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Dynamic in-lake spawning migrations by female sockeye salmon

Young DB, Woody CA. Dynamic in-lake spawning migrations by female sockeye salmon.
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Abstract – Precise homing by salmon to natal habitats is considered the primary mechanism in the evolution of population-specific traits, yet few studies have focused on this final phase of their spawning migration. We radio tagged 157 female sockeye salmon (*Oncorhynchus nerka*) as they entered Lake Clark, Alaska, and tracked them every 1–10 days to their spawning locations. Contrary to past research, no specific shoreline migration pattern was observed (e.g., clockwise) nor did fish enter a tributary unless they spawned in that tributary. Tributary spawning fish migrated faster (mean = 4.7 km·day^{-1}, SD = 2.7, vs. 1.6 km·day^{-1}, SD = 2.1) and more directly (mean linearity = 0.8, SD = 0.2, vs. 0.4, SD = 0.2) than Lake Clark beach spawning fish. Although radio-tagged salmon migrated to within 5 km of their final spawning location in an average of 21.2 days (SD = 13.2), some fish migrated five times the distance necessary and over 50 days to reach their spawning destination. These results demonstrate the dynamic nature of this final phase of migration and support studies indicating a higher degree of homing precision by tributary spawning fish.

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Key words: sockeye salmon; migration; lake; radio telemetry

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Introduction

Pacific salmon (*Oncorhynchus* spp.) generally return to their natal habitats to spawn, a behaviour referred to as 'homing.' The homing process includes long directed migrations through the ocean where salmon may rely, in part, on the earth's magnetic field to orient towards home (Quinn & Groot 1983; Quinn 1984; Ogura & Ishida 1995). When salmon migrate into freshwater, they rely primarily on olfactory cues imprinted during their early life history (Hasler & Scholz 1983; Dittman & Quinn 1996) to navigate to natal lakes and streams. Sockeye salmon (*Oncorhynchus nerka*) are thought to be 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; Quinn 2005). While many studies have focused on the oceanic (French et al. 1976; Groot & Quinn 1987) and riverine (Killick 1955; Eiler et al. 1992) phases of homing in sockeye salmon, few have focused on the final in-lake migration to spawning habitats.

Past research provides some information on this final in-lake phase of migration. Burger et al. (1995) found that radio-tagged sockeye salmon migrated in a clockwise pattern in Tustumena Lake, Alaska, and that 80% of tagged fish migrated directly to spawning habitats, whereas 20% of tagged fish entered one tributary prior to spawning at a different location. Sockeye salmon displaced from spawning grounds in lake systems tend to migrate along lake shorelines and generally return to their original capture locations (Hartman & Raleigh 1964; Varnavsky & Varnavskaya 1985; Blair & Quinn 1991; Ueda et al. 1998). Blair & Quinn (1991) found that sockeye salmon displaced from tributary spawning habitats had greater site fidelity than those displaced from beaches.

Information on final in-lake migration dynamics are currently lacking in the sockeye salmon literature. Such information is essential to managers of in-lake

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subsistence fisheries, to those charged with mitigation of development in and near sockeye salmon lakes and for those who study salmonid homing and evolution. Here, we focus on the final in-lake migration of sockeye salmon returning to diverse spawning habitats within a pristine ecosystem. Specific objectives were to test whether sockeye salmon exhibit specific migration patterns to different spawning areas and to examine how rapidly and directly they migrate to spawning habitats.

Materials and methods

Study site

The Lake Clark watershed (60°01′N, 154°45′W) is located within the Kvichak River drainage in southwest Alaska (Fig. 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 66-km long and 5- to 8-km wide with an average depth of 103 m, maximum depth of 262 m and a drainage area of 7620 km^2 (Anderson 1969). Glaciers, steep mountains, glacial rivers and high precipitation (average 203 cm annually) characterise the upstream end of the watershed while lowland tundra, small mountains, clear and organically stained streams and low precipitation (average 64 cm annually) characterise the downstream end (Jones & Fahl 1994; Brabets 2002). Six primary tributaries empty into Lake Clark with glacier-fed tributaries providing approximately half of the annual water budget (Fig. 1; Table 1; Brabets 2002). Run off from glacial tributaries is the highest between June and September and creates a seasonal turbidity gradient along the length of Lake Clark from the turbid (~10 NTU) upstream to the clear (≤2 NTU) downstream (Brabets 2002; Wilkens 2002). The watershed is currently pristine with one small permanent community (population <200) along the lakeshore. Between 2000 and 2003, counting towers on the Newhalen River estimated an average escapement of 216,000 sockeye salmon to Lake Clark annually (Woody 2004).

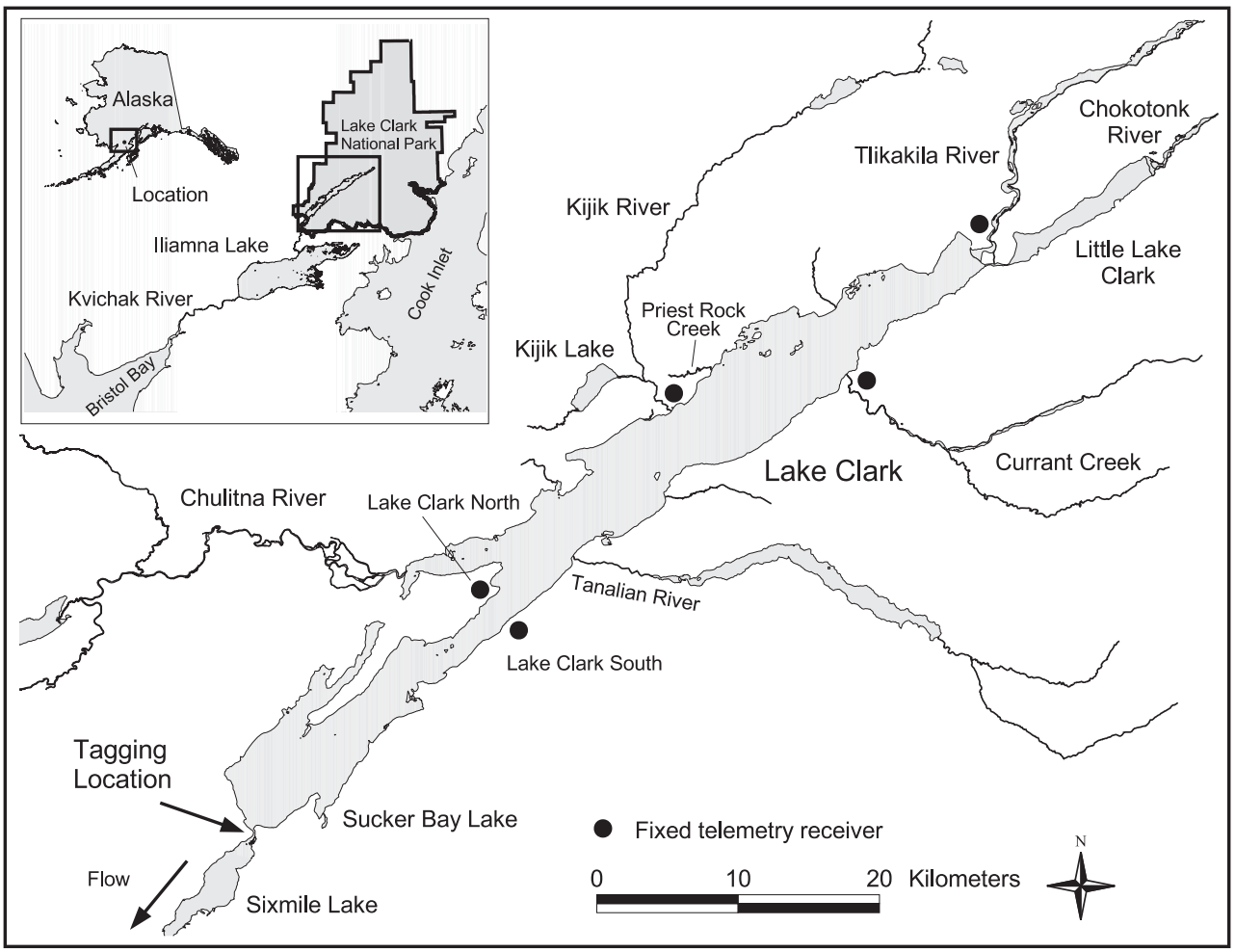

Fig. 1. Location of tributaries, tagging site and fixed telemetry receivers in the Lake Clark watershed.

Table 1. Ranges in discharge and selected water-quality constituents for major tributaries to Lake Clark, 1999–2001. [Based on data from Brabets (2002).]

Tributary	Source	Discharge ($m^3 \cdot s^{-1}$)	Temperature (°C)	Suspended sediment ($mg \cdot l^{-1}$)	Basin area (km^2)
Lake Clark outlet	Lake fed	242–674	4–12	1–5	7629
Chulitna River	Bog fed	37–210	1–15	4–9	3000
Tanalian River	Lake fed	5–168	5–14	1–5	532
Kijik River	Lake fed	12–85	3–13	2–123	773
Currant Creek	Glacier fed	8–78	1–8	3–282	428
Tlikakila River	Glacier fed	1–340	0–10	5–710	1613
Chokotonk River	Glacier fed	7–62	0–10	9–211	436

Radio-tagging, -tracking and telemetry equipment

Migrating adult female sockeye salmon were captured at the outlet of Lake Clark (Fig. 1) with nylon beach seines (62 m × 2.4 m–3.7 m; 10.2 cm mesh) and radio tagged throughout the run (15 July to 9 August 2001). Only females were tagged because they exhibit stronger spawning site fidelity than males (Mathisen 1962; Foote 1990), and because a companion study was focused on proportional distribution among spawning habitats (Young 2004). Fish were captured between 08:00 and 19:59 hours with 1-h fishing sessions determined using a random number table. Fish were not tagged at night (between 20:00 and 07:59 hours), because >90% of sockeye salmon migrate into Lake Clark during the day (Poe & Rogers 1984; USGS unpublished data). Tags were proportionally distributed throughout the run based on daily salmon abundance estimated from tower counts made 10 km downstream (Poe & Rogers 1984; Woody 2004); we tagged approximately 10 fish·day^{-1} during large migration periods (>10,000 fish·day^{-1}) and 5 fish·day^{-1} during smaller migration periods.

Radio-tagging protocols followed Eiler et al. (1992) and Burger et al. (1995). Captured sockeye salmon were placed in a submerged tagging cradle, identified as male or female and measured from mid-eye to hypural plate. Anaesthesia was not used during the tagging procedure. A glycerine-coated radio tag was inserted into the stomach of a subset of the captured female salmon using a 6-mm diameter PVC tube (Monan et al. 1975; Burger et al. 1995), with the antenna protruding out of the fish mouth. After tagging, fish were placed in a mesh holding pen (1.5 m × 1.5 m × 1.5 m with 2.5-cm mesh) to recover and were released when they could swim away on their own volition. The tagging procedure took, on average, less than 1 min.

Tagged fish were tracked every 1–10 days using fixed-wing aircraft or boats and 24 h·day^{-1} at fixed radio telemetry receivers (Fig. 1). Aerial surveys were flown along the shoreline of Lake Clark and its tributaries at an altitude between 200 and 300 m and airspeed between 100 and 130 kph. Boat tracking was conducted around the lake perimeter and islands approximately 300 m offshore and at a maximum speed of 30 kph. During aerial and boat-tracking events, a global positioning system receiver recorded the location where a tagged fish was detected. Fish were detected within 1 km of actual positions during aerial surveys and within 400 m during boat surveys based on field tests with planted transmitters (USGS unpublished data).

Radio telemetry equipment consisted of high-frequency (149–150 MHz) VHF radio tags, scanning receivers and 4-element Yagi and H antennas (Lotek Engineering Inc., Newmarket, ON, Canada). Digitally coded radio tags, model MCFT-3A (Lotek Wireless Inc., Newmarket, ON, Canada), measured 16 mm × 46 mm and weighed 15.6 g, which was less than 2% of body weight of tagged fish as generally recommended (Winter 1996). Radio tags transmitted every 2 s, 24 h·day^{-1} with a tag life of approximately 380 days.

A companion study examined radio tag retention and tag-related mortality (Ramstad & Woody 2003). During this study, overall tag retention in sockeye salmon was high [0.98, 95% confidence interval (CI): 0.92–1.00] and mortality of tagged salmon (0.02, 95% CI: <0.01–0.08) was low and similar to that of untagged controls (0.03, 95% CI: <0.01–0.15).

Data analyses

Data collected during radio-tracking events and at fixed telemetry receivers were condensed for data analyses. If a fish was detected multiple times during an aerial or boat-tracking event, the record with the highest signal strength (0.25 dB resolution) was selected. Data collected at fixed telemetry receivers were condensed to one record per fish for a 24-h period using the signal strength criterion. Six radio-tagged fish that migrated to spawning locations downstream of the tagging site were excluded, because they did not enter Lake Clark.

Five measures were derived to characterise the in-lake migration of female sockeye salmon including nearshore/offshore migration, travel time (days), net speed (km·day^{-1}), linearity and arrival date at

spawning locations. 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. Telemetry receivers located along the north and south shore of Lake Clark (Fig. 1) monitored the nearshore and offshore movements of radio-tagged sockeye salmon between 16 July and 12 August 2001. These receivers detected fish passage within 400 m of the lakeshore based on tests with planted transmitters to depths of 5 m (USGS unpublished data). Radio-tagged salmon detected by receivers were considered to have migrated along the shoreline, whereas fish that were not detected but subsequently located up-lake were considered to have travelled offshore. Travel time was estimated as the number of days between tagging and arrival at a spawning location. Net speed of migration was estimated as the distance to a spawning location divided by travel time. Linearity, a measure of how straight a course was travelled (Batschelet 1981), was estimated as the distance to a spawning location divided by the straight-line distance between all relocation data points. Distances between successive positions were determined with the Animal Movement Analyst Extension (Hooge & Eichenlaub 2000) for ArcView (Environmental Systems Research Institute, Inc., Redlands, CA, USA) geographic information system. 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. Arrival date at a spawning location was calculated with the equation: $AD = (D + PD)/2$, where AD is the arrival date, D the day a fish was first detected at a spawning location and PD the previous day a fish was detected. One-way analysis of variance (ANOVA, SPLUS software version 6.0; Lucent Technologies Inc., Murray Hill, NJ, USA) was used to assess differences in mean travel time, migration speed and linearity because of spawning habitat. Spawning habitats were either tributary rivers and lakes or Lake Clark beaches (LC).

Migration timing into tributaries and the number of days female salmon milled at tributary mouths were estimated using both radio-tracking and fixed telemetry receiver data. Receivers located on Kijik River, Currant Creek and Tlikakila River (Fig. 1) determined the date that tagged fish migrated upstream. The date of river entry into tributaries without a fixed telemetry receiver was estimated with the equation: $RE = (D + PD)/2$, where RE is the date of river entry, D the day a fish was first detected in a tributary and PD the previous day detected. The number of days fish milled at the mouth of a tributary was estimated with the equation: $MD = RE - AD$, where MD is milling days, RE the recorded or estimated date of river entry and AD the arrival date at the tributary mouth. Two-way analysis of variance was used to assess the mean migration timing into tributaries because of 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

We tracked 142 of 157 radio-tagged female sockeye salmon to spawning locations within the Lake Clark watershed between late July and early September 2001. Six salmon migrated to spawning locations outside the study area and 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 relocated 17.7 times (SD = 5.7, range: 7–33) with over 2500 relocations made during the study. After tagging, female sockeye salmon either migrated directly to spawning locations, followed a linear path but took a relatively long time to arrive, or swam indirectly and slowly to spawning locations. Twenty-five per cent of the Lake Clark fish migrated directly into Lake Clark, 50% milled at the lake outlet for several days and 25% migrated downstream into Sixmile Lake (mean = 11.3 days, SD = 5.7 days, range: 4–26). After entering Lake Clark, salmon usually migrated to an area of the lake, which was near their spawning location. For example, salmon that eventually spawned near the tagging site tended to remain in the lower end of the lake (Fig. 2). Ninety-three per cent of radio-tagged salmon arrived at spawning locations by 6 September (Fig. 2).

Generally, radio-tagged salmon migrated along the shoreline, although some fish were detected crossing through the middle of the lake. At the Lake North and Lake South telemetry receivers, 83% of radio-tagged fish were detected travelling nearshore (Fig. 1). Of these, 75% were detected along the south shore, 10% were detected along the north shore, and 15% were detected by both receivers indicating that salmon moved through the middle of the lake. Tracking data also indicate that radio-tagged fish made frequent trips through the middle of the lake while migrating to spawning locations.

The travel time and net speed of migration to spawning locations were, on average, 21.2 days (SD = 13.2) and 3.5 $km \cdot day^{-1}$ (SD = 2.9, range: 0.1–11.0 $km \cdot day^{-1}$; Table 2). Travel time to tributaries was, on average, 12 days shorter than that to LC spawning locations (Table 2) and fish generally arrived sooner at spawning locations closer to the

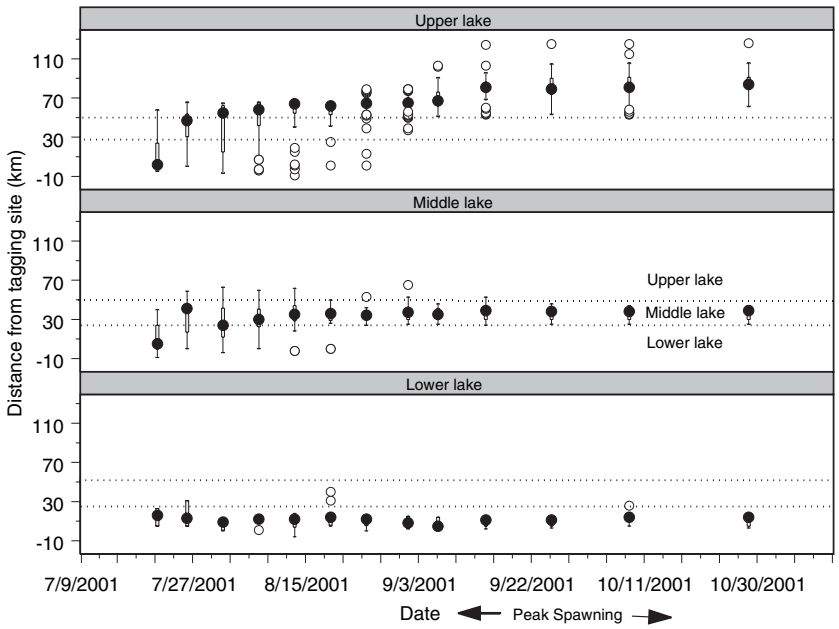

Fig. 2. Distance-radio-tagged sockeye salmon were located from the tagging site by date; boxes comprise central 50% of data, filled circles indicate median and empty circles indicate outliers. Negative distance values indicate salmon that migrated downstream of the tagging site.

Table 2. Speed of migration, days migrated and linearity of migration to spawning locations in Lake Clark 2001. Spawning habitat was either Lake Clark beaches (LC) or tributary rivers or lakes (Trib).

Area	Location	Water	Peak spawning date	Distance (km)	*N*	Travel time (days)		Speed (km·day^{-1})		Linearity		Arrival date		
						Average	SD	Average	SD	Average	SD	Mean	Min	Max
Sucker Bay Lake	Trib	Clear	30 August	7	2	3.0	2.8	4.2	4.0	0.7	0.4	28 July	20 July	4 August
Kijik Lake	Trib	Clear	25 September	42	20	8.3	4.4	6.0	2.4	0.8	0.2	31 July	21 July	22 August
Priest Rock Creek	Trib	Clear	11 October	46	1	24.5	NA	1.9	NA	0.4	NA	25 August	NA	NA
Currant Creek	Trib	Turbid	25 September	53	3	15.3	10.7	5.0	3.5	0.7	0.2	8 August	28 July	26 August
Little Lake Clark	Trib	Turbid	7 October	66	31	20.4	9.5	4.4	3.3	0.7	0.2	14 August	25 July	29 August
Tlikakila River	Trib	Turbid	1 October	66	33	19.0	7.9	4.2	2.1	0.8	0.1	13 August	28 July	2 September
All tributaries	Trib			7–66	90	16.7	9.4	4.7	2.7	0.8	0.2	10 August	20 July	2 September
Lake Clark beaches	LC			4–63	52	29.1	15.2	1.6	2.1	0.4	0.2	25 August	26 July	22 September
All clear		Clear		4–46	42	14.4	13.5	3.9	3.5	0.6	0.3	9 August	20 July	19 September
All turbid		Turbid		30–66	100	24.1	12.0	3.4	2.6	0.6	0.3	18 August	25 July	22 September
All drainages				1–66	142	21.2	13.2	3.5	2.9	0.6	0.3	16 August	20 July	22 September

tagging site (Table 2; Fig. 3). Seventy-five per cent of tagged salmon travelled at speeds greater than 10 km·day^{-1} at some point in their migration, and five salmon exceeded 48 km·day^{-1} (~2 km·h^{-1}). Tributary spawning fish migrated faster (mean = 4.7 km·day^{-1}, SD = 2.7 vs. 1.6 km·day^{-1}, SD = 2.1) than LC spawning fish (one-way ANOVA, $P < 0.001$) and fish migrated fastest to the Kijik River and Sucker Bay Lake drainages (Table 2).

Radio-tagged sockeye salmon migrated to spawning locations with varying degrees of linearity. Eighteen per cent of fish migrated directly to spawning locations (linearity = 1.0; Fig. 4a) while another 11% made extensive movements before settling at a spawning location (linearity <0.25; Fig. 4b). Tributary spawning fish migrated more directly (mean linearity = 0.8, SD = 0.2 vs. 0.4, SD = 0.2) than LC spawning fish (one-way ANOVA, $P < 0.001$; Table 2). One LC spawning salmon travelled 307 km within Lake Clark, although its spawning location was only 55 km from the tagging site.

Radio-tagged sockeye salmon were not detected in a tributary of Lake Clark unless they spawned in that tributary. That is, no salmon were detected in one tributary and then subsequently spawned in another tributary system or at LC. Tributary spawning fish milled at the mouth of tributary streams, on average, for 17.4 days (SD = 13.6, range: 0–59 days), before migrating upstream. Salmon congregated shortest at the mouth of Sucker Bay Lake (mean = 9.2 day, SD = 6.0) and Kijik River (mean = 2.3 days, SD = 2.6) and longest at the mouth of Currant Creek (mean = 36.3, SD = 12.5) and Tlikakila River (mean = 26.8, SD = 8.5; Fig. 5a). Salmon migrated

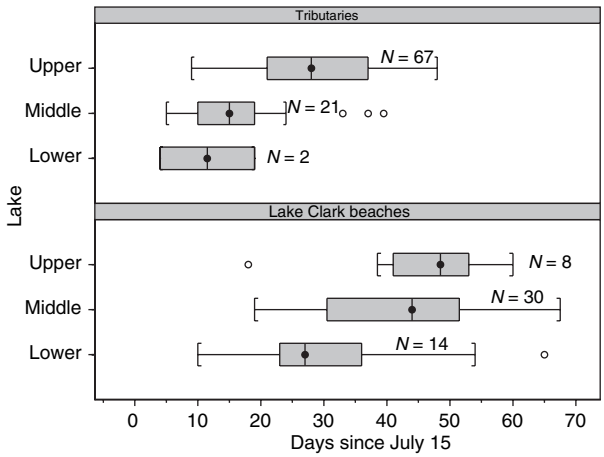

Fig. 3. Date-radio-tagged sockeye salmon arrived at spawning locations by lake section and habitat type; boxes comprise central 50% of data, filled circles indicate median and empty circles indicate outliers. Tributaries include both tributary rivers and tributary lakes.

into tributaries associated with a lake system earlier than tributaries without a lake system and entered clear water tributaries earlier than glacially turbid tributaries (Table 2; Fig. 5b; two-way ANOVA: tributary type $P < 0.001$, water turbidity $P < 0.001$). One radio-tagged salmon that migrated into the spring-fed Priest Rock Creek in early October was an exception to this general pattern (Fig. 5b).

Discussion

This study provides the first detailed examination of in-lake spawning migrations of female sockeye salmon, which is the essential information to in-lake fishery managers. While our data are limited to a sample of the movements of female radio-tagged fish within Lake Clark, general migration patterns were clearly evident. For example, after entering the lake, tagged fish migrated more directly and faster to tributary rivers and lakes than to LC spawning locations. Assuming directed travel equates to homing, this is consistent with genetic studies (Varnavskaya et al. 1994; Habicht et al. 2004; Ramstad et al. 2004), homing experiments (Blair & Quinn 1991) and otolith microchemistry data (Quinn et al. 1999). Another pattern observed was that tagged fish primarily migrated along the lakeshore to reach spawning locations corroborating prior findings (Blair & Quinn 1991; Burger et al. 1995). The lack of an obvious nearshore migration pattern within Lake Clark contrasts with the clockwise pattern observed in a similar study (Burger et al. 1995).

Prior to this research, we assumed that in-lake migration to spawning locations would be both rapid and direct, because sockeye salmon are considered very precise in their homing (Foerster 1968; Quinn 1993; Hendry et al. 1995; Quinn 2005) and excessive movements would be energetically costly, perhaps compromising reproduction (Brett 1995). Although we observed this behaviour for fish returning to two tributary lake systems of Lake Clark, the slow speed and excessive distance that some sockeye salmon travelled were unanticipated. The mean speed of migration observed within Lake Clark was 40% slower than that observed in a similar study by Burger et al. (1995) and substantially slower than 50 km·day^{-1} or 2.0 km·h^{-1} observed in the marine (French et al. 1976), riverine (Killick 1955; Quinn 1988) and lacustrine (Blair & Quinn 1991) environments. If radio-tagged fish had travelled at a rate of 50 km·day^{-1}, they would have reached their spawning location within 2 days rather than the mean of 21 days we observed. Our study may not be representative of male sockeye salmon movements, as they typically arrive earlier than females at spawning grounds (Morbey 2000).

Several factors may explain the relatively slow in-lake migration to spawning locations. First, it is possible that the tagging procedure altered fish behaviour as others have documented sublethal tagging effects (e.g., Gray & Haynes 1979). This is unlikely, as the tagging procedure was rapid (~1 min); a concurrent tagging effect study showed no increase in mortality (Ramstad & Woody 2003), and milling behaviour observed at the lake outlet was consistent with observations by Burger et al. (1995). Secondly, it is possible that our sampling interval was insufficient to detect the true movement and speed of radio-tagged fish travelling within Lake Clark. While our data certainly underestimate the movement of salmon during their in-lake migration, this scenario seems unlikely, given the large sample size ($N = 142$), large number of data points collected (>2500) and the consistency in the migration patterns among tagged fish. Thirdly, arriving at spawning locations quickly in lake systems may not be necessary, because sockeye salmon populations tend to migrate into nursery lakes about 1 month before spawning begins (Hodgson & Quinn 2002). During the time between lake entry and spawning, salmon may continue to migrate to specific sites or hold within the lake until they become sexually mature. Finally, the process of searching for an adequate spawning location may take longer than navigating through the oceanic and riverine environments. Of these alternatives, our data suggest that the slow migration speed can be attributed to salmon holding in areas of the lake during their migration rather than randomly searching for spawning locations.

Different natal lakes used by juvenile salmon may explain the relatively fast migration by tagged fish to

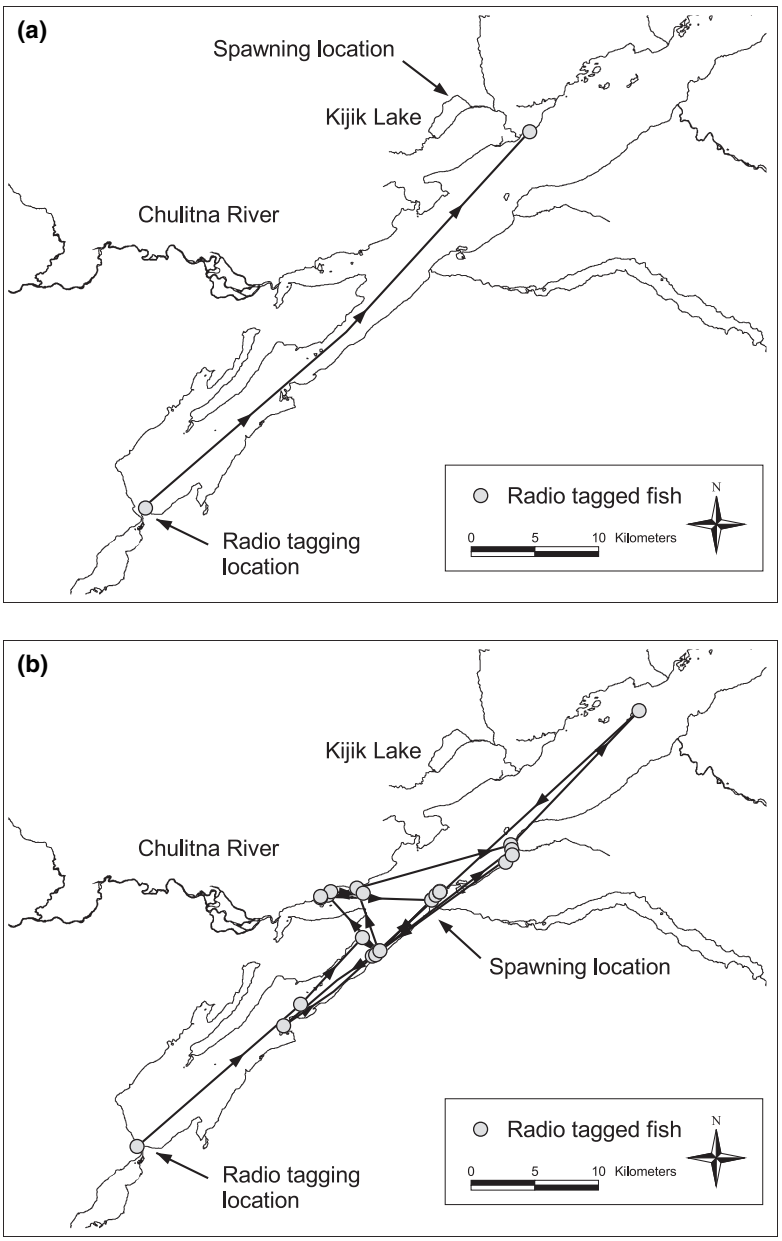

Fig. 4. Example of radio-tagged sockeye salmon that migrated directly (a) and indirectly (b) to spawning locations. Linearity was calculated as the shortest distance in water from the tagging site to within 5 km of the spawning location or mouth of the spawning stream divided by the straight-line distance between all relocation data points.

Kijik River and Sucker Bay Lakes. Both tributary lakes provide rearing habitat for juvenile salmon and a stable environment for adult salmon to congregate prior to spawning. Experimental research has demonstrated that salmon return to waters where they were reared and that the most sensitive period for olfactory imprinting is just prior to seaward migration (see reviews by Hasler & Scholz 1983; Dittman & Quinn 1996). Perhaps, salmon migrated faster to these lakes simply because they were reared and imprinted on the unique odours of these waters rather than Lake Clark. Although we did not collect fin clips from tagged fish to assess this natal lake hypothesis, genetic data collected in a concurrent study (Ramstad et al. 2004) found that both the Kijik River and Sucker Bay Lake spawning populations are highly divergent compared with other populations within the Lake Clark drainage.

Radio-tagged fish that were less direct in their migration could have been searching for an appropriate spawning location, milling, or swimming throughout the lake, because they had energy reserves beyond that needed for successful reproduction. Indirect migrations to beach spawning locations may be attributable to beaches having similar physical and chemical characteristics. In contrast, the unique water chemistry and flows of tributaries (e.g., Brabets 2002) are likely easier for salmon to recognise. It is also possible that salmon were milling within the lake waiting for the proper environmental and physical cues to trigger migration to a specific spawning location. Most fish that wandered confined their

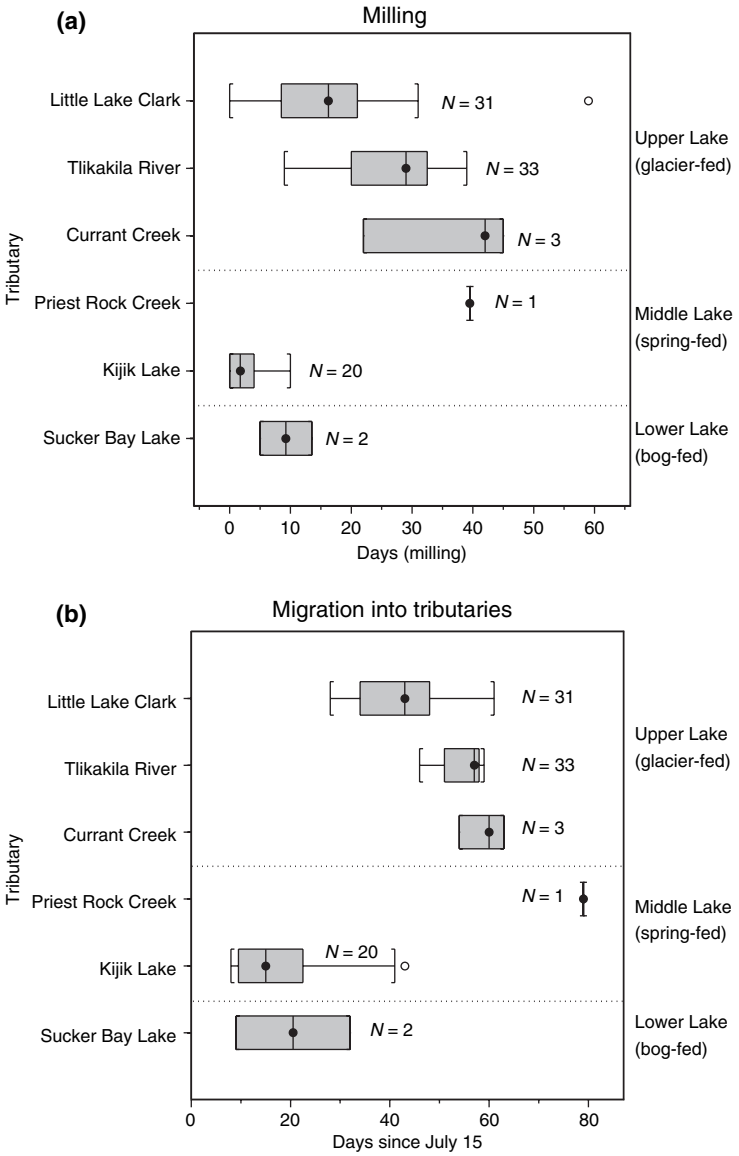

Fig. 5. Days-radio-tagged salmon milled at the mouth of tributaries (a) and date salmon migrated into tributaries of Lake Clark (b); boxes comprise central 50% of data, filled circles indicate median and empty circles indicate outliers.

movements to a region of the lake that was near their final spawning location. Finally, while conserving energy during migration is considered important for successful reproduction (Brett 1995; Rand & Hinch 1998), prespawning salmon may have had excess energy reserves that allowed them to migrate throughout the lake. In 2001, approximately 70% of the Lake Clark return was composed of large salmon that had spent 3 years in the ocean (Woody 2004). The degree of wandering might be less in lakes with smaller fish (e.g., two-ocean fish) and a longer migration.

We did not observe any obvious exploring or proving behaviour by female sockeye salmon as all tagged fish detected in a tributary spawned in that tributary. This observation suggests a high level of precision to tributary habitats, although without complimentary genetic data we are unable to verify that tagged fish were returning to natal sites. The absence of exploring behaviour contrasts with results from a similar study (Burger et al. 1995), where approximately 16% of tributary spawners and 21% of beach spawners migrated into one tributary, before settling at other spawning locations. The wandering into tributaries and difference in homing precision observed by Burger et al. (1995) may be attributable to an active rearing and stocking programme in Tustumena Lake (Kyle 1992). Early imprinting of these stocks on their natal streams may have been compromised, because eggs were incubated in a hatchery and fry were released at the mouths of their respective natal tributaries (Kyle 1992), thereby leading to the higher percentage of wandering.

The upstream migration of sockeye salmon into glacially turbid tributaries coincided with cooling temperatures, lower water levels and a dramatic decrease in the concentration of suspended sediments. For example, the upstream migration into the Tlikakila River occurred in late August/early September when

suspended sediment in the river decreased from a high of 710 $mg \cdot l^{-1}$ in June to 71 $mg \cdot l^{-1}$ in September (Brabets 2002). The similar timing of upstream migration among glacier-fed rivers in the watershed suggests an adaptive response to seasonal turbidity cycles. Jensen & Mathisen (1987) noted that sockeye salmon generally migrate into glacial systems later than into clear systems. Such a behavioural adaptation would result in deposition of eggs on a decreasing turbidity cycle, thereby reducing adverse effects of fine sediments on embryo survival (Chapman 1988).

Sockeye salmon populations have suffered decline throughout their range in the last century (Baker et al. 1996; Gustafson et al. 1997; McKinnell et al. 2001; Fair 2003). Because these fish exhibit spatially and temporally predictable migrations to and from the seas (Burgner 1991), verification of similar predictable patterns during their in-lake migration would be useful to managers of freshwater fisheries. The directed migration to tributaries observed in this study suggests that tributary spawners may be distinct populations and should be monitored and managed separately. In the case of specific populations with low effective population sizes (Habicht et al. 2004; Ramstad et al. 2004), knowing how such populations migrate through a lake system would facilitate conservation efforts by managers. Further studies are needed to determine variation in movement patterns among lakes, factors that influence movements and timing and possible sex-specific differences in migratory behaviour.

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