



State of Alaska
Department of Fish and Game
Division of Sport Fish

Nomination Form
Anadromous Waters Catalog

Region USGS Quad(s)
 Anadromous Waters Catalog Number of Waterway
 Name of Waterway USGS Name Local Name
 Addition Deletion Correction Backup Information

For Office Use

Nomination #	<u>11-077</u>	<u>[Signature]</u>	<u>6/13/11</u>
		Fisheries Scientist	Date
Revision Year:	<u>2012</u>	<u>[Signature]</u>	<u>6/13/11</u>
Revision to:	Atlas _____ Catalog _____	Habitat Operations Manager	Date
	Both <u>X</u>	<u>[Signature]</u>	<u>1/4/2011</u>
Revision Code:	<u>BZ</u>	AWC Project Biologist	Date
		<u>[Signature]</u>	<u>9/29/11</u>
		Cartographer	Date

OBSERVATION INFORMATION

Species	Date(s) Observed	Spawning	Rearing	Present	Anadromous
Sockeye salmon (5)	2001	X			<input checked="" type="checkbox"/>
					<input type="checkbox"/>
					<input type="checkbox"/>
					<input type="checkbox"/>
					<input type="checkbox"/>

IMPORTANT: Provide all supporting documentation that this water body is important for the spawning, rearing or migration of anadromous fish, including: number of fish and life stages observed; sampling methods, sampling duration and area sampled; copies of field notes; etc. Attach a copy of a map showing location of mouth and observed upper extent of each species, as well as other information such as: specific stream reaches observed as spawning or rearing habitat; locations, types, and heights of any barriers; etc.

Comments: Change species designation from sockeye salmon present to spawning based on observations by Dan Young (NPS) cited in "Distribution and Characteristics of Sockeye Salmon Spawning Habitats in the Lake Clark Watershed, Alaska" Tech Rpt. NPS/NRWRD/NRTR-2005/338 (attached)

Name of Observer (please print): Daniel Young
 Signature: _____ Date: 1/14/2011
 Agency: NPS
 Address: Lake Clark NP, AK

This certifies that in my best professional judgment and belief the above information is evidence that this waterbody should be included in or deleted from the Anadromous Waters Catalog.

Signature of Area Biologist: _____ Date: _____ Revision 05/08
 Name of Area Biologist (please print): _____



Distribution and Characteristics of Sockeye Salmon Spawning Habitats in the Lake Clark Watershed, Alaska

Daniel B. Young



The National Park Service Water Resource Division is responsible for providing water resources management policy and guidelines, planning, technical assistance, training, and operational support to units of the national park system. Program areas include water rights, water resources planning, regulatory guidance and review, hydrology, water quality, watershed management, watershed studies and aquatic ecology.

Technical Reports

The National Park service disseminates the results of biological, physical and social research through the Natural Resource Technical Report Series. Natural resources inventories and monitoring activities, scientific literature reviews, bibliographies, and proceedings of technical workshops and conferences are also disseminated through this series.

Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the National Park Service

Copies of this report are available from the following:

National Park Service
Water Resource Division (970) 225-3500
1201 Oak Ridge Drive, Suite 250
Fort Collins, CO 80525

National Park Service
Technical Information Center (303) 969-2130
Denver Service Center
P.O. Box 25287
Denver, CO 80225-0287

Cover Photos:

Top Left Photo: Radio tagged sockeye salmon

Top Right Photo: Radio tracking on Lake Clark

Bottom Left: Glacially turbid spawning habitat in the upper Tlikakila River

Bottom Right: Clear-water spawning habitat in Little Kijik River

Distribution and Characteristics of Sockeye Salmon Spawning Habitats in the Lake Clark Watershed, Alaska

Daniel B. Young¹

¹National Park Service
Port Alsworth, AK 99653

Technical Report/NPS/NRWRD/NRTR-2005/338

AUGUST, 2005

This report constitutes the completion report for PMIS project #54327 funded by the NPS Biological Resources Management Division component of the Natural Resource Challenge



National Park Service - Department of the Interior
Fort Collins - Denver - Washington

United States Department of the Interior • National Park Service

CONTENTS

CONTENTS.....	iv
LIST OF FIGURES	v
LIST OF TABLES.....	v
LIST OF APPENDICES.....	vi
ACKNOWLEDGEMENTS.....	vi
EXECUTIVE SUMMARY	1
INTRODUCTION	2
STUDY AREA	3
OBJECTIVES.....	4
METHODS	5
Spawning distribution	5
Spawning Activity	5
Characteristics of spawning habitat	5
Land ownership and development	7
Subsistence and sport fishing use	7
RESULTS	7
Spawning distribution	7
Spawning activity.....	7
Characteristics of Spawning Habitat.....	9
Land ownership and development	12
Subsistence and sport fishing use	13
LITERATURE CITED	19
APPENDIX.....	24

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Location of Lake Clark and Lake Clark National Park and Preserve relative to Bristol Bay and Cook Inlet, Alaska	3
2	Lake Clark watershed in Lake Clark National Park and Preserve.....	4
3	Location of tagging site, telemetry receivers, habitat sampling sites, and tributaries within the Lake Clark watershed	6
4	Spawning locations of radio tagged sockeye salmon in the Lake Clark watershed, 2000 and 2001.....	8
5	Spawning locations relative to land ownership within the Lake Clark	12
6	Subsistence fishing locations within the Lake Clark watershed	16
7	Sport fishing locations for sockeye salmon within the Lake Clark watershed	17

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Tagging and tracking summary for radio tagged adult sockeye salmon in Lake Clark watershed, 2000 and 2001.....	9
2	Characteristics of spawning habitat in Lake Clark and Tazimina River watersheds, 2000 – 2001	10
3	Characteristics of tributary inputs to Lake Clark at time of spawning activity 1999 – 2001.....	11
4	Subsistence harvest of sockeye salmon by community, in numbers of fish, Kvichak River drainage, Bristol Bay, 1983-03.....	14
5	Sport fish harvest of sockeye salmon by location, in numbers of fish, Kvichak River drainage, Bristol Bay, 1977 -2003	15

APPENDICES

<u>Appendix</u>	<u>Page</u>
1 Lake Clark and Kvichak River sockeye salmon escapement, in numbers of fish from 1980 – 1984 and 2000 – 2004.....	24
2 Spawning locations identified by radio telemetry and visual observation in Lake Clark, 2000 and 2001.....	25
3 Physical properties and water-quality characteristics of streamflow samples collected from the tributaries of Lake Clark, 1999 through 2001.....	27
4 Inshore commercial catch and escapement of sockeye salmon in the Naknek - Kvichak District by river system, in numbers of fish, Bristol Bay, 1983-2004	29

ACKNOWLEDGEMENTS

This project was a collaborative effort between the United States Geological Survey, Alaska Science Center (USGS ASC) and the National Park Service (NPS), Lake Clark National Park and Preserve. Funding was provided by the NPS Biological Resources Management Division component of the Natural Resource Challenge, U.S. Geological Survey, and U.S. Fish and Wildlife Service. Jim Tilmant (NPS) provided project oversight and helpful editorial comments. Carol Ann Woody (USGS ASC) provided guidance, and encouragement throughout this project. Kristina Ramstad, Ph.D. candidate at the University of Montana, conducted the habitat assessment portion of this study. Helpful editorial comments were made by M. Flora of the NPS Water Resources Division, J. Putera (NPS), and J. Margraf and G. Haas of the University of Alaska Fairbanks. D. Palmer, R. Brown, and E. Spangler provided technical advice and support. A special thanks to all the field assistants who contributed to this project.

EXECUTIVE SUMMARY

This report describes findings from a sockeye salmon *Oncorhynchus nerka* radio telemetry and spawning habitat study conducted in the Lake Clark watershed in 2000 and 2001. The primary objectives of this research were 1) to locate and map all major spawning aggregations 2) to determine basic characteristics of spawning habitats, and 3) to determine the distribution of private land uses and subsistence/sport use locations in relation to salmon spawning habitats.

To determine spawning distributions, 332 adult sockeye salmon were radio tagged as they entered Lake Clark in 2000 and 2001. Fish were relocated every 1-10 days by boat, plane, or remote solar powered receiver. On average, a radio tagged fish was relocated 12.7 times (range, 3 - 33) and over 3,500 relocations were made. Thirty-five spawning areas were identified, including three sites downstream of the tagging area and five sites identified by visual observation or seining. Eighteen areas were newly identified. Most Lake Clark sockeye salmon spawn in the Tlikakila River, Kijik watershed and along beaches of Lake Clark and Little Lake Clark. Spawning habitat locations were mapped into the Geographic Information System (GIS) for Lake Clark National Park and Preserve. Surprisingly, over 60% of radio tagged salmon spawned in turbid glacial waters; most of which were adjacent to an obvious clear water source.

Sockeye salmon spawning habitat was examined from a subset of spawning sites identified by radio telemetry. Basic characteristics including water temperature, turbidity, water depth, channel width, slope, and spawning substrate were collected. Water quality data were collected from the outlet of spawning tributaries during a concurrent study (Brabets 2002). Surface water temperature at spawning habitats ranged from 3.1° Celsius (C) to 12.9° C. Habitats in the glacier-fed Currant Creek and Tlikakila River as well as the spring-fed Priest Rock Creek were cooler than other habitats. Spawning habitats in the upper portion of the watershed were turbid due to runoff from glacial melt. However, the timing of spawning activity in turbid habitats coincided with a dramatic decrease in the concentration of suspended sediment and turbidity. Tributary spawning habitats were in less than one meter of water and spawning channels were on average less than 50 meters in width. Spawning substrate was variable among sites and ranged from habitat dominated by small fines in the headwaters of Tlikakila River to boulder dominated habitat in Little Lake Clark and Sucker Bay Lake. Water quality parameters were all within acceptable range for freshwater aquatic life.

Subsistence and sport fishing data were summarized using data collected during previous studies and by National Park Service (NPS) staff. Existing GIS coverages of land ownership were used to compare the location of spawning habitats relative to land ownership. Current development within the Lake Clark watershed was documented by NPS staff. Subsistence fishing for migrating sockeye salmon occurs throughout Lake Clark near seasonal and year-round residences. Residents of Nondalton harvest red fish (spawning sockeye salmon) from spawning areas. Sport harvest occurs at the outlet of Lake Clark, the outlet of Tanalian River, and within the Kijik Lake drainage. Subsistence and sport fishers currently harvest less than one percent of the Lake Clark escapement. About 75% of identified spawning habitats are adjacent to privately owned lands, many slated for development. Proactive measures should be taken to conserve these habitats.

INTRODUCTION

Lake Clark National Park and Preserve (LACL) is located in southcentral/southwest Alaska (Figure 1). Its 4 million acres straddle the Chigmit Mountains, which bridge the Aleutian Range to the southwest and the Alaska Range to the north. Approximately one-third of the park and preserve is located in the Cook Inlet drainage of south-central Alaska and two-thirds is located in the Kvichak, Kuskokwim, and Nushagak River drainages in southwest Alaska. The Kvichak River drainage, which includes the Iliamna Lake (11,137 km²) and Lake Clark watersheds (9,583 km²; Demory et al. 1964), is one of the world's most productive spawning and rearing habitats for sockeye salmon.

LACL was established in 1980 as part of the Alaska National Interest Lands Conservation Act (ANILCA). The primary purposes stated in the park's enabling legislation were 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).

Sockeye salmon originating from Lake Clark are important to the economy, culture, and ecosystem of the Bristol Bay region. The Lake Clark system produces an estimated 7-30% of the annual escapement of sockeye salmon to the Kvichak River drainage (Poe and Rogers 1984, Woody 2004) and historically, the Kvichak River drainage has been the largest contributor to the commercial salmon fishery in Bristol Bay. Sockeye salmon are an integral part of local Alaskan native culture (Unrau 1992) and continue to provide subsistence for contemporary users (Alaska Department of Fish and Game 2003). Ecologically, sockeye salmon are an important food resource for over 40 species of mammals and birds (Bennett 1995; Willson 1995; Wilson and Halupka 1995), and represent a significant source of marine derived nutrients that sustain freshwater ecosystem productivity (Kline et al. 1993).

Since 1996, sockeye salmon returns to the Kvichak River and Lake Clark watersheds have declined for unknown reasons. The Kvichak River escapement has failed to meet its minimum escapement goal in four of the last five years (ADFG 2004) and the recent (2000 – 2004) escapement of sockeye salmon to Lake Clark is about 75% lower than was documented from 1980 – 1984 (Appendix 1; Poe and Rogers 1984, Woody 2004). The decline has affected subsistence, commercial, and sport fisheries and caused the governor of Alaska to declare the region an economic disaster area. Depressed sockeye salmon returns concerned fishers and resource managers and initiated new research and monitoring programs in the Lake Clark watershed.

The purpose of this report is to summarize findings regarding sockeye salmon spawning habitats located in the Lake Clark watershed. This project represents one facet of integrated salmon ecology/water resource studies that were primarily completed in Lake Clark from 1999 - 2001. Completed projects include: Water quality of the Tlikakila River and five major tributaries to Lake Clark, Lake Clark National Park and Preserve, Alaska, 1999 – 2001 (Brabets 2002), Historical sockeye salmon data of Lake Clark, Alaska (Ramstad 2002), The limnology of Lake Clark, Alaska (Wilkens 2002), Nondalton traditional ecological knowledge of freshwater fish (Stickman et al. 2003), Lake Clark sockeye salmon population assessment (Woody et al. 2003), Founding events influence genetic population structure of sockeye salmon (*Oncorhynchus*

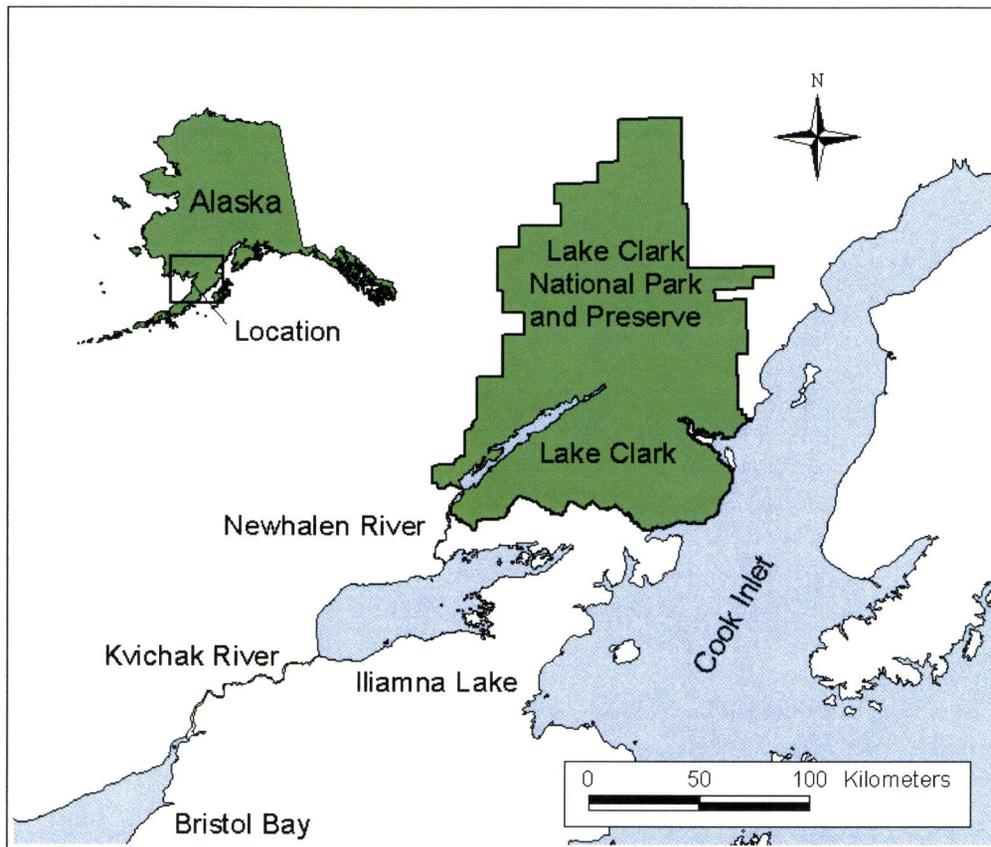


Figure 1. Location of Lake Clark and Lake Clark National Park and Preserve relative to Bristol Bay and Cook Inlet, Alaska.

nerka) in Lake Clark, Alaska (Ramstad et al. 2004), Population monitoring of Lake Clark and Tazimina River sockeye salmon, Kvichak River watershed, Bristol Bay, Alaska 2000 – 2003 (Woody 2004), and The migration and spawning distribution of sockeye salmon within Lake Clark, Alaska (Young 2004).

STUDY AREA

Lake Clark (60° 01 N, 154° 45 W) is the second largest lake (267 km²) in the Kvichak River drainage, and the largest body of water in LACL (Figure 2). It is a long (74 km), narrow (2.5 to 8 km), and deep (mean depth of 103 m) glacial lake with a drainage area of 7,620 km² (Anderson 1969, Brabets 2002). Six primary tributaries including three glacial tributaries, two lake-fed tributaries, and one organically stained tributary feed Lake Clark (Brabets 2002). In addition to the six primary tributaries, numerous small glacial, clear, and organically stained streams 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). Glacial tributaries provide approximately half of Lake Clark’s annual water budget and transport large

amounts (0.4 – 1.5 million tons) of suspended sediment into the lake each year (Brabets 2002). During the summer months (June – October) when runoff from glacial tributaries is highest, a turbidity gradient is established along the length of Lake Clark from the turbid (~10 NTUs) northeast to the clear (≤ 2 NTUs) southwest (Brabets 2002, Wilkens 2002).

OBJECTIVES

The objectives of this study were to:

1. Locate and map all major spawning aggregations, including those in glacial regions
2. Determine basic characteristics of spawning habitats
3. Determine the distribution of private land uses and subsistence/sport use locations in relation to salmon spawning habitats.

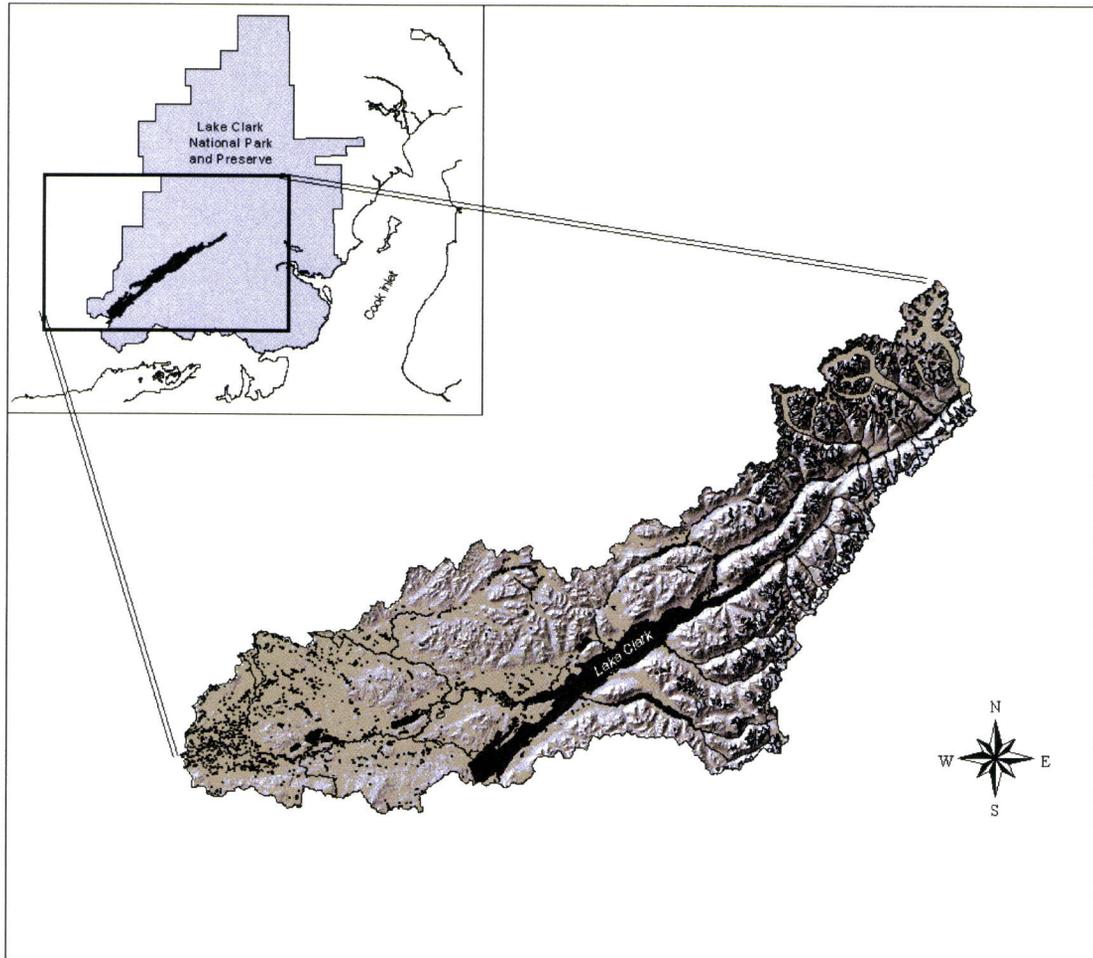


Figure 2. Lake Clark watershed in Lake Clark National Park and Preserve, Alaska.

METHODS

Spawning distribution

Radio telemetry was used to determine the spawning distribution of sockeye salmon in the Lake Clark watershed. Methods regarding radio tagging and tracking are briefly summarized below. Please refer to Young (2004) for more detailed description of these methods.

Adult sockeye salmon ($n = 332$; $n = 175$ in 2000; $n = 157$ in 2001) were captured with a nylon beach seine as they entered Lake Clark (Figure 3) 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 in the morning (0800 to 1359) and afternoon (1400 to 1959). Approximately six fish/day were tagged in 2000 and five fish/day were tagged in 2001. To tag a more representative sample of the run in 2001, 10 fish were tagged per day during large migrations as most sockeye salmon migrate into Lake Clark within two weeks (Poe and Rogers 1984, Woody 2004). Large migrations ($> 10,000$ fish/day) were identified at a counting tower located 10 km downstream of the tagging site (Woody 2004).

Tagged fish were tracked every one to ten days using fixed-wing aircraft or boats and 24 hours/day at fixed radio telemetry receivers (Figure 3). During aerial and boat tracking events, a GPS receiver recorded the location of the plane or boat when a tagged fish was detected (latitude and longitude in the North America Dataset 27 datum (NAD27)). Fixed telemetry receivers monitored fish passage within 400 m of the lakeshore based on tests with planted transmitters. Fish were tracked to within 1 km during initial aerial and boat surveys and to within 400 m during spawning surveys, based on field tests with planted transmitters. A fish was considered to be at its spawning location if (i) it was relocated within 400 m of its previous location at least twice within three weeks, (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 areas with limited visibility (glacially turbid beach and tributary habitats).

Spawning Activity

Sockeye salmon spawning activity within the Lake Clark drainage was assessed by visual observation in clear water habitats and by beach seine or tangle net in waters with limited visibility. Peak spawning was estimated as the time when half of the female salmon were in spawning condition and half were spawned out.

Characteristics of spawning habitat

Basic spawning habitat and water quality data were collected from a subset ($n = 9$ of 32) of spawning habitats identified in the Lake Clark watershed (K. Ramstad, University of Montana, unpublished data; Figure 3). Sampling sites were chosen to represent a range of habitat types (beach, inlet tributary, outlet tributary; glacial and non-glacial) at varying distances from each other throughout the Lake Clark system. An additional spawning habitat in the Tazimina River drainage (Figure 3) was also surveyed. At each spawning site four transects were established for sampling water quality and physical habitat parameters. Transects at riverine spawning areas

were perpendicular to the stream channel covering the wetted width from stream bank to stream bank. Transects at beach spawning sites were perpendicular to the shoreline from wetted shore to a depth of approximately one meter. Surface water temperature and turbidity measurements were collected at the beginning, middle and end of each transect. Surface water temperature ($^{\circ}\text{C}$) was measured to the nearest degree Celsius with a hand held thermometer. Incubation temperature ($^{\circ}\text{C}$) was measured intergravel with a StowAway Tidbit temperature logger (Onset Computer Corporation, Bourne, Massachusetts) from 11 October to 30 May. Turbidity (NTU) was measured with a pocket turbidimeter (Hach Company, Loveland, Colorado). Water depth (cm) was measured every meter along the transect using a fiberglass stadia rod. For each spawning site, an average temperature and turbidity value was calculated. The slope of beach spawning habitats was estimated as the distance from the lake shoreline to the offshore extent of the transect divided by water depth. Spawning substrate was estimated using the Wolman pebble-count technique (Wolman 1954, Kondolf 1992).

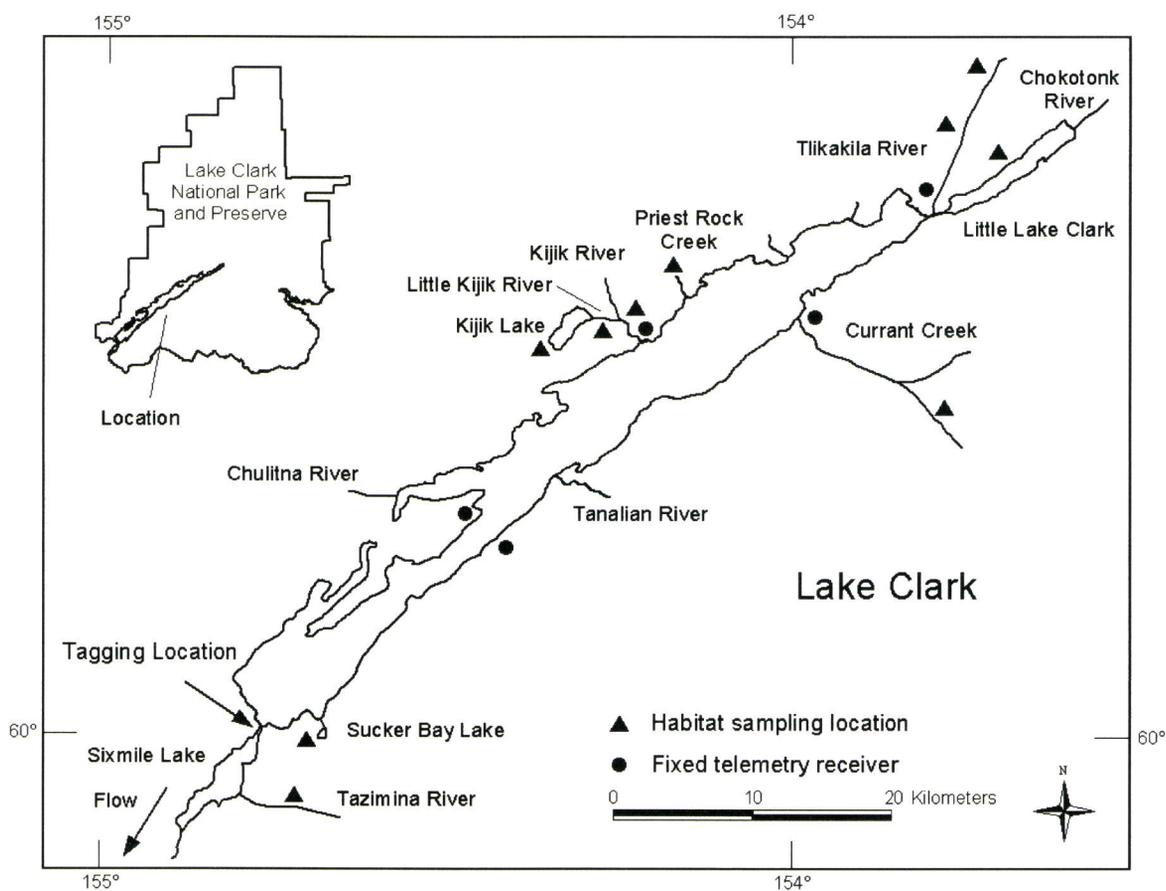


Figure 3. Location of tagging site, telemetry receivers, habitat sampling sites, and tributaries within the Lake Clark watershed.

Water quality data (conductivity, pH, dissolved oxygen, suspended sediments, and temperature) and stream discharge (m^3/s) were collected monthly from six tributaries of Lake Clark during a concurrent study (see methods in Brabets 2002). Although these water quality samples were not

collected at spawning habitats, they provide valuable information regarding general water quality within these tributaries.

Land ownership and development

Existing GIS coverages of land ownership were used to compare the location of spawning habitats relative to land ownership (National Park Service 2001). Current development within the Lake Clark watershed was documented by NPS staff during 2000 and 2001.

Subsistence and sport fishing use

Subsistence and sport fishing data were summarized using data collected during previous studies and during interviews with National Park Service (NPS) staff. Subsistence fishing areas were identified during Traditional Ecological Knowledge (TEK) studies in the Lake Clark area (Morris 1986, Stickman et al. 2003) and during patrols of the Lake Clark shoreline by NPS staff. Sport fishing locations were identified in the Lake Clark drainage by LACL staff during radio telemetry surveys and during a 1999 creel survey of the Kijik River drainage. Subsistence and sportfish harvest data were summarized from the Alaska Department of Fish and Game (ADFG) management reports.

RESULTS

Spawning distribution

Spawning locations were determined for 282 of 332 radio tagged sockeye salmon (Figure 4). 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 1). 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.

Spawning activity

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). Fish spawned earliest in Sucker Bay Lake and latest in the turbid waters of Little Lake Clark and Tlikakila River. Spawning activity was generally earlier in warmer water habitats and later in cooler water. For example, peak spawning in Tazimina River (12.9° C) and Lake Clark outlet (11° C) was in August/early September, whereas spawning in the spring-fed Priest Rock Creek (4.5° C) was in mid October (Appendix 2, Table 2 and 3).

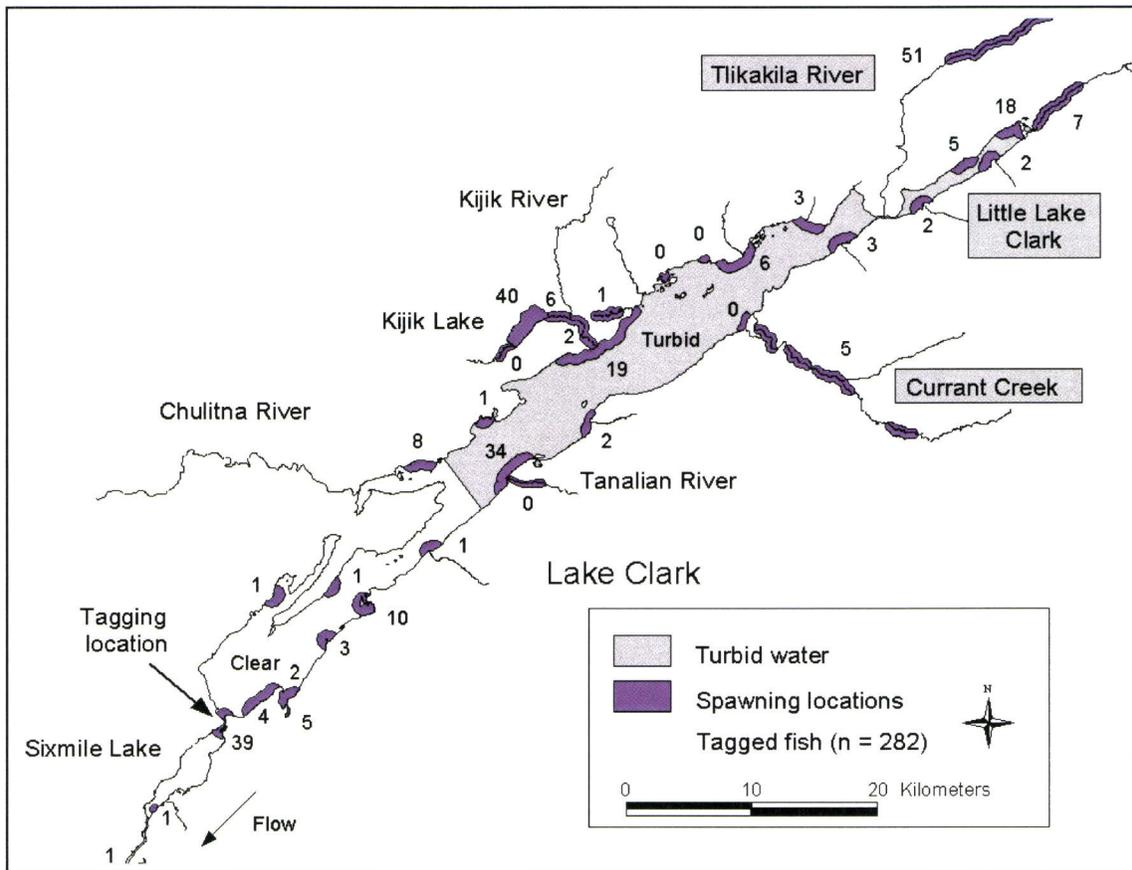


Figure 4. Spawning locations of radio tagged sockeye salmon in the Lake Clark watershed, 2000 and 2001. The number of tagged fish per spawning location is indicated. Five spawning locations (labeled with a 0) were located by visual observation or seining. Shaded areas indicate glacially turbid waters (≥ 5 NTU) with limited visibility.

Spawning activity in turbid locations in the Lake Clark watershed coincided with a dramatic decrease in suspended sediment concentrations and an increase in specific conductance. 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 (Appendix 2; Brabets 2002). The concentration further declined to 9 mg/L in October when peak spawning ended. During this same time period, specific conductance was 40 $\mu\text{s}/\text{cm}$, 32 $\mu\text{s}/\text{cm}$, 55 $\mu\text{s}/\text{cm}$, and 91 $\mu\text{s}/\text{cm}$ indicating an increased contribution of groundwater inflow to the system (Appendix 3; Brabets 2002).

Thirty two spawning areas were identified in the Lake Clark watershed (Figure 4, Appendix 2). 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 4, Appendix 2). An additional five spawning locations were identified in the Lake Clark watershed by visual observation or seining (Figure 4, Appendix 2). Although 32 spawning locations were identified

in the Lake Clark watershed, 70% of radio tagged fish returned to five spawning locations including the Tlikakila River (21%), the Kijik River drainage (20%), and beach spawning areas off the mouth of the Tanalian (14%), Kijik (8%), and Chokotonk Rivers (7%) (Figure 4, Appendix 2). Please see Young (2004) for more detailed results concerning migration patterns and spawning distribution of radio tagged fish.

Seventy percent of radio tagged fish returned to beach spawning sites and 30% returned to tributary rivers in the Lake Clark watershed (Table 1). Of the beach spawners, 57% spawned in Lake Clark, 24% in Kijik Lake, 16% in Little Lake Clark, and 3% in Sucker Bay Lake. Seventy one percent (n = 51) of the tributary spawners spawned in the Tlikakila River.

Table 1. Tagging and tracking summary for radio tagged adult sockeye salmon in Lake Clark watershed, 2000 and 2001.

Category	Number of salmon		
	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 area	134 (76%)	148 (94%)	282 (85%)
Spawning Distribution			
Downstream spawning areas*	35 (26%)	6 (4%)	41 (15%)
Lake Clark spawning areas	99 (74%)	142 (96%)	241 (85%)
Beach spawning habitat	71 (72%)	98 (69%)	169 (70%)
Tributary spawning habitat	28 (28%)	44 (31%)	72 (30%)

* Includes spawning areas at the outlet of Lake Clark, in Sixmile Lake, and in the Newhalen River (Figure 4).

Characteristics of Spawning Habitat

Beach spawning habitats were located in both glacially turbid (≥ 5 NTU) and clear (< 5 NTU) water and were typically next to inlet tributaries or springs (Table 2). The slope of beach spawning habitats ranged between 0.04 in Kijik Lake to 0.13 in Little Lake Clark. The spawning substrate at beach spawning habitats was predominately comprised of medium-sized gravel (≥ 4 mm, < 64 mm) except at Little Lake Clark where more than half of the substrate was large boulders (Table 2).

Table 2. Characteristics of spawning habitat in Lake Clark and Tazimina River watersheds. Mean water temperature during incubation (intergravel - 11 Oct to 30 May) and spawning (surface), mean turbidity during spawning, mean water depth, mean channel width, and percent frequency of small ($<4\text{mm}$), medium ($\geq 4, <64\text{mm}$), and large ($\leq 64\text{mm}$) substrate by spawning habitat (K. Ramstad, University of Montana, unpublished data).

Spawning location	Ecotype	Date	Temperature ($^{\circ}\text{C}$)			Turbidity (NTU)	Water depth (m)	Channel width (m)	Slope	Percent substrate		
			Incubation	Spawning	Spawning					Small	Medium	Large
Sucker Bay Lake	Beach	9/15/2000	3.0	11.3	11.3	2.7	0.68	0.07	11	41	49	
Kijik Lake S. Beach	Beach	10/5/2000	-	9.0	9.0	0.7	0.45	0.04	16	80	4	
Little Lake Clark	Beach	10/8/2000	-	6.4	6.4	11.6	0.83	0.13	2	32	66	
Tazimina River	Tributary	8/26/2001	1.3	12.9	12.9	0.4	0.60		11	75	14	
Kijik River	Tributary	9/20/2001	1.8	7.5	7.5	2.2	0.46		17	70	13	
Little Kijik River	Tributary	9/19/2000	3.0	11.0	11.0	0.6	0.47		10	87	3	
Priest Rock Creek	Tributary	10/11/2001	4.5	4.9	4.9	1.6	0.51		66	32	2	
Currant Creek	Tributary	9/24/2001	-	5.0	5.0	7.0	0.47		24	52	24	
Lower Tlikakila River	Tributary	10/12/2000	1.5	3.1	3.1	6.2	0.36		24	56	20	
Upper Tlikakila River	Tributary	9/26/2001	-	5.0	5.0	8.1	0.32		73	26	1	

Tributary spawning habitats were also located in both glacially turbid (≥ 5 NTU) and clear (< 5 NTU) water and were generally shallow (< 0.7 m) channels with small to medium sized substrate (Table 2). The average channel width ranged from 9 m in Currant Creek to 52 m in Little Kijik River. The average water depth for all tributary habitats was 0.46 meters and the shallowest stream channels were located in the Tlikakila River. Spawning activity in the Tlikakila River was generally confined to side-channels off the main river. Spawning substrate in tributary habitats was mostly comprised of medium-sized gravel except in the upper Tlikakila River and Priest Rock Creek which were dominated by small (< 4 mm) fines (Table 2).

Water quality and discharge data collected by Brabets (2002) were relatively consistent among tributaries (Table 3, Appendix 3). Specific conductance ranged between 45 $\mu\text{s}/\text{cm}$ and 91 $\mu\text{s}/\text{cm}$, pH ranged between 7.0 and 7.5, and dissolved oxygen ranged between 10.3 mg/L and 16.5 mg/L for all sites (Table 3). Suspended sediment concentrations were greatest in the glacier-fed Tlikakila River and Currant Creek. Stream discharge ranged between 7 m^3/s and 87 m^3/s except for at the outlet of Lake Clark which ranged between 246 m^3/s and 433 m^3/s (Table 3). Water temperatures ranged from a low of 0.0° C in Chokotonk and Tlikakila Rivers to a high of 13.0° C in the Tazimina River (Table 3).

Table 3. Characteristics of tributary inputs to Lake Clark at time of spawning activity 1999 - 2001 (From Brabets 2002).

Tributary	Discharge (m^3/s)	Specific conductance ($\mu\text{s}/\text{cm}$)	pH	Water temperature (°C)	Dissolved oxygen (mg/L)	Suspended sediments (mg/L)
Chokotonk River	7	45 - 74	7.1 - 7.2	0.0 - 6.5	11.6 - 12.2	9
Currant Creek	8 - 25	55 - 74	7.0 - 7.4	2.0 - 6.5	11.6 - 14.9	3 - 25
Kijik River	12 - 22	85 - 88	7.0 - 7.3	3.5 - 8.5	11.2 - 13.5	2 - 6
Lake Clark Outlet	246 - 433	57 - 62	7.0 - 7.3	8.5 - 11.0	10.8 - 12.4	1 - 5
Tanalian River	13 - 18	44 - 52	7.0 - 7.2	5.5 - 10.5	10.3 - 12.0	1 - 3
Tlikakila River	21 - 87	55 - 91	7.2 - 7.5	0.0 - 8.0	11 - 16.5	9 - 118

Land ownership and development

Seventy five percent of the spawning areas were adjacent to private or Native corporation lands (Figure 7; National Park Service 2001). Non-Federal lands in the Lake Clark watershed are comprised of Native corporation land, native allotments, subdivided corporation or allotments, and private parcels. Four Native corporations including Kijik Corporation, Tanalian Incorporated, Bristol Bay Native Corporation (BBNC), and Cook Inlet Region Incorporated (CIRI) own or have selected land adjacent to spawning areas in the Lake Clark watershed. Lands adjacent to spawning areas in the Kijik Lake drainage have been selected (pending conveyance) by CIRI. Kijik Corporation owns the surface property rights on land adjacent to spawning areas in the southwest region of the watershed while BBNC owns the subsurface property rights. Tanalian Incorporated owns land adjacent to spawning areas near the community of Port Alsworth (population 103) on the south shore of Lake Clark. There are more than 100 individual parcels of land along the Lake Clark shoreline including native allotments, subdivisions (Keyes Point, Portage Creek, and Dice Bay), and land associated with the town of Port Alsworth.

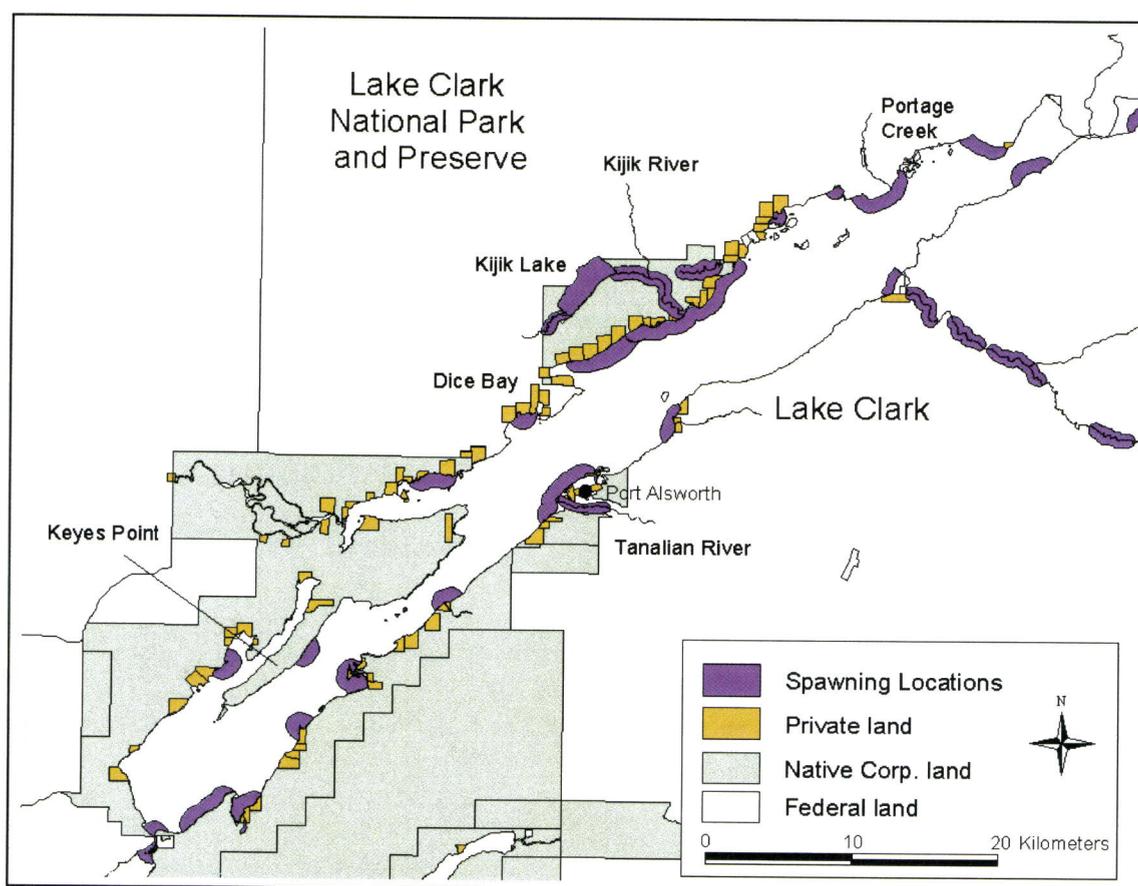


Figure 5. Spawning locations relative to land ownership within the Lake Clark watershed (National Park Service 2001). Seventy five percent of the spawning sites identified in the Lake Clark watershed were adjacent to private land, and most of this land (73%) remains undeveloped.

More (61%) radio tagged fish returned to spawning areas adjacent to private land than federally protected land, and most (74%) returned to areas that are currently undeveloped. Current development is primarily limited to seasonal and year-round residences and fishing/hunting lodges. Access to these lands is provided by boat or aircraft. Several small roads connect parcels of land within Port Alsworth and Keyes Point. Small runways provide access to private parcels at Tommy Creek, Miller Creek, Kijik Outlet, Chulitna Bay, and Dice Bay and large runways (3000 - 4000 ft) provide access to the communities at Port Alsworth and Keyes Point (Figure 7). The greatest concentration of development adjacent to a spawning habitat is located on the southwest shore of Lake Clark in the community of Port Alsworth. Other areas of concentrated development adjacent to spawning areas include Keyes Point subdivision and Stinson Lake subdivision at Dice Bay. The Keyes Point subdivision is composed primarily of summer cabins and currently has small (2.5 acres) lots for sale at an affordable price (\$15,000).

Subsistence and sport fishing use

Subsistence fishing was documented throughout Lake Clark with most fishing occurring near permanent residences, seasonal fish camps, or spawning areas (Figure 5; Morris 1986, Stickman et al. 2003). Subsistence fishing occurs in July and August for migrating sockeye salmon and in September and October for redfish (spawning sockeye salmon). The harvest of salmon in July/August occurs along the shoreline of Lake Clark adjacent to permanent residences or seasonal fish camps whereas the harvest of redfish in September/October occurs at spawning sites. The primary redfish harvest location within Lake Clark is at the outlet of the Kijik River adjacent to historic Kijik Village.

Sockeye salmon harvests by Port Alsworth subsistence permit holders from the period 2001 to 2003 averaged 1,510 fish, compared to a recent 10-year average (1991 to 2000) of 3,067 sockeye salmon (Table 4; ADFG 2004).

Sport fishing for Lake Clark sockeye salmon is limited within the Lake Clark watershed and primarily occurs outside the park boundary at the outlet of Iliamna Lake (Kvichak River) and along the Newhalen River (Figure 1; Dunaway and Jaenicke 2000). During the period 1993 to 1997 the sport fish harvest for sockeye salmon in the Kvichak River and Newhalen River was 2,730 fish and 6,991 fish respectively (Table 5). In contrast, the harvest of sockeye salmon from Lake Clark during this same time period was 497 fish (Table 5; Dunaway and Sonnichsen 2000). During the period 2000 to 2003, the average sport fish harvest of sockeye salmon from Lake Clark was 242 fish (Walker et al. 2003, Jennings et al. 2004, ADFG^d, ADFG^f).

Within the Lake Clark drainage, anglers fish for sockeye salmon from mid July to mid August at the outlet of Lake Clark, the mouth of the outlet tributary for Sucker Bay Lake, the mouth of the Tanalian River, the mouth of Kijik River, and within the Kijik Lake drainage (Figure 6). Within the Kijik system, anglers primarily fish large pools in the upper and lower sections of the Little Kijik River. In 1999, anglers harvested 57 sockeye salmon from the Kijik Lake drainage between 1 August and 16 August (unpublished data).

Table 4. Subsistence harvest of sockeye salmon by community, in numbers of fish, Kvichak River drainage, Bristol Bay, 1983-03^{ab} (From ADFG 2004).

Year	Levelock	Igiugig	Pedro Bay	Kokhanok	Iliamna-Newhalen	Nondalton	Port Alsworth	Other ^e	Total
1983	4,800	3,300	10,400	20,100	23,800	29,400	4,700		96,500
1984	8,100	6,300	12,100	24,400	15,900	29,100	4,600		100,500
1985	6,600	3,400	12,900	21,900	22,300	14,900	4,500		86,500
1986	6,400	1,600	6,700	18,300	17,000	6,600	3,300		59,900
1987	5,700	c	7,300	16,500	27,500	11,800	3,200		72,000
1988	3,500	c	5,500	14,400	29,800	20,700	3,200	d	77,100
1989	5,100	1,200	6,700	13,000	24,700	18,500	2,200	d	71,400
1990	4,700	2,200	6,600	12,400	18,800	27,300	3,200	1,400	76,600
1991	1,029	1,712	9,739	17,184	29,094	4,163	2,755	1,110	66,786
1992	4,374	1,056	6,932	11,477	29,633	13,163	2,954	2,559	72,148
1993	4,699	1,397	6,226	18,810	19,067	17,890	3,254	2,780	74,123
1994	1,467	1,201	8,747	15,771	15,553	15,246	3,074	3,284	64,343
1995	3,756	497	5,359	14,412	20,134	4,188	2,892	3,441	54,679
1996	1,120	2,309	5,219	14,011	14,787	11,856	3,263	2,307	54,872
1997	1,062	2,067	5,501	8,722	19,513	17,194	2,348	3,101	59,508
1998	2,454	1,659	3,511	10,418	16,165	13,136	2,678	3,635	53,656
1999	1,276	1,608	5,005	10,725	14,129	17,864	4,282	2,834	57,723
2000	1,467	1,981	1,815	7,175	6,679	11,953	3,200	2,720	36,990
2001	908	779	2,118	9,447	8,132	7,566	1,958	1,901	32,808
2002	625	2,138	2,687	9,847	9,417	5,508	1,201	1,578	33,001
2003	737	1,081	2,135	9,771	13,824	8,016	1,370	1,591	38,495
20 Year Avg.	3,457	2,022	6,553	14,450	19,105	14,901	3,138	2,512	65,057
1983-92	5,030	2,596	8,487	16,966	23,853	17,563	3,461	1,690	77,943
1993-02	1,883	1,564	4,619	11,934	14,358	12,240	2,815	2,758	52,170

^a Harvests are extrapolated for all permits issued, based on those returned. Harvest estimates from 1991 are rounded to the nearest hundred fish.

^b Harvest estimates prior to 1990 are based on the community where the permit was issued; estimates from 1990 to the present are based on community of residence and include fish caught only in the Kvichak District.

^c No permits issued.

^d No permits issued. Only residents of the Naknek/Kvichak watershed could obtain subsistence permits.

^e Subsistence harvests by non-Kvichak River watershed residents.

Table 5. Sport fish harvest of sockeye salmon by location, in numbers of fish, Kvichak River drainage, Bristol Bay, 1977 -2003 (modified from ADFG management reports^{abcde}).

Year	Kvichak River	Newhalen River	Lake Clark
1977	583	805	420
1978	380	1,479	648
1979	283	1,163	1,022
1980	654	715	155
1981	400	1,490	292
1982	639	1,786	220
1983	603	1,671	603
1984	898	2,581	449
1985	1,827	2,623	106
1986	102	238	0
1987	1,805	4,185	110
1988	526	2,414	0
1989	4,769	14,508	252
1990	2,988	6,093	246
1991	1,249	9,523	143
1992	1,964	6,509	510
1993	2,923	9,889	297
1994	4,001	7,973	782
1995	3,811	7,859	800
1996	2,139	4,795	91
1997	778	4,440	515
1998	2,910	6,830	159
1999	3,516	6,356	161
2000	3,554	3,414	148
2001	4,017		473
2002	2,147		34
2003	2,754		314
Average	1,934	4,556	331

^a 1977 - 1998 data summarized in Dunaway and Sonnichsen (2001)

^b 1999 data from Howe et al. (2001)

^c 2000 data from Walker et al. (2003)

^d 2001 data from Jennings et al. (2004)

^e 2002 – 2003 data from ADFG website (ADFG^d ADFG^f)

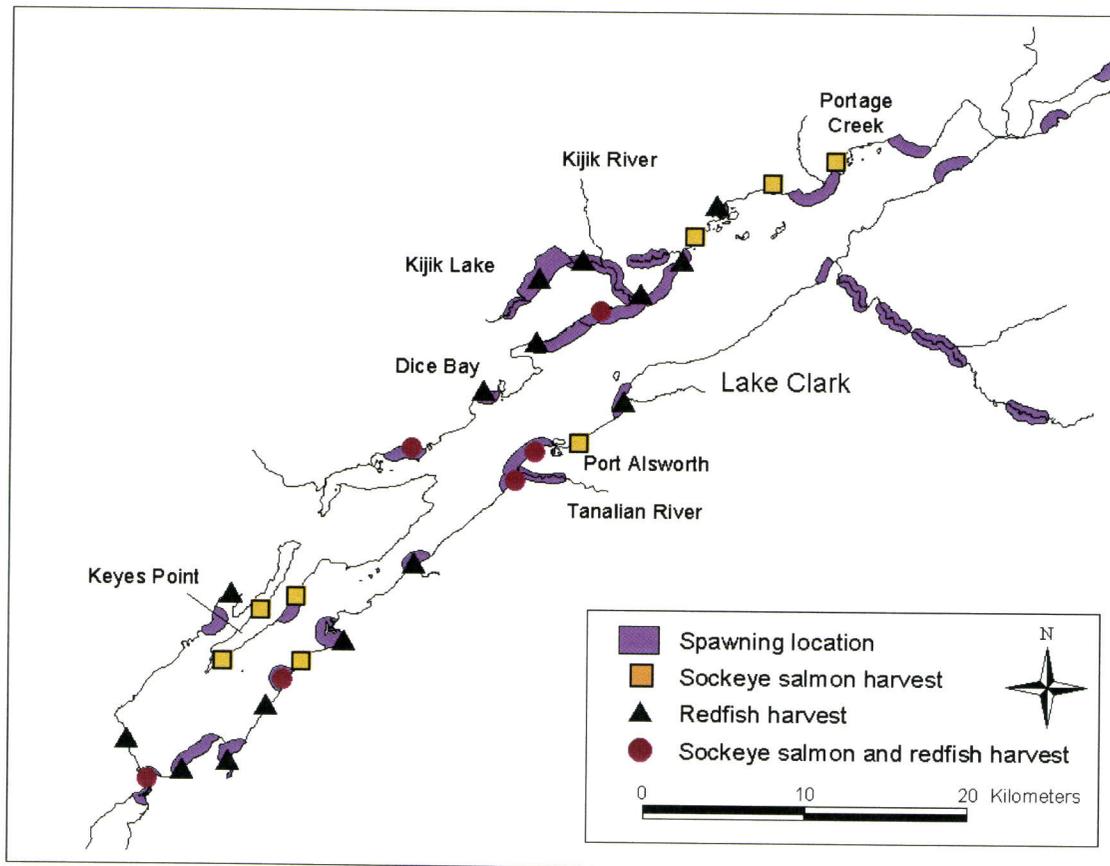


Figure 6. Subsistence fishing use within the Lake Clark watershed. Harvests of sockeye salmon occur both in July when salmon enter the system (sockeye salmon harvest) and in September/October when salmon are at spawning locations (redfish harvest).

DISCUSSION

Spawning locations for sockeye salmon have been underestimated in the Lake Clark watershed. Compared to previous scientific research (Demory et al. 1964, Smith 1964, Anderson 1968, Russell 1980, Jensen and Mathisen 1987, Parker and Blair 1987, Regnart 1998), this study documented 18 new spawning locations. Compared to traditional ecological knowledge, 10 new spawning locations were identified (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 65% of Lake Clark sockeye salmon spawn in glacially turbid locations (Figure 4). Glacially turbid waters have obviously limited the accurate assessment of sockeye salmon spawning locations and distribution in the Lake Clark watershed.

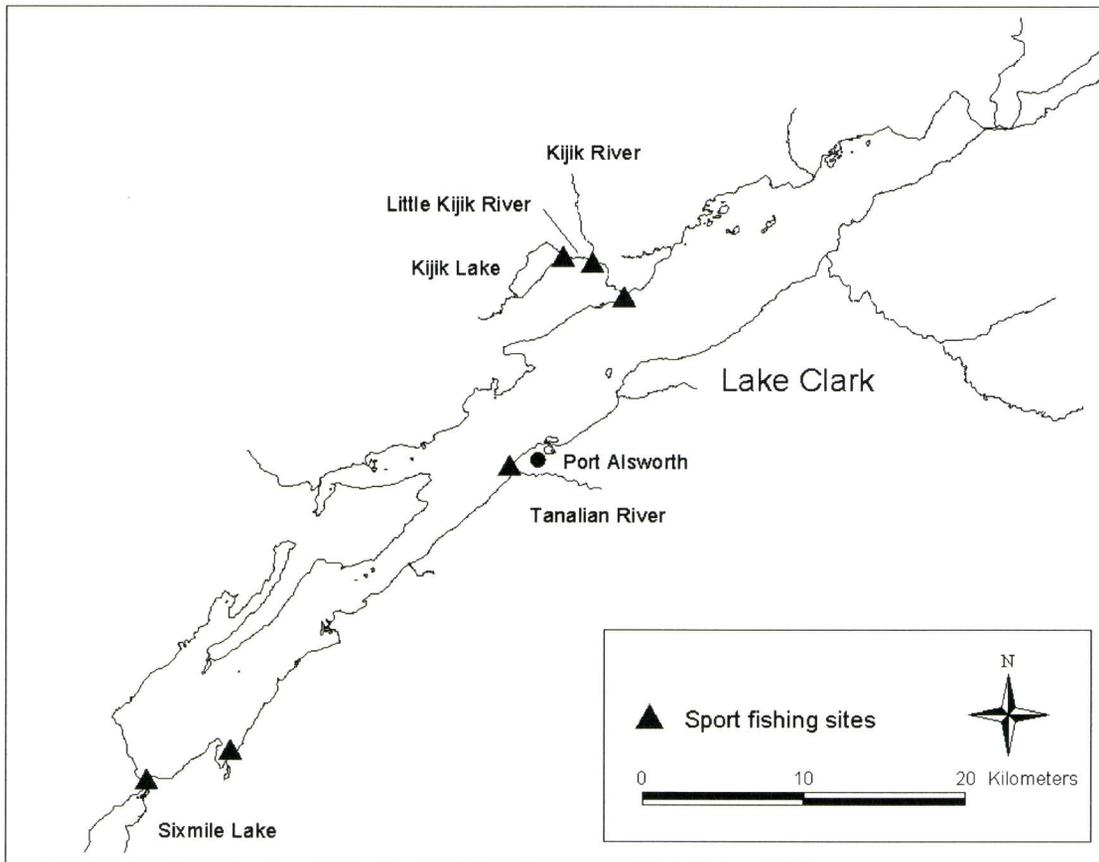


Figure 7. Sport fishing use for sockeye salmon within the Lake Clark watershed.

Radio telemetry was an effective tool to identify sockeye salmon spawning habitat within the Lake Clark watershed. Seventy-six percent of tagged fish were tracked to spawning areas in 2000 and 94% in 2001. During both years of the study, most tagged fish were tracked to spawning areas within the Lake Clark drainage. In 2000, however, 26% of tagged fish migrated to a spawning area just downstream of the tagging site. While some of these fish may have been affected by the clove oil anesthetic or died after tagging, it is more likely these fish were captured while milling in close proximity to their spawning location. Of the fish tracked downstream, most were captured after August 9, 2000 and displayed phenotypic characteristics of spawning sockeye salmon. In 2001, the tagging period was shortened and less than 5% of tagged fish were tracked to downstream spawning areas.

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.

Water quality data collected from spawning habitats and tributaries of Lake Clark (Brabets 2002) were within acceptable levels for sockeye salmon spawning and survival. All pH observations were near neutral and within the EPA's criteria (pH range of 6.5 – 9.0) for freshwater aquatic life (USEPA 1987). Dissolved oxygen ranged between 9.4 mg/L and 14.9 mg/L, which were within the acceptable range for spawning sockeye salmon (Bjornn and Reiser 1991). Turbidity values and suspended sediment concentrations were highest in the glacial rivers and Little Lake Clark but still within state standards for streams and lakes (Lloyd 1987).

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).

Surface water temperatures measured at spawning sites (Table 2) and tributaries (Table 3) were mostly within acceptable levels for sockeye salmon (Reiser and Bjornn 1991). Surface water and incubation temperatures measured at spawning habitats were sufficient for sockeye salmon spawning activity and incubation. Surface water temperatures measured at the outlet of the Tlikakila and Chokotonk Rivers (Table 3; Brabets 2002), however, were not sufficient for salmon survival and not surprisingly, no spawning activity was documented in these areas.

Spawning substrate was variable among Lake Clark sites yet within acceptable ranges for sockeye salmon spawning habitat. Generally, sockeye salmon prefer spawning habitat with small to medium sized gravel (Burgner 1991) such as was found in Tazimina River and the Kijik Lake drainage (Table 2). The large concentration of small substrate observed in the headwaters of the Tlikakila River was similar to what has been documented in sockeye salmon redds in the glacier-fed Taku River in southeast Alaska (Lorenz and Eiler 1991). The large percentage of larger substrate in Little Lake Clark was similar to spawning habitats in other sockeye systems (see reviews by Foerster 1968, Burgner 1991). Spawning substrate samples in Priest Rock Creek may be biased toward small fines because there were fewer than one hundred fish to remove fine sediment from the spawning gravels, and beaver activity in the area has increased sedimentation of the spawning habitat.

Turbid water and poor visibility limited the assessment of beach spawning habitats in Lake Clark and Little Lake Clark. While spawning activity was confirmed in these areas, habitat assessment was limited. In Little Lake Clark, substrate samples were collected in shallow, turbid water and may not represent habitat used by spawning salmon. Further work is needed to more precisely define beach spawning habitats in turbid habitats. Hydroacoustics could be used to delineate critical spawning habitat and focus future habitat studies.

Subsistence and sport harvests of sockeye salmon within the Lake Clark watershed are currently at low levels and represent less than one percent of the annual escapement of sockeye salmon to

Lake Clark (Poe and Rogers 1984, Woody 2004). In contrast, commercial fisheries in Bristol Bay harvest, on average, 53% of the annual sockeye salmon return to the Kvichak, Alagnak, and Naknek Rivers (Appendix 4).

Recent declines in the subsistence and sport harvests of sockeye salmon in the Kvichak River drainage are likely the result of decreased salmon escapement to the system (Table 4, Table 5, Appendix 4). The Kvichak River system has failed to reach its minimum escapement goal in seven of the last nine years (ADFG 2004). An especially low return of sockeye salmon in 2000 caused the ADFG to close the sport fishery (ADFG^a). In 2001, 2002, and 2003 limits on the sport fishing harvest were similarly enacted due to poor returns (ADFG^b ADFG^c, ADFG^e).

Decreased subsistence harvest of sockeye salmon in the Lake Clark watershed may also be the result of recent NPS restrictions on subsistence fisheries. On May 21, 2001, subsistence fishing with nets in LACL, including all of Lake Clark, was restricted to federally qualified local rural residents. This restriction applies to anyone who is not a permanent resident of Iliamna, Lime Village, Newhalen, Nondalton, Pedro Bay, or Port Alsworth, or who does not have a Section 13.44 subsistence use permit issued by the park superintendent. Prior to this restriction, any Alaskan resident was eligible to harvest subsistence fish from Lake Clark. Since the restriction was established, fewer permits have been issued and the subsistence harvest for sockeye salmon has decreased (ADFG 2003).

Development on private lands could harm important salmon spawning habitat in the Lake Clark watershed. Spawning areas most susceptible to future development on privately owned land include Kijik Lake and associated drainages, Tanalian Point/Port Alsworth, Dice Bay, and Keyes Point. As the number of permanent and seasonal residents increase in the Lake Clark area, more private land will be subdivided, sold, and developed. For example, subdivisions have recently been created in the Dice Bay and Keyes Point areas. Construction and land clearing at these sites could harm spawning habitats. Similarly, development in the Kijik River drainage and in Port Alsworth has the potential to impact a large proportion of Lake Clark spawning sockeye salmon. Further, proposed bridges across the Tanalian River and Newhalen River, as well as proposed mining activity in the headwaters of the Chulitna River, could adversely affect water quality and habitat critical for Lake Clark sockeye salmon spawning and rearing.

LITERATURE CITED

- ADFG^a. 2000 Southcentral – Region 2 Sport Fishing Emergency Order No.: 2-RS-5-13-00. Alaska Department of Fish and Game, Division of Sport Fish.
<http://www.sf.adfg.state.ak.us/statewide/eonr/index.cfm>
- ADFG^b. 2001 Southcentral – Region 2 Sport Fishing Emergency Order No.: 2-RS-5-12-01. Alaska Department of Fish and Game, Division of Sport Fish.
<http://www.sf.adfg.state.ak.us/statewide/eonr/index.cfm>
- ADFG^c. 2002 Southcentral – Region 2 Sport Fishing Emergency Order No.: 2-RS-5-09-02. Alaska Department of Fish and Game, Division of Sport Fish.
<http://www.sf.adfg.state.ak.us/statewide/eonr/index.cfm>

- ADFG^d. Kvichak River drainage area sport fish harvest and effort by fisheries and species, 2002, Alaska Department of Fish and Game, Division of Sport Fish.
<http://www.sf.adfg.state.ak.us/Statewide/ParticipationAndHarvest/main.cfm>
- ADFG^e. Southcentral – Region 2 Sport Fishing Emergency Order No.: 2-RS-5-11-03; Alaska Department of Fish and Game, Division of Sport Fish.
<http://www.sf.adfg.state.ak.us/statewide/eonr/index.cfm>
- ADFG^f. Kvichak River drainage area sport fish harvest and effort by fisheries and species, 2003; Alaska Department of Fish and Game, Division of Sport Fish.
<http://www.sf.adfg.state.ak.us/Statewide/ParticipationAndHarvest/main.cfm>
- ADFG^g. 2004 Bristol Bay salmon fishery season summary. Alaska Department of Fish and Game, Division of Commercial Fisheries.
<http://www.cf.adfg.state.ak.us/region2/finfish/salmon/bbayhome.php>
- ADFG. 2001. Alaska Department of Fish and Game Division of Commercial Fisheries annual management report, 2000, Bristol Bay Area. Anchorage, Alaska.
- ADFG. 2003. Alaska Subsistence Fisheries 2002 Annual Report. Alaska Department of Fish and Game, Division of Subsistence. Juneau, Alaska.
- ADFG. 2004. Alaska Department of Fish and Game Division of Commercial Fisheries Annual Management Report, 2003, Bristol Bay Area. Anchorage, Alaska.
- Anderson, J.W. 1968. Addendum to spawning ground catalog of the Kvichak River system, Bristol Bay, Alaska. University of Washington, Fisheries Research Institute Circular No. 68-2.
- Anderson, J.W. 1969. Bathymetric measurements of Iliamna Lake and Lake Clark, Alaska. University of Washington, Fisheries Research Institute Circular No. 69-17.
- 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.
- Bennett, A.J. 1995. Bald eagle productivity in Lake Clark National Park and Preserve. Unpublished Progress Report. National Park Service-LACL, Port Alsworth, 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 of the sockeye salmon in a glacially turbid lake: evidence for population differentiation. Transactions American Fisheries Society 124: 1-15.

- Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1-117 in Groot, C., and L. Margolis, editors. Pacific Salmon Life Histories, University of British Columbia Press, Vancouver, British Columbia, Canada.
- Bjornn, T.C., and D.W. Reiser. 1991. Habitat requirements of salmonids in streams. American Fisheries Society Special Publication 19: 83-138.
- 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.
- Dunaway, D.O., and M.J. Jaenicke. 2000. Area management report for the recreational fisheries of the Southwest Alaska Sport Fish Management Area, 1998. Alaska Department of Fish and Game, Fishery Management Report No. 00-3, Anchorage.
- Dunaway, D.O., and S. Sonnichsen. 2001. Area management report for the recreational fisheries of the Southwest Alaska Sport Fish Management Area, 1999. Alaska Department of Fish and Game, Fishery Management Report No. 01-6, Anchorage.
- Foerster, R.E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Fisheries Research Board of Canada Bulletin 162.
- Howe, A.L., R.J. Walker, C. Olness, K. Sundet, and A.E. Bingham. 2001. Participation, catch, and harvest in Alaska sport fisheries during 1999. Alaska Department of Fish and Game, Fishery Data Series No. 01-8, Anchorage.
- Jennings, G.B., K. Sundet, A.E. Bingham, and D. Sigurdsson. 2004. Participation, catch, and harvest in Alaska sport fisheries during 2001. Alaska Department of Fish and Game, Fishery Data Series No. 04-11, Anchorage.
- 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 [ed.]. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Government of Canada, Department of Fisheries and Oceans, Ottawa, Ontario
- Jones, S.H., and C.B. Fahl. 1994. Magnitude and frequency of floods in Alaska and conterminous basins of Canada: U.S. Geological Survey Water-Resources Investigations Report 93-4179.
- 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: II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

- evidence of the Kvichak River watershed, Bristol Bay, southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2350-2365.
- Kondolf, G.M. 1992. The Pebble Count Technique for Quantifying Surface Bed Material Size in Instream Flow Studies. *Rivers* 3: 80-87.
- Lloyd, D.S. 1987. Turbidity as a water quality standard for salmonid habitats in Alaska. *North American Journal of Fisheries Management* 7: 34-45.
- 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.
- 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.
- 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 ground in the Lake Clark-Tazimina River watershed. University of Washington, Fisheries Research Institute FRI-UW-8703.
- 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.
- Ramstad, K.M. 2002. Historical sockeye salmon data of Lake Clark, Alaska. Unpublished report, Lake Clark National Park and Preserve, Port Alsworth, Alaska.
- 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.
- Reiser, D.W. and Bjornn, T.C. 1979. Habitat requirements of anadromous salmonids. General Technical Report PNW-96. U.S. Department of Agriculture, Portland, Oregon.
- Regnart, J.R. 1998. Kvichak River sockeye salmon spawning ground surveys, 1955-1998. Alaska Department of Fish and Game, Regional Information Report 2A98-38.
- Russell, R. 1980. A fisheries inventory of waters in the Lake Clark National Monument area. Alaska Department Fish Game.
- 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. USFWS Office of Subsistence Management, Fisheries Resource Monitoring Program, Final Report No. FIS 01-075, Anchorage, Alaska.
- Unrau, H.D. 1992. Lake Clark National Park and Preserve historic resource study. U. S. Department of Interior. National Park Service. Anchorage, Alaska.
- USEPA. U.S. Environmental Protection Agency. 1987. Quality Criteria for Water. EPA Publication 440/5-86- 001. United States Government Printing Office, Washington D.C.
- Walker R.J., C. Olnes, K. Sundet, A.L. Howe, and A.E. Bingham. 2003. Participation, catch, and harvest in Alaska sport fisheries during 2000. Alaska Department of Fish and Game, Fishery Data Series No. 03-05, Anchorage.
- Wilkins, A.X. 2002. The limnology of Lake Clark, Alaska. Masters thesis. University of Alaska Fairbanks.
- Willson, M.F. 1995. Biodiversity and ecological processes. *in* R. Szaro, editor, Biodiversity in managed landscapes. Oxford University Press, New York.
- Willson, M. and K. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. *Conservation Biology* 9: 489-497.
- Wolman, M.G. 1954. A method of sampling coarse river-bed material. *Transactions of the American Geophysical Union* 35: 951-956.
- Woody, C.A., K.M. Ramstad, D.B. Young, G.K. Sage and F.W. Allendorf. 2003. Lake Clark sockeye salmon population assessment. Final report for study 00-042 U. S. Fish and Wildlife Service, Office of Subsistence Management.
- 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.
- Young, D.B. 2004. The migration and spawning distribution of sockeye salmon within Lake Clark, Alaska. Masters thesis. University of Alaska Fairbanks.

APPENDIX

Appendix 1. Lake Clark and Kvichak River sockeye salmon escapement, in numbers of fish, from 1980 – 1984 and 2000 – 2004 (modified from ADFG 2004 and Woody 2004).

Year	Lake Clark escapement ^{abc}	% of Kvichak	Kvichak River escapement ^d
1980	1,502,898	7	22,505,268
1981	231,714	13	1,754,358
1982	147,294	13	1,134,840
1983	702,792	20	3,569,982
1984	3,091,620	29	10,490,670
2000	172,902	10	1,827,780
2001	222,414	20	1,095,348
2002	203,670	29	703,884
2003	264,690	16	1,686,804
2004	554,520	10	5,463,942
1980 - 1984 Average	1,135,264	16	7,891,024
2000 - 2004 Average	283,639	17	2,155,552

^a 1980 - 1984 data from Poe and Rogers (1984)

^b 2000 - 2003 data from Woody (2004)

^c 2004 data unpublished, National Park Service, Port Alsworth, Alaska

^d ADFG (2004)

Appendix 2. Spawning locations identified by radio telemetry and visual observation in Lake Clark, 2000 and 2001. Distance was calculated from the tagging site at the outlet of Lake Clark. Private land and Development adjacent to spawning areas were recorded as present (Yes = Y) or not present (No = N).

ID	Drainage	Specific location	Latitude	Longitude	Habitat type	Spawning activity	Distance (km)	Private land	Development	Number of tagged fish		
										2000	2001	Total
1	Newhalen River ^a	Horseshoe Bend ^a	59.8824614	-154.8709529	Tributary		19	-		0	1	1
2	Sixmile Lake ^a	Simile lake ^a	59.9548997	-154.8532472	Beach		8	-		0	1	1
3	Sixmile Lake ^a	Lake Clark outlet ^a	60.0196571	-154.7575543	Tributary	8/25-9/15	1	N	N	35	4	39
4	Lake Clark	Outlet South	60.0268979	-154.7133590	Beach	9/1-9/30	4	Y	N	1	3	4
5	Lake Clark	Sucker Bay	60.0357855	-154.6573315	Beach	9/1-9/30	8	Y	N	1	1	2
6	Sucker Bay Lake	Sucker Bay Lake	60.0215469	-154.6636382	Beach	8/25-9/15	9	Y	N	3	2	5
7	Lake Clark	Snowshoe Bay	60.1067853	-154.6851025	Beach	9/1-9/30	11	Y	N	0	1	1
8	Lake Clark	Chi Point	60.0755617	-154.6042180	Beach	9/1-9/30	12	Y	Y	2	1	3
9	Lake Clark	Keyes Point	60.1147003	-154.6036866	Beach	9/1-9/30	15	Y	Y	0	1	1
10	Lake Clark	Flat Island	60.0981051	-154.5407755	Beach	9/1-10/15	16	Y	N	3	7	10
11	Lake Clark	22 Creek	60.1413319	-154.4593394	Beach	9/15-9/30	22	Y	Y	1	0	1
12	Lake Clark	Chulitna Bay	60.2049753	-154.4763469	Beach	9/15-10/15	30	Y	N	2	5	7
13	Lake Clark	Tanalian Point	60.1939450	-154.3508224	Beach	9/15-10/15	31	Y	Y	17	17	34
14	Tanalian River ^b	Tanalian River ^b	60.1858212	-154.2740385	Tributary	9/15-9/30	31	Y	N	0	0	0
15	Lake Clark	Dice Bay	60.2348902	-154.3872065	Beach	9/1-9/30	33	Y	N	0	1	1
16	Lake Clark	Tommy	60.2285721	-154.2337341	Beach	9/15-10/15	38	Y	Y	2	0	2
17	Lake Clark	Kijik Outlet	60.2807490	-154.2648977	Beach	9/15-10/15	41	Y	Y	12	7	19
18	Kijik Lake	Kijik River	60.2978737	-154.2432988	Tributary	9/15-10/15	45	Y	N	2	0	2
19	Kijik Lake	Little Kijik River	60.3078998	-154.2932831	Tributary	9/15-10/15	49	Y	N	5	1	6
20	Lake Clark	Aggie's Beach ^b	60.33869	-154.13223	Beach	9/15-10/15	49	Y	Y	0	0	0
21	Priest Rock Creek	Priest Rock Creek	60.3084707	-154.2287282	Tributary	9/25-10/15	52	Y	N	0	1	1
22	Lake Clark	Currant Outlet Beach ^b	60.29969	-154.01009	Beach	9/15-10/15	52	Y	N	0	0	0
23	Kijik Lake	Kijik Lake	60.2870340	-154.3447792	Beach	9/15-10/31	52	Y	N	21	19	40
24	Kijik Lake ^b	Kijik Lake Tributaries ^b	60.28577	-154.34395	Tributary	9/25-10/15	53	Y	N	0	0	0
25	Lake Clark	Corey's Beach ^b	60.35162	-154.06406	Beach	9/15-10/15	53	Y	Y	0	0	0
26	Lake Clark	Portage Creek	60.3458561	-154.0298919	Beach	9/15-10/15	54	Y	N	3	3	6
27	Currant Creek	Currant Creek	60.2292195	-153.8007299	Tributary	9/15-9/30	57	N	N	2	3	5
28	Lake Clark	Hatchet Point	60.3745545	-153.9141226	Beach	9/15-10/15	62	Y	Y	0	3	3

-Continued-

Appendix 2. (page 2 of 2).

ID	Drainage	Specific location	Latitude	Longitude	Habitat type	Spawning activity	Distance (km)	Private land	Develop-ment	Number of tagged fish		
										2000	2001	Total
29	Lake Clark	Middle Ridge	60.3607695	-153.8619178	Beach	9/15-10/15	64	N	N	1	2	3
30	Little Lake Clark	Cave Falls	60.3856850	-153.7529883	Beach	9/15-10/15	71	N	N	0	2	2
31	Little Lake Clark	Little Lake Clark N	60.4183515	-153.6965771	Beach	9/15-10/15	76	N	N	0	5	5
32	Little Lake Clark	Little Lake Clark S	60.4175140	-153.6557679	Beach	9/15-10/15	77	N	N	0	2	2
33	Little Lake Clark	Chokotonk Outlet	60.4437421	-153.6218053	Beach	9/15-10/31	80	N	N	2	16	18
34	Little Lake Clark	Chokotonk River	60.4669812	-153.5423128	Tributary	9/15-10/15	86	N	N	1	6	7
35	Tiikakila River	Tiikakila River	60.5537441	-153.5067036	Tributary	9/15-10/15	98	N	N	18	33	51

^a Identified by radio telemetry, but not included in estimates of spawning distribution.

^b Identified by visual observation or seining – no radio tags were tracked to this location.

Appendix 3. Physical properties and water-quality characteristics of streamflow samples collected from the tributaries of Lake Clark, 1999 through 2001 (modified from Brabets 2002)

Tributary	Date	Discharge (m ³ /s)	Specific conductance (µs/cm)	pH	Water temperature (°C)	Dissolved oxygen (mg/L)	Suspended sediments (mg/L)
Chokotonk River	10/14/1999	7	74	7.1	0.0	11.6	9
Chokotonk River	9/17/2001		45	7.2	6.5	12.2	
Currant Creek	9/15/1999	25	51	7.0	6.0	12.6	25
Currant Creek	10/17/1999	8	74	7.3	2.0	11.6	7
Currant Creek	9/19/2000	8	71	7.4	6.5	14.9	3
Currant Creek	9/25/2001	19	55	7.0	5.5	13.7	
Kijik River	9/14/1999	22	88	7.1	7.5	12.3	2
Kijik River	10/13/1999	12	88	7.3	3.5	11.2	6
Kijik River	9/19/2000	17	85	7.6	7.5	13.5	3
Kijik River	9/25/2001	13	86	7.0	8.5	11.7	
Lake Clark Outlet	9/13/1999	433	58	7.3	11.0	11.8	1
Lake Clark Outlet	10/12/1999	306	62	7.3	11.0	11.8	1
Lake Clark Outlet	9/22/2000	246	58	7.0	8.5	12.4	5
Lake Clark Outlet	9/25/2001	300	57	7.2	10.0	10.8	
Tanalian River	10/14/1999	15	52	7.0	5.5	10.3	3
Tanalian River	9/20/2000	14	50	7.2	8.5	12.0	1
Tanalian River	9/13/2001	18	50	7.1	10.5	10.4	1
Tanalian River	9/24/2001	13	44	7.0	10.0	11.4	
Tlikakila River	9/16/1999	86	55	7.2	6.0	13.3	71
Tlikakila River	10/14/1999	25	91	7.3	0.0	11.6	9
Tlikakila River	9/21/2000	21	71	7.5	8.0	11.0	118
	Minimum	13	44	7.0	0.0	10.3	2
	Maximum	433	91	7.6	11.0	14.9	118
	Average	168	65	7.2	6.8	12.0	25

Appendix 4. Inshore commercial catch and escapement of sockeye salmon in the Naknek-Kvichak District by river system, in numbers of fish, Bristol Bay, 1983-2004 (modified from ADFG 2001, ADFG 2004)

Year	Catch	% of Total Run	Escapement				Total Run
			Kvichak ^a	Alagnak ^{bc}	Naknek ^a	Total	
1980	15,120,457	37	22,505,268	297,900	2,644,698	25,447,866	40,568,323
1981	10,992,809	75	1,754,358	82,210	1,796,220	3,632,788	14,625,597
1982	5,005,802	66	1,134,840	239,300	1,155,552	2,529,692	7,535,494
1983	21,559,372	83	3,569,982	96,220	888,294	4,554,496	26,113,868
1984	14,546,710	55	10,490,670	215,370	1,242,474	11,948,514	26,495,224
1985	8,179,093	47	7,211,046	118,030	1,849,938	9,179,014	17,358,107
1986	2,892,171	46	1,179,322	230,180	1,977,645	3,387,147	6,279,318
1987	4,986,002	41	6,065,880	154,210	1,061,806	7,281,896	12,267,898
1988	3,480,836	40	4,065,216	194,630	1,037,862	5,297,708	8,778,544
1989	13,809,956	59	8,317,500	196,760	1,161,984	9,676,244	23,486,200
1990	17,272,224	65	6,970,020	168,760	2,092,578	9,231,358	26,503,582
1991	10,475,206	56	4,222,788	277,589	3,578,508	8,078,885	18,554,091
1992	9,395,948	59	4,725,864	224,643	1,606,650	6,557,157	15,953,105
1993	8,907,876	60	4,025,166	347,975	1,535,658	5,908,799	14,816,675
1994	16,327,858	63	8,337,840	242,595	990,810	9,571,245	25,899,103
1995	20,279,581	64	10,038,720	215,713	1,111,140	11,365,573	31,645,154
1996	8,211,983	74	1,450,578	306,750	1,078,098	2,835,426	11,047,409
1997	589,311	18	1,503,732	218,115	1,025,664	2,747,511	3,336,822
1998	2,595,439	41	2,296,074	252,200	1,202,172	3,750,446	6,345,885
1999	9,452,972	53	6,196,914	481,600	1,625,364	8,303,878	17,756,850
2000	4,727,061	56	1,827,780	451,300	1,375,488	3,654,568	8,381,629
2001	5,280,538	62	1,095,348	267,000	1,830,360	3,192,708	8,473,246
2002	1,407,621	38	703,884	335,661	1,263,918	2,303,463	3,711,084
2003	3,348,453	37	1,686,804	3,676,146	1,831,170	7,194,120	10,542,610
2004	4,786,694	37	5,500,134	5,396,592	1,939,374	12,836,100	17,622,831
25 Year Average	8,945,279	53	5,075,029	587,498	1,556,137	7,218,664	16,163,946
1985-94 Average	9,572,717	54	5,512,064	215,537	1,689,344	7,416,945	16,989,662
1995-04 Average	6,067,965	48	3,229,997	1,160,108	1,428,275	5,818,379	11,886,352

^a Tower count

^b Aerial survey estimates

^c Tower count for Alagnak River in 2003 and 2004



As the nation’s principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

LACL D-29, August 2005

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

DANIEL B. YOUNG*

National Park Service, Lake Clark National Park and Preserve, Port Alsworth, Alaska 99653, USA

CAROL ANN WOODY¹

U.S. Geological Survey, Alaska Science Center,
4230 University Drive, Suite 201, Anchorage, Alaska 99508, USA

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 km²

* Corresponding author: dan_young@nps.gov

¹ Present address: US: Science and Education, 6601 Chevigny Street, Anchorage, Alaska 99502, USA

Received December 20, 2005; accepted November 2, 2006
Published online March 15, 2007

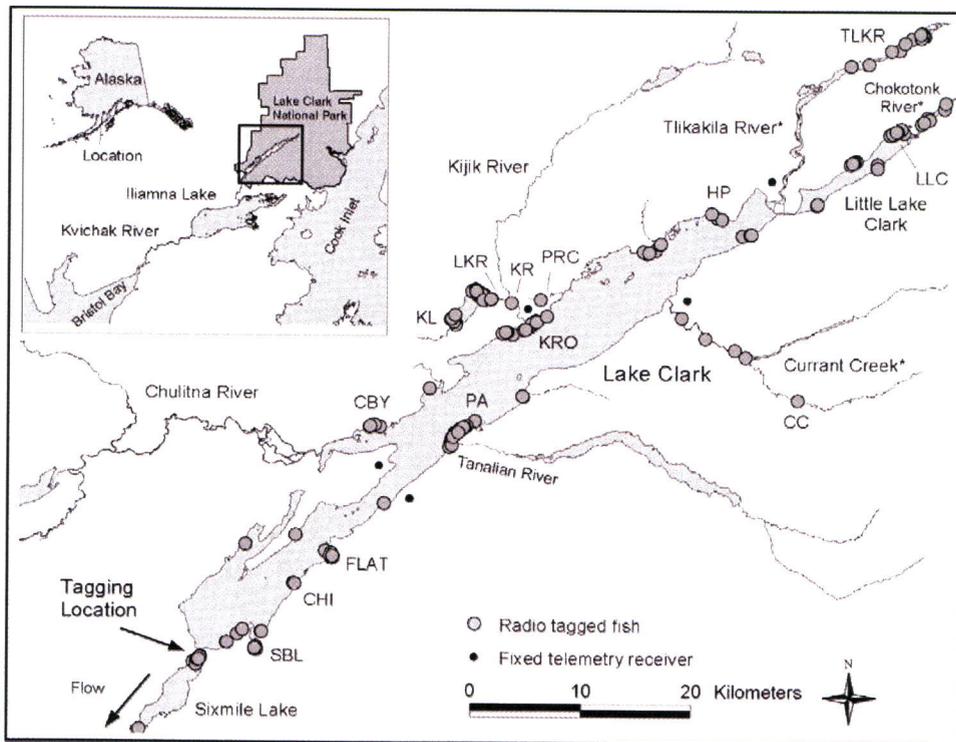


FIGURE 1.—Map of Lake Clark, Alaska, including tagging location, fixed telemetry receivers, and spawning areas for radio-tagged sockeye salmon. Asterisks denote glacier-fed tributaries. Refer to Table 2 for spawning distribution data and spawning site identification codes.

(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
Carrant 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		
Carrant 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 $T = 0.44(\text{SSC})^{0.858}$. 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

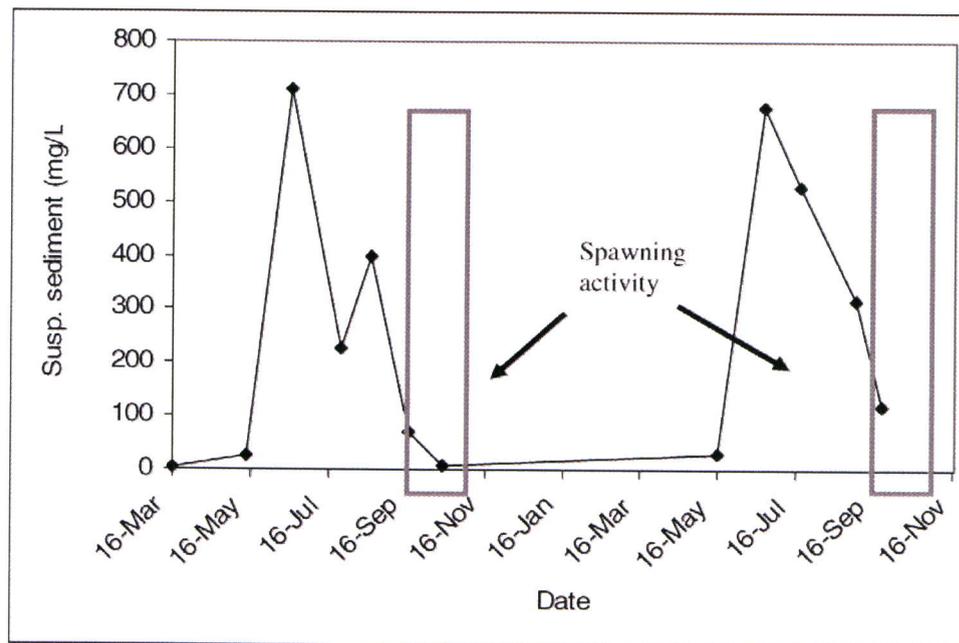


FIGURE 2.—Sockeye salmon spawning activity and suspended sediment concentration in the Tlikakila River, Alaska, from 16 March 1999 to 16 September 2000 (suspended sediment data are from Brabets 2002).

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).

Acknowledgments

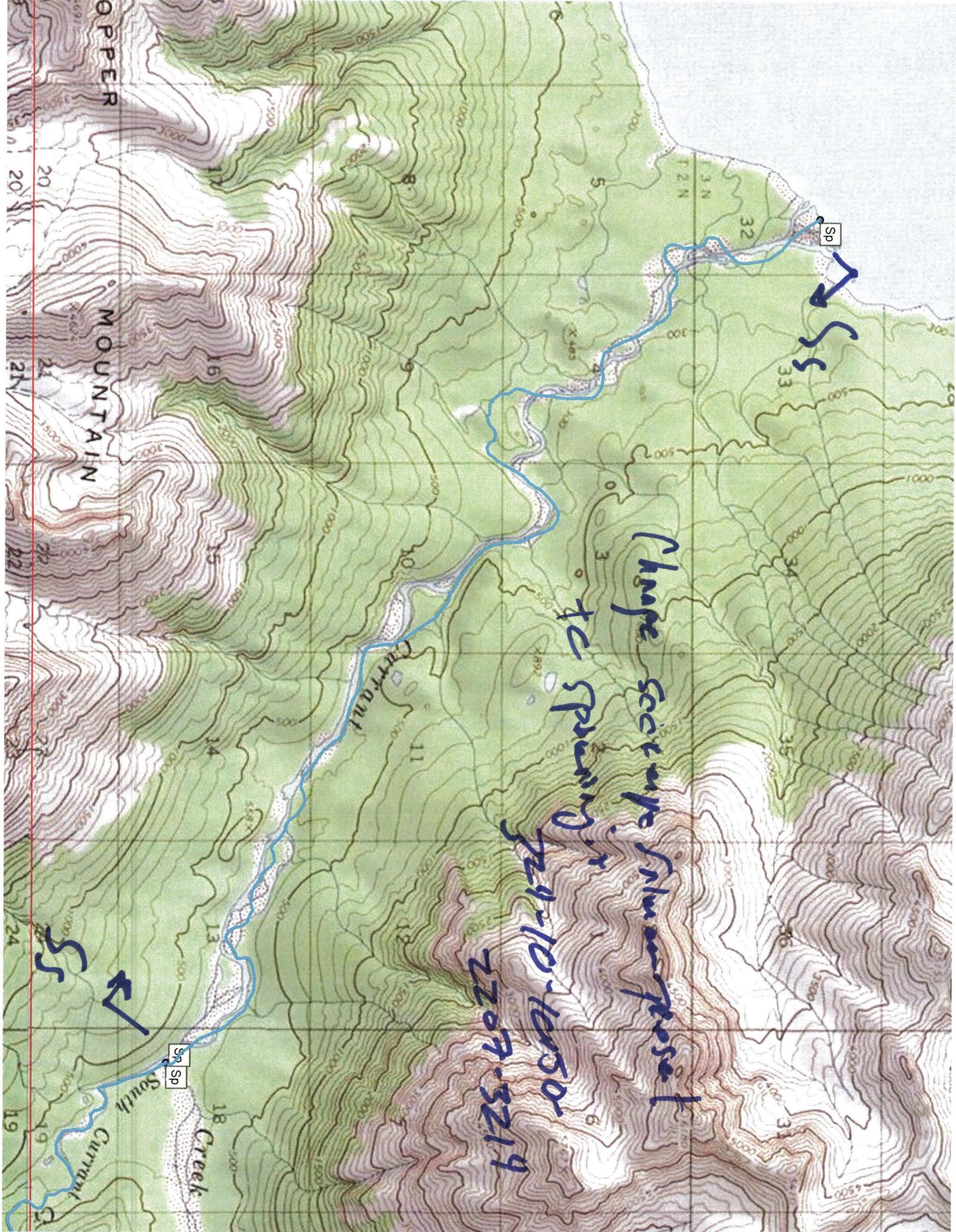
This project was a collaborative effort between the USGS Alaska Science Center (ASC), Alaska Cooperative Fish and Wildlife Research Unit, and NPS Lake Clark National Park and Preserve. Funding support was provided by USGS ASC, U.S. Fish and Wildlife Service Office of Subsistence Management, and NPS. Invaluable assistance with project design and implementation was provided by K. Ramstad. Helpful editorial comments were made by J. Margraf, G. Haas, and B. Smoker of the University of Alaska Fairbanks. Statistical reviews and editorial comments were provided by J. H. Reynolds. Radiotelemetry advice and support were provided by D. Palmer, R. Brown, and E. Spangler. A special thanks to all the field assistants who contributed to this project. Reviews by R. Gregory, J. Miller, and an anonymous reviewer greatly improved this manuscript.

References

- Anderson, J. W. 1969. Bathymetric measurements of Iliamna Lake and Lake Clark, Alaska. University of Washington, Fisheries Research Institute Circular 69–17, Seattle.
- Barton, L. H. 1992. Tanana River, Alaska, fall chum salmon radio telemetry study. Alaska Department of Fish and Game, Fishery Research Bulletin 92–01, Anchorage.
- 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.
- Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Pages 120–124 in H. D. Smith, L. Margolis, and C. C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Canadian Special Publications of Fisheries and Aquatic Sciences 96.
- 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. Healey. 1982. A review of salmon escapement estimation techniques. Canadian Technical Report of Fisheries and Aquatic Sciences 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 Fisheries 488.
- Eiler, J. H., B. D. Nelson, 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.
- Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Hausle, D. A., and D. W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 105:57–63.
- Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43:1946–1959.
- Jensen, K. A., and O. A. Mathisen. 1987. Migratory structure of the Kvichak River sockeye salmon (*Oncorhynchus nerka*) escapement, 1983. Canadian Special Publication of Fisheries and Aquatic Sciences 96:101–109.
- 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, and J. M. Edmundson. 1990. The exclusion of limnetic cladocera from turbid glacier-meltwater lakes. Ecology 71:57–67.
- 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.
- 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.
- 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.
- Murphy, M. L., K. V. Koski, J. M. Lorenz, and J. F. Thedinga. 1997. Downstream migrations of juvenile Pacific salmon (*Oncorhynchus* spp.) in a glacial transboundary river. Canadian Journal of Fisheries and Aquatic Sciences 54:2837–2846.
- Parker, S. S., and G. R. Blair. 1987. Aerial surveys of sockeye salmon abundance on spawning grounds in the Lake Clark-Tazimina River watershed. (FRI-UW-8703). University of Washington, Fisheries Research Institute, Seattle.
- 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.
- Poe, P. H., and D. E. Rogers. 1984. 1984 Newhalen River adult salmon enumeration program (FRI-UW-8415). University of Washington, Fisheries Research Institute, Seattle.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland.
- 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, Anchorage.
- 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.
- Siitonen, L., and G. A. E. Gall. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri*. Aquaculture 78:153–161.
- Silverstein, J. T. 1993. A quantitative genetic study of coho salmon (*Oncorhynchus keta*). Doctoral dissertation. University of Washington, Seattle.
- 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.
- Stewart, D. C., G. W. Smith, and A. F. Youngson. 2002. Tributary - specific variation in timing of return of Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. Canadian Journal of Fisheries and Aquatic Sciences 59:276–281.
- Wilkens, A. X. 2002. The limnology of Lake Clark, Alaska. Master'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. Pages 195–216 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.
- Woody, C. A. 2004. Population monitoring of sockeye salmon from Lake Clark and the Tazimina River, Kvichak River

- watershed, Bristol Bay, Alaska, 2000–2003. U.S. Fish and Wildlife Service, Office of Subsistence Management, Final Report 01–095, Anchorage, Alaska.
- Woody, C. A. In press. Tower counts. *In* Sampling protocols for salmonids. American Fisheries Society. Bethesda, Maryland.
- 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.
- Young, D. B., and C. A. Woody. In press. Dynamic in-lake spawning migrations by female sockeye salmon. *Ecology of Freshwater Fish*.



Change site up stream present
to spawning

724-10-1050

7207-3219

Sp

Sp

OPPER

MOUNTAIN

CUTTANT

South Creek

Curran

