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Riverine Spawning by Sockeye Salmon in the Taku River, Alaska and British Columbia

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Abstract.—Radio telemetry was used to determine the distribution of sockeye salmon *Oncorhynchus nerka* returning to spawn in the glacial Taku River in 1984 and 1986, and to locate and characterize spawning areas used by this species. During the study, 253 sockeye salmon were tracked as they moved upriver; 204 of these were followed to spawning areas. Only 37% of the 204 fish traveled to areas associated with lakes; the remaining 63% returned to "riverine" areas—river areas without lakes (42% to the Taku River main stem, 17% to the Nakina River, and 4% to other rivers). Sockeye salmon spawning in riverine areas used a variety of habitat types, including main-river channels, side channels, tributary streams, and upland sloughs. Most (55%) of the radio-tagged fish that returned to the Taku River main stem were tracked to side-channel spawning areas. Half of the 471 adult sockeye salmon sampled in main-stem spawning areas had migrated to sea as juveniles before their first winter. This study showed that many sockeye salmon returning to the Taku River do not depend on lakes, and that riverine sockeye salmon make up a major portion of the run in some river systems.

Sockeye salmon *Oncorhynchus nerka*, an important commercial species in the north Pacific Ocean, spawns in many river systems along the western coast of North America and the eastern coast of Asia. This species typically spawns in flowing water close to lakes (Ricker 1966; Foerster 1968), although incidents of sockeye salmon spawning in areas without lakes (hereafter referred to as riverine areas) have been reported (Gilbert 1918; Wood et al. 1987).

Many glacial rivers in Alaska are important producers of sockeye salmon. However, the large size and turbidity of these rivers make it difficult to observe returning salmon and to locate spawning sites. In 1984 and 1986, we used radio telemetry to follow the movements of adult sockeye salmon in the glacial Taku River in southeastern Alaska and northwestern British Columbia. When our study began, relatively little was known about Taku River sockeye salmon except the location of certain spawning areas, run timing, and catch levels from the commercial fishery. Our telemetry data indicate that many Taku River sockeye salmon spawn in riverine areas remote from lakes. This paper describes the evidence for this rarely reported behavior.

Study Area

The Taku River drains a watershed of over 16,000 km^2, most of it in British Columbia (Figure 1). The Taku River's main stem is extensively braided with numerous side channels. Northern and central tributaries carry fast-moving water restricted to single channels; easternmost tributaries are slow and meandering. The water in many ar-

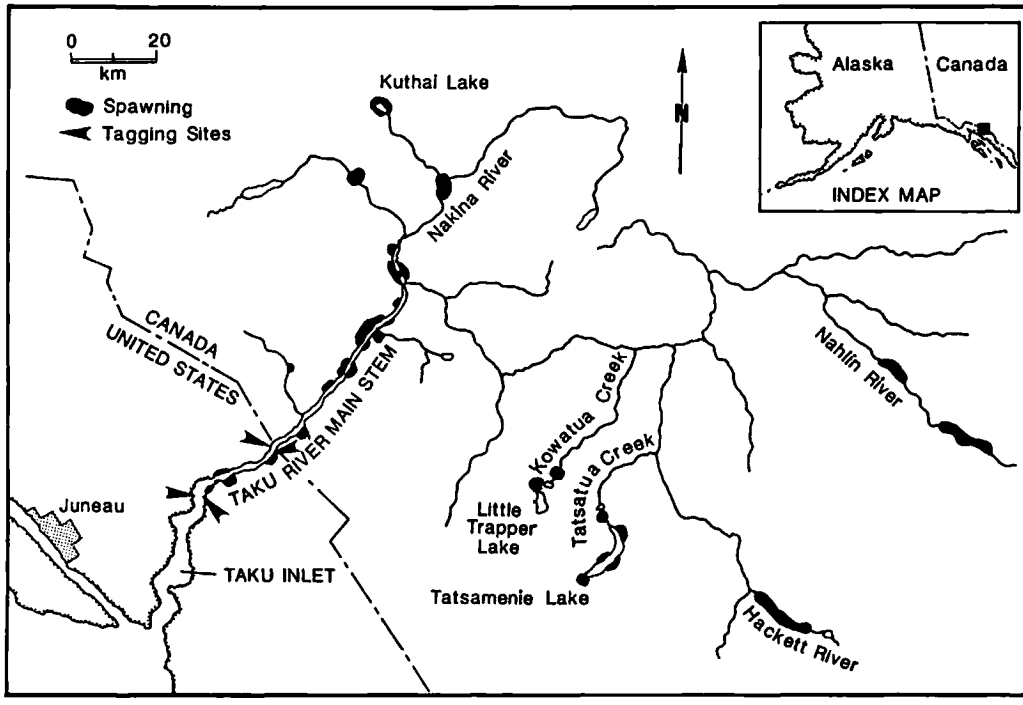


FIGURE 1.—Spawning areas used by radio-tagged sockeye salmon in the Taku River drainage.

eas is kept extremely turbid by glacial runoff. Most of the system is accessible only by aircraft.

Six species of Pacific salmonids *Oncorhynchus* spp. return to the Taku River to spawn. Returning sockeye salmon are commercially harvested by U.S. fishermen in seawater near the mouth of the river and by Canadian fishermen along the river just beyond the USA–Canada border. From 1985 to 1990, an average of 169,300 adult sockeye salmon returned to the Taku River, of which an estimated 88,300 fish escaped beyond the fisheries (Anonymous 1992).

Methods

Adult sockeye salmon migrating upstream were captured with fish wheels (Meehan 1961) near the mouth of the Taku River from 16 July to 22 August 1984 and from 21 June to 1 September 1986. During 1984, only the last third of the run was sampled, based on population estimates of sockeye salmon for the system (Clark et al. 1986). The entire run was sampled in 1986, except for a few fish entering the river in early June.

The fish were placed in a tagging cradle submerged in a trough of fresh water. Anesthesia was not used during the tagging procedure. A radio transmitter (30–31 MHz range) equipped with motion and mortality sensors (Eiler 1990) was inserted through the mouth and placed in the stomach. Each fish was also marked externally with a spaghetti tag attached below the dorsal fin (Wydoski and Emery 1983). The tagging procedure took approximately 5 min per fish. The fish were released in quiet water out of the main current.

Sockeye salmon tagged with radio transmitters were located weekly from boats or fixed-wing aircraft equipped with receiving antennas (Eiler 1989). We continued the surveys until the fish restricted their movements within a specific area. We used the transmitters' mortality sensor to determine whether fish died while in transit to spawning areas; these fish were eliminated from the analysis. During late August and September, helicopters equipped with receiving antennas were used to pinpoint radio-tagged fish in localized areas and to access these sites for collecting samples and observing fish.

Small beach seines (20 m long and 3 m deep, with 38-mm-square mesh) were used to capture sockeye salmon in turbid sections of the main stem by targeting on the location of radio-tagged fish. We determined spawning condition by the coloration and physical characteristics of the fish (Foerster 1968) and the ease with which eggs and

TABLE 1.—Habitat types used to describe spawning areas of sockeye salmon on the Taku River main stem in Alaska and British Columbia.

Habitat type	Description
Main channel	Primary river channel with high water velocity and year-round stream flow. Changes in groundwater and tributary inflow have inconsequential effects on overall stream characteristics. Suspended sediment and turbidity are high from late spring to fall
Side channel	Secondary river channel with shallower depth, lower water velocity, and smaller bed material than main channel. Water may enter directly from the main channel during periods of high flow. Suspended sediment and turbidity usually are high from late spring to fall
Upland slough	Area that conveys upwelling groundwater and small tributaries to the main channel but is not connected at its upper end to the main channel. Often associated with beaver ponds
Tributary	Stream whose characteristics are influenced by basin hydrology and morphology rather than by main-channel conditions (except at its mouth). Often associated with upland sloughs and beaver ponds
Tributary mouth	Area from main-channel junction to the uppermost point of influence by the main channel or slough backwaters
Lake	Lentic environment receiving water from springs, surface runoff, or small tributaries
Upwelling basin	Shallow off-channel water body formed by upwelling groundwater and flowing into main channel

milt were exuded (McNeil and Bailey 1975). We took scales to determine age and residence time in fresh water (Clutter and Whitesel 1956) and tissue samples for electrophoretic analysis of genetic characteristics (Utter et al. 1984).

Sections of the drainage where lakes were absent, or where barriers prevented access to lakes by juvenile or adult salmon, were designated as riverine areas. Most lakes within the Taku River are in terminal areas in the upper reaches of the drainage (Figure 1). Although juvenile salmon in some river systems migrate upstream from their birth sites to nursery areas (Burgner 1991), the distances involved on the Taku River make it unlikely that juvenile salmon from the main stem or other riverine areas travel to these lentic habitats to rear. Two small glacial lakes, less than 10 km^2 in area, are within several kilometers of the main stem and may provide limited rearing habitat for juvenile sockeye salmon, but limited seining suggests that the number of juvenile salmon using these areas is low (M. L. Murphy, Auke Bay Fisheries Laboratory, personal communication).

Classifying fish that remained in the main stem was complicated by the fact that this section of the river is used as a travel corridor by fish moving to upper reaches of the drainage, and that most of the main stem is usually very turbid. We considered radio-tagged fish to be destined for the main stem if they (1) restricted their movements to a localized area in the main stem or remained active into September, because our observations indicated that most spawning by sockeye salmon in the upper reaches of the drainage had been completed by mid-September, (2) were observed exhibiting spawning behavior, or (3) were recovered in spawning or postspawning condition.

Documented spawning areas were classified into habitat types (Table 1) adapted from classifications by Sedell et al. (1983) and Murphy et al. (1989). River turbidity, limited helicopter use, and difficulties in accessing certain areas made it impossible to verify spawning activity and habitat types for all fish classified as returning to the main stem.

Results

Tagging

We tagged 375 sockeye salmon with radio transmitters during the study: 93 in 1984 and 282 in 1986 (Table 2). Of these, 253 (67%) fish were tracked as they moved upriver from the tagging site. The remaining fish disappeared after starting upriver, died after being tagged (due to predation or handling), or moved back into seawater.

Distribution

Of the 253 radio-tagged fish that we tracked upriver, 49 were caught in the Canadian fishery,

TABLE 2.—Tagging and tracking summary for radio-tagged adult sockeye salmon in the Taku River, 1984 and 1986.

Group	Number of fish		
	1984	1986	Total
Tagged	93	282	375
Tracked upriver from tagging site	74 (80%)	179 (63%)	253 (67%)
Caught in Canadian fishery	19 (26%)[a]	30 (18%)[b]	49 (19%)[a]
Tracked to spawning areas	55 (74%)[a]	149 (83%)[a]	204 (81%)[a]

[a] Percent of fish that moved upriver.
[b] Percent of 167 fish that moved upriver into Canada; 12 of the 179 fish tagged with radio transmitters remained in the U.S. portion of the river.

including one that had been in the main stem 47 d before it was caught in 1984, and 204 were tracked to spawning areas throughout the river system (Table 2). Seventy-six (37%) of these 204 fish traveled to areas associated with lake systems (Table 3) along Kowatua and Tatsatua creeks (Figure 1). The remaining 128 (63%) fish returned to riverine areas: 85 (42%) to the main stem, 35 (17%) to the Nakina River, and 8 (4%) to other areas of the drainage including the Nahlin and Hackett rivers.

We were able to observe spawning activity by both radio-tagged and untagged sockeye salmon in clear-water sections of the Nakina, Nahlin, and Hackett rivers, and the Taku River main stem. Although portions of the Nakina River and most of the main stem are usually turbid, we were able to locate redd sites and visually document spawning there by radio-tagged and untagged fish—sporadically in 1984, and for an extended period in 1986 when normally turbid side channels and main channel edges cleared as a result of several weeks without precipitation and unusually low water levels.

All sockeye salmon observed in riverine areas during the fall exhibited the coloration and physical characteristics typical of spawning sockeye. Of the nearly 500 main-stem sockeye salmon captured and examined, including 13 radio-tagged fish, all were in spawning or postspawning condition.

In 1984, we tracked a greater percentage of fish to the main stem and a lesser percentage to the Nakina River and Kowatua Creek than we did in 1986 (Figure 2). Only the last third of the run (mid-July to late August) was sampled in 1984, and its distribution was not representative of the entire run. Mark–recapture studies indicate that most of the fish destined for the Nakina River and Kowatua Creek in 1984 entered the river before late July (Clark et al. 1986).

TABLE 3.—Types of area used by radio-tagged sockeye salmon spawning in the Taku River, 1984 and 1986.

Area	Number of fish		
	1984	1986	Total
All spawning areas	55	149	204
Lake systems	17 (31%)	59 (40%)	76 (37%)
Riverine areas[a]	38 (69%)	90 (60%)	128 (63%)

[a] Areas not associated with lake systems.

Spawning Areas

Sockeye salmon returning to the Taku River basin spawned in a variety of habitats. The fish reaching lakes spawned in effluent and tributary streams and along lake shores. In riverine areas, sockeye salmon (hereafter referred to as riverine sockeye salmon or riverine spawners) used various habitat types for spawning, including main-river channels, side channels, tributaries, and upland sloughs.

Of the 85 radio-tagged fish that returned to the main stem, the spawning habitats of 56 were identified (Table 4). Side channels were the most important spawning habitat; 31 of the 56 (55%) radio-tagged fish were in side channels, often in the same locales as chum salmon *O. keta*. Other habitat types used for spawning along the main stem were small tributaries, tributary mouths, upland sloughs, and upwelling basins. Several radio-tagged fish remained in turbid main-channel areas late into the fall, and we were unable to determine whether these fish were spawning or holding there before moving to other areas to spawn. Several radio-tagged fish held in the main channel, in one case for up to 22 d, before moving to known spawning areas. Weekly aerial counts of sockeye salmon in clear-water spawning areas during late August and September also suggest that main-stem fish may hold in other locales before moving to spawning areas.

Certain reaches of the main stem were used extensively by spawning salmon. For example, of the 85 radio-tagged fish that returned to the main stem, 17 (20%) were localized in several interconnected side channels. Radio-tagged fish were less concentrated in other main-stem areas.

Freshwater Residence Times

Residence times as juveniles in fresh water were determined from scale growth patterns for 471 adult sockeye salmon sampled at eight spawning

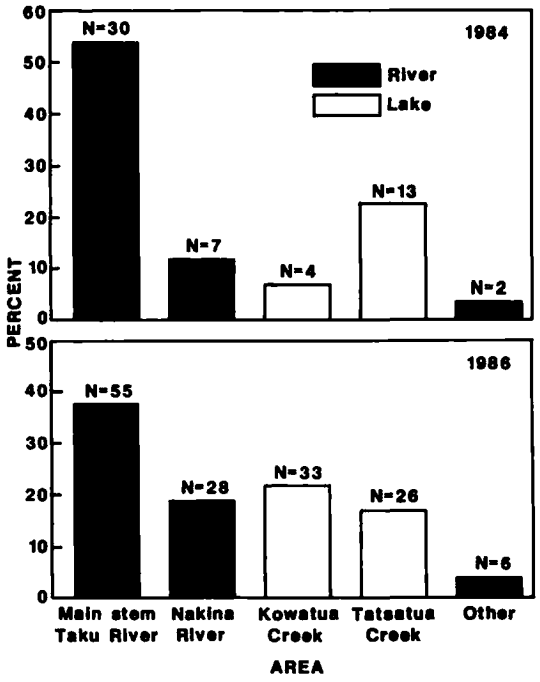


FIGURE 2.—Distributions of radio-tagged, adult sockeye salmon in the Taku River system during 1984 and 1986.

sites on the Taku River main stem. About half (235) of these fish, hereafter referred to as sea-type sockeye salmon (Wood et al. 1987), had migrated to sea as juveniles before their first winter; 236 fish overwintered in fresh water before migrating to sea (Table 5). Sea-type spawners predominated in side channels, where 64% (of the 302 fish sampled) were sea-type; only 6% (of the 106 fish sampled) in main-stem tributaries were sea-type (Table 5).

Discussion

Sockeye salmon are typically thought to spawn in streams that drain to and from lakes and along lake shores (sometimes to depths of 30 m) where seepage outflows occur (Ricker 1966; Foerster 1968). Before our work in 1984, it was estimated that 60–70% of the sockeye salmon returning to the Taku River spawned in the vicinity of Little Trapper Lake (D. J. Ingledue, Alaska Department of Fish and Game, unpublished data), one of several lakes in the upper drainage (Figure 1). In contrast, our study showed that most (63%) radio-tagged sockeye salmon in the Taku River returned to riverine areas, previously considered unsuitable for this species. Tagged fish using riverine areas

TABLE 4.—Spawning habitats used by radio-tagged sockeye salmon in the Taku River main stem, 1984 and 1986. Habitat types are defined in Table 1.

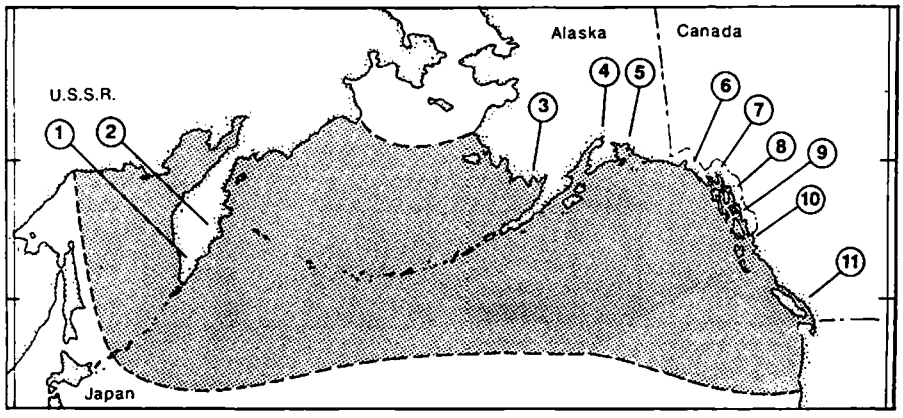
Habitat type	Number of fish		
	1984	1986	Total
Side channel	11 (46%)	20 (63%)	31 (55%)
Upland slough	5 (21%)	2 (6%)	7 (13%)
Tributary	1 (4%)	7 (22%)	8 (14%)
Tributary mouth	1 (4%)	0	1 (2%)
Upwelling basin	6 (25%)	3 (9%)	9 (16%)
Total	24	32	56

probably were not strays, because large numbers of untagged fish were observed in these areas and sockeye salmon home with great precision to their natal streams; less than 1% of sockeye salmon strayed between rivers in southern British Columbia (Quinn et al. 1987). Electrophoretic analysis of sockeye salmon sampled at different times and from different sections of the Taku River basin indicates that sockeye salmon from the main stem are genetically distinct from sockeye salmon returning to the major lake systems (C. M. Guthrie and A. J. Gharrett, Auke Bay Laboratory, personal communication). The genetic differences observed suggest that main-stem fish comprise one or more separate subpopulations in the drainage.

Counts of adult sockeye salmon at weirs in the major lake systems provide additional evidence that riverine spawning is important in the Taku River drainage. Escapement estimates of sockeye salmon in the Taku River averaged more than 88,000 fish from 1985 to 1990. However, weir counts from the major lake systems during this period averaged only 18,000 fish (Anonymous 1992), and our telemetry study indicated that lake systems in the drainage without weirs were not used extensively for spawning.

TABLE 5.—Freshwater residence times of juvenile sockeye salmon that emigrated to sea and subsequently returned as adults to various spawning habitats in the Taku River main stem, 1986. The percentage distribution of age at emigration within each habitat type is in parentheses; N = sample size. Habitat types are defined in Table 1.

Habitat type	Number of fish			
	Age (years) at emigration			
	0	1	2	N
Side channel	194 (64%)	104 (35%)	4 (1%)	302
Upwelling basin	35 (56%)	28 (44%)	0	63
Tributary	6 (6%)	96 (90%)	4 (4%)	106
Total	235	228	8	471



1. Bolshaya River (Semko 1954, cited by Foerster 1968)
2. Kamchatka River (Bugaev 1984)
3. Nushagak and Mulchatna Rivers (Russell 1989)
4. Susitna River (Anonymous 1983)
5. Copper River and Prince William Sound Systems (Sharr et al. 1988)
6. East Alsek River (Pahlke and Riff 1988)
7. Chilkat River (S. McPhearson, Alaska Department of Fish and Game, P.O. Box 20, Douglas, AK)
8. Taku River (this study)
9. Stikine River (Craig 1985)
10. Gingit Creek, Nass River Drainage (Ricker 1966)
11. Harrison River, Fraser River Drainage (Foerster 1968)

FIGURE 3.—Examples of river drainages where sockeye salmon have been observed spawning in areas not associated with lake systems. The shaded area represents the known geographic range of sockeye salmon.

Riverine spawning by sockeye salmon has been reported from the Harrison River in southern British Columbia (Gilbert 1918) to rivers on the Kamchatka Peninsula in Siberia (Semko 1954) (Figure 3). However, the extent of riverine spawning is difficult to determine from the formal literature alone; many references are anecdotal or only imply that riverine spawning occurs. Riverine spawning by sockeye salmon in both large and small river systems is more common than previously thought, based on our analysis of the formal literature and of other available data such as stream survey counts (Alaska Department of Fish and Game, Commercial Fisheries Division, unpublished data) and maps showing spawning locations (Alaska Department of Fish and Game, Habitat Division, unpublished data).

Riverine spawners make up a major segment of the population in some rivers. Our study showed a strong component of riverine spawners in the Taku River drainage; a similar pattern probably exists in the Stikine River (Craig 1985; Wood et al. 1987). In the Nushagak and lower Mulchatna rivers in the Bristol Bay area (Figure 3), Russell et al. (1989) reported 60,000–150,000 riverine spawners from an estimated escapement of 550,000 sockeye salmon. No lakes exist on the East Alsek River (Figure 3), and all the sockeye salmon are riverine spawners; an estimated 37,000 sockeye salmon returned to this river in 1986 (Pahlke and Riffe 1988).

The cumulative importance of small populations of riverine sockeye salmon is undoubtedly underestimated. Riverine sockeye salmon occur in numerous stream systems of Prince William Sound and the Copper River delta in south-central Alaska (Sharr et al. 1988), the Yakutat area in southeastern Alaska (Pahlke and Riffe 1988), and the lower portion of the Nass River in northern British Columbia (D. Southgate, Canadian Department of Fisheries and Oceans, personal communication). Individually, these stocks may be small; collectively, their contribution is important.

The main reason that riverine areas have been considered unsuitable for spawning sockeye salmon is the perceived lack of juvenile rearing habitat. After emerging from redds, juvenile sockeye salmon typically rear in lakes for one or more years before migrating to sea (Foerster 1968). However,

sockeye salmon in some river systems have adopted alternative strategies that compensate for the lack of typical rearing areas. Juvenile sockeye salmon rear in the main Stikine River (Wood et al. 1987) and the Taku River main stem (Murphy et al. 1989). Sea-type sockeye salmon have been reported by Gilbert (1918), Bugaev (1984), Wood et al. (1987), and Heifetz et al. (1989).

During our study, most of the sockeye salmon sampled in main-stem spawning areas were sea-type fish. Fewer sea-type sockeye salmon returned to main-stem tributaries (areas associated with beaver ponds and upland sloughs) than to main-stem side channels and upwelling basins. Juvenile sockeye salmon rear in beaver ponds and upland sloughs in the lower Taku River (Murphy et al. 1989), and these habitats may account for the lower incidence of sea-type fish. Fewer than 2% of the sockeye salmon sampled at lakes within the Taku River drainage during 1986 were sea-type (McGregor and Walls 1987), although levels have ranged as high as 19% for fish returning to lakes on Tatsatua Creek (McGregor and Jones 1989). Because riverine sockeye salmon can rear in rivers or migrate to sea during their first year, they can use a wider range of areas and habitats than sockeye salmon that require lake systems.

The radio-tagged fish that migrated to lake systems selected spawning sites typical for this species—sites with medium-sized to small gravel, little silt, and moderate stream flows (Foerster 1968). However, sockeye salmon returning to the Taku River main stem used atypical spawning sites—substrates covered with sediment from glacial runoff, a condition typically considered detrimental to the incubation and survival of eggs and pre-emergent fry (Phillips et al. 1975; Hausle and Coble 1976). Silt proportions at redds in the main stem were two to four times higher than previously reported in the literature (Lorenz and Eiler 1989). Although the substrate was cleared of sediment during redd construction, silt accumulated after spawning activity had ceased, covering the redds. However, spawning was localized within certain areas of the Taku River main stem. Lorenz and Eiler (1989) found an association between spawning sites on the main stem and upwelling groundwater, and speculated that upwellings bring enough oxygen to eggs to maintain their viability despite heavy silt loads. Associations of salmonid spawning with upwelling water have long been noted (Foerster 1968).

Little information is available on the productivity of riverine sockeye salmon compared to those that spawn in areas associated with lakes. In riverine areas, the lack of lacustrine rearing habitat, extreme changes in main-channel and side-channel water levels (making these areas susceptible to freezing or desiccation), and heavy silt loads may result in low or highly variable production by riverine spawners. However, the large returns of riverine sockeye salmon in some systems suggest that these are not always limiting factors.

Our study indicates that many sockeye salmon returning to the Taku River spawn in riverine areas typically not associated with this species. Riverine spawning has been reported, if only anecdotally, throughout the species' range. The ability of sockeye salmon in some drainages to spawn and rear in riverine as well as in lake areas contributes to the species' adaptability and success.

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