AN ABSTRACT OF THE DISSERTATION OF

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Carl B. Schreck

Chinook salmon, *Oncorhynchus tshawytscha*, returning to the Yukon River basin and other large river systems in western Alaska have declined dramatically since the late 1990s. This continuing trend has raised concerns over the future status of the returns, and severely impacted commercial and subsistence fisheries within the drainage. Management is further complicated by the mixed-stock composition of the run, the presence of other temporally similar salmon species, and the need to equitably allocate harvests between the numerous fisheries and user groups scattered throughout the basin. Detailed information is needed on Chinook salmon run characteristics to better understand and manage the returns, and facilitate conservation efforts. However, this goal is exacerbated by the massive size and remote nature of the basin, the large number of highly mobile fish, and the compressed timing of the run. To address these challenges, radio telemetry was used to determine the stock composition and spawning distribution of the returns, and the migratory characteristics of the fish. The migratory patterns exhibited by returning salmon provide a number of insights into the status of the run. Since the Yukon River is essentially free-flowing (i.e., not regulated), this study also presented an opportunity to document the distribution and upriver movements of large returns of wild Chinook salmon under natural conditions.

During 2002-2004, returning adult Chinook salmon were captured in the lower Yukon River (approximately 300 km upriver from the river mouth), tagged with radio transmitters, and tracked upriver using remote tracking stations located on important migratory routes and major spawning tributaries. Aerial tracking surveys were used to locate fish in spawning areas and between stations. The fish responded well to the

capture and handling procedures, with most (2,790, 98%) resuming upriver movements. Although the fish initially displayed a negative tagging response, with slower migration rates observed immediately after release, the duration of this response was relatively short (several days) and less severe as the fish moved upriver. Independent measures indicated that the swimming speeds and timing of the fish upriver from the tagging area were comparable to untagged fish, suggesting that the tagging methods used were relatively benign.

Fish returned to spawning areas throughout the basin, ranging from several hundred to over 3,000 km from the tagging area. Distribution patterns were similar across years, suggesting that the principal components of the run were identified. Most spawning fish were clustered in a number of key tributaries, with smaller numbers of fish located in other spatially isolated areas. The fish typically returned to clear water tributaries that were relatively entrenched, had moderate gradients, and were associated with upland areas. Fish were largely absent in lowland reaches characterized by meandering, low gradient, highly alluvial channels often associated with main river floodplains. There was suggestive evidence of mainstem spawning in reaches of the Upper Yukon. The status of fish remaining in other mainstem areas was less certain, and may represent local spawning activity or fish that died while in-transit to upriver areas.

Although Chinook salmon spawned throughout the basin, the run was dominated by two regional components (Tanana and Upper Yukon), which annually comprised over 70% of the return. Substantially fewer fish returned to other areas ranging from 2-9% of the return, although the collective contribution of these stocks was appreciable. Most regional returns consisted of several principal stocks and a number of small, spatially isolated populations. Regional and stock composition estimates were similar across years even though differences in run abundance were reported, suggesting that these abundance differences were not related to regional or stock-specific differences. Run timing was relatively compressed compared to rivers in the southern portion of the range, with most stocks passing through the lower river over a 6-week period, ranging from 16 to 38 d. Run timing was generally earlier for stocks traveling farther upriver, although exceptions were noted. Lower basin stocks were primarily later run fish.

Pronounced differences were observed in the migration rates (km/d) exhibited by regional stocks. Substantially slower swimming speeds were observed for fish returning to terminal tributaries in the lower basin ranging from 28-40 km/d compared to 52-62 km/d for upper basin stocks. The migratory patterns (migration rates in sequential reaches) of the fish also showed distinct regional differences. Average migration rates through the lower river were remarkably similar for the different stocks, ranging from 57-62 km/d, with most stocks exhibiting a general decline as the fish moved farther upriver. Tanana River stocks displayed a pronounced reduction in swimming speed after leaving the Yukon River main stem, with migration rates declining to 24 km/d on average as the fish approached their terminal tributaries. Conversely, upper basin stocks exhibited a relatively gradual (but variable) overall decline in migration rate even though these fish were traveling substantially greater distances upriver. Average migration rates for upper basin stocks ranged from 43-61 km/d as the fish approached their terminal tributaries.

There was substantial variation in the migratory patterns exhibited by individual fish, although these patterns tended to be similar to the patterns exhibited by the regional stocks, particularly as the fish moved farther upriver from the tagging area. The dominant source of variation among fish reflected the average migration rate, with individual fish traveling slower in the lower basin exhibiting consistently slower migration rates as they moved upriver compared to their faster moving counterparts. This migratory pattern was consistent across stocks, and on average explained 74% of the within-stock variation in migration rate represented by the multivariate data. The second source of variation in migration rate reflected a shift in the relative swimming speeds of the individual fish as they progressed upriver. Although movement rates declined for nearly all of the fish during the migration, differences were observed in the pattern of the decline. Fish with faster migration rates in the lower river exhibited a pronounced decline in swimming speed as they moved upriver, whereas fish moving slower in the lower river displayed a more gradual decline in migration rate. On average, this migratory pattern explained 22% of the within-stock variation in migration rate represented by the multivariate data.

Most fish (98%) exhibited continuous upriver movements and strong fidelity to the rivers they entered. However a small number of fish (n = 66) deviated from this pattern. Some of these individuals initially passed their final destination and continued upriver for varying distances before reversing direction, swimming back downstream, and entering their terminal tributary. Although most of these excursions were relatively short (< 30 km), there were several instances where fish traveled hundreds of kilometers out of their way. Thirty-four fish tracked to terminal tributaries subsequently left these rivers, and traveled to other terminal tributaries within the basin (n = 31) or were harvested in upriver fisheries (n = 3). Although most of these incidents involved nearby tributaries, major diversions were also observed, with several fish traveling over 300 km to natal rivers after leaving the initial tributary.

Chinook salmon returns to the Yukon River typically consisted of a series of distinct and sizable increases in the number fish entering the river over the course of the run, commonly referred to as pulses. A large number of fish (n = 251) were radio tagged over a 4-day period during a pulse in 2003 to provide information on the progression of the pulse as it moved upriver. The time taken by the pulse to move past subsequent upriver locations increased as the fish moved farther upriver from the tagging area, with the fish passing sites located 580 and 800 km upriver over a span of 14 and 21 d, respectively. Although not surprising considering the extensive variation in migration rates observed among individual fish, this finding does suggest that these pulses do not represent cohesive aggregates of fish moving upriver.

Unlike the well established methods used to estimate other life history characteristics, the development of quantitative methods for analyzing and modeling fish movements has lagged noticeably behind, due in part to the complexity associated with movement data and (prior to the advent of telemetry) the difficulty of collecting this type of information on free-ranging individuals. Two fundamentally different analytical approaches, hierarchical linear regression models and multivariate ordination, were used during this study to evaluate factors thought to influence the upriver movements of the fish. In spite of the inherent differences, both methods provided strikingly similar results, indicating that the study findings were not dependent on the approach used, and suggesting that the results were plausible based on the information available and the weight of evidence.

Both analytical methods had advantages, and provided complementary information. With hierarchical linear models, it was possible to simultaneously evaluate a wide range of explanatory variables (in our case, both biological and environmental), which provided standardized comparisons and simplified the interpretation of the results. Since both fixed and random effects were incorporated in the models, it was possible to account for sources of variation when insufficient information was available to identify the underlining factors – an important consideration since few field studies provide comprehensive data. With multivariate ordination, separate analyzes were needed to examine the relationships between the migration rates and the biotic and physical variables. In addition to being cumbersome, this limitation made it more difficult to compare the relative influence of the different factors and interactions between factors. However, ordination was very useful as an exploratory tool. Although compartmentalized by stock, across fish comparisons were simple and relatively straightforward. Because the explanatory variables were evaluated separately in relation to the ordination score assigned to the fish, it was possible to examine and compare highly correlated variables. Ordination was also able to identify overall patterns within the data and assess the relative importance. While this can be accomplished within the framework of linear regression using mixture models to determine whether multiple distributions exist within the data, the process is much simpler with ordination.

The migratory patterns of the fish were influenced by a wide range of factors, with evidentiary support for complex, multi-faceted relationships. Physical features of the basin demonstrated stronger explanatory power, accounting for over 70% of the observed variation in migration rate compared to 18% for the biological characteristics of the fish. Parameter estimates associated with the steepness of the migratory route and remaining distance the fish had to travel to reach their natal rivers were most strongly correlated with migration rate, with consistent relationships observed across stocks. Migration rates were also noticeably slower in extensively braided reaches of the basin. The weaker relationships between migration rate and biotic factors may reflect stabilizing

selection on long-distance migrants. Smaller fish exhibited minimally faster swimming speeds on average than larger individuals. This relationship was stronger in highly braided reaches. Run timing was positively related to migration rate for most stocks. Surprisingly, upper basin stocks traveling farther upriver displayed progressively negative relationships, suggesting that late-run fish were moving slower. Ancillary information suggests that this decline may relate to deteriorating fish condition later in the season.

Distribution and Movements of Chinook Salmon, *Oncorhynchus tshawytscha*, Returning to the Yukon River Basin

By

John H. Eiler

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APPROVED:

Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

John H. Eiler, Author

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CONTRIBUTION OF AUTHORS

Chapter 2: Ted Spencer and Richard Driscoll helped design the study, assisted with field work, and helped summarize the data collected. Carl Schreck helped interpret the data, and provided guidance in the development of the written summary. All authors provided editorial support.

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DEDICATION

This dissertation is dedicated to the late Monty Millard, whose insight, enthusiasm, and commitment to Yukon River salmon – and the people who depend on the resource – was instrumental in bringing large-scale telemetry studies to the basin.

To Nancy, the love of my life, who kept the home fires burning, and whose patience, love, encouragement, and support made this all possible.

Distribution and Movements of Chinook Salmon, *Oncorhynchus tshawytscha*, returning to the Yukon River basin

INTRODUCTION

General Information

Pacific salmon (*Oncorhynchus* spp.) are an iconic species throughout the northern Pacific Rim, and have been an integral part of the history, culture, art, and economy of the region. They are members of the family Salmonidae, which also includes trout (*Oncorhynchus* and *Salmo* spp.), char (*Salvelinus* spp.), whitefish (*Coregonus*, *Prosopium,* and *Stenodus* spp.), huchen and taimen (*Hucho* spp.), and arctic grayling (*Thymallus arcticus*) (Helfman et al. 1997; Nelson et al. 2004). Most Pacific salmon are anadromous. Born in coastal rivers and streams, juvenile salmon rear in freshwater for up to several years before migrating to sea, where they remain for most of their life before returning as adults (typically to their natal streams) to spawn (Groot and Margolis 1991). Non-anadromous forms have also evolved when local populations become land-locked (Moyle and Cech 2004). Pacific salmon are semelparous, and die a few days or weeks after spawning (Quinn 2005).

Of the seven recognized species of Pacific salmon (Groot and Margolis 1991), Chinook salmon (*O. tshawyscha*) are considered one of the most valuable. Their large size (adults may weigh in excess of 40 kg) and high quality flesh make them highly prized by fishers. Although typically less abundant than other commercially harvested salmon, the annual exvessel value of Chinook salmon in Alaska alone averaged over $19.4 million (USD) during 2000-2010 (data from State of Alaska web site http://www.adfg. alaska.gov/index.cfm?adfg=commercialbyfisherysalmon.salmoncatch). Chinook salmon occur from central California, north along the coasts of western Canada, Alaska, and eastern Russia, and south along the Asian coast to the Kamchatka peninsula. Chinook salmon are predacious, and become increasingly piscivorous after entering marine waters (Healy 1991). They have a streamline, fusiform body typical of rover-predator fish, and exhibit a subcaragiform swimming style (i.e., propulsion provided by the posterior body and caudal fin) well suited for a wide-ranging anadromous species, providing power for fast acceleration and sustained speeds over long distances while maintaining maneuverability in relatively confined environments such as rivers and streams (Webb 1975; Helfman et al. 1997).

Chinook salmon have a complex and varied life history which includes two primary behavioral forms. Fish returning to rivers in the northern portion of their range (i.e., from northern British Columbia to eastern Russia) are often described as stream-type (Gilbert 1913). These fish typically spend 1-2 years in freshwater before migrating to sea, exhibit extensive offshore migrations, remain in marine waters for 1-6 years, return to their natal rivers during the spring or summer, and spawn several months later (Healey 1991). In contrast, Chinook salmon in the southeastern portion of their range exhibit both stream-type and sea-type (Gilbert 1913) forms. Sea-type fish migrate to sea during their first year of life, remain in coastal waters, return to their natal rivers during the fall, and spawn within a few days or weeks (Healy 1991). Sea-type fish generally spawn in the lower reaches of large river drainages or small coastal streams. Chinook salmon in the southernmost extent of their range in North America (e.g., Sacramento River, CA) also return to natal rivers in winter, hold in the drainage for several months, and spawn in spring and summer. The variation in timing likely reflect differences in spawning, egg development, and spring emergence requirements in relation to environmental conditions (e.g., water temperature and flow), or problems related to accessing spawning areas.

Spawning Migration

The spawning migration of Chinook salmon (and other Pacific salmon) has received considerable attention due in part to the large and cyclical nature of the returns, the relative proximity of migration routes and spawning grounds to human populations, and the enormous value they represent in terms of commercial, sport, and subsistence fisheries. The returning salmon also serve an important biological function by providing a major nutritional “boost” to the freshwater communities associated with coastal and interior river systems within the region. In addition to functioning as prey to numerous predators and scavengers, the carcasses of the spawned out fish provide the nutritional basis for the next generation of salmon and other stream life (Brett 1983; Cederholm et al. 1999; Naiman et al. 2002).

Fish migrations have been defined as directed movements exhibited by a large segments of a population that occur on a cyclical basis, with fish actively swimming extended distances between separate and distinct habitats within a predictable period of time (Northcote 1978). For salmon, their anadromous life style and associated seaward migration provide an opportunity to escape from the relatively sterile habitats of their natal streams in favor of the more productive conditions of the marine environment (Quinn 2005). However, this strategy carries with it the burden of having to return to their natal streams to spawn, and the extreme physical demands associated with this migration. In addition to being in suitable physical condition, the fish must also select the migratory timing and swimming behavior that will enable them to reach their natal river, migrate upstream, and arrive on the spawning grounds when conditions are favorable. This task presents the fish with a migratory dilemma. In addition to traveling substantial distances within a limited period of time, the fish must conserve their energy resources during the migration to ensure that they reach their final destination with sufficient reserves to avoid predation, compete with other individuals, and reproduce. To be successful, the fish must strike a balance between these two conflicting needs.

Marine phase of migration.— Salmon begin their spawning migration at sea, but the factors that initiate this behavior are poorly understood. Unlike many freshwater species that migrate and spawn in response to changes in river conditions, salmon must initiate their migration based on indirect cues. Photoperiod has often been proposed as a probable mechanism for initiating migratory behavior (Quinn 2005, Hinch et al. 2006). Body size and energy reserves presumably play a role as well, since the behavior and energetics of the fish are closely linked to the extreme physical demands associated with migration. Fish that begin the migration in optimal condition presumably have a distinct advantage.

Although the methods used by salmon to navigate during the migration and to locate natal rivers are poorly understood, a number of possibilities have been suggested, including the use of the Earth's magnetic field, celestial orientation, or a combination of several mechanisms (Leggett 1977, Brett 1983, Quinn 2005). As the fish arrive in coastal areas, they rely increasingly on olfactory cues (Hasler et al. 1978).

Salmon exhibit several important physiological changes during the marine phase of the spawning migration, including a pronounced shift in the osmoregulatory system preparatory to the transition from the marine to freshwater environment (McCormick 2001) and endocrine changes associated with sexual maturation (Hinch et al. 2006). Endocrine changes may include the development of the gonads and secondary sexual characteristics, particularly for fish returning to small coastal drainages with short in-river migrations.

Freshwater phase of migration.— Salmon often initiate upriver movements soon after reaching their natal rivers. Lengthy delays in estuaries can increase the risk of predation, elevate stress levels, and amplify energy use (Hinch et al. 2006). In spite of these disadvantages, other patterns have been reported. Salmon may hold for varying periods of time in response to environmental conditions (Quinn 2005; Mundy and Evenson 2011). Some salmon stocks, particularly those destined for small coastal tributaries (i.e., fish traveling short distances to reach spawning grounds) hold in estuaries for extended periods until sexually mature before commencing upriver movements (Gilhousen 1980, Brett 1995).

Salmon stop feeding after entering freshwater, and exhibit a true catabolic state ranging in duration from several weeks to months (Quinn 2005, Hinch et al. 2006). The cessation of feeding has severe repercussions on the returning salmon, since the fish must hereafter rely solely on existing energy reserves. As a result, the behavioral patterns employed and environmental conditions encountered during the migration can have a significant impact on upriver movements (Blackbourn 1987, Quinn 1990).

Salmon migrations can be grouped into two basic patterns: coastal/lower river and upper river. Fish returning to coastal stream and lower reaches of large river drainages typically begin their upriver migration sexually mature, travel short distances, and spawn relatively close to saltwater. Fish returning to upper reaches of large drainages enter rivers when only partially mature (i.e., gonads not fully developed), and move substantial distances over an extended period of time (Gilhousen 1980, Brett 1995), often spawning hundreds of kilometers or more from the sea (Eiler et al. 1992; Keefer et al. 2004). The type of pattern exhibited has major implications on the migratory behavior and energetics of the fish. Only individuals that have acquired adequate energy stores prior to entering freshwater can sustain upriver movements long enough to reach upper headwater areas in large drainages, while the constraints on coastal and lower river fish are much less severe (Brett 1995).

Size-specific migratory patterns have also been reported. Larger fish, which are typically older, often precede smaller fish during the migration, and typically arrive first on the spawning grounds. Quinn (2005) speculated that this pattern may reflect the relative benefits of feeding longer in the marine environment. Larger fish would receive proportionally less benefit by remaining at sea, and their behavior may reflect an emphasis on optimal timing for migration and reproduction. Smaller fish that remain in the marine environment several weeks longer may improve their overall condition, even though it potentially results in less optimal timing. By arriving later on the spawning grounds, smaller individual may also minimize competition with larger and more aggressive fish (Quinn 2005). Differences by sex have also been reported, with males often entering rivers and arriving on spawning grounds before females. However, the significance of this pattern is not fully understood, because females, not males, select and prepare redd sites (Quinn 2005).

Swimming Behavior

Although salmon are capable of swimming continuously for extended periods of time (Brett 1973), the behavioral patterns and swimming speeds employed can have a significant impact on overall performance. Swimming speed is particularly critical since it directly affects the use of energy reserves. Beamish (1978) categorized swimming speed into three basic categories that are still commonly used: sustained, prolonged, and burst. Sustained swimming, which occurs under aerobic conditions, consists of swimming speeds that can be maintained for extended periods (i.e., greater than 200 minutes) without resulting in muscle fatigue. Prolonged swimming speeds are shorter in duration (i.e., 2-200 minutes), and are comprised of a mixture of aerobic and anaerobic activity. If maintained, prolonged swimming will eventually result in fatigue. Burst swimming represents the greatest speeds the fish are capable of, ranging from 10 to 20 body lengths per seconds, and can only be maintained for short periods (i.e., less than 20 seconds). Burst swimming is completely anaerobic, incurring an oxygen debt that must be repaid. However, the capacity for short-term, high performance swimming is essential for returning salmon, since it enables them to avoid predators and negotiate high velocity currents encountered during the upriver migration (Beamish 1978).

The metabolic demands of swimming, in terms of oxygen and energy consumption, increase as the fish approach their maximum sustainable speed (Brett 1983). Fish are capable of traveling faster, but must engage in either prolonged or burst swimming, which uses substantially more energy and cannot be maintained over an extended period. Slow speeds use less energy, but often are not efficient in terms of the energy used for the distance traveled. Brett (1983) estimated optimal swimming speed (i.e., minimum cost per distance traveled) as one body length per second, or approximately 1.8 km/h. Swimming at optimal speed would be particularly advantageous for fish traveling extended distances; however, this may not be feasible when encountering high velocity currents.

Although river flow is a primary means of orientation during the upriver migration, the energy costs of swimming against the current can be substantial (Brett 1995, Hinch et al. 2006). The migratory route traveled by the fish can have a major impact on swimming performance. Gilhousen (1980) determined that sockeye salmon returning to reaches with greater change in elevation experienced substantially greater energy expenditures than other stocks, even when those stocks were traveling up to 40% farther to reach their final destination. The energy expenditures incurred when traveling through areas with extreme flows can be severe, and in extreme cases can result in delayed upriver movements and increased mortality (Crossin et al. 2004; Rand and Hinch 1998).

Hinch and Rand (2000) reported that sockeye salmon routinely adjusted their swimming speed based on the water flows encountered, swimming near optimal speed when currents were slow, and at greater speeds as water velocity increased. When traveling through more challenging reaches, the fish exhibited a mixture of speeds, employing sustained speeds 76% of the time, prolonged speeds 18% of time, and burst speeds 6% of time (Hinch et al 2002). In contrast, Brown and Geist (2002) reported that Chinook salmon only exhibited burst speeds 2% of the time during passage through difficult reaches on the Klickitat River. The differences observed may relate to the larger size of Chinook salmon, and represent greater swimming capacity for this species (i.e., the ability to generate greater levels of swimming power without having to rely on burst speeds), although dissimilarities between the drainages may also have been a factor. Although burst swimming is effective and may be critical in negotiating challenging reaches, this behavior is energetically costly and likely used sparingly (Hinch et al. 2006). Salmon are also adept at selecting travel routes that minimize the energy expended (Standen et al. 2002, Hinch et al. 2002).

Body morphology undoubtedly plays a role in the swimming patterns exhibited by salmon. The generalized body form of salmon is adapted for fast acceleration and prolonged cruising speeds (Webb 1995), physical characteristics that make it ideal for long upriver migrations with variable flow regimes. Although similar in most respects, differences in body shape have been noted between coastal/lower river and upper river stocks. Crossin et al. (2004) observed that Fraser River sockeye salmon with difficult travel routes tended to have shorter, rounder bodies than stocks with less challenging migrations, and speculated that this form might favor energy conservation. It has also been reported that Chinook and sockeye salmon with the longest migrations are generally smaller in size compared with populations migrating shorter distances, even though larger bodies would presumably be able to store more energy reserves, and therefore be an advantage (Gustafson et al. 1997, Roni 1992 cited by Quinn 2005). Smaller fish, which are likely weaker swimmers, usually travel close to shore, ostensibly to take advantage to the slower currents present there (Brett 1983, Burgner 1991, Hinch et al 2002). Larger salmon are stronger swimmers, and are therefore able to swim farther away from the bank where they are presumably safer from predation. However, Hughes (2004) demonstrated that larger fish may swim farther from shore to avoid wave drag, which is a function of body size and water depth. By swimming farther from the bank, larger individuals are able to swim deep enough to avoid this effect, which makes swimming more efficient in spite of the faster offshore currents.

Energetics of Migration

An overview of the migratory movements of salmon would be incomplete without discussing the associated energy cost, since the patterns and behaviors exhibited are so closely linked to the resources available and utilized. Several forms of energy are used by migrating salmon. Lipids are the primary fuel source, including both unsaturated fats and long-chain saturated fats (Brett 1973). Saturated fats are typically used early in the migration. Unsaturated fats become increasingly important as the stores of saturated fat are depleted (Brett 1995). Hendry and Berg (1999) reported that stored lipids are used primarily to supply the energy needed for upriver migration and egg production. The relative amount of stored lipids in migrating salmon is usually a good indication of the distance and duration of the upriver migration (Crossin et al. 2004). Fraser River sockeye salmon, bound for spawning areas in the upper reaches of the drainage, enter freshwater with substantial more energy stores compared to populations bound for nearby coastal streams, with lipid reserves comprising 12-15% and 2-9% of the somatic tissue, respectively (Brett 1995). Similar patterns have been reported for other salmon species (Brett 1995). Regardless of the migratory pattern exhibited, almost all of the lipid reserves are depleted during the migration. Studies that sampled salmon before and after the upriver migrations determined that swimming activity typically depleted between 75-98% of the body fat, which comprised about half of the energy reserves of the fish (Brett 1995). The depletion rates were highest for long distance migrants, and were particularly severe for females (Gilhousen 1980, Hendry and Berg 1999). Fish size also affected energy expenditures, with large fish using relatively more energy to complete the migration than smaller fish (Hinch et al. 2006).

Proteins are used primarily for the development of secondary sexual characteristics and metabolism during spawning. When lipid stores are depleted, salmon may also derive some energy for swimming by metabolizing proteins, particularly during the final stages of the migration (Brett 1995). However, using proteins causes deterioration in muscle tissue, resulting in reduced muscle mass and decreased swimming performance, which likely explains why proteins are not used extensively for upriver migration. This may also be a reason that secondary sexual characteristics develop later in the migratory process (Brett 1995). Compared to the drastic reduction in lipids, protein levels for Fraser River sockeye salmon declined from 20% at river entry to 17-18% on the spawning ground, and ultimately decreased to 15% at the time of death (Brett 1995). Despite the use of energy stores, fish weights remain relatively constant during the upriver migration due to the fact that water is absorbed and retained. Water levels increased from 66% to over 75% in Fraser River sockeye salmon. This process serves to preserve the body form of the fish even though the flesh is deteriorating (Brett 1995, Quinn 2005).

Upper river salmon have the additional burden of having to partition their energy stores to support both migratory activities and gamete formation (Crossin et al. 2004). Coastal/lower river fish are not encumbered by this requirement, since gonad maturation usually occurs prior to entering freshwater, and their energy stores are therefore used primarily for migration and spawning activities (Brett 1995). Of the total energy available to upper river females, an estimated 55% is used for swimming, while 23% is used to ripen gonads and reproduce (Brett 1983). Females with more arduous migration often allocate less energy to gonad development (Kinnison et al. 2001), presumably to ensure that they are able to successfully reach their final destination and spawn.

Females allocate significantly more energy to gonad development than do males. Brett (1995) reported differences of 14% and 2% for female and male sockeye salmon, respectively. Hinch et al. (2006) speculated that swimming patterns that conserved energy would be more strongly selected for in female salmon than in their male counterparts due to the greater energy demands associated with reproduction. Telemetry studies on Fraser River sockeye salmon suggested that females have different swimming patterns that are more efficient in the use of energy. In difficult passages, females exhibited more sustained and prolonged swimming speeds, while males exhibit a disproportionately higher rate of burst swimming (Hinch et al. 2006). As a result, energetic costs within these reaches were substantially higher for males than females. Males and females exhibited similar swimming patterns and energy expenditures in the less arduous river sections (i.e., simpler channel formation and more moderate flows) commonly encountered during most of the spawning migration (Standen et al. 2002).

Status of Yukon River Chinook Salmon

Large numbers of Chinook salmon return to the Yukon River located in Alaska and Yukon Territory. These returns are an integral part of the Yukon River ecosystem and have a major economic impact on the basin. Although run abundance is difficult to estimate, harvest levels during 1961-2010 ranged from 38,964 (2009) to 220,511 (1980) fish (JTC 2011), and are thought to represent between 30-50% of the return (T. Lingnau, Alaska Department of Fish and Game, Anchorage, AK, personal communication). Chinook salmon support important commercial and subsistence fisheries throughout the basin. They are a principal food source in many remote communities and often provide the primary source of income for local residents. Chinook salmon returns are jointly managed by the U.S. and Canada to maintain adequate spawning escapements, provide harvest opportunities, and ensure adequate fish passage into the Canadian portion of the drainage (Yukon River Salmon Act 2000, JTC 2011). A number of factors complicate these efforts, including increasing harvest demands, variable run abundance, and the movement of the fish across international borders and management jurisdictions. Chinook salmon are harvested in widely scattered fisheries, which further confounds allocation and harvest issues, and often results in conflicts between different users groups, particularly lower and upper basin fishers. Assessing the impact of multiple fisheries on the return can be difficult.

Chinook salmon returns to the basin were relatively stable until the late 1990s when dramatic declines in abundance and harvest levels were reported (JTC 2001). This trend has continued during subsequent years, and resulted in closures or drastic reductions in commercial fisheries, severe restrictions in subsistence harvests, and difficulties meeting regional and basin-wide escapement goals (JTC 2011).

Prior to the crash, run assessment efforts within the basin focused primarily on determining harvest levels, run abundance and timing, basic run structure (i.e., age composition, sex ratio, and fish size), regional composition particularly in relation to the contribution of U.S. and Canadian stocks, and escapement estimates in selected terminal tributaries. Stock-specific information on run characteristics was needed to better understand and manage the returns, and facilitate conservation efforts and harvest allocations. However, obtaining this type of information presented a significant challenge. The basin is vast, draining a watershed of over 855,000 km^2. The main river alone flows for over 3,000 km from its headwaters in Canada and has several sizable tributaries. The basin is remote, with access to most areas limited to boat or aircraft. The nature of the Chinook salmon return also complicates data collection efforts, with large numbers of fast-moving fish entering the river over a short period of time (i.e., six weeks), traveling at relatively deep depths (i.e., exceeding 20 m in the lower river), and distributing widely throughout the basin.

Research Objectives

A telemetry study was initiated in 2000 to provide stock-specific information on Chinook salmon returns in the Yukon River basin. Returning adults were captured in the lower river, tagged with radio transmitters, and tracked upriver during their spawning migration. Work in 2000-2001 focused on developing capture methods, improved telemetry equipment for tracking the fish, and the infrastructure necessary for a study of this size and scope. Large-scale tagging and basin-wide monitoring programs were conducted in 2002-2004.

The study focused on four principal objectives, which are discussed in the following chapters: spawning distribution, stock composition and timing, migratory phenology, and factors affecting upriver movements. Chapter 2 describes the spawning distribution of the radio-tagged fish within the basin. The migratory tendencies of Pacific salmon tend to promote the creation of isolated populations (Moyle and Cech 2004). In large river basins, this can result in returns comprised of numerous and widely scattered stocks. Documenting complex stock structures can be difficult, particularly in remote drainages or in rivers with limited visibility. The telemetry information collected during this study on spawning distribution helped identify principal components of the return (including both major and minor stocks) and provided the stock affiliation and timing data used in subsequent chapters to address other research objectives. These data also identified important spawning areas and reaches needing protection, and helped direct other research efforts and assessment projects. A primary assumption in tagging studies is that the capture and handling procedures do not adversely affect the fish (i.e., tagged and untagged fish behave the same), or that any effect is limited in severity and duration, and ultimately has negligible effect. This chapter details the methods used during the study and evaluates the response exhibited by fish in relation to this assumption.

Chapter 3 describes the stock composition of the returns and associated stock-specific run timing. The distribution data described in Chapter 2 directly reflects the final destination of individuals within the radio-tagged sample. Although sufficient for some research objectives, this type of information can be misleading when indiscriminately expanded to describe the larger population. Telemetry data from the study were used to estimate the contribution of U.S. and Canadian fish returning to the basin (i.e., nation of origin estimates), making it necessary to develop more rigorous analytical methods. Chapter 3 describes the approach used during the study to address potential bias, including temporal changes in run abundance in the lower river (which result in disproportional tagging at the capture site) and disproportional removal of tagged individuals due to the presence of fisheries throughout the basin. Comparisons with Chinook salmon returns in other large river drainages are also discussed.

Chapter 4 describes the migratory patterns exhibited by Yukon River Chinook salmon stocks during their spawning migration, and compares these results to those from Chinook salmon migration studies in other large river drainages. In addition to traveling substantial distances, Chinook salmon returning to large river drainages must conserve their energy resources during the migration in order to reach their final destination with sufficient reserves to reproduce. The swimming patterns employed during the spawning migration undoubtedly play a critical role in this process. Fish movements are inherently difficult to quantify. The fish are often difficult to observe, and the data collected must incorporate variability in both spatial and temporal scales (Turchin 1998). Information from traditional tagging methods (i.e., attachment of external markers) is typically limited to differences in time and distance from the release site to the recapture location with no sense of what happened in between. The lack of detailed movement information has often led to generalized assumptions related to migratory patterns.

The advent of telemetry and its application to fish species has greatly enhanced the ability to collect detailed information on fish movements. The stock-specific migratory patterns observed during this study are compared with commonly held assumptions and results from salmon studies in other large drainages. Although logistically challenging due to its massive size and isolated nature, the Yukon River provides a unique opportunity to study salmon migratory patterns. It is one of the few large free-flowing river systems not impounded by dams, and the movements observed likely reflect normal swimming patterns. Chinook salmon stocks returning to the basin exhibit diverse spawning migrations, ranging from relatively short migrations (hundreds of kilometers) to some of the longest migrations recorded for the species (i.e., fish traveling over 2,500 km), providing a good basis of comparison with other river systems.

A number of factors potentially influence the migratory patterns exhibited by Chinook salmon returning to their natal streams. Chapter 5 expands on the information discussed in the previous chapter by examining the relationship between the movements exhibited by Chinook salmon in relation to the biological characteristics of the fish and physical features of the basin. Several working hypotheses are developed to provide a context for explaining fish movements in relation to these factors. Two statistical approaches, hierarchical linear regression and multivariate ordination, are used to analyze the data, and these results are compared. The results are also compared with other studies that have attributed fish movements to other factors.

Finally, Chapter 6 provides a summary of the study results, and discusses how the information provided can be used to enhance our understanding of the biology and management of multiple-stock salmon returns in large river drainages.

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Distribution and Tagging Response of Wild Chinook Salmon Returning to a Large, Free-flowing River Basin

John H. Eiler[1,2], Ted R. Spencer[3], Richard J. Driscoll[3], and Carl B. Schreck[2]

[1]National Marine Fisheries Service, Alaska Fisheries Science Center
Auke Bay Laboratories, Juneau, Alaska 99801, USA

[2]U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit
Department of Fisheries and Wildlife, Oregon State University
Corvallis, Oregon 97331, USA

[3]Alaska Department of Fish and Game, Division of Commercial Fisheries
Anchorage, Alaska 99518, USA

***Abstract*. —** Radio telemetry was used to determine the distributional patterns and spawning site locations for Chinook salmon returning to a large, free-flowing river basin. A total of 2,860 fish were radio tagged in the lower Yukon River and tracked upriver. Fish traveled to spawning areas throughout the basin, ranging from several hundred to over 3000 km from the tagging site. Distribution patterns were similar across years, suggesting that the principal components of the run were identified. Most spawning fish were clustered in a number of principal tributaries, with smaller numbers of fish located in other spatially-isolated areas. The cumulative contribution of these minor stocks was appreciable, comprising between 28-31% of the tagged sample. There was evidence of possible mainstem spawning in reaches of the Upper Yukon. The status of fish remaining in other mainstem areas was less certain, and may represent local spawning activity or fish that died while in-transit to upriver areas. Large-scale elevation and physiographic information were useful in categorizing spawning areas. The fish generally responded well to the capture, handling, and tagging procedures with most (2,790, 97.6%) resuming upriver movements, although the fish initially displayed a negative tagging response, with slower migration rates observed immediately after release. The duration of this response was relatively short (several days) and less severe as the fish moved upriver. Independent estimates suggest that the swimming speed and run timing of the radio-tagged fish were comparable to untagged fish. These findings indicate that the methods associated with tagging used were relatively benign.

Keywords: Chinook salmon, spawning distribution, tagging response, Yukon River, radio telemetry, tag recoveries

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) spawn in natal rivers and streams throughout the northern Pacific Rim, ranging from small coastal drainages to vast river basins (Healey 1991, Heard et al. 2007). This species displays a wide range of life history strategies and behavioral forms, with returns often composed of multiple age classes, complex population structures, and variable run timing. The biological implications of this diversity undoubtedly reflect the opportunities and constraints experienced by the fish during the upriver migration and subsequent spawning. Information on the spawning distribution of the return, stock-specific abundance, location of spawning sites, and the degree of spawning activity within those areas provides a number of insights into the suitability of the conditions encountered by the fish during the upriver migration and after reaching their final destination. Increasingly, human activities and anthropogenic factors are impacting Chinook salmon populations (and other salmon species) in rivers throughout their range. Basic information, including a comprehensive inventory of the stock-specific components of the run and the location of both major and minor spawning areas, is fundamental to better understanding and managing Chinook salmon returns, and when needed, facilitating conservation efforts. However, obtaining this type of information is particularly challenging in large, free-flowing rivers where the ability to access and evaluate the run is limited.

Large numbers of Chinook salmon return to the Yukon River basin, a large northern river in Alaska and northwestern Canada. Although less numerous than other salmon species, Chinook salmon support important commercial and subsistence fisheries throughout the basin, and are an integral part of the Yukon River ecosystem. Because of the international nature of the drainage, Chinook salmon returns are jointly managed by the U.S. and Canada to maintain acceptable spawning escapements, support subsistence fisheries for local residents, and provide commercial and sport fishing opportunities when appropriate (Yukon River Salmon Act 2000).

Similar to other river drainages, managing the multiple stocks returning to the Yukon River poses numerous challenges. These issues are exacerbated due to the massive size and remote nature of the basin, difficulties associated with determining the stock-specific abundance and timing of the returns, the presence of other temporally similar species of salmon (most notably summer chum salmon *O. keta*), and the need to equitably allocate harvests between the numerous fisheries and user groups scattered throughout the basin. Management within the basin has been further complicated by recent trends in run abundance and composition. Chinook salmon returns were relatively stable until the late 1990’s when dramatic declines in abundance were reported (JTC 2001, Heard et al. 2007). This trend has continued during subsequent years, and resulted in the closure or drastic reductions in commercial fisheries, severe restrictions in subsistence harvests, and difficulties in meeting regional and basin-wide escapement goals (ENS 2012, JTC 2012). Annual harvests within the basin averaged 155,480 fish from 1961 to 1997, compared to less than 82,500 fish during 1998-2011 (based on data from JTC 2012). Just over 38,960 fish were harvested in 2009. Similar trends have been observed for Chinook salmon in other large rivers in western Alaska (Heard et al. 2007). Possible reductions in fish size (JTC 2006) and shifts in age composition to younger fish (based on data from Karpovich and Dubois 2007 and Schumann and Dubois 2012) have also been reported for Yukon River Chinook salmon returns.

Due to these trends, detailed information is needed on the status and run characteristics of Yukon River Chinook salmon to better understand and manage the returns and to facilitate conservation efforts. Various assessment methods have been used, including enumeration weirs, counting towers, test fisheries, sonar counts, and intensified spawning ground surveys and sampling (JTC 2006, Hayes et al. 2008). Although fundamental, these methods either provide information specific to particular tributaries or stocks, or generalized information about the entire run without reference to the different components. Developing technologies have made it possible to collect information on a more comprehensive scale. Genetic stock identification (GSI) is increasingly being used to estimate run composition and timing within the basin and in local fisheries (Beacham et al. 1989, Smith et al. 2005, Flannery 2012, Decovitch and Howard 2011). Due to technical advances in equipment and tracking capabilities, radio telemetry can provide quantitative information on salmon distribution and movements on both a basin-wide and stock-specific scale. Unlike other approaches, telemetry is capable of providing progressive information on the fish as they migrate upriver.

Radio telemetry has been used effectively to provide information on Pacific salmon (Burger et al. 1985, Eiler et al. 1992, Hinch et al. 2002, Cooke et al. 2004) including studies specifically on Chinook salmon in other large rivers, most notably the Columbia River (Geist and Dauble 1998, Reischel and Bjornn 2003, Keefer 2004). However, this river is heavily regulated, with controlled flows and pathways associate with the numerous hydroelectric dam located throughout the basin (Federal Columbia River Power System 2001). Further, Chinook salmon returns within the basin are composed of both wild and hatchery stocks (Myers et al. 1998). In contrast, the Yukon River basin is essentially free-flowing – only a small, passable hydroelectric dam ~ 2500 km upriver from the river mouth impedes the natural flow of water – providing an opportunity to document the upriver movements and distribution of wild Chinook salmon under natural conditions, but making tracking and monitoring more difficult.

Tagging and effectively tracking large numbers of highly mobile fish in the Yukon River is extremely challenging due to the vast and remote nature of the basin. Preliminary studies were conducted in 2000-2001 to develop the telemetry equipment, capture and tracking methods, and infrastructure needed for a study of this magnitude. Based on this initial work, large-scale radio tagging and basin-wide monitoring programs were conducted during 2002-2004. The primary objectives of the study were to determine the in-river distribution, nation of origin, and stock composition and timing of the return. Detailed information on distribution was needed to provide a comprehensive inventory of the component stocks that make up the return, facilitate the collection of genetic samples from previously unidentified populations to update GSI baselines, and document the location of important spawning areas within the basin – information essential to on-going conservation and management efforts. In this paper, we describe the upriver dispersal, spawning distribution, and final destination of Chinook salmon radio tagged in the lower Yukon River. Because adverse effects from capture and handling can potentially bias study results, we also examine the post-tagging response and upriver movements of the radio-tagged fish in relation to this concern.

Methods

Study Area

The Yukon River basin drains a watershed of more than 855,000 km^2. The main river alone flows for more than 3,000 km from its headwaters in Canada to the Bering Sea (Figure 1). The river is relatively deep, with channel depths exceeding 20 m in the lower basin compared to 12-14 m downstream of the Yukon-Tanana River confluence and 5-7 m near the U.S.-Canada border (distances of ~ 1100 km and 2000 km from the river mouth, respectively). Several major tributaries flow into the Yukon River main stem, including the Koyukuk and Tanana rivers in the United States; the Stewart, White, Pelly, and Teslin rivers in Canada; and the Porcupine River, which transects both countries. The basin also includes numerous medium and small-sized tributaries. In addition to its large size, the Yukon River is the fifth largest drainage in North America in terms of total annual discharge, and exhibits considerable temporal variability with greater flows during the summer months (Brabets et al. 2000, Yang et al. 2009). The basin is remote, with access to most areas limited to boat or aircraft.

Most reaches of the basin consist of a primary river channel with occasional side channels and sloughs, although the Yukon River main stem is extensively braided in the area commonly referred to as the Yukon Flats (Figure 1). Sections of the Tanana River, White River, and the Canadian main stem are also noticeably braided. Water visibility in many areas is extremely poor, particularly in the Tanana and White rivers due to turbidity from glacial activity in the upper headwaters of these drainages. Regional designations were based on geographic location and the general geomorphology of the area; e.g., lower reaches of the Porcupine River were considered part of the Yukon Flats due to similarities in landscape and river characteristics.

Chinook salmon are a major source of food in many remote communities, and provide a source of income for local residents. Subsistence and commercial fisheries occur throughout the basin with most fishing effort concentrated near villages along the Yukon River main stem (JTC 2012). Fish are also harvested in a number of tributaries including the Koyukuk, Tanana, Chandalar, Porcupine, Stewart, Pelly, and Teslin rivers (Figure 1). Limited sport fishing takes place in a number of clear water tributaries within the basin.

Fish Capture and Handling

Adult Chinook salmon were captured with drift gill nets in the lower Yukon River near the village of Russian Mission (Figure 1). This site was selected because it 1) consisted of a relatively narrow, unbraided sections of river, increasing the probability of capturing a representative sample, 2) was downriver of most known Chinook salmon spawning areas (i.e., only the Andreafsky River, located approximately 190 km downriver, was not included), and 3) was upriver of significant commercial and subsistence fisheries lower in the basin. During 2002, fish were also captured near the village of Marshall, located approximately 90 km downriver from Russian Mission. Local fishers were contracted to fish the area from early June to mid-July, with project personnel handling the fish and collecting data. Both day (0900-1700) and night (1800-0200) shifts were fished during the study.

The fish were captured with drift gill nets constructed with No. 21 seine twine and 21.5 cm mesh size. The nets were 46 m long, 7.6 m deep, and hung at a 2:1 ratio. This configuration was effective for capturing Chinook salmon while minimizing chum salmon (*O. keta*) bycatch. The nets were monitored continually, and fish removed immediately after capture. The netting was cut to facilitate removal and minimize injuries. A dip net, constructed with soft, fine-mesh netting, was used to lift fish into the boat for tagging. A maximum of two fish (the first two uninjured individuals encountered) were tagged per drift to minimize both handling time and potential sampling bias if stocks of fish were poorly mixed. The remaining fish were released from the gill net while still in the river. Fish retained for tagging were placed in a neoprene-lined tagging cradle submerged in a tote of fresh water. A pump circulated river water into the tote while the fish were being processed. Anesthesia was not used during the procedure.

Fish were tagged with pulse-coded radio transmitters in the 150-151 MHz frequency range manufactured by Advanced Telemetry Systems (Isanti, Minnesota)[1]. The transmitters (5.4 cm long, 2.0 cm in diameter, with a 30-cm transmitting antenna, and weighing 20 g) were gently inserted through the mouth and into the stomach using a plastic tube 0.7 cm in diameter. Each transmitter emitted a unique signal, based on a combination of frequency and signal pattern (as described by Eiler 2012), making it possible to identify individual fish. Transmitters were also equipped with a motion sensor and activity monitor (as described by Eiler 1990). The motion sensor, an integrated tilt switch sensitive to movement, inserted additional signal pulses into the signal burst each time the transmitter moved. The activity monitor changed the signal pattern to an inactive mode if the motion sensor was not triggered for 24 hours; the signal reverted to the original pattern if the motion sensor was activated. Transmitters had a minimum battery life of 90 days. Fish were marked externally with spaghetti tags attached just below the dorsal fin (as described by Wydoski and Emery 1983) to help identify tagged individuals caught in fisheries or located in spawning areas.

Information on the physical characteristics of the fish was also recorded, including body length (mid-eye to fork of tail) and external color (iridescent silver, silver, and blush – silver with reddish tinges). Iridescent silver indicated that the fish were not as advanced in their transition to freshwater as those with silver coloration; the initial onset of spawning coloration (blush) provided an external sign of advancing sexual maturation. A tissue sample was taken from the axillary process for genetic stock

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA or U.S. Geological Survey.

identification studies, and scales were collected to provide age data (as described by DeVries and Frie 1996). Data on sex were not collected because of difficulties in distinguishing sex in the lower river due to the lack of distinct external characteristics. Fish were released back into the main river immediately after the tagging procedure was completed. Handling, from removal of the net from the water to release, took about 6 to 8 minutes per fish.

Tracking Procedures

Radio-tagged fish that moved upriver were tracked with remote tracking stations (as described by Eiler 1995) placed at 40 sites throughout the basin (Figure 1). The sites were located on important migratory routes and major tributaries. Pairs of stations were placed at sites with special significance, including Paimiut, lower Koyukuk River, Manley, Rapids, Yukon Border, and Porcupine Border, to avoid loss of data due to technical problems with the equipment, damage from bears (*Ursus* spp.), or other unforeseen difficulties. The stations consisted of several integrated components, including a computer-controlled receiver developed by Advanced Telemetry Systems and satellite uplink (Campbell Scientific, Logan, Utah). A self-contained power system – consisting of a bank of six 6-volt, sealed lead-acid batteries connected in series and parallel (12 V, 610 Ah) and charged by two 80-W solar panels – supplied continual power to the stations.

Fish within reception range were identified and recorded by the stations. Nearly all the fish passing the sites were detected. Fish were periodically missed, particularly by stations at Paimiut and the Yukon-Anvik River confluence likely due to fish swimming at deeper depths; main channel depth at these sites was 25 m and 16 m, respectively. These fish were subsequently recorded at stations farther upriver. Information collected included the date and time the fish were present at the site, signal strength of the transmitter, and the orientation of the fish in relation to the station (i.e., upriver or downriver from the site). The information was summarized and recorded at 10-minute intervals, and used to estimate the date and time the fish moved past the station. Because of the isolated nature of the sites, the data collected, including information on the operational performance of the station (e.g., power levels, whether the reference transmitter at the site was properly recorded), were transmitted every hour to a geostationary operational environmental satellite (GOES) and relayed to a receiving station operated by NOAA, National Environmental Satellite and Data Information Service near Washington D.C.. These data were accessed daily via the Internet, and uploaded to an Oracle-based database (Oracle, Redwood Shores CA) for analysis and a geographical information system (GIS) mapping program (ArcGIS, Version 10.0, Esri, Redlands CA) for spatial comparisons (Eiler and Masters 2000). The program flagged information that indicated problems with stations operations so that corrective action could be taken, and created daily summaries of the upriver movements of the fish to facilitate other research activities. Fish records were systematically reviewed post-season to verify passage at the sites and to ensure that the movements reflected a sequential progression past the stations.

The response of the fish to the capture and handling procedures was evaluated based on the resumption of upriver movements and the swimming behavior exhibited by the fish after release. Fish that passed Paimiut (the first station site, located approximately 62 km upriver from Russian Mission) were considered to have resumed upriver movements. Swimming behavior was assessed by comparing migration rates (km/d) of the fish from their release site to Paimiut in relation to the distance traveled. The distance to Paimiut varied since fish were captured, tagged, and released while drifting through the tagging area. Distances ranged from 29-94 km for fish tagged at Russian Mission to 139-152 km for fish tagged at Marshall in 2002. Only fish traveling to natal streams substantial distances upriver from Paimiut (> 700 km) were included in this analysis to avoid confounding issues between swimming speed and proximity to spawning areas. Differences in migration rates between the first two sections of river traversed by the fish, from the release site to Paimiut and from Paimiut to the Yukon-Anvik River confluence (133 km upriver from Paimiut), were also compared for these fish.

Fish tracked to terminal tributaries within the basin (i.e., their final destination) were classified as distinct spawning stocks. The status of fish last located in non-terminal reaches, such as sections of the Yukon River main stem, was less certain since these individuals could represent fish spawning in nearby areas or fish in-transit to spawning areas farther upriver. Based on information provided by the stations, periodic aerial surveys were conducted to locate fish between station sites and upriver of stations on terminal tributaries. Fish were tracked from fixed-wing aircraft and helicopters as described by Eiler (2012). Helicopters were used to access remote areas to determine the status of the fish and recover transmitters. Tracking receivers equipped with an integrated global positioning system (GPS) receiver were used during the surveys to standardize the location estimates of the fish. Although it was beyond the scope of this study to characterize spawning habitat, the GIS mapping program was used to compare the final locations of the fish with elevation and physiographic overlays of the basin (provided by U.S. Geological Survey, http://agdc.usfs.gov/data/usgs/water/yukon.html). General river type as described by Rosgen (1994) was also noted for terminal tributaries.

Fishers within the basin were asked to report any radio-tagged fish they caught, and steps were taken to promote this cooperative effort, including a reward system for the tags returned, regular presentations at fishery meetings, information flyers posted in local communities, and personal discussions with local fishers (which often had the most impact but was difficult to implement on a large scale). Fish were considered to have been harvested if their transmitters were located out of the water in villages or fish camps during aerial surveys, even if the recovery was not reported.

Results

Fish Capture and Tagging

Fishing commenced in early June and continued until the end of the run in mid-July when catch rates were low (Table 1). The drift gill nets designed for the study were effective for capturing Chinook salmon in suitable condition for tagging, based on the number of uninjured and physically active fish caught. A total of 2,860 fish were captured and radio tagged, with transmitters deployed throughout the run (Figure 2). Bycatch was minimal, even though large numbers of summer chum salmon were present in the lower river during this period. Tagging operations were delayed until 9 June in 2002 (compared to 3 June in 2003 and 2004), and it is likely that the earliest fish passing through the area were not sampled, although harvest data from fisheries near the river mouth (JTC 2002) suggest that minimal coverage was lost due to the delay.

Six-year-old fish were the dominant age group (67.2%) in the tagged sample, ranging from 63.2% to 69.3% during the 3-year study. The remaining fish were primarily 5-year-olds (20.5%, ranging from 18.1% to 22.1%), with smaller proportions of 7-year-olds (8.1%), 4-year-olds (4.1%), 8-year-olds (0.07%), and 3-year-olds (0.03%). Most juveniles (99.8%) migrated to saltwater after one year of life, with only five individuals remaining for a second year. Fish length was similar during the three years of the study, averaging 833 mm and ranging from 395 mm to 1,075 mm. Fish passing through the lower river were primarily bright, iridescent silver in color during the first several weeks of June, with increasing numbers of dull silver fish later in the run (Figure 2). Small numbers of blush-colored fish were observed from mid-June to the end of the run. This general pattern was observed for all three years of the study, although the prevalence of iridescent silver fish was nominally greater over the course of the run in 2003. Color differences were also observed in relation to the final destination of the fish. Most fish traveling to Canadian reaches of the basin were iridescent silver when captured near Russian Mission, while fish destined for spawning areas lower in the basin were increasingly silver in color (Figure 3). Blush-colored fish were primarily late run fish returning to lower basin tributaries.

Tagging Response

Most fish (2,790, 97.5%) resumed upriver movements after release (Table 1), and were either harvested in upriver fisheries (874, 30.6%) or traveled to upriver reaches of the basin (1,917, 67.0%). Similar results were observed across years. The 70 fish (2.5%)

not located upriver either regurgitated their transmitters, died after release due to handling, predation, or undocumented encounters with local fishers, or had transmitters that malfunctioned. None of the fish harvested in upriver fisheries, captured and released at assessment projects, or recovered in spawning areas were missing their transmitter (i.e., both the transmitter and external spaghetti tag were present), suggesting that regurgitation was not a major factor.

Although most fish resumed upriver movements, passing Paimiut several days after release (averaging 1.6 and 3.4 days for fish tagged near Russian Mission and Marshall, respectively) the migration rates initially observed after tagging suggest that the fish were negatively affected by the capture, handling, and tagging methods (hereafter collectively referred to as the tagging effect). Fish that ultimately traveled to upper reaches of the basin (> 700 km upriver from Paimiut) exhibited progressively faster swimming speeds as they moved farther away from the tagging site (Figure 4). Migration rates from the release site to Paimiut for fish tagged near Russian Mission averaged 34.4 km/d (95% confidence interval from 33.7 to 35.1 km/d) compared to 44.7 km/d for fish tagged near Marshall (95% confidence interval from 42.5 to 46.9 km/d). In addition, there was convincing evidence of a positive relationship between migration rate and the distance fish traveled to reach Paimiut ($p < 0.001$ with 1256 df), with fish moving 1.4 km/d faster on average for every 10 km increase in distance traveled after release.

A similar pattern was also observed for upper river fish traveling between Paimiut and the Yukon-Anvik River confluence (Figure 4). Most fish (1234, 98%) displayed an increase in swimming speed between these two sites, with migration rates for individual fish increasing on average by 22.0 km/d. Differences in migration rates between these two sites were less for fish tagged at Marshall, with swimming speeds increasing on average by 15.6 km/d (95% confidence interval from 13.7 to 17.5 km/d) compared to 22.6 km/d for Russian Mission fish (95% confidence interval from 22.0 to 23.2 km/d). These findings suggest that Marshall fish had recovered more by the time they reached Paimiut, and as a result were showing less difference in swimming speeds compared to fish released closer to Paimiut. The geomorphic and hydrological characteristics of these two reaches were similar, suggesting that the differences observed primarily reflected the time since release and distance traveled rather than the conditions encountered by the fish.

Fishery Recoveries

A total of 874 radio-tagged fish were harvested in fisheries throughout the Yukon River basin, representing between 25% and 35% of the tagged sample (Table 1). Most fish (659, 75.4%) were harvested in U.S. fisheries along the Yukon River main stem, with smaller numbers caught in the Tanana, Koyukuk, and Porcupine rivers (Table 2). Fish caught in main stem fisheries in the U.S. were likely composed of both U.S. and Canadian stocks, although fish caught in the U.S. fishery near Eagle (Figure 1) were assumed to be destined for spawning areas in Canada. Canadian catches were composed primarily of Upper Yukon River fish (130, 14.9%) harvested in both main stem reach and several large tributaries (Table 2). Small numbers of fish were also caught in Canadian reaches of the Porcupine River.

Based on aerial surveys that included villages along the Tanana River and Yukon River main stem, over 200 (27%) of the 737 radio-tagged fish harvested by U.S. fishers were not reported, comprising 20.9%, 29.7% and 30.4% of the tagged sample annually. A similar phenomenon was observed in Canadian reaches, although the extent was more difficult to assess due to the proximity of some Canadian fisheries to possible spawning areas.

Upriver Distribution

Radio-tagged fish traveled to areas throughout the Yukon River basin with 2,120 fish tracked to upriver areas or recovered in terminal fisheries (Table 3, Figure 5). Although nominal differences were observed for both regional areas and specific spawning tributaries, the distribution patterns were similar across years. Upper Yukon and Tanana River fish were consistently the largest components (Figure 6), averaging 45.0% and 23.7% of the tagged sample, respectively, and collectively comprising between 66.2% and 70.3% of the sample annually. The proportions of fish returning to terminal areas in other regions were substantially less, ranging from an average of 2.1% for Upper Koyukuk fish to 6.9% for fish traveling to Lower Yukon tributaries (Table 3).

A majority (424, 50.1%) of the 846 Upper Yukon fish not harvested in main stem fisheries were tracked to large tributaries, including the Stewart (77 fish), Pelly (159 fish), and Teslin (156 fish) rivers (Table 4). Although the White River is also a sizable drainage, only 32 fish returned to this area. The remaining fish (237, 28.0%) were scattered among small and medium-sized tributaries within the region, with relatively few fish (1-37 individuals) located in most of these areas (Table 4). The Big Salmon River was a notable exception with 101 fish tracked to this tributary. A sizable number of fish (145, 17.1%) were last located in turbid reaches of the Yukon River main stem upriver from the Yukon-Pelly confluence (Figure 1). Smaller numbers of fish (40, 4.7%) remained in main stem reaches downriver from this site. The percentages across years were comparable (Table 4).

Most (353, 78.1%) of the 452 Tanana fish not harvested in Tanana River fisheries were tracked to medium-sized tributaries (i.e., Chena, Salcha, and Goodpaster rivers) in the middle reaches of the drainage (Table 4). The remaining fish (53, 11.7%) returned to other small and medium-sized tributaries, ranging from just a few individuals (1-4 fish) in most of these areas to 32 (7.1%) fish in the Kantishna River. Forty-six fish (10.2%) remained in reaches of the main Tanana River.

Although fewer fish were tracked to other regions (Figure 6), the distribution patterns were similar to that observed in the Tanana, with most fish traveling to one or two principal tributaries and smaller numbers of fish spawning in isolated areas. For example, most (102, 89.5%) of the 114 fish returning to tributaries in the Yukon Flats were tracked to the Chandalar and Sheenjek rivers (Figure 1, Figure 5). Similarly, 105 (71.2%) of the fish that traveled to Lower Yukon tributaries were tracked to spawning areas in the Anvik River. It should be noted that the contribution of the smaller groups of fish was still considerable when considered cumulatively. Fish returning to tributaries with less than 15 tagged individuals represented between 27.6% and 31.3% of tagged sample annually. In addition to the fish tracked to terminal tributaries, 201 fish (9.5% of the tagged sample not harvested in main stem fisheries) were last recorded in non-terminal reaches of the Yukon River main stem. This component included 121 fish (5.7%) located in turbid reaches of the Lower Yukon and Middle Yukon, and 80 fish (3.8%) located in the Yukon Flats (Table 3).

Spawning Areas

Most fish returned to clear water tributaries that were relatively entrenched, had moderate gradients, and were associated with relatively narrow valleys and gentle slopes. These areas were classified as low, rolling uplands and rolling uplands (similar to classifications described by Brabets et al. 2000), and hereafter referred to collectively as upland areas. Fish were largely absent in lowland reaches characterized by meandering, low gradient, highly alluvial channels often associated with main river floodplains. For example, most fish in the Lower Yukon, Middle Yukon, Upper Koyukuk, and Upper Porcupine were located on the periphery of main river floodplains (Figure 5). A similar pattern was observed in the Yukon Flats, with the exception of Sheenjek River fish which spawned from the lower reaches of the river to the upper headwaters (Figure 7). Although distant (~ 70 km) from the Yukon River main stem, Chandalar River fish returning to lower spawning reaches also utilized lowland areas. Most Tanana River fish returned to upland tributaries, in particular the Chena, Salcha, and Goodpaster rivers. Fish distributed widely within these rivers, spawning from near the river mouth to sites in the upper reaches (Figure 7). In contrast, Tolovana River fish were conspicuously absent in lowland areas near the river mouth, ultimately traveling to the upper reaches of the river. Remarkably few fish returned to the numerous main river tributaries flowing north across the Tanana Flats, although small clusters of fish were located in the Kantishna and Nenana rivers, and individual fish were periodically tracked to small main river tributaries. On the other end of the physiographic scale, relatively few fish in U.S. regions returned to areas associated with moderately rugged mountains, such as headwater reaches in the Upper Koyukuk and Chandalar rivers (Figure 5). The few fish present were located in lower reaches of these areas.

Physiographic features in the Upper Yukon consisted primarily of uplands areas with relatively narrow floodplains. Moderately rugged mountains were generally located along the periphery of the region. Most Upper Yukon fish returned to upland areas, and in general were more widely distributed (both within the region and within their terminal tributary) than fish in other regions of the basin (Figure 5), although clusters of fish were still observed in some reaches. For the most part, fish were largely absent from moderately rugged mountain reaches. A notable exception was the Big Salmon River, which had sizable numbers of fish returning during all three years of the study. GIS overlays categorizing the basin in relation to permafrost, wetlands, and lake systems did not display strong associations with the distribution of the fish.

Some differences were observed in the spawning distribution of fish within their terminal tributaries. Fish returning to the Teslin River displayed a negative relationship between the distance traveled from the tributary mouth and run timing. Fish tagged early in the run traveled primarily to spawning area in the upper reaches, whereas later run fish generally spawned in lower reaches of the drainage. However, this observation was not typical of the return. Fish returning to most terminal tributaries exhibited either no relationship or a slightly negative relationship between distance traveled and run timing. Of the four major stocks returning to the Upper Yukon, only Teslin River fish did not exhibit this pattern, whereas comparable numbers of early and late run fish traveled to the upper reaches of the Stewart, Pelly, and Big Salmon rivers (Figure 8). A similar relationship was observed for the other major and minor stocks within the basin.

Discussion

Chinook Distribution

The approaches used to capture, tag, and track the upriver movements of Yukon River Chinook salmon were remarkably successful in spite of the logistical challenges associated with the study. The modified gill nets were effective at capturing adequate numbers of fish in the lower river in suitable condition for tagging. Bycatch was minimal, even though large numbers of chum salmon were present in the lower river during the Chinook salmon migration. The fish responded well to the capture, handling, and tagging procedures, with most fish (97.5%) resuming upriver movements. The percentage of fish not moving upriver during the study (2-3%) was comparable or lower than reported for salmon telemetry studies in other river systems (e.g., Burger et al. 1985, Matters and Sandford 2003, Keefer et al. 2004), although study differences (e.g., capture and tagging methods, condition of the fish, proximity to saltwater, river type) and how the data were reported (i.e., how post-release fish were categorized) make direct comparisons difficult. The combination of satellite-linked tracking stations and coordinated aerial surveys (based on the station data), and the integrated database and GIS mapping program were effective at collecting and summarizing telemetry data in-season, and made it possible to accurately monitor fish movements, prioritize field activities, and provide information on the status of the run to fishery managers.

Chinook salmon returns during this study consisted of an aggregate of spatially distinct populations, with fish returning to spawning areas throughout the basin. Fish in the Upper Yukon were widely distributed. In contrast, fish returning to the other regions were conspicuously clumped in relatively isolated areas. The spawning distribution represented by the tagged samples was remarkably consistent during the three years of the study, suggesting that the composition of the run was relatively stable during this period. However, it should be noted that disproportional tagging in the lower river and disproportional harvests in upriver fisheries potentially bias stock composition estimates based solely on the distribution of the radio-tagged fish. Stock composition and timing estimates for the returns that account for these confines are presented separately (Chapter 3). Both major and minor stocks were consistently represented by the tagged samples, including several extremely small stocks (e.g., Beaver Creek and Black River fish in the Yukon Flats) suggesting that the principal components of the return were identified. There was good agreement between the final destination of the fish tracked to upriver areas and genetic stock identification estimates (Flannery et al. 2012), indicating that the fish were returning with relative precision to natal streams.

Chinook salmon escapement estimates during the study ranged from poor to average compared to estimates from 1989-1997, which represent escapements prior to the decline in run abundance (JTC 2002, 2004, 2005). Information is not available on how larger escapements would impact spawning distribution. The distribution of both radio-tagged and untagged Chinook salmon in the Taku River, a large coastal basin in Alaska and northwestern British Columbia, extended beyond designated index areas used to assess run abundance (J. Eiler, National Marine Fisheries Service, Juneau, AK, unpublished report). These index areas were initially established when escapement levels were low (P. Kissner, fishery biologist, Alaska Department of Fish and Game, Juneau, AK 99801, personal communication), suggesting that the original distribution reflected optimal spawning habitat, and that less optimal sites were being utilized as escapement levels increased.

Site selection by spawning salmon has been attributed to a variety of factors, including thermal and flow regimes, channel morphology, substrate characteristics, and accessibility (Neilson and Banford 1983, Lorenz and Eiler 1989, Berman and Quinn 1991, Geist and Dauble 1998, Isaak et al. 2007). Yukon River Chinook salmon presumably share similar behaviors, selecting sites that facilitate spawning activities, enhance egg deposition, development, and survival, and provide access to suitable juvenile rearing areas. However, detailed information on habitat characteristics within the basin is limited, and typically restricted to localized areas (Durst 2001, von Finster 2006), making it difficult to account for the distributional patterns displayed by returning salmon. In spite of this constraint, comparing telemetry data from this study with large-scale basin features showed several distinguishable patterns, with most fish returning to clear, moderately entrenched, upland rivers with moderate gradients and located in areas with modest relief. Although spawning often extended into upper reaches of the tributaries, fish were generally absent in headwater areas likely due to increased gradient and associated shifts in stream substrate and flow (as described by Church 2006).

Fish were generally absent in low gradient reaches associated with floodplains and wide river valleys, areas typically characterized by marginally entrenched, meandering rivers and streams. This pattern was particularly apparent in U.S. reaches of the basin where lowland areas were more prevalent. All fish destined for Lower Yukon and Middle Yukon tributaries traveled to forested upland areas distinct from the Yukon River floodplain. Most spawning in the Tanana River drainage was concentrated in upland tributaries, with relatively few fish returning to the numerous low-gradient rivers flowing across the vast Tanana Flats, a glacial outwash plain characterized by broken forests and muskeg (Durst 2001). Fish returning to the Kantishna (Tanana) and Sheenjek (Yukon Flats) rivers, were notable exceptions, and further assessment of these area may provide additional insights into the factors associated with spawning site selection.

Relatively few fish returned to spawning areas in the Upper Koyukuk. Lower and middle reaches of this drainage flow through lowland flats associated with muskeg, off-channel sloughs, and broken timber. Chinook salmon colonizing new areas may be less likely to make exploratory forays into relatively slow moving, low gradient rivers, even though upper reaches may potentially contain suitable spawning habitat. However, other limiting factors seem likely, since population (once established) would presumably increase in abundance over time and expand into adjoining areas if suitable conditions were present. Although comparable in size to other large Canadian tributaries, relatively few fish returned to the White River. Lower reaches of this drainage are extensively braided and extremely turbid from glacial runoff, but Milligan et al. (1985) reported that suitable spawning and rearing habitat appeared to be limited in the upper reaches of the drainage suggesting that utilization was not related solely to migratory conditions.

It is often assumed that fish traveling farther upriver generally exhibit earlier run timing than those fish migrating shorter distances. Arriving earlier would presumably provide additional time for these fish to reach their natal streams when spawning conditions were optimal. Run timing in the Yukon River was generally earlier for stocks traveling farther upriver with lower basin stocks primarily composed of later run fish, although exceptions were observed (Chapter3). However, the distribution of fish within terminal tributaries did not reflect this pattern, with comparable numbers of early and late run fish distributed throughout the spawning areas. Although not surprising for small and medium-sized tributaries where the upriver movements of the fish were more limited, this pattern was also observed in the larger tributaries within the basin, with some fish traveling in excess of 500 km upriver from the tributary mouth. The Teslin River was the lone exception within the basin, with spatial and temporal differences in the spawning distribution of the fish. This difference was likely due to the added complexity of the drainage associated with Teslin Lake – a large lake system (120 km long and 5 km wide) located approximately 195 km upriver from the Yukon-Teslin River confluence – and the presence of extensive spawning areas both upriver and downriver from the lake. Although early run fish spawned primarily in upper reaches of the drainage, with some fish spawning over 500 km upriver from the tributary mouth, later run fish spawned predominantly in the lower reaches downstream from the lake.

Non-terminal Areas

The status of the fish last located in non-terminal areas is uncertain, particularly those fish in U.S. reaches of the Yukon River main stem. In addition to serving as a migratory corridor for fish traveling farther upstream, these areas potentially support local spawning populations. Mainstem spawning by Chinook salmon has been reported in other large rivers, including the Sacramento (Yoshiyama 1998) and Columbia (Chapman 1943, Swan 1989, Dauble and Geist 2000). Chapman (1943), describing observations in the Columbia River prior to dam construction, reported fish spawning in the main river channel at depths in excess of 4 m. More recent studies have located Chinook salmon redds in water exceeding 6 m (Swan 1989). Mainstem spawning has been reported in Canadian reaches of the Upper Yukon (Milligan et al. 1985), although the extent was not determined due to turbid conditions. In addition to reports from local fishers, mainstem sampling late in the season (when fish in-transit to tributaries farther upriver were not present) recovered fish in spawning condition.

Large-scale efforts to verify spawning activity in non-terminal reaches were not feasible during this study due to the turbid nature of these areas, the scattered distribution of the fish, and the logistical difficulties associated with accessing and evaluating the sites. However, several findings provided suggestive evidence of mainstem spawning in the Upper Yukon. Most fish remaining in mainstem areas traveled to upper reaches of the region, a pattern indicative of directed movements. A more random distribution would generally be expected if individuals were in a progressively weakened state and dying while in transit. In addition, telemetry-based stock composition estimates for mainstem fish in the Upper Yukon (Chapter 3) were comparable to GSI estimates of the Canadian returns in 2008-2012 (P. A. Milligan, fishery biologist, Department of Fisheries and Oceans Canada, Whitehorse, Yukon Territory, unpublished data). The GSI estimates were based on samples taken near Eagle, Alaska, using the Canadian GSI baseline (updated in 2011) as a standard for stock allocation. The concordance between these two fundamentally different methods not only provides compelling evidence for the presence of mainstem spawning, but also corroborates the distribution information provided by this study and the methods used to obtain it. In contrast, only nominal information is available to suggest spawning by Chinook salmon in the main Tanana River, with most non-terminal fish returning to middle and upper reaches of the drainage. Some of the area identified in the upper reaches were also used by spawning chum salmon, and may represent spawning sites for Chinook salmon.

It is unknown if there is suitable salmon spawning habitat in U.S. reaches of the Yukon River main stem. Spawning by other salmonids, including inconnu (*Stenodus leucichthys*), whitefish (*Coregonus* spp.), and cisco (*Coregonus* spp.), has been reported in mainstem areas of the Yukon Flats (Brown et al. 2012). Alternatively, Chinook salmon last located in U.S. reaches may have ultimately spawned in mainstem tributaries scattered along the water course; many of these were not surveyed due to costs and logistical constraints. Based on our findings, fish returning to these tributaries would likely travel to upland reaches on the periphery of the Yukon River floodplain, which would simplify future survey efforts. A radio-tagged fish was serendipitously located during an over flight of the upper Hodzana River, a small mainstem tributary located in the Yukon Flats, suggesting that other mainstem tributaries may also support small spawning populations. Untagged Chinook salmon have been reported in other small and medium-sized mainstem tributaries not surveyed during our study (Johnson and Daigneault 2008), although these sightings may also represent exploratory behavior exhibited by fish traveling farther upriver.

An alternate explanation is that non-terminal fish represent tagged individuals that died while in-transit to upriver spawning areas due to latent effects from handling, natural causes (e.g., disease, poor physical condition, or predation), injuries from encounters with fishing gear, or unreported fishery recoveries. Potential impacts associated with tagging effects are discussed below in more detail. Since the late 1990s, the fish parasite *Ichthyophonus* has been reported in Yukon River Chinook salmon, and sampling studies have suggested that infected fish destined for the Tanana River and the upper basin may succumb to the parasite while in-transit to spawning areas (Kocan and Hershberger 2006). While latent effects from handling and disease can’t be definitely ruled out as possible effects, the migratory patterns of the fish suggest that these contributing factors do not fully explain the presence of fish in non-terminal areas. Slower swimming speeds would be expected for fish in the process of dying while in-transit to areas farther upriver. However, most non-terminal fish did not exhibit this pattern, with only 30 individuals (1.5% of the tagged sample) exhibiting migration rates that were noticeably slower than those exhibited by fish harvested in fisheries or tracked to terminal tributaries in the Lower Yukon, Middle Yukon, and Yukon Flats (Chapter 4).

The most likely explanation is that non-terminal fish represent undocumented fishery recoveries or fish that experience fishery related injuries. Migration rate of non-terminal fish were similar to those of fish harvested in mainstem fisheries. Although some non-terminal fish were located in isolated areas, most were concentrated in the vicinity of villages and fishing camps, and often interspersed with confirmed fishery recoveries; a more random distribution would be expected for fish experiencing impaired swimming behavior from other causes. Physical injuries from encounters with fishing gear may also result in impaired swimming performance and undocumented mortality for fish within areas with intensive fishing pressure. Incidents of fish regurgitating transmitters when captured and removed from fishing gear were also reported and may be a factor.

The importance of local support for research efforts is often underestimated. In the case of tagging studies, fishers are frequently reluctant to report tag recoveries due to the perception that the information will ultimately result in harvest restrictions or other unwanted management actions. In some remote communities, there is also a general distrust of outsiders and government programs. Extensive efforts were taken during this study to inform and encourage fishers to report tag recoveries. The success of this effort was obviously mixed, with substantial numbers of the tagged fish known to have been harvested not reported. Some fishers reportedly threw transmitters back in the river, confounding efforts to determine the status of fish remaining in mainstem areas; only transmitters located out of water, and in villages and fish camps were counted as unreported tag recoveries. The extent of this practice is unknown, making it difficult to assess the impact. Ironically, several issues of interest to local fishers could have been addressed with an unambiguous assessment of fish status in mainstem areas. For example, the parasite *Ichthyophonus* was a major concern throughout the basin due to its effect on flesh quality and the potential impact on escapement vis-à-vis elevated mortality levels. Telemetry, in conjunction with accurate harvest information, provided an opportunity to address this issue by revealing the proportion of fish not completing their upriver migration due to non-fishery related causes and the spatial distribution of these individuals. Future outreach efforts that emphasize how study results will be used to address local and basin-wide concerns would likely increase the effectiveness of these programs. The findings from this study also demonstrate the importance of designing telemetry-based studies that incorporate independent assessments of fish status to confirm the integrity of the information collected.

Tagging Response

A basic assumption in any tagging study is that the capture and handling methods do not adversely affect the fish (i.e., tagged fish behave the same as untagged fish) or that any effect is limited in severity and duration, and ultimately has negligible impact. In the case of migrating salmon, methods that violate these assumptions undoubtedly bias information on the upriver movements and in extreme cases may even alter the final destination of the fish, underscoring the need to evaluate the response exhibited by fish after release to validate the veracity of the data collected.

The procedures used can have a variety of effects on fish performance, ranging from minimal influence to impaired behavior, exhaustion, and death. In addition to physical injury, the stress experienced by the fish can also be a major factor, and can have an immediate or latent effect on the performance capabilities (Schreck 1981, Schreck and Li 1991, Schreck 2000, Schreck 2010), behavior (Schreck et al. 1997), and reproductive fitness and motivation of the fish (Schreck et al. 2001, Schreck 2010). Sub-lethal effects may also increase the vulnerability of the fish to other limiting factors, such as adverse environmental conditions, increased performance demands, and the associated allostatic loads (Schreck 1981, Schreck and Li 1991, Schreck 2010); stressors likely experienced during the upriver migration due to the extended distances traveled, and the need to avoid predation and compete with other salmon after reaching spawning areas. Budy et al. (2002) speculated that the cumulative effects of stress may be delayed for some time due to the complex interactions with other potential sources of mortality. Latent and sub-lethal effects are often difficult to assess, particularly in large remote river drainages where access to the fish is limited. Tagged fish that stop moving and die soon after release are relatively easy to identify with telemetry, whereas impaired movements upriver are more difficult to distinguish, particularly when the final destination and typical movement patterns of the fish are not known, and in some cases may be the primary study objective.

The severity of the tagging effect can be influenced by a number of factors, including the methods used during the procedure (e.g., capture technique, surgical vs.

non-surgical tagging), environmental conditions (particularly temperature), and the maturity, physical condition, and size of the fish (Bridger and Booth 2003). While our study was based on free-ranging, adult salmon radio tagged gastrically (i.e., transmitters inserted through the mouth and placed in the stomach), due to logistical constraints most research on tagging effects in salmon has focused on laboratory studies of juvenile tagged surgically with transmitters inserted into the abdominal cavity. Jepsen et al. (2001) reported that cortisol levels (an indicator of stress) in juvenile Chinook salmon increased substantially and remained elevated for 24-48 hours after tagging, whereas fish that were only handled returned to pre-trauma levels within several hours. These findings also suggest that the effects from radio tagging were short term, with tagged fish returning to normal cortisol levels within several days. Tagged and untagged Atlantic salmon (*Salmo salar*) smolts exhibited comparable swimming speeds during controlled endurance tests, although performance was influenced by fish and transmitter size (McCleave and Stred 1975). In contrast, Adams et al. (1998) reported adverse impacts on swimming performance for juvenile Chinook salmon 21 days after radio tagging, but fish size and tagging method were again contributing factors.

Although less definitive due to study differences and the inherent limitations in interpreting results due to confounding factors, *in situ* studies on adult salmon provide insight related to tagging effect. Stress indicators, including elevated cortisol, lactate, and glucose levels, were related to lower return rates for sockeye salmon (*O. nerka*) tagged during the marine phase of their spawning migration to natal streams in the Fraser River (Cooke et al. 2006). Decreasing tagged-untagged ratios in upriver recovery areas were observed for spaghetti-tagged chum salmon during mark-recapture studies on the Yukon River, suggesting that capture and handling increased mortality rates (Bromaghin et al. 2007). During a companion study, radio-tagged chum salmon handled in the same manner (i.e., held in fish wheel live boxes prior to tagging) exhibited delayed upriver movements and slower migration rates than fish radio tagged and released immediately after capture, suggesting that the stress associated with being held negatively affected the response exhibited by the fish (J. Eiler, National Marine Fisheries Service, Juneau, AK, unpublished report). Over the course of several studies, differences in tagging response were also observed in relation to species tagged, and proximity to both saltwater and spawning areas. Comparisons between adult Chinook salmon tagged with passive integrated transponders (PIT) and radio transmitters in the lower Columbia River found no evidence that radio tagging adversely affected the migratory behavior and upriver movements (Matter and Sandford 2003). The wide range of responses reported by these (and other) studies is not particularly surprising considering the diverse set of circumstances and conditions involved, including differences in river characteristics, species, fish characteristics (life stage, physical features, and condition), and the capture, handling, and tagging methods used.

Although the fish during our study responded well to the capture, handling, and tagging procedures (with 97.5% resuming upriver movements), there is evidence that they initially displayed a negative tagging effect. Migration rates between the tagging area and Paimiut were significantly slower than in reaches immediately upriver. Chinook salmon within the basin generally exhibit a progressive decline in migration rate as they move upriver and neared their natal streams (Chapter 4). Although general increases in swimming speed are periodically observed in upriver areas, they are typically associated with major changes in the physical features of the basin. For example, most fish (78%) displayed faster swimming speeds after leaving the highly braided Yukon Flats. River characteristics from the tagging area to the Yukon-Anvik River confluence were fairly similar, suggesting that the slower migration rates exhibited by the fish immediately after release were likely tagging induced. Differences in migrations rates at Paimiut and the Yukon-Anvik River confluence also showed that fish tagged farther downstream (i.e., that had traveled farther distances after release) were swimming considerably faster, and were progressively less variable as they moved upriver past the station sites, suggesting that these individuals had recovered more fully and were beginning to exhibit more normal swimming patterns. These findings suggest that although the tagging effect was relatively widespread among fish in the sample, with some individual still exhibiting residual effects 200 km upriver from their release site, it was relatively short in duration (several days) and less influential during the later stages. Caution is obviously needed when assessing movement data from tagging studies due to the potential bias associated with tagging effect. Migration rate estimates during this study censored information downstream of Paimiut due to concerns that it did not reflect normal upriver movements (Chapter 4).

It is not definitely known whether the reduced migration rates exhibited by the fish immediately after release represented a reduction in swimming speed or an aberrant migratory pattern. Limited fine-scale tracking from boats within the general vicinity of the tagging area determined that at least some fish held in mainstem eddies for several hours after tagging (presumably recovering from the event), although other fish resumed upriver movements immediately after release. A similar pattern was also observed just upriver from the tagging area, with fish holding in quiet water (e.g., eddies, slough mouths, and downstream side of islands), although it is not known whether this reflected normal migratory behavior or was an artifact of the tagging effect. Numerous other salmon telemetry studies have reported fish dropping downstream and temporarily delaying their upriver movements after tagging (Gray and Haynes 1979, Burger et al. 1985, Bernard et al. 1999).

Fish experiencing latent or long-term tagging effects would be expected to show reduced vitality and impaired movements as they moved upriver. The actual response would likely be expressed as slower than normal migration rates, migratory patterns exhibiting an accelerated decline in swimming speed, or truncated movements (i.e., atypical distribution). Fish traveling extended distances would presumably be particularly susceptible to long-term or latent effects. However, the upriver movements exhibited by fish during this study did not display these patterns. Migration rates of fish returning to the upper basin (i.e., fish traveling the farthest distances) ranged from 52 to 62 km/d among the different stocks (Chapter 4). By comparison, migration rates of adult Chinook salmon in mainstem reaches of the Columbia River averaged around 35 km/d (Keefer et al. 2004, Goniea et al. 2006). Although Yukon River Chinook salmon exhibited a general decline in migration rate as the fish moved upriver and neared their natal streams, the migratory pattern varied between reaches and was more reflective of changes in river characteristics than impaired swimming behavior (Chapter 5). As previously mentioned, fish remaining in non-terminal areas may represent mortality associated with latent tagging effects. However, the proximity of these fish to local fisheries and the movement patterns exhibited prior to arriving at their final location suggests that other factors may better explain their presence in these areas.

Several indirect measures also support the notion that the migration rates observed during this study were comparable to normal, non-impaired movements. Information on the timing of distinct pulses of Chinook salmon harvested in village fisheries along sequential reaches of the Yukon River main stem suggests that untagged fish were traveling between 48 and 56 km/d (T. Vania, fishery management biologist, Alaska Department of Fish and Game, Anchorage, personal communication); migration rates similar to those of the radio-tagged fish. Yukon River Chinook salmon radio tagged at Rapids (Figure 1) in 1998 traveled an average of 53 km/d during their upriver migration (JTC 1998). These rates were comparable to those observed for upper basin fish tagged during this study, even though the fish tagged at Russian Mission traveled substantially farther after being released. In addition, there was a high degree of concordance between Chinook salmon sonar counts in the Big Salmon River (located in the upper headwaters of the basin) during 2005 and the composite timing (2002-2004) of radio-tagged fish passing the tracking station near the river mouth (Figure 1). Key metrics for the two methods (i.e., the arrival date of the first fish, last fish, peak count, and 90% cumulative count) were within a couple days of each other (Mercer and Wilson 2006). The arrival date of the first fish showed the greatest difference (4 days), although this may relate to delays in the lower river associated with the tagging effect. Comparable timing patterns were observed at the sonar site during 2006-2011 (B. Mercer, fishery biologist, Whitehorse, Yukon Territory, personal communication). Similar observations were made at assessment projects on the Yukon River main stem (e.g., test fish wheels located at Rapids) and in major spawning tributaries, with the radio-tagged fish mirroring the timing of untagged fish.

Schreck (2000) suggested that the impact of stress on swimming performance and survival is dependent on the severity, duration, and frequency of the stress experienced by the fish. The physical nature and severity of capture and handling related injures will undoubtedly influence the immediate and long-term response as well. To address these concerns, a number of steps were taken during this study to minimize physical injuries and handling induced stress to the fish. The gill nets used to capture the fish were constructed with seine twine instead of monofilament to minimize injuries and make it easier to remove the fish from the mesh. The mesh was cut to further facilitate removal. The relatively short nets and the fishing methods employed (e.g., retrieving the nets as soon as fish were detected, retaining only two fish per set regardless of the number caught) undoubtedly reduced the number of fish captured and tagged. However these methods substantially reduced the time needed to process the catch and complete the tagging, and likely reduced the stress experienced by the fish. Capture and handling methods used can have a major impact on tagging response. In an extreme case, steelhead (*O. mykiss*) were captured and radio tagged as a sample of opportunity in an existing sockeye salmon test fishery using standard fishing methods (i.e., large, commercial gill nets fished for one hour periods). Only 49 (43%) of the 113 steelhead capture were judged to be in suitable condition for tagging, and only 8 of these moved upriver after release (Beere 1991), further illustrating the importance of handling issues.

Technical aspects related specifically to tagging, such as transmitter size and attachment methods, can also have considerable impact on how tagged fish behave after release. Several recent review articles discuss these issues in detail (Bridger and Booth 2003, Liedtke and Rub 2012). The tagging equipment and techniques used during this study were based on methods used successfully in previous salmon studies in large rivers (Eiler et al. 1990, Eiler et al. 1992, Eiler 1995). The results from the current study suggest that these methods were relatively benign.

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Table 1.— Tagging dates and numbers of fish capture, tagged, tracked upriver, and not located upriver after release for Chinook salmon radio tagged in the lower Yukon River during 2002-2004. Percentages of the total fish tagged are in parentheses.

	2002	2003	2004	All years
Start of tagging	9 June	3 June	3 June	3-9 June
End of tagging	13 July	14 July	19 July	13-19 July
Captured	1,310	2,312	2,107	5,729
Tagged	768	1,097	995	2,860
Moved upriver	751 (97.8)	1,081 (98.5)	958 (96.3)	2,790 (97.6)
Upriver location[1]	481 (62.6)	810 (73.8)	625 (62.8)	1,916 (67.0)
Harvested in fishery	270 (35.2)	271 (24.7)	333 (33.4)	874 (30.6)
Not located upriver	17 (2.2)	16 (1.5)	37 (3.7)	70 (2.4)

[1] Fish located upriver from Paimiut tracking stations.

Table 2.— Numbers of radio-tagged Chinook salmon harvested in regional fisheries in the Yukon River basin during 2002-2004. Percentages of the total are in parentheses.

Fishery	2002	2003	2004	All Years
Combined (U.S.)	235 (87.0)	226 (83.4)	276 (82.9)	737 (84.3)
Yukon River main stem	222 (82.2)	196 (72.3)	241 (72.4)	659 (75.4)
Tanana River	12 (4.4)	25 (9.2)	32 (9.6)	69 (7.9)
Koyukuk River	1 (0.4)	4 (1.5)	3 (0.9)	8 (0.9)
Porcupine River		1 (0.4)		1 (0.1)
Combined (Canada)	35 (13.0)	45 (16.6)	57(17.1)	137 (15.7)
Yukon River main stem	24 (8.9)	21 (7.7)	37 (11.1)	82 (9.4)
Yukon River tributaries[1]	10 (3.7)	21 (7.7)	17 (5.1)	48 (5.5)
Porcupine River	1 (0.4)	3 (1.1)	3 (0.9)	7 (0.8)
Total	270	271	333	874

[1] Principally the Stewart, Pelly, and Teslin rivers.

Table 3.— Distribution of Chinook salmon radio tagged in the lower Yukon River basin during 2002-2004. Fish harvested in terminal fisheries are included. Fish harvested in natal streams are considered to have reached their final destination. Percentages of the total are in parentheses.

Region	Final location	2002	2003	2004	All years
Lower Yukon	Yukon tributaries	49 (9.4)	39 (4.5)	59 (8.1)	147 (6.9)
	Yukon River[1]	2 (0.4)	1 (0.1)	21 (2.9)	24 (1.1)
	Combined areas	51 (9.8)	40 (4.6)	80 (11.0)	171 (8.1)
Middle Yukon	Yukon tributaries[2]	32 (6.1)	39 (4.5)	33 (4.6)	104 (4.9)
	Yukon River[1]	19 (3.6)	41 (4.7)	37 (5.1)	97 (4.6)
	Combined areas	51 (9.8)	80 (9.1)	70 (9.7)	201 (9.5)
Upper Koyukuk	Koyukuk tributaries	5 (1.0)	14 (1.6)	17 (2.3)	36 (1.7)
	Koyukuk fisheries	1 (0.2)	4 (0.5)	3 (0.4)	8 (0.4)
	Combined areas	6 (1.2)	18 (2.1)	20 (2.8)	44 (2.1)
Tanana	Tanana tributaries	103 (19.8)	159 (18.2)	144 (19.9)	406 (19.2)
	Tanana River	6 (1.2)	12 (1.4)	28 (3.9)	46 (2.2)
	Tanana fisheries	9 (1.7)	19 (2.2)	22 (3.0)	50 (2.4)
	Combined areas	118 (22.6)	190 (21.7)	194 (26.8)	503 (23.7)
Yukon Flats	Yukon tributaries	30 (5.8)	60 (6.9)	24 (3.3)	114 (5.4)
	Yukon River[1]	26 (5.0)	31 (3.5)	23 (3.2)	80 (3.8)
	Combined areas	56 (10.7)	91 (10.4)	47 (6.5)	194 (9.2)
Upper Porcupine	Porcupine tributaries	11 (2.1)	27 (3.1)	9 (1.3)	47 (2.2)
	Porcupine fisheries	1 (0.2)	4 (0.4)	3 (0.4)	8 (0.4)
	Combined areas	12 (2.3)	31 (3.5)	12 (1.7)	55 (2.6)
Upper Yukon	Yukon tributaries	139 (26.7)	323 (36.9)	199 (27.5)	661 (31.2)
	Yukon River[1]	55 (10.6)	74 (8.5)	56 (7.7)	185 (8.7)
	Canadian fisheries[3]	33 (6.3)	28 (3.2)	46 (6.4)	107 (5.0)
	Combined areas	227 (43.6)	425 (48.6)	301 (41.6)	953 (45.0)
Total		521	875	724	2,120

[1] Mainstem reaches including associated tributaries not monitored with tracking stations or aerial surveys.

[2] Including fish destined for tributaries in the lower Koyukuk River.

[3] Including fish caught in the U.S. fishery near Eagle, Alaska.

Table 4.— Distribution of Chinook salmon radio tagged in the lower Yukon River basin during 2002-2004 by stock. Fish harvested in natal streams are included. Percentages of the annual total are in parentheses.

Region	Stock	2002	2003	2004	All years
Lower Yukon	Anvik	34 (7.1)	31 (3.8)	40 (6.2)	105 (5.4)
	Bonasila	10 (2.1)	6 (0.7)	14 (2.2)	30 (1.5)
	Innoko	5 (1)	2 (0.2)	5 (0.8)	12 (0.6)
	Yukon River[1]	2 (0.4)	1 (0.1)	21 (3.2)	24 (1.2)
Middle Yukon	Nulato	19 (4)	15 (1.8)	11 (1.7)	45 (2.3)
	Gisasa[2]	4 (0.8)	11 (1.3)	8 (1.2)	23 (1.2)
	Kateel[2]	1 (0.2)			1 (0.1)
	Melozitna	1 (0.2)	1 (0.1)	3 (0.5)	5 (0.3)
	Nowitna	1 (0.2)	2 (0.2)	3 (0.5)	6 (0.3)
	Tozitna	6 (1.3)	10 (1.2)	8 (1.2)	24 (1.2)
	Yukon River[1]	19 (4.0)	41 (5.0)	37 (5.7)	97 (5.0)
Upper Koyukuk	Koyukuk River	5 (1.0)	7 (0.9)	10 (1.5)	22 (1.1)
	Hogatza		1 (0.1)		1 (0.1)
	Henshaw		1 (0.1)	2 (0.3)	3 (0.2)
	South Fork		3 (0.4)	5 (0.8)	8 (0.4)
	Middle Fork		2 (0.2)		2 (0.1)
Tanana	Lower Tanana River[1]	2 (0.4)	2 (0.2)	8 (1.2)	12 (0.6)
	Kantishna	8 (1.7)	15 (1.8)	9 (1.4)	32 (1.6)
	Tolovana	2 (0.4)	5 (0.6)	5 (0.8)	12 (0.6)
	Nenana		3 (0.4)	1 (0.2)	4 (0.2)
	Middle Tanana River[1]	3 (0.6)	4 (0.5)	12 (1.8)	19 (1.0)
	Clear			3 (0.5)	3 (0.2)
	Chena	30 (6.3)	40 (4.9)	30 (4.6)	100 (5.1)
	Moose		1 (0.1)		1 (0.1)

	Salchaket		1 (0.1)		1 (0.1)
	Salcha	47 (9.9)	58 (7.1)	68 (10.5)	173 (8.9)
	Upper Tanana River[1]	1 (0.2)	6 (0.7)	8 (1.2)	15 (0.8)
	Goodpaster	16 (3.4)	36 (4.4)	28 (4.3)	80 (4.1)
Yukon Flats	Beaver	1 (0.2)	3 (0.4)	2 (0.3)	6 (0.3)
	Hodzana			1 (0.2)	1 (0.1)
	Chandalar	15 (3.1)	35 (4.3)	14 (2.2)	64 (3.3)
	Sheenjek	12 (2.5)	20 (2.4)	6 (0.9)	38 (2.0)
	Black	2 (0.4)	2 (0.2)	1 (0.2)	5 (0.3)
	Yukon River[1]	26 (5.5)	31 (3.8)	23 (3.5)	80 (4.1)
Upper Porcupine	Coleen			3 (0.5)	3 (0.2)
	U.S. tributaries	3 (0.6)		1 (0.2)	4 (0.2)
	Old Crow River		2 (0.2)	1 (0.2)	3 (0.2)
	Porcupine River (Can)[3]	5 (1.0)	10 (1.2)	1 (0.2)	16 (0.8)
	Whitestone[3]		1 (0.1)		1 (0.1)
	Miner[3]	3 (0.6)	14 (1.7)	3 (0.5)	20 (1.0)
Upper Yukon	Charley	2 (0.4)	3 (0.4)	1 (0.2)	6 (0.3)
	Kandik	1 (0.2)	1 (0.1)		2 (0.1)
	Nation		2 (0.2)	2 (0.3)	4 (0.2)
	Chandindu[3]	1 (0.2)	5 (0.6)	1 (0.2)	7 (0.4)
	Klondike[3]	6 (1.3)	19 (2.3)	12 (1.8)	37 (1.9)
	Sixtymile[3]			1 (0.2)	1 (0.1)
	Stewart[3]	21 (4.4)	30 (3.7)	26 (4.0)	77 (4.0)
	White[3]	8 (1.7)	12 (1.5)	12 (1.8)	32 (1.6)
	Pelly[3]	32 (6.7)	79 (9.6)	48 (7.4)	159 (8.2)
	Below Yukon-Pelly[1,3]	13 (2.7)	13 (1.6)	14 (2.2)	40 (2.1)
	Above Yukon-Pelly[1,3]	42 (8.8)	61 (7.4)	42 (6.5)	145 (7.4)

	Big[3]		1 (0.1)		1 (0.1)
	Tatchun[3]	4 (0.8)	3 (0.4)	3 (0.5)	10 (0.5)
	Nordenskiold[3]	2 (0.4)	8 (1.0)	2 (0.3)	12 (0.6)
	Little Salmon[3]	2 (0.4)	17 (2.1)	3 (0.5)	22 (1.1)
	Big Salmon[3]	17 (3.6)	59 (7.2)	25 (3.8)	101 (5.2)
	Teslin[3]	36 (7.5)	71 (8.7)	49 (7.5)	156 (8.0)
	Hootalinqua[3]	7 (1.5)	7 (0.9)	9 (1.4)	23 (1.2)
	Takhini[3]		6 (0.7)	5 (0.8)	11 (0.6)
Total		477	820	650	1,947

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[1] Reaches of the Yukon River main stem including associated tributaries not monitored with tracking stations or aerial surveys.

[2] Tributaries in the lower reaches of the Koyukuk River.

[3] Canadian reaches of the basin.

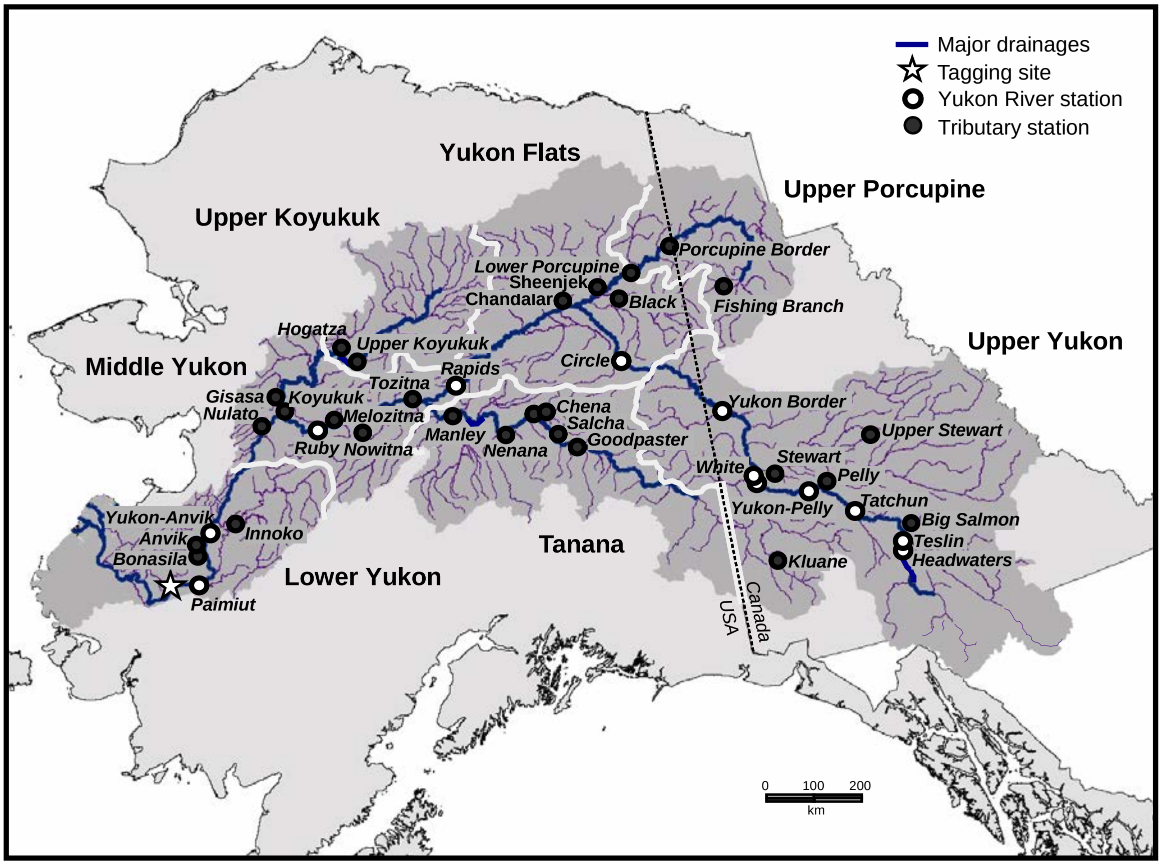

Figure 1.— Map of the Yukon River basin showing the regional areas, major drainages, lower river tagging site near Russian Mission, and tracking stations on both the Yukon River main stem and associated tributaries.

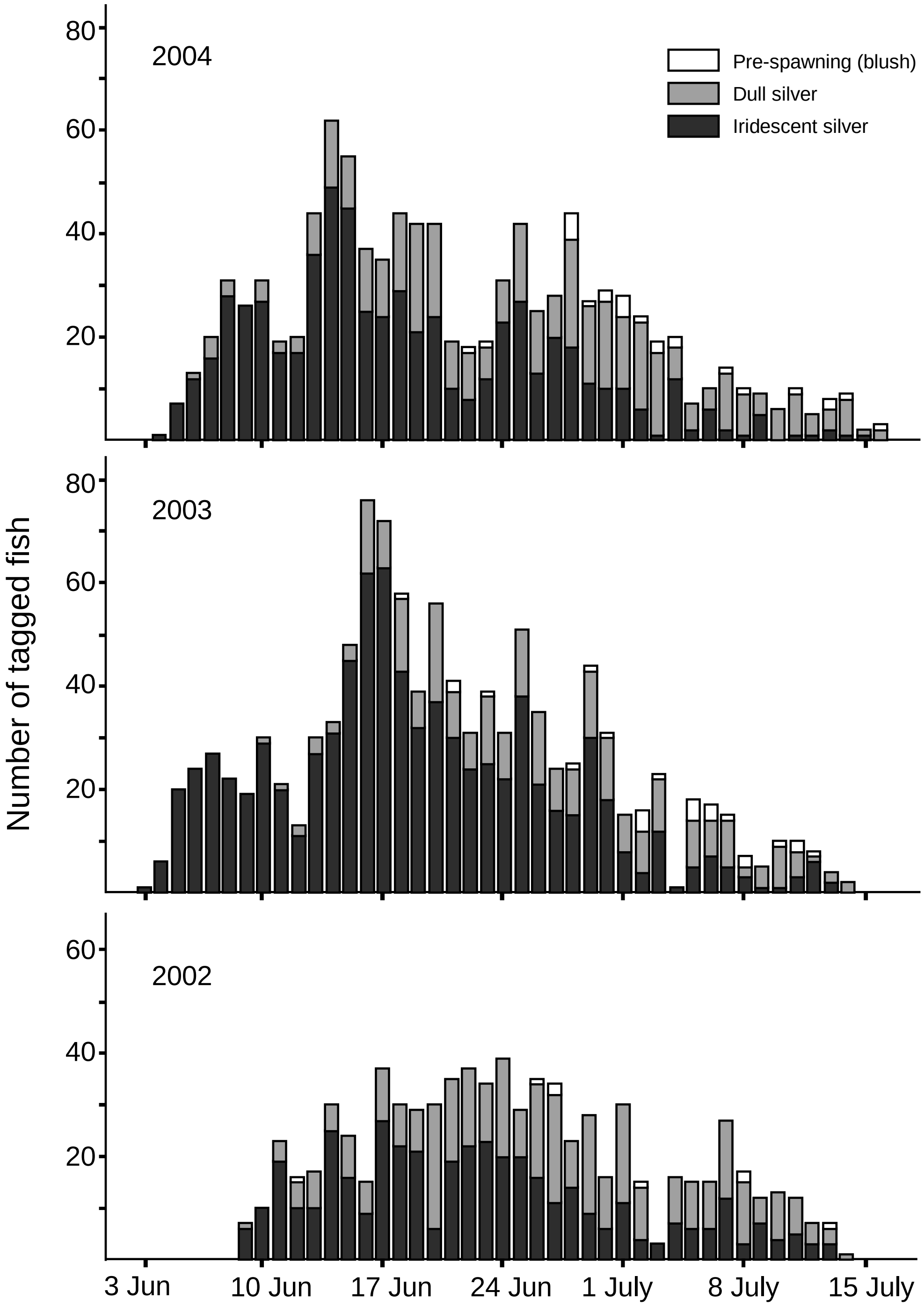

Figure 2.— Daily numbers of Chinook salmon radio tagged in the lower Yukon River during 2002-2004. Skin coloration is indicated, ranging from iridescent silver to blush (i.e., external sign of sexual maturation).

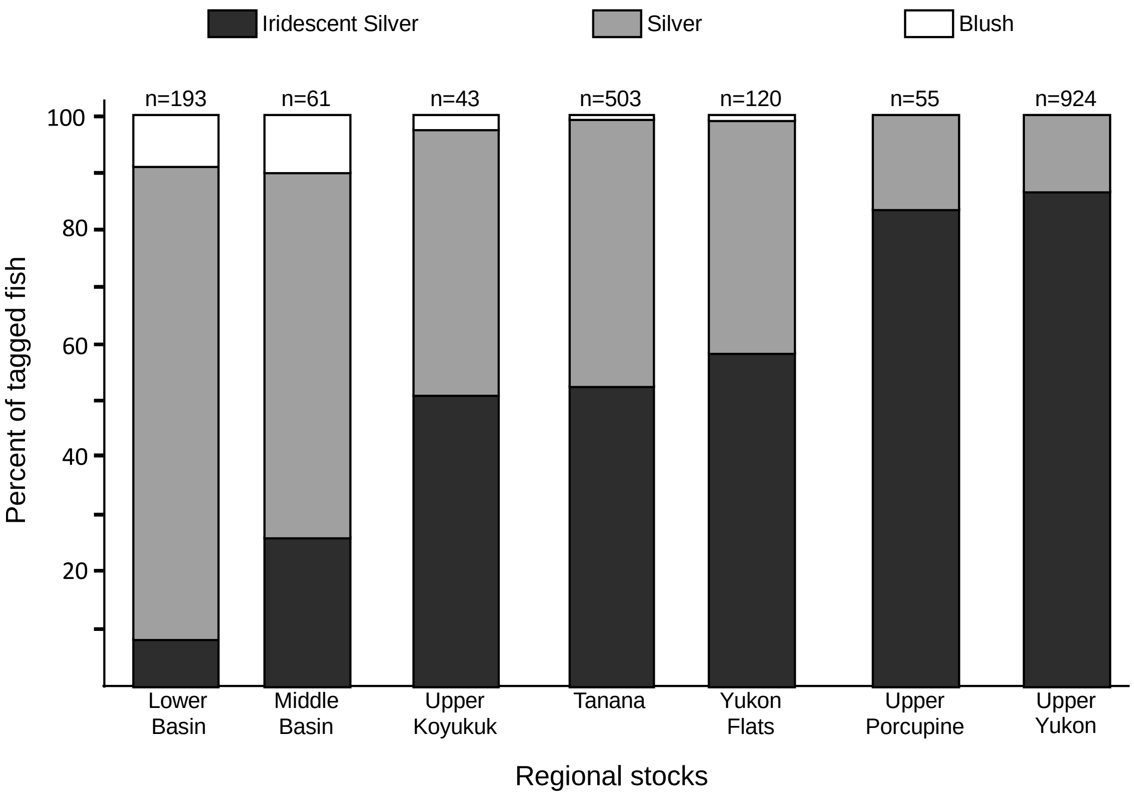

Figure 3.— Skin color of Chinook salmon radio tagged in the lower Yukon River during 2002-2004 and tracked to regional areas of the basin. Blush coloration representing external signs of sexual maturation.

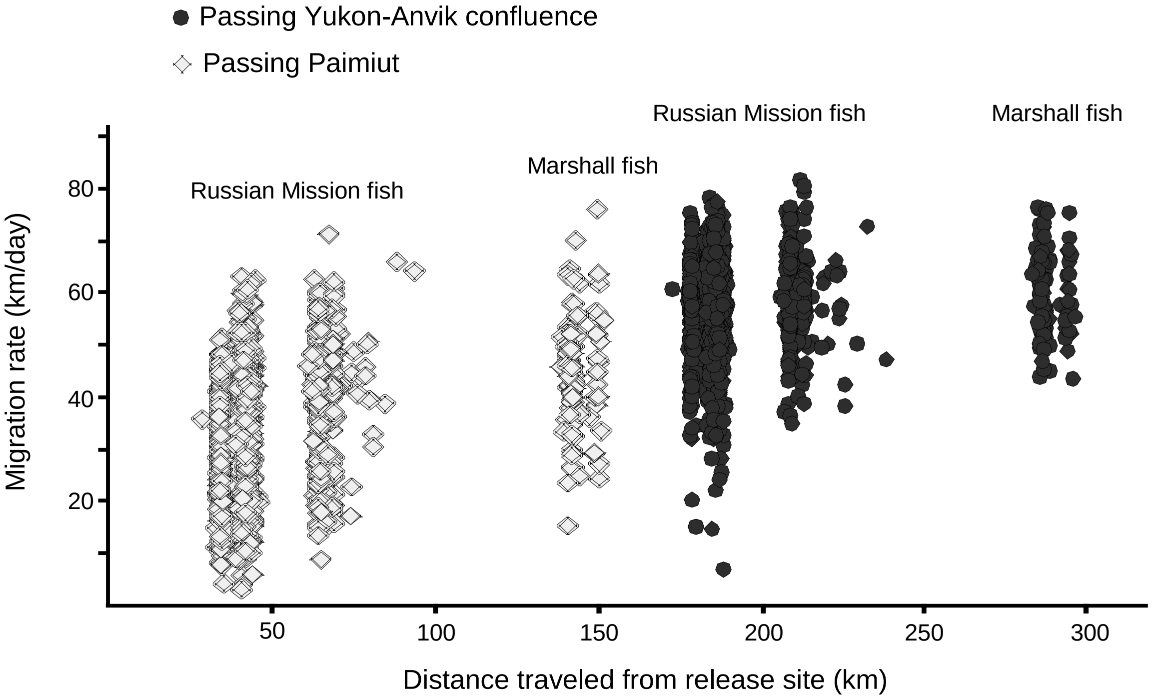

Figure 4.— Migration rates of radio-tagged Chinook salmon passing remote tracking stations in the lower Yukon River near Paimiut and the Yukon-Anvik River confluence. Fish were captured with drift nets (varying release sites) near the villages of Russian Mission (2002-2004) and Marshall (2002).

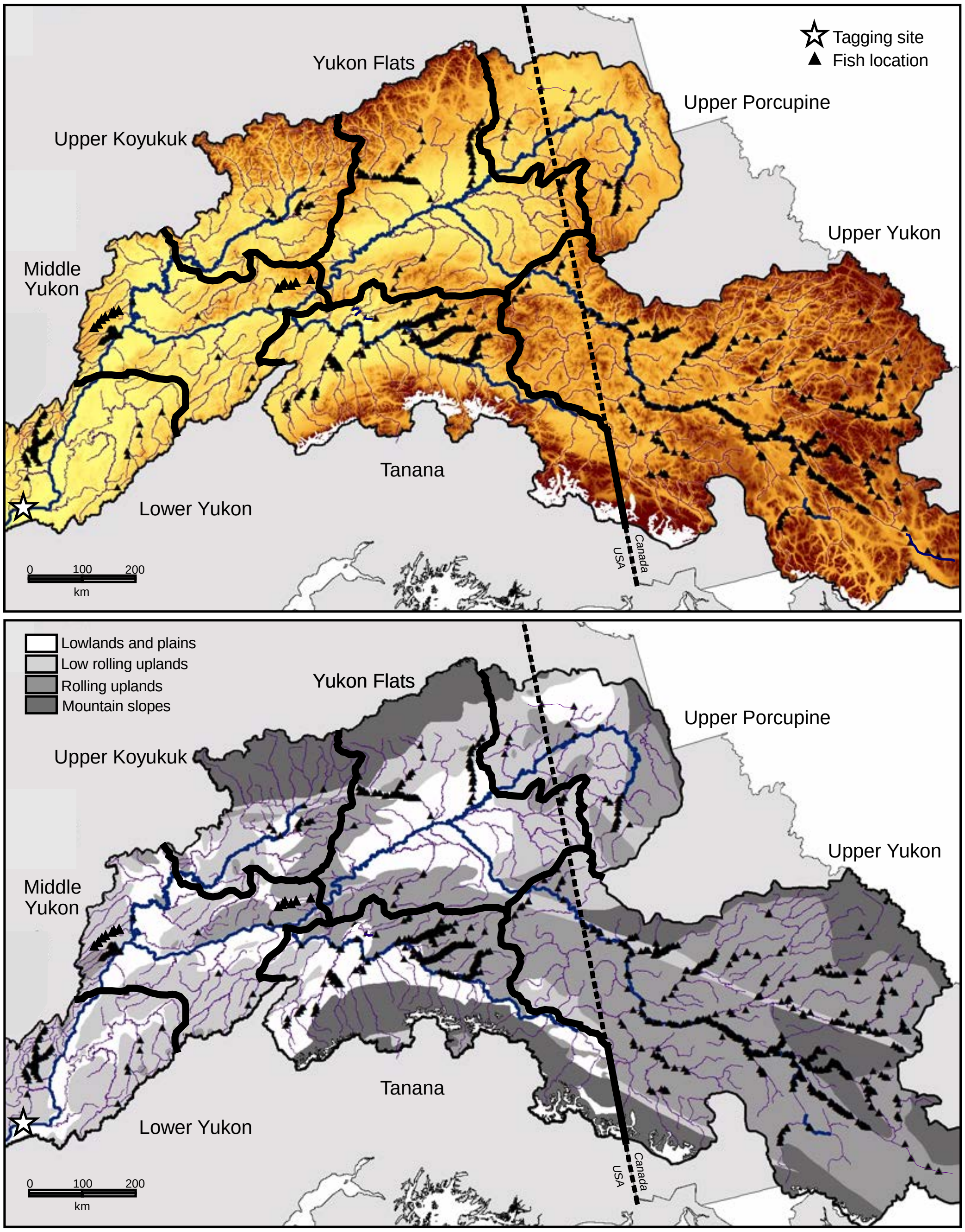

Figure 5.— Final location (dark triangles) of Chinook salmon radio-tagged in the lower Yukon River during 2002-2004. Regional areas, tagging site, basin topography (upper panel), and physiographic features (lower panel) are indicated. Topographic and physiographic overlays provided by U.S. Geological Survey (Anchorage, AK).

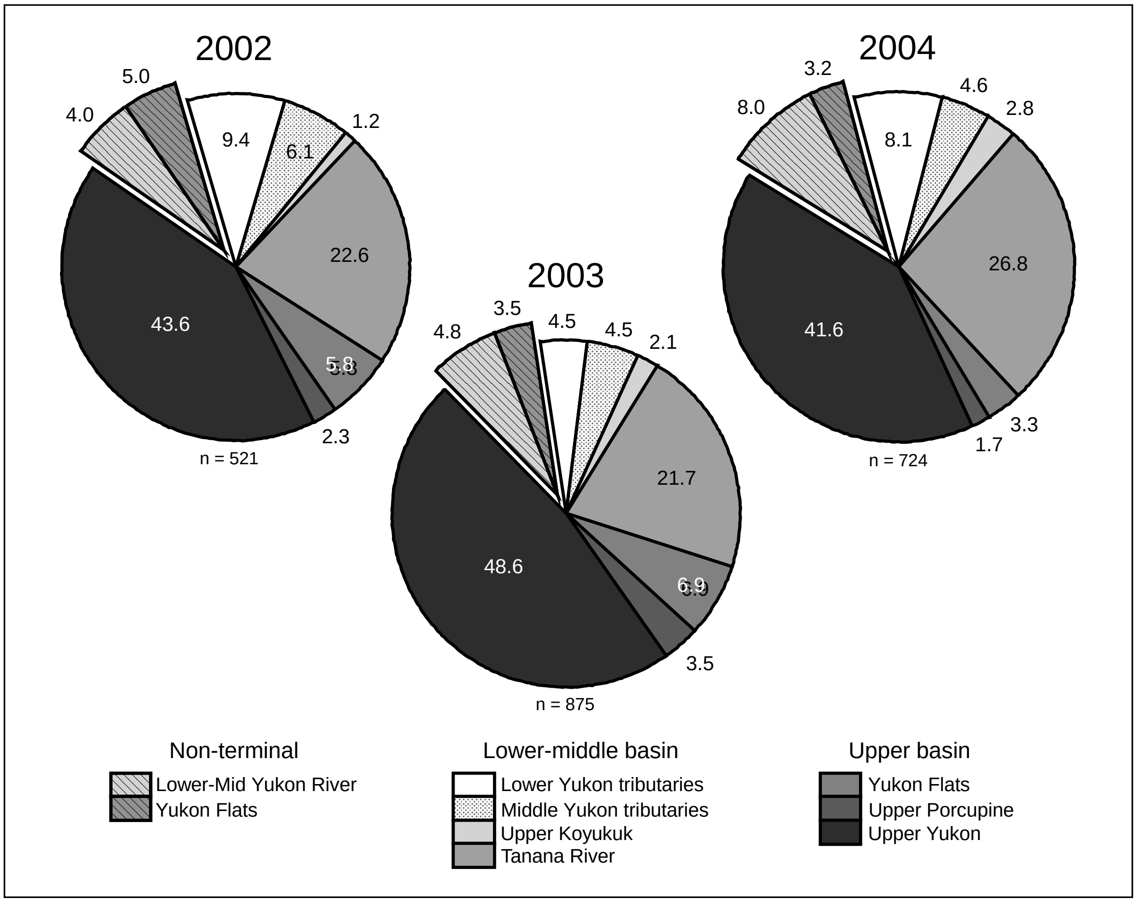

Figure 6.— Distribution of Chinook salmon radio tagged in the lower Yukon River during 2002-2004. Percentages of the total number of fish that moved upriver and were not harvested in U.S. reaches of the Yukon River main stem are indicated.

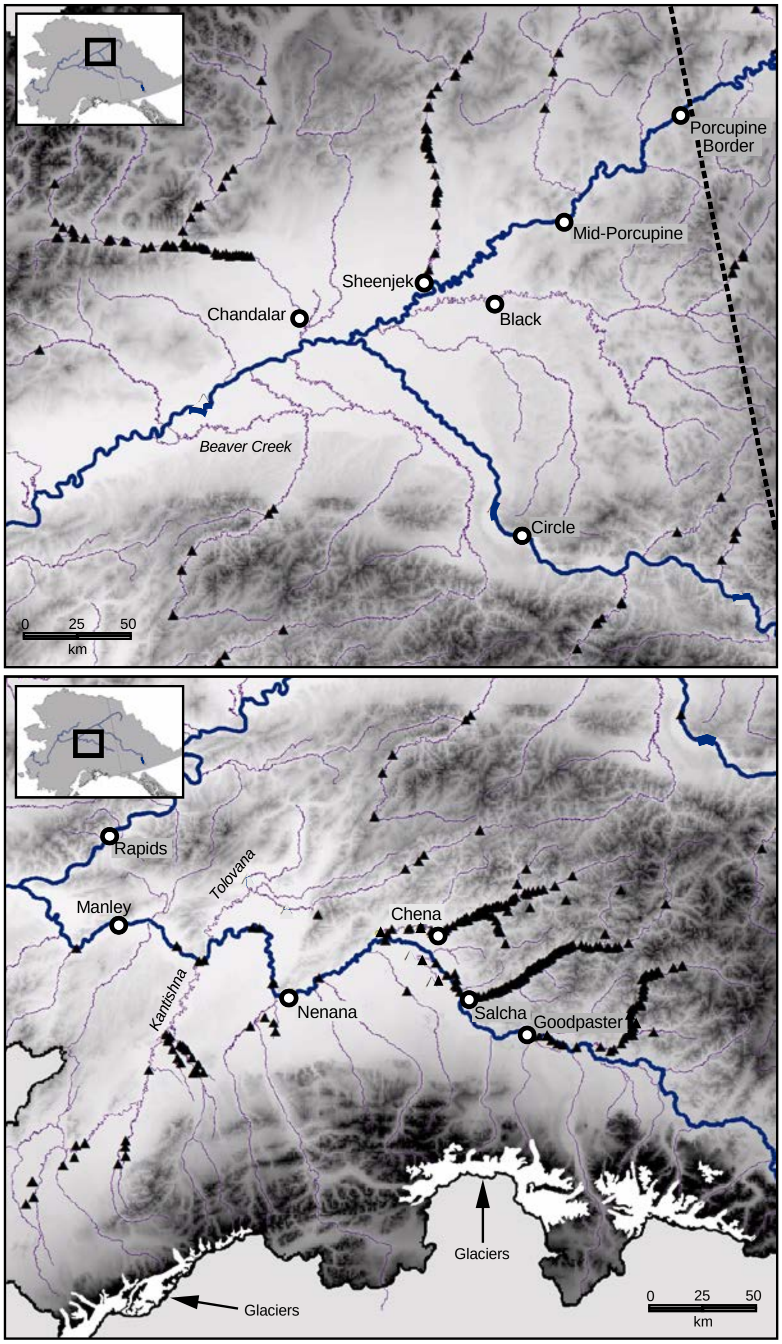

Figure 7.— Distribution (dark triangles) of Chinook salmon radio tagged in the lower Yukon River and tracked to terminal spawning areas in the Tanana River and Yukon Flats during 2002-2004. Topographic (upper panel) and physiographic (lower panel) features of the regions are shown.

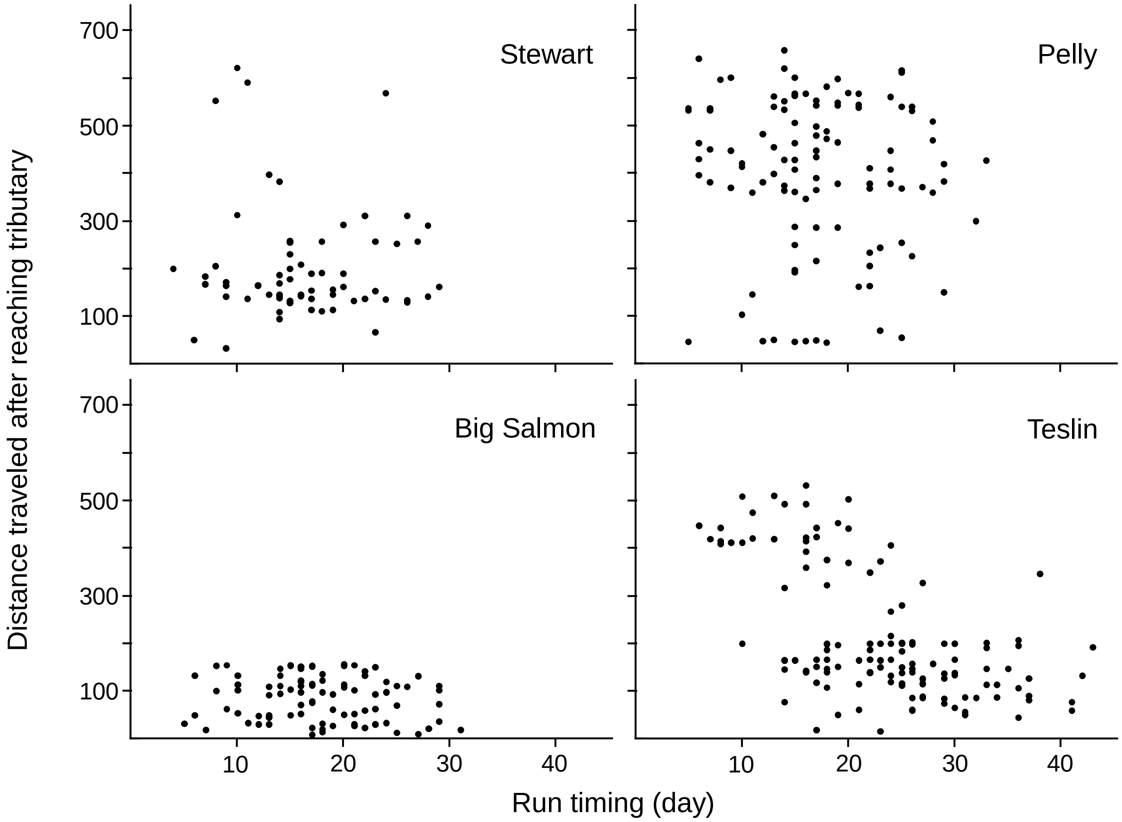

Figure 8.— Comparison of distance traveled by Chinook salmon after arriving at terminal tributary in relation to run timing based on capture date at Russian Mission. Fish representing four principal stocks returning to the upper Yukon River are shown, including three stocks returning to large tributary drainages (Stewart, Pelly, and Teslin) and one stock returning to a smaller tributary (Big Salmon) with fish traveling < 200 km to reach spawning sites. June 5 was designated as Day 0 for run timing estimates.

Stock Composition and Timing of Wild, Chinook Salmon Returning to a Large, Free-flowing River Basin

John H. Eiler[1,2], Michele M. Masuda[1], Ted R. Spencer[3], and Carl B. Schreck[2]

[1]National Marine Fisheries Service, Alaska Fisheries Science Center
Auke Bay Laboratories, Juneau, Alaska 99801, USA

[2]U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit
Department of Fisheries and Wildlife, Oregon State University
Corvallis, Oregon 97331, USA

[3]Alaska Department of Fish and Game, Division of Commercial Fisheries
Anchorage, Alaska 99518, USA

***Abstract*.—** Telemetry-based distribution data were used to estimate stock composition and timing of Yukon River Chinook salmon returns during 2002-2004. Daily and seasonal composition estimates were calculated for component stocks based on the distribution of 2,790 radio-tagged fish weighted by daily indices of abundance and adjusted to account for the disproportional harvest of tagged fish in upriver fisheries. Although Chinook salmon spawned throughout the basin, the run was dominated by two regional components comprising over 70% of the return. Substantially fewer fish returned to other areas ranging from 2-9% of the return, although their collective contribution was appreciable. Most regional returns consisted of several principal stocks and a number of small, spatially isolated populations. Regional and stock composition estimates were similar across years even though differences in run abundance were reported, suggesting that these abundance differences were not related to regional or stock-specific differences. Run timing was relatively compressed compared to rivers in the southern portion of the species' range, with most stocks passing through the lower river over a 6-week period, ranging from 16 to 38 d. Run timing was generally earlier for stocks traveling farther upriver, although exceptions were noted. Lower basin stocks were primarily later run fish. Although differences were observed, there was general agreement between our composition estimates and those from other assessment projects within the basin, suggesting that the telemetry-based estimates provided a plausible approximation of the return. The short duration of the run, complex stock structure, and temporally similar stock timing complicate the management of the Yukon River returns.

Keywords: Chinook salmon, stock composition, run timing, Yukon River, radio telemetry

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) spawn in natal rivers and streams throughout the northern Pacific Rim, ranging from small coastal drainages to vast river basins (Healey 1991, Heard et al. 2007). This species displays a wide range of life history strategies and behavioral forms, with returns often composed of multiple age classes, complex population structures, and variable run timing. The biological implications of this diversity undoubtedly reflect the opportunities and constraints experienced by the fish during the upriver migration and subsequent spawning. For example, river drainages with protracted salmon returns presumably provide a wider range of options to the returning fish than those with more compressed run timing. Similarly, information on the abundance, stock composition, and spawning distribution of the return provide a number of insights into the conditions encountered by the fish both during the migration and after reaching their final destination. Increasingly, human activities and anthropogenic factors are impacting Chinook salmon populations (and other salmon species) in rivers throughout their range, emphasizing the need to better understand the run characteristics of these returns. Determining the stock structure and associated timing of the returns is instrumental to better understanding and managing Chinook salmon and facilitating conservation efforts when the need arises. However, obtaining this type of detailed information is particularly challenging in large, free-flowing rivers where the ability to access and evaluate the run is limited.

Large numbers of Chinook salmon return to the Yukon River basin, a large, northern river in Alaska and northwestern Canada. Although less numerous than other salmon species, Chinook salmon support important commercial and subsistence fisheries throughout the basin, and are an integral part of the Yukon River ecosystem. Because of the international nature of the drainage, Chinook salmon returns are jointly managed by the U.S. and Canada to maintain acceptable spawning escapements, support subsistence fisheries for local residents, and provide commercial and sport fishing opportunities when appropriate (Yukon River Salmon Act 2000).

Similar to other river drainages, managing the multiple stocks returning to the Yukon River poses numerous challenges. These issues are exacerbated due to the massive size and remote nature of the basin, difficulties associated with determining the stock-specific abundance and timing of the returns, the presence of other temporally similar species of salmon (most notably summer chum salmon *O. keta*), and the need to equitably allocate harvests between the numerous fisheries and user groups scattered throughout the basin. Management within the basin has been further complicated by recent trends in run abundance and composition. Chinook salmon returns were relatively stable until the late 1990's when dramatic declines in abundance were reported (JTC 2001, Heard et al. 2007). This trend has continued during subsequent years, and resulted in the closure or drastic reductions in commercial fisheries, severe restrictions in subsistence harvests, and difficulties in meeting regional and basin-wide escapement goals (ENS 2012, JTC 2012). Annual harvests within the basin averaged 155,480 fish from 1961 to 1997, compared to less than 82,500 fish during 1998-2011 (based on data from JTC 2012). Just over 38,960 fish were harvested in 2009. Similar trends have been observed for Chinook salmon in other large rivers in western Alaska (Heard et al. 2007). Possible reductions in fish size (JTC 2006) and shifts in age composition to younger fish (based on data from Karpovich and Dubois 2007 and Schumann and Dubois 2012) have also been reported for Yukon River Chinook salmon returns.

Due to these trends, detailed information is needed on the status and run characteristics of Yukon River Chinook salmon to better understand and manage the returns and to facilitate conservation efforts. Various assessment methods have been used, including enumeration weirs, counting towers, test fisheries, sonar counts, and intensified spawning ground surveys and sampling (JTC 2006, Hayes et al. 2008). Although fundamental, these methods either provide information specific to particular tributaries or stocks, or generalized information about the entire run without reference to the different components. Developing technologies have made it possible to collect information on a more comprehensive scale. Genetic stock identification (GSI) is increasingly being used to estimate run composition and timing within the basin and in local fisheries (Beacham et al. 1989, Smith et al. 2005, Flannery 2012, Decovitch and Howard 2011). Due to technical advances in equipment and tracking capabilities, radio telemetry can provide quantitative information on salmon distribution and movements on both a basin-wide and stock-specific scale.

Radio telemetry has been used effectively to provide information on Pacific salmon (Burger et al. 1985, Eiler et al. 1992, Hinch et al. 2002, Cooke et al. 2004) including studies specifically on Chinook salmon in large rivers, most notably the Columbia River (Geist and Dauble 1998, Reischel and Bjornn 2003, Keefer 2004). However, this river is heavily regulated, with controlled flows and pathways associate with numerous hydroelectric dam located throughout the basin (Federal Columbia River Power System 2001). Further, Chinook salmon returns within the basin are composed of both wild and hatchery stocks (Myers et al. 1998). In contrast, the Yukon River basin is essentially free-flowing – only a small, passable hydroelectric dam located ~ 2500 km upriver from the river mouth impedes the natural flow of water – providing an opportunity to document the upriver movements and distribution of wild Chinook salmon under natural conditions. However, tagging and effectively tracking large numbers of these highly mobile fish in the Yukon River is extremely challenging due to the vast and remote nature of the basin.

During 2002-2004, a basin-wide radio telemetry study was conducted to determine the nation of origin, stock composition and timing, and spawning distribution of Chinook salmon returning to the Yukon River basin. Radio-tagged fish were tracked to spawning areas throughout the basin, from lower river tributaries to the upper headwaters, distances ranging from several hundred kilometers to over 3000 km upriver from the tagging area near Russian Mission (Chapter 2). Although distribution information from the radio-tagged sample can be used to approximate the stock composition and timing of the returns, these estimates are potentially biased by differential sampling and harvests. Accurate information on stock composition and timing is essential for effectively managing salmon returns in large river basins, particularly those with compressed run timing, complex stock structures, spatially separate fisheries, and differential fishing pressure over the course of the run. These considerations take on added significance due to the importance of salmon returns to local communities, and (in the case of the Yukon River) the international nature of the associated fisheries. Here, we present an approach for estimating stock composition and timing using telemetry-based distribution data that addresses these issues, and discuss the implications of composition and timing patterns for Chinook salmon returns in large river basins.

Methods

Study Area

The Yukon River basin drains a watershed of more than 855,000 km^2. The main river alone flows for more than 3,000 km from its headwaters in Canada to the Bering Sea (Figure 1). The river is relatively deep, with channel depths exceeding 20 m in the lower basin compared to 12-14 m downstream of the Yukon-Tanana River confluence and 5-7 m near the U.S.-Canada border (distances of ~ 1100 km and 2000 km from the river mouth, respectively). Several major tributaries flow into the Yukon River main stem, including the Koyukuk and Tanana rivers in the United States; the Stewart, White, Pelly, and Teslin rivers in Canada; and the Porcupine River, which transects both countries. The basin also includes numerous medium and small-sized tributaries. In addition to its large size, the Yukon River is the fifth largest drainage in North America in terms of total annual discharge, and exhibits considerable temporal variability with greater flows during the summer months (Brabets et al. 2000, Yang et al. 2009). The basin is remote with limited access to most areas.

Most reaches of the basin consist of a primary river channel with occasional side channels and sloughs, although the Yukon River main stem is extensively braided in the area commonly referred to as the Yukon Flats (Figure 1). Sections of the Tanana River, White River, and the Canadian main stem are also noticeably braided. Water visibility in many areas is extremely poor, particularly in the Tanana and White rivers due to turbidity from glacial activity in the upper headwaters of these drainages. Regional designations were based on geographic location and the general geomorphology of the area; e.g., lower reaches of the Porcupine River were considered part of the Yukon Flats due to similarities in landscape and river characteristics.

Chinook salmon are a major source of food in many remote communities, and provide a source of income for local residents. Subsistence and commercial fisheries occur throughout the basin with most fishing effort concentrated near villages along the Yukon River main stem (JTC 2012). Fish are also harvested in a number of tributaries including the Koyukuk, Tanana, Chandalar, Porcupine, Stewart, Pelly, and Teslin rivers (Figure 1). Limited sport fishing takes place in a number of clear water tributaries within the basin.

Fish Tagging and Tracking

Details regarding the methods used to capture, tag, and track the fish are described in Chapter 2. Briefly, adult Chinook salmon were captured with drift gill nets in the lower Yukon River near the village of Russian Mission (Figure 1). This site was selected because it 1) consisted of a relatively narrow, unbraided section of river, increasing the probability of capturing a representative sample, 2) was downriver of most known Chinook salmon spawning areas (i.e., only the Andreafsky River, located approximately 190 km downriver, was not included), and 3) was upriver of significant commercial and subsistence fisheries lower in the basin. During 2002, fish were also captured near the village of Marshall, located approximately 90 km downriver from Russian Mission. Local fishers were contracted to fish the area from early June to mid-July, with project personnel handling the fish and collecting data. Both day (0900-1700) and night (1800-0200) shifts were fished during the study.

Fish were tagged with pulse-coded radio transmitters manufactured by Advanced Telemetry Systems (Isanti, Minnesota)[1]. The transmitters (5.4 cm long, 2.0 cm in

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA or U.S. Geological Survey.

diameter, with a 30-cm transmitting antenna, and weighing 20 g) were gently inserted through the mouth and into the stomach of the fish. Each transmitter emitted a unique signal, making it possible to identify individual fish, and was equipped with a motion sensor and activity monitor (as described by Eiler 2012). The fish were also marked externally with spaghetti tags attached just below the dorsal fin (as described by Wydoski and Emery 1983) to help identify tagged individuals caught in fisheries or located in spawning areas. The methods used to describe the physical characteristics of the fish are described in Chapter 2.

Fish that moved upriver were tracked with remote tracking stations (as described by Eiler 1995) placed at 40 sites throughout the basin (Figure 1). The sites were located on important migratory routes and major tributaries. Pairs of stations were placed at sites with special significance, including Paimiut, lower Koyukuk River, Manley, Rapids, Yukon Border, and Porcupine Border, to avoid loss of data due to technical problems with the equipment, damage from bears (*Ursus* spp.), or other unforeseen difficulties. Aerial tracking surveys were conducted with fixed-wing aircraft and helicopters to locate fish that traveled to areas between station sites and upriver of stations on terminal tributaries. The equipment and methods used to track and relocate the fish are described by Eiler (2012).

Fish that passed the first station site (hereafter referred to as Paimiut), located approximately 62 km upriver from Russian Mission, were considered to have resumed upriver movements. Fish tracked to terminal tributaries within the basin were considered to have reached their final destination, and were classified as distinct spawning stocks. Since fidelity to natal rivers was strong during the study (Chapter 4), fish harvested in terminal tributaries were assumed to be destined for those areas, and considered part of the local population. The status of fish last located in non-terminal reaches, such as sections of the Yukon River main stem, was less certain because they could represent fish spawning in nearby areas or fish in-transit to spawning grounds farther upriver. Many non-terminal areas were turbid and hard to access, making verification of spawning activity unfeasible.

Estimating Stock Composition

Efforts to estimate stock composition were confounded by several factors. Returning Chinook salmon passing through the lower Yukon River are composed of a number of distinct stocks that differ in magnitude and run timing. In addition, varying portions of the fish are intercepted in fisheries before reaching their final destination. Stock composition estimates in the lower river (i.e., near Russian Mission) were therefore based on the distribution of radio-tagged fish tagged per day (Chapter 2), weighted by daily indices of abundance at the capture site, and adjusted to account for tagged fish removed in upriver fisheries. This approach provided an estimate of the relative abundance of stocks passing through the lower river on both a daily and seasonal basis. The daily estimates were used to determine the run timing pattern of the regional components of the return and the individual stocks. The number of radio-tagged fish released on day *t* was denoted as $R = (R_1, \ldots, R_t)'$. These fish were assumed to represent a random sample from the mixture of Chinook salmon stocks passing through the tagging area each day. A total of 46 final destinations (designated as stocks) were included in the analysis, and the unknown stock proportions of the mixture on day *t* were denoted by $\theta_t = (\theta_{t,1}, \ldots, \theta_{t,46})'$. Final destinations included 42 terminal areas (i.e., tributaries with confirmed spawning activity) and four non-terminal areas. The numbers of fish escaping to spawning areas from releases on day *t* were denoted as $r_t = (r_{t,1}, \ldots, r_{t,46})'$.

Fifteen fisheries upriver from the tagging area were defined for the analysis (Figure 2); 14 of these (Fishery 1 through 14) potentially alter the initial stock composition estimates at the tagging site because they disproportionally intercept stocks traveling to upriver spawning areas (i.e., stocks traveling farther upriver are exposed to more fishing pressure than lower river stocks). The first fishery (Fishery 0) was downstream of all spawning areas, and therefore was assumed to exploit the stocks equally. Radio-tagged fish caught in Fishery 0 were subtracted from the initial releases to provide a corrected set of daily releases, namely $R = (R_1, \ldots, R_t)'$, and were not considered further in this analysis. Fish destined for any spawning stock *s* were exposed to a downriver subset of the 14 remaining fisheries. The collection of these fishery indices was denoted by F_s. Catches in the 14 fisheries from releases of day t were denoted by $C_t = (c_{t,1},\ldots,c_{t,14})'$, and the corresponding exploitation rates (i.e., fractions of the tagged fish entering and removed by each fishery) were denoted by $\phi_t = (\phi_{t,1},\ldots,\phi_{t,14})'$. The set of stock indices of upriver stocks passing through fishery f were denoted by S_f, $f = 1,\ldots,14$.

The naive assumption of stock composition being equal to the observed distribution of radio-tagged fish escaping to spawning areas was rejected because of the inherent bias due to the disproportional fishing pressure experienced by upper basin stocks. Observed counts of radio-tagged fish among spawning areas and catches were modeled so that the effects of unequal harvests among the stocks would not bias estimates of the stock composition at the tagging site. A probability model was developed using the schematic for the migration routes, fisheries, and spawning areas in the Yukon River basin (Figure 2). Counts of fish in the escapements and catches from a daily release were assumed to have the multinomial distribution,

$$p(r_{t,1},\ldots,r_{t,46},c_{t,1},\ldots,c_{t,14}) = \left(\frac{R_t!}{\prod_{s=1}^{46} r_{t,s}! \prod_{f=1}^{14} c_{t,f}!} \right) \prod_{s=1}^{46} \left(\theta_{t,s} \cdot \psi_{t,s}\right)^{r_{t,s}} \prod_{f=1}^{14} \left(\mu_{t,f}\right)^{c_{t,f}}$$

$$\sum_{s=1}^{46} \theta_{t,s}\psi_{t,s} + \sum_{f=1}^{14} \mu_{t,f} = 1, \quad t = 1,\ldots,T, \tag{1}$$

where $\psi_{t,s} = \prod_{j \in F_s} \left(1 - \phi_{t,j}\right)$ is the probability that a fish destined for stock *s* escapes downriver fisheries, $\mu_{t,f} = \prod_{j \in H_f} \left(1 - \phi_{t,j}\right) \cdot \phi_{t,f} \cdot \sum_{s \in S_f} \theta_{t,s}$ is the probability that a tagged fish released on day *t* is caught in fishery *f*, and H_f is the set of indices for fisheries downstream from fishery *f*. The Lagrange function for the unknowns given the recoveries and catches from day *t*, which is the likelihood function with an added term to constrain the daily probabilities to equal 1, is

$$\log L(r,c;\theta_t,\phi_t) = \kappa + \sum_{s=1}^{46} r_{t,s} \log(\theta_{t,s}\cdot\psi_{t,s}) + \sum_{f=1}^{14} c_{t,f} \log(\mu_{t,f}) + \gamma\left(\sum_{s=1}^{46}\theta_{t,s}\psi_{t,s} + \sum_{f=1}^{14}\mu_{t,f} - 1\right), \qquad (2)$$

where κ is a constant and γ is a constant called the Lagrange multiplier. The Lagrange function was maximized by values of $\theta_{t,s}$ as shown in Table 4 of Eiler et al. (2006) with known values of $\phi_{t,f}$ given by

$$\phi_{t,f} = c_{t,f} \bigg/ \left(R_t - \sum_{s\in G_f} r_{t,s} - \sum_{j\in H_f} c_{t,j} \right),\ f = 1,\ldots,14, \qquad (3)$$

where G_f is the set of indices for stocks downstream from fishery *f*. Although the estimates of daily stock composition were of interest, they do not reflect the changes in magnitude of the daily returns passing Russian Mission. The unknown daily numbers of fish passing this site were denoted as $E_1, E_2,\ldots, E_T$, and their season total as $E_. = \sum_{i=1}^{T} E_i$.

The daily fraction of the total return passing the tagging area were denoted as

$$\pi_i = E_i / E_.,\ i = 1,\ldots T. \qquad (4)$$

Daily fraction of the total season return to the basin that pass the capture site were estimated from the catch rates of gill nets used to capture the fish for tagging. Gill nets were expected to capture fish in proportion to daily effort. Daily catches, $X_1,\ldots, X_T$, were assumed to be Poisson random variables with expected values,

$$\lambda_t = \lambda h_t E_t = (\lambda E_.) h_t \frac{E_t}{E_.} = \lambda_0 h_t \pi_t, \quad t = 1,\ldots,T \qquad (5)$$

Where $\lambda_0 = \lambda E_.$ is a constant proportional to the total return, and h_t is the number of units of effort fished on day *t*. Maximum likelihood estimates of the daily migration fractions, $\pi = (\pi_1,\ldots,\pi_T)'$, can be shown to be the time series of normalized catch per effort,

$$\hat{\pi}_t = Y_t \bigg/ \sum_{j=1}^{T} Y_j = (X_t / h_t) \bigg/ \left(\sum_{t'=1}^{T} X_{t'} / h_{t'} \right), \quad t = 1,\ldots,T \qquad (6)$$

The maximum likelihood estimate of λ_0 is $\hat{\lambda}_0 = \sum_{t=1}^{T} X_t / h_t$.

Daily fractions of the total season return to the basin that are destined for any particular stock equal the products of the stock's daily proportions, $\theta_{t,s}$, and the corresponding daily fractions of the total season return passing the tagging site, namely $\omega_{t,s} = \pi_t \theta_{t,s}$. These stock-specific daily fractions of the total return were estimated by the daily products of the estimates of stock composition, $\theta_{t,s}$, and the daily migration fractions, $\hat{\pi}_t$, from Equation 6,

$$\hat{\omega}_{t,s} = \hat{\pi}_t \hat{\theta}_{t,s}, \quad s = 1,\ldots,46; t = 1,\ldots,T. \tag{7}$$

Finally, the estimated fraction of the total season return to the Yukon River basin that belonged to any stock s equals the sum,

$$\hat{\alpha}_s = \sum_{t=1}^{T} \hat{\omega}_{t,s}, \quad s = 1,\ldots,46. \tag{8}$$

To evaluate the sampling variation in estimates, a parametric bootstrap was performed. First random bootstrap samples of daily gillnet catches, $X_1^*, X_2^*,\ldots, X_T^*$, were drawn from Poisson distributions with expected values of the X_t^* determined from the maximum likelihood estimates and equal to $\hat{X}_t = \hat{\lambda}_0 h_t \hat{\pi}_t$, $t = 1,2,\ldots, T$. These random catches were used to compute corresponding bootstrap catch rates $Y_1^*, Y_2^*,\ldots, Y_T^*$, and daily migration fractions, π_t^*, $t = 1,\ldots, T$. Next, independent daily multinomial samples of radio-tagged fish, either migrating to the possible stocks, $r^*_{t,1}, r^*_{t,2},\ldots, r^*_{t,S}$, or caught in the various fisheries, $c^*_{t,1},\ldots, c^*_{t,14}$, from the daily known numbers released, R_t, were drawn with probabilities equal to the original maximum likelihood estimates from Equation 1.

Bootstrap samples of tagged fish in catches and escapements were used to compute the corresponding bootstrap estimates for stock proportions, such as $\hat{\theta}_{t,s}$, just as with the original counts of tagged fish. Finally, bootstrap estimates for stock proportions were weighted by the bootstrap daily migration fractions. The next bootstrap sampling began with another draw of the daily gillnet catches and tagged numbers migrating to the possible stocks or caught in the fisheries, followed by computation of the bootstrap estimates of daily catch rates, daily migration fractions, daily stock compositions, and weighted stock compositions.

Stock composition estimates were based on the assumption that fish allocated to designated stock groups (both terminal and non-terminal) represented spawning populations. Non-terminal reaches that included fish in-transit to areas farther upriver (i.e., undocumented fishery harvests, or fish that died due to disease, injury, poor physical condition, or predation prior to reaching their final destination) would bias composition estimates, and underestimate the contribution of upriver stocks. To address this concern, stock composition estimates were recalculated with all fish remaining in non-terminal areas categorized as in-transit and treated as fishery recoveries.

Inter-annual differences in stock–group composition estimates were tested using a multivariate test for proportions outlined by Edgington (1995). Edgington's test statistic, based on a geometrical approach, is the sum of squared deviations from proportion means summed over the dependent variables and weighted by sample size. Following Edgington's notation (1995), we defined the test statistic with no weighting as

$$SS_B = SS_{B(1)} + SS_{B(2)} + \ldots + SS_{B(G)},$$ where

G is the number of stock groups,

$SS_{B(i)} = (C_{i,2002} - \bar{C}_i)^2 + (C_{i,2003} - \bar{C}_i)^2 + (C_{i,2004} - \bar{C}_i)^2$,

$C_{i,\text{year}}$ is the composition estimate for stock group i of that year, and

$\bar{C}_i$ is the stock-group composition estimate averaged over the three years.

Significance of the test was determined from the reference distribution generated from the parametric bootstrap that was used in evaluating sampling variation in the stock composition estimates. The test statistic was computed for each of the bootstrap composition estimates, and the *P*-value was determined as the proportion of test statistics that were greater than or equal to the observed test statistic.

Results

Tagging and Upriver Movements

Fishing commenced in early June and continued until the end of the run in mid-July when catch rates were low. Annual differences in run timing were observed based on catch per unit effort (CPUE) data from the Russian Mission tagging site (Figure 3). In 2002, several distinct pulses of fish moved through the lower river from early to mid-June, with declining numbers observed during late June and July. The 2003 return exhibited a more bell-shaped curve. Although several pulses of fish were observed in early and late June, the peak of the run was pronounced with most fish passing Russian Mission during 15-19 June. The peak of the run was less pronounced in 2004, with several distinct pulses moving through the lower river during middle and late June.

A total of 2,860 Chinook salmon were captured and radio tagged, with transmitters deployed throughout the run (Figure 3). The fish responded well to the capture, handling, and tagging procedures, with most resuming upriver movements after release (Table 1). A total of 2,790 (97.6%) fish passed Paimiut, and traveled to upriver reaches (1,917, 67.0%) or were caught in upriver fisheries (874, 30.6%). Seventy fish (2.4%) were not located upriver, and either regurgitated their transmitters, died after release due to handling, predation, or undocumented encounters with local fishers, or had transmitters that malfunctioned. None of the fish harvested in upriver fisheries, examined and released at assessment projects, or recovered in spawning areas were missing their transmitter (i.e., both the transmitter and external spaghetti tag were present), suggesting that regurgitation was not a major factor.

A total of 874 radio-tagged fish were harvested in fisheries throughout the Yukon River basin, representing between 25% and 35% of the tagged sample (Table 1). Most fish (659, 75.4%) were harvested in U.S. fisheries along the Yukon River main stem, with smaller numbers caught in the Tanana, Koyukuk, and Porcupine rivers (Table 2). Fish harvested in main stem fisheries were likely composed of both U.S. and Canadian stocks, although fish caught near Eagle, Alaska (U.S.-Canada border) were assumed to be destined for spawning areas in Canada. Canadian catches were composed primarily of Upper Yukon fish (130, 14.9%) harvested in both main stem reaches and several large tributaries (Table 2). Small numbers of fish were also caught in Canadian reaches of the Upper Porcupine.

Stock Composition and Timing

Chinook salmon returns were composed primarily of Upper Yukon and Tanana fish, collectively comprising between 71.5 and 72.5% of the return during the three years of the study. Upper Yukon fish were the largest component, ranging from 47.2 to 52.3% of the return (Figure 4). Most Upper Yukon fish (28.0 to 32.7% of the return) traveled to large Canadian tributaries, principally the Stewart, Pelly, and Teslin rivers, and the medium-sized Big Salmon River (Table 3, Figure 5). A number of minor stocks were also present in scattered tributaries, with average composition estimates ranging from 0.3% (Charley River) to 2.6% (White River). Collectively these stocks represented between 8.1 and 10.0% of the return. Upper Yukon fish also remained in reaches of the Yukon River main stem and small associated tributaries, principally in the middle reaches (upstream of the Yukon-Stewart River confluence) and upper reaches (upstream of the Yukon-Pelly River confluence) of the drainage, comprising 3.8 to 4.8% and 4.4 to 5.3% of the return, respectively. Tanana fish were also a major regional component, ranging from 19.3 to 24.3% of the return (Figure 4). This assemblage also consisted of a combination of major and minor stock (Table 3, Figure 5), with most fish (15.6 to 18.8%) returning to the Chena, Salcha, and Goodpaster rivers. Unlike the Upper Yukon, minor stocks represent a substantially smaller proportion of the return (1.5 to 1.7%). Tanana fish also remained in reaches of the Tanana River or traveled to small tributaries associated with the main river, primarily in the middle and upper reaches of the drainage (Table 3).

By comparison, the proportions of the run returning to the Yukon Flats and Upper Porcupine were relatively small (Figure 4). Upper Porcupine stocks ranged from 2.1 to 3.9% of the return, with most fish traveling to the upper headwaters of the drainage.

Composition estimates for fish returning to tributaries within the Yukon Flats ranged from 3.3 to 6.9% of the return, with Chandalar River fish (1.7 to 4.0%) and Sheenjek River fish (1.0 to 2.5%) constituting the principal stocks (Table 3, Figure 5). Substantially smaller percentages of the run returned to Black River and Beaver Creek. Fish were also allocated to reaches of the Yukon River main stem and associated mainstem tributaries (Figure 4).

Chinook salmon also returned to spawning areas in the lower and middle basin. Composition estimates for Lower Yukon tributaries ranged from 3.3 to 6.1% of the return. This component was composed primarily of Anvik River fish (2.6 to 4.1%) with smaller proportions returning to the Innoko and Bonasila rivers (Table 3, Figure 5). Middle Yukon stocks, consisting of fish traveling to medium-sized tributaries along the Yukon River corridor and lower Koyukuk River, were also relatively minor components, with most fish returning to the Nulato (1.3 to 1.9%) and Tozitna (1.0 to 1.2%) rivers, and smaller percentages in the Gisasa, Melozitna, and Nowitna rivers. Similarly, headwater stocks in the Upper Koyukuk were a minor component, ranging from 1.1 to 1.9% of the return. As in the upper basin, fish remained in reaches of the Yukon River main stem or traveled to small associated tributaries, ranging from 2.9 to 5.7% in the Lower Yukon and from 0.8 to 1.5% in the Middle Yukon.

Stock composition estimates were relatively consistent during the three years of the study. There was no evidence of inter-annual differences by region ($SS_B = 0.0048$, $p = 0.80$), suggesting that the relative contribution of the regional components was fairly stable during this period. A similar pattern was observed for individual stocks. Only the Little Salmon River showed substantial inter-annual difference, with a higher proportion of the run returning to this tributary in 2003 than during the other two years of the study (Figure 5). Ancillary observations on the spawning grounds also reflected this pattern. Composition estimates for Salcha River fish were noticeably lower in 2003, but within the bounds of the 95% confidence intervals of the other years.

The composition estimates derived using the two allocation methods for non-terminal reach (i.e., all fish treated as spawning locally vs. all fish treated as in-transit to spawning areas farther upriver) were similar (Figure 6). Upper Yukon fish were most discordant, with estimates of 50.6, 51.6 and 46.7% of the return (2002, 2003, and 2004, respectively) when non-terminal fish were considered local spawning populations compared to 56.7, 57.9, and 53.8% of the return (2002, 2003, and 2004, respectively) when these fish were treated as in-transit to spawning areas farther upriver. Stock composition estimates for Tanana fish increased to a lesser extent; from 20.9, 19.3, and 24.4% when non-terminal fish were treated as spawning populations to 21.6, 20.4, and 26.2% when non-terminal fish were assumed to be in-transit to upriver areas. Difference in stock composition estimates for other regions were minimal (i.e., less the 1%).

Chinook salmon stocks passing through the lower Yukon River (i.e., moving past Russian Mission) exhibited different run timing patterns. Tanana and Upper Yukon fish were present throughout the run, but were most abundant during middle to late June (Figure 7). Although substantially less abundant, stocks traveling to the Yukon Flats and Middle Yukon exhibited the same general pattern. Lower Yukon stocks displayed later run timing, with most fish passing Russian Mission during late June and July. These regional patterns were consistent during the three years of the study, showing progressively later run timing for stocks lower in the basin. Median run timing for Upper Yukon, Yukon Flats, and Tanana fish was prior to 20 June compared to early July for Lower Yukon stocks (Figure 7). Run timing for Middle Yukon fish was generally later than upper basin stocks, particularly during 2002.

In addition to regional patterns, differences in run timing were also observed for individual stocks. Stocks returning to lower reaches of the Upper Yukon, such as the Klondike and Stewart rivers, were primarily early run fish, whereas those traveling to tributaries farther upriver (e.g., Teslin River fish) exhibited later and more protracted run timing (Figure 8). Fish remaining in middle and upper reaches of the main stem also exhibited this pattern, passing Russian Mission from early June to mid-July. Headwater stocks were also primarily middle and late run fish, although the run timing of these fish was more compressed than Teslin River and main stem fish. Run timing for Upper Porcupine fish was generally early in the run and relatively compressed.

The principal stocks returning to the Yukon Flats (Chandalar and Sheenjek rivers) were predominantly middle run fish, although both displayed protracted run timing with fish present from early June to mid July (Figure 9). The three dominant Tanana stocks (Chena, Salcha, and Goodpaster rivers) exhibited a similar pattern with most fish passing Russian Mission from middle to late June, although fish from these stocks were also prevalent in early June and present during July. Kantishna River fish, in addition to being less abundant, had later and more compressed run timing. Middle and Lower Yukon stocks displayed a progressive shift in run timing, with stocks traveling farther upriver typically passing Russian Mission earlier in the run. The timing of Middle Yukon stocks ranged from middle June for fish returning to the Tozitna River (786 km upriver from Russian Mission) to middle June-early July for fish returning to the Nulato River (453 km upriver from Russian Mission). Most Lower Yukon stocks (e.g., Anvik River fish and Bonasila River fish) passed Russian Mission later in the run.

Although some stocks exhibited relatively compressed run timing, most were passing through the lower river over an extended period. The time taken by stocks to move past Russian Mission averaged 28 d, ranging from 16 d (Klondike River fish) to 38 days (Teslin River fish), with some stocks present throughout the run (Figure 10). The timing patterns exhibited by individual stocks were relatively consistent during the three years of the study. Annual differences in lower river passage were typically less than five days for most stocks using the 50th percentile as a relative measure of timing (Figure 10). Small sample sizes for some stocks, such as Tozitna River fish in 2002, resulted in imprecise timing estimates and hampered assessment efforts.

In general, run timing was progressively earlier for stocks traveling farther upriver. Stocks returning to spawning tributaries closest to Russian Mission (e.g., Bonasila and Anvik rivers approximately 160 km and 180 km upriver, respectively) exhibited the latest timing, with 50% of the fish passing through the lower river by early July (Figure 11). Whereas 50% of the Klondike River fish (which traveled in excess of 1800 km to reach their terminal tributary) passed Russian Mission prior to mid-June. However, stock timing was comparable for many stocks throughout the middle and upper basin, particularly during 2003 and 2004, even though the distances traveled ranged from 700 km to 2300 km. Contrary to the general pattern, fish traveling to the Teslin River and Upper Yukon headwaters (distances in excess of 2400 km from Russian Mission) displayed later run timing than other Upper Yukon stocks, with median run timing of 23-28 June and 12-18 June, respectively (Figure 10). The distances used in these comparisons were minimum estimates, reflecting the distance fish traveled from Russian Mission to the mouth of their terminal tributary. Fish returning to the large, Upper Yukon tributaries (i.e., Stewart, White, Pelly, and Teslin rivers) typically traveled substantially farther after arriving at the river mouth compared to the medium and small rivers typical of spawning tributaries in other regional areas, suggesting an even weaker association between lower river passage and distance traveled by Upper Yukon stocks.

Discussion

Information on stock composition and timing, used in conjunction with estimates of run abundance, is essential for understanding and managing salmon returns in large river basins. This is particularly true in drainages with widely scattered fisheries and varying harvest regimes that can have differential impact on individual stocks and over time affect the overall stock structure of the return. During this study, the composition of Chinook salmon returns varied substantially among regional areas and specific stocks. The runs were consistently dominated by Tanana and Upper Yukon stocks, comprising over 70% of the return annually. Substantially fewer fish traveled to other regional areas, ranging from less than 2% (Upper Koyukuk) to approximately 9% (Yukon Flats) of the return. Collectively the contribution of these smaller stock groups was substantial, and management focusing only on the most prominent components could potentially jeopardize a significant proportion of the return.

Regional components of the returns typically consisted of several dominant stocks, but also included a number of small, isolated populations. Upper Yukon returns were dominated by stocks returning to several prominent tributaries (i.e., Stewart, Pelly, Big Salmon, and Teslin) representing 60-63% of the local return, with the remainder traveling to other tributaries and main stem reaches. This pattern was even more evident in the other areas. Fish returning to the Chena, Salcha, and Goodpaster rivers were the predominant Tanana stocks, comprising 80-90% of the local return. Most fish returning to the Yukon Flats were destined for the Chandalar and Sheenjek rivers, and similar patterns were observed in the other regions. Compared to the Upper Yukon, minor stocks were less prevalent in the other regions. For example, although numerous rivers flow into the Tanana River, spawning populations were only located in a small number of isolated tributaries, suggesting that suitable spawning conditions were less available within this drainage.

Complex stock structures have been reported for Chinook salmon returns in drainages throughout their range, including rivers in Kamchatka (Vronskiy 1972), Alaska and northwestern Canada (Burger et al. 1985, Pahlke and Etherton 1999, Stuby 2007), and the Washington-California coast (Fulton 1968, Yoshiyama et al. 1998, Brannon et al. 2004). The composition of these returns may be even more complex than reported, because stock structure is often based on general in-river distribution, which tends to group fish by specific tributaries and may underestimate the underlying diversity. For example, Teslin River fish in the Upper Yukon exhibited spatial and temporal differences in distribution associated with geomorphic features within the Teslin River (Chapter 2) and potentially represent multiple stocks. Based on a finer scale, Chinook salmon have been reported in over 110 spawning streams in just the Canadian section of the Upper Yukon (von Finster 2006). Keefer et al. (2004) noted that Chinook salmon returns to major tributaries in the Columbia River were often considered single stocks even though other criteria suggested that more than one discrete spawning population was present.

The stability of stock structure over time can have a major effect on how harvest regimes impact salmon returns and the effectiveness of conservation efforts. During our study, regional and stock composition estimates were remarkably similar across years, with substantial differences observed for only a few stocks. Conversely, abundance estimates during the same period indicated substantial variation in the magnitude of the run among years, with estimates of large Chinook salmon (length > 655 mm MEFT) for each of the three years respectively, approximating 125 K, 262 K, and 230 K fish based on mark-recapture experiments (Spencer et al. 2009) and 93 K, 245 K, and 110 K fish based on lower river sonar counts at Pilot Station, located 197 km upriver from the river mouth (JTC 2006). In spite of the sizable differences (particularly in 2004), both methods indicated a substantial increase in run abundance during 2003. Other assessment projects in localized areas also reflected this trend (JTC 2006, Hayes et al. 2008). Combined with the stock composition estimates from our study, these findings suggest that the annual shifts in run abundance during 2002-2004 were not based on regional differences in abundance, but were reflected by most regional and stock-specific components of the return. Subsequent stock composition studies would be useful in determining the consistency of this pattern.

In spite of the distances traveled by the fish (ranging from several hundred kilometers to over 3000 km upriver from the Russian Mission tagging area), run timing exhibited by Yukon River Chinook salmon was relatively compressed, with fish passing through the lower river during a 5-6 week period in late spring and early summer. Other rivers in western Alaska exhibit similar patterns, with run timing becoming progressively more protracted in drainages farther south along the western coast of North America (Burger et al 1985, Department of Fisheries and Oceans 1999, Pahlke and Etherton 1999, Savereide 2005, Stuby 2007). Chinook runs are also more protracted in the Kamchatka River in the Russian Far East (Vronskiy 1972). Chinook salmon returns to rivers in the southern portion of their range in North American extend throughout most of the year, with fish classified into distinct spring-summer and fall runs (Fulton 1968, Healy 1991, Myers et al. 1998, Yoshiyama et al. 1998). Winter runs of Chinook salmon also occur in the Sacramento River, with fish essentially passing through the lower river year round (Yoshiyama et al. 1998). The spring-summer components of these southern rivers, which are analogous in many ways to returns in Alaska and northwestern Canada, typically exhibit more protracted run timing than observed during our study. In the Columbia

River, spring-summer Chinook salmon passed through the lower river at Bonneville Dam over a 16-17 week period from early April through July (Keefer et al. 2004).

Chinook salmon traveling greater distances during the freshwater phase of their spawning migration are generally thought to enter natal rivers earlier in the run than lower river stocks, and management is often based on these temporal differences (Fulton et al. 1985, Myers et al. 1998, Yoshiyama et al. 1998). However, in spite of the extreme disparity in distances traveled (ranging from several hundred to over 3000 km), most Yukon River stocks were temporally similar. Tanana and Upper Yukon fish, the largest components of the return, exhibited similar peaks in abundance and substantial overlap in run timing. Timing differences were most distinct between stocks destined for lower reaches of the Upper Yukon (early run) and Lower Yukon tributaries (late run), but even these stocks exhibited overlap. The presumed timing pattern (i.e., late run fish traveling shorter distances) was further contradicted by the timing of Upper Yukon fish traveling to headwater tributaries and upper mainstem areas, which traveled substantially farther than other stocks but exhibited extended run timing with fish passing through the lower river late in the return. Run timing patterns exhibited by the stocks presumably reflect adaptive behaviors that enhance spawning success in relation to the environmental conditions encountered. Although supportive evidence is not available for the Yukon River basin, the relatively compressed run timing exhibited by the fish indicate a narrow biological window in relation to the factors affecting the upriver migration, site selection, and spawning activities.

Compared to rivers with more protracted returns, the short duration of the Yukon River run, combined with temporal similarities and extensive overlap in lower river passage, limits the usefulness of stock timing information for managing in-river fisheries. Marine and atmospheric conditions occasionally delay river entry by Yukon River Chinook salmon (Mundy and Evenson 2011), which further compresses or shifts the overall run timing, and may further complicate management by increasing the overlap in the timing of regional and stock-specific components of the return. Timing differences could potentially be used to manage the harvest of lower basin fish based on the later timing of these stocks. However, the magnitude of this component of the run is substantially less, and upper basin fish are still passing through the lower river during this period (albeit at lower levels) limiting the utility of this approach. In addition, local fishers generally prefer to fish Chinook salmon earlier in the run due to reduced flesh quality as the run progresses, and to ensure that adequate numbers of fish are harvested to meet their needs.

Validity of Stock Composition Estimates

As with other tagging studies, an inherent limitation with telemetry data is that it most directly reflects the movements and behavior of individuals within the tagged sample. Although sufficient for some research objectives, this information can be misleading when indiscriminately expanded to describe a larger population. The approach used during this study to estimate stock composition was designed to address bias related to temporal changes in abundance at the tagging site and to account for the disproportional harvest of tagged fish traveling farther upriver. Although generally similar, differences were observed between the regional distribution of the radio-tagged fish (Chapter 2) and the stock composition estimates derived from these data (Figure 12). The greatest disparity was observed for Upper Yukon fish, with differences between the two methods ranging from 3.7% in 2003 to 8.0% in 2002. Differences were greater (9.3 to 13.1%) when fish remaining in non-terminal reaches were treated as in-transit to areas farther upriver. Upper Yukon stocks traveled farther and were subjected to heavier fishing pressure over the course of the migration than fish returning to other regional areas, disproportionally increasing the number of tagged fish harvested and biasing stock composition estimate. Conversely, Tanana fish traveled shorter distances, were subjected to less fishing pressure, and showed negligible differences between the sample proportions and the stock composition estimates (Figure 12). Similarly, Lower Yukon fish were exposed to substantially less fishing pressure, and sample percentages were somewhat higher than the stock composition estimates, particularly during 2002.

Tagging studies on migrating salmon often attempt to deploy tags in proportion to run abundance, relying on historical records or run timing estimates from assessment projects farther downriver. However, annual variation in timing and problems associated with the accuracy of in-season indices can frustrate these efforts. During our study, a general attempt was made to tag fish proportionally, but discrepancies periodically occurred. For example, a disproportional number of fish were tagged late in the run during 2002 (Figure 3), which tended to underestimate upper basin stocks with earlier run timing and inflate estimates of later run stocks. Lower Yukon fish, which were more prevalent later in the run, comprised 13% of the tagged sample compared to 6% of the return based on stock composition estimates. Random or selective (e.g., tagging every third fish captured) sampling has been used to account for temporal differences, alleviating some of these limitations (Johnson et al. 1992, Savereide 2005). However, this approach may be ineffectual when changing river conditions alter fishing efficiency, or impractical when there are problems capturing adequate numbers of fish. The method used during our study did not depend on proportional tagging, eliminated the need to sub-sample the fish captured, and addressed the problems associated with disproportional harvests of tagged individuals during their upriver migration.

Capture and tagging efforts during this study were sufficient to obtain fairly inclusive samples of the component stocks. In addition to the major segments of the return, minor stocks scattered throughout the basin were consistently represented (e.g., from fish returning to the Innoko River in the Lower Yukon to Tatchun Creek in the Upper Yukon). The population size of some of these stocks was relatively small. Fish returning to Beaver Creek in the Yukon Flats were identified as a component stock during all three years of the study. Less than 200 Chinook salmon were counted at an enumeration weir on this tributary during 1999-2000 (Collin et al. 2002). Stocks known to be major components of the return, based on other assessment projects within the basin, were also well represented by the telemetry-based estimates. For example, Chinook salmon returning to the Chena and Salcha rivers reportedly have some of the largest escapements within the U.S. portion of the basin (Schultz et al. 1994), a finding similar to our results.

Stock composition estimates were based on the premise that fish in designated stock groups represented local spawning populations. Fidelity to natal rivers was strong during the study (Chapter 4), and fish that traveled to terminal tributaries were assumed to have reached their final destination. The status of fish in non-terminal reaches was less certain, potentially representing individuals that died while in-transit to upriver areas or fish spawning locally. Stock composition estimates that included in-transit fish would underestimate the contribution of stocks traveling farther upriver, whereas estimates that excluded all non-terminal fish would potentially overestimate upriver stocks. Although definitive information on the status of non-terminal fish was not available, an analysis of the distribution and final location of these individuals suggests that non-terminal reaches likely included both in-transit and spawning fish (Chapter 2). Separate composition estimates based on both extremes (i.e., all non-terminal fish spawning locally vs. all non-terminal fish in-transit), were reasonably similar, suggesting minimal bias related to the treatment of non-terminal fish. The actual stock composition for the basin is likely between these two estimates.

The accuracy of stock composition estimates is of particular interest in the Yukon River basin, since information on country of origin is needed to implement conservation and allocation efforts between the U.S. and Canada. Upper Yukon fish were used to represent the Canadian contribution, since most (99%) were destined for Canadian reaches of the basin. In general, our country of origin estimates were consistent with other estimates reported for the basin. Scale pattern analysis from the early 1980s suggested that Canadian-origin fish in the Upper Yukon comprised between 42% and 54% of the return (Anon 1985). Based on catch and escapement information in the early 1980s, Milligan et al. (1985) estimated that approximately 50% of the return was made up of Canadian stocks, ranging from 44% to 51% in years with low returns and 48% to 57% in years of greater abundance. GSI estimates of the Canadian contribution from 1987 to 1990 averaged 53% of the return, ranging from 42% to 61% (Wilmot et al.

1992). Not all stocks were included in the GSI baseline used for this analysis, most notably fish returning to the Yukon Flats, which undoubtedly biased these estimates to some extent. Additional sampling, based on the telemetry information, was subsequently conducted in the basin to enhance the GSI baseline (Templin et al. 2006, Flannery et al. 2012). Based on the updated baseline, seasonal composition trends determined from mixed-stock fisheries in the lower Yukon River during 1987-1990 and 2002-2003 (Templin et al. 2005) were similar to those observed during our study. Conversely, lower contribution estimates have been proposed based on GSI sampling in the lower Yukon River during 2005-2011, with Canadian contribution averaging around 40% of the return (T. Hamazaki, fishery statistician, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication).

Sampling methods may partially explain some of the differences in the country of origin estimates reported. Because of size selectivity associated with larger mesh gill nets (Fujimori and Tokai 2001, Fukuwaka et al. 2008), we assume that the length frequency of our tagged sample was not representative of the entire run. Smaller fish (i.e., 3-year-olds and 4-years-olds) were likely underrepresented and the composition estimates more reflective of the older aged fish. Younger age classes made up 4.4% of the tagged sample during the three years of the study (Chapter 2). Definitive information on stock-specific length frequency is not readily available for Chinook salmon returns in the Yukon River basin, due to the variety of methods used to collect these data and the inherent logistical constraints, although it is generally believed that average fish size is less in lower basin stocks. If true, this would suggest that our estimates for lower basin fish were biased low. However, 3-year-old and 4-years-old fish are generally considered minor run components, with some estimates as low as 4-5% of the return (Beacham et al 1989, Hayes et al. 2008), although higher percentages are periodically reported (as described by Spencer et al. 2009), which would suggest that sampling bias associated with fish size had minimal effect on our composition estimates.

There was general agreement between our stock composition and timing estimates and other stock assessment projects within the basin. Large numbers of Chinook salmon are visually counted from counting towers on the Chena and Salcha rivers (Schultz et al. 1994). Although these counts are considered minimum estimates due to periodically high water and poor viewing conditions (Doxey et al. 2005), general timing patterns observed for radio-tagged fish (based on station records) and untagged fish (based on the visual counts) were similar. There was also general agreement between our composition estimates for Upper Yukon stocks and those based on GSI sampling at fish wheels near the U.S.-Canada border during 2005-2007 (P. A. Milligan, fishery biologist, Department of Fisheries and Oceans Canada, Whitehorse, Yukon Territory, unpublished data). Our estimates for Stewart River fish ranged from 8-14% of the Canadian return (4-7% of the entire return) compared to GSI estimates of 9-15%.

Similar patterns were observed for the other major stocks, including the Pelly River (18-20% vs. 13-21%), Big Salmon River (10-15% vs. 10-11%), and Teslin River (19-20% vs. 10-19%). Smaller stocks showed less agreement. Estimates for the Klondike River (3-5% vs. 1-4%) and Nordenskiold River (1-2% vs. <1%) were comparable, whereas the White River (3-8% vs. 1-2%) and Chandindu River (2-4% vs. 7-12%) were more disparate. GSI estimates for the Chandindu River were substantially higher than what is credible, likely due to sampling bias related to the proximity of this river to the fish wheel site and associated bank orientation of the fish (P. A. Milligan, fishery biologist, Department of Fisheries and Oceans Canada, Whitehorse, Yukon Territory, personal communication).

Minimal information is available on the abundance and timing of Chinook salmon stocks in the Lower Yukon, with most assessment efforts upriver of Russian Mission limited to carcass sampling and periodic aerial surveys in the Anvik River (Sandone 1994, Templin 2006). Although not particularly instructive, the spawning distribution of radio-tagged fish in the Anvik River (Chapter 2) conformed to local information for this tributary. The general pattern of agreement between our study and other fundamentally different assessment methods used within the basin (e.g., genetics, index surveys in spawning areas), particularly for the larger stock groups, suggests that the telemetry-based stock composition and timing estimate provide a plausible approximation of the return.

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Table 1.— Tagging dates and numbers of fish capture, tagged, tracked upriver, and not located upriver after release for Chinook salmon radio tagged in the lower Yukon River during 2002-2004. Percentages of the total fish tagged are in parentheses.

	2002	2003	2004	All years
Start of tagging	9 June	3 June	3 June	3-9 June
End of tagging	13 July	14 July	19 July	13-19 July
Captured	1,310	2,312	2,107	5,729
Tagged	768	1,097	995	2,860
Moved upriver	751 (97.8)	1,081 (98.5)	958 (96.3)	2,790 (97.6)
Upriver location[1]	481 (62.6)	810 (73.8)	625 (62.8)	1,917 (67.0)
Harvested in fishery	270 (35.2)	271 (24.7)	333 (33.4)	874 (30.6)
Not located upriver	17 (2.2)	16 (1.5)	37 (3.7)	70 (2.4)

[1] Fish located upriver from Paimiut tracking stations.

Table 2.— Numbers of radio-tagged Chinook salmon harvested in regional fisheries in the Yukon River basin during 2002-2004. Percentages of the total are in parentheses.

Fishery	2002	2003	2004	All Years
Combined (U.S.)	235 (87.0)	226 (83.4)	276 (82.9)	737 (84.3)
Yukon River main stem	222 (82.2)	196 (72.3)	241 (72.4)	659 (75.4)
Lower Yukon	81 (30.0)	38 (14.0)	64 (19.2)	183 (20.9)
Middle Yukon	55 (20.4)	45 (16.6)	69 (20.7)	169 (19.3)
Yukon Flats	77 (28.5)	106 (39.1)	99 (29.7)	282 (32.3)
Upper Yukon[1]	9 (3.3)	7 (2.6)	9 (2.7)	25 (2.9)
Koyukuk River	1 (0.4)	4 (1.5)	3 (0.9)	8 (0.9)
Tanana River	12 (4.4)	25 (9.2)	32 (9.6)	69 (7.9)
Porcupine River		1 (0.4)		1 (0.1)
Combined (Canada)	35 (13.0)	45 (16.6)	57 (17.1)	137 (15.7)
Yukon River main stem	24 (8.9)	21 (7.7)	37 (11.1)	82 (9.4)
Border to Dawson	15 (5.6)	14 (5.2)	25 (7.5)	54 (6.2)
Upriver of Dawson	9 (3.3)	7 (2.6)	12 (3.6)	28 (3.2)
Yukon River tributaries[2]	10 (3.7)	21 (7.7)	17 (5.1)	48 (5.5)
Porcupine River	1 (0.4)	3 (1.1)	3 (0.9)	7 (0.8)
Total	270	271	333	874

[1] Near Eagle, AK downriver from U.S.-Canada border; fish comprised of Canadian stocks.

[2] Principally the Stewart, Pelly, and Teslin rivers.

Table 3.— Stock composition estimates of Chinook salmon returns in 2002-2004 based on the distribution of radio-tagged fish weighted by catch per unit effort information at the tagging site and adjusted for the harvests of tagged individuals in upriver fisheries. Percentage of the return and 95% confidence intervals (in parentheses) are indicated.

Region	Stock	2002	2003	2004
Lower Yukon	Innoko	0.7 (0.1, 1.4)	0.2 (0.0, 0.5)	0.5 (0.1, 1.0)
	Bonasila	0.9 (0.4, 1.5)	0.4 (0.1, 0.8)	1.5 (0.7, 2.3)
	Anvik	3.0 (2.0, 4.1)	2.6 (1.8, 3.5)	4.1 (2.9, 5.6)
	Yukon River[1]	2.9 (1.5, 4.5)	4.4 (3.2, 5.7)	5.7 (4.1, 7.4)
Middle Yukon	Nulato	1.9 (1.0, 2.8)	1.3 (0.7, 2.0)	1.7 (0.7, 2.8)
	Gisasa	0.3 (0.1, 0.6)	1.0 (0.4, 1.6)	0.8 (0.3, 1.4)
	Lower Koyukuk[1]	0.1 (0.0, 0.3)		0.7 (0.2, 1.3)
	Melozitna	0.1 (0.0, 0.5)	0.1 (0.0, 0.3)	0.3 (0.0, 0.7)
	Nowitna	0.2 (0.0, 0.8)	0.2 (0.0, 0.5)	0.4 (0.0, 1.0)
	Tozitna	1.2 (0.4, 2.3)	1.1 (0.4, 1.8)	1.0 (0.4, 1.8)
	Yukon River[1]	0.8 (0.3, 1.4)	0.8 (0.3, 1.5)	1.5 (0.7, 2.3)
Upper Koyukuk	Upper tributaries[2]	1.1 (0.2, 2.2)	1.9 (1.0, 2.8)	1.7 (0.9, 2.7)
Tanana	Main river (lower)[1]	0.2 (0.0, 0.6)	0.2 (0.0, 0.5)	0.9 (0.3, 1.7)
	Kantishna	1.1 (0.4, 2.0)	1.4 (0.8, 2.2)	1.2 (0.5, 2.0)
	Tolovana	0.4 (0.0, 1.1)	0.5 (0.1, 1.0)	0.6 (0.1, 1.3)
	Main river (middle)[1]	0.3 (0.0, 0.8)	0.7 (0.2, 1.2)	1.3 (0.5, 2.2)
	Chena	5.3 (3.4, 7.5)	4.8 (3.4, 6.2)	4.3 (2.8, 5.9)
	Salcha	10.7 (7.5, 14.2)	6.4 (4.9, 8.0)	10.1 (7.9, 12.4)
	Main river (upper)[1]	0.1 (0.0, 0.4)	1.0 (0.4, 1.6)	2.2 (1.2, 3.5)
	Goodpaster	2.8 (1.5, 4.5)	4.4 (3.0, 5.8)	3.6 (2.4, 5.0)
Yukon Flats	Main stem (lower)[1,3]	0.1 (0.0, 0.4)	2.5 (1.5, 3.6)	2.8 (1.7, 4.2)
	Beaver	0.1 (0.0, 0.4)	0.3 (0.0, 0.8)	0.4 (0.0, 1.0)
	Chandalar	3.4 (1.9, 5.2)	4.0 (2.8, 5.4)	1.7 (0.9, 2.8)
	Sheenjek	2.5 (1.2, 4.2)	2.4 (1.4, 3.4)	1.0 (0.3, 1.9)
	Black	0.4 (0.0, 1.1)	0.2 (0.0, 0.6)	0.1 (0.0, 0.3)

	Main stem (upper)[1,4]	0.3 (0.0, 0.8)	1.2 (0.5, 2.0)	0.4 (0.0, 0.8)
Upper Porcupine	U.S. tributaries	0.6 (0.0, 1.6)		0.8 (0.2, 1.5)
	Upper tributaries[5]	2.7 (1.0, 4.7)	3.9 (2.6, 5.3)	1.3 (0.5, 2.4)
Upper Yukon	Charley	0.3 (0.0, 0.9)	0.4 (0.0, 0.8)	0.2 (0.0, 0.5)
	Kandik-Nation	0.6 (0.0, 2.2)	0.3 (0.0, 0.7)	0.3 (0.0, 0.9)
	Main stem (lower)[1]	1.8 (0.6, 3.4)	0.9 (0.3, 1.6)	0.9 (0.2, 1.8)
	Klondike[5]	1.6 (0.5, 3.2)	2.5 (1.5, 3.7)	2.0 (1.0, 3.1)
	Main stem (middle)[1]	3.8 (2.2, 5.8)	4.3 (3.0, 5.7)	4.8 (3.2, 6.5)
	Stewart[5]	7.2 (4.0, 10.3)	4.2 (2.9, 5.7)	4.7 (3.0, 6.5)
	White[5]	4.0 (0.9, 7.9)	1.6 (0.8, 2.5)	2.2 (1.1, 3.4)
	Pelly[5]	9.2 (6.2, 12.6)	10.0 (8.0, 12.1)	9.4 (7.1, 11.8)
	Tatchun[5]	0.7 (0.1, 1.6)	0.3 (0.0, 0.6)	0.4 (0.0, 1.0)
	Main stem (upper)[1]	4.9 (3.1, 6.9)	4.4 (3.0, 5.8)	5.3 (3.6, 7.1)
	Nordenskiold[5]	0.7 (0.0, 1.9)	1.2 (0.5, 2.1)	0.3 (0.0, 0.8)
	Little Salmon[5]	0.2 (0.0, 0.9)	2.1 (1.2, 3.2)	0.4 (0.0, 0.9)
	Big Salmon[5]	5.2 (2.9, 7.8)	8.1 (6.2, 10.0)	4.7 (3.1, 6.4)
	Teslin[5]	9.9 (5.9, 14.4)	10.4 (8.4, 12.5)	9.2 (7.0, 11.7)
	Headwaters[5]	1.5 (0.6, 2.8)	1.6 (0.8, 2.5)	2.3 (1.2, 3.6)

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[1] Non-terminal mainstem reaches, including small tributaries associated with the main river.

[2] Combined tributaries in upper reaches of the drainage.

[3] From Rapids to Yukon-Porcupine River confluence.

[4] Upriver from Yukon-Porcupine River confluence.

[5] Canadian reaches of the basin.

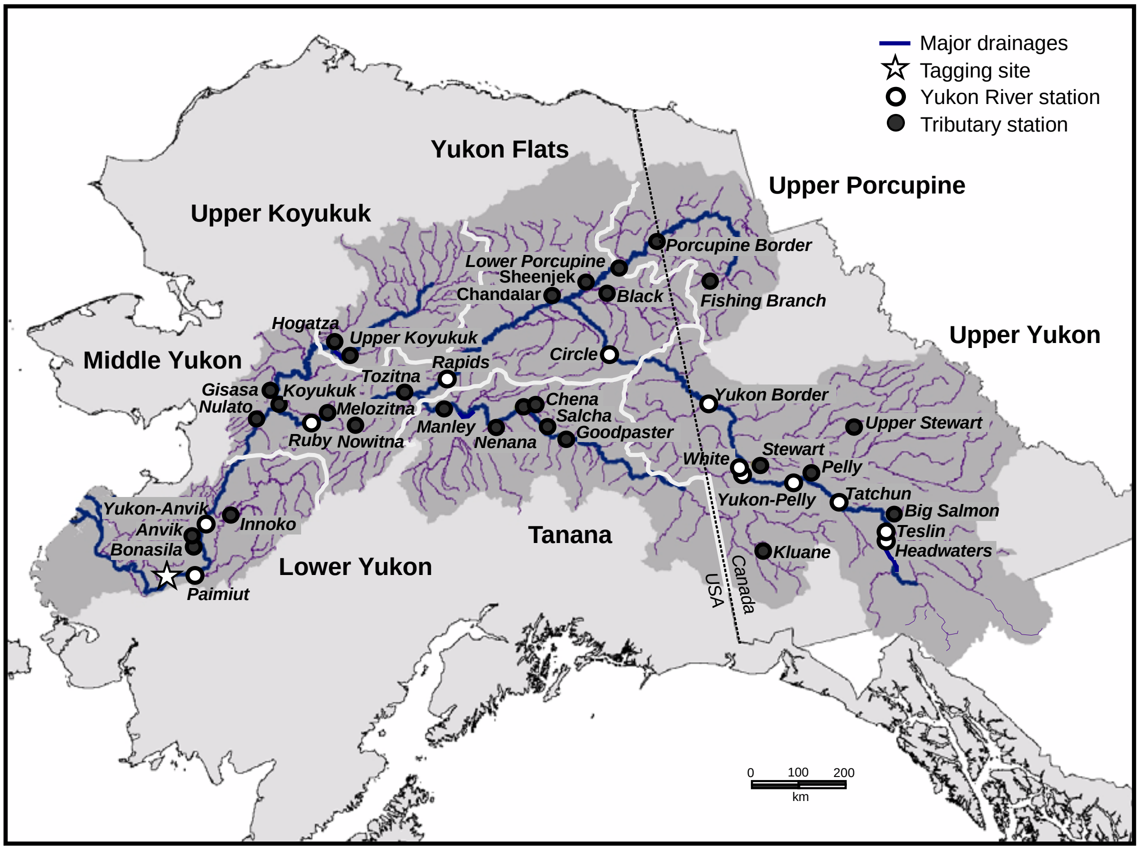

Figure 1.— Map of the Yukon River basin showing the regional areas, major drainages, lower river tagging site near Russian Mission, and tracking stations on both the Yukon River main stem and associated tributaries. Stations at key locations on the migratory route (e.g., confluence of major rivers) and on principal spawning tributaries are indicated.

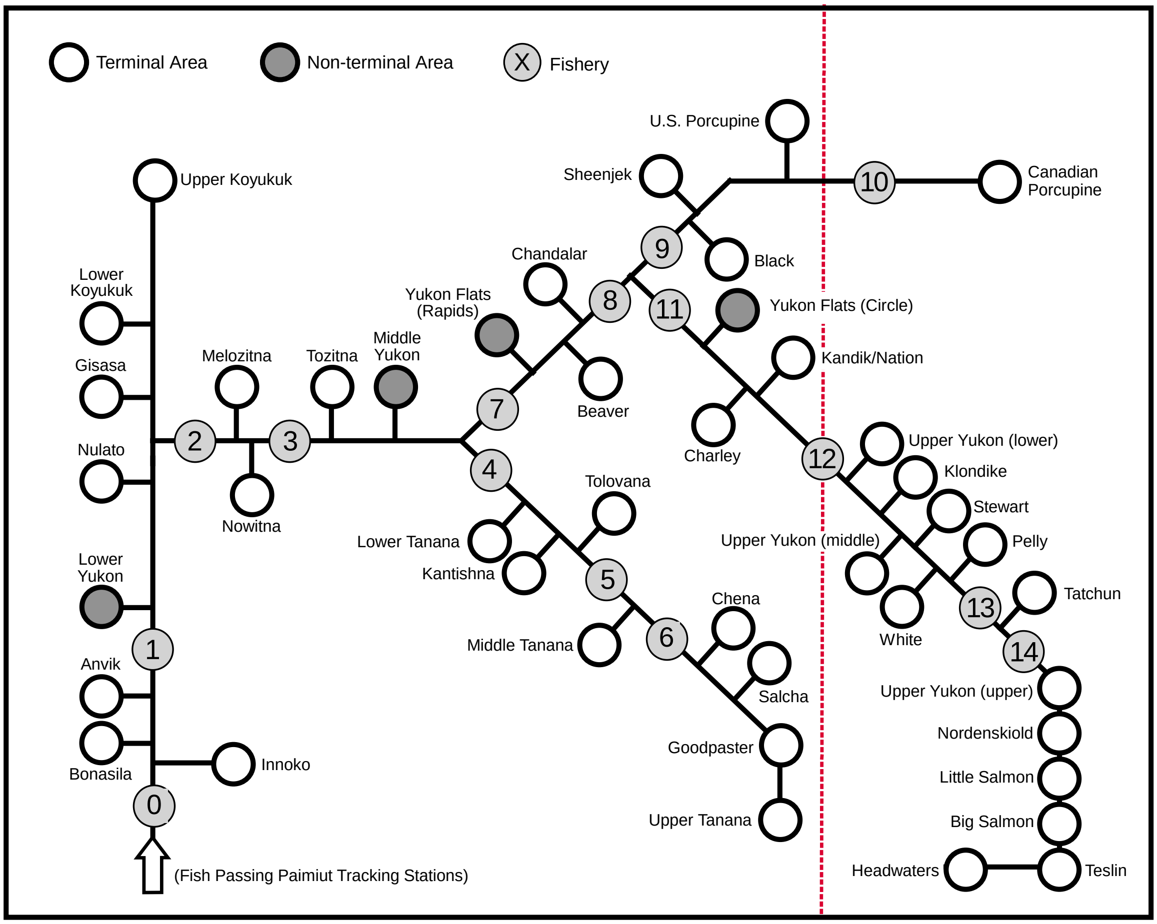

Figure 2.— Migration model for calculating stock composition estimates of Chinook salmon returns in the Yukon River basin based on the distribution of radio-tagged fish, weighted by daily measures of abundance at the tagging site, and adjusted to account for tagged fish removed in upriver fisheries. Spatial relationships of the fisheries and component stocks are indicated.

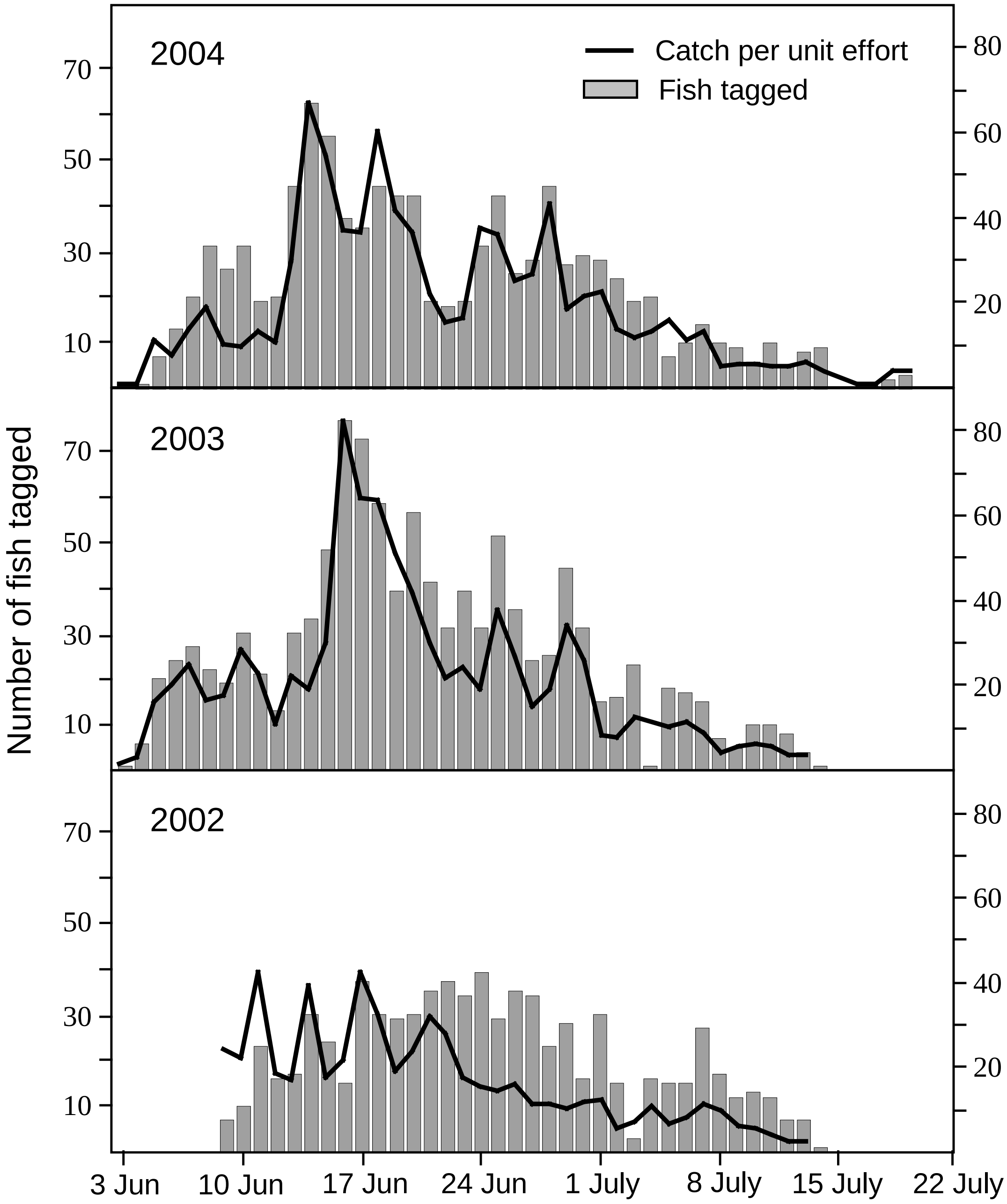

Figure 3.— Number of Chinook salmon radio tagged in the lower Yukon River and daily catch per unit effort information for Chinook salmon captured at the Russian Mission tagging site during 2002-2004.

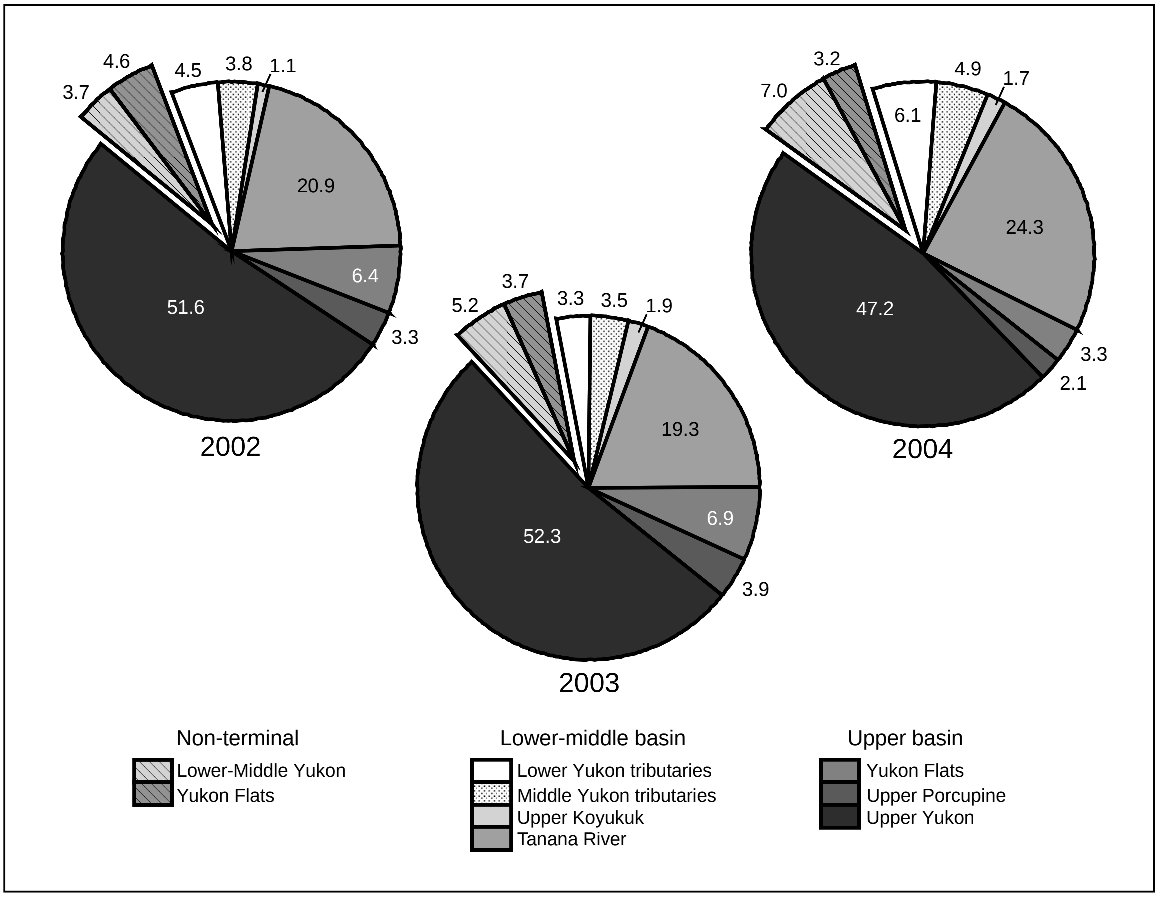

Figure 4.— Regional composition of Yukon River Chinook salmon returns in 2002-2004 based on the distribution of radio-tagged fish weighted by catch per unit effort information at the Russian Mission tagging site and adjusted for the harvest of tagged individuals in upriver fisheries.

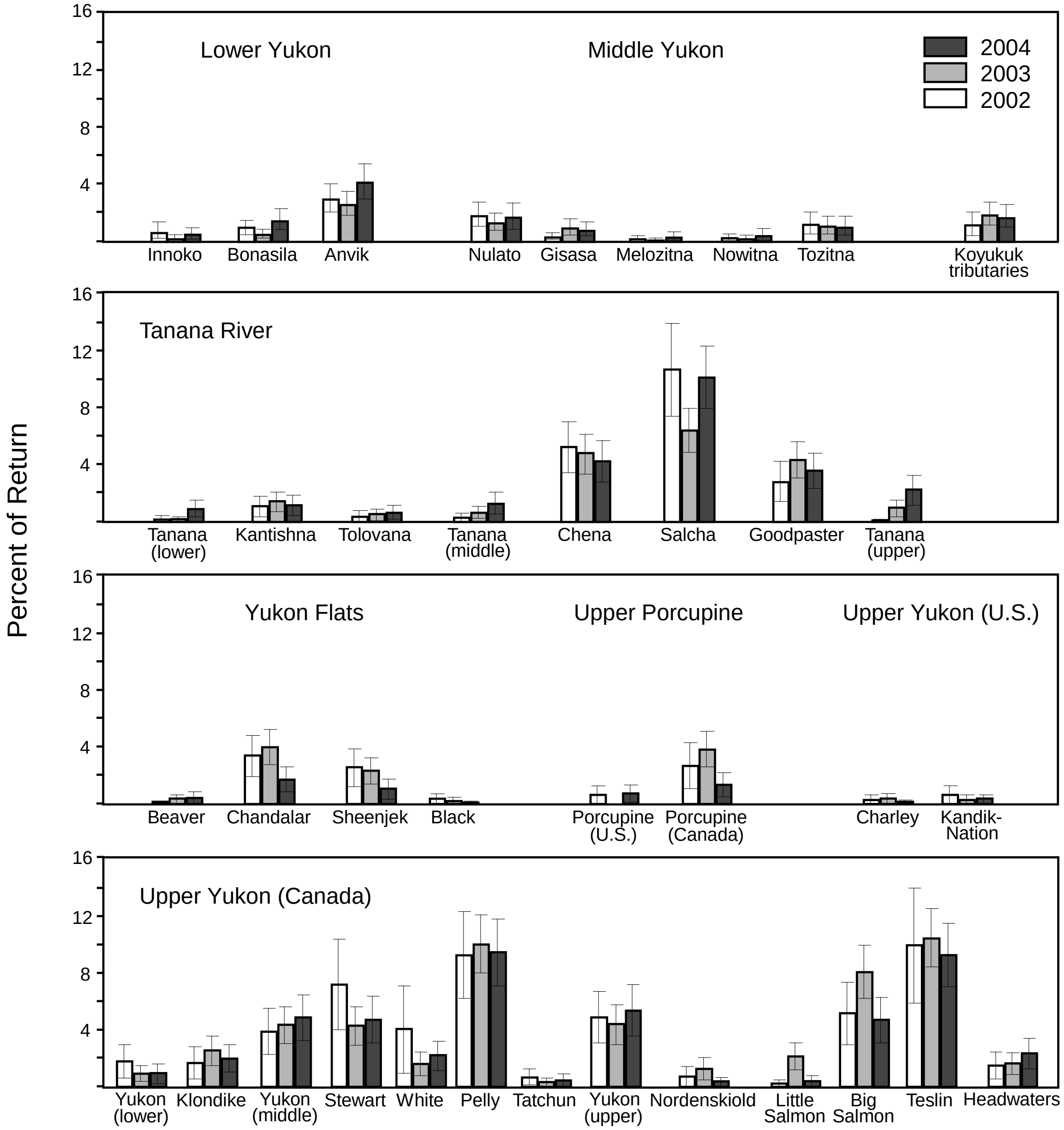

Figure 5. — Stock composition of Chinook salmon returning to terminal reaches of the Yukon River basin in 2002-2004, based on the distribution of radio-tagged fish weighted by catch per unit effort information at the Russian Mission tagging site and adjusted for the harvest of tagged individuals in upriver fisheries. Composition estimates and 95% confidence interval are indicated. Fish returning to small tributaries associated with mainstem areas included in main river estimates.

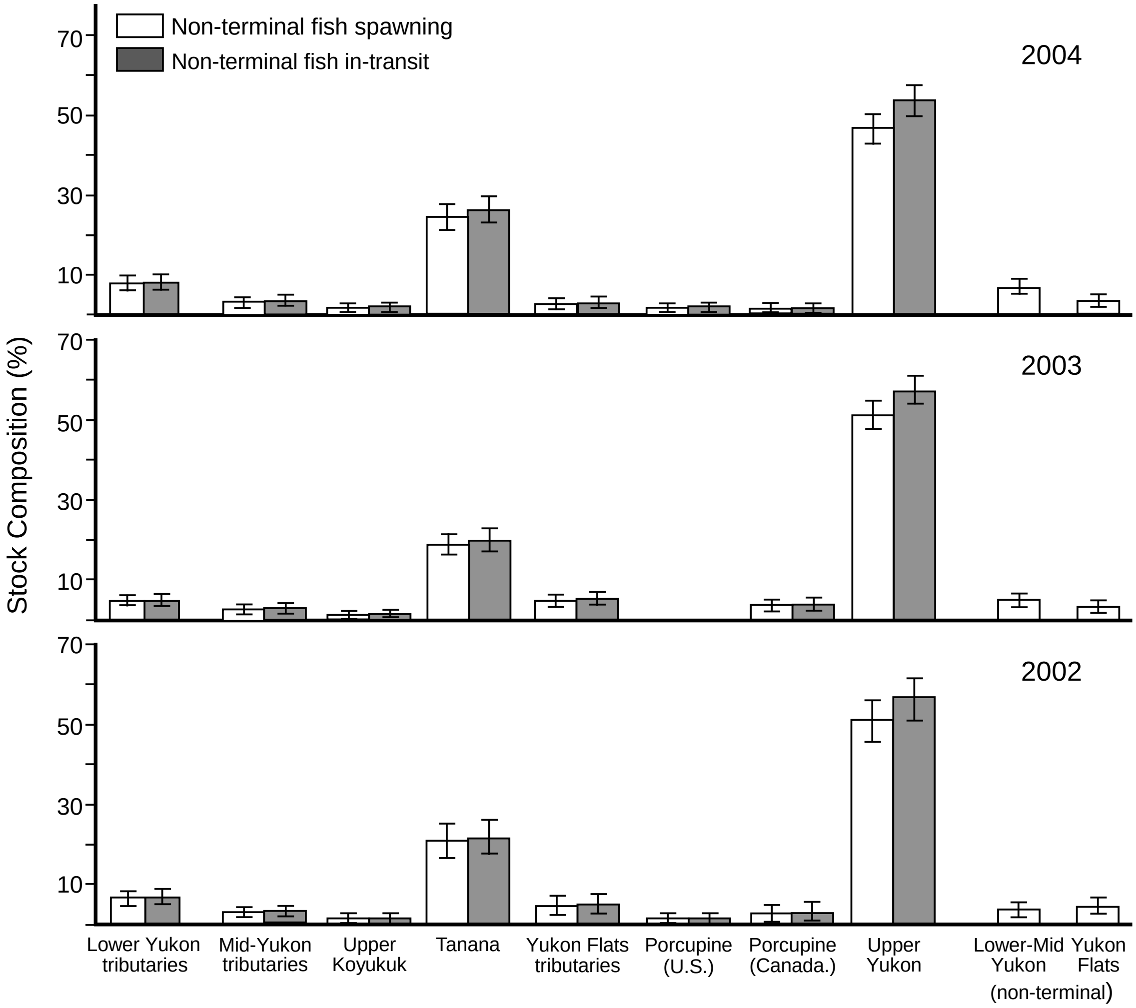

Figure 6.— Comparison of stock composition estimates of Yukon River Chinook salmon returns in 2002-2004 based the presumed status of fish remaining in non-terminal reaches of the U. S. Yukon River main stem (i.e., categorized as fish in-transit to spawning areas farther upriver or fish spawning in local areas). Non-terminal areas include associated mainstem tributaries not monitored during the study. Composition estimates and 95% confidence intervals are provided.

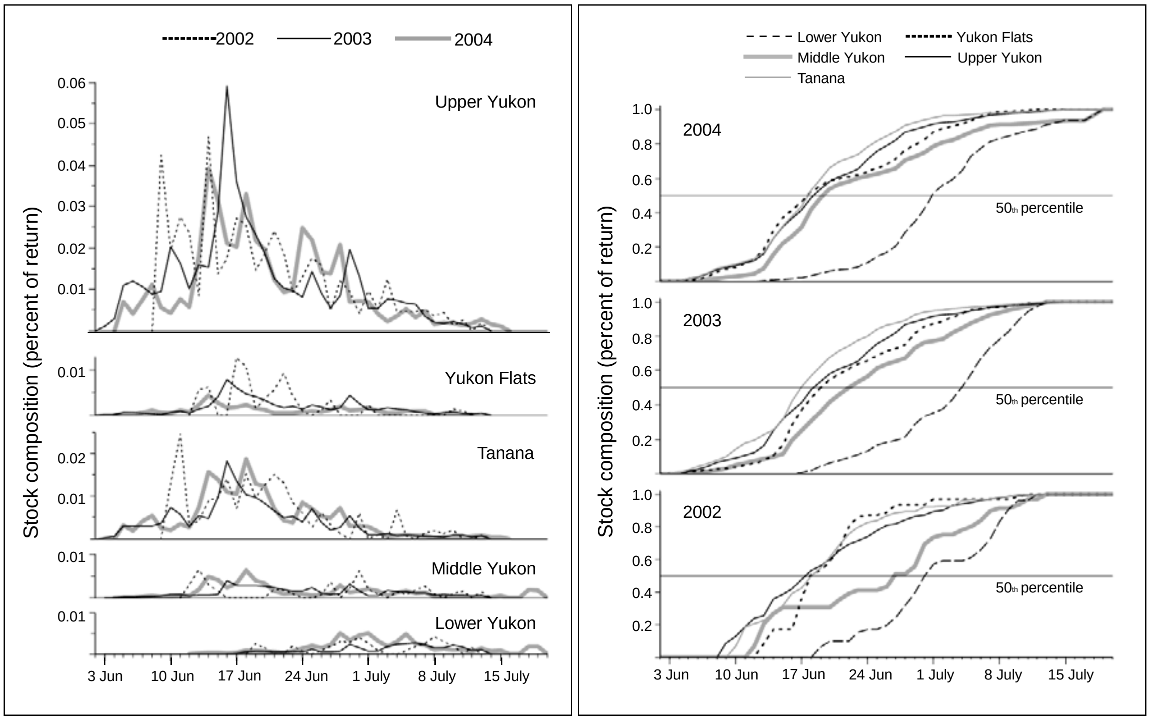

Figure 7.— Lower river run timing of regional aggregates of Chinook salmon returning to terminal reaches of the Yukon River basin in 2002-2004 based on daily stock composition estimates. Daily percentage of the return (left panel) and cumulative percentage of the regional return (right panel) are shown by regional components. The 50th percentile is indicated for the cumulative percentages.

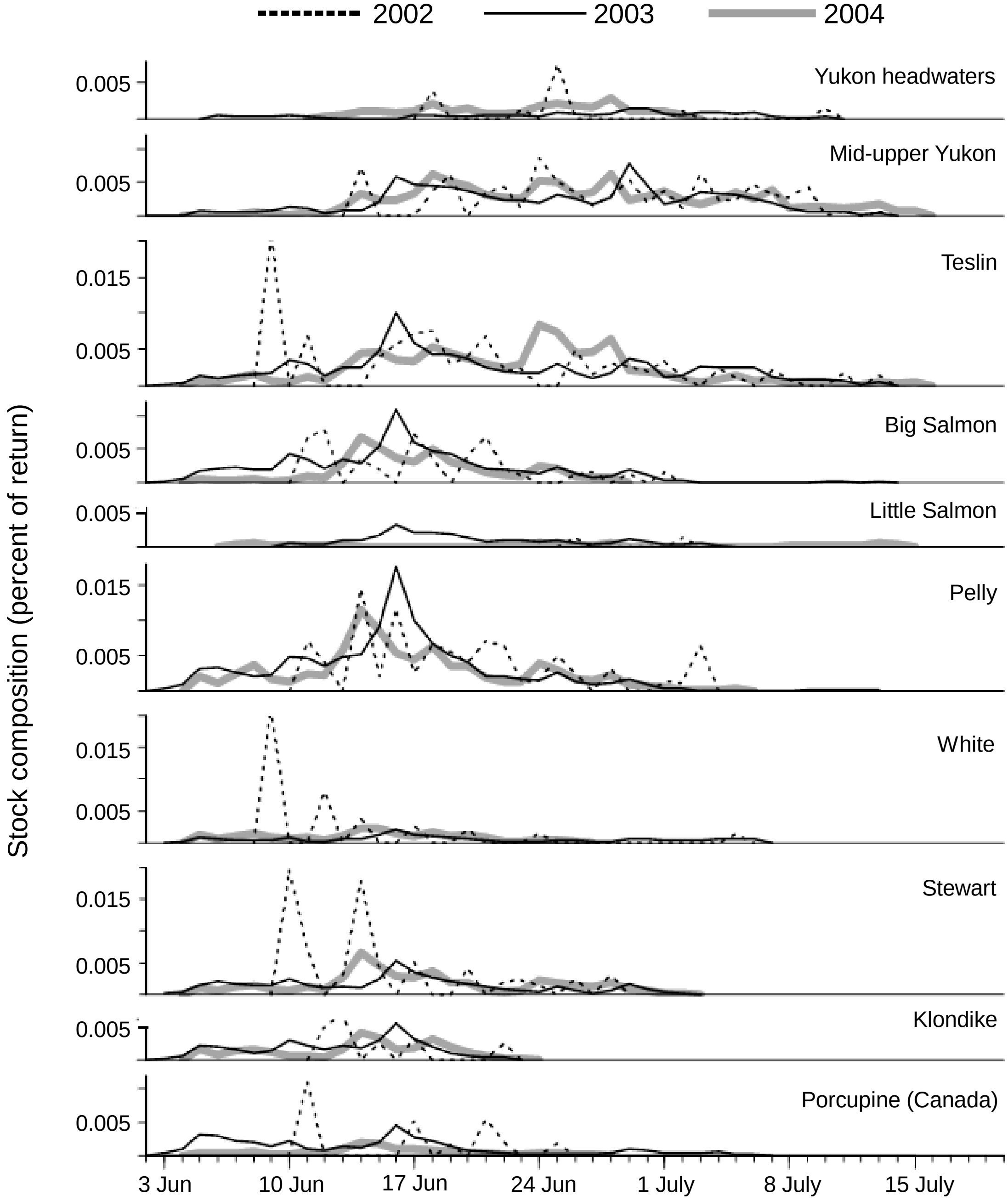

Figure 8.— Lower river run timing of the principal Chinook salmon stocks returning to the Upper Yukon and Upper Porcupine in 2002-2004 based on daily stock composition estimates of the return.

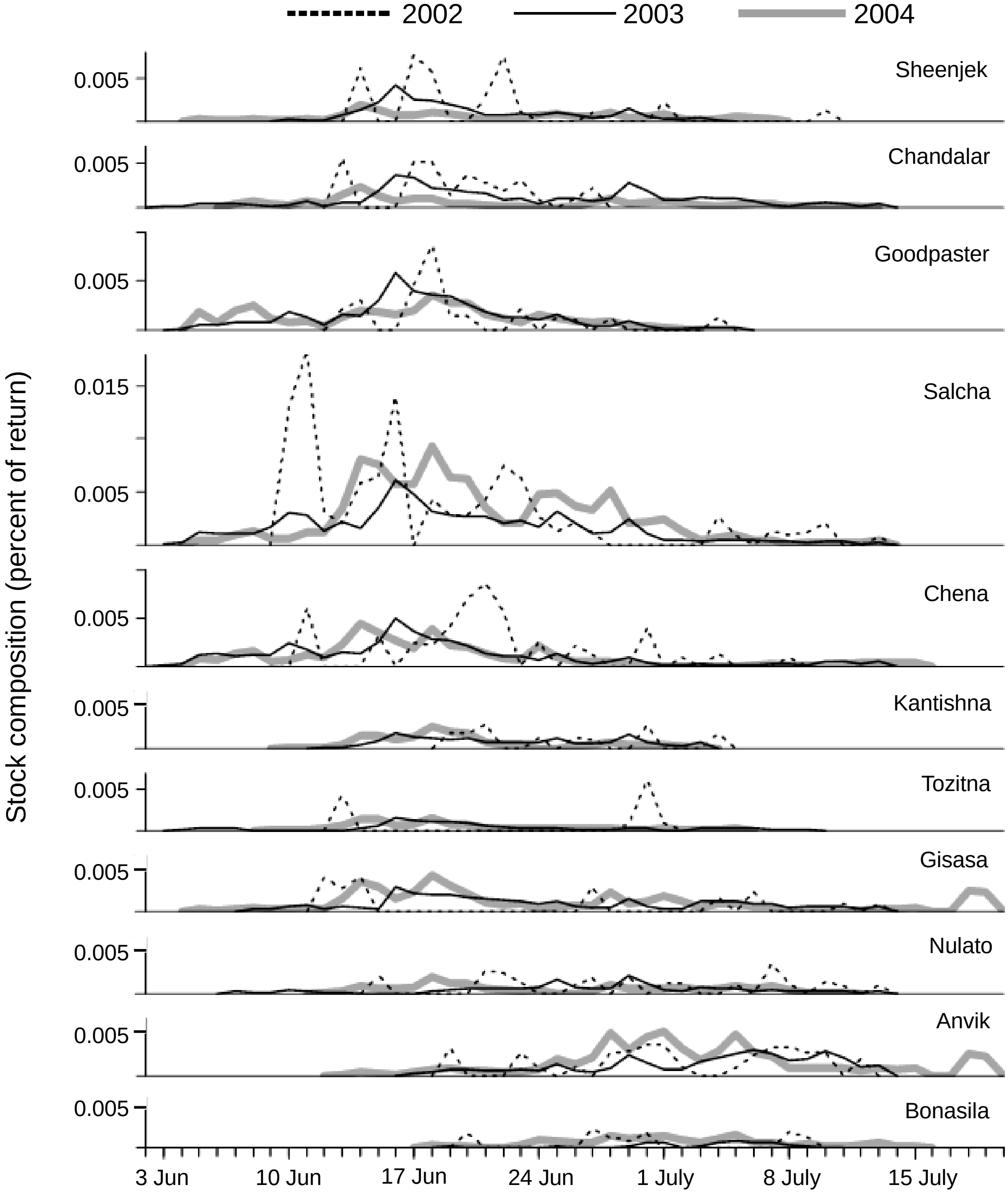

Figure 9.— Lower river run timing of the principal Chinook salmon stocks returning to U.S. reaches of the basin in 2002-2004 based on daily stock composition estimates of the return. Note difference in scale from Figure 8 for percentage of the return.

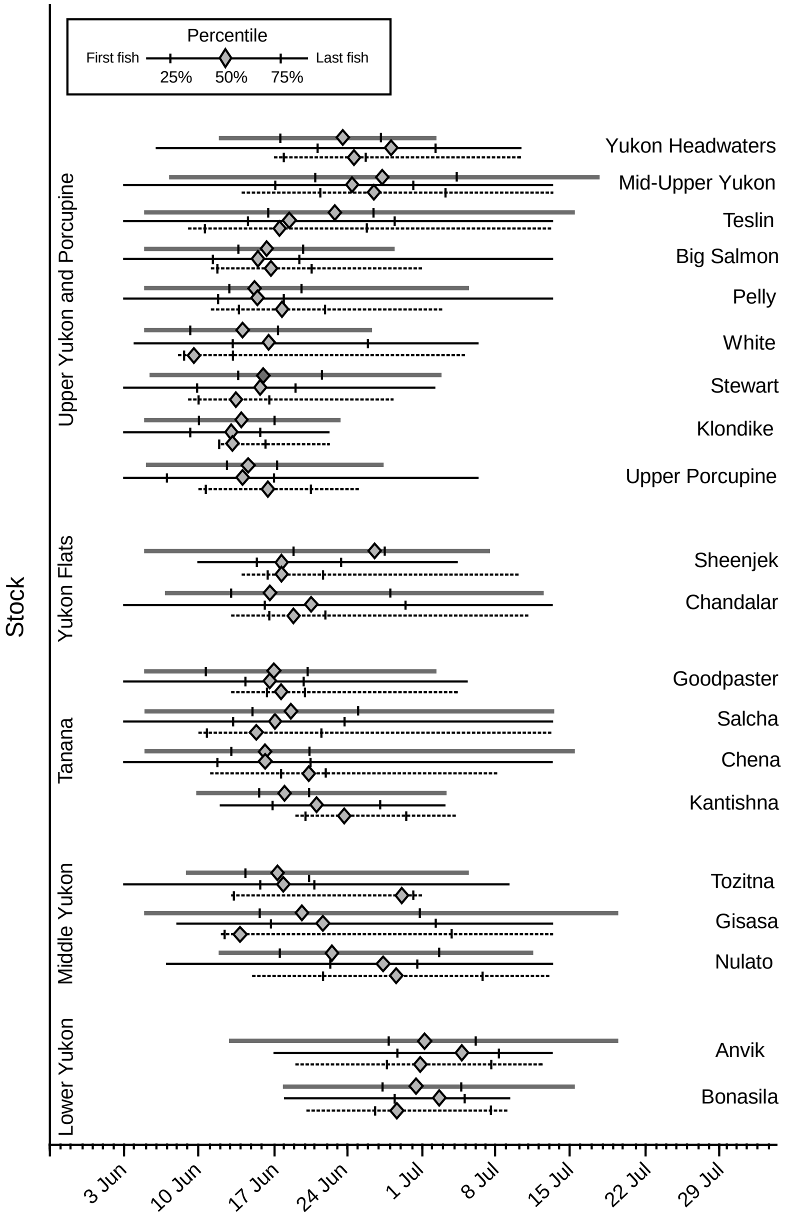

Figure 10.— Lower river run timing of Chinook salmon stocks returning to terminal reaches of the Yukon River basin based on stock composition estimates of the return in 2002 (dotted line), 2003 (solid, thin line), and 2004 (solid, thick line). The presence of the stock (first to last fish) and cumulative percentages (25th, 50th, and 75th percentile) are indicated.

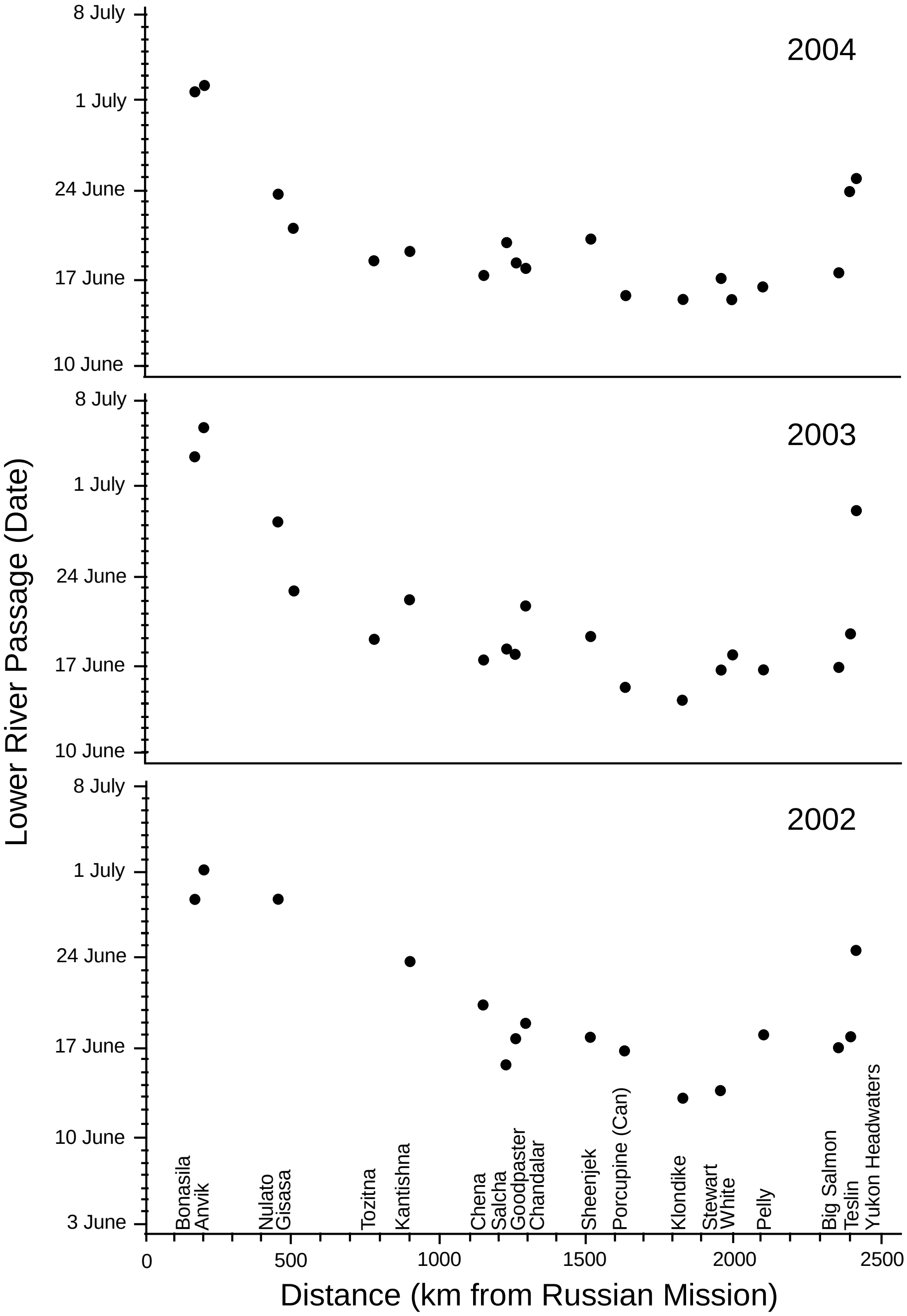

Figure 11.— Comparison of lower river passage of Chinook salmon stocks (based on 50th percentile) returning to the Yukon River basin in 2002-2004 with the distance traveled by the fish to reach their natal rivers.

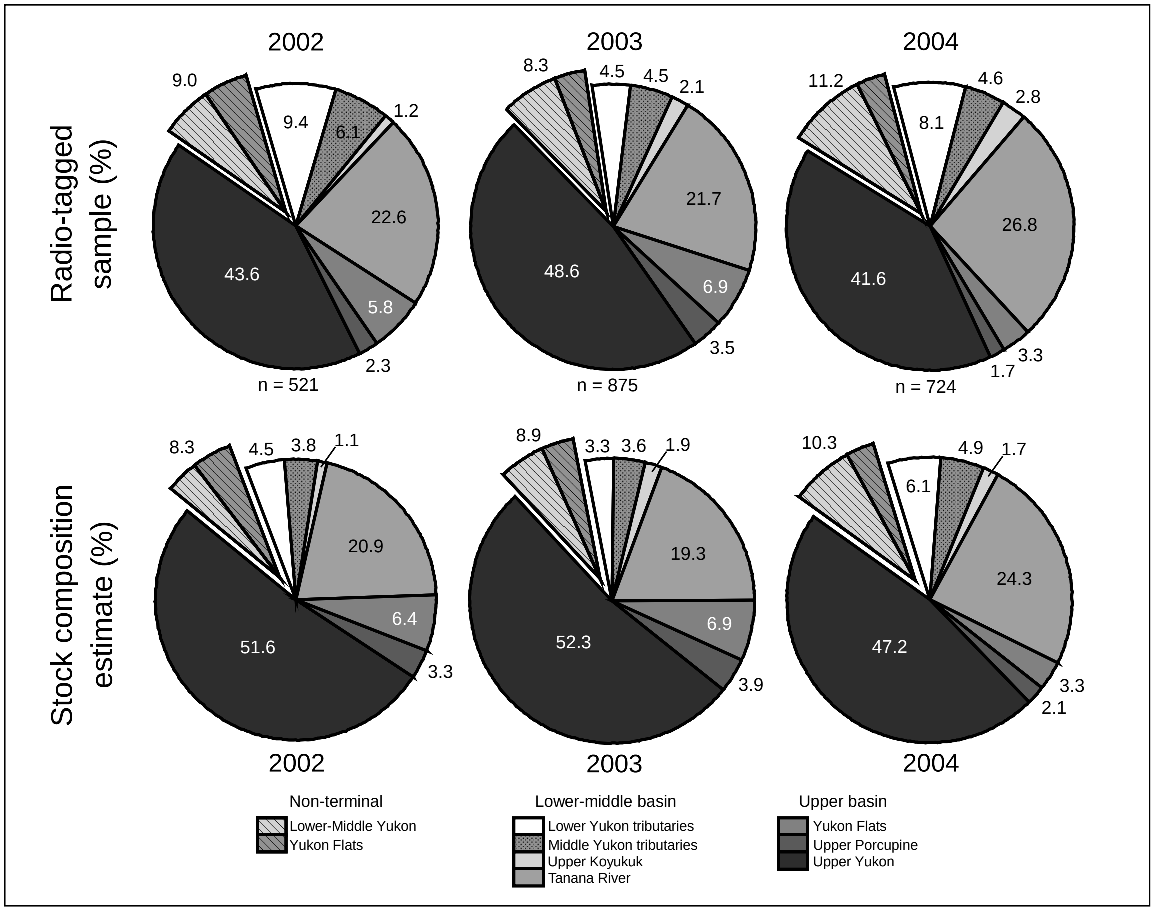

Figure 12.— Comparison of the regional distribution of Chinook salmon radio tagged in the lower Yukon River, and stock composition estimates based on these data, but weighted by daily measures of abundance at the tagging site and adjusted to account for the harvest of tagged fish in upriver fisheries.

Migratory Patterns of Wild Chinook Salmon Returning to a Large, Free-flowing River Basin

John H. Eiler[1,2], Carl B. Schreck[2], and Allison N. Evans[3]

[1]National Marine Fisheries Service, Alaska Fisheries Science Center
Auke Bay Laboratories, Juneau, Alaska 99801, USA

[2]U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit
Department of Fisheries and Wildlife, Oregon State University
Corvallis, Oregon 97331, USA

[3]Department of Fisheries and Wildlife, Oregon State University
Corvallis, Oregon 97331, USA

***Abstract*. —** Radio telemetry was used to determine the migratory patterns of Chinook salmon returning to the Yukon River basin during 2002-2004. A total of 2,860 fish were radio tagged and tracked upriver. Most fish exhibited continual upriver movements and strong fidelity to the tributaries entered. A small percentage (2.5%) deviated from this pattern, and exhibited atypical movements. Average migration rates were substantially slower for lower basin stocks (28-40 km/d) compared to upper basin stocks (52-62 km/d). Regional differences in migratory patterns (rates in sequential reaches) were observed. Although migration rates were similar in the lower river (57-62 km/d), Tanana stocks showed pronounced declines as they moved upriver, with migration rates of 24 km/d near terminal tributaries. Yukon Flats and Upper Yukon stocks exhibited gradual declines in migration rates (43-61 km/d near terminal tributaries) even though they traveled farther. Migratory patterns among individual fish within a stock showed substantial variation in migration rate, but tended to reflect regional patterns. Differences between consistently fast and consistently slow fish explained 74% of the within-stock variation, whereas relative shifts in migration rates between “hares” (fast fish becoming slower) and “tortoises” (slow but steady fish) explained 22% of the variation. Pulses of fish were not cohesive. Fish tagged over a 4-d period passed sites 580 and 872 km upriver over a 14-d and 16-d period, respectively. Migration rates were substantially faster and the percentage of aberrant movements considerably less than reported for Columbia River Chinook salmon, and may reflect pristine conditions within the basin and wild origins of the fish.

Keywords: Chinook salmon, spawning migration, upriver movements, migratory patterns, Yukon River, radio telemetry

Introduction

Pacific salmon (*Oncorhynchus* spp.) migrations have received considerable attention due to the large numbers of fish and cyclical nature of the returns, the extraordinary distances traveled, and the economic and biological importance of the resource. Fish migrations are generally defined as cyclical and directed movements by large segments of a population actively swimming extended distances between separate and distinct habitats (Northcote 1978). These migratory movements typically occur within a predictable period of time, and serve to bring populations into contact with resources that either enhance or are essential for growth, survival, or reproduction. The anadromous life style and associated seaward migration of salmon provide an opportunity for the fish to escape from the relatively sterile habitats of their natal streams in favor of the more productive conditions of the marine environment (Quinn 2005). However, this life history strategy carries with it the burden of having to return to freshwater to spawn and the extreme physical demands associated with the migration. This task presents the fish with a migratory dilemma. In addition to being in suitable physical condition, the fish must select the migratory timing and swimming behaviors that will enable them to return to suitable rivers, migrate upstream, and arrive on the spawning grounds when conditions are favorable. At the same time, the fish must also conserve energy resources during the migration to ensure that they reach their final destination with sufficient reserves to reproduce. To be successful, the fish must strike a balance between these two conflicting requirements.

Large numbers of Chinook salmon (*O. tshawytscha*) return to the Yukon River basin, a large northern river in Alaska and northwestern Canada. These returns are composed of multiple stocks distributed throughout the basin (Chapter 2), support important commercial and subsistence fisheries in both the U.S. and Canada, and are an integral part of the Yukon River ecosystem. The upriver movements of the fish are characterized by long-distance migrations. While fish returning to lower river tributaries may only travel several hundred kilometers and arrive on the spawning grounds within several weeks, some upper basin stocks travel over 3200 km from saltwater and take over 60 days to reach their final destination. Fish returning to the upper headwaters exhibit some of the longest salmon migrations recorded in freshwater.

Increasingly, both environmental and anthropogenic factors are impacting Chinook salmon populations (and other salmon species) in rivers throughout their range, underscoring the need to better understand the run characteristics of these returns. Although recognized as an important population parameter, detailed information on salmon movements in large rivers is often limited due to the effort and costs associated with implementing large-scale monitoring programs over extended distances and periods of time. Advances in biotelemetry, including the development of equipment systems robust enough to track large numbers of highly mobile fish over vast areas, have substantially enhanced the ability to collect movement data, and have been used effectively on migrating salmon (Burger et al. 1985, Eiler et al. 1992, Hinch et al. 2002, Keefer et al. 2004).

Chinook salmon returns in the Yukon River basin were relatively stable until the late 1990s when dramatic declines in abundance were reported (JTC 2001, Heard et al. 2007). This trend has continued during subsequent years, and resulted in the closure or drastic reductions in commercial fishing, severe restrictions in subsistence harvests, and difficulties in meeting regional and basin-wide escapement goals (ENS 2012, JTC 2012). In response to these declines, basin-wide telemetry studies were conducted during 2002-2004 to determine the nation of origin, stock composition and timing, and spawning distribution of the returns. Although not the primary objective, the study also provided detailed information on upriver movements. In this paper we describe the regional and stock-specific migratory patterns of the radio-tagged fish over the course of the spawning migration. We also compared the upriver movements of the fish with those observed in other large river basins. Many large rivers with sizable Chinook salmon returns are heavily regulated with controlled flows and impounded reaches, and are frequently comprised of both wild and hatchery fish. In contrast, the Yukon River basin is essentially free-flowing and composed of wild stocks. Only a small, passable hydroelectric dam ~ 2500 km upriver from the river mouth impedes the natural flow of water. Less than 3% of the returning fish pass this site, and a naturally-occurring lake < 35 km downstream minimizes any impact that might be caused by the restricted flow. Sizeable numbers of fish were radio tagged during the study, making meaningful comparisons possible for fish traveling varying distances and providing an opportunity to document the migratory patterns of Chinook salmon under natural conditions.

Methods

Study Area

The Yukon River basin drains a watershed of more than 855,000 km^2. The main river alone flows for more than 3,000 km from its headwaters in Canada to the Bering Sea (Figure 1). The river is relatively deep, with channel depths exceeding 20 m in the lower basin compared to 12-14 m downstream of the Yukon-Tanana River confluence and 5-7 m near the U.S.-Canada border (distances of ~ 1100 km and 2000 km from the river mouth, respectively). In addition to its large size, the Yukon River is the fifth largest drainage in North America in terms of total annual discharge, and exhibits considerable temporal variability with greater discharge during the summer months (Brabets et al. 2000, Yang et al. 2009).

Several major tributaries flow into the Yukon River main stem, including the Koyukuk and Tanana rivers in the United States; the Stewart, White, Pelly, and Teslin rivers in Canada; and the Porcupine River, which transects both countries. The basin also includes numerous medium and small-sized tributaries. Most reaches of the basin consist of a primary river channel with occasional side channels and sloughs, although the Yukon River main stem (hereafter referred to simply as the main stem) is extensively braided in the area commonly referred to as the Yukon Flats (Figure 1). Sections of the Tanana River, White River, and the Canadian main stem are also noticeably braided. Water visibility in many areas is extremely poor, particularly in the Tanana and White rivers due to turbidity from glacial activity in the upper headwaters of these drainages.

Regional designations used during the study were based on geographic location and the general geomorphology of the area; e.g., lower reaches of the Porcupine River were considered part of the Yukon Flats due to similarities in landscape and river characteristics. The Yukon River basin is extremely remote, with access to most areas limited to boat or aircraft.

Chinook salmon are a major source of food in many remote communities, and provide a source of income for local residents. Subsistence and commercial fisheries occur throughout the basin with most fishing effort concentrated near villages along the main stem (JTC 2012). Fish are also harvested in a number of tributaries including the Koyukuk, Tanana, Chandalar, Porcupine, Stewart, Pelly, and Teslin rivers (Figure 1). Limited sport fishing takes place in a number of clear water tributaries within the basin.

Fish Tagging and Tracking

Details regarding the methods used to capture and tag the fish are described in Chapter 2. Briefly, adult Chinook salmon were captured with drift gill nets in the lower Yukon River near the village of Russian Mission located 303 km upriver from the Yukon River mouth (Figure 1). During 2002, fish were also captured near the village of Marshall, located approximately 90 km downstream from the principal tagging area. Local fishers were contracted to fish these areas from early June to mid-July, with project personnel handling the fish and collecting the data. Both day (0900-1700) and night (1800-0200) shifts were fished during the study. The information recorded on the physical characteristics of the fish is described in Chapter 2.

The fish were tagged with pulse-coded radio transmitters in the 150-151 MHz frequency range manufactured by Advanced Telemetry Systems (Isanti, Minnesota)[1]. The transmitters (5.4 cm long, 2.0 cm in diameter, with a 30-cm transmitting antenna, and weighing 20 g) were gently inserted through the mouth and into the stomach of the fish. Each transmitter emitted a unique signal, based on a combination of frequency and

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA or U.S. Geological Survey.

signal pattern (described by Eiler 2012), making it possible to identify individual fish. Transmitters were also equipped with a motion sensor and activity monitor (described by Eiler 1990). The motion sensor, an integrated tilt switch sensitive to movement, inserted additional signal pulses into the signal burst each time the transmitter moved. The activity monitor changed the signal pattern to an inactive mode if the motion sensor was not triggered for 24 hours; the signal reverted to the original pattern if the motion sensor was activated. Transmitters had a minimum battery life of 90 days. The fish were marked externally with spaghetti tags attached just below the dorsal fin (described by Wydoski and Emery 1983) to help identify tagged individuals caught in fisheries or located in spawning areas.

Radio-tagged fish that moved upriver were tracked with remote tracking stations (described by Eiler 1995) placed at 40 sites throughout the basin (Figure 1). The sites were located on important migratory routes and major tributaries. Pairs of stations were placed at sites with special significance, including Paimiut, lower Koyukuk River, Manley, Rapids, Yukon Border, and Porcupine Border, to avoid loss of data due to technical problems with the equipment, damage from bears (*Ursus* spp.), or other unforeseen difficulties. The stations consisted of several integrated components, including a computer-controlled receiver (Advanced Telemetry Systems), satellite uplink (Campbell Scientific, Logan, Utah), and directional receiving antennas oriented upriver and downriver to provide information on the general location of the fish in relation to the site. A self-contained power system – consisting of a bank of six 6-volt, sealed lead-acid batteries connected in series and parallel (12 V, 610 Ah) and charged by two 80-W solar panels – supplied continual power to the stations.

Fish within reception range were identified and recorded by the stations. Most fish passing the sites were detected. The information collected included the date and time the fish were present at the site, signal strength of the transmitter, and the orientation of the fish in relation to the station (i.e., upriver or downriver from the site). The information was summarized and recorded at 10-minute intervals. Fish were periodically missed, particularly at Paimiut and the Yukon-Anvik River confluence (comprising 24%

and 15% of the fish passing the station, respectively) and to a lesser extent at Ruby (7%), presumably due to fish swimming at deeper depths; main channel depth at these sites was 25 m, 16 m, and 14 m, respectively. These fish were subsequently recorded at stations farther upriver. Essentially all fish (99-100%) were recorded by stations near the Koyukuk River mouth (6 m depth), Manley (8 m depths), Rapids (10 m depths) and at the other main stem and tributary sites.

Because of the isolated nature of the sites, the data collected by the stations, including information on operational performance (e.g., power levels of station components, whether the reference transmitter at the site was properly recorded), were transmitted every hour to a geostationary operational environmental satellite (GOES) and relayed to a receiving station operated by NOAA, National Environmental Satellite and Data Information Service near Washington D.C.. These data were accessed daily via the Internet, and uploaded to a computerized database (Oracle, Redwood Shores CA) for analysis and geographical information system (GIS) mapping program (ArcGIS, Version 10.0, Esri, Redlands CA) for spatial comparisons (Eiler and Masters 2000). The program flagged information that indicated problems with station operations so that corrective action could be taken, and created daily summaries of the upriver movements of the fish to facilitate other in-season research activities.

Based on information provided by the stations, periodic aerial surveys were conducted to locate fish between station sites and upriver of stations on terminal tributaries. Fish were tracked from fixed-wing aircraft and helicopters as described by Eiler (2012). Helicopters were used to access remote areas to determine the status of the fish and recover transmitters. Tracking receivers equipped with an integrated global positioning system (GPS) receiver were used during the surveys to standardize the location records of the fish.

Determining Migratory Patterns

Fish that passed Paimiut (the first station site, located approximately 62 km upriver from Russian Mission) were considered to have resumed upriver movements.

Fish tracked to terminal tributaries within the basin were classified as members of distinct spawning stocks. The status of fish last located in non-terminal reaches, such as sections of the main stem, was less certain since these individuals could represent fish spawning in local areas or fish that died while in-transit to spawning areas farther upriver. Fishers within the basin were asked to report any radio-tagged fish they caught, and steps were taken to promote this cooperative effort, including a reward system for the tags returned, regular presentations at fishery meetings, information flyers posted in local communities, and personal discussions with local fishers. Fish were considered to have been harvested if their transmitters were located out of the water in villages or fish camps during aerial surveys, even if the recovery was not reported.

The tracking records of each fish were systematically reviewed post-season to verify passage by the station sites, and to confirm that the movements represented a sequential series of stations. The time of passage (i.e., date and time the fish move past a station) was determined by comparing the progressive change in signal strength of the transmitter detected by the station’s directional antennas, and was designated as the time that the strongest signal shifted from the downriver antenna to the upriver antenna.

Migration rates (km/d) between sequential stations were determined for fish that resumed upriver movements and had complete migratory histories (i.e., recorded by all stations along their migratory route). These rates were based on the distance traveled between the two stations and the time taken to reach the second site. Travel time between stations was calculated based on the date and time of passage at the two sites. Due to the size of the basin and scope of the study, it was not possible to determine the actual pathways taken by the fish. Therefore, distance traveled was estimated based on the assumption that fish were primarily traveling along the thalweg. This approach avoided underestimating distance by not transcribing migratory routes through areas inaccessible to fish (e.g., islands, dewatered channels), and avoided overestimating distance traveled by assuming that fish were not following the most circuitous route. This approach likely provided relatively accurate distance estimates in reaches where the river consisted primarily of the main channel with occasional side channels and sloughs (i.e., limited options for the migrating fish) – conditions typical for most of the basin – but was potentially less accurate in highly braided reaches where the fish had an opportunity to select a variety of pathways. "Slower" migration rates in these areas could reflect additional time taken by fish to move through the reach via a more circuitous route, rather than a reduction in swimming speed. The calculated distances were based on the GIS mapping program previously mentioned. Migration rate was selected as the most appropriate measure of upriver movement since it normalized differences in the distance traveled between sequential stations, which ranged from 20 km to 639 km.

To standardize comparisons, only fish tracked upriver and detected by all sequential stations along their migratory route were included in the analysis. Although the fish responded well to the capture and tagging procedures, with most (97%) resuming upriver movements, there was also evidence of a negative tagging effect, with slower migration rates observed immediately after release (Chapter 2). This response was relatively short in duration (several days) and less severe as the fish moved upriver. Based on these findings, movement data between the tagging site and Paimiut were not included in the analysis to avoid incorporating tagging-induced behavior that could bias results. Migration rates between Paimiut and the Yukon-Anvik River station (133 km upriver from Paimiut) were used as the initial estimate of upriver movements. Fish continuously moving upriver and remaining in the terminal tributary they entered were deemed to be exhibiting typical migratory movements. Fish that deviated from this pattern (hereafter referred to as atypical movements) were considered separately. Fish tracked to terminal tributaries were used to determine migration rates for specific stocks. Information for regional components of the run was based on the fish tracked to the terminal tributaries within the area or harvested in main river fisheries in terminal regions (i.e, Upper Koyukuk, Tanana, Upper Porcupine, and Upper Yukon). Fish harvested in mainstem fisheries in the Lower Yukon, Middle Yukon, and Yukon Flats were excluded since these individual were potentially destined for regional areas farther upriver. Due to the small number of Yukon River stations in the Lower Yukon (i.e., most stations within the region were located on terminal tributaries), the information on these fish was limited to stock-specific comparisons.

The migration rates of individual fish in sequential reaches of the basin were compared by stock using nonmetric multidimensional scaling (NMS), a nonparametric, multivariate ordination technique (Kruskal 1964, Mather 1976). NMS was selected over other ordination methods because it can accommodate nonnormal or discontinuous data, does not assume linearity, is based on ranked distances, which improves its ability to extract information from non-linear relationships, can be used with any distance measure or data transformation, and is generally considered the most effective ordination method for ecological data (McCune and Grace 2002). Separate ordinations were conducted for individual stocks returning to terminal tributaries (i.e., within-stock analyses). Stocks with a minimum of three stations along their migratory route and represented by $\geq$ 20 radio-tagged fish were analyzed. Only fish recorded by all stations along the migratory route and ultimately located at spawning sites within the terminal tributary were included in the sample. The main data matrix used in the analysis consisted of individual fish (rows) by stations along the migration route of the stock (columns), with the cells denoting the fish's migration rate for the reach.

The multivariate data were reduced to a small number of continuous synthetic variables (axes) representing the gradients of variation that best characterized differences in individual fish movements during the upriver migration based on the original, multivariate data. NMS iteratively searched for an ordination with low stress as measured by the relationship between ranked distances in the original multidimensional space and those in the reduced dimensions (Peterson and McCune 2001). The ordination was conducted with PC-ORD software (MjM Software Design, Gleneden Beach Oregon) using the "slow and thorough" autopilot mode to determine the minimum stress value from 250 runs for up to six-dimensional configurations. A Monte Carlo test was performed using 250 runs of randomized data to determine if the ordination solution provided significantly more reduction in stress than expected by chance ($\alpha \approx 0.05$). Euclidean distance measurements (McCune and Grace 2001) were used to calculate the dissimilarity matrix. This metric was selected because movement data is continuous (i.e., all matrix combinations were possible), and absolute differences (versus proportional differences) in migration rate, which were our primary interest, are adequately reflected by this measure.

The synthetic axes created by NMS were interpreted using Pearson's correlation (r), Kendall's non-parametric rank correlation (τ), and scatter plots of the data to characterize the relationship between migration rates at sequential stations and the axis scores of the individual fish. The percentage of the variation in the original data represented by the ordination was calculated with Pearson's coefficient of determination (r^2).

Results

Regional and Stock-specific Movements

General Movements and Migration Rates

Fishing commenced in early June and continued until the end of the run in mid-July when catch rates were low. Large numbers of Chinook salmon (n = 2,860) were captured and radio tagged, with transmitters deployed throughout the run. The final destinations of the 2,790 fish that resumed upriver movements are summarized in Chapter 2. Of the 2,626 fish with migratory information (i.e., tracked past multiple stations), 2,560 fish (97.5%) displayed typical upriver movements (Table 1). Anomalous movements were exhibited by the remaining fish, and are described below. Migration rates were determined for the regional components of the return based on 1,097 fish with complete migratory histories (i.e., recorded by all stations passed); 877 fish of these fish were tracked to terminal tributaries and used to describe the upriver movements of specific stocks.

The average migration rate of the fish was 51 km/d (SD = 10.7), but pronounced differences were observed among regions, stocks, individual fish, and reaches of the basin. Substantially slower migration rates were observed for fish returning to terminal tributaries lower in the basin (Table 2). Average migration rates for Lower Yukon stocks ranged from 28-40 km/d compared to 45-46 km/d for the three principal Tanana stocks (Chena River, Salcha River, and Goodpaster River), and 52-62 km/d for fish returning to the Yukon Flats, Upper Porcupine, and Upper Yukon, hereafter referred to collectively as the upper basin. Although slower than upper basin fish, Middle Yukon stocks also exhibited progressively faster migration rates in relation to distance traveled. Fish returning to the Nulato River (391 km upriver from Paimiut) averaged 39 km/d compared to 51 km/d for Tozitna River fish traveling over 720 km upriver from Paimiut. Compared to stocks in other regions, Upper Koyukuk fish displayed faster swimming speeds, averaging 66 km/d. Although the Yukon-Koyukuk River confluence is relatively low in the basin (420 km from Paimiut), Upper Koyukuk fish traveled to spawning areas in the upper reaches of the drainage, distances in excess of 1200 km from Paimiut. Migration rates were more variable for stocks returning to the lower reaches of the basin. The coefficient of variation for Lower Yukon and Middle Yukon stocks ranged from 31-40% and 20-28%, respectively, compared to lower estimates for Upper Koyukuk (9%), Tanana (9-16%), and upper basin stocks (5-15%) (Table 2).

Migratory Patterns

Migration rates in sequential reaches of the basin (hereafter referred to as the migratory pattern) showed distinct regional differences in relation to distance travel and the nature of the river (i.e., main stem vs. tributary reach). As before, Lower Yukon and Middle Yukon stocks were uniformly slower than those traveling farther upriver (Figure 2). Conversely, migration rates in the lower reaches of the basin (i.e., downriver of both the Yukon-Koyukuk River confluence and Yukon-Tanana River confluence) were remarkably similar for stocks returning to the Upper Koyukuk, Tanana, and upper basin (ranging from 57-60 km/d) in spite of the disparate distances ultimately traveled by these fish to reach their terminal tributaries. However, major differences were observed in the migratory patterns of these regional components as the fish moved farther upriver. Upper Koyukuk fish swam considerably faster (72 km/d) after leaving the main stem (Figure 2). No stations were located in the upper reaches of this drainage, making it difficult to characterize the movements of these fish as they approached their final destination. However, ancillary information based on estimated migration rates for several fish harvested in nearby villages (40 km/d) and one fish recovered at an enumeration weir located 1,190 km upriver from Paimiut on the Henshaw River (31 km/d) suggests that Upper Koyukuk stocks exhibit a considerable reduction in migration rate as they near spawning areas. Upper Porcupine fish displayed a similar migratory pattern, with comparable migration rates while traveling through mainstem reaches compared to other upper basin stocks, followed by a pronounced increase in swimming speed as fish left the main stem and moved up the Porcupine River (Figure 2). Migration rates for fish passing the station near the U.S. – Canada border (1,570 km from Paimiut) averaged 68 km/d. Because of the braided nature of the Yukon-Porcupine River confluence, the initial Porcupine River station (1,448 km from Paimiut) was located 216 km upriver from the confluence and reflected movements in both the Yukon and Porcupine rivers. Upper Porcupine fish traveled hundreds of kilometers past the U.S. – Canada border to reach spawning areas, but no arrival information was available to assess swimming speed as they approached their final destination.

In contrast to Upper Koyukuk and Upper Porcupine stocks, Tanana fish displayed a pronounced decline in migration rate after leaving the main stem. As previously mentioned, migration rates were relatively fast downstream of the Yukon-Tanana River confluence and comparable to upper basin stocks moving through the area. However, Tanana fish swam progressively slower after leaving the main stem, with migration rates declining to 24 km/d on average as the fish arrived at their terminal tributaries (Figure 2). A similar pattern was observed for Middle Yukon fish returning to the Gisasa River, located in the lower reaches of the Koyukuk River. Migration rates for these fish declined from 51 to 26 km/d after leaving the main stem (Figure 3).

Yukon Flats and Upper Yukon fish returned to a number of large, medium, and small-sized tributaries flowing into the main stem. These stocks exhibited a conspicuously different migratory pattern, characterized by a relatively gradual but erratic overall decline in migration rate as the fish moved upriver. Migration rates were similar to other upper river stocks as the fish moved through the lower reaches of the basin. Unlike the pronounced decline exhibited by Tanana fish, migration rates initially increase for stocks continuing up the main stem past the Yukon-Tanana River confluence (Figure 2). A series of notable declines in swimming speed were subsequently observed as the fish traveled through the highly braided Yukon Flats (937-1,400 km from Paimiut), and mainstem reaches downstream of the Yukon-White River confluence (1,902 km from Paimiut), upstream of the Yukon-Pelly River confluence (2,048 km from Paimiut), and upstream of the Yukon-Teslin River confluence in the upper headwaters of the basin (2,333 km from Paimiut). Migration rates increased following these declines, although the overall trend was toward slower swimming speeds.

Similar migratory patterns were exhibited by stocks returning to the Tanana, Yukon Flats, and Upper Yukon (Figure 3). Migration rates for the two principal stocks in the Yukon Flats were essentially the same. Fish returning to the Goodpaster River were only nominally faster on average than the other principal Tanana stocks (Chena River and Salcha River fish). Migratory patterns were comparable for the four major Upper Yukon stocks (i.e., Stewart River, Pelly River, Big Salmon River, and Teslin River). These stocks comprised between 61-77% of the regional return based on stock composition estimates (Chapter 3). Several Upper Yukon stocks deviated from the regional pattern as the fish neared their terminal tributaries, including Pelly River and Teslin River fish. Both of these stocks returned to large tributaries and showed an increase in swimming speed during the final stage of their mainstem migration (Figure 3). Klondike River fish were consistently faster on average than other Upper Yukon stocks, whereas Little Salmon and headwater fish were noticeably slower throughout the migration. The migratory patterns of Middle Yukon stocks varied substantially, although less information was available to assess these movements due to the limited number of stations in the lower reaches of the basin. Migration rates declined dramatically for Nulato and Gisasa fish as they approached their final destination, whereas Tozitna River fish exhibited a relatively modest reduction in swimming speed (from 54 to 49 km/d) during the upriver migration (Figure 3).

Major differences in migration rate were observed as stocks approached their terminal tributaries. Compared to Tanana River fish, stocks returning to the Yukon Flats and Upper Yukon did not exhibit a pronounced decline (Figure 3). Final migration rates for Chandalar River and Sheenjek River fish averaged 52 and 53 km/d, respectively. These stocks traveled less than 230 km upriver past their final station to reach spawning areas, distances comparable to those exhibited by the principal Tanana River stocks (Table 3). Similar migration rates were observed for Upper Yukon fish returning to the Stewart (53 km/d) and Pelly (59 km/d) rivers. Although last located in the main stem (73 km downriver from their terminal tributary, and approximately 110-190 km from spawning areas), Klondike River fish averaged an impressive 61 km/d. Somewhat slower migration rates were observed for stocks returning to headwater areas, most notably Big Salmon River (43 km/d) and Teslin River (49 km/d) fish which traveled in excess of 2300 km from Paimiut to reach their terminal tributary.

Direct comparisons between the migratory patterns exhibited by Tanana and upper basin stocks were confounded to some extent by differences in the migratory routes. Tanana fish left the main stem and traveled substantial distances up the Tanana River prior to nearing terminal tributaries, whereas upper basin stocks spent most of the migration in the main stem. Based on the distances traveled (from Paimiut to spawning sites in the terminal tributaries), fish returning to the Chena, Salcha, and Goodpaster rivers spent 56-62% of the migration in mainstem reaches, compared to 85-90% for Yukon Flats fish, 84-90% for Upper Yukon fish returning to large tributaries (Stewart, Pelly, and Teslin rivers) and 89-96% for Upper Yukon fish returning to medium-sized tributaries. Similar to Tanana stocks, some Stewart River, Pelly River, and Teslin River fish traveled substantial distances (in excess of 500 km) after leaving the main stem (Table 3). Limited information is available on movements within the tributaries due to the scope of the study. However, ancillary information from the Stewart River suggests that fish in the upper reaches of this drainage continued to exhibit relatively fast swimming speeds. Estimated migration rates for several fish harvested in fisheries over 260 km upriver from the Yukon-Stewart River confluence ranged from 50-57 km/d after entering the Stewart River. Similarly, migration rates ranging from 46-54 km/d were recorded for several fish that passed the tracking station operated in the upper reaches of the drainage (327 km upriver from the Yukon-Stewart River confluence) during 2004. The relatively fast migration rates exhibited by Upper Yukon stocks returning to medium-sized tributaries were also notable, with Klondike River, Little Salmon River, and Big Salmon River fish traveling less than 190 km to spawning areas after reaching their terminal tributary (Table 3), further suggesting that Upper Yukon fish were exhibiting a different migratory pattern with swimming speed less strongly associated with proximity to spawning areas. Based on the coefficient of variation (Table 3), migration rates of Upper Yukon stocks were also less variable than Tanana fish as they approach their natal rivers.

Within-stock Migratory Patterns

In contrast to the similarities observed among stocks within the same region (Figure 3), there was considerable variation in the migratory patterns exhibited among fish within those stocks. Migration rates at the sequential stations varied widely among individuals as illustrated by the fish returning to the Salcha and Big Salmon rivers (Figure 4). Other stocks within the basin also exhibited considerable variation among fish (Appendix A). Although individual differences in migration rate were observed (i.e., wide range of swimming speeds among fish at specific stations), the migratory patterns exhibited by the fish generally reflected the average migratory pattern exhibited by the stock. For example, most fish returning to the Salcha River exhibited relatively consistent migration rates at the first three stations, followed by a pronounced decline at the fourth and fifth station (Figure 4). The tendency for individuals within a stock to exhibit the same general migratory pattern (i.e., increasing or decreasing migration rate) between sequential stations was particularly noticeable as the fish moved farther upriver from Paimiut.

Two primary sources of variation in migration rate were identified for individual fish based on the within-stock ordinations of 11 stocks that met the sample criteria (Table

4). Usable ordinations were obtained for all the stocks examined as illustrated by Salcha River fish (Figure 5). The dominant source of variation among individuals (represented by Axis 1) reflected the average migration rate of the fish, with the axis gradient ranging from slower fish (lower axis scores) to faster fish (higher axis scores). Simply stated, individual fish traveling slower in the lower basin exhibited consistently slower migration rates as they moved upriver compared to their faster moving counterparts, as reflected by the positive relationship between migration rate and the Axis 1 scores for the sequential stations (Figure 6). Similarly, fish with faster migration rates in the lower basin continued to display faster swimming speeds as they moved upriver relative to the slower fish. This source of variation among fish is visually evident in the raw data from the Big Salmon River stock (Figure 4), with fish exhibiting faster than average migration rates in the lower river remaining faster than average at upriver sites. This migratory pattern was observed across stocks, and on average explained 74% of the within-stock variation in migration rate represented by the multivariate data, ranging from 53% for White River fish to 94% for Chandalar River fish (Table 4).

The second source of variation in migration rate (represented by Axis 2) reflected a shift in the relative swimming speeds of the individual fish as they progressed upriver. Although movement rates declined for nearly all of the fish within a stock during the migration, differences were observed in the pattern of the decline. Fish with faster migration rates in the lower river exhibited a pronounced decline in swimming speed as they moved upriver, as reflected by the progressive change from a positive relationship to a negative relationship between migration rate and the Axis 2 scores for the sequential stations (Figure 6). Conversely, fish moving slower in the lower river displayed a more gradual decline in migration rate. In many ways the two patterns were analogous to the proverbial characters in Aesop’s fable *The Hare and the Tortoise* (Aesop 2003), with fish exhibiting both hare-like (initially fast then slowing down) and tortoise-like (slow and steady) movements. The axis gradient ranged from fish exhibiting tortoise-like movements (lower axis scores) to those displaying hare-like movements (higher axis scores) – hereafter designated as “tortoises” and “hares”. Based on within-stock comparisons of the outermost 10% of both the highest and lowest Axis 2 scores (as shown in Figure 5), fish exhibiting the hare pattern ultimately displayed slower migration rates as they neared their terminal tributaries than the fish with the tortoise pattern (Figure 7). Similarly, although direct comparisons were difficult due to differences among fish in run timing and other potentially confounding factors, the time taken by fish to reach their terminal tributaries was comparable for both tortoises and hares in spite of the substantially faster swimming speeds initially displayed by the hares. On average, this migratory pattern explained 22% of the within-stock variation in migration rate represented by the multivariate data, ranging from 6% for Chandalar River fish to 39% for White River fish (Table 4). Orthogonality was essentially 100% for Axis 2, suggesting that the information represented was not redundant in relation to Axis 1.

The variation represented by Axis 1 and Axis 2 reflect a continuum in the migratory patterns exhibited by the fish, with every fish falling somewhere along both gradients. Simply stated, individuals express different degrees of both the fast fish-slow fish and tortoise-hare pattern. Comparisons of the outermost 10% of both the highest and lowest Axis 2 scores where used to identify fish exhibiting the most hare-like and tortoise-like migratory patterns. Similarly, extreme Axis 1 scores represented fish with migration rates that were either more consistently slower (negative values) or faster (positive values) than other fish within the stock. As show in Figure 5, several Salcha River fish exhibiting the tortoise pattern (slow and steady) on Axis 2 also displayed the consistently slower pattern on Axis 1. Not surprisingly, fish displaying the hare pattern (initially fast, followed by a prominent decline) on Axis 2 displayed neither the consistently slow nor consistently fast pattern on Axis 1.

Migratory patterns were also determined for fish last located in non-terminal reaches of the basin and harvested in main stem fisheries. Of particular interest were fish tracked to the lower and upper reaches of the Yukon Flats (937-1,400 km from Paimiut), which had a more extensive migratory history than fish in lower reaches of the basin (i.e., greater number of station records) and provided a greater basis of comparison. The migratory patterns observed were comparable for both groups (Figure 8) and were also similar to the migratory patterns exhibited by upper basin stocks (as illustrated in Figure 4). Small numbers of both non-terminal and harvested fish exhibited migration rates that were substantially slower than typically observed in main stem reaches. Similar results were observed for the entire radio-tagged sample, with only 30 fish (1.5% of the tagged sample) exhibiting migration rates that were noticeably slower than those of fish harvested in fisheries or tracked to terminal tributaries in the Lower Yukon, Middle Yukon, and Yukon Flats.

Atypical Movements

Most of the fish tracked past multiple stations (2,560, 97.5%) exhibited continuous upriver movements and strong fidelity to the rivers they entered. Of the 1,680 fish tracked to terminal tributaries and not harvested in terminal fisheries (i.e., individuals with the option to leave), 1,620 fish (96.5%) moved varying distances upriver to spawning sites and remained for the duration of the run. Sixty-six (2.5%) fish tracked past multiple stations deviated from this pattern and displayed atypical movements. Two types of atypical movements were observed: bypassing terminal tributaries and movements between terminal tributaries. Twenty-three fish initially passed their final destination and continued upriver for varying distances, before reversing direction, swimming back downstream, and entering their terminal tributary. Some of these excursions were relatively short, with fish moving less than 30 km upriver past their final destination before reversing direction and moving back downstream, whereas others were fairly extensive with fish traveling hundreds of kilometers out of their way (Table 5). In two extreme cases, fish moved upriver past the Circle station (1,399 km upriver from Paimiut) before reversing direction and traveling to terminal areas in the Chandalar River and Upper Porcupine. The distances reported in Figure 5 represent minimum estimates, because it is not known how far upriver the fish ultimately traveled. The time spent upriver from the farthest station these individuals passed ranged from several hours to 8-9 days. Nine other fish displayed downriver movements, but were not tracked to terminal tributaries and were instead last located in mainstem areas or harvested in mainstem fisheries.

Thirty-four fish tracked to terminal tributaries subsequently left these rivers, and traveled to other terminal tributaries within the basin (n = 31) or were harvested in upriver fisheries (n = 3). Most of these fish (23, 68%) were observed moving between the Bonasila River and Anvik River in the Lower Yukon. The fish were initially recorded by the Bonasila station (approximately 5 km upriver from the Yukon-Bonasila River confluence) and remained in the lower reaches of the drainage for a short time (usually for several hours, although one fish remained for several days) before moving back to the main stem and traveling to the Anvik River, located 17 km farther upriver. Similar short incursions were observed in other tributaries, including the Nulato (n = 1) and Melozitna (n = 1) rivers in the Middle Yukon, Chena River (n = 1) in the Tanana, and the Stewart (n = 2) and Pelly (n = 1) rivers in the Upper Yukon, with fish entering and remaining in the lower reaches of the drainage for a limited period of time (typically < 1 d) before moving back downstream and resuming their upriver migration. These incidents were not limited to fish moving between nearby rivers. The Nulato River fish that exhibited this behavior ultimately traveled to the Teslin River in the Upper Yukon, a distance of 1,950 km.

Major diversions from the typical migratory route were also observed during the study. A fish tracked to the Sheenjek River in the Yukon Flats left this terminal tributary after 6 days and traveled downstream to the Chandalar River, a distance of over 100 km. Even more extreme, two fish tracked past the Porcupine Border station (a distance of over 337 km from the Yukon-Porcupine River confluence) ultimately returned to the main stem, traveled upriver to the upper reaches of the Upper Yukon, and were located in spawning areas in the Pelly and Teslin rivers.

Upriver Progression of a Fish Pulse

Based on catch per unit effort (CPUE) data from the Russian Mission tagging site, Chinook salmon returns exhibited a series of distinct and sizable increases in the number of fish moving through the lower river within a relatively short period of time (i.e., several days), hereafter referred to as pulses. These pulses were observed at varying times over the course of the run (Chapter 3). In 2002, several distinct pulses of fish moved through the lower river from early to mid-June, with declining numbers observed during late June and July. The 2003 return exhibited a more bell-shaped curve. Although several pulses of fish were observed in early and late June, the peak of the run was pronounced with the largest daily totals passing Russian Mission during 15-18 June (Figure 9). The peak of the run was less pronounced in 2004, with several distinct pulses moving through the lower river during middle and late June. More detailed information on the magnitude and timing of the run during 2002-2004 is presented in Chapter 3.

A total of 251 fish were radio tagged over a 4-day period (15-18 June) during the peak of the run in 2003 to provide information on the progression of the pulse as it moved upriver from Russian Mission (Figure 9). Collectively, these fish past the Yukon-Anvik River station (195 km upriver) over a 9-day period from 18-26 June. The time taken by the pulse to move past subsequent sites continued to increase as the fish moved farther upriver from Russian Mission (Figure 10). The fish took 14 d to pass Ruby, a distance of 579 km (Table 6). The reduced samples representing the pulse at locations farther upriver reflected the harvest of tagged fish in mainstem fisheries and fish that left the main stem and moved into terminal tributaries along the migratory route. Most of the pulse (168 fish) continued moving up the main stem, passing the Rapids station (872 km from Russian Mission) over a 16-day period from 27 June to 12 July (Figure 10). Passage times were similar at both the Circle station (15 d) and Yukon Border station (19 d), distances of 1,461 and 1,764 km from Russian Mission, respectively (Table 6). Passage at mainstem stations farther upriver ranged from 16 to 24 d for fish passing the Teslin (n = 16) and Tatchun (n = 51) stations, located 2,395 and 2,197 km from Russian Mission, respectively.

The portion of the pulse that left the main stem and continued up the Tanana River (n = 50 fish) took 27 d to pass Manley, and 24 d to pass Nenana, distances of 897 and 1,072 km from Russian Mission, respectively (Table 6). However, passage duration at these two sites was heavily influence by several fish that arrived substantially later than the other fish in the sample. Passage duration was 8 d at Manley and 11 d at Nenana when these fish were censored. The time of passage for fish moving upriver from Nenana and passing station on terminal tributaries was 22 d at the Chena River station (10 fish), 5 d at the Salcha River station (10 fish), and 16 d at the Goodpaster station (17 fish). The distances of these stations from Russian Mission ranged from 1,210 to 1,264 km.

Discussion

General Movements

Chinook salmon returning to spawning areas in the Yukon River basin face a number of challenges. In addition to the substantial distances traveled, the fish must respond to the environmental conditions encountered along the way and reach spawning area when conditions are favorable. They must also arrive with sufficient energy reserves to avoid predation, select appropriate spawning sites, compete with other individuals, select mates, and successfully reproduce. The ability to accomplish these tasks is implicitly tied to the movements of the fish. Slower swimming speeds use less energy, but are often inadequate in relation to the time available to complete the migration and traverse the extended distances involved. Optimal swimming speed (i.e., minimum cost per distance traveled) has been estimated as one body length per second (Brett 1983), or approximately 1.8 km/h (43 km/d) for an average sized Chinook salmon in the Yukon River. Swimming at optimal speed would be particularly advantageous for fish traveling extended distances, but may be insufficient when moving upriver against strong currents or when time is limited. Environmental and temporal constraints may force fish to swim in a less energy-efficient manner, as suggested by our findings where average migration rates for most stocks typically exceeded optimal swimming speed until the end of the migration. The migratory strategies and swimming behaviors displayed by the fish likely reflect the varied approaches used to address these issues.

Most fish during our study exhibited continuous upriver movements and displayed strong fidelity to the terminal tributaries they initially entered. The fish moved upriver at relatively fast rates of speed, with average migration rates ranging from 45 to 66 km/d for upper river stocks, suggesting that these fish were moving well above optimal swimming speed. Migration rates for fish returning to spawning areas in the lower basin were substantially slower, ranging from 26 to 40 km/d. The slower swimming speeds were likely related to the shorter distances these fish traveled to reach their final destination. The migration rates exhibited by lower basin fish were also more variable than those displayed by stocks returning to spawning areas farther upriver (Table 2). The compressed run timing of the return (~ 6 weeks, Chapter 3) and the extended distances traveled (in some cases over 3000 km from the tagging area) may limit the swimming options available to fish traveling considerable distances and needing to reach terminal sites within a restricted period of time, and may account for the reduced variability observed in upper basin stocks. Although precise timing information is not available on spawning activity within the basin, information from spawning ground surveys suggest that the peak of spawning in regional areas is generally confined to a 2-3 week period, with spawning in the upper basin occurring later in the season compared to lower and middle basin tributaries (Chapter 5). This relatively narrow window (presumably related to environmental constraints associated with access to spawning grounds, spawning conditions within these areas, and offspring survival) may explain the relatively compressed run timing and rapid migration rates exhibited by the return.

Comparable information on the migration rates of Chinook salmon in other large river systems is limited due to the logistical challenges and costs associated with large-scale monitoring programs. Basin-wide telemetry studies in the Columbia River provided useful comparisons. Both the Yukon River and Columbia River studies encompassed large river basins, relied on tracking stations located on principal migratory routes and spawning tributaries, and tracked large numbers of radio-tagged fish to terminal spawning areas. Swimming speeds in riverine reaches of the Columbia River were substantially slower than observed during our study, with most spring-summer

Chinook salmon migrating at rates between 10 and 30 km/d (Keefer et al. 2004). Median migration rates in low gradient reaches of the Columbia River main stem (Hanford Reach, 553-639 km from the river mouth) were consistently < 40 km/d, whereas rates in the lower Snake River (759 km from the river mouth) ranged between mid-30 and mid-40 km/d. Median migration rates in other reaches of the basin were substantially less. Similar to our study, lower basin stocks generally displayed slower migration rates. Fall Chinook salmon exhibited a similar pattern, with median migration rate of approximately 38 km/d in the lower reaches of the basin (Goniea et al. 2006). Weekly migration rates were mostly between 30 and 45 km/d when water temperatures were below 21^{o}C, but decreased by about 50% at higher temperatures (Goniea et al. 2006).

Differences between the two river basins potentially explain some of the disparity observed in Chinook salmon migration rates. Compared to the largely pristine and free-flowing conditions in the Yukon River basin, the Columbia River is heavily regulated, with controlled flows and inundated reaches associate with the numerous hydroelectric dams located throughout the drainage (Federal Columbia River Power System 2001). These structures have fundamentally altered the hydrological characteristics of the system, and resulted in diminished summer discharge, earlier warming of the lower river, higher peak temperatures, and later cooling in the fall (Quinn and Adams 1996, Quinn et al. 1997). The consequences of these changes on migrating salmon vary widely between species and between years, and are not well understood (Keefer et al. 2004b). In contrast to the relatively slow migration rates in riverine areas, Chinook salmon displayed rapid movements through impounded reaches, likely due the reduced water velocities encountered. Median migration rates in reservoirs associated with the lower Columbia River and Snake River dams ranged from 47-77 km/d, and were influenced by run timing, distance traveled, river discharge, and water temperature (Keefer et al. 2004b).

In addition to other anthropogenic effects associated with human population centers and activities along the Columbia River, the origins of the fish may also play a role. Chinook salmon returns to the basin are composed of both wild and hatchery stocks (Myers et al. 1998). Differences in migratory movements have been reported between wild and hatchery fish (Connor and Garcia 2006, Keefer et al. 2008, Westley et al. 2013), and may explain some of the disparity in migration rates observed between the Yukon River and Columbia River studies. Chinook salmon returning to the Yukon River basin are also near the northern extent of their range, and may be environmentally constrained to a relatively narrow migratory window, necessitating faster swimming speeds to reach terminal tributaries when spawning conditions are optimal. In contrast, Chinook salmon runs in the southern portion of their North American range extend throughout most of the year (Fulton 1968, Healy 1991, Myers et al. 1998, Yoshiyama et al. 1998), and likely face a less restricted range of environmental conditions and migratory options. However, Chinook salmon returning to the Copper River in south-central Alaska also exhibited relatively slow migration rates, ranging from approximately 4 km/d in the lower river to 14 km/d in the upper reaches of the basin. This drainage is highly glacial and relatively moderate in size, with the main river flowing < 300 km from its headwaters to the sea, and the heavy silt loads and shorter distances traveled by the fish are likely contributing factors. Migration rates for Chinook salmon returning to the relatively clear, moderately sized Klamath River (located within the southern portion of the range) averaged 21 km/d (Strange 2010).

Migratory Patterns

Most fish exhibited a general decline in migration rate as they moved upriver and approached their terminal tributaries. However, pronounced differences were observed in the migratory patterns exhibited by stocks returning to different regions (Figure 3). Most upper river stocks exhibited similar migration rate when moving through lower and middle reaches of the main stem, ranging from 57-60 km/d. This changed as fish left the main stem and entered tributaries, likely in response to the river conditions encountered, changes in physiological condition, and the innate behavior of the fish as they approached spawning areas. All Tanana stocks exhibited a pronounced decline in migration rate after leaving the main stem. These fish traveled 150-500 km farther upriver prior to reaching their terminal tributaries. Although river discharge in the Tanana River was substantially less than in the main stem (Chapter 5), the drainage is extremely turbid from glacial runoff which may impact swimming performance. The reduced migration rates may also reflect efforts to conserve energy reserves during the final stages of the migration or searching behavior as the fish attempt to locate their terminal tributary.

In contrast, Upper Koyukuk fish swam considerably faster after leaving the main stem, averaging 72 km/d at their final stations. River size, discharge, and turbidity were noticeably less in the Koyukuk River, which undoubtedly provided less arduous swimming conditions for the fish. However, proximity to spawning areas was likely a contributing factor with faster swimming speeds observed for fish traveling farther distances upriver. The migration rates of fish returning to the Gisasa River, located in the lower Koyukuk River drainage, declined dramatically (from 51 to 26 km/d) after leaving the main stem. These fish only traveled 96 km from the Koyukuk River mouth to their terminal tributary, compared to over 770 km for Upper Koyukuk fish. Migratory information on Upper Koyukuk fish is incomplete due to the lack of stations in the upper reaches of the drainage, but ancillary information suggests that these stocks also exhibited a reduction in swimming speed as they approach their final destination.

Upper basin stocks returning to tributaries in the Yukon Flats and Upper Yukon exhibited a conspicuously different migratory pattern, characterized by a gradual decline in movement rate as the fish moved upriver, punctuated by periodic increases. Increases in swimming speed were observed at varying distances from the final destination of the fish, suggesting that these patterns were more likely relate to local geomorphic or hydrological characteristics of the basin rather than the physiological condition of the fish or proximity to spawning areas. Most fish continuing up the main stem past the Yukon-Tanana River confluence displayed increased migration rates; river discharge and turbidity downriver from this site were substantially greater due to outflow from the Tanana River. Migration rates declined for over 99% of the fish traveling through the highly braided Yukon Flats. Although migration rates generally declined as fish moved upriver, the subsequent increase displayed by fish after leaving the Yukon Flats suggests that the slower swimming speeds within this area were in response to the physical features encountered.

Unlike Tanana fish, upper basin stocks returning to the Yukon Flats and Upper Yukon did not exhibit a prominent decline in migration rate as they approached their terminal tributaries. For example, when comparing fish moving through the Yukon Flats, the migration rates of Chandalar River fish (arriving at their terminal tributary) were comparable to those of Upper Yukon stocks with hundreds of kilometers still to travel. Slower movements by salmon approaching spawning areas are often attributed to increased efforts by the fish to search for and locate spawning areas. The lack of a prominent reduction in migration rate suggests that upper basin fish were either not having difficulty recognizing the environmental cues used to home to their final destination (i.e., extensive searching was not necessary), or that these cues were not readily apparent until the fish were in the general vicinity due to the size and substantial discharge associated with mainstem reaches. Although the migratory patterns for upper basin stocks generally declined as the fish progressed upriver, swimming speeds for several headwater stocks actually increased during the final leg of their mainstem migration. In addition to the reduced river size and discharge associated with these reaches, which presumably afforded less challenging swimming conditions, many of these fish still had to travel considerable distances after arriving at their terminal tributary prior to reaching spawning sites (e.g., over 500 km farther for some Teslin River fish), which may have been a contributing factor.

The migratory patterns for stocks returning to the same region were remarkably similar for Tanana, Yukon Flats, and Upper Yukon fish (Figure 3). These similarities suggest that the differences in migration rate observed in sequential reaches of the basin were not unique to certain stocks (e.g., reduced swimming speed in the Yukon Flats was displayed by all stocks passing through this area). Differences were observed among Middle Yukon stocks, but these were at least partly due to less extensive station coverage in the lower basin, and the geomorphic and spatial differences between the tributaries. A review of the literature did not reveal comparable information on the migratory patterns of Chinook salmon stocks in other river systems. As previously mentioned, Keefer et al. (2004) reported on the migration rates of spring-summer Chinook salmon aggregates in selected reaches of the Columbia River, but did not describe the sequential movements of the fish within the basin.

In contrast to the similarities exhibited by Yukon River Chinook salmon stocks returning to the same region, within-stock movements were more varied. The migratory patterns exhibited by the fish reflected two sources of variation: fast fish vs. slow fish and tortoises vs. hares. The fast fish-slow fish migratory pattern explained most of the variation in migration rate and was relatively apparent when graphically comparing individual movements. Although the fish tended to reflect the general migratory pattern of the stock, the range in migration rate between the slowest and fastest individuals was often considerable (Figure 4, Appendix A). Appreciable variation was also explained by the tortoise-hare pattern, ranging from 19-25% and 20-31% for the principal Tanana and Upper Yukon stocks (i.e., the largest components of the run), respectively, but this pattern was less apparent when comparing groups of individual fish and would have been difficult to identify based solely on visual inspection of the data.

Detailed information on salmon movements is often not available to fishery managers, and the methods for incorporating it into the decision making process not always straight forward. However, in conjunction with information on run timing and stock structure, movement data can provide a number of insights into the passage of fish through upriver fisheries and the status of the return. Movement data can be particularly important in large drainages with widely scattered fisheries where management actions in the lower river potentially impact harvests farther upstream. The migratory patterns of the fish can also be used to assess other issues related to the return. For example, since the late 1990s there has been concern within the Yukon River basin over the presence of the fish parasite *Ichthyophonus* and its impact on Chinook salmon returns. Sampling studies have suggested that infected fish succumb to the parasite while in-transit to Tanana and upper basin spawning areas (Kocan and Hershberger 2006). During our study, a number of fish were tracked to non-terminal areas associated with the main stem

(Chapter 2). The status of these fish was uncertain due to turbid conditions in these areas, and the difficulties associated with accessing and sampling the sites. Although these individuals may have spawned in local areas, they may also represent fish that died while in-transit to spawning areas farther upriver due to disease or handling stress, or reflect unreported harvests in local fisheries. Although latent effects from disease or handling can't be definitively ruled out, the migratory patterns of the fish tracked to non-terminal areas suggest that other factors were involved. Reduced stamina and progressively slower swimming speeds would be expected for fish in a weakened state or in the process of dying while in-transit to areas farther upriver (Kocan et al 2006b, 2009). Reduced swimming ability has also been reported in parasitized sockeye salmon (*O. nerka*) (Moles and Heifetz 1998). However, most non-terminal fish did not exhibit this trend, exhibiting migration rates that were similar to those displayed by fish harvested in main stem fisheries or tracked to nearby terminal tributaries. There is suggestive evidence, based on the final location of the non-terminal fish, that at least a portion of these individuals represent unreported fishery harvests (Chapter 2), an interpretation supported by the migratory patterns exhibited by the fish.

The migratory patterns documented during this study also provide a baseline for future comparisons. Smaller fish exhibited faster migration rates during the upriver migration (Chapter 5). Possible reductions in fish size (JTC 2006) and shifts in age composition to younger fish (based on data from Karpovich and Dubois 2012) have been reported within the basin and may affect the migratory patterns exhibited by the returns. Climate change is also a major concern. Due to the extended migrations exhibited by many of the stocks, Yukon River fish could be seriously affected by prolonged exposure to water temperatures elevated above optimal limits. Reported effects from increased temperatures on migrating salmon range from reduced stamina (Farrell et al. 2008), pronounced shifts in run timing, swimming speeds, and increased use of thermal refuges (Quinn et al. 1997, Berman and Quinn 1991, Keefer et al. 2004, Goniea et al. 2006), and elevated mortality (Gilhousen 1990, Macdonald 2000). The accelerated progression of disease and its increased severity under warmer temperature regimes (Wedemeyer 1996) would also likely impact the swimming performance and stamina of the fish (Kocan et al. 2009).

The migratory similarities exhibited by stocks within the same region (Figure 3) would seemingly provide a mechanism for tracking in-season movements and managing in-river fisheries. However, the underlying complexities exhibited by individual fish introduce a number of complications. Most of the individual variation in migration rate within a stock was explained by the fast fish-slow fish migratory pattern. This pattern would tend to amplify spatial differences, with consistently faster fish tending to outdistance their slower moving counterparts over time. Although a divergent trend would initially be expected for fish displaying the tortoise-hare pattern, the pronounced decline exhibited by the (initially faster) hares combined with the consistent (albeit initially slower) swimming speed of the tortoises would tend to reverse this tendency as the fish approached their final destination. Individual variation in run timing, combined with the varied migratory patterns exhibited by the fish, would further confound efforts to assess stock-specific movements.

Fine-scale movements were not routinely examined during this study, due to the vast size of the basin, limited resources, and focus on other research objectives. As previously mentioned, the location of stations on key migratory routes and tributaries limited the information collected on movements within localized areas. However, the substantial distances between spawning tributaries likely minimized the inherent bias this created. Limited boat tracking between Russian Mission and Paimiut showed that radio-tagged fish regularly shifted from the main river channel into adjoining eddies. It is not known whether the fish exhibited this pattern farther upriver, although local fishers often fish mainstem eddies with drift gill nets and set (stationary) gill nets are frequently positioned at the upper end of major eddies, suggesting that these areas are routinely use by migrating salmon. Salmon moving upriver reportedly seek out and use current as a directional cue (Arnold 1974). While this behavior would help fish avoid selecting circuitous or unsuccessful migratory routes, the energetic costs of swimming against strong current can be substantial (Brett 1995, Hinch et al. 2006). The routine use of mainstem eddies would presumably reduce the energy expended by the fish, while allowing them to stay in close proximity to the main current.

It is not known whether Chinook salmon within the basin spent appreciable periods of time resting during the upriver migration. Several fish held in slack water just downstream of islands immediately after moving upriver from the tagging site, although it is not known whether this behavior was typical of movements farther upriver or was a short-term response to being captured and tagged. The migration rates estimated during this study were based on the assumption that the fish were continually moving upriver. Prolonged holding by the fish would bias these estimates low, and suggest that the fish were actually swimming at faster speeds. However, this seems unlikely given the relatively fast migration rates observed during this study, suggesting that holding by the fish during the upriver migration was limited. Delayed upriver movements have been reported in other river systems for salmon utilizing terminal refuges (Goniea et al. 2006) and encountering velocity barriers. Rand and Hinch (1998) found that Fraser River sockeye salmon (*O. nerka*) passing a velocity barrier at the Hell's Gate site exhibited behavioral strategies that included periods of stasis punctuated by swimming bursts. However, Standen et al. 2002 reported that pink salmon (*O. gorbuscha*) moving through reaches of the Fraser River with relatively fast, turbulent flows generally displayed faster, less energy-efficient swimming patterns in spite of the increased energetic costs, presumably to minimize travel time through these areas since significant delays could seriously affect arrival times on spawning grounds and negatively impact spawning success.

Atypical Movements

Although most fish exhibited continual movements upriver during the migration and strong fidelity to natal rivers, small numbers of fish exhibited aberrant movements. Most of the movements that deviated from the typical pattern represented short exploratory incursions by the fish into rivers downstream from their final destination. Fish moving from the Bonasila River to the Anvik River (located in the Lower Yukon) were the most common example, representing 68% of the observations. These two rivers were in close proximity to each other (17 km), drained adjacent watersheds, and likely had water with similar chemical characteristics. The use of olfactory cues by adult salmon to home to natal rivers is well established (Hasler 1971), and incursions by fish into nearby tributaries with similar characteristics is understandable and may be more common than generally thought. There were few opportunities during our study to document movements between nearby tributaries due the size of the basin, the considerable distances between rivers with spawning populations, and limitations on the number of stations deployed, but it is likely that fish encountering river conditions similar to those of their final destination would exhibit similar exploratory patterns. No fish were observed moving from the Anvik River to the Bonasila River, suggesting that the fish were searching for their terminal tributary as they moved progressively upriver.

The frequency of between-tributary movements appears related to the distance traveled by the fish and the proximity of the tributaries. Unlike the Bonasila and Anvik rivers (located in the Lower Yukon), no exchange was observed for Tanana fish returning to the Salcha and Goodpaster rivers (located 96 km apart), even though both rivers supported large Chinook salmon returns and drained adjacent (and similar) upland watersheds. The same result was observed for fish returning to the Chena and Salcha rivers (located 66 km apart), although the city of Fairbanks is located along the lower Chena River, and undoubtedly influences the chemical characteristics of the river. Even so, one Goodpaster River fish initially moved a short distance up the Chena River before reversing directions several hours later, returning to the Tanana River, and moving upriver to its final destination. Similarly, only a few Upper Yukon fish exhibited between-tributary movements even though numerous rivers and streams within the area supported spawning populations. Distances between these rivers were typically greater than 30 km and proximity may be a factor.

Small numbers of fish exhibited more convoluted movements, traveling substantial distances out of their way and initially entering rivers that were considerably different than their final destination. The movements between the upper Porcupine River (which drains an interior plateau and is characterized by broad river valleys underlain by permafrost, Brabets et al. 2000) and upland tributaries in the Upper Yukon were prime examples. Similarly, the fish initially tracked to the Sheenjek River traveled over 70 km through the lower Porcupine River, and remained in the Sheenjek River for over 6 d before moving back downstream and traveling to spawning areas in the Chandalar River. Similar movements were observed for radio-tagged chum salmon (*O. keta*), with fish traveling to both the Chandalar and Sheenjek rivers subsequently leaving these tributaries and traveling to spawning areas in the other river (J. Eiler, National Marine Fisheries Service unpublished report). These observations may reflect the general proximity of the two rivers and similarities between the watersheds. Both rivers drain the lower foothill of the Brooks Range and flow across the Yukon Flats, and may provide similar environmental cues important to the homing salmon.

Small numbers of fish (~ 1% of those tracked past multiple stations) initially bypassed their terminal tributary and continued traveling upriver before doubling back. These movements were likely inadvertent (i.e., the fish failing to detect the environment cues from their natal rivers during the initial passage), particularly since the extreme distances traveled by the fish are an energetic challenge and extraneous movements would presumably have a decidedly negative impact. Although some bypass movements were relatively short (< 30 km), most were fairly extensive with minimum distances traveled ranging from 70 to over 360 km. However, this observation may be an artifact of the methods used to monitor the fish (i.e., stations). Because of the limited number of stations and their placement on key migratory routes and tributaries, we were not able to document small-scale migratory patterns, and it is possible that generalized searching and bypass movements may be more common in localized areas near terminal tributaries.

The frequency of atypical movements in the Yukon River was substantially less than observed for Chinook salmon in the Columbia River. Keefer et al. (2008) reported that over 14% of the radio-tagged fish in their study exhibited between-tributary movements, and that a substantial percentage (> 75%) of the lower basin fish initially bypassed their natal rivers. Based on these observations, they suggested that direct point-to-point movement by salmon *en route* to natal stream may be less common than previously thought. Since limited information was available on the migratory patterns of Chinook salmon in other large river systems, fine-scale movements of sockeye salmon in a small Alaskan river (Burger et al. 1995), which displayed localized movements between small, lake-shore tributaries, were used to support this view. However, our findings suggest that Chinook salmon in large, free-flowing rivers exhibited relatively typical (i.e., directed) upriver movements, with less than 3% of the fish exhibiting either between-tributary or extended bypass movements. As previously mentioned, our study was not designed to document small-scale movements in localized areas, but movements between adjacent tributaries supporting large Chinook salmon stocks were relatively rare compared to those in the Columbia River. In addition to the impounded and highly regulated nature of the drainage, Chinook salmon returns to the Columbia River are composed of both wild and hatchery stocks (Myers et al. 1998), which as previously discussed may impact the behavior and migratory movements displayed by the fish. Keefer et al. (2008) noted that atypical movements were more frequently displayed by Chinook salmon originating from hatcheries, particularly when considering Snake River stocks in the upper basin. Incidents were also greater for later run fish, particularly when river temperatures exceeded 19^{o}C.

Similarities were also observed in the atypical migratory patterns displayed by Yukon River and Columbia River Chinook salmon. Between-tributary movements were most common in lower reaches of the basin where several tributaries entered the main stem in close proximity to each other. Keefer et al. (2008) speculated that this pattern was related to greater main stem flows and more complex mixtures of olfactory cues in the lower Columbia River compared to areas farther upriver where spawning tributaries were more widely spaced and river discharge substantially less. Although not entirely analogous to the Yukon River basin (i.e., numerous tributaries in the Upper Yukon supported spawning populations of Chinook salmon), river discharge in upper reaches of the basin was substantially less and derived from fewer sources of water than in the lower river, undoubtedly providing less ambiguous olfactory cues for the returning fish.

Keefer et al. (2008) noted that bypass movements were more common for lower basin stocks, particularly when terminal tributaries were near dams, suggesting that homing behavior was less precise in impounded reaches and large migratory corridors compared to smaller, free-flowing rivers where less searching would be needed to locate natal streams. Based on observations that migrating salmon tended to migrate along shorelines and orient on plumes of water from upriver spawning tributaries (Daum and Osborne 1998, Reischel and Bjornn 2003), they also speculated that bypass movements may be associated with fish traveling on the opposite side of the river from their terminal tributary and missing the olfactory cues, particularly in mainstem areas with substantial flows. Regional differences were less obvious during our study, although these comparisons were based on very small numbers of fish due to the low incidence of this behavior. Eight Anvik River fish (11% of the fish tracked to this tributary) displayed bypass movements compared to only one fish (3.5%) traveling to the nearby Bonasila River, whereas three fish (14%) returning to the Tozitna River (over 720 km upriver from Paimiut) exhibited this pattern. Tributary size may be a factor. Sixteen (70%) of the fish that showed bypass movements returned to medium-sized tributaries flowing into the Yukon River main stem: the Bonasila, Anvik, Nulato, and Tozitna rivers. The main stem was fairly sizable at these sites, ranging from 1,200-1,400 m wide and 14-16 m deep (Yukon-Anvik confluence) to 800-1,000 m wide and 12-14 m deep (Yukon-Tozitna confluence), and it is possible that the tributary discharge (and the associated olfactory signal used by the homing salmon) may periodically be obscured by the main stem flow. The three fish that bypassed the Tozitna River were somewhat surprising. There is strong evidence that Tanana River and Yukon River fish start exhibiting bank orientation several hundred kilometers downstream of the Yukon-Tanana confluence (Schultz et al. 1994) due to the distinct river characteristics of the two drainages, and most Tozitna River fish would presumably be traveling along the same side of the river as their terminal tributary. Several islands are located just downstream from the Yukon-Tozitna confluence, and the added geomorphic complexity may influence the localized movements of the passing fish.

Upriver Progression of a Fish Pulse

Large pulses of fish moving upriver through the Yukon River main stem are routinely used by fishery managers to identify and target different components of the return (D. Bergstrom, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication). During years of low abundance, fisheries are closed as the pulses pass upriver to manage harvests and enhance spawning ground escapements. Similar actions are taken as these fish move farther upriver through successive fisheries. In addition to monitoring the relative magnitude of the run, genetic stock identification information (described by Decovitch and Howard 2011) for fish passing through the lower river provide in-season estimates of the regional composition and provide a means to minimize harvests on stocks of concern. However, the integrity of these pulses as they move upriver can impact the effectiveness of the management actions taken.

Large numbers of fish were tagged during the pronounced pulse in 2003 because it provided a strong signal that could be tracked upriver. The timing of the tagged fish as they passed upriver sites suggests that pulses of fish are not amalgamated, and that subsequent signals detected farther upriver likely represent different combinations of fish. Attrition caused by fishery harvests and fish moving from the main stem into adjoining tributaries resulted in the continuous reduction in the magnitude of both the pulse and tagged sample, which was expected. However, the temporal spread of the pulse would be expected to remain relatively constant if the pulse was cohesive. Instead, the time taken by these fish to pass successive upriver sites became progressively more protracted as the distance upriver increased. The fish passing the tagging site over a four day period took nine days to pass the main stem station located 195 km upriver, and 2-3 weeks to pass sites approximately 600 and 900 km upriver, respectively. This lack of temporal continuity is not surprising considering the substantial variation exhibited among individual fish. As previously discussed, the fast fish-slow fish migratory pattern (which explained most of the observed variation in migration rates) would be expected to result in a divergent trend. Although a strong pulse was still apparent at the upriver sites, the composition of this aggregate appears to consist of a fraction of the original fish, as well as a combination of slower moving fish overtaken by the pulse and faster moving fish that had "joined" the pulse for a period of time. Understanding this dynamic can help assess the impact of harvests in upriver fisheries.

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Table 1.— Tagging dates and numbers of Chinook salmon capture in the lower Yukon River, radio tagged, and tracked upriver passed the first tracking station site (Paimiut) during 2002-2004. The numbers of fish exhibiting typical (only upriver movements) and atypical migratory patterns are presented. The percentage of the fish that moved upriver and were recorded by multiple stations is in parentheses. The number of fish that exhibited typical movements and were recorded by all sequential stations along their migratory route is also indicated.

	2002	2003	2004	All years
Start of tagging	9 June	3 June	3 June	3-9 June
End of tagging	13 July	14 July	19 July	13-19 July
Captured	1,310	2,312	2,107	5,729
Tagged	768	1,097	995	2,860
Moved upriver past Paimiut	751	1,081	958	2,790
Tracked past multiple stations	683	1,050	893	2,626
Typical migratory pattern	666 (97.5)	1,031 (98.2)	863 (96.6)	2,560 (97.5)
Regional fish[1]	242	470	385	1,097
Terminal tributary fish[2]	196	394	287	877
Atypical migratory pattern	17 (2.5)	19 (1.8)	30 (3.4)	66 (2.5)

[1] Fish tracked to terminal tributaries or harvested in main river fisheries in terminal regions, and recorded by all stations along the migratory route.

[2] Fish tracked to terminal tributaries and recorded by all stations along the migratory route.

Table 2.— Migration rate (km/d) of radio-tagged Chinook salmon with complete migratory histories (recorded by all tracking stations along their migratory route) returning to terminal tributaries in the Yukon River basin during 2002-2004. Stocks represented by less than 10 fish are not listed. The number of tracking stations along the migratory route, number of fish, and average migration rate, standard error (SE) and coefficient of variation (CV) are indicated for the principal stocks of the return.

Region	Stock	Stations	n	Migration rate	SE	CV (%)
Lower Yukon	Bonasila	2	22	39.5	2.6	31.1
	Anvik	2	50	27.9	1.6	39.6
Middle Yukon	Nulato	3	27	39.1	2.1	28.2
	Gisasa	4	13	41.3	2.3	19.8
	Tozitna	4	16	50.5	2.7	21.3
Upper Koyukuk	Koyukuk[1]	4	23	65.7	1.3	9.3
Tanana	Kantishna	4	21	54.8	1.1	9.4
	Chena	6	56	45.8	1.0	15.5
	Salcha	6	96	45.2	0.5	11.4
	Goodpaster	6	52	46.0	0.7	10.9
Yukon Flats	Chandalar	5	26	56.7	1.5	13.8
	Sheenjek	5	10	56.3	0.9	5.3
Upper Porcupine	Canadian stocks[2]	6	30	59.6	1.6	15.1
Upper Yukon	Klondike	6	24	61.6	0.9	7.2
	Stewart	7	56	57.2	0.9	11.1
	White	6	24	59.2	0.7	5.6
	Pelly	9	97	57.4	0.5	9.0
	Little Salmon	9	11	52.6	2.0	12.9
	Big Salmon	10	56	53.8	0.6	7.9
	Teslin	10	81	54.5	0.7	10.8
	Headwaters[3]	10	19	52.2	0.8	7.0

[1] Composite of headwater stocks, including Henshaw, South Fork, and Middle Fork rivers.

[2] Primarily Miner River fish, but also including fish returning to the Old Crow River and Whitestone River.

[3] Including fish returning to the Takhini River and other headwater tributaries.

Table 3.— Travel distances associated with the last tracking station passed by radio-tagged Chinook salmon stocks returning to terminal tributaries in the Yukon River basin during 2002-2004. Distances from the last station to the first station in the lower basin (Paimiut), the Yukon River main stem (Yukon), and spawning sites within the tributary (final) are presented. The stations were typically located on the terminal tributary near the mouth. Stocks with the last station located on the Yukon River main stem are indicated, with the distance still to travel to reach the tributary in parentheses. The number of fish, migration rate for the reach (from the previous station to the last station), standard error (SE) and coefficient of variation (CV) are also presented. Stocks represented by less than 10 fish or lacking spawning sites information are not listed.

			Distance from station (km)					
Region	Stock	n	Paimiut	Yukon[1]	Final[2]	Rate	SE	CV(%)
Tanana	Chena	56	1148	405	1-105	25.7	1.1	31.3
	Salcha	96	1147	404	0-168	23.5	0.6	23.8
	Goodpaster	52	1243	500	32-188	24.3	0.7	20.2
Yukon Flats	Chandalar	26	1205	25	6-222	52.2	2.2	21.6
	Sheenjek	10	1312	80	57-188	52.7	1.1	6.9
Upper Yukon	Klondike[3]	24	1702	(74)	38-114	60.5	1.4	11.2
	Stewart	56	1900	21	7-622	52.7	1.0	13.9
	Pelly	97	2063	15	44-641	58.5	0.8	13.4
	Little Salmon[3]	11	2135	(93)	22-57	41.3	1.9	15.2
	Big Salmon	56	2319	30	18-155	42.9	1.0	16.9
	Teslin[3]	81	2333	(6)	9-526	48.8	1.0	18.1

[1] Confluence of the Yukon River and the terminal tributary.

[2] Distance traveled from last station to spawning sites within the tributary (final location of fish). Reflects distance from the tributary mouth to spawning sites for stocks with last station on Yukon River main stem.

[3] Final station located on Yukon River main stem downriver from the terminal tributary.

Table 4.— Yukon River Chinook salmon stocks analyzed using within-stock ordination to describe the migration patterns of individual fish returning to terminal tributaries. Pearson's r^2 values represent the proportion of the multivariate data explained by the synthetic variables (axes).

Region	Stock	n	Migration rate	SE	CV (%)	Pearson's r^2 Axis1	Axis2	Total
Tanana	Kantishna	20	54.9	1.2	9.7	0.919	0.079	0.998
	Chena	51	47.2	0.8	12.7	0.769	0.185	0.954
	Salcha	91	47.0	0.4	8.9	0.695	0.254	0.949
	Goodpaster	51	49.6	0.7	9.9	0.730	0.231	0.961
Yukon Flats	Chandalar	20	59.0	1.3	9.8	0.936	0.056	0.992
Upper Yukon	Klondike	24	63.1	0.9	6.8	0.739	0.177	0.916
	Stewart	48	58.7	0.8	9.2	0.726	0.250	0.976
	White	24	60.9	0.7	5.3	0.526	0.389	0.915
	Pelly	77	58.0	0.5	7.4	0.680	0.244	0.924
	Big Salmon	53	53.5	0.6	7.9	0.728	0.203	0.931
	Teslin	70	53.8	0.7	10.2	0.660	0.311	0.971

Table 5.— Extra distance traveled (km) and time spent (d) by radio-tagged Chinook salmon that initially bypassed their terminal tributary and continued swimming upriver before reversing direction and traveling to their final destination in the Yukon River basin during 2002-2004. The extra distance is a minimum estimate because the actual distance traveled by the fish past the farthest upriver station is unknown.

Farthest (last) upriver station	Final destination	Fish[1]	Total fish	Extra distance traveled (km)[2]	Time upriver last station (d)
Yukon-Anvik	Anvik River	8 (11.3)	71	28	2.2 (0.1-8.0)
Yukon-Anvik	Bonasila River	1 (3.5)	29	70	6.2
Ruby	Nulato River	4 (9.8)	41	303	1.9 (0.1-4.7)
Ruby	Upper Koyukuk	1 (3.6)	28	110	6.7
Upper Tanana	Salcha River	1 (0.6)	164	110	0.1
Rapids	Tozitna River	3 (14.3)	21	179	4.0 (0.6-9.4)
Mid-Porcupine	Sheenjek River	1 (2.7)	37	303	5.0
Circle	Upper Porcupine	1 (2.2)	46	340	2.3
Circle	Chandalar River	1 (1.5)	65	368	1.2
Yukon-White	White River	2 (6.9)	29	13	0.5 (0.3-0.7)

[1] Numbers of fish exhibiting bypass movements. Percentage of total number of fish with complete migratory histories and tracked to final destination is in parentheses.

[2] Based on distance from terminal station (final destination) to farthest station upriver and return.

Table 6.— Passage dates for Yukon River Chinook salmon radio tagged during the peak of the run and tracked upriver during 2003. Distances of the upriver locations from Russian Mission, number of fish, and numbers of days taken by the group of tagged fish to pass the sites are presented. The reduced sample size at the upriver locations reflects the harvest of radio-tagged fish in mainstem fisheries and the movement of fish into other terminal tributaries along the migratory route.

Location	Distance from tagging (km)	n	Passage dates	Passage duration (d)
Russian Mission (tagging site)	--	251	15-18 Jun	4
Yukon-Anvik River station	195	226	18-26 Jun	9
Ruby station	579	217	23 Jun – 6 Jul	14
Manley station (Tanana River)[1]	897	50	30 Jun – 26 Jul	27
Nenana station (Tanana River)[1]	1,072	40	2-25 Jul	24
Rapids station (Yukon River)	872	168	27 Jun – 12 Jul	16
Circle station (Yukon River)	1,461	116	7-21 Jul	15
Yukon Border station	1,764	104	11-29 Jul	19

[1] Includes several fish tagged during the pulse, but moving substantially later past the site.

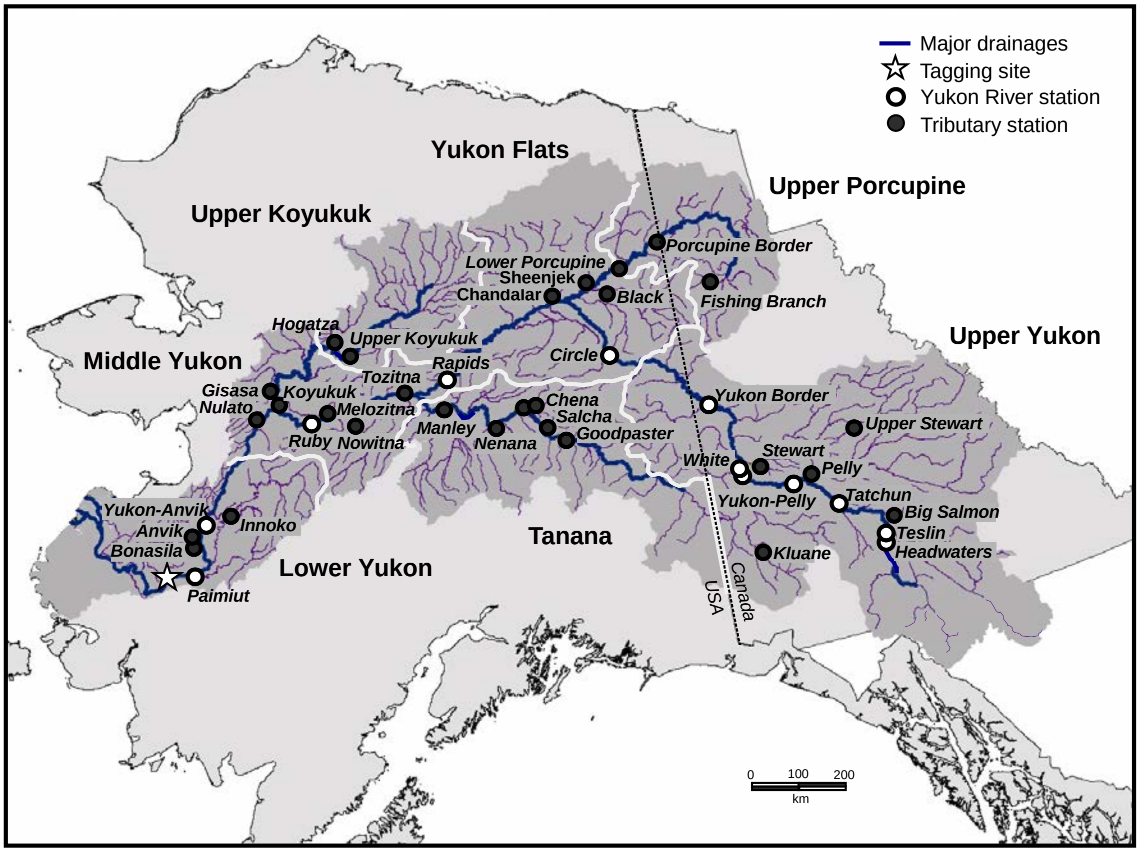


Figure 1.— Map of the Yukon River basin showing the regional areas, major drainages, lower river tagging site near Russian Mission, and tracking stations on both the Yukon River main stem and associated tributaries.

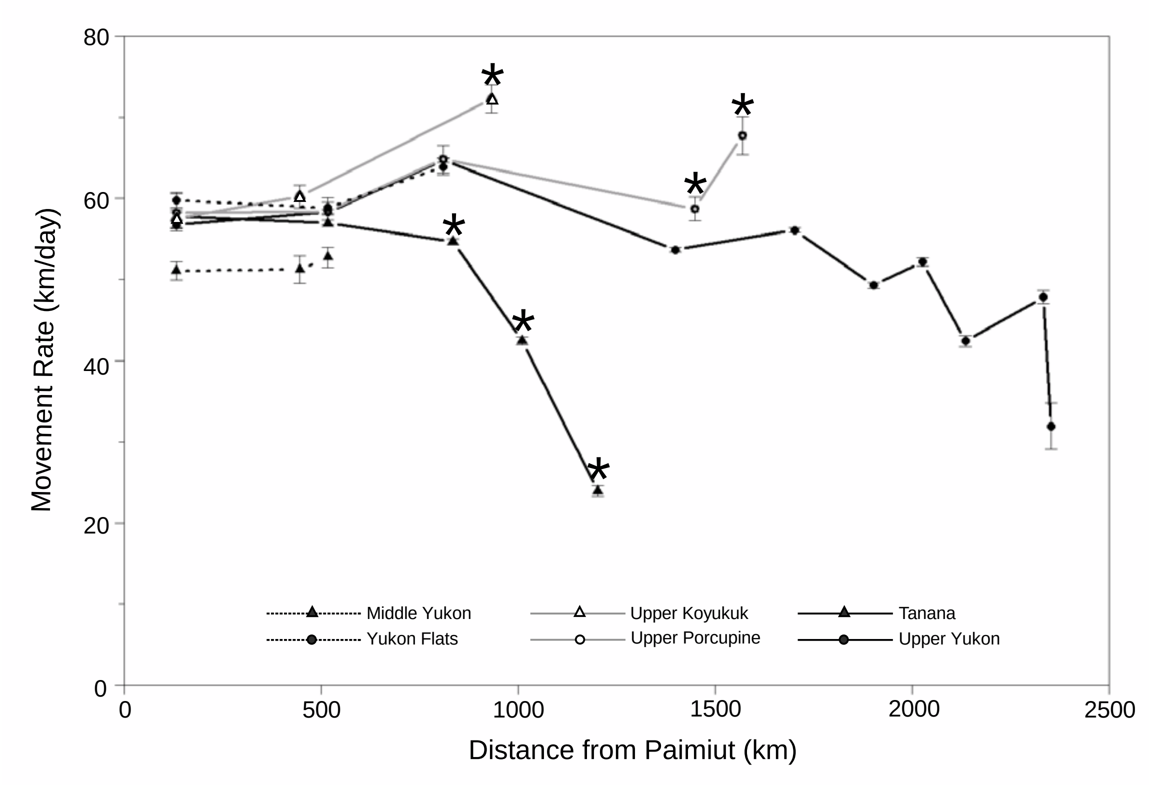


Figure 2.— Migration rates by distance traveled for Chinook salmon returning to regional areas of the Yukon River basin during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated. Estimates and standard error are based on fish with complete migratory histories (recorded by all stations passed). Migration rates in basin tributaries (i.e., fish that have left the Yukon River main stem) are also indicated (*). Regional estimates were not available for Lower Yukon stocks due to the limited number of Yukon River stations in this region.

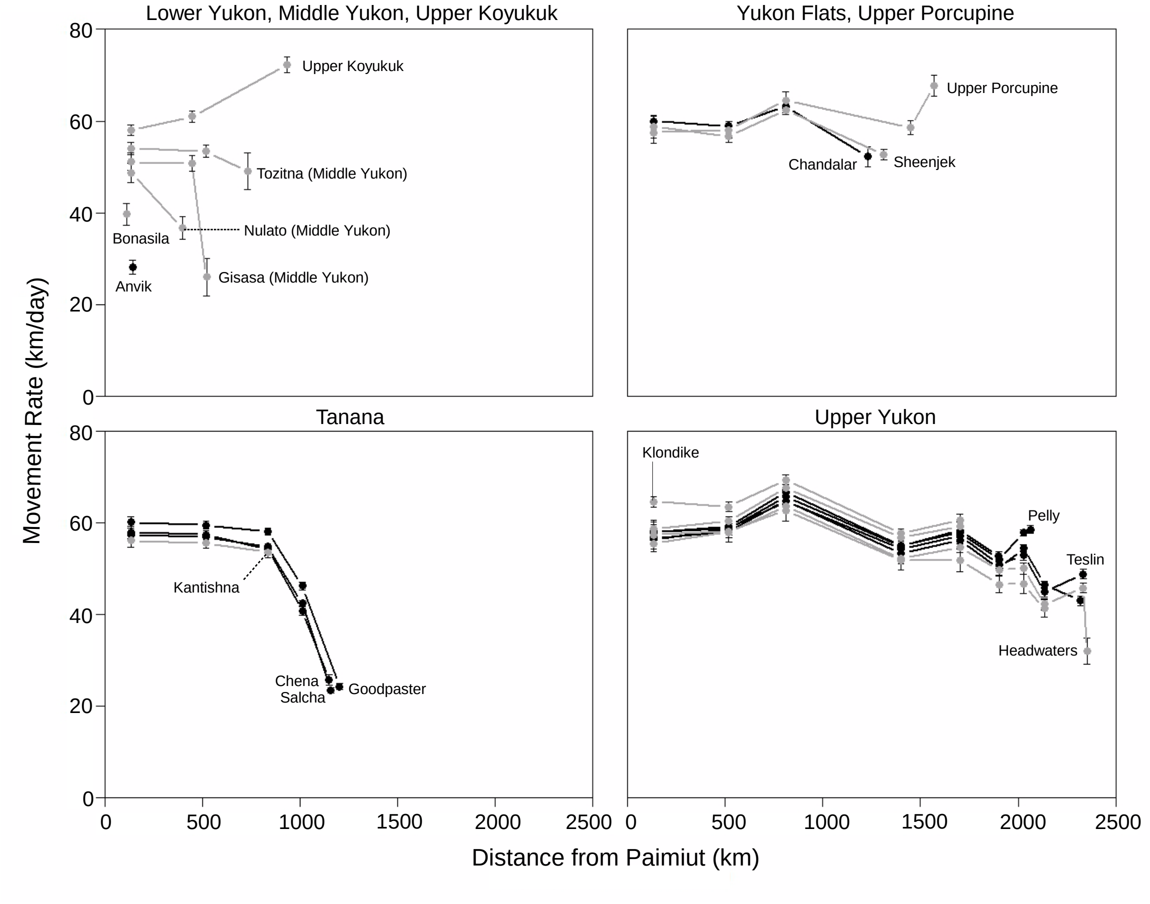


Figure 3.— Migration rates by distance traveled for the principal Chinook salmon stocks returning to regional areas of the Yukon River basin during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated. Estimates and standard error are based on fish with complete migratory histories (recorded by all stations passed).

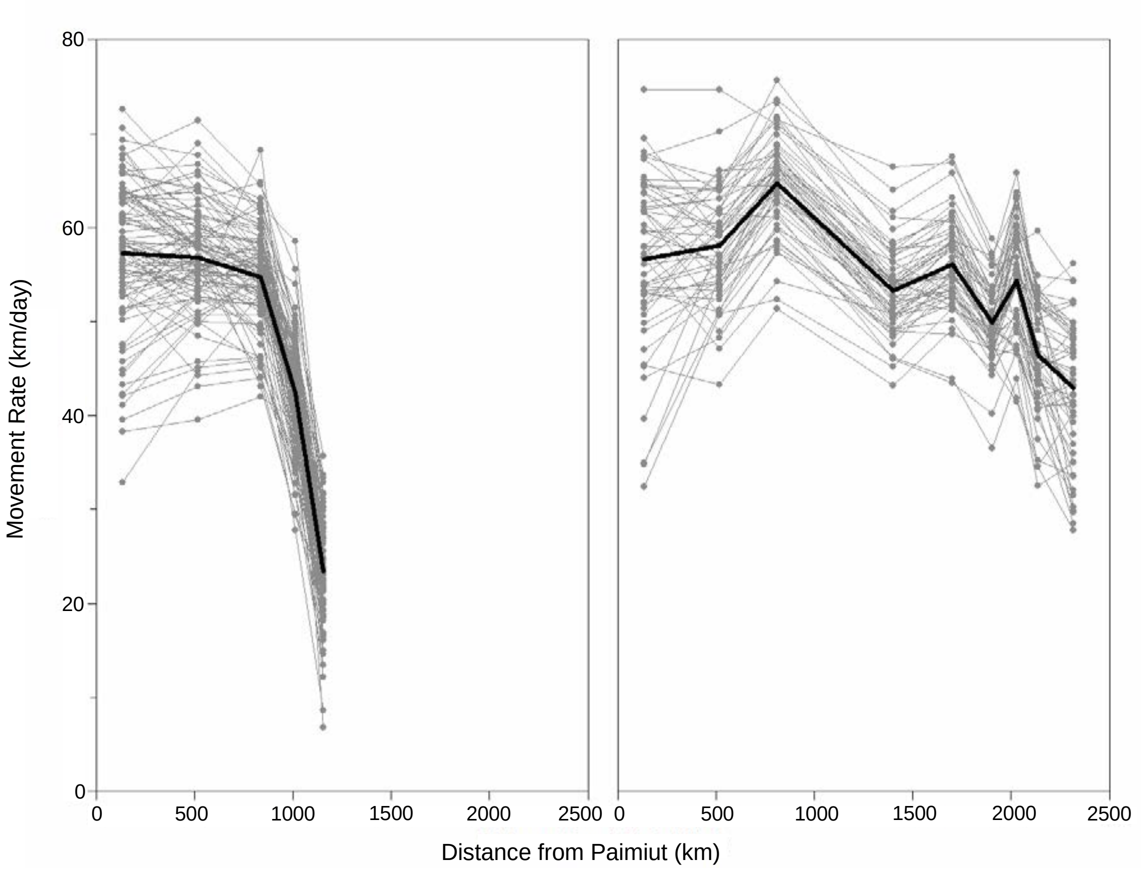


Figure 4.— Migration rates by distance traveled for individual Yukon River Chinook salmon returning to the Salcha and Big Salmon rivers during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated.

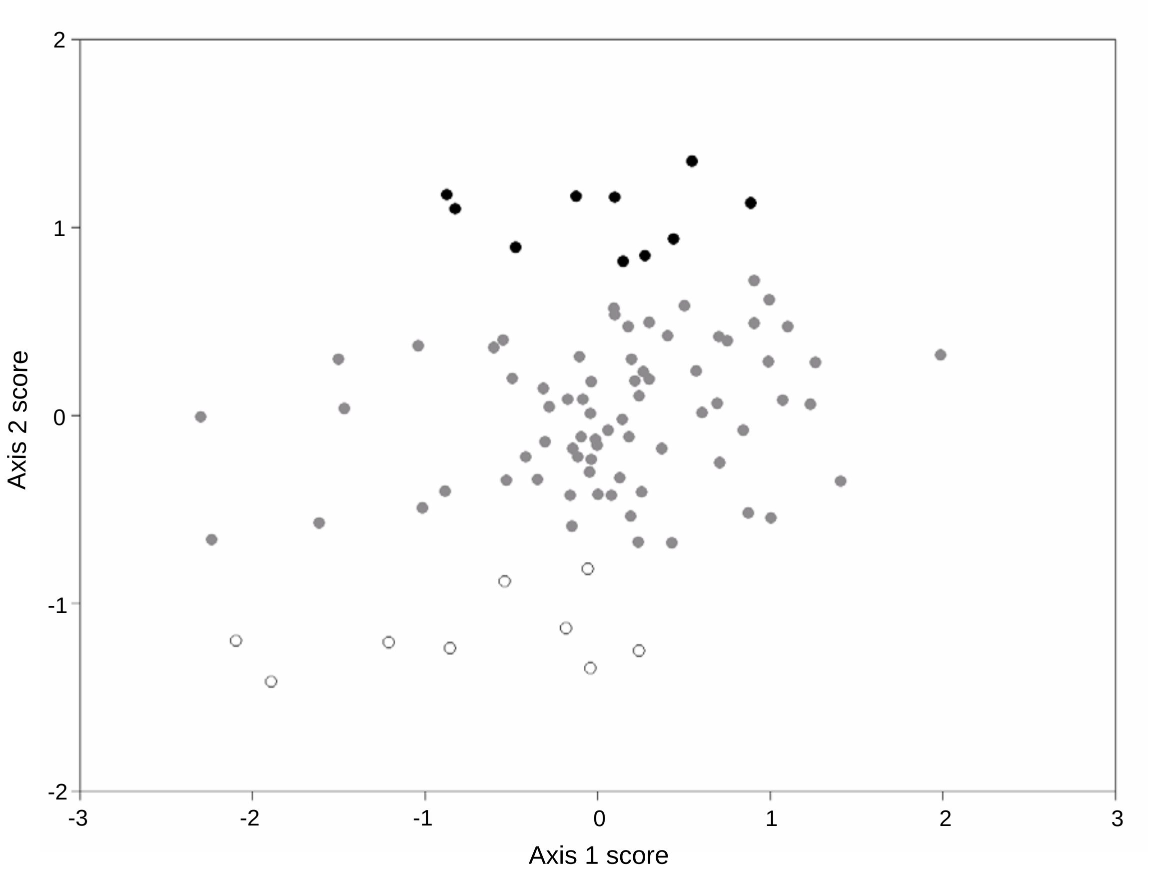


Figure 5.— Nonmetric multidimensional scaling (NMS) ordination based on upriver migration rates of 96 Yukon River Chinook salmon returning to the Salcha River and recorded by five sequential tracking stations located along the migratory route during 2002-2004. The upper 10% (dark circles), central 80% (open circles), the lower 10% (dark triangles) of the Axis 2 scores of the fish are indicated.

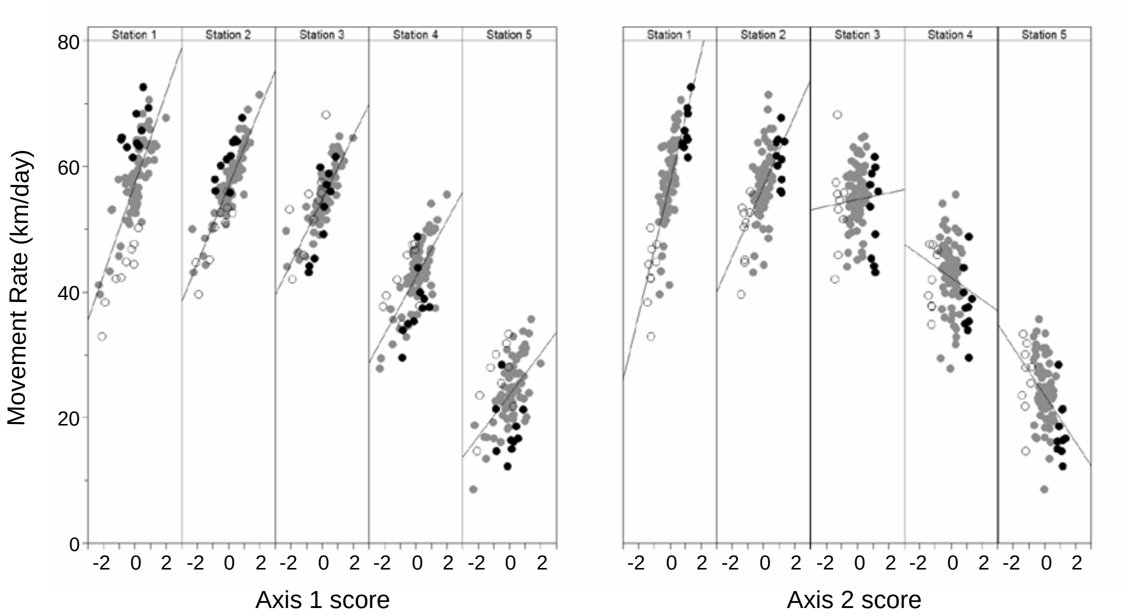


Figure 6.— Relationship between migration rates and nonmetric multidimensional scaling (NMS) ordination scores for 96 Yukon River Chinook salmon returning to the Salcha River during 2002-2004. Both the Axis 1 and Axis 2 scores and associated regression lines are presented for the five sequential tracking stations located along the migratory route. The upper 10% (black circles, referred to as “hares”), central 80% (gray circles), the lower 10% (open circles, referred to as “tortoises”) of the Axis 2 scores of the fish are indicated.

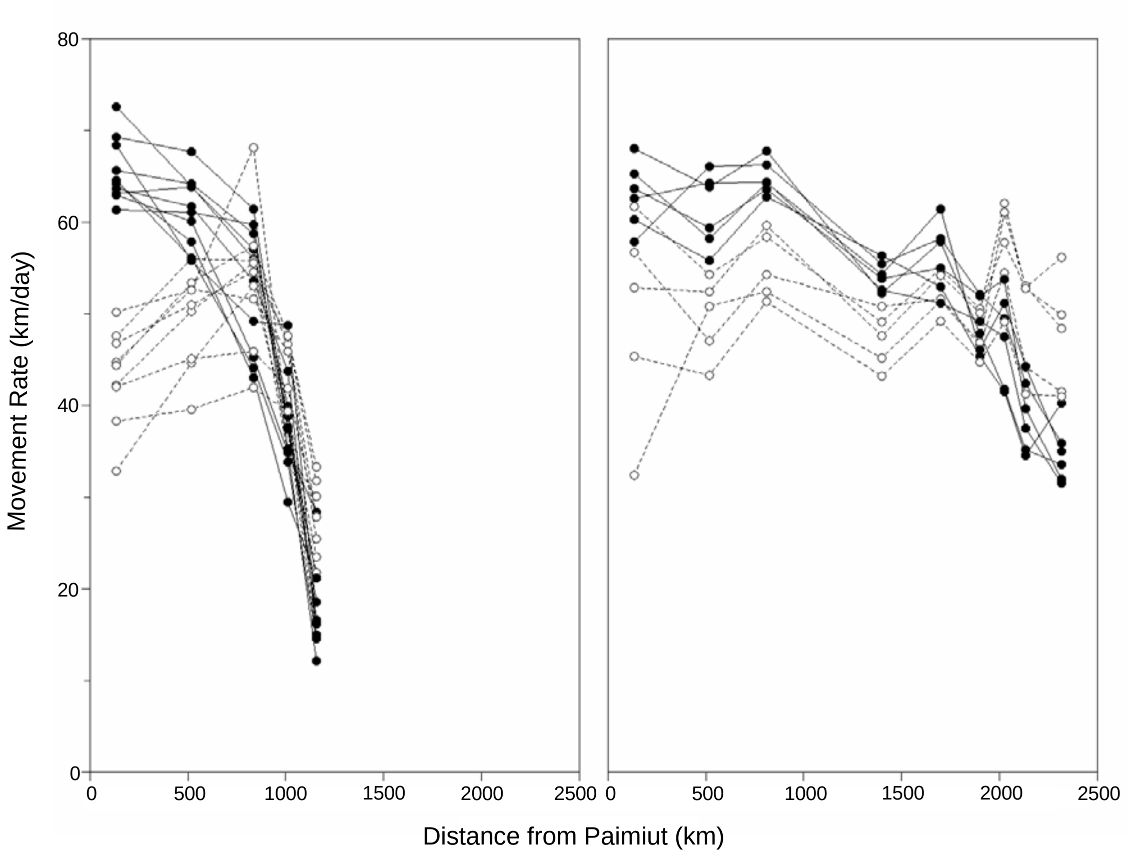


Figure 7.— Migration rates by distance traveled for individual Yukon River Chinook salmon returning to the Salcha and Big Salmon rivers during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated. The fish shown include the upper 10% (dark circles, referred to as “hares”) and the lower 10% (open circles, referred to as “tortoises”) of the Axis 2 scores from a nonmetric multidimensional scaling (NMS) ordination.

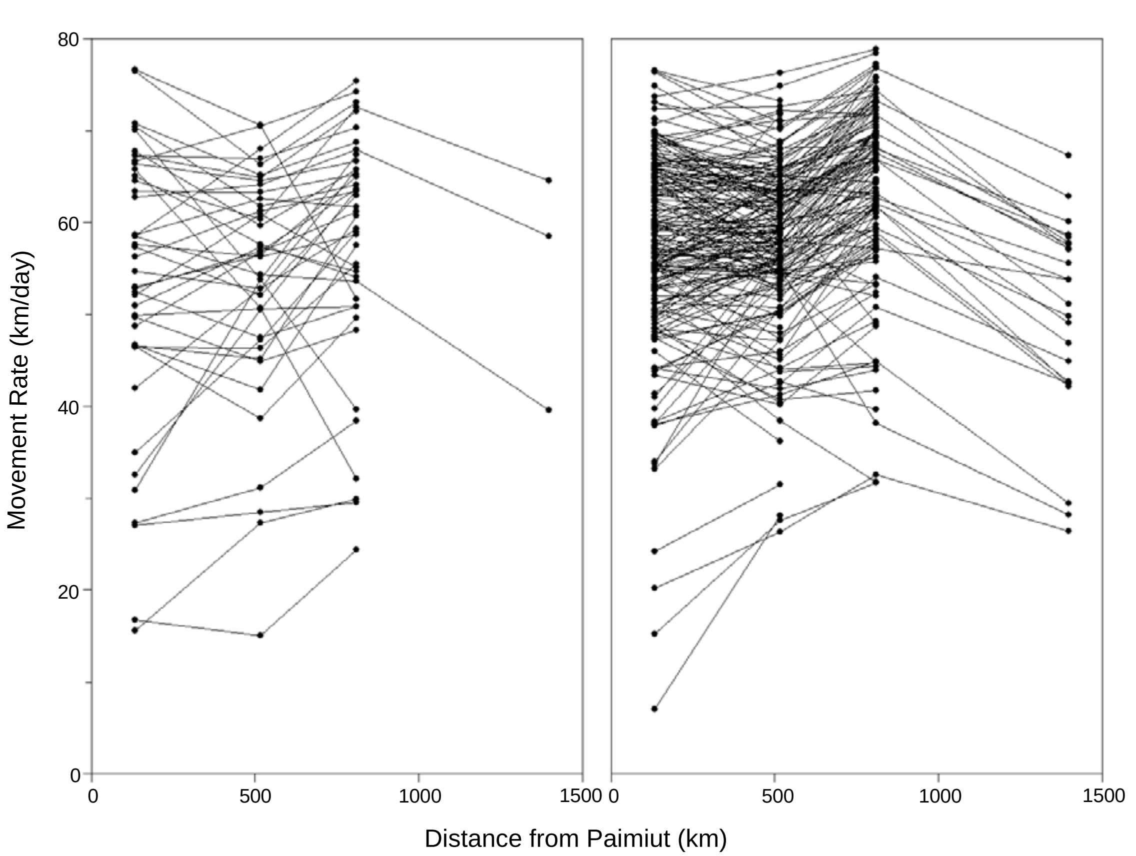


Figure 8.— Migration rates by distance traveled for individual Yukon River Chinook salmon tracked to non-terminal areas (left panel) or harvested in mainstem fisheries (right panel) in the Yukon Flats during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated.

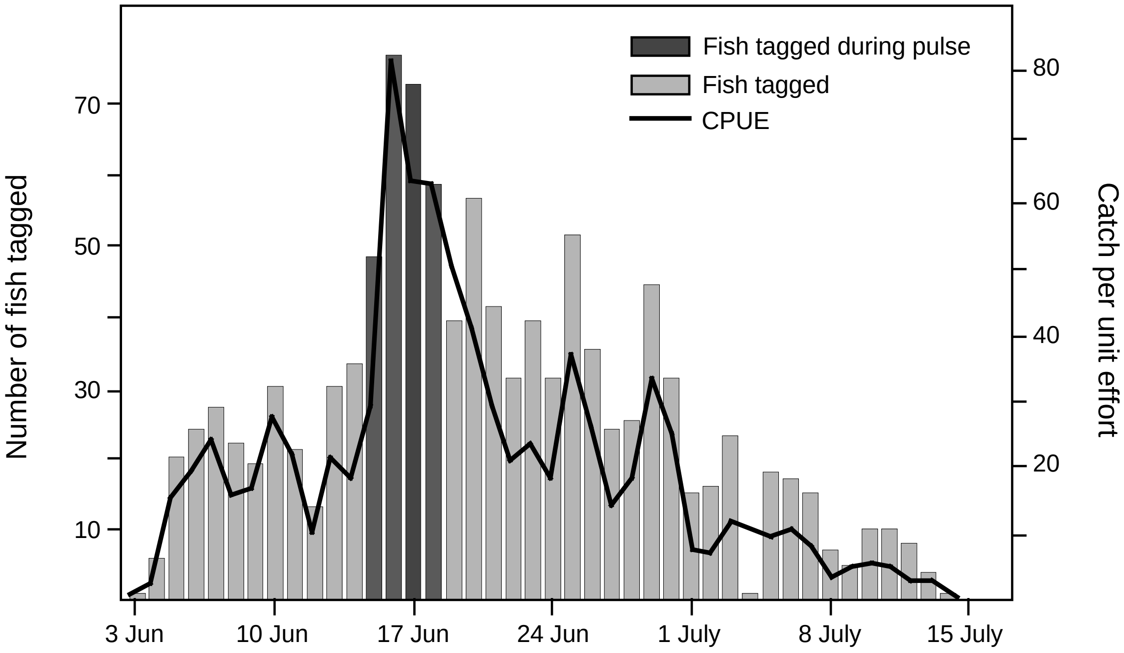


Figure 9.— Daily number of Chinook salmon radio tagged in the lower Yukon River and daily catch per unit effort information for Chinook salmon captured at the Russian Mission tagging site during 2003. The fish tagged during the pulse associate with the peak of the run (15-18 June) are indicated.

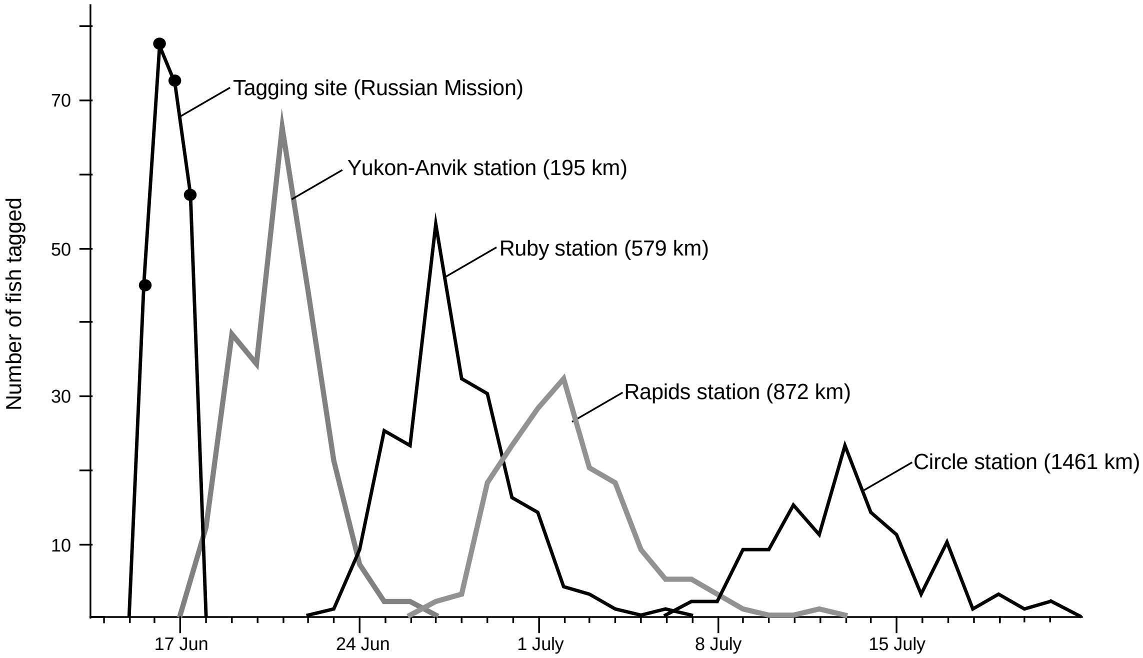
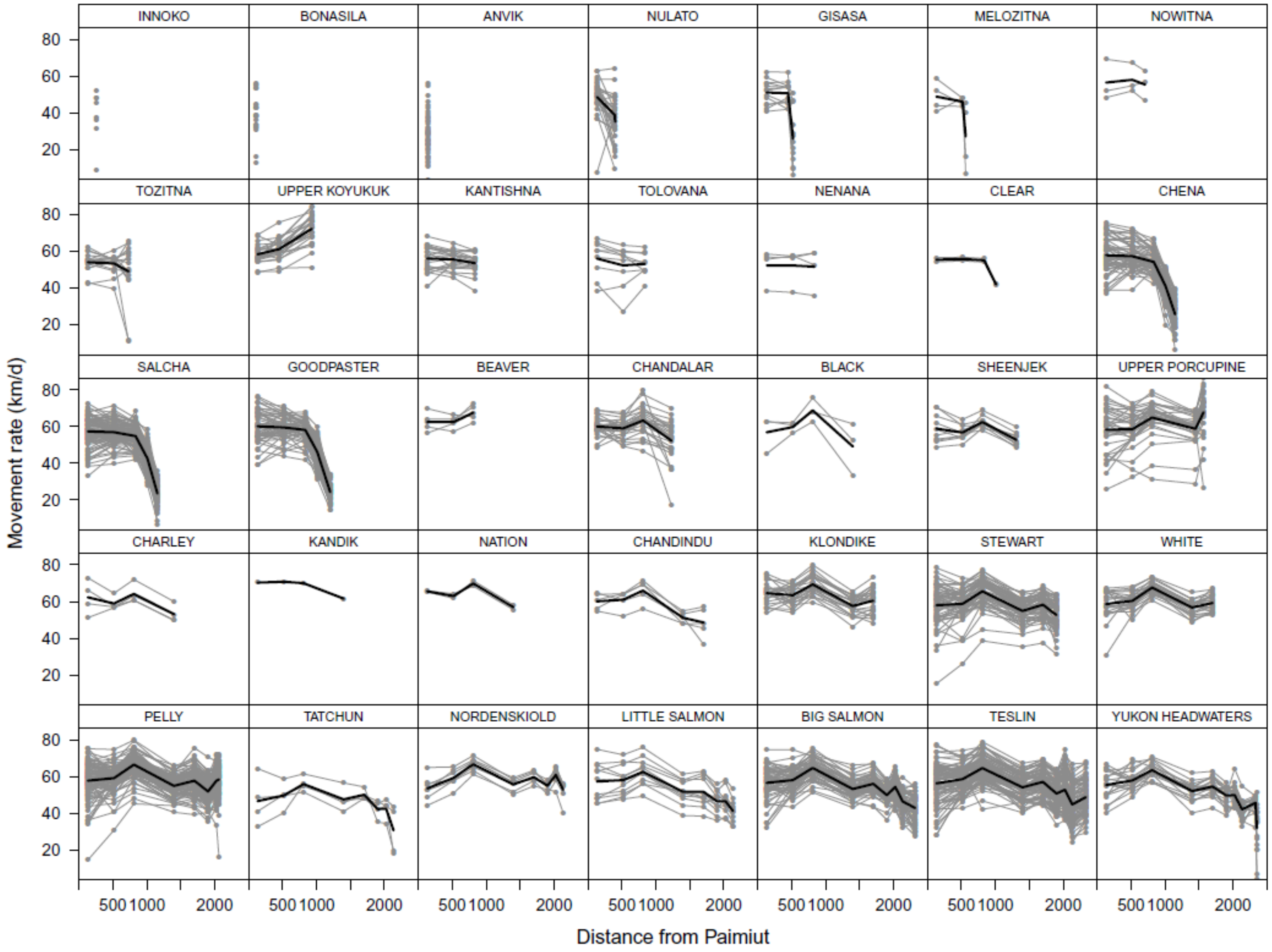
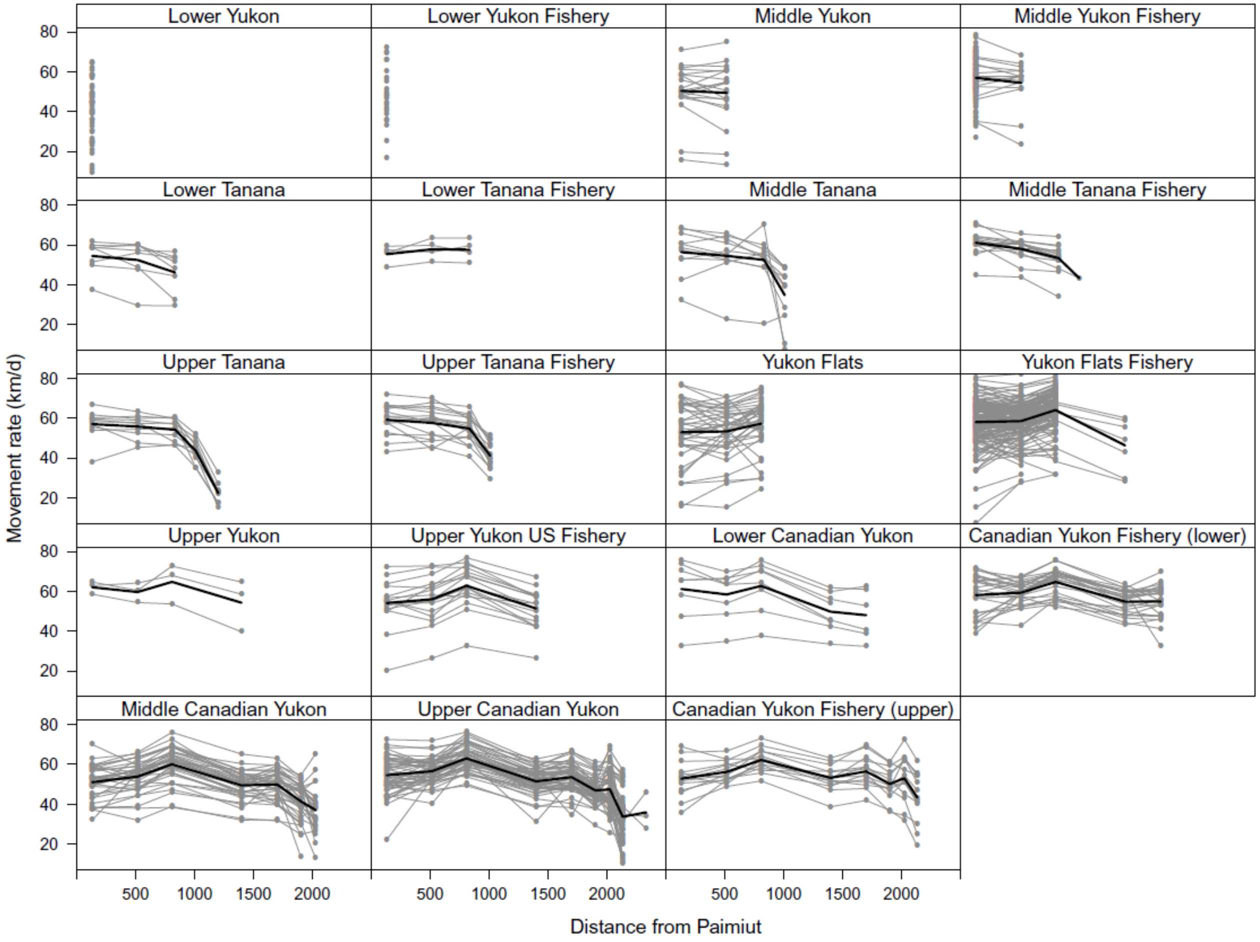


Figure 10.— The upriver progression of fish tagged during the pulse of Chinook salmon moving past the Russian Mission tagging site during 15-18 June 2013 and located at successive upriver locations. Points indicate the daily number of fish tagged. Distances upriver from the tagging site are in parentheses.

Appendix A.— Migration rates by distance traveled for Chinook salmon returning to terminal tributaries in the Yukon River basin during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated by the points.



Appendix B.— Migration rates by distance traveled for Chinook salmon harvested in fisheries or last located in non-terminal reaches of the Yukon River basin during 2002-2004. The locations of tracking stations along the migratory route used to record the fish are indicated by the points.



Factors Affecting the Spawning Migration of Chinook Salmon in a Large, Free-flowing River Basin as Determined by Different Analytical Methods

John H. Eiler[1,2], James T. Peterson[2], Carl B. Schreck[2], and Allison N. Evans[3]

[1]National Marine Fisheries Service, Alaska Fisheries Science Center
Auke Bay Laboratories, Juneau, Alaska 99801, USA

[2]U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit
Department of Fisheries and Wildlife, Oregon State University
Corvallis, Oregon 97331, USA

[3]Department of Fisheries and Wildlife, Oregon State University
Corvallis, Oregon 97331, USA

Abstract. — Upriver migration rates exhibited by radio-tagged Chinook salmon in sequential reaches of the Yukon River basin were compared to the physical features of the basin and biological characteristics of the fish. The data were analyzed with hierarchical linear regression models and within-stock multivariate ordination. Similar results were observed with both analytical methods, suggesting that the findings were not dependent on the approach used. Upriver movements were influenced by a wide range of factors, with evidentiary support for complex, multi-faceted relationships. Physical features of the basin demonstrated stronger explanatory power, accounting for over 70% of the observed variation in migration rate compared to 18% for biotic factors. Parameter estimates associated with the steepness of the migratory route and remaining distance were most strongly correlated with migration rate, with consistent relationships observed across stocks. Migration rates were noticeably slower in extensively braided reaches of the basin. Although river discharge was negatively related to the movements of Tanana River fish, no relationship was observed for Upper Yukon fish passing into Canada. The weaker relationships between migration rate and biotic factors may reflect stabilizing selection on long-distance migrants. Smaller fish exhibited minimally faster swimming speeds on average than larger individuals. This relationship was stronger in highly braided reaches. Run timing was positively related with migration rate for most stocks. Surprisingly, upper basin stocks traveling farther upriver displayed progressively negative relationships, suggesting that late-run fish were moving slower. Ancillary information suggests that this decline may relate to deteriorating fish condition later in the season.

Keywords: Chinook salmon, spawning migration, migration rate, swimming speed, Yukon River, radio telemetry

Introduction

After spending multiple years at sea, Chinook salmon (*Oncorhynchus tshawytscha*) return to natal rivers and streams throughout the northern Pacific Rim, ranging from small coastal drainages to vast river basins (Healy 1991, Heard et al. 2007). The fish often travel substantial distances after entering freshwater to reach suitable spawning areas. These lengthy migrations represent an energetic challenge, particularly because the fish stop feeding during this period and exhibit a catabolic state for the duration of their lives (Brett 1995). The cessation of feeding has severe repercussions, because the fish must rely solely on existing energy reserves. Although this behavior is less of a concern for populations spawning in small coastal rivers or tributary streams near saltwater, the energetic constraints on fish traveling extended distances inland are much more severe. These fish have the added burden of having to partition energy reserves to support both gamete formation and the physical demands associated with migration. Fish traveling shorter distances are not encumbered by this restriction, because sexual maturation typically occurs prior to entering freshwater (Brett 1995, Crossin et al. 2004).

In addition to being in suitable physical and physiological condition for the long arduous journey, salmon must select the migratory timing and swimming patterns that enable them to complete the migration when local conditions are favorable (e.g., adequate water levels and flow for accessing spawning sites, suitable water quality and temperatures for egg development and survival) and when other sexually mature fish are present. The fish must also arrive at their final destination with sufficient energy reserves to avoid predation, complete sexual maturation, compete with other individuals for redd sites and mating privileges, and reproduce. Not surprisingly, the swimming behavior exhibited by the fish during the migration and the environmental conditions encountered can have a significant impact on the success of the fish in reaching their final destination and reproducing (Blackbourn 1987, Quinn 1990). Run timing for Chinook salmon returning to the Yukon River is relatively compressed compared to rivers in the southern parts of their range (Chapter 3), suggesting a relatively narrow window when proximal conditions are favorable for spawning. For example, the Yukon River is covered with ice for over half of the year, which may influence run timing, whereas the more southerly river (e.g., Columbia River and Sacramento River) are typically ice free year round.

The physical and energetic challenges associated with the spawning migration are amplified in large river systems such as the Yukon River in Alaska and northwestern Canada. Yukon River Chinook salmon spawn throughout the basin. While fish returning to lower river tributaries may only travel several hundred kilometers and arrive on the spawning grounds within a couple of weeks, some upper basin fish travel over 3200 km from the mouth and take over 60 days to reach their final destination (Chapter 4). Understanding the factors that influence these movements can provide insights into the constraint imposed by the migration on returning salmon and the potential impact this may have on reproductive success.

In spite of the severe logistical challenges, movement studies in the Yukon River basin present several distinct advantages. The basin is essentially free flowing, providing an opportunity to document long-distance migratory patterns and assess the factors influencing these movements under natural conditions. Only a small, passable hydroelectric dam located on the Yukon River main stem ~ 2500 km upriver from the river mouth impedes the natural flow of water. Less than 3% of the returns pass this site, and a naturally-occurring lake < 35 km downstream minimizes any impact that might be caused by the restricted flow. Sizeable numbers of Chinook salmon return to the basin (Spencer et al. 2009) with major stocks spawning in different regional areas (Chapter 3), making meaningful comparisons possible for fish traveling varying distances and subjected to a range of migratory conditions. The information is also timely. Chinook salmon returns to the Yukon River basin were relatively stable until the late 1990’s when dramatic declines in abundance and harvest levels were reported (JTC 2001). This trend has continued during subsequent years, and resulted in closures or drastic reductions in commercial fisheries, severe restrictions in subsistence harvests, and difficulties in meeting regional and basin-wide escapement goals (ENS 2012, JTC 2012). Similar trends have been observed in other large rivers in western Alaska (Heard et al. 2007).

Better understanding of the migratory patterns and the factors affecting these movements would be beneficial to managers responsible for assessing changes in run abundance, escapements, stock composition, and age structure.

In response to declining abundance, a basin-wide telemetry study was conducted to provide detailed information on the run characteristics of Chinook salmon returning to the Yukon River basin. The overall objectives were to determine the nation of origin (U.S. vs. Canada), stock composition and timing, and spawning distribution of the returns. An unintended benefit of the study was that it also provided information on the upriver movements of the fish. Movement data can provide a number of insights into the status and underlying dynamics of salmon returns, particularly in large river basins. In Chapter 4, we described the migratory patterns of Chinook salmon returning to the Yukon River basin. Here, we examine the biological and physical factors that potentially affect these movements. Movement data is messy, since it encompasses both spatial and temporal aspects of an animal's life history. Unlike the well established methods used to estimate abundance, survival, and mortality, the quantitative methods for analyzing and modeling animal movements had lagged noticeably behind (Turchin 1998). Recent technological advances, particularly in the field of biotelemetry, have dramatically improved the ability to document salmon movements, and increasing efforts have been made to analyze these migratory patterns (Keefer et al. 2004, Salinger and Anderson 2006, Cooke et al. 2008). In this paper, we compare two distinctly different analytical methods for examining complex data – hierarchical linear models and non-parametric multivariate ordination – to assess the utility of these methods for analyzing salmon movements.

Methods

Study Area

The Yukon River basin drains a watershed of more than 855,000 km^2. The main river alone flows for more than 3,000 km from its headwaters in Canada to the Bering

Sea (Figure 1). The river is relatively deep, with channel depths exceeding 20 m in the lower basin compared to 12-14 m downstream of the Yukon-Tanana River confluence and 5-7 m near the U.S.-Canada border (distances of ~ 1100 km and 2000 km from the river mouth, respectively). Several major tributaries flow into the Yukon River main stem, including the Koyukuk and Tanana rivers in the United States; the Stewart, White, Pelly, and Teslin rivers in Canada; and the Porcupine River, which transects both countries. The basin also includes numerous medium and small-sized tributaries. In addition to its large size, the Yukon River is the fifth largest drainage in North America in terms of total annual discharge, and exhibits considerable temporal variability with greater flows during the summer months (Brabets et al. 2000, Yang et al. 2009). The basin is remote with limited access to most areas.

Most reaches of the basin consist of a primary river channel with occasional side channels and sloughs, although the Yukon River main stem is extensively braided in the area commonly referred to as the Yukon Flats (Figure 1). Sections of the Tanana River, White River, and the Canadian main stem are also noticeably braided. Water visibility in many areas is extremely poor, particularly in the Tanana and White rivers due to turbidity from glacial activity in the upper headwaters of these drainages. Regional designations were based on geographic location and the general geomorphology of the area; e.g., lower reaches of the Porcupine River were considered part of the Yukon Flats due to similarities in landscape and river characteristics.

Fish Capture, Tagging, and Tracking

Details regarding the methods used to capture, tag, and track the fish are described in Chapter 2. Briefly, returning adult Chinook salmon were caught with drift gill nets near the village of Russian Mission (located approximately 300 km upriver from the river mouth) during 2002-2004 and Marshall (located approximately 90 km downriver from Russian Mission) during 2002. The fish were tagged with pulse-coded radio transmitters manufactured by Advanced Telemetry Systems (Isanti, Minnesota)[1]. The transmitters were gently inserted through the mouth and into the stomach of the fish. Each transmitter emitted a unique signal (as described by Eiler 2012), making it possible to identify individual fish, and was equipped with a motion sensor and activity monitor (as described by Eiler 1990). The fish were also marked externally with spaghetti tags attached just below the dorsal fin (as described by Wydoski and Emery 1983) to help identify tagged individuals caught in fisheries or located in spawning areas.

Information on the physical characteristics of the fish was also recorded, including body length (mid-eye to fork of tail) and external color (iridescent silver, silver, and blush – silver with reddish tinges). Iridescent silver indicated that the fish were not as advanced in their transition to freshwater as those with silver coloration; the initial onset of spawning coloration (blush) provided an outward sign of advancing sexual maturation. A tissue sample was taken from the axillary process for genetic stock identification studies, and scales were collected to provide age data (as described by DeVries and Frie 1996). Data on sex were not collected because of difficulties in distinguishing the sexes in the lower river due to the lack of distinct external characteristics. Fish were released back into the main river immediately after the tagging procedure was completed.

Radio-tagged fish that moved upriver were tracked with remote tracking stations (as described by Eiler 1995) located at 40 sites throughout the basin (Figure 1). The stations were placed on important migration routes and major tributaries of the drainage. Pairs of stations were located at sites with special significance (e.g., major confluence, international border), including Paimiut, lower Koyukuk River, lower Tanana River, Rampart Rapids, Yukon Border, and Porcupine Border, to avoid loss of data due to technical problems with the equipment, damage from bears (*Ursus* spp.), or other unforeseen difficulties. Aerial tracking surveys were conducted with fixed-wing aircraft and helicopters to locate fish that traveled to areas between station sites and upriver of

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA or U.S. Geological Survey.

stations on terminal tributaries. The equipment and methods used to track and relocate the fish are described by Eiler (2012).

Upriver Movements

Radio-tagged fish that passed the first station site (hereafter referred to as Paimiut), located approximately 62 km upriver from Russian Mission, were considered to have resumed upriver movements. Fish tracked to terminal tributaries within the basin (i.e., their final destination) were classified as distinct spawning stocks. Since fidelity to natal rivers was strong during the study, fish harvested in terminal tributaries were assumed to be destined for those areas, and considered part of those populations. The status of fish last located in non-terminal reaches, such as sections of the Yukon River main stem, was less certain because they could represent fish spawning in nearby areas or fish in-transit to spawning grounds farther upriver. Many non-terminal areas were turbid and hard to access, making verification of spawning activity difficult. Fish last recorded in these areas were not included in the analysis.

Migration rates (km/d) between sequential stations were determined for fish tracked to terminal tributaries within the basin (Chapter 4). These data were used to describe the movements exhibited by the fish within different reaches of the basin. Migration rate was considered a good measure of upriver movement since it normalized differences in the distance traveled between stations, which ranged from 20 km to 639 km. Scatter plots of the data comparing the distance and time traveled exhibited a linear relationship, suggesting that movement rate was a suitable measure. Movement data between the tagging site and Paimiut were not included in the analysis to avoid incorporating tagging-induced behavior that could bias results. The methods used to determine the time taken and distance traveled by the fish between stations are described in Chapter 4. Elevation for the fish locations was determined in the field using GPS receivers (Garmin, Olathe, KS) and verified post-season using electronic overlays of the basin (ArcGIS, Version 10.0, Esri, Redlands CA).

Statistical Analysis

Telemetry-generated movement data typically consist of multiple observations recorded over time and at varying locations for the tagged individuals, which in the case of this study were used to calculate migration rates for sequential reaches of the basin (see Chapter 2). These observations represent repeated measures; which violate statistical assumptions of independence, can result in aggregation bias and erroneous estimates of precision, and preclude the use of more traditional regression models (as discussed by Raudenbush and Bryk 2002). To account for the problems associated with repeated measures, we explored a variety of statistical methods for analyzing the data, including the comparison of clustered trajectories (as described by Hafner et al. 2006), probabilistic Bayesian networks (as described by Neapolitan 2004), and various derivations of linear regression models used for both fisheries and non-fisheries applications (as described by Salinger and Anderson 2006, Dixon et al. 2008). Ultimately, we selected two distinct analytical methods to identify and evaluate the factors affecting the upriver movements of the fish: hierarchical linear regression (as described by Raudenbush and Bryk 2002), also known as mixed-effects models because both fixed and random effects are incorporated, and non-parametric multivariate ordination (as described by McCune and Grace 2001). These two methods were selected because they seemed most suitable for the type of information typically collected during fish telemetry studies, and because they represented fundamentally different analytical approaches, thereby providing a robust comparison of the various approaches available.

Hierarchical Linear Regression Models

Hierarchical liner regression models are useful for analyzing complex data structures. They differ from conventional linear regression in that dependence among the repeated measures (and any associated temporal and spatial autocorrelation) is accounted for by including random effects (Snijders and Bosker 1999). The telemetry data collected during this study had a hierarchical structure consisting of repeated observations for individual fish (level 1), which were nested within individual stocks (level 2). The location of the observations (station site) was also treated as a random effect due to within-site dependence that could not be accounted for by the covariates. Whereas the fixed-effects of the model reflected the average relationship between the response and predictor variables (e.g., migration rate in relation to river gradient), the random effects estimated the variance remaining after accounting for the covariates. Incorporating random effects also made it possible to compare variation among levels, whereas traditional linear regression analyzes all effects at a single level (Raudenbush and Bryk 2002).

A hierarchical linear regression model was developed with a lower and upper level component. The lower level model was constructed as:

$$Y_{ijk} = \beta_{0j} + \beta_{pj} X_{pijk} + \beta_q X_{qijk} + \ldots + r_i + r_k + r_{ijk}$$

where Y_{ijk} was the migration rate for fish i from stock j at station k, β_{0j} and β_{pj} were the intercept and effect of the explanatory variable p on migration rate, respectively, varying randomly among stocks, X_{pijk} was the value of variable p, β_q was the fixed effect of the explanatory variable q on migration rate, X_{qijk} was the value of variable q, r_i and r_k were the random effects associated with fish and station, which were assumed to be normally distributed with a mean of zero and random-effect-specific variance, and r_{ijk} was the residual. The upper level of the model was:

$$\beta_{0j} = \gamma_{00} + \gamma_{01} * W_{1j} + \ldots + \gamma_{0S} * W_{Sj} + u_{0j}$$
$$\beta_{pj} = \gamma_{p0} + \gamma_{p1} * W_{1j} + \ldots + \gamma_{pS} * W_{Sj} + u_{pj}$$

where W_{Sj} represented the stock-specific variable, γ_{00} was the mean intercept, γ_{p0} was the mean slope, γ_{01} and γ_{0S} were the effect of the stock-specific variables (1,2,…s) on the intercept, γ_{p1} and γ_{pS} were the effect of the stock-specific variables (1,2,…s) on the slope, and u_{0j} and u_{pj} were the random effects of stock on the intercept and slopes, respectively, which were assumed to be normally distributed with a mean of zero and random-effect-specific variance. Both u_{0j} and u_{pj} represented the unique effects associated with stock that were unexplained by the explanatory variables, which would equal zero if all the variation in the upper-level model was accounted for. Simply stated, explanatory variables, some varying by stock, were incorporated into the model to explain the observed variation in migration rate. Individual fish, stocks and stations were treated as random effects to explain and partition the remaining variation exhibited by migration rate after accounting for the explanatory variables. Random effects also reflected the unique effect of the explanatory variables varying randomly by stock (i.e., how much the slopes for these factors varied among stocks).

Model development.— Several candidate hypotheses (hereafter referred to as themes) were developed *a priori* as described by Anderson (2008). The themes provided a framework for examining the relationship between migration rate and potential explanatory variables, and for evaluating the relative empirical support for the different factors. The themes included:

- ***Motivation***: Salmon have limited time to complete their upriver migration, reach their final destination, and spawn. Migration rates are therefore affected by the time available to the fish (i.e., late run fish have less time to complete their upriver migration compared to early run fish) and the distance they must travel. Fish with greater limitations (e.g., less time available and farther distances to travel) will exhibit faster swimming speeds. This theme assumes that the movement patterns exhibited by the fish are genetically based (i.e., heritable traits rather than a response to the environmental conditions encountered).
- ***Fatigue***: Swimming upstream against current is strenuous activity. Migration rates are affected by the cumulative effort expended by the fish in relation to the conditions encountered. Fish that have traveled extended distances under strenuous conditions will be more fatigued than those that have traveled shorter distances. Likewise, fish that have experienced arduous migratory conditions over extended distances will be more fatigued than those that have traveled comparable distances under less demanding circumstances.

- ***Ability***: Migration rates are impacted by the physical capabilities and physiological condition of the fish. Stronger fish with greater energy reserves will exhibit better swimming performance than weaker individuals with marginal reserves. Similarly, fish that are more sexual mature are using energy reserves for both movement and reproduction (e.g., physical changes, gamete formation and maturation), and swimming performance will be adversely affected.
- ***Environment***: Migration rates are affected by the physical characteristics of the river, with reduced swimming performance in areas with complex geomorphology and adverse local conditions (e.g., swift currents, steep gradients).

Explanatory variables representing the biological and behavioral characteristics of the fish and the physical features of the basin were assigned to the theme that best described the nature of their (potential) relationship to migration rate.

The explanatory variables *length*, *age*, *color*, *run timing*, and *final destination* were used to describe the biological and behavioral characteristics of the fish. Fish passage through the lower river, based on capture date at the tagging site, was used as a proxy for *run timing*. *Final destination* was designated by both region (Figure 1) and stock affiliation. Explanatory variables were also used to describe the physical features associated with the migratory routes, including several measures of distance traveled, elevation, and river characteristics. Since the final destination of the fish was known, distance estimates were calculated for the total distance traveled (from Paimiut to the final station located on the fish's terminal tributary), current distance traveled (from Paimiut to the station where the fish was recorded for that particular observation), and the distance remaining to reach the final destination (from the station for that particular observation to the final station).

River elevation within the basin ranged from relatively low sections in the Lower Yukon and Middle Yukon to increasingly higher reaches in headwater areas (Figure 2). Elevation change and river gradient (i.e., elevation change in relation to distance) were determined for the entire migratory route traveled by the fish (from Paimiut to the final station), the cumulative route (from Paimiut to the station for that particular observation), and the between-station reaches. Efforts were also made to identify basic differences in river characteristics within the basin. The Yukon Flats (Figure 1) is a unique area, and was categorized as extensively braided compared to other reaches used by migrating fish.

Other potential factors were harder to quantify due to the vast size, complexity, and dynamic nature of the drainage. For example, data on river discharge and stage was only available at several locations within the basin, and how these factors influenced conditions downriver, in both a spatial and temporal sense is not well understood. Even if discharge and stage data could be accurately extrapolated to downriver sites, comparisons with telemetry data would be further complicated by differences in scale. These variables were therefore not incorporated in the analysis in deference to the principal of Occam's razor that, all things being equal, fewer assumptions usually provide the most likely explanation (Walsh 1979).

A global model (i.e., model containing all the possible predictors thought to influence migration rate) was developed using the theme parameters. This multi-step process included the selection of the model variables and associate error structure. Since there was reason to believe that some of the explanatory variables exhibited a similar relationship to migration rate, the themes were first refined by identifying and eliminating highly correlated predictor variables to reduce problems associated with multicollinearity. Pairwise comparisons were made of all continuous variables using Pearson's correlations (*r*) calculated with S-Plus (Version 7.0 for Windows, TIBCO Spotfire Inc., Seattle WA) to determine the degree of correlation (values ranging from -1.0 to 1.0). Pairs with values < -0.7 or > 0.7 were considered highly correlated (Moore and McCabe 1993). Because highly correlated variables were redundant in relation to migration rate, these terms were systematically exchanged (i.e., one discarded and replaced with the other) and tested using the procedures described below to avoid over fitting the model.

The second step consisted of developing a series of models using all of the non-correlated variables. Alternate models were constructed by systematically replacing variables with the highly correlated counterparts that had been previously discarded, so that all possible combinations of variables were represented. Although highly correlated with *reach gradient*, *cumulative gradient* was retained in the model since it was the sole variable representing the theme ***Fatigue***. Further analysis comparing changes in parameter estimates and standard errors in models with and without both variables indicated minimal bias and variance inflation when both variables were included. The interim global models were then fit to the data using R statistical software (Version 2.13.1, lme4 library, http://www.r-project.org) to determine the most appropriate combination of variables. Goodness-of-fit was determined by examining box, normal probability (QQ), and residual plots to verify that the statistical assumptions of independence, normality, and equal variance were met. The relative fit of the models to the data was determined using Akaike's Information Criteria (AIC, Akaike 1973). The models were ranked, with the lowest AIC score indicating the best approximating model and associated variables given the data and the set of interim models.

Finally, a similar process was used to determine how best to represent the random effects error structure of the global model. Although not the primary objective of the analysis, determining the error structure made it possible to partition and estimate the variation in migration rate not explained by the covariates. Using the global model variables, interim models with different error structures were constructed and fit to the data; including *fish* nested within *stock*, *fish* nested within *stock* and varying by *station*, *station* nested within *stock*, *station* nested within *stock* and varying by *fish*, varying by *fish* and *station* with *stock* fixed, and varying by *fish* and *station* with *stock* fixed and with selected explanatory variables nested within *stock*. The relative support for each model was evaluated using AIC, with the lowest calculated value indicating the best approximating error structure. Goodness of fit was assessed as previously described. The best approximating error structure and theme variables were designated as the global model.

Forty-eight candidate models were systematically constructed from the global model using all possible combinations of the four themes (including main effects and within-theme interactions) and the most plausible theme interactions. The set of candidate models ranged from relatively simple models (single theme) to the global model (most complex with all themes and theme interactions represented).

Model assessment.— A primary objective was to identify the model (or models) that best described the migration rate. To this end, the candidate models (derived from the global model) were fit to the data using R statistical software. The relative support for each model was estimated using AIC and Akaike weights (w_i) as described by Burnham and Anderson (2002). The number of parameters (K) used to estimate AIC included the fixed effects, random effects, and random-effect covariances incorporated when two or more random effects were included in the model. The models were ranked by AIC, with the lowest value representing the most likely (i.e., best) model. Given that more than one model might be plausible, Akaike weights (ranging from zero to one, with the highest value signifying the most plausible model) were used to estimate the likelihood that the candidate model provided the best fit. Similarly, Akaike weight ratios (best model w_i /alternate model w_i) were used to estimate the likelihood that the alternate models were comparable to the best model (Burnham and Anderson 2002). Alternate models with Akaike weight ratios within 12% of the best model (as described by Royall 1997 for evaluating strength of evidence) were considered plausible. Rather than basing model inferences on a single model, the plausible models were used as a confidence set for assessing model selection uncertainty, similar to a confidence interval for parameter estimates (Burnham and Anderson 2002). The relative importance of the theme parameters was also estimated by summing the Akaike weights for all models that contained the theme (Burnham and Anderson 2002). Both the primary themes and theme interactions were evaluated in this manner. Pearson's coefficient of determination (r^2) was used to estimate the proportion of the variability in migration rate accounted for by the model.

Parameter estimates for the fixed and random effects were reported for models in the confidence set. The data were standardized (i.e., independent variables scaled with mean = 0 and standard deviation = 1) to provide a relative measure of the magnitude of the relations, making it possible to compare the effect each variable had on migration rate in relation to the other variables, and to reflect the full range of the data (as described by Raudenbush and Bryk 2002). While AIC, ΔAIC, w_i, and relative importance weights provided evidentiary support for determining which explanatory variables were related to fish movements, the parameter estimates indicated the magnitude of the effect (i.e., factors with larger parameter estimates were more strongly related to migration rate). The precision of the fixed effect variables was determined by calculating the 95% confidence interval (as described by Sokal and Rohlf 1969). The magnitude and precision of the parameter estimates were used to infer biological importance in relation to migration rate. Data plots were used to illustrate the relationship between migration rate and important variable interactions. The amount of variation accounted for by the explanatory variables was estimated by comparing the random-effect estimates from the best model with estimates from the random-effects analysis of variance (ANOVA) fit to the data.

The random-effect estimates for *fish* and *station* reflected the predictable variation in migration rate among individual fish and sites not accounted for by the fixed-effect explanatory variables. The random effect *stock* was not a random sample, because all known spawning populations were included in the analysis, and the estimate therefore represented the predictable variation among these particular stocks. The magnitude of the variation between individual fish, stocks, and stations was determined by dividing the standard deviation by the mean migration rate to provide a mean-normalized estimate of variance (similar to a coefficient of variation) and to identify the random effects exhibiting substantial differences. Similarly, the variation of the explanatory variables that varied by stock was determined by dividing the standard deviation by the parameter estimate. Empirical Bayes plots (Raudenbush and Bryk 2002) were used to show the variability of the stock-specific relationships.

Multivariate Ordination

Migration rates in sequential reaches of the basin were compared across individual fish within a stock (fish movements) using nonmetric multidimensional scaling (NMS), a nonparametric ordination technique (Kruskal 1964, Mather 1976). NMS was selected over other ordination methods because it can accommodate nonnormal or discontinuous data, does not assume linearity, is based on ranked distances, which improves its ability to extract information from non-linear relationships, can be used with any distance measure or data transformation, and is generally considered the most effective ordination method for ecological data (McCune and Grace 2002). Separate ordinations were conducted for each stock (i.e., within-stock analyses). Stocks with a minimum of four stations along the migration route and represented by $\geq$ 20 radio-tagged fish tracked to the terminal tributary were analyzed. Only fish that exhibited progressive movements upriver (i.e., only moving upstream), were recorded by all tracking stations along the migration route, and ultimately located at spawning sites within the terminal tributary were included in the sample.

The main data matrix used in the analysis consisted of individual fish (rows) by stations along the migration route of the stock (columns), with the cells denoting each fish's migration rate for the particular reach. The multivariate data were reduced to a small number of continuous synthetic variables (axes) representing both the strongest correlations between the response variables and the combined gradients of variation among the original movement data. NMS iteratively searched for an ordination with low stress as measured by the relationship between ranked distances in the original multidimensional space and those in the reduced dimensions (Peterson and McCune 2001). The ordination was conducted with PC-ORD software (MjM Software Design, Gleneden Beach Oregon) using the "slow and thorough" autopilot mode to determine the minimum stress value from 250 runs for up to six-dimensional configurations. A Monte Carlo test was performed using 250 runs of randomized data to determine if the ordination solution provided significantly more reduction in stress than expected by chance ($\alpha \approx 0.05$). Euclidean distance (McCune and Grace 2001) was used to calculate the dissimilarity matrix. This metric was considered suitable because movement data is continuous (i.e., all matrix combinations were possible), and absolute differences in migration rate (versus proportional differences), which were our primary interest, are adequately reflected by this measure. The meaning of the synthetic axes was interpreted using Pearson's *r*, Kendall's non-parametric rank correlation (τ), and scatter plots of the data to characterize the relationship between migration rates at sequential stations and the axis scores of the individual fish. The percentage of the variation in the original data represented by the ordination was determined by calculating Pearson's r^2 between the Euclidean distance for each pair of fish in both the ordination and original data.

A second matrix was created for each stock, consisting of the individual fish (rows) by explanatory variables (columns), and used to examine the relationship between migration rate and the biological characteristics (e.g., length, age, and color) and behavioral characteristics (e.g., run timing, time of arrival at the terminal tributary, and several measures of distance traveled) of the fish. The relationship between the axes scores and the explanatory variables was determine using Pearson's *r* and Kendall's τ to examine the correlation of each variable in relation to the axis score. Effect size (i.e., relative strength of the relationship between migration rate and the explanatory variables) was interpreted as weak for correlations approximating 0.10, moderate for correlations approximating 0.30, and strong for correlations approximating or greater than 0.50 (Cohen 1988).

A second series of within-stock ordinations was conducted comparing migration rates at sequential stations (movements by station) to examine the relationship between migration rates and the physical features of the basin represented by conditions at the station sites. The same analytical approach (NMS ordination and Euclidean distance measures), stock selection criteria, and evaluation measures were used. The main data matrix consisted of stations along the migration route of the stock (rows) by individual fish (columns), with the cells denoting the fish's migration rate at that particular station. A second matrix was created for each stock, consisting of stations along the migratory route (rows) by explanatory variables (columns), and was used to examine the relationship between migration rates for specific reaches of the basin and the physical features associated with the migratory route (including several measures of river gradient and distance traveled).

Assessing Effect of River Stage and Flow

Although river stage and flow (represented by discharge) potentially influence fish movements, data for these factors were only available at three sites within the study area; on the Yukon River main stem near the villages of Rampart (upriver from the Yukon-Tanana confluence) and Eagle (downriver from the U.S. Canada border), and on the Tanana River near the village of Nenana (Figure 1, Figure 3). The lack of information for other reaches of the basin and concerns over extrapolating stage and flow information to distant locations stymied efforts to incorporate these variables in the hierarchical linear model and multivariate ordination. Instead, linear regression was used to compare discharge with the migration rates exhibited by fish in reaches immediately downriver from Nenana (between the Manley and Nenana stations) and Eagle (between the Circle and Yukon Border stations). Information from Rampart was not included in the analysis because a substantial portion of the reach between the Ruby and Rapids stations was downstream from the Yukon-Tanana River confluence (Figure 1), and was therefore not reflective of the discharge at the Rampart site.

Separate multiple linear regression models were fit to data from the two sites using R statistical software. The models were constructed for each site as:

$$Y_i = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_p X_p + e_i, \quad i = 1, \ldots, n,$$

where Y_i was the migration rate within the reach for fish i, β_0 the intercept, β_p the coefficient of the p explanatory variables, and e_i the residual error. Similar to previous analyses, the explanatory variables *year*, *length*, *color*, *run timing*, *final destination* (stock), *distance* (from Paimiut to the spawning site within the terminal tributary), and *cumulative gradient* were used to describe the biological and behavioral characteristics of the fish and physical features of the migration route. Both *year* and *color* were categorical variables, with 2002 and iridescent silver used as the reference variables, respectively. The explanatory variable *discharge* was calculated as the average discharge at the site for the period that the fish were traveling through the downstream reach; discharge values for partial days were pro-rated based on the proportion of time that the fish were present. As before, pairwise comparisons were made of all continuous predictor variables using Pearson's *r* to identify potential problems with multicollinearity. River stage was highly correlated with discharge at the sites (*r* ~ 1.0), and was not used in the analysis since discharge was considered a better proxy for flow. *Discharge* was retained in all models. Other non-significant variables and interactions were removed from the model, and the reduced version fit to the data. Box, normal probability (QQ), and residual plots were used to verify that the statistical assumptions of independence, normality, and equal variance were adequately met.

Results

Fish Tagging and Migration Rates

Large numbers of Chinook salmon (n = 2,860) were captured and tagged during this study. The fish responded well to the handling procedures, with most (2790, 97.6%) resuming upriver movement after release. The average migration rates was 51 km/d, ranging from 28-40 km/d for stocks returning to natal streams in the Lower Yukon to 58-63 km/d for Porcupine River stocks (Table 1). Detailed information on run characteristics (e.g., stock composition, timing, spawning distribution, and migratory patterns) is presented separately (Chapter 2, Chapter 3, and Chapter 4). The upriver movements of 1,421 fish, representing 49 stocks, were analyzed using hierarchical linear models to determine the relationship between migration rate and associated factors; the remaining fish did not meet the established criteria and were excluded from the analysis. Due to the stricter sample criteria required, the migration rates of 542 fish, representing 11 stocks, were examined with multivariate ordination (Table 1).

Hierarchical Linear Regression

Factors Related to Migration Rate

Based on the model selection process, *fish*, *stock*, *station*, *length*, *color*, *run timing*, *remaining distance*, *cumulative gradient*, *reach gradient*, and *river type* were considered the best approximating variables and included in the global model (Table 2).

The model treated *fish*, *stock*, and *station* as random effects, with several fixed-effect variables (*reach gradient*, *remaining distance*, and *run timing*) varying by *stock*. Diagnostic plots indicated that the statistical assumptions of independence, normality, and equal variance were met. The explanatory variables from the global model were used to represent the underlying themes, with ***Motivation*** characterized by *run timing* and *remaining distance*, ***Fatigue*** by *cumulative gradient*, ***Ability*** by *length* and *color*, and ***Environment*** by *river type* and *reach gradient*.

Factors associated with *fish, stock,* and *station* accounted for 87.9% of the variation in migration rate based on the random effects ANOVA. Substantial differences were observed among the random effects, with *fish* accounting for 13% of the total variation, compared to 5% for *stock*, and 71% for *station* (Table 3). Approximately 12% of the observed variation was not explained by the random effects.

Forty-eight candidate models were fit to the data using hierarchical linear regression. The ten best approximating models are listed in Table 4. Relative importance weights for the themes and associated interactions indicated that all four themes were comparable and highly probable explanations of migration rate given the existing data (Table 5). Evidence for theme interactions differed substantially. The importance weights indicated strong support for ***Fatigue*** x ***Ability*** and ***Ability*** x ***Environment***, while the support for both ***Motivation*** x ***Ability*** and ***Fatigue*** x ***Environment*** was approximately three times less (Table 5).

Best approximating model.— The best approximating model mirrored the results obtained from the relative importance weights. This model contained the explanatory variables from the four themes, and the ***Fatigue*** x ***Ability*** and ***Ability*** x ***Environment*** theme interactions. The main effect variables included *reach gradient*, *cumulative gradient*, *river type, remaining distance*, *length*, *color*, and *run timing*. The variable interactions are listed in Table 6. Based on the Pearson's r^2 estimate, the model accounted for approximately 87% of the observed variation in migration rate. The explanatory variables associated with the model accounted for 31% of the variation explained by *fish*, *stock*, and *station*. Differences were observed among the random effects. Several variables were used to explain the variation in migration rate exhibited among individual fish, including *length*, *run timing*, and *color*. These variables were marginally descriptive, accounting for only 2% of the variation associated with *fish* in the random-effects ANOVA. The predictable variation remaining after these factors were accounted for was relatively large (5.1, Table 6), suggesting that the average swimming speed (48 km/d) would be expected to vary up to 5.1 km/d for similar fish. Migration rates were estimated to vary up to 11% between individuals (based on the mean-normalized estimate of variance) when all other conditions were held constant at average values, indicating that 11% of the observed variation was caused by factors not included in the model.

Compared to *fish,* the variables used to explain the variation in migration rate among stocks (including *reach gradient*, *cumulative gradient*, *remaining distance,* and *river type*) were relatively informative, accounting for 27% of the variation observed for *stock* in the random-effects ANOVA. The predictable variation in migration rate after these factors were accounted for was noticeably less (Table 6), with the average swimming speed for similar stocks varying on average by up to 2.7 km/d. Stocks were estimated to vary about 6% when all other conditions were held constant at average values, suggesting that 6% of the observed variation was caused by other factors.

The random effect *station* exhibited substantially more variation than *fish* and *stock*. The explanatory variables used in the best approximating model to explain the variation in migration rate among stations (including *reach gradient*, *cumulative gradient*, *remaining distance*, and *river type*) were relatively descriptive, accounting for over 36% of the variation observed in the random-effects ANOVA. The predictable variation in migration rate after these variables were accounted for was ± 9.8 km/d (Table 6), with migration rates varying up to 20% when all other conditions were held constant at average values.

Alternate models.— Four alternate models were considered plausible explanations of the data, and were included in the confidence set of models (Table 4). Based on Pearson's r^2 estimates, each of the models accounted for approximately 87% of the observed variation in migration rate. Based on comparisons with the random effects ANOVA, the explanatory variables in the alternate models accounted for about 31% of the variation in migration rate explained by the random effects, with the factors associated with *fish*, *stock*, and *station* accounting for 2-3%, 27-29%, and 36% of the variation, respectively. These proportions were similar to those exhibited by the best model.

In general, the composition of the alternate models was similar to the best approximating model. The most plausible alternative contained the same main effect and interaction terms as the best model, plus the additional theme interaction ***Motivation*** x ***Ability***, suggesting that the variable interactions *run timing* x *length*, *remaining distance* x *length*, *remaining distance* x *color*, and *remaining distance* x *run timing* x *length* also related to migration rate. Based on the Akaike weight ratio, this model was 2.4 times less likely to explain the data than the best model (Table 4). The second alternate model also contained the same main effect and interaction terms as the best model, but included the additional theme interaction ***Fatigue*** x ***Environment***, which consisted of the *cumulative gradient* x *river type* interaction. This model was 2.7 times less likely to explain the data than the best model (Table 4). The third alternate model was the global model, suggesting that there was evidentiary support for all the underlying themes and theme interactions, although this model was 7.7 times less likely to explain the data than the best model. Lastly, there was support for the fourth alternate model, which was a subset of the best model. This model contained all four themes but only the ***Fatigue*** x ***Ability*** theme interaction, and was 11.7 times less likely to explain the data than the best model (Table 4).

Parameter Estimates

Parameter estimates from the best approximating model were used to evaluate the explanatory variables in relation to migration rate with all other factors held constant at average values. The other models in the confidence set were not included in this analysis, based on the fact that the magnitude and precision of the parameter estimates held in common with the best model were comparable (Table 6, Figure 4). The parameter estimates unique to the alternate models were small and relatively imprecise, suggesting that the variables were weakly related to migration rate and that the support for these models was largely due to the variables held in common with the best model.

Physical features.— Several physical features associated with the river basin were strongly related to migration rate. *Reach gradient* was on average strongly and negatively related across all stocks (Table 6, Figure 4). Although the 95% confidence interval was relatively wide, its range was almost entirely negative, suggesting that fish traveling through steeper areas consistently exhibited slower swimming speeds. Based on the parameter estimate, fish moved an average of 1.8 km/d slower for every 0.1 m/km increase in gradient within the reach. Migration rate among similar stocks varied approximately 1 km/d on average based on the predicted variation associated with the random effects (Table 6). The mean-normalized estimate of variance was relatively small (24%), suggesting that although there was some stock to stock variability, the effect of reach gradient was similar and predominantly negative for most stocks. Plots of the relationship between migration rate and individual stocks reflected this trend, with negative and relatively uniform slopes (Figure 5). Between-stock differences were minimal, particularly for stocks using relatively gradual (< 0.4 m/km) migratory routes. Stock-specific slopes were more variable for fish returning to the Upper Yukon, with stocks destined for terminal tributaries in the lower reaches of this region (e.g., Klondike River) displaying relatively uniform slopes and generally faster migration rates than stocks traveling farther upriver and subjected to steeper gradients. In contrast, Tanana River fish returning to the Salcha and Goodpaster rivers displayed similar slopes compared to stocks lower in the drainage even though they encountered substantially steeper slopes (Figure 5), suggesting that other influences in addition to *reach gradient* were a factor.

The cumulative gradient experienced by the fish was also strongly and negatively related to migration rate. The estimate was relatively imprecise, with a wide confidence interval that encompassed zero (Table 6, Figure 4). However, the confidence interval was predominantly negative, suggesting that the relationship between *cumulative* *gradient* and migration rate was generally consistent and biologically meaningful, with steeper migratory routes resulting in slower swimming speed. This parameter estimate indicates that fish swam 4.5 km/d slower on average for every 0.1 m/km increase in *cumulative gradient*.

Remaining distance was on average strongly and positively related to migration rate across stocks (Table 6, Figure 4). The parameter estimate was relatively precise, indicating that fish with greater distances still to travel before reaching their terminal tributaries consistently exhibited faster migration rates than those closer to their spawning areas. The estimate suggests that fish swam 0.42 km/d faster on average for every 100 km increase in distance left to travel. Swimming speed was estimated to vary up to 1.7 km/d on average among similar stocks (Table 6). Based on the mean-normalized estimate of variance, the effect of *remaining distance* on migration rate varied by 65% on average among stocks. *Remaining distance* was positively related to migration rate for most stocks, with relatively uniform slopes for fish returning to spawning areas in the Lower Yukon and Middle Yukon (Figure 6). Similar to *reach gradient*, stocks destined for the Upper Yukon displayed more variability. Slopes for stocks returning to lower reaches within the region (e.g., Klondike River) were comparable to stocks farther downriver. Conversely, *remaining distance* was positively (but more weakly) related to migration rate for Upper Yukon fish traveling to the Stewart, White, and Pelly rivers (middle reaches), while headwater stocks exhibited the most variability ranging from slightly positive to weakly negative (Figure 7).

Fish characteristics.— Compared to the physical features of the basin, the relationship between migration rate and the biological and behavioral characteristics of the fish was less pronounced. The parameter estimate for *length* was moderately negative in relation to migration rate and relatively precise (Table 6, Figure 4), suggesting that larger individuals traveled somewhat slower than smaller fish. Swimming speeds averaged 1.1 km/d less for every 100 mm increase in length. Observed lengths of the sample ranged from 400 mm to 1060 mm, suggesting a 6-7 km/d difference between the smallest and largest fish. A similar pattern was observed for *color*. The parameter estimate was small but precise, with migration rate positively related to this factor (Table 6, Figure 4), suggesting that fish displaying blush coloration moved slightly faster than those without external signs of sexual maturation.

Run timing was on average weakly related to migration rate, with a precise parameter estimates centered near zero (Table 6, Figure 4). However, the mean-normalized estimate of variance was extremely large (2494%), indicating substantial stock to stock variation and suggesting that although *run timing* had minimal predictive power across stocks, it was strongly correlated with the movements of certain populations. Regional differences were observed. For stocks in the Lower Yukon, Middle Yukon, and Yukon Flats, *run timing* tended to be either weakly related or slightly positive in relation to migration rate (Figure 8). Anvik River fish (Lower Yukon) were a notable exception, exhibiting the strongest relationship compared to all other stocks within the basin and swimming an estimated 1.9 km/d faster for every 7-day increase in *run timing*. *Run timing* was positively related to migration rate for Tanana River fish, with the major stocks (Chena, Salcha, and Goodpaster) exhibiting the steepest slopes (Figure 8), and traveling an estimated 0.8 to 1.7 km/d faster for every 7-day increase in run timing. Tanana River fish were present throughout the run, and the consistent pattern among stocks suggests that later run fish returning to this drainage were routinely swimming faster than early run fish.

The relationship between migration rate and *run timing* was more variable for upper basin stocks. This pattern was particularly evident in the Upper Yukon. Stocks returning to lower reaches of the region consisted primarily of early-middle run fish and exhibited slightly positive slopes (Figure 9), similar to stocks returning to the Tanana River and Yukon Flats. Conversely, slopes were consistently negative for Upper Yukon fish traveling to the Stewart, White, and Pelly rivers (middle reaches) and the upper headwater, suggesting that late run fish were generally swimming slower than their early run counterparts.

Parameter Interactions

Several parameter interactions were strongly related to migration rate. Although the parameter estimate for *river type* was extremely imprecise and not biologically meaningful when considered separately, the interaction *river type* x *length* was strongly negative (Table 6, Figure 4). The confidence interval was exclusively negative, indicating a predictive relationship. Length was more strongly related to migration rates for fish traveling through the extensively braided Yukon Flat, with the smallest fish swimming 22.8 km/d faster on average than the largest fish (Figure 10). Simply stated, with all other conditions being equal, the largest fish would take 4.8 days longer on average than the smallest fish to travel through the area (a distance of approximately 600 km). The relationship between migration rate and length was less pronounced for fish in single-channel reaches, with the smallest fish swimming 6.8 km/d faster on average than the largest fish (Figure 10). With all other conditions being equal, the largest fish would take 1.7 days longer on average than the smallest fish to swim 600 km in a non-braided reach. The lower range of swimming speeds in Figure 10 for single-channel reaches reflects the basin-wide movements of the fish. This can be somewhat misleading since Yukon River Chinook salmon show a general reduction in migration rate as they moved upriver and approach their terminal tributaries (Chapter 4). The range of swimming speed for fish traveling through single-channel reaches in the lower basin would be substantially faster.

The parameter estimate for the *remaining distance* x *run timing* interaction was moderately positive and precise in relation to migration rate (Table 6, Figure 4), suggesting that both early and late run fish traveled faster when the distance from their terminal tributary was greater. Late run fish exhibited a stronger relationship than their early run counterparts. Late run fish with substantial distances still to travel (e.g., 2300 km to reach their terminal tributary) swam up to 14.4 km/d faster on average than fish with minimal distances remaining (Figure 10). Differences among early run fish were less apparent. Individuals with substantial distances left to travel swam up to 4.7 km/d faster on average than those with minimal distances remaining. Comparisons between early and late run fish suggested that late run fish with more than 700 km remaining to reach their terminal tributaries tended to exhibit greater swimming speeds than early run fish with comparable distances still to travel, swimming up to 7.1 km/d faster (Figure 10). Late run fish with less than 500 km left to travel were comparable or somewhat slower than their early run counterparts, although the predictable variation was less pronounced with differences up to 2.7 km/d for fish with the shortest remaining distances.

The parameter estimate for the *cumulative gradient* x *color* interaction was moderately positive and precise in relation to migration rate (Table 6, Figure 4). However, prominent differences were observed for the three color phases, with the two extremes (iridescent silver and blush) displaying an inverse relationship to migration rate (Figure 10). Iridescent silver fish that traversed steep (0.24 m/km) migratory routes traveled 4.4 km/d slower on average than those with gradual (0.06 m/km) routes, while blush fish with steep migratory routes traveled 3.4 km/d faster on average than those with gradual routes. Differences between these two color types were more pronounced for routes with steeper gradients. Both iridescent silver and blush fish exhibited comparable rates when the migratory routes were relatively gradual (0.06 - 0.12 m/km), but the discrepancy between the two became progressively larger as *cumulative gradient* increased (Figure 10). Blush fish with steep routes traveled up to 6.7 km/d faster on average than iridescent silver fish subjected to the same conditions. By contrast, silver fish were weakly related to migration rate (Figure 10), suggesting a transitional response in swimming speed in relation to color. Swimming speed for silver fish was similar to the other color phases when migratory routes were relatively gradual, but showed little change as *cumulative gradient* increased. Silver fish with steep migratory routes were only 0.5 km/d slower than silver fish with gradual routes.

Multivariate Ordination

Two primary sources of variation in migration rate were identified for individual fish (fish movements) based on the within-stock ordinations of the 11 stocks (Table 7). The dominant source of variation between fish (represented by Axis 1) reflected the average migration rate of the fish, with the axis gradient ranging from slower fish (lower axis scores) to faster fish (higher axis scores). Simply stated, individual fish traveling slower in the lower basin exhibited consistently slower migration rates as they moved upriver compared to their faster moving counterparts. Similarly, fish with faster migration rates in the lower basin continued to display faster swimming speeds as they moved upriver relative to the slower fish. On average, this migratory pattern explained 74% of the within-stock variation in migration rate represented by the multivariate data, ranging from 53% for White River fish to 94% for Chandalar River fish (Table 7).

The second source of variation in migration rate (represented by Axis 2) reflected a shift in the relative swimming speeds of the individual fish as they progressed upriver. Although movement rates declined for nearly all of the fish during the migration (Chapter 4), differences were noted in the pattern of the decline. Fish with faster migration rates in the Lower Yukon exhibited a pronounced decline in swimming speed as they moved upriver. Conversely, fish moving slower in the Lower Yukon displayed a more gradual decline in migration rate. Fish exhibiting the first migratory pattern (i.e., initially faster swimming speeds, followed by a pronounced declined) ultimately displayed slower migration rates as they neared their terminal tributaries than the fish with initially slower swimming speeds but the more gradual decline – hereafter designated as “hares” and “tortoises” in reference to the proverbial characters from Aesop’s fables (Aesop 2003) as described in Chapter 4. The axis gradient ranged from fish exhibiting the hare behavior (higher axis scores) to those displaying the tortoise behavior (lower axis scores). On average, this pattern explained 22% of the within-stock variation in migration rate represented by the multivariate data, ranging from 6% for Chandalar River fish to 39% for White River fish (Table 7). Orthogonality was essentially 100% for Axis 2, suggesting that the information represented was not redundant in relation to Axis 1.

The within-stock ordinations comparing migration rates at sequential stations (movements by station) consistently identified a single source of variation for the different stocks, with the axis gradient ranging from reaches with faster swimming speeds (lower axis scores) to slower swimming speeds (higher axis scores). Although differences in average migration rate were observed among stocks (Chapter 4), within a stock, migration rates at stations in the lower and middle basin were generally faster with slower swimming speed at stations in the upper reaches. On average, this pattern explained 89% of the within-stock variation in migration rate represented by the multivariate data, ranging from 77% for Pelly River fish to 99% for Chena River and Goodpaster River fish (Table 7).

No useful ordination was found for the movements by station of several stocks, including Stewart River fish in the Upper Yukon (Table 7). Several other stocks with usable ordinations followed the same migratory route before continuing on to terminal tributaries farther upriver, including the Pelly, Big Salmon, and Teslin (Figure 1). Within-stock ordinations were conducted for these stocks with the migration rates for stations upriver from the Yukon-Stewart River confluence excluded. In all three cases, no useful ordination was found, suggesting that the structure in the data for these stocks (reflected by the ordination when all migration data was included) related primarily to the movements exhibited during the final stages of the migration. Stewart River fish exhibited substantial variation in swimming speed during their migration through the lower basin. A within-stock ordination with the movement data from the first main stem station upriver from Paimiut excluded resulted in a useable ordination, suggesting that the lack of an identifiable migration pattern for this stock was due to both the extreme variation in migration rate observed among fish within the lower basin and the lack of consistent differences among stations as the fish moved upriver and neared their terminal tributary.

Comparisons across stocks, based on the separate within-stock ordinations, suggest that the explanatory variables associated with the biological and behavioral characteristics of the fish were not strongly correlated with either average migration rate (represented by the Axis 1 scores) or the position of the fish on the tortoise-hare gradient (represented by the Axis 2 scores)(Figure 11). Correlation coefficients typically ranged from weakly to moderately correlated, although exceptions were observed for individual stocks. Teslin River fish with faster average migration rates tended to traveled farther distances after reaching their terminal tributary (and consequently farther total distances), passed through the Lower Yukon earlier in the run, and arrived earlier at terminal tributaries, whereas fish with slower average migration rates typically traveled shorter distances, had later run timing, and arrived later at their terminal tributaries. Goodpaster, Stewart, and White River fish also exhibited strong correlations between average migration rate (Axis 1) and specific explanatory variables (Figure 11). Similarly, several Upper Yukon stocks exhibited strong correlations between the tendency of the fish to exhibit tortoise or hare-like behavior (i.e., position on the Axis 2 gradient) and several explanatory variables, although there was no consistent pattern across stocks. There was also no evidence of within-stock or across stock differences for the categorical variables *year*, *age*, and *color*.

Although strong correlations were not typically observed, similarities across stocks suggest several consistent (albeit weak) relationships based on weight of evidence (Weed 2005). Average migration rates (represented by the Axis 1 scores) were negatively related across stocks to fish length (Figure 11), suggesting that larger fish generally traveled slower than smaller fish. Both Klondike and White River fish returning to the Upper Yukon exhibited strong relationships, whereas this relationship was generally weak for Tanana River stocks. Consistent trends were also observed across stocks for the relationship between average migration rate and distance traveled. Fish swimming greater distances to reach spawning sites generally traveled faster, as illustrated by the positive correlation between the Axis 1 scores and both total distance traveled and the distance traveled after reaching terminal tributaries. Correspondingly, the percentage of distance traveled in the Yukon River main stem showed a negative relationship, with faster swimming speeds for fish traveling shorter distances after reaching their natal streams (i.e., spawning closer to the mouth of their terminal tributary. Tanana River stocks consistently exhibited a moderate to strong relationship between migration rate and distance traveled. A greater disparity was observed in the Upper Yukon, with Klondike and Teslin River fish exhibiting a strong relationship, while the other Upper Yukon stocks displayed a relatively weak relationship. A consistent trend was also observed between average migration rate and when fish reached their terminal tributary (arrival date), with slower moving fish arriving later than faster fish (Figure 11). In contrast, the relationship between average migration rate and run timing varied across stocks, ranging from strongly negative to moderately positive. Regional similarities were observed for Tanana River stocks, with slower fish typically passing through the lower river earlier in run and later run fish exhibiting faster migration rates. Surprisingly, a strong negative relationship was observed for the stock with the longest migration (Teslin), suggesting that later run fish exhibited slower swimming speeds than their early run counterparts. In summary, fish with faster average migration rates tended to be smaller in length and travel greater distances, and arrive earlier at terminal tributaries than fish with slower swimming speeds. Although these patterns were consistent across stocks, the correlations were not strong, indicating a general but weak relationship between migration rate and the biotic factors of the fish.

Based on comparisons across stocks, the tendency of fish to exhibit the tortoise or hare-like migratory pattern was not consistently related to the biotic factors of the fish (Figure 11). However, regional relationships were evident for some variables. Moderately strong correlations between the position on the tortoise-hare gradient and fish length were observed for Tanana River stocks returning to the middle reaches of the drainage (Chena, Salcha, and Goodpaster), suggesting that larger fish tended to exhibit more hare-like migratory patterns, whereas smaller fish tended to be more tortoise-like in their movements. Only White River fish displayed a strongly negative relationship suggesting the opposite behavior. The tortoise-hare migratory patterns of Upper Yukon stocks consistently exhibited a positive relationship to run timing, with early run fish more tortoise-like and late run fish more hare-like in their movements (Figure 11). Headwater stocks, including Big Salmon and Teslin River fish exhibited the strongest relationships. A similar relationship between arrival timing at the terminal tributary and the tendency to display tortoise or hare-like movements was observed among stocks for Upper Yukon fish. Unlike average migration rates (represented by Axis 1), the relationship between the various measures of distance traveled and the position on the tortoise-hare gradient varied widely across stocks, with estimates ranging from strongly negative to strongly positive. In summary, although regional patterns were observed, when considered across stocks, none of the biotic factors of the fish were consistently related to the tendency of the fish to exhibit tortoise or hare-like movements.

In contrast to the biological and behavioral characteristics of the fish, the physical features associated with the migratory route were strongly correlated with the average swimming speeds at each station (as represented by movements by station, Axis 1). Recall that higher axis scores reflect stations with slower average migration rates. Based on the within-stock ordinations of migration rates at sequential stations (movements by station), distance from Paimiut was consistently and strongly correlated across stocks, with slower swimming speeds exhibited at stations located farther upriver (i.e., general slowing trend as the fish neared their terminal tributary). Similarly, both cumulative gradient (from Paimiut to the current station) and reach gradient (from previous station) were consistently and strongly correlated with migration rate, with slower swimming speeds exhibited by fish exposed to steeper gradients. Only White River fish were weakly correlated, suggesting that the decline is swimming speed exhibited by this stock was less pronounced as the fish moved upriver and encountered steeper gradients. The correlation coefficients for these physical features were much stronger than those observed for the biotic variables from the fish movement ordinations.

Migration Rates in Relation to River Discharge

The relationship between migration rate and river discharge varied at the two gauging stations sites. Parameter estimates were weak and imprecise for fish passing Eagle (Table 8). Conversely, there was convincing evidence of a negative relationship for fish passing Nenana, with fish moving 0.4 km/d slower on average (95% confidence interval ranging from -0.5 to -0.3) for every 1000 cfs increase in discharge. Based on this estimate, a substantial increase (in the tens of thousands) would be needed to elicit a meaningful response (e.g., fish swimming 4 km/d slower for a 10,000 cfs increase). The seasonal range in discharge at Nenana averaged 33,000 cfs during the period when fish were present, suggesting an estimated decease of ~ 12 km/d between the lowest and highest discharge levels. After passing Nenana, Tanana River fish travel between 76 and 190 km to reach terminal tributaries, typically arriving within 6-8 d, suggesting that even major changes in discharge had minimal overall effect on the upriver migration of these stocks.

The parameter estimates from this analysis (Table 8) also provided an additional measure of the relationship between migration rate and other associated factors. Although based on information from a localized reach and representing distinct segments of the return, the results were similar to those observed for both the hierarchical linear model and the dominant migratory pattern identified by ordination. The explanatory variable *length* was negatively related for all three analytical methods, with larger fish swimming slower on average than smaller individuals. Fish passing Nenana and Eagle were swimming 1.4 and 1.0 km/d slower, respectively, for every 100 mm increase in length. Site differences were observed for *run timing*. This variable was positively correlated at Nenana and negatively correlated at Eagle, with fish swimming 2.0 km/d faster and 1.3 km/d slower, respectively, for every 7 d increase in lower river passage. Similar results were generally observed for the other two analytical methods used during the study (hierarchical linear model and the multivariate ordination), although some Upper Yukon stocks also demonstrated a positive relationship (Figure 8, Figure 11). A consistent relationship was also displayed by *color*. Fish passing Nenana and Eagle that were iridescent silver when tagged at Russian Mission swam 1.3 and 2.0 km/d slower on average than fish with dull silver coloration. Few blush-colored fish traveled past the Nenana and Eagle sites. Finally, all three analytical methods (hierarchical linear model, multivariate ordination, and this regression analysis) showed positive correlations between migration rate and travel distance for Tanana River fish. Fish passing Nenana were swimming 3.1 km/d faster on average for every 100 km increase in distance traveled. In contrast, no relationship was observed for fish passing Eagle. This difference was also indicated in both the hierarchical linear model and within-stock ordination, with the relationship of Upper Yukon stocks ranging from no correlation to strongly positive (Figure 6, Figure 11).

Based on the adjusted Pearson's r^2 estimate, the regression model for Nenana accounted for approximately 41% of the observed variation in migration rate. The amount of variation explained by these variables was substantially less for fish passing Eagle (adjusted $r^2 = 0.117$), suggesting that the variation observed at this site was largely due to factors not included in the model.

Discussion

Factors Affecting Movements

The evidentiary measures examined suggest that the upriver movements displayed by Yukon River Chinook salmon were influenced by a wide range of factors. Relative importance weights from the hierarchical linear models showed support for all of the underlying themes that we examined. All of the plausible models contained the four principal themes (***Motivation***, ***Fatigue***, ***Ability***, and ***Environment***), and each theme included model parameters strongly correlated with migration rate. The confidence set of plausible models included the global model, further indicating that all of the explanatory themes and theme interactions were influential, although the magnitude of the effect differed substantially among variables. The fish exhibited two distinct sources of variation in their migratory pattern, and although consistent relationships were observed across all stocks between average migration rates and certain biological and behavioral explanatory variables, none of these factors were consistently related to the tendency of fish to exhibit either tortoise or hare-like movements. The ordination of migration rates at sequential stations (movements by station) revealed strong correlations across all stocks between average swimming speed and the variables characterizing the migratory route, indicating the influence of physical factors on migration rate. These findings suggest that there is a complex, multi-faceted relationship between upriver movements and the biological characteristics of the fish (physical abilities, physiological state, and inherent behavior), the conditions encountered during the migration (distance to suitable spawning sites, and the physical features and hydrological characteristics of the basin), and the physiological response of the fish to those conditions (physical limitations, fatigue, and depletion of energy reserves).

Physical features of the basin demonstrated the strongest relationship with migration rate and explained most of the variation exhibited by the fish. The random effects ANOVA indicated that the variation among stations explained over 70% of the observed variation in migration rate. Parameter estimates associated with basin characteristics, particularly the steepness of the migratory route and the distance still to travel (i.e., remaining distance), were relatively large compared to other factors in the models, further indicating the importance of the physical surroundings. Correlation estimates from the within-stock ordinations of movements by station reflected the same pattern.

By comparison, the biological and behavioral characteristics of the fish (biotic factors) were more weakly related to upriver movements. The random effects ANOVA indicated that the variation among fish and among stocks only explained 13% and 5% of the observed variation, respectively. Parameter estimates for fish length, color, and run timing were less strongly related to migration rate than those associate with the physical features of the basin. Similar results were obtained for the within-stock ordinations of fish movements. In spite of the dominant influence attributed to the physical features of the basin, our findings suggest that biotic factors were still an important part of the equation. Although substantially less than observed for *station*, the variation in migration rate explained by *fish* and *stock* in the hierarchical linear models was still appreciable (18%), and the associated parameter estimates, while not strongly correlated, were relatively precise, indicating predictable (albeit weak) relationships. A number of the biotic variables in the within-stock ordinations also showed definite trends across stocks suggesting a consistent relationship, with several stocks displaying strong correlations. The nature of the primary source of variation uncovered by the multivariate ordination (i.e., fish with faster migration rates in the lower reaches of the basin continuing to swim comparatively faster than "slower" fish as they moved upriver) further suggests that migration rate was influenced by individual characteristics and was not impacted solely by the fish's surroundings. Based on the relative importance weights, there was also more support for theme interactions that represented a combination of both basin features and fish characteristics than for interactions that reflected these attributes separately. For example, parameter estimates in the hierarchical linear models were small for *length* and highly variable for *river type*, but the interaction of these two factors was strongly correlated with migration rate and relatively precise.

Indirect evidence also supports the contention that biotic factors influenced upriver movements. In addition to differences among stocks returning to different regions, migration rates observed for fish returning to the same terminal tributary varied widely, a pattern observed across stocks within the basin (Chapter 4). With the possible exception of the highly braided Yukon Flats (where multiple pathways were available), fish within a stock utilize the same migratory route and encounter the same range of physical features during their upriver migration, suggesting that other factors were influencing swimming speed. Although temporal changes in river hydrology could potentially impact stocks with protracted run timing, river stage and discharge were generally less variable from mid-June to mid-August when fish were moving upriver (Figure 3) and swimming speeds among individual fish during weekly periods (when hydrological conditions were comparable) were still highly variable. Migration rates for Tanana River fish were negatively related to river discharge near the village of Nenana, but no relationship was observed for fish migrating up the Yukon River main stem near Eagle, further indicating that multiple factors were at work.

It would be naive to assume that the physical and physiological attributes of the fish have no effect on swimming ability. In addition to being intuitive, numerous authors have reported differences in performance in relation to size, sex, and species (Brett 1995, Hinch et al. 2002, Brown and Geist 2002, Hinch et al. 2006). Salmon are capable of swimming continuously for extended periods of time, but the swimming speed used can be critical since it directly affects when the fish reach natal streams and the amount of energy expended in the process. Slower speeds may be more energy efficient (Beamish 1978, Brett 1983), but may be insufficient for long migrations or for making headway against strong currents. Beamish (1978) categorized swimming speed into three basic categories that are still commonly used; sustained, prolonged, and burst. Sustained swimming speeds can be maintained over an extended period with optimal oxygen and energy consumption and without undue muscle fatigue. The metabolic demands of swimming increase as the fish approach their maximum sustainable speed. Prolonged and burst swimming speeds are occasionally necessary to negotiate high velocity currents or avoid predation, but these faster modes are energetically costly and cannot be maintained over an extended period without resulting in fatigue (Beamish 1978).

While the connection between migration rate and the biological characteristics of the fish seems apparent, the relatively weak relationships observed during this study suggest that the traits exhibited by the fish were relatively well adapted to the spawning migration. Wild (i.e., non-hatchery) Chinook salmon home to natal streams with considerable fidelity (Healey 1991, McIsaac and Quinn 2011, Flannery 2012), and the selective pressures inflicted by local conditions would be expected to routinely eliminate less fit individuals and over time reduce the range of biological and behavioral characteristics expressed by the returns. The acute rigors associated with the extended upriver migration of Yukon River Chinook salmon (even fish spawning in lower basin tributaries traveled hundreds of kilometers to reach suitable spawning sites) would presumably accentuate the distillation of desirable traits, although some variation would still be expected due to chance, the extreme genotypic diversity of salmonids, annual variation in river conditions, and distributional differences of the fish. Conversely, the strong influence of basin characteristics on upriver movements is understandable due to the immediacy of the demands placed on the fish by existing conditions. In spite of the overarching (and sometime conflicting) need to conserve energy during the migration while reaching suitable spawning areas within a prescribed period of time, the fish must respond directly to the physical and physiological challenges imposed by faster currents, steeper gradients, extreme distances, or a combination of these and other factors.

Although the response to these immediate demands is undoubtedly shaped by the intrinsic capabilities of the fish, the general fitness of the return would tend to lessen the relative impact of these biotic factors among individuals.

While the hierarchical linear models were able to account for most (88%) of the variation in migration rate, the explanatory variables used to express these differences were not very descriptive. Variables associated with basin characteristics only explained 36% of the observed variation, and those related to the biological traits of the fish were substantially less informative, suggesting that other influential factors or complex interactions between factors were not incorporated in the models. This result is not particularly surprising considering the size and complexity of the basin (and the difficulties involved in identifying and categorizing pertinent features), the minimal information available on the physical and physiological status of the fish, and the logistical limitations imposed not only on adequately describing the upriver movements with sufficient resolution, but in determining the river conditions actually experienced by the fish during the migration. The implications of these issues are discussed in the following sections. In spite of the obvious limitations, the study provided a number of specific insights into the underlining factors associated with upriver movements.

Migratory Route and Basin Features

River gradient and migratory distance exhibited the strongest relationships to migration rate. Fish with steeper migratory routes (both cumulatively and within the immediate reach) were predicatively slower, after accounting for other factors. This pattern was consistent for all Yukon River stocks. Gilhousen (1980) reported that measures of average river slope provided the best indication of the difficulty experienced by migrating sockeye salmon (*O. nerka*) in the Fraser River.

Fish with farther to travel (i.e., greater remaining distance in the hierarchical linear model or shorter distance from Paimiut in the station ordination) displayed faster migration rates on average, with slower swimming speeds as they neared their terminal tributaries. This pattern was consistent for most stocks, suggesting that migration rates generally declined as the fish move upriver, although exceptions were observed for both stocks and different reaches of the basin (discussed below). Upper Yukon fish demonstrated a progressively weaker association between migration rate and remaining distance, with headwater stocks which had the longest migrations (e.g., some fish traveling over 3200 km) demonstrating no discernible relationship. Migration rates for several headwater stocks increased during the final leg of their journey through the Yukon River main stem (Chapter 4). In addition to reduced river size and discharge during this stage of the migration, which presumably afforded less arduous swimming conditions, many of these fish traveled considerable distances after reaching their terminal tributary (e.g., over 500 km farther for some Teslin River fish), which may have played a role in the swimming speeds exhibited. Upper Koyukuk fish also showed an increase in migration rate as they moved upriver, likely in response to the river conditions encountered. Migration rates for both Koyukuk and upper basin stocks were comparable downriver of the Yukon-Koyukuk River confluence, but Upper Koyukuk fish swam considerably faster (averaging 72 km/d) after leaving the Yukon River main stem (Chapter 4). The size, discharge, and turbidity of the Koyukuk River were noticeably less than the main stem, and likely had an effect on swimming speed, although proximity to natal streams was undoubtedly a contributing factor. The migration rates of fish returning to the Gisasa River, located in the lower Koyukuk River drainage, declined dramatically (averaging 26 km/d) after leaving the Yukon River main stem. These fish only traveled 96 km from the Koyukuk River mouth to their terminal tributary, compared to over 700 km for those traveling to the upper reaches of the drainage. Other factors further complicate the relationship between migration rate and migratory distance. Late run fish with farther to travel had faster migration rates than early run fish under similar circumstances. These fish presumably had less time than early run fish to complete the migration and reach spawning sites when conditions were suitable, and the faster swimming speeds likely compensate for this limitation.

The total distance traveled by the fish was less important than either river gradient or remaining distance. The most plausible hierarchical models did not include measures of total distance, indicating that other factors better explained the observed variation in migration rate. Lower basin stocks, which traveled considerably shorter total distances (ranging from 150 to 700 km upriver from Russian Mission) moved substantially slower than stocks traveling farther upriver (Table 1), possibly due to the proximity of the fish to their terminal tributaries. However, middle and upper basin stocks did not reflect this pattern. The migration rates of fish returning to the Yukon Flats and Upper Yukon were comparable, even though stocks in the Yukon Flats were traveling much shorter distances; 1230 to 1680 km compared to 1500 to 3100 km for Upper Yukon fish. Fish destined for the Klondike River, which were primarily early run fish, were consistently faster than other Upper Yukon stocks that traveled farther upriver and had later run timing (Chapter 4). Klondike River fish spawned noticeably earlier than stocks farther upriver (Figure 12), possibly due to colder water temperatures in the drainage and the related effect on the developing progeny (T. Tanner, Department of Fisheries and Oceans Canada, Whitehorse, Yukon Territory, personal communication), and the faster swimming speeds may reflect this difference in timing. Other authors have noted ambiguities associated with total distance traveled. Gilhousen (1980) reported that total distance traveled by sockeye salmon in the Fraser River was less influential than the steepness of the route, even for fish traveling up to 40% farther.

Conversely, there was a pronounced relationship between migration rate and the distance traveled by fish after reaching terminal tributaries. Comparisons across stocks in the fish movements ordination showed a consistent trend, with faster migration rates for fish spawning farther upstream. This trend presumably reflects the additional time needed by fish to reach outlying areas. Surprisingly, this relationship was relatively weak for several Upper Yukon stocks returning to large tributaries with widely scattered spawning, including the Stewart and Pelly rivers. Spawning in these tributaries ranged from near the mouth to over 600 km upstream (median distances of 165 and 421 km, respectively). Only the Teslin River with fish spawning over 500 km from the mouth (median distance of 166 km) was strongly correlated, probably due to the added complexity within the drainage introduced by Teslin Lake, and the temporally and spatially separate spawning areas (Chapter 4). In contrast, Chena, Salcha, and

Goodpaster River fish were moderately to strongly correlated, even though the spawning distribution of these stocks was more localized, ranging from near the tributary mouth to < 170 km upstream with median distances of 53, 54, and 82 km, respectively. It is interesting to noted that the relationship for fish exhibiting the tortoise-hare migratory pattern varied widely, ranging from strongly negative to strongly positive.

As previously mentioned, migration rates across stocks and (to a lesser extent across fish) varied consistently within certain reaches of the basin, indicating a strong relationship with the physical features of the surrounding area. Fish entering the Tanana River exhibited a pronounced decline in migration rate, while swimming speeds increased for those continuing up the Yukon River main stem. Notable declines in swimming speed were displayed by upper basin fish in the Yukon Flats and downriver of the Yukon-White River confluence. These migratory patterns were undoubtedly influenced by the geomorphology of the river. The vast majority of fish (99%) traveling through the highly braided Yukon Flats exhibited a reduction in swimming speed. Although migration rates generally declined as fish moved upriver (Chapter 4), the subsequent increase displayed by most fish (78%) after leaving the Yukon Flats suggests that the slower swimming speeds observed within this area were likely in response to the physical or hydrological features encountered.

Parameter estimates from the hierarchical linear models for *river type* (single-channel vs. highly braided reaches) were highly variable with no predictive power. However, this was at least partly due to difficulties in categorizing reach characteristics, and the lack of fine-scale tracking data in localized areas. Only the Yukon Flats was designated as braided due to the extensive braiding throughout the reach. Less extensive braiding was observed in other reaches of the basin, but the prevalence and extent, as well as the accessibility and use of these areas by migrating salmon, was difficult to assess. Although not as extreme as the Yukon Flats, portions of the main stem downstream from the Yukon-White River confluence were moderately braided and considerably more turbid due to glacial runoff from the White River. Similar to the Yukon Flats, migration rate were consistently less within this reach, with 97% of the fish displaying slower migration rates, while most fish (73%) upriver from the confluence again showed an increase in swimming speed.

Although side channels provide alternate pathways with reduced flow (a potential advantage), the added complexity of highly braided reaches may force migrating fish to swim slower as they make their way upriver. The negative relationship between migration rate and fish length was even more pronounced in the highly braided Yukon Flats, suggesting that smaller fish were either more apt or better able to take advantages of local conditions in ways that enhanced swimming performance. The "slower" speeds observed in the Yukon Flats may also be an artifact of how distance traveled was calculated (Chapter 4), and may instead indicate that fish were diverting from main channel routes (i.e., reflecting the additional time taken to move through the reach via a more circuitous pathway rather than a reduction in swimming speed). However, this explanation seems less likely because of the stronger relationship between migration rate and fish length in braided reaches, which would imply that larger fish were more likely to diverge from main channel pathways than smaller fish.

River flow is often considered a major influence on salmon movements, but assessing its impact is a challenge. While increasing water velocity has routinely been shown to reduce swimming performance under controlled conditions (Brett 1995), varied responses have been reported for *in situ* studies on salmon (Trepanier et al. 1996, Quinn et al. 1997, Salinger and Anderson 2006). Free-flowing rivers are extremely dynamic, their irregular shapes and non-laminar flow often creating a highly variable velocity gradient (Leopold et al. 1964). Conditions are further complicated by seasonal changes and the diverse geomorphology typical in large drainages. Hydrological data is often limited to localized areas, and attempting to extrapolate this information to distant locations is fraught with assumptions and potential bias. For example, high water (often associated with increased water velocity in main river channels) may also inundate peripheral areas, creating additional waterways with reduced flow. Detailed models that "accurately" project flow to downriver sites in both a spatial and temporal sense may provide a relative measure of conditions when fish are present. However, even with better information, the effect of these conditions on upriver movements is likely confounded by the behaviors used by migrating salmon to adjust to adverse situations.

Migrating salmon use current as a directional cue for orientation (Arnold 1974), and have been reported to seek out high flows when moving through impounded reaches (Thorstad et al. 2003). In large free-flowing rivers, proximity to strong main-channel currents reduces the risk of selecting circuitous or unsuitable migratory routes. However, the energetic costs of swimming against fast current can be substantial (Beamish 1978, Brett 1995), and in extreme cases can result in delayed upriver movements and increased mortality (Rand and Hinch 1998, Crossin et al. 2004). It is unlikely that general measures of river stage and flow reflect the conditions actually experienced by the fish, since salmon routinely select travel routes that optimize swimming performance and adjust swimming speeds in response to river conditions (Hinch and Rand 2000, Hinch et al. 2002, Brown and Geist 2002, Standen et al. 2002). Ancillary tracking data from this study suggests that fish routinely selected pathways within the main river that reduced exposure to the main current while maintaining close contact for orientation (Chapter 4). Documenting the actual pathway used by the fish (even with the aid of telemetry) and determining the river conditions actually subjected to is difficult at best, particularly when assessing large-scale movements. The varied and sometimes contradictory results reported in the literature may be due, at least in part, to these limitations.

Dissimilar results were observed when comparing migration rates and river discharge at Eagle (upper Yukon River) and Nenana (Tanana River). Although no relationship was observed at Eagle, Tanana River fish exhibited a negative relationship even though overall discharge levels at Nenana were substantially less than at the other site (Figure 3). The fish passing Eagle had traveled farther and were subjected to steeper river gradients (both cumulative and within the reach), indicating that attributes other than basin features were likely involved. The migratory stage and physiological state of the fish may be contributing factors. Most fish passing Eagle still had extended distances to travel, while Tanana River fish were nearing their final destination. It is well established that salmon use olfactory cues to differentiate the chemical signature of their natal streams (Hasler 1971), and the slower swimming speeds at Nenana may reflect the additional time and effort needed by the fish to detect and isolate these cues in the face of the increasing water. The Tanana River is also extremely turbid with glacial silt from the upper reaches of the drainage. Increasing discharge may result in higher silt loads, which could negatively impact migrating fish. On the other hand, salmon use a substantial portion of their energy reserves during the upriver migration, particularly those fish traveling extended distances (Gilhousen 1980, Brett 1995, Hendry and Berg 1999). Chinook salmon harvested in the Tanana River near Manley (Figure 1) were more sexually mature (based on flesh quality, coloration, and gamete development) than those caught a comparable distance up the Yukon River main stem near Rapids (S. Zuray, Yukon River subsistence fisher, Tanana, AK, personal communication). Since faster swimming speeds have higher energetic costs, the slower migration rates observed in relation to increasing flow may represent either the inability of maturing fish to maintain the faster speeds or a behavioral response designed to conserve remaining energy reserves under more challenging conditions. The Pearson's r^2 estimate for the Nenana regression was substantially higher than observed for Eagle. Although the significance of this difference is open to interpretation, it may be that some explanatory variables become more influential as fish approach their natal streams and other considerations become less demanding.

Fish Characteristics

Although adequate numbers of fish were sampled during the study, relatively few parameters were available to describe individual characteristics. Fish length and run timing provided definitive measures. In contrast, fish coloration only provided an indirect and relatively imprecise measure of sexual maturity. Fish passing through the lower river were generally at an early stage of maturation, with most (98%) displaying either the iridescent or dull silver coloration. The small number, restricted timing and limited distribution of blush-colored fish (primarily late run fish destined for Lower Yukon tributaries) further limited the utility and explanatory power of this parameter.

The stereotypic body type of salmon is adapted for fast acceleration and prolonged cruising speeds (Webb 1975), making it ideal for extended migrations against variable currents. Larger body size would presumably have a number of advantages, including greater physical strength for swimming and intra-specific competition during spawning (e.g., mate selection, redd construction and defense), as well as increased capacity for gamete production. Larger fish are generally considered stronger swimmers, with smaller individuals traveling closer to shore ostensibly to take advantage of the slower current (Brett 1983, Burgner 1991, Hinch et al 2002). Bank affinity has also been observed for smaller species, also thought to be weaker swimmers. Pink salmon (*O. gorbuscha*) have difficulty swimming at the maximum speeds displayed by sockeye salmon, and require more energy to maintain the same swimming speed (Brett 1995). However, Hughes (2004) proposed that larger salmon swim farther offshore to avoid wave drag, which is a function of body size and water depth. Salmon generally swim near the river bottom to take advantage of the reduced velocity associated with the boundary layer (Schlichting 1979). By swimming farther from the bank, larger fish are also able to swim deep enough to avoid wave drag, making swimming more efficient in spite of the faster offshore currents.

Surprisingly, the results from both the hierarchical linear model and multivariate ordination suggest that smaller fish were swimming minimally faster on average than larger fish. Because of the large-scale tracking methods used during the study, it is not known whether this pattern represented smaller fish swimming faster at a constant rate, utilizing a better combination of speeds (i.e., variable rates), or selecting more efficient pathways that resulted in a faster overall rate. Sockeye and pink salmon in the Fraser River displayed similar mean swimming speeds (even though sockeye salmon were considered more powerful swimmers), but employed substantially different swimming patterns. Sockeye salmon displayed more variability, regularly alternating between sustained and burst speeds, while pink salmon generally swam at a steadier rate using a combination of sustained and prolonged speeds (Hinch et al. 2002). Positive relationships between energy costs associated with swimming and fish size have been reported for a variety of species, with larger fish using relatively more energy to complete upriver migration than smaller fish (Jonsson et al. 1997, Leonard and McCormick). Hinch et al. (2002) reported that larger salmon (standardized by species and sex) typically displayed less energy-efficient swimming patterns than smaller individuals. Since energy depletion rates are particularly severe for long-distant migrants (Gilhousen 1980, Brett 1995, Hendry and Berg 1999), the lower transportation costs associated with smaller size may be an advantage in relation to swimming speed. Morphological differences have been noted between coastal and upper river salmon populations. Several authors have reported that Chinook and sockeye salmon with longer, more difficult migrations are smaller in size than populations traveling shorter distances (Gustafson et al. 1997, Crossin et al. 2004, Roni and Quinn 1995). In contrast, Yukon River Chinook salmon tracked to lower basin tributaries were smaller on average than middle and upper basin stocks, with generally larger fish destined for tributaries in the Yukon Flats and Upper Porcupine.

The relationship between migration rates and fish size may be confounded by the lack of other pertinent information. Sex was not recorded for fish tagged during this study due to the lack of external characteristics in the lower river, and efforts to determine sex based on genetic characteristics were unsuccessful (B. Flannery, U.S. Fish and Wildlife Service, Anchorage, AK, personal communication). Female Chinook salmon returning to the Yukon River basin are generally comparable in size or somewhat larger than males; similarly, smaller fish are typically males (Karpovich and DuBois 2007), and the slower swimming speeds exhibited by smaller fish during this study may related to sex-linked differences. Female salmon are generally considered less powerful swimmers. Salmon traveling extended distances to reach spawning areas must partition energy reserves to support both swimming and gamete production. Since females allocate more energy to reproduction, they presumably have less to devote to upriver movements (Brett 1995, Kinnison et al. 2001, Crossin et al. 2004). Female salmon in the Fraser River employed more energy-efficient swimming patterns than males (i.e., more sustained and prolonged speeds, with less burst swimming), particularly in constricted reaches with higher flows (Rand et al. 1998, Hinch et al. 2002). Female Chinook salmon in the Klickitat River (Columbia River basin) were less likely to make it past waterfalls than males (Brown and Geist 2002). However, average swimming speeds were similar for male and females during fine-scale telemetry studies on both Fraser River sockeye and pink salmon (Hinch et al. 2002), suggesting that the relationship between sex and swimming speeds is uncertain.

Run timing also appeared to be an influential factor. Late run fish, particularly those traveling considerable distances, would be expected to have faster migration rates since they presumably have less time to reach suitable spawning areas. Early run fish traveling to the same destination would (in theory) have the option of swimming at slower speeds that are more energy efficient, although arriving earlier on the spawning grounds likely has selective advantages (Foerster 1968, Healey 1991, Quinn 2005). Temporal differences in hydrological conditions (e.g., higher flow regimes earlier in the season) may also temper this assumption to some extent. During this study, Middle Yukon fish reflected this pattern, with positive relationships between migration rate and run timing observed across stocks. Mixed results were observed in the Lower Yukon, but this was likely due to the small numbers of fish tracked to terminal tributaries with minor stocks. The relationship between migration rate and run timing was positively correlated for stocks with adequate samples (e.g., Anvik, Nulato, and Tozitna rivers). The strong relationship displayed by Anvik River fish (Figure 8) was likely influenced by the relatively short distances these fish traveled from the tagging site (< 300 km) and the relatively early spawning period compared to upper basin stocks (Figure 12).

Surprisingly, Upper Yukon stocks showed a progressively negative relationship (relative to the distance traveled to reach their terminal tributaries) between run timing and migration rate, indicating that later run fish were swimming slower than early run fish after accounting for other factors. The spawning distribution of Teslin River fish may partially explain this anomalous observation. Although early run fish traveled to spawning sites throughout the drainage, with some fish spawning over 500 km from the tributary mouth, later run fish spawned predominantly in the lower reaches downstream from Teslin Lake (< 200 km from the mouth, Chapter 4). The shorter distances traveled may have influenced the swimming speeds exhibited by these fish. However, this distribution pattern was unique compared to other Upper Yukon stocks. Although spawning in the Big Salmon River was more confined (< 160 km from the mouth), both early and late run fish were distributed throughout the utilized area. A similar pattern was observed in the Pelly River, even though these fish were spawning up to 660 km from the mouth.

Fishers along the Yukon River main stem from Rapids to Eagle report a progressive decline in the condition of Chinook salmon over the course of the run, with a marked deterioration in flesh quality (both in terms of firmness and color) and an increase in secondary sexual characteristics including changes in physical features and spawning coloration (S. Zuray, Yukon River subsistence fisher, Tanana, AK, personal communication, A. Bassich, Yukon River subsistence fisher, Eagle, AK, personal communication). Salmon primarily metabolize proteins for the development of secondary sexual characteristics, resulting in the deterioration of muscle tissue, reduced muscle mass, and decreased swimming performance (Brett 1995). Fish passing Eagle traveled varying distances to reach spawning sites, and the combined effect of remaining distance and deteriorating condition may explain the increasingly negative relationship observed between run timing and migration rate. Klondike River fish, which traveled 270-360 km after passing Eagle, displayed a positive correlation similar to stocks lower in the basin. Fish traveling to middle and headwater reaches traveled substantially farther (e.g., 450-1100 km for Pelly River fish, 750-1260 km for Teslin River fish), and the increasingly negative correlation for these stocks may reflect an escalation in the effect of condition on swimming performance. Spawn timing is influenced by the ability of the fish to access the sites (i.e., acceptable water levels and flow), the sexual maturity of the fish, and the water temperature regimes and associated degree days needed by salmon eggs to develop and hatch when local conditions are optimal for juvenile survival (Alederdice and Velsen 1978, Murray and Beacham 1986, Healey 1991). Spawning in the Upper Yukon occurred considerably later than in the lower and middle basin (Figure

12), and the anomalous relationship between run timing and swimming speed suggests that the window for reaching spawning sites is sufficiently wide (in relation to local conditions) to accommodate this migratory pattern.

In addition to the lack of data on sex, information was not obtained for several other factors that potentially affect upriver movements, including the physiological condition of the fish. Lipid content provides a relative measure of condition and the length of the migration. Salmon with longer migrations typically enter freshwater with greater energy reserves compared to populations bound for nearby coastal streams (Brett 1995, Crossin et al. 2004). As previously mentioned, conversations with local fishers suggest that the condition of Yukon River Chinook salmon varied both spatially and temporally over the season, and there is suggestive evidence that individual variation in condition likely impacted swimming performance. Similarly, the pathogen *Ichthyophonus* is present in Yukon River Chinook salmon, and potentially affects the movements and survival of infected individuals (Kocan and Hershberger 2006, Kocan et al. 2009).

Although the ability of returning salmon to successfully migrate upriver is implicitly tied to their physical and physiological capabilities, more invasive techniques for determining sex, maturation, physiological condition, and disease infection rates (e.g., blood and tissue samples) were not employed in order to minimize stress and handling injuries that could adversely impact swimming performance. Even with procedures designed to minimize handling (used during this study), upriver movements were adversely impacted for a short time immediately after release (Chapter 2). Additional sampling procedures that might exacerbate this response were therefore avoided to increase the likelihood that the behavior exhibited by fish in the tagged sample would reflect that of untagged fish. Water temperature also controls fish behavior by regulating the underlining metabolic rates (Fry 1971), and has been shown to have varying effects on salmon movements (Brett 1995, Trepanier et al. 1996, Quinn et al. 1997, Salinger and Anderson 2006). Similar to hydrological conditions, information on water temperature was not readily available for the basin and was not incorporated as a factor.

Methods for Analyzing Movement Data

Two fundamentally different analytical approaches were used during this study to evaluate factors thought to influence the upriver movements of the fish. In spite of the inherent differences, both methods provided strikingly similar results, indicating that the study findings were not dependent on the approach used, and suggesting that the results were plausible based on the information available and the weight of evidence. Disparate results between the methods would have inspired less confidence in the findings, and raised additional questions related to the suitability of the two approaches.

Both analytical approaches had advantages. As previously discussed, hierarchical linear models separately compared individual movement records in relation to the biological characteristics of the fish and the physical features of the basin and migratory route. The sequential movements of individual fish were not considered analytically. Because of the less stringent sample criteria (e.g., not limited by the number of stations or the number of fish tracked within a stock), the hierarchical linear models were able to use the entire data set, which provided more extensive coverage of the basin (Table 1). More importantly, we were able to evaluate the suite of explanatory variables (both biological and environmental) simultaneously, which provided standardized comparisons and simplified the interpretation of the results. As illustrated by this study, obtaining information pertinent to the migratory patterns of the fish is often difficult or impossible. By using random effects, the models were able to account for sources of variation even when insufficient information was available to identify the underlining factors.

Conversely, multivariate ordination compared migration rates in sequential reaches across individual fish by stock, thereby retaining the linkage between multiple movement records for the individual fish. However, separate analyzes were needed to examine the relationships between migration rate and the biotic and physical variables. In addition to being cumbersome, it was also more difficult to compare the relative influence of the different factors and interactions between factors, whereas the hierarchical linear model facilitated explicit evaluation of the interactions. However, ordination was very useful as an exploratory tool. Although compartmentalized by stock, across fish comparisons were simple and relatively straightforward. Because the explanatory variables were evaluated separately in relation to the axis score of the fish, it was possible to examine and compare highly correlated factors. Ordination was also able to identify overall patterns within the data and assess the relative importance. While this can be accomplished within the framework of linear regression using mixture models to determine whether multiple distributions exist within the data, the process is much simpler with ordination.

As with all research efforts, the methods used to collect and analyze the data ideally reflect the principal questions being asked. The analytical methods used during this study had different strengths, but in many ways were complementary. Although similar results were obtained with the two methods, multivariate ordination was better suited for exploring the data and identifying the general migratory patterns exhibited by the fish. Conversely, hierarchical linear models were more appropriate for determining the specific factors influencing those migratory patterns, and would be more applicable to studies focusing on this objective. Using both methods in tandem substantially enhanced our confidence in the results obtained and provided additional insights not apparent when the methods were used separately.

As demonstrated by this study, it is possible to obtain usable information on salmon movements collected under less than ideal circumstances. Careful review is of course needed to understand the intricacies and limitations of the data, and identify potential sources of bias. That being said, we suggest that the judicious use of robust, analytical models can be used to analyze telemetry data from studies designed to address other research objectives. Even when these efforts do not present a complete picture of the situation at hand, they can often provide the foundation needed to effectively develop future research efforts.

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Table 1.— Average migration rate (km/d) for stocks analyzed with hierarchical linear models and multivariate ordination. The number of remote tracking stations (RTS) along the migration route, standard deviation (SD) of the migration rate, and number of fish by stocks used in each analysis are also indicated. Stocks represented by less than 10 fish are combined by region and listed simply as minor stocks.

			Average migration rate (SD)			
Region	Stock	RTS	Hierarchical linear model	n	Within-stock[1] ordination	n
Lower Yukon	Innoko	2	32.4 (14.9)	8		
	Bonasila	2	39.5 (12.3)	22		
	Anvik	2	27.9 (11.0)	50		
Middle Yukon	Nulato	3	39.1 (11.0)	36		
	Gisasa	4	41.6 (7.4)	23		
	Tozitna	4	51.8 (10.3)	21		
	Minor stocks [2]	4	48.4 (10.5)	12		
Upper Koyukuk	Koyukuk	4	66.9 (5.9)	19		
	Minor stocks [3]	4	62.5 (7.0)	14		
Tanana	Kantishna	4	54.6 (5.0)	32	54.9 (5.3)	20
	Tolovana	4	53.2 (9.2)	11		
	Chena	6	46.3 (6.7)	100	47.2 (6.0)	55
	Salcha	6	44.8 (5.0)	172	47.0 (4.2)	91
	Goodpaster	6	46.0 (4.8)	79	49.6 (4.9)	51
	Minor stocks [4]	5	51.1 (6.3)	9		
Yukon Flats	Chandalar	5	56.8 (6.6)	65	59.0 (5.8)	20
	Sheenjek	5	59.2 (5.4)	37		
	Minor stocks [5]	5	60.8 (7.5)	11		
Upper Porcupine	Porcupine	6	58.5 (10.8)	23		
	Miner	6	62.6 (6.2)	19		
	Minor stocks [6]	6	57.9 (3.6)	7		
Upper Yukon	Klondike	6	60.6 (4.3)	37	63.1 (4.3)	24
	Stewart	7	57.1 (6.2)	77	58.7 (5.4)	48
	White	6	59.3 (3.8)	29	60.9 (3.2)	23
	Pelly	9	56.4 (5.7)	157	58.0 (4.3)	77
	Nordenskiold	9	57.8 (3.9)	11		
	Little Salmon	9	52.5 (6.5)	22		
	Big Salmon	10	54.1 (4.4)	101	53.5 (4.2)	53
	Teslin	10	53.8 (5.5)	153	54.0 (5.9)	70
	Headwaters	10	51.8 (4.6)	23		
	Takhini	10	51.1 (1.8)	11		
	Minor stocks [7]	5-9	54.1 (7.3)	30		
Entire basin	All stocks	2-10	51.4 (10.5)	1,421		542

[1] Differences across stocks based on comparison of ordination results for individual stocks.
[2] Including Kateel, Melozitna, and Nowitna rivers.
[3] Including fish returning to the Hogatza, Henshaw, South Fork, and Middle Fork rivers.
[4] Including fish returning to Clear, Moose, and Salchaket creeks.
[5] Including fish returning to Beaver Creek, Hodzana River and Black River.
[6] Including fish returning to Coleen River (U.S.), and Old Crow and Whitestone rivers (Canada).
[7] Including fish returning to Charley, Kandik, and Nation rivers (U.S.), and Chandindu River, Sixtymile River, Big Creek, and Tatchun Creek (Canada).

Table 2.— Underlying themes and fixed-effect explanatory variables used to describe the relationship between migration rates exhibited by Yukon River Chinook salmon and the biological characteristics of the fish and physical features of the basin. The best approximating variables included in the global model are indicated. Variables *fish*, *stock*, and *station* were treated as random effects.

Theme	Global model	Explanatory variable	Description
Motivation	x	Run timing	Day fish captured in lower river
	x	Remaining distance	Distance (current to last station)
		Total distance	Distance (Paimiut to final station)
		Total elevation change	Elevation change (Paimiut to final station)
Fatigue	x	Cumulative gradient[1]	Gradient (Paimiut to current station)
		Current distance	Distance (Paimiut to current station)
		Elevation change	Elevation change (Paimiut to current station)
Ability	x	Length	Length of fish (mid-eye to fork of tail)
	x	Color[2]	Skin color of fish in lower river[2]
		Age	Combined years in fresh and salt water
Environment	x	Reach gradient	Gradient from previous to current station
	x	River type[3]	Primarily channel characteristics of in reach[3]
		Reach distance	Distance (previous to current station)
		Reach elevation change	Elevation change (previous to current station)

[1] Change in elevation divided by the distance traveled by the fish.
[2] Comparing fish with iridescent silver, dull silver, and blush coloration when tagged.
[3] Comparing primarily single-channel vs. highly braided reaches.

Table 3.— Variance estimates for random-effect ANOVA used to describe the observed variation in the upriver migration rates of Yukon River Chinook salmon. Standard deviation (SD) is used to describe the predictable variation in migration rate exhibited by the parameters. Percentage of the total model variation is in parentheses.

Parameter	Variance	(%)	SD
Fish	26.58	(12.6)	5.16
Stock	9.77	(4.6)	3.13
Station	149.03	(70.7)	12.21
Residual	25.53	(12.1)	5.05
Total	210.91		

Table 4.— Ten best approximating models fit to the 2002-2004 Yukon River Chinook salmon movement data. Models were ranked based on Akaike's Information Criteria (AIC) scores, with the lowest value representing the best approximation. Model themes (which included both main effects and within-theme interactions) and theme interactions are indicated. Models were considered plausible based on Akaike weights estimates (w_i) and Akaike weight ratios.

Themes[1]	Theme interactions	AIC Score	” AIC Value	K	w_i	Weight Ratio
All themes[2]	Fatigue x ability Ability x environment	46126.52		13	0.45	
All themes[2]	Fatigue x ability Ability x environment Motivation x ability	46128.29	1.77	17	0.19	2.42
All themes[2]	Fatigue x ability Ability x environment Fatigue x environment	46128.52	2.00	14	0.17	2.72
All themes[2,3]	Fatigue x ability Ability x environment Motivation x ability Fatigue x environment	46130.29	3.77	18	0.07	6.59
All themes[2]	Fatigue x ability	46130.60	4.08	9	0.06	7.70
All themes	Fatigue x ability Motivation x ability	46131.43	4.91	13	0.04	11.66
All themes	Fatigue x ability Fatigue x environment	46132.60	6.08	10	0.02	20.87
All themes	Fatigue x ability Motivation x ability Fatigue x environment	46133.42	6.90	14	0.01	31.60
Motivation Ability Environment	Ability x environment Motivation x ability	46142.35	15.83	14	0.00	2243.50
All themes	Ability x environment Motivation x ability	46144.25	17.73	15	0.00	4487.00

[1] Including motivation, fatigue, ability, and environment.

[2] Plausible model; together plausible models constituted confidence set of models.

[3] Global model.

Table 5.— Akaike importance weights for the primary themes and theme interactions used to describe the upriver movements of Yukon River Chinook salmon. Importance weights were estimated by summing the Akaike weights from individual candidate models containing the theme parameters. Importance weight equals one when parameters are present in all model with an Akaike weight value greater than zero.

Theme	Number of models containing theme	Importance weight
Motivation	31	1.00
Fatigue	36	1.00
Ability	39	1.00
Environment	36	1.00
Fatigue x ability	15	0.99
Ability x environment	15	0.87
Motivation x ability	13	0.31
Fatigue x environment	14	0.27

Table 6.— Parameter estimates for random effect and fixed-effect variables from the two best-approximating hierarchical linear regression models used to explain the upriver migration rates of Yukon River Chinook salmon. The standard deviation (SD) is presented for the random effects and standard error (SE) and 95% confidence interval for the fixed effects. The model intercept represents the average movement rate.

			95% confidence interval	
Parameter	Estimate[1]	SD or SE	Lower	Upper
Best-approximating model (w_i = 0.45)				
Random effects				
Fish	25.95	5.09		
Stock	7.16	2.68		
Reach gradient	0.93	0.97		
Remaining distance	2.71	1.65		
Run timing	1.49	1.22		
Station	95.14	9.75		
Residual	23.05	4.80		
Fixed effects				
Intercept	48.01	1.93	44.23	51.78
Reach gradient	-4.06	2.26	-8.49	0.38
River type	2.71	22.42	-41.22	46.65
Cumulative gradient	-2.87	2.05	-6.89	1.15
Remaining distance	2.51	0.57	1.39	3.63
Length	-0.96	0.44	-1.82	-0.10
Color	0.79	0.39	0.03	1.55
Run timing	-0.05	0.28	-0.60	0.50
Reach gradient x river type	-3.61	51.77	-105.27	97.85
Length x river type	-2.26	0.97	-4.17	-0.36
Run timing x remaining distance	1.28	0.07	1.14	1.41
Cumulative gradient x color	1.35	0.35	0.67	2.03
Color x reach gradient	-0.65	0.31	-1.25	0.05
Cumulative gradient x length	-0.52	0.11	-0.74	-0.29
Color x river type	0.32	0.56	-0.78	1.42
Length x color	0.20	0.31	-0.41	0.81
Length x reach gradient	-0.18	0.11	-0.39	0.03
Most plausible alternate model (w_i = 0.19)				
Random effects	25.90	5.09		
Fish	7.023	2.65		

Stock	1.53	1.24		
Reach gradient	2.78	1.67		
Remaining distance	0.95	0.98		
Run timing	95.09	9.75		
Station	23.03	4.80		
Fixed effects				
Intercept	48.03	1.93	44.25	51.81
Reach gradient	-4.28	2.26	-8.71	0.16
Cumulative gradient	-2.69	2.10	-6.81	1.43
River type	2.63	22.43	-41.34	46.60
Remaining distance	2.48	0.70	1.10	3.86
Color	0.84	0.43	0.00	1.68
Length	-0.66	0.47	-1.58	0.26
Run timing	-0.07	0.28	-0.62	0.49
Reach gradient x river type	-3.67	51.77	-105.15	97.80
Length x river type	-2.18	0.97	-4.09	-0.27
Cumulative gradient x color	1.31	0.45	0.43	2.19
Run timing x remaining distance	1.29	0.07	1.15	1.42
Cumulative gradient x length	-0.61	0.17	-0.94	-0.28
Color x reach gradient	-0.58	0.31	-1.18	0.02
Color x river type	0.35	0.57	-0.76	1.47
Run timing x length[2]	0.22	0.17	-0.11	0.56
Length x reach gradient	-0.19	0.11	-0.40	0.03
Timing x remaining distance x length[2]	-0.13	0.07	-0.26	0.01
Remaining distance x length[2]	-0.11	0.13	-0.36	0.14
Length x color	-0.08	0.35	-0.76	0.60
Remaining distance x color[2]	0.05	0.32	-0.58	0.68

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[1] Random effect estimate is a variance component.

[2] Parameters unique to plausible alternative model; not represented in best-fitting model.

Table 7. Yukon River Chinook salmon stocks analyzed with within-stock ordination to describe the migration rates of individual fish (fish movements) and for different reaches of the basin (reach movements). Pearson's r^2 values represent the proportion of the multivariate data explained by the synthetic variables (axes). Missing values indicate no useful ordination.

			Fish movements			Reach movements
Region	Stock	n	Axis1 r^2	Axis2 r^2	Total r^2	Axis1 r^2
Tanana	Kantishna	20	0.919	0.079	0.998	
	Chena	51	0.769	0.185	0.954	0.987
	Salcha	91	0.695	0.254	0.949	0.819
	Goodpaster	51	0.730	0.231	0.961	0.987
Yukon Flats	Chandalar	20	0.936	0.056	0.992	
Upper Yukon	Klondike	37	0.739	0.177	0.916	0.821
	Stewart	48	0.726	0.250	0.976	
	White	24	0.526	0.389	0.915	0.793
	Pelly	77	0.680	0.244	0.924	0.770
	Big Salmon	53	0.728	0.203	0.931	0.931
	Teslin	70	0.660	0.311	0.971	0.904

Table 8. Relationship between migration rates of Yukon River Chinook salmon, river discharge at three sites within the basin, and the biological characteristics of the fish passing the site using linear regression. River discharge was retained in all models. Other non-significant variables were removed and the model rerun. The stocks and number of fish passing the site, parameter estimates, standard error (SE), and 95% confidence interval are indicated. Year and color are categorical variable, with 2002 and iridescent silver used as reference variables, respectively.

Site	Region	n	Parameter	Estimate	SE	95% CI
Nenana	Tanana	329	Discharge[1]	-0.420	0.041	-0.50 to -0.34
			Length	-0.014	0.003	-0.02 to -0.01
			Color[2]	1.299	0.611	0.10 to 2.50
			Color[3]	3.576	3.657	-3.62 to 10.77
			Run timing	0.284	0.045	0.20 to 0.37
			Distance traveled[4]	0.031	0.005	0.02 to 0.04
			Year 2003	-0.06	0.795	-1.63 to 1.50
			Year 2004	2.721	0.775	1.20 to 4.25
Eagle	Upper Yukon	527	Discharge[1]	-0.017	0.021	-0.00 to 0.00
			Length	-0.011	0.003	-0.12 to -0.00
			Color[2]	2.003	0.865	0.30 to 3.70
			Run timing	-0.189	0.038	-0.26 to -0.11
			Year 2003	-0.491	0.818	-2.10 to 1.12
			Year 2004	2.380	0.807	0.79 to 3.97

[1] Representing discharge in units of 1,000 cfs.
[2] Comparing fish with iridescent silver and dull silver coloration at the tagging site.
[3] Comparing fish with iridescent silver and blush coloration at the tagging site.
[4] Distance from Paimiut to final spawning site.

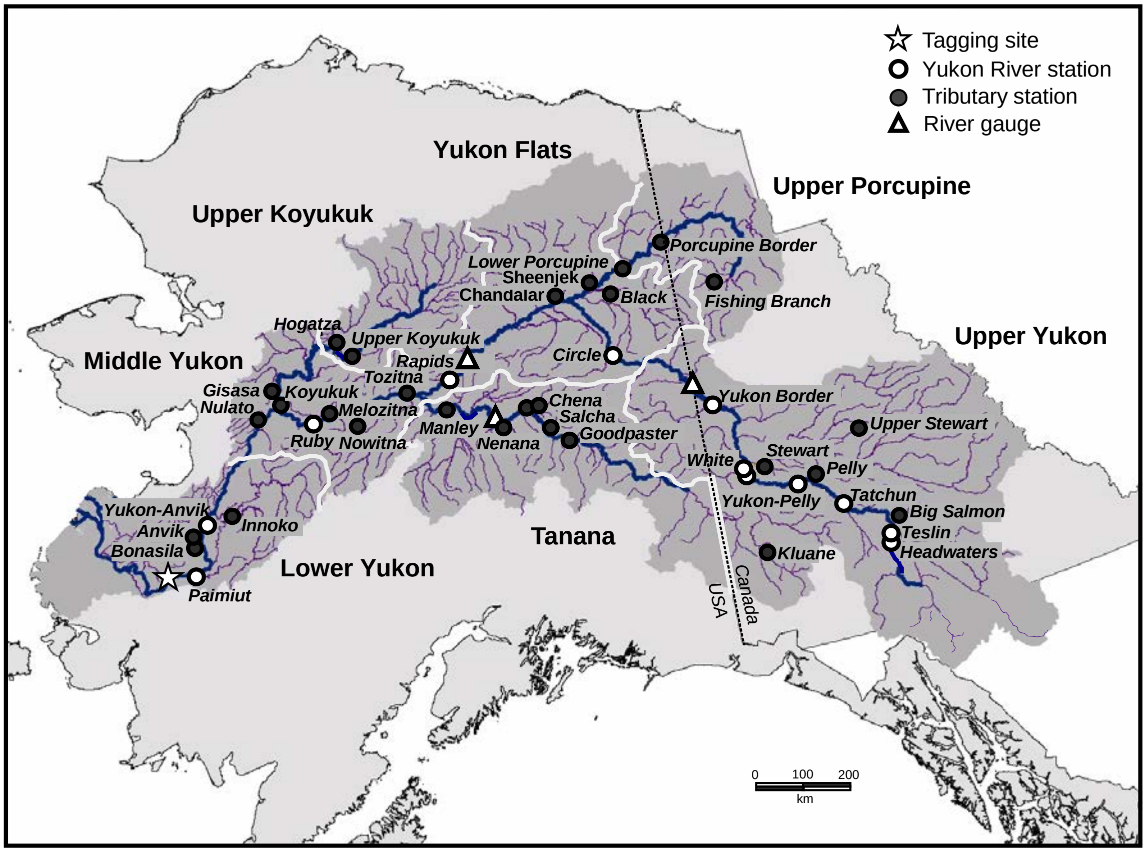

Figure 1.— Map of the Yukon River basin (shaded area) showing the regional areas, major drainages, lower river tagging site, tracking stations on both the Yukon River main stem and associated tributaries, and river gauge locations.

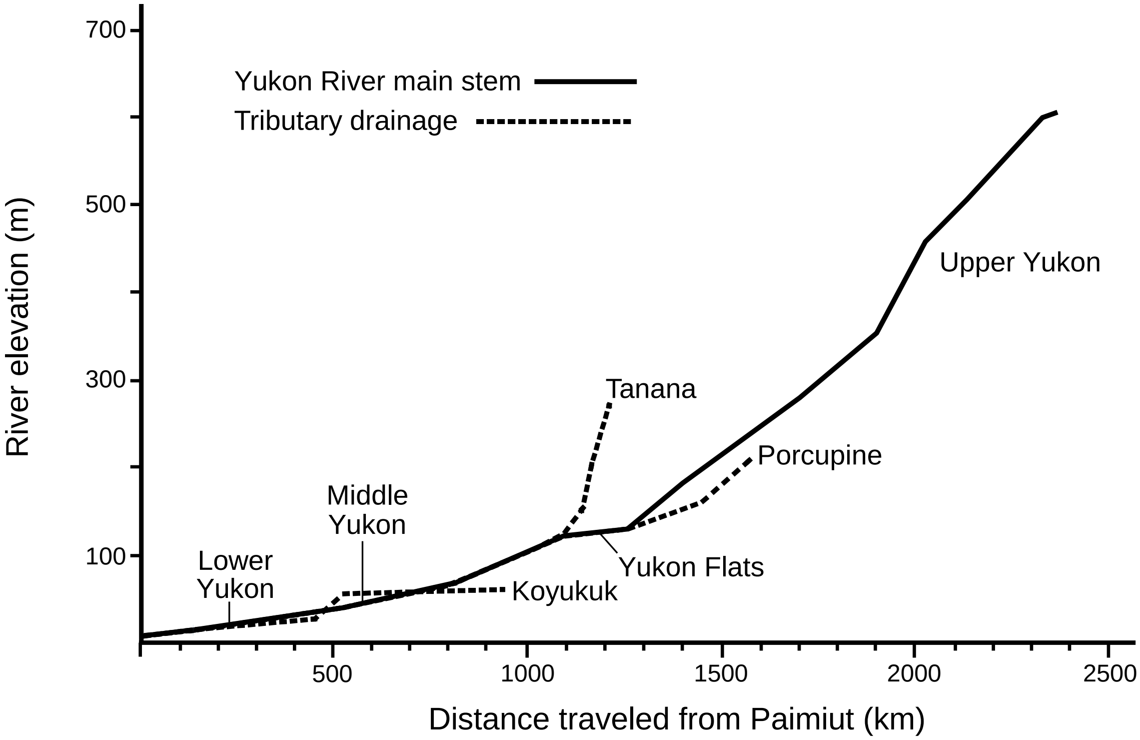

Figure 2.— Elevation of the principal drainages of the Yukon River basin used as travel routes by Chinook salmon during their upriver migration. Coverage extends from Paimiut to the location of tracking stations on terminal tributaries.

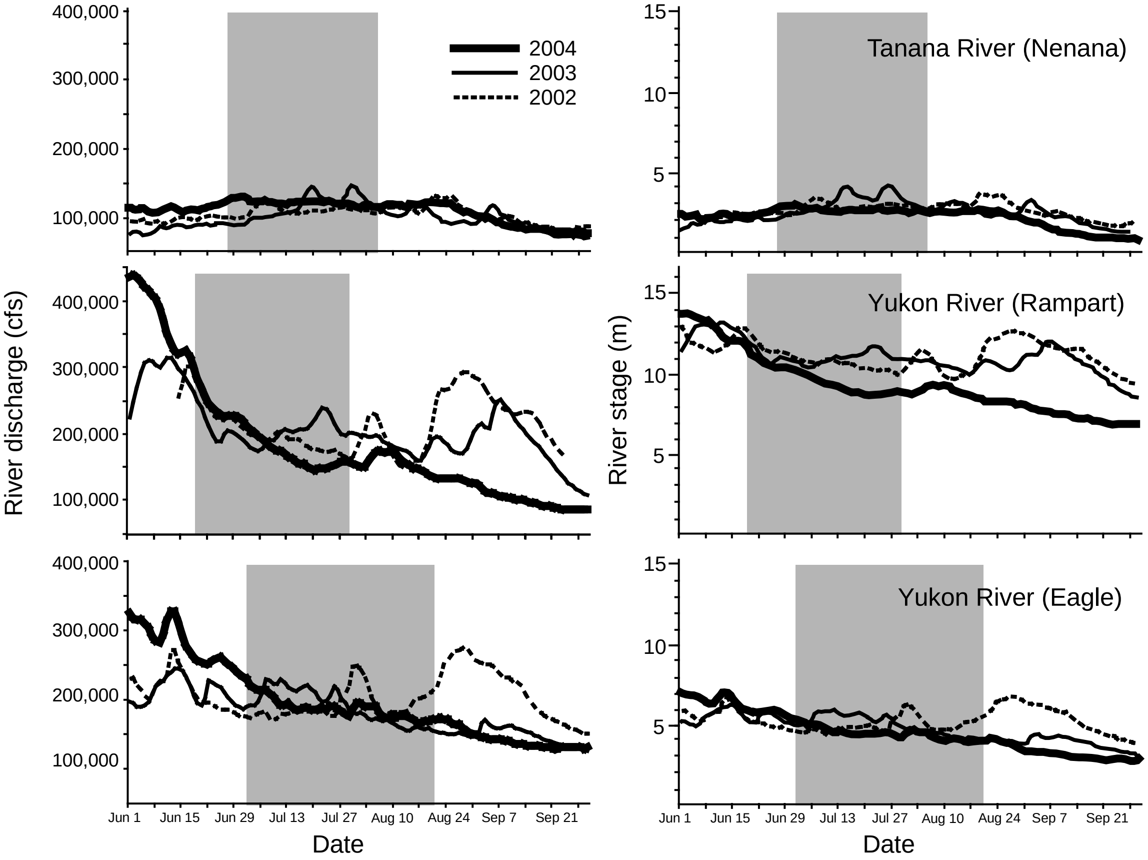

Figure 3.— River discharge and stage at sites on the Yukon River near the villages of Rampart (upriver from the Yukon-Tanana River confluence) and Eagle (near the U.S.-Canada border) and on the Tanana River near Nenana during 2002-2004 (data provided by the U.S. Geological Survey, National Water Information System). Shaded areas indicate the dates when returning adult Chinook salmon were present.

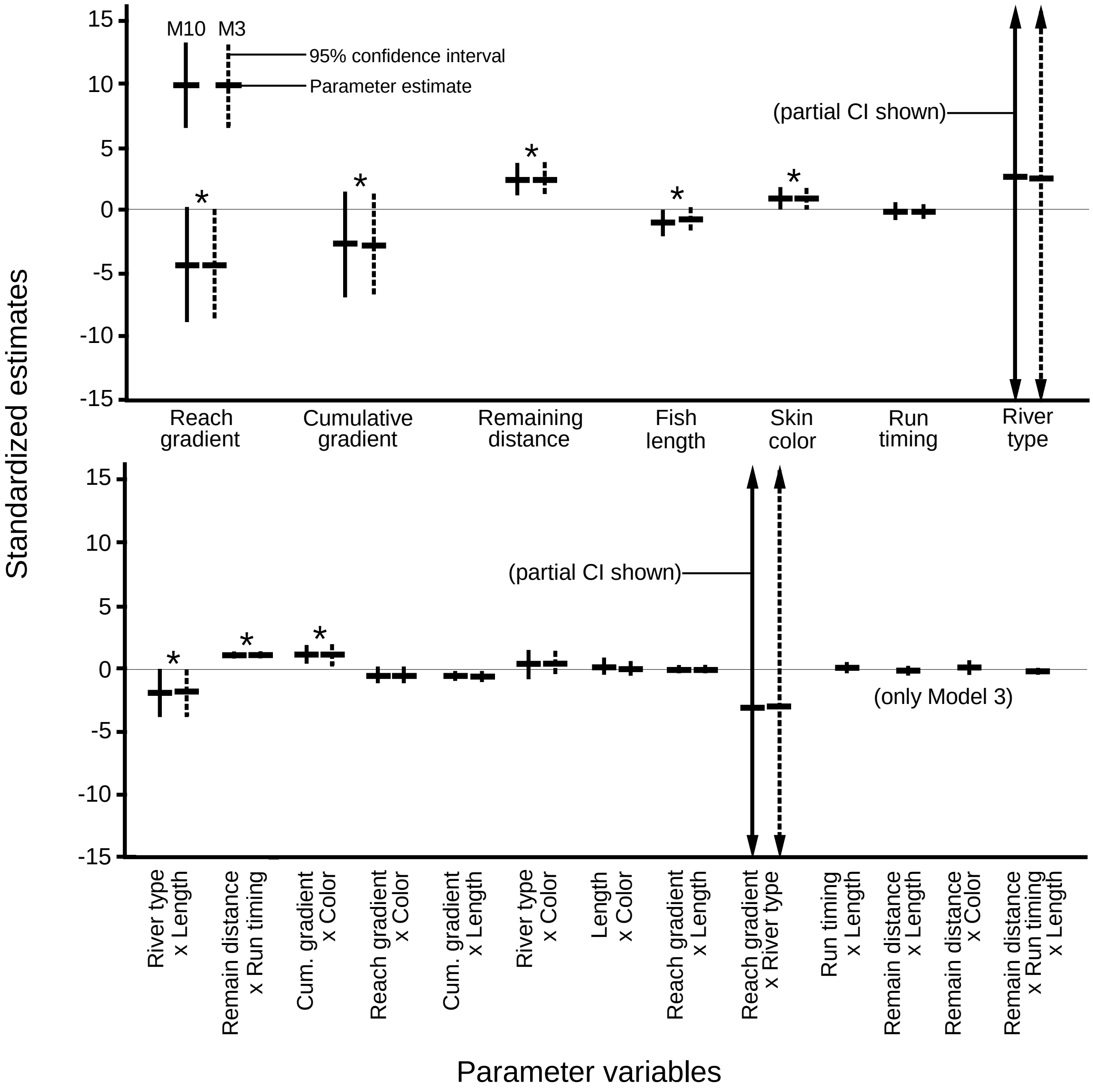

Figure 4.— Parameter estimates and 95% confidence intervals of the fixed-effect explanatory variables (both main effects and interactions) from the two best-fitting hierarchical linear regression models used to evaluate the factors affecting upriver migration rates of Yukon River Chinook salmon. The confidence intervals for the main effect *river type* and interaction *river type* x *reach gradient* were excessively wide (-41 to 47 and -105 to 98, respectively) and are not shown in their entirety. Asterisks denote factors with appreciable parameter effect on migration rate.

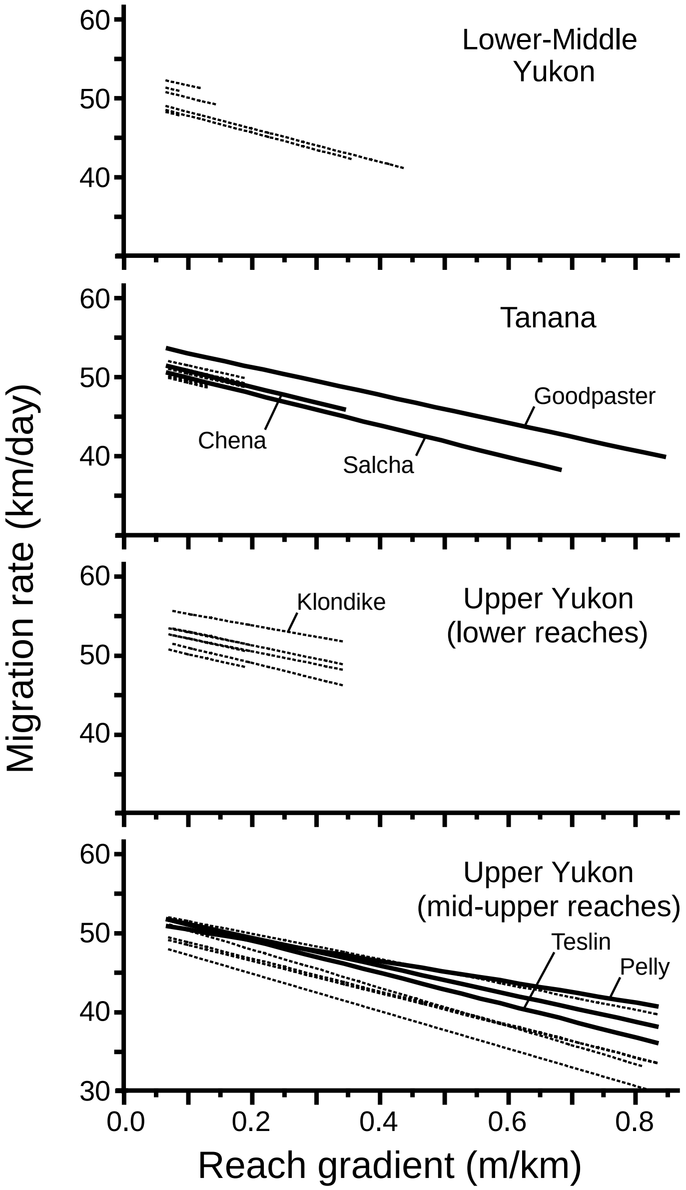

Figure 5.— Empirical Bayes estimates of the relationship between migration rate and *reach gradient* for stocks of Yukon River Chinook salmon, including lower and middle Yukon River stocks, Tanana River stocks, and upper Yukon River stocks from both the lower reaches (downstream from the Yukon-Stewart River confluence) and middle to upper reaches (from the Stewart River to the upper headwaters). Solid lines indicate major stocks; dotted lines indicate minor stocks. Selected stocks are also indicated.

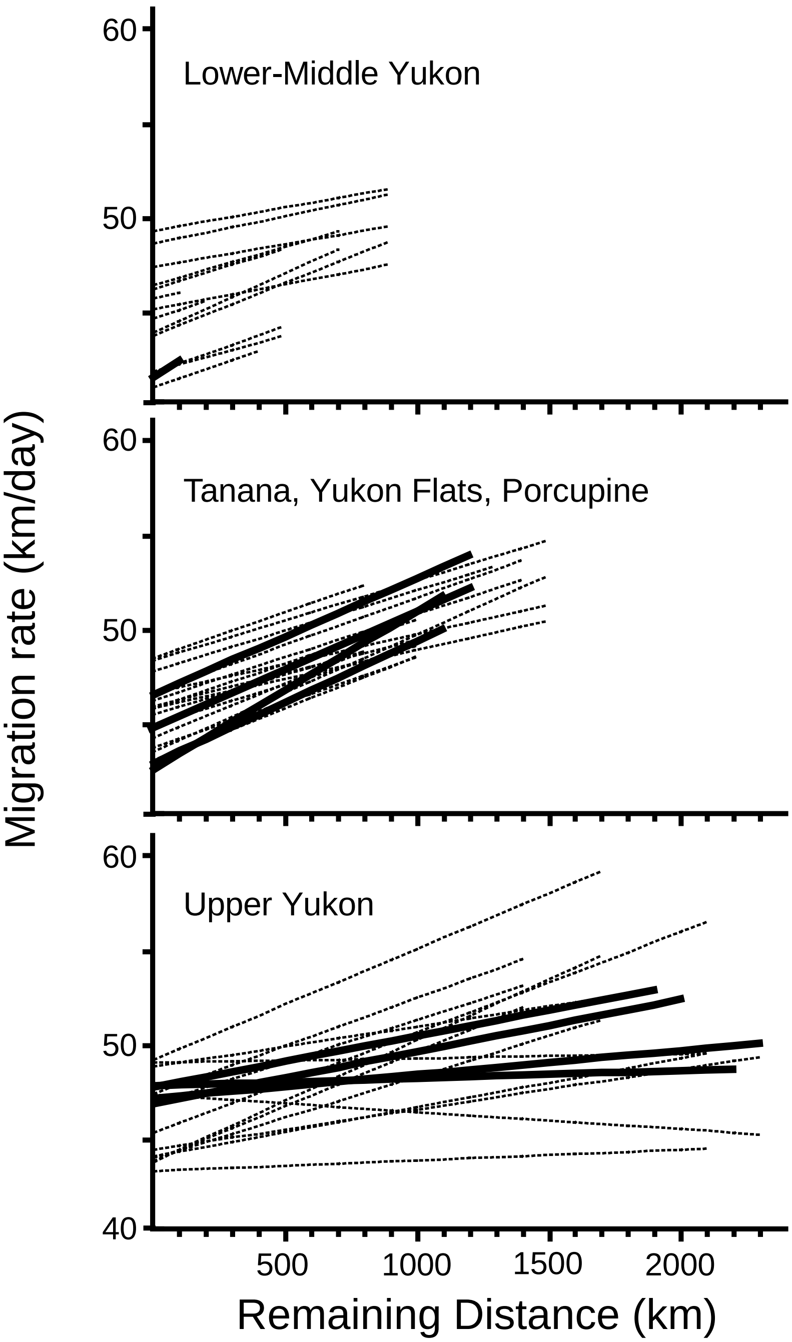

Figure 6.— Empirical Bayes estimates of the relationship between migration rate and *remaining distance* for Yukon River Chinook salmon, including lower and middle Yukon River stocks; Tanana River, Yukon Flats, and Porcupine River stocks; and upper Yukon River stocks. Solid lines indicate major stocks; dotted lines indicate minor stocks.

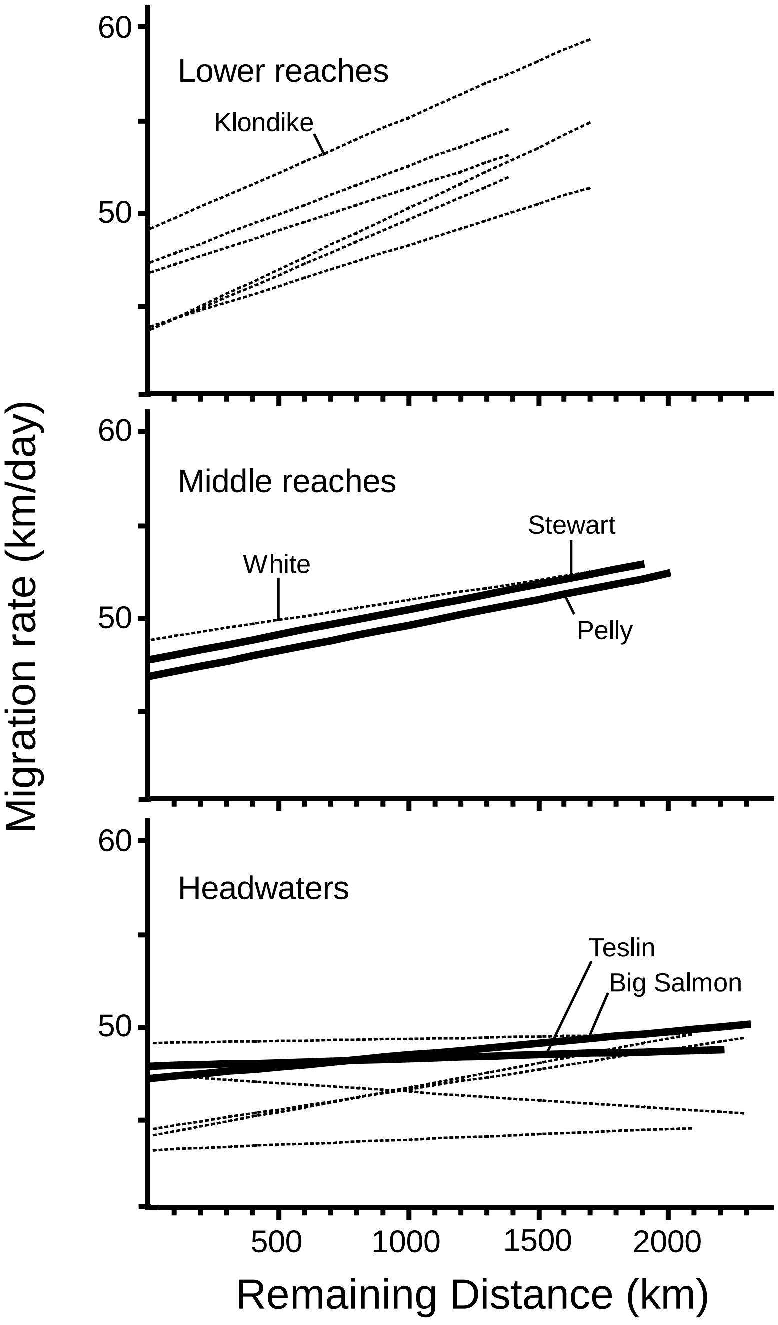

Figure 7.— Empirical Bayes estimates of the relationship between migration rate and *remaining distance* for Yukon River Chinook salmon returning to the upper Yukon River, including the lower, middle, and headwater reaches. Solid lines indicate major stocks; dotted lines indicate minor stocks. Selected stocks are also indicated.

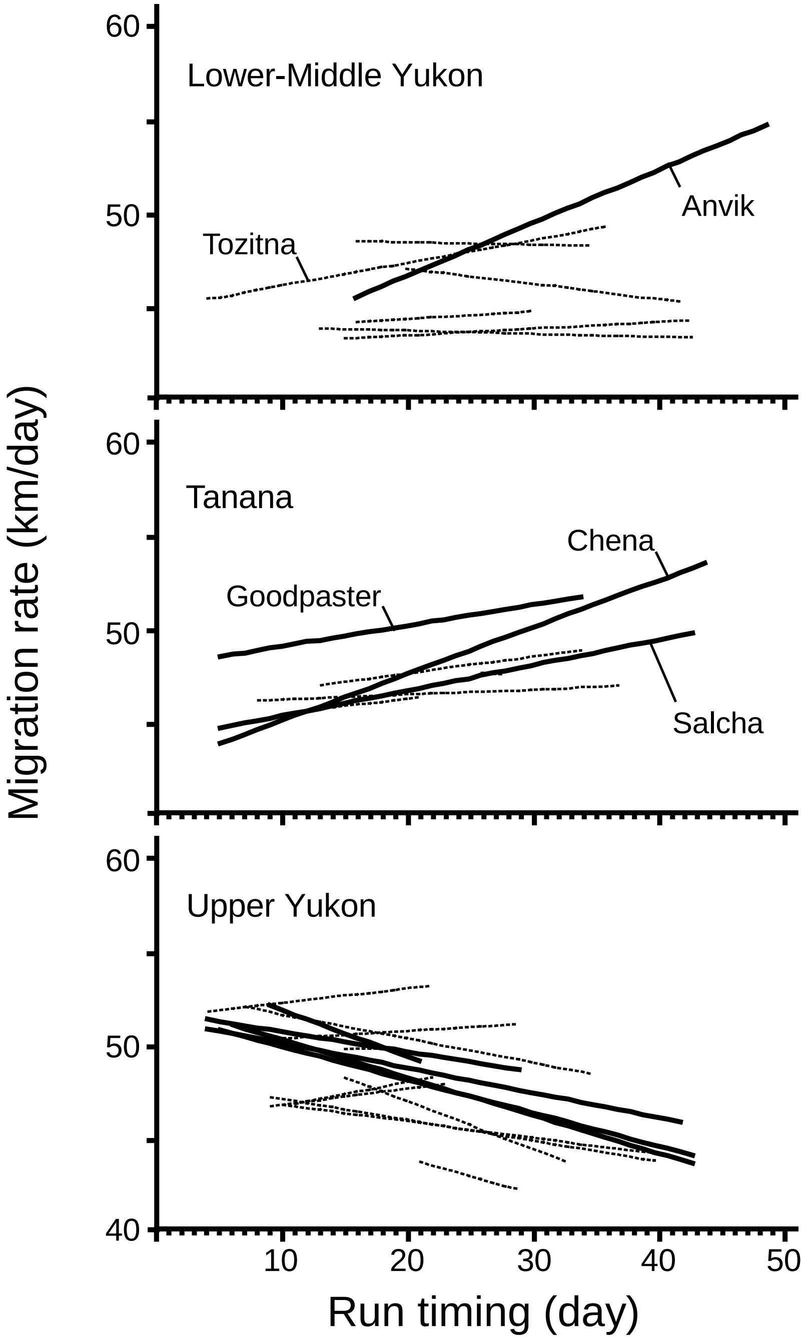

Figure 8.— Empirical Bayes estimates of the relationship between migration rate and *run timing* for Yukon River Chinook salmon, including lower and middle Yukon River stocks, Tanana River stocks, and upper Yukon River stocks. Solid lines indicate major stocks; dotted lines indicate minor stocks. Selected stocks are also indicated.

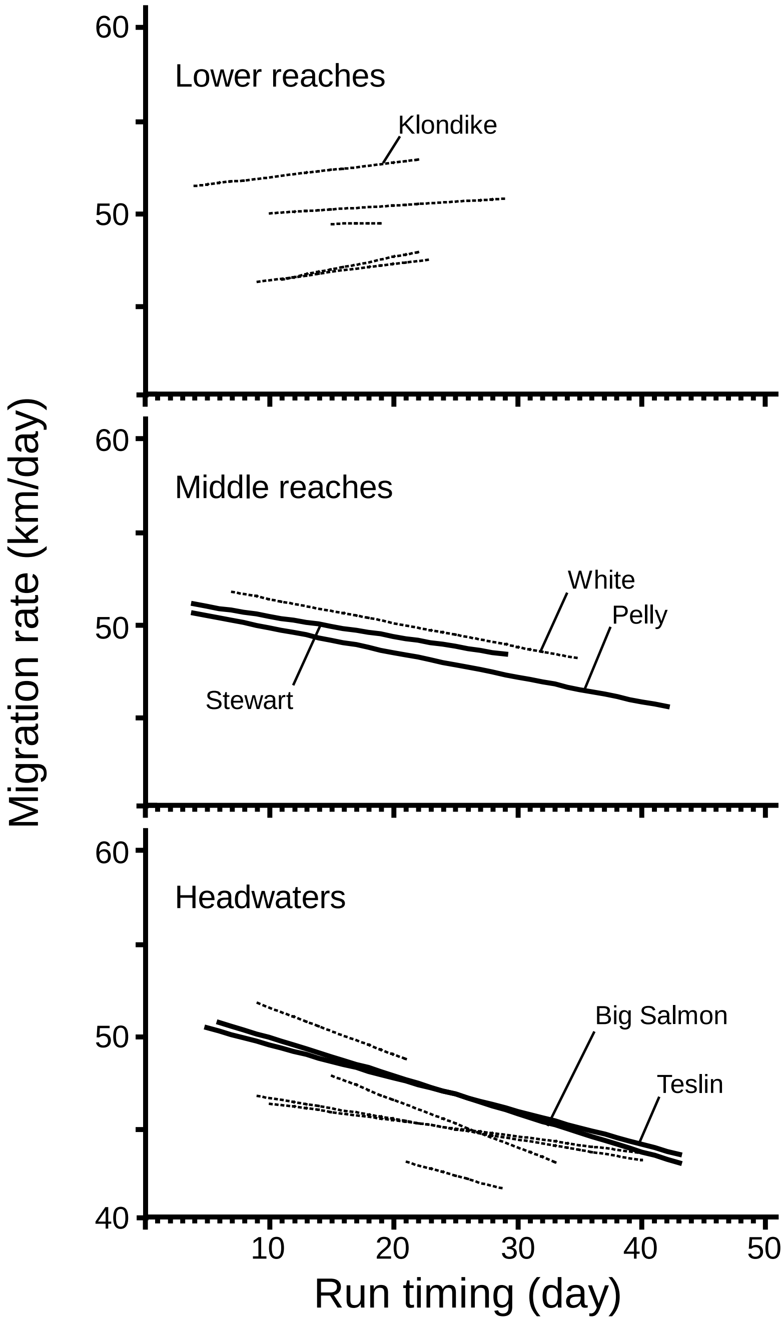

Figure 9.— Empirical Bayes estimates of the relationship between migration rate and *run timing* for Yukon River Chinook salmon returning to the upper Yukon River, including the lower, middle, and headwater reaches. Solid lines indicate major stocks; dotted lines indicate minor stocks. Selected stocks are also indicated.

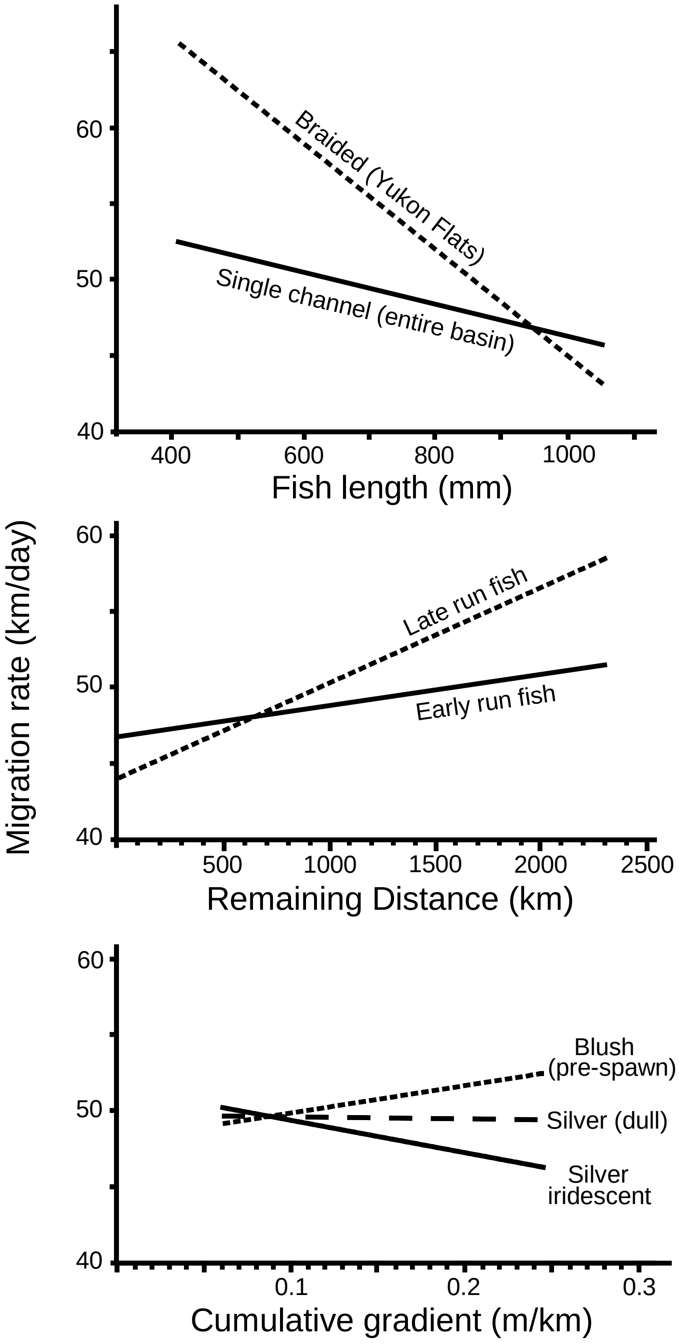

Figure 10.— Predicted relationships between migration rate of Yukon River Chinook salmon and the *river type* x *length* (top panel), *remaining distance* x *run timing* (middle panel), and *cumulative gradient* x *color* (bottom panel) interactions. The explanatory variables were constrained to reflect the observed data.

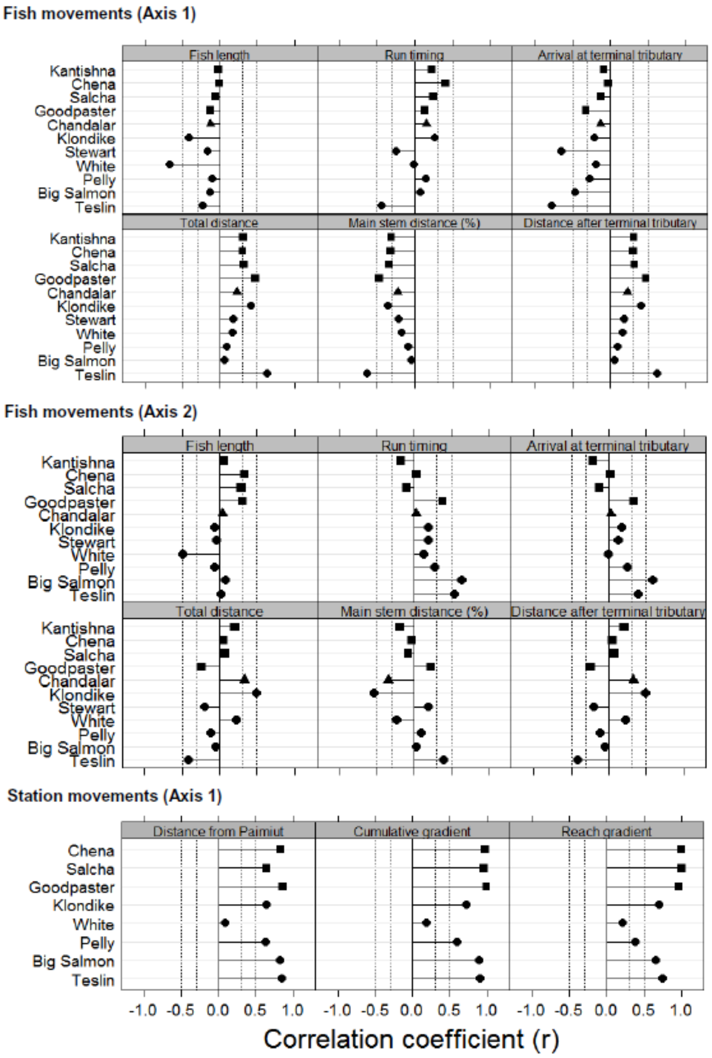

Figure 11.— Correlation coefficients for within-stock ordination of Yukon River Chinook salmon stocks comparing explanatory variables with the migration patterns exhibited by individual fish (fish movements, Axis 1 and Axis 2) and recorded at tracking stations along the migration route (station movements). Stocks are listed by distance traveled, with Teslin River fish traveling the farthest. Regional differences are represented by squares, triangles, and circles for Tanana River, Yukon Flats, and upper Yukon River stocks, respectively. The gradient values for the axis scores are listed in the text. Several stocks did not provide a usable ordination for station movements and are not listed.

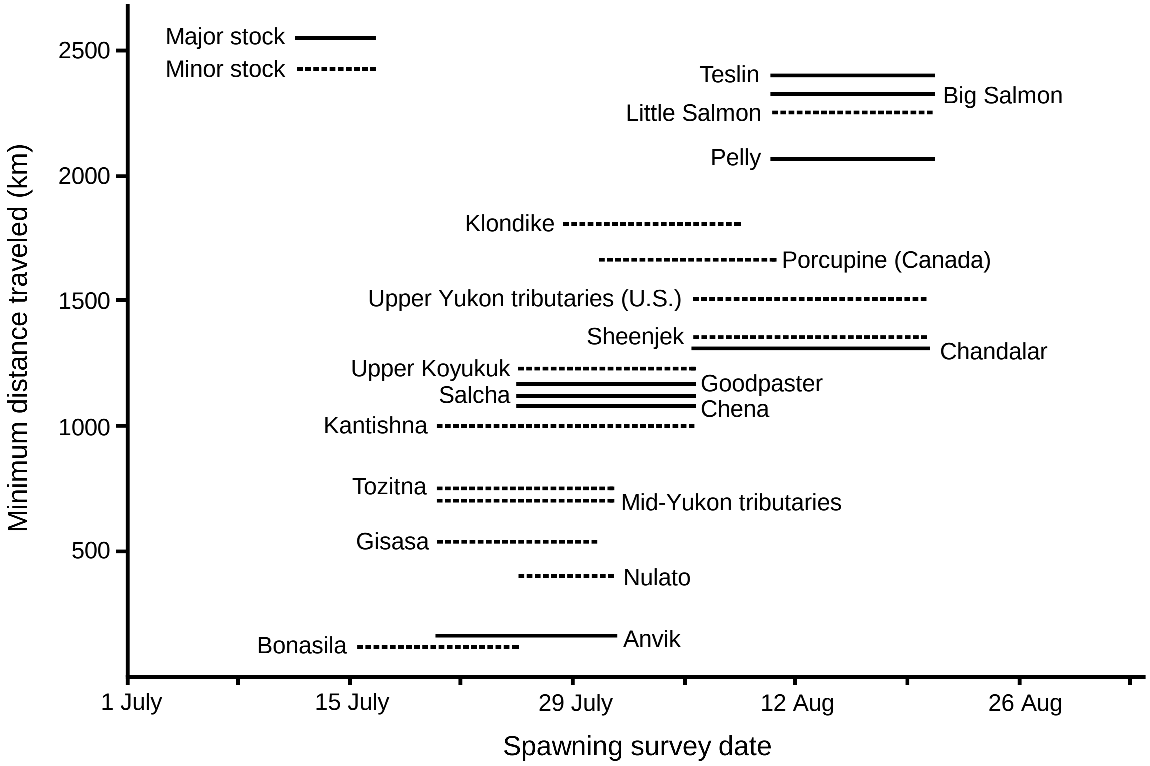

Figure 12.— Timing of aerial spawning ground surveys used to enumerate Chinook salmon in major tributaries of the Yukon River basin. Major and minor stocks are indicated. Timing data provided by the Alaska Department of Fish and Game and the Department of Fisheries and Oceans Canada.

GENERAL CONCLUSION

In many ways, the story behind this study started years before the first fish was tagged. I began working for the National Marine Fisheries Service (NMFS) in the early 1980s. At that time the U.S. and Canada were struggling to resolve a number of issues related to the coast-wide management of Pacific salmon (*Oncorhynchus* spp). These efforts had been ongoing since the 1950s, and at times the only common ground, in what were often rather contentious discussions, seemed to be the recognition that the problems needed to be addressed. Increasingly, the transboundary rivers were becoming an issue. These were large coastal rivers located primarily in Canada, but flowing through the U.S. into the marine waters of southeastern Alaska. Sizeable runs of salmon returned to these rivers, and supported long-standing marine fisheries. The development and expansion of in-river fisheries in Canada raised a number of issues related to the management of the returns and harvests allocations between the two countries.

Limited information was available on salmon returns in these rivers, and a cooperative, research effort, involving the NMFS, Alaska Department of Fish and Game, and Department of Fisheries and Oceans Canada, was initiated to start filling in some of the blanks. Although traditional fishery techniques (e.g., enumeration weirs, fishery-based mark-recapture studies) provided information on run timing and abundance, the large size and turbid conditions of these rivers complicated efforts to collect information on the spawning distribution and stock structure of the returns. As so often happens, different experiences and perspectives can have a synergetic effect. Prior to my work on salmon, I had used radio telemetry on a number of wildlife studies. Although numerous adjustments were ultimately needed to tailor this approach to salmon returns in large transboundary rivers, telemetry provided a means to accomplish many of the research objectives that would have been difficult (if not impossible) to address with more conventional methods.

At the time, fish telemetry was still in its infancy. Most telemetry studies involved small numbers of fish in localized areas. The existing equipment and tracking techniques were generally inadequate for the task of monitoring the movements of large numbers of fish over vast distances and prolonged periods of time. Transmitters either lacked sufficient signal strength and life, or were inordinately large. Tracking equipment, which was sufficient for monitoring the localized movements of small numbers of fish, was functionally cumbersome and operationally inadequate on a larger scale. Major improvements were made over the intervening years through a series of large-scale projects and integrated feasibility studies. Many of these advances were a direct result of the cooperative efforts between researchers and vendors, often overcoming technical limitations with innovative approaches and the creative use of new technologies. Smaller transmitters with greater reception range, life, and encoded signals for distinguishing greater numbers of individual fish became available with the trend toward higher quality, miniaturized electrical components. Transmitters equipped with sensors to help remotely monitor the status of fish in turbid areas were developed to substantiate unexpected results that were initially viewed skeptically (Eiler et al. 1992). Tracking receivers with internal global positioning system (GPS) links were developed and used to standardize and electronically record the locations of radio-tagged fish, eliminating the cumbersome process of physically marking the positions on maps, and transcribing and summarizing the data by hand.

One of the major advances was the shift from mobile tracking to the use of remote tracking stations. It soon became apparent that the established methods of tracking fish by boat or aircraft were inadequate for large, basin-wide studies conducted over extended periods of time. In addition to the problems associated with maintaining contact with the fish, the costs and general wear-and-tear on the researchers from long, frequent survey flights was substantial. The need for information on fall-run species (returning to spawning tributaries when weather conditions were marginal for flying) further demonstrated the limitations of conventional tracking methods, and led to the development of the satellite-linked tracking station system (described by Eiler 1995) ultimately used during the Yukon River study. One of the unsung heroes of this story is Jim Olsen (NMFS, U.S.-Canada program manager) who understood the need, saw the potential, and steadfastly supported the development of this technology in spite of considerable criticism during the process. Stationary tracking is now routinely used for both large and small-scale fish telemetry studies. Enhanced database capabilities made it possible to more efficiently summaries the often voluminous amounts of data collected during these studies (Eiler and Masters 2000). Although websites that display study results in real time are now commonplace, this “novel” approach was essential for evaluating station performance in-season, planning field operations (based on the upriver movements of the fish), and updating collaborators from other agencies.

It is often the combination of incremental steps that make major undertakings possible. The combination of technical advances described above, in conjunction with the insights gained from previous studies, provided the foundation necessary to conduct basin-wide studies on Yukon River salmon despite the massive size and limited access of the drainage, and the difficulties associated with keeping track of large numbers of highly mobile, long-distance migrants. Even with this advantage, two years of preliminary work were needed to locate suitable capture sites, fine-tune capture and handling procedures, install the system of tracking stations, and develop the infrastructure needed for a study of this size and scope.

The importance of Yukon River Chinook salmon also influenced and shaped the study. The salmon resource within the basin is unique due to the enormity of its impact. The river and its tributaries drain over a third of interior Alaska and most of the Yukon Territory. Salmon are central to the fabric of life within the basin. Every year the returns provide a major nutritional boost to the ecosystem. Most interior communities are located on the river, and have strong traditions of fishing for salmon. Discussions and management decisions related to fishing and salmon harvests are not abstract, but have a direct impact on local residents. Numerous disputes have erupted over the years (not only between U.S. and Canadian agencies, but between lower and upper river fishers) regarding Chinook salmon harvests, allocations between user groups, and escapement levels. Efforts to resolve these issues have been exacerbated by the continuing decline in run abundance. Although local fishers occasionally voiced concerns that we (as researchers) were not treating the fish respectfully or with sufficient care, in reality it was impossible not to be conscience of the importance of the returns to local communities. Many of the capture and handling methods used during the study were specifically designed to lessen adverse effects on the fish. The tagging response and upriver movements exhibited by the fish demonstrate that large-scale capture and handling efforts can be effective when steps are taken to minimize adverse effects.

No field study is perfectly designed or flawlessly executed. Key factors are occasionally overlooked, unforeseen circumstances invariably arise, seemingly minor issues can have a disproportional effect, and some objectives are simply unattainable despite the best of efforts. Even when studies are well planned, limited funding, logistical considerations, and competing objectives often affect the type and quality of data collected. Several factors influenced the outcome of this study. Although the tagging and tracking methods provided reliable data (Chapter 2), the study was primarily designed to determine the composition, timing, and spawning distribution of the returns. The methods used to track the fish reflected these goals, limiting to some extent the information provided on upriver movements. Stationary tracking provided detailed and comparable information for different reaches of the basin and different groups of fish, but relatively few stations were located in the lower river, limiting the migratory information on lower basin stocks. While station placement was less critical for determining fish distribution, logistical considerations frequently made it difficult (or impossible) to position stations at the best sites for calculating migratory rates (e.g., river confluences, transitional sites between river types), and alternative approaches were sometimes required (Eiler 2012). Operational costs and other research priorities also restricted the coverage of minor stocks, and limited the information on fine-scale movements. As previously mentioned, potentially important information on fish characteristics (e.g., sex and fish condition) was sacrificed in deference to concerns over handling issues, and detailed hydrological and temperature data, which may have provided useful insights on fish response, were not available.

It is often necessary to evaluate and manage natural resources based on the best information available. Handling effects, information gaps, data resolution (i.e., scale) and compatibility issues, and tradeoffs between research goals and operational restrictions are common problems in fish movement studies. These concerns are exacerbated by the complexities associated with Chinook salmon returns in large free-flowing rivers, with individual movements reflecting a diverse and dynamic amalgamation of internal traits and external influences. In spite of these shortcomings, even less than perfect efforts can supply valuable information. The data obtained during this study provided a number of insights into the spawning distribution, stock structure, upriver movements, and factors associated with the migratory patterns of these fish, and in some cases called into question some conventional view. The study also highlighted several areas needing additional research, including the:

- Effect of changes in run characteristics on the spawning distribution, stock structure and timing, and migratory patterns of the returns
- Migratory patterns of lower river fish and minor stocks within the basin.
- Comparative studies on the migratory patterns exhibited by upper headwater stocks.

There is increased concern over the continuing decline in Chinook salmon returns in the Yukon River basin (ENS 2012) and the perceived reduction in fish size (JTC 2006). Possible causes run the gamut from harvest practices (e.g., marine bycatch, gear selectivity in riverine fisheries) to environmental shifts related to climatic changes and the associated impacts on the ecosystem. Migratory patterns provide a functional measure of the fish that can be monitored temporally over the course of the run. Comparative information on upriver movements in relation to run characteristics (e.g., abundance, stock composition, and timing), and in concert with data on an expanded suite of explanatory factors could provide needed insights into the status of the returns. The seemingly incongruous relationship (i.e., negative) between swimming speed and fish size observed during this study may provide new perspectives into the tradeoffs between size, swimming performance, and transportation costs, and address the possible implications associated with current population trends.

Headwater stocks in the Upper Yukon exhibit some of the longest salmon migrations in a free-flowing river, and are undoubtedly subjected to extreme selective pressures. Although similarities in migratory patterns were observed between these fish and those traveling shorter distances, anomalies were also observed in relation to several principal factors. Comparative studies of these stocks would enhance our understanding of the contributing factors and evolutionary forces constraining Chinook salmon migrations. There is also ancillary evidence from this study that the physiological condition of the fish influenced the migratory patterns of upper headwater stocks, and (by inference) may potentially impact reproductive success particularly in light of current environmental trends. Fish condition is likely impacted by a number of factors, ranging from climatic shifts in the Bering Sea which have been shown to affect temperature regimes and forage fish populations (Hollowed et al. 2012, Stabeno et al. 2012) to changes in river condition (e.g., temperature and flow) that may alter the energetic costs incurred during the migration. Movement studies that incorporated measures of physiological condition would provide invaluable insights.

Movement data are messy, since they encompass both spatial and temporal aspects of an animal’s life history. Turchin (1998), in his seminal work on animal movements, observed that unlike the well developed approaches for estimating population density, survival, and mortality, quantitative methods for analyzing and modeling animal movements had lagged noticeably behind. However, advances in biotelemetry and computational capabilities have radically changed the technological and analytical landscape, making it possible to collect and evaluate detailed and (at times) voluminous amounts of information on animal movements. This transformation has unquestionably energized research efforts in this field. Salmon migrations have received considerable attention due to the large and cyclical nature of the returns, the extraordinary distances traveled, and the economic and biological importance of the resource, with efforts to both quantitatively describe and analyze migratory movements and the contributing factors (Keefer et al. 2004, Salinger and Anderson 2006, Cooke et al. 2008).

In spite of these advances, research objectives often focus on other higher priority objectives (e.g., abundance, distribution, stock structure, and habitat use). Since detailed information on salmon movements is often not available to fishery managers, the methods for incorporating it into the decision making process are not always apparent or straight forward. However, in conjunction with other information on run characteristics, movement data can provide a number of insights into the passage of fish through upriver fisheries and the status of the return. Movement data can be particularly important in large drainages with widely scattered fisheries where management actions in the lower river potentially impact harvests farther upstream. As demonstrated during this study, it is possible to glean usable information on salmon movements collected under less than ideal circumstances. Careful review is of course needed to understand the intricacies and limitations of the data, and identify sources of potential bias. That being said, the judicious use of robust, analytical methods can be used to effectively mine existing telemetry data from studies designed to address other research objectives. Even when these efforts do not present a complete picture of the situation at hand, they can often provide the foundation needed to effectively develop future research efforts.

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