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Pattern of Shoreline Spawning by Sockeye Salmon in a Glacially Turbid Lake: Evidence for Subpopulation Differentiation

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Abstract.—Alaskan sockeye salmon *Oncorhynchus nerka* typically spawn in lake tributaries during summer (early run) and along clear-water lake shorelines and outlet rivers during fall (late run). Production at the glacially turbid Tustumena Lake and its outlet, the Kasilof River (south-central Alaska), was thought to be limited to a single run of sockeye salmon that spawned in the lake's clear-water tributaries. However, up to 40% of the returning sockeye salmon enumerated by sonar as they entered the lake could not be accounted for during lake tributary surveys, which suggested either substantial counting errors or that a large number of fish spawned in the lake itself. Lake shoreline spawning had not been documented in a glacially turbid system. We determined the distribution and pattern of sockeye salmon spawning in the Tustumena Lake system from 1989 to 1991 based on fish collected and radiotagged in the Kasilof River. Spawning areas and times were determined for 324 of 413 sockeye salmon tracked upstream into the lake after release. Of these, 224 fish spawned in tributaries by mid-August and 100 spawned along shoreline areas of the lake during late August. In an additional effort, a distinct late run was discovered that spawned in the Kasilof River at the end of September. Between tributary and shoreline spawners, run and spawning time distributions were significantly different. The number of shoreline spawners was relatively stable and independent of annual escapement levels during the study, which suggests that the shoreline spawning component is distinct and not surplus production from an undifferentiated run. Since Tustumena Lake has been fully deglaciated for only about 2,000 years and is still significantly influenced by glacier meltwater, this diversification of spawning populations is probably a relatively recent and ongoing event.

Shoreline spawning in lakes is one of several reproductive adaptations of sockeye salmon *Oncorhynchus nerka* throughout eastern Asia and the Pacific Northwest of North America. Although spawning commonly occurs in rivers, tributaries, springs, and outlet streams adjacent to lakes, shoreline spawning in lakes can be extensive in some populations (Burgner 1991). For example, shoreline spawning occurs on Russia's Kamchatka Peninsula (Yegorova 1977; Bazarkin 1990), in British Columbia (Foerster 1968; Brannon 1987), and in many Alaskan drainages, particularly those

in Bristol Bay (Burgner et al. 1969) and on Kodiak Island (Gard and Drucker 1963).

Reports of shoreline spawning in lakes by sockeye salmon are often anecdotal, perhaps because of a historical consensus that shoreline spawning is of minor significance (Rounsefell 1958; Straty 1964; Foerster 1968). Burgner et al. (1969) believed that production from shoreline spawning is more variable than production from stream spawning. Other authors have considered shoreline spawners in lakes to be part of large runs in rivers (Williams 1987) or to be individuals forced to

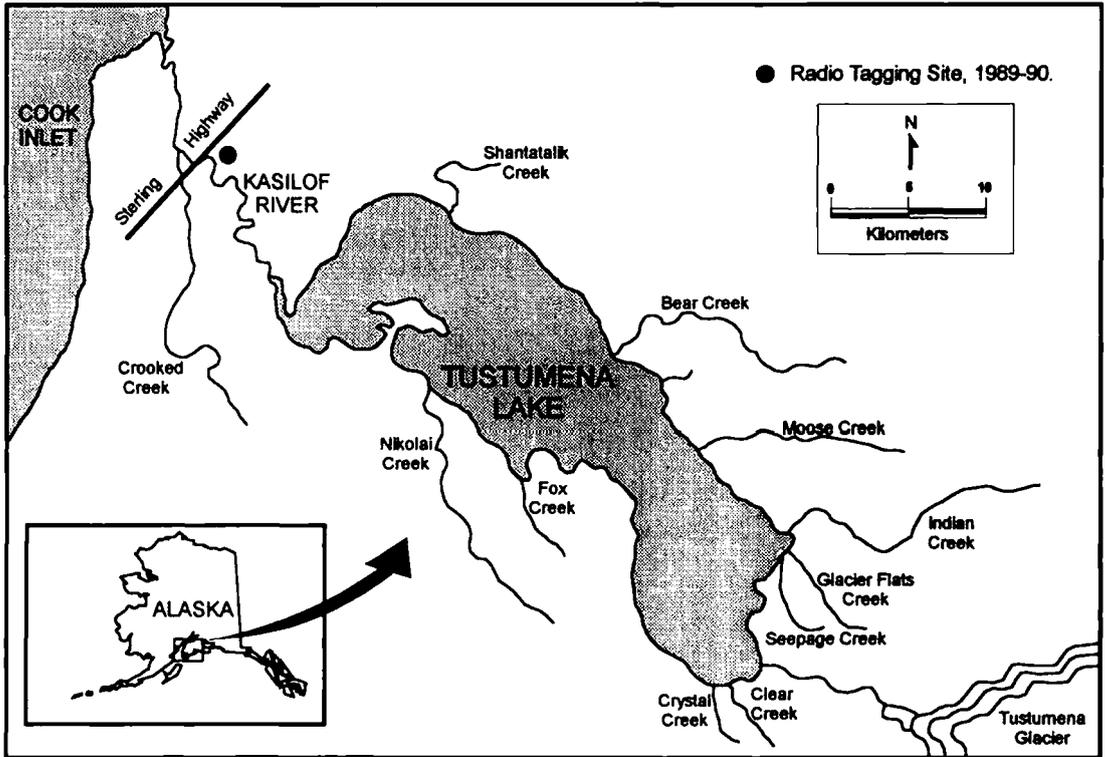


FIGURE 1.—Tustumena Lake study area on the Kenai Peninsula, south-central Alaska. In 1991, some fish were captured at a site closer to the mouth of the Kasilof River.

spawn in suboptimal habitat as spawner densities increased (West and Mason 1987). However, where lake spawning has been observed in Alaska, the sockeye salmon are often late-run fish that are genetically discrete from the early-run sockeye salmon spawning in lake tributaries (Wilmot and Burger 1985). Late-run sockeye salmon spawn along the shoreline and lake outlets in Alaska's Russian (Nelson 1983), Karluk (Owen et al. 1962), Chignik (Narver 1968), and Brooks river systems (Hartman et al. 1963). Such observations suggest that shoreline-spawning sockeye salmon may be distinct populations whose reproduction is not surplus within a single run.

For several reasons, the incidence and relative importance of lake spawning by sockeye salmon has been difficult to ascertain. Spawners are not confined to specific areas (such as streams) where accurate observations can be made. Direct observations from boats and aircraft have been used in Alaska to estimate shoreline spawning by sockeye salmon in Bristol Bay lakes (Metsker 1967), Iliamna Lake (Kerns and Donaldson 1968), and Wood River lakes (Burgner et al. 1969). However,

such studies are limited to observations of fish in the shallows of clear-water lakes and cannot account for individuals at depths greater than about 12 m, where spawning may occur (Kerns and Donaldson 1968). Visual surveys are extremely limited by turbidity in Alaska's numerous glacial lakes. Also, visual surveys result in point-in-time estimates and may not account for the "multiple waves" of late-arriving sockeye salmon that are known to occur in some drainages (Merrell 1964; Kerns and Donaldson 1968). These point estimates preclude a determination of total residence time in the lake and may result in incomplete and misleading interpretations of the value of shoreline spawning.

Radio tracking has been used successfully to locate spawning salmon when direct observation is limited (Burger 1981; Eiler 1990). The application of telemetry to determine shoreline spawning could surmount the logistical difficulties experienced by other investigators, especially in glacially turbid lakes where shoreline spawning cannot be visually observed.

Tustumena Lake (Kenai Peninsula, Alaska)

drains into Cook Inlet (Figure 1) and has supplied about 20% of the inlet's annual sockeye salmon harvest (Kyle 1992). Shoreline spawning was suspected to occur in Tustumena Lake, but the glacially turbid waters of the lake prevented visual observation and precluded assessment of its importance. The only known spawning areas at Tustumena Lake were its clear-water tributaries, where sockeye salmon were enumerated visually (Kyle 1992). Because the availability of spawning habitat was believed to limit sockeye salmon production from Tustumena Lake, hatchery-incubated juveniles have been released each year since 1976 to supplement natural reproduction (Van Ray et al. 1983). The overall reason for our study was to determine if sockeye salmon reproduced only in Tustumena Lake tributaries. This information could have implications for continued hatchery enhancement in the drainage.

Indirect evidence of shoreline spawning by Tustumena Lake sockeye salmon emerged from side-scanning sonar observations of adult returns in the Kasilof River, the lake's outlet (Kyle 1992). When visual estimates of the number of spawning salmon in lake tributaries each year (1976–1987) were compared with the number of fish enumerated by sonar, 20–40% of the sonar counts could not be accounted for in the drainage. This discrepancy suggested either lake spawning or large counting errors.

The available sonar counts indicated that the spawning escapement (those fish that survived commercial and sport fisheries) was a single run of sockeye salmon (mid-June to early August), with a peak in migration during mid-July of each year (Kyle 1992). Thus, if shoreline spawning by sockeye salmon was occurring at Tustumena Lake, it was not the typical pattern observed in several Alaskan drainages that had two distinct runs: early-run tributary spawners and late-run lake shoreline and lake outlet spawners.

The objectives of our study were to (1) determine the location and timing of sockeye salmon spawning in the various habitats of the Tustumena Lake drainage, (2) estimate the proportion of salmon spawning along the shoreline of the lake, and (3) analyze the annual variation in observed patterns and the factors (for example, run timing, number of spawners returning to the lake, and tributary hydrology) that might influence the success and significance of shoreline spawning.

Study Site

Tustumena Lake (60°10'N, 150°55'W) drains over 1,375 km² on the Kenai National Wildlife

Refuge in south-central Alaska (Figure 1). This oligotrophic lake is the largest on the Kenai Peninsula, with a surface area of about 294 km², a mean depth of 24 m, and a maximum depth of 320 m (Kyle 1992). Nine clear-water tributaries drain into the lake, but meltwater from nearby Tustumena Glacier produces high turbidity (52 nephelometric turbidity units, NTU) that limits the lake's euphotic zone to a depth of 1.1 m (Koenings and Burkett 1987; Lloyd et al. 1987). The Kasilof River (annual average discharge, 2.13×10^9 m³/year; Koenings et al. 1986) is glacially turbid and flows about 30 km from the lake outlet to Cook Inlet.

Thermographs installed in three tributaries and in three shoreline areas of the lake recorded peak summer temperatures of 11 and 12°C, respectively. The mean daily precipitation in the study area during summer ranged from 0.03 to 0.15 mm (Figure 2). Lake water level peaked in August and September each year but dropped 2–3 m each winter through early spring.

Methods

We implanted radio transmitters in adult sockeye salmon during their upstream migration in the Kasilof River and radio-tracked the tagged salmon to spawning locations. Radio-tagging was conducted during three migration seasons, 1989–1991. In 1989 and 1990, adult sockeye salmon were captured with a fish wheel (Meehan 1961) operated by the Alaska Department of Fish and Game (ADFG) in the Kasilof River, about 8 km upstream from Cook Inlet (Figure 1). Because low flows precluded operation of the fish wheel during much of the 1991 season, 152 fish were captured with a gill net (11-cm mesh size; 18 m long \times 4.2 m deep) about 2 km upstream of the Kasilof River's mouth. The remainder (37) were captured in the fish wheel.

Radio-tagging.—Radio-tagging procedures were similar to those used by Burger et al. (1985). Fish captured by fish wheel or gill net were transferred to a holding tank that contained fresh river water, where they were anesthetized in a 50-mg/L solution of tricaine (MS-222) for 2–3 min. Each fish was held with its ventral side upward and its lower jaw raised while a glycerin-coated transmitter was gently pushed into the anterior portion of the stomach with plexiglass tubes (Monan et al. 1975). The transmitter antenna was left protruding from the mouth. Each fish was identified to sex and measured (mid-eye to fork of tail) to the nearest millimeter; several scales were removed for age analysis. A 5-cm colored dart tag was inserted near

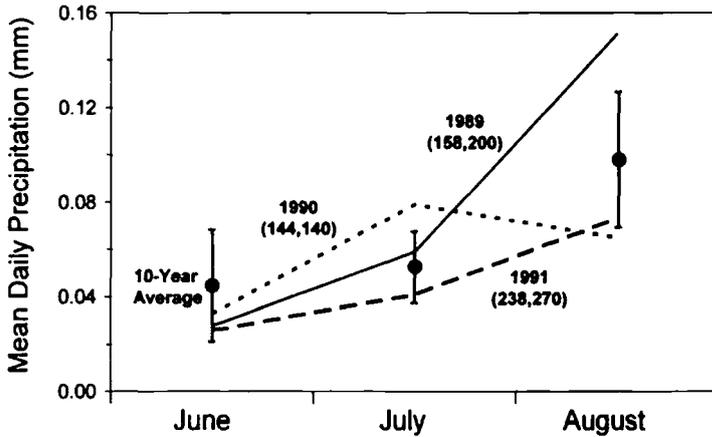


FIGURE 2.—Comparison of mean daily precipitation and 10-year average precipitation levels (mm) during summer months for each study year (1989–1991) at U.S. Weather Service Cooperative Station 50-4425, Kasilof, Alaska. (Vertical bars are 95% confidence intervals. Numbers in parentheses are annual sockeye salmon escapements to the Kasilof River.)

the dorsal fin to aid in recovery of radio-tagged fish on the spawning grounds. The tagging procedure averaged about 4 min per fish. Each tagged fish was allowed to recover in a holding pen (usually for 10–15 min) on the shoreline of the Kasilof River until it could swim away.

Our radiotelemetry equipment (Advanced Telemetry Systems, Isanti, Minnesota) consisted of low-frequency (40–41 MHz) transmitters, scanning receivers, and direction-sensitive loop antennas similar to those used by Burger et al. (1985). In 1989, a 20-g transmitter of 19.5-mm diameter by 55.5-mm length was used. However, we found the unit too large to use on fish less than 480 mm in length because of its potential to rupture their stomachs. Thus, a smaller transmitter (15.5 × 46.5 mm at 12.5 g) was used in 1990 and 1991 to permit tagging of all length-classes. (The smallest was 420 mm.) Each transmitter had a minimum lifespan of 90 d and a unique radio frequency to permit tracking of individual fish. In Tustumena Lake (water conductivity <120 μ S/cm), the 30-cm external wire antenna produced signals that could be detected over distances of at least 0.8 km on the ground and 1.6 km from an airplane.

The number of radio-tagged fish was distributed throughout each season in proportion to the 10-year average daily sonar counts for the system (ADFG, unpublished data) from mid-June to early August. This schedule ensured placement of the greatest number of radio tags in fish during the historic peak in upstream migration. In the final study year, however, we tagged nine fish in the

lower 2–3 km of the Kasilof River before (early June) and seven fish in the upper river after (late August) the established schedule to determine if early and late migrants behaved differently from fish tagged between mid-June and early August.

Radio-tracking.—We tracked fish by boat (Winter et al. 1978), aircraft (Gilmer et al. 1981), or foot every 2–3 d. Initially, an inflatable raft was used to float the Kasilof River from its origin at the lake outlet to determine riverine locations of newly tagged fish. Later, a jet boat was used to locate fish in the lake and to access lake tributaries for foot surveys. Use of the aircraft at altitudes of approximately 300 m above the ground (Burger et al. 1985) enabled us to survey the entire Tustumena Lake watershed and other drainages (such as the nearby Kenai River), to detect any tagged fish that may have strayed from the study area.

Fish positions were determined within 2–3 m of actual positions during foot and boat surveys and within 100 m during aircraft surveys, based on field tests with planted transmitters. Precise locations were obtained near the mouths of Tustumena Lake tributaries and during late-season periods when salmon were observed or thought to be spawning. A more general location (plotted on topographic maps after visual triangulation of prominent landmarks) was used during active pre-spawning migration in the lake and for locating fish in tributaries not accessible by boat or foot.

Spawning criteria.—Although determination of actual spawning times and locations among tagged fish was somewhat subjective, we attempted to min-

imize the subjectivity by establishing specific criteria related to distances between sites where fish were relocated and frequency of relocation. After we radio-tracked fish upstream in the Kasilof River and through Tustumena Lake, tagged fish were assigned a final destination (spawning area) if (1) they were relocated on at least two subsequent occasions during a 2-week interval in an area having a radius less than 100 m, (2) no additional migration was detected, and (3) untagged spawning or spawned-out sockeye salmon were observed (tributary foot survey) or sampled (gill net) in the areas selected by tagged fish. In cooperation with ADFG biologists, we conducted up to three foot surveys of the lake tributaries each season to observe spawning sockeye salmon. Gill netting was conducted at a depth averaging 4 m for about 4 h each week (late July through early September) to verify the presence and spawning condition of sockeye salmon along the lake shoreline. Two foot surveys of the lake's shoreline were conducted during April (1991) to look for evidence of shoreline spawning in areas once submerged by lake water.

The spawning times of tagged fish were determined from radio-tracking records of the calendar days when tagged individuals were located at their final spawning destination. We assumed that tagged sockeye salmon remained at their spawning locations between radio-tracking periods. For example, a tagged fish relocated in a specific reach of tributary on 26 July, 31 July, 5 August, and 10 August was assumed to have remained at this location from 26 July through 10 August. The numbers of tagged fish at the various spawning areas were summed by calendar day to develop histograms of spawning times. The median was used to estimate the peak spawning date of tagged fish that selected tributary and shoreline spawning areas. Although stream life of female sockeye salmon on their spawning grounds has been reported to vary from 6 to 19 d (Burgner 1991), no data were available for stream life of sockeye salmon in the Tustumena Lake drainage. Thus, we chose the median spawning date ± 5 d as a range for peak spawning of tagged fish.

Data analysis.—Of several fish tagged before and after the established schedule in 1991, the nine fish tagged in early June were included in all data analyses because they entered Tustumena Lake and exhibited spawning behavior similar to fish tagged between mid-June and early August. The seven fish tagged at the end of August were excluded because they exhibited unique spawning behavior and did not enter the lake.

To test for sampling bias, the age and length compositions of tagged fish were compared with age and length compositions of untagged sockeye salmon sampled from the fish wheel by ADFG (King and Tarbox 1991; Kyle 1992); chi-square tests of independence and Kolmogorov-Smirnov (K-S) two-sample procedures were used for this purpose (Daniel 1990). Run and spawning times of radio-tagged fish were analyzed to test for interannual variation within and among tributary and shoreline spawners. Anderson-Darling (A-D) k -sample tests were used to evaluate interannual variation because of the need to simultaneously compare $k > 2$ distributions (Scholz and Stephens 1987). When A-D results were significant, multiple-pairwise K-S tests were performed to determine which distribution pairs were significantly different. The critical significance level for each pairwise comparison was set at $\alpha = 0.1/[k(k - 1)]$, where k was the total number of values compared and 0.1 was the experimentwise error rate (Daniel 1990). Among radio-tagged fish, chi-square analysis was used to test the hypothesis that the proportions of radio-tagged fish selecting tributary and shoreline areas were independent of the sampling year. When chi-square results were significant, analysis of residuals (Everitt 1977) was used to determine which observations were significantly different from their expected values (expected value calculated for the chi-square test of independence). Based on radio-tagged fish, tests for differences between proportion estimates of shoreline and tributary spawners and proportion variance estimates were performed according to Zar (1974). Methods for determining sample size and power ($1 - \beta$; β = the probability of making a type II error, given a preselected α) for proportion estimates were obtained from Snedecor and Cochran (1967). The age and length composition and the spawning and run times of tagged sockeye salmon that selected tributaries and shoreline areas were compared with K-S tests. The minimum migration rate (km/d) at which each fish moved between locations was the straight-line distance from each position divided by the time (d) between observations.

The total spawning escapement of sockeye salmon into Tustumena Lake was estimated each year by ADFG (Kyle 1992) with Bendix side-scanning sonar in the Kasilof River as described by Gaudet (1990). The annual number of shoreline spawners was estimated by multiplying the total escapement estimate by the proportion of radio-tagged fish that we classified as shoreline spawners. Similarly, confidence intervals were calculated

TABLE 1.—Disposition of 564 adult sockeye salmon radio-tagged and tracked in the Kasilof River, Tustumena Lake drainage, Alaska, 1989–1991.

Category	Number (%) of fish in:			
	1989	1990	1991	Total
Posttagging distribution				
Number tagged	202	173	189	564
Deaths ^a	12 (6)	14 (8)	2 (1)	28 (5)
Never found	27 (13)	35 (20)	15 (8)	77 (14)
Returned to seawater	13 (7)	16 (9)	7 (4)	36 (6)
Strays to other drainages ^b	6 (3)	1 (1)	3 (1)	10 (2)
Tracked upstream	144 (71)	107 (62)	162 (86)	413 (73)
Spawning distribution				
No determination ^c	43	24	22	89
Remaining spawners	101	83	140	324
Lake tributaries	69 (68)	46 (55)	109 (78)	224 (69)
Lake shoreline	32 (32)	37 (45)	31 (22)	100 (31)

^a These fish gradually drifted downstream to permanent positions near the estuary and were assumed to be dead.

^b Most of these fish were relocated in the Kenai River drainage.

^c These fish entered Tustumena Lake and its tributaries but relocation data were insufficient to determine the final spawning area.

by applying the upper and lower bounds of the confidence interval for the shoreline spawner proportion estimates to the annual escapement. The estimated numbers of shoreline spawners were compared to the escapements to determine if shoreline spawning was related to fish density.

Results

Tagged Fish

We implanted radio transmitters in 564 adult sockeye salmon from early June through early August: 202 in 1989, 173 in 1990, and 189 in 1991 (Table 1). Peak numbers of tagged fish were released in mid-July of each year. The ratio of male to female sockeye salmon averaged 1:0.9 in the 3-year study. Lengths of tagged fish (mid-eye to fork of tail) ranged from 480–630 mm in 1989, but sockeye salmon as small as 420 mm were tagged in 1990 and 1991 (Figure 3).

On average, tagged sockeye salmon were longer than untagged fish (ADFG fish wheel samples) in two of the three study years (Figure 3). The length distribution of radio-tagged fish differed significantly from that of untagged fish in 1989 (K-S test, $D_{\max} = 0.228$, $P < 0.01$) and 1991 (K-S test, $D_{\max} = 0.253$, $P < 0.001$), but not in 1990 (K-S test, $D_{\max} = 0.099$, $P = 0.117$). The predominant age structure of tagged and untagged sockeye salmon in all years consisted of fish that had spent their first year in freshwater and either 2 or 3 years (age 1.2 or 1.3) at sea. However, tagged fish were somewhat older than untagged fish and their age composition differed from untagged fish in all 3 years (1989: $\chi^2 = 14.7$, $df = 3$, $P < 0.01$; 1990:

$\chi^2 = 10.15$, $df = 3$, $P < 0.02$; 1991: $\chi^2 = 50.79$, $df = 3$, $P < 0.001$). In 1989 age-1.2 fish composed 44% of the untagged sockeye salmon removed from the fish wheel for measurement by ADFG, but only 28.9% of our tagged fish. In 1991 age-2.3 fish composed only 5.8% of the untagged sample, but 19.4% of our tagged sockeye salmon.

Spatial Distribution of Tagged Salmon

Of the 564 sockeye salmon tagged during the 3-year study, 413 (73%) were radio-tracked upstream of the release site in the Kasilof River (Table 1). About 8% returned to seawater, some of which were relocated as "strays" in a different drainage (Kenai River). Some of the remaining sockeye salmon (5%) were assumed to have died because they gradually drifted downstream to the estuary, whereas others (14%) were never relocated after release. We made over 1,000 relocations of radio-tagged fish after their release in each year of study.

A spawning area was identified in the lake or in a tributary for 324 sockeye salmon (Table 1) based on an average of 8.3 relocations (range, 3–17) per radio-tagged fish. These fish constitute the basis of our analyses because the established spawning criteria were met. For 89 additional fish that entered the lake, either relocations were too few or we detected no localized movement believed to be typical of spawning behavior.

Of the 324 fish for which spawning destinations were determined, 100 fish (31%) were tracked to shoreline spawning areas in Tustumena Lake, and 224 fish (69%) spawned in lake tributaries (Table

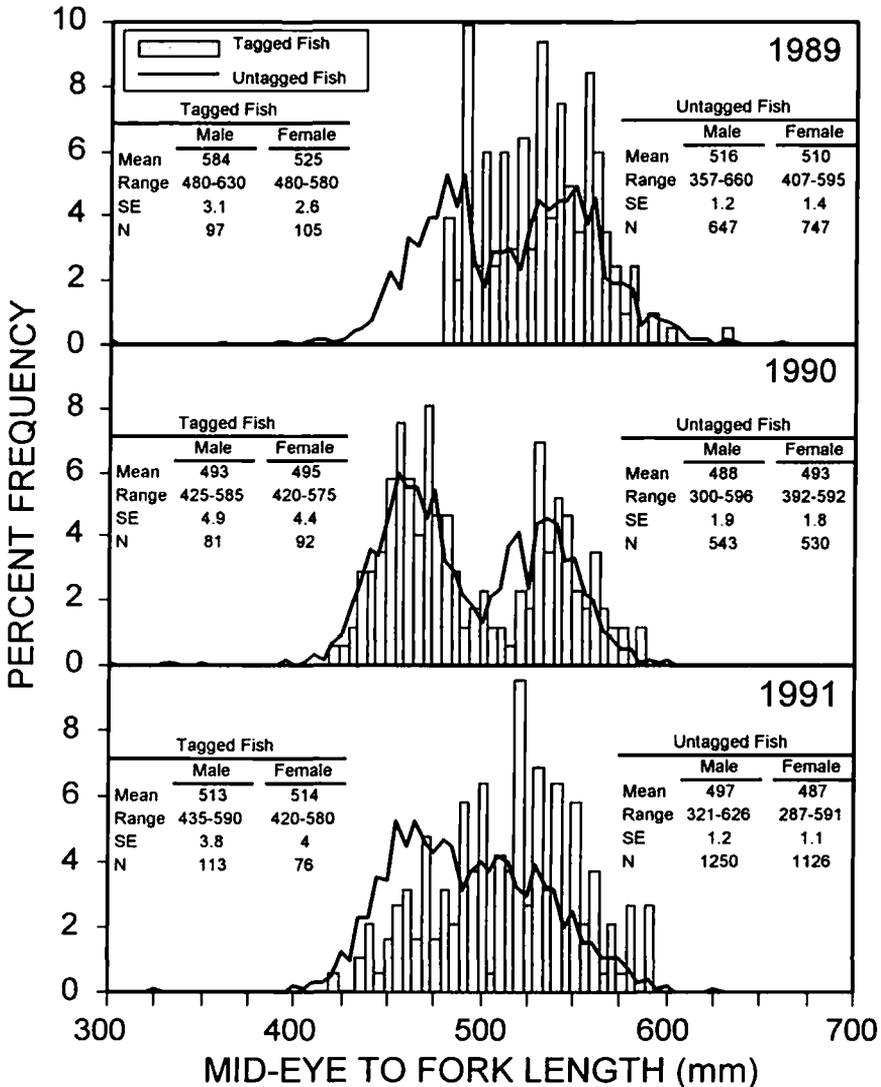


FIGURE 3.—Numbers and lengths (mid-eye to fork of tail) of radio-tagged and untagged adult sockeye salmon from the Kaslof River, Alaska, 1989–1991. (Untagged fish were sampled with a fish wheel and the values are unpublished data, Alaska Department of Fish and Game, Commercial Fisheries Division, Soldotna.)

1). The relative proportions of lake shoreline and tributary spawners were significantly different among years ($\chi^2 = 12.3$, $df = 2$, $P < 0.002$). Analysis of residuals indicated that the observed number of shoreline spawners was significantly higher than the expected value in 1990 (37 fish observed versus 25.6 expected) and significantly lower than the expected value in 1991 (31 fish observed versus 43.2 expected).

Neither the number nor the proportion of shoreline spawners appeared related to total escapement or to the June–August precipitation levels (used as

an index of tributary water volume). The estimated numbers of shoreline spawners did not increase with increased escapements (Figure 4). Rather, the numbers of shoreline spawners appeared relatively stable, ranging from 50,100 (1989) to 64,200 (1990), while escapements ranged from 144,000 (1990) to 238,000 (1991). Also, the lowest proportion (0.22) of shoreline spawning occurred during the year (1991) with the lowest observed precipitation (Figure 2) and the highest escapement (Figure 4).

Among tagged sockeye salmon, no consistent

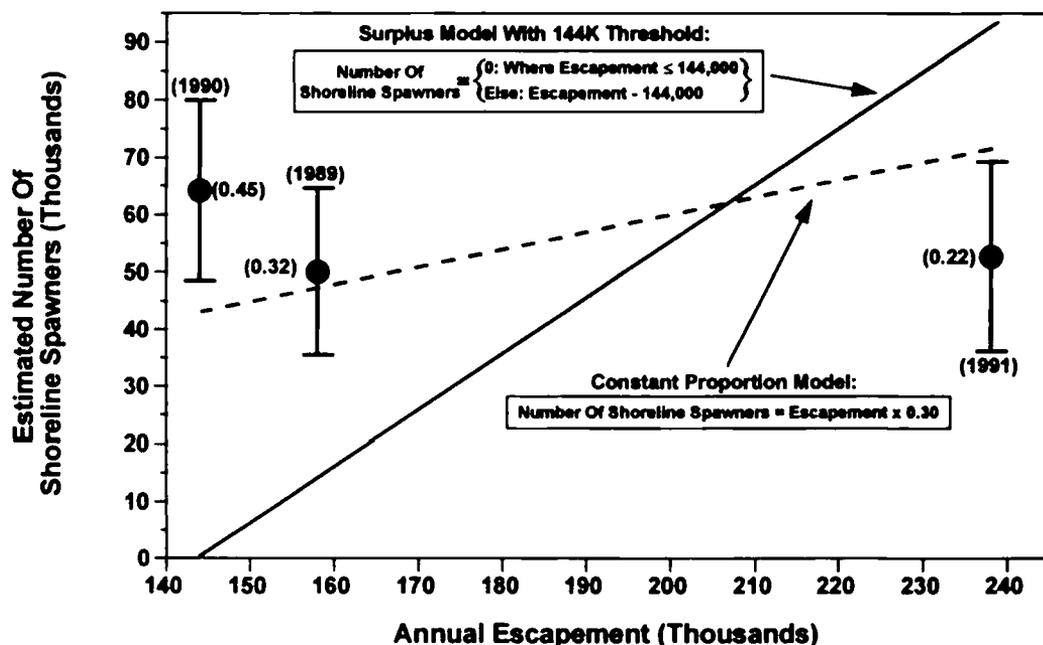


FIGURE 4.—Comparison of the estimated numbers of sockeye salmon shoreline spawners (95% confidence intervals shown by vertical bars) with annual sockeye salmon escapements, Tustumena Lake, Alaska, 1989–1991. (A constant proportion model is shown as a dashed line whereas a surplus model is shown as a solid line. Year and estimated proportion of shoreline spawners are in parentheses.)

differences were evident in the age or length structure between fish classified as shoreline or tributary spawners. While the length distributions were significantly different in 1991 (K-S test, $D_{\max} = 0.373$, $P = 0.002$), the difference between mean lengths was only 10 mm. Age compositions were significantly different only in 1989 ($\chi^2 = 6.82$, $df = 2$, $P = 0.033$).

Prior to our study we estimated that an annual sample size of 200 radio-tagged fish would allow us to estimate the proportion of shoreline spawners (p) and tributary spawners (q) in a “worst case” scenario ($p = q = 0.5$) with 95% confidence within $\pm 7\%$ of the true population proportion ($d = 0.07$, $\alpha = 0.05$). Despite intensive tracking, however, we determined spawning areas for only an average 57% (50% in 1989, 48% in 1990, and 74% in 1991) of the tagged fish (Table 1). The reduced sample sizes resulted in estimated confidence intervals for the proportions of shoreline spawners that were 0.32 ± 0.092 (1989), 0.45 ± 0.109 (1990), and 0.22 ± 0.069 (1991). Thus, we were 95% confident that our estimates were within 7–11% of the true population. Only the proportion estimates for 1990 and 1991 were significantly different ($Z = 3.46$, $P = 0.0005$).

Tagged fish that selected shoreline habitat spawned predominately in two areas of the lake (Figure 5), each of which was in proximity to an upland source of water. One of these areas was located between Bear and Moose creeks, near a small tributary; the other was near springs between Clear and Seepage creeks in the southeast corner of the lake. During the shoreline foot surveys (April 1991), the springs contained about 300 newly emerged yolk-sac fry in shallow pools of water a few meters from the lake.

Timing

There was little interannual variation in the run times of tagged fish classified as either shoreline or tributary spawners. There was no significant difference in the run timing of shoreline spawners among years (A–D test, $T_{akN} = -0.019$, $P > 0.39$). Although the overall analysis of run times for tributary spawners showed a significant difference (A–D test, $T_{akN} = 4.67$, $P < 0.002$), this difference was the result of only one pairwise comparison (1989 versus 1991; K-S test, $D_{\max} = 0.266$, $P < 0.008$). When we excluded the nine fish we tagged in early June 1991 (see above), no significant differences existed (K-S test, $D_{\max} = 0.217$, $P >$

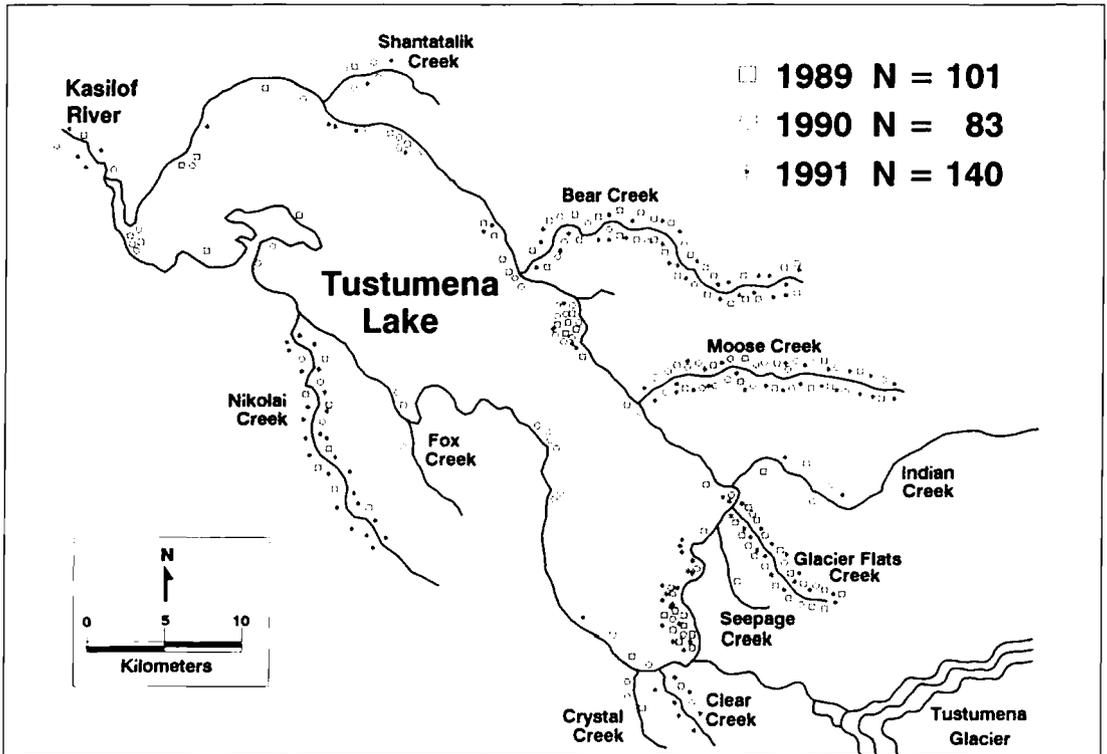


FIGURE 5.—Spawning destinations of sockeye salmon radio-tagged in the Tustumena Lake drainage, Alaska, 1989–1991. (Tagged individuals are denoted by symbols that correspond to the tagging year. Symbol positions are generalized to illustrate drainage-wide distributions and are not precise spawning locations.)

0.05). Therefore, all years were pooled for a comparison between tributary and shoreline spawning fish. Radio-tagged fish destined for tributary spawning areas migrated earlier than shoreline spawning fish (K–S test, $D_{\max} = 0.506$, $P = 0.0001$; Figure 6), whether the several fish tagged in early June of 1991 were included or not.

As with run timing, tagged fish that entered Tustumena Lake tributaries spawned earlier than sockeye salmon that spawned in shoreline areas. Spawning peaked by mid-August in all tributaries, whereas spawning peaked in lake shoreline areas during the last 2 weeks of August (data for all years combined; Figure 6). Although the spawning time distributions of radio-tagged fish did exhibit interannual variation (tributary: A–D test, $T_{ukN} = 114.4$, $P < 0.0001$; shoreline: A–D test, $T_{ukN} = 139.5$, $P < 0.0001$), the above differences between tributary and shoreline spawners were consistent across years based on K–S tests (1989: K–S test, $D_{\max} = 0.291$, $P = 0.0001$; 1990: K–S test, $D_{\max} = 0.318$, $P = 0.0001$; 1991: K–S test, $D_{\max} = 0.592$, $P = 0.0001$). The median date of spawning

was consistently earlier for tagged fish that selected tributaries than for those that selected shoreline areas (1989: 13 versus 19 August; 1990: 20 versus 26 August; 1991: 14 versus 29 August). The interannual variation we observed in run and spawning times of radio-tagged fish was also present in ADFG sonar data (1989–1991) that estimated escapement timing (A–D test, $T_{ukN} = 115.4$, $P < 0.0001$).

Our estimates of spawning times were consistent with results we obtained from visual tributary surveys and shoreline test netting. The more than 400 fish that were captured during August and September of each year by test netting confirmed that sexually mature sockeye salmon were present by mid-August in the same shoreline areas selected by tagged fish. Sockeye salmon believed to be spawning were captured at these sites in late August, and spawned-out fish were captured in early September.

Lake outlet spawning in the Kasilof River was identified as a third reproductive pattern for this system. Three fish tagged from late July to early

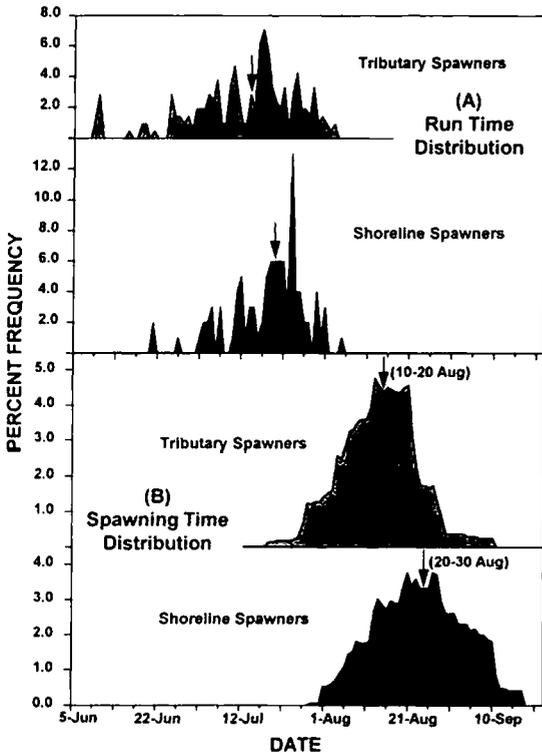


FIGURE 6.—Run (A) and spawning (B) time distributions of radio-tagged sockeye salmon that spawned in tributaries and shoreline areas of Tustumena Lake, Alaska, 1989–1991. Median dates are indicated by arrows. Peak spawning ranges (median date \pm 5 d) are in parentheses.

August (one in 1989, two in 1990) selected the upper Kasilof River as a final spawning destination. The seven mature but unspawned sockeye salmon we radio-tagged in this location at the end of August (1991) all remained in the upper river and did not enter Tustumena Lake, undertaking only localized movement. Test netting in each year confirmed the presence of unspawned mature sockeye salmon in the upper Kasilof River during early September and spawning individuals about 2–3 km downstream of the lake outlet during the last 2 weeks of September.

Behavior of Tagged Salmon

Radio-tagged fish migrated upstream in the Kasilof River at a rate averaging 4.2 km/d (range, 0.8–14.6) over the 3-year study. Once in the lake, most salmon congregated for 3–6 d just upstream of the lake's outlet in a cove formed by a peninsula of land to the immediate east (Figure 5), after which fish migration resumed at an average 5.3 km/d (range, 1.1–19.8). The predominant pattern

of movement was in a clockwise direction around the lake (69% of fish).

Prespawning tagged fish were located frequently at the mouths of tributaries during their migration, and they typically moved in proximity to the lake's shoreline. About 16% (36 of 224) of the fish classified as tributary spawners entered other streams for brief periods (<4–5 d) during their prespawning migration. The remainder (84%) appear to have homed directly to a single tributary. Twenty-one percent (21 of 100) of the shoreline spawners entered the lower 1–2 km of a tributary for 2–3 d at the onset of their migration around Tustumena Lake, whereas the remainder never left the lake. Thus, 79% of the shoreline spawners appear to have homed directly to a shoreline spawning site. Tagged sockeye salmon did not migrate through the middle of Tustumena Lake. Of two fish relocated there, both were believed to have been spawned-out dead or dying sockeye salmon.

Discussion

Determination of the incidence and pattern of lake shoreline spawning by sockeye salmon represents a new application of radiotelemetry. On average, one-third of the sockeye salmon spawned along the lake's shoreline, which corresponds well with the proportion of fish previously unaccounted for by stream surveys and sonar counts. The incidence (22–45%; mean, 31%) of shoreline spawning by sockeye salmon at Tustumena Lake was within the range of variation reported for shoreline spawners elsewhere. Among sockeye salmon returning to the Wood River system from 1955 to 1962, the incidence of lake spawning averaged 3% in Aleknagik Lake and 47% in Lake Nerka (Burgner et al. 1969). Although the extremely turbid nature of Tustumena Lake (>50 NTU) negated our efforts to locate redds, a few hundred yolk-sac fry were found during our shoreline surveys after lake levels had dropped. This finding and the annual use of shorelines by spawning adults suggest that shoreline spawning occurs in Tustumena Lake. We know of no previous descriptions of shoreline spawning by sockeye salmon in a glacially turbid lake.

Although spawning may have occurred along much of the lake shoreline, most fish apparently spawned in two areas: a site on the eastern shoreline near a small tributary and a site in the southeast corner of the lake (Figure 5) about 10 m from upwelling springs that we observed during shoreline surveys. The springs allowed continued watering of redds in an area where much of the shore-

line was exposed to air during seasonal periods of low lake levels. Additionally, springs may provide a selective advantage for egg incubation, similar to upwelling areas used by sockeye salmon in Iliamna Lake (Olsen 1968). Subsurface currents (Kerns and Donaldson 1968) may oxygenate the eggs of shoreline spawners in areas of Tustumena Lake remote from upland water sources. Frequent strong winds from Tustumena Glacier generate waves up to 2 m that probably produce such currents.

Spawning by sockeye salmon in subarctic drainages along shorelines and in lake outlets commonly peaks late in the season (typically mid-September), whereas in tributaries spawning occurs earlier in the season (usually mid-July through mid-August). This pattern has been observed in the Karluk (Owen et al. 1962; Gard et al. 1987), Russian (Engel 1972; Nelson 1983), Chignik (Narver 1968), Brooks (Hartman et al. 1963), and Kenai (Burger, unpublished data) river systems in Alaska, and in Russia (Bazarkin 1990) and Canada (Williams 1987). The late-returning sockeye salmon that spawn along the beaches and outlets of Karluk and Russian lakes are genetically distinct (reproductively isolated) from the early spawning fish that enter tributaries (Wilmot and Burger 1985). In systems such as Iliamna Lake, distinct early and late runs of sockeye salmon have not been detected (Jensen and Mathisen 1987), but spawning times are later along mainland beaches (Demory et al. 1964) than in tributaries or island beaches (Olsen 1968; Blair et al. 1993). The warmer temperatures observed in some sockeye salmon beach-spawning areas (Brannon 1987) and the moderating effects of lakes on outlet rivers (Carmack et al. 1979) may select for later spawning times in various beach and lake outlet spawning populations. Despite late-season spawning, the development rate of embryos in lake outlet areas is enhanced by the warming influence of the lake—a strategy used by late-run chinook salmon *Oncorhynchus tshawytscha* in Alaska's Kenai River (Burger et al. 1985) and apparently by sockeye salmon in British Columbia (Brannon 1987).

The lake outlet spawning pattern we observed at Tustumena Lake was typical of other late-run sockeye salmon populations in Alaska. The late September spawning in the outlet of the lake was substantially later than the mid-August spawning in the tributaries. Although we radio-tagged only seven fish in the outlet area, all were tracked to spawning areas in the upper Kasilof River by mid-September, and spawning was verified with gill

nets during the last 2 weeks of September. Recently completed genetic studies (Burger, unpublished data) suggest a distinct population: 10 of 20 outlet-spawning sockeye salmon had a mitochondrial DNA haplotype not observed in over 160 fish sampled from other spawning areas in the drainage.

Unlike the lake outlet spawners, shoreline spawners in Tustumena Lake did not demonstrate distinct, widely separate late-run characteristics common in other Alaskan populations. Peak spawning of tributary and shoreline spawners differed by only 1–2 weeks and there was considerable overlap. However, we suggest that shoreline spawners may represent an actively differentiating subpopulation. First, the run timing of shoreline spawners peaked significantly later than that of tributary spawners. Second, the spawning time distributions between tributary and shoreline spawners were statistically different and consistent with the difference in run timing. Although interannual variability in run and spawning times of radio-tagged fish was observed, it was consistent with the annual variation in the escapement timing documented by ADFG during sonar enumeration of returning adults. Third, most of the radio-tagged fish that spawned along the shoreline (79 of 100 fish) homed directly to shoreline spawning areas. Finally, there is no evidence that the shoreline spawners were surplus to tributary capacity at Tustumena Lake. If shoreline spawners were merely surplus production from the tributaries or part of an undifferentiated population of salmon, the highest incidence of shoreline spawning would be expected in years of peak escapements. Increased beach spawning was observed at Iliamna Lake in years having large escapements of sockeye salmon (Burgner et al. 1969). If shoreline spawning were surplus production, a threshold response could be expected: shoreline spawning would not occur below the level of escapement that represented tributary capacity, whereas escapement levels above the threshold would force salmon to spawn in shoreline areas. Our results do not support a surplus hypothesis because the estimated number of shoreline spawners did not increase with increased escapement (Figure 4). Further, a constant proportion model (shoreline spawning as a fixed proportion of total escapement) does not appear to fit our data because the lowest proportion of shoreline spawners (1991, 0.22) occurred at the highest observed escapement (Figure 4). Although three data points are insufficient for a conclusive test, the only model supported by our data is a constant

population model. That is, the numbers of shoreline spawners appear relatively constant and independent of total escapement. In addition, if shoreline spawners were surplus production we would expect increased use of shoreline spawning habitat in years when less tributary habitat was available (i.e., during periods of low stream flows). Although stream flow data were unavailable, we noted marginal spawning conditions because of extremely low water levels in several lake tributaries in 1991. Mean daily rainfall, an index of tributary water volume, was near its 10-year low during the summer of 1991, when the incidence of shoreline spawning was also lowest. These observations contradict the argument that shoreline spawners are surplus to tributary capacity. The relatively constant numbers of shoreline spawners during our study may be a reflection of the more stable incubation environment that lakes (as opposed to tributaries) are thought to provide (Brannon 1987; Burgner 1991).

Although sockeye salmon colonization can occur quickly following glacial recessions (Milner and Bailey 1989), differentiation of distinct subpopulations should require substantially more time. The Karluk Lake drainage, for example, has been free from glacial influence for more than 10,000 years (D. Mann, University of Alaska, Fairbanks, personal communication) and supports both shoreline- and outlet-spawning populations of late-run sockeye salmon. Late-run shoreline and outlet spawners also occur at Russian, Chignik, and Brooks lakes, all of which are clear-water systems no longer under glacial influence. However, colonization of Tustumena Lake has been limited to the last few thousand years. Tustumena Glacier (Figure 1) extended into the southern portion of the lake until about 2,000 years ago, with minor readvances occurring as recently as 300 years ago (Karlstrom 1964). To the extent that a lake's moderating effect on water temperature is an important factor in selecting for late spawning time in salmon populations (Burger et al. 1985; Brannon 1987), favorable conditions for late spawning would be expected at habitats farthest from glacial influence. Tustumena Glacier still intrudes turbid, cold meltwater (summer $<1.0^{\circ}\text{C}$) into the distal corner of the lake, some 55 km from the lake's outlet into the Kasilof River, where we have documented a genetically distinct late run (Burger, unpublished data). To the extent that lake temperatures are increasing as the glacier continues to recede, later spawning and further differentiation of the lake-

spawning component may occur similar to the pattern observed in other Alaskan drainages.

There are some noteworthy sample size considerations for future radio-tagging when the objective is to determine factors influencing the percentage of fish using shoreline habitat. Given our average tag "loss" of 43%, power analysis indicates that an annual sample size of about 690 would be required to detect an increase in the incidence of shoreline spawners from 0.30 to 0.40 ($\alpha = 0.05$, $\beta = 0.25$). If the criteria are relaxed ($\alpha = 0.1$, $\beta = 0.25$), a sample size of about 535 tags would be required to detect the same difference with a 75% probability. On the other hand, annual samples of 555 ($\alpha = 0.05$, $\beta = 0.25$) or 444 ($\alpha = 0.1$, $\beta = 0.25$) would be required to detect a decrease from 0.30 to 0.20. Therefore, investigators must determine what level and direction of change is of significance to their study objectives.

Unavoidable conditions required the use of different sampling procedures in this study. During 1990, when it was possible to capture all fish to be tagged from the fish wheel, there was no apparent size bias and no significant difference in the age and length composition of fish tracked to tributary and shoreline spawning sites. Conditions in 1989 and 1991 required different sampling strategies and the age and length compositions of radio-tagged salmon were biased toward older and larger fish, compared with samples of several hundred untagged fish. However, there were no consistent differences in the ages or lengths of tributary and shoreline spawners among years. In 1991, when length distributions of tributary and shoreline spawners were significantly different, the difference in mean length was only 10 mm; thus, our sampling should not have resulted in the overrepresentation of shoreline or tributary spawners. Although Blair et al. (1993) found smaller, younger sockeye salmon spawning along island beaches in Iliamna Lake, other workers (Narver 1968; Burgner et al. 1969) found larger, older sockeye salmon spawning in shoreline areas. Gard et al. (1987) found no consistent differences in the freshwater or ocean ages between early- and late-run sockeye salmon at Karluk Lake. Such discrepancies imply local adaptations to various spawning habitats (Taylor 1991).

This study demonstrates that Tustumena Lake sockeye salmon comprise multiple runs that exhibit different spawning behavior and may warrant designation as distinct populations. Our data also imply the existence of lake outlet and shoreline

spawning areas, which suggests that more spawning habitat is available in the drainage than previously thought. Genetic integrity and fitness of the subpopulations identified in our study may be important considerations for evaluating future hatchery enhancement in this drainage. Although adaptation may occur within surprisingly small geographical (Taylor 1991) and time scales (Quinn and Unwin 1993), additional research is necessary to determine whether these groups represent locally adapted populations. Further analysis is also necessary to answer questions concerning the depth distribution of shoreline spawners, spawning habitat characteristics, and embryo survival rates that were not addressed in our study.

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