Habitat Utilization by Juvenile Pacific Salmon (*Onchorynchus*) in the Glacial Taku River, Southeast Alaska

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Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, southeast Alaska. Can. J. Fish. Aquat. Sci. 46: 1677–1685.

Habitat utilization was determined in summer 1986 by sampling 54 sites of nine habitat types: main channels, backwaters, braids, channel edges, and sloughs in the river; and beaver ponds, terrace tributaries, tributary mouths, and upland sloughs on the valley floor. Physical characteristics were measured at all sites, and all habitats except main channels (current too swift for rearing salmon) were seined to determine fish density. Sockeye (*Oncorhynchus nerka*) averaged 23 fish/100 m^2, nearly twice the density of coho (*O. kisutch*) and four times that of chinook (*O. tshawytscha*), 14 and 6 fish/100 m^2, respectively. Sockeye were age 0, 27–84 mm fork length (FL), and most abundant in upland sloughs, beaver ponds, and tributary mouths. Coho were ages 0 and 1, 33–132 mm FL, and most abundant in beaver ponds and upland sloughs. Chinook were age 0, 40–93 mm FL, and more abundant than the other species in habitats with faster currents (1–20 cm/s), particularly channel edges. Each species was absent from about one-quarter of the seining sites of each habitat type. Thus, the lower Taku River provides important summer habitat for juvenile salmon, but many suitable areas were unoccupied, possibly because of their distance from spawning areas and poor access for colonizing fish.

En été 1986, pour connaître l'utilisation de l'habitat, on a échantillonné 54 points dans 9 types d'habitats : bras principaux, eaux dormantes, bras anastomosés, zones riveraines et portions marécageuses de la rivière ainsi qu'étangs de castors, tributaires de terrasse, embouchure de tributaires et marécages sur le fond de la vallée. On a mesuré les caractéristiques physiques à tous les points d'échantillonnage et l'on a senné tous les habitats, sauf les canaux principaux (où le courant est trop rapide pour l'élevage du saumon) afin de déterminer la densité de poissons. La densité moyenne de saumons rouges (*Oncorchynchus nerka*) était de 23 poissons/100 m^2 ce qui est à peu près le double de la densité de saumons coho (*O. kisutch*) et quatre fois la densité de saumons quinnat (*O. tshawytscha*) qui étaient respectivement de 14 et 6 poissons/100 m^2. Les saumons rouges étaient de la classe d'âge 0 et mesuraient 27–84 mm de longueur à la fourche (LF); ils étaient surtout abondants dans les marécages du fond de la vallée, les étangs de castors et à l'embouchure des tributaires. Les saumons coho étaient de classe d'âge 0 et 1, mesuraient 33–132 mm de LF et abondaient surtout dans les étangs de castors et les marécages du fond de la vallée. Enfin, les saumons quinnat étaient de classe d'âge 0, mesuraient 40–93 mm de LF et étaient plus nombreux que les autres dans les habitats où les courants sont plus rapides (1–20 cm/s), particulièrement dans les zones riveraines. Chacune des espèces était absente d'environ un quart des points de sennage dans les différents types d'habitats. Le cours inférieur de la rivière Taku est donc un habitat d'été important pour le saumon juvénile, mais un bon nombre de zones propices étaient inoccupées, peut-être parce qu'elles se trouvent à distance des eaux de fraye et qu'elles sont difficilement accessibles pour les poissons cherchant un milieu à coloniser.

Received July 25, 1988
Accepted June 16, 1989
(J9820)

Reçu le 25 juillet 1988
Accepté le 16 juin 1989

The glacial Taku River, which originates in British Columbia and flows through Southeast Alaska, is an important producer of Pacific salmon (*Oncorhynchus* spp.) for both United States and Canadian fisheries (Clark et al. 1986). The U.S./Canada Pacific Salmon Treaty establishes goals to manage the salmon stocks in such "transboundary" rivers for conservation, optimum production, and equitable sharing by the two countries (Natural Resources Consultants 1986). To accomplish these goals, information is needed on habitat utilization by juvenile salmon so that the stocks can be managed for maximum production from available habitat. Although chinook (*O. tshawytscha*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon are known to rear in the lower reaches of turbid Alaska rivers (Alaska Department of Fish and Game 1983; Wood et al. 1987; J. Edgington and J. Lynch, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833 USA, unpubl. data), their use of this habitat is ill-defined. The purpose of this study was to determine patterns of habitat utilization by juvenile salmon in summer in the lower Taku River.

Study Area

The Taku River originates in northern British Columbia and flows through the Coast Range Mountains to Taku Inlet 40 km east of Juneau, Alaska (Fig. 1). The watershed is composed of 16 000 km^2, 95% of which is in Canada. Most of the year, the river is turbid with glacial silt. River flow is low (<100 m^3/s) in winter and high (>700 m^3/s) during snowmelt in June (Clark et al. 1986). Each summer, the lower river floods when ice dams impounding a lake on the Tulsequah River, 7 km upstream of the U.S./Canada border, suddenly break, sometimes tripling the river flow.

Five species of salmon occur in the drainage and are exploited by Canadian and Alaskan fisheries. Sockeye is the most numer-

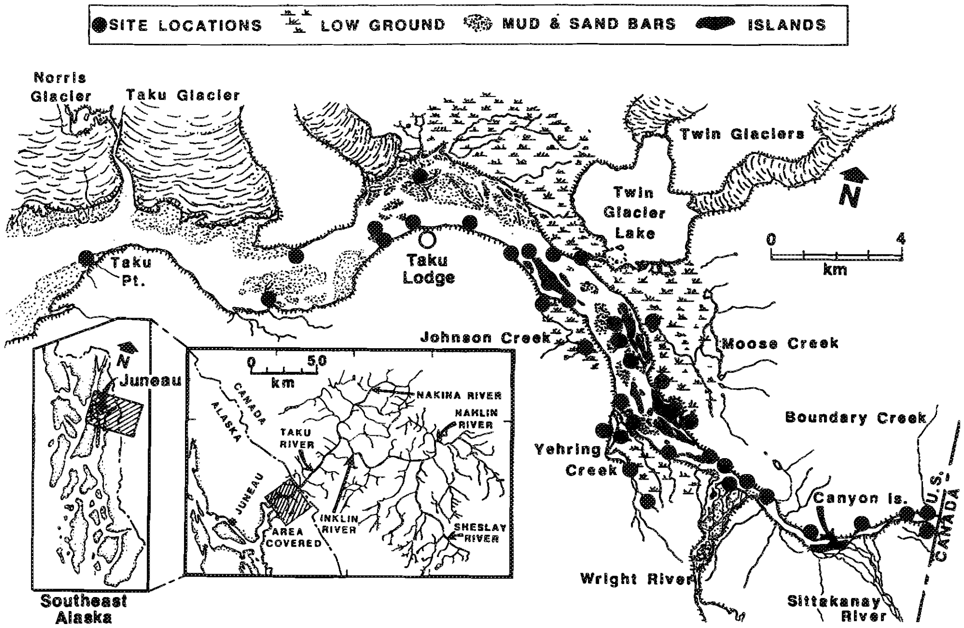

FIG. 1. Study area and locations of sampling sites in the lower Taku River, Southeast Alaska.

ous and valuable species in Taku River fisheries, with an annual harvest of about 100 000 fish (McPherson and McGregor 1986). Chinook stocks have been depressed and the fishery restricted since the 1970s. Annual adult returns of spring chinook recently have averaged 7500; in the 1950s, returns were typically about 25 000 (Kissner 1984). Adult returns of the other species are not well known, but are estimated to average 170 000 coho, 80 000 pink (*O. gorbuscha*), and 70 000 chum (*O. keta*) salmon (Alaska Department of Fish and Game, Commercial Fish Division, Juneau, unpubl. data).

This study was limited to the lower 28 km of the river between the river mouth at Taku Point and the U.S./Canada border, including off-channel areas on the valley floor (Fig. 1). In this area, the river flows within a wide (2–4 km), U-shaped glacial valley. The active river channel expands from 400 m wide at the border to nearly 3 km wide near the mouth. The river is extensively braided, and the substrate changes from mixed sand, gravel, and cobble near the border to mostly sand and silt near the mouth. Downstream of Taku Lodge, river height fluctuates 0–3 m daily during summer because of tidal influence as the river backs up during high tide; however, salt water does not intrude upstream beyond Taku Point.

Off-channel habitats on the valley floor consist of small, spring-fed streams often impounded by beaver dams, as well as tributary streams and rivers which drain valley slopes and flow across the valley floor to the river. Tributaries are glacial, humic (organic stain), or clear, depending on source and season. Sitka spruce (*Picea sitchensis*) and cottonwood (*Populus trichocarpa*) dominate high ground, and willow (*Salix* spp.) and red alder (*Alnus rubra*) flourish on low ground.

Methods

To determine habitat utilization by juvenile salmon, the habitat classification systems of Sedell et al. (1983); Alaska Department of Fish and Game (1983); and Edgington and Lynch (J. Edgington and J. Lynch, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833 USA, unpubl. data) were adapted to classify habitat into two broad categories:

TABLE 1. Definitions of habitat types for classifying salmon rearing areas of the lower Taku River, Alaska.

Habitat type	Definition
River habitats	
Main channel	Area of main river flow; turbid, deep, turbulent, and rapid (>30 cm/s).
Braid	Shallow channel across mudflat or channel bar; water velocity moderate (10–30 cm/s).
Channel edge	Margin of main channels with moderate water velocity (<30 cm/s).
Slough	Slough formed when sediment and organic debris block the head of a braid or branch of a main channel. Water velocity varies from slow (0–15 cm/s) at low stage to rapid at high stage.
Backwater	Slack water formed by obstructions, such as a point bar in the main channel.
Off-channel habitats	
Terrace trib	Stream flowing across the valley floor to the river; may be glacial, humic, or clear.
Trib mouth	Lower reach of a tributary affected by the river; often has slack water.
Beaver pond	Terrace tributary impounded by beaver dam.
Upland slough	A slough fed by spring or terrace tributary; has outlet to the river.

(1) river habitats within the active river channel, and (2) off-channel habitats on the valley floor. Each category was divided further according to water velocity regime, for a total of five river habitats and four off-channel habitats (Table 1). A total of 54 sites (3 to 17 of each type) were selected to give a representative sample of available habitat. Each site was sampled once between 8 July and 18 September 1986. Habitat types were sampled in random order to eliminate temporal bias. All habitat types except main channels were sampled for both habitat characteristics and fish density.

To describe habitat, selected physical characteristics were measured at each site. Water depth (measured with a meter stick) and velocity (measured at mid-depth with a current meter) were measured at one-quarter, one-half, and three-quarters across the middle of each station; pieces of large woody debris (>10 cm diameter) were counted; and water temperature was taken. Turbidity of a water sample from each site was determined to the nearest 50 Jackson turbidity units (JTU) by titrating a standard suspension into distilled water and comparing it with the sample (American Public Health Association 1971).

To estimate fish density, at least three separate stations spaced 50 m apart at each of 49 sites were seined for fish. Main channels, except for channel edges, were assumed too swift (mean, 102 cm/s) to contain rearing salmon (Hillman et al. 1987) and were not seined. Where water was too deep to wade (beaver ponds, sloughs, and tributary mouths), a beach seine (15.2 m long, 2 m deep, 6-mm mesh) was set from a boat and retrieved from shore; the area seined was 37 m^2. Where water was shallow enough to wade (channel edges, braids, backwaters, and terrace tributaries), a pole seine (3 m long, 1.2 m deep, 6-mm mesh, and fixed with a pole at each end) was pulled against the current parallel to shore for 20 m; the area sampled was 54 m^2. Stations with woody debris were seined by working the net around the debris; however, seining probably was less effective in dense debris than in other areas.

The number of fish at each station was estimated by the removal method (Zippin 1958), based on at least three passes with a seine. The removal method minimized bias from using different capture methods in the different habitat types. During sampling, probability of capture was assumed constant, and immigration and emigration were assumed negligible. Salmon probably did not avoid the seine in most areas because of turbidity. Population estimates were divided by the area seined to compute density, and density at each site ws computed as the mean at the stations. Fish were anesthetized with MS-222, identified to species, counted, and measured for fork length (FL). Scales were taken from up to 25 fish of each species to determine age: age-0 fish were young-of-the-year, and age-1 fish had one winter annulus. After sampling, fish were released where they had been captured.

Overlap in habitat use (Horn 1966) between salmon species was calculated as

$$C = \frac{2 \sum_{i=1}^{n} X_i Y_i}{\sum_{i=1}^{n} X_i^2 + \sum_{i=1}^{n} Y_i^2}$$

where C is overlap and X_i and Y_i are catches of species X and Y from habitat type i of the n habitat types, as a proportion of the total catches in all samples. Overlap ranges from 0 (complete segregation) to 1 (complete overlap), and values greater than 0.6 are considered significant (Zaret and Rand 1971).

Total populations of juvenile salmon in the area of the lower river between Taku Point and the U.S./Canada border were estimated from the mean fish densities and total area of each habitat type in the lower river. Area of habitats was measured with a computer by digitizing outlines of habitats drawn on aerial photographs (Fig. 2; U.S. Department of Agriculture, Agricultural Stabilization and Conservation Service, August 1977; scale, 1:6272). Area of channel edges was computed from the length of main channels by assuming an average edge width of 3 m. This edge width approximated the area of reduced current in most channels and equalled the length of the net used to sample fish. Confidence limits for total populations were computed from the variance for the stratified population mean (Cochran 1953). To determine degrees of freedom, the number of potential sites was computed for each habitat type by dividing its total area by the mean area sampled in the sites of that type.

Results

Sockeye, coho, and chinook were the most abundant salmonids. Overall sockeye density at 49 sites averaged 23 fish/100 m^2, nearly twice the density of coho (14 fish/100 m^2) and four times that of chinook (6 fish/100 m^2). Dolly Varden (*Salvelinus malma*) also were captured, but in low mean density (<1 fish/100 m^2). A few chum salmon, steelhead trout (*O. mykiss*) and cutthroat trout (*O. clarki*) also were caught, and sculpins (*Cottus* spp.), sticklebacks (*Gasterosteus aculeatus*), and whitefish (*Prosopium* spp.) sometimes were abundant, but numbers were not analyzed.

Salmon Size and Age

Sockeye and chinook were predominantly (99%) age 0, and ranged from 27 to 84 mm and 40 to 93 mm FL, respectively; coho were mixed ages 0 and 1, and ranged from 33 to 132 mm FL (Fig. 3). Age composition of coho differed between beaver ponds and other habitats: beaver ponds averaged 89% age 1, and other habitats averaged 96% age 0. Length frequency distributions of sockeye, chinook, and age-1 coho were approximately normal, whereas that of age-0 coho was highly skewed, with a concentration in the smallest length classes.

Mean FL increased during the study period, indicating apparent growth (Fig. 4). From early July to mid-September, sockeye mean FL increased 0.25 mm/d, from 40 to 58 mm; age-0 coho mean FL increased 0.14 mm/d, from 39 to 49 mm; and chinook mean FL increased 0.15 mm/d, from 55 to 66 mm. Except for some beaver ponds, all habitat types had similar mean FL. In beaver ponds in the south-facing Sockeye Creek drainage (Fig. 1), sockeye and age-0 coho were significantly ($P<0.025$; *t*-test) larger than expected, based on the regression equations, probably because of warmer water in the ponds (Table 2). The regression of chinook mean FL on date had more variation and a lower R^2 than that of the other species. Some of this variation was caused by a trend in chinook size with location in the river. Chinook mean FL was negatively correlated ($r = -0.67$; $P<0.01$) with distance from the river mouth and decreased from 70 mm in the tide-influence zone to 62 mm at the U.S./Canada border (Fig. 5).

Habitat Utilization

Physical characteristics of the sites differed significantly ($P<0.05$; Kruskal–Wallis test) between habitat types (Table 2). Mean water velocity was lowest (0–5 cm/s) in sloughs, backwaters, tributary mouths, upland sloughs, and beaver ponds; intermediate (10–21 cm/s) in braids, channel edges, and terrace tributaries; and highest (102 cm/s) in main channels. Mean depth ranged from 0.3 m in braids to 1.0 m in beaver ponds and 2.9 m in main channels. Typically, river habitats were turbid (means, 240–400 JTU), whereas off-channel habitats were clear or humic (means, 20–208 JTU). Large woody debris was common in terrace tributaries but absent from upland sloughs. Water temperature was 2–4°C higher in beaver ponds and upland sloughs than in channel edges, braids, and terrace tributaries. Temperature of channel edges and braids was not significantly correlated with distance from Taku Point ($r=0.22$; $P=0.13$;

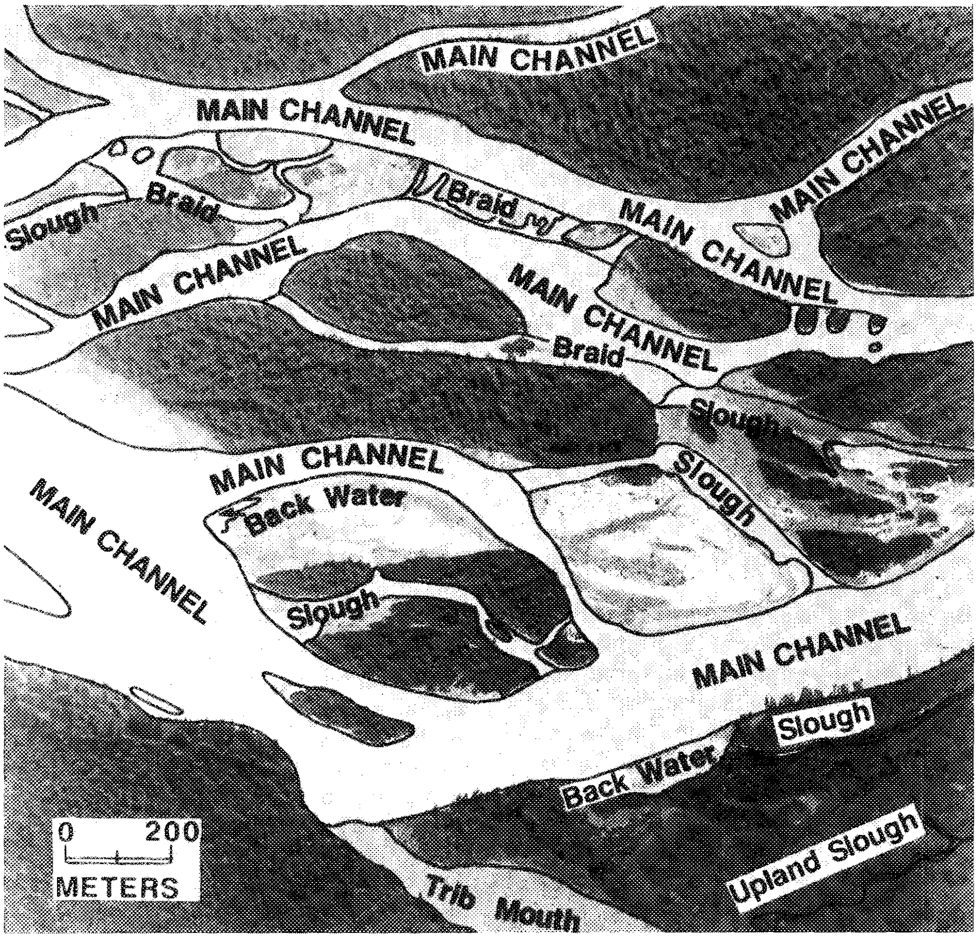

FIG. 2. Example of an aerial photograph of a section of the lower Taku River, with habitat types delineated.

from Taku Point ($r=0.22$; $P=0.13$; $n=28$); thus, temperature did not change longitudinally along the river.

Distribution of salmon was most closely related to water velocity, and turbidity had a secondary influence. Sockeye and coho occupied significantly ($P<0.05$; Kolmogorov–Smirnov test) slower current than chinook (Fig. 6). Sockeye and coho densities were highest in still or slow water (≤10 cm/s), whereas chinook density was highest in slow-to-moderate current (1–20 cm/s). All species were virtually absent from areas with currents greater than 30 cm/s. Correlations (r) between fish densities and turbidity in all 49 sites were weak: 0.14 ($P=0.16$) for chinook, −0.24 ($P=0.05$) for sockeye, and −0.32 ($P=0.01$) for coho. Differences in water velocity may have masked effects of turbidity. For sites with suitable water velocity (≤10 cm/s for sockeye and coho and 1–20 cm/s for chinook, based on relationships in Fig. 6), both sockeye and coho had significantly ($P<0.01$; Kruskal–Wallis test) lower density in highly turbid (≥400 JTU) than in less turbid water (Fig. 7). Chinook density, however, was similar ($P>0.05$) in areas of different turbidity.

Mean salmon density in the habitat types corresponded to water velocity but also differed between the river and off-channel areas (Fig. 8). Sockeye were most abundant (means, 36–73 fish/100 m^2) in sloughs in the river and tributary mouths, beaver ponds, and upland sloughs off channel — all habitats with mean water velocity less than 10 cm/s (Table 2). Coho almost exclusively occupied off-channel habitats with slow water; the highest mean densities were in beaver ponds and upland sloughs (58–59 fish/100 m^2). Coho were consistently scarce (means, 1–3 fish/100 m^2) in river habitats, even those with slow water. Chinook primarily were in river habitats, particularly sloughs and channel edges (means, 6–8 fish/100 m^2), and off-channel terrace tributaries and tributary mouths (means, 5–8 fish/100 m^2) — all habitats with mean water velocity 3–15 cm/s. Chinook were virtually absent (mean, <1 fish/100 m^2) from beaver ponds and upland sloughs. Differences in density between habitat types were significant ($P<0.05$; $N=49$; Kruskal–Wallis test) for coho and chinook but not for sockeye ($P=0.35$) because sockeye were absent from several beaver ponds and upland sloughs.

Each species was present in only about three-quarters of the sites, and even the most suitable habitat often was unoccupied (Fig. 8). Sockeye, for example, were absent from one-half of the beaver ponds and one-quarter of the upland sloughs, yet density exceeded 150 fish/100 m^2 in some of these habitats. Maximum density within a habitat type, a measure of habitat suitability, was unrelated to occurrence of a species in the habitat. Habitat types with extremely low maximum density (≤5 fish/100 m^2) had low percent frequency of occurrence (%FO), but in others, %FO averaged 74% and was not correlated ($r=0.00$) with maximum density (i.e. unrelated to suitability).

Overlap (C) in habitat use was high (0.80) between sockeye and coho, moderate (0.38) between sockeye and chinook, and low (0.18) between coho and chinook. Mean densities of sock-

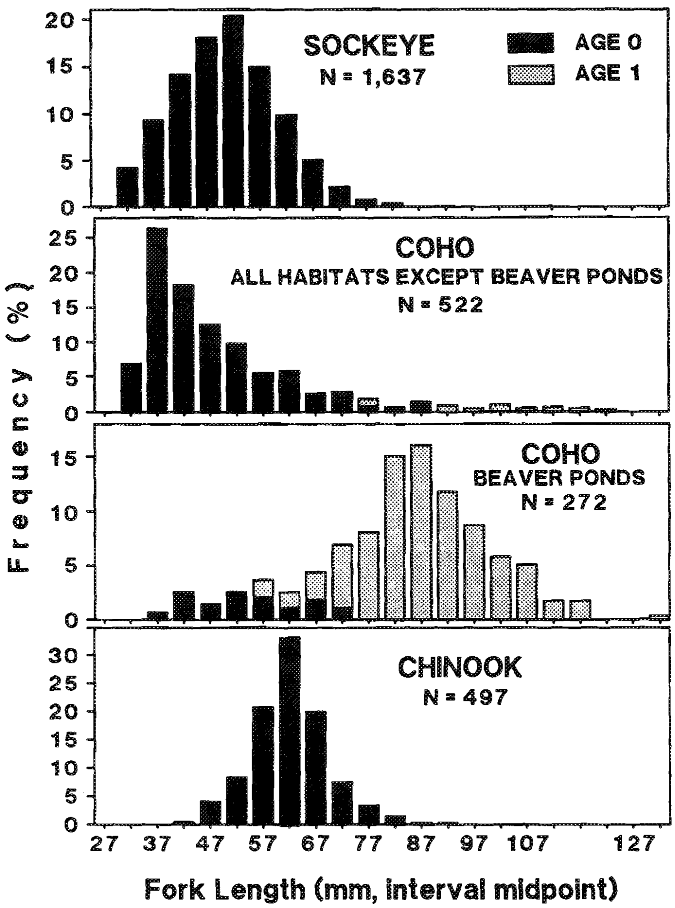

FIG. 3. Frequencies of fork length (in 5-mm intervals) and age classes of juvenile sockeye, coho, and chinook salmon from the lower Taku River, Alaska, July–September 1986.

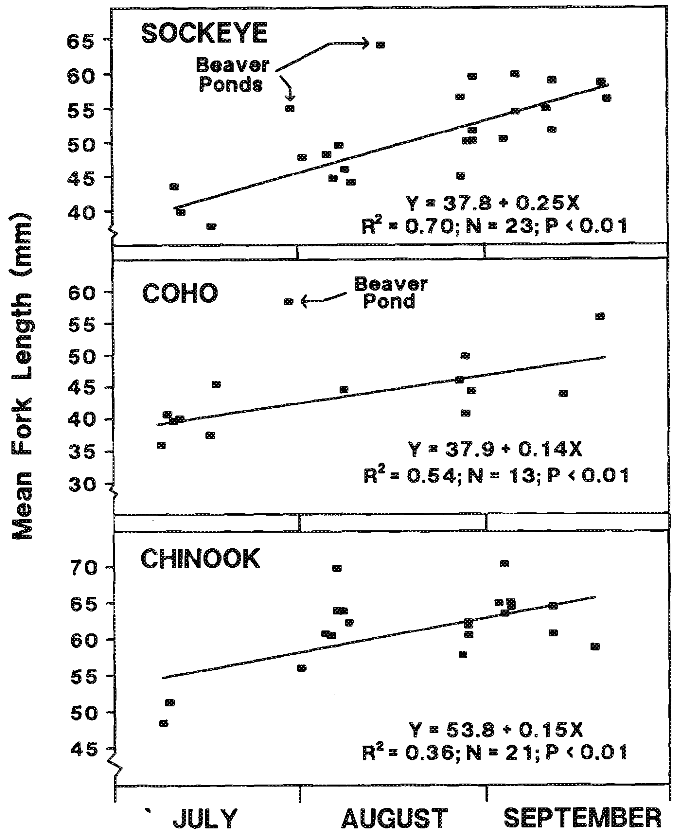

FIG. 4. Mean length of age-0 sockeye, coho, and chinook salmon in the lower Taku River, Alaska, July–September 1986. Regression equations relate mean FL (Y) to number of days (X); day 1 = July 1. Data are from sites with at least six FL measurements. The three labeled points representing beaver ponds were outliers and were not used in the regressions.

eye and coho in the habitat types also were positively correlated (rank correlation $r_s = 0.83$; $P<0.01$; $n=8$), whereas coho and chinook were negatively correlated ($r_s = -0.75$; $P<0.05$). Both sockeye and coho were abundant in upland sloughs, beaver ponds, and tributary mouths; however, sockeye were less abundant in terrace tributaries and more abundant in sloughs and backwaters than were coho. Coho and chinook generally occupied different habitats, with the exception that both species occurred in moderate density in terrace tributaries and tributary mouths. Each species, however, occurred independently of the others ($P>0.50$; Chi-square test; $n=49$). Presence of coho at a site, for example, did not influence occurrence of sockeye and chinook.

Total wetted area of the lower Taku River and its off-channel habitats was 1932 ha and consisted mostly of main channels and braids (Table 3). Main channels, which were too swift for rearing salmon, comprised 70% of the area, and braids, which were marginal habitat, comprised 21% of the area. All other river habitats were only 4% of the area, and all off-channel habitats were only 5% of the area. Because of the large area of braids, the greatest number of sockeye and chinook were in this habitat, even though mean density in braids was low. The habitats with highest mean densities, however, were only a small part of the total area. Tributary mouths and beaver ponds, for example, were only 2.2% of the area but accounted for 52% of the coho. Estimated total populations were 641 000 sockeye; 293 000 coho; and 248 000 chinook, for a total of 1 million salmon of the three species. Because of a large variance in salmon density within habitat types, the 95% confidence intervals were wider than ±50% of the estimated total populations.

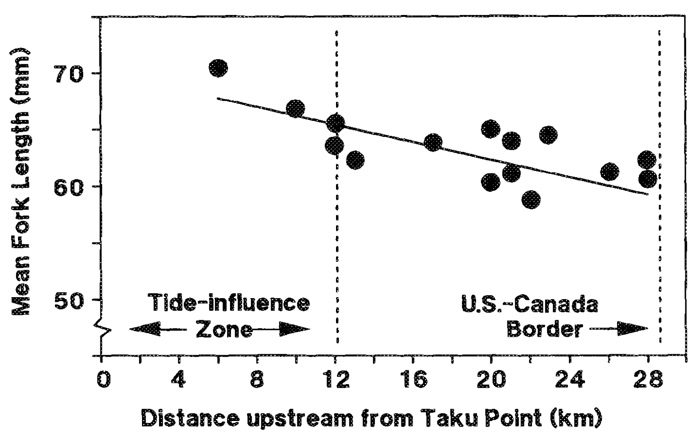

FIG. 5. Longitudinal trend in mean fork length of juvenile chinook salmon in channel-edge and braid habitats in the lower Taku River, Alaska, July–September 1986. Data are from sites with at least six FL measurements.

Discussion

Fish Density

The results indicate that the lower Taku River and associated

TABLE 2. Mean physical characteristics of habitat types in the lower Taku River, Alaska, summer 1986. Habitat types are defined in Table 1. Ranges are in parentheses.

	River habitats					Off-channel habitats			
	Main channel	Braid	Channel edge	Slough	Backwater	Terrace tributary	Tributary mouth	Beaver pond	Upland slough
Number of sites	5	5	17	5	3	5	6	4	4
Water velocity (cm/s)	102 (30–240)	19 (10–27)	11 (3–30)	3 (0–16)	1 (0–1)	15 (11–20)	5 (0–15)	0 (0–1)	1 (0–2)
Water depth (m)	2.9 (1.6–3.8)	0.3 (0.2–0.5)	0.4 (0.2–0.6)	0.5 (0.3–0.7)	0.6 (0.4–0.7)	0.5 (0.4–0.7)	0.8 (0.2–1.2)	1.0 (0.6–1.4)	0.9 (0.2–1.4)
Turbidity (JTU[a])	400 (400–400)	400 (400–400)	383 (100–600)	240 (0–400)	400 (400–400)	20 (0–100)	208 (0–400)	25 (0–100)	150 (0–300)
LWD[b] (No./station)	0.07 (0.0–1.0)	0.07 (0.0–0.3)	0.17 (0.0–1.0)	0.13 (0.0–0.7)	0.17 (0.0–0.5)	0.27 (0.1–1.0)	0.06 (0.0–0.3)	0.08 (0.0–0.7)	0.00 (0.0–0.0)
Water temperature (°C)	8.0 (4.6–9.8)	8.7 (7.2–10.7)	7.9 (4.6–9.7)	10.3 (7.9–11.9)	9.5 (8.3–10.6)	9.1 (8.3–11.2)	9.5 (6.9–12.8)	12.0 (9.5–15.4)	11.4 (9.4–16.2)

[a]Jackson turbidity units.
[b]Large wood debris (>10 cm diameter).

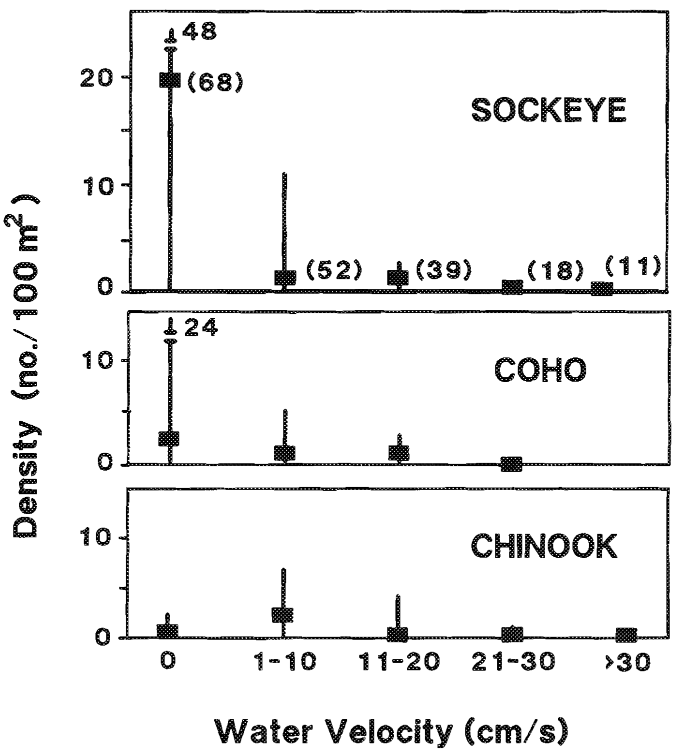

FIG. 6. Density of juvenile sockeye, coho, and chinook salmon in relation to water velocity at 188 seining stations in the lower Taku River, Alaska, July–September 1986. Symbols are medians, bars are interquartile ranges, and number of stations (N) is in parentheses.

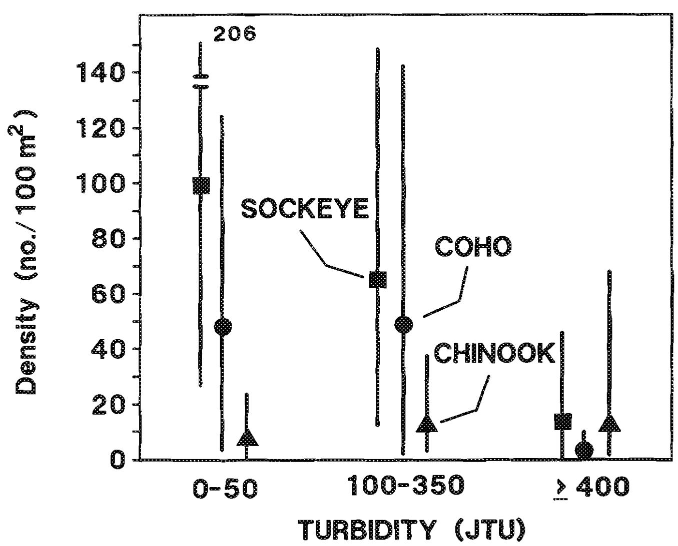

FIG. 7. Density of juvenile sockeye, coho, and chinook salmon in relation to turbidity in the lower Taku River, Alaska, July–September 1986. Data are from sites with suitable mean water velocity, based on relationships in Fig. 6 (≤10 cm/s for sockeye and coho, and 1–20 cm/s for chinook). Symbols are means and bars are ranges. Number of sites per species were 9–10 at 0–50 NTU, 4–5 at 100–350 NTU, and 16–18 at ≥400 NTU.

off-channel areas provide rearing habitat for an estimated 1 million juvenile sockeye, coho, and chinook salmon. This may be an underestimate, however, because of our methods. Seining within accumulations of woody debris probably underestimated true fish densities. Also, the number of sites was insufficient to provide reliable estimates of mean density for all habitat types, and some important areas may have been missed. Although much of the area covered by the aerial photographs was checked on the ground, some areas had poor access and could not be verified. Further, density data for fish were not normally distributed, and parametric statistics may have given biased estimates of total populations and confidence intervals. Thus, these estimates should be considered only approximations of the actual total populations of juvenile salmon in the lower river.

Two types of juvenile sockeye probably were present in the lower river: "river-type" sockeye, which rear in rivers for 1 yr; and "sea-type" sockeye, which migrate to sea as underyearlings (Wood et al. 1987). Based on adult scales, about 40% of the adult sockeye that spawn in the mainstem Taku River went to sea as underyearlings, and 60% wintered in fresh water (McPherson and McGregor 1986). Age-0 sockeye migrate to sea from the Taku River primarily from late June through September at a mean FL of 55 mm (Murphy et al. 1988). Thus, many of the juvenile sockeye we caught in the river may have been migrating to sea and only temporarily rearing in the lower river. River-type and sea-type sockeye also are present in other

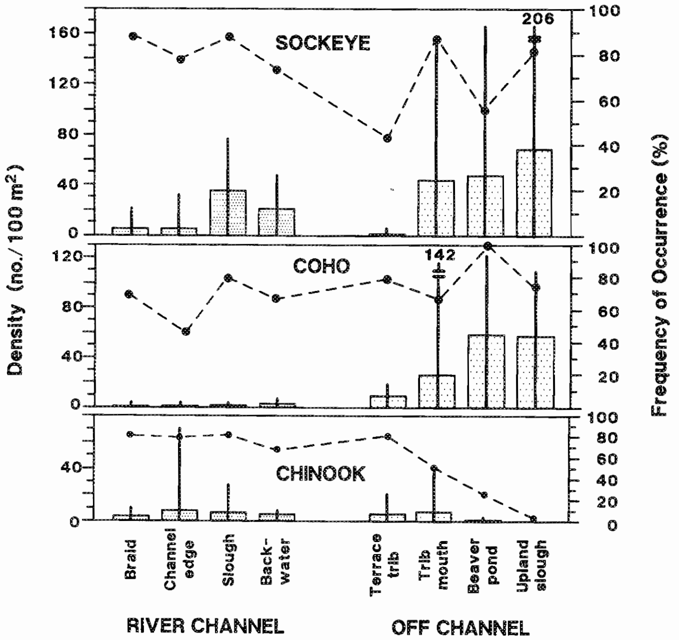

FIG. 8. Density and frequency of occurrence of juvenile sockeye, coho, and chinook salmon by habitat type in the lower Taku River, Alaska, July–September 1986. Histograms and bars show mean and range of density; shaded circles connected by dashed lines show frequency of occurrence. Number of sites sampled per habitat is shown in Table 2.

glacial Alaska rivers, including the Copper, Stikine, and Susitna Rivers, as well as smaller, nonglacial rivers of the northeastern coast of the Gulf of Alaska (McPherson 1987).

Densities of salmon in the lower Taku River were comparable to other studies. The range in mean density of coho in off-channel habitats (9–59 fish/100 m^2) was similar to the range in density in numerous small streams in Southeast Alaska (18–74 fish/100 m^2; Elliott and Hubartt 1983; Murphy et al. 1984; Murphy et al. 1986). In ponds and upland sloughs, mean sockeye density per unit water volume (0.38 fish/m^3; based on area seined and depth of the net or habitat) was within the range of densities in Babine Lake, B.C. (0.1–1.7 fish/m^3; Johnson 1961), and was greater than the average for Southeast Alaska lakes (0.1/m^3; J. Koenings, Alaska Department of Fish and Game, P.O. Box 3150, Soldotna, AK 99669 USA, pers. comm.). Mean chinook density in channel edges (8 fish/100 m^2) was similar to the density (14 fish/100 m^2) in channel edges of the Stikine River, Alaska (J. Edgington and J. Lynch, Alaska Department of Fish and Game, P.O. Box 667, Petersburg, AK 99833 USA, unpubl. data) but less than 15% of chinook density in an Idaho stream (56–69 fish/100 m^2; Hillman et al. 1987).

Size and Growth

Changes in size of juvenile salmon indicate apparent growth. From early July to mid-September, mean FL of sockeye and chinook increased 0.25 and 0.15 mm/d, respectively, and the mean FL of both species in September (58 and 66 mm, respectively) was similar to the mean FL of age-1 smolts (65 and 76 mm, respectively) that migrate to sea in June (Murphy et al. 1988). Mean FL of age-0 coho increased 0.14 mm/d, but the mean FL attained in September (49 mm) was only 58% of the mean FL of age-1 smolts (85 mm) that migrate to sea in June (Murphy et al. 1988). Growth of age-0 coho probably was

TABLE 3. Area, mean fish density, and total population of juvenile salmon by habitat type in the U.S. part of the Taku River. Standard error of fish density is in parentheses.

Habitat type	Area		Fish density (No./100 m^2)			Total population (thousands)		
	(ha)	(%)	Sockeye	Coho	Chinook	Sockeye	Coho	Chinook
River habitats								
Main channel*	1342	69.5	0	0	0	0	0	0
Braid	408	21.1	5.5 (4.1)	1.0 (0.8)	3.4 (1.6)	224	41	139
Channel edge	36	1.9	5.8 (2.2)	1.0 (0.3)	8.4 (4.4)	21	3	30
Slough	36	1.9	35.8 (12.7)	1.2 (0.4)	6.5 (5.1)	129	4	23
Backwater	9	0.5	21.1 (14.2)	2.9 (2.6)	5.1 (2.6)	19	3	5
Off-channel habitats								
Terrace tributary	52	2.7	1.4 (1.2)	9.4 (3.9)	5.3 (4.0)	7	49	28
Tributary mouth	29	1.5	44.2 (24.0)	26.3 (23.1)	7.5 (5.8)	128	76	22
Beaver pond	13	0.7	47.9 (39.7)	58.6 (27.6)	0.9 (0.9)	62	76	1
Upland slough	7	0.4	73.4 (45.6)	58.2 (26.9)	0.0 (0.0)	51	41	0
Totals	1932	100.2				641	293	248
95% Confidence interval						±451	±173	±184

*Main channels were too swift to seine, and were assumed not to contain rearing salmon because of swift current.

underestimated because of ongoing migration of newly emerged coho into the study area.

Except for beaver ponds, apparent growth was similar in the different habitat types. Mean FL of sockeye and coho were larger in beaver ponds than in other habitats, indicating faster growth because of higher temperature. The increasing trend in mean chinook FL from the U.S./Canada border toward the river mouth probably was not caused by differences in temperature, as temperature of the river did not differ longitudinally within the study area. Instead, the increase in chinook FL toward the river mouth may have been caused by different times of migration into the lower river from upstream. The larger fish closer to the river mouth may have emerged and migrated to the lower river before the smaller chinook upstream.

Habitat Utilization

Distributions of fish primarily depended on water velocity, and salmon used all types of habitat except where current exceeded 30 cm/s. In some streams (Lister and Genoe 1970; Everest and Chapman 1972), chinook and coho inhabit areas with current as fast as 70 cm/s where coarse substrate (20–40 cm diameter) provided cover from the fast current. In the active channel of the lower Taku River, substrate is mostly compacted gravel, sand, and mud, providing little cover from the turbulent flow, and the only suitable habitat occurs along the channel edge. In comparable streams with heavy sediment loads in New Zealand and Idaho, chinook also primarily used areas with current less than 30 cm/s (Glova and Duncan 1985; Hillman et al. 1987).

The river's turbidity had only a secondary influence on fish distribution, even though such high turbidity should severely impact fish. Bisson and Bilby (1982) showed that juvenile coho avoid turbidity greater than 70 nephelometric turbidity units (NTU), which is much lower than the typical 200 NTU of the Taku River in summer. Coho did avoid the river, perhaps because of turbidity, but sockeye and chinook occurred in both the turbid river and in clearwater off-channel areas. Lloyd et al. (1987) deduced that turbidity affects Alaska fishes by reducing aquatic primary production and impairing feeding. Being an optical property, turbidity is a poor measure of abrasive properties of suspended sediment (Warren 1971), and the glacial silt in the Taku River may not adversely affect fish. Turbidity effects, furthermore, were confounded with other differences between the river and off-channel habitats. For example, habitat stability, as measured by fluctuations in water level, was greater off channel than in the river.

Although the salmon species showed significant overlap, competition probably was important in only a few types of habitat. Competition between coho and chinook probably was unimportant because of low overlap in habitat, and because high turbidity and low fish density probably minimized social interactions in the river. As in the Sixes River, Oregon (Stein et al. 1972), coho and chinook occupied different habitats (coho in off-channel areas and chinook in the river), probably without actual territorial conflict. Competition between coho and sockeye, however, could occur because both species reached high density in upland sloughs and beaver ponds where clear water allowed visual contact. Differences in diet could alleviate such competition. In sloughs of the lower Fraser River, B.C., sockeye ate mostly Cladocera and Copepoda (Birtwell et al. 1987), which differs from the typical coho diet of Chironomidae, Plecoptera, and Ephemeroptera in streams (Koski and Kirchhofer 1984).

Suitable sites in the lower river frequently were unoccupied by juvenile salmon, apparently because of incomplete colonization. Spawning habitat is limited in the lower Taku River; most spawning in the mainstem is 15–50 km upstream of the U.S./Canada border; although tributaries along the lower river have some spawning populations (Eiler et al. 1988; Elliott and Kuntz 1988). Thus, many of the juvenile salmon in the lower river originated from upstream, and underuse of habitat probably resulted from incomplete colonization by downstream migrants. Even in lakes, for example, limited dispersal can cause inefficient use of rearing area. More than two-thirds of the juvenile sockeye in Babine and Nilkitkwa Lakes, B.C., concentrated in only 11% of the available rearing area near their entrance to the lakes (Johnson 1956).

Beaver dams present further obstacles to colonizing fish. Sockeye were present in only one-half of the beaver ponds. Coho were present in all the ponds but were mostly age-1 parr; age-0 coho were usually scarce or absent. The low frequency of occurrence of age-0 sockeye and coho indicates that the ponds were not fully colonized. Colonization of beaver ponds along the lower Taku River probably requires high water levels, such as during Tulsequah River floods (Thedinga et al. 1988) or fall freshets (Peterson 1982).

Salmon production possibly could be enhanced if the lower Taku River habitats were fully colonized by fish. Full colonization of off-channel habitat is needed to maximize smolt production because these areas provide most of the suitable rearing habitat for sockeye and coho. Although off-channel habitats comprise only 5% of the lower river's total area, they contained 39 and 83% of the total summer populations of juvenile sockeye and coho, respectively. Because salmon populations in glacial rivers have not been adequately studied, information is lacking on population dynamics and species interactions. Additional research, therefore, is needed to define factors that limit salmon production in the lower river before enhancement programs are initiated.

Acknowledgments

This research was partially funded through provisions of the U.S./Canada Pacific Salmon Treaty. We thank R. Bradshaw, J. Greiner, and R. Stone for help in maintaining field facilities. C. Hawkes verified and summarized the raw data and digitized areas of habitats on aerial photographs. We thank J. Eiler, J. Helle, S. Ignell, P. Kissner, M. Lorenz, L. Shaul, and A. Wertheimer for reviewing an early draft of this paper. C. A. Dolloff and an anonymous reviewer suggested changes that greatly improved this paper.

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