Comparison of Spawning Areas and Times for Two Runs of Chinook Salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska

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Burger, C. V., R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times for two runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Can. J. Fish. Aquat. Sci. 42: 693–700.

From 1979 to 1982, 188 chinook salmon (*Oncorhynchus tshawytscha*) were tagged with radio transmitters to locate spawning areas in the glacial Kenai River, southcentral Alaska. Results confirmed that an early run entered the river in May and June and spawned in tributaries, and a late run entered the river from late June through August and spawned in the main stem. Spawning peaked during August in tributaries influenced by lakes, but during July in other tributaries. Lakes may have increased fall and winter temperatures of downstream waters, enabling successful reproduction for later spawning fish within these tributaries. This hypothesis assumes that hatching and emergence can be completed in a shorter time in lake-influenced waters. The time of upstream migration and spawning (mid- to late August) of the late run is unique among chinook stocks in Cook Inlet. This behavior may have developed only because two large lakes (Kenai and Skilak) directly influence the main-stem Kenai River. If run timing is genetically controlled, and if the various components of the two runs are isolated stocks that have adapted to predictable stream temperatures, there are implications for stock transplantation programs and for any activities of man that alter stream temperatures.

De 1979 à 1982, on a fixé des transmetteurs radio à 188 saumons quinnats (*Oncorhynchus tshawytscha*) afin de localiser les frayères dans la rivière glaciaire Kenai, dans le centre sud de l'Alaska. Les résultats ont corroboré l'hypothèse suivante : des géniteurs avaient pénétré dans la rivière en mai et juin et avaient frayé dans les tributaires et d'autres avaient remonté plus tard, de la fin juin à la fin d'août, et s'étaient reproduits dans le cours principal. La fraie a atteint son maximum en août dans les tributaires de lacs, et en juillet dans les autres. L'apport d'eaux lacustres a peut-être entraîné une augmentation de la température des eaux d'aval, en automne et en hiver ; ceci aurait permis la réussite de la fraie des géniteurs tardifs dans ces tributaires. Il ressort de la présente hypothèse que l'éclosion et l'émergence peuvent s'effectuer plus rapidement dans les eaux sous l'influence d'un lac. L'époque de la montaison et de la fraie (de la mi-août à la fin d'août) des géniteurs tardifs est unique parmi les stocks de saumon quinnat peuplant l'inlet Cook. Le fait que deux grands lacs (Kenai et Skilak) influencent directement le cours principal de la rivière Kenai peut avoir mené au développement d'un tel comportement. Si l'époque de la remonte est génétiquement contrôlée et que les diverses composantes des deux remontes sont des stocks isolés qui se sont adaptés à des températures lotiques prévisibles, ceci pourrait avoir des répercussions sur les programmes de transplantation de stocks et sur toute activité humaine entraînant une modification de la température de l'eau.

Received April 26, 1984
Accepted December 31, 1984
(J7768)

Reçu le 26 avril 1984
Accepté le 31 décembre 1984

Multiple runs of chinook salmon (*Oncorhynchus tshawytscha*) have been documented in several rivers in the Pacific Northwest (Scott and Crossman 1973). Spring runs of chinook salmon spawn in headwater areas of rivers such as the Columbia, whereas summer and fall runs appear to spawn lower in the drainage (Fulton 1968). Salmonids tend to spawn earlier in northern than in southern latitudes (Godin 1981). Unlike streams in southern latitudes where multiple runs of salmonids occur over widely differing times of the year, runs in Alaska overlap to a greater degree presumably because summers are short and water temperatures colder.

The Kenai River (Fig. 1) is a popular recreation area in southcentral Alaska. Fifteen percent of the statewide sport fishing occurs there, focusing on chinook salmon which attain weights ranging up to 40 kg. Chinook salmon currently account for over 70 000 angler days of fishing effort in the Kenai each summer (Hammarstrom 1981).

Creel censuses by the Alaska Department of Fish and Game since the early 1970's suggest that two runs of chinook salmon occur in the Kenai River. Angler success was high in mid-June, decreased in early July, and then increased again in mid-July (Hammarstrom 1981) (Fig. 2). Earlier, a similar pattern occurs in the marine sport fishery in Cook Inlet, about 20 km south of the Kenai River mouth (Fig. 2). Analysis of scales from adults harvested in the Kenai River suggests that these fish as juveniles spend 1 yr in freshwater (Hammarstrom 1981) and thus, they are "stream-type" chinook salmon (Healey 1983). Although 5-yr-

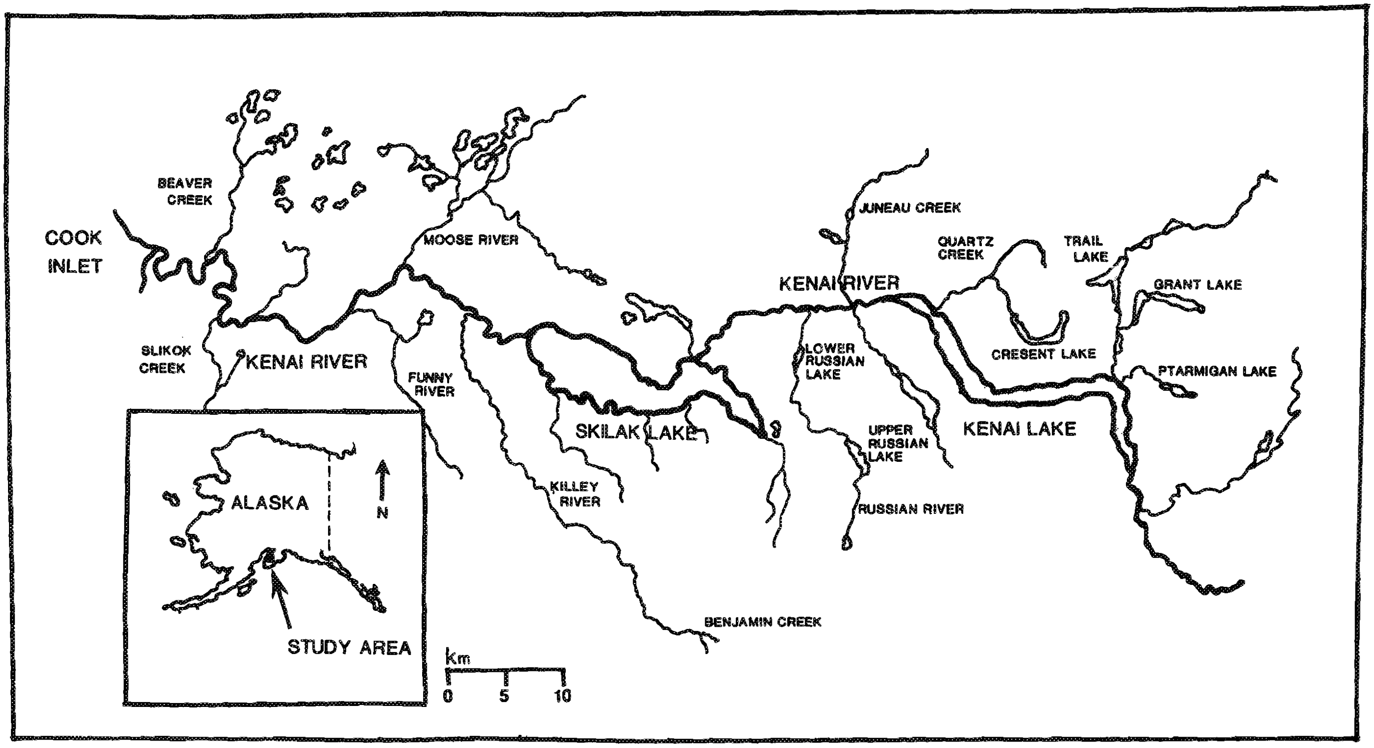

FIG. 1. Location of the Kenai River and tributaries in southcentral Alaska.

old fish dominate each peak in abundance, fish harvested from the late peak were larger; in 1980, for example, their average weight was 17.4 kg compared with 16.1 kg for fish in the early peak (Hammarstrom 1981). These differences led fishery managers to conclude that early and late runs of chinook salmon occurred; however, the glacially turbid water in the Kenai River prevented direct observation of the time and location of fish spawning. Such observations would provide more certain evidence that the two runs indeed represented discrete populations.

We describe the results of a study to locate and characterize chinook salmon spawning areas in the Kenai River System, and to determine spawning times for fish of the two apparent runs. On the basis of these data, we develop a hypothesis to explain the factors determining the time of spawning and the distribution of this species in the Kenai River.

Materials and Methods

Study Site

The Kenai River originates from Kenai Lake and flows through Skilak Lake before reaching Cook Inlet, a total distance of 136 km (Fig. 1). The river has a mean annual flow of about 140 m^3/s, peak discharges of 550–850 m^3/s (Scott 1982), and a drainage basin of about 3000 km^2.

Radio Tagging and Tracking

After preliminary tests, we chose radio tagging as the tool by which to track chinook salmon to their spawning areas in the Kenai River, and to determine time of spawning in the main-stem river. Several other researchers have used radio telemetry to determine salmonid migrational behavior (Knight et al. 1977; Liscom et al. 1978; Winter et al. 1978; Gray and Haynes 1979) and spawning areas (Lough 1980; Spence 1981).

We used low-frequency (40 MHz) radio telemetry equipment developed by Smith-Root, Inc., Vancouver, WA. The encapsulated transmitters were cylindrical (9.6 cm long by 1.8 cm diameter) and had external antennas 18 cm long. Transmitters were designed to operate for 80–90 d on lithium batteries. Different frequencies (40.600–40.740 MHz) and pulse rates (1, 2, or 3 pulses per second) were used to identify individual fish during each season of tagging. Transmitters were tested in water before field use to verify their operation and frequency.

Fish were captured in the lower 20 km of the Kenai River by drifting a small-mesh (13-cm, stretch mesh) gill net (18.0 m long and 2.4 m deep) from a boat. Chinook salmon encountering this net became entangled by their teeth and jaws. Once netted, fish were quickly retrieved and transferred to a holding tank containing fresh river water where they were anesthetized.

The fish was held with its ventral side upward and its lower jaw raised while a glycerin-coated transmitter was pushed gently into the anterior portion of the stomach with Plexiglas tubing (method modified from Monan and Liscom 1975). The external antenna extended into the mouth, where it was attached to the upper jaw posterior to the vomer with a stainless-steel fishhook. An external disc tag was affixed near the dorsal fin of each radio-tagged salmon to aid in recovery of the transmitter from the sport fishery or from fish on the spawning grounds. Length (mid-eye to fork) of each tagged fish was measured. The fish then was transferred to the river near the shoreline, where it was held by its caudal peduncle until it could forcefully swim away. The entire process from capture to release averaged 25 min per fish, mainly because both anesthetization and recovery were gradual. Each fish was out of the water for only a short time, during insertion of the transmitter.

In four field seasons, 188 Kenai River chinook salmon were radio tagged: 33 from 25 June to 31 July 1979; 25 from 19 May to 30 June and 19 from 16 July to 31 July 1980; 62 from 13 May to 25 August 1981; and 49 from 20 May to 6 July 1982. Most

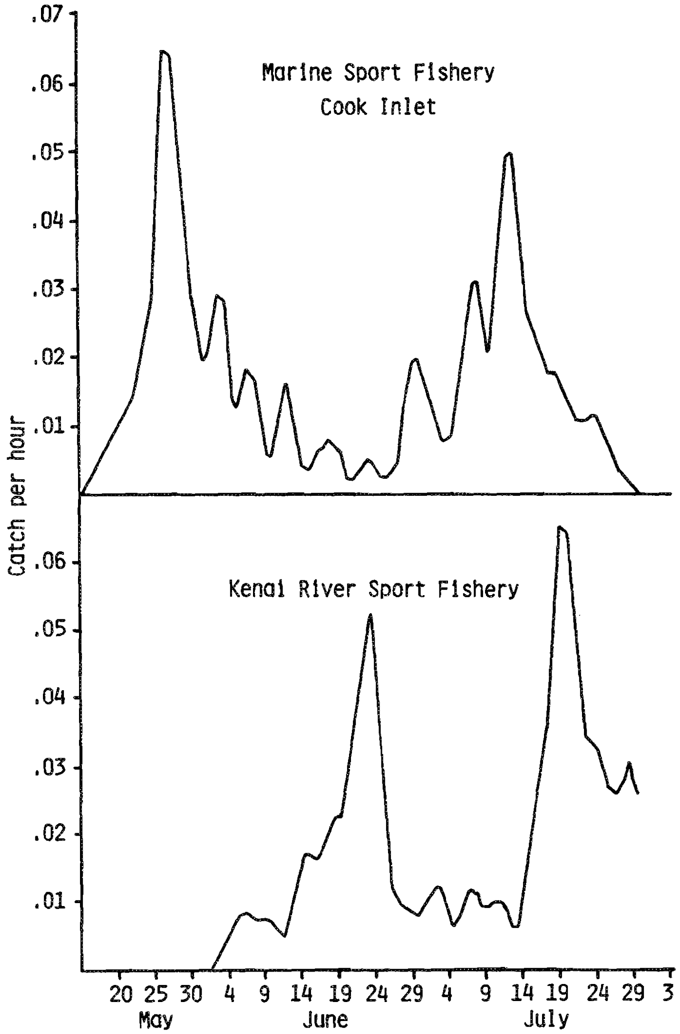

FIG. 2. Catch per hour of chinook salmon by date in the marine sport fishery (Cook Inlet) and in the Kenai River, Alaska, 1980 (from Hammarstrom 1981). (Data are based on boat counts, angler counts, and angler interviews until closure of the sport fishery on 31 July.)

fish were tagged and released at km 20, an area influenced by tides only to the degree that water velocity decreased at high tide. Females outnumbered males by a ratio of 1.5:1. The mean length of the tagged fish (mid-eye to fork) was 98.7 cm (range 65–117 cm). Although these fish were not weighed, we estimated that the weights of the smallest and largest fish tagged were about 8 and 32 kg.

We attempted to locate radio-tagged fish from boats or airplanes at least every 2 d with manual and scanning receivers. From boats, it was possible to determine the strongest or weakest (null) signal from the transmitter with a direction-sensitive loop antenna. We could locate, with two or more of these measurements, the exact position of each fish by triangulation, accurate to ±3 m. Characteristic conductivities (70–100 μS/cm) and depths (<6 m) of the Kenai River resulted in a transmitter signal range that averaged more than 0.8 km from a boat. Tracking flights from an airplane were made to supplement data obtained by boat. Loop antennas were attached to the struts of an aircraft with hose clamps and positioned to face aft with the most sensitive planes of the antennas directed toward the river. When the aircraft was at an altitude of about 300 m, transmitter signal range exceeded 1.6 km.

Development of Criteria for Spawning Areas and Times

Criteria were established to determine spawning areas and times for radio-tagged fish. "Final destinations" (spawning areas) for tagged fish were defined as areas where milling behavior (limited movements in a local area) occurred following an upstream migration. (In a few instances, data from fish that selected areas near or just downstream from their release sites were accepted because milling was detected and redds were found in those areas.)

Our day-to-day relocations allowed us to detect decreases in migration rates and the onset of milling behavior. It was possible to assign most tagged fish to one of four reaches of the main stem or to a tributary as a final destination. Tagged fish that were relocated on at least five different occasions and that demonstrated milling behavior after migrating upstream were assigned first to one of these reaches or to tributaries to determine their distribution within the drainage. Our ability to define spawning areas more precisely within these broad categories depended on the frequency and consistency of additional relocations. For example, two or more subsequent relocations without upstream movement by fish in a reach of river having a radius of up to 1.6 km connotated a general spawning area. Specific spawning areas and times were identified in the main-stem river if supplementary relocations made from a boat on two or more occasions demonstrated the presence of a tagged fish in the same particular pool or area of the river (usually having a radius ≤10 m and never exceeding 100 m) for a period of at least 8 d.

Test netting with a small-mesh gill net was used to assess the condition of fish caught in these areas, to determine whether our criteria for spawning times of tagged chinook were representative of those of untagged fish. Eventual downstream "drifting" by some tagged fish was a further indication that spawning was complete.

In tributary streams inaccessible to boats, such as the Killey and Funny rivers, our criteria were broadened because we had to rely on techniques (airplane tracking) that were less accurate than those deployed from a boat. A specific spawning area in a tributary was defined as the kilometre of river where relocations were made on two or more occasions following cessation of upstream movement by tagged fish. Spawning times were periods when a tagged fish was relocated within a 3.2-km radius of this area for at least a 5-d period. Since we did not track with airplanes every day, we assumed that a fish remained in an area when it was found there on each of two or more successive flights.

Peak spawning times in four areas of the main stem and in the Killey and Funny rivers were determined by comparing tracking records of tagged individuals within each area. The 10-d period of peak spawning was defined as the interval of time that had the highest frequency of tagged fish meeting the criteria for spawning. In some tributaries (Juneau, Slikok, and Benjamin creeks) it was possible to evaluate spawning by direct observation, and such observations supplemented the telemetry data. Several main-stem areas where tagged salmon were presumed to have spawned were surveyed periodically each year, during low-flow conditions (late September through April), to verify whether milling areas of tagged fish were actual spawning sites, and to locate additional redds. A few of the redds were excavated to determine the presence and depth of chinook salmon ova. Sieves (64, 16, 8, and 2 mm) were used to determine the predominant size of spawning gravels.

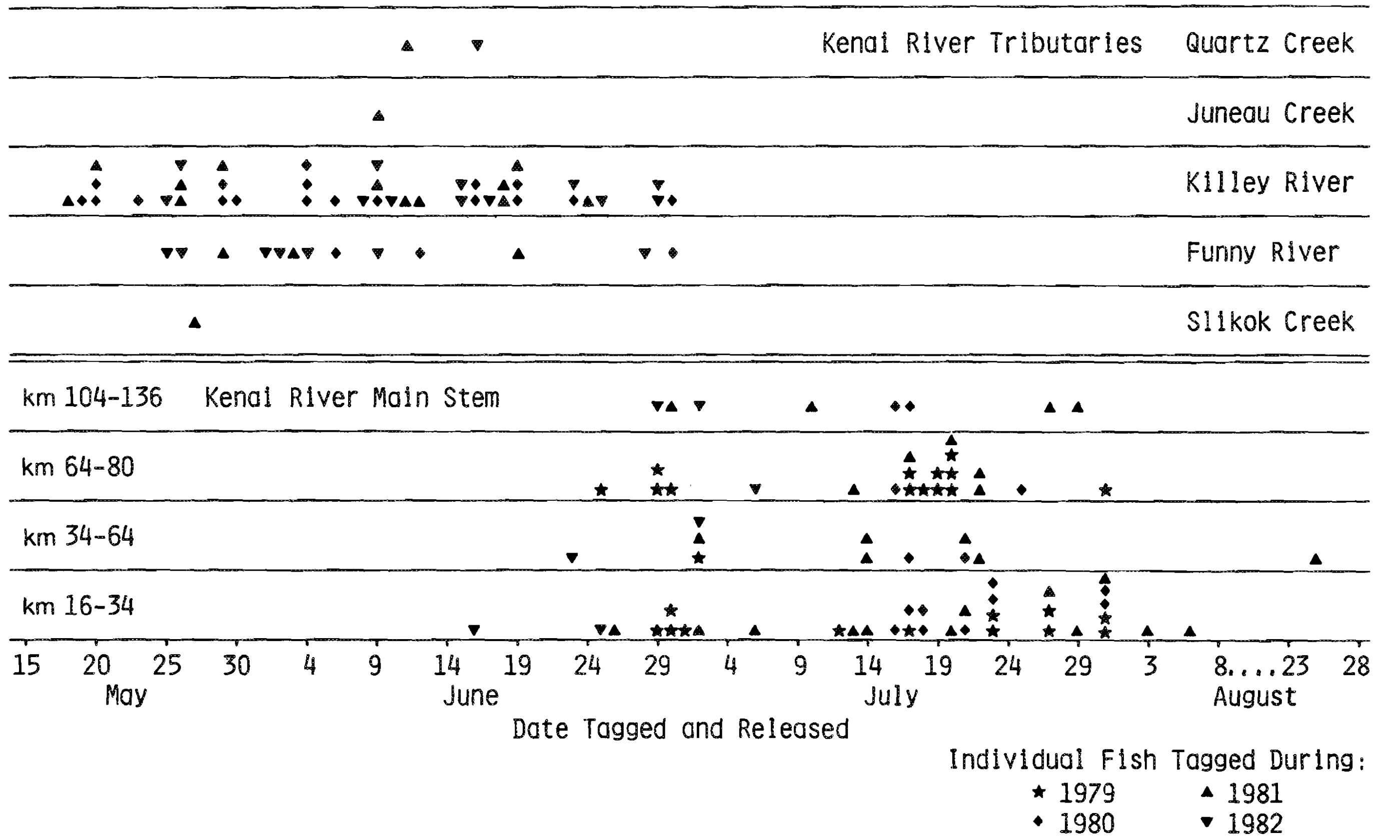

FIG. 3. Final destinations versus date tagged and released for radio-tagged chinook salmon in the Kenai River, Alaska, 1979–82. Fish that spawned in tributaries are shown above the double line and those that spawned in the main-stem river are shown below the double line. (Skilak Lake, km 80–104, is not represented because chinook salmon did not spawn there.)

Results

Distribution of Tagged Chinook Salmon

Most fish remained at or downstream from their release site during recovery. Within 2 d after tagging, about 52% of the 188 tagged fish were >2 km upstream from their release site, 16% were within 2 km of the release site, and 32% were >2 km downstream from the release site. Within 1 wk after tagging, 79% of the fish were upstream of their release site.

We obtained an average of 17 relocations (range 5–34) per fish tagged. Of 188 tagged salmon, 134 could be placed within one of four general reaches of the Kenai River main stem or a tributary as a final destination, and 74 of these met our criteria for determining specific spawning areas and times. Anglers caught 25 of the tagged fish during the 4-yr study, and 20 (probably strays or injured fish) were radio tracked downstream to the lowest reaches of the Kenai River and subsequently lost. These fish presumably returned to Cook Inlet (three were caught in the gill nets of Cook Inlet commercial fishermen), since they could not be relocated again in the river. (Several fish moved downstream to the estuary temporarily but then returned to the river and migrated to upstream locations.) Data for the remaining nine fish were not obtained or could not be used for a variety of reasons, including transmitter failure or unreported angler harvest.

Comparison of the final destinations of 134 tagged fish with the dates of tagging and release each year (Fig. 3) showed that fish entering the river in May and June were destined for tributaries, while fish that entered the river from late June through August spawned in the main stem. Except for one fish radio tagged on 16 June and one on 23 June 1982, all fish that spawned in the main stem were captured and tagged on or after 25 June in each year. The early run was upstream of the main-stem sport fishery (river km 0–80) by early July, while the late run was just entering the river. This time interval between runs coincided with the annual period of low angler success in the main stem.

Most of the fish tagged in the early run spawned in the Killey and Funny rivers (Fig. 3) downstream from Skilak Lake (Fig. 1). A few, however, spawned in Juneau and Quartz creeks, upstream from Skilak Lake. Fish in the late run spawned primarily in two areas of the main stem — below Skilak Lake (km 64–80) and in the lower Kenai River between km 16 and km 34. Some fish from the late run, however, also migrated through Skilak Lake and spawned in the main stem below Kenai Lake.

Spawning Areas and Times

Of 74 specific spawning areas located by radio telemetry, 47 were for early-run fish in tributaries, most of which were located throughout the Killey River. Benjamin Creek, in the headwaters of the Killey River (Fig. 1), was identified as an important spawning area because several tagged fish were tracked to this stream or to its confluence with the Killey River each July. Although a waterfall restricted the usable habitat in Benjamin Creek to only 1.2 km, the estimated numbers of adult chinook salmon in this stream during helicopter and ground surveys were 1000 in 1980 and 600 in 1981. In mid-July 1982, a radio transmitter was recovered from a partly spent fish in Benjamin

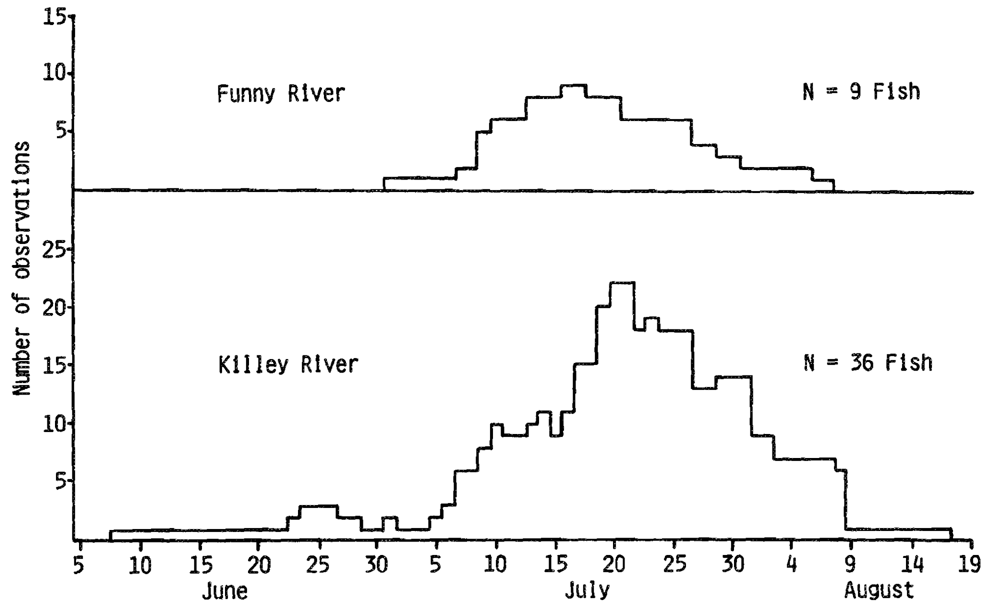

FIG. 4. Estimated peak spawning times of radio-tagged chinook salmon in the Funny and Killey rivers, as determined by intermittent airplane tracking during 1980, 1981, and 1982.

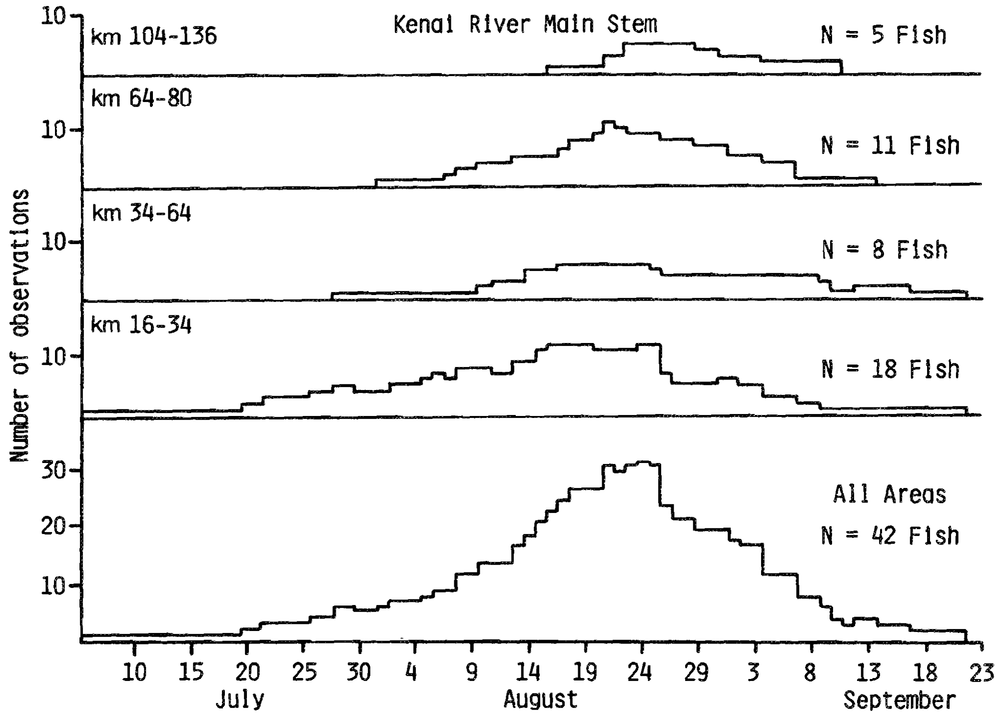

FIG. 5. Estimated peak spawning times of radio-tagged chinook salmon in the main-stem Kenai River, as determined by radio tracking from boats and airplanes during 1979, 1980, and 1981. (Skilak Lake, km 80–104, is not represented because chinook salmon did not spawn there.)

Creek, confirming that tagged as well as untagged fish were present in the spawning population.

The number of tagged fish that met our spawning criteria in the Killey and Funny rivers (1980–82) was greatest between 17 and 27 July and 12 and 22 July, respectively (Fig. 4). Tagged fish that entered other tributaries were too few to determine spawning areas or times by radio telemetry alone. One tagged fish was found in Juneau Creek from 29 July to 7 August 1981, and was recovered in a spent condition. As judged by our observations of redds and of about 50 adults in Juneau Creek in 1981, spawning was estimated to have peaked from 27 July to 6 August. Another tagged fish was tracked to Slikok Creek, where we observed about 40 spawners and estimated that spawning had peaked from 13 to 23 July.

Twenty-seven tagged fish met our criteria for determining specific spawning areas in the main-stem Kenai River from 1979 to 1981; 15 others spent at least 8 d in an area of the river with a radius of up to 1.6 km. Of this total of 42 fish, 15 were tracked to the lower Kenai main stem and 11 to the area below Skilak Lake. Spawning of tagged fish in the Kenai River main stem peaked from 16 to 26 August (Fig. 5). Test netting also indicated that peak spawning was in mid- to late August:

unspawned fish were captured in early August but spent salmon were found in early September.

Daily thermal readings at km 34 in the Kenai River from 1979 to 1981 (collected by the U.S. Department of Commerce; J. Dubendorf, Box 67, Soldotna, AK, pers. comm.) showed that maximum annual temperatures of about 12°C were recorded during the first 10 d of August. Because temperatures decline after this period and chinook salmon spawn during the latter part of August, spawning in the main stem occurred while water temperatures were declining.

Low-flow surveys confirmed that most chinook salmon that spawned in the main stem did so from km 16 to 34, and from km 64 to 80, where more meanders and vegetated islands occur than in the middle Kenai River. Redds were located frequently at the upstream tips of vegetated islands in loose, clean gravels. Gravel in predominant substrates used by spawners ranged from 1.6 to 6.4 cm in diameter.

Time of residence at spawning areas was computed for tagged fish in each run. Early-run fish spent an average of 13.0 d at tributary spawning areas and late-run fish an average of 18.4 d in main-stem spawning areas.

Discussion

Our data, when coupled with the sport harvest information collected by the Alaska Department of Fish and Game, provide strong evidence that two runs of chinook salmon exist in the Kenai River and demonstrate the existence of at least two discrete spawning stocks. Early-run fish were radio tracked to five (Fig. 3) of nine streams known to produce chinook salmon in the Kenai drainage. The four tributaries never used by tagged fish receive small numbers of chinook salmon each year, and fish destined for these tributaries were evidently missed during sampling. We conclude that early-run fish spawn in Kenai River tributaries (primarily in the Killey and Funny rivers) and that late-run fish spawn in the main stem.

Radio tagging did not appear to have any impact on fish behavior that would negate the value of the results. Most fish recovered from any handling stress within 2 d after tagging and resumed upstream migrations. Tagged fish in three tributaries were observed to be present in association with spawning, untagged fish.

Length of residence at the spawning area for most tagged fish from the early run (average was 13.0 d) exceeded the 5-d criterion we imposed. Length of residence of most late-run fish (average was 18.4 d) exceeded the 8-d criterion imposed. Recent research in the Nechako River, B.C., showed residency of 6–25 d ($\bar{x} = 14.5$) at redds by chinook salmon (Neilson and Banford 1983), consistent with our data. Kamchatka River chinook salmon were observed on redds from 10 to 23 d (Vronskiy 1972). Although some of our tagged salmon appeared to spawn in more than one adjacent area, we assumed that spawning occurred in the area occupied for the longest period.

More meanders and vegetated islands occur in the two areas of the main stem most heavily used by late-run chinook (Fig. 3) than in other sections of the river. Redds often were near the upstream tips of these islands, where loose mounds of clean gravel were available. Stuart (1953) found consistent downward currents through gravel mounds that were strongest below the apex of the mound. Other researchers, using dyes, found that riffles with a convex profile had a downward direction of water exchange through the center of the mound (Vaux 1962). In the Kenai River, vegetated islands facilitate gravel mound formations, which presumably allow favorable subsurface flows for egg incubation and hence, a selective advantage for spawning salmon.

The median date of the spawning migration among salmonids generally occurs progressively earlier in the year with increasing latitude (Godin 1981). Multiple runs of chinook salmon have not been reported elsewhere in Alaska. The timing of the runs of chinook salmon stocks in southcentral Alaska is similar to that of the early-run fish in the Kenai. Apparently, conditions are not favorable for two runs of chinook salmon in these and other Alaskan streams. The obvious question is, what is the reason for the existence of a unique run of late-spawning chinook salmon in the Kenai River?

Our radio-tagging data suggested a tendency for spawning to occur progressively later as distance from Cook Inlet increased. We compared spawning times of tagged fish from both runs to evaluate this observation, supplementing our data with results of our stream surveys and those of the Alaska Department of Fish and Game, Soldotna, AK (unpubl. data), because tagged fish had not used four tributaries that were known producers of chinook salmon. The 10-d peak spawning period was that interval of time when the highest frequency of adults were on the spawning grounds. The midpoint of this interval was chosen for purposes of comparison. Although spawning time and distance of tributaries from Cook Inlet appear related, spawning peaked nearly 20 d later in the Russian River than in the next upstream tributary, Juneau Creek (Table 1). Distance of spawning grounds is not the major determinant for differences among stock arrival times (Miller and Brannon 1981).

The Russian River is influenced by two lakes (Fig. 1). Our untested hypothesis is that these lakes have warmed the fall and winter water temperatures of the Russian River sufficiently to result in selection for later spawning, an event that is probably now under genetic control. This sequence of events assumes that there is an optimal emergence time for fry each spring. Thus, if adults returned to the Russian River to spawn in July instead of late August (as now occurs; Table 1), the accumulated temperature units for their ova might result in premature emergence and poor fry survival, thus removing early spawners from the gene pool. If spawning occurred too late (for example, mid-September), delayed emergence could produce the same end result.

For each tributary where peak spawning occurs in August (Table 1), a lake influences the drainage (Fig. 1). Where peak spawning occurs in July (Killey and Funny rivers and Slikok Creek), there are no lake influences. Thus, for early-run chinook salmon in the Kenai River, lake influences and spawning times appear to be correlated, the later spawning times occurring in lake-influenced streams. The influence of Kenai and Skilak lakes on the Kenai River main stem (Fig. 1) is therefore a likely explanation for the existence of this unique late run of chinook salmon in Cook Inlet.

We have postulated that tributary spawners are early-run chinook salmon that enter the river during May and June. Because fish in certain tributaries spawn in late August (see Table 1; Grant and Ptarmigan creeks and Russian River), it might appear that these salmon must delay spawning. Our data, however, are insufficient to address this point. Our radio tracking records demonstrate that the small number of tagged fish selecting Quartz and Juneau creeks (Fig. 3) arrived there by late July, just prior to the early-August spawning period. Tagged fish selecting the Killey and Funny rivers arrived there by early July, just prior to the mid-July spawning period.

TABLE 1. Summary of peak spawning times of chinook salmon in the Kenai River drainage, Alaska.

Drainage	Estimated peak spawning period		Distance from Cook Inlet (km)
	Dates	Midpoint	
Kenai River tributaries			
Grant Creek	16–26 Aug.[a]	21 Aug.	171.2
Ptarmigan Creek	21–31 Aug.[a]	26 Aug.	168.0
Crescent Creek	1–11 Aug.[a]	6 Aug.	147.2
Quartz Creek	1–11 Aug.[a]	6 Aug.	140.8
Juneau Creek	27 July – 6 Aug.[b]	1 Aug.	130.0
Russian River	15–25 Aug.[a]	20 Aug.	121.6
Killey River	17–27 July[c]	22 July	70.8
Funny River	12–22 July[c]	17 July	49.0
Slikok Creek	13–23 Aug.[b]	18 July	30.0
Kenai River main stem			
All four reaches combined	16–26 Aug.[c]	21 Aug.	—

[a]Determined by stream survey, Alaska Department of Fish and Game, Soldotna, AK (unpubl. data).
[b]Determined by radio tracking and stream survey (this study).
[c]Determined by radio tracking (this study).

Similarly, late-run fish did not delay spawning in the main stem. It is tempting to speculate that the late-August spawners in three tributaries are actually late-run chinook salmon, an argument that can be clarified only by more extensive tagging, but one that is more consistent with our hypothesis.

We hypothesize that Kenai River chinook salmon have adapted to predictable thermal regimes in the home stream and that selection has occurred for stock-specific run times that insure the presence of adults at spawning areas just prior to the optimum spawning period. This promotes specific emergence times that enhance survival of the fry.

Temperature data on the Kenai River and its tributaries are inadequate to enable us to test our hypothesis. It is generally known, however, that the volume of water flowing through a lake results in a considerable heat loss from the topmost layers of the lake, and the larger the lake, the longer is its cooling process each autumn (Ruttner 1964). Ruttner also noted that if a lake outlet is wide and shallow, the heat loss from the lake to the outlet increases. Hydrological studies on the Kenai River (Scott 1982) show that Skilak and Kenai lakes act as reservoirs that influence the flow regime of the river. The wide lake outlets are shallow extensions of these lakes, particularly the outlet of Skilak Lake where the width averages about 200 m (Scott 1982). Other researchers support the contention that outflows can receive heat from lakes by advection. The Thompson River provides inflow and outflow for Kamloops Lake, British Columbia. Carmack et al. (1979) studied temperature relationships in this drainage from 1974 to 1975. They found that the temperature of the river at its point of inflow peaked in late August at about 15°C and fell to 0°C from January to early March. The river near the lake outflow, however, was warmer — the temperature peaked at about 17°C in early September and gradually fell only as low as about 1°C during the last several days of February (Carmack et al. 1979). Such findings support our argument that differences in spawning times for chinook salmon in lake-fed streams in the Kenai drainage are temperature related.

Variability in the thermal regime of the home river has been suggested as the principal factor influencing reproductive strategies in American shad (*Alosa sapidissima*) (Leggett and Carscadden 1978). Other researchers have suggested that the thermal regime of the home river affects salmon spawning times. For example, pink salmon (*O. gorbuscha*) were found spawning early in cold (inland) streams in southeastern Alaska and later in warmer (coastal) streams (Sheridan 1962). Sheridan showed that despite a 46-d difference in spawning times between Kadashan and Klawock creeks, pink salmon ova in both streams received about the same number of temperature units by spring, so that fry in both streams emerged at about the same time. Miller and Brannon (1981), who offered a model for the evolution of life history patterns in Pacific salmonids, suggested that local temperature regimes are most responsible for ecological isolation of stocks, that the incubation period is dictated by temperature, and that therefore the time of egg deposition is predetermined for each habitat for optimal fitness of fry. Thus, there is evidently strong selection pressure on spawning times to insure hatching and emergence at the most favorable time each spring (Godin 1981).

Rich and Holmes (1929, cited in Ricker 1972) reported that offspring from fall chinook salmon transplanted to a stream in the Columbia River Basin that normally produced only spring chinook salmon returned during the normal times for fall fish, a result that indicates that run timing is under genetic control. If run timing is genetically controlled, and the various components of the early run (and the late run) are reproductively isolated stocks that have adapted to predictable stream temperatures, there are implications for stream rehabilitation and enhancement programs in the Kenai River drainage, events that have not yet occurred. For example, if a self-perpetuating run is to be established in a stream currently devoid of salmon, our hypothesis implies that the donor stock must be thermally adapted to a temperature regime similar to that of the stream being enhanced. We suggest that in a given drainage, the success of natural spawning by transplanted stocks will be determined, in part, by their compatability with the temperature regime of the stream enhanced.

Man-made reservoirs associated with hydroelectric development can affect temperatures in receiving waters (Hecky 1984; Heggberget and Wallace 1984). A small hydroelectric facility is planned in the upper Kenai River System, and several such facilities are planned in other Alaskan rivers. If migrations and spawning times of indigenous stocks are predetermined for predictable environmental conditions, the implications associated with changes in temperature regimes resulting from these types of development must also be considered.

Acknowledgments

The Division of Ecological Services, U.S. Fish and Wildlife Service, funded this study. The Alaska Department of Fish and Game was a major cooperator, and personnel from various divisions assisted us, especially L. Flagg, S. Hammarstrom, S. Logan, and R. Reddick. We thank M. Healey (Canadian Department of Fisheries and Oceans), J. McIntyre (U.S. Fish and Wildlife Service), E. Salo (University of Washington), F. Wangaard (Colorado State University, emeritus), and J. Winter (State University College, Fredonia, NY) for critically reviewing this manuscript; R. Bailey and A. Knight (U.S. Fish and Wildlife Service) and K. Liscom and his staff (National Marine Fisheries Service) for suggestions on radio telemetry techniques; D. Schmidt (Alaska Department of Fish and Game) for his many helpful suggestions; and L. Van Ray and J. Freidersdorff (U.S. Fish and Wildlife Service) for assistance and logistical support. A. Danielson, L. Dugan, D. Gray, A. Palmisano, M. Thompson, R. Uberuaga, and M. Wenger assisted with data collection.

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