Downstream migrations of juvenile Pacific salmon (*Oncorhynchus* spp.) in a glacial transboundary river

Michael L. Murphy, K V. Koski, J. Mitchel Lorenz, and John F. Thedinga

Abstract: Migrations of juvenile Pacific salmon (*Oncorhynchus* spp.) in the glacial Taku River (seventh order) were studied to assess movement from upriver spawning areas (in British Columbia) into lower-river rearing areas (in Alaska). Differences between fyke-net catches in the river and seine catches in the river's estuary indicated that many downstream migrants remained in the lower river instead of migrating to sea. In particular, age-0 coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) moved downriver from May to November but were not caught in the estuary. Age-0 sockeye salmon (*O. nerka*), coho presmolts, and other groups delayed entry into the estuary after moving downriver. We tagged groups of juvenile coho (ages 0–2) from the fyke net with coded-wire to determine when they left the river. One-third of all tags recovered from sport and commercial fisheries occurred 2–3 years later, showing that many coho remained in fresh water for 1–2 years after moving to the lower river. Lower-river areas of large glacial rivers like the Taku River can provide essential rearing habitat for juvenile salmon spawned upriver and are important to consider in integrated whole-river management of transboundary rivers.

Résumé : L'étude des migrations de saumons du Pacifique juvéniles (*Oncorhynchus* spp.) dans la Taku, rivière d'origine glaciaire (septième ordre) visait à évaluer leur déplacement des frayères d'amont (en Colombie-Britannique) vers les aires d'alevinage en aval (en Alaska). Les différences relevées entre les captures au verveux dans la rivière et les captures à la senne dans l'estuaire ont montré que de nombreux saumons en avalaison demeuraient dans le cours inférieur au lieu de descendre en mer. En particulier, les saumons cohos (*O. kitsutch*) et les quinnats (*O. tshawytscha*) d'âge 0 descendaient le cours de la rivière de mai à novembre, mais ils n'étaient pas capturés dans l'estuaire. Les saumons rouges (*O. nerka*) d'âge 0, les pré-smolts de coho et d'autres groupes retardaient leur entrée dans l'estuaire après leur descente. Des groupes de cohos juvéniles (0–2 ans) capturés dans des verveux ont été marqués avec un fil de fer codé afin d'établir à quel moment ils quittaient la rivière. Le tiers de toutes les étiquettes ont été récupérées 2–3 ans plus tard auprès de pêcheurs sportifs et de pêcheurs commerciaux. De nombreux cohos demeurent donc en eau douce pendant 1–2 ans après être descendus dans le cours inférieur de la rivière. Les zones d'aval des grandes rivières d'origine glaciaire comme la Taku peuvent offrir un habitat d'alevinage essentiel aux saumons juvéniles d'amont, et il est important de les prendre en compte dans la gestion intégrée des cours d'eau transfrontières.
[Traduit par la Rédaction]

Introduction

Salmonid habitat in large (greater than sixth order) rivers can be viewed as a patch-dynamic system with connectivity among patches provided by fish migration (Stanford and Ward 1992). In such rivers, habitat patches theoretically should vary along the river continuum corresponding to systematic gradients in physical and biological variables (Leopold et al. 1964; Vannote et al. 1980), so that different habitat patches needed at different life stages are distributed systematically. Upriver areas likely have coarse alluvium and upwelling groundwater (Dunne and Leopold 1978) important for spawning (Eiler et al. 1992) whereas lower-river areas often have limited spawning habitat because of excessive fine sediment and reduced upwelling as the result of low substrate porosity and low floodplain slope (Stanford and Ward 1992). Despite limited spawning habitat, lower-river areas often have abundant low-gradient habitats suitable for rearing. This longitudinal pattern is especially evident in glacial rivers (Murphy et al. 1989; Bryant 1991) because of their extremely high sediment load which strongly affects habitat formation.

Salmonid habitat in large rivers, therefore, requires integrated whole-river management to conserve ecological connectivity and habitat function for all life stages (Stanford and Ward 1992). When such rivers cross national boundaries, international cooperation is required to manage the stocks and their habitat.

The Taku River, flowing from British Columbia into Southeast Alaska (Fig. 1), is an example of a large (seventh order), glacial transboundary river where salmonid habitat in the upper and lower river serves different functions. The upper river has many areas for spawning (Lorenz and Eiler 1989) because gradient is sufficient to export fine sediment and upwellings are common; however, the high gradient and high water velocity reduce habitat for rearing (Lorenz et al. 1991).

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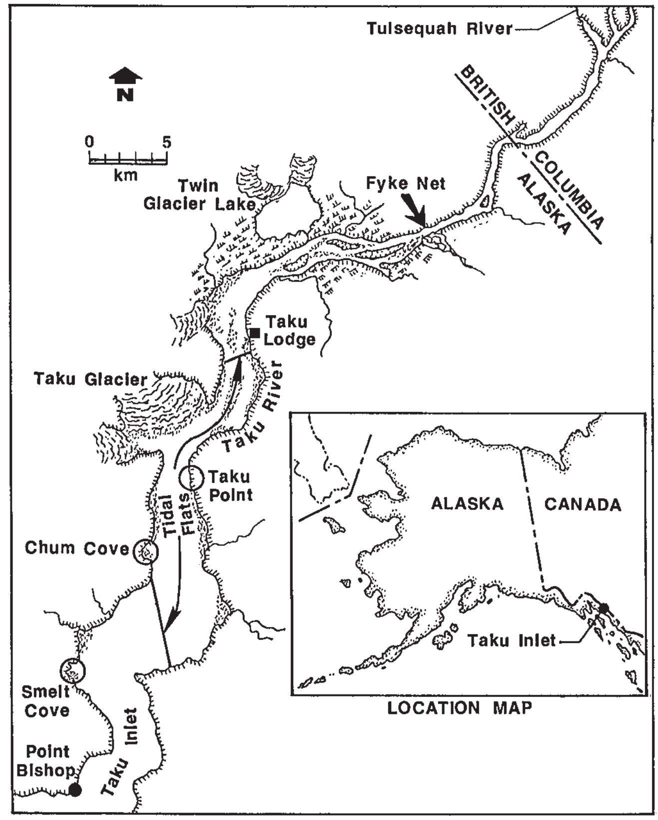
M.L. Murphy,[1] K V. Koski, J.M. Lorenz, and J.F. Thedinga. Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 11 305 Glacier Highway, Juneau, AK 99801-8626, U.S.A.

[1] Author to whom all correspondence should be addressed. e-mail: mike.murphy@noaa.gov

Conversely, the lower river has extensive habitat for rearing because of braided channels, wide floodplain, and broad tidal flats, but its unstable channels, excessive fine sediment, and lack of upwellings limit spawning (Murphy et al. 1989; Lorenz et al. 1991). Even though virtually all chinook salmon (*Oncorhynchus tshawytscha*), 95% of sockeye salmon (*O. nerka*), and 76% of coho salmon (*O. kisutch*) spawn upstream of the U.S.–Canada border (Eiler et al. 1991, 1992; J. Eiler, NMFS Auke Bay Laboratory, 11 305 Glacier Highway, Juneau, AK, personal communication), an estimated 1 million juveniles of these species rear in the lower river downstream of the border (Murphy et al. 1989). Thus, the different functions of upriver and lower-river habitats need to be understood to improve international management and enhancement efforts.

The objectives of this study were to describe the time, size, and age at which juvenile salmonids in the Taku River migrate from upriver spawning areas into the lower river and to determine the amount of time they spend there before going to sea. Previous studies have examined downstream migrations of juvenile salmonids in the Taku River (Meehan and Siniff 1962; Heifetz et al. 1987; Murphy et al. 1991) and in the similar but larger Stikine River, Alaska (Wood et al. 1987), but they did not distinguish between juveniles remaining in the lower river and migrants passing through to the estuary. In the present study, we monitored juvenile salmonids in both the river and estuary, and we marked downstream migrants with coded-wire tags to corroborate the age at which they left the river and went to sea.

Fig. 1. Sites for capturing migrant juvenile salmon by fyke net in the Taku River and by beach seine at Taku Point, Chum Cove, and Smelt Cove in the estuary.



Study area

The Taku River originates in British Columbia and empties into Taku Inlet, 40 km from Juneau, Alaska (Fig. 1). The watershed area is 16 000 km^2, over 90% of which is in Canada; the river main stem is about 70 km long and nearly 60% is in Canada. Important fisheries include gillnet fisheries in Taku Inlet in the United States and in the river main stem in Canada, as well as troll and local sport fisheries. Sockeye salmon is the most important commercial species, with recent adult returns averaging 195 000 fish (Pacific Salmon Commission 1993). Escapements recently averaged over 10 000 chinook and about 70 000 coho salmon (Pacific Salmon Commission 1991). Pink salmon (*O. gorbuscha*) runs vary widely and are low in even-numbered years and high (about 1 million) in odd-numbered years (Clark et al. 1986). Chum salmon (*O. keta*) returns are unknown.

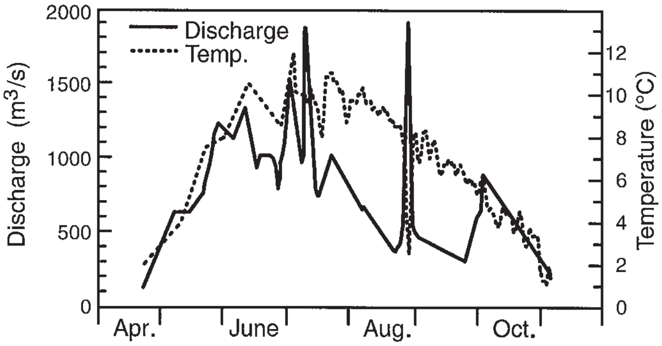
The Taku River is typical of many large, salmon-producing rivers in Alaska and western Canada. Because it is glacier fed, it is turbid, has rapid fluctuations in flow, and transports a large sediment load. From late spring through summer, turbidity in the lower river averages about 200 nephelometric turbidity units (NTU) and discharge usually exceeds 500 m^3/s (Clark et al. 1986). Discharge is low (<100 m^3/s) in winter when the river freezes over and increases rapidly during snowmelt in May and June to a maximum of about 1000 m^3/s, and turbidity and discharge generally decrease thereafter. The lower river floods at least once each summer, when an ice-dammed lake on the Tulsequah River, a tributary entering the Taku River about 7 km upstream of the border (Fig. 1), suddenly drains when the dam breaks (Clark et al. 1986). During these flash floods (jokulhlaups), river discharge can double and subside in 3 days.

This study was limited to the area downstream of the U.S.–Canada border, including the lower 28 km of river and 30 km of estuary. In the lower-river area, the river flows within a wide (2–4 km) U-shaped glacial valley. 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. Water is swift, averaging about 21 cm/s, and channel gradient is <0.1% (Lorenz et al. 1991). The active river channel expands from 400 m at the border to nearly 3 km wide near the mouth. The main channel is about 5 m deep and 200 m wide.

The estuary is a narrow (1–6 km wide) fiord 30 km long, extending from the mouth of Taku Inlet to the end of tidal flats near Taku Lodge (Fig. 1). Water is turbid, and suitable habitats for salmonid rearing, such as low-gradient beaches (Celewycz 1989) and tidal sloughs (Heifetz et al. 1989), are uncommon.

Juvenile salmon also occupy upriver areas in Canada, particularly the mainstem Taku River, its major tributaries, and headwater lakes (Kissner 1984; Lorenz et al. 1991). Compared with the lower river, the upper mainstem river is generally narrower (<100 m), has higher gradient (0.1 to >0.2%), lower summer turbidity (<150 NTU), and faster water velocity (averaging 45 cm/s in the upper 18 km). Only about 25% of the upper river has habitable water velocity for juvenile salmon (<30 cm/s) in summer compared with over 50% of the lower river (Lorenz et al. 1991).

Fig. 2. Discharge and temperature of the Taku River, late April to November 1987.



Methods

River sampling

To monitor downstream migrations, a fyke net was set in the lower river, 17 km upstream from the estuary (Fig. 1), and fished for 2–3 days in each of 20 sampling periods in 1987, beginning shortly after ice left the river in late April and ending shortly before ice reformed in November. Sampling periods were every week from 22 April to 6 August and every 2–4 weeks thereafter until 4 November.

The net had an opening 3 m wide by 1.5 m deep and formed a 12-m-long funnel of 13-mm mesh leading to a cod end of 6-mm mesh that led to a floating live-box. The net was set 4 m from shore perpendicular to and within the main river flow. Depending on river stage, water at the net entrance was 1.5–5 m deep and current was 43–85 cm/s. The net was positioned just below the water surface to avoid floating debris. The mesh quickly became coated with fine debris but functioned well as long as the cod end remained open. During each sampling period, the net and live-box were removed from the river and cleaned every 1–23 h to prevent the cod end from clogging and the live-box from filling with sediment.

Each time the net was pulled, captured fish were anesthetized and counted. We measured fork length (FL) of up to 100 fish of each species, 50 (not consciously selected) from the first part and 50 from the last part of the catch, and took scale samples (up to 150/month) representing the size range of each species (except pink and chum fry) to determine age. Life stage was categorized as parr (parr marks present), smolt (silvery color indicating skin guanine; Rodgers et al. 1987), or presmolt (transitional). Catch data were standardized by dividing the number caught by hours fished.

Although the fyke net was small compared with the river's size, it was effective at sampling fish. At the peak of the spring migration, for example, the net caught as many coho in 9 h (480 fish) as Meehan and Siniff (1962) caught in 1 week of continuous sampling with a scoop trap 4 km upriver from our site. The net's efficiency, based on recapture of fin-clipped fish released 5–6 km upstream of the net, ranged from 1% for chinook and sockeye smolts in spring to 8% for age-0 coho in summer (Murphy et al. 1991). Fast, turbulent water and high turbidity reduced fish avoidance of the net. Efficiency was inversely related to river discharge and turbidity (Murphy et al. 1991), indicating that fish did not avoid the net when turbidity declined. Small fry (<45 mm FL), however, could pass through the 13-mm mesh, but capture efficiency probably increased as the mesh became coated with debris. Based on recapture of marked fish (Murphy et al. 1991), the fyke net was not biased by size selectivity, except for underrepresenting small fry.

River discharge (measured at the fyke net) changed seasonally during the study (Fig. 2). Discharge at various river stages was estimated from the channel's cross-sectional area (measured with electronic distance and depth meters) and mean velocity at 1-m depth (measured with a current meter). Discharge was then regressed on river stage (determined by staff gauge) to estimate discharge for each sampling period. Discharge increased from 100 m^3/s in late April to nearly 2000 m^3/s on 9 July during a Tulsequah River flood and then declined to 200 m^3/s in November. This decline was interrupted by a second Tulsequah River flood on 28 August.

Changes in river temperature (measured each sampling period with a thermometer from 22 April to 8 July, and thereafter with a thermograph every 2 h) and turbidity (measured with a turbidimeter) generally paralleled discharge. Temperature rose from 2°C in late April to 12°C in July and declined to nearly 0°C in November (Fig. 2). Temperature dropped to 3°C in a few hours during the Tulsequah flood in August. Turbidity averaged about 200 NTU but varied directly with discharge, ranging from 18 NTU during low water in November to nearly 400 NTU during Tulsequah floods.

Table 1. Number and fork length (FL) of three groups of coded-wire-tagged juvenile coho released 5–6 km upstream of the fyke net in the Taku River, number recaptured after 2–10 days, and estimated tag retention.

Age group	FL range (mm)	Tagging period	Number released	Number recaptured (%)	Tag retention (%)
1 and 2	50–120	May–June	5189	210 (4.0%)	99.0
0	34–45	May–June	606	8 (1.3%)	87.5
0	45–90	Aug.–Sept.	4177	300 (7.2%)	96.7

Coded-wire tagging

In 1989, the fyke net was operated from April to September at the same location as in 1987 to capture coho for coded-wire tagging. Only coho were tagged because virtually all chinook go to sea at age 1 and the other species are not sampled for coded-wire tags in the fisheries. Coho were tagged, adipose-fin clipped, and released in quiet water 5–6 km upstream. Fish showing stress or descaling were not tagged and were released downstream. Twice each week, a group of 25 tagged fish were held in live-boxes for 24 h to estimate handling mortality. Mortality was <1%. Different codes were used to tag three groups of fish: (1) age-1 and age-2 parr, smolts, and presmolts (50–120 mm FL) in May and June, (2) age-0 fry (34–45 mm FL) in May and June, and (3) age-0 parr (45–90 mm FL) in August and September.

Recaptures in the fyke net, which generally occurred within 2–10 days, were used to estimate tag retention (Table 1). Recaptured coho were checked for tags with a tag detector and released downstream. Of 5189 age-1 and age-2 fish tagged in May and June, 210 (4.0%) were recaptured in the fyke net and 208 (99.0%) had retained their tags. Of 606 fry tagged, eight (1.3%) were recaptured and seven (87.5%) had tags. Of 4177 age-0 parr tagged in August and September, 300 (7.2%) were recaptured and 290 (96.7%) had tags. Accounting for tag loss, the total number of valid tags released was about 10 000. Data on recovery of coded-wire-tagged adults in subsequent fisheries were provided by the Alaska Department of Fish and Game (K. Crandall, Alaska Department of Fish and Game, P.O. Box 3-2000, Juneau, AK 99802, personal communication).

Data from the recovered coded-wire tags were used to determine when fish left fresh water. Except for coho jacks, which spend only one summer at sea, all Alaska coho spend two summers and one winter at sea before returning to spawn (Gray et al. 1981). Tagged adult coho recovered in the fisheries must have left fresh water the previous year. Jacks and adults are separated by size during port sampling, and jacks are generally not caught in the fisheries. Therefore, the time the adults spent at sea is known, and the time they spent in fresh water can be determined by difference.

Estuary sampling

To monitor fish in the estuary, we established three study sites: Taku Point near the middle tidal flats, Chum Cove in the lower tidal flats,

Fig. 3. Species composition of juvenile salmon caught during (A) April–November 1987 by fyke net in the Taku River and (B) May–August 1987 by beach seine in the river's estuary.

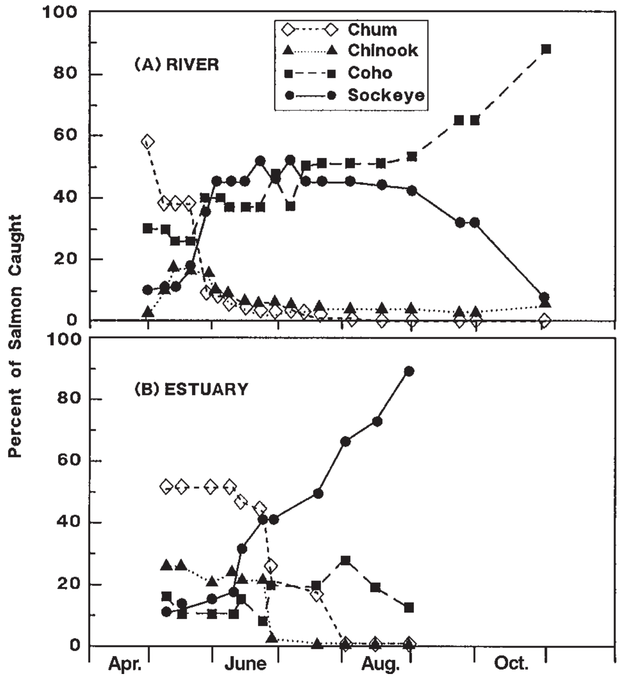
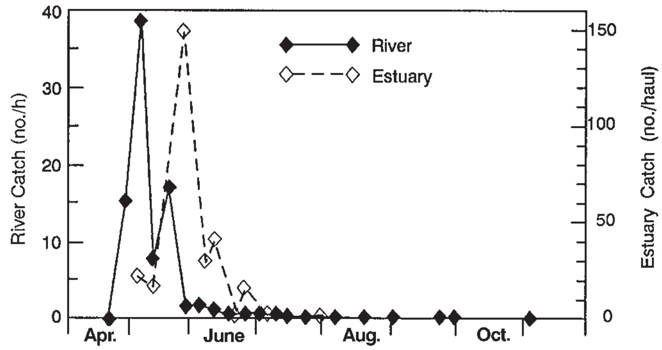


Fig. 4. Catch of age-0 chum during April–November 1987 by fyke net in the Taku River and May–August 1987 by beach seine in the river's estuary.



and Smelt Cove in the outer basin (Fig. 1). Two beaches at each site were seined (one haul each) weekly from 8 May to 26 June and every 2 weeks thereafter until 28 August.

To catch fish in the estuary, we used a beach seine (37 × 2 m, with 6-mm-mesh central bag and 16-mm-mesh wings). The seine was set parallel to and 40 m from shore with a skiff and retrieved onto shore with ropes. Catch was treated the same as for the fyke net. For logistical reasons, Taku Point was seined at high tide and the other sites at midtide.

The three estuary sites represented a longitudinal gradient in salinity and turbidity. Taku Point had low salinity (<3‰), was adjacent to river and tidal currents, and had shallow water (<3 m deep) and a sandy beach. Chum Cove had moderate salinity (5–26‰) modified by a small fresh-water stream (first order); it was sheltered from currents and had shallow water (<4 m deep) and a rocky beach. Smelt Cove had moderate salinity (5–25‰) also modified by a first-order stream; it was sheltered from currents and had deep water (>8 m deep) and a rocky beach. For comparison, salinity at Point Bishop at the mouth of Taku Inlet (Fig. 1) ranged from 16 to 28‰. Water temperature was similar at the three sites: 6°C in early May, 8–13°C in July, and 5°C in late August (low because of a Tulsequah flood). Turbidity decreased with distance from the river: Secchi disk visibility was only 5–25 cm at Taku Point compared with 20–60 cm at Chum and Smelt coves and 100–150 cm at Point Bishop.

Results

The catch differed between the river and estuary and changed seasonally in both areas (Fig. 3). The river catch (over 10 000 salmon) was dominated by chum fry in May, age-0 sockeye and coho from May to September, and age-0 coho from September to November. The estuary catch (2600 salmon) was dominated by chum fry in May and June and age-0 sockeye in July and August. The river catch was 49% coho, 35% sockeye, 10% chum, 6% chinook, and <1% pink. The estuary catch was 61% chum, 20% sockeye, 10% chinook, 7% coho, and 2% pink.

Chum salmon

Most chum moved downstream in May and were caught in the estuary from mid-May to late June (Fig. 4). Peak river catch was on 7 May, 3 weeks before the peak estuary catch. Modal FL of downstream migrants was 40 mm in both May and June, as small chum continuously migrated downstream. Chum in the river in June ranged up to 60 mm FL, indicating some riverine growth. Chum in the estuary were similar in size to those in the river in May, but averaged 7 mm larger ($P < 0.001$, *t*-test) than in the river in June (Fig. 5).

Chinook salmon

Chinook smolts moved downstream and through the estuary in May and June (Fig. 6). Peak catch in the river was on 7 May and in the estuary 3 weeks later. Smolts ranged from 54 to 120 mm FL (mean 74 mm); 98% were age 1 and 2% were age 2 (Fig. 7). Small numbers of age-0 chinook moved downstream throughout the study period, particularly August–November, but only two age-0 chinook were caught in the estuary. Mean FL of age-0 chinook from the fyke net increased from 39 mm in May to 63 mm in November (Fig. 7).

All age-2 and many large age-1 chinook migrated early. Age-2 chinook were caught only in May, and chinook smolts in the estuary in May averaged 5 mm larger than migrants in the river ($P < 0.01$, *t*-test; Fig. 7). In June, however, smolts were the same mean FL (76–77 mm) in both the river and estuary because mean FL increased in the river during May and June whereas it remained nearly constant in the estuary.

Coho salmon

Coho were abundant migrants and exhibited several migration patterns (Fig. 8). Smolts, presmolts, and parr (92% age-1 and 8% age-2) moved downstream primarily in May and June. A large catch of age-1 parr occurred around 7 May, associated with increased river discharge, and catch of age-1 parr declined sharply thereafter. Smolts and presmolts in the river peaked in late May and declined to zero in July. Coho smolts were in the estuary from early May to mid-August, peaking around 4 June, 1 week after peak catch of smolts in the river.

Age-0 coho also moved downstream in large numbers. Catch was high in early May, low but steady in June, and

Fig. 5. Length frequencies (3-mm increments) of age-0 chum from (A) the Taku River and (B) estuary during May–June 1987. Means and sample sizes are shown for each month.

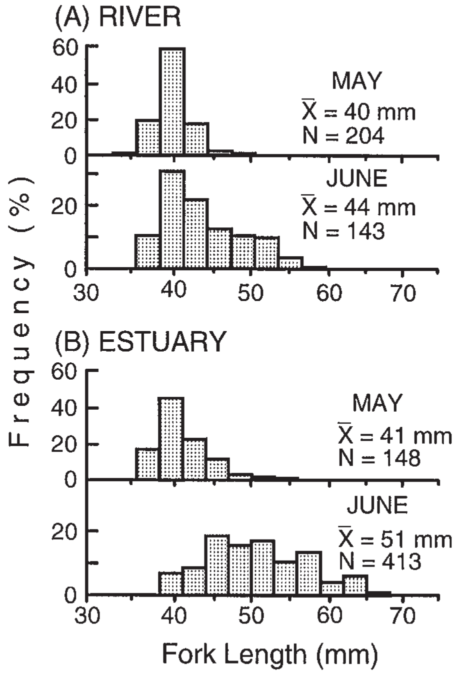


Fig. 6. Catch of juvenile chinook by age-class during April–November 1987 by fyke net in the Taku River and May–August 1987 by beach seine in the river's estuary.

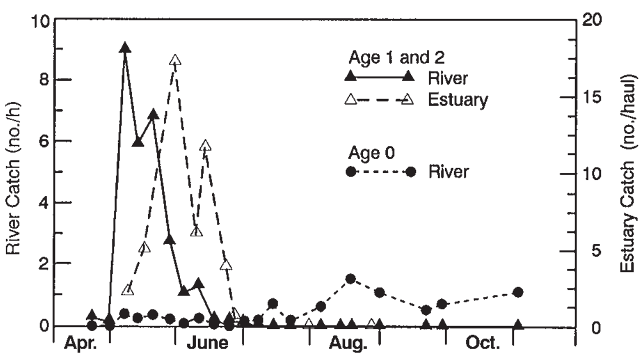
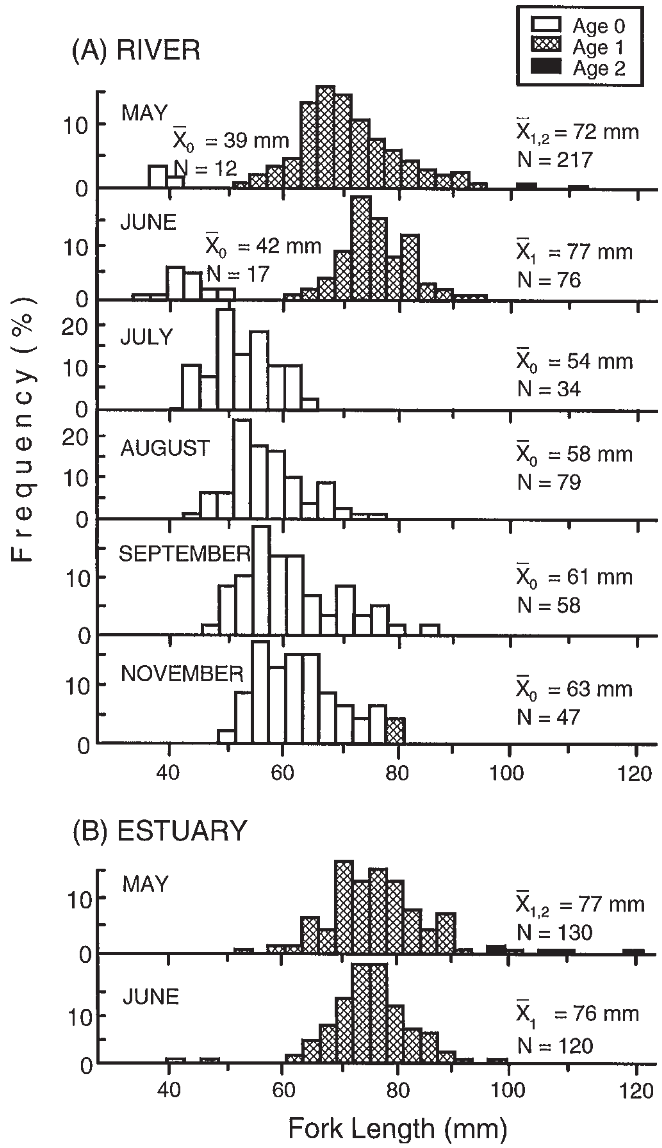


Fig. 7. Length frequencies (3-mm increments) by age-class of juvenile chinook during (A) May–November 1987 from the Taku River and (B) May–June 1987 from the river's estuary. Means and sample sizes are shown for each class.



increased from July to November (Fig. 8). In May, many small fry (35 mm mean FL) moved downstream as river discharge increased; in August–November, larger age-0 parr (49–60 mm mean FL) moved downstream as the river receded (Figs. 8 and 9). Although many age-0 coho migrated downstream in the river, only 16 were caught in the estuary, and 14 of these were caught at the mouths of the small streams in Chum and Smelt coves. All age-0 coho caught in the estuary were <45 mm FL.

Age, size, and developmental stage of coho differed between the river and estuary. In May, 33% of coho smolts in the estuary were age 2, compared with 17% of presmolts and smolts in the river; but in June, most age-2 coho had left, and age-2 coho comprised <5% of migrants in both the river and estuary (Fig. 9). In May and June, parr from the fyke net averaged 62 mm FL, and smolts and presmolts averaged 87 mm, approximately the same as smolts in the estuary (90 mm in May and 85 mm in June). Although many age-1 parr were

Fig. 8. Catch of juvenile coho by stage and age-class during April–November 1987 by fyke net in the Taku River and May–August 1987 by beach seine in the river's estuary. Smolt and presmolt data from the river are combined.

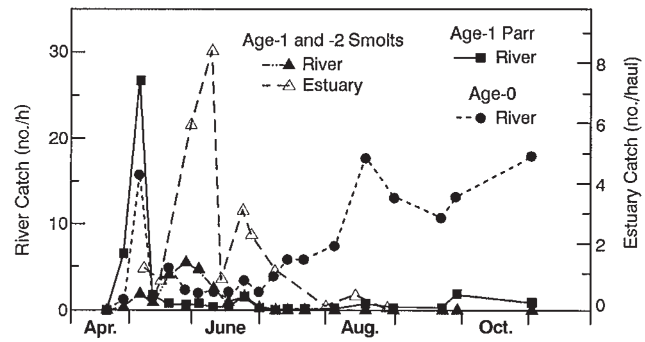


Fig. 9. Length frequencies (3-mm increments) of juvenile coho by age-class during (A) May–November 1987 from the Taku River and (B) May–June 1987 from the river's estuary. Means and sample sizes are shown for each age-class.

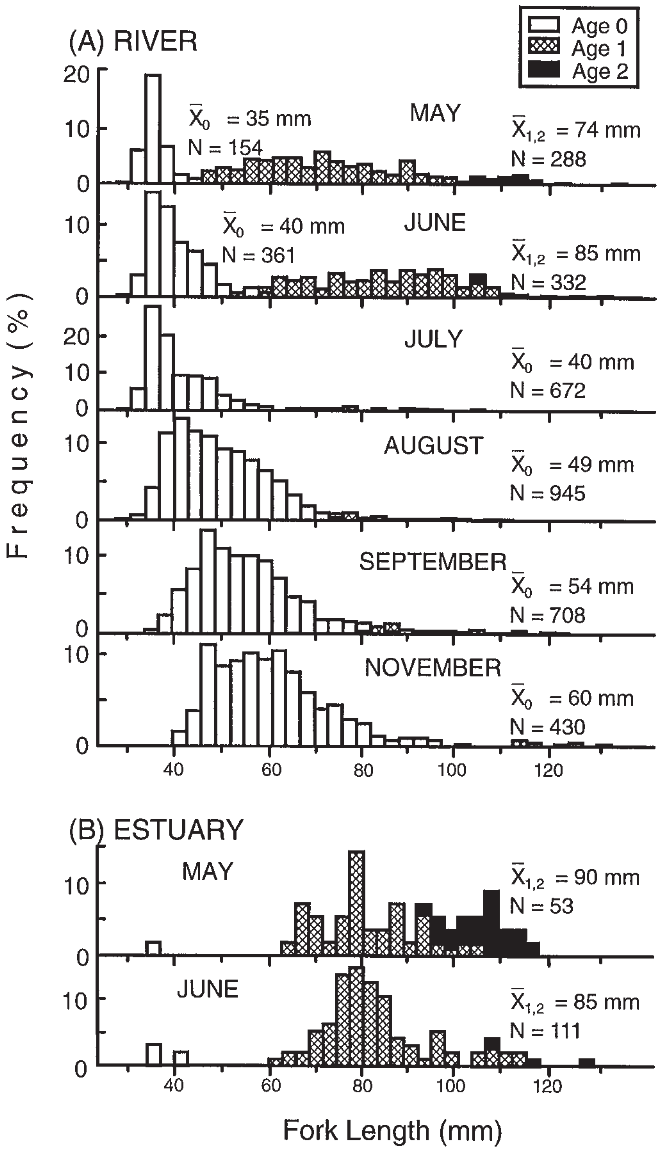
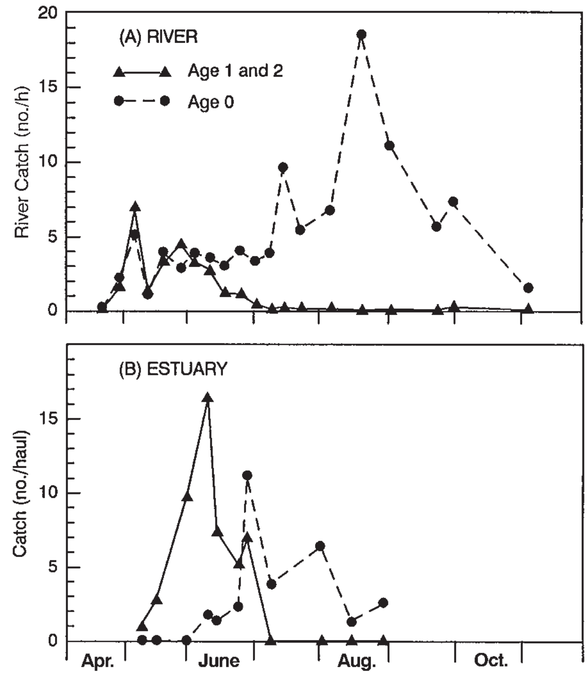


Fig. 10. Catch of juvenile sockeye by age-class during (A) April–November 1987 by fyke net in the Taku River and (B) May–August 1987 by beach seine in the river's estuary.



caught in the river in early May, no parr were caught in the estuary.

Sockeye salmon

Sockeye also exhibited several migration patterns (Fig. 10). Age-1 and age-2 smolts moved downstream and through the estuary in May and June. Catch of smolts in the river peaked twice: first in early May and again in late May. Peak catch in the estuary was in early June.

Sockeye smolts consisted of two size groups, of which the larger tended to migrate earlier. In May, the two modal FL frequencies were more evident in the estuary than in the river. A primary mode occurred at 58–63 mm (age-1 smolts) and a secondary mode at 70–75 mm (about one-third were age-2 smolts) (Fig. 11). Smolts averaged 6 mm larger in the estuary than in the river ($P < 0.001$, t-test) in May, but in June, after most of the larger size group had left the estuary, smolts were the same mean FL (65 mm) in both areas.

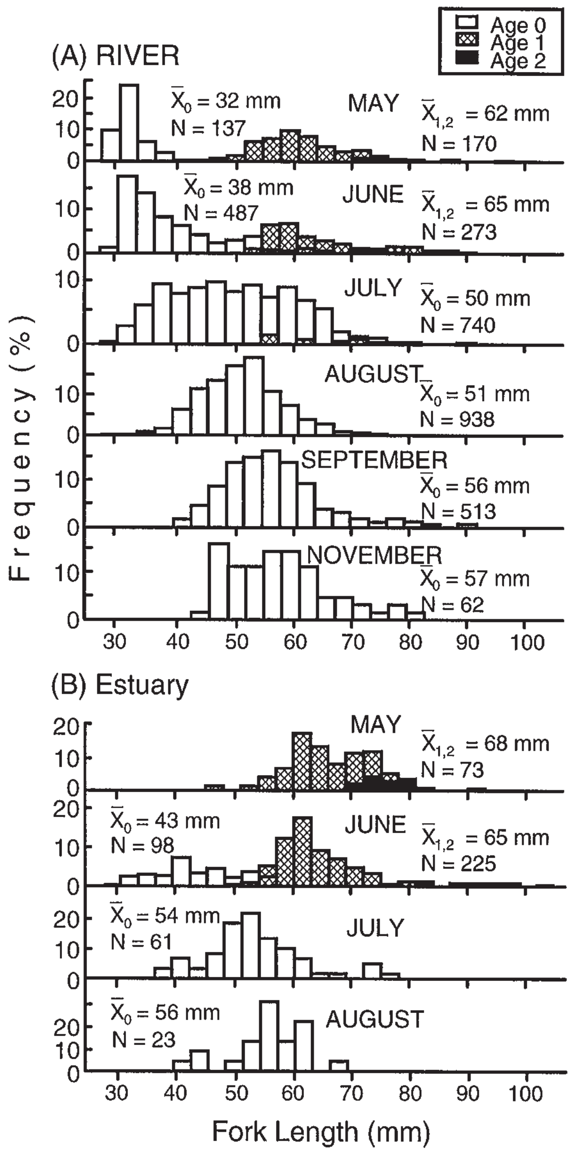
Age-0 sockeye also consisted of two size groups that moved downstream at different times. The first group consisted of small fry (32 mm mean FL) that moved downstream in May and June, but they were not caught in the estuary until mid-June (Fig. 10). Few small fry (<35 mm) were caught in the estuary, although many moved into the lower part of the river (Fig. 11).

The second group of age-0 sockeye to migrate consisted of larger fish (>50 mm mean FL) that moved downstream in summer. Catch in the river increased sharply in early July, peaked in August, and declined through September (Fig. 10). Between 30 June and 7 July, FL frequencies in the river changed from being strongly skewed with a dominant mode at 35 mm FL to being broadly bimodal with a dominant mode at 59 mm FL. Mean FL increased sharply in early July, and regressions of mean FL on sampling date differed ($P < 0.01$, F-test) before and after 7 July, separated by a 10-mm gap (Fig. 12), resulting from the sudden migration of the distinctly larger fish.

Unlike age-0 coho and chinook, many age-0 sockeye were caught in the estuary from mid-June through late August (Fig. 10). Estuary catch increased sharply in late June, 2 weeks before river catch increased. Estuary catch, however, declined in August whereas river catch was still increasing. The increased catch in the river in August was probably due to increasing efficiency of the fyke net as river discharge decreased, and the population of migrants probably peaked in late June (Murphy et al. 1991).

Age-0 sockeye caught in the estuary were larger than those caught in the river (Fig. 11). In July and August, mean FL was 54–56 mm in the estuary compared with 50–51 mm in the river, and variance in FL in July was significantly greater ($P <$

Fig. 11. Length frequencies (3-mm increments) of juvenile sockeye by age-class during (A) May–November 1987 from the Taku River and (B) May–August 1987 from the river's estuary. Means and sample sizes are shown for each age-class.



0.01, F-test) in the river than in the estuary. The FL frequencies differed significantly ($P < 0.001$, Kolmogorov–Smirnov test) between the river and estuary because sockeye <50 mm FL were less common in the estuary catch than in the river catch whereas larger sockeye were represented similarly in the river and estuary. The absence of the smaller sockeye in the estuary indicates that they remained in the lower river until they reached a threshold size of about 50 mm.

Coded-wire tag returns

From the tag group consisting of age-1 and age-2 coho parr, presmolts, and smolts tagged in May and June 1989, an estimated 7.4% were subsequently caught as adults in sport and commercial fisheries (Table 2). Three-quarters of the recaptures were in 1990, indicating that these fish had migrated to sea in 1989, the same year as they were tagged. One-quarter of the recaptures were in 1991, indicating that these fish had remained in fresh water another year after migrating to the lower river.

Fig. 12. Change in mean fork length of age-0 sockeye from the Taku River during 29 April – 4 November 1987. Broken lines were fitted to the data before and after 7 July. Total number of fish measured was 2877.

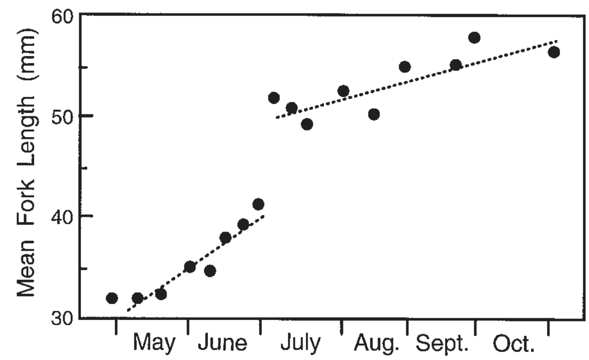


Table 2. Number and fork length (FL) of three groups of coded-wire-tagged juvenile coho released in the Taku River in 1989 and estimated number of tagged adults caught in fisheries in 1990–1992 (recovery data provided by K. Crandall (Alaska Department of Fish and Game, personal communication)).

Age group	FL range (mm)	Tagging period	Number released[a]	Adults in fisheries[b]		
				1990	1991	1992
1 and 2	50–120	May–June	5137	287	93	0
0	34–45	May–June	530	0	21	0
0	45–90	Aug.–Sept.	4039	0	24	43

[a]Number after accounting for estimated tag loss.

[b]Estimated number based on Alaska Department of Fish and Game port sampling program (K. Crandall, personal communication).

Age-0 coho tagged in 1989 were recovered as adults in fisheries in both 1991 and 1992 (Table 2), indicating that they remained in fresh water 1–2 years after migrating to the lower river. From the 530 tagged coho fry released in spring, an estimated 21 adults (4.0% of the fry released) were caught in fisheries in 1991, having gone to sea at age 1. From the 4039 tagged age-0 parr released in August and September, 67 (1.7%) were later caught as adults in 1991 and 1992. Most (64%) of these recoveries were in 1992, having remained in fresh water for two winters after migrating to the lower river.

Discussion

Salmon habitat in the Taku River can be viewed as an interconnected patch-dynamic system, with most spawning habitat located in the upper river and substantial rearing habitat in the lower river, connected by continuous downstream migrations of juveniles from April to November. The migrations had several distinct components: migrations of smolts, age-1 parr, and age-0 fry in spring and migration of age-0 parr in summer and fall.

Smolt migration

In spring, the lower river functioned as a staging area where presmolts completed smoltification before going to the estuary, as shown by differences in peak catch, size, age, and developmental stage of fish between the river and estuary. Catch of downstream migrants in the river peaked 1–3 weeks earlier than catch in the estuary, indicating about a 1- to 3-week delay in the lower river. Differences in size, stage, and age between downstream migrants and fish in the estuary indicated that the largest and oldest fish moved directly to the estuary whereas the smaller fish reared for a time in the lower river. Many coho presmolts and parr that moved to the lower river in May and June probably became smolts there before descending to the estuary in July and August.

Timing of the smolt migration in our study was similar to that in other Alaska studies. The peak for chum and chinook was also the first week of May in the Taku River in 1961 (Meehan and Siniff 1962). The peak for coho smolts was also in mid-May to late May in the Taku River in 1961 (Meehan and Siniff 1962), as well as in other Southeast Alaska streams (Crone and Bond 1976; Thedinga and Koski 1984; Elliott et al. 1989). Sockeye smolts in the Taku River in 1961 showed a bimodal migration, with peaks in early May and in late May to mid-June (Meehan and Siniff 1962), corresponding closely to the two peaks in our study.

Compared with the 1961 Taku River study by Meehan and Siniff (1962), smolt size in our study was similar for chinook but smaller for coho and sockeye. Chinook smolts averaged 73 mm in 1961 and 74 mm in 1987. Coho smolts averaged 93 mm (46% age-1 and 54% age-2) in 1961 compared with 87 mm (86% age-1 and 14% age-2) in 1987. Stages of coho migrants in our study were difficult to distinguish because "smolts" had not fully smoltified and parr from the turbid river often had indistinct parr marks and faded coloration. Including the smaller parr with smolts could explain why smolts in our study were smaller and younger than in Meehan and Siniff's (1962) study. Similarly, modal FLs of sockeye smolts in our study were 10–20 mm smaller than in Meehan and Siniff's (1962) study. The difference could have been caused by a change in contributions from different headwater lakes (McPherson et al. 1988), which can change the modal FL of migrants (Peven 1987).

Age-1 parr migration

The spring migration of age-1 coho parr in the Taku and other large rivers probably consists of fish leaving wintering areas. Timing of this migration appears to be linked to the first substantial increase in river discharge in spring or early summer (Murphy et al. 1991). In the nonglacial Situk River, Alaska, many age-1 coho parr moved downstream in spring, but the peak migration was in June during the first large freshet (Johnson et al. 1994; Thedinga et al. 1994), rather than in early May as in the Taku River. A significant age-1 parr migration was missing, however, in studies of smaller Alaska streams (e.g., Crone and Bond 1976; Thedinga and Koski 1984).

Like coho parr in the Taku River, Atlantic salmon (*Salmo salar*) parr in Newfoundland rivers also migrate downstream in spring, starting before and overlapping the migration of smolts (Cunjak et al. 1989; Birt et al. 1990). Unlike coho parr, however, Atlantic salmon parr are found throughout the estuary; larger parr apparently become smolts, but smaller parr return to the river to overwinter and mature and can ultimately represent a significant portion of a river's total salmon production (Cunjak et al. 1989). This is analogous to the situation in the Taku River where our coded-wire tagging showed that age-1 coho parr that migrate to the lower river represent a substantial part of the river's total coho production.

Results from the coded-wire tagging showed that many coho parr migrants in spring remained in fresh water for another year. If we assume that our tagging was random across the population of downstream migrants, the estimated proportion of migrants that remained in fresh water, based on the 24% tag recovery in the 1991 fisheries, would be about one-quarter of the total 1989 spring migration of age-1 and age-2 coho. This proportion would be much higher if we could account for fresh-water mortality resulting from the additional year of rearing in the river. For example, an overwinter mortality of 65% (Crone and Bond 1976) would mean that roughly 50% of the total migration of age-1 and age-2 coho in spring 1989 remained in fresh water until 1990.

The age-1 coho migrants that remained in the lower river probably reared mostly in off-channel habitats on the river terrace (Murphy et al. 1989). Off-channel beaver ponds, in particular, are likely rearing areas for the age-1 parr migrants, as coho in beaver ponds along the lower Taku River are mostly (89%) age-1 compared with mostly (96%) age-0 in all other types of habitat (Murphy et al. 1989). High river discharge during the spring migration probably helps coho gain access to these off-channel habitats. We cannot be certain about where the migrants that remained in fresh water actually spent the intervening year before going to sea. They might also have left the lower Taku River and reared in fresh water in other streams in the area.

The recovery of coded-wire tags in the fisheries indicated good survival of these parr. The 7.4% total recovery of tags in the fisheries over 2 years was similar to the 10% tag recovery from coho smolts tagged in 1989 as they left Yehring Creek, a tributary of the lower river (Elliott and Sterritt 1990).

Fry migration

The downstream movement of newly emerged fry is a typical event in many streams. As young salmonids emerge, they are often swept downstream (Ottaway and Clarke 1981) or are forced to emigrate by dominant fish (Mason and Chapman 1965). In the Taku River and its tributaries, many newly emerged fry are probably swept downstream, but some stocks may have behavioral adaptations that cause fry to move downstream in spring to colonize available habitat in the lower river. Chinook fry principally use channel edges and side sloughs in the main river, sockeye fry use sloughs and ponds both in the river and off-channel, and coho fry mainly use off-channel areas (Murphy et al. 1989).

Many of the age-0 sockeye migrants eventually entered the estuary after rearing for a time in the lower river. Because sockeye must be at least 50 mm FL to survive in seawater (Heifetz et al. 1989), they initially rear in fresh or brackish water. In our study, age-0 sockeye went to the estuary in summer at a mean FL of 55 mm. Thus, the newly emerged sockeye that moved downstream in spring apparently did not go to the estuary immediately but reared in the lower river until mid-June.

Results from coded-wire tagging indicate that survival of coho fry migrants in the lower river was comparatively high. The 4% tag recovery from coho fry tagged in spring 1989 and recovered in the fisheries in 1991 compares favorably with the

10% tag recovery from smolts leaving Yehring Creek tagged in spring 1989 and recovered in 1990 (Elliott and Sterritt 1990). Assuming similar exploitation rates in the fisheries, the difference in recoveries in these two groups (age-0 fry migrants and age-1 and age-2 Yehring Creek smolts) indicated that survival of coho migrants during the additional year in fresh water was approximately 40%.

Age-0 parr migration

The summer migration of age-0 parr in the Taku River differs from the typical pattern in most streams. Age-0 parr usually move during fall storms as they leave summer rearing areas for winter habitat; they seldom move during summer low flow (Crone and Bond 1976; Murphy et al. 1984). The summer migration in the Taku River also differs from that in the Situk River, where downstream movement occurred during freshets (Thedinga et al. 1994); in the Taku River, movement occurred during declining flow.

The summer migration in the Taku River was probably caused by shrinking habitat upriver as discharge dropped 75% between June and September. Densities of juvenile coho and sockeye are directly related to pool or lake volume (Murphy et al. 1986; Koenings and Burkett 1987); hence, decreased volume could cause them to migrate. Although spawning is mostly in upriver areas, sampling in late summer found few age-0 coho and sockeye in the upper main stem and much available habitat dewatered because of low river discharge (Lorenz et al. 1991). Thus, rearing capacity upriver may be limited by low water in summer, and many juveniles spawned there probably survive by migrating to the lower river.

This habitat limitation as the result of declining water levels probably occurs in many rivers. Total commercial catch of coho off Washington and Oregon is directly related to the amount of summer streamflow when the juveniles are in streams (Smoker 1955; Mathews and Olson 1980). The limitation may be most severe in glacial rivers because of geomorphic and hydrologic factors (Ritter 1978; Milner and Petts 1994). Glacial river channels generally are dominated by aggradation resulting from high sediment supply, resulting in wide, shallow channels. Jokulhlaups from ice-dammed lakes further work to create channels that are extremely wide relative to normal flow. The hydrograph shows wide seasonal variation, dominated by an early-summer maximum produced by snow and icemelt and a winter minimum when runoff declines to virtually zero. The combination of a high width-to-depth ratio and declining water levels in summer results in widespread dewatering of fish habitat.

The fate of age-0 summer migrants varies by species. All adult coho and chinook returning to the Taku River show one or more fresh-water annuli on their scales, whereas about 11% of adult sockeye do not show a fresh-water annulus (Kissner 1984; McPherson et al. 1988). Thus, age-0 coho and chinook migrants remain in fresh water whereas some age-0 sockeye migrate to sea. Coded-wire tag recoveries in our study show that many age-0 parr that migrated downriver in August and September survived and reared in fresh water for 1–2 years after migrating to the lower river.

Results from the coded-wire tag recoveries indicate that the age-0 coho parr that migrated downstream in summer survived well compared with those in other areas of the Taku River. Between 1986 and 1990, over 91 000 age-0 coho parr in 14 tag groups were coded-wire tagged in late summer at various sites in the Taku River drainage in Canada, including tributary rivers and Tatsamenie Lake (Department of Fisheries and Oceans (Canada) and Alaska Department of Fish and Game, unpublished data). The tag recoveries from these groups in fisheries ranged from 0.0 to 2.2% and averaged 1.1%; recovery of adults from the age-0 parr in our study was 1.7%. Thus, assuming similar fisheries exploitation rates, survival of migrants to the lower river was better than the average for juveniles rearing upriver.

Conclusion

Although upriver areas of the Taku River contain most of the spawning habitat, lower-river areas have essential rearing areas for juvenile salmon that contribute significantly to the river's total salmon production. The concept of salmonid habitat as a patch-dynamic system is important in management of any large river where habitats with different functions in salmonid life history are located in different parts of the system. When the river crosses national boundaries, as in the glacial transboundary rivers of Alaska and British Columbia, fish stocks and their habitat require international cooperation in integrated whole-river management.

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