

The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska

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Abstract: This study examined the influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on the density, growth rate, body condition, and survival to outmigration of juvenile coho salmon on the Copper River Delta, Alaska, USA. During the fall of 1999 and 2000, fish rearing in beaver ponds that received spawning salmon were compared with fish from ponds that did not receive spawners and also with fish from ponds that were artificially enriched with salmon carcasses and eggs. The response to spawning salmon was variable. In some ponds, fall-spawning salmon increased growth rates and improved the condition of juvenile coho salmon. The enrichment with salmon carcasses and eggs significantly increased growth rates of fish in nonspawning ponds. However, there was little evidence that the short-term growth benefits observed in the fall led to greater overwinter growth or survival to outmigration when compared with fish from the nonspawning ponds. One potential reason for this result may be that nutrients from spawning salmon are widely distributed across the delta because of hydrologic connectivity and hyporheic flows. The relationship among spawning salmon, overwinter growth, and smolt production on the Copper River Delta does not appear to be limited entirely to a simple positive feedback loop.

Résumé : Notre étude examine l'influence de la présence des saumons coho (*Oncorhynchus kisutch*) à reproduction automnale sur la densité, le taux de croissance, la condition corporelle et la survie des jeunes saumons coho jusqu'à l'émigration du printemps dans le delta du fleuve Copper, Alaska, É.-U. À l'automne 1999 et 2000, nous avons comparé les poissons élevés dans des étangs de castors qui reçoivent des saumons en fraye à des poissons provenant d'étangs qui ne reçoivent pas de reproducteurs et enfin à des poissons provenant d'étangs qui ont été artificiellement enrichis de carcasses et d'oeufs de saumons. La réaction à la présence de saumons reproducteurs est variable. Dans certains étangs, les saumons à reproduction automnale augmentent le taux de croissance et améliorent la condition des jeunes saumons coho. L'enrichissement par l'addition de carcasses et d'oeufs de saumons augmente significativement le taux de croissance des poissons dans les étangs qui ne contiennent pas de reproducteurs. Cependant, il y a peu d'indications que les bénéfices de croissance à court terme observés à l'automne entraînent une meilleure croissance durant l'hiver ou une plus grande survie jusqu'à l'émigration, par comparaison avec les poissons provenant des étangs qui ne reçoivent pas de reproducteurs. Une explication potentielle de ce résultat est que les nutriments provenant des saumons reproducteurs sont peut-être largement répartis dans tout le delta à cause de la connectivité hydrologique et des flux hyporhéiques. La relation entre les saumons reproducteurs, la croissance au cours de l'hiver et la production de saumoneaux dans le delta du fleuve Copper ne semble pas se limiter seulement à une simple boucle de rétroaction positive.

[Traduit par la Rédaction]

Introduction

The spawning and death of semelparous anadromous Pacific salmon (*Oncorhynchus* spp.) is recognized as an inte-

gral ecological process in freshwater ecosystems throughout the North Pacific Rim. Studies have revealed that this process influences primary productivity of streams (Richey et al. 1975; Wipfli et al. 1998) and the population dynamics

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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).

The transport and delivery of marine-derived nutrients into streams by spawning salmon may be 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). This potentially results in larger numbers of adults returning to spawn, thus continuing the cycle.

A critical element of this positive feedback hypothesis is that juvenile salmonids experience heightened growth rates and greater survival to smolt outmigration because of energy acquired from eggs and carcasses. 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).

Spawning salmon can directly and indirectly impact food availability and growth rates of juvenile, stream-rearing salmonids (Bilby et al. 1996, 1998; Eastman 1996). 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; Piorkowski 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 that can dislodge 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 (*Oncorhynchus kisutch*) 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 pristine streams of the Copper River Delta provide an excellent opportunity to examine the relationship between

fall-spawning coho salmon and juvenile coho salmon. Most streams on the Copper River Delta have large runs of coho salmon from September through November. Beaver ponds dominate stream habitats on the Copper River Delta and generally have sufficient depth and cover to provide excellent rearing and overwinter 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). Beaver ponds downstream of spawning habitats may be hotspots of juvenile coho salmon productivity because spawning salmon and carcasses could 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 with those rearing in ponds without influence from spawning salmon and also with those rearing in ponds that were artificially enriched with salmon carcasses and eggs. The study focused on four main questions. (i) Were growth rates and body condition of juvenile coho salmon increased during salmon spawning? (ii) Were densities and growth rates of juvenile coho in beaver ponds with access to spawning salmon greater than those without such access? (iii) Could growth rates of juvenile coho in ponds without access to spawning salmon be increased through experimental introduction of salmon carcasses and eggs? (iv) Were smolt growth and survival to outmigration 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.

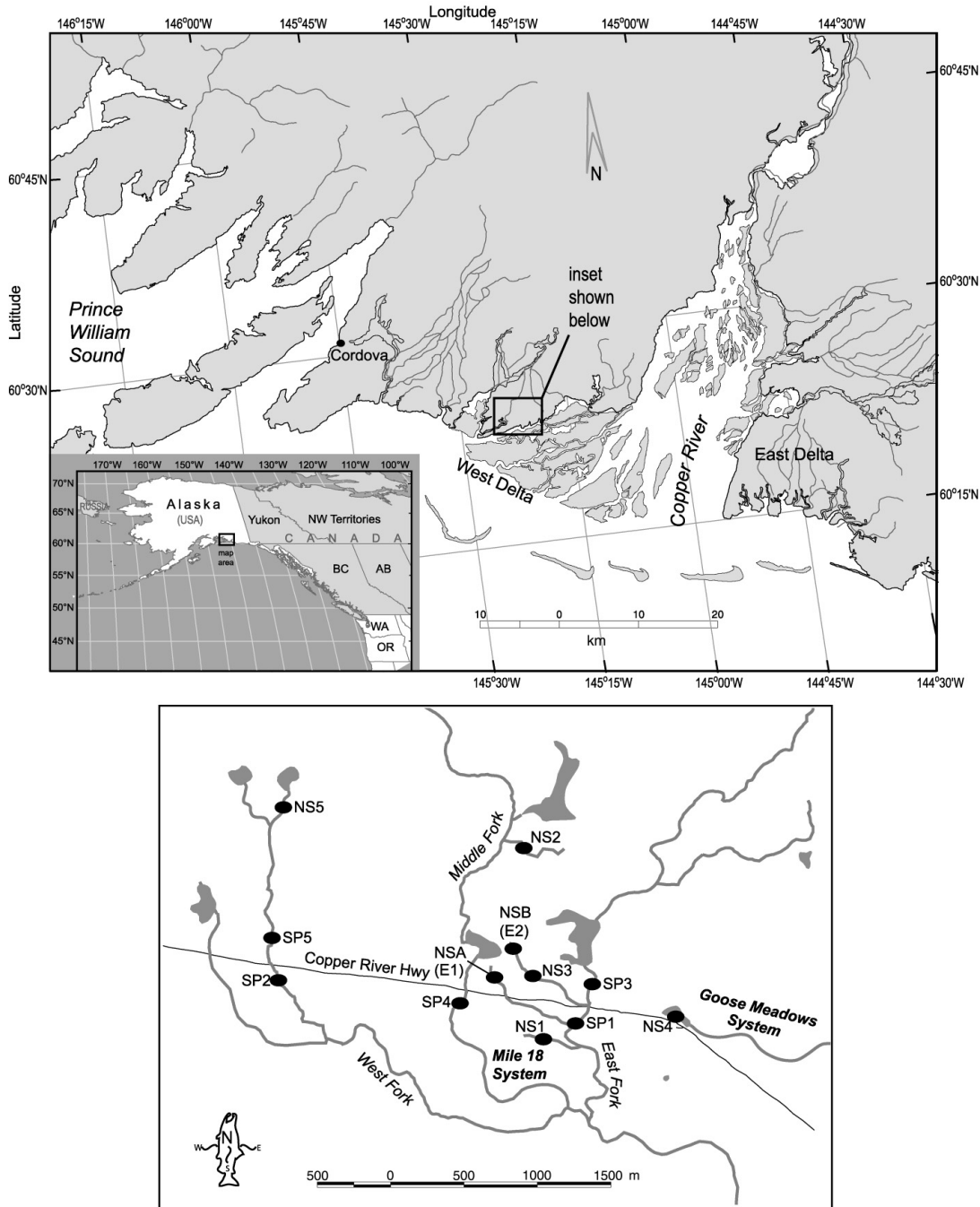
Materials and methods

Study area

The study was conducted in 12 beaver ponds located in two stream systems on the Copper River Delta, Alaska (Fig. 1). Eleven of the study ponds were in the Mile 18 stream system (60°26'N, 145°20'W) and one pond was located in an adjacent system known as Goose Meadows (60°26'N, 145°19'W; Fig. 1). The Mile 18 stream system is a fourth-order coastal floodplain river with a catchment area of ~15 km² and 21 km of stream channels. Mean stream surface gradient is 1%. The area receives ~380 cm of rainfall annually. Approximately 75% of the juvenile-rearing habitat is beaver ponds. Mean annual discharge is estimated at 1.0 m³·s⁻¹ and wetted widths are ~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 of the study ponds, except for surface area, were generally similar (Table 1). Pond sizes ranged from 324 to 4300 m². Primary cover for fish was

Fig. 1. Location of the study stream systems on the Copper River Delta, Alaska (USA,) and the study beaver ponds (lower inset map).



emergent aquatic vegetation and overhanging terrestrial vegetation. There were some pieces of small wood associated with the beaver dams, lodges, and caches in each pond, but large wood was not common.

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

ing (NSA(E1) and NSB(E2)) were artificially enriched with salmon carcasses and eggs during the second year of the study. 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, six fish were seen spawning in and above pond NS4 (Table 1). Adult coho salmon entered these stream systems in early September, and spawning began in the last week of

Table 1. Characteristics of the 12 beaver ponds and influence of spawning coho salmon (*Oncorhynchus kisutch*) during fall 1999 and 2000 on the Copper River Delta, Alaska.

Pond	Pond area (m ²) ^a	Max depth (m)	Water temperature during spawning (°C) ^b		Peak spawner count ^c	
			15 Sept. – 11 Oct.	11 Oct. – 8 Nov.	1999	2000
Ponds with no direct influence by spawning salmon, artificially enriched in 2000						
NSA(E1)	704	1.2	8.3	5.2	0	0
NSB(E2)	1779	1.1	7.8	4.8	0	0
Mean (SE)	1242 (538)	1.2 (0.1)	8.1 (0.3)	5.0 (0.2)	—	—
Ponds with direct influence by spawning salmon						
SP1	1588	1.7	6.6	3.6	234	194
SP2	1394	0.97	6.6	3.5	223	271
SP3	1011	—	6.2	4.4 ^d	—	200
SP4	4298	1.5	7.8	4.9 ^d	243	136
SP5	3147	—	7.1	4.6 ^d	87	92
Mean (SE)	2288 (260)	1.4 (0.2)	6.9 (0.3)	4.2 (0.3)	197 (37)	179 (30)
Ponds with no direct influence by spawning salmon						
NS1	1432	1.7	7.1	3.7	—	0
NS2	1231	1.6	5.9	3.5	—	0
NS3	324	—	7.2	4.8 ^d	—	0
NS4	9829	1.5	7.6	4.9 ^d	—	6
NS5	692	1.8	6.7	4.9 ^d	—	0
Mean (SE)	2702 (1793)	1.7 (0.1)	6.9 (0.3)	4.4 (0.3)	—	—

Note: Standard error (SE) is given after mean in parentheses.

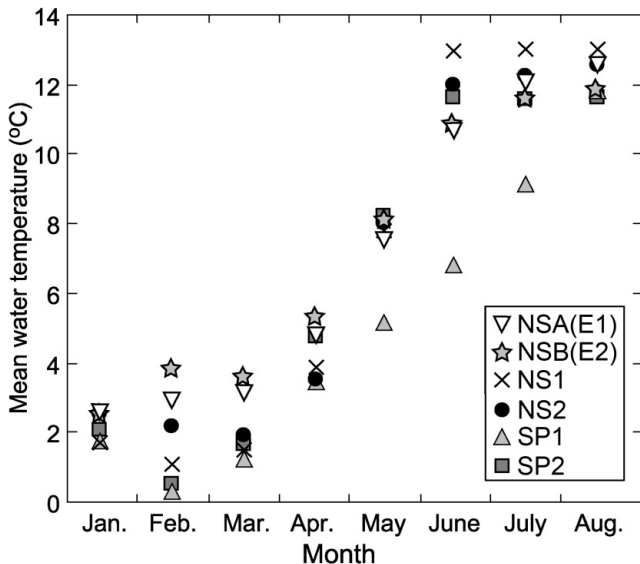
^aPond surface area measured using geographic information system (GIS) software.

^bMean water temperatures between sample dates during spawning in 2000 are shown. Temperatures were recorded hourly with Onset™ HOBO temperature data loggers placed midwater column at the deepest location in each pond.

^cPeak count of spawners and carcasses within ponds and upstream of ponds is given. Approximate distance upstream that was included for each site was 100 m.

^dTemperature recorders were removed during the week of 1 November rather than the week of 8 November.

Fig. 2. Mean water temperatures between sample dates over the summer and fall 2000 and over the winter and spring of 2001 in the beaver ponds with juvenile coho salmon (*Oncorhynchus kisutch*) tagged with passive integrated transponder (PIT) tags on the Copper River Delta, Alaska.



September. Peak counts of spawning salmon in the Mile 18 stream system were made in the third week of October in both years.

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).

Riparian habitats were similar around the ponds and dominated by Sitka alder (*Alnus sinuata*) and willow (*Salix* spp.). Sweetgale (*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 vulgaris*). 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. Threespine stickleback (*Gasterosteus aculeatus*), slimy sculpin (*Cottus cognatus*), coastrange sculpin (*Cottus aleuticus*), Dolly Varden (*Salvelinus malma*), and coastal cutthroat trout (*Oncorhynchus clarkii*) were also present in some ponds.

Density, growth rate, and body condition

In 1999, four ponds were sampled monthly beginning the week of 23 August and ending the week of 17 November. 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 and eggs. The other

Table 2. Schedule of introduction, volume of eggs, and number and biomass of carcasses added to the enriched ponds on the Copper River Delta, Alaska, in 2000.

Week of spawning run	Litres of eggs (and biomass, kg)		No. of carcasses (and biomass, kg)	
	NSA(E1)	NSB(E2)	NSA(E1)	NSB(E2)
1 Oct. – 7 Oct.	2 (2.6)	4 (5.2)	0	0
8 Oct. – 14 Oct.	3 (3.9)	6 (7.8)	4 (15.5)	11 (42.7)
15 Oct. – 21 Oct.	3 (3.9)	7 (9.1)	6 (23.3)	14 (54.4)
22 Oct. – 28 Oct.	2 (2.6)	4 (5.2)	8 (31.1)	20 (77.7)
29 Oct. – 4 Nov.	1 (1.3)	2 (2.6)	16 (62.2)	26 (101)
5 Nov. – 11 Nov.	1 (1.3)	2 (2.6)	13 (50.5)	25 (97.7)
12 Nov. – 18 Nov.	0	0	3 (11.7)	4 (15.5)
Total	12 (15.6)	25 (32.5)	50 (194)	100 (389)

Note: The volume of eggs was added throughout the entire pond at several times over the course of the week. Carcasses were introduced one at a time during the week and randomly distributed throughout the ponds.

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 5 July and ending the week of 8 November. 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 h to capture fish during each monthly sample. Traps were set once overnight in each pond during the months of October and November during both years, because water temperatures were below 6 °C and trap efficiency declined dramatically.

Growth rates of juvenile coho salmon were estimated by recapturing fish marked with passive integrated transponder (PIT) tags. During August and September 1999 and July, August, and September 2000, all individuals >60 mm from each pond were PIT-tagged, which gave them an individual identification number. Captured fish >60 mm were anesthetized with MS-222 (tricaine methanesulfate), measured to the nearest 1 mm fork length, and weighed wet to the nearest 0.1 g on an analytical balance and tagged. On these sampling dates, all fish <60 mm were measured and a subsample of 100 fish was weighed. 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 >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 following equation:

$$(1) \quad G_r = \{[(W_{t+1} - W_t)W_t^{-1}]D^{-1}\} \times 100$$

where G_r is the relative growth rate expressed as percent 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 relation between initial size and growth rates was examined (Lang 2003). There was no relation between size and growth rate, and we therefore did not consider size class in analyses for this study.

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. This was done with the fish captured from four ponds in 1999 and 12 ponds in 2000.

Six new ponds were sampled in 2000, three of which were naturally influenced by spawning (SP3–SP5 in Fig. 1). The other three ponds were not influenced by spawning salmon (NS3–NS5 in Fig. 1). Coho salmon were captured from the six new ponds using similar methods employed in the original ponds, except that fewer traps were used (~60% less effort) and a random subsample of 100 fish >60 mm was taken from the total number captured.

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

Table 3. Estimated density (fish·m⁻²) and standard error (SE) of estimate of juvenile coho salmon (*Oncorhynchus kisutch*) in six beaver ponds on the Copper River Delta, Alaska, during August and September 1999 and July, August, and September 2000.

Pond	1999		2000		
	August	September	July	August	September
Fish >60 mm					
Ponds with no direct influence by spawning salmon, artificially enriched in 2000					
NSA(E1)	0.28 (0.01)	0.35 (0.003)	No estimate ^a	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) ^b
Mean	0.17 (0.12)	0.25 (0.11)	0.15	0.18 (0.02)	0.25 (0.03)
Ponds with direct influence by spawning salmon					
SP1	0.28 (0.01)	0.40 (0.04) ^c	No estimate ^a	0.14 (0.003) ^b	0.18 (0.05) ^b
SP2	0.29 (0.01) ^b	0.30 (0.01)	0.26 (0.02)	0.23 (0.01) ^b	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)
Ponds with no direct influence by spawning salmon					
NS1	—	—	0.17 (0.001)	0.20 (0.01)	0.36 (0.01)
NS2	—	—	0.11 (0.01)	0.08 (0.001) ^b	0.10 (0.001)
Mean	—	—	0.14 (0.03)	0.14 (0.06)	0.23 (0.13)
Fish <60 mm					
Ponds with no direct influence by spawning salmon, artificially enriched in 2000					
NSA(E1)	0.18 (0.01)	0.20 (0.01)	2.89 (0.49) ^c	1.43 (0.04) ^b	1.59 (0.02)
NSB(E2)	0.07 (0.001) ^b	0.29 (0.01)	0.39 (0.14)	0.18 (0.01) ^b	0.29 (0.01) ^b
Mean	0.13 (0.06)	0.25 (0.05)	1.64 (1.25)	0.81 (0.63)	0.94 (0.65)
Ponds with direct influence by spawning salmon					
SP1	2.11 (2.60) ^c	1.39 (0.35)	No estimate ^a	0.52 (0.02)	0.88 (0.01)
SP2	0.53 (0.05) ^c	0.26 (0.01)	2.16 (0.32)	0.79 (0.02) ^b	0.85 (0.09)
Mean	1.32 (0.79)	0.83 (0.57)	2.16	0.66 (0.14)	0.87 (0.02)
Ponds with no direct influence by spawning salmon					
NS1	—	—	No estimate ^a	0.03 (0.01)	0.05 (0.01)
NS2	—	—	0.80 (0.07) ^c	0.26 (0.03) ^c	0.28 (0.002)
Mean	—	—	0.8	0.15 (0.12)	0.17 (0.12)

^aNo estimates were obtained as a result of poor depletion (equal or greater numbers captured on successive occasions as compared with the first).

^bEstimates may be biased low (i.e., high proportion of total catch being captured on the first trap).

^cEstimates may be biased high (i.e., poor depletion). (Based on χ^2 goodness-of-fit test where $p = 0.05$.)

from females if present and separated with a 2 cm mesh screen. Measured portions of eggs were placed in Ziploc[®] bags and stored in a refrigerator until introduction into the ponds. One female provided about 0.7 L (0.9 kg) 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 (see Table 2). 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 (see Table 2).

Overwinter growth rate and survival to outmigration

A smolt weir was operated from 18 April to 2 July 2001 at the mouth of the Mile 18 stream system. 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 funnel supported by fence posts (upstream migrants). Fish were funneled into wooden holding boxes (0.6 m × 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 scanned with an AVID[™] PIT-tag scanner. Tagged fish were anesthetized with MS-222, weighed to the nearest 0.1 g on an analytical balance, and fork length was measured. 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.

Overwinter growth was estimated based on the PIT-tagged fish recaptured at the weir. Growth rates (percent weight gain per day) were calculated using the time periods from capture in September, October, and November to recapture at outmigration. These time periods were used because they included the influence of spawning, if present, and overwinter and spring growth.

Survival to smolt outmigration was calculated as the percentage of tagged fish that were recaptured at the weir from the total number initially 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

Table 4. Capture data for juvenile coho salmon (*Oncorhynchus kisutch*) >60 mm tagged with passive integrated transponder (PIT) tags in beaver ponds on the Copper River Delta, Alaska.

Pond	July			August			September			October			November					
	Total no. captured	Total no. captured	No. recaptured	Total no. captured	Total no. captured	No. recaptured	Total no. captured	Total no. captured	Total no. captured	Total no. captured	Total no. captured	Total no. captured	Total no. captured	Total no. captured	Total no. captured	No. recaptured	% recaptured	
1999																		
NSA(E1)	151	101	NA	220	168	116	185	158	76.8	76.8	106	41.6	109	58	22.7			
NSB(E2)	84	320	NA	138	457	63	158	75.1	75.1	51	32.1	104	23	14.5				
SP1	360	226	NA	421	261	97	41	24.3	24.3	10	2.5	42	13	3.3				
SP2	337	293	NA	374	326	191	76	56.7	56.7	19	5.1	47	4	1.1				
2000																		
NSA(E1)	72	101	45	168	116	71	32	51.4	51.4	12	5.5	137	15	6.9				
NSB(E2)	231	320	143	457	289	289	118	70.8	70.8	36	6.3	344	79	13.7				
SP1	151	226	22	261	35	35	47	10.4	10.4	13	2.3	160	14	2.5				
SP2	279	293	122	326	173	173	19	38.4	38.4	8	1.3	30	6	1.0				
NS1	207	255	105	399	182	182	420	50.3	50.3	230	63.5	358	78	21.5				
NS2	122	101	86	116	99	99	36	72.3	72.3	10	6.5	60	7	4.5				

Note: Total number 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. Percent recaptured is the number of fish with PIT tags that in the sample month expressed as a percentage of all the PIT tags that were placed in the pond prior to the sample month. See text for definition of pond types. Because ponds were not sampled in July of 1999, there were no recaptured fish in August of 1999 (NA).

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). MARK performs a χ^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 χ^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 the true abundance tends to be underestimated (White et al. 1982; Riley and Fausch 1992). A poor depletion (greater or equal numbers captured on successive occasions as compared with the first occasion) can also be responsible for failure of χ^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 of 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.

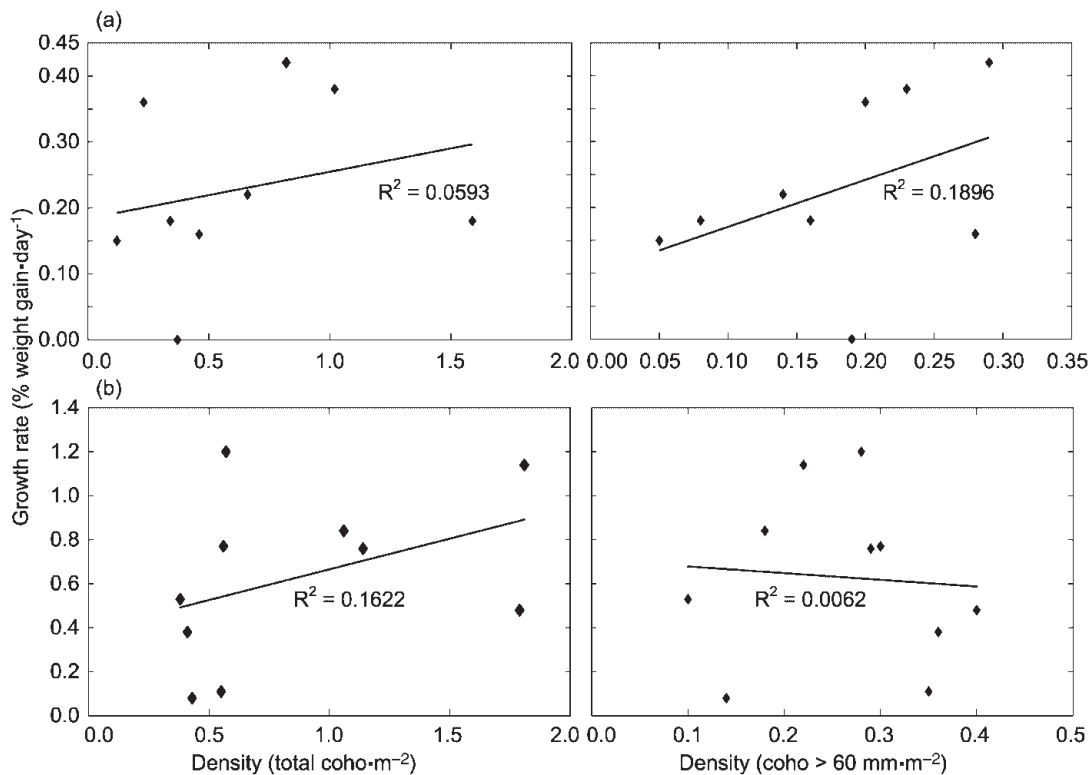
The response of growth rate to spawning and enrichment within individual ponds was compared with *t* tests. In this analysis, the mean growth rates of fish in the August–September time period were compared with growth during the September–October and September–November periods within each pond. Wilcoxon 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 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:

$$(2) \quad \ln \text{ weight} = \beta_0 + \beta_1(\ln \text{ length}) + \beta_2(\text{sample time}) + \beta_3(\ln \text{ length})(\text{sample time})$$

where β_0 is the intercept determined by the regression, β_1 is the slope of the regression, β_2 is a coefficient for the indicator of sample time (September vs. November), and β_3 is the

Fig. 3. Linear relationship between growth and density of passive integrated transponder (PIT)-tagged juvenile coho salmon (*Oncorhynchus kisutch*) trapped in beaver ponds on the Copper River Delta, Alaska. Densities at the beginning of the growth periods shown were used in the analysis, and total density was the combined density estimate of coho salmon >60 mm and <60 mm in length. (a) August–September; (b) September–October.



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 significant differences between samples (before vs. during) (Eastman 1996).

Results

Influence of spawning on density of salmon rearing in beaver ponds

In 1999, there were no significant differences in estimated density of fish (>60 mm) between the spawning and non-spawning ponds (Table 3; $p = 0.49$ and 0.53 for August and September estimates, respectively; t tests). There was high variation between the densities rearing in the two non-spawning ponds in both months (Table 3). In 2000, there were no significant differences in estimated fish densities (>60 mm) among the three pond types (Table 3; $p = 0.76$ and 0.98 for August and September estimates, respectively; analysis of variance (ANOVA) F tests). Again there was high variation between the densities of fish rearing in the nonspawning ponds (Table 3). Fish density (>60 mm) increased over time in most ponds during both years, but most increases were small and were likely the result of recruitment of fish from the 50 mm size class rather than immigration into ponds. Movement of tagged fish among ponds was minimal. Only 29 fish (0.6% of the total fish marked) were ever recaptured in ponds other than where they were

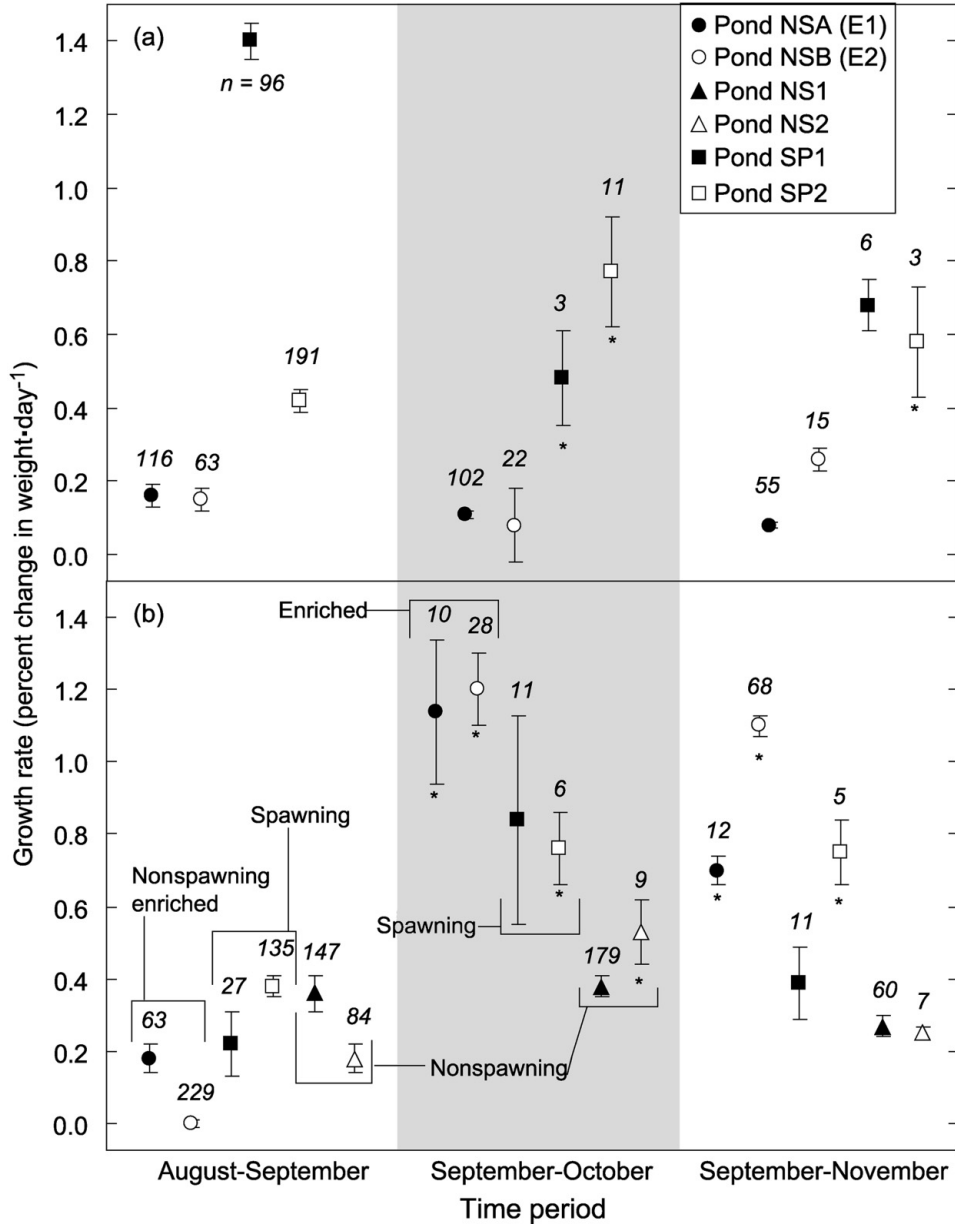
marked. There were two exceptions to this low rate of immigration observed for fish >60 mm. In pond NS1, estimated density nearly doubled between August and September 2000. In pond NSB(E2), estimated density nearly tripled between the August and September 1999 samples (Table 3). The large increase in the total number of fish >60 mm captured during trapping (Table 4) provides additional evidence that fish moved into these ponds.

There was high variability in estimated densities within and among pond types for fish <60 mm (Table 3). In 1999, there were no significant differences between the pond types in either month ($p = 0.37$ and 0.49 (two-sided) for August and September, respectively; t tests). In 2000, there were no significant differences among the three pond types ($p = 0.51$ and 0.40 for August and September, respectively; ANOVA F tests). Although the variability within and between ponds was great, there was a general pattern of greater fish density (<60 mm) in the ponds adjacent to spawning habitats. In August and September, the estimated mean density of fish <60 mm in the ponds adjacent to spawning habitats was three to four times that in the nonspawning ponds (Table 3). The exception was in pond NSA(E1) where high densities of fish <60 mm were found during July, August, and September of 2000 (Table 3).

Influence of spawning on growth rate during spawning

We tagged 4609 juvenile coho salmon over 2 years: 1886 fish in 1999 and 2723 fish in 2000. The percentage of PIT-

Fig. 4. Estimated mean growth rates (± 1 standard error) of passive integrated transponder (PIT)-tagged juvenile coho salmon (*Oncorhynchus kisutch*) recaptured over the time periods before (August–September) and during (September–October, September–November) spawning in (a) 1999 and (b) 2000 on the Copper River Delta, Alaska. Numbers next to each frame indicate sample sizes for estimates. An asterisk (*) denotes a significant difference ($p < 0.05$) in growth of fish recaptured in a particular pond during spawning periods (September–October, September–November) as compared with those that were captured in the same pond before spawning (August–September).



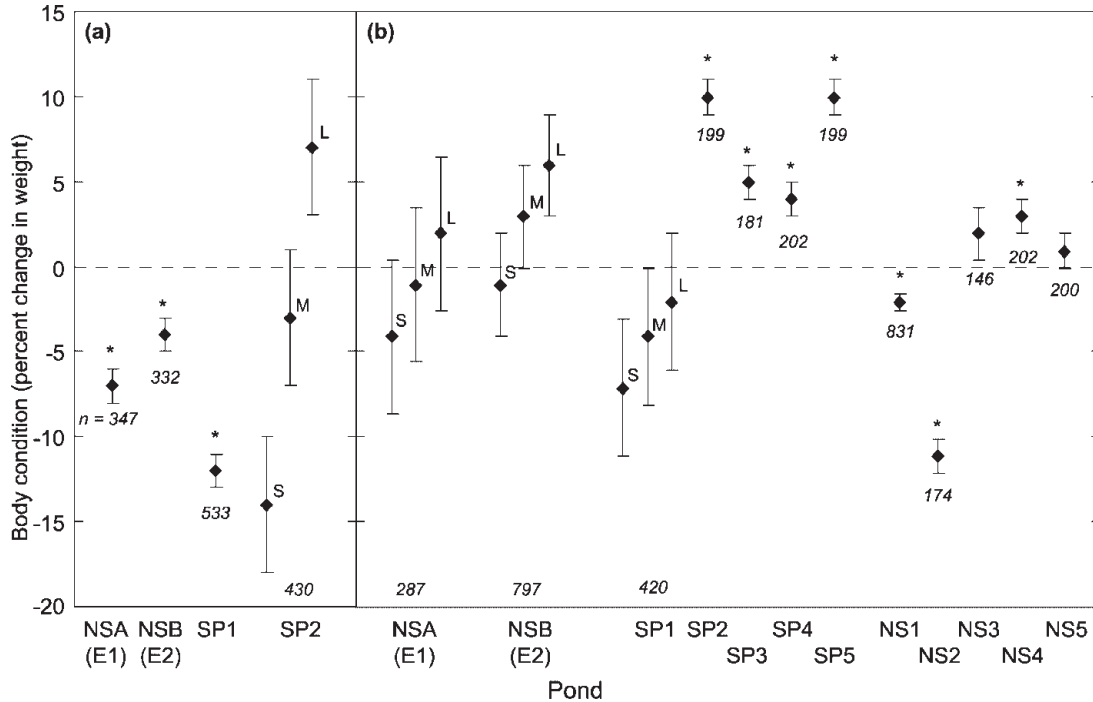
tagged fish recaptured in the ponds during monthly sampling varied from 1.0% to 76.8% (Table 4). Recapture percentages tended to be highest in August and September and were lowest during spawning in October and November. Total number of fish >60 mm captured during the monthly samples generally decreased during spawning periods (Table 4).

There was no evidence of a density-dependent effect on growth rate in this study (Fig. 3). There was no significant relationship between total fish density or specific size class densities and growth rates during any of the time periods when both growth and density could be measured (August–

September: total density, $p = 0.52$; density for fish > 60 mm, $p = 0.24$. September–October: total density, $p = 0.25$; density for fish > 60 mm, $p = 0.83$).

In 1999, growth rates of recaptured PIT-tagged fish were consistently greater in both the spawning ponds (SP1 and SP2) over all of the time periods (Fig. 4). There was no significant ($p > 0.05$) change in growth rate between time periods within either nonspawning pond (NSA and NSB, 1999). In the spawning ponds (SP1 and SP2), there were differences in growth rates between time periods but the patterns of growth were different (Fig. 4). In pond SP1, growth rates

Fig. 5. The influence of spawning on body condition of juvenile coho salmon (*Oncorhynchus kisutch*) >60 mm captured in four beaver ponds in 1999 (a) and 12 beaver ponds in 2000 (b). The percent change in weight was predicted by regression models for fish of the same length sampled during spawning (November) as compared with before spawning (September). Negative values indicate a decrease in weight during spawning compared with before spawning. An asterisk (*) denotes that the regression was significant ($p < 0.001$). In ponds where interaction was significant (i.e., regression lines not parallel), three representative lengths (S = 60 mm, M = 80 mm, L = 100 mm) were used to get the corresponding percent change in weight. Numbers next to each frame indicate sample sizes for estimates.



decreased significantly ($p < 0.001$, two-sided t tests) during both spawning time periods relative to before spawning (Fig. 4). In pond SP2, growth rates increased in both time periods during spawning relative to before spawning. The estimated difference in mean growth rate for fish in this pond was significant ($p = 0.01$, two-sided t tests) between the August–September and the September–October time periods but not between the August–September and the September–November time periods ($p = 0.44$, two-sided t test).

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, which corresponded with the addition of salmon eggs and carcasses. The nonspawning 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. 4). Growth rates significantly increased in ponds NSA(E1) and NSB(E2) ($p < 0.001$ in both ponds and time periods; t tests) during the egg and carcass enrichment relative to that before enrichment (Fig. 4).

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, two-sided 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 ($p = 0.005$, two-sided t test).

Influence of spawning on body condition during spawning

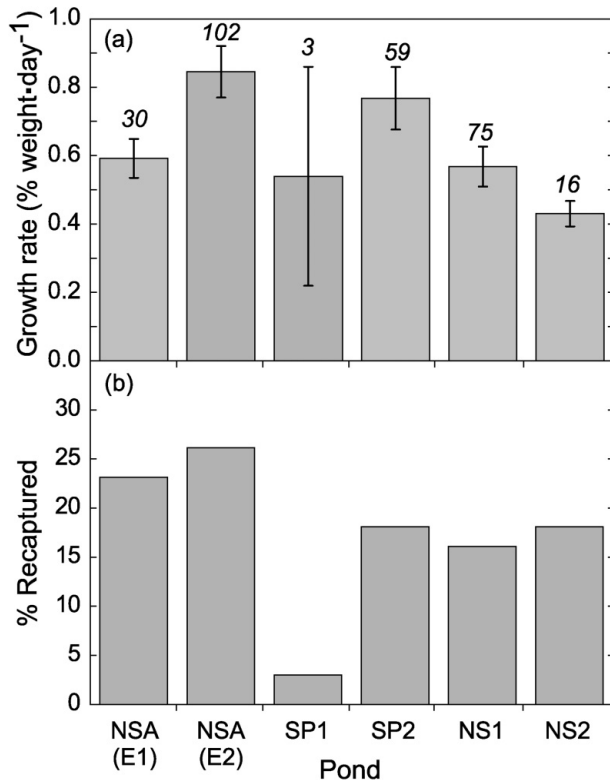
In 1999, spawning did not improve the body condition of most juvenile coho salmon. In ponds NSA, NSB, and SP1, fish of the same length weighed significantly less ($p < 0.001$) during spawning as compared with fish sampled in these ponds before spawning (Fig. 5a). In pond SP2, there was a significant ($p < 0.05$) interaction between the length–weight relationships before and during spawning. This indicated that the response of fish body condition to spawning depended on fish size. Larger fish (~100 mm) weighed more during spawning than before spawning, but the medium (~80 mm) and small (~60 mm) fish weighed less during spawning than before (Fig. 5a).

In 2000, the body condition of juvenile coho salmon in the spawning ponds generally improved during the spawning period. In ponds SP2–SP5, fish of the same length were significantly ($p < 0.001$) heavier during spawning than before (Fig. 5b). The increase in mean weight for fish of the same length in these ponds ranged from 4.2% to 11.4%. In pond SP1, the response of body condition to spawning varied with fish size, but condition was always less during spawning regardless of fish size (Fig. 5b).

In the enriched ponds, the body condition of medium-sized fish in pond NSB(E2) and of larger fish in both ponds were improved by the presence of carcasses and eggs (Fig. 5b). Small fish in both ponds did not show an improvement in body condition during the enrichment.

The change in body condition of juvenile coho salmon in the nonspawning ponds (NS1–NS5) varied during the spawning period (Fig. 5b). In two of five ponds (NS1 and NS2),

Fig. 6. Estimated mean (\pm standard error) growth rate (a) and survival to outmigration (b) of recaptured passive integrated transponder (PIT)-tagged juvenile coho salmon (*Oncorhynchus kisutch*) over the time period from the fall 2000 to smolt outmigration in the spring 2001 on the Copper River Delta, Alaska.



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. 5b). There was no major change in body condition associated with the spawning period in pond NS3 and NS5 (Fig. 5b). In pond NS4, the body condition of fish was significantly ($p < 0.0001$) improved during the spawning period.

Influence of spawning on overwinter growth rate and survival to outmigration

There was no significant difference in growth rate or survival over the winter between the ponds based on the recapture of PIT-tagged fish at the weir (Fig. 6; growth, $p = 0.22$; survival, $p = 0.23$; ANOVA F tests).

Discussion

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 nonspawning ponds. Although growth rates of fish in the spawning ponds were generally greater during the spawning period, small sample sizes, few replicates, and high variation gave little power to statistically test for a pond type (spawning vs. nonspawning) effect on growth rate.

The influence from spawning salmon on stream system productivity may not be easily discerned in all stream sys-

tems, over broad spatial scales, or in complex natural habitats such as the Copper River Delta. Other studies have documented variation in the responses of salmonids to artificial enrichment (Wilzbach et al. 2005) and in the response of stream biota to natural spawning (Chaloner et al. 2004). The effects of spawning may also be masked in stream systems where responses are limited by other habitat factors, such as canopy coverage (Wilzbach et al. 2005). The ponds that were used in this study were similar in physical characteristics, had open canopies, and no light limitations. However, there may have been high connectivity between the pond types owing to hydrologic and hyporheic flows that would enable nonspawning sites to be indirectly influenced by nutrients from spawning salmon. The nonspawning ponds may also receive salmon-derived nutrients from carcasses through animal transport and floodplain sources (Ben-David et al. 1998; O'Keefe and Edwards 2003). Hicks et al. (2005) found that the concentration of marine-derived nitrogen and carbon in various food organisms of juvenile salmonids in the ponds examined in the current study were similar. This suggests a strong hyporheic connection between ponds in our study system. In nonspawning ponds that may be connected in this manner, the 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 in the following spring (Wipfli et al. 1998).

At the individual pond level, the enrichment, and to some degree natural spawning, had immediate positive influences on the growth rate and body condition of juvenile coho salmon in the fall. These results are consistent with other studies concerning the influence of spawning on the growth of juvenile salmonids (Bilby et al. 1998; Wipfli et al. 2003). These studies were conducted in small stream habitats and artificial channels. Our study confirms that egg and carcass additions can be successful in boosting the short-term growth of juvenile coho salmon rearing in natural beaver pond habitats as well.

Salmon eggs appeared to be the main resource responsible for increased growth and body condition during enrichment. The diets of fish in the enriched ponds were dominated by eggs (Hicks et al. 2005). During the enrichment, most whole carcasses were intact, with minimal conditioning or decomposition, thus making them unavailable as an immediate food source to juvenile coho salmon. Salmon eggs, on the other hand, were immediately available for consumption by fish in these ponds. Diet analysis of the fish rearing in these ponds confirmed that few juvenile coho salmon consumed carcass flesh during the enrichment (Hicks et al. 2005).

Fish size mattered in the relative influence of enrichment on body condition. Larger fish were of better body condition than smaller fish rearing in the enriched ponds during the enrichment. The most plausible explanation for this result is that the availability and consumption of salmon eggs was greater for larger fish. Larger fish have a greater gape with which to consume eggs, and the larger the fish the more eggs that could potentially be consumed. Smaller fish may consume fewer eggs because of a reduced capacity to swallow an egg. Competition for eggs may also limit the number of eggs available to smaller fish. In feeding experiments,

Foote and Brown (1998) found that larger sculpins could eat more sockeye salmon (*Oncorhynchus nerka*) eggs than smaller ones. We do not know for sure whether salmonid juveniles were limited in number of eggs consumed or through competition in our study, but these results indicate that competition or lower consumption by smaller fish may have occurred.

The ability to trap juvenile coho salmon dropped substantially during the spawning period. This contrasts with results from other studies where densities increased because fish were attracted to spawning salmon (Bilby et al. 1998; Foote and Brown 1998). In this study, we used minnow traps (a passive method) to capture juvenile coho salmon. The salmon eggs used to bait these traps may not have had enough attractive capacity during spawning because other eggs and food resources may have been plentiful. Electrofishing (Bilby et al. 1998) and visual observation (Foote and Brown 1998) were used to document fish presence on spawning grounds in other studies.

Our study is one of only a few that has documented the response of juvenile salmonids to natural spawning in pristine stream systems where spawning salmon abundance and habitats have not been drastically reduced from historic conditions. Eastman (1996) found that juvenile coho salmon, rainbow trout (*Oncorhynchus mykiss*), and Arctic char (*Salvelinus alpinus*) exhibited increased growth and body condition during spawning by sockeye salmon in the Wood Lakes system, Alaska. In our study, increased growth rates and improved body condition in juvenile coho salmon were generally observed during spawning in ponds with spawning salmon. However, this was not always the case. In pond SP1, the presence of spawning salmon did not confer widespread or detectable benefits to juvenile coho salmon. There were also ponds without spawning that exhibited increased growth and improved body condition relative to before spawning.

There are many reasons why these ponds may not have fit the expected pattern. In a natural system, the full suite of foods and environmental conditions were available to the fish. The highest growth rates of fish observed during the study were from pond SP1 before spawning from August–September 1999. This time period coincides with high rainfall on the Copper River Delta (32.8 cm from 23 August to 15 September, National Oceanic and Atmospheric Administration weather station, Cordova airport). The upper reaches of this system, especially the East Fork consist of high gradient, contained channels that typically result in “flashy” rain and snowmelt events (Blanchet 1983). 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, ~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. In this case, the short-term benefits of flood-related resource availability might have far outweighed that from spawning salmon.

The presence of Sitka alder may also lessen the dependence of spawning fish as a nutrient source in nonspawning ponds. Sitka alder, a nitrogen fixer, is a dominant component

of the riparian plant community around beaver ponds on the Copper River Delta. Alder can represent a major source of nutrients to aquatic communities (Volk et al. 2003) and may be as influential as salmon carcasses in terms of nitrogen enrichment (R.T. Edwards, USDA Forest Service, Pacific Northwest Research Station, 2770 Sherwood Lane, Juneau, AK 99801, USA, personal communication). Alder leaf fall coincides with the arrival of spawning coho salmon on the Copper River Delta and may provide an equal boost in food and nutrient input to the nonspawning ponds.

The fall may also be a time of increased aquatic and terrestrial invertebrate abundance. The diets of fish in the natural spawning and nonspawning ponds were similar and composed mostly of aquatic invertebrates (Hicks et al. 2005). Eggs and carcass material only accounted for a small percentage of the diet of sampled fish in the spawning ponds (Hicks et al. 2005). Corixidae were particularly abundant during spawning in all of the ponds, and they were a major dietary component of juvenile coho salmon in the fall and early winter.

Management implications

This study suggests that enrichment of natural beaver pond habitats with salmon carcasses and eggs can have immediate impacts on the growth rates of juvenile salmonids. Most salmon nutrient restoration efforts have focused on the introduction of carcasses only. To maximize immediate effectiveness for juvenile fish, salmon eggs should be included along with carcasses. Eggs are more readily available and have greater energy content than carcasses. 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.

Fisheries managers should consider the geographic region and the limiting factors associated with the stream system and fish population of interest before incorporating nutrient enrichment projects. Limiting factors such as canopy coverage or overwinter habitat may reduce the potential for carcass and egg enrichments to work. Wilzbach et al. (2005) suggested that in light-limited systems, canopy removals might be more beneficial than enrichment. Enrichment alone may not be enough to increase productivity and smolt abundance in streams with degraded habitats that limit juvenile capacity. 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 limited the number of smolts produced. Some combination of enrichment, stream habitat improvement, and canopy removal may be needed to restore highly degraded systems.

Gende et al. (2002) noted that it is important to validate experimental results in natural stream environments and to explore potential site- or system-specific variability in the response of freshwater systems to spawning salmon. In our study, the response of juvenile coho salmon to fall-spawning salmon was variable. In most ponds, natural spawning positively influenced short-term growth and body condition in

the fall, and carcass and egg enrichment greatly increased the growth of fish rearing in ponds that were not naturally exposed to spawning. However, there was little evidence that the short-term benefits observed in the fall led to greater overwinter growth rates or survival to outmigration when compared with fish from ponds that were not directly influenced by spawning salmon in the fall. One potential reason for this result may be that nutrients from spawning salmon are widely distributed across the delta because of hydrologic connectivity and hyporheic flows. There may also be other important factors unrelated to spawning salmon that are important for smolt production. The relationship among spawning salmon, overwinter growth, and smolt production on the Copper River Delta does not appear to be limited to a simple positive feedback loop.

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