Spawning Habitat and Redd Characteristics of Sockeye Salmon in the Glacial Taku River, British Columbia and Alaska

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Abstract.—Spawning habitats of sockeye salmon Oncorhynchus nerka in the Taku River and its tributaries in British Columbia and Alaska were studied to determine habitat use and redd characteristics in a glacial river system. We used radiotelemetry to track adult sockeye salmon to 26 spawning reaches, and 63 spawning sites were sampled for habitat characteristics. Over 40% of the sockeye salmon in the sampling area had a freshwater age of zero, and most of these spawned in main channels or off-channel areas. The availability of upwelling groundwater influenced habitat use in the main stem of the river; upwelling groundwater was detected in nearly 60% of the sites sampled in main-stem areas. Spawning sites with upwelling groundwater had lower water velocities and more variable substrate compositions than sites without upwelling groundwater. Redds had two to four times more fine sediment than previously reported. The probability of use was greatest when substrate had less than 15% fine sediment, water velocity was between 10 and 15 cm/s, and intragravel temperature was between 4.5 and 6.0°C.

Large numbers of salmon Oncorhynchus spp. are produced in glacial rivers in Alaska and British Columbia, but little is known about the spawning habitat of these fish. In some glacial rivers, sockeye salmon O. nerka spawn along the main stem (Wood et al. 1987; Eiler et al. 1988), which is unusual for this species because main-stem areas offer little or no access to lacustrine rearing habitat for young sockeye salmon. In the Taku River, some juvenile sockeye salmon apparently overwinter in areas along the river; however, a study of scale patterns indicated that more than 50% of main-stem spawners in the Taku River migrated to sea during their first year without overwintering in fresh water (Eiler et al. 1988). Sockeye salmon with this unusual life history are referred to as zero-check fish because they do not have a freshwater annulus, or check, on their scales. Little is known about the habitat used by zero-check sockeye salmon; however, some authors (Semko 1954; Wood et al. 1987) have suggested that the life history of these fish may be influenced by their incubation habitat (i.e., spawning habitat).

The objectives of this study were to locate and describe the spawning sites of sockeye salmon in a glacial river where the young fish have little or no access to lacustrine rearing habitat.

Study Area

The Taku River flows about 60 km southwest through the heavily forested and glaciated Coast Range Mountains to the sea, about 40 km east of Juneau, Alaska (Figure 1). Nearly 95% of the 16,000-km² watershed is in British Columbia, Canada, and about 25% is glaciated or under permanent snowpack. The study area encompassed the principle main-stem spawning areas in a 75-km river section, including the lower portion of the Nakina River (Figure 1). About 50% of the sockeye salmon that return to the river spawn in this section, and over 40% of these are zero-check fish (Eiler et al. 1988).

Within the study area, the Taku River flows through a U-shaped glacial valley with a 2-4-km wide floodplain that covers much of the valley bottom. The river often is braided, and a typical cross section has several main channels (about 2-3 m deep and >100 m wide) and many small, unstable side channels and sloughs. Most water within the river channel is highly turbid, except for small areas of clear, upwelling groundwater. Summer flow averages 150 m³/s (J. E. Clark and colleagues, Alaska Department of Fish and Game, unpublished). An alluvial-colluvial terrace up to 2 km wide often is present along the valley margin. Many small tributaries cross this terrace, where they are often impounded by beaver dams. These tributaries are clear, organically stained, or turbid, depending on their source. The turbidity of the main stem and glacial tributaries varies with discharge and decreases during periods of low flow.

Methods

Adult sockeye salmon were trapped in fish wheels (Meehan 1961), tagged, and released at three sites in the lower Taku River (Figure 1) be-
FIGURE 1.—Sockeye salmon spawning areas and sites sampled for habitat characteristics in the Taku River, British Columbia-Alaska, 1986. Arrows represent sites where fish were captured, tagged, and released.

between mid-June and late August 1986. Radio transmitters that included a mercury switch to indicate movement were placed in the stomachs (McCleave et al. 1978), and spaghetti tags were attached below the dorsal fins of 282 sockeye salmon. Sex and length (mideye to fork of caudal fin) of each fish were recorded before release into quiet water above the capture site. Radio-tagged fish were tracked to spawning areas by aircraft or boat.

Most spawning areas used by tagged sockeye salmon were sampled from late August through September 1986. Although we could not sample deep, swift areas of the main channel, we observed that most of these areas had armored or cemented substrate that would make spawning difficult; telemetry also indicated that only one tagged fish may have spawned there.

Aerial and ground observations of habitat characteristics (e.g., channel geometry and water clarity) were used to classify each spawning reach as one of three habitat types (classifications adapted from J. R. Sedell and colleagues, U.S. National Park Service, unpublished). 

Main channel refers to the portion of the floodplain that contains surface water at normal river stages; water in the main channel is deep and often swift. Off-channel refers to the area within the river floodplain that is influenced mainly during floods and is fed by high flows or groundwater. Terrace tributary refers to a stream located on the river terrace fed by runoff from valley slopes or by groundwater; water velocity in a terrace tributary depends on gradient, and the stream is generally shallow.

Habitat measurements.—Data on spawning habitat characteristics were collected from 63 sockeye salmon spawning sites in 26 spawning reaches (i.e., isolated groups of redds). Most redds sampled were observed easily, but in a few deep or turbid sites we tracked fish directly to redd sites by following radio signals caused by the fish’s digging movements. Individual sockeye salmon redds were identified in 40 of the 63 spawning sites that were sampled. At the other 23 sites, spawning sockeye salmon were observed, but their redds overlapped or were otherwise obscured so redd dimensions could not be measured. Data presented for sites where redds could not be measured are means of three to five measurements of habitat variables other than redd dimensions from the area where spawning was observed.

In 19 spawning reaches, up to three redds were located and measured for areal dimensions, water depth and velocity, substrate composition, and water temperature, and these data then were analyzed by analysis of variance. Water depth to the surface of the surrounding substrate was recorded to the nearest centimeter. Water velocity (cm/s) was determined from the average of velocities taken with an electronic current meter at 20 and 80% of the water depth. Substrate composition was estimated visually from surficial sediments in the bowl and tailspill of each redd (Figure 2) and was expressed by percentage of three general substrate size-classes: fine sediment (<2 mm in diameter), gravel (2 mm–10 cm), and coarse (>10 cm). When compared to volumes from sieved samples (McNeil and Ahnell 1964), our visual estimates of substrate composition at 10 sites were within plus or minus 6% for fine sediment, generally underestimated gravel by less than 5%, and overestimated coarse sediment by less than 8%. Surface and intragravel (15 cm into the substrate) temperatures were measured to the nearest 0.1°C at each site with a digital electronic thermometer. Similar temperature measurements were taken in nearby areas where no redds had been constructed.

The presence of upwelling groundwater was detected in most cases by observation of fine sedi-
ment particles that were lifted into the water column as groundwater left the substrate. In some cases, a large difference (>1.5°C) between intragravel temperatures at and away from redds also indicated the presence of upwelling groundwater.

We noted the general spawning behavior (i.e., prespawning, active spawning, or postspawning; Mathisen 1962) of most sockeye salmon within each spawning reach during initial site examination. After habitat characteristics had been measured, we captured 7–110 fish with seines from 23 reaches to measure their physical characteristics. We measured lengths and noted physical condition (i.e., ripeness, egg retention, and body condition; Foerster 1968) of the fish as a measure of spawning stage and redd maturity. Scales were taken from each fish and aged by the Alaska Department of Fish and Game's Stock Biology Group.

Seven habitat variables (water depth, redd area, average water velocity, water temperature, intragravel temperature, % fine sediment, and % coarse sediment) from each redd were compared among habitat types by single-classification analysis of variance. Fisher's modified least-significant-difference procedure was used to compare the variables among habitat types. Significances of the F-values from the analyses were determined by a randomization test (Edgington 1980). A chi-square test was applied to determine if significant relationships existed between some variables. We used frequency analysis to describe the optimum range of several habitat variables and developed probability-of-use curves (Bovee and Cochnauer 1977) for percent of fine sediment in the substrate, average water velocity, and intragravel temperature.

Results

The river was low and clear, compared to its condition in most years (Paul Kissner, Alaska Department of Fish and Game, personal communication), but sockeye salmon spawned in about the same locations and habitats as in a year with a more average flow (Eiler et al. 1988). Areal dimensions taken from 40 sockeye salmon redds showed a mean length of 2.3 m, a mean width of 1.7 m, and a mean area of 4.0 m². Temperatures at the redds averaged 6.8°C in the water column and 6.5°C in the substrate. Substrate in the redds was variable and ranged from nearly 80% fine sediment to over 70% coarse sediment among different sites (Figure 3). Mean water depth at spawning sites in the main channel (58.3 cm) was significantly greater (P < 0.05) than at off-channel (37.3 cm) or terrace tributary sites (37.3 cm). Mean water depth at spawning sites in the main channel (58.3 cm) was significantly greater (P < 0.05) than at off-channel (37.3 cm) or terrace tributary sites (37.3 cm). Mean water depth at spawning sites in the main channel (58.3 cm) was significantly greater (P < 0.05) than at off-channel (37.3 cm) or terrace tributary sites (37.3 cm). Mean water depth at spawning sites in the main channel (58.3 cm) was significantly greater (P < 0.05) than at off-channel (37.3 cm) or terrace tributary sites (37.3 cm). Mean velocity at off-channel sites (6.3 cm/s) was significantly less (P < 0.05) than at either main-channel (15.5 cm/s) or terrace tributary sites (17.4 cm/s). Because hydraulic characteristics were, in part, used to separate habitat types, we expected water depth and velocity to differ among habitats. Redd area in the main channel averaged 4.5 m², significantly greater (P < 0.05) than redds constructed off-channel or in terrace tributaries (3.4 and 3.3 m², respectively). Redd width, rather than redd length, caused the differences in redd area between habitat types (P < 0.02). The average width of redds in the main channel (1.9 m) was more than 25% greater than their average width off-channel (1.5 m) or in tributaries (1.4 m).

Differences in redd area between the three habitats were not caused by differences either in fish size or spawning stage of localized populations. The size of female sockeye salmon could affect redd dimensions, but mean length was not signif-
FIGURE 3.—Means, 95% confidence intervals (CI), and ranges for spawning habitat characteristics in areas with and without upwelling groundwater in the Taku River, British Columbia-Alaska, 1986. Absolute differences in surface temperature and intragravel temperature between redds and nearby sites without redds are represented by $T_S$ and $T_I$, respectively.

icantly different among habitat types. Spawning stage was also similar (chi-square test, $P > 0.05$) in all habitat types; 85% of fish that we sampled were in a postspawning stage. Thus, we assumed that most redds were complete and that stage of construction did not affect their dimensions in any habitat type.

Zero-check sockeye salmon were significantly more likely (chi-square test, $P < 0.01$) to be found in main-channel and off-channel habitats than in
Figure 4.—Probability of use by spawning sockeye salmon for (A) percent fine sediment, (B) water velocity, and (C) intragravel temperature in the Taku River, British Columbia-Alaska 1986.

Table 1.—Mean values by habitat type for selected characteristics of sockeye salmon spawning habitat in the Taku River, British Columbia-Alaska, 1986. Ninety-five-percent confidence intervals are in parentheses. Asterisks denote significant differences (F-test, \( P < 0.05^* \)) among sample means for a characteristic.

<table>
<thead>
<tr>
<th>Habitat characteristic</th>
<th>Main channel</th>
<th>Off channel</th>
<th>Terrace tributary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redd area* (m²)</td>
<td>4.5</td>
<td>3.4</td>
<td>3.3</td>
</tr>
<tr>
<td></td>
<td>(3.8-5.3)</td>
<td>(2.7-4.0)</td>
<td>(2.4-4.3)</td>
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<tr>
<td>Water depth* (cm)</td>
<td>58.3</td>
<td>37.3</td>
<td>37.3</td>
</tr>
<tr>
<td></td>
<td>(57.5-59.0)</td>
<td>(36.4-38.1)</td>
<td>(36.5-38.1)</td>
</tr>
<tr>
<td>Mean water velocity* (cm/s)</td>
<td>15.5</td>
<td>6.3</td>
<td>17.4</td>
</tr>
<tr>
<td></td>
<td>(7.7-23.3)</td>
<td>(3.9-8.7)</td>
<td>(8.4-26.5)</td>
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<tr>
<td>Fine sediment, (%)*</td>
<td>23.3</td>
<td>21.8</td>
<td>22.2</td>
</tr>
<tr>
<td></td>
<td>(11.2-35.5)</td>
<td>(13.9-29.7)</td>
<td>(14.1-30.3)</td>
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<tr>
<td>Gravel (%)*</td>
<td>64.5</td>
<td>68.5</td>
<td>64.3</td>
</tr>
<tr>
<td></td>
<td>(51.0-78.0)</td>
<td>(68.3-76.7)</td>
<td>(55.0-73.5)</td>
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<tr>
<td>Water column temperature (°C)</td>
<td>6.9</td>
<td>6.5</td>
<td>6.8</td>
</tr>
<tr>
<td></td>
<td>(6.3-7.5)</td>
<td>(5.8-7.2)</td>
<td>(6.1-7.5)</td>
</tr>
<tr>
<td>Intragravel temperature (°C)</td>
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</tr>
<tr>
<td></td>
<td>(5.6-6.7)</td>
<td>(5.3-6.8)</td>
<td>(5.9-7.4)</td>
</tr>
</tbody>
</table>

* Fine sediment, <2 mm in diameter; gravel, 2 mm–10 cm in diameter.

Discussion

Spawning by sockeye salmon in the lower Taku River seems particularly unlikely because of high sediment loads, unstable channel conditions, and little access to the typical lacustrine rearing habitat associated with this species; however, our study showed that this glacial river does provide suitable spawning habitats for sockeye salmon. Habitat diversity, created by the dynamic hydrology of the Taku River floodplain and adaptation to alternative life history patterns by sockeye salmon has produced the population described in this study. Our results show the types of habitat used by this species in these areas.
sockeye salmon population and identify some key habitat variables.

The significant differences in water velocity and depth among habitat types probably represent differences among our classification types rather than differences among the groups of fish using them. Water velocity in off-channel areas, for example, was significantly lower than in the other two habitat types, but in off-channel spawning areas, very little water was flowing at the velocity most probable for use (about 10-15 cm/s; Figure 4). Water at main-channel redd sites was significantly deeper than in other habitats; however, the deepest off-channel and tributary spawning areas rarely reached even the average depth (about 58 cm: Table 1) of the main-channel redds. Thus, in some spawning reaches, optimum hydraulic characteristics were probably not as important as other factors in defining spawning sites.

Our data do not support any obvious explanation of differences in redd width among habitat types. Sockeye salmon were usually the only salmon species observed in spawning areas where most of the largest redds were found and were observed spawning on 93% of the redds measured in turbid main-channel areas. Chum salmon Oncorhynchus keta also were observed in some spawning areas, and in a few cases their generally larger redds (Burner 1951) could have been mistaken for sockeye salmon redds in deep, turbid main-channel areas. A more likely cause, however, is that high turbidity in main channels decreased visibility and thus decreased territorial behavior that can cause sockeye salmon to construct smaller redds (Mathisen 1962). Sockeye salmon that spawn in turbid water also may be more disoriented than those in clear water and simply may wander laterally while constructing redds. This would result in wider redds in turbid main channels than in clearer off-channel and tributary areas.

Habitat characteristics of Taku River spawning sites, except for percent fine sediment, were within ranges reported in the literature. Other habitat characteristics (percent coarse sediment and water velocity) were highly variable but not unusual. No difference was detected in substrate composition between habitat types in this study, probably because fish selected such a wide range of spawning substrates. Sockeye salmon in the Taku River apparently are similar to other sockeye salmon populations (Ricker 1966; Foerster 1968) in that spawning substrate often varies widely within the same population, particularly where spawning reaches are associated with upwelling ground-water. Spawning by sockeye salmon in coarse sediment similar to that in our study area has been observed in the Kispiox River, British Columbia (Foerster 1968). However, we saw more than twice as much fine sediment in the average sockeye salmon redd in the Taku River than in any sockeye salmon redd measured with methods similar to ours (Burner 1951) or with more quantitative methods (Hoopes 1972).

Sockeye salmon probably construct redds in areas with high levels of fine sediment in the Taku River because of the lack of suitable spawning habitat without fine sediment in glacial rivers. In some spawning areas, redds were constructed in reaches where gravel beds were covered by glacial or organic silts. Spawning sockeye salmon usually had removed much of this fine material during spawning but, as in other years, it probably was reintroduced during the incubation period. Thus, the amount of surficial fine sediment present during critical incubation and emergence periods may have been underestimated when we measured sediment composition soon after the redds were complete.

Many studies have shown that high percentages of fine sediment, often less than those in the Taku River spawning reaches, have detrimental effects on salmonid egg-to-fry survival (Koski 1966; Hall and Lantz 1969; Phillips et al. 1975; Hausle and Coble 1976). However, the size composition of spawning substrate does not affect the survival of embryos of rainbow trout Oncorhynchus mykiss incubated in streams with upwelling groundwater (Sowden and Power 1985).

Upwelling groundwater commonly is associated with spawning areas of sockeye salmon (Semko 1954; Hanamura 1966; Foerster 1968) and other salmonids, such as chum salmon (Helle 1980), rainbow trout (Sowden and Power 1985), and brook trout Salvelinus fontinalis (Greeley 1932). Brook trout will actively select spawning sites with upwelling water (Webster and Eriksdottir 1976) and often spawn in areas with upwelling water and sandy or silty substrate, even when clean, uncompacted gravel containing no upwelling water is available nearby (Witzel and MacCrimmon 1983). Taku River sockeye salmon often construct redds near locations of upwelling groundwater detectable by our methods and spawn in low-velocity water with a wide range of substrates and water temperatures.

Our data show that areas with detectable upwelling of groundwater have a wider range of differences in surface temperature between redds and
nearby sites without redds; however, there is no difference in average surface temperatures between areas with or without detectable upwelling (Figure 4). Therefore, although upwelling groundwater may influence surface water temperature in spawning reaches, fish probably did not select redd sites in upwelling areas because of a temperature difference between spawning sites and surrounding areas.

Spawning in areas with upwelling groundwater offers three advantages: the hydraulic action of upwelling groundwater within the substrate provides a loose and unconsolidated substrate for spawning and fry emergence, unlike the compacted substrate we observed in much of the Taku River study area; sockeye salmon fry have developed specialized behavior to emerge from gravel beds covered by uncompacted fine sediments (Bams 1969); and upwelling groundwater provides a more constant incubation temperature and may not freeze as readily as surface water (Sheridan 1962).

Taku River sockeye salmon that spawned in reaches with upwelling groundwater used wider ranges of substrate sizes and low velocity probably because upwelling water and spawning sites in these reaches were in ecotones between coarse, permeable sediments carrying groundwater, and finer, less permeable sediments that force groundwater to surface. Several studies show that intragravel flow volume is positively correlated with both salmonid egg-to-fry survival and the success of fry emergence (Coble 1961; Silver et al. 1963; Shumway et al. 1964) because intragravel flow constantly replenishes the oxygen supply to eggs and alevins and carries away metabolites. Therefore, intragravel flow is the most important component of salmonid incubation (Foerster 1968; Reiser and Bjornn 1979). The volume of intragravel flow from upwelling groundwater in Taku River spawning areas is unknown, but it may be an important factor in egg-to-fry survival of sockeye salmon. If fish spawning in areas with upwelling groundwater are not dependent on the infusion of surface water to provide adequate intragravel flow, substrate composition and surface water velocity are probably not as important for successful incubation and emergence of fry.

Although upwelling groundwater provides many benefits to spawning and incubating sockeye salmon, it often has low levels of dissolved oxygen and high levels of dissolved minerals that can adversely affect salmonid egg-to-fry survival (Leitritz and Lewis 1980). We did not evaluate water chemistry or egg-to-fry survival in Taku River spawning areas; however, other studies indicate that sockeye salmon are well-adapted to incubation in the type of adverse conditions sometimes caused by groundwater. Sockeye salmon can incubate at lower levels of oxygen (as low as 3 mg/L) than many other salmonids (Semko 1954; E. L. Brandon, University of Washington, unpublished), and egg-to-fry survival rates may be higher (15-75%; Semko 1954) in areas containing upwelling groundwater than in other spawning areas (<20% survival rate; Foerster 1968). Thus, even if groundwater quality in Taku River spawning areas is poor, conditions may still be adequate for sockeye salmon egg-to-fry development.

In conclusion, sockeye salmon spawning in the Taku River and lower Nakina River floodplains used a wide range of water depths, water velocities, and substrate conditions, but constructed redds in areas that provided good intragravel flow. The variability in habitat characteristics among spawning sites made it difficult to determine why specific redd sites were used, and many factors may have played a role; however, upwelling groundwater may have been the most important of these factors. This study showed that main-channel spawning sites of sockeye salmon often were associated with upwelling groundwater and that spawning sites with upwelling groundwater were selected in all habitats regardless of temperature or substrate. In areas without detectable levels of upwelling groundwater, sockeye salmon spawned in reaches with narrower ranges of velocity, temperature, and substrate composition. This study also indicated that sockeye salmon incubated within the floodplain were more likely to become zero-checks, but those incubated in tributaries were likely to overwinter in fresh water.

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