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[Article]

Spawning Distribution of Sockeye Salmon in a Glacially Influenced Watershed: the Importance of Glacial Habitats

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Abstract.—The spawning distribution of sockeye salmon *Oncorhynchus nerka* was compared between clear and glacially turbid habitats in Lake Clark, Alaska, with the use of radiotelemetry. Tracking of 241 adult sockeye salmon to 27 spawning locations revealed both essential habitats and the relationship between spawn timing and seasonal turbidity cycles. Sixty-six percent of radio-tagged sockeye salmon spawned in turbid waters (≥5 nephelometric turbidity units) where visual observation was difficult. Spawning in turbid habitats coincided with seasonal temperature declines and associated declines in turbidity and suspended sediment concentration. Because spawn timing is heritable and influenced by temperature, the observed behavior suggests an adaptive response to glacier-fed habitats, as it would reduce embryonic exposure to the adverse effects of fine sediments.

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, springs, and lake shorelines (for reviews, see Groot and Margolis 1991 and Quinn 2005).

Glacier-fed rivers and lakes, which are characterized by high summer turbidity, variable flows, and large concentrations of suspended fine sediments (Koenings et al. 1986, 1990; Lloyd et al. 1987; Brabets 2002), are generally considered poor spawning habitat for Pacific salmon (Groot and Margolis 1991) because fine sediments can smother developing embryos (Phillips et al. 1975; Hausle and Coble 1976; Everest et al. 1987). More specifically, fine sediments can inhibit oxygenation, metabolic waste transfer, and fry emergence (Everest et al. 1987), resulting in higher mortality levels. Studies indicate that survival to emergence of salmonids is inversely related to the percentage of fine sediments in a redd (Holtby and Healey 1986; Chapman 1988).

Although the adverse effects of fine sediments on salmon egg and embryo survival are well documented (Holtby and Healey 1986; see review by Chapman 1988), many glacial rivers and lakes support productive salmon stocks. Traditionally, spawning in these systems was assumed to occur in associated clear-water tributaries and lakes (e.g., Burger et al. 1995). However, recent studies suggest that glacially turbid spawning habitats are more important for Pacific salmon production than previously thought (Burger et al. 1985, 1995; Eiler et al. 1992). Because even low turbidity levels (e.g., 4 nephelometric turbidity units [NTU]) inhibit visual observation of spawning salmon (Cousens et al. 1982; Lloyd et al. 1987), the actual distribution of salmon in glacier-fed watersheds has probably been underestimated.

The objectives of this study were to (1) identify the spawning locations of sockeye salmon *O. nerka* in the Lake Clark watershed and assess their distribution relative to water turbidity and (2) examine the relationship between spawn time and suspended sediment concentration (SSC) within individual tributaries. Such information is essential to conservation of contemporary salmon populations because it has implications for the definition and conservation of essential spawning habitats, abundance estimates, and population management (Knudsen 2000).

Study Area

The Lake Clark watershed (60°01′N, 154°45′W), located within the Kvichak River drainage in southwest Alaska (Figure 1), includes Lake Clark and six primary tributaries. Lake Clark is a semiglacial oligotrophic lake that is 66 km long and 5–8 km wide; it has an average depth of 103 m, a maximum depth of 322 m, and a drainage area of 7,620 km^2

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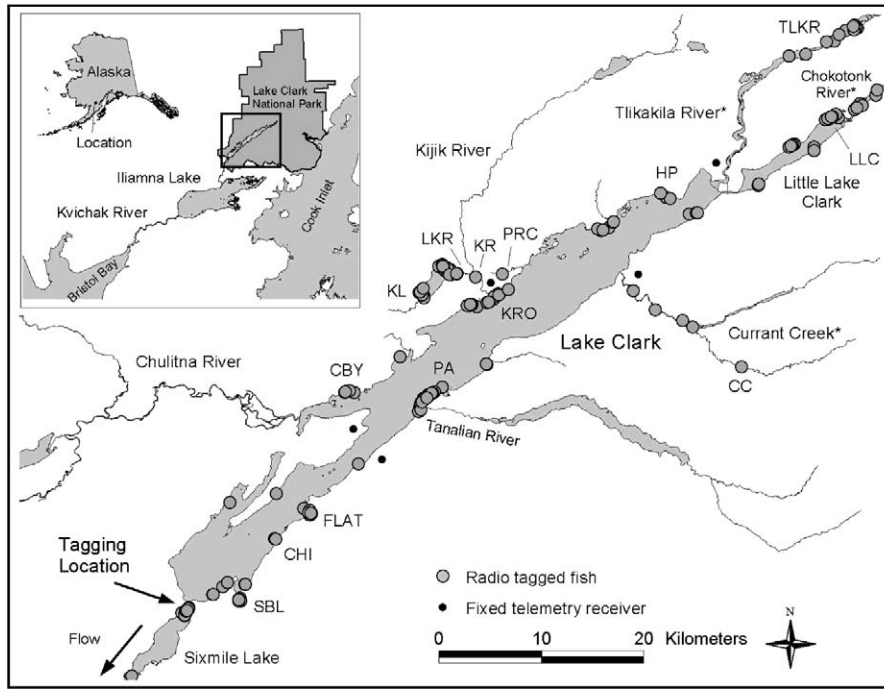

FIGURE 1.—Map of Lake Clark, Alaska, including tagging location, fixed telemetry receivers, and spawning areas for radio-tagged sockeye salmon. Asterisks denote glacier-fed tributaries. Refer to Table 2 for spawning distribution data and spawning site identification codes.

(Anderson 1969; Wilkens 2002). Of the tributaries, three are glacier fed, two are clear, and one is organically stained (Table 1; Brabets 2002). Seasonal runoff from glacial tributaries is highest between June and September, which creates a turbidity gradient along the length of the lake from the turbid upstream to the relatively clear (~2 NTU) downstream (Brabets 2002; Wilkens 2002).

The Lake Clark watershed is a significant producer of sockeye salmon (200,000–3,100,000 fish/year; Poe

TABLE 1.—Ranges in discharge, temperature, and suspended sediment concentration (SSC) for the six major tributaries to Lake Clark, Alaska, 1999–2000 (data from Brabets [2002]).

Tributary	Water source	Basin area (km^2)	Discharge (m^3/s)	Temperature (°C)	SSC (mg/L)						
					Mar	May	Jun	Jul	Aug	Sep	Oct
				1999							
Lake Clark outlet	Lake	7,629	306–606	5–11			1	2	1	1	1
Chulitna River	Bog	3,000	40–116	1–12			9	4	5	5	5
Tanalian River	Lake	532	5–168	6–12			5	3	1	1	3
Kijik River	Lake	773	12–50	4–13			123	8	3	2	6
Currant Creek	Glacier	428	8–76	2–8			193	82	103	25	7
Chokotonk River	Glacier	436	7–62	0–10			208	80	107		9
Tlikakila River	Glacier	1,613	1–340	0–9	5	25	710	227	397	71	9
				2000							
Lake Clark outlet	Lake	7,629	244–484	5–12			1	1	3	5	
Chulitna River	Bog	3,000	37–112	8–15			5	5	5	5	
Tanalian River	Lake	532	14–46	9–12		2	1	1	2	1	
Kijik River	Lake	773	17–35	7–12			3	2	3	3	
Currant Creek	Glacier	428	8–78	5–7			9	162	282	3	
Chokotonk River	Glacier	436	27–43	5–7			25	211			
Tlikakila River	Glacier	1,613	21–182	0–9		29	676	525	318	118	

and Rogers 1984; Woody 2004) and contains numerous glacier-fed tributaries that are potential spawning habitat. Previous studies (Demory et al. 1964; Smith 1964; Jensen and Mathisen 1987; Parker and Blair 1987; Regnart 1998) provide salmon spawning data from clear-water portions of the watershed, but the extent of sockeye salmon use in the glacially turbid portions was unknown. Estimated escapement of sockeye salmon to the Lake Clark system during this study was 172,902 fish in 2000 and 224,414 fish in 2001 (Woody 2004). The watershed is currently pristine and hosts one small, permanent community of about 200 people.

Methods

Capture and tagging protocols, telemetry equipment, and tag retention.—We used radiotelemetry to examine the spawning distribution of sockeye salmon between clear and glacially turbid habitats in Lake Clark. Adult sockeye salmon ($N = 332$; 93 males and 82 females in 2000; 157 females in 2001) were captured with seines as they migrated into Lake Clark (Figure 1) between 15 July and 23 August 2000 and between 15 July and 9 August 2001. Fish were radio-tagged during randomly selected fishing sessions between 0800 and 1959 hours because more than 90% of the salmon migration into Lake Clark is diurnal (Poe and Rogers 1984; National Park Service [NPS], unpublished data). Radio-tagging protocols followed those of Eiler et al. (1992) and Burger et al. (1995). Captured sockeye salmon were placed in a tagging cradle and identified as male or female; a glycerin-coated radio tag was inserted into the stomach of each fish (Monan et al. 1975; Burger et al. 1995) in such a way that the antenna protruded from the mouth. After tagging, fish recovered in an in-river mesh holding pen ($1.5 \times 1.5 \times 1.5$ m; 2.5-cm mesh) if necessary and were then released.

Radiotelemetry equipment consisted of high-frequency (149–150 MHz) VHF radio tags, scanning receivers, and four-element Yagi and H antennas (Lotek Wireless, Inc., Newmarket, Ontario). Radio tags were digitally coded to identify individual fish and weighed less than 2% of body weight of tagged fish, as is generally recommended (Winter 1996). In 2000, we used model MCFT-3E radio tags (Lotek Wireless, Inc.), which measured 14.5×49.0 mm, weighed 15.6 g in air, and transmitted every 3 s continuously over a 24-h period. In 2001, we changed the model and transmission rate of our tags to increase the reception range of tagged fish during tracking events. The tags used in 2001 were model MCFT-3A radio tags, which measured 16×46 mm, weighed 19 g in air, and transmitted every 2 s.

In 2001, several capture and tagging protocols were changed to better achieve study objectives. First, the tagging period was shortened by 2 weeks to minimize the capture and tagging of salmon that spawn at the lake outlet. Second, the number of fish tagged per day was changed to better distribute the tags in proportion to the run. In 2000, 6 fish were tagged per day, whereas in 2001 we tagged 5 fish when fewer than 10,000 fish migrated past a local counting tower and 10 fish when more than 10,000 fish passed the tower (Woody 2004, in press). Third, only female salmon were tagged in 2001 because females exhibit stronger spawning site fidelity to specific spawning locations than males (Mathisen 1962). Fourth, the sampling procedure was streamlined in 2001, making an anesthetic unnecessary in the tagging procedure. In 2000, fish were anesthetized with a clove oil mixture before tagging (Woody et al. 2002) to reduce handling stress from sampling of fin clips (for genetic analysis), scales (for aging), and morphometric measures, whereas in 2001 fish were only measured and radio-tagged. This change resulted in a decreased average handling time (including recovery) from 5 min in 2000 to 1 min in 2001.

Radio tag retention and potential tagging effects were examined during a companion study (Ramstad and Woody 2003). During that study, the overall tag retention in sockeye salmon was high (mean = 0.98; 95% confidence interval [CI] = 0.92–1.00) and the mortality of tagged salmon (mean = 0.02; 95% CI = <0.01–0.08) was low and similar to that of untagged controls (mean = 0.03; 95% CI = <0.01–0.15).

Radio-tracking protocol and spawning criteria.—Tagged fish were tracked every 1–10 d with fixed-wing aircraft or boats and were tracked 24 h/d at fixed radiotelemetry receivers (Figure 1). Aerial surveys were flown along Lake Clark shorelines and tributaries at an altitude between 200 and 300 m and an airspeed between 100 and 130 km/h. Boat tracking followed lake and island perimeters about 300 m offshore and at a maximum speed of 30 km/h. During tracking events, a Global Positioning System 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 if (1) it entered a tributary stream or lake, or (2) it was located in the same area (within 400 m) twice within a 3-week period and no further migration occurred, and (3) spawning or spawned-out sockeye salmon were observed in that area. We verified spawning in turbid areas by fishing (seine or gill nets). Salmon that migrated to spawning habitats downstream of the tagging location ($n = 41$) were excluded from

analyses because they were outside our defined study area.

Turbidity measurements.—Water turbidity was measured from a subset of spawning habitats (n = 24) during spawning activity with a pocket turbidimeter (Hach Company, Loveland, Colorado). We collected water samples when approximately half of the female sockeye salmon were spawning and half were spawned out. Spawning habitats were categorized as either turbid (≥5 NTU) or clear (<5 NTU) after Koenings et al. (1986, 1990) and Lloyd et al. (1987), who indicated that turbidity levels greater than 4 NTU affected observer ability to detect salmon during aerial surveys. We measured turbidity rather than SSC 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.

Spawn time and suspended sediment concentration.—The relationship between spawn time and SSC was assessed in Lake Clark's tributaries with data collected concurrently by Brabets (2002). Spawn time throughout the drainage was determined by visual observation of spawning activity on redds and by manual assessment of female spawning condition (e.g., spawning females expelled eggs with light pressure to the abdomen; U.S. Geological Survey [USGS], unpublished data). For comparative purposes, SSC values were converted to turbidity (T) units with the equation $T = 0.44(\mathrm{SSC})^{0.858}$. This equation (from Lloyd et al. 1987) relates SSC and turbidity with the use of paired data from streams throughout Alaska.

Data analyses.—Each year, the proportion of tagged fish spawning in turbid sites rather than clear sites was tested against random chance with a binomial test. Three chi-square tests of homogeneity were conducted: (1) the proportion of tagged fish spawning in turbid sites rather than clear sites was compared between study years; (2) the proportion of tagged fish spawning in tributary sites rather than beach sites was compared between study years; and (3) for the year both sexes were tagged, the proportion of tagged fish spawning in turbid sites rather than clear sites was compared between sexes.

Results

We determined spawning locations for 282 of 332 radio-tagged fish (Figure 1). Of these, 241 migrated to spawning locations within the Lake Clark watershed (N = 27) and 41 migrated to spawning locations (N = 3) outside of our study area (Figure 1). Fish not tracked to spawning locations were either never located, were lost after being tracked into Lake Clark, or did not meet our criteria for determining a final spawning location (see Methods). On average, radio-tagged fish tracked to spawning locations were located 12.7 times (range = 3–33), and over 3,500 locations were made during the two study years.

Within the Lake Clark drainage, 66% of tagged fish migrated to turbid habitats (≥5 NTU) and 70% migrated to five primary spawning locations, including Kijik Lake, Tlikakila River, Little Lake Clark, and beach spawning locations at the mouths of the Tanalian and Kijik rivers (Table 2; Figure 1). During both years of the study, more tagged fish spawned in turbid habitats than in clear-water habitats (binomial test: P = 0.11 in 2000, P = 0.00 in 2001). Turbidity readings at the time of spawning ranged from a low of 0.3 NTU in clear-water habitats (median = 2.1 NTU) to a high of 14.2 NTU in turbid habitats (median = 7.8 NTU; Table 2). Turbid spawning habitats (N = 14) included 3 glacier-fed rivers and 11 beach spawning habitats in Little Lake Clark and the upper portion of Lake Clark (Figure 1). Clear-water spawning habitats (N = 13) included 2 lake-fed rivers, 1 spring-fed stream, and 10 beach spawning habitats in Kijik Lake, Sucker Bay Lake, and the lower portion of Lake Clark (Figure 1; Table 2).

Despite protocol changes between 2000 and 2001, the spawning distribution of tagged salmon was similar between years by both water turbidity ($\chi^2 = 3.114$, df = 1, $P = 0.07$) and habitat type ($\chi^2 = 0.0949$, df = 1, P = 0.76). In 2000, when both sexes were tagged, there was no difference in the distribution of male and female sockeye salmon relative to water turbidity ($\chi^2 = 0.047$, df = 1, $P = 0.826$).

Spawning activity in Lake Clark's glacier-fed tributaries coincided with a decline in SSC. For example, spawning in the glacier-fed Tlikakila River occurred in September, after SSC decreased from a high of 710 mg/L (123 NTU) in June to a relatively high (compared with clear-water habitats) 71 mg/L (17 NTU) in September (Table 1; Figure 2; Brabets 2002). The SSC further declined to 9 mg/L (3 NTU) in October, when most spawning ended (Table 1; Figure 2). A similar pattern was observed for fish spawning in the other glacier-fed tributaries (Table 1).

Discussion

This is the first study to describe the relationship between spawn timing and the annual pattern of natural turbidity in a large glacial lake system. The upstream migration (Young and Woody, in press) and spawning of sockeye salmon in glacially turbid tributaries of Lake Clark coincided with cooling temperatures, declining water levels, and decreasing SSC (Brabets 2002). Such behavior suggests an adaptive response by fish to seasonal turbidity cycles, as heritable phenotypic traits under selection, such as adult spawn time

TABLE 2.—Spawning distribution of radio tagged sockeye salmon in the Lake Clark (Alaska) watershed during 2000 and 2001. Spawning habitats were categorized by water turbidity at the time of spawning activity: clear <5 nephelometric turbidity units [NTU] and turbid ≥5 NTU.

Spawning site	Site	Drainage	Habitat type	Turbidity category	Date sampled	Turbidity (NTU)	Number of tagged fish		
							2000	2001	Total
SBL	Sucker Bay Lake	Sucker Bay Lake	Beach	Clear	30 Aug	2.3	3	2	5 (2.0%)
KR	Kijik River	Kijik River	Tributary	Clear	20 Sep	0.4	2	0	2 (1.0%)
LKR	Little Kijik River	Kijik River	Tributary	Clear	18 Sep	0.4	5	1	6 (2.0%)
KL	Kijik Lake	Kijik River	Beach	Clear	25 Sep	0.3	21	19	40 (17.0%)
PRC	Priest Rock Creek	Priest Rock Creek	Tributary	Clear	11 Oct	1.4	0	1	1 (0.4%)
CC	Currant Creek	Currant Creek	Tributary	Turbid	25 Sep	7.1	2	3	5 (2.0%)
LLC	Little Lake Clark	Little Lake Clark	Beach	Turbid	7 Oct	14.2	2	18	20 (8.0%)
TLKR	Tlikakila River	Tlikakila River	Tributary	Turbid	12 Oct	8.5	18	33	51 (21.0%)
CHI	Chi Point	Lake Clark	Beach	Clear	24 Sep	2.7	2	1	3 (1.0%)
FLAT	Flat Island	Lake Clark	Beach	Clear	13 Sep	3.1	3	7	10 (4.0%)
CBY	Chulitna Bay	Lake Clark	Beach	Clear	21 Sep	4.4	2	5	7 (3.0%)
PA	Port Alsworth	Lake Clark	Beach	Turbid	25 Sep	5.1	17	17	34 (14.0%)
KRO	Kijik River Outlet	Lake Clark	Beach	Turbid	30 Sep	5.3	12	7	19 (8.0%)
HP	Hatchet Point	Lake Clark	Beach	Turbid	30 Sep	6.7	0	3	3 (1.0%)
	All other sites						10	25	35 (15.0%)
	All clear			Clear			41	42	83 (34.0%)
	All turbid			Turbid			58	100	158 (66.0%)
	All beach		Beach				71	98	170 (71.0%)
	All tributary		Tributary				28	44	72 (29.0%)
	All sites in Lake Clark drainage						99	142	241

(Siitonen and Gall 1989; Silverstein 1993; Stewart et al. 2002) and incubation duration (Brannon 1987), would be affected by both thermal and suspended sediment cycles in glacial systems. Spawning later would increase fitness by reducing the exposure of developing embryos to the adverse effects of fine sediments (Chapman 1988).

Another mechanism allowing salmon to exploit turbid habitats may be their use of spawning habitats associated with upwelling groundwater or springs. Although we did not assess this directly, we observed that most spawning habitats were associated with a clear-water source. Lorenz and Eiler (1989) found that sockeye salmon redds in a glacial river were associated

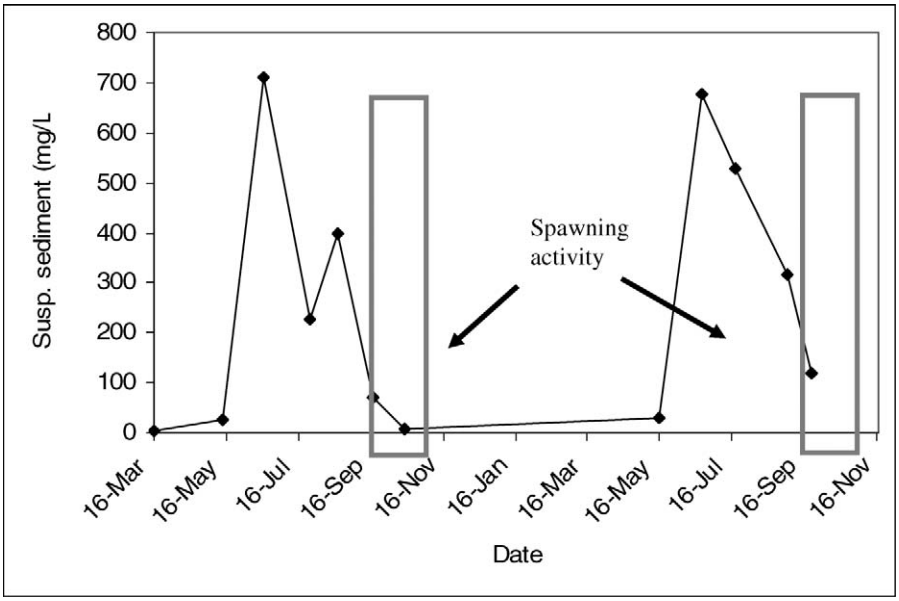

FIGURE 2.—Sockeye salmon spawning activity and suspended sediment concentration in the Tlikakila River, Alaska, from 16 March 1999 to 16 September 2000 (suspended sediment data are from Brabets 2002).

with upwelling groundwater and springs and suggested that these inputs were sufficient to remove fine sediments from spawning substrates. Burger et al. (1995) indicated that sockeye salmon used spawning locations in a glacial lake that were adjacent to inlet tributaries or springs. Hyporheic flow in these areas may similarly remove sediments from the spawning substrate. In addition to removing sediments from spawning substrates, upwelling groundwater and springs provide a relatively warm winter incubation environment for developing embryos (Quinn 2005). Because water temperature primarily determines incubation rate in salmonids (Brannon 1987), this association helps explain the late spawn time in the relatively cold glacier-fed tributaries.

Poor visibility in turbid waters may explain why limited spawning activity has been documented in glacial habitats. Lloyd et al. (1987) reported that an absolute turbidity as low as 4 NTU was sufficient to limit the direct observation of salmon during aerial surveys. While we did not specifically examine this relationship, our data and visual observations during radio-tracking support this finding. For example, compared with previous aerial surveys in the Lake Clark system that relied on visual observation (Parker and Blair 1987; Regnart 1998), our study documented 18 new spawning locations, and most of the newly identified sites were located in turbid habitats.

Other researchers have similarly used radiotelemetry to identify new spawning locations in glacially turbid waters for Chinook salmon *O. tshawytscha* (Burger et al. 1985; Savereide 2003), chum salmon *O. keta* (Barton 1992), and sockeye salmon (Eiler et al. 1992; Burger et al. 1995). Thirty percent of radio-tagged sockeye salmon in Tustumena Lake, Alaska, spawned in waters of 50 NTU (Burger et al. 1995). About 40% of radio-tagged sockeye salmon returned to the main stem of the Taku River (Alaska and British Columbia), where turbidities reach 200 NTU (Eiler et al. 1992; Murphy et al. 1997). Before research on the Taku River, it was estimated that most (60–70%) sockeye salmon spawned in clear-water lakes in the upper watershed (Eiler et al. 1992).

Findings from this study have 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. Relative to evolutionary history, sockeye salmon recolonized much of the Pacific Rim since the Pleistocene glaciation (Wood 1995), and behavioral adaptations observed in this study (e.g., spawning on a declining turbidity gradient and in regions associated with clear waters) are probably the product of natural selection for spawn timing that improves embryo survival in an otherwise harsh environment. If this behavior is correlated across a larger geographic range, it will help explain how sockeye salmon successfully colonized such environments postglaciation (Wood 1995).

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