THE MIGRATION AND SPAWNING DISTRIBUTION OF SOCKEYE SALMON WITHIN LAKE CLARK, ALASKA

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Abstract

Recent declines in the number of sockeye salmon *Onchorynchus nerka* returning to Lake Clark, Alaska have caused economic hardship in the region and raised resource concerns among local subsistence users and Federal managers. A lack of information regarding the distribution of spawning habitats in the glacially turbid Lake Clark watershed instigated this research. Radio telemetry was used to 1) determine the in-lake movement patterns of adult sockeye salmon and 2) identify sockeye salmon spawning locations. Sockeye salmon were radio tagged at they entered Lake Clark and tracked to spawning locations. After entering Lake Clark, sockeye salmon usually migrated to a region of the lake that was within 15 km of their spawning location. Tagged fish migrated faster and more directly to spawning locations in tributary rivers and lakes than to Lake Clark beaches. Thirty three spawning locations were identified in the Lake Clark watershed including 18 new spawning locations compared to previous scientific research and ten compared to traditional local knowledge. Most radio tagged sockeye salmon (65%) returned to spawning locations in glacially turbid waters and most spawning locations (75%) were adjacent to privately owned lands. Proactive measures should be taken to conserve both migration corridors and spawning habitats.

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Acknowledgements

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Introduction

This thesis describes findings from a sockeye salmon *Onchorynchus nerka* radio telemetry study conducted in the Lake Clark watershed in 2000 and 2001. The primary objectives of this research were 1) to determine how sockeye salmon migrate within Lake Clark to spawning locations, and 2) to identify sockeye salmon spawning locations within the glacially turbid watershed.

Recent declines in the number of sockeye salmon returning to Lake Clark instigated this study. Historically, sockeye salmon escapement to the Lake Clark/Newhalen River drainage ranged between 240,000 and 3.1 million sockeye salmon (average = 1.1 million fish; Poe and Rogers 1984). Since 2000, escapements have been relatively low with an average of 220,000 sockeye salmon returning per year (Woody 2004).

Annual sockeye salmon returns to the Lake Clark area are important to the culture, economy, and ecosystem of the Bristol Bay region. Lake Clark sockeye salmon have been an integral part of Alaskan native culture since prehistoric times (Unrau 1992), and continue to provide subsistence for contemporary users (Alaska Department of Fish and Game 2002). Lake Clark is situated within Lake Clark National Park and Preserve, which was established in 1980 in part to "…protect the watershed necessary for the perpetuation of the red [sockeye] salmon fishery in Bristol Bay…" and to "…protect habitats for populations of fish and wildlife…" (ANILCA 1980). Ecologically, sockeye salmon are an important food resource for over 40 species of Alaskan mammals, fish and birds (Willson and Halupka 1995), and represent a significant source of marine derived nutrients that sustain freshwater ecosystem productivity (Kline et al. 1993).

Despite the recognized importance of Lake Clark sockeye salmon to both humans and the ecosystem, the basic biological information necessary for effective salmon management is lacking. No information exists regarding the spawning migration of sockeye salmon within Lake Clark. Glacially turbid waters within Lake Clark have limited the visual observations of spawning locations within the watershed. Recent studies in other glacial systems have identified Pacific salmon spawning in similarly turbid habitats (Burger et al. 1985, Eiler et al. 1992, Burger et al. 1995), implying that unidentified spawning congregations may exist in the Lake Clark watershed.

Identification of spawning locations is especially important in the Lake Clark watershed given that 60% of the Lake Clark shoreline is adjacent to private land (NPS 2001). Future development on these lands could potentially impact migration corridors and critical spawning habitats. Distribution maps of sockeye salmon migration patterns and spawning areas will allow managers to work with landowners and other agencies to protect critical sockeye salmon habitat.

Chapter 1: The spawning migration of sockeye salmon within Lake Clark, Alaska[1]

Abstract

The spawning migration of sockeye salmon *Oncorhynchus nerka* within Lake Clark, Alaska was examined using radio telemetry. In 2001, sockeye salmon (n = 142) were tagged as they entered the lake and tracked to spawning locations. Radio tagged salmon generally migrated to a region of the lake that was within 15 km of their final spawning location. Some salmon, however, migrated for more than 50 days and further than five times the necessary distance before arriving at spawning locations. Sockeye salmon migrated faster and more directly to spawning locations in tributary rivers and lakes than to Lake Clark beaches. Fish that spawned in tributaries congregated at the mouth of their tributary system for an average of 17.4 days (SD = 13.6, range: 0 - 59 days) before migrating upstream. Radio tagged sockeye salmon did not enter a tributary system unless they spawned in that tributary. This study provides one of the first detailed examinations of in-lake spawning migrations of sockeye salmon and demonstrates that the final homing process is more dynamic than previously thought.

Introduction

Pacific salmon *Oncorhynchus* spp. generally return to their natal habitats to spawn, a behavior referred to as “homing”. The homing process includes long directed migrations through the ocean where salmon may rely, in part, on the earth’s electromagnetic spectrum to orient toward home (Quinn and Groot 1983, Quinn 1984, Ogura and Ishida 1995). Once salmon reach landfall, they rely primarily on olfactory cues learned during their early life history (Hasler and Scholz 1983, Dittman and Quinn 1996) to navigate to natal lakes and streams. Sockeye salmon *O. nerka* are thought to be

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[1] Prepared for submission to Transactions of the American Fisheries Society. Young, D. B., and C. A. Woody. The spawning migration of sockeye salmon within Lake Clark, Alaska. Transactions of the American Fisheries Society.

especially precise in homing because they generally return to and spawn in habitats associated with a lake where their offspring rear for one or more years before migrating to the sea (reviewed in Foerster 1968, Burgner 1991).

While many studies have focused on adult sockeye salmon migrations in the ocean (French et al. 1976, Groot and Quinn 1987) and riverine environments (Killick 1955, Eiler et al. 1992), limited information exists regarding the final in-lake migration of sockeye salmon to spawning locations. Limited data collected during radio telemetry studies indicate that most sockeye salmon migrate directly to spawning locations after entering a lake system (Burger et al. 1995, Schubert and Scarborough 1996). In Tustumena Lake, Alaska, approximately 80% of radio tagged sockeye salmon swam directly to spawning locations although some migrated into one tributary before settling at another tributary or beach spawning habitat (Burger et al. 1995). Most sockeye salmon did not migrate randomly through Tustumena Lake, but followed the shoreline in a clockwise direction.

Homing experiments provide additional information regarding the migratory behavior of sockeye salmon in lakes. During these experiments, displaced adult sockeye salmon generally migrated back to the original capture location (Hartman and Raleigh 1964, Varnavskyi and Varnavskaya 1985, Blair and Quinn 1991, Ueda et al. 1998). In Iliamna Lake, Alaska, displaced sockeye salmon tended to migrate along the lake shoreline and were more likely to return to a tributary spawning habitat than beach spawning habitats (Blair and Quinn 1991).

The Lake Clark watershed in southwest Alaska (Figure 1.1) is an ideal location to further study the in-lake spawning migration of sockeye salmon. Lake Clark is located within Lake Clark National Park and Preserve which was established in part to protect habitats critical for sockeye salmon populations. Each year sockeye salmon migrate to a variety of pristine spawning habitats throughout Lake Clark and its tributaries. Monitoring the in-lake movements of sockeye salmon in Lake Clark will provide insight into the timing and migration patterns of sockeye salmon returning to these different spawning habitats. Such information is critical for population management and for understanding divergence patterns within a species.

To investigate how sockeye salmon migrate through a lake system, adult sockeye salmon were radio tagged as they entered Lake Clark and tracked to spawning locations. Specific study objectives were to: 1) determine where sockeye salmon migrate through the lake relative to the lake shoreline, 2) determine the net speed of migration through Lake Clark to spawning locations, 3) determine how directly sockeye salmon migrate to spawning locations.

Study Site

The Lake Clark watershed (60° 01 N, 154° 45 W) is located within the larger Kvichak River drainage in southwest Alaska (Figure 1.1). It includes Lake Clark (267 km^2), the sixth largest lake in Alaska and the largest body of water in Lake Clark National Park and Preserve. Lake Clark is a semi-glacial oligotrophic lake that is approximately 66-km long and 2.5 – 8-km wide with an average depth of 103 m, maximum depth of 322 m, and a drainage area of 7,620 km^2 (Anderson 1969, Wilkens 2002). The lake is composed of three major basins, hereafter referred to as the lower, middle and upper basins (Figure 1.2). The lower basin is distinctly separated while the middle and upper basins are less distinct. Six primary tributaries empty into the middle and upper basins of Lake Clark and provide the majority of the inflow to the lake (Figure 1.2, Table 1.1; Brabets 2002). In addition, numerous smaller streams that are glacially turbid, clear, or organically stained flow into Lake Clark.

Glaciers, steep mountains, glacial rivers, and high precipitation (average 203 cm annually) characterize the northeast end of the watershed while lowland tundra, small mountains, clear and organically stained streams, and low precipitation (average 64 cm annually) characterize the southwest end (Jones and Fahl 1994, Brabets 2002). Glacier-fed tributaries provide approximately half of Lake Clark's annual water budget and transport 0.4 – 1.5 million tons of suspended sediment into the lake each year (Brabets

2002). Runoff from glacial tributaries is highest between June and September creating a turbidity gradient along the length of Lake Clark from the turbid (~10 NTU) northeast to the clear (≤ 2 NTU) southwest (Brabets 2002, Wilkens 2002).

Methods

Radio tagging

Migrating adult sockeye salmon were captured at the outlet of Lake Clark (Figure 1.2) with nylon beach seines (62 m x 2.4 m - 3.7 m; 10.2-cm mesh) and radio tagged throughout the run (15 July to 9 August 2001). Captures were made during randomly selected fishing sessions between 0800 and 1959 hours. A random number table was used to select one-hour fishing sessions throughout the day. Radio tagging did not occur at night (between 2000 and 0759 hours) because > 90% of sockeye salmon migrate into Lake Clark during the day (Poe and Rogers 1984). Approximately five fish were tagged per day during small migrations and 10 fish were tagged per day during large migrations. The two-tiered tagging regime was used to distribute the tags in proportion to the run as most sockeye salmon migrate into Lake Clark within two weeks (Poe and Rogers 1984, Woody 2004). A counting tower located 10 km downstream of the tagging site (Woody 2004) identified large migrations (> 10,000 fish/day).

Radio tagging protocols were similar to previous radio telemetry studies of sockeye salmon (e.g., Eiler et al. 1992, Burger et al. 1995). After capture, sockeye salmon were placed in a mesh live well in the stream (1.5 m x 1.5 m x 1.5 m; 2.5-cm mesh size). A subset of female salmon captured in the net were placed in a tagging cradle with ventral side up and lower jaws raised so that a glycerin-coated radio tag could be inserted into their stomachs using a 6-mm diameter PVC tube (Monan et al. 1975, Burger et al. 1995). After the tagging procedure, fish were released at the location of capture after recovering in the mesh live well. The tagging procedure took, on average, less than one minute.

Radio tag retention was examined during a companion study (Ramstad and Woody 2003). During this study, the overall tag retention in sockeye salmon was high (0.98, 95% confidence interval (CI), 0.92-1.00) and mortality of tagged salmon was low and similar to that of untagged controls (0.02, 95% CI<0.01 – 0.08).

Telemetry equipment

Radio-telemetry equipment consisted of high frequency VHF radio tags, scanning receivers, and 4-element Yagi and H antennae (Lotek Engineering, Inc., Newmarket, Ontario, Canada). Digitally coded radio tags measured 14.5 x 49 mm and weighed 12.9 g in air, which was less than 2% of body weight of tagged fish as generally recommended (Winter 1996). Radio tags transmitted 24 hours per day with a two second burst rate and tag life was approximately 380 days, which well exceeded the known spawning period (< 120 days) of any sockeye salmon spawning population in the Lake Clark watershed (Demory et al. 1964, Regnart 1998).

Radio tracking

Fixed-wing aircraft or boats were used to track radio tagged fish every one to ten days and fixed radio telemetry receivers monitored fish passage 24 hours per day (Figure 1.2). Aerial surveys were flown (with an H antenna mounted on each wing strut) along the shoreline of Lake Clark and its tributaries at an altitude between 200 and 300 m and an airspeed between 100 and 130 kph (Gilmer et al. 1981). Aerial flights were not flown up tributaries until it was determined that fish could have moved into the area; e.g., fish were recorded past a fixed telemetry station on the tributary. Boat tracking was conducted around the lake perimeter and islands approximately 300 m offshore and at a maximum speed of 30 kph. Two 4-element Yagi antennae, mounted to the boat hull and positioned at 45° angles scanned the areas forward of the boat. Fixed telemetry receivers consisted of an enclosure box, a telemetry receiver, two 4-element Yagi antennae, an antenna switchbox, and a sealed lead-acid battery powered by a solar panel.

During aerial and boat tracking events, a global positioning system (GPS) receiver recorded the location where a tagged fish was detected. Fish were tracked to within 1 km during aerial surveys and within 400 m during boat surveys, based on field tests with planted transmitters.

Data summation

Data collected during radio tracking events and at fixed telemetry receivers were condensed for data analyses. If fish were recorded multiple times during an aerial or boat tracking event, the record with the highest signal strength was selected. Comparison between signal strengths was made using a reference gain on the telemetry receiver. Data collected at fixed telemetry receivers were condensed to one record per fish for a 24-hour period. If fish were recorded multiple times in one day at a fixed telemetry receiver, the record with the highest signal strength was selected. Six radio tagged fish that migrated to spawning locations downstream of the tagging site were excluded because they exhibited unique spawning migrations and did not enter Lake Clark.

Data analyses

A salmon was considered to have migrated to its spawning location when it was located within 5 km of its spawning location or mouth of its spawning stream and no further migration occurred except into a tributary system. Distance to a spawning location was defined as the shortest distance in water from the tagging site to the spawning location. Migration days were defined as the number of days elapsed between tagging and arrival at a spawning location. Arrival date at a spawning location was calculated with the formula:

$$AD = (D+PD)/2$$

AD = arrival date
D = day first detected at spawning location
PD = previous day detected

Near shore/off shore movements

Fixed telemetry receivers, located 25 km up-lake of the tagging site (Figure 1.2) monitored the near shore and off shore migration of radio tagged sockeye salmon between 16 July and 12 August 2001. The receivers monitored fish passage within 400 m of the lakeshore based on tests with planted transmitters to depths of five meters. Radio tagged salmon that were tracked up-lake and were detected by one of the receivers were classified near shore migrants. Salmon that were tracked up-lake and were not detected by the telemetry receivers were classified off shore migrants.

Speed of migration

The speed sockeye salmon migrated within Lake Clark was calculated two different ways. First, the speed of migration was estimated to fixed telemetry receivers located 25 km up-lake from the tagging site (Figure 1.2; Lake North and Lake South). Second, the speed of migration was estimated from the tagging site to spawning locations. One-way analysis of variance (ANOVA, SPLUS software version 6.0, Lucent Technologies Inc.) was used to assess differences in migration speed due to spawning habitat. Spawning habitats were either tributary rivers and lakes (Trib) or Lake Clark beaches (LC).

Linearity of migration

The linearity of migration was used to estimate how directly sockeye salmon migrated to spawning locations. Linearity, a measure of how straight a course was traveled, was calculated as the distance from the tagging site to the spawning location or spawning stream divided by the straight-line distance between all re-location data points. If a radio tagged salmon migrated directly to a spawning location its linearity value would equal one. If a radio tagged salmon followed a circuitous path, the linearity value would be less than one. One-way analysis of variance was used to assess differences in mean linearity values due to spawning habitat.

Milling and migration into tributaries

The number of days radio tagged salmon congregated at the mouth of their tributary system was calculated from the date of arrival to the date of river entry. Fixed telemetry receivers recorded the exact date fish migrated into Kijik River, Currant Creek, and Tlikakila River (Figure 1.2). For other tributaries, the mean date of river entry was estimated as:

$$RE = (D+PD)/2$$

RE = river entry
D = day first detected in tributary
PD = previous day detected

Two- way analysis of variance (SPLUS software version 6.0, Lucent Technologies Inc.) was used to assess the mean migration timing into tributaries due to tributary type and water clarity. Tributary types were tributary rivers or tributary lakes and water turbidity was either turbid from glacial meltwater or clear.

Results

Spawning migration

One hundred forty two of 157 radio tagged sockeye salmon migrated to spawning locations within the Lake Clark watershed. Six salmon migrated to spawning locations downstream of the tagging site. Nine salmon lacked sufficient data to determine a final spawning location. On average, radio tagged fish that migrated to spawning locations in the Lake Clark watershed were re-located 17.7 times (SD = 5.7, range: 7 – 33) with over 2,600 re-locations made during the study.

Radio tagged sockeye salmon migrated throughout the Lake Clark and Sixmile Lake drainages before arriving at spawning locations in the Lake Clark watershed. Approximately 25% percent of the 142 radio tagged sockeye salmon migrated downstream into Sixmile Lake before entering Lake Clark (average = 11.3 days, SD = 5.7 days, range: 4 - 26). Fifty percent milled at the lake outlet for several days before entering Lake Clark and 25% migrated directly into Lake Clark. After entering Lake Clark, salmon usually migrated to a region of the lake that was within 15 km of their spawning location. For example, salmon that spawned near the tagging site remained in the lower basin of the lake (Figure 1.3).

Near shore/off shore movements

Most (83%) radio tagged sockeye salmon were detected traveling near shore at the Lake North and Lake South telemetry receivers (Figure 1.2). Of these, 75% were detected along the south shore and 15% were detected along the north shore. Fifteen percent, however, were recorded by both receivers indicating that some salmon moved through the middle of the lake to reach the opposite shoreline. In addition, radio telemetry data indicate that many sockeye salmon migrated between shorelines during their travels to spawning locations.

Speed of migration

Sockeye salmon migrated to fixed telemetry receivers located 25 km up-lake of the tagging site at an average net speed of 5.7 km/day (SD = 6.1, range: 0.9 – 27.0 km/day). Sockeye salmon migrated to spawning locations at an average speed of 3.5 km/day (SD = 2.9, range: 0.1 – 11.0 km/day). Seventy five percent of salmon traveled at speeds > 10 km/day at some point in their migration and five salmon traveled at speeds > 48 km/day (~ 2 km/hour). Radio tagged salmon migrated, on average, faster to tributary rivers and lakes than to Lake Clark beaches (one-way ANOVA, $P < 0.001$; Figure 1.4). Sockeye salmon migrated fastest to the Kijik and Sucker Bay Lake drainages (Table 1.2).

Linearity of migration

Radio tagged sockeye salmon migrated to spawning locations with varying degrees of linearity. Fifteen percent of fish migrated directly to spawning locations (linearity = 1.0, Figure 1.5 A) while 11% made extensive movements before settling at a spawning location (linearity <0.25, Figure 1.5 B). One salmon traveled 307 km within

Lake Clark although its spawning location was only 55 km from the tagging site. Sockeye salmon migrated less directly to Lake Clark beaches than to tributary streams and lakes (one-way ANOVA, $P < 0.001$; Figure 1.6, Table 1.2).

Timing

Radio tagged salmon migrated to spawning locations within the Lake Clark watershed between late July and early September. On average, this was 21.2 days (SD = 13.2) after they were tagged (Table 1.2). Tagged salmon migrated to tributaries earlier than Lake Clark beaches (one-way ANOVA, $P < 0.001$) and generally migrated to the lower basin earlier than the upper basin (Figure 1.6). Ninety three percent of radio tagged salmon had arrived at spawning locations by 6 September (Figure 1.4).

Milling and migration into tributaries

Fish that spawned in tributaries congregated at the mouth of their tributary system for an average of 17.4 days (SD = 13.6, range: 0 - 59 days) before migrating upstream. There was a significant difference in the number of days radio tagged salmon milled at the mouth of their spawning streams due to drainage (one-way ANOVA, $P < 0.001$). Salmon milled shortest at the mouth of Sucker Bay Lake and Kijik River in the lower basin, and longest at the mouth of Currant Creek and Tlikakila River in the upper basin (Figure 1.8 A).

Radio tagged salmon migrated into the Kijik and Sucker Bay Lake drainages earlier than other tributaries (Figure 1.8 B). Salmon migrated into tributaries associated with a lake system earlier than tributaries without a lake system and entered clear water tributaries earlier than glacially turbid tributaries (two-way ANOVA: tributary type $P < 0.001$, water turbidity $P < 0.001$). One radio tagged salmon that migrated into the clear waters of Priest Rock Creek in early October was an exception to this general pattern (Figure 1.8).

Radio tagged sockeye salmon did not enter a tributary system unless they spawned in that tributary. That is, no salmon entered one tributary and then subsequently spawned in another tributary system or at Lake Clark beaches. However, one salmon that migrated into Kijik Lake eventually migrated downstream to spawn in Little Kijik River (Figure 1.2).

Discussion

This study provides one of the first detailed examinations of in-lake spawning migrations of sockeye salmon and demonstrates that the final homing process is more dynamic than previously thought. The slow speed and excessive distance that some sockeye salmon traveled to spawning locations in the Lake Clark watershed was unexpected because sockeye salmon are considered very precise in their homing (Foerster 1968, Quinn 1993) and excessive movements would be energetically costly, perhaps compromising reproduction (Brett 1995). Therefore, one would assume movements to spawning locations would be both rapid and direct.

The average net speed (3.5 km/day or 21 days) sockeye salmon migrated to spawning locations in the Lake Clark watershed was similar to observations from other lake systems, yet slower than expected. Sockeye salmon migrate within Babine Lake, on average, for 27 days before arriving at spawning grounds (unpublished data, C. Groot, Department of Fisheries and Oceans, personal communication). In Tustumena Lake, sockeye salmon migrate to spawning locations at an average net speed of 5.7 km/day (Burger et al. 1995), which is almost twice the speed observed within Lake Clark. The slow migration through Lake Clark was unexpected because sockeye salmon can swim 50 km/day or 2.0 km/hour during their homing migration through marine (French et al. 1976), riverine (Killick 1955, Quinn 1988), and lacustrine (Blair and Quinn 1991) environments. The delayed arrival to spawning locations could indicate that tagged salmon were resting after migrating into Lake Clark, were searching within the lake for spawning locations, or were waiting for the proper environmental and genetic cues to arrive.

The excessive in-lake movement of some radio tagged sockeye salmon was counterintuitive because migration (e.g., Rand and Hinch 1998) and reproduction (Healy et al. 2003) are energetically costly. Sockeye salmon stop eating after entering freshwater and must rely on energy reserves for their final journey to spawning locations. Previous research indicates that 41-80% of energy reserves are consumed during upstream migration and reproduction (Hendry and Berg 1999). Conserving energy during migration is considered important (Rand and Hinch 1998) because depleting reserves would result in insufficient energy resources for gamete production, courtship behavior, and nest defense (Brett 1995). Perhaps the energy stores available to Lake Clark salmon are sufficient to support movement throughout the lake before spawning begins. In 2001, approximately 70% of the Lake Clark return was comprised of large salmon that had spent three years in the ocean (Woody 2004). The degree of wandering might be less in years when smaller fish (e.g., two-ocean fish) return to Lake Clark and have decreased energy reserves. Most research regarding the energetics of freshwater migration and reproduction has occurred in the Fraser River drainage in British Columbia where salmon may migrate up to 1,000 km before arriving at natal lakes. In contrast, the 200 km that salmon travel to Lake Clark is relatively short.

This study demonstrates that sockeye salmon migrate more directly to tributary rivers and lakes than to beach spawning locations. Assuming directed travel equates to homing, this is consistent with homing experiments where adult sockeye salmon were displaced between beach and tributary spawning habitats (Blair and Quinn 1991). Genetic (Habicht et al. 2004, Ramstad et al. 2004) and otolith microchemistry data (Quinn et al. 1999) further suggest that sockeye salmon home more precisely to tributaries than beach spawning habitats. Migration is likely more direct to tributaries because they have unique water chemistries, flows, and temperature regimes (e.g., Brabets 2002) that make them easier to recognize than beach spawning habitats.

Further demonstrating migration precision, all sockeye salmon that entered a tributary of Lake Clark, remained within that tributary to spawn. This observation contrasts with results from Tustumena Lake where approximately 16% of tributary spawners and 21% of beach spawners migrated into one tributary before settling at spawning locations (Burger et al. 1995). The difference in homing precision observed by Burger et al. (1995) may be attributable to an active rearing and stocking program in Tustumena Lake (Kyle 1992). Early imprinting of these stocks on their natal streams may have been compromised because fry were released at the mouths of their respective natal tributaries (Kyle 1992) thereby leading to the higher percentage of wandering.

The most precise migrations within Lake Clark were to the Kijik and Sucker Bay Lake drainages. Radio tagged salmon tended to migrate both quickly (speed) and directly (linearity) into these lakes. A recent population genetic study in Lake Clark found a high level of divergence of Kijik and Sucker Bay Lake populations compared to other populations within the lake, indicating a high degree of homing precision to these habitats (Ramstad et al. 2004). Both lakes provide a stable environment for adult sockeye salmon to congregate until spawning commences and may provide important rearing habitat for juvenile salmon. Experimental research indicates that the most sensitive period for olfactory imprinting occurs just before juvenile salmon migrate to sea (Hasler and Scholz 1983, Dittman and Quinn 1996). Perhaps salmon migrated more precisely to these lakes simply because they reared and imprinted on the unique odors of these waters rather than Lake Clark.

The upstream migration of sockeye salmon in glacially turbid tributaries coincided with cooling temperatures, lower water levels, and a dramatic decrease in the concentration of suspended sediment in the water. The similar timing of upstream migration among glacier fed rivers in the watershed suggests an adaptive response to seasonal turbidity cycles. Jensen and Mathisen (1987) noted that sockeye salmon generally migrate into glacial systems later than into clear systems. Such a behavioral adaptation would result in deposition of eggs on a decreasing turbidity cycle, thereby reducing adverse effects of fine sediments on embryo survival (Chapman 1988).

Similar to previous studies radio tagged salmon primarily migrated along the shoreline to spawning locations (Blair and Quinn 1991, Burger et al. 1995). Some salmon, however, moved through the middle of the lake, which contrasts observations made within Tustumena Lake, Alaska (Burger et al. 1995). No obvious pattern of near shore migration was observed, which contrasts the clockwise pattern observed within Tustumena Lake.

This study provides one of the first detailed examinations of in-lake spawning migrations of sockeye salmon and demonstrates that the final homing process is more dynamic than previously thought. Salmon migrated more precisely to tributary rivers and lakes than to Lake Clark beaches and this has implications for studies of salmon genetic population structure and evolution (Futuyma 1986, Avise 1994). Direct migration to tributaries may be attributable to tributaries having unique water chemistries and flows, which are easier to recognize than beach spawning locations. Indirect movements to spawning locations could indicate that sockeye salmon were searching for natal sites or had energy reserves beyond that needed for successful reproduction. These results have direct implications for the management of sockeye salmon stocks within Lake Clark and glacial habitats around the Pacific Rim. Directed migrations to tributaries suggest that tributaries spawners are distinct populations and should be monitored and managed separately. Within Lake Clark, there appears to be population structuring within lake basins. Future research is needed to further assess in-lake spawning migrations and population structuring within lake systems.

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Literature Cited

Anderson, J. W. 1969. Bathymetric measurements of Iliamna Lake and Lake Clark, Alaska. University of Washington, Fisheries Research Institute Circular No. 69-17.

Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York, New York.

Blair, G. R., and T. P. Quinn. 1991. Homing and spawning site selection by sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. Canadian Journal of Zoology 69:176-181.

Brabets, T. P. 2002. Water quality of the Tlikakila River and five major tributaries to Lake Clark, Lake Clark National Park and Preserve, Alaska, 1999-2001. U.S. Geological Survey Water Resources Investigations Report 02-4127.

Brett, J. R. 1995. Energetics. Pages 1-68 in C. Groot, L. Margolis, and C. Clark, editors. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver, British Columbia.

Burger, C. V., J. E. Finn, and L. Holland-Bartels. 1995. Pattern of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for population differentiation. Transactions of the American Fisheries Society 124:1-15.

Burgner, R.L. 1991. Life history of sockeye salmon (Oncorhynchus nerka). Pages 1-117 in C. Groot,, and L. Margolis, editors. Pacific salmon life histories, University of British Columbia Press, Vancouver, British Columbia.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society. 117:1-21.

Demory, R. L., R. F. Orrell, and D. R. Heinle. 1964. Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. U.S. Fish and Wildlife Service Special Scientific Report No. 488.

Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199:83-91.

Eiler J., D. N. Bonita, and R. F. Bradshaw. 1992. Riverine spawning by sockeye salmon in the Taku River, Alaska and British Columbia. Transactions of the American Fisheries Society 121:701-708.

Foerster, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Fisheries Research Board of Canada Bulletin 162.

French, R., H. Bilton, M. Osako, and A. Hartt. 1976. Distribution and origin of sockeye in offshore waters of the North Pacific Ocean. International North Pacific Fisheries Commission Bulletin No. 34.

Futuyma, D. J. 1986. Evolutionary biology. Sinauer Associates, Inc. Sunderland, Massachusetts.

Gilmer, D. S., L. M. Cowardin, R. L.Duval, L. M. Mechlin, C. W. Shaiffer, V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U.S. Fish and Wildlife Service Resource Publication 140.

Groot, C., and Quinn, T. P. 1987. Homing migration of sockeye salmon, *Oncorhynchus nerka*, to the Fraser River. Fisheries Bulletin 85:455-469.

Habicht, C., J. B. Olsen, L. Fair, and J. E. Seeb. 2004. Smaller effective population sizes evidenced by loss of microssatellite alleles in tributary-spawning populations of sockeye salmon from the Kvichak River, Alaska drainage. Environmental Biology of Fishes 69:51-62.

Hartman, W. L., and R. F. Raleigh. 1964. Tributary homing of sockeye salmon at Brooks and Karluk lakes, Alaska. Journal of the Fisheries Research Board of Canada 21:485-504.

Hasler, A. D., and A. T. Scholz. 1983. Olfactory imprinting and homing in salmon. Springer-Verlag, Berlin.

Healey, M. C., R. Lake, and S. G. Hinch. 2003. Energy expenditures during reproduction by sockeye salmon (*Oncorhynchus nerka*). Behavior 140:161-140.

Hendry, A. P., and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Canadian Journal of Zoology 77:1663-1675.

Jensen, K. A., and O. A. Mathisen. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983. Pages 101-109 in H.D. Smith, L. Margolis, and C. C. Wood, editors. Sockeye salmon (*Onchorhyncus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96.

Jones, S. H., and Fahl, C. B. 1994. Magnitude and frequency of floods in Alaska and conterminuous basins of Canada: U.S. Geological Survey Water-Resources Investigations Report 93-4179.

Killick, S. R. 1955. The chronological order of Fraser River sockeye salmon during migration, spawning, and death. International Pacific Salmon Fisheries Community Bulletin 7.

Kyle, G. B. 1992. Summary of sockeye salmon (*Oncorhynchus nerka*) investigations in Tustumena Lake, 1981-1991. Alaska Department of Fish and Game Division of Fisheries Rehabilitation, Enhancement, and Development Report No. 122. Juneau, Alaska.

Monan, G. E., J. H. Johnson, and G. F. Esterberg. 1975. Electronic tags and related tracking techniques aid in study of migrating salmon and steelhead trout in the Columbia River basin. U.S. National Marine Fisheries Service Marine Fisheries Review 37:9-15.

Ogura, M. And Y. Ishida. 1995. Homing behavior and vertical movements of four species of Pacific salmon (*Oncorhynchus spp.*) in the central Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 52:532-540.

Poe, P. H., and D. E. Rogers. 1984. 1984 Newhalen River adult salmon enumeration program. University of Washington, Fisheries Research Institute Final Report - Contract 14007-00011. Stone and Webster Engineering Corporation. FRI-UW-8415.

Quinn T. P. 1984. Homing and straying in Pacific salmon. Pages 357-362 in McCleave J. D., G. P. Arnold, and J. Dodson , editors. Mechanisms of Migration in Fishes. Plenum Press, NewYork.

Quinn, T. P. 1988. Estimated swimming speeds of migrating adult sockeye salmon. Canadian Journal of Zoology 66: 2160-2163.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29-44.

Quinn, T. P., and C. Groot. 1983. Orientation of chum salmon (*Oncorhynchus keta*) after internal and external magnetic field alteration. Canadian Journal of Fisheries and Aquatic Sciences 40:1598-1606.

Quinn, T. P., E. C. Volk, and P. P. Hendry. 1999. Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Zoology 77:766-775.

Ramstad, K. M., and C. A. Woody. 2003. Radio tag retention and mortality of adult sockeye salmon. North American Journal of Fisheries Management 23:978-982.

Ramstad, K. M., C. A. Woody, G. K. Sage, and F. W. Allendorf. 2004. Founding events influence genetic population structure of sockeye salmon (*Oncorhynchus nerka*) in Lake Clark, Alaska. Molecular Ecology 13:277-290.

Rand, P. S., and S. G. Hinch. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. Canadian Journal of Fisheries and Aquatic Sciences 55:1832-1841.

Regnart, J. R. 1998. Kvichak River sockeye salmon spawning ground surveys, 1955-1998. Alaska Department of Fish and Game, Regional Information Report 2A98-38.

Schubert, N. D., and G. C. Scarborough. 1996. Radio telemetry observations of sockeye salmon (*Oncorhynchus nerka*) spawners in Chilko River and Chilko Lake: Investigation of the role of stress in a mark/recapture study. Canadian Technical Report of Fisheries and Aquatic Sciences 2131.

Ueda, H., M. Kaeriyama, K. Mukasa, A. Urano, H. Kudo, T. Shoji, Y. Tokumitsu, K. Yamauchi, and K. Kurihara. 1998. Lacustrine sockeye salmon return straight to their natal area from open water using both visual and olfactory cues. Chemical Senses 23:207-212.

Varnavskiy, V. S., and N. V. Varnavskaya. 1985. Assessment of straying between groups of early spawning sockeye salmon, *Oncorhynchus nerka*, in Nakhichinskoye Lake, Kamchatka. Journal of Ichthyology 25:136-139.

Wilkens, A. X. 2002. The limnology of Lake Clark, Alaska. M.S. thesis. Univerisity of Alaska Fairbanks.

Winter, J. D. 1996. Advances in underwater biotelemetry. Pages 555-590 in B. R. Murphy, and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Woody, C. A. 2004. Counting tower data for the Newhalen and Tazimina Rivers, 2000-2003. Final Report 01-095. U.S. Fish and Wildlife Service Office of Subsistence Management, Anchorage, Alaska.

Tables

Table 1.1. Characteristics of tributary inputs to Lake Clark. [From Wilkens (2002); based on data from Brabets (2002), May to October of 1999 – 2001].

Tributary	Basin	Source	Discharge (m^3/s)	Temperature (°C)	Suspended sediment (mg/L)	Basin area (km^2)
Lake Clark outlet	Lower	Lake-fed	242-674	4-12	1-5	7,629
Chulitna River	Middle	Bog-fed	37-210	1-15	4-9	3,000
Tanalian River	Middle	Lake-fed	5-168	5-14	1-5	532
Kijik River	Middle	Lake-fed	12-85	3-13	2-123	773
Currant Creek	Upper	Glacier-fed	8-78	1-8	3-282	428
Tlikakila River	Upper	Glacier-fed	1-340	0-10	5-710	1,613
Chokotonk River	Upper	Glacier-fed	7-62	0-10	9-211	436

Table 1.2. Linearity, speed of migration, and days migrated to spawning location by drainage, Lake Clark, 2001. Location was either Lake Clark beaches (LC) or tributary rivers or lakes.

							Speed (km/day)		Speed (days)		Linearity		Arrival date		
Area	Location	Basin	Water	Peak spawning date	Distance (km)	n	Avg.	Std Dev.	Avg.	Std Dev.	Avg.	Std Dev.	Mean	Min.	Max.
Lake Clark	LC	Lower	Clear	15-Sep	4 - 15	14	2.1	3.8	16.4	13.0	0.4	0.3	16-Aug	26-Jul	19-Sep
Lake Clark	LC	Middle	Turbid	25-Sep	25 - 44	30	1.2	0.6	32.9	12.5	0.3	0.1	28-Aug	4-Aug	21-Sep
Lake Clark	LC	Upper	Turbid	25-Sep	53 - 63	8	2.0	1.2	36.9	15.9	0.6	0.2	30-Aug	3-Aug	14-Sep
Sucker Bay Lake	Trib	Lower	Clear	30-Aug	7	2	4.2	4.0	3.0	2.8	0.7	0.4	27-Jul	20-Jul	4-Aug
Kijik Lake	Trib	Middle	Clear	25-Sep	42	20	6.0	2.4	8.3	4.4	0.8	0.2	30-Aug	21-Jul	22-Aug
Priest Rock Creek	Trib	Middle	Clear	11-Oct	46	1	1.9	NA	24.5	NA	0.4	NA	24-Aug	24-Aug	24-Aug
Currant Creek	Trib	Upper	Turbid	25-Sep	53	3	5.0	3.5	15.3	10.7	0.7	0.2	7-Aug	28-Jul	26-Aug
Little Lake Clark	Trib	Upper	Turbid	7-Oct	66	31	4.4	3.3	20.4	9.5	0.7	0.2	13-Aug	25-Jul	29-Aug
Tlikakila River	Trib	Upper	Turbid	1-Oct	66	33	4.2	2.1	19.0	7.9	0.8	0.1	12-Aug	28-Jul	2-Sep
All Lake Clark	LC				4 - 63	52	1.6	2.1	29.1	15.1	0.4	0.2	25-Aug	26-Jul	22-Sep
All tributaries	Trib				7 - 66	90	4.7	2.7	16.7	9.3	0.8	0.2	10-Aug	20-Jul	2-Sep
All Lower Basin		Lower			4 - 15	16	2.3	3.8	14.8	13.0	0.4	0.3	14-Aug	20-Jul	19-Sep
All Middle Basin		Middle			25 - 44	51	3.1	2.9	23.1	15.6	0.5	0.3	17-Aug	21-Jul	21-Sep
All Upper Basin		Upper			53 - 63	75	4.1	2.7	21.3	11.0	0.8	0.2	15-Aug	25-Jul	14-Sep
All Clear			Clear		4 - 46	42	3.9	3.5	14.4	13.5	0.6	0.3	9-Aug	20-Jul	19-Sep
All Turbid			Turbid		30 - 66	100	3.4	2.6	24.1	12.0	0.6	0.3	18-Aug	25-Jul	22-Sep
All drainages					1 - 66	142	3.5	2.9	21.2	13.2	0.6	0.3	16-Aug	20-Jul	22-Sep

Table 1.3. Date salmon migrated into tributaries of Lake Clark, 2001. Tributary type was either a tributary lake (Lake) or tributary river (Trib).

					Date of entry into tributaries		
Tributary	Basin	Source	Tributary Type	n	Mean	Min.	Max.
Sucker Bay Lake	Lower	Bog-fed	Lake	2	6-Aug	25-Jul	18-Aug
Kijik Lake	Middle	Spring-fed	Lake	20	3-Aug	24-Jul	28-Aug
Priest Rock Creek	Middle	Spring-fed	Trib	1	3-Oct		
Currant Creek	Upper	Glacier-fed	Trib	3	13-Sep	8-Sep	17-Sep
Tlikakila River	Upper	Glacier-fed	Trib	33	8-Sep	1-Sep	13-Sep
Little Lake Clark	Upper	Glacier-fed	Lake	31	27-Aug	13-Aug	15-Sep

Figures

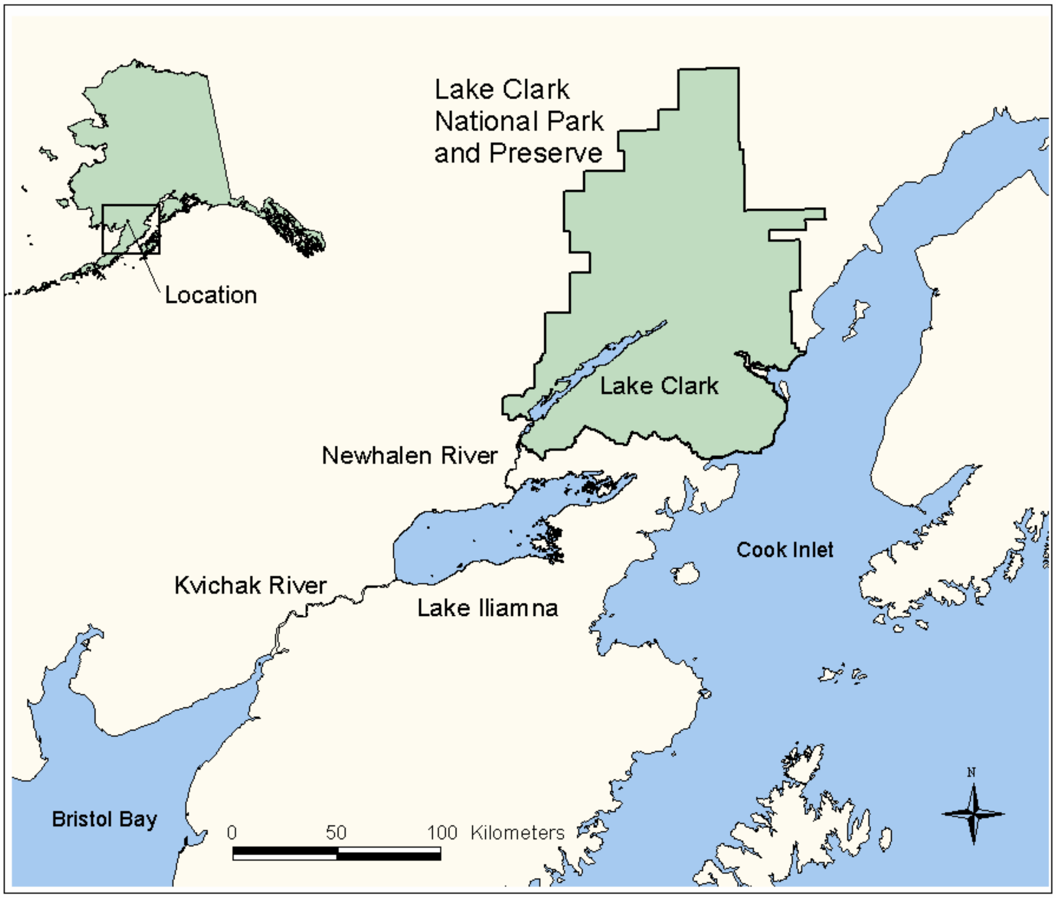

Figure 1.1. Location of Lake Clark relative to Bristol Bay, Alaska.

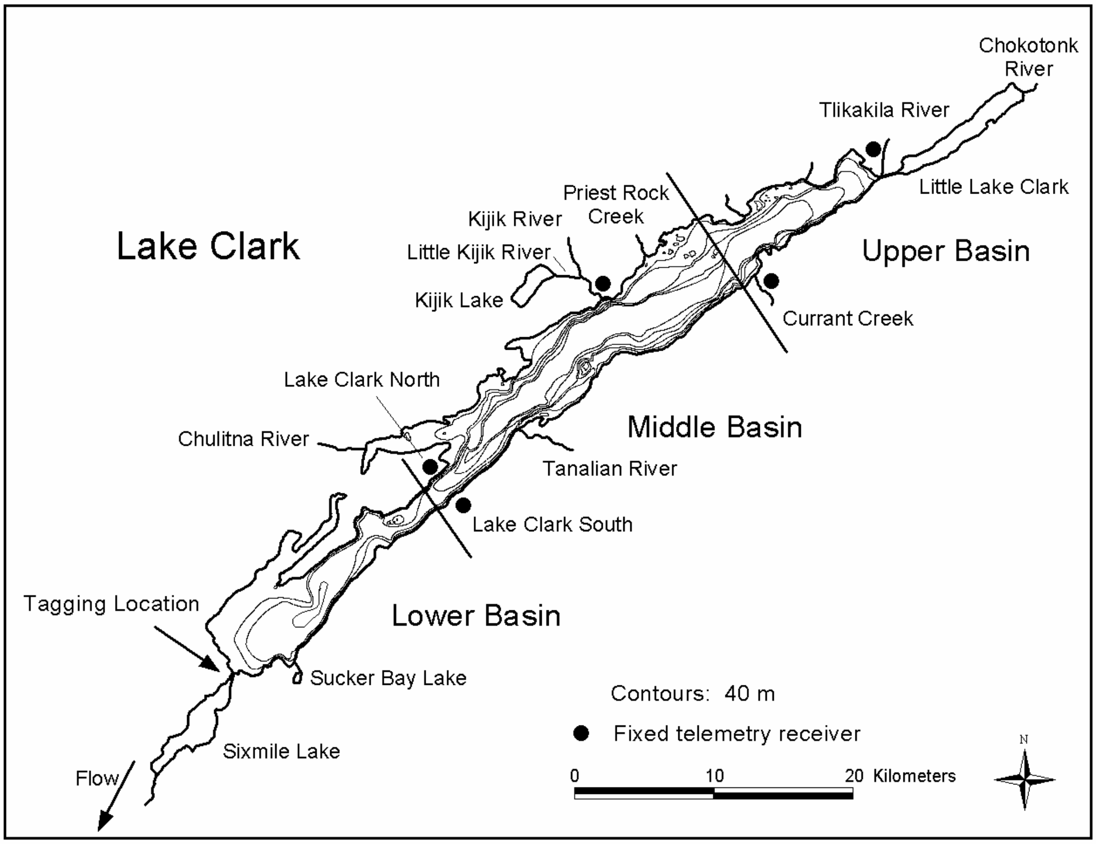

Figure 1.2 Location of lake basins, tributaries, tagging site, and fixed telemetry receivers in the Lake Clark watershed (contours redrawn from Anderson 1969).

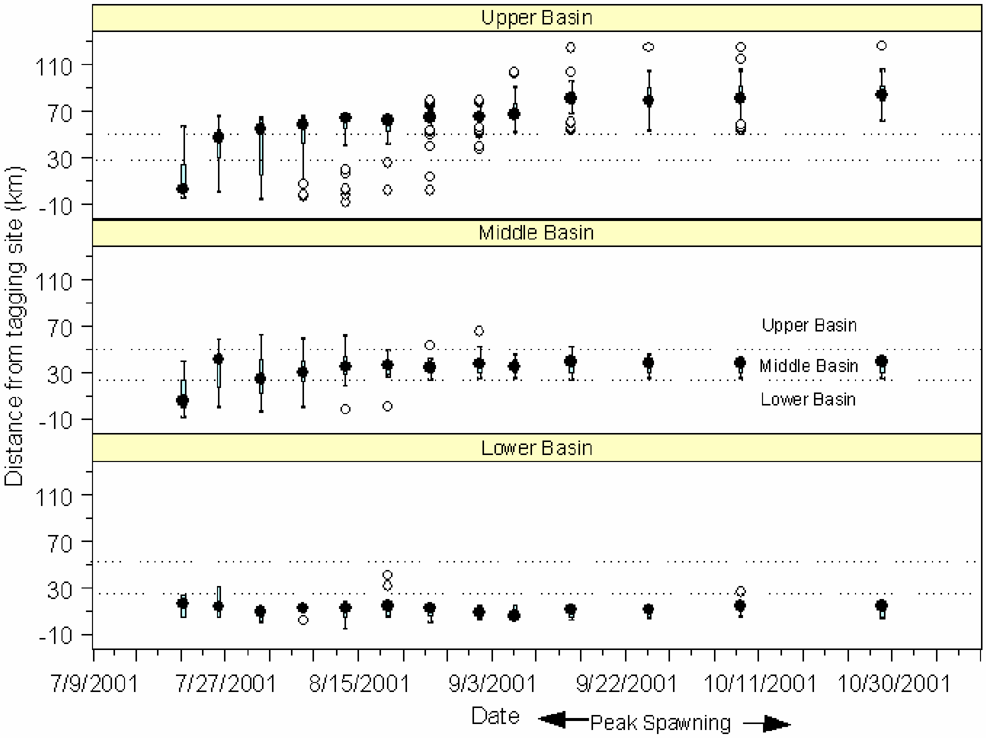

Figure 1.3. Distance radio tagged sockeye salmon were located from the tagging site by date; boxes comprise central 50% of data, filled circles indicate median, and empty circles indicate outliers. Negative distance values indicate salmon that migrated downstream of the tagging site. Radio tagged fish generally migrated to a particular lake basin. Ninety three percent of radio tagged fish had arrived at spawning locations by 3 September.

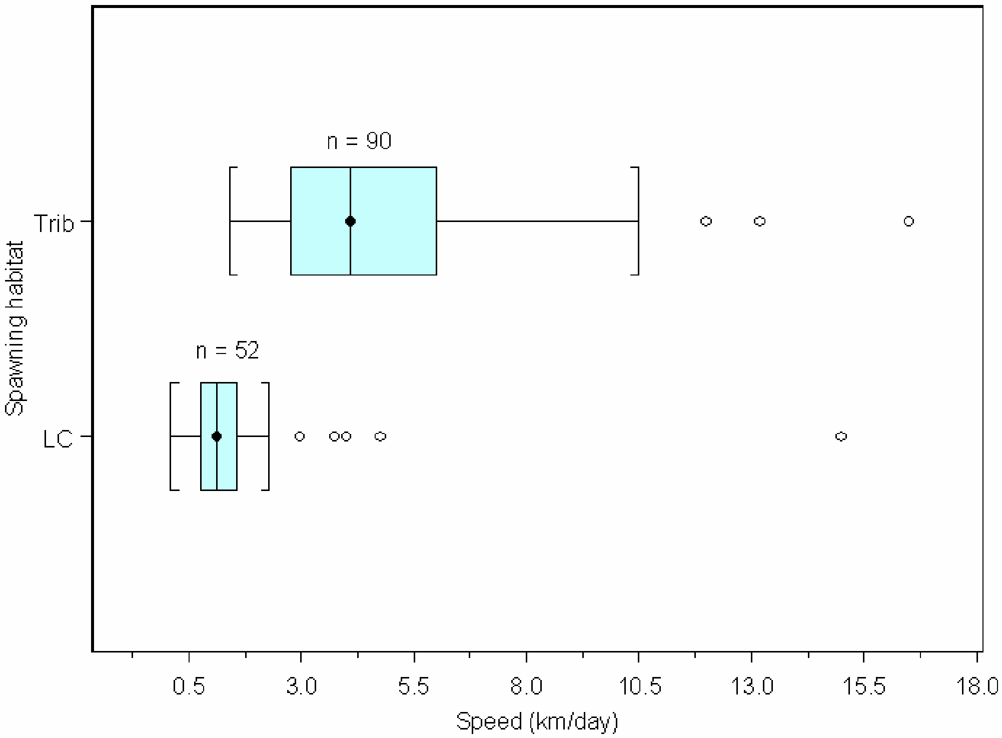

Figure 1.4. Speed of migration to spawning locations by habitat type; boxes comprise central 50% of data, filled circles indicate median, and empty circles indicate outliers. Habitat types were either tributary rivers and lakes (Trib) or Lake Clark beaches.

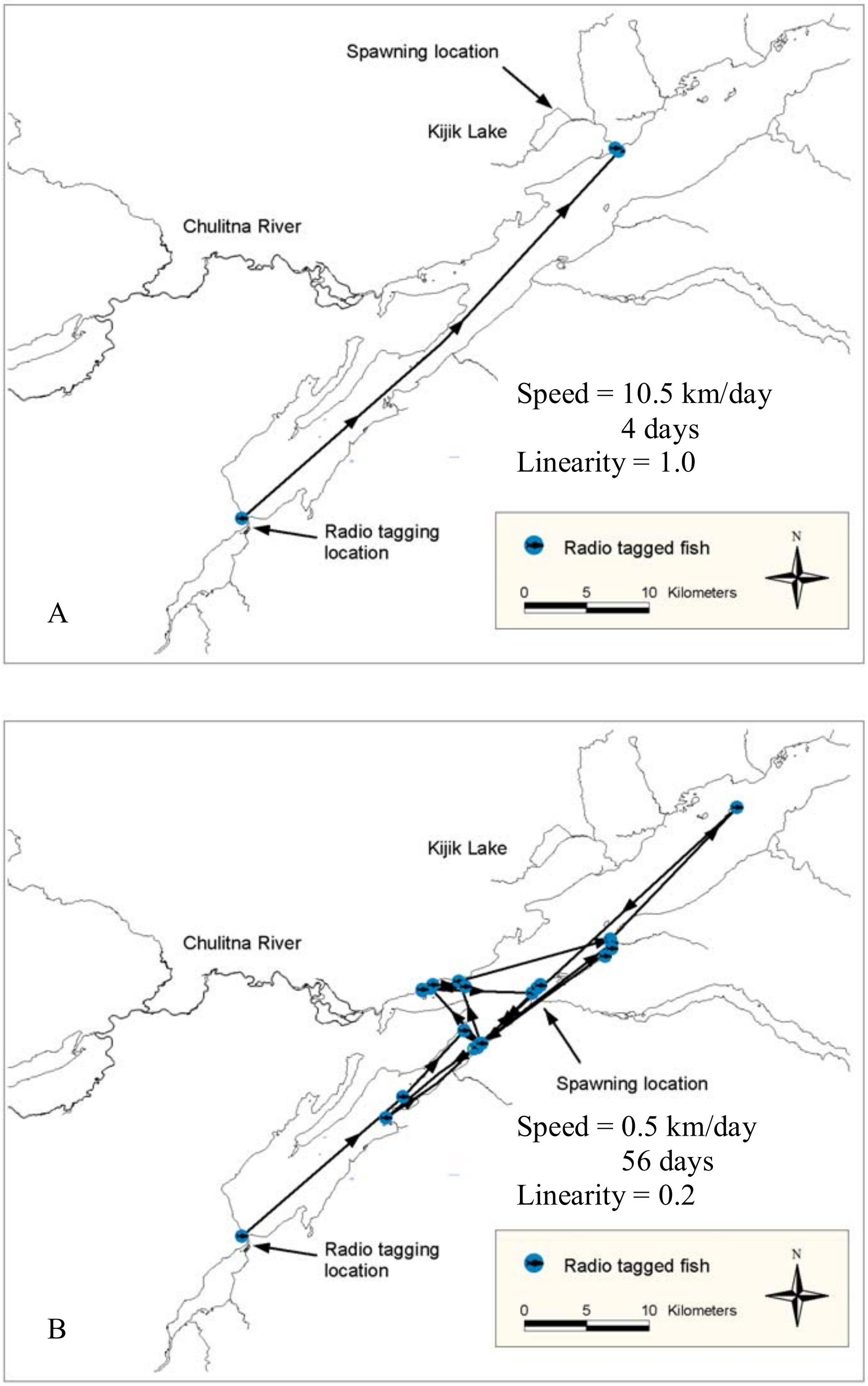

Figure 1.5. Example of radio tagged sockeye salmon that migrated directly (A) and indirectly (B) to spawning locations. Linearity was calculated as the shortest distance in water from the tagging site to within 5 km of the spawning location or mouth of the spawning stream divided by the straight-line distance between all re-location data points.

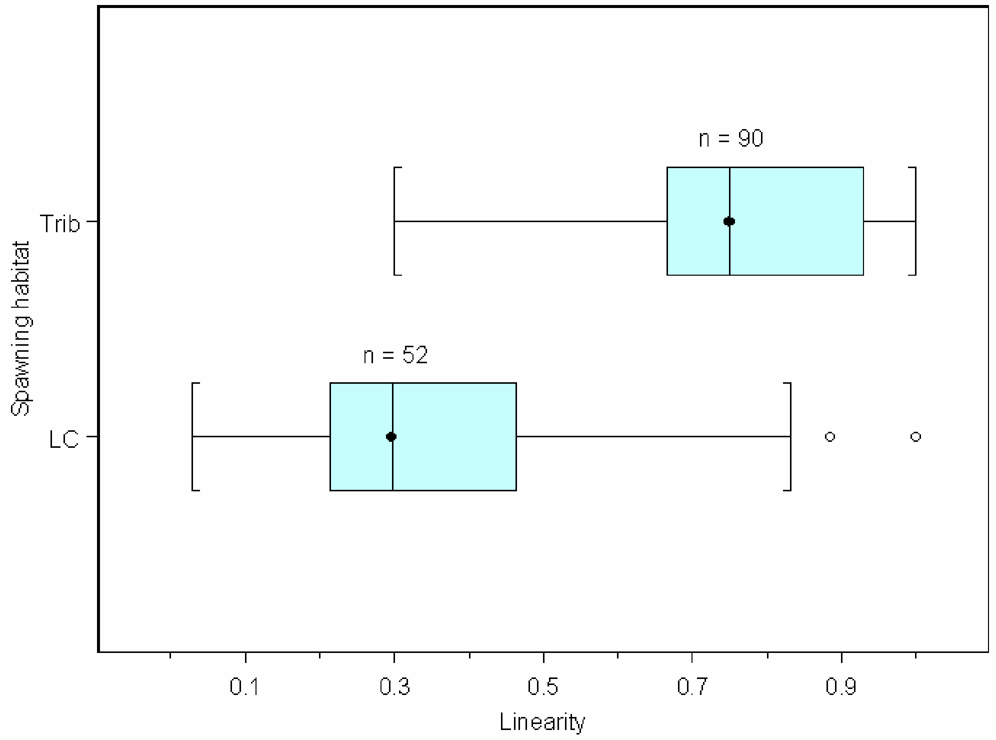

Figure 1.6. Linearity of migration for radio tagged salmon returning to spawning locations by habitat type; boxes comprise central 50% of data, filled circles indicate median, and empty circles indicate outliers. Habitat types were either tributary rivers and lakes (Trib) or Lake Clark beaches (LC). Linearity was calculated as the shortest distance in water from the tagging site to within 5 km of the spawning location or mouth of the spawning stream divided by the straight-line distance between all re-location data points.

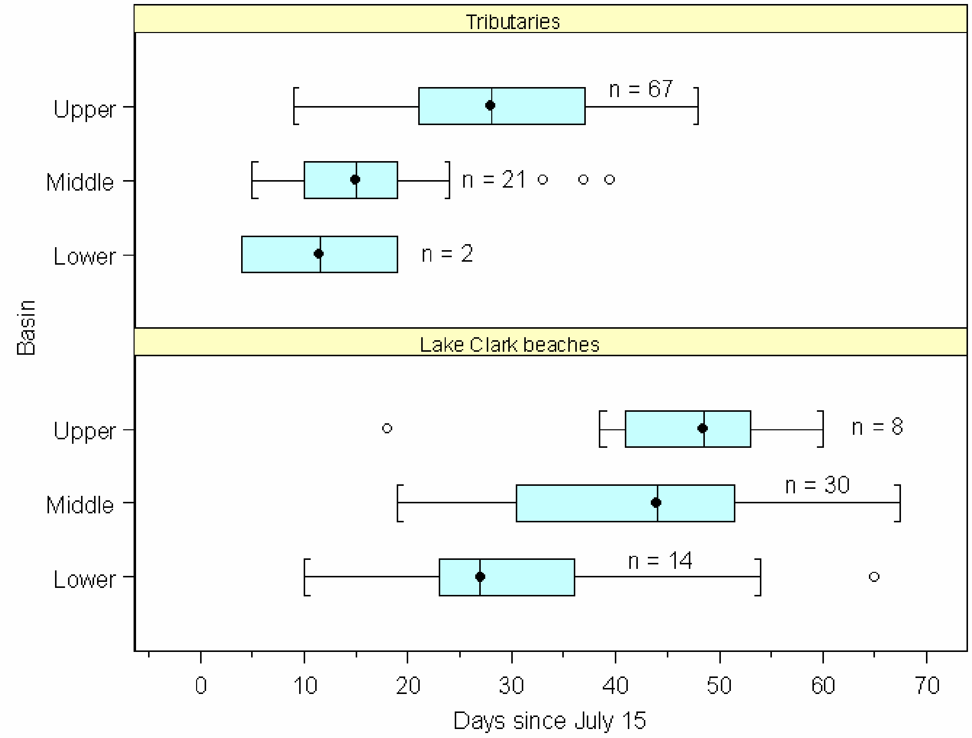

Figure 1.7. Date radio tagged sockeye salmon arrived at spawning locations by lake basin and habitat type; boxes comprise central 50% of data, filled circles indicate median, and empty circles indicate outliers. Tributaries include both tributary rivers and tributary lakes.

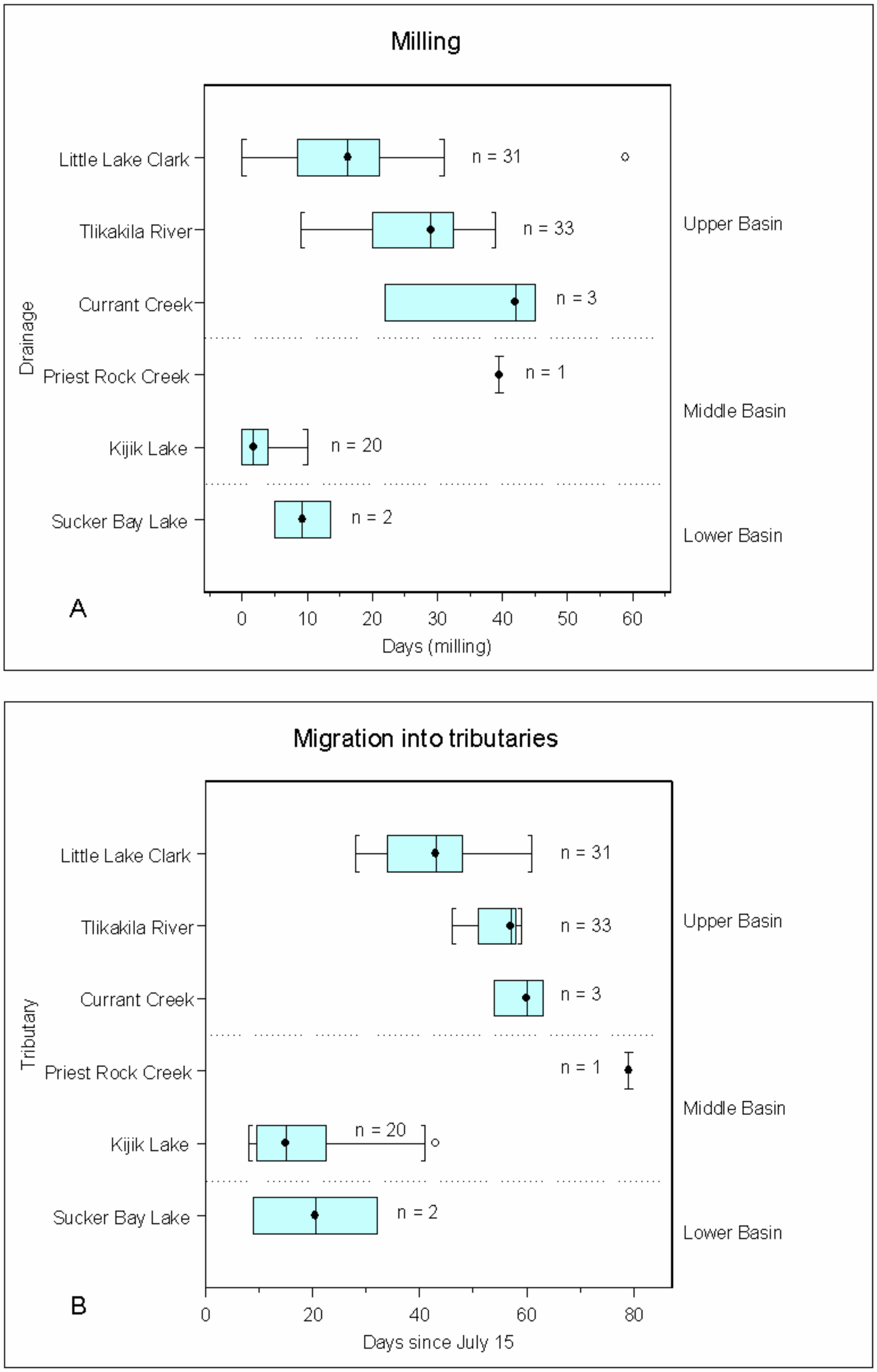

Figure 1.8. Days radio tagged salmon milled at the mouth of tributaries (A) and date salmon migrated into tributaries of Lake Clark (B); boxes comprise central 50% of data, filled circles indicate median, and empty circles indicate outliers.

Chapter 2: The spawning distribution of sockeye salmon in a glacially influenced lake: the importance of turbid habitats[1]

Abstract

The spawning distribution of sockeye salmon *Oncorhynchus nerka* was examined in the Lake Clark watershed, Alaska using radio telemetry. The Lake Clark watershed has a distinct dichotomy of turbid and non-turbid habitats due to the input of glacial meltwater in the northeastern end of the lake. During the two study years, 241 adult sockeye salmon were tracked to 27 spawning locations in the Lake Clark watershed. An additional five spawning locations were identified by visual observation or seining. Most radio tagged sockeye salmon (65%) returned to spawning locations in turbid waters that were adjacent to an obvious clear water source. Spawning activity in turbid waters was relatively late and coincided with a dramatic decrease in suspended sediments. The assumed impact of fine sediments on salmonid egg and embryo survival in naturally turbid systems appears to have been overestimated and poorly understood.

Introduction

Pacific salmon *Oncorhynchus* spp. spawn in a variety of habitats throughout their natural range in the northern basin of the Pacific Ocean. Their spawning locations are typically associated with clear, cool, and well-oxygenated water and may include rivers, streams, tributaries, springs and lake shorelines (for a review see Groot and Margolis 1991).

Glacially turbid rivers and lakes are generally considered poor spawning habitat for Pacific salmon (Groot and Margolis 1991). Glacier-fed waters are characterized by high turbidity, variable flows, large concentrations of suspended fine sediments, and silty substrates (Koenings et al. 1986, 1990, Lloyd et al. 1987). Studies suggest that large concentrations of fine sediments in redds can smother eggs and embryos, and thus

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adversely affect their survival (Phillips et al. 1975, Hausle and Coble 1976, Everest et al. 1987). Fine sediments can inhibit oxygenation, metabolic waste transfer, and fry emergence (Everest et al. 1987). In his review on the effects of fine sediments in salmonid redds, Chapman (1988) indicated that survival to emergence usually relates negatively to the percentage of fine sediments in a redd.

Although the effects of fine sediments on egg and embryo survival are well documented (Chapman 1988), many glacial rivers and lakes support productive salmon stocks. Spawning in turbid systems was traditionally explained through the assumption that it simply occurred in associated clear tributaries and lakes (e.g., Burger et al. 1995). Recent studies suggest that glacially turbid spawning locations are significantly more important for Pacific salmon production than previously thought (Burger et al. 1985, Eiler et al. 1992, Burger et al. 1995). The turbid nature of these glacier-fed waters has hindered the accurate assessment of spawning locations by conventional visual census (Cousens 1982). Absolute turbidities between 4 and 8 nephelometric turbidity units (NTU) may be sufficient to limit the direct observation of salmon during aerial surveys (Lloyd et al. 1987).

Information regarding the spawning locations of sockeye salmon *Oncorhynchus nerka* in the Lake Clark watershed (Figure 2.1) has been limited to visual surveys of spawning locations. Approximately half of the drainage is turbid due to glacial influences, and the extent of sockeye salmon use in these waters is unknown. Historic spawning surveys (Demory et al. 1964), traditional tagging studies (Smith 1964, Jensen and Mathisen 1987), and aerial surveys (Parker and Blair 1987, Regnart 1998) suggested that most spawning activity occurred in clear water tributaries and tributary lakes. Although limited spawning has also been documented in turbid regions of the watershed (Smith 1964, Jensen and Mathisen 1987, Parker and Blair 1987, Regnart 1998), the importance of these locations for overall salmon production remains unknown. Unidentified spawning locations likely exist as sockeye salmon have been documented spawning in similarly turbid waters elsewhere (e.g., Eiler et al. 1992, Burger et al. 1995). To identify the spawning locations of sockeye salmon in the Lake Clark watershed and assess the distribution relative to water turbidity, adult sockeye salmon were radio tagged as they entered Lake Clark and tracked to spawning locations. This information is critical for accurate stock assessment, population management, and protection of critical spawning habitats (Knudsen 2000).

Study Site

The Lake Clark watershed (60° 01 N, 154° 45 W) is located within the larger Kvichak River drainage in southwest Alaska (Figure 2.1). It includes Lake Clark (267 km^2), which is the sixth largest lake in Alaska and the largest body of water in Lake Clark National Park and Preserve. Lake Clark is a semi-glacial oligotrophic lake that is approximately 66-km long and 2.5 – 8-km wide with an average depth of 103 m, maximum depth of 322 m, and a drainage area of 7,620 km^2 (Anderson 1969, Wilkens 2002). The lake is composed of three major basins, hereafter referred to as the lower, middle and upper basins (Figure 2.2). The lower basin is distinctly separated while the middle and upper basins are less distinct. Six primary tributaries empty into the middle and upper basins of Lake Clark and provide the majority of the inflow to the lake (Table 2.1; Brabets 2002). In addition, numerous smaller streams that are glacially turbid, clear, or organically stained flow into Lake Clark.

Glaciers, steep mountains, glacial rivers, and high precipitation (average 203 cm annually) characterize the northeast end of the watershed while lowland tundra, small mountains, clear and organically stained streams, and low precipitation (average 64 cm annually) characterize the southwest end (Jones and Fahl 1994, Brabets 2002). Glacier-fed tributaries in the upper basin provide approximately half of Lake Clark's annual water budget and transport 0.4 – 1.5 million tons of suspended sediment into the lake each year (Table 2.1; Brabets 2002). Runoff from glacial tributaries is highest between June and September creating a turbidity gradient along the length of Lake Clark from the turbid (~10 NTU) northeast to the clear (≤ 2 NTU) southwest (Brabets 2002, Wilkens 2002). Lake Clark is therefore an ideal location to study the spawning distribution of sockeye salmon relative to water turbidity because approximately half of the watershed is turbid and half is clear when spawning activity occurs.

Methods

Radio tagging

Migrating adult sockeye salmon were captured at the outlet of Lake Clark (Figure 2.2) with nylon beach seines (62 m x 2.4 m - 3.7 m with 10.2 cm mesh) and radio tagged throughout the run (15 July to 23 August 2000 and 15 July to 9 August 2001). Captures were made during randomly selected fishing sessions between 0800 and 1959 hours. In 2001, the tagging period was shortened by two weeks to minimize the capture and tagging of salmon that spawn at the lake outlet. Approximately six fish per day were tagged in 2000 and five fish per day in 2001. In order to tag an even more representative sample of the run in 2001, ten fish per day were tagged during the peak of salmon migration into Lake Clark. A counting tower located 10 km downstream of the tagging site identified the peak migration period (> 10,000 fish/day; Woody 2004).

Radio tagging protocols were similar to previous radio telemetry studies of Pacific salmon (Eiler et al. 1992, Burger et al. 1995). After capture, sockeye salmon were placed in a mesh live well in the stream (1.5 m x 1.5 m x 1.5 m with 2.5 cm mesh). Captured sockeye salmon were placed in a tagging cradle, identified as male or female, and measured from mid-eye to hypural plate. A subset of salmon captured in the net were then turned with ventral side up and with their lower jaws raised so that a glycerin-coated radio tag could be inserted into their stomachs using a 6-mm diameter PVC tube (Monan et al. 1975, Burger et al. 1995). After the tagging procedure, fish were released at the location of capture after recovering in the mesh live well.

In 2000, fish were anesthetized with a clove-oil mixture prior to the tagging procedure (Woody et al. 2002) while in 2001 no anesthesia was used. An anesthetic was used in 2000 to reduce the handling stress from additional sampling of fin clips for genetics, scales for aging, and measures of body length and depth. In 2001, an anesthetic was unnecessary because fish were only measured and radio tagged (Eiler et al. 1992).

The change in the tagging procedure resulted in a decreased handling time from five minutes in 2000 to one minute in 2001.

Both sexes were tagged in 2000 while only females were tagged in 2001. The tagging of only females in 2001 was done to better identify specific spawning locations because females exhibit stronger site fidelity (Mathisen 1962).

Radio tag retention was examined during a companion study (Ramstad and Woody 2003). During this study, the overall tag retention in sockeye salmon was high (0.98, 95% confidence interval (CI), 0.92-1.00) and mortality of tagged salmon was low and similar to that of untagged controls (0.02, 95% CI<0.01 – 0.08).

Radio telemetry equipment

Radio-telemetry equipment consisted of high frequency VHF radio tags, scanning receivers, and H and 4-element Yagi antennae (Lotek Engineering, Inc., Newmarket, Ontario, Canada). Digitally coded radio tags measured 14.5 x 49 mm and 12.9 g in 2000 and 16 mm x 46 mm and 15.6 g in 2001. A larger radio tag was used in 2001 to increase the reception range of tagged fish during tracking. Radio tags weighed less than 2% of body weight of tagged fish as generally recommended (Winter 1996). Radio tags transmitted 24 hours per day with a three second burst rate in 2000 and a two second burst rate in 2001. The shorter burst rate was used in 2001 to further minimize the scan time during tracking events. Tag life was approximately 380 days, which well exceeded the known spawning period (< 120 days) of any sockeye salmon spawning populations in the Lake Clark watershed (Demory et al. 1964, Regnart 1998).

Radio tracking

Radio tagged fish were tracked every five to ten days using fixed-wing aircraft or boats and were monitored 24 hours per day at fixed radio telemetry receivers (Figure 2.2). Aerial surveys were flown with an H antenna mounted on each wing strut along the shoreline of Lake Clark and its tributaries at an altitude between 200 and 300 m and an airspeed between 100 and 130 kph (Gilmer et al. 1981). Aerial flights were not flown up tributaries until it was determined that fish could have moved into the area; e.g., fish were recorded past a fixed telemetry receiver on the tributary. Boat tracking was conducted around the lake perimeter and islands approximately 300 m offshore and at a maximum speed of 30 kph. Two 4-element Yagi antennae, mounted to the boat hull and positioned at 45° angles scanned the areas forward of the boat. Fixed telemetry receivers consisted of an enclosure box, a telemetry receiver, two 4-element Yagi antennae, an antenna switchbox, and a sealed lead-acid battery powered by a solar panel. The receiver at the Kijik and Tlikakila River monitored fish passage in both 2000 and 2001. The receivers located at Lake Clark North, Lake Clark South and Currant Creek monitored fish passage in 2001 (Figure 2.2).

During aerial and boat tracking events, a global positioning system (GPS) receiver recorded the location where a tagged fish was detected. Fish were tracked to within 1 km during aerial surveys and to within 400 m during boat surveys, based on field tests with planted transmitters.

A fish was considered to be at its final spawning location when (i) it was relocated within 400 m of its previous location at least twice within three weeks or entered its spawning stream, (ii) no further migration occurred, and (iii) spawning or spawned out sockeye salmon were observed in that area. A beach seine or tangle net was used to verify spawning in glacially turbid locations with limited visibility.

Data summation

Data collected during radio tracking events and at fixed telemetry receivers were condensed for data analyses. If fish were recorded multiple times during an aerial or boat tracking event, the record with the highest signal strength was selected. Comparison between signal strengths was made using a reference gain on the telemetry receiver. Data collected at fixed telemetry receivers were condensed to one record per fish for a 24-hour period. If fish were recorded multiple times in one day at a fixed telemetry receiver, the record with the highest signal strength was selected. Forty-one radio tagged fish that migrated to spawning locations downstream of the tagging site were excluded because they exhibited unique spawning migrations and did not enter Lake Clark.

Spawning locations – glacially turbid vs. clear water

Spawning locations were classified as clear (< 5 NTU) or glacially turbid (≥ 5 NTU) according to whether observers were likely to see spawning salmon during aerial surveys (Lloyd et al. 1987). This criterion has also been used to distinguish between glacially turbid and clear lakes in Alaska (Koenings et al. 1986, 1990). Turbidity was measured at the time of peak spawning using a pocket turbidimeter (Hach Company, Loveland, Colorado, USA). Turbidity was used to classify spawning locations because it was easy to measure, was a good indicator of suspended fine sediments (Lloyd et al. 1987), and was a variable of biological interest and suspected importance.

The formula Lloyd et al. (1987) used to model the relationship between turbidity and suspended sediment concentration from 34 streams in Alaska was used to convert suspended sediment concentrations collected by Brabets (2002) into turbidity values (NTU).

$$T = 0.44(SSC)^{0.858}$$

T = turbidity (NTU)

SSC = suspended sediment concentration (mg/L)

Data analyses

To determine if radio tagged sockeye salmon were a representative sample of salmon entering Lake Clark, one-way analysis of variance (ANOVA, S-PLUS software version 6.0, Lucent Technologies Inc.) was used to compare the length (mid-eye to hypural plate) of radio tagged and untagged salmon. A chi square test of independence (S-PLUS software version 6.0, Lucent Technologies Inc.) was used to test the hypothesis that the proportion of radio tagged fish selecting glacially turbid and clear spawning locations was independent of sex and sample year.

Results

Radio tagging

The lengths of captured tagged and untagged fish ranged between 404 mm and 592 mm (Table 2.2). On average, tagged salmon were the same size as untagged salmon due to sex and sample year (Table 2.2). That is, tagged and untagged females were the same size in 2000 ($P = 0.277$), as were males in 2000 ($P = 0.996$), and females in 2001 ($P = 0.220$).

Spawning locations

Three hundred thirty-two adult sockeye salmon were radio tagged as they entered Lake Clark: 175 (93 male, 82 female) in 2000, 157 (all female) in 2001. Spawning locations were determined for 282 radio tagged sockeye salmon (Figure 2.3). Eighty five percent of tagged fish returned to spawning locations within the Lake Clark watershed and 15% returned to spawning locations downstream of the tagging site (Table 2.3). Fish not tracked to spawning locations were either never located, lost after being tracked into Lake Clark, or lacked sufficient relocation data to determine a spawning location. On average, radio tagged fish tracked to spawning locations were relocated 12.7 times (range, 3 – 33) with over 3,500 relocations made during the two study years.

Radio tagged salmon returned to 30 spawning locations including 27 locations in the Lake Clark watershed and three located downstream of the tagging site (Figure 2.3, Appendix 2.A, Appendix 2.B, Appendix 2.C). An additional five spawning locations were identified in the Lake Clark watershed by visual observation or seining (Figure 2.3, Appendix 2.D). Radio tagged salmon returned to 20 spawning locations ($N = 16$ for females only) in 2000 and 27 spawning locations in 2001. Tagged salmon were documented at 18 of these spawning locations during both years of the study (Appendix 2.B). Although radio tagged salmon returned to 30 spawning locations, 70% returned to five primary spawning locations within the Lake Clark watershed. These five spawning locations were Kijik Lake, Tlikakila River, and beach spawning locations at the mouths of the Tanalian, Kijik, and Chokotonk Rivers (Figure 2.3, Appendix 2.B).

Spawning locations - glacially turbid vs. clear water

Approximately 50% of the spawning locations identified in the Lake Clark watershed were located in turbid waters. Turbidity values at spawning locations ranged from a low of 0.3 NTU in Kijik Lake to a high of 15.0 NTU in Little Lake Clark. During both years of the study, more radio tagged salmon returned to spawning locations in turbid waters than clear waters (Figure 2.4). In 2000, there was no difference in the spawning distribution of male and female sockeye salmon relative to water turbidity ($X^2 = 0.047$, df = 1, P = 0.826). In 2001, more tagged fish spawned in glacially turbid waters than in 2000 ($X^2 = 3.619$, df = 1, P = 0.057).

Most spawning locations were adjacent to a clear water source. Beach spawning habitats were typically located adjacent to inlet tributaries, springs, or outwash plains. In turbid rivers, radio tagged salmon generally spawned in the middle to upper reaches of the rivers in side channels.

Despite changes in the tagging procedure between 2000 and 2001, the spawning distribution of sockeye salmon within the Lake Clark drainage was similar between years by both water turbidity (59% and 70% returned to turbid waters) and ecotype (72% and 69% returned to beach spawning habitats).

Spawn timing

Spawning was observed from late August until mid November with spawning activity ranging from several weeks at some locations (e.g., Sucker Bay Lake) to over two months at others (e.g., Kijik Lake). Peak spawning activity throughout the watershed generally occurred between 15 September and 15 October (Appendix 2.B). Fish spawned earliest in the clear waters of Sucker Bay Lake and latest in the turbid waters of Little Lake Clark and Tlikakila River.

Spawning activity in turbid locations of the Lake Clark watershed coincided with a dramatic decrease in suspended sediment concentrations (Figure 2.5). In the glacier-fed Tlikakila River, spawning began when temperatures cooled and the concentration of suspended sediments decreased from a high of 710 mg/L (125 NTU) in June to 71 mg/L (15 NTU) in September (Figure 2.5; Brabets 2002). The concentrations further declined to 9 mg/L (2 NTU) in October when peak spawning ended.

Discussion

Spawning locations for sockeye salmon have been underestimated in the Lake Clark watershed. Compared to historic scientific research, this study documented 18 new spawning locations (Figure 2.6, Appendix 2.B). Compared to traditional ecological knowledge (TEK), 10 new spawning locations were identified (Figure 2.7, Appendix 2.B; Morris 1986, Stickman et al. 2003). Most of the newly identified spawning locations were in turbid areas of the watershed. Historic aerial surveys that relied on visual observation suggested that 50 – 90% of Lake Clark sockeye salmon spawned in clear water tributaries (Parker and Blair 1987, Regnart 1998). In contrast, this study indicates that most sockeye salmon (65%) spawn in glacially turbid locations (Figure 2.4). Turbid waters have obviously limited the accurate assessment of sockeye salmon spawning locations and distribution in the Lake Clark watershed.

Other researchers have similarly revealed new spawning locations for Chinook salmon *Oncorhnchus tschawytscha* (Burger et al. 1985, Savereide 2003), chum salmon *O. keta* (Barton 1992) and sockeye salmon (Eiler et al. 1992, Burger et al. 1995) in glacially turbid waters. Thirty percent of radio tagged sockeye salmon that returned to Tustumena Lake, Alaska, spawned in waters with a turbidity of 50 NTU (Burger et al. 1995). Forty-two percent of radio tagged sockeye salmon returned to the mainstem of the Taku River, Alaska and British Columbia, where turbidities reach 200 NTU (Eiler et al. 1992, Murphy et al. 1997). Prior to research on the Taku River, it was estimated that most (60-70%) sockeye salmon spawned in lakes in the upper watershed (Eiler et al. 1992).

Similar to observations in other glacial systems, most spawning locations in the Lake Clark watershed were associated with a clear water source, such as an inlet tributary. Lorenz and Eiler (1989) suggested that upwelling groundwater and springs are sufficient to remove fine sediments from the spawning substrates in turbid rivers. Sockeye salmon that spawned in turbid waters along the shoreline of Tustumena Lake preferred locations adjacent to inlet tributaries or springs (Burger et al. 1995). Hyporheic flow in these areas may similarly remove sediments from the spawning substrate.

Spawning activity by sockeye salmon in glacially turbid tributaries coincided with cooling temperatures, lower water levels, and a dramatic decrease in the concentration of suspended sediment in the water. The similar timing of spawning activity among glacier fed rivers in the watershed suggests an adaptive response to seasonal turbidity cycles. Jensen and Mathisen (1987) observed sockeye salmon generally migrate into glacial systems later than into clear systems. Such a behavioral adaptation would result in deposition of eggs on a decreasing turbidity cycle, thereby reducing adverse effects of fine sediments on embryo survival (Chapman 1988).

Ideally, 500 sockeye salmon should have been tagged and tracked to spawning locations to determine the relative contribution of each spawning aggregation (Thompson 1987). Given that 241 sockeye salmon were tracked to spawning locations in the Lake Clark watershed, the observed spawning distribution was representative of the true distribution with a confidence interval of 70% and with a maximum absolute error of 5% (Thompson 1987).

The impact of fine sediments on salmonid embryo survival in naturally turbid systems appears to have been overestimated and poorly understood. This is the first study to describe the relationship between spawn timing and the annual pattern of natural turbidity in a large glacial river. This finding has important implications for both management and further understanding of sockeye salmon evolution. Relative to management, it is likely that sockeye salmon exploit other glacial systems currently discounted as poor habitat. For example, initial surveys of the glacially turbid Tlikakila River in the Lake Clark watershed estimated that there was 0% available salmon spawning habitat (Demory et al. 1964). To determine the presence or absence of salmon in other turbid systems, biologists should either sample the mouth of glacial rivers prior to upstream migration or potential spawning habitats associated with clear water inputs. Relative to evolutionary history, sockeye salmon have recolonized much of the Pacific Rim since the Pleistocene glaciation (Wood 1995) and the behavioral adaptations observed in this study, e.g. spawning on a declining turbidity gradient and in regions associated with clear waters, could be the product of natural selection for migration timing that improves embryo survival in an otherwise harsh environment. If regular associations like this are verified in other glacial systems, it could help explain how sockeye salmon successfully colonized such environments post-glaciation (Wood 1995). This information collectively has important conservation and management implications ranging from proper escapement enumeration to protection of critical spawning and rearing habitat.

This study provides the first comprehensive examination of sockeye salmon spawning locations in the Lake Clark watershed. Spawning locations have historically been underestimated due to high glacial turbidity in some parts of the system. Prior to this research, it was unknown that 75% of the spawning locations were adjacent to private land (Figure 2.8). Now, National Park Service managers and private land owners can take proactive measures to conserve these habitats. The recognition and further understanding of salmon use of and adaptations to turbid habitats is important toward both effective fisheries management and understanding the evolutionary history of sockeye salmon.

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Literature Cited

Anderson, J. W. 1969. Bathymetric measurements of Iliamna Lake and Lake Clark, Alaska. University of Washington, Fisheries Research Institute Circular No. 69-17.

Barton, L. H. 1992. Tanana River, Alaska, fall chum samlon radio telemetry study. Alaska Department of Fish and Game, Fishery Research Bulletin No. 92-01, Anchorage, Alaska.

Brabets, T. P. 2002. Water quality of the Tlikakila River and five major tributaries to Lake Clark, Lake Clark National Park and Preserve, Alaska, 1999-2001. U.S. Geological Survey Water Resources Investigations Report 02-4127.

Burger, C. V., J. E. Finn, and L. Holland-Bartels. 1995. Pattern of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for population differentiation. Transactions of the American Fisheries Society 124:1-15.

Burger, C. V., R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times of two runs of Chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 42:693-700.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1-21.

Cousens, N. B., G. A. Thomas, D. G. Swann, and M. C. Healy. 1982. A review of salmon escapement estimation techniques. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1108.

Demory, R. L., R. F. Orrell, and D. R. Heinle. 1964. Spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. U.S. Fish and Wildlife Service Special Scientific Report No. 488.

Eiler J., D. N. Bonita, and R. F. Bradshaw. 1992. Riverine spawning by sockeye salmon in the Taku River, Alaska and British Columbia. Transactions of the American Fisheries Society 121:701-708.

Everest, F. H., R. L. Beschta, J. C. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 143-190 in E.O. Salo and T.W. Cundy, editors, Streamside Management: Forestry and Fishery Interactions. Institute of Forest Resources, University of Washington, Seattle, Washington.

Gilmer, D. S., L. M. Cowardin, R. L.Duval, L. M. Mechlin, C. W. Shaiffer, V. B. Kuechle. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U.S. Department of the Interior, Fish and Wildlife Service Resource Publication 140.

Groot, C., and L. Margolis. 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, British Columbia.

Hausel, D. A., and D. W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout (*Salvelinus fontinalus*). Transactions of the American Fisheries Society 105:57-63.

Jensen, K. A., and O. A. Mathisen. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983. Pages 101-109 in H.D. Smith, L. Margolis, and C. C. Wood, editors. Sockeye salmon (*Onchorhyncus nerka*) population biology and future management. Canadian Special Publication of Fisheries and Aquatic Sciences 96:101-109.

Jones, S. H., and Fahl, C. B. 1994. Magnitude and frequency of floods in Alaska and conterminuous basins of Canada: U.S. Geological Survey Water-Resources Investigations Report 93-4179.

Knudsen, E. E. 2000. Managing Pacific salmon escapements: the gaps between theory and reality. Pages 237-272 in E.E. Knudsen, C.R. Steward, D.D. Macdonald, J.E. Williams, and D.W. Reiser, editors. Sustainable fisheries management: Pacific salmon. Lewis Publishers, Boca Raton, Florida.

Koenings, J. P., R. D. Burkett, G. B. Kyle, J.A. Edmundson, and J. M. Edmundson. 1986. Trophic level responses to glacial meltwater intrusion in Alaskan lakes. Pages 179-194 in D.L. Kane, editor. Proceedings: cold regions hydrology symposium. American Water Resources Association, Bethesda, Maryland.

Koenings, J. P., R. D. Burkett, and J. M. Edmundson. 1990. The exclusion of limnetic cladocera from turbid glacier-meltwater lakes. Ecology 7:57-67.

Lloyd, D. S., J. P. Koenings, and J. D. LaPerriere. 1987. Effects of turbidity in fresh waters of Alaska. North American Journal of Fisheries Management 7:18-33.

Lorenz, J. M., and J. H. Eiler. 1989. Spawning habitat and redd characteristics of sockeye salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118:495-502.

Mathisen, O. A. 1962. The effects of altered sex ratios on the spawning of red salmon. Pages 137-248 in T.S.Y. Koo, editor. Studies of Alaska red salmon. University of Washington Press, Seattle, Washington.

Monan, G. E., J. H. Johnson, and G. F. Esterberg. 1975. Electronic tags and related tracking techniques aid in study of migrating salmon and steelhead trout in the Columbia River basin. U.S. National Marine Fisheries Service Marine Fisheries Review 37:9-15.

Morris, J. M. 1986. Subsistence production and exchange in the Iliamna Lake region, southwest, Alaska. Technical Paper Number 136. Alaska Department of Fish and Game, Juneau, Alaska.

Murphy, M. L., K. V. Koski, J. M. Lorenz, and J. F. Thedinga. 1997. Downstream migrations of juvenile Pacific salmon (Oncorhynhus spp.) in a glacial transboundary river. Canadian Journal of Fisheries and Aquatic Sciences 54:2837-2846.

National Park Service, Alaska Support Office, Land Resources Program Center. 2001. National Park Service land status – federal, state, native, and private. Anchorage, Alaska.

Parker, S. S., and G.R. Blair. 1987. Aerial surveys of sockeye salmon abundance on spawning grounds in the Lake Clark-Tazimina River watershed. University of Washington, Fisheries Research Institute FRI-UW-8703.

Phillips, R. W., R. L. Lantz, E. W. Claire, and J. R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104:461-466.

Ramstad, K. M., and C. A. Woody. 2003. Radio tag retention and mortality of adult sockeye salmon. North American Journal of Fisheries Management 23:978-982.

Regnart, J. R. 1998. Kvichak River sockeye salmon spawning ground surveys, 1955-1998. Alaska Department of Fish and Game, Regional Information Report 2A98-38.

Savereide, J. W. 2003. Inriver abundance, spawning distribution, and run timing of Copper River Chinook salmon in 2002. Alaska Department of Fish and Game, Fishery Data Series No. 03-21, Anchorage, Alaska.

Smith, H. D. 1964. The segregation of red salmon in the escapements to the Kvichak River system, Alaska. U.S. Fish and Wildlife Service Special Scientific Report – Fisheries 470.

Stickman, K., A. Baluta, M. McBurney, and D. Young. 2003. K'ezghlegh Nondalton traditional ecological knowledge of freshwater fish. Final Report FIS 01-075. U.S. Fish and Wildlife Service Office of Subsistence Management, Anchorage, Alaska.

Thompson, S. K. 1987. Sample size for estimating multinomial proportions. The American Statistician 41: 42-46.

Wilkens, A. X. 2002. The limnology of Lake Clark, Alaska. M.S. thesis. University of Alaska Fairbanks.

Winter, J. D. 1996. Advances in underwater biotelemetry. Pages 555-590 in B.R. Murphy, and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Wood, C. 1995. Life history variation and population structure in sockeye salmon. American Fisheries Society Symposium 17:195-216.

Woody, C. A., J. Nelson, and K. Ramstad. 2002. Clove oil as an anaesthetic for adult sockeye salmon: field trials. Journal of Fish Biology 60:340-347.

Woody, C. A. 2004. Population monitoring of sockeye salmon from Lake Clark and the Tazimina River, Kvichak River watershed, Bristol Bay, Alaska, 2000-2003. Final Report 01-095. U.S. Fish and Wildlife Service Office of Subsistence Management. Anchorage, Alaska.

Tables

Table 2.1. Characteristics of tributary inputs to Lake Clark. [From Wilkens (2002); based on data from Brabets (2002), May to October of 1999 – 2001].

Basin	Tributary	Type	Discharge (m^3/s)	Temperature (°C)	Suspended sediment (mg/L)	Basin area (km^2)
Upper	Chokotonk River	glacier-fed	7-62	0-10	9-211	436
Upper	Tlikakila River	glacier-fed	1-340	0-10	5-710	1,613
Upper	Currant Creek	glacier-fed	8-78	1-8	3-282	428
Middle	Kijik River	lake-fed	12-85	3-13	2-123	773
Middle	Tanalian River	lake-fed	5-168	5-14	1-5	532
Middle	Chulitna River	bog-fed	37-210	1-15	4-9	3,000
Lower	Lake Clark outlet	lake-fed	242-674	4-12	1-5	7,629

Table 2.2. Mid-eye to hypural length (mm) of tagged and untagged adult sockeye salmon captured at the outlet of Lake Clark, 2000 and 2001.

2000	Male		Female	
	Tagged	Untagged	Tagged	Untagged
Mean	510	510	484	479
Range	404-592	409-583	404-552	377-546
Standard error	4.1	5.0	4.0	4.0
n	93	81	82	187

2001	Male		Female	
	Tagged	Untagged	Tagged	Untagged
Mean	0	546	526	522
Range	0	409-616	415-591	411-511
Standard error	0	1.3	2.0	2.1
n	0	474	157	187

Table 2.3. Tagging and tracking summary for radio tagged adult sockeye salmon in Lake Clark watershed, 2000 and 2001.

	Number of salmon		
Category	2000	2001	Total
Tagged	175	157	332
Never located	8 (5%)	0	8 (2%)
Lost / no determination	33 (19%)	9 (6%)	42 (13%)
Tracked to spawning location	134 (76%)	148 (94%)	282 (85%)
Spawning Distribution			
Lake Clark spawning locations	99 (74%)	142 (96%)	241 (85%)
Downstream spawning locations	35 (26%)	6 (4%)	41 (15%)

Figures

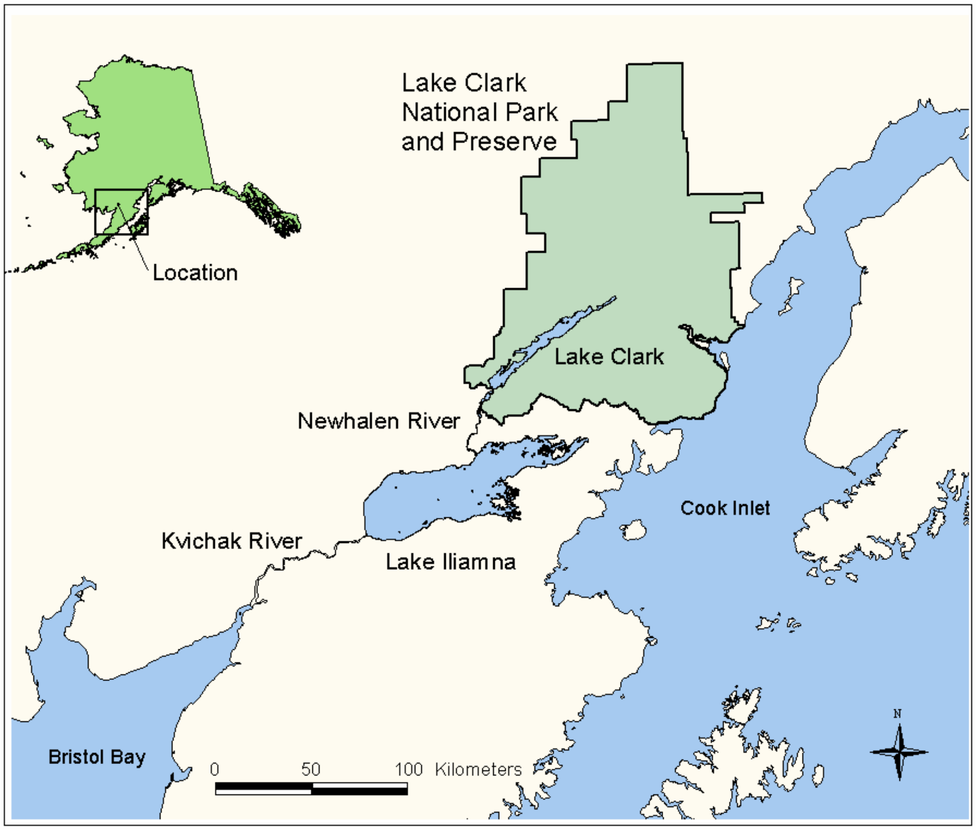


Figure 2.1. Location of Lake Clark relative to Bristol Bay, Alaska.

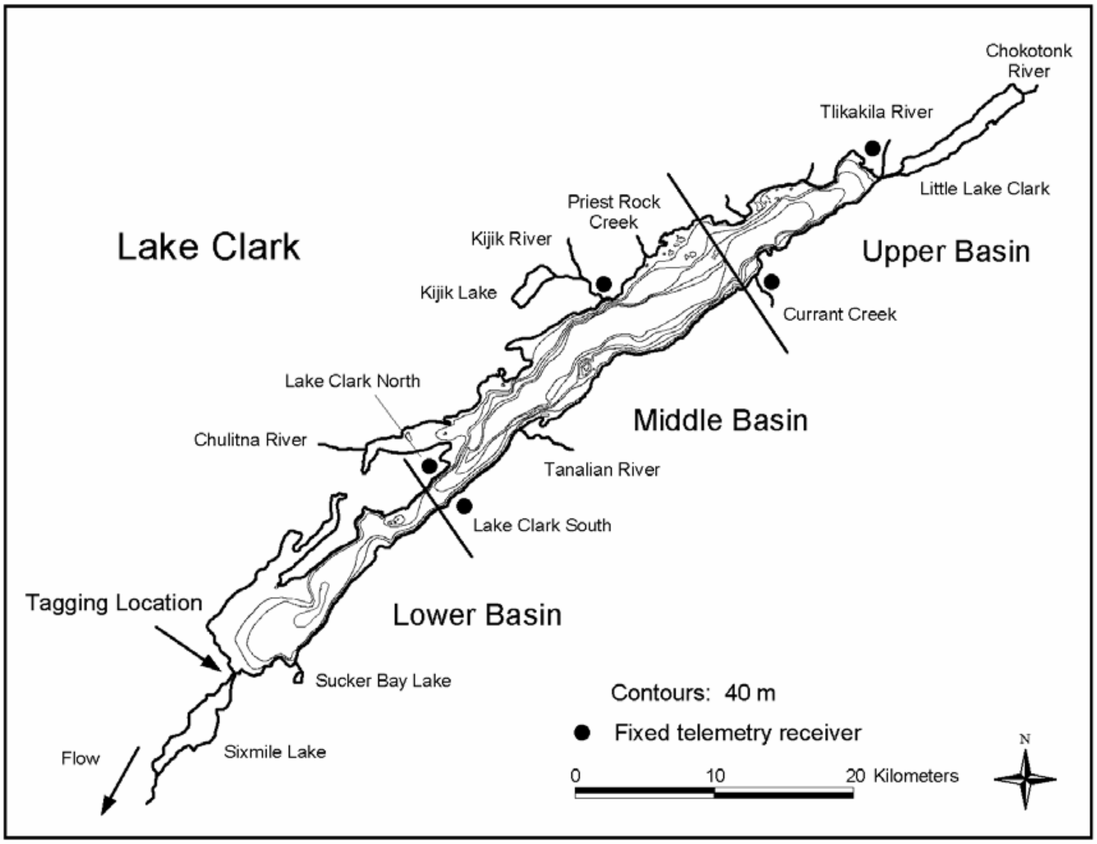


Figure 2.2. Location of lake basins, tributaries, tagging site, and fixed telemetry receivers in the Lake Clark watershed (contours redrawn from Anderson 1969). The receiver at Kijik River and Tlikakila River monitored fish passage in both 2000 and 2001. The Lake Clark North, Lake Clark South, and Currant Creek receivers monitored fish passage in 2001.

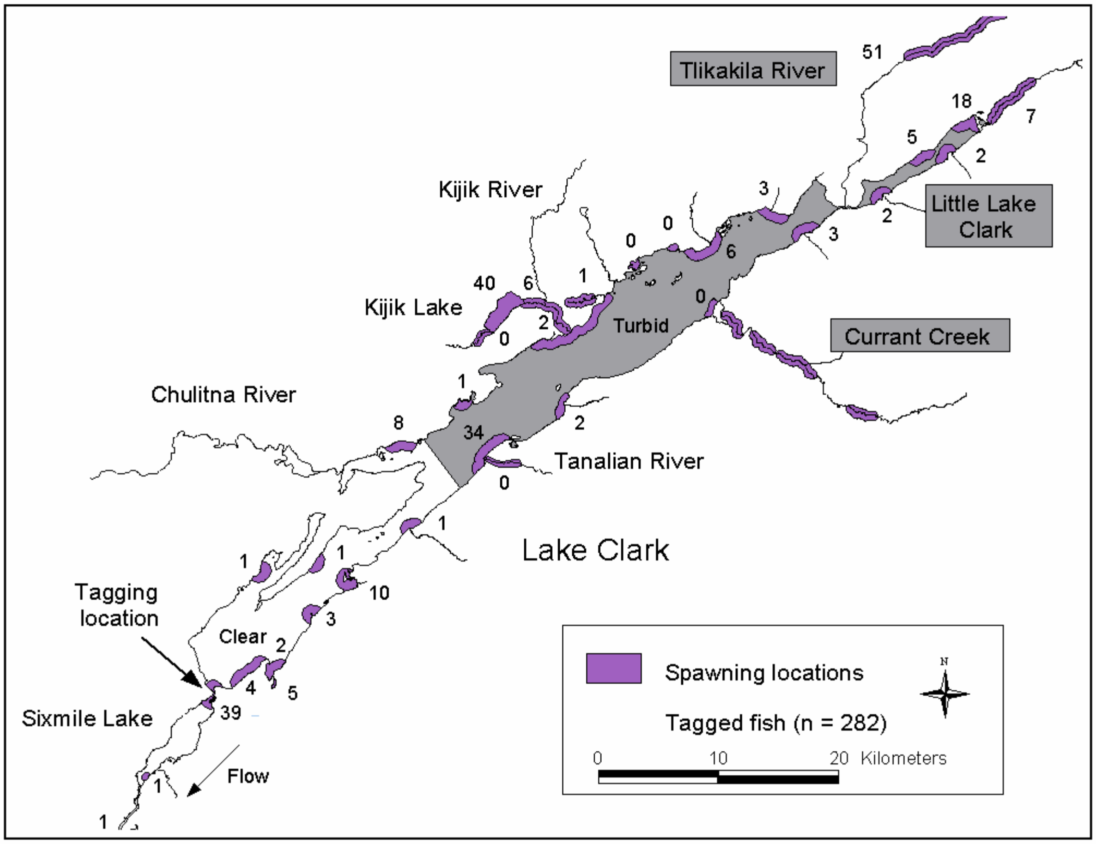


Figure 2.3. Spawning locations of radio tagged sockeye salmon in the Lake Clark watershed, 2000 and 2001. The number of tagged fish per spawning location is indicated. Five spawning locations (labeled with a 0) were located by visual observation or seining. Shaded areas indicate glacially turbid waters with limited visibility.

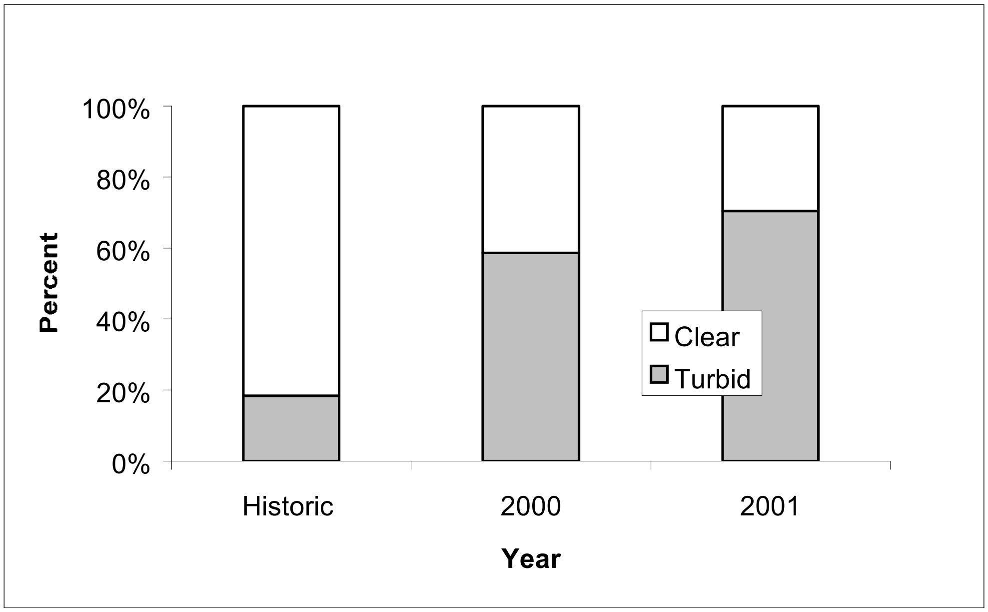


Figure 2.4. Proportion of radio tagged salmon that returned to clear (< 5 NTU) and turbid (≥ 5 NTU) spawning locations in the Lake Clark watershed. Historic data reflect the proportion of salmon counted in clear and turbid habitats during aerial surveys from 1968 to 1983 (Regnart 1998).

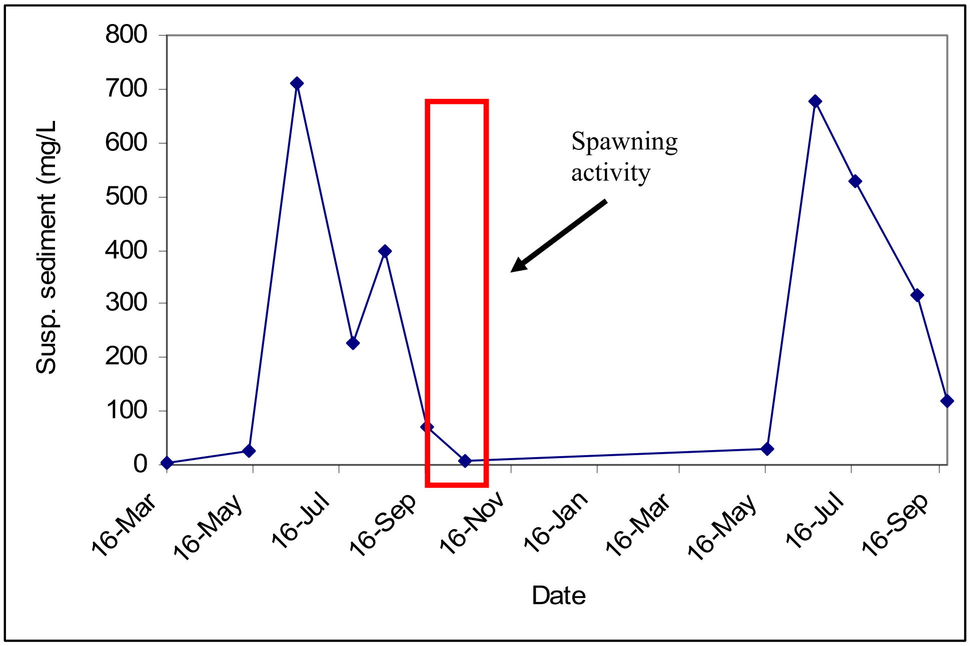


Figure 2.5. Sockeye salmon spawning activity and suspended sediment concentration in the Tlikakila River by date (data redrawn from Brabets 2002).

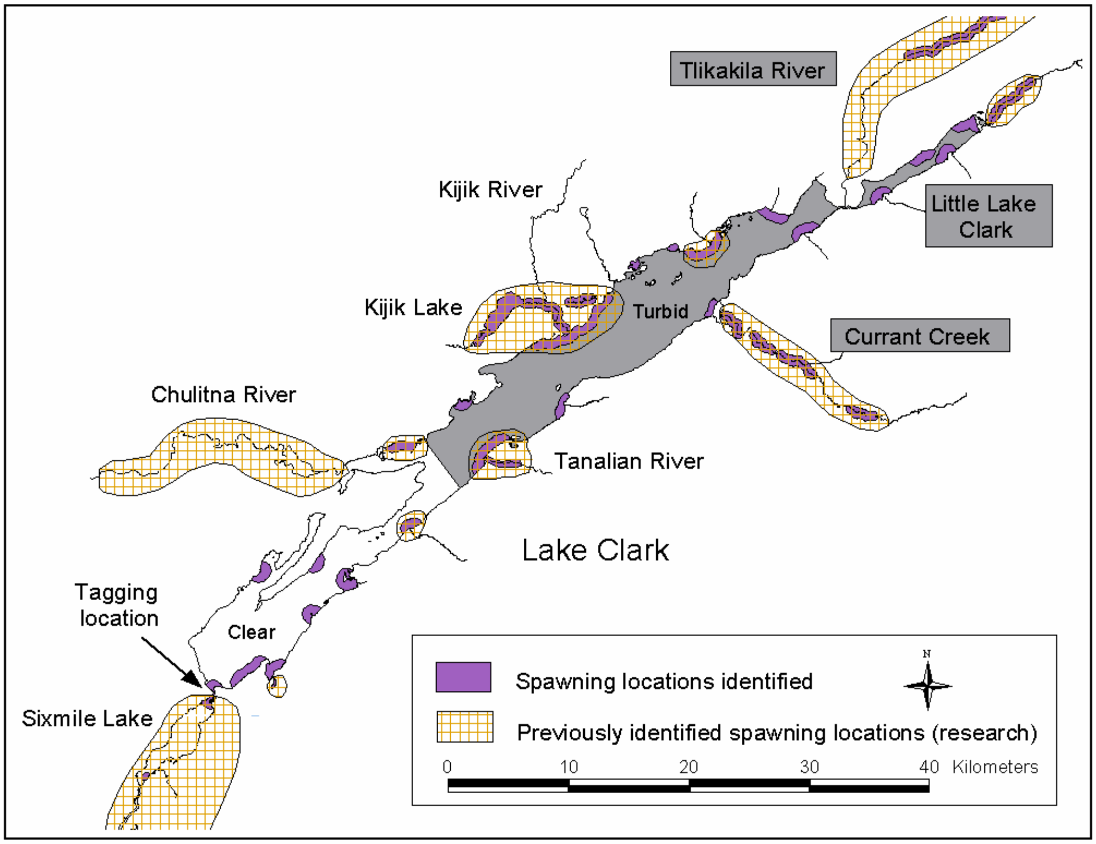


Figure 2.6. Spawning locations identified during this study and during historic aerial surveys and previous tagging studies (Smith 1964, Jensen and Mathisen 1987, Parker and Blair 1987, Regnart 1998). Shaded areas indicate glacially turbid waters with limited visibility.

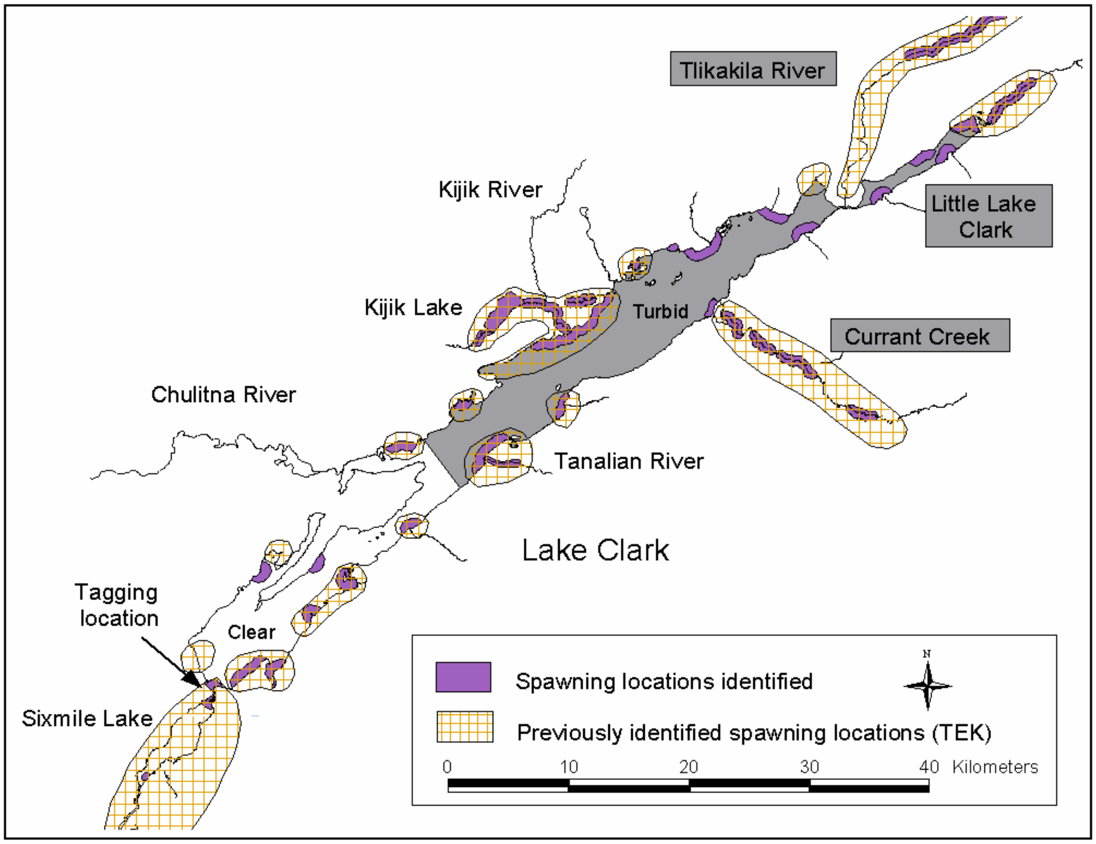


Figure 2.7. Spawning locations identified during this study and during interviews with local residents (traditional ecological knowledge (TEK); Morris 1986, Stickman et al. 2003). Shaded areas indicate glacially turbid waters with limited visibility.

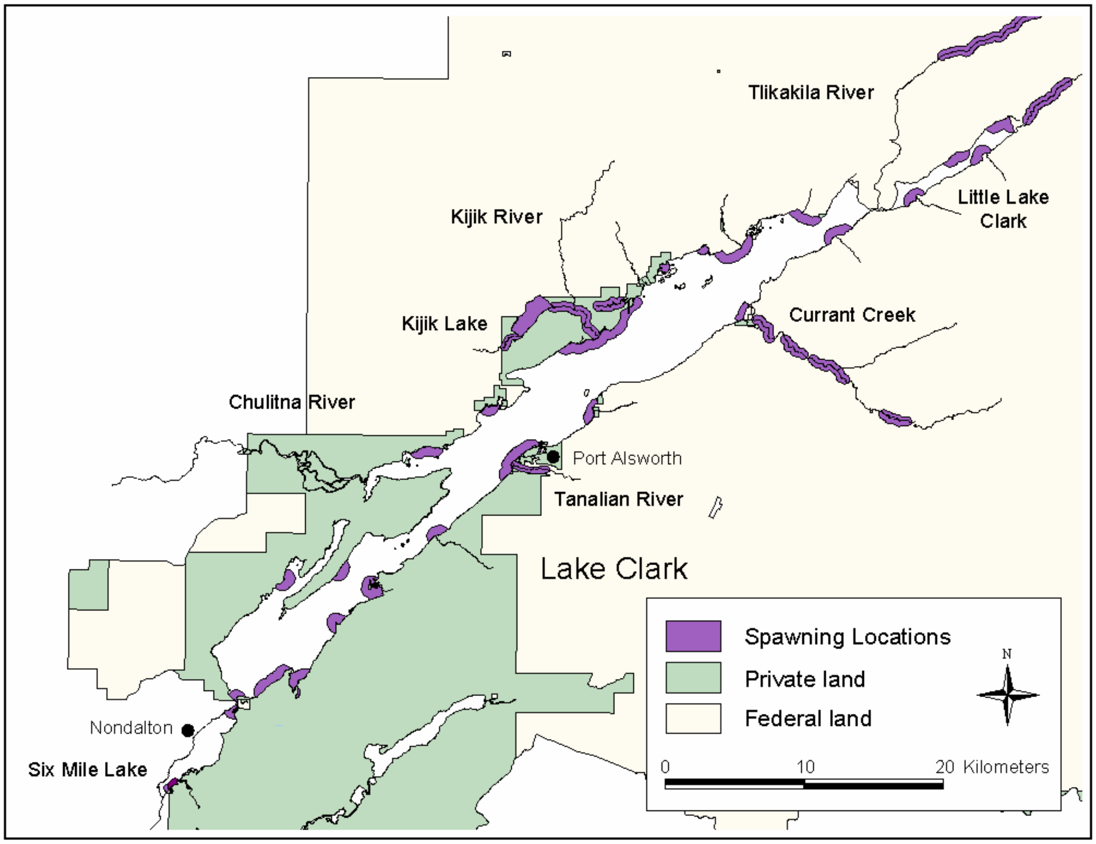
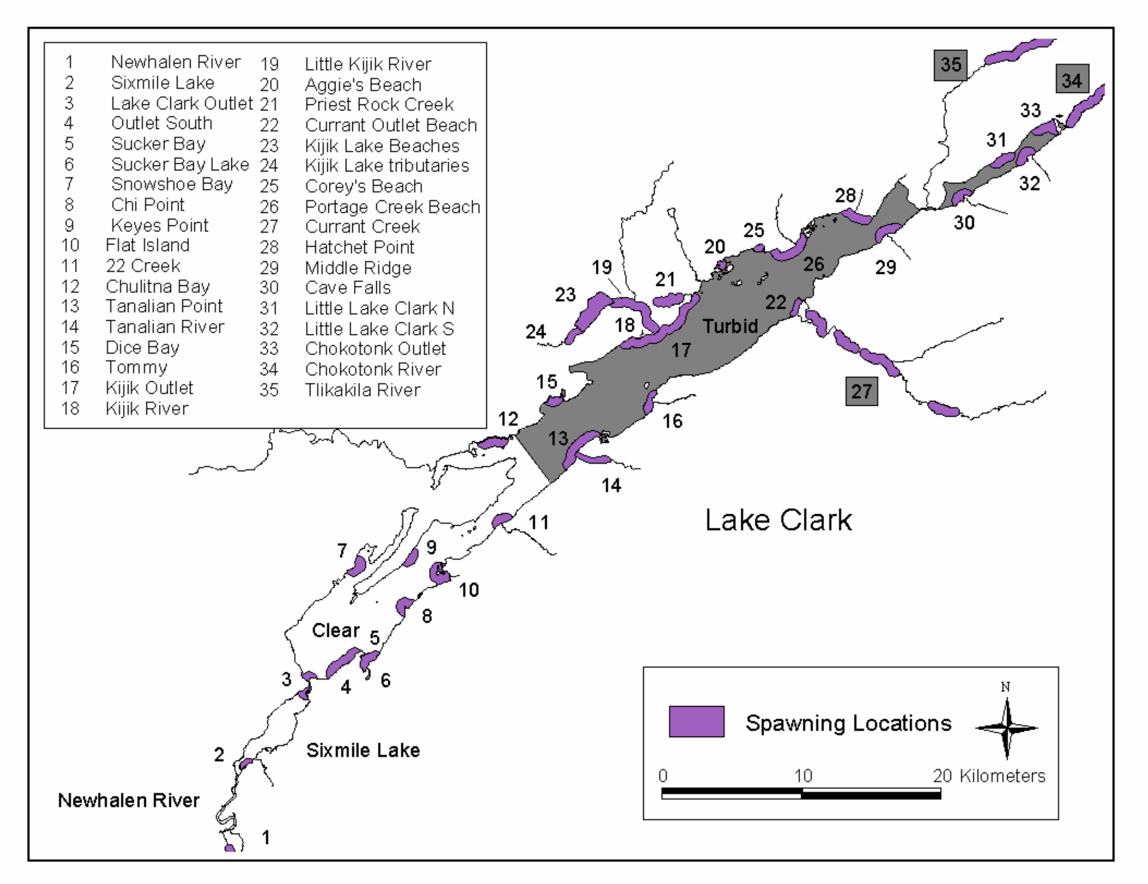


Figure 2.8. Spawning locations relative to land ownership within the Lake Clark watershed (National Park Service 2001).

Appendices



Appendix 2.A. Key to spawning locations identified during this study. Numbers indicate ID of spawning locations. Shaded areas indicate glacially turbid waters with limited visibility.

Appendix 2.B. Distribution of radio tagged salmon within the Lake Clark watershed. Ecotypes were beach (Bch) and tributary (Trib) spawning habitats. Water was clear (Clr; < 5 NTU) or glacially turbid (Tur; ≥ 5 NTU) and was measured at time of peak spawning activity. Distance was calculated from the tagging site at the lake outlet. Spawning activity documented during previous scientific research (Hist) and by traditional ecological knowledge (TEK) was recorded as present (Y) or not present (N). Private land data were collected in other studies and were recorded as present (Y) or not present (N).

												Number of tagged fish					
ID	Drainage	Specific location	Latitude	Longitude	Eco-type	Water	Spawning activity	Distance (km)	Hist.	TEK	Private land	2000		2001		Total	
4	Lake Clark	Outlet South	60.02690	-154.71336	Bch	Clr	9/1-9/30	4	N	N	Y	1	(1%)	3	(2%)	4	(2%)
5	Lake Clark	Sucker Bay	60.03579	-154.65733	Bch	Clr	9/1-9/30	8	Y	Y	Y	1	(1%)	1	(1%)	2	(1%)
6	Sucker Bay Lake	Sucker Bay Lake	60.02155	-154.66364	Bch	Clr	8/25-9/15	9	Y	Y	Y	3	(3%)	2	(1%)	5	(2%)
8	Lake Clark	Chi Point	60.07556	-154.60422	Bch	Clr	9/1-9/30	12	N	Y	Y	2	(2%)	1	(1%)	3	(1%)
9	Lake Clark	Keyes Point	60.11470	-154.60369	Bch	Clr	9/1-9/30	15	N	N	Y	0		1	(1%)	1	(0.4%)
10	Lake Clark	Flat Island	60.09811	-154.54078	Bch	Clr	9/1-10/15	16	N	Y	Y	3	(3%)	7	(5%)	10	(4%)
11	Lake Clark	22 Creek	60.14133	-154.45934	Bch	Clr	9/15-9/30	22	Y	Y	Y	1	(1%)	0		1	(0.4%)
12	Lake Clark	Chulitna Bay	60.20498	-154.47635	Bch	Clr	9/15-10/15	30	Y	Y	Y	2	(2%)	5	(4%)	7	(3%)
13	Lake Clark	Tanalian Point	60.19395	-154.35082	Bch	Tur	9/15-10/15	31	Y	Y	Y	17	(17%)	17	(12%)	34	(14%
15	Lake Clark	Dice Bay	60.23489	-154.38721	Bch	Tur	9/1-9/30	33	N	Y	Y	0		1	(1%)	1	(0.4%)
16	Lake Clark	Tommy	60.22857	-154.23373	Bch	Tur	9/15-10/15	38	N	Y	Y	2	(2%)	0		2	(1%)
17	Lake Clark	Kijik Outlet	60.28075	-154.26490	Bch	Tur	9/15-10/15	41	Y	Y	Y	12	(12%)	7	(5%)	19	(8%)
18	Kijik Lake	Kijik River	60.29787	-154.24330	Trib	Clr	9/15-10/15	45	Y	Y	Y	2	(2%)	0		2	(1%)
19	Kijik Lake	Little Kijik River	60.30790	-154.29328	Trib	Clr	9/15-10/15	49	Y	Y	Y	5	(5%)	1	(1%)	6	(2%)
21	Priest Rock Creek	Priest Rock Creek	60.30847	-154.22873	Trib	Clr	9/25-10/15	52	Y	Y	Y	0		1	(1%)	1	(0.4%)
23	Kijik Lake	Kijik Lake	60.28703	-154.34478	Bch	Clr	9/15-10/31	52	Y	Y	Y	21	(21%)	19	(13%)	40	(17%)
26	Lake Clark	Portage Creek	60.34586	-154.02989	Bch	Tur	9/15-10/15	54	Y	N	Y	3	(3%)	3	(2%)	6	(2%)
27	Currant Creek	Currant Creek	60.22922	-153.80073	Trib	Tur	9/15-9/30	57	Y	Y	N	2	(2%)	3	(2%)	5	(2%)
28	Lake Clark	Hatchet Point	60.37455	-153.91412	Bch	Tur	9/15-10/15	62	N	N	Y	0		3	(2%)	3	(1%)

- Continued -

Appendix 2.B. (page 2 of 2)

												Number of tagged fish					
ID	Drainage	Specific location	Latitude	Longitude	Eco-type	Water	Spawning activity	Distance (km)	Hist.	TEK	Private land	2000		2001		Total	
29	Lake Clark	Middle Ridge	60.36077	-153.86192	Bch	Tur	9/15-10/15	64	N	N	N	1	(1%)	2	(1%)	3	(1%)
29	Little Lake Clark	Cave Falls	60.38569	-153.75299	Bch	Tur	9/15-10/15	71	N	N	N	0		2	(1%)	2	(1%)
31	Little Lake Clark	Little Lake Clark N	60.41835	-153.69658	Bch	Tur	9/15-10/15	76	N	N	N	0		5	(4%)	5	(2%)
32	Little Lake Clark	Little Lake Clark S	60.41751	-153.65577	Bch	Tur	9/15-10/15	77	N	N	N	0		2	(1%)	2	(1%)
33	Little Lake Clark	Chokotonk Outlet	60.44374	-153.62181	Bch	Tur	9/15-10/31	80	N	Y	N	2	(2%)	16	(11%)	18	(7%)
34	Little Lake Clark	Chokotonk River	60.46698	-153.54231	Trib	Tur	9/15-10/15	86	Y	Y	N	1	(1%)	6	(4%)	7	(3%)
35	Tlikakila River	Tlikakila River	60.55374	-153.50670	Trib	Tur	9/15-10/15	98	Y	Y	N	18	(18%)	33	(23%)	51	(21%)
	Total:											99		142		241	

Appendix 2.C. Distribution of radio tagged salmon that migrated downstream of the tagging site. Ecotypes were beach (Bch) and tributary (Trib) spawning habitats. Water was clear (Clr; < 5 NTU) or glacially turbid (Tur; ≥ 5 NTU) and was measured at time of peak spawning activity. Distance was calculated from the tagging site at the lake outlet. Spawning activity documented during previous scientific research (Hist) and by traditional ecological knowledge (TEK) was recorded as present (Y) or not present (N). Private land data were collected in other studies and were recorded as present (Y) or not present (N).

												Number of tagged fish		
ID	Drainage	Specific location	Latitude	Longitude	Eco-type	Water	Spawning activity	Distance (km)	Hist.	TEK	Private land	2000	2001	Total
1	Newhalen River	Horseshoe Bend	59.88246	-154.87095	Trib	Clr		19	Y	Y		0	1	1
2	Sixmile Lake	Fish Camp	59.95490	-154.85325	Bch	Clr		8	Y	Y		0	1	1
3	Sixmile Lake	Lake Clark outlet	60.01966	-154.75755	Trib	Clr	8/25-9/15	1	N	Y	N	35	4	39
	Total:											35	6	41

Appendix 2.D. Spawning locations within the Lake Clark watershed identified by visual observation or seining. Ecotypes were beach (Bch) and tributary (Trib) spawning habitats. Water was clear (Clr; < 5 NTU) or glacially turbid (Tur; ≥ 5 NTU) and was measured at time of peak spawning activity. Distance was calculated from the tagging site at the lake outlet. Spawning activity documented during previous scientific research (Hist) and by traditional ecological knowledge (TEK) was recorded as present (Y) or not present (N). Private land data were collected in other studies and were recorded as present (Y) or not present (N).

												Number of tagged fish		
ID	Drainage	Specific location	Latitude	Longitude	Eco-type	Water	Spawning activity	Distance (km)	Hist.	TEK	Private land	2000	2001	Total
14	Tanalian River	Tanalian River	60.18582	-154.27404	Trib	Clr	9/15-9/30	31	Y	Y	Y	0	0	0
20	Lake Clark	Aggie's Beach	60.33869	-154.13223	Bch	Tur	9/15-10/15	49	N	Y	Y	0	0	0
22	Lake Clark	Currant Outlet Beach	60.29969	-154.01009	Bch	Tur	9/15-10/15	52	N	N	Y	0	0	0
25	Lake Clark	Corey's Beach	60.35162	-154.06406	Bch	Tur	9/15 - 10/15	53	N	N	Y	0	0	0
24	Kijik Lake	Kijik Lake Tributaries	60.28577	-154.34395	Trib	Clr	9/25-10/15	53	Y	Y	Y	0	0	0
	Total:											0	0	0

Conclusions

- This study provides one of the first detailed examinations of in-lake spawning migrations of sockeye salmon and provides the first comprehensive survey of spawning locations within this drainage. Sockeye salmon spawning locations in the Lake Clark watershed have historically been underestimated due to high glacial turbidity in some parts of the system.

- Radio tagged salmon migrated faster and more directly to spawning locations in tributary rivers and lakes than to Lake Clark beaches. Salmon may migrate more precisely to tributaries simply because they can detect the unique odors and flow of tributaries easier than beach spawning habitats. The fastest and most directed migrations were to clear-water tributary lakes. It is likely that salmon migrate more precisely to these locations because they reared and imprinted on the odors of these lakes rather than Lake Clark.

- After entering Lake Clark, sockeye salmon generally migrated to a basin of the lake that was within 15 km of their final spawning location. Within a lake basin, some salmon made extensive movements until spawning activity began. These excessive movements could indicate that salmon were searching for natal sites. Alternatively, salmon may know the location of natal sites but wait to select a nest site and spawn.

- Directed migrations to tributaries suggest that tributaries spawners are distinct populations and should be monitored and managed separately. Sucker Bay Lake, Kijik Lake, and Priest Rock Creek are genetically distinct populations (Ramstad et al. 2004). Within Lake Clark, there appears to be population structuring within lake basins.

- Radio telemetry and visual observations identified 33 spawning locations within the Lake Clark watershed. Eighteen new spawning locations were identified compared to previous scientific research whereas ten new locations were identified compared to traditional local knowledge.

- Approximately two-thirds of the radio tagged salmon returned to spawning locations in turbid habitats. Data collected during this study further suggest that turbidities as low as 5 NTU are sufficient to limit the accurate assessment of the spawning activity.

- Upstream migration and spawning activity in glacially turbid waters coincided with cooling temperatures, lower water levels, and decreased suspended sediment concentrations. Delayed migration and spawning likely limits the adverse effects of silt and fine sediments on egg and embryo survival.

- More than two thirds of spawning locations identified could be impacted by future development on private land.

Recommendations

- The migration of sockeye salmon through lakes should be examined further. Slow and imprecise movements within lakes could indicate that animals are straying from natal sites. Coupling radio telemetry data with genetic research in future studies could help determine the origin of radio tagged salmon.

- Further work is needed to more precisely define spawning habitat boundaries in the Lake Clark drainage. Hydroacoustics could be used to provide a better estimate of spawning boundaries and delineate critical spawning habitat.

- Radio telemetry should be repeated in years of greater sockeye salmon abundance. Current results represent spawning distribution during years of relatively low abundance, and it is likely that additional spawning areas would be identified during years of greater abundance.

- Because many spawning locations could be impacted by future development on private land, the National Park Service should be proactive in educating and working with private landowners to ensure responsible development and prevent degradation of critical spawning habitats.

Literature Cited

Alaska Department of Fish and Game (ADFG). 2002. Alaska Department of Fish and Game Division of Commercial Fisheries annual management report 2001. 2001 Bristol Bay Area Region Information Report No. 2A02-18, Anchorage, Alaska.

ANILCA. 1980. Alaska National Interest Lands Conservation Act. 16 U.s.C. 3101 et seq. (1988), Dec 2 1980, Stat. 2371, Pub. L. pages 96-487.

Burger, C. V., J. E. Finn, and L. Holland-Bartels. 1995. Pattern of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for population differentiation. Transactions of the American Fisheries Society 124:1-15.

Burger, C. V., R. L. Wilmot, and D. B. Wangaard. 1985. Comparison of spawning areas and times of two runs of Chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 42:693-700.

Eiler J., D. N. Bonita, and R. F. Bradshaw. 1992. Riverine spawning by sockeye salmon in the Taku River, Alaska and British Columbia. Transactions of the American Fisheries Society 121:701-708.

Kline, T. C., Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, P. L. Parker, and R. S. Scalan. 1993. Recycling of elements transported upstream by runs of Pacific salmon: evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Canadian Journal of Fish and Aquatic Sciences 50:2350-2365.

National Park Service, Alaska Support Office, Land Resources Program Center. 2001. National Park Service land status – federal, state, native, and private. Anchorage, Alaska.

Poe, P. H., and D. E. Rogers. 1984. 1984 Newhalen River adult salmon enumeration program. University of Washington, Fisheries Research Institute Final Report - Contract 14007-00011. Stone and Webster Engineering Corporation. FRI-UW-8415.

Unrau, H. D. 1992. Lake Clark National Park and Preserve historic resource study. U.S. Department of Interior. National Park Service, Anchorage, Alaska.

Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489-497.

Woody, C. A. 2004. Population monitoring of sockeye salmon from Lake Clark and the Tazimina River, Kvichak River watershed, Bristol Bay, Alaska, 2000-2003. Final Report 01-095. U.S. Fish and Wildlife Service Office of Subsistence Management, Anchorage, Alaska.