRON study reach. These estimates of returning adults are close to the returns that are counted during the USFWS weir operations (refer to Table 1) even though our estimates are only from riverine sockeye in a relatively short section of the Kwethluk River. Our estimates

suggest that more sockeye are being produced than is currently counted by USFWS weir operations and commercial and subsistence harvest levels may have a larger impact on sockeye populations than is currently recognized.

DISCUSSION

The diversity and abundance of lateral flood plain habitats within the Kwethluk River clearly proved to be important for spawning and rearing riverine sockeye. We found that adult riverine sockeye move throughout the entire river system, but spawn exclusively in off-channel spring brook and side channel habitats, where as in the two other riverine sockeye studies, spawning occurred in the main channel, terrace tributaries, side channels, and upland sloughs (Lorenz and Eiler 1989; Eiler et al. 1992). Within the SaRON study reach, over 50% of the available off-channel habitat was composed of spring brooks and side channels. These results show that there is an abundance of riverine spawning habitat available throughout the Kwethluk River and overall a lot more spawning habitat for riverine sockeye compared to lake-type sockeye.

In the Taku River, juvenile sockeye were primarily found rearing in main channel sloughs, tributary mouths, beaver ponds, and upland sloughs of the river flood plain (Murphy et al. 1989). However, we found riverine sockeye reared exclusively in spring brooks, beaver ponds, and backwaters. These habitats made up over 70% of the available off-channel habitat and within the SaRON study reach, there is over five times more river rearing habitat (907,440 m²) than the lake rearing habitat (170,000 m²). However, in 2007 another upper Kwethluk spring-fed lake was found to support lake-type sockeye (M. McPhee, Flathead Lake Biological Station, personal communication) and the total lake rearing habitat may be slightly underestimated.

Our results showed that lake-type sockeye spawned in the alluvial fans and outlets streams of Boundary Lakes, which has been shown for many lake-type populations (c.f., Burgner 1991). Within spawning research sites, 100 % of riverine and 85 % lake-type sockeye redds were constructed in areas dominated by hyporheic-groundwater, which has also been found by others, to be a key attribute of riverine (Lorenz and Eiler 1989) and lake-type (e.g., Foerster 1968) spawning habitats. However, sockeye have been

found to spawn in areas that more dependent in wave action than upwelling groundwater in lakes (Leonetti 1997).

We found no correlation between the water depth and velocity where riverine sockeye constructed redds which as been reported by others (Hoopes 1972; Burgner 1991), but water depth was probably a contributing factor in the high bear predation in the Boundary Lake outlet. We did not see much variation in the sediments used in redd construction between sites, although the D50 found in sockeye redds were within the size range found in other lake-type sockeye studies (reviewed by Keeley and Slaney 1996). But, lake-type sockeye have been found to spawn in a variety of sediment types, ranging from coarse granitic sand to large boulders, where in sockeye do not build a redd and simply deposit their embryos in sand or crevices between large boulders (Foerster 1968; Kerns and Donaldson 1968; Olsen 1968). Thus, sockeye can virtually spawn in any type of bed-sediment and in some cases, excavated areas where the stream bed was composed of 100% fine sediments to find upwelling areas. These results suggest that water depth, water velocity, and bed-sediments are not the key habitat attributes that determine redd placement by sockeye but rather a function of what is available within habitats dominated by upwelling hyporheic-groundwater. We and others (e.g., Baxter and Mcphail 1999; Baxter and Hauer 2000; Geist 2000; Geist and Dauble 1998) suggest that surface water-groundwater exchange should be included when assessing habitat suitability, conservation, and restoration for sockeye and other salmonid spawning habitats in rivers and lakes.

The water chemistries between redds and areas adjacent to redds in any riverine or lake-type spawning sites did not vary considerably. All redds contained levels of DO and pH that were above the 5.0 mg·L⁻¹ and 4.5 lethal levels found for salmonids (Crisp 1993). Furthermore, we showed that riverine and lake-type sockeye did not spawn in areas with downwelling surface water-groundwater exchange. These results suggest that spawning riverine and lake-type sockeye do not select spawning habitat at a microscale, but rather at a larger, more reach scale. Specific conductance readings taken in riverine sockeye redds and in the surface water, showed that the upwelling groundwater in redds was closer to surface water than to phreatic groundwater of the alluvial aquifer (Geist and Dauble 1989; Geist et al. 2002). These results suggest that the hyporheic-groundwater

flow paths within spawning channels were probably relatively short and predominantly recharged by the main channel.

The benefits of upwelling groundwater to incubating embryos, has been documented in salmonids (Sowden and Power 1985; Leman 1992; Curry et al. 1995; Cope 1996; Baxter and McPhail 1999). In 1999, Baxter and McPhail found that bull trout selected areas of upwelling groundwater and that these areas provided consistently higher over-winter incubation temperatures leading to higher over-winter survival. Although, we couldn't extensively document the temperature patterns throughout the incubation period in riverine or lake-type sockeye redds, the few iButtons that did continue recording into the winter, suggests the same temperature pattern. If floodplain intergravel redd temperatures remained at 4.0 °C throughout the incubation period, than riverine sockeye embryo survival to emergence would be around 40 to >96 % (Murray and Mcphail 1988; Beacham and Murray 1989) In general, some spring brook spawning and rearing sites were over 6 °C warmer than the main channel during the winter and never dropped to 0 °C, suggesting that both riverine sockeye embryos and juveniles in these sites may have higher over-winter survival than main channel spawning salmonids, during the harsh winter conditions of southwestern Alaska.

We found that riverine sockeye redds had higher temperatures and an increased number of degree days than lake (lake-type sockeye) redds however, the rate of embryonic development is not constant in relation to temperature (Aldering and Velsen 1978). Sockeye embryos have evolved incubation strategies that adjust to declining temperatures and compensate by increasing development rate per unit of temperature decrease (Brannon 1987). Thus, with the offset of spawning time between riverine and lake-type sockeye we would expect lake-type sockeye embryos to compensate for the drop in temperatures and emerge nearly a month earlier. This difference in emergence time may have some explanation for the increased size that we documented in lake rearing sockeye compared to spring brook rearing sockeye in the summer.

Scale analysis from adults confirmed that both riverine and lake-type sockeye over-wintered in the Kwethluk and that floodplain rearing sockeye were indeed riverine and not sea-type. The mean lengths of floodplain rearing juveniles in the fall were nearly the equal to (or greater than) what Murphy et al. (1989) found during their flood plain

habitat surveys of the lower Taku River (mean=58 mm) and what Robins et al. (2005) showed for over 40 years of lake-type sockeye data from Lake Aleknagik, Alaska. Juveniles rearing in beaver ponds and some backwaters were considerably larger than springbrook rearing juveniles. However, because we did not find any adults spawning in these habitats, this could be attributed to a difference emergence time, giving older age (in days or potentially weeks) juveniles a growth advantage over spring brook juveniles that emerged later. Nonetheless, springbrook rearing juveniles had an absolute growth rate in length of .23 to .27 mm · d⁻¹, showing that sockeye rearing in spring brooks grow very rapidly and reached sizes similar to backwater and beaver ponds in the fall, even though they may emerge later.

The temperatures in all habitat types were within the 5-17 °C “zone of efficiency” for >20% conversion of food to flesh found by Brett (1971a) for sockeye rearing under constant temperatures. However, we found that beaver ponds and backwaters had higher water temperatures during the summer and were closer to the optimum growth efficiency of 11.5 °C (Brett 1971a), but dropped to 0 °C for most of the winter compared to spring brooks. These results suggest that spring brook rearing juveniles might be able to feed and grow more during winter and may have higher over-winter survival than fish in other habitat types.

The lengths and weights of sockeye smolts that rear in large nursery lakes around the Pacific Rim are highly variable, but the lengths all of the Kwethluk smolts that were measured in 2007 were within the range for age 1 and 2 lake-type smolts (cf., Burgner 1991). Likewise, the mean length of Kwethluk River sockeye smolts were nearly the same mean length (65 mm) and within the range (45 to 88) that was reported by Murphy et al. (1988) for Taku River smolts. Moreover, over 90% of smolts were at or above the 60 mm size threshold size that has been found when Alaska sockeye lakes are believed to be at carrying capacity (Koenings and Kyle 1997) and leads to a mean smolt-to-adult survival rate of 13% in northern latitudes (Koenings et al. 1993). These results suggest that both riverine and lake-type juveniles reach a size range during their first year of growth that produces smolts that have a high chance for saltwater survival.

Lake-type sockeye are considered a specialized predator, preying predominantly on zooplankton as juveniles and make copepods and cladocerans the mainstay of their

diet (Forester 1968; Eggers 1978; Burgner 1991). The productivity and decline of lake-type populations has been linked to the abundance of zooplankton populations in sockeye nursery lakes (e. g., Burgner 1991; Koenings and Kyle 1997). On the contrary, this study is the first to describe and quantify the diet of river rearing sockeye and our results showed that riverine sockeye are more of an opportunistic predator, feeding on a variety of invertebrate prey. Yet, floodplain habitats also provide sockeyes preferred prey and zooplankton is utilized by multiple species of salmonids rearing in floodplain habitats (T. Tappenbeck, unpublished data). There can be up to seven different species fish rearing in one site, with total fish densities ranging from 1.4 to 4.6 fish · m⁻². It may be this opportunistic feeding strategy that allows sockeye to coexist and thrive within these habitat types, in the face of substantial interspecific competition for food resources.

Riverine populations have higher genetic diversity and lower population structure than lake-type populations (Gustafson and Winans 1999, Beacham et al. 2004). These findings have led some to hypothesize that riverine sockeye are the primary colonizing form of the species and play a dominant role in sustaining sockeye populations in dynamic glacial systems (Wood et al. 1987; Wood 1995; Wood 2007). Genetic and population structure analysis by McPhee et al. (2008, submitted) on Kwethluk sockeye discussed herein revealed three pertinent things: 1) riverine populations did indeed have higher genetic diversity and weaker population structure than lake-type populations; 2) estimates of *N_e* (effective population size) were not primarily responsible for the differences in population structure suggesting, increased straying of riverine populations; 3) riverine populations were more closely related to riverine populations from the Taku River, British Columbia, Canada than the lake-type populations within the same catchment, suggesting that lake-type and riverine sockeye may have colonized the Kwethluk River separately or that lake-type populations may have branched off from the colonizing riverine population.

Our study coupled with the genetic results of this companion study underscores the importance and ability of riverine sockeye populations to thrive within the dynamic floodplain landscapes of large rivers. Moreover, the alteration of spawning and rearing habitat by beaver is prevalent throughout the catchment. We observed beaver's damming spring brooks that were used in previous years by spawning riverine sockeye and in one

case beaver's dammed a spring brook after sockeye had spawned (T. Tappenbeck, personal observation). However, in the following year juvenile sockeye were documented rearing in the newly created beaver pond. Likewise, in 2006, beavers built a dam that partially blocked the Boundary Lake outlet and limited lake spawning. While, in 2007, beavers completely dammed the outlet of Boundary Lake and no adults were observed spawning within the lake (M. McPhee, Flathead Lake Biological Station, personal communication). Thus, the behavior of beavers and the heterogeneity of floodplain habitats in the Kwethluk, may drive small scale colonization events where by, roving populations of riverine sockeye annually search for new habitats to spawn. Where as, lake-type sockeye have high site fidelity and home tightly to the Boundary Lakes in which they reared. This may prove to be detrimental to lake-type populations when lake spawning and rearing habitats become unavailable or decrease in productivity (Schindler et al. 2005) and it may be the riverine life history strategy that allows sockeye populations to persist in rivers with dynamic floodplains and ecosystem engineers.

Sockeye salmon have evolved life histories that thrive in the complex habitats of large flood plain rivers. Lake, river, and sea -type life histories can be found within the same catchment (Wood et al. 1987; Murphy et al. 1997) and over 50% of the rivers around the Pacific Rim are large complex floodplain river systems (M. Luck, Flathead Lake Biological Station, unpublished data). Thus, the dynamic landscapes of these river systems provide opportunities for life history and genetic diversity, allowing multiple populations with distinct life histories strategies, to coexist within the same river system. Life history diversity is a natural advantage in the face climate and other environmental changes that could otherwise cause extinction (Schindler et al. 2003). We conclude that riverine sockeye take advantage of the complexity of large river systems and that floodplain habitats are key spawning and rearing habitats for this species. This life history strategy may more important in sustaining sockeye salmon populations throughout the Pacific Rim than is currently acknowledged.

RECOMMENDATIONS FOR FUTURE STUDY

Our study showed that lateral floodplain habitats are important spawning and rearing habitats for sockeye salmon in the Kwethluk River. We recommend that fisheries managers obtain a better understanding if how many river systems within the Kuskokwim River catchment and throughout the Pacific Rim, support riverine sockeye populations. In 2006, the Commercial Fisheries Division of the Alaska Department of Fish and Game (ADF&G) began an upper catchment wide radiotelemetry study to investigate which upper Kuskokwim River tributaries sockeye salmon returned to spawn. They found that a majority of the upper Kuskokwim River sockeye were returning to the Holitna River (which has no nursery lakes) and Telaquana Lake (of the Stony River catchment), which supports a large lake-type population (Sara Gilk, ADF&G, personal communication). This research began because of our observations and work on the Kwethluk River and the fact that in 2005 a tributary of the Holitna River, the Krogrukluk River had record returns of over 37,000 sockeye (Jasper and Molyneaux 2007). The work of ADF&G and SaRON, which is expanding to other river systems around the Pacific Rim, will help determine the overall contribution of riverine populations to the total sockeye salmon production in the Kuskokwim River and around the Pacific Rim. We recommend that both riverine and lake-type sockeye populations be separately managed and monitored during commercial and subsistence harvests. While, completing detailed studies of the spawning and rearing ecology of riverine sockeye within the Kuskokwim River and other rivers around the Pacific Rim.

In river systems, such as the Kwethluk River, understanding how growth rates and accumulated energetic reserves or nutritional condition (i.e., stored lipids) available for over-winter survival and smoltification of juvenile riverine sockeye compare to juvenile lake-type sockeye are important to continue to understand how floodplain rearing habitats compare in productivity to lake rearing habitats. Our scale analysis of Kwethluk River adults showed that both riverine and lake-type sockeye reared in the Kwethluk River for a least one year. However, juveniles migrate to the ocean before we begin field research in the spring. We recommend that (1+) year-old ocean migrants be captured during USGS smolt trap operations. Scales and otoliths should be collected from a subsample of

migrating fish and otolith microchemistry analysis should be conducted to determine where each fish reared (lake or river), based on the water chemistry analysis (or signature) of the Boundary Lakes and floodplain habitats. Once, microchemistry analysis is completed and fish are sorted into their respective rearing habitats and life history types, an analysis of nutritional condition and growth rates can be determined for riverine and lake-type juveniles.

We observed that once sockeye salmon spawned in spring brooks and side channels dominated by ground water, an apparent release of nutrients ensued and there was a noticeable increase of algae on rocks in sockeye redds. We recommend a study into how sockeye and other species that spawn in off-channel habitats dominated by groundwater upwelling, facilitate the release of nutrients by disturbing the bed-sediments, thus making more nutrients available to aquatic and terrestrial plants and animals. This study would increase our understanding of how salmon function as ecosystem engineers. It may be that salmon increase the release of nutrients from the ground water or hyporheic water that would otherwise be released very slowly through normal hydrologic processes. Likewise, it may be that sockeye and other species that spawn in off-channel habitats may directly spread MDN throughout the flood plain, rather than fall flooding, which may occur after peak salmon die-off. Thus, bringing nutrient rich flesh and eggs to aquatic and terrestrial organisms that would otherwise be obtained from indirect pathways (e.g., surface water-groundwater interactions and through food web transfer) and potentially increasing the overall productivity off-channel habitats.

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