Lake Clark Sockeye Salmon Population Assessment

Final Report for Study 01-042

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EXECUTIVE SUMMARY

Recent declines in the number of sockeye salmon returning to Lake Clark caused economic hardship in the region and raised resource concerns among local subsistence users and Federal managers. This final report describes findings from a two year study with two primary objectives: 1) to identify sockeye salmon spawning areas using radio telemetry, and 2) to describe genetic variation within and divergence among spawning populations.

Radio Telemetry Research: A lack of information regarding spawning habitat distribution in Lake Clark instigated this study. To determine spawning distributions, 332 adult sockeye salmon were radio tagged as they entered Lake Clark in 2000 and 2001. Fish were relocated every 5-10 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 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. 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.

Genetics Research: Prior to this study genetic information was lacking for Lake Clark originating sockeye salmon populations. Molecular genetic markers provide managers with more precise tools with which to identify and manage fish populations. Small clips of fin tissue (non-lethal) were obtained from 1,442 sockeye salmon representing 13 Lake Clark and 2 northeastern Lake Iliamna spawning populations in 2000 and 2001. Allele frequencies differed significantly across 11 microsatellite loci in 94 of 105 pair-wise population comparisons. Pair-wise estimates of F_{ST} ranged from zero to 0.089. There is significant genetic divergence between populations of Lake Clark and Sixmile Lake, the latter being more similar to fish of Lake Iliamna. The reduced numbers of alleles and strong divergence of most Lake Clark populations relative to Lake Iliamna/Sixmile Lake populations suggest a bottleneck or period of low population abundance, resulting in reduced genetic diversity. The greatest bottleneck effect detected and the most genetically distinct population was found in Sucker Bay Lake. Possible causes of these bottlenecks include reductions in effective population size associated with recent poor returns or colonization of new spawning habitats. Samples shared with the Alaska Department of Fish and Game for a Bristol Bay wide analysis indicate Lake Clark originating sockeye salmon are easily distinguished from other lake originating Bristol Bay stocks of sockeye salmon.

CHAPTER 1. IDENTIFICATION AND MAPPING OF LAKE CLARK SOCKEYE SALMON SPAWNING HABITATS

ABSTRACT

Radio telemetry was used to identify and map sockeye salmon spawning habitats in glacially influenced Lake Clark, Kvichak River watershed, Alaska. Two hundred eighty-two adult sockeye salmon were radio tagged and tracked to spawning grounds. Thirty-five spawning areas were identified, including 18 previously unidentified. Comparison of radio telemetry data with past aerial population surveys indicate sockeye salmon spawning habitat use and distribution in Lake Clark was underestimated, likely due to poor visibility associated with glacial habitats. Although glacially turbid waters are not considered suitable incubation environments because fine sediments can suffocate embryos, more than 60% of radio tagged fish spawned in such waters. Over 50% of identified spawning areas are along the shores of Lake Clark and Little Lake Clark and about 75% of spawning areas are adjacent to private land. Proposed development on these lands could negatively impact critical spawning habitats if protective measures are not in place.

INTRODUCTION

The purpose of this study was to identify spawning habitats of sockeye salmon *Onchorynchus nerka* in the Lake Clark watershed. A lack of information regarding spawning habitat distribution in Lake Clark instigated this study. Lake Clark National Park and Preserve was established in 1980 in part to "…protect the watershed necessary for the perpetuation of the red [sockeye] salmon fishery in Bristol Bay…" and to "…protect habitats for populations of fish and wildlife…" (ANILCA 1980). To protect habitats, the location of spawning areas used by sockeye salmon must be known.

The Lake Clark watershed is a significant producer of sockeye salmon to the Bristol Bay fishery, the largest sockeye salmon fishery in the world. Annually, Lake Clark sockeye salmon may comprise from 6 to 80% of the total Kvichak River return (Rogers and Poe 1984). The Kvichak River escapement, historically the largest in the world, ranges from 0.3 to 55 million fish (Rogers and Poe 1984, Rogers et al. 1999, ADFG 2002).

Annual returns of sockeye salmon to Lake Clark are important to the economy, culture, and ecosystem of the Bristol Bay region. Continued declines in the returns of sockeye salmon to Bristol Bay have impacted commercial, subsistence and sport fisheries and caused the governor

of Alaska to declare the region an economic disaster area five of the last seven years. Lake Clark sockeye salmon have been an integral part of Alaskan native culture since prehistoric times (Unrau 1992), and are the primary subsistence resource for contemporary users (ADFG 2002). Ecologically, sockeye salmon are an important food resource for over 40 species of mammals and birds (Bennett 1995, Wilson 1995, Wilson and Halupka 1995), and represent a significant source of marine derived nutrients that sustain freshwater ecosystem productivity (Kline et al. 1993).

Despite the recognized importance of Lake Clark sockeye salmon to humans and the ecosystem, basic biological information necessary for effective salmon management is lacking. Past spawning ground surveys (both aerial and ground surveys) and tagging studies indicated most sockeye salmon in the Lake Clark watershed spawn in clear water habitats (Demory et al. 1964, Anderson 1968, Smith 1964, Jensen and Mathisen 1987, Regnart 1998). Glacially turbid waters were thought to provide limited spawning habitat (range: 0 to 39%, average =10%; Regnart 1998). Research at Tustumena Lake, on the Kenai Peninsula indicates that 30% of the total sockeye salmon escapement spawned along glacially turbid beaches (Burger et al. 1995). Therefore, it is likely that unidentified spawning congregations exist in the Lake Clark watershed.

Knowing the location and extent of spawning is critical for accurate stock assessment and population management. "Protecting habitats" presumes having identified their distribution. Identification of spawning habitats is especially important in the Lake Clark watershed given that 60% of the Lake Clark shoreline is adjacent to private land. If the National Park Service and private landowners know where spawning areas are located, then protective measures can be implemented.

To identify and map sockeye salmon spawning habitats in the Lake Clark watershed, sockeye salmon were radio tagged as they entered Lake Clark and tracked to spawning grounds. The location of spawning areas was examined relative to water clarity and land ownership.

OBJECTIVES

1)   Locate spawning habitats using radio telemetry.
2)   Map spawning habitats in a Geographic Information System database.
3)   Determine spawner distribution by water clarity: Glacial (> 5 Nephelometric Turbidity Units (NTUs)); or Clear (≤ 5 NTUs).
4)   Determine spawner distribution by land ownership: Federal (National Park Service) or Private.

STUDY AREA

Lake Clark (60° 01 N, 154° 45 W) is the second largest lake (267 km^2) in the Kvichak River drainage, and the largest body of water in Lake Clark National Park and Preserve (Figure 1). 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 km^2 (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 (203 cm annual average) characterize the northeast end of the watershed while lowland tundra, small mountains, clear and organically stained streams, and low precipitation (64 cm annual average) 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 Nephelometric Turbidity Units (NTUs)) northeast to the clear (≤ 2 NTUs) southwest (Brabets 2002, Wilkens 2002).

METHODS

Radio Tagging

Migrating adult sockeye salmon were captured at the outlet of Lake Clark (Figure 2) with a nylon beach seine (62 m x 2.4 m - 3.7 m; 10.2-cm mesh) and radio tagged throughout the run (July 15 to August 23, 2000 and July 15 to August 9, 2001). Captures were made during randomly selected fishing sessions in the morning (0800 to 1359 hours) and afternoon (1400 to 1959 hours). Approximately six fish per day were tagged in 2000 and five fish per 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 Mathisen 1981; Poe and Rogers 1984; U.S. Geological Survey, unpublished data). Large migrations (greater than 10,000 fish per day) were identified at a U.S. Geological Survey monitoring site located 10 km downstream of the tagging site.

Tagging procedures were similar to other radio telemetry studies of sockeye salmon (Eiler et al. 1992, Burger et al. 1995). After capture, sockeye salmon were placed in a mesh live well in the stream (1.5 m x 1.5 m x 1.5 m; 2.5 cm mesh size). In 2000, fish were anesthetized with a clove-oil mixture prior to the tagging procedure (Woody et al. 2002), while in 2001 no anesthesia was used. Captured sockeye salmon were placed in a tagging cradle, identified as male or female,

and measured to the nearest 1 mm (mid-eye to hypural plate). Then, with the ventral side facing up and lower jaw raised, a glycerin-coated radio transmitter was inserted into the stomach using a 6 mm diameter Polyvinyl Chloride tube (Monan et al. 1975, Burger et al. 1995). After the tagging procedure, fish recovered in a live well and were released at the point of capture. Tagging took, on average, less than 5 minutes in 2000 and less than 1 minute in 2001. The difference in tagging duration between years reflects longer handling time and anesthetic use in 2000, and less handling and no anesthetic use in 2001. Both sexes were tagged in 2000 to monitor male and female movements, while only females were tagged in 2001 to better identify contemporary spawning sites, as females exhibit stronger site fidelity (Burgner 1991).

Telemetry Equipment

Radio-telemetry equipment (Lotek Engineering, Inc., Newmarket, Ontario) included high frequency VHF (149-150 MHz) transmitters, scanning receivers, and antennae (4-element yagi and H antennae). Digitally coded transmitters (2000: model MCFT-3E, 14.5 x 49 mm; 2001: model MCFT-3A, 16 mm x 46 mm) were used to track a large number of fish at one time. In 2001, a larger radio transmitter (MCFT-3A) was used to increase the reception range of tagged fish during tracking events. Transmitter weight in air (2000: 12.9 grams; 2001: 15.6 grams) was less than 2% of body weight as recommended by Winter (1983). Tags transmitted 24 hours a day with a 3-second burst rate in 2000 and a 2-second burst rate in 2001. The shorter burst rate in 2001 minimized scan time during tracking events. Tag life (greater than 380 days) exceeded estimated peak-spawning times of all previously identified spawning populations in the Lake Clark watershed (Demory et al. 1964, Anderson 1968, Regnart 1998).

Radio Tracking

Tagged fish were tracked every five to ten days using fixed-wing aircraft or boats and 24 hours a day at fixed radio telemetry stations. Aerial surveys were flown (with an H antenna mounted on each wing strut) along the shoreline of Lake Clark and its tributaries at an altitude of 200 - 300 m at airspeeds between 100 and 130 km per hour (Gilmer et al. 1981). Aerial flights were not flown up tributaries until it was determined that fish could have moved into the area (for example, fish were recorded past a fixed telemetry station on the tributary). Boat tracking was conducted around the perimeter of the lake and islands approximately 300 m offshore and at a maximum speed of 30 km per hour. Two 4-element yagi antennae, mounted to the boat hull and positioned at 45° angles scanned the areas slightly forward of the boat. Fixed telemetry stations monitored fish passage 24 hours per day on Lake Clark, Currant Creek, Kijik River, and the Tlikakila River (Figure 2). In 2000, only the Kijik River and Tlikakila River fixed stations were operational while all sites were operational in 2001.

During aerial and boat tracking events, a Global Positioning System receiver was used to record the location of the plane or boat when a tagged fish was detected (latitude and longitude in the North America Dataset 27 datum). Based on field tests with planted transmitters, fish were tracked to within 1 km of their actual location during initial aerial and boat surveys and to within 400 m during spawning surveys. Spawning locations in areas only accessible by aircraft could only be determined to within 1 km. If fish were recorded multiple times during a tracking event, the record with the highest signal strength was selected. Comparison between signal strengths was made using a reference gain on the telemetry receiver.

A fish was considered to be at its spawning destination if 1) it was relocated within a spawning area at least twice within three weeks, 2) no further migration occurred, and 3) 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).

Habitat Classification

Spawning areas were classified by water type as glacially turbid (≥ 5 NTUs) or clear (< 5 NTUs) based on Koenings et al. (1986 and 1990). Turbidity was measured at peak spawning with a pocket turbidimeter (Hach Company, Loveland, Colorado). Time of peak spawning (summarized in Regnart 1998) was used to classify spawning areas because discharge of suspended sediment loads from glaciers can vary by season (Brabets 2002). For example, in 1999 suspended sediment loads into the Tlikakila River were: 5 mg/L in March; 25 mg/L in May; 710 mg/L in June; 71 mg/L in September; and 9 mg/L in October (Brabets 2002).

Spawning Habitat Distribution - Public Versus Private Land

Identified spawning locations were mapped into a Geographic Information System and compared to available Geographic Information System land status data (National Park Service 2001). Land owned by native corporations or private individuals was categorized as private land; land owned by the Federal government was categorized as Federal. Development on private land, such as houses, cabins, fuel storage, roads, or runways, within 500 m of spawning areas was also documented.

RESULTS

Radio Tagging

Three hundred thirty-two adult sockeye salmon were tagged with radio transmitters as they entered Lake Clark: 175 (93 males, 82 females) in 2000; 157 (all female) in 2001. Lengths of tagged and untagged captured fish ranged from 404 mm to 592 mm (Table 1). On average, tagged salmon were the same size as untagged captured salmon (one-way analysis of variance, α = .05).

Spawning Areas And Timing

Spawning areas were determined for 282 of 332 radio tagged sockeye salmon (Figure 3). Most (85%) tagged fish returned to spawning areas within Lake Clark, though some (15%) were tracked to spawning areas downstream of the tagging site (Table 2). Fish not tracked to spawning sites were either never located, lost after being tracked into Lake Clark, or lacked sufficient relocation data to determine a spawning area. On average, radio tagged fish tracked to spawning areas were relocated 12.7 times (range, 3 – 33 times) with over 3,500 relocations made during the two study years.

Thirty-five spawning areas were identified, including three sites downstream of the tagging area and five sites identified by visual observation or seining (Figure 3, Appendix 1). Radio tagged fish were tracked to 20 spawning areas (N = 16 for females only) in 2000 and 27 spawning areas in 2001. Tagged fish used 18 of these spawning areas in both study years. Although many spawning areas were identified, most (70%) radio tagged sockeye salmon returned to five primary spawning areas within the Lake Clark watershed. These included the glacially turbid Tlikakila River (20%), the clear waters of the Kijik River drainage (20%), and glacially turbid beach habitats off the mouth of the Tanalian (14%), Kijik (8%), and Chokotonk Rivers (7%).

Sockeye salmon spawned within the Lake Clark drainage from late August until mid November; spawning occurred from several weeks (Sucker Bay Lake) to more than two months (Kijik Lake). Fish spawned earliest in Sucker Bay Lake and the outlet river of Lake Clark. Peak spawning occurred between September 15 and October 15. All sockeye salmon (including several radio tagged fish) captured at spawning areas had acquired secondary sexual characteristics (Foerster 1968).

Habitat Classification - Glacially Turbid Versus Clear Water

Spawning occurred in both glacially turbid and clear waters (Figure 3), but more tagged fish returned to glacially turbid than clear habitats (Figure 4). Glacial spawning areas included Lake Clark (> 5 NTUs) and Little Lake Clark (> 10 NTUs) beaches; and Currant Creek, Chokotonk River, and Tlikakila River (> 5 NTUs) riverine habitats (Figure 3). Clear spawning areas included Lake Clark, Kijik Lake, and Sucker Bay Lake (≤ 5 NTUs) beaches; and Kijik River, Little Kijik River, and Priest Rock Creek (≤ 1 NTU) riverine habitats (Figure 3, Appendix 1). More tagged fish spawned in glacial areas in the upper watershed (for example, Tlikakila River and Little Lake Clark) in 2001 than in 2000. Conversely, fewer tagged fish spawned in the clear waters of Kijik Lake in 2001 than 2000.

Tagged fish generally entered clear water tributaries earlier than glacially turbid tributaries. For example, tagged fish entered the clear Kijik River and Sucker Bay Lake from mid July to mid September. In contrast, they entered the turbid Tlikakila River, Chokotonk River, and Currant Creek from late August to mid September. One exception was clear Priest Rock Creek, which tagged fish entered from late September to early October. Seventy percent of tagged fish returning to Kijik River swam upstream by August 4, although no spawning occurred until September. River entry in the Tlikakila River occurred from August 25 to September 13 and coincided with reduced turbidity loads from glaciers due to colder temperatures (from 676 mg/L in June 2000 to 113 mg/L in September 2000; Brabets 2002). Spawning activity, however, was not visually detected from the air until late September or early October. Even then, only fish in shallow side channels were visible.

Spawning Habitat Distribution - Public Versus Private Land

Seventy-five percent of the spawning areas identified during this study are adjacent to private land (Figure 5), and most of this land (73%) is currently undeveloped. More (61%) radio tagged fish returned to spawning areas adjacent to private land than federally protected land, and most (74%) returned to spawning areas that are currently undeveloped (Table 3, Appendix 1). The greatest concentration of development is located on the southwest shore of Lake Clark at the outlet of the Tanalian River. The community of Port Alsworth (population ~ 100) is adjacent to spawning grounds in this area.

DISCUSSION

Sockeye salmon have adapted to use a variety of spawning habitats throughout the Lake Clark watershed (Figure 3). Migrating salmon enter Lake Clark over a relatively brief interval during

July and August, and spawning activity occurs from late August until the middle of November. Spawning activity can extend over weeks (for example, Sucker Bay Lake) or months (for example, Kijik Lake).

Glacial waters, both riverine and beaches, provide critical spawning habitat for sockeye salmon in Lake Clark. While spawning activity occurs in both glacial and clear habitats (Figure 3), more than half of the tagged fish spawned in glacial habitats each study year (Figure 4, Appendix 1). This is consistent with research at Tustumena Lake on the Kenai Peninsula, Alaska, where 30% of sockeye salmon spawn in glacially turbid areas along the lakeshore (Burger et al. 1995). Unlike Tustumena Lake, Lake Clark sockeye salmon spawn in both glacially turbid beach and tributary habitats (Burger et al. 1995). On the Taku River in southeast Alaska and British Columbia, sockeye salmon spawn in glacial river habitats (Eiler et al. 1992).

Radio telemetry was effective at identifying sockeye salmon spawning sites within both glacial and clear areas of 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 just milling in the capture area before returning downstream to spawn. Swift water currents in this area would tend to transport most carcasses downstream past the spawning site into Sixmile Lake (Figure 3). Most fish tracked to the downstream spawning site were captured after August 9, 2000, and had acquired phenotypic characteristics of spawning sockeye salmon (Burgner 1991). In 2001, the tagging season was shortened and less than 5% of tagged fish were tracked to downstream spawning areas.

Radio tagged fish returned to all sites identified in previous spawning surveys except for the Twenty-two Creek and Chulitna River drainages (Figure 6, Appendix 2). Additionally, no spawning activity was observed in either of these drainages.

The Twenty-two Creek drainage has been identified as a potential spawning area since 1964 (Demory et al. 1964, Regnart 1998), although no fish have ever been recorded spawning in the stream (Parker and Blair 1987). During this study, one radio tagged fish was tracked to a beach spawning area at the mouth of Twenty-two Creek. It is likely that the few fish counted in this area during aerial surveys spawned along the shoreline of Lake Clark rather than in the stream.

The slow moving, organically stained Chulitna River is thought to have limited spawning habitat for sockeye salmon (Demory et al. 1964). Less than 10 sockeye salmon have been observed in the Chulitna River (Russell 1980), and some tags from a study by Smith (1964) were recovered there. However, Smith (1964) noted that the tags from his study were collected "…in part or in whole from personal use fisheries." Since there are no records of personal use fisheries for sockeye salmon in the Chulitna River (Stickman et al. 2003), it is likely that Smith's (1964) tags were recovered from a known spawning area in Chulitna Bay. When Jensen and Mathisen (1987) repeated Smith's (1964) study, their tags were recovered in Chulitna Bay rather than Chulitna River. Although unidentified spawning areas may exist in this drainage, radio tagging results indicate that Chulitna River provides limited spawning habitat for sockeye salmon.

Historic aerial spawning ground surveys underestimated the size and distribution of Lake Clark sockeye salmon populations. This is not surprising since turbid conditions and deep water limit visual observations (Cousens et al. 1982). Estimating annual returns in glacial systems is also complicated by annual and seasonal variation in the amount of suspended sediments loaded into the watershed (Brabets 2002). For example, aerial surveyors might see more sockeye salmon in glacial rivers from one year to the next simply because of changes in visibility rather than changes in abundance.

Approximately 50% of radio tagged fish spawned on beach areas along the shores of Lake Clark each year of the study. While aerial surveyors have been aware that spawning occurs in these areas ("Lake Clark beaches" in Regnart 1998), they have had difficulty identifying specific spawning sites or documenting spawning activity (Appendix 2). During this study, 22 spawning areas were identified along the shores of Lake Clark and Little Lake Clark beaches, while only 5 areas were documented previously (Figure 6, Appendix 1).

Complete assessment of all spawning areas is important because underestimating the number of spawners could lead to inaccurate harvest management decisions. Nevertheless, aerial surveys provide useful long-term index data on the spawning activity in clear water areas (≤ 1 NTUs) such as the Kijik Lake drainage and Priest Rock Creek. Both historic and recent aerial surveys have identified the Kijik Lake drainage as an important spawning area within the watershed (Appendix 2). However, aerial survey estimates indicate that 70% of Lake Clark sockeye salmon spawn in the Kijik drainage, while less than 30% of radio tagged fish returned to this area.

Surprisingly, peak spawning times were similar in both glacial and clear riverine and beach habitats. This may be due to the association of most spawning areas, in both turbid and clear habitats, with clear water inlet sources including springs, tributaries, and upwelling. Groundwater upwelling sites in glacial rivers clear silt from the spawning substrate and provide a warm water incubation environment characteristic of late spawning salmon (Burgner 1991, Eiler et al. 1992, Burger et al. 1995). Spawning in the glacial waters may be delayed until the suspended sediment load decreases. Spawning in tributaries typically occurs earlier than spawning along beaches (Burgner 1991, Burger et al. 1995).

Development on private lands could harm important salmon spawning habitat in the Lake Clark watershed. Most spawning areas are adjacent to private land, although most sites remain undeveloped (Figure 5, Table 3, Appendix 1). Nevertheless, as the number of permanent and seasonal residents increases 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 on Tanalian Point 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 a proposed open pit copper mine in the headwaters of the Chulitna River, could adversely affect water quality and habitat critical for Lake Clark sockeye salmon spawning and rearing.

Chapter 2. Bottleneck Effects Explain Genetic Population Structure of Sockeye Salmon in Lake Clark, Alaska

ABSTRACT

Lake Clark, Alaska contributes 6% to 80% of the Kvichak River return of sockeye salmon to the Bristol Bay fishery, the largest salmon fishery in the world. Continued declines in salmon returns to the Kvichak River drainage has focused research on development of molecular genetic markers to allow more precise management of the commercial fishery. This study describes genetic divergence patterns among and genetic variation within spawning populations of sockeye salmon throughout Lake Clark and northeastern Lake Iliamna. Fin tissue was collected from 1,442 sockeye salmon representing 13 Lake Clark and 2 northeastern Lake Iliamna spawning populations. Allele frequencies differed significantly across 11 microsatellite loci in 94 of 105 pair-wise population comparisons. Pair-wise estimates of F_{ST} ranged from zero to 0.089. There is significant genetic divergence between populations of Lake Clark and Sixmile Lake, the latter being more similar to fish of Lake Iliamna. The reduced numbers of alleles and strong divergence of most Lake Clark populations relative to Lake Iliamna/Sixmile Lake populations suggest a bottleneck associated with the colonization of Lake Clark by sockeye salmon. The greatest bottleneck effect detected, and the most genetically distinct population, was Sucker Bay Lake. Possible causes of these bottlenecks include reductions in effective population size associated with recent poor returns or colonization of new spawning habitats.

INTRODUCTION

Understanding the pattern of genetic variation among and within populations is critical for effective management of species. The genetic population structure of a species provides a basis for defining management units, identifying populations with unusual genetic composition, and recognizing populations at risk of extinction due to low genetic diversity (Avise 1994). Population structure is positively associated with genetic diversity and resilience to disturbance; large, highly structured populations have high genetic diversity and probability of persistence (Giesel 1974, Altukhov 1981). In contrast, small, panmictic populations are vulnerable to inbreeding, demographic stochasticity, genetic drift, causing reduced evolutionary potential, and increased probability of extinction (Cornuet and Luikart 1996, Luikart et al. 1998, Soulé and Mills 1998).

Sockeye salmon *Oncorhynchus nerka* are a highly structured species due to their homing tendencies and ability to colonize new habitats. Specific natal homing promotes reproductive isolation and genetic structuring between populations of sockeye salmon (Ricker 1972, Quinn 1985, Quinn and Dittman 1990). Lakes are focal points of homing, and genetic divergence is typically greater among populations spawning in different lakes than among spawning populations within the same lake (Wood et al. 1994, Wood 1995, Seeb et al. 2000, Withler et al. 2000). However, there is often significant genetic divergence among spawning populations within lakes due to isolation of populations spawning in different habitat types or at different times (Wilmot and Burger 1985, Varnavskaya et al. 1994a, 1994b, Wood 1995, Ramstad 1998, Woody et al. 2000).

Sockeye salmon are vulnerable to loss of genetic variation due to severe reductions in effective population size (bottleneck effects; Avise 1994) because they are excellent colonizers that can quickly establish spawning populations with few individuals (Milner 1987, Milner and Bailey 1989, Milner et al. 2000). Random changes in allele frequencies due to imperfect sampling of the allele frequencies between generations (genetic drift) causes loss of genetic variation during a bottleneck and promotes genetic divergence among populations while reducing genetic diversity within them (Avise 1994). Thus genetic drift may drive the genetic population structure of sockeye salmon through bottleneck effects associated with colonization events.

Loss of allelic variation is greater than loss of heterozygosity during a bottleneck (Maruyama and Fuerst 1985, Allendorf 1986). Therefore, recently bottlenecked populations exhibit higher heterozygosity than would be expected if they were in mutation-drift equilibrium given their number of alleles. Rare alleles, having frequency ≤ 0.1, are lost in higher proportion than those of moderate or high frequency. Thus, recently bottlenecked populations can be identified by an excess of heterozygosity (relative to their number of alleles and assuming mutation-drift equilibrium), a reduction in number of alleles, and a disproportionate loss of rare alleles (Cornuet and Luikart 1996, Luikart et al. 1998).

OBJECTIVES

1) Test for genetic divergence among spawning populations of sockeye salmon in Lake Clark and between Lake Clark and Lake Iliamna.
2) Test for reduced genetic variation (bottlenecks) within spawning populations of sockeye salmon in Lake Clark and relative to populations in Lake Iliamna.

STUDY AREA

Lake Clark is the sixth largest lake in Alaska (surface area of 267 km^2, mean depth 103 m; Anderson 1969), and the largest body of water in Lake Clark National Park and Preserve (Figure 7). Glacially turbid water flows into the northeast end of Lake Clark and drains through Sixmile Lake and the Newhalen River to Lake Iliamna. These waters and the Kvichak River comprise the Kvichak system, which has historically been the largest contributor of sockeye salmon to the Bristol Bay fishery (0.3 to 55 million fish; Faire 2000), the largest sockeye salmon fishery in the world. Lake Clark sockeye salmon comprise 6% to 80% of the annual Kvichak return; support commercial, subsistence, and recreational fisheries; and provide critical marine derived nutrients to the Lake Clark ecosystem (Rogers and Poe 1984, Rogers et al. 1997, Kline et al. 1993, Wilson and Halupka 1995). Fishery managers are concerned about recent dramatic declines in the number of sockeye salmon returning to the Kvichak system (Regnart 1998, Faire 2000), as well as the impacts of fisheries and continued shoreline development on sockeye salmon within Lake Clark National Park and Preserve.

Lake Clark is geologically young, having been created by glacial retreat approximately 15 to 12 thousand years ago (P. Heiser, University of Alaska, Anchorage, personal communication). Present day sockeye salmon spawning habitats vary in the time they have been ice-free, suggesting they similarly vary in the time they were first colonized by sockeye salmon. Thus, sockeye salmon populations within Lake Clark may vary greatly in their age, and those spawning in younger habitats may have experienced recent bottlenecks. For example, sockeye salmon spawn in an area of the Upper Tlikakila River that was deglaciated approximately one to two hundred years ago (P. Heiser, University of Alaska, Anchorage, unpublished data). This study describes the genetic population structure of sockeye salmon within Lake Clark. Two null hypotheses were investigated: 1) no genetic divergence has occurred and 2) no difference in genetic variation exists among the spawning populations of sockeye salmon studied. This work will help fishery managers define and prioritize conservation units of Lake Clark sockeye salmon as they attempt to mitigate impacts of fisheries and planned shoreline development within Lake Clark National Park and Preserve.

METHODS

Sample Collection

Fin tissue from 15 Lake Clark and two Lake Iliamna populations were collected for this study (Figure 7, Table 4). Samples of about 100 individuals from each of three Lake Clark populations (Currant Creek, Priest Rock Creek, Kijik River) and two Lake Iliamna populations (Lower Talarik Creek, Fuel Dump Island) were collected in a single year. Samples of about 50

individuals were collected from 10 additional Lake Clark populations in each of two years to examine inter-annual variation in allele frequencies within populations. Post spawning or spawning fish were captured on their spawning grounds by seine and tangle net. A fin clip (approximately 5mm^2) was collected and stored in 100% EtOH from each fish sampled.

Sample sizes for most populations approximate 100 (Table 4), which provide a 95% probability of detecting an allele having a frequency of 0.015 or greater. The exception is Priest Rock Creek, for which only 65 samples were obtained. While this lower sample size reduces the ability to detect rare alleles, the number of fish sampled represented a large fraction of the estimated 150 fish present at this site. Thus, allele frequencies based on this small sample are probably representative of this population.

Microsatellite Genotyping

Total DNA was extracted using the Puregene$^®$ DNA Isolation Tissue Kit (Gentra Systems, Minneapolis, Minnesota). Concentration of DNA was measured with a DyNA Quant 200 Fluorometer (Hoefer, San Francisco, California) after rehydration in Tris-EDTA. Working stocks for each sample were diluted with deionized water to concentrations of 50ng/µl. Fish were genotyped at 11 microsatellite loci (Table 5). Primers were directly labeled with infrared flurophore IRD700 and IRD800 (LI-COR, Lincoln, Nebraska). The DNA was amplified in 10µl polymerase chain reactions (PCR): 200 µmol each dNTP, 4 pmol each primer, 10 mM Tris-HCl (pH 8.3), 1.5 mM MgCl$_2$, 50 mM KCl, 0.01% each of gelatin, NP-40 and Triton-x 100, and 0.5 units of DNA polymerase (Promega and/or Perkin-Elmer) in a series of five PCRs. Profiles for PCR were: 94°C for 2 min followed by 35-40 cycles of 15 sec to 1 min at 94°C, 15 sec to 1 min at annealing temperature and 30 sec to 1 min at 72°C. Blank reactions, in which all constituents were present but template DNA, were included in each PCR to detect sample contamination.

DNA was electrophoresed on a 6% denaturing polyacrylamide gel, and PCR products were scored relative to a known size standard on a LI-COR DNA Analyzer Global Edition IR2 and a LI-COR DNA Sequencer Long Reader 4200 using V4.03 Gene ImagIR software (Scanalytics, Inc., Fairfax, Virginia). An individual fish with known allele sizes was included on every gel and a second gel reader proofed allele sizes to insure accuracy and consistency of scoring across gels. Individuals representing 10% of genotyped fish were reamplified and scored a second time. Comparison of initial and repeated scores revealed a genotyping error rate of less than 2%. All differences between initial and repeated scores were resolved and corrected.

Departures from Hardy-Weinberg proportions (Guo and Thompson 1992) and heterogeneity of allele frequencies were tested using GENEPOP version 3.2 (Raymond and Rousset 1995). The proportion of genetic variation due to population subdivision was estimated as F_{ST} and computed in FSTAT, version 1.2 (Goudet 1995), and calculated according to Weir and Cockerham (1984). Principal component analysis was performed using the covariance matrix of allele frequencies in MINITAB, version 11 (State College, PA), after omitting the largest allele at each locus to allow for the non-independence of allele frequencies within a locus (Johnson 1998). Sequential Bonferroni adjustments were made for all multiple comparisons (Rice 1989).

Reduced genetic variation due to bottleneck effects was assessed in BOTTLENECK, version 1.2.02 (Cornuet and Luikart 1996). The program uses a Wilcoxon sign-rank test (Luikart 1997) to assess heterozygosity excess relative to a non-bottlenecked population in mutation-drift equilibrium having the same number of alleles. This test assumes selective neutrality of markers that conform to the infinite alleles model of mutation, the populations are panmictic and closed to immigration, and data are available from at least 10 independent loci (Cornuet and Luikart 1996, Waples 2002). The number of alleles observed in a population is highly dependent on sample size. Therefore, allelic diversity was assessed as allelic richness, which is a measure of the number of alleles per population weighted by sample size (El Mousadik and Petit 1996). Allelic richness was calculated and compared among major population groups following El Mousadik and Petit (1996) in FSTAT, version 1.2 (Goudet 1995). Finally, alleles within populations were grouped into each of ten frequency classes (Luikart et al. 1998) and the proportion of rare alleles (frequency < 0.1) present in major population groups were compared with a one tailed, nonparametric Mann-Whitney test (Zar 1984).

RESULTS

The total number of alleles per locus ranged from 5 to 21, and the mean number of alleles per population and locus ranged from 3.1 to 10.9 (Table 5, Appendix 3). All loci were polymorphic in all samples. Mean expected heterozygosity ranged from 0.46 to 0.52, and mean number of alleles ranged from 4.3 to 7.1 per population over all loci. There was no evidence of deviation from Hardy-Weinberg proportions at any locus, in any sample. There were no significant inter-annual differences in allele frequencies ($P > 0.05$), so samples collected from the same population in different years were pooled for further analysis.

Genetic Divergence Among Major Population Groups

There were significant differences in allele frequencies in 89 of 105 pair-wise population comparisons (Table 6). Estimates of F_{ST} ranged from 0 to 0.089 and were greatest between Lake Iliamna and Lake Clark populations. Lake Clark populations were divergent from Sixmile Lake populations, the latter being more similar to Lake Iliamna fish. The Sucker Bay Lake population was highly divergent from all other populations surveyed.

Principal component analysis supported this pattern (Figure 8). The first principal component explained 57% of the total genetic variation and differentiated between three major groups of populations: 1) Lake Iliamna and Sixmile Lake, 2) Sucker Bay Lake, and 3) Lake Clark. The second principal component explained 16% of the total genetic variation, further differentiated the Sucker Bay Lake population, and explained the difference between populations of Iliamna and Sixmile Lakes. Iliamna/Sixmile Lake populations had a pair-wise F_{ST} of 0.048 (95% CI, 0.018 – 0.082) with Sucker Bay Lake and 0.054 (95% CI, 0.023 – 0.086) with Lake Clark. Between Sucker Bay Lake and Lake Clark populations, F_{ST} was 0.060 (95% CI, 0.021 – 0.111). Thus, there was significant and similar genetic divergence between these three major population groups.

Genetic Divergence within the Lake Clark Group

First, the data suggest major genetic divergence between fish spawning in Sucker Bay Lake, and remaining Lake Clark populations (Figure 8, Table 6). There was also significant genetic structuring within the Lake Clark group: all populations spawning above the outlet of Lake Clark with the exception of Sucker Bay Lake. There was no difference in allele frequencies between the two Kijik Lake populations sampled, Little Kijik River and Kijik Lake South Beach, and pair-wise F_{ST} within Lake Clark was greatest between Kijik Lake and other populations (range from 0.008 to 0.024). Priest Rock Creek differed in allele frequencies from all other populations sampled. This pattern of divergence within Lake Clark was supported by principal component analysis (Figure 9). The first principal component explained 44% of the genetic variation within Lake Clark and separated the Kijik Lake populations from all others. The second principal component explained 19% of the genetic variation and differentiated the Priest Rock Creek population.

Genetic Diversity and Bottleneck Effects

A significant bottleneck effect was detected in Sucker Bay Lake ($P < 0.005$; Figure 10). The mean expected heterozygosity calculated from observed allele frequencies (0.502) was far in excess of that expected if this population were in mutation-drift equilibrium (0.388). In addition,

the Sucker Bay Lake sample had less than half the number of alleles found in Iliamna/Sixmile Lake samples (47 versus 105). Allelic richness among Sucker Bay Lake fish was 4.16, which was significantly lower than that of Iliamna/Sixmile Lake (5.55, $P < 0.001$). Allelic richness within Lake Clark fish was 4.96. While this was also greater than that of the Sucker Bay Lake population, the difference is only marginally significant ($P = 0.084$). A lower proportion of rare alleles relative to Iliamna/Sixmile Lake also suggest a bottleneck in Sucker Bay Lake. Fish in Sucker Bay Lake possess approximately 37% fewer rare alleles than fish in Iliamna/Sixmile Lake (Figure 11).

The data also suggest a bottleneck among fish of Lake Clark relative to Iliamna/Sixmile Lake. Eight of the 10 populations in Lake Clark have an excess of heterozygosity relative to that expected at mutation-drift equilibrium, though these differences are not statistically significant ($P = 0.517$; Figure 10). However, there is a significant reduction in allelic richness ($P < 0.001$) of Lake Clark populations (4.96) relative to Iliamna/Sixmile Lake populations (5.99). We found a total of 105 alleles in the 383 Iliamna/Sixmile Lake fish sampled and only 92 alleles in the 959 Lake Clark fish sampled, although sample sizes greatly favored finding more alleles in Lake Clark populations. Though the mean proportion of rare alleles is significantly lower in Lake Clark (0.58+ 0.02 95% CI) than Iliamna/Sixmile Lake (0.64 + 0.06 955 CI) populations ($U_{4, 10}$ = 37, P = 0.01), there is nearly complete overlap in the confidence intervals of these estimates. Thus, there is no significant difference in mean proportion of rare alleles between Iliamna/Sixmile Lake and Lake Clark group populations. However, 8 of 10 Lake Clark populations have a lower proportion of rare alleles than all four Iliamna/Sixmile Lake populations (Figure 11). While this difference is not dramatic (Lake Clark mean 0.585, SE 0.010; Iliamna/Sixmile Lake mean 0.641, SE 0.010), it is consistent with our prediction that a bottleneck occurred among fish of Lake Clark relative to Iliamna/Sixmile Lake.

DISCUSSION

Genetic Divergence Among Major Population Groups

Significant genetic divergence was found between populations of Lake Clark and Sixmile Lake (Lake Clark Outlet, Tazimina River), the latter being more similar to fish of Lake Iliamna. This result was surprising because Sixmile Lake is geographically closer to Lake Clark than to Iliamna, and the Newhalen River is also a barrier to fish migration at high water velocities (Poe and Mathisen 1981, 1982). Nevertheless, the overall pattern of genetic variation suggests the primary divergence is found at the confluence of Lake Clark and Sixmile Lake and between some populations that are very close geographically.

Satellite imagery shows the presence of a major outwash fan from the Tazimina Valley (P. Heiser, University of Alaska, Anchorage, personal communication), and it is possible that glaciers and outwash at Sixmile Lake could have caused isolation and divergence between

sockeye salmon of Lake Clark and Lake Iliamna. There is also a significant difference in spawning time between these areas that could maintain this isolation. Peak spawning of the Tazimina River and Lake Clark Outlet populations typically occurs between August 25 and September 15, while peak spawning of Lake Clark populations occurs approximately one week (Kijik Lake populations) to more than a month (Tlikakila River, Little Lake Clark Beach) later. Some of the greatest genetic differences among sockeye salmon spawning in the same lake have been found between populations with different spawning times (Varnavskaya et al. 1994b).

Spawning times overlap and geographic distances are small between fish of Sixmile Lake and Sucker Bay Lake, so temporal and spatial isolation do not explain the high level of genetic divergence between these groups. Sucker Bay Lake is a beach spawning population and Sixmile Lake a stream spawning population, so differences in spawning habitat may promote reproductive isolation between these populations. Significant genetic divergence is often found between beach and stream spawning populations of sockeye salmon within the same nursery lake (Varnavskaya et al. 1994a, Wood 1995).

Genetic Divergence within The Lake Clark Group

There is significant population structure within Lake Clark, although many populations are genetically similar. Fish spawning in Kijik Lake (South Beach and Little Kijik River outlet) do not differ from one another in allele frequencies, but are significantly different from other populations of Lake Clark. Similarly Priest Rock Creek fish are highly different from all other Lake Clark populations. As in Sixmile Lake, some of the greatest divergence between populations within Lake Clark is found between proximate populations with similar spawning times. Little genetic divergence was found between fish spawning in different habitat types (beach, tributary). Thus, the pattern of genetic divergence within Lake Clark sockeye salmon is not one of simple isolation by distance, spawning time, or spawning habitat type.

Genetic Diversity and Bottleneck Effects

Both the reduced numbers of alleles in most Lake Clark populations and the strong divergence between Lake Clark and Iliamna/Sixmile Lake populations suggest a bottleneck associated with the colonization of Lake Clark by sockeye salmon. The fact that reduced allelic diversity is common to eight of the 10 populations in this group suggests an event that reduced the overall genetic diversity of Lake Clark sockeye salmon.

The divergence between Sucker Bay Lake and all other populations is likely due to genetic drift from a bottleneck effect. Reduced allelic richness, reduced total numbers of alleles, and excessive heterozygosity in Sucker Bay Lake relative to all other populations support this hypothesis. A bottleneck could be due to a recent reduction in effective population size or an

older event associated with colonization of Sucker Bay Lake. Traditional ecological knowledge of local Dena'ina elders suggest recent reductions in the numbers of fish spawning in Sucker Bay Lake (M. McBurney, National Park Service, Anchorage. personal communication), and aerial spawning surveys also suggest a recent reduction in number of spawners (Regnart 1998). However, a bottleneck effect associated with the colonization of Sucker Bay Lake by sockeye salmon cannot be ruled out based on these data.

It is possible that other bottlenecks have occurred within Lake Clark as well, although no statistically significant bottleneck effects were found in Lake Clark except for the Sucker Bay Lake population. Priest Rock Creek has reduced allelic diversity relative to other populations within Lake Clark. This creek has been severely impacted by beaver dam building in recent years, and the number of returning sockeye salmon has been greatly reduced from historic levels (Regnart 1998). A similar reduction in allelic diversity is also present in Upper Tlikakila River. This is an extremely young habitat uncovered by receding glaciers within the last 200 years (P. Heiser, University of Alaska, Anchorage, personal communication), and loss of genetic variation may be due to a bottleneck effect associated with colonization.

Absence of significant bottleneck effects within most Lake Clark populations may be due to low polymorphism of our markers or reduced genetic variation within Lake Clark. The moderately polymorphic microsatellites used here have low numbers of alleles, which makes them insensitive to loss of genetic variation. Highly polymorphic microsatellites, or mitochondrial DNA, may provide better resolution in detecting bottlenecks. Because of its maternal and haploid mode of inheritance, mitochondrial DNA has one quarter the effective population size of nuclear markers (microsatellites), and, therefore, is four times as sensitive to bottlenecks (Nei and Tajima 1981, Birky et al. 1983).

Management Relevancy of Findings

The strong divergence between Lake Clark and Lake Iliamna populations provides fishery managers with a tool to differentiate between fish returning to the different lakes. Tissue from approximately 1,100 sockeye salmon from 11 Lake Clark spawning populations have been shared with Alaska Department of Fish and Game for use in Bristol Bay mixed stock fishery analyses. These samples will allow inclusion of Lake Clark sockeye salmon in their microsatellite, allozyme, and mitochondrial DNA baselines, and may ultimately provide harvest rate estimates for Lake Clark sockeye salmon. The ability to differentiate between Lake Iliamna and Lake Clark sockeye salmon would also allow juvenile stock dynamics to be studied within the lakes, estimates of stock contributions to smolt production to be made, and distribution of stocks at sea to be examined.

These findings provide a valuable foundation for fishery managers of Lake Clark National Park and Preserve to define population units for conservation and fishery management, to identify population groups for long term monitoring, and to prioritize imperiled populations for conservation action. The reduced genetic diversity within most Lake Clark sockeye salmon

populations, particularly the Sucker Bay Lake population, suggests that conservation of these populations may be a high priority for Lake Clark and Bristol Bay fishery managers.

Chapter 3 Study Conclusions and Recommendations

CONCLUSIONS

1)   Sockeye salmon spawning habitats in the Lake Clark watershed have historically been greatly underestimated due to high glacial turbidity in some parts of the system. This study provides the first comprehensive survey of spawning areas within this drainage.

2)   Radio telemetry and visual observations resulted in the identification and mapping of 33 spawning sites within the Lake Clark watershed, including 18 previously unidentified sites.

3)   Sockeye salmon spawn in both glacial and clear water habitats, but two thirds of radio tagged fish returned to spawning areas in glacial waters.

4)   More than half of the spawning areas identified were located along the shores of Lake Clark and Little Lake Clark.

5)   More than two thirds of the spawning areas identified could be impacted by future development on private land.

6)   The magnitude of genetic differentiation among spawning populations of Lake Clark sockeye salmon is larger than that typically found between populations within the same lake.

7)   There is significant genetic divergence between populations of Lake Clark and Sixmile Lake, with Sixmile Lake fish being more similar to those in Lake Iliamna.

8)   The reduced numbers of alleles and strong divergence of most Lake Clark populations relative to Lake Iliamna/Sixmile Lake populations suggest a bottleneck associated with the colonization of Lake Clark by sockeye salmon. The greatest bottleneck effect detected, and the most genetically distinct population, was the one in Sucker Bay Lake.

9)   Sucker Bay Lake and Priest Rock Creek populations have reduced numbers of spawners and genetic diversity.

RECOMMENDATIONS

1) Further work is needed to more precisely define spawning habitat boundaries in the Lake Clark drainage. While radio telemetry identified general spawning areas, results cannot be used to determine the extent of these areas. The glacial nature of the watershed made determining these boundaries quite difficult, but hydroacoustics could provide information to more precisely estimate boundaries and delineate critical spawning habitat.

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

3) Spawning areas identified during the current study should be compared with information gathered from traditional ecological knowledge studies being conducted within this area to determine whether there have been changes from historic spawning patterns.

4) Lake Clark, Sixmile Lake, and Lake Iliamna comprise distinct population groups that should be monitored and managed separately. Special consideration should be given to conserving populations within Sucker Bay Lake, Kijik Lake, and Priest Rock Creek because these are the most genetically divergent populations surveyed.

5) Additional genetic analysis with more sensitive markers, such as mitochondrial DNA, should be pursued to better resolve and identify genetic bottlenecks.

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

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LITERATURE CITED

Alaska Department of Fish and Game (ADFG). 2002. Alaska Department of Fish and Game Division of Commercial Fisheries annual management report 2001. 2001 Bristol Bay area region information report No. 2A02-18. Anchorage, Alaska.

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

Allendorf, F.W. 1986. Genetic drift and the loss of alleles versus heterozygosity. Zoo Biology 5:181-190.

Altukhov, Y.P. 1981. The stock concept from the viewpoint of population genetics. Canadian Journal of Fisheries and Aquatic Sciences 38:1523-1538.

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.

Avise, J.C. 1994. Molecular Markers, Natural History and Evolution. Chapman and Hall, New York, New York.

Banks, M.A., M.S. Blouin, B.A. Baldwin, V.K. Rashbrook, H.A. Fitzgerald, S.M. Blankenship, and D. Hedgecock. 1999. Isolation and inheritance of novel microsatellites in Chinook salmon (*Oncorhynchus tschawytscha*). Journal of Heredity 90:281-288.

Bennett, A.J. 1995. Bald eagle productivity in Lake Clark National Park and Preserve. Unpublished Progress Report. National Park Service-LACL, Port Alsworth, AK.

Birky, C.W., Maruyama, T., and Fuerst, P. 1983. An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. Genetics 103:513-527.

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.

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

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.

Cornuet, J.M., and G. Luikart. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics 144:2001-2014.

Cousens, N.B., G.A. Thomas, D.G. Swann, and M.C. Healy. 1982. A review of salmon escapement estimation techniques. Canadian Technical Report of Fisheries and Aquatic Sciences 1108.

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

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

El Mousadik, A., and R.J. Petit. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinos* (L.) Skeels] endemic to Morocco. Theoretical and Applied Genetics 92:832-839.

Estoup, A., P. Presa, F. Krieg, D. Vaiman, and R. Guyomard. 1993. $(Ct)_n$ and $(Gt)_n$ microsatellites: a new class of genetic markers for *Salmo trutta* L. (brown trout). Journal of Heredity 71:488-496.

Faire, L. 2000. Report to the Alaska Board of Fisheries on spawning escapement goal evaluations for Bristol Bay salmon. Alaska Department of Fish and Game Regional Information Report No. 2A00-38, Anchorage, Alaska.

Gilmer et al. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U.S. Department of Interior, Fish and Wildlife Service Resource Publication 140.

Giesel, J.T. 1974. Fitness and polymorphism for net fecundity distribution in iteroparous populations. American Naturalist 103:321-331.

Goudet, J. 1995. Fstat version 1.2: a computer program to calculate F-statistics. Journal of Heredity 86:485-486.

Guo, S.W., and E.A. Thompson. 1992. Performing the exact test of Hardy-Weinberg
  proportions for multiple alleles. Biometrics 48:361-372.

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

Johnson, D.E. 1998. Applied Multivariate Methods for Data Analysis. Brooks/Cole Publishing,
  Pacific Grove, California.

Jones, S.H., and Fahl, C.B. 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: evidence in the
  Kvichak River watershed, Bristol Bay, southwestern Alaska. Canadian Journal of
  Fisheries and Aquatic Sciences 50:2350-2365.

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

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

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

Luikart, G. 1997. Usefulness of molecular markers for detecting population bottlenecks and
  monitoring genetic change. Doctoral dissertation, University of Montana, Missoula.

Luikart, G., F.W. Allendorf, J.M. Cornuet, and W.B. Sherwin. 1998. Distortion of allele
  frequency distributions provides a test for recent population bottlenecks. Journal of
  Heredity 89:238-247.

Maruyama T., and P.A. Fuerst. 1985. Population bottlenecks and non-equilibrium models in
  population genetics II. Number of alleles in a small population that was formed by a
  recent bottleneck. Genetics 111:675-689.

Milner, A.M. 1987. Colonization and ecological development of new streams in Glacier Bay
  National Park, Alaska. Freshwater Biology 18:53-70.

Milner, A.M., and R.G. Bailey. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. Aquaculture and Fisheries Management 20:179-192.

Milner, A.M., E.E. Knudsen, C. Soiseth, A.L. Robertson, D. Schell, I.T. Phillips, and K. Magnusson. 2000. Colonization and development of stream communities across a 200 year gradient in Glacier Bay National Park, Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences 57:2319-2335.

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(2):9-15.

Morris, D.B., K.R. Richard, and J.M. Wright. 1996. Microsatellites from rainbow trout (*Oncorhynchus mykiss*) and their use for genetic study of salmonids. Canadian Journal of Fisheries and Aquatic Sciences 53:120-126.

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

]Nei, M. and F. Tajima. 1981. DNA polymorphism detectable by restriction endonucleases. Genetics 105:207-217.

Nelson, R.J., and T.D. Beacham. 1999. Isolation and cross species amplification of microsatellite loci useful for study of Pacific salmon. Animal Genetics 30:225-244.

O'Connell, M., R.G. Danzmann, J. Cornuet, J.M. Wright, and M.M. Ferguson. 1997. Differentiation of rainbow trout (*Oncorhynchus mykiss*) populations in Lake Ontario and the evaluation of the stepwise mutation and infinite allele mutation models using microsatellite variability. Canadian Journal of Fisheries and Aquatic Science 54:1391-1399.

Olsen, J.B., S.L. Wilson, E.J. Kretschmer, K.C. Jones, and J.E. Seeb. 2000. Characterization of 14 tetranucleotide microsatellite loci derived from sockeye salmon. Molecular Ecology 9:2185-2187.

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 O.A. Mathisen. 1981. Enumeration of sockeye salmon escapements to the Newhalen River-Lake Clark system in 1979 and 1980. University of Washington, Fisheries Research Institute (unpublished report).

Poe, P.H., and O.A. Mathisen. 1982. 1981 Newhalen river sockeye escapement studies. University of Washington, Fisheries Research Institute Report FRI-UW-8211, Seattle, Washington.

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. Sone and Webster Engineering Corp. FRI-UW-8415.

Quinn, T.P. 1985. Homing and the evolution of sockeye salmon, (*Oncorhynchus nerka*). Contributions in Marine Science 27 (Supplement):353-366.

Quinn, T.P., and A.H. Dittman. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. Trends in Ecology and Evolution 5:174-177.

Ramstad, K.M. 1998. Morphological, life history and genetic comparison of early and late run sockeye salmon (*Oncorhynchus nerka*) of Bear Lake, Alaska. Master of Arts thesis, University of Washington, Seattle, Washington.

Raymond, M. and F. Rousset. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

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, Alaska.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 19-160 *in* R.C. Simon and P.A. Larkin, editors. The Stock Concept in Pacific Salmon. University of British Columbia Press, Vancouver, British Columbia, Canada.

Rogers, D.E., and P.H. Poe. 1984. Escapement goals for the Kvichak River system. University of Washington, Fisheries Research Institute Report FRI-UW-8407, Seattle, WA.

Rogers, D.E., C. Foote, T. Quinn, and B. Rogers. 1997. Alaska salmon research, annual report-1996 to Bristol Bay processors. University of Washington, Fisheries Research Institute Report FRI-UW-9702, Seattle, Washington.

Rogers, D.E., T. Quinn, and B. Rogers. 1999. Alaska salmon research, annual report to Bristol Bay processors. University of Washington, Fisheries Research Institute No. FRU-UW-9904.

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 of Fish and Game (unpublished report).

Scribner, K.T., J.R. Gust, and R.L. Fields. 1996. Isolation and characterization of novel salmon microsatellite loci: cross-species amplification and population genetic applications. Canadian Journal of Fisheries and Aquatic Science 53:833-841.

Seeb, L.W., C. Habicht, W.D. Templin, K.E. Tarbox, R.Z. Davis, L.K. Brannian, and J.E. Seeb. 2000. Genetic diversity of sockeye salmon of Cook Inlet, Alaska, and its application to management of populations affected by the *Exxon Valdez* oil spill. Transactions of the American Fisheries Society 129:1223-1249.

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.

Smith, C.T., B.F. Koop, and R.J. Nelson. 1998. Isolation and characterization of coho salmon (*Oncorhynchus kisutch*) microsatellites and their use in other salmonids. Molecular Ecology 7:1614-1616.

Soulé, M.E. and L.S. Mills. 1998. No need to isolate genetics. Science 282:1658-1659.

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

Varnavskaya, N.V., C.C. Wood, and R. J. Everett. 1994a. Genetic variation in sockeye salmon (*Oncorhynchus nerka*) populations of Asia and North America. Canadian Journal of Fisheries and Aquatic Science 51(Supplement1):132-146.

Varnavskaya, N.V., C.C. Wood, R.J. Everett, R.L. Wilmot, V.S. Varnavsky, V.V. Midanaya, and T. P. Quinn. 1994b. Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*) within lakes of Alaska, British Columbia, and Kamchatka, Russia. Canadian Journal of Fisheries and Aquatic Sciences 51:147-157.

Waples, R. S. 2002. Definition and estimation of effective population size in the conservation of endangered species. Pages 147-168 *in* S. R. Beissinger and D. R. McCullough, editors. Population Viability Analysis. University of Chicago Press, Chicago, Illinois.

Weir, B.S., and C.C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358-1370.

Wilkens, A.X. 2002. The limnology of Lake Clark, Alaska. Master of Science thesis, University of Alaska Fairbanks.

Wilmot, R.L., and C.V. Burger. 1985. Genetic differences among populations of Alaskan sockeye salmon. Transactions of the American Fisheries Society 114:236-243.

Wilson, M.F. 1995. Biodiversity and ecological processes. *in* R. Szaro, editor. Biodiversity in managed landscapes. Oxford University Press, New York.

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

Winter, J.D. 1983. Underwater biotelemetry. Pages 371-395 *in* L.A. Nielsen and D.L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Withler, R.E., K.D. Le, J. Nelson, K. Miller, and T.D. Beacham. 2000. Intact genetic structure and high levels of genetic diversity in bottlenecked sockeye salmon (*Oncorhynchus nerka*) populations of the Fraser River, British Columbia, Canada. Canadian Journal of Aquatic and Fishery Science 57:1985-1998.

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

Wood, C.C., B.E. Riddell, D.T. Rutherford, and R.E. Withler. 1994. Biochemical genetic survey of sockeye salmon (*Oncorhynchus nerka*) in Canada. Canadian Journal of Aquatic and Fishery Science 51(Supplement 1):114-131.

Woody, C.A., J. Olsen, J. Reynolds, and P. Bentzen. 2000. Temporal variation in phenotypic and genotypic traits in two sockeye salmon populations, Tustumena Lake, Alaska. Transactions of the American Fisheries Society 129:1031-1043.

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

Zar, J.H. 1984. Biostatistical analysis, 2nd edition. Prentice Hall, New Jersey.

FIGURES
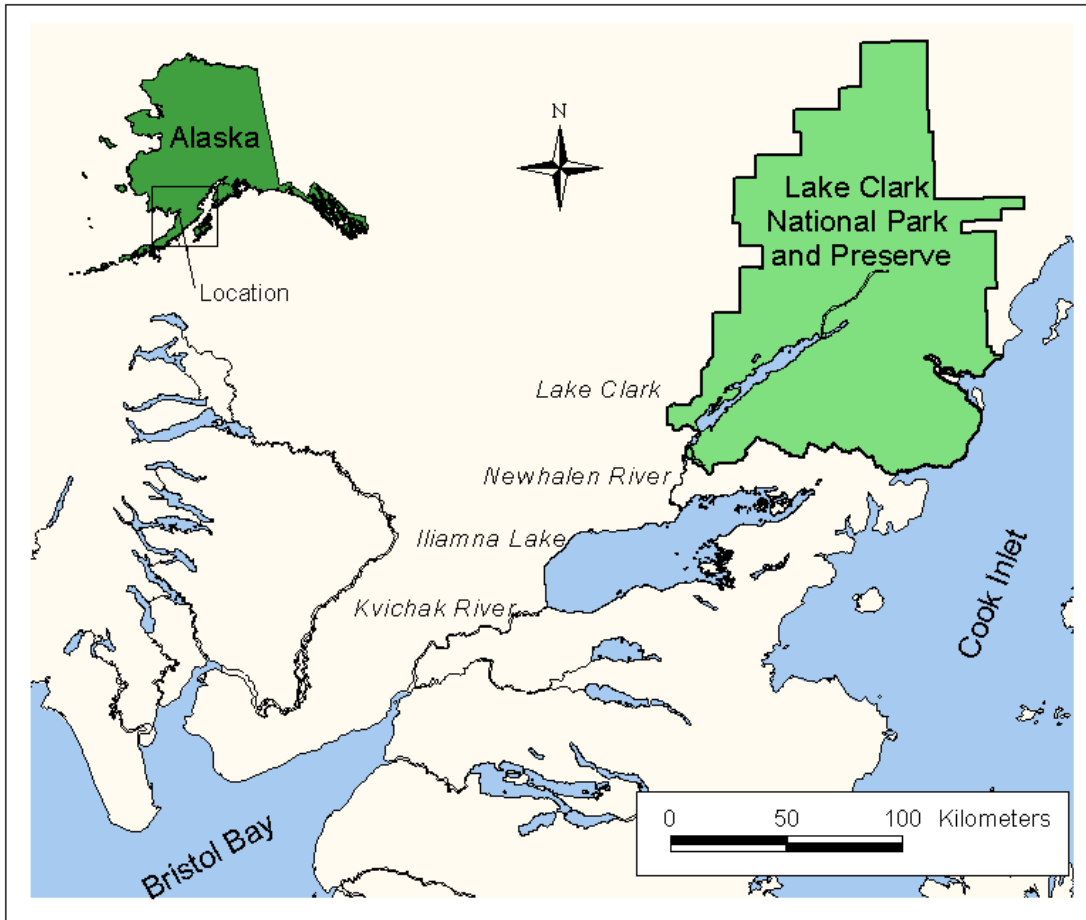
Figure 1. Location of Lake Clark relative to Bristol Bay, Alaska.
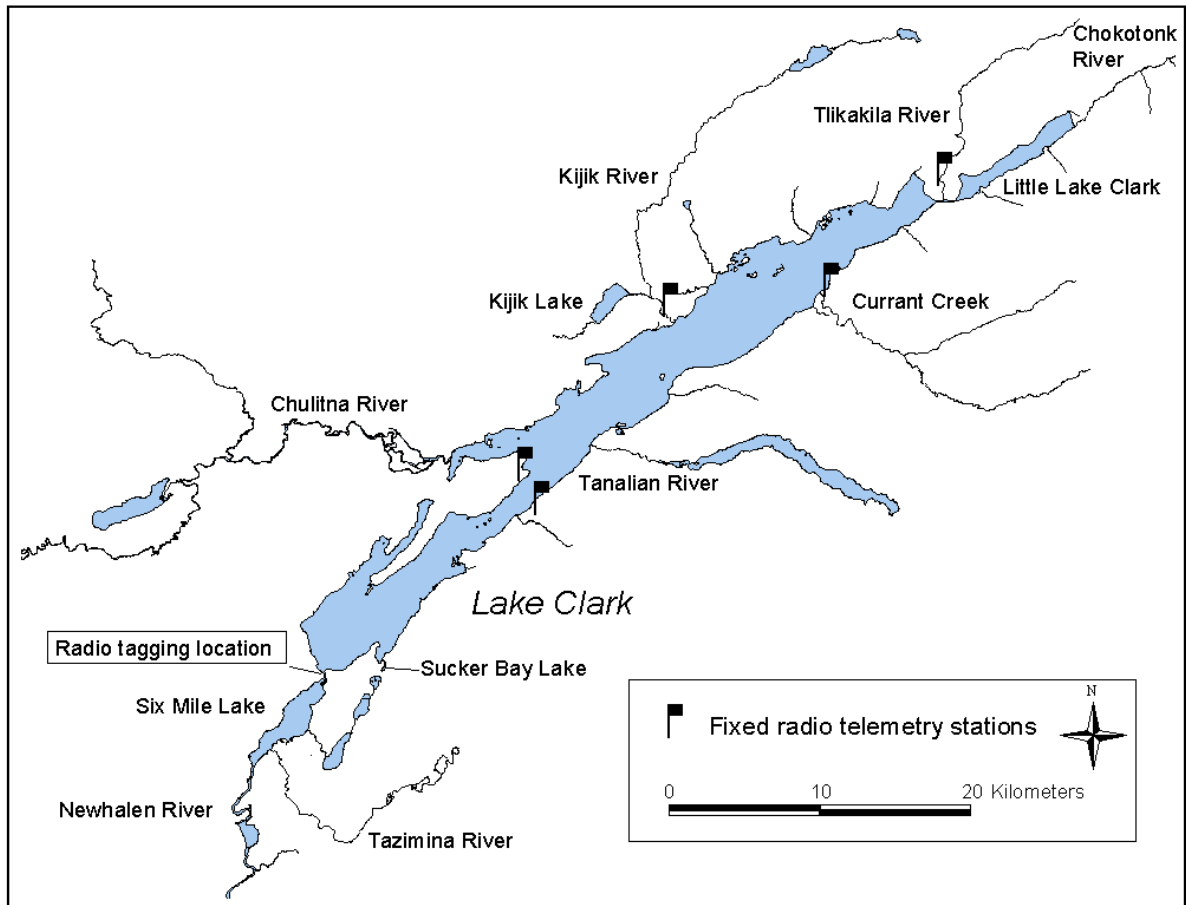
Figure 2. Location of fixed radio telemetry stations in the Lake Clark watershed, 2000 and 2001. In 2000, only the Kijik River and Tlikakila River fixed stations were operational.

Figure 3. Comprehensive map of spawning areas identified by radio telemetry and visual observation in clear (C) and glacial (G) waters of Lake Clark, 2000 and 2001. The number of tagged fish per spawning area is indicated. An additional five sites (labeled with a 0) were located by visual observation or seining. The line across the middle of Lake Clark denotes the boundary between glacial and clear beach spawning habitats. Note the large number of spawning habitats in glacial waters (>5 NTUs).

Figure 4. Proportion of glacial (> 5 NTUs) and clear (≤ 5 NTUs) spawning habitats identified by aerial surveys (A) and radio telemetry (R), historic, 2000, and 2001. Historic aerial survey data are from 1968 - 1983 (Regnart 1998). The aerial survey in 2000 was flown by Alaska Department of Fish and Game.
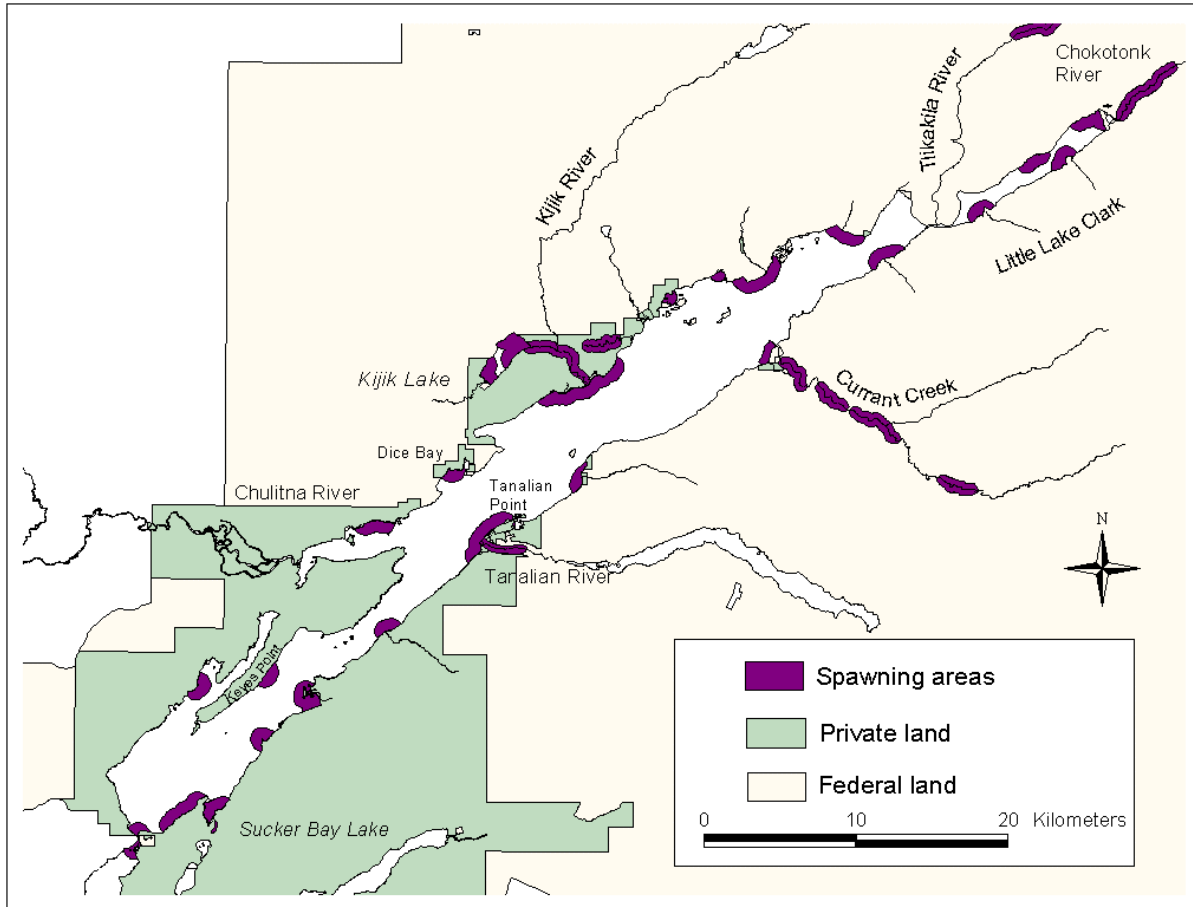
Figure 5. Spawning areas identified by radio telemetry and visual observation relative to land ownership in Lake Clark, 2000 and 2001.
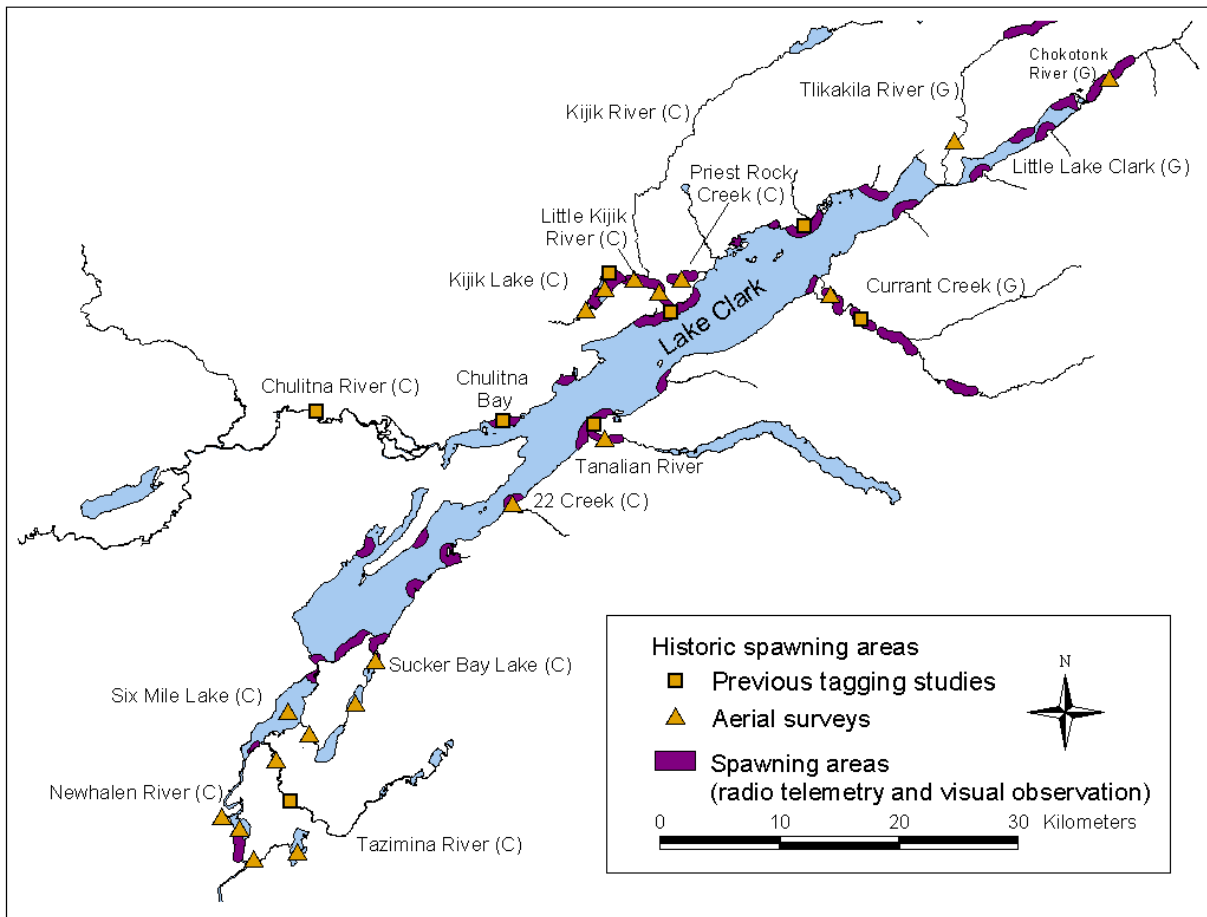
Figure 6. Comparison of spawning areas in Lake Clark identified by radio telemetry and visual observation in this study and spawning areas identified during historic aerial surveys (Parker and Blair 1987, Regnart 1998) and previous tagging studies (Smith 1964, Jensen and Mathisen 1987).
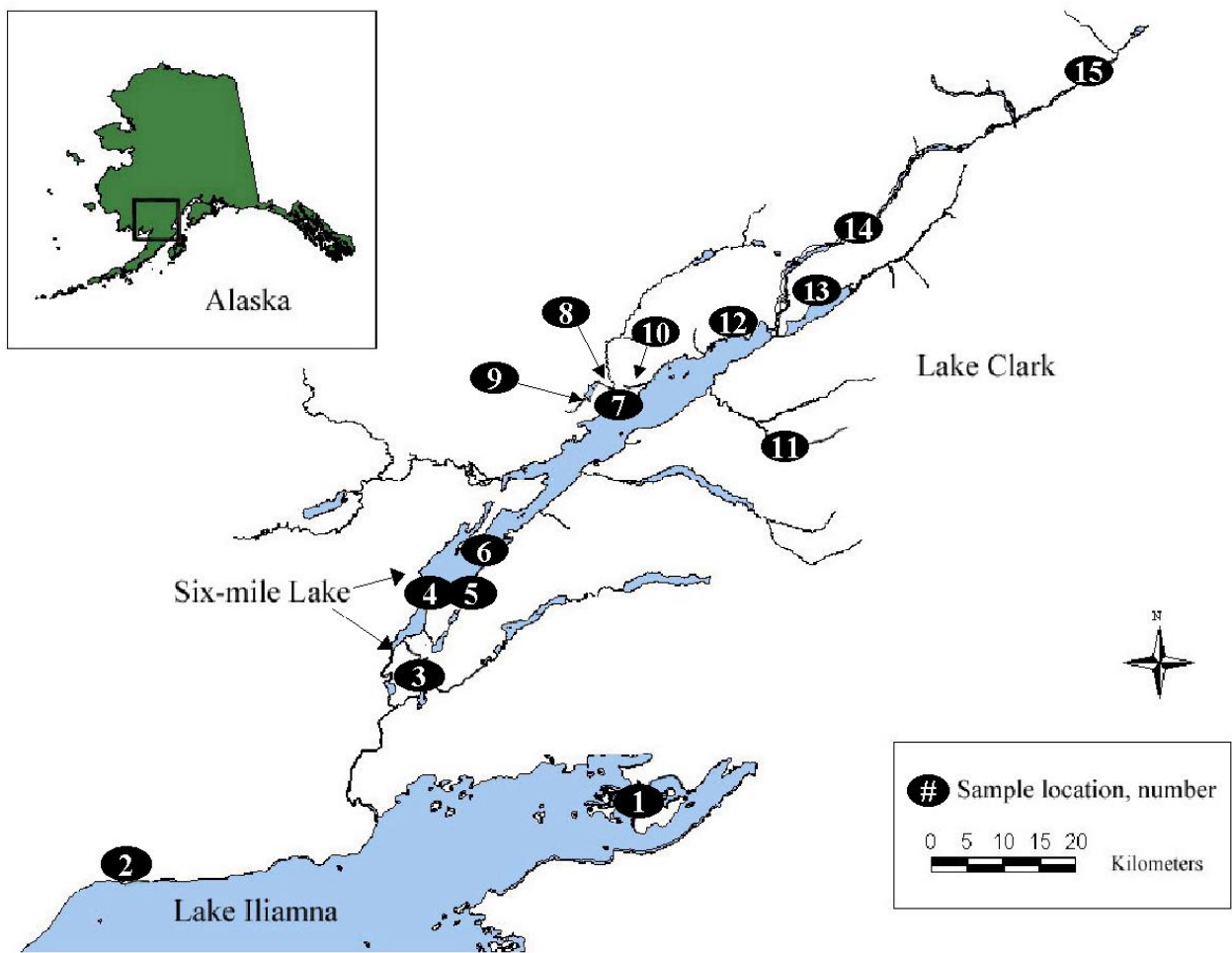
Figure 7. Map of Lake Clark, Sixmile Lake, and Lake Iliamna with genetic sampling sites shown. Refer to Table 4 for population names.
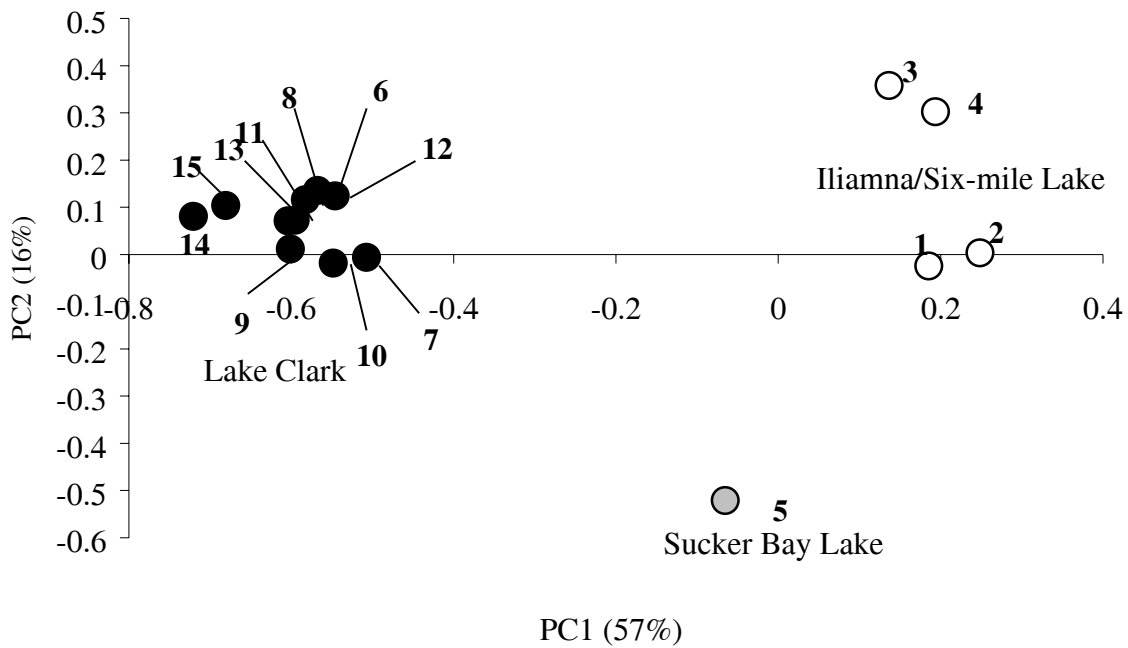
Figure 8. Principal component analysis of allele frequencies at 11 microsatellite loci. Percentages in parentheses indicate amount of variation explained by each principal component. Three major population groups are detected: Iliamna/Sixmile Lake = outlined, Lake Clark = black, and Sucker Bay Lake = shaded points. Refer to Table 4 for population names.
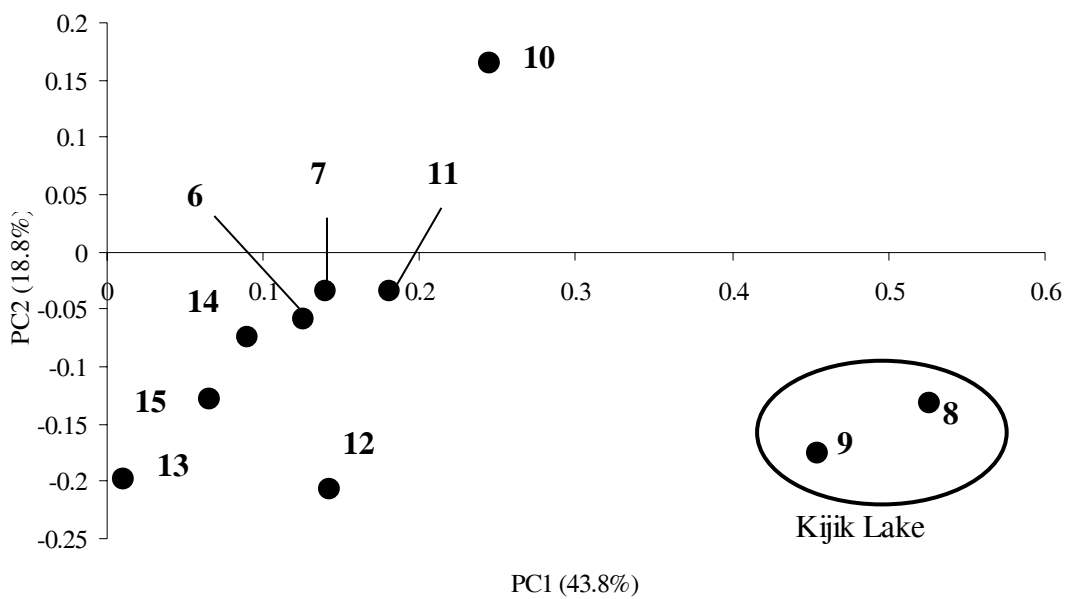
Figure 9. Principal component analysis of Lake Clark population allele frequencies at 11 microsatellite loci. Highly divergent populations of Kijik Lake and Priest Rock Creek are identified. Percentages in parentheses indicate amount of variation explained by each principal component. Refer to Table 4 for population names.
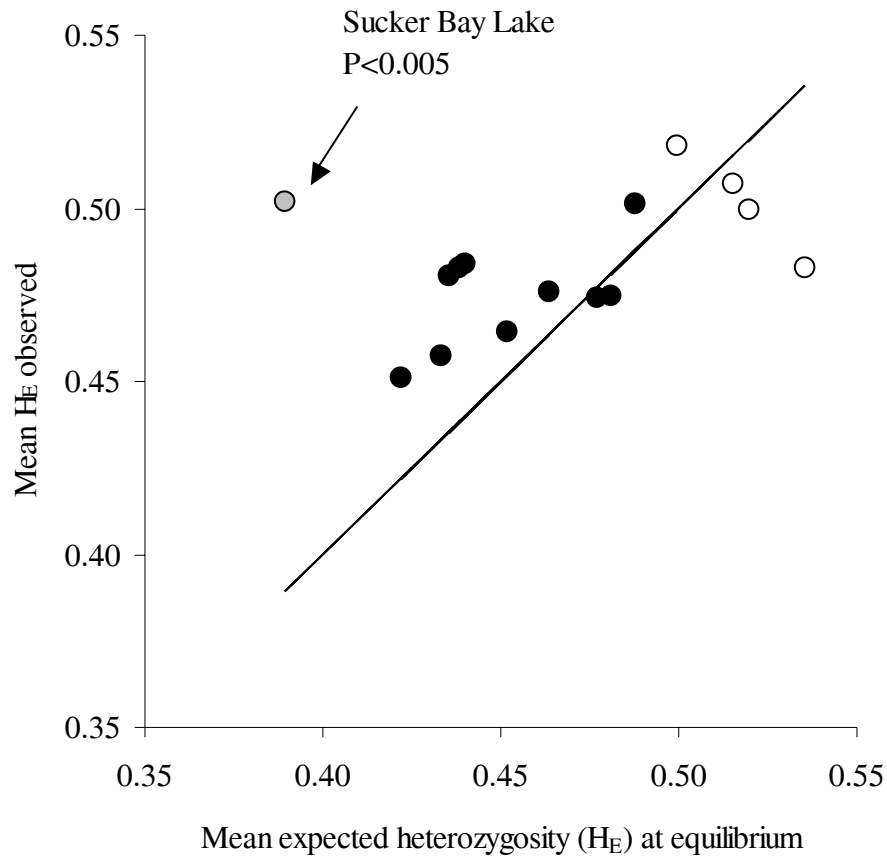
Figure 10. Relationship between mean expected heterozygosity (H_E) observed and expected under the Infinite Alleles Model of mutation (IAM). Recently bottlenecked populations will have greater heterozygosity (H_E) than expected at migration-drift equilibrium with the same number of alleles due to the loss of rare alleles. Non-bottleneck populations will have an H_E that is equal to or less than that expected under IAM (on or below equality line). Three major population groups are coded as follows: Iliamna/Sixmile Lake = outlined, Lake Clark = black, and Sucker Bay Lake = shaded circles.
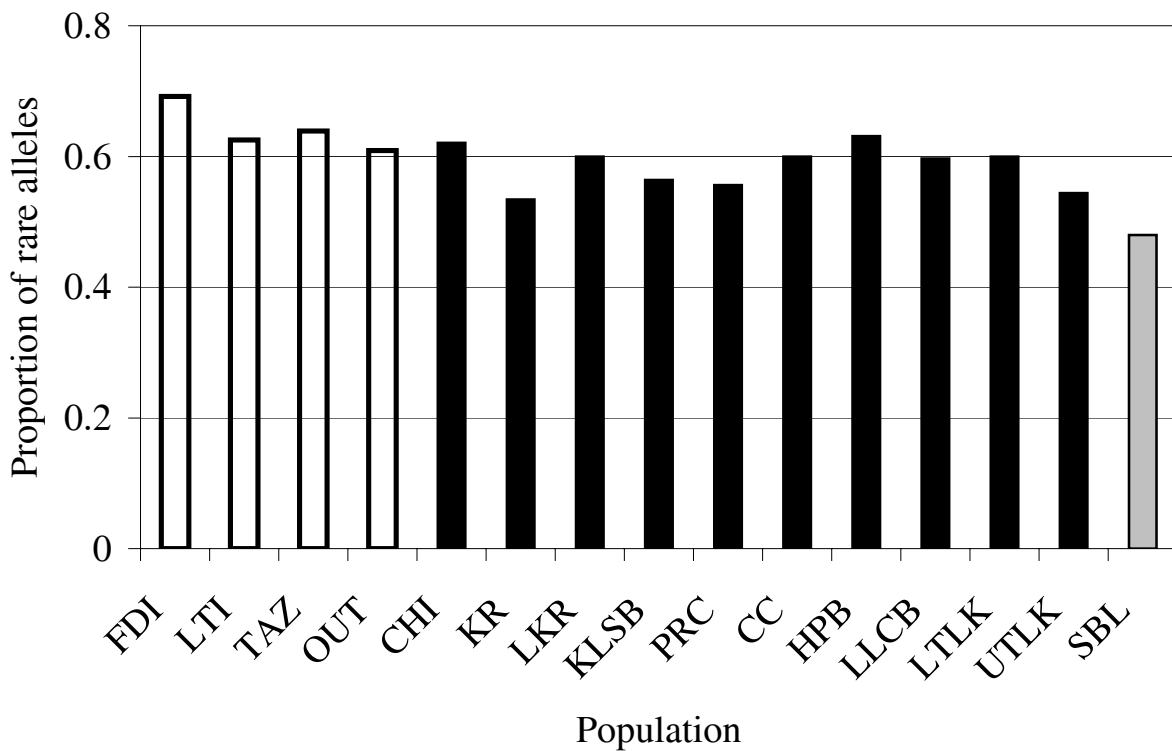
Figure 11. Proportion of rare alleles (frequency less than or equal to 0.1) by population. Three major population groups are coded as follows: Iliamna/Sixmile Lake = outlined, Lake Clark = black, and Sucker Bay Lake = shaded bar. Refer to Table 4 for population names.

TABLES

Table 1. Mid-eye to hypural length (mm) of tagged and untagged adult sockeye salmon captured at the outlet of Lake Clark, 2000 and 2001.

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

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

Table 2. Tagging and tracking summary for radio tagged adult sockeye salmon in Lake Clark watershed, 2000 and 2001.

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

[a]These include spawning areas at the outlet of Lake Clark, Sixmile Lake, and Newhalen River.

Table 3. Number and percent distribution of spawning radio tagged fish relative to land ownership and development in Lake Clark, Alaska, 2000 and 2001.

Land Category	2000	2001	Total
Private	75 (76%)	73 (51%)	148 (61%)
Federal	24 (24%)	69 (49%)	93 (39%)
Development	34 (34%)	29 (20%)	63 (26%)
No Development	65 (66%)	113 (80%)	178 (74%)

Table 4. Sample size (N), heterozygosity (H_E), and allelic richness (number of alleles corrected for sample size) of sockeye salmon populations sampled in Lake Clark, Sixmile Lake, and Lake Iliamna sockeye. Allelic richness is standardized to the lowest sample size (N=65).

		Site	N	H_E	Mean no. alleles	Allelic richness
1	FDI	Fuel Dump Island, Iliamna	87	0.48	7.1	6.50
2	TCI	Talarik Creek, Iliamna	97	0.50	6.5	5.97
3	TAZ	Tazimina River	99	0.51	6.5	5.83
4	OUT	Lake Clark Outlet	100	0.52	6.3	5.65
5	SBL	Sucker Bay Lake	100	0.50	4.3	4.16
6	CHI	Chi Point	99	0.48	6.0	5.42
7	KR	Kijik River	99	0.48	5.3	4.90
8	LKR	Little Kijik River	98	0.46	5.0	4.62
9	KLSB	Kijik Lake South Beach	100	0.45	5.0	4.58
10	PRC	Priest Rock Creek	65	0.48	4.9	4.91
11	CC	Currant Creek	100	0.48	5.5	5.03
12	HPB	Hatchet Point Beach	99	0.50	5.9	5.34
13	LLCB	Little Lake Clark Beach	100	0.47	5.6	5.12
14	LTLK	Lower Tlikakila	100	0.46	5.5	4.90
15	UTLK	Upper Tlikakila	100	0.48	5.2	4.75

Table 5. Microsatellite loci analyzed including multiplex annealing temperatures and allelic variation per locus and population.

Locus	Annealing temperature (°C)	Allelic size range	Total no. alleles per locus	Mean no. alleles per population	Reference
Oki1-1	56	106-122	5	3.1	Smith et al. 1998
Oki1-2	56	140-164	7	3.0	Smith et al. 1998
Omy325	56	118-174	21	10.9	O'Connell et al. 1997
uSat60	58	112-136	12	5.6	Estoup et al. 1993
One21	58	110-152	16	10.1	Scribner et al. 1996
Ots3	48	74-100	12	4.0	Banks et al. 1999
One18	52	163-189	12	6.1	Scribner et al. 1996
One13	52	154-174	11	5.9	Scribner et al. 1996
One105	52	124-144	6	4.5	Olsen et al. 2000
Ots107	48	90-130	9	4.1	Nelson and Beacham 1999
Omy77	48	85-121	14	5.4	Morris et al. 1996

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Table 6. Pair-wise F_{ST} (below diagonal) and comparisons of allele frequencies (above diagonal) between sockeye salmon populations sampled in Lake Clark and Lake Iliamna. Number of loci with significant differences in allele frequencies is given for comparisons with significantly different allele frequencies over all loci. Refer to Table 4 for population names.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK
FDI	-	4	7	7	11	8	7	7	8	6	10	6	7	10	8
TCI	0.016	-	8	7	11	8	11	8	7	7	9	9	9	10	10
TAZ	0.043	0.023	-	NS	9	7	9	10	10	8	8	9	10	10	9
OUT	0.026	0.018	0.003	-	9	7	10	8	10	8	7	9	10	10	9
SBL	0.054	0.045	0.065	0.061	-	8	8	9	9	7	8	7	9	8	7
CHI	0.060	0.062	0.052	0.051	0.063	-	NS	2	2	1	NS	NS	NS	NS	NS
KR	0.052	0.055	0.052	0.049	0.044	0	-	4	3	1	1	NS	9	10	0
LKR	0.065	0.071	0.069	0.066	0.077	0.014	0.017	-	NS	2	2	3	4	4	4
KLSB	0.067	0.071	0.071	0.069	0.064	0.012	0.011	0.001	-	3	1	2	4	1	2
PRC	0.062	0.057	0.058	0.058	0.050	0.004	0.005	0.012	0.012	-	2	2	2	2	2
CC	0.067	0.065	0.056	0.057	0.057	0	0	0.011	0.008	0.002	-	1	2	NS	NS
HPB	0.055	0.060	0.053	0.048	0.060	0.001	0.004	0.013	0.010	0.009	0.004	-	NS	0	NS
LLCB	0.070	0.069	0.059	0.061	0.060	0.003	0.005	0.024	0.017	0.013	0.005	0.002	-	NS	NS
LTLK	0.089	0.085	0.069	0.074	0.069	0.003	0.006	0.018	0.013	0.007	0	0.006	0.004	-	NS
UTLK	0.076	0.077	0.065	0.066	0.067	0	0.003	0.018	0.013	0.007	0	0.001	0	-0.001	-

APPENDIX

Appendix 1. Spawning locations identified by radio telemetry and visual observation in Lake Clark, 2000 and 2001. Water type (glacial > 5 NTUs or clear < 5 NTUs) was categorized at time of peak spawning activity. Distance was calculated from the tagging site at the outlet of Lake Clark. Historic aerial survey data are from the Fisheries Research Institute, University of Washington 1968 to 1983 (Regnart 1998). Land status (e.g. private) adjacent to spawning areas was recorded as present (Y) or not present (N).

ID	Spawning location	Specific location	Latitude	Longitude	Habitat type	Water type	Peak spawning	Distance (km)	Historic	Private land	Development	Number of tagged fish		
												2000	2001	Total
1	Newhalen River[a]		59.8824614	-154.8709529	Stream	Clear		19	Y	-	-	0	1 *	1 *
2	6 Mile Lake[a]		59.9548997	-154.8532472	Beach	Clear		8	Y	-	-	0	1 *	1 *
3	Lake Clark Outlet[a]		60.0196571	-154.7575543	Stream	Clear	8/25-9/15	1	N	N	N	35 *	4 *	39 *
4	Lake Clark Beaches	Outlet South	60.0268979	-154.7133590	Beach	Clear	9/1-9/30	4	N	Y	N	1 (1.0%)	3 (2.1%)	4 (1.7%)
5	Lake Clark Beaches	Sucker Bay	60.0357855	-154.6573315	Beach	Clear	9/1-9/30	8	Y	Y	N	1 (1.0%)	1 (0.7%)	2 (0.8%)
6	Sucker Bay Lake		60.0215469	-154.6636382	Beach	Clear	8/25-9/15	9	Y	Y	N	3 (3.0%)	2 (1.4%)	5 (2.1%)
7	Lake Clark Beaches	Snowshoe Bay	60.1067853	-154.6851025	Beach	Clear	9/1-9/30	11	N	Y	N	0	1 (0.7%)	1 (0.4%)
8	Lake Clark Beaches	Chi Point	60.0755617	-154.6042180	Beach	Clear	9/1-9/30	12	N	Y	Y	2 (2.0%)	1 (0.7%)	3 (1.2%)
9	Lake Clark Beaches	Keyes Point	60.1147003	-154.6036866	Beach	Clear	9/1-9/30	15	N	Y	Y	0	1 (0.7%)	1 (0.4%)
10	Lake Clark Beaches	Flat Island	60.0981051	-154.5407755	Beach	Clear	9/1-10/15	16	N	Y	N	3 (3.0%)	7 (4.9%)	10 (4.1%)
11	Lake Clark Beaches	22 Creek	60.1413319	-154.4593394	Beach	Clear	9/15-9/30	22	Y	Y	Y	1 (1.0%)	0	1 (0.4%)
12	Lake Clark Beaches	Chulitna Bay	60.2049753	-154.4763469	Beach	Clear	9/15-10/15	30	Y	Y	N	2 (2.0%)	5 (3.5%)	7 (2.9%)
13	Lake Clark Beaches	Tanalian Point	60.1939450	-154.3508224	Beach	Glacial	9/15-10/15	31	Y	Y	Y	17 (17.2%)	17 (12%)	34 (14.1%)
14	Tanalian River[b]		60.1858212	-154.2740385	Stream	Clear	9/15-9/30	31	Y	Y	N	0	0	0
15	Lake Clark Beaches	Dice Bay	60.2348902	-154.3872065	Beach	Glacial	9/1-9/30	33	N	Y	N	0	1 (0.4%)	1 (0.4%)
16	Lake Clark Beaches	Tommy	60.2285721	-154.2337341	Beach	Glacial	9/15-10/15	38	N	Y	Y	2 (2.0%)	0	2 (0.8%)
17	Lake Clark Beaches	Kijik Outlet	60.2807490	-154.2648977	Beach	Glacial	9/15-10/15	41	Y	Y	Y	12 (12.1%)	7 (4.9%)	19 (7.9%)
18	Kijik River		60.2978737	-154.2432988	Stream	Clear	9/15-10/15	45	Y	Y	N	2 (2.0%)	0	2 (0.8%)
19	Little Kijik River		60.3078998	-154.2932831	Stream	Clear	9/15-10/15	49	Y	Y	N	5 (5.1%)	1 (0.7%)	6 (2.5%)
20	Lake Clark Beaches	Aggie's Beach[b]	60.33869	-154.13223	Beach	Glacial	9/15-10/15	49	N	Y	Y	0	0	0
21	Priest Rock Creek		60.3084707	-154.2287282	Stream	Clear	9/25-10/15	52	Y	Y	N	0	1 (0.7%)	1 (0.4%)
22	Lake Clark Beaches	Currant Outlet Beach[b]	60.29969	-154.01009	Beach	Glacial	9/15-10/15	52	N	Y	N	0	0	0
23	Kijik Lake Beaches		60.2870340	-154.3447792	Beach	Clear	9/15-10/31	52	Y	Y	N	21 (21.2%)	19 (13.4%)	40 (16.6%)
24	Kijik Lake Tributaries		60.28577	-154.34395	Stream	Clear	9/25-10/15	53	Y	Y	N	0	0	0
25	Lake Clark Beaches	Corey's Beach[b]	60.35162	-154.06406	Beach	Glacial	9/15 - 10/15	53	N	Y	Y	0	0	0
26	Lake Clark Beaches	Portage Creek	60.3458561	-154.0299919	Beach	Glacial	9/15-10/15	54	Y	Y	N	3 (3.0%)	3 (2.1%)	6 (2.5%)

-Continued-

Appendix 1. (page 2 of 2).

					Habitat	Water	Peak	Distance		Private	Develop-	Number of tagged fish		
ID	Spawning location	Specific location	Latitude	Longitude	type	type	spawning	(km)	Historic	land	ment	2000	2001	Total
27	Currant Creek		60.2292195	-153.8007299	Stream	Glacial	9/15-9/30	57	Y	N	N	2 (2.0%)	3 (2.1%)	5 (2.1%)
29	Lake Clark Beaches	Middle Ridge	60.3607695	-153.8619178	Beach	Glacial	9/15-10/15	64	N	N	N	1 (1.0%)	2 (1.4%)	3 (1.2%)
29	Lake Clark Beaches	Cave Falls	60.3856850	-153.7529883	Beach	Glacial	9/15-10/15	71	N	N	N	0	2 (1.4%)	2 (0.8%)
31	Lake Clark Beaches	Little Lake Clark N	60.4183515	-153.6965771	Beach	Glacial	9/15-10/15	76	N	N	N	0	5 (3.5%)	5 (2.1%)
32	Lake Clark Beaches	Little Lake Clark S	60.4175140	-153.6557679	Beach	Glacial	9/15-10/15	77	N	N	N	0	2 (1.4%)	2 (0.8%)
33	Lake Clark Beaches	Chokotonk Outlet	60.4437421	-153.6218053	Beach	Glacial	9/15-10/31	80	N	N	N	2 (2.0%)	16 (11.3%)	18 (7.5%)
34	Chokotonk River		60.4669812	-153.5423128	Stream	Glacial	9/15-10/15	86	Y	N	N	1 (1.0%)	6 (4.2%)	7 (2.9%)
35	Tlikakila River		60.5537441	-153.5067036	Stream	Glacial	9/15-10/15	98	Y	N	N	18 (18.2%)	33 (23.2%)	51 (21.2%)

[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.

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Appendix 2. Comparison of percent spawning distribution among habitats of Lake Clark sockeye salmon identified by aerial survey (A) and radio telemetry (R).

Spawning Location	Habitat Type	Water Type	Peak Spawning	Percent spawning distribution by location[a]				
				Historic (A)	2000 (A)	2000 (R)	2001 (R)	Total (R)
Tlikakila River	Stream	Glacial	9/15-10/15	7	14	18	23	21
Chokotonk River	Stream	Glacial	9/15-10/15	2	3	1	4	3
Currant Creek	Stream	Glacial	9/15-9/30	0	13	2	2	2
Priest Rock Creek	Stream	Clear	9/25-10/15	5	0	0	1	0
Tanalian River	Stream	Clear	9/15-9/30	1	0	0	0	0
22 Creek	Stream	Clear	9/15-9/30	0	0	0	0	0
Little Kijik River	Stream	Clear	9/15-10/15	18	15	5	1	2
Kijik River	Stream	Clear	9/15-10/15	9	5	2	0	1
Kijik Lake Tributaries	Stream	Clear	9/25-10/15	3	3	0	0	0
Kijik Lake Beaches	Beach	Clear	9/15-10/30	41	44	21	13	17
Sucker Bay Lake	Beach	Clear	8/25-9/15	5	3	3	1	2
Lake Clark Beaches	Beach	Both	9/1-10/30	9	0	47	54	51

[a] Aerial survey data for 1968-1983 was the most comprehensive and flown by the same University of Washington observer (Pat Poe, present address: Bonneville Power Association, Portland, OR). Aerial survey data for 2000 was collected by Alaska Department of Fish and Game.

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Appendix 3. Microsatellite allele frequencies and sample sizes of Lake Clark sockeye salmon by locus and population. Refer to Table 4 for population names.

	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
Oki1-1																
N	87	97	99	100	100	99	99	98	100	65	100	99	100	100	100	54
106	0.006	0.005	0.005	-	-	0.010	0.015	-	-	-	0.005	0.010	0.025	-	0.015	0.056
110	0.816	0.876	0.793	0.790	0.680	0.682	0.626	0.770	0.740	0.700	0.655	0.667	0.630	0.630	0.625	0.806
114	0.178	0.119	0.202	0.210	0.320	0.308	0.354	0.230	0.255	0.292	0.340	0.303	0.330	0.370	0.355	0.102
118	-	-	-	-	-	-	-	-	0.005	0.008	-	0.020	0.015	-	0.005	0.037
122	-	-	-	-	-	-	0.005	-	-	-	-	-	-	-	-	-
Oki1-2																
N	87	97	99	100	100	99	99	98	100	65	100	99	100	100	100	54
140	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-
144	-	-	-	-	-	0.005	-	-	-	-	0.015	0.015	0.005	0.010	-	-
148	0.672	0.598	0.692	0.675	0.670	0.753	0.722	0.577	0.560	0.723	0.705	0.682	0.740	0.750	0.740	0.463
152	-	0.021	-	0.005	-	-	-	-	-	-	-	-	-	-	-	0.009
156	0.299	0.361	0.293	0.305	0.315	0.237	0.278	0.418	0.440	0.277	0.280	0.303	0.255	0.240	0.260	0.528
160	0.029	0.015	0.015	0.015	-	0.005	-	0.005	-	-	-	-	-	-	-	-
164	-	-	-	-	0.015	-	-	-	-	-	-	-	-	-	-	-
Omy325																
N	87	97	99	100	100	99	99	98	100	65	100	99	100	100	100	54
118	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-
134	-	-	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-
138	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-
140	0.184	0.103	0.030	0.080	0.005	0.056	0.061	0.020	0.025	0.008	0.040	0.086	0.04	0.035	0.08	0.009
142	-	0.010	-	-	-	-	-	-	-	0.031	0.010	-	-	-	-	0.009
144	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.056

-Continued-

Appendix 3. (page 2 of 7)

Omy325 (continued)

	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
146	-	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-
148	-	0.005	0.005	-	-	0.010	-	-	-	-	0.035	0.020	0.005	0.020	0.010	0.009
150	0.017	-	-	0.005	0.005	0.010	0.030	0.036	0.040	0.023	0.020	0.030	0.025	0.015	0.040	0.019
152	0.115	0.211	0.187	0.110	0.200	0.328	0.318	0.449	0.340	0.431	0.390	0.263	0.290	0.385	0.355	0.093
154	0.080	0.010	0.005	0.020	0.095	0.076	0.101	0.051	0.095	0.077	0.090	0.066	0.065	0.085	0.055	0.120
156	0.259	0.418	0.515	0.485	0.275	0.162	0.136	0.097	0.100	0.185	0.105	0.167	0.135	0.110	0.105	0.352
158	0.230	0.134	0.182	0.225	0.350	0.293	0.298	0.281	0.355	0.146	0.265	0.333	0.365	0.300	0.315	0.111
160	0.034	0.041	0.015	0.030	0.015	0.030	0.025	0.041	0.015	0.031	0.030	0.010	0.025	0.035	0.025	0.111
162	0.023	0.046	0.010	0.015	0.020	0.015	0.015	0.005	0.005	-	0.015	-	-	0.005	-	0.028
164	0.029	0.005	0.010	0.005	-	-	-	0.005	-	0.023	-	0.005	0.020	0.005	-	-
166	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.019
168	0.011	0.005	0.005	0.005	0.035	0.020	0.010	0.015	0.020	0.046	-	0.020	0.030	0.005	0.015	0.009
170	0.006	-	-	0.005	-	-	-	-	0.005	-	-	-	-	-	-	-
172	-	0.005	-	0.010	-	-	0.005	-	-	-	-	-	-	-	-	0.056
174	0.006	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-

uSat60

	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
N	87	97	99	100	100	98	99	98	100	65	100	98	100	100	100	54
112	-	-	0.010	0.010	-	-	-	-	-	0.038	-	-	0.005	-	-	-
114	0.011	-	0.010	0.010	-	0.041	0.035	0.046	0.035	0.023	0.035	0.041	0.020	0.025	0.090	-
116	0.011	-	0.005	0.005	-	0.005	0.005	-	-	-	-	0.005	-	-	-	-
118	0.603	0.608	0.773	0.735	0.475	0.745	0.717	0.811	0.770	0.677	0.750	0.668	0.650	0.770	0.690	0.426
120	0.006	0.005	0.005	0.005	-	0.005	-	-	0.010	-	-	-	-	-	-	0.046
122	0.017	0.026	0.056	0.045	-	0.010	-	-	-	-	0.035	0.005	0.005	-	-	0.120
124	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

-Continued-

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	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
uSat60 (continued)																
126	-	-	-	-	0.020	-	-	-	-	0.015	0.005	0.005	-	-	-	-
128	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
130	0.333	0.345	0.131	0.175	0.505	0.189	0.237	0.138	0.180	0.246	0.175	0.265	0.320	0.200	0.220	0.398
134	0.006	0.010	0.010	0.015	-	0.005	0.005	0.005	0.005	-	-	0.010	-	0.005	-	0.009
136	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-
One21																
N	87	97	99	100	99	99	99	98	100	65	100	99	100	100	100	54
110	-	-	-	-	-	-	-	-	-	-	-	-	0.005	-	-	-
124	0.011	-	-	-	0.010	-	-	-	-	-	-	0.005	-	-	-	-
126	0.017	0.015	-	-	-	0.005	0.035	0.005	0.005	0.023	0.005	0.005	0.005	0.005	-	0.046
128	-	0.010	0.005	-	-	0.010	0.005	-	-	0.008	0.015	-	0.005	0.005	0.005	-
130	0.247	0.165	0.268	0.330	0.066	0.131	0.116	0.163	0.080	0.069	0.145	0.167	0.170	0.105	0.150	0.407
132	0.023	0.031	0.040	0.045	-	0.010	0.005	-	0.010	-	-	-	-	-	0.005	0.056
134	0.011	-	0.172	0.135	0.035	0.020	0.005	-	0.010	-	0.005	0.020	0.010	0.005	0.010	-
136	0.063	0.067	0.056	0.035	-	0.086	0.066	0.010	0.015	0.046	0.020	0.076	0.035	0.065	0.065	0.056
138	0.034	0.036	0.030	0.020	-	0.010	-	0.015	0.010	0.038	0.030	0.005	0.025	0.010	0.005	0.019
140	0.345	0.371	0.313	0.240	0.768	0.475	0.515	0.582	0.625	0.600	0.535	0.444	0.500	0.600	0.495	0.287
142	0.172	0.165	0.091	0.140	0.101	0.172	0.197	0.133	0.105	0.131	0.145	0.197	0.130	0.115	0.140	0.093
144	0.052	0.108	0.015	0.040	0.020	0.051	0.040	0.087	0.120	0.077	0.090	0.061	0.080	0.090	0.120	0.028
146	0.011	0.015	0.005	0.005	-	0.020	0.015	0.005	-	0.008	0.010	0.015	0.040	-	0.005	-
148	0.006	0.010	-	0.005	-	0.005	-	-	0.020	-	-	0.005	-	-	-	0.009
150	0.006	-	0.005	0.005	-	0.005	-	-	-	-	-	-	-	-	-	-
152	-	0.005														

-Continued-

Appendix 3. (page 4 of 7)

	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
Ots3																
N	87	97	99	100	100	98	99	96	100	65	100	99	100	100	100	54
74	-	0.005	-	0.005	-	-	-	-	-	-	-	-	-	-	-	0.176
78	-	-	-	-	-	-	-	-	-	-	0.020	-	0.005	-	0.005	-
82	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-
84	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-
86	0.011	-	-	-	-	-	0.015	-	0.005	-	-	0.005	-	-	-	-
88	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-
90	0.891	0.881	0.763	0.715	0.785	0.939	0.929	0.880	0.940	0.923	0.915	0.904	0.940	0.900	0.945	0.417
92	-	0.010	-	-	-	-	-	0.016	-	-	0.010	-	-	0.005	-	-
94	0.052	0.067	0.136	0.150	0.200	0.061	0.056	0.094	0.055	0.054	0.055	0.081	0.050	0.090	0.045	0.028
96	0.040	0.031	0.091	0.125	0.015	-	-	-	-	0.023	-	0.010	0.005	0.005	0.005	0.370
98	-	0.005	-	0.005	-	-	-	-	-	-	-	-	-	-	-	0.009
100	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
One18																
N	87	97	99	100	100	99	99	97	100	65	100	99	100	100	100	54
163	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-
169	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.130
171	0.316	0.412	0.338	0.315	0.205	0.207	0.177	0.170	0.135	0.177	0.140	0.177	0.220	0.165	0.150	0.120
173	0.017	0.005	0.010	-	-	-	-	0.005	-	-	-	-	-	-	-	0.046
175	-	-	0.061	0.020	0.090	0.116	0.126	0.072	0.075	0.046	0.095	0.076	0.110	0.075	0.115	0.019
177	-	-	-	-	-	0.005	0.005	-	-	-	-	0.005	-	-	0.005	-
179	-	-	-	0.005	0.160	0.005	0.020	-	-	0.008	0.030	-	0.005	0.035	0.030	-
181	0.218	0.304	0.328	0.395	0.405	0.520	0.530	0.469	0.530	0.585	0.565	0.510	0.505	0.570	0.550	0.176

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	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
One18 (continued)																
183	-	-	-	-	-	-	-	-	-	-	0.010	0.005	-	-	0.005	-
185	0.431	0.258	0.258	0.265	0.140	0.146	0.141	0.278	0.255	0.177	0.160	0.222	0.140	0.150	0.130	0.509
187	0.011	-	0.005	-	-	-	-	-	-	-	-	0.005	0.005	-	-	-
189	0.006	0.015	-	-	-	0.005	-	0.005	0.005	0.008	-	-	0.015	0.005	0.015	-
One13																
N	87	97	99	100	100	99	99	97	100	65	100	99	100	99	100	54
154	0.006	0.021	-	-	-	-	-	-	-	-	-	-	-	-	-	-
156	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
158	0.006	-	0.010	-	-	0.025	0.025	-	0.005	0.031	-	0.025	0.005	-	-	-
160	0.236	0.397	0.510	0.380	0.415	0.444	0.429	0.340	0.420	0.377	0.485	0.449	0.550	0.545	0.510	0.204
162	0.017	0.015	0.051	0.050	0.030	0.020	0.020	0.041	0.005	0.077	0.035	0.030	0.040	0.025	0.045	0.278
164	0.006	0.026	0.005	0.020	-	-	-	0.005	-	-	-	-	0.005	0.005	-	0.028
166	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-
168	0.695	0.495	0.303	0.475	0.545	0.490	0.505	0.577	0.550	0.500	0.470	0.480	0.390	0.399	0.435	0.472
170	0.006	-	0.111	0.070	-	0.015	0.010	0.021	0.005	-	-	0.010	-	-	-	0.009
172	0.017	0.041	0.005	0.005	0.010	0.005	0.010	0.015	0.015	0.015	0.010	0.005	0.010	0.025	0.010	0.009
174	0.006	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-
One105																
N	87	97	99	100	98	99	99	98	100	65	100	99	100	100	100	54
124	-	-	-	-	-	0.010	0.005	-	-	-	0.005	-	-	-	-	-
128	-	-	0.005	0.005	0.020	0.005	-	0.010	-	-	0.005	0.005	0.005	-	0.005	0.019
132	0.822	0.784	0.773	0.775	0.699	0.763	0.803	0.832	0.835	0.723	0.800	0.793	0.845	0.795	0.780	0.630
136	0.126	0.113	0.101	0.110	0.133	0.172	0.162	0.092	0.105	0.177	0.145	0.141	0.120	0.170	0.145	0.139

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	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
One105 (continued)																
140	0.046	0.103	0.061	0.060	0.107	0.051	0.020	0.066	0.060	0.100	0.040	0.051	0.025	0.030	0.040	0.213
144	0.006	-	0.061	0.050	0.041	-	0.010	-	-	-	0.005	0.010	0.005	0.005	0.030	-
Ots107																
N	86	97	99	100	100	99	99	98	100	65	100	99	100	100	100	54
90	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	0.185
102	-	-	0.015	0.010	-	-	-	-	-	-	-	-	-	-	-	-
106	-	-	-	0.005	0.080	-	-	-	-	0.008	0.005	-	-	-	-	-
110	-	-	-	-	-	-	-	-	0.005	-	-	-	0.005	0.005	-	-
114	0.035	0.021	0.005	0.015	-	0.005	-	0.005	-	-	0.005	-	-	-	-	0.065
118	0.895	0.835	0.823	0.825	0.840	0.753	0.793	0.730	0.755	0.762	0.750	0.682	0.730	0.705	0.710	0.630
122	0.058	0.113	0.152	0.145	0.080	0.232	0.187	0.219	0.215	0.208	0.235	0.293	0.230	0.270	0.260	0.065
126	0.012	0.010	-	-	-	0.010	0.020	0.046	0.025	0.023	0.005	0.025	0.035	0.020	0.030	0.037
130	-	0.021	-	-	-	-	-	-	-	-	-	-	-	-	-	0.019
Omy77																
N	87	97	99	100	100	98	99	97	98	65	100	99	100	100	100	54
85	-	-	-	-	-	-	-	-	-	-	-	-	-	0.005	-	-
89	-	-	-	-	-	-	-	-	-	-	0.005	-	-	0.010	0.005	-
97	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.093
99	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.019
101	-	-	-	-	-	-	-	-	-	-	-	0.005	-	0.005	-	0.056
103	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
105	0.431	0.325	0.455	0.440	0.330	0.750	0.621	0.768	0.719	0.692	0.685	0.753	0.765	0.745	0.765	0.287
107	0.006	0.010	-	-	-	0.005	-	-	-	-	0.005	0.005	-	0.005	-	0.028

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Appendix 3. (page 7 of 7)

Omy77 (continued)

	FDI	TCI	TAZ	OUT	SBL	CHI	KR	LKR	KLSB	PRC	CC	HPB	LLCB	LTLK	UTLK	TUST
109	0.500	0.577	0.505	0.500	0.560	0.209	0.273	0.170	0.189	0.238	0.260	0.172	0.180	0.150	0.175	0.352
111	0.006	0.062	0.010	0.010	0.010	0.015	0.005	0.005	0.010	0.023	-	-	0.015	0.015	0.005	0.056
113	0.023	0.005	0.015	0.020	0.100	0.015	0.101	0.057	0.082	0.046	0.050	0.066	0.040	0.065	0.050	0.009
115	0.023	0.021	0.015	0.030	-	0.005	-	-	-	-	-	-	-	-	-	0.046
119	0.006	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.046
121	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.009