

AN ABSTRACT OF THE THESIS OF

Dirk W. Lang for the degree of Master of Science in Fisheries Science presented on June 13, 2003.

Title: The Influence of Fall-Spawning Salmon on Growth and Production of Juvenile Coho Salmon Rearing in Beaver Ponds on the Copper River Delta, Alaska.

Abstract approved: Redacted for privacy  
  
Gordon H. Reeves

This thesis examined the influence of fall-spawning coho salmon on the density, growth rate, body condition, and survival to outmigration of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska. During the fall of 1999 and 2000 fish rearing in ponds that received spawning salmon were compared to ponds that did not receive spawners, and to ponds that were artificially enriched with salmon carcasses and eggs. Juvenile coho salmon responded variably to fall-spawning salmon. There were no consistent patterns associated with the two naturally occurring pond types (spawning vs no spawning). In some ponds, fall-spawning salmon increased growth rates and improved the body condition of juvenile coho salmon. Enrichment with salmon carcasses and eggs significantly increased growth rates of fish in non-spawning ponds. For some ponds, the relative influence of spawning and enrichment on body condition depended on fish size. There was no evidence that the influence of fall-spawning resulted in greater smolt production. Fall-spawning salmon provide important food resources that can benefit juvenile coho salmon rearing in beaver ponds on the Copper River Delta. However, other factors such as nutrients from riparian vegetation and catchment characteristics that control hydrology and thermal regimes are important to coho salmon smolt production.

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The Influence of Fall-Spawning Salmon on Growth and Production of Juvenile Coho  
Salmon Rearing in Beaver Ponds on the Copper River Delta, Alaska.

by  
Dirk W. Lang

A THESIS

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## CONTRIBUTION OF AUTHORS

Dr. Jim Hall assisted with data collection during the field season of 2000. He was also involved in the writing and editing of Chapter 2.

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# The Influence of Fall-Spawning Salmon on Growth and Production of Juvenile Coho Salmon Rearing in Beaver Ponds on the Copper River Delta, Alaska.

## Chapter 1—Introduction

The spawning and death of semelparous anadromous Pacific salmon (*Oncorhynchus* spp.) is recognized as an integral ecological process in freshwater ecosystems throughout the North Pacific Rim. Studies have revealed that salmon spawners play a role in the primary productivity of streams (Richey et al. 1975; Wipfli et al. 1998) and in population dynamics and growth of secondary consumers (Wipfli et al. 1999), including juvenile salmonids (Eastman 1996; Bilby et al. 1998; Wipfli et al. 2003). Although studies have focused on the individual components involved in these processes, there is still much to be learned about the ecological relationships and consequences of spawning salmon (Gende et al. 2002).

Annual migrations of spawning salmon can bring a large amount of nutrients to freshwater ecosystems, and these salmon-derived nutrients are incorporated into freshwater food webs, including fishes (Kline et al. 1993; Piorkowski 1995; Bilby et al. 1996). During spawning, eggs that are not buried in the substrate can be consumed by juvenile salmonids. Carcasses can be consumed directly by juvenile fish and by organisms that serve as a food for juvenile salmonids (Wipfli et al. 1998, 2003). Salmon eggs can be a large proportion of the diet of juvenile salmonids (Bilby et al. 1998).

Salmon eggs appear to be an abundant and energy-rich food resource that is made available to stream-rearing fishes during spawning (Bilby et al. 1998; Foote and Brown 1998; Fukushima et al. 1998). Salmon eggs can be especially important for juveniles during the fall or winter months, when fish may be ingesting less food. High quality foods supply more energy per unit ingested. Since metabolic rates are depressed at lower water temperatures and some of the energy ingested above that required for maintenance can be stored, juveniles with access to eggs could experience positive growth during the winter (Weatherley 1972; Brett 1979). Excess energy can also be stored as lipid reserves to be utilized when less favorable conditions of food availability exist (Weatherley 1972), and lipid content of fish at the onset of winter is important in overwinter survival (Toneys and Coble 1980; Cunjak et al. 1998).

Increased quantity and quality of food resources can have direct effects on the growth rates of juvenile anadromous salmon rearing in habitats near spawning salmon. Bilby et al. (1998) observed an increase in weight, condition factor, and density of juvenile steelhead (*O. mykiss*) and coho salmon (*O. kisutch*) in response to the addition of carcasses to a small stream in Washington State. Juvenile salmonids rearing in two streams of the Wood Lake system in Alaska were estimated to increase in weight by 12% and 17% during the peak of sockeye salmon (*O. nerka*) spawning activity (Eastman 1996). Wipfli et al. (2003) recorded increased growth rates of juvenile coho salmon with increasing amounts of salmon tissue and eggs in a mesocosm experiment and found higher growth rates of resident cutthroat trout (*O. clarki*) and Dolly Varden (*Salvelinus malma*) in a stream in Alaska enriched with salmon carcasses.

However, studies that have examined the influence of spawning salmon on growth rates of juvenile salmonids are limited. Most of these studies have been conducted in experimental streams, above natural barriers to migration of anadromous salmon, or in small streams that have been altered by management activities (Bilby et al. 1996; Bilby et al. 1998; Wipfli et al. 2003). The applicability of these results to larger, more complex natural aquatic systems is unknown. It is important to validate experimental results in natural stream environments and to explore potential site/system-specific variability in growth rate and productivity in response to spawning salmon (Gende et al. 2002). This information will be important in future management of local fisheries and will provide a broader scientific understanding of the relationship between spawning salmon and juvenile salmonids (Gende et al. 2002).

Salmon populations in the U.S. Pacific Northwest have declined substantially in recent decades (Nehlsen et al. 1991). As a result, the salmon-derived nutrient linkage has probably been greatly reduced or completely eliminated from many freshwater systems (Cederholm et al. 1999; Gresh et al. 2000). In response to the cultural oligotrophication associated with diminished returns of salmon and salmon-derived nutrients, fisheries managers have begun to apply nutrients or salmon carcasses to aquatic systems as a restoration technique (Johnston et al. 1990; Budy et al. 1998; USDA Forest Service 2001). Nutrient additions can be used as a temporary restoration measure, but they will never replace all of the complex ecological processes associated with natural salmon spawning (Cederholm et al. 1999). Salmon populations in naturally functioning aquatic systems of Canada and Alaska may serve

as important reference systems where the ecological processes associated with spawning salmon can be studied with fewer human impacts. These systems may prove critical to obtaining a more complete understanding of the relationship between spawning salmon and their ecosystems. A better understanding of these processes should ultimately benefit efforts to restore spawning salmon and salmon-derived nutrients to the nutrient-deprived systems in the Pacific Northwest.

The Copper River Delta (CRD), Alaska provides an excellent opportunity to examine the relationship between spawning salmon and stream-rearing juvenile coho salmon in relatively pristine stream systems. Most clear-water streams on the CRD have very large runs of coho salmon during the fall and early winter. Beaver ponds are one of the most dominant freshwater habitats types on the CRD, and these ponds contain depth and cover that provide excellent rearing habitat for juvenile coho salmon (Nickelson et al. 1992; Cunjak 1996). Beaver ponds are depositional habitats that act as sinks trapping sediments, nutrients, and organic material, including salmon carcasses, which are important for sustaining aquatic productivity (Cederholm et al. 1989; Wipfli et al. 1998). Spawning areas on the Delta are quite often directly upstream of beaver ponds, and spawning also occurs within beaver ponds. Therefore, beaver ponds downstream of spawning habitats may be "hotspots" of productivity for juvenile coho salmon because spawning salmon and carcasses are potentially a significant source of food and nutrients that stimulate food webs available to fish rearing in these ponds.

Spawning runs are temporally predictable for a given species within a given stream, and this may have implications for the potential of spawning to influence juvenile salmonid growth. Spawning of coho salmon on the CRD begins in mid to late September and often persists into January. It has been assumed that growth of juvenile salmonids ceases in the late fall because water temperatures are typically lower than 5°C. This temperature is considered the lower limit of growth for salmonids (Elliott 1994). However, the presence of an abundant, high quality food item, coupled with low water temperatures, may offset the effect of low water temperatures and lead to relatively efficient growth at cooler water temperatures (Brett 1971). Fall and winter runs of spawning salmon may supply such food resources and growth opportunities for juvenile coho salmon on the CRD.

Understanding the relationship between spawning salmon and production of juvenile coho salmon on the CRD may provide a great benefit to both the economic community and land managers who wish to sustain healthy populations. Coho salmon provide commercial, recreational, and subsistence opportunities to the local economy. Much of the 3,000-km<sup>2</sup> CRD is public land managed by the USDA Forest Service (2002) and current policy (Alaska National Interest Lands Conservation Act of 1980) mandates that fisheries resources on it be preserved. The major factors influencing coho salmon productivity are currently unknown.

This thesis examines the influence of fall-spawning coho salmon on the growth rate, density, and smolt production of juvenile coho salmon rearing in beaver pond habitats of the CRD. Density, growth rates, and survival to outmigration of juvenile

coho salmon were compared between fish rearing in ponds directly influenced by spawning salmon, ponds that were not influenced by spawners, and ponds that were experimentally/artificially enriched with salmon carcasses and eggs.

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## Chapter 2—The Influence of Fall-Spawning Salmon on Growth and Production of Juvenile Coho Salmon Rearing in Beaver Ponds on the Copper River Delta, Alaska

The transport and delivery of marine-derived nutrients into freshwater streams by spawning salmon (*Oncorhynchus* spp.) is responsible, in part, for the high productivity of coastal Alaskan systems, especially in light of their oligotrophic nature (Mathisen et al. 1988; Kyle et al. 1997). The annual subsidy of nutrients from returning anadromous salmonids may induce a positive feedback loop where increases in productivity of multiple trophic levels lead to increased production of juvenile salmonids in streams (Michael 1995; Schmidt et al. 1998; Wipfli et al. 1998). Consequently, larger numbers of adults should return to spawn as the cycle is completed. Growth and size have important implications in the overwinter survival of stream-rearing juveniles (Smith and Griffith 1994; Quinn and Peterson 1996) and in the ocean survival of smolts (Hager and Noble 1976; Bilton et al. 1982; Holtby et al. 1990). Critical elements of this positive-feedback hypothesis are that juvenile salmonids experience heightened growth rates and greater survival to smolt outmigration due to energy acquired from eggs and carcasses.

Spawning salmon can directly and indirectly impact food availability and growth rates of juvenile stream-rearing salmonids (Bilby et al. 1996; Eastman 1996; Bilby et al. 1998). Carcasses and eggs from spawning salmon supply food and salmon-derived nutrients to freshwater ecosystems, and these nutrients are incorporated into freshwater food webs, including stream-rearing juvenile salmonids (Kline et al. 1993; Piorowski 1995; Bilby et al. 1996). Fish can feed directly on carcasses and eggs

(Bilby et al. 1998). Nutrients from carcasses can also be obtained by fish through the consumption of macroinvertebrates that feed directly on carcasses and on fungi and bacteria that colonize decaying carcasses (Wipfli et al. 1999). Spawning salmon can also increase invertebrate prey availability by their disturbance of streambed substrates and by dislodging benthic organisms (Peterson and Foote 2000).

Salmon eggs can make up a large portion of the diet of juvenile anadromous salmonids and resident trout during spawning (Eastman 1996; Bilby et al. 1998). Eggs are a high calorie food item (Bilby et al. 1998; Foote and Brown 1998), so their consumption can have short-term as well as long-term benefits. Spawning by coho salmon often occurs in the late fall or early winter, when metabolic rates may be depressed because of low water temperatures. A high quality food such as eggs supplies more energy per unit ingested, and some of the energy ingested above that required for maintenance can be stored (Weatherley 1972). The presence of an abundant, high quality food item, coupled with low water temperatures may lead to relatively efficient growth (Brett 1971). The excess energy can be stored as lipid reserves that can be utilized when food availability decreases in the winter (Weatherley 1972).

The relatively unimpacted streams of the Copper River Delta, southcentral Alaska (Delta) provide an excellent opportunity to examine the relationship between spawning salmon and juvenile coho salmon (*O. kisutch*). Most clear-water streams on the Delta have large runs of coho salmon during the fall and early winter. Beaver ponds dominate stream habitats on the Delta and generally have sufficient depth and

cover to provide excellent rearing habitat for juvenile coho salmon (Nickelson et al. 1992; Cunjak 1996). Beaver ponds also act as sinks that trap sediments, nutrients, and organic material, including salmon carcasses, which should be important to aquatic productivity (Cederholm et al. 1989; Wipfli et al. 1999). Therefore, beaver ponds downstream of spawning habitats may be "hotspots" of juvenile coho salmon productivity because spawning salmon and carcasses may stimulate food webs available to fish rearing in these ponds.

The purpose of this study was to examine the influence of fall-spawning coho salmon on the growth rate, density, and smolt production of juvenile coho salmon rearing in beaver pond habitats of the Copper River Delta. Density, growth rate, and survival to outmigration of juvenile coho salmon rearing in ponds directly influenced by spawning salmon were compared to those rearing in ponds without influence from spawning salmon, and to those rearing in ponds that were artificially enriched with salmon carcasses and eggs. Four main questions were the focus: (1) were growth rates and body condition increased during salmon spawning?; (2) were densities and growth rates of juveniles in beaver ponds with access to spawning salmon greater than those without such access?; (3) could growth rates of juveniles in pond without access to spawning salmon be increased through experimental introduction of salmon carcasses and eggs?; and (4) was smolt growth and overwinter survival related to the presence of spawning salmon, carcasses, and eggs? A better understanding of the relationship between spawning salmon and juvenile coho salmon productivity may be important in

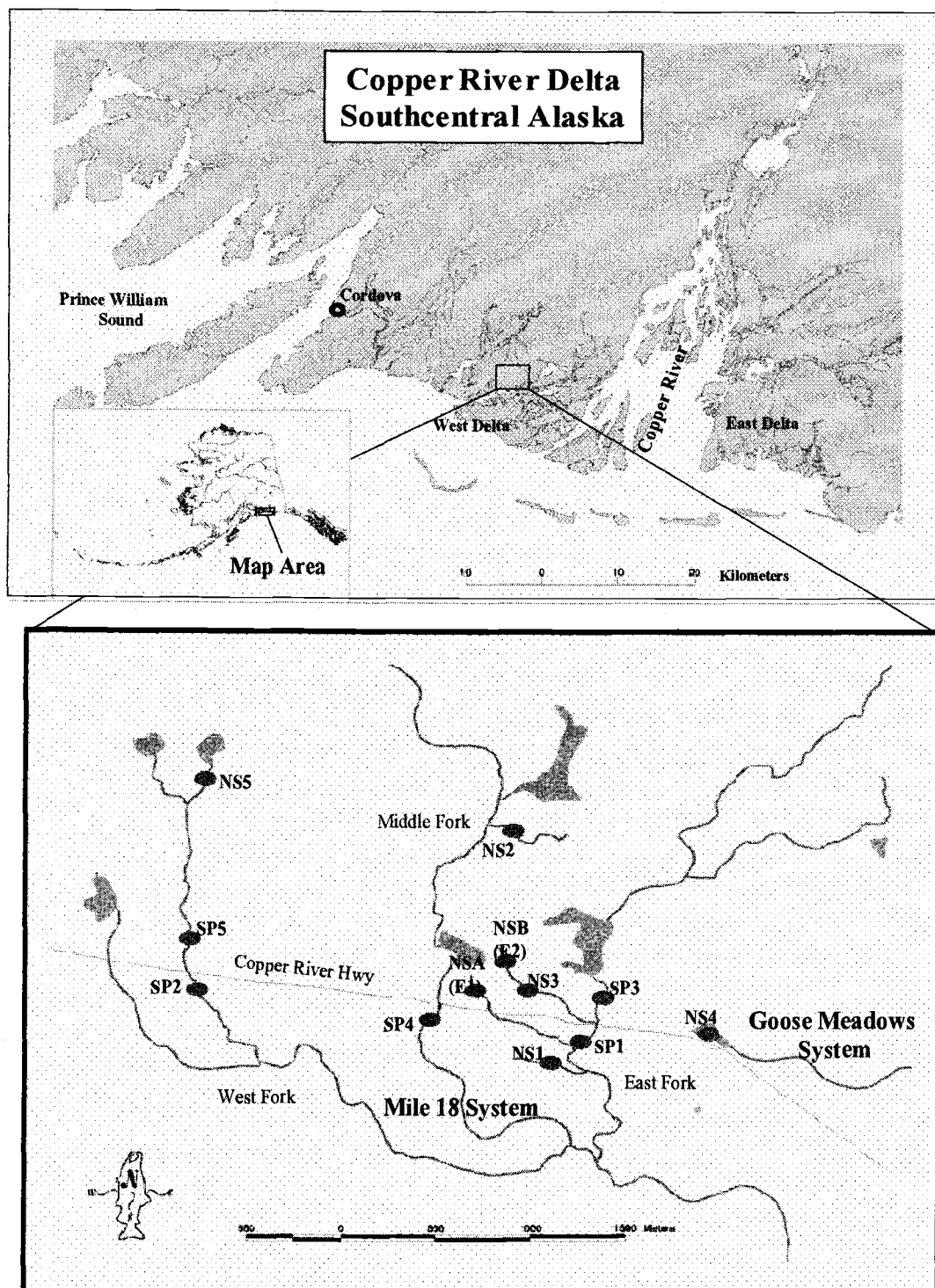
future management of local fisheries and provide valuable insight into the ecological processes associated with spawning salmon in natural systems.

### Study Area

The study was conducted in 12 beaver ponds located in two stream systems on the Copper River Delta, Alaska (Fig.1) in 1999 and 2000. Eleven of the study ponds were in the Mile 18 stream system ( $60^{\circ} 26' N$ ,  $145^{\circ} 20' W$ ) and one pond was located in an adjacent system known as Goose Meadows ( $60^{\circ} 26' N$ ,  $145^{\circ} 19' W$ ; Fig.1). The Mile 18 stream system is a fourth-order coastal floodplain river with a catchment area of approximately  $15 \text{ km}^2$  and 21 km of ephemeral stream channels. Mean stream surface gradient is 1%. The area receives approximately 380 cm of rainfall annually. Mean discharge is estimated at  $7.0 \text{ m}^3 \cdot \text{s}^{-1}$  and wetted widths are approximately 9 m during mean summer flow. The substratum is composed of alluvial gravels and cobbles. The Goose Meadows system is similar in size and other physical stream system characteristics.

The physical characteristics and degree of influence by spawning salmon varied between beaver ponds used in the study (Table 1). Of the 12 ponds, 5 were directly downstream of spawning habitats and, therefore, influenced by spawning (SP1–SP5) while another 5 of the ponds (NS1–NS5) were located in side channels or upstream of spawning areas (Fig. 1; Table 1). Two other ponds that were not

**Figure 1.** Location of the study ponds in two stream systems on the West Copper River Delta, southcentral Alaska.



influenced by spawning (NSA (E1) and NSB (E2)) were artificially enriched with salmon carcasses and eggs during the second year of the study. Pond sizes ranged from 324 to 4,298 m<sup>2</sup> and maximum depths were between 1.0 and 1.8 m (Table 1).

**Table 1.** Characteristics of the 12 beaver ponds and influence from spawning salmon during the fall of 1999 and 2000.

Pond	Pond area (m <sup>2</sup> ) <sup>a</sup>	Max depth (m)	Water temperature during spawning (°C) <sup>b</sup>		Peak spawner count <sup>c</sup>	
			Sept. 15–Oct. 11	Oct. 11–Nov. 8	1999	2000
NSA(E1)	704	1.2	8.3	11.6	0	0
NSB(E2)	1779	1.1	7.8	10.8	0	0
Mean(SE)	1242(538)	1.2(0.1)	8.1(0.3)	5.0(0.2)		
SP1	1588	1.7	6.6	3.6	234	194
SP2	1394	0.97	6.6	3.5	223	271
SP3	1011	NI	6.2	4.4*	no count	200
SP4	4298	1.5	7.8	4.9*	243	136
SP5	3147	NI	7.1	4.6*	87	92
Mean(SE)	2288(620)	1.4(0.2)	6.9(0.3)	4.2(0.3)	197(37)	179(30)
NS1	1432	1.7	7.1	3.7		0
NS2	1231	1.6	5.9	3.5		0
NS3	324	NI	7.2	4.8*		0
NS4	9829	1.5	7.6	4.9*		6
NS5	692	1.8	6.7	4.9*		0
Mean(SE)	2702(1793)	1.7(0.1)	6.9(0.3)	4.4(0.3)		

<sup>a</sup> Pond surface area measured using Geographic Information System (GIS) software.

<sup>b</sup> Mean water temperatures between sample dates during spawning in 2000.

Temperatures were recorded hourly with Onset™ HOBO temperature data loggers placed mid-water column at the deepest location in each pond.

<sup>c</sup> Peak count of spawners and carcasses within ponds and upstream of ponds.

Approximate distance upstream that was included for each site was 100m.

\* Temperature recorders were removed during the week of Nov. 1 rather than the week of Nov 8.

NI = no information collected

The mean number of fish observed during on-the-ground counts of spawning coho salmon in the stream directly above the influenced ponds was 197 and 179 fish in 1999 and 2000 respectively. The non-influenced ponds typically are not directly influenced by spawning salmon, but in some instances a few adult fish will get into these ponds. In 2000, 6 fish were seen spawning in and above pond NS4 (Table 1).

Water temperatures were monitored from July 2000 through August 2001 in six of the ponds (Fig. 2). In 2000, mean water temperatures between sample dates were recorded for all 12 ponds in time periods when salmon spawning occurred (Table 1). During spawning, mean water temperatures were similar between ponds (Table 1). The mean water temperature in pond SP1 was lower than in the other ponds throughout the spring and early summer months (Mar–June).

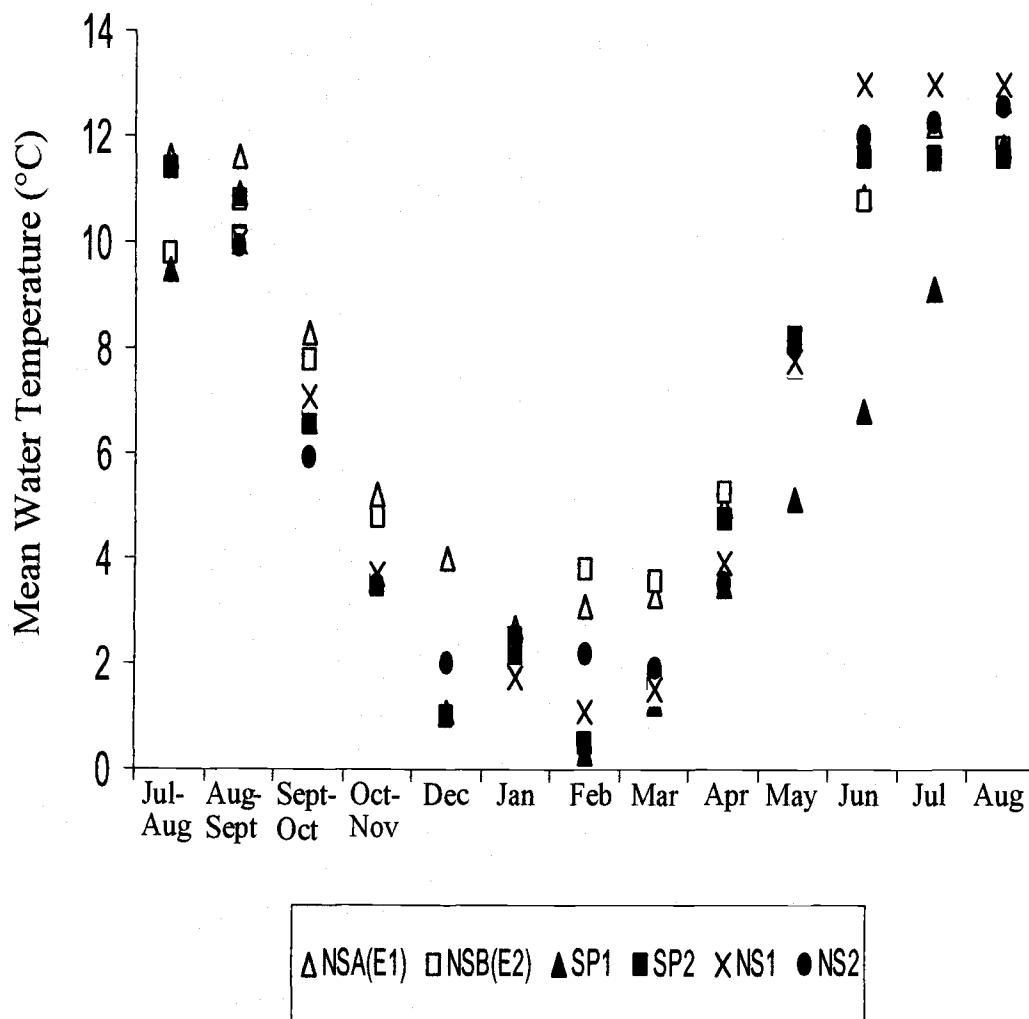
Riparian habitats were similar around the ponds and dominated by Sitka alder (*Alnus sinuata*) and willow (*Salix spp.*). Sweet gale (*Myrica gale*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*) were present to a much lesser degree. The aquatic plant communities were similar in all of the ponds. The dominant species included *Potamogeton spp.*, burr reed (*Zostera spp.*), sedges (*Carex spp.*), and mare's tail (*Hippuris spp.*). Canopy cover was zero on all of the ponds. Pond substrates were predominantly composed of sand, silt, and organic material, but spawning-influenced ponds contained small pockets of gravels and cobbles where salmon spawned.



Age-0 and age-1 coho salmon were present in all the ponds. Three-spined stickleback (*Gasterosteus aculeatus*), slimy sculpin (*Cottus cognatus*), Dolly Varden (*Salvelinus malma*), and coastal cutthroat trout (*O. clarki*) were also present in some ponds.

In 1999 and 2000, adult coho salmon entered these stream systems in early-September and spawning began in the last week of September. Peak counts of spawning salmon in the Mile 18 stream system were made in the third week of October in both years.

**Figure 2.** Mean water temperatures between sample dates over the summer and fall 2000 and over the winter and spring months of 2001 in the beaver ponds with PIT-tagged juvenile coho salmon. All temperatures were recorded with Onset™ HOBO temperature data loggers. The standard error of the mean water temperatures during each time interval in each pond ranged from 0.01 to 0.09. See text for pond codes.



## Study Design and Methods

### Density, Growth Rate, and Body Condition

In 1999, four ponds were sampled monthly beginning the week of August 23 and ending the week of November 17. Two of these ponds (SP1 and SP2 in Fig. 1) were directly downstream of spawning habitats and therefore juvenile coho salmon had access to salmon carcasses, eggs, and other food resources associated with spawning. The other two ponds were located in side-channels or in stream sections above available spawning habitats (ponds NSA(E1) and NSB(E2) in Fig. 1).

In 2000, six ponds were sampled monthly beginning the week of July 5 and ending the week of November 8. Beginning in October 2000, ponds NSA(E1) and NSB(E2) were experimentally enriched with salmon carcasses and eggs. Ponds SP1 and SP2 were sampled again and two ponds that were not influenced by spawning salmon were added to serve as controls to the enrichment (NS1 and NS2 on Fig. 1).

Juvenile coho salmon were captured each month with wire-mesh minnow traps baited with salmon roe. Traps were placed at approximately 10-m intervals in a grid-like fashion throughout each pond. Traps were set three times for 1.0–1.5 hrs to capture fish during each monthly sample. When water temperatures dropped below 6°C trap efficiency declined dramatically and traps were set once overnight in each pond.

Growth rates of juvenile coho salmon were estimated by recapturing fish marked with Passive Integrated Transponder (PIT) tags. Captured fish were

anesthetized with MS-222, measured to the nearest 1 mm fork length (FL), and weighed wet (WW) to the nearest 0.1 g on an analytical balance. During August and September 1999 and July, August, and September 2000, individuals over 60 mm from each pond were PIT-tagged, which gave them an individual identification number. For fish under 60 mm, a sub-sample of 100 fish was anesthetized, weighed, and measured. Thereafter only the length of fish under 60 mm was measured. All captured fish were used to estimate abundance and to formulate length-frequency distributions in the ponds. To identify PIT tags, all juvenile coho salmon over 60 mm were scanned with an AVID™ PIT-tag receiver after the initial August 1999 and July 2000 trappings. The PIT-tag identification number was recorded along with the weight and length of the fish. After processing, all fish were placed into a recovery pen and released upon completion of the last trap set.

Percent weight gain per day was used as a measure of growth for individual recaptured PIT-tagged fish and was calculated with the equation:

$$(1) \quad Gr = (((W_{t+1} - W_t) * W_t^{-1}) * D^{-1}) * 100$$

Where Gr is the relative growth rate expressed as percent of initial weight gained per day over the growth period from capture at time t to recapture at time t + 1,  $W_t$  is the weight of an individual at time t,  $W_{t+1}$  is the weight of an individual at time of recapture, and D is the number of days occurring between time t and time t+1.

The influence of spawning on age-0 coho salmon was examined by comparing the change in mean length between a "before" spawning sample and a "during" spawning or enrichment sample. All age-0 coho salmon captured in the September and

November samples in both years from each pond were used in this portion of the study. In 2000, six new ponds were sampled in addition to the ponds containing PIT-tagged fish. Three of the new ponds were naturally influenced by spawning and are referred to as Spawn 3, Spawn 4, and Spawn 5 (SP3–5 in Fig. 1). The other three ponds were not influenced by spawning salmon and are referred to as No Spawn 3, No Spawn 4, and No Spawn 5 (NS3–5 in Fig. 1). Age-0 coho salmon were captured from the six new ponds using similar methods employed in the original ponds except that fewer traps were used (approximately 60% less effort) and only a random subsample of 200 fish ( $100 < 60$  mm and  $100 > 60$  mm) was taken from the total number captured. In all the ponds, scale samples were taken from 10 fish in each 10-mm size class. Scales were taken from a location just behind the dorsal fin and above the lateral line. Scale samples, along with length-frequency histograms, were used to determine age distribution and separate the age-0 cohort for each pond and sample period.

All juvenile coho salmon  $> 60$  mm captured from the ponds in September and November were used in a weight-length regression analysis to compare the change in body condition of fish between a “before spawning” and a “during spawning” sample (Eastman 1996). The time and methods of capturing these fish were the same as for the change in length of age-0 coho salmon.

#### Experimental Enrichment with Salmon Carcasses and Eggs

Carcass and egg introductions attempted to mimic timing and magnitude of the natural spawning processes occurring in the Mile 18 stream system. During spawning

in 1999 and 2000, field crews conducted weekly on-the-ground escapement surveys and recorded the number of spawners occurring within and directly upstream of ponds SP1 and SP2. The total number of spawning salmon within and above the ponds and the carcasses per area of pond were calculated at various times throughout the spawning run. Estimates from 1999 were used to calculate the expected number of carcasses needed for the introduction in 2000. Surveys conducted in 2000 were used to evaluate escapement numbers and timing of the run. Introduction of salmon eggs and carcasses to ponds E1 and E2 began in the first week of October 2000 (Table 2). We collected 77 returning adult coho salmon from the Mile 18 stream system by hook-and-line. Fish were measured from mid-eye to tail fork to the nearest 1 cm and weighed to the nearest 0.1 kg. Egg skeins were removed from females if present and separated with a 2-cm mesh screen. Measured portions of eggs were placed in zip-lock bags and stored in a refrigerator until introduction into the ponds. One female provided about 0.67 L of eggs after separation. Storage was typically 2–3 days. The remaining whole fish were either frozen or placed directly into the ponds in a random fashion from a small boat. Frozen fish were thawed and placed randomly into the ponds at later dates. An additional 73 post-spawned carcasses were collected by hand from the Mile 18 stream and placed directly into the ponds or frozen for introduction at a later time. Mean weight of the spawners captured by hook-and-line methods were used to estimate biomass of the 73 carcasses. Some of the fish captured by hook-and-line methods were post-spawned but many were not.

**Table 2.** Schedule of introduction, volume of eggs, and number and biomass of carcasses added to the enriched ponds in 2000. The volume of eggs was added throughout the entire pond at several times over the course of the week. Carcasses were introduced at one time during the week and randomly distributed throughout the ponds.

<u>Week of Spawning Run</u>	<u>Volume of eggs (Liters)</u>		<u>Added number of carcasses and biomass (kg)</u>	
	<u>Enriched 1</u>	<u>Enriched 2</u>	<u>Enriched 1</u>	<u>Enriched 2</u>
1 (10/01/00 - 10/07/00)	2	4	0	0
2 (10/08/00 - 10/14/00)	3	7	4 (15.5)	11 (42.7)
3 (10/15/00 - 10/21/00)	3	6	6 (23.3)	14 (54.4)
4 (10/22/00 - 10/28/00)	2	4	8 (31.1)	20 (77.7)
5 (10/29/00 - 11/04/00)	1	2	16 (62.2)	26 (101)
6 (11/05/00 - 11/11/00)	1	2	13 (50.5)	25 (97.7)
7 (11/12/00 - 11/18/00)	0	0	3 (11.7)	4 (15.5)
<b>Total</b>	12	25	50 (194)	100 (389)

### Overwinter Growth Rate and Survival to Outmigration

Fisheries personnel from the Cordova Ranger District (CRD) operated a smolt weir from April 18 to July 2, 2001 at the mouth of the Mile 18 stream system. The weir was constructed of several 4-m long aluminum panels with pickets and 1.25-cm diamond mesh Vexar™ screens fastened to the panels. Vexar skirts extended past the bottom of the panels and were buried in the stream substrate and overlaid with sandbags. Boat anchors, fence posts, and wooden braces were also used to anchor the weir to the bank and substrate. The weir spanned the entire stream channel in a

downstream-facing V-formation. Migrating fish were funneled to the tip of the V by the weir itself (downstream migrants) or by a vexar funnel supported by fence posts (upstream migrants). Fish were funneled into wooden holding boxes (0.6 x 1.2 m), one on either side of the weir, catching upstream and downstream migrants. The boxes were checked daily during the period of operation. All outmigrating juvenile coho salmon were collected from the downstream box and processed at a station on the stream bank adjacent to the weir. These fish were scanned with an AVID™ PIT-tag scanner. Tagged fish were anesthetized with MS-222, weighed to the nearest 0.1g on an analytical balance, and measured (FL). After recovery, the fish were released 50 m downstream of the weir. Juvenile coho salmon captured in the upstream box were scanned for PIT tags and then released 50 m upstream of the weir. Only PIT-tagged individuals were weighed and measured prior to release from the upstream box. Overwinter growth was calculated over the time period from September to smolt outmigration with percent weight gain per day (equation 1). This time period would include the influence of spawning, if present, and the overwinter and spring growth prior to outmigration. Survival to smolt outmigration was calculated as the percentage of tagged fish that were recaptured at the weir from the total number tagged in each pond during the previous summer and fall.

### **Statistical Analyses**

Abundance of juvenile coho salmon rearing in the ponds was estimated with the removal method when water temperatures were above 6°C and the multiple trap-



set schemes were incorporated (Zippin 1958; Bryant 2000). By October in both years, water temperatures had dropped below 6°C and minnow traps were set out once overnight. Thus, no depletion population estimates were computed after September.

The computer software Program MARK was used to obtain population estimates for juvenile coho salmon with the removal method (Zippin 1958; White and Burnham 1999). Program Mark performs a  $X^2$  goodness-of-fit test to check the assumption of equal probability of capture required in the removal model (White et al. 1982). Failure of the  $X^2$  goodness-of-fit test can result from having a high probability of capture on the first occasion relative to the other occasions, in which case estimates tend to underestimate the true abundance (White et al. 1982; Riley and Fausch 1992). A poor depletion (greater or equal numbers captured on successive occasions as compared to the first occasion) can also be responsible for failure of  $X^2$  goodness-of-fit tests. A poor depletion tends to overestimate true abundance (White et al. 1982).

Mean growth rates of recaptured PIT-tagged fish between monthly samples were calculated for each pond, resulting in three and four time periods in 1999 and 2000, respectively. Fish had to be captured in both the beginning and ending dates of a monthly time period to be included in the analysis of growth for that period. For example, to be included in the August–September estimate of growth, a PIT-tagged fish had to be captured in the August and in the September samples in a given pond. Few fish were recaptured in November that had also been captured in October; therefore, we did not use the October–November time period in our analysis. However, sufficient numbers of fish were recaptured in November that had been

captured in September, so this time period was used to compare growth. Spawning and enrichment began in mid-September and at the start of October, so the time periods from September–October and September–November were considered time periods “during spawning” while the ones “before spawning” included August–September 1999, and July–September and August–September 2000.

The response of growth rate to spawning and enrichment within individual ponds was compared with *t* tests. In this analysis, the mean growth rates of fish in the August–September time period were compared to growth during the September–October and September–November period within each pond. Wilcoxon rank-sum tests were performed with the same data and were in agreement with the *t* test results. The results of the *t* test with unequal variances were reported if the Brown-Forsythe’s Test for homogeneity in variances was significant ( $p < 0.05$ ).

Weight-length regressions were used to compare body condition of juvenile coho salmon  $> 60$  mm between spawning periods in 2000 (Cone 1989). A test for significance between “before spawning” (September) and “during spawning” (November) samples within each pond was done with the multiple regression model:

$$(2) \text{Ln Weight} = \beta_0 + \beta_1 \text{Ln length} + \beta_2 \text{sample time} + \beta_3 \text{Ln length} * \text{sample time}$$

where  $\beta_0$  was the intercept determined by the regression,  $\beta_1$  was the slope of the regression,  $\beta_2$  was a coefficient for the indicator of sample time (September vs November), and  $\beta_3$  was the coefficient of the interaction term. If the slopes were not significantly different (test for  $\beta_3 = 0$ ;  $p > 0.05$ ), this variable was dropped from the

model and the parallel lines model was used to test for the significance differences between samples (before vs during) (Eastman 1996).

## Results

### Density

The estimated densities of fish > 60 mm were similar between pond types (Table 3). In September of 2000, going into the spawning period, the mean estimated densities of fish > 60 mm were between 0.23 and 0.25 fish/m<sup>2</sup> (Table 3). In general, fish density (> 60 mm) was estimated to increase over the sample dates in both years; however most increases were small and may have resulted from recruitment of fish from the 50-mm size class. Two exceptions were in pond NS1, where estimated density nearly doubled between August and September 2000 and in pond NSB(E2), where estimated density nearly tripled between the August and September 1999 samples (Table 3). A large increase in the total number of fish > 60 mm captured (Table 4), and the length-frequency distributions between sample dates provide additional evidence that fish migrated into these ponds.

There was more variability in estimated densities within and between pond types for fish < 60 mm. We expected that densities of fish < 60 mm would be greater in ponds adjacent to spawning areas because recruitment of age-0 fish should be high and in general this was the case. The estimated mean density of fish < 60 mm in the ponds adjacent to spawning habitats was 3 – 4 times that in the no spawning ponds

**Table 3.** Estimated density (fish/m<sup>2</sup>) of juvenile coho salmon in six beaver ponds during August and September 1999 and July, August, and September 2000. Values are number of fish/m<sup>2</sup> (1 SE).

Pond	1999		July	2000	
	August	September		August	September
<b>&gt; 60 mm</b>					
NSA(E1)	0.28 (0.01)	0.35 (0.003)	No Est.	0.16 (0.01)	0.22 (0.004)
NSB(E2)	0.05 (0.001)	0.14 (0.003)	0.15 (0.004)	0.19 (0.004)	0.28 (0.01) <sup>U</sup>
Mean	0.17 (0.12)	0.25 (0.11)	0.15	0.18 (0.02)	0.25 (0.03)
SP1	0.28 (0.01)	0.40 (0.04) <sup>O</sup>	No Est.	0.14 (0.003) <sup>U</sup>	0.18 (0.05) <sup>U</sup>
SP2	0.29 (0.01) <sup>U</sup>	0.30 (0.01)	0.26 (0.02)	0.23 (0.01) <sup>U</sup>	0.29 (0.02)
Mean	0.29 (0.01)	0.35 (0.01)	0.26 (0.02)	0.19 (0.05)	0.23 (0.06)
NS1			0.17 (0.001)	0.20 (0.01)	0.36 (0.01)
NS2			0.11 (0.01)	0.08 (0.001) <sup>U</sup>	0.10 (0.001)
Mean			0.14 (0.03)	0.14 (0.06)	0.23 (0.13)
<b>&lt; 60 mm</b>					
NSA(E1)	0.18 (0.01)	0.20 (0.01)	2.89 (0.49) <sup>O</sup>	1.43 (0.04) <sup>U</sup>	1.59 (0.02)
NSB(E2)	0.07 (0.001) <sup>U</sup>	0.29 (0.01)	0.39 (0.14)	0.18 (0.01) <sup>U</sup>	0.29 (0.01) <sup>U</sup>
Mean	0.13 (0.06)	0.25 (0.05)	1.64 (1.25)	0.81 (0.63)	0.94 (0.65)
SP1	2.11 (2.60) <sup>O</sup>	1.39 (0.35)	No Est.	0.52 (0.02)	0.88 (0.01)
SP2	0.53 (0.05) <sup>O</sup>	0.26 (0.01)	2.16 (0.32)	0.79 (0.02) <sup>U</sup>	0.85 (0.09)
Mean	1.32 (0.79)	0.83 (0.57)	2.16	0.66 (0.14)	0.87 (0.02)
NS1			No Est.	0.03 (0.01)	0.05 (0.01)
NS2			0.80 (0.07) <sup>O</sup>	0.26 (0.03) <sup>O</sup>	0.28 (0.002)
Mean			0.8	0.15 (0.12)	0.17 (0.12)

No Est. – No estimates obtained as a result of poor depletion (equal or greater numbers captured on successive occasions as compared to the first).

<sup>O</sup> – Estimates may be biased high due to poor depletion.

<sup>U</sup> – Estimates may be biased low due to high proportion of total catch being captured on the first trap occasion.

(Table 3). However, high densities of fish < 60 mm were found in pond NSA(E1) during July, August, and September of 2000 (Table 3).

#### Growth Rate and Body Condition

We tagged 4,609 juvenile coho salmon over 2 years: 1,886 fish in 1999 and 2,723 fish in 2000. The percentage of PIT-tagged fish recaptured in the ponds during monthly sampling varied from 1.0% to 76.8% (Table 4). Recapture percentages tended to be highest in August and September and were lowest in October and November, especially in ponds SP1 and SP2 during periods of spawning (less than 5%). Total number of fish > 60 mm captured during the monthly samples decreased during spawning periods (Table 4).

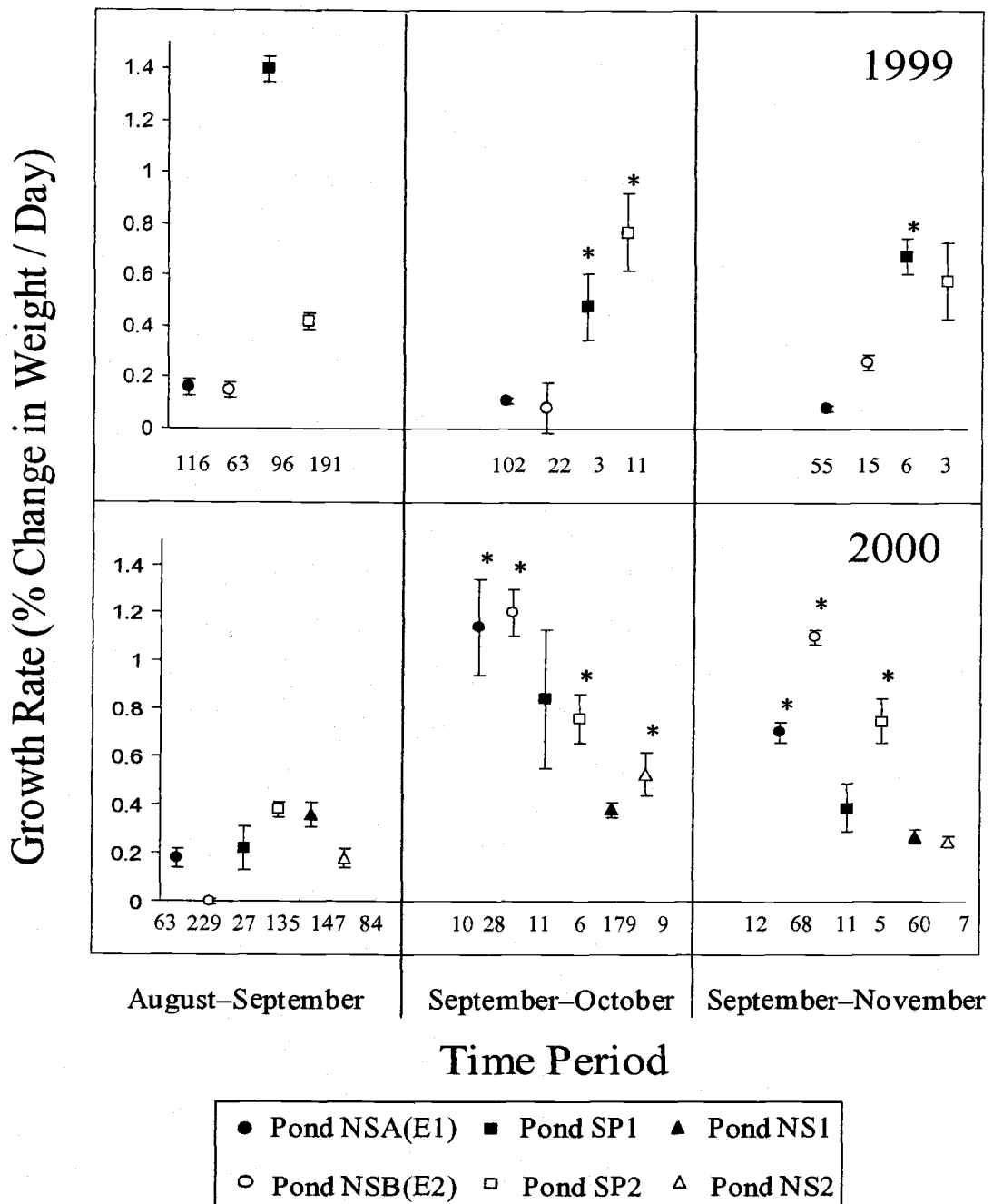
The pattern of growth between ponds and within pond types was variable (Fig. 3). In 1999, growth rates of recaptured PIT-tagged fish in ponds NSA and NSB were consistently lower than in ponds SP1 and SP2 over all of the time periods (Fig. 3). There was no significant ( $p > 0.05$ ) change in growth rate between time periods within either non-spawning pond (NSA and NSB, 1999; Fig. 3). On the other hand, results indicated significant ( $p < 0.05$ ) differences in growth rates of PIT-tagged fish between time periods in ponds SP1 and SP2, but the patterns of growth were different. Mean growth rates decreased significantly ( $p < 0.001$ ;  $t$  tests) during both spawning time periods relative to before spawning in pond SP1 (Fig. 3). In pond SP2, growth rates increased in both time periods during spawning relative to before spawning. The

**Table 4.** Capture data for juvenile coho salmon > 60 mm in the PIT-tag studied beaver ponds. Total captured is all coho salmon > 60 mm captured during the particular sample month. Number recaptured is the number of fish with PIT-tags that were captured during the sample month. Percentage recaptured is the number of fish with PIT-tags that were captured in the sample month expressed as a percentage of all the PIT-tags that were placed in the pond prior to the sample month.

Pond	July		August		September			October			November		
	Total captured	Total captured	Number recaptured	Percentage recaptured	Total captured	Number recaptured	Percentage recaptured	Total captured	Number recaptured	Percentage recaptured	Total captured	Number recaptured	Percentage recaptured
<b>1999</b>													
NSA(E1)		151	NA	NA	220	116	76.8	185	106	41.6	109	58	22.7
NSB(E2)		84	NA	NA	138	63	75.1	158	51	32.1	104	23	14.5
SP1		360	NA	NA	421	97	24.3	41	10	2.5	42	13	3.3
SP2		337	NA	NA	374	191	56.7	76	19	5.1	47	4	1.1
<b>2000</b>													
NSA(E1)	72	101	45	62.5	168	71	51.4	32	12	5.5	137	15	6.9
NSB(E2)	231	320	143	61.9	457	289	70.8	118	36	6.3	344	79	13.7
SP1	151	226	22	14.6	261	35	10.4	47	13	2.3	160	14	2.5
SP2	279	293	122	43.7	326	173	38.4	19	8	1.3	30	6	1.0
NS1	207	255	105	50.7	399	182	50.3	420	230	63.5	358	78	21.5
NS2	122	101	86	70.5	116	99	72.3	36	10	6.5	60	7	4.5

NA – Ponds were not sampled in July of 1999, therefore there were no recaptured fish in August of 1999.

**Figure 3.** Estimated mean growth rates ( $\pm 1$ SE) of PIT-tagged juvenile coho salmon recaptured over the time periods before (Aug–Sept) and during (Sept–Oct, Sept–Nov) spawning in 1999 (top) and 2000 (bottom). Numbers at the bottom of each frame indicate sample sizes for estimates. \* denotes a significant difference ( $p < 0.05$ ) in growth of fish recaptured in a particular pond during spawning periods (Sept–Oct, Sept–Nov) as compared to those that were captured in the same pond before spawning (Aug–Sept).



estimated difference in mean growth rate for fish in this pond was significant ( $p = 0.01$ ;  $t$  tests) between the Aug–Sept and the Sept–Oct time periods.

In 2000, the highest mean growth rates for recaptured PIT-tagged fish were observed in the enriched ponds (NSA(E1) and NSB(E2)) over the spawning time periods. This growth corresponds with the addition of salmon eggs and carcasses. The non-influenced ponds (NS1, NS2) had the lowest growth rates during the spawning time periods, whereas the spawning-influenced ponds (SP1, SP2) exhibited an intermediate level of growth (Fig. 3). Growth rates significantly increased in ponds NSA(E1) and NSB(E2) ( $p < 0.001$  in both ponds and time periods;  $t$  tests) during the artificial enrichment relative to before enrichment (Fig. 3).

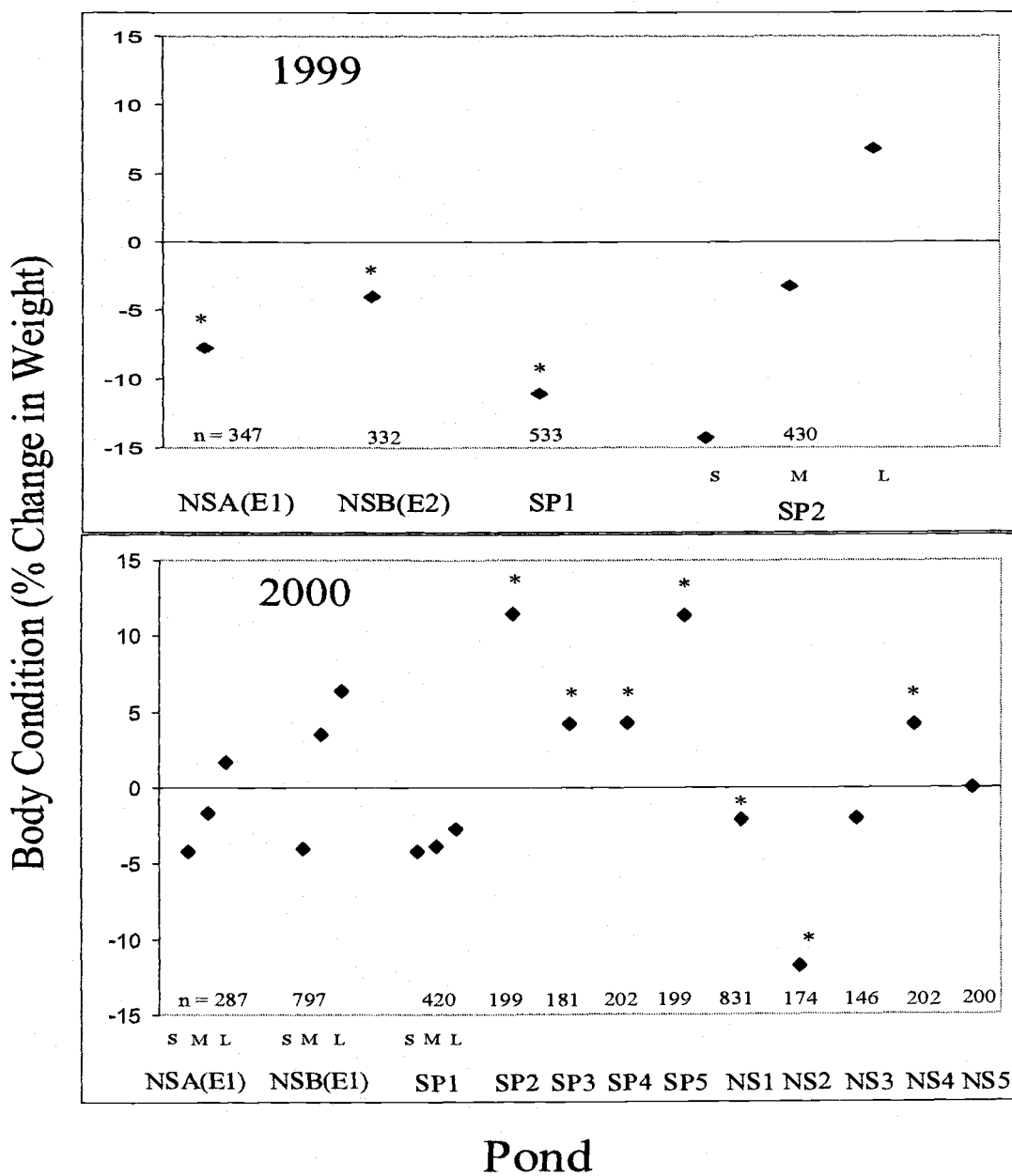
Growth rates increased in the spawning-influenced ponds over the spawning time periods relative to that before spawning in 2000. However, the differences in growth rate between time periods were significant only in pond SP2 ( $p = 0.01$  for both periods;  $t$  tests).

In pond NS1 growth rates did not differ significantly between any of the time periods but in pond NS2 growth rates significantly increased during the September–October time period relative to the August–September time period ( $p = 0.005$ ).

In 1999 spawning did not improve the body condition of most juvenile coho salmon. In ponds NSA, NSB, and SP1, fish of the same length weighed significantly less during spawning as compared to fish sampled in these ponds before spawning. (Fig. 4). In pond SP1 the larger sized fish ( $\approx 100$  mm) weighed more during spawning



**Figure 4.** The influence of spawning on body condition of juvenile coho salmon > 60 mm captured in the 4 beaver ponds in 1999 (top) and 12 beaver ponds in 2000 (bottom). Values are the mean percent change in weight of fish of the same length sampled during spawning (Nov.) as compared to before spawning (Sept.). Negative values indicate a decrease in mean weight during spawning compared to before spawning. \* denotes that the change was significant ( $p < 0.001$ ). In ponds with interaction, three representative lengths (S = 60 mm, M = 80 mm, L = 100mm) were used to get the corresponding change in mean weight. Sample sizes are as indicated above x-axis.



than before spawning but the medium ( $\approx 80$  mm) and small ( $\approx 60$  mm) sized fish weighed less during spawning (Fig. 4).

In 2000, the body condition of juvenile coho salmon in the spawning ponds was generally improved during the spawning period. In four out of five of these ponds, fish of the same length were significantly ( $p < 0.001$ ) heavier during spawning (Fig. 4). The increase in mean weight for fish of the same length ranged from 4.2 – 11.4 % (Fig. 4). In pond SP1 body condition varied with the size of the fish but was always less during spawning regardless of fish size (Fig. 4).

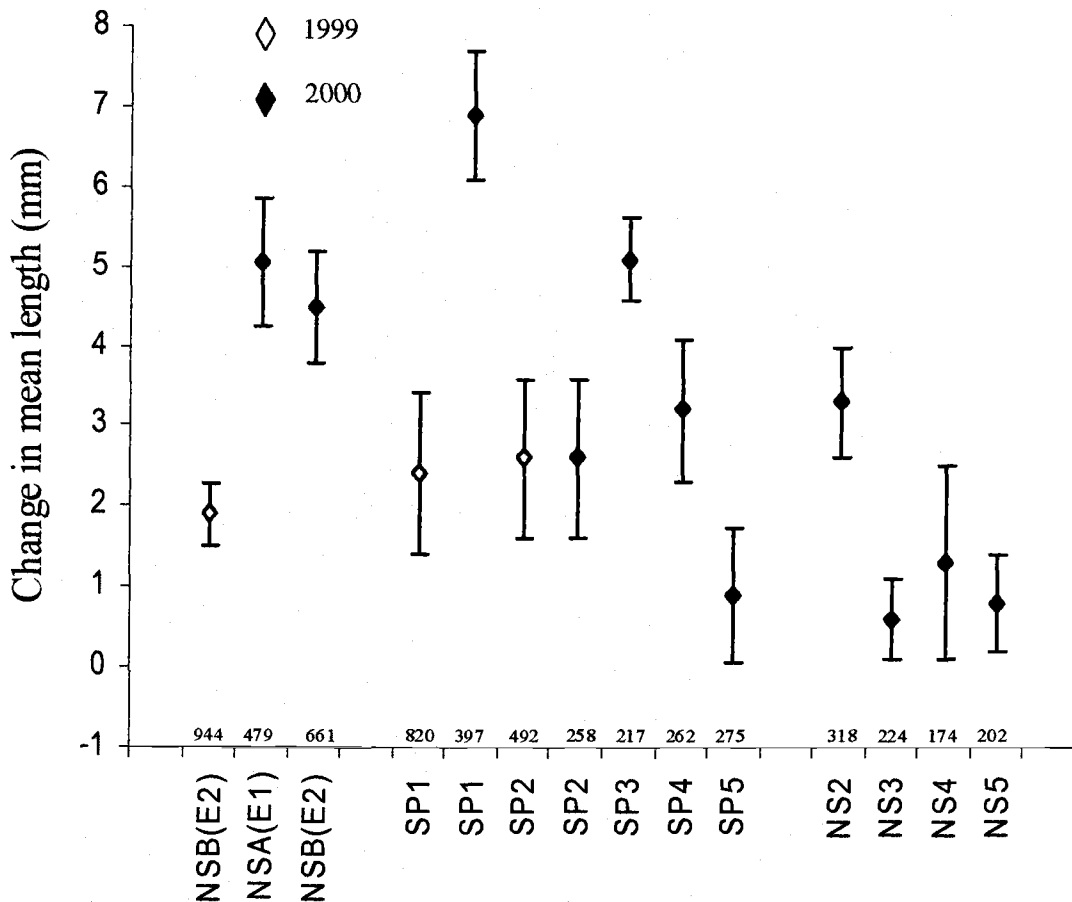
In the enriched ponds, the body condition of medium ( $\approx 80$  mm) sized fish in pond NSB(E2) and larger sized fish ( $\approx 100$  mm) in both ponds were improved by the presence of carcasses and eggs (Fig. 4). Small ( $\approx 60$  mm) fish from either pond did not show an improvement in body condition during the enrichment.

The body condition of juvenile coho salmon in the no-spawning ponds was affected variably during the spawning period. In two of five ponds, body condition decreased significantly ( $p \leq 0.0001$ ) during spawning. The decrease in mean weight for fish of the same length was 2.1% (NS1) and 11.8 % (NS2) (Fig. 4). There was no significant change in body condition associated with the spawning period in pond NS3 and NS5 (Fig. 4). In pond NS4, the body condition of fish was significantly ( $p < 0.0001$ ) improved during the spawning period.

There was no consistent pattern observed in the growth of age-0 coho salmon (Fig. 5). In 2000, the estimated change in lengths between periods before and during spawning was generally greater in the enriched and spawning ponds than in the no

spawning ponds, but the variance associated with these estimates indicate that the differences were not significant (Fig. 5). Mean length of age-0 fish could not be determined in pond NSA in 1999 or NS1 in 2000 because length frequency distributions and scale analysis did not reveal distinct size and age class separations.

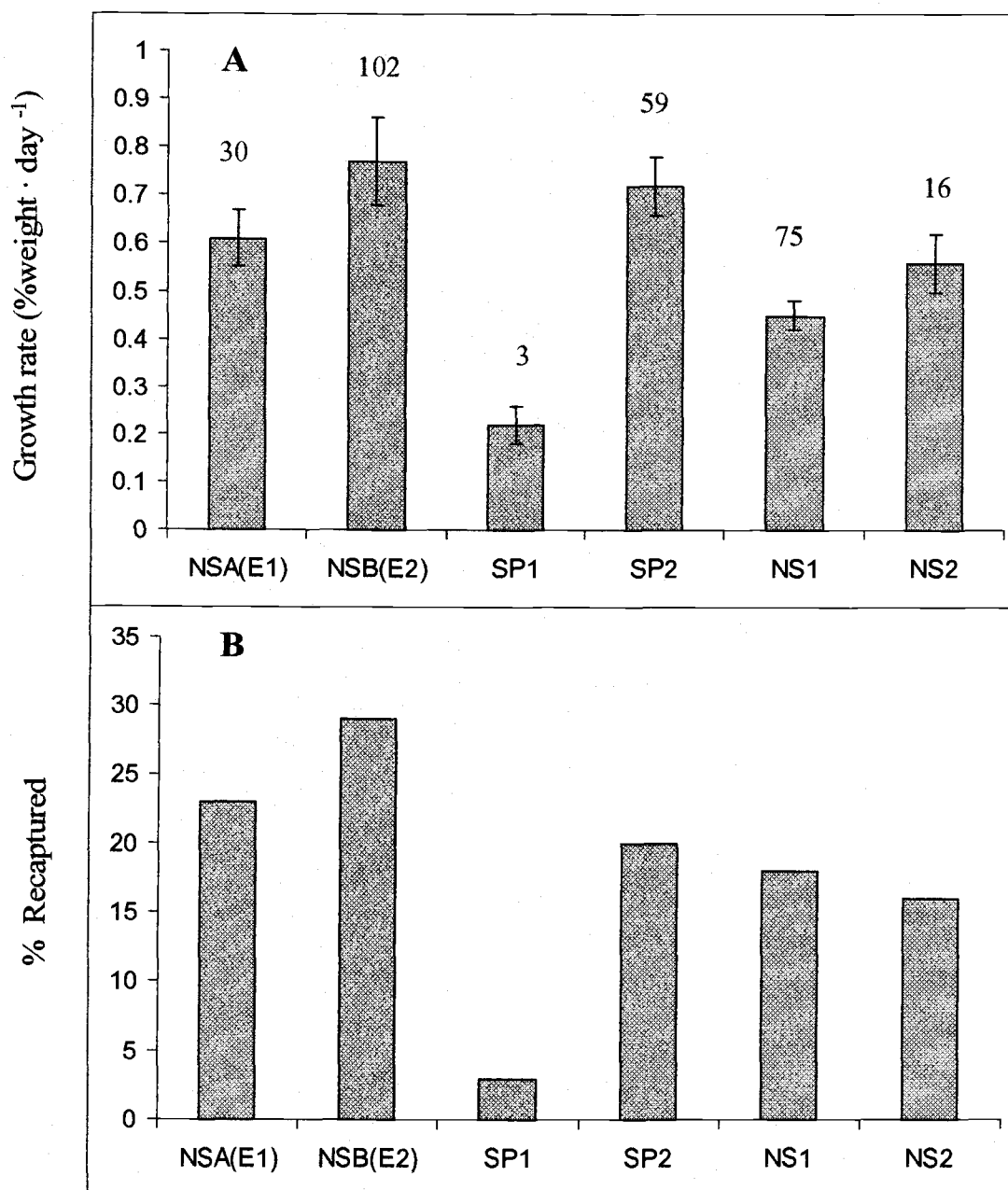
**Figure 5.** Estimated change in mean length of age-0 coho salmon captured in the beaver ponds. Values are the differences in mean length ( $\pm 1$  SE) between samples in September (before spawning) and November (during spawning). Sample sizes for each estimate is given on x-axis above the respective pond.



### Overwinter Growth Rate and Survival to Outmigration

Survival to outmigration was related to growth rates; fish from ponds with higher growth rates had greater rates of survival to outmigration (Fig. 6). However, there were no distinct patterns or differences in either variable between the ponds (Table 5). The highest estimated mean growth rates and survival were observed in the enriched ponds (NSA(E2), NSB(E2)) and one of the spawning ponds (SP2). However, the lowest estimated mean growth rate and survival were observed in pond SP1, which was influenced by spawning salmon (Fig. 6).

**Figure 6.** Estimated mean growth rate (A) and survival to outmigration (B) of recaptured PIT-tagged juvenile coho salmon over the time period from the fall 2000 to smolt outmigration in the spring 2001. Estimated growth values are means ( $\pm 1$  SE) calculated for fish during the September–Outmigration time period (Spring 2001).



## Discussion

### Density

The density and size class structure of juvenile coho salmon rearing in the beaver ponds were generally influenced by proximity to spawning areas. The mean densities of juvenile coho salmon < 60 mm in the spawning-influenced ponds were estimated to be approximately 3–4 times greater than in the non-influenced ponds by September. The mean change in length of age-0 coho salmon did not statistically differ between the ponds. If densities during spawning were similar to the September estimates, then the spawning-influenced ponds supported more age-0 juvenile coho salmon.

There was no difference in the estimated density of fish > 60 mm between the ponds in September. This suggests higher food resource availability in the spawning-influenced ponds over the spawning period. Fish > 60 mm in the spawning-influenced ponds were able to maintain equal or higher growth rates than in the non-spawning ponds over spawning periods even though total fish density was greater. Greater total densities of fish in the spawning ponds may have been one reason for the lack of a difference between spawning and no spawning ponds in terms of growth and survival to outmigration. In this sense, there were more fish rearing in the spawning ponds, but they did not necessarily produce more smolts.

The ability to trap juvenile coho salmon dropped substantially during the spawning period and therefore density estimates were not obtained after September.

Increased fish densities during spawning have been observed in other studies (Bilby et al. 1998; Foot and Brown 1998). Fish may move into spawning areas of streams in order to take advantage of the additional food resources associated with spawning. This study was unable to determine if fish densities increased in the spawning ponds.

#### Growth rate, Body Condition, and Survival to Smolt Outmigration

The influence of natural spawning on growth rate and body condition of juvenile coho salmon was quite variable between years, ponds, and sizes of fish. There were no consistent patterns observed in these variables for spawning and non-spawning ponds. Although growth rates of fish in the spawning ponds were generally greater during the spawning period, small sample sizes and few replicates gave little power to statistically test for a pond type (spawning vs non-spawning) effect on growth rate.

At the individual pond level, there was some indication that natural spawning positively influenced growth rates and body condition of juvenile coho salmon in the late fall and early winter. In pond SP2, growth rates significantly increased in all but one of the spawning time periods tested over both years. In 2000, body condition improved significantly in all of the spawning ponds except SP1. Eastman (1996) found that growth and body condition of trout and char increased in response to natural spawning by sockeye salmon in the Wood Lakes system, Alaska.

The artificial enrichment of ponds with salmon eggs and carcasses significantly increased growth rates of juvenile coho salmon. Fish rearing in these ponds responded quickly, and exhibited rapid growth over the periods that coincided with the artificial enrichment. Juvenile coho salmon readily used the additional food resources and substantially benefited. Carcass and egg enrichments have resulted in immediate growth benefits for juvenile anadromous salmonids in other studies (Bilby et al. 1998; Wipfli et al. 2003).

On the Copper River Delta, the timing of these benefits could be important for overwinter survival (Quinn and Peterson 1996). Fall-spawning salmon provide eggs, carcasses, and benthic invertebrates that can be consumed by juvenile coho salmon just prior to winter (Bilby et al. 1998; Peterson and Foote 2000). The overwinter period is critical for many Alaskan freshwater fish populations (Reynolds 1997). In 2000, most spawning-influenced ponds had heavier fish during spawning. That these fish were heavier for fish of the same length before spawning may indicate storage of lipids. Lipid reserves at the onset of winter are important for overwinter survival of fish (Toneys and Coble 1980; Cunjak et al. 1998). However, in this study there was no clear evidence that increased growth rate or improved body condition in the fall led to greater survival to outmigration.

In some ponds, the relative influence of spawning or enrichment on body condition depended on fish size. Body condition improved with increasing fish size in the enriched ponds during the enrichment and in ponds SP1 (2000) and SP2 (1999) during spawning. The most plausible explanation for this result is that the availability



and consumption of salmon eggs was greater for larger fish. Salmon eggs are the most valuable food resource associated with spawning. They are energy rich (Bilby et al. 1996; Foote and Brown 1998) and abundant during spawning (Fukushima et al. 1998). Other studies (Eastman 1996; Bilby et al. 1998) found that salmon eggs dominated the diets of stream-rearing resident trout and juvenile anadromous salmonids during spawning. During the enrichment, most whole carcasses were intact, with minimal conditioning or decomposition, thus making them unavailable as a food source to juvenile coho salmon. Salmon eggs, on the other hand, were immediately available for consumption by fish in these ponds. Larger fish have enough gape to consume eggs and the larger the fish the more eggs that can be consumed. Smaller fish consume fewer eggs and there may be a threshold size at which gape size prohibits egg consumption. Competition for eggs may also limit the number of eggs available to smaller fish.

The size and duration of spawning runs have implications for the availability of salmon eggs and other salmon-derived food resources. More spawning fish and prolonged spawning result in higher potential for egg availability through egg spill or the superimposition of redds (Fukushima et al. 1998). Invertebrate prey densities can increase with increasing carcass densities (Wipfli et al. 1998), and the number invertebrates drifting in the water column can increase with number of spawning fish present on redds (Peterson and Foote 2000). In this study, the numbers of spawning fish counted above the naturally influenced ponds was similar, yet there was a high degree of variability in growth rate and body condition between years. High growth

rate in the before period in pond SP1 and the density of fish < 60mm rearing in both ponds may explain some of this variation.

The variability observed between and within ponds indicates that there are other important factors influencing growth and survival to outmigration. The fall and early winter period coincides with other potentially abundant food and nutrient resources that can be utilized by juvenile coho salmon. Sitka alder, a nitrogen fixer, is a dominant component of the riparian plant community around beaver ponds. Alder can represent a major source of nutrients to aquatic communities (Volk et. al. 1998) and may be as influential as salmon carcasses in terms of nitrogen enrichment (O'keefe and Edwards, in review). The fall is also a time of increased aquatic and terrestrial invertebrate abundance. Corixidae were abundant in all ponds during the spawning time periods. From mid-September to early-October, large clouds of corixids were flying above and swimming within all of the ponds. Terrestrial invertebrates can be an important prey item for juvenile salmonids in the fall, especially in streams dominated by deciduous riparian vegetation (Wipfli 1997).

Hydrology and catchment characteristics may play a role in the observed patterns of growth rate and survival to outmigration for the spawning ponds. Pond SP1 was located in the East Fork of the Mile 18 stream system whereas pond SP2 was in the West Fork. The East Fork is mostly fed by hillslope runoff, while the Middle and West Forks are mostly ground water fed from the Sheridan Glacier River. The upper reaches of the East Fork consist of high gradient, contained channels that typically result in 'flashy' rain and snowmelt events (Blanchet 1983). The highest growth rates

of fish observed during the study were from pond SP1 over the August–September time period in 1999, which coincides with a period of very high rainfall on the Delta (32.8 cm from Aug 23–Sept 15; NOAA weather station, Cordova airport). Flashy streams can benefit fish through frequent flood events that increase availability of drifting invertebrate prey species (Pearson and Franklin 1968) and through access to food resources on floodplains and in side channels (Junk et al. 1989; Giannico and Healey 1998). During sampling in September 1999 at pond SP1, approximately 3 m of floodplain habitat was accessible to fish on either side of the normal pond bank. Juvenile coho salmon were captured on the floodplains and pond margins and had exceptional body condition and gut fullness. Many of the larger fish (> 85 mm) had the features of smolts (e.g. silvery, faint parr marks) and none of these fish were recovered in the weir the following spring. These fish likely outmigrated in the late fall or early winter.

The East Fork was also colder than the West and Middle Forks over the spring months, likely as a result of runoff from snowmelt. Lower temperatures could have influenced overwinter growth rates and survival to outmigration. Mean water temperatures in pond SP1 were generally below 6°C through the month of June whereas mean temperatures by June in the other ponds were over 10°C. Only 3% of the fish tagged in this pond were recaptured at the weir and low growth rates of these fish indicated poor overwinter conditions. These data suggest either high mortality for fish overwintering in pond SP1 or failure to recapture these fish at the weir. As

mentioned, some of the fish tagged in this pond probably smolted and migrated out in the fall. The rapid growth of fish in this pond from the fall through early winter may induce a fall smolt outmigration. Those that stayed behind experienced relatively cold spring water temperatures, and this may have influenced growth rates of the few fish captured at the weir in 2001.

Another potential reason that differences in growth rates and survival to smolt outmigration were not greater between the three pond types is the potential connectivity between habitats. The non-spawning ponds may receive salmon-derived nutrients from upstream, hyporheic, riparian, and floodplain sources (Ben-David et al. 1998; O'Keefe and Edwards 2002). This type of influence from spawning salmon may not result in immediate growth benefits like that associated with direct consumption of eggs and carcasses, but it may affect growth rates and overwinter survival through increased prey abundance and productivity in the ponds over the winter or following spring (Wipfli et al. 1998).

### Conclusion and Management Implications

Juvenile coho salmon responded variably to fall-spawning salmon on the Copper River Delta. There were no consistent patterns associated with the two naturally occurring pond types (spawning vs no spawning). In some ponds, fall-spawning salmon increased growth rates and improved the body condition of juvenile coho salmon and enrichment with salmon carcasses and eggs significantly increased

growth rates of fish in non-spawning ponds. In the enriched ponds, and some spawning ponds, the relative influence of spawning and enrichment on body condition varied by fish size. There was no evidence that increased growth rate and body condition in the fall resulted in greater smolt production. Other factors such as nutrients from riparian vegetation and catchment characteristics that control hydrology and thermal regimes may play an important role in smolt production.

This study and others (Bilby et al. 1998; Wipfli et al. 2003) have indicated that enrichment of streams with salmon carcasses and eggs can have immediate impacts on the growth rates of juvenile salmonids. Stream enrichment may be an effective means to boost growth rates of fish. In order to maximize immediate effectiveness for juvenile fish, salmon eggs should be included along with carcasses. Artificial enrichment with eggs and carcasses may be best considered a temporary, short-term restoration technique with the ultimate goal of producing viable runs of wild spawning salmon. Given the critically low numbers of wild spawning fish (Nehlsen et al. 1991) and the severe disruption of the salmon-derived nutrient linkage of many streams in the Pacific Northwest (Cederholm et al. 1999; Gresh et al. 2000), carcass and egg enrichments may be able to accelerate restoration efforts for some salmon populations.

However, results from this study indicate that in a complex, natural stream system, smolt production may not be as closely correlated with spawning salmon as some research has suggested. Increased growth rates and body condition associated with enrichment and natural fall spawning did not necessarily lead to increased overwinter growth and survival to outmigration. Recent studies concerning the

influence of spawning on growth of juvenile salmonids were conducted in small streams that have been altered by land management activities, in streams above natural barriers to the migration of anadromous salmon, or in experimental streams (Bilby et al. 1996; Bilby et al. 1998; Wipfli et al. 2003). These studies also focused on the immediate influence of spawning on growth and implied that there would be a corresponding relationship to smolt production. In natural, complex streams there are many other factors that can be important in influencing longer-term growth rates and ultimately smolt production. Supplemental feeding of coho salmon in a natural stream during the summer increased growth and carrying capacity, but failed to produce greater numbers of smolts the following spring (Mason 1976). Mason (1976) concluded that overwinter habitat controlled the number of smolts produced. Managers should be familiar with the limiting factors associated with the fish population of interest before incorporating nutrient enrichment projects. Adding nutrients to streams with degraded habitats that limit juvenile capacity will likely fail to produce greater numbers of smolts.

Gende et al. (2002) noted that it is important to validate experimental results in natural stream environments and to explore potential site/system-specific variability in the response of freshwater systems to spawning salmon. On the Copper River Delta, the response of juvenile coho salmon to fall-spawning salmon was variable and these results suggest other potential factors are important in smolt production. Naturally functioning stream environments will have increased layers of complexity but can

provide valuable insight into the relative importance of spawning salmon to stream rearing salmonids and the ecosystems in which they are a part.

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### Chapter 3—Conclusion

Juvenile coho salmon responded variably to fall-spawning salmon on the Copper River Delta. There was not a consistent difference in density, growth rate, body condition, and survival to outmigration between the two naturally occurring pond types (spawning vs no spawning). In some ponds, fall-spawning salmon increased growth rates and improved the body condition of juvenile coho salmon and enrichment with salmon carcasses and eggs significantly increased growth rates of fish in non-spawning ponds. In the enriched ponds, and some spawning ponds, the relative influence of spawning and enrichment on body condition varied by fish size. There was no evidence that increased growth rate and body condition in the fall resulted in greater smolt production.

In some beaver ponds, fall-spawning salmon positively influenced the growth rates and body condition of juvenile coho salmon > 60 mm. The increased growth and condition in the fall and early winter comes at an important time for stream-rearing fishes in Alaska (Reynolds 1997). The winters are long and cold, with water temperatures as low as 1°C from December – March. Heightened growth rates prior to this period has implications in the overwinter survival of salmonids (Smith and Griffith 1994; Quinn and Peterson 1996). The availability of eggs to juvenile coho salmon during spawning may be the most beneficial component of spawning because of their high caloric content. Ingestion of eggs can lead to rapid growth (this study) and may supply juvenile coho salmon with excess energy that can be stored as lipid

reserves and utilized during the overwinter period (Cunjak et al. 1998). The potential benefit from eggs to juvenile coho salmon may depend on fish size. Gape size of smaller fish may limit the consumption or number of eggs consumed.

Although natural spawning and enrichment directly benefited growth rates and body condition in the fall, there was not a corresponding effect on overwinter growth and survival to outmigration. Increased growth rates and body condition associated with enrichment and natural fall spawning did not necessarily lead to increased overwinter growth and survival to outmigration. In complex, natural streams, smolt production may not be as closely correlated with spawning salmon as some recent research has suggested. Recent studies have observed increased growth rates and body condition as a result of spawning and discussed the implications for smolt production. (Bilby et al. 1998; Wipfli et al. 2003). However, these studies have been conducted in artificial streams or streams that have been altered by land management activities. Other studies have linked numbers of returning adult salmon to the adult escapement numbers during the returning salmonid's juvenile stage in freshwater (Michael 1995). Even though widely accepted notions regarding growth, size, overwinter survival, and smolt survival (Holtby et al. 1990; Smith and Griffith 1994; Quinn and Peterson 1996) support these assertions, the direct evidence linking spawning salmon to increased smolt production has been lacking. This study provided no evidence that increased fall growth rates resulting from spawning salmon led to increased smolt production.

On the Copper River Delta, there are other factors that can be important in influencing longer-term growth rates and ultimately smolt production. Our results

suggest that nutrients from riparian vegetation and catchment characteristics that control hydrology and thermal regimes may play an important role in smolt production. The East Fork of the Mile 18 and pond SP1 was of particular interest. Increased fall growth rates can occur in the fall prior to spawning, apparently as a result of frequent and/or severe flooding. Floodplain effects and temperature regimes may be involved with an age-1 life history pattern not previously known for coho salmon smolts in the Mile 18.

Several questions arise from this study. One is the relative benefit of nutrients from alder and riparian vegetation compared to nutrients associated with spawning salmon. Another question is the relative benefit of eggs compared to carcasses for juvenile coho salmon production. Results from a study focused on that question would provide valuable insight into the potential shortcomings of only introducing carcasses as part of efforts to enhance depleted salmonid populations. Another question would focus the effect of the late fall and early winter growth on survival to smolting. This would require an intense effort monitoring smolt production from different portions of the watershed. Also it would require determining smolt production over a greater portion of the year rather than only in the spring. Knowledge gained from such studies would further increase our understanding of the importance of returning adults to the long-term production of salmonid populations.

Gende et al. (2002) noted that it is important to validate experimental results in natural stream environments and to explore potential site/system-specific variability in the response of freshwater systems to spawning salmon. On the Copper River Delta,

the response of juvenile coho salmon to fall-spawning salmon was highly variable and these results suggest other potential factors are important in smolt production.

Naturally functioning stream environments will have increased layers of complexity but can provide valuable insight into the relative importance of spawning salmon to stream rearing salmonids and the ecosystems in which they are a part.



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