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ARTICLE

Swimming depths and water temperatures encountered by radio-archival-tagged Chinook Salmon during their spawning migration in the Yukon River basin

John H. Eiler[1] | **Michele M. Masuda**[1] | **Allison N. Evans**[2]

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

[2]Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Corvallis, Oregon 97331, USA

Correspondence
John H. Eiler
Email: alaska.jeiler@gmail.com

Abstract

Objective: Historically, Chinook Salmon *Oncorhynchus tshawytscha* have supported important fisheries throughout the Yukon River basin, but dramatic declines in abundance since the late 1990s have resulted in smaller returns, severe reductions in harvests, and difficulties in meeting escapement goals. These observations coincide with major climatic changes in the northern Pacific, characterized by a general warming trend throughout the region. Our objective was to document the migratory patterns of the fish in relation to the environmental conditions encountered in order to assess the impact of climate change and help manage the returns.

Methods: We used radio-archival tags to track the distribution and movements of adult Chinook Salmon returning to the Yukon River to spawn. The tags were equipped with sensors that recorded the swimming depth of the fish and water temperatures encountered during the upriver migration. Spawning ground surveys and fishery returns were used to recover the tags to download the sensor data.

Result: Ninety-five (71.4%) of the 133 tags tracked upriver were recovered, including 35 (26.3%) returned by fishermen and 60 (45.1%) retrieved on the spawning grounds. Upriver movements were characterized by continuous and highly variable fluctuations in depth throughout the migration, ranging from <5 m to >20 m in the lower river and progressively less as fish moved upstream into shallower waters. Swimming depth was not influenced by time of day. Temperatures encountered by the fish were generally warmer in 2004, but this pattern was not consistent throughout the basin and was driven by conditions in the lower main stem, with temperatures frequently >18°C and periodically exceeding 21°C. There was no obvious behavioral response to the warm conditions, with comparable movements and survival rates when conditions were cooler. Temperatures in terminal tributaries often exceeded the upper range generally considered optimal during spawning (13°C), but signs of impaired behavior or prespawning mortality were not observed. A thermal diel pattern was evident as fish left the main stem and approached their spawning grounds, with temperatures declining from early evening to early morning and increasing during daylight hours, suggesting that assessments based on average daily temperature may not adequately reflect exposure to suboptimal conditions.

Conclusion: Although the fish during our study frequently encountered temperatures associated with adverse effect on salmon, impaired behavior and increased mortality were not evident. However, the current warming trend occurring throughout the northern Pacific is predicted to continue and may impact salmon populations more severely. Our findings provide a baseline for comparing past conditions and migratory patterns with those of present and future returns. Radio-archival tags not only provided site-specific information, but substantially increased the number of tags recovered, with a recovery rate considerably higher than reported for most archival tag studies. The ability to obtain larger samples and more representative results is a major advantage for addressing many resource issues currently facing fishery managers and local communities.

KEYWORDS

Chinook Salmon, climate change, radio-archival tags, spawning migration, swimming depth, water temperature, Yukon River

INTRODUCTION

After spending a considerable portion of their lives at sea (typically several years), Chinook Salmon *Oncorhynchus tshawytscha* return to spawn in rivers throughout the northern Pacific, ranging from small coastal drainages to vast river basins (Healey 1991; Heard et al. 2007). Sizeable numbers of Chinook Salmon return to spawning areas in the Yukon River, a massive river basin in Alaska and northwestern Canada (JTC 2021). These returns support important subsistence and commercial fisheries throughout the basin and are an integral part of the riverine ecosystem.

The upriver migration presents a formidable challenge for the fish, which must travel substantial distances (from hundreds to thousands of kilometers) to reach their natal streams (Eiler et al. 2014). In addition to the physical demands associated with swimming upstream against strong currents (Beamish 1978; Brett 1995) and increasing elevation (Gilhousen 1980), there are also physiological costs incurred while in transit related to the sexual maturation of the fish and the production of gametes (Brett 1995; Crossin et al. 2004). These demands are exacerbated by the fact that salmon stop feeding as they enter freshwater and must rely on stored energy reserves (Brett 1995; Quinn 2018). To succeed, the fish must be able to complete the migration within a specific period of time, arrive on the spawning grounds when conditions are favorable, compete with conspecifics for suitable spawning sites and mates, avoid predation, and have sufficient energy left to spawn and defend their redds. Most salmon have minimal energy reserves after spawning (Brett 1995; Hendry and Berg 1999), and any factor that increases metabolic costs during the migration may have a detrimental effect on the performance of the fish and may ultimately determine whether they successfully reproduce (Martin et al. 2015).

Impact Statement

Chinook Salmon returns to the Yukon River have declined dramatically in recent years, creating social and economic hardships in many rural communities. This decline coincides with the general warming trend observed throughout the northern Pacific. Although the long-term effects of this trend are not fully understood, the impact on Pacific salmon may become increasingly severe. This paper looks at the upriver movements of Yukon River Chinook Salmon in relation to the water temperatures encountered, and examines the impact of elevated temperatures during the migration. Our findings provide a baseline for comparing past conditions and migratory patterns with those of present and future returns.

Dramatic reductions in abundance were reported for Chinook Salmon populations in the Yukon River and other drainages throughout the northern Pacific in the late 1990s (Heard et al. 2007; Jones et al. 2020). This decline has continued during subsequent years and resulted in diminished returns, severe reductions in harvests, and difficulties in meeting escapement goals (Evenson et al. 2009). Reductions in fish size and shifts in age composition to younger individuals have also been reported (Lewis et al. 2015; Ohlberger et al. 2018). These trends have created social and economic hardships in many rural communities as well as concern over the long-term health of the returns. Information on run characteristics (e.g., abundance, stock and age composition, and migratory patterns) and environmental conditions within the basin is needed to more precisely assess Chinook Salmon returns, track population trends, and identify the root causes associated with recent shifts in abundance, fish size, and age structure (ADFG Chinook Salmon Research Team 2013).

Over the last several decades, major climatic changes have occurred in the northern Pacific, characterized by a general warming trend throughout the region (Walsh et al. 2011). Corresponding shifts in both large-scale oceanic patterns (Kilduff et al. 2015; Mantua 2015) and localized conditions (Chittenden et al. 2010) have been linked to reduced marine survival in Pacific salmon *Oncorhynchus* spp. Measurable effects have also been reported in the freshwater environment, with some of the most pronounced changes occurring in both the Arctic and subarctic regions (Carey et al. 2017). Increasing temperatures in rivers used by Pacific salmon and the potential impact on these populations have become a major concern. Although differences have been reported, particularly in relation to species and life stage, 18°C has often been considered a critical threshold during the spawning migration, with temperatures above this level associated with adverse effects on the returning adults (Brett 1971; McCullough 1999). Altered run timing, disrupted migratory patterns, and increased mortality have been attributed to elevated temperatures in a number of drainages within the southern range of Pacific salmon, including the Sacramento (Peterson et al. 2020), Klamath (Strange 2010), Columbia (Keefer et al. 2008), and Fraser (Hinch et al. 2012) rivers. Although these issues have been less evident for salmon in northern rivers, there is increasing concern that these populations may also be at risk (von Biela et al. 2022).

Understanding the vulnerability of Chinook Salmon to increasing temperatures and the impact on in-river movements and survival is complicated by the vast size and dynamic hydrology of large river drainages. These constraints are routinely compounded by a lack of information on the swimming patterns of the fish and the nominal environmental data available, which are often limited to isolated sampling sites and may not adequately reflect the conditions encountered by the fish. In 2002–2004, a basin-wide telemetry study was conducted to determine the run characteristics of Chinook Salmon returning to the Yukon River basin, including the spawning distribution, stock composition, run timing, and migratory patterns of the returns (Eiler et al. 2014, 2015). As part of this study, Chinook Salmon were tagged with radio-archival tags to provide site-specific information on the swimming depths of the fish and the water temperatures encountered during the spawning migration. In this paper, we compare the swimming patterns exhibited by regional Chinook Salmon stocks and the thermal conditions experienced by the fish as they traveled upriver through different reaches of the basin.

METHODS

Study area

The Yukon River basin drains a watershed of over 855,000 km^2. The main river alone (hereafter referred to as the "main stem") flows for more than 3,000 km from its headwaters in Canada to the Bering Sea (Figure 1). Several major tributaries flow into the 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 areas are remote, with access limited to boat or aircraft. The Yukon River is also one of the largest drainages in North America in terms of annual discharge and exhibits considerable seasonal variability, with substantially greater flows during summer (Brabets et al. 2000; Yang et al. 2009). The entire drainage freezes over in winter, with ice breakup taking place during the spring. Several reaches are extremely turbid during the summer from glacial runoff, including the Tanana River, the White River, and sections of the main stem downstream of these tributaries. River elevation ranges from sea level to over 500 m in the upper headwaters.

The main stem is relatively deep, with channel depths exceeding 20 m in the lower river compared to 12–14 m downstream of the Yukon–Tanana River confluence and 8–10 m near the U.S.–Canada border (distances of ~1,100 and 2,000 km from the river mouth, respectively). Most reaches consist of a primary river channel with occasional side channels and sloughs, although the main stem is extensively braided in the area commonly referred to as the Yukon Flats. Sections of the Tanana River, the White River, and the Canadian main stem are also highly braided. Regional designations (Figure 1) are based on the geographic location and geomorphology of the area (e.g., lower reaches of the Porcupine River are included as part of the Yukon Flats due to similarities in landscape and river characteristics).

Subsistence fishing and commercial fishing occur throughout the basin, with most effort concentrated near villages along the main stem (JTC 2021). Fish are also harvested in reaches of the Koyukuk, Tanana, Chandalar, Porcupine, Stewart, Pelly, and Teslin rivers. Limited

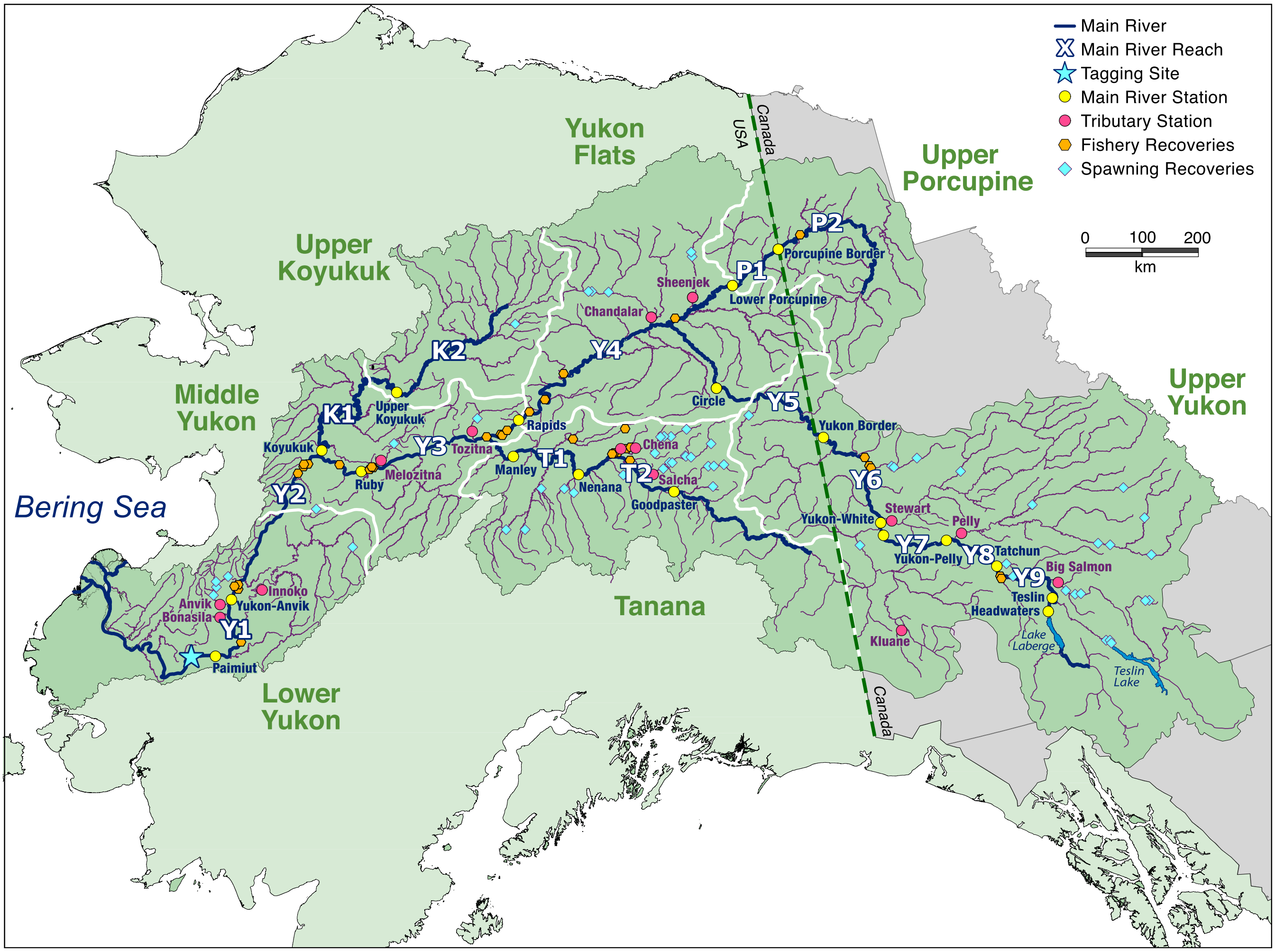

FIGURE 1 Map of the Yukon River basin, showing the regional areas, major drainages, tagging site, tracking stations on both the main rivers and associated tributaries, and the final location of radio-archival-tagged Chinook Salmon harvested in the fishery or recovered in spawning tributaries. Main river reaches (Y = Yukon River main stem; K = Koyukuk River; T = Tanana River; P = Porcupine River) are also indicated.

sportfishing takes place in a number of clear-water tributaries. The fisheries are managed to provide essential spawning escapements, subsistence harvests for local residents, and commercial fishing and sportfishing opportunities when sufficient fish are available.

Fish capture and tagging

Adult Chinook Salmon were captured in the lower river near the village of Russian Mission (~300 km from the river mouth) during 2002–2004 (Figure 1). The methods used were described by Eiler et al. (2014). Briefly, the fish were captured from early June to mid-July with drift gill nets that were specifically designed to minimize capture-related injuries. The nets were monitored continually, and the fish were removed immediately after capture. Fish were randomly selected for tagging (a maximum of 2 fish/drift) and were placed in a neoprene-lined tagging cradle that was submerged in a trough filled with river water. Fresh river water was continually pumped into the trough while the fish were being processed. Anesthesia was not used during the tagging procedure.

The fish were tagged with radio-archival tags manufactured by Advanced Telemetry Systems. The tags (which were 6.6 cm long and 2.0 cm in diameter, had a 30-cm transmitting antenna, and weighed 20 g) were gently inserted through the mouth and placed in the stomach of the fish. The tags had a minimum battery life of 90 days.

Each tag included a radio transmitter that emitted a unique pulse-coded signal on a single frequency (151.033 MHz), making it possible to effectively track the fish while still identifying specific individuals. The transmitter was also equipped with a motion sensor and activity monitor (Eiler 1995). The motion sensor inserted additional signal pulses (distinct from the basic signal pattern) each time the transmitter moved. The activity monitor changed the signal from the basic pattern to an inactive mode if the motion sensor was not triggered for 24 h; the signal reverted to the original pattern if the motion sensor was activated. Fish with transmitters that continually registered as inactive over three consecutive days were assumed to have died.

The archival component of the tag recorded water temperature and depth every 3 min. The temperature sensor was accurate to ±0.5°C and was capable of responding rapidly to temperature changes. Tags transferred from 25°C water (room temperature) to 3°C water accurately reflected the temperature change in <2 min (Advanced Telemetry Systems, unpublished data). Depth estimates were based on information from the tag's pressure sensor and were accurate to ±1.0 m (Advanced Telemetry Systems, unpublished data). Since pressure decreases with increasing elevation, these data were adjusted to account for changes in elevation as the fish moved upriver. Signal pattern information from the transmitter's activity monitor (i.e., active or inactive mode) was also recorded and stored every 3 min during 2003–2004.

Fish tagged with radio-archival tags were marked externally with pink spaghetti tags attached below the dorsal fin as described by Wydoski and Emery (1983) to help identify individuals that were caught in fisheries or located in spawning areas. Fish length (mid-eye to fork of tail) was also recorded. Scales were collected to provide age data as described by DeVries and Frie (1996). Information on sex was not collected due to the lack of distinct external characteristics during this stage of the upriver migration. Fish were released back into the main stem immediately after tagging. Handling and tagging, from removal from the net to release, took about 6–8 min.

Fish tracking

Fish that moved upriver were tracked with remote tracking stations as described by Eiler (1995, 2012). The stations were located on important travel corridors and major tributaries of the drainage (Figure 1). Fish within reception range were detected and recorded by the station. The information collected included the identity of the fish, the date and time it was present at the site, the signal strength of the transmitter, and its relative position in relation to the station (i.e., upriver or downriver from the site). Changes in signal strength and the relative position of the fish were used to determine when it moved past the station. Due to the isolated nature of the sites, telemetry data were transmitted every hour to a geostationary operational environmental satellite, relayed to a receiving station operated by the National Environmental Satellite and Data Information Service (National Oceanic and Atmospheric Administration), and accessed daily via the Internet.

Aerial surveys were conducted to locate fish between station sites and upriver of stations on terminal tributaries. Both fixed-wing aircraft and helicopters were used as described by Eiler (2012). Tracking receivers, each equipped with an integrated GPS receiver, were used to identify and record the locations. Helicopters were used to access the sites to recover the tags so that the archival data could be downloaded. Fish that were recovered intact (i.e., alive or recent mortality) were necropsied to determine their general condition. Tagged fish were also caught in fisheries and at salmon assessment projects (e.g., enumeration weirs, test fisheries), and steps were taken to encourage the return of any tags that were recovered (Eiler et al. 2014).

Data analysis

Tracking station data were systematically reviewed postseason to determine when fish passed the station sites and to confirm that the movements represented a sequential series of locations. Aerial survey data were used to corroborate these results. Fish that passed the first station site (Paimiut; Figure 1), located 62 km upriver from Russian Mission, were considered to have resumed upriver movements. The archival data collected between the tagging site and Paimiut were excluded from the analysis since radio-tagged Chinook Salmon typically exhibited a post-tagging effect immediately after release, which could potentially bias results (Eiler et al. 2014).

Swimming depth and water temperature were summarized for each fish by year, reach, and final destination (region and stock). Fish that were harvested in main-stem fisheries (i.e., where the final destination was unknown) were analyzed separately. Depth and temperature data were linked to the position of the fish when it passed the station sites. Location estimates between sequential stations were interpolated based on the known distance and time taken by the fish to travel between the sites. The movement rate of the fish within the reach was assumed to be constant. The metric “hours after release” was used instead of distance when comparing data that included records from terminal tributaries, since the absence of tracking stations in the upper reaches of these drainages limited information on the movement patterns of the fish as they approached their spawning grounds. Fish passing lower-river stations (particularly Paimiut and the Yukon–Anvik River confluence) were occasionally not detected, presumably due to reduced signal reception associated with the deeper depths and local topography of these sites. In these cases, station passage was estimated by prorating the overall movement rate from the combined reach to the two separate reaches based on stock-specific movement rates from the 2002–2004 basinwide telemetry study (Eiler et al. 2015).

The radio-archival data show variation in depths for individual fish and provide information on temperature exposure by depth. We can determine whether temperature exposure for the fish is related to depth (e.g., whether deeper waters are related to cooler temperatures). However, without temperature data within the entire water column, we cannot infer any preference the fish may have had for certain depths or temperatures. The use of Pearson's product-moment correlation coefficients allowed us to measure any association between temperature and depth for the fish during the upriver migration without regard to causation (i.e., one variable depends on the other). The association between temperature and depth could be particularly important as baseline information for future comparisons in light of general warming trends in the region. River depths in the upper reaches of the basin are generally shallower than those in the lower river, and temperatures are typically cooler. To control for these regional differences, we calculated correlation coefficients for different reaches that were relatively uniform in depth (based on approximate starting and ending depths) and had similar channel characteristics. We selected reach Y2 in the lower basin and reach Y5 in the upper basin for the comparison (Figure 1). Data for all 3 years were pooled, and fish that migrated through reach Y5 were not included in the analysis of reach Y2; hence, the two data sets were independent. The reach Y2 data included fish that were subsequently harvested in the Yukon Flats; some of these fish were likely destined for spawning areas in the Upper Yukon. We tested significance of the correlations (null hypothesis: the population correlation is equal to zero) without regard to the direction of the association even though it is generally thought that deeper waters are cooler (and, conversely, that shallower waters are warmer). Because observations for individual fish were recorded at varying intervals of time, we used a modified *t*-test that accounts for autocorrelation of serial observations. The modified test reduces the degrees of freedom based on an approximation of the variance of the sample correlation coefficient (Clifford et al. 1989). We used the software PASSaGE (Rosenberg and Anderson 2011) to apply the modified *t*-test for testing the significance of the correlation between one-dimensional spatial processes to the temporal data.

We used ANOVA to determine whether the temperatures recorded for the fish differed between years. Because observations for individual fish were recorded serially, we computed average temperature for each fish within reaches Y2 and Y5 and we fitted separate one-way ANOVAs to average temperature data. We tested all pairwise comparisons between years using an α of 0.10 and the Bonferroni method for multiple comparisons. The ANOVAs and multiple comparisons were fitted with S-PLUS version 8.0 (TIBCO Software, Inc.).

We modeled the migration rate of the fish with a generalized linear mixed-effects model as a function of both fixed effects—temperature, reach (Y1–Y9; T1–T2), fish length, and the interaction between reach and temperature—and random effects (see below). We computed the migration rate and average temperature for each fish by reach. One approach to account for an individual's correlated observations (across reaches for these data) is to include a random intercept that varies over the fish and follows some distribution. For this model, the migration rate of the fish has random effects at two levels: the effects for year and the effects for fish within year. The random effects, including the within-fish variability, were assumed to be independent and normally distributed with a mean of zero and some variance. The model was fitted with the function lme in S-PLUS (Pinheiro and Bates 2002).

River depth and channel configuration were determined at several station sites, including Paimiut, the Yukon–Anvik River confluence, Ruby, and Manley. Similar information was obtained from salmon assessment projects in the lower Yukon River and near the Yukon U.S.–Canada border (C. Pfisterer, Alaska Department of Fish and Game, unpublished data) and at Rapids (S. Zuray, Yukon River fisherman, unpublished data).

RESULTS

Tagging and tag recovery

A total of 137 Chinook Salmon were tagged with radio-archival tags: 23 fish in 2002, 37 fish in 2003, and 77 fish in 2004 (Table 1). Most of the fish in 2002 and 2003 were tagged during the middle of the run. Tagging was expanded in 2004 to include early run and late-run fish (Figure 2). Four-ocean-age fish (i.e., fish that remained in the marine environment for 4 years) were the predominant age-class, comprising 61.6% of the sample. The remainder consisted primarily of 3-ocean-age fish (22.4%), with smaller numbers of younger (9.6%) and older (6.4%) individuals. The fish averaged 815 mm (SD = 106) in length, ranging from 560 to 1,060 mm (Table 1). Length and age data were unbalanced among years due to the expanded

TABLE 1 Number, age, and length (mid-eye to fork of tail) of Chinook Salmon tagged with radio-archival tags in the Yukon River basin. Percentages by age-class are given in parentheses.

		Age				Length (mm)	
Year	Number of fish	2-ocean	3-ocean	4-ocean	>4-ocean	Average ± SD	Range
2002	23		4 (18.2)	18 (81.8)		836 ± 71	695–935
2003	37		8 (23.5)	22 (64.7)	4 (11.8)	846 ± 93	670–1,025
2004	77	12 (17.4)	16 (23.2)	37 (54.6)	4 (5.8)	794 ± 117	560–1,060
Total	137	12 (9.6)	28 (22.4)	77 (61.6)	8 (6.4)	815 ± 106	560–1,060

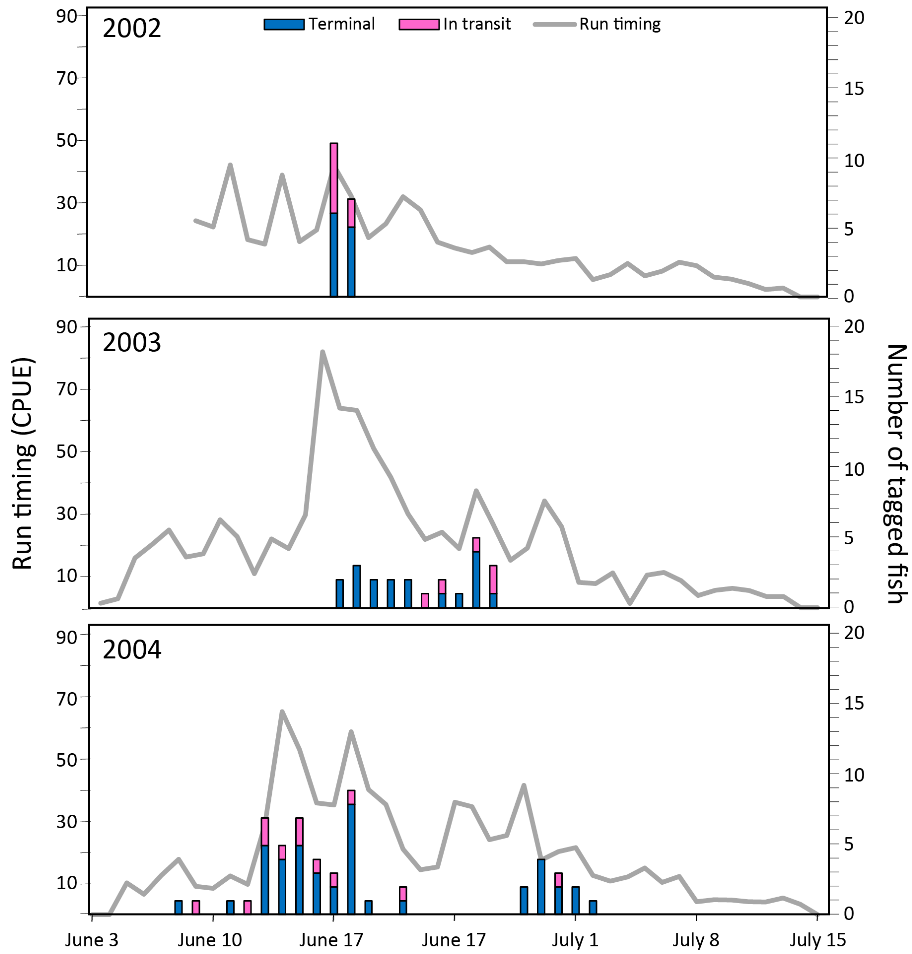

FIGURE 2 Chinook Salmon run timing (based on CPUE data at the tagging site) and the number of radio-archival-tagged fish recovered in the Yukon River basin. The status of the fish (recovered in terminal spawning tributaries or harvested while in transit to their final destination) by tagging date is shown.

tagging in 2004. Similar to the basinwide telemetry study (Eiler et al. 2014), both 2-ocean-age and >4-ocean-age fish were represented in the 2004 sample. Both length and age were significantly different among years based on one-way ANOVAs (length: $F = 3.7 \sim F_{2,\,134}$, $P = 0.03$; age: $F = 4.5 \sim F_{2,\,122}$, $P = 0.01$), with the 2004 sample comprised of smaller and younger fish overall.

The fish responded well to the capture and tagging procedures, with most (135; 98.5%) moving upriver, including two fish with malfunctioning tags that were not detected by the stations but were subsequently caught in mainstem fisheries. Two fish were not located after release and either regurgitated their tags, had malfunctioning transmitters, or died near the tagging site due to handling, predation, or undocumented encounters in the local fishery.

Overall, 133 fish were tracked upriver, with most either caught in fisheries or located in terminal reaches of the basin. Ninety-five (71.4%) tags were recovered, including

35 (26.3%) returned by fishermen and 60 (45.1%) retrieved during spawning ground surveys (Table 2). Upper Yukon fish comprised 28.4% of the sample, ranging from 24.1% in 2004 to 34.8% in 2003 (Figure 3). Tanana fish were also a major component, particularly during 2003 (30.4%) and 2004 (33.3%). Smaller numbers of fish were recovered in the other regional areas, collectively comprising 18.0% of the sample.

The fish that were recovered in terminal spawning areas were often clustered in several tributaries (Figure 1). Of the 31 fish returning to the Tanana River, 22 (71.0%) were recovered in the Chena, Salcha, and Goodpaster rivers. Clusters of fish were also located in the Anvik, Chandalar, and Sheenjek rivers. Upper Yukon fish were more widely distributed, with most located in several large-sized (Stewart, Pelly, White, and Teslin) and medium-sized (Klondike, Big Salmon) rivers. The status of the fish ranged from live individuals (both prespawning and spawned out) to those killed by predators or that had died and were in various stages of decay. None of the fish that had died and could still be examined exhibited signs of prespawning mortality. Fishery recoveries were scattered from the lower river to the upper reaches of the basin (Figure 1), including 24 fish (25.3%) caught in main-stem fisheries within the Lower Yukon, Middle Yukon, and Yukon Flats. These fish were potentially in transit to areas farther upriver and were treated as nonterminal recoveries.

TABLE 2 Recovery of Chinook Salmon tagged with radio-archival tags in the Yukon River basin during 2002–2004. Percentages of the number of fish tracked upriver are given in parentheses.

		Spawning ground survey		Fishery		
Year	Number of fish tracked upriver[a]	Recovered	Not recovered[b]	Returned	Not returned	All recoveries
2002	23	6 (26.1)	5 (21.7)	12 (52.2)		18 (78.3)
2003	37	17 (45.9)	12 (32.4)	6 (16.2)	2 (5.4)	23 (62.2)
2004	73[a]	37 (50.7)	16 (21.9)	17 (23.3)	3 (4.1)	54 (74.0)
Total	133	60 (45.1)	33 (24.8)	35 (26.3)	5 (3.8)	95 (71.4)

[a]Not including two fish with malfunctioning tags that moved upriver and were caught in fisheries.

[b]Tags were located but not accessible.

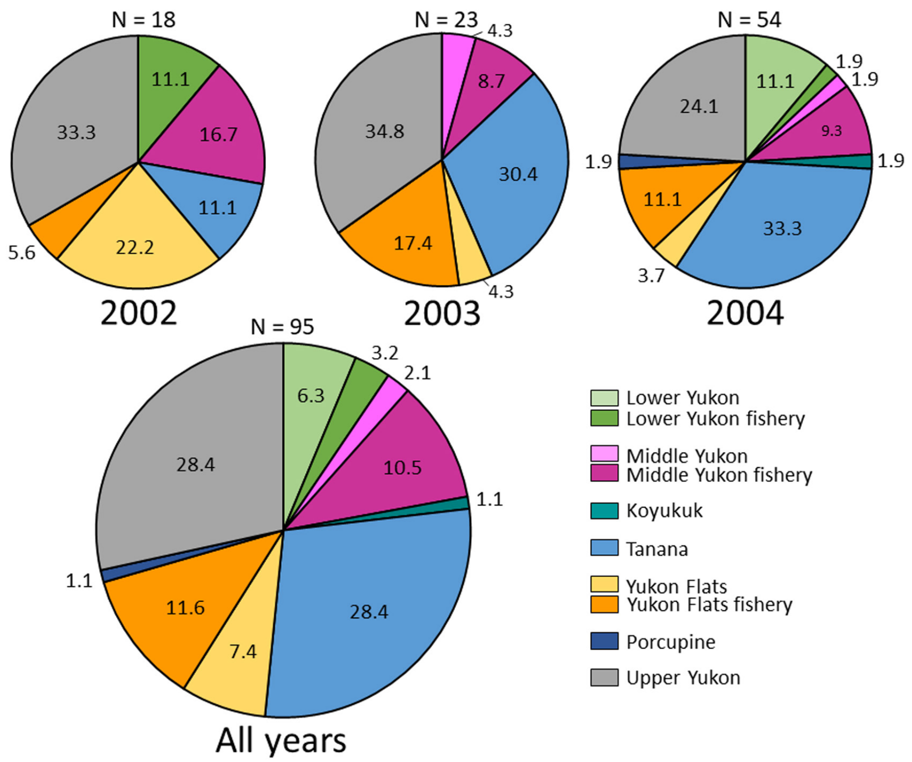

FIGURE 3 Regional recoveries (%) of Yukon River Chinook Salmon tagged with radio-archival tags during 2002–2004. Fish that were harvested in main-stem fisheries in the Lower Yukon, Middle Yukon, and Yukon Flats were potentially in transit to areas farther upriver.

Information on the upriver movements, swimming depth, and water temperatures encountered during the spawning migration was summarized for each fish by year, reach, time since release at the tagging site, distance traveled upriver, region, and final destination (stock). Fish harvested in main-stem fisheries were considered separately since their final destination was unknown. These data have been archived and are available online (Eiler et al. 2022a).

Swimming depth

The upriver movements of the fish during the spawning migration were characterized by continuous and highly variable fluctuations in depth, as illustrated by an Upper Yukon fish traveling to the Teslin River (Figure 4). The swimming depth of this fish immediately upriver of Paimiut (reach Y1) averaged 10.3 m (SD = 5.3) but ranged from 1.4 to 27.6 m (Figure 4, lower left panel). Channel depth within this section of river varied from 24 to 26 m at Paimiut and from 15 to 17 m at the Yukon–Anvik River confluence, suggesting that the fish was periodically traveling in the deepest parts of the river. Although swimming depth became progressively less as the fish moved farther upstream into shallower water, it continued to exhibit this variable pattern. Swimming depth in reach Y5 averaged 2.4 m (SD = 1.0) but ranged from 0.6 to 9.8 m (Figure 4, lower middle panel). Channel depth near the Yukon border (1,626 km upriver from Paimiut) was generally between 8 and 10 m, again suggesting that the fish was periodically traveling in the deepest part of the channel. Prior to entering Teslin Lake, swimming depth in the lower Teslin River averaged 2.6 m (SD = 0.9), ranging from 0.7 to 6.2 m (Figure 4, lower right panel). Time of day did not appear to influence the swimming depth of the fish.

A similar pattern was displayed by a fish returning to the Tanana River, with continuous fluctuations in depth as it moved upriver (Figure 5). Swimming depth averaged 11.7 m (SD = 5.7) in reach Y1 but ranged from 3.2 to 29.2 m (Figure 5, lower left panel). Although swimming depth became progressively less as the fish moved farther

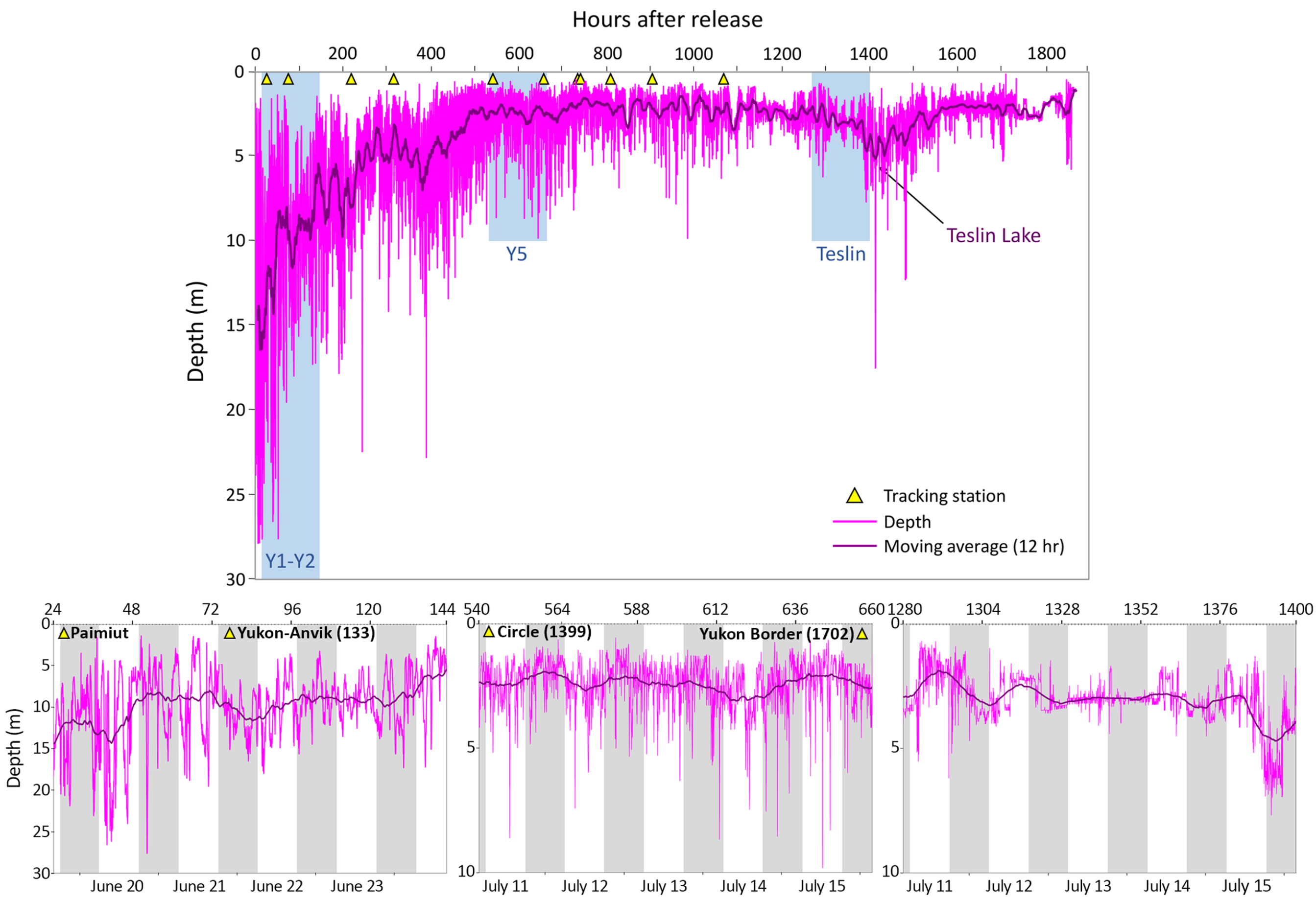

FIGURE 4 Swimming depth of a Yukon River Chinook Salmon during the upriver migration to its spawning grounds in the Teslin River in 2004. The bottom panels show depth during 120-h periods in different reaches of the basin (indicated by blue shading); note differences in the *Y*-axis scale. The tracking stations passed by the fish are shown; the distance (km) from the initial station at Paimiut is given in parentheses. Gray shading represents the time between 1800 and 0600 hours.

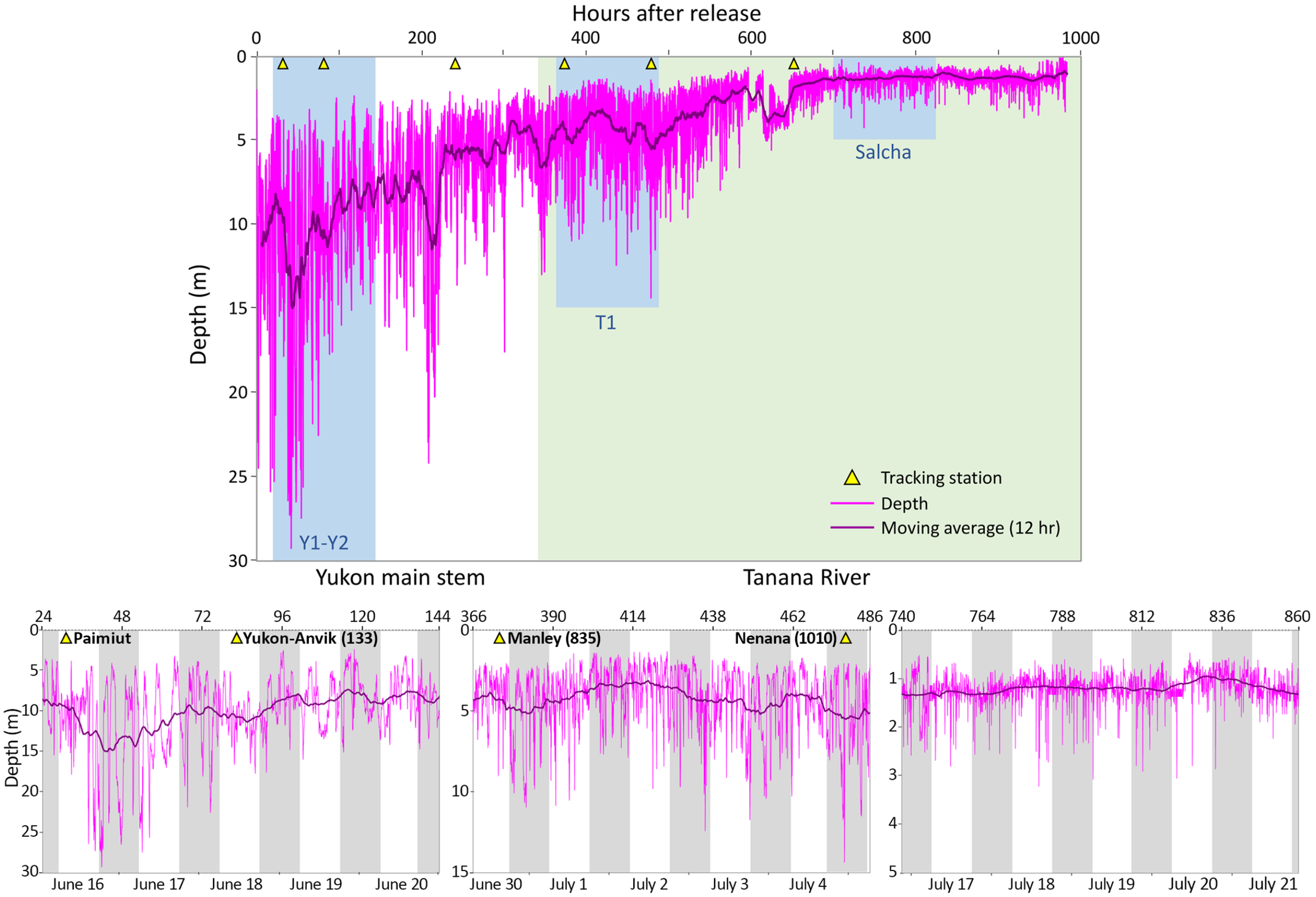

FIGURE 5 Swimming depth of a Yukon River Chinook Salmon during the upriver migration to its spawning grounds in the Salcha River in 2004. The bottom panels show depth during 120-h periods in different reaches of the basin (indicated by blue shading); note differences in the *Y*-axis scale. The tracking stations passed by the fish are shown; the distance (km) from the initial station at Paimiut is given in parentheses. Gray shading represents the time between 1800 and 0600 hours. The green background represents the Tanana River drainage.

upstream into shallower water, it continued to exhibit this variable pattern. Swimming depth in the lower Tanana River (reach T1) averaged 4.2 m (SD = 2.0) but ranged from 1.3 to 14.3 m (Figure 5, lower middle panel). Channel depth near Manley (92 km upstream from the Yukon–Tanana River confluence) was approximately 7–8 m, suggesting that the fish was periodically traveling through relatively deep sections of the river. Swimming depth in the Salcha River downstream from the fish's spawning site averaged 1.3 m (SD = 0.4) but ranged from 0.2 to 4.2 m (Figure 5, lower right panel). Depth did not appear to be influenced by the time of day.

The fluctuating patterns of these two individuals were similar to those exhibited by other Upper Yukon and Tanana fish (the two principal components of the sample) as well as fish returning to the other regional areas. For example, swimming depth was highly variable for all fish passing through reach Y1, ranging from <5 to over 20 m, with depth exceeding 25 m for 61% of the fish. Average depth in reaches Y1–Y3 (hereafter referred to as the "lower main stem") was comparable for both Upper Yukon and Tanana stocks during all 3 years of the study, with Upper Yukon fish swimming somewhat deeper on average (Figure 6). Swimming depth became progressively less as the fish moved farther upstream into shallower water. Average depth for Upper Yukon fish ranged from 4.3 m in reach Y4 to 2.4 m in reach Y7. Tanana fish traveled shorter distances but exhibited a similar reduction in depth as they neared their terminal tributary. Between-year differences in swimming depth were minimal for both regional stocks.

Although other regional stocks were represented by relatively few fish, the same general swimming depth pattern was observed (Figure S1 available in the Supplement in the online version of this article). Lower Yukon fish returning to the Innoko River (dark-green box plot) displayed substantially shallower depths on average in reach Y1 than the other stocks, but this may relate to the proximity of their terminal tributary. These fish traveled substantial distances after entering the Innoko River, spawning in the upper headwaters (Figure 1), but they traveled <50 km upriver from Paimiut before reaching the Yukon–Innoko

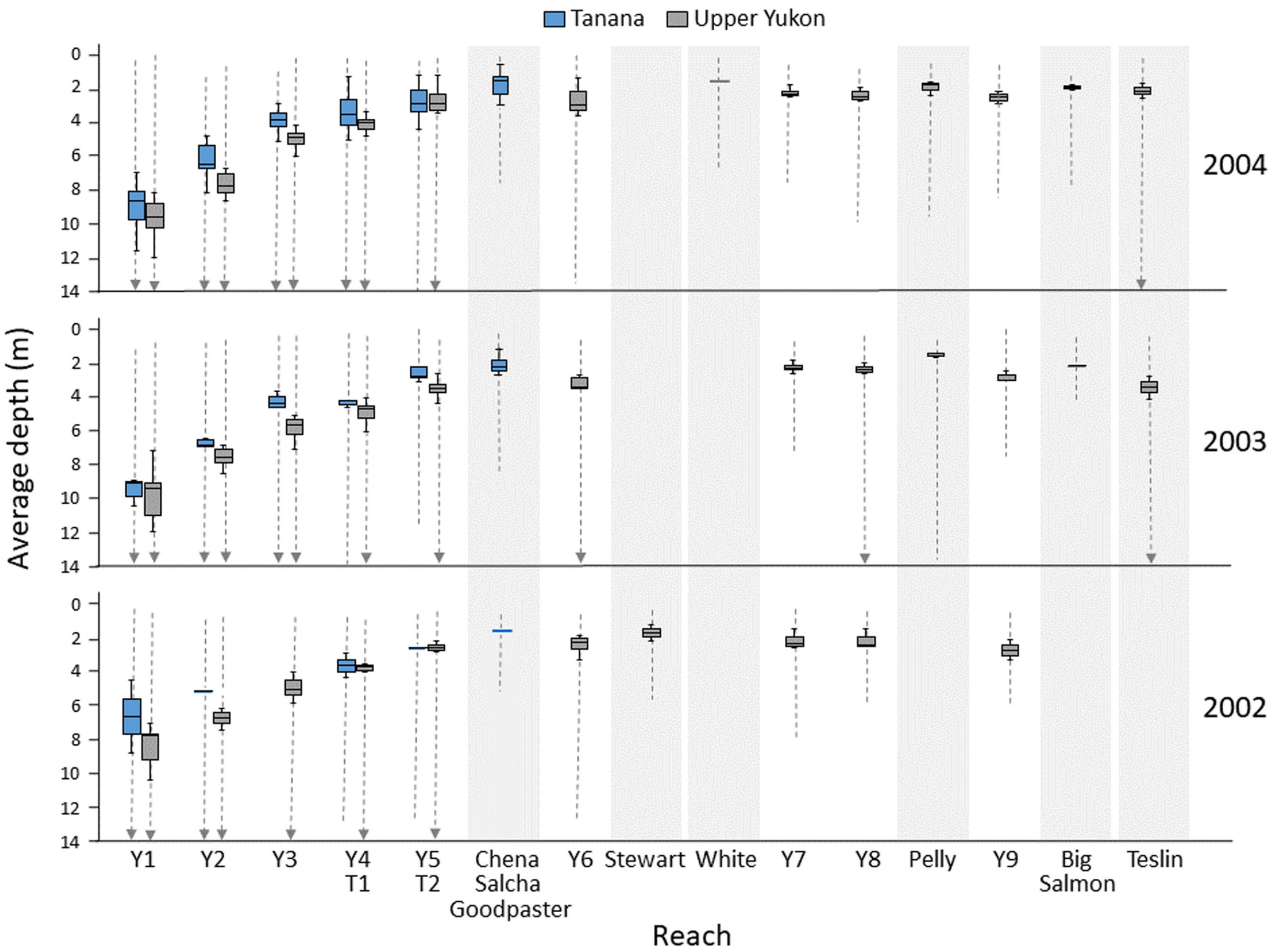

FIGURE 6 Box plots of the average swimming depth by reach for Yukon River Chinook Salmon traveling to spawning grounds in the Tanana and Upper Yukon during 2002–2004. Terminal reaches are shaded gray. Dashes represent individual fish. Dotted gray lines show the range of depths; arrows indicate depths exceeding 14 m.

River confluence. Although beyond the scope of this paper, individual fish and stock-specific swimming depth patterns are described by Eiler et al. (2022b).

Thermal conditions

Upriver migration

There was considerable variation in the thermal conditions encountered by fish during the upriver migration, with differences observed among years, regional stocks, and reaches of the basin. The patterns exhibited by Upper Yukon stocks in 2004 were similar to those of the Teslin River fish shown in Figure 7. Water temperatures increased substantially as the fish traveled through the lower main stem and were consistently >18°C in reaches Y2 and Y3 before declining in the Yukon Flats (reach Y4). Temperatures increased again upstream of the Yukon–White River confluence (reach Y7) before declining as the fish moved farther upriver. Similar patterns were observed in the lower main stem for Tanana stocks, as illustrated by the fish depicted in Figure 8, with temperatures increasing substantially in reaches Y2 and Y3 but declining abruptly after the fish entered the Tanana River (green background). Fish returning to other regional areas exhibited similar patterns in main-stem reaches, such as the Porcupine fish shown in Figure 9. Lower Yukon stocks experienced temperatures well above 18°C before entering their terminal tributaries, with the highest temperatures (in excess of 23°C) recorded over a 4-h period for an Innoko River fish.

By comparison, the thermal conditions encountered during 2002 and 2003 were generally cooler in the lower main stem, although they occasionally exceeded 18°C (Figure 9). Temperatures >20°C were not observed during 2003 and occurred only briefly in 2002. Upper Yukon fish encountered warmer conditions as they progressed

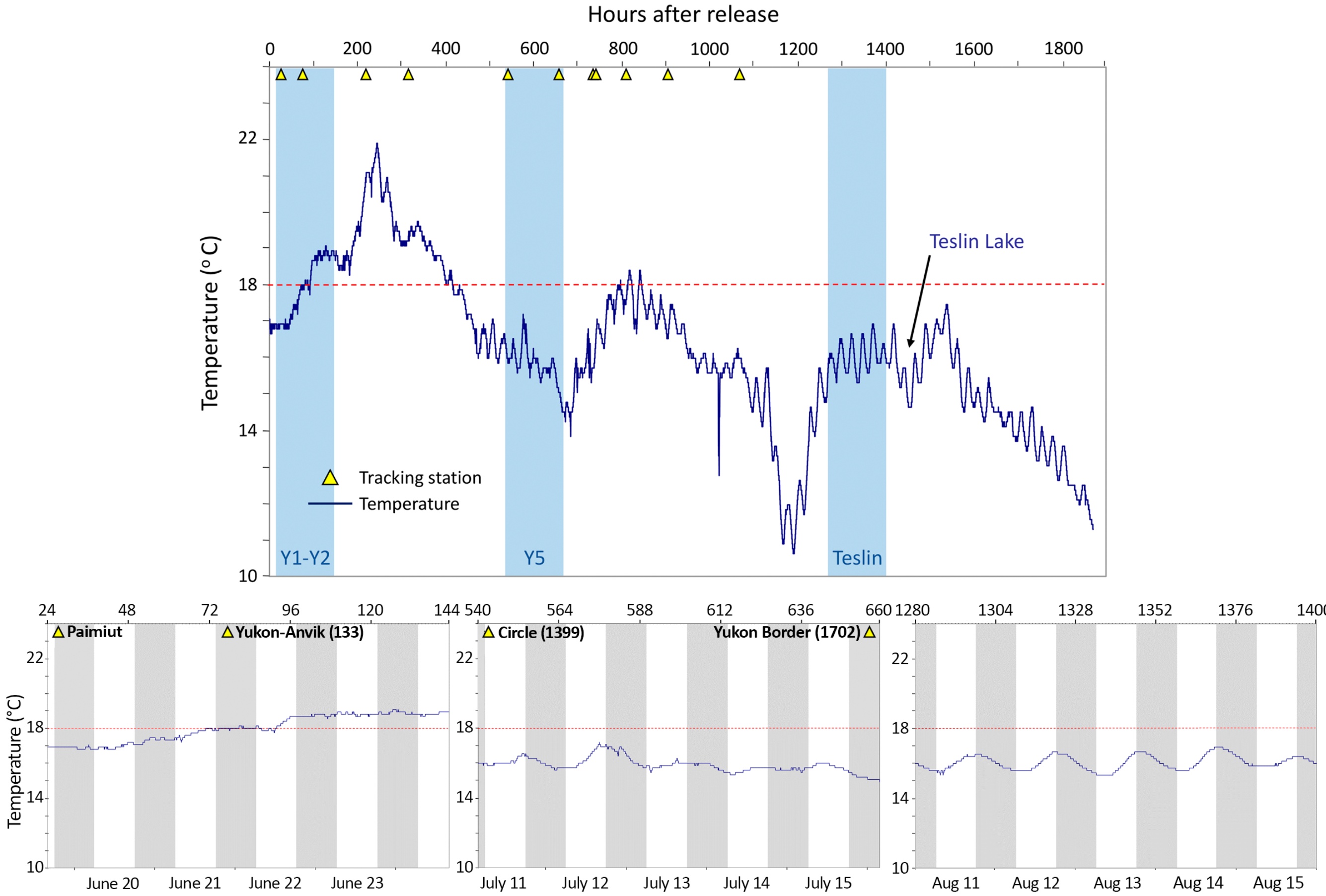

FIGURE 7 Water temperatures encountered by a Yukon River Chinook Salmon during the upriver migration to its spawning grounds in the Teslin River in 2004. The bottom panels show temperature during 120-h periods in different reaches of the basin (indicated by blue shading). The tracking stations passed by the fish are shown; the distance (km) from the initial station at Paimiut is given in parentheses. Gray shading represents the time between 1800 and 0600 hours. Red lines signify the temperature threshold associated with heat stress in Pacific salmon.

upriver, with temperatures periodically exceeding 18°C in upper reaches of the main stem (Y5–Y7) before declining as the fish approached their terminal tributaries. The other regional stocks exhibited similar trends in main-stem reaches. Tanana fish experienced a pronounced decline in temperature after leaving the main stem during all 3 years, with temperatures predominantly <18°C. Temperatures in the Tanana River were noticeably cooler during 2003, whereas the limited information from 2002 suggests that conditions were comparable to those in 2004. The average hourly difference between the minimum and maximum temperatures experienced by the fish (across all combinations of year and reach) was 0.16°C per hour and mirrored the patterns shown in Figure 9 (Figure S2). Individual fish and stock-specific patterns are described by Eiler et al. (2022b).

Average temperatures recorded for fish migrating through reach Y2 were significantly different between years (F = 150.3 ~ $F_{2,\ 48}$, P <0.001) and were highest in 2004 (mean = 18.7°C, SD = 0.5), followed by 2003 (mean = 17.5°C, SD = 0.3) and 2002 (mean = 15.2°C, SD = 0.6). All pairwise comparisons between years were significantly different. Average temperatures recorded for fish migrating through reach Y5 were also significantly different between years (F = 14.3 ~ $F_{2,\ 24}$, P <0.001) and were highest in 2002 (mean = 17.5°C, SD = 0.5), followed by 2003 (mean = 17.2°C, SD = 0.6) and 2004 (mean = 15.8°C, SD = 0.9). For all pairwise comparisons between years, 2004 was significantly different than 2002 and 2003.

We also examined the relationship between migration rate and the average temperature recorded for the fish by reach. The generalized linear mixed-effects model of the migration rate was fitted with restricted maximum likelihood. The covariate average temperature was not significant (F = 0.38 ~ $F_{1,\ 264}$, P = 0.54).

Terminal tributaries

Thermal conditions were substantially cooler as fish left main-stem reaches and entered their terminal tributaries, with temperatures typically <18°C (Figure 10).

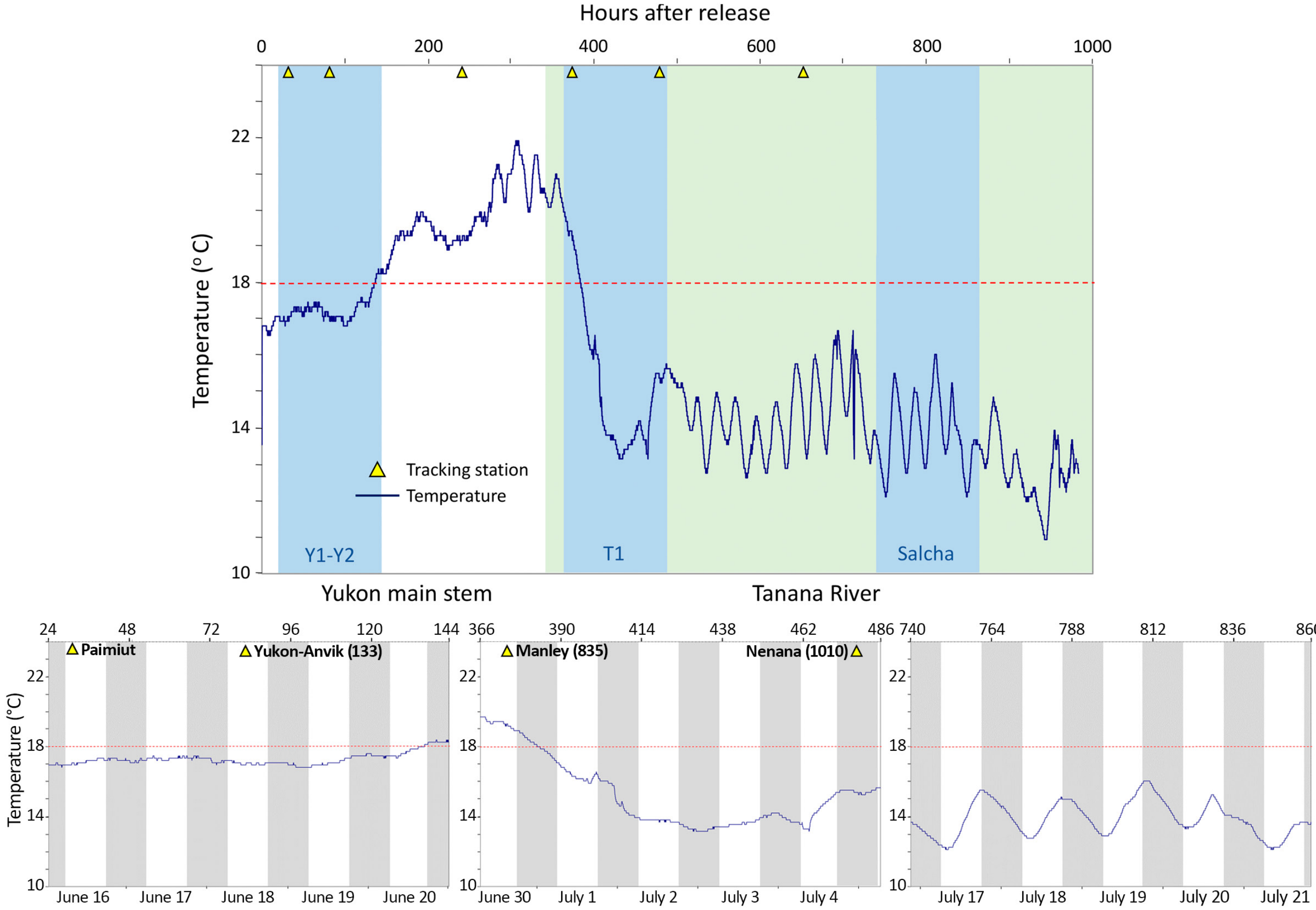

FIGURE 8 Water temperatures encountered by a Yukon River Chinook Salmon during the upriver migration to its spawning grounds in the Salcha River in 2004. The bottom panels show temperatures during 120-h periods in different reaches of the basin (indicated by blue shading). The tracking stations passed by the fish are shown; the distance (km) from the initial station at Paimiut is given in parentheses. Gray shading represents the time between 1800 and 0600 hours. Red lines signify the temperature threshold associated with heat stress in Pacific salmon. The green background represents the Tanana River drainage

Temperatures were similar among Upper Yukon fish during 2003 and 2004, whereas Tanana fish encountered somewhat cooler temperatures in 2003 than in 2004. Conditions were generally warmer in small main-stem tributaries of the Lower Yukon and Middle Yukon during 2004. However, spatial differences were observed, with temperatures declining as the fish moved farther upstream. For example, the average temperature for the Middle Yukon fish returning to the Melozitna River in 2004 was 18.5°C for the first 10 days after the fish entered the river compared to 16.4°C during the last 10 days it was present on the spawning grounds. Similar patterns were observed for Lower Yukon fish returning to the Innoko and Anvik rivers. Limited information is available for the Koyukuk River, with only one fish spawning in the upper headwaters of the drainage (Figure 1). Temperatures in the lower section of the drainage (reach K1) and in the initial section of reach K2 averaged 18.5°C and 17.4°C, respectively, compared to 12.6°C when the fish was on its spawning grounds.

Although time of day did not appear to influence the temperatures encountered during much of the upriver migration, a pronounced diel pattern was observed as fish left the main stem and approached their spawning grounds, with temperatures declining from early evening to early morning (from 1800 to 0600 hours) and increasing during daylight hours, as shown in Figures 7 and 8 (lower right panel). This pattern was observed for all fish that were tracked to terminal tributaries.

Cumulative exposure

Cumulative exposure of the fish to higher temperature ranges showed pronounced differences in relation to both reach and year. Temperatures ≥18°C were more prevalent in the lower basin than farther upriver (Figure 11). Reach Y3 was a conspicuous hot spot, particularly during 2004, when Upper Yukon fish traveling through the area were exposed to temperatures above the 18°C threshold

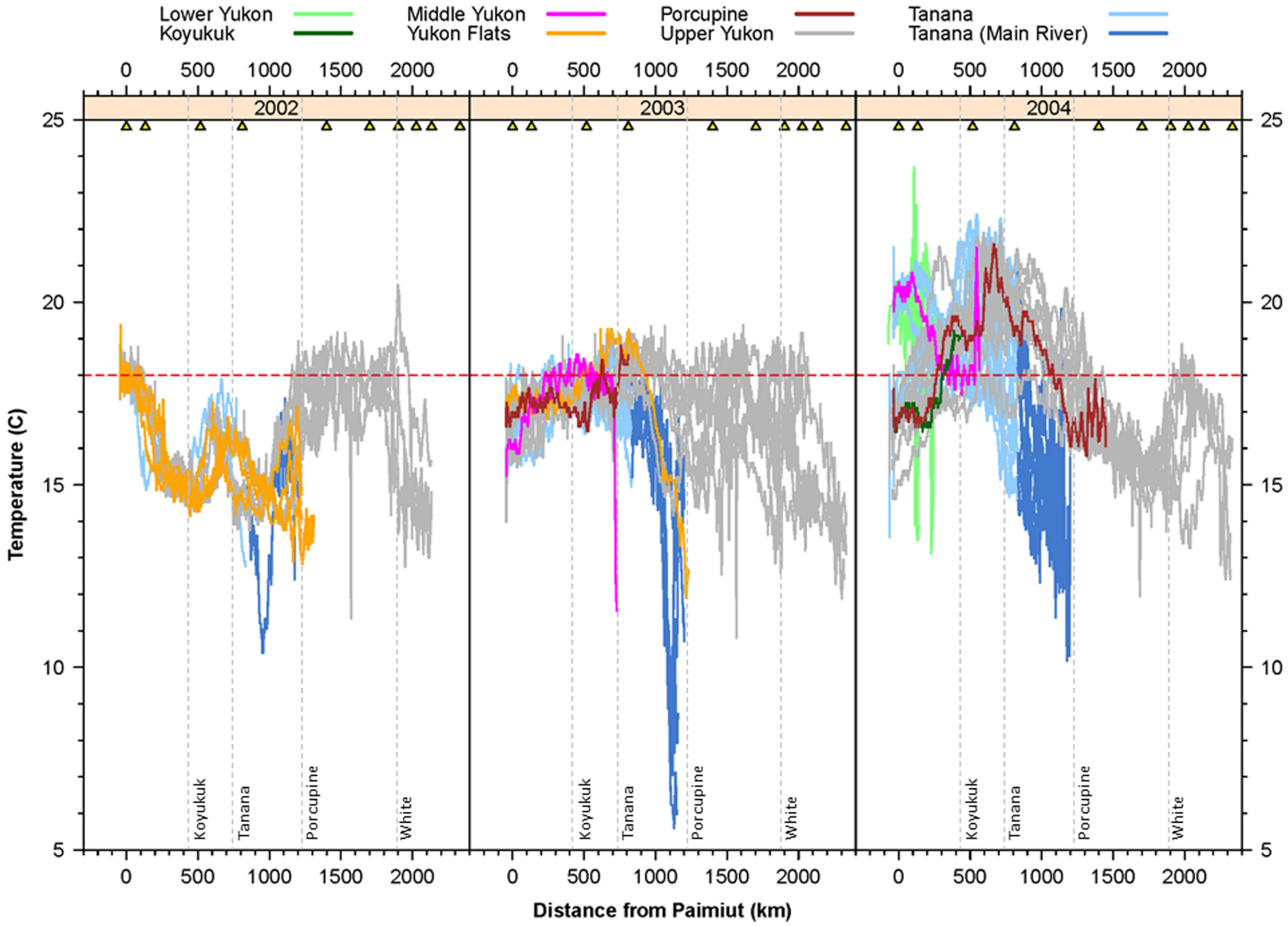

FIGURE 9 Water temperatures (°C) encountered by Chinook Salmon in the Yukon River main stem during their spawning migration in 2002–2004. The final destination of the fish by region is indicated. Water temperatures in the Tanana River upstream of the Manley tracking station are also shown (dark blue). The confluence of the main stem with several major drainages is indicated. Triangles denote the locations of tracking stations along the main stem. The red line represents the temperature threshold associated with heat stress in Pacific salmon.

over 94% of the time compared to 33% in 2003 and 0% in 2002. Temperatures ≥21°C were not observed in 2002 and 2003 but were encountered 14% of the time during 2004. Similar patterns were exhibited by the other regional stocks traveling through this area, with greater exposure to temperatures ≥18°C during 2004 compared to the two previous years. Temperatures ≥21°C were not observed during 2002–2003, whereas the proportion of time above this level in 2004 ranged from 9.2% for Middle Yukon fish to 13.2% for Tanana fish. Although the final destination could not be determined for fish that were harvested in nonterminal main-stem fisheries, these individuals also experienced increased exposure to elevated temperatures as they traveled through this reach (Figure S3).

Exposure to temperatures above the 18°C threshold was also greater in other main-stem reaches during 2004, including Y1, Y2, and Y4, as well as the lower section of the Tanana River (reach T1). However, thermal conditions within the basin were not consistently warmer. Cooler temperatures were observed downstream of the Yukon–White River confluence in 2004 compared to 2002–2003 (Figure 9). Greater exposure to temperatures ≥18°C was also observed in reaches Y5 and Y6 in both 2002 and 2003, ranging from 25.1% to 32.3% of the time within the reach, whereas temperatures above this threshold were not encountered during 2004 (Figure 11). Warmer conditions were observed in main-stem reaches upstream of the Yukon–White River confluence (Y7 and Y8), but exposure levels were similar across years.

Exposure to elevated temperatures was substantially less in terminal spawning tributaries. Temperatures ≥18°C were not observed for the three major Tanana stocks: Chena, Salcha, and Goodpaster rivers (Figure 11). Upper Yukon fish returning to the Stewart and Pelly rivers encountered temperatures in excess of this threshold, but exposure was minimal (<2% of the time) and occurred

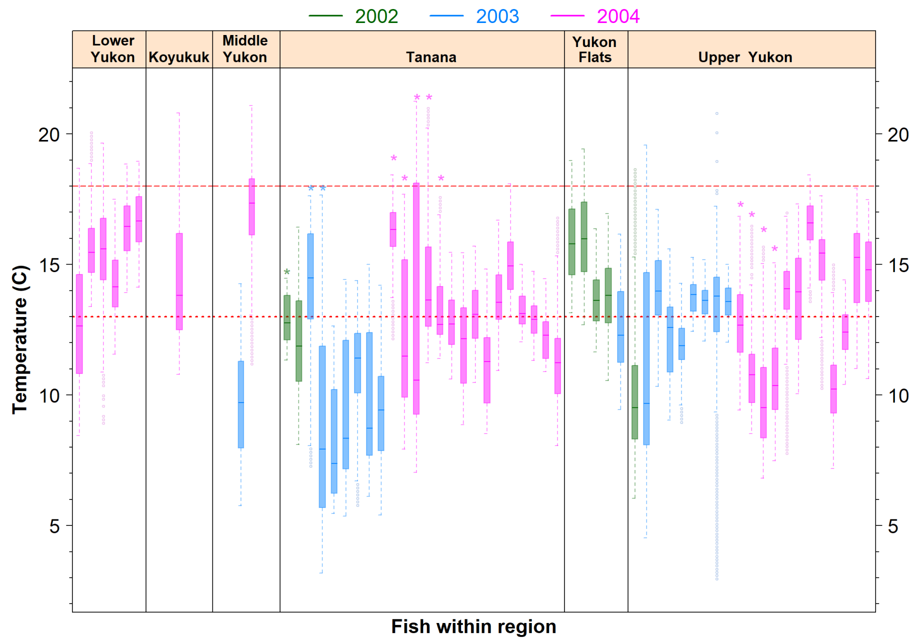

FIGURE 10 Box plots of water temperatures (°C) encountered by Yukon River Chinook Salmon in terminal spawning tributaries during 2002–2004. The final destination of the fish by region is indicated. Asterisks denote fish that returned to tributary streams without a tracking station and include temperatures from the last main-stem (Upper Yukon fish) or Tanana River (Tanana fish) reach. The dashed red line signifies the temperature threshold associated with heat stress in Pacific salmon; the dotted red line represents the upper temperature level that is considered optimal during spawning.

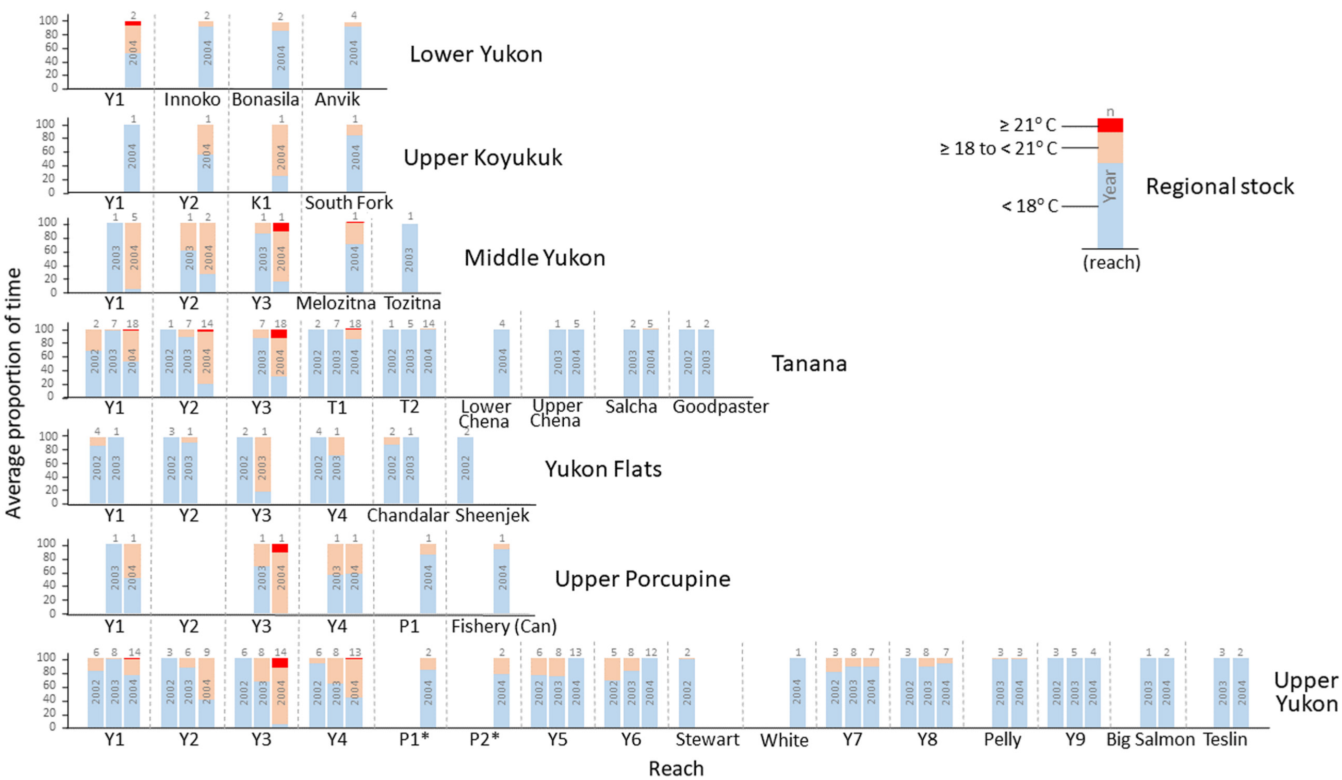

FIGURE 11 Average proportion (%) of time that Yukon River Chinook Salmon were exposed to different water temperature ranges during their upriver migration to spawning grounds in 2002–2004 by reach and final destination. Asterisks denote atypical movements by the fish.

near the tributary mouth. The proportion of time that Lower Yukon and Koyukuk fish were exposed to elevated temperatures was also limited, ranging from 8.0% to 15.7%, respectively. With regard to the Middle Yukon stocks, temperatures ≥18°C were not observed for the Tozitna River fish in 2003, but temperatures in excess of the 18°C threshold were encountered 32.0% of the time for the Melozitna River fish in 2004, including temperatures ≥21°C, which were encountered 2% of the time. As previously mentioned, cooler temperatures were encountered as these fish moved upstream and approached their spawning grounds.

Relationship between temperature and depth

We examined the relationship between average temperature and depth based on reaches in both the lower (reach Y2) and upper (reach Y5) Yukon River basin. Both reaches consisted of a primary river channel, with occasional side channels and sloughs. Reach Y2 had a starting depth of 16 m and an ending depth of 14 m over a distance of 385 km. Excluding fish in the Y5 sample, a total of 51 individuals traveled through reach Y2 during the 3 years of the study. Only one correlation coefficient was significant using an α of 0.10 and a Bonferroni correction of 1/51 (Table S1 available in the Supplement in the online version of this article), providing evidence of no relationship between the depths and temperatures recorded for the fish. The significant correlation (−0.12 for an Upper Yukon fish) was low and negative, indicating a weak relationship between higher temperatures and shallower depths. Correcting for the large number of tests resulted in low power to detect a significant relationship between temperature and depth; however, patterns can be inferred from the correlation values and signs (i.e., positive or negative). Most of the correlations (63%) were negative, indicating that higher temperatures experienced by the fish may be weakly associated with shallower depths.

Reach Y5 had starting and ending depths of 8–10 m over a distance of 590 km. Overall, 27 fish migrated through this reach during the 3 years of the study. Only one correlation coefficient was significant using an α of 0.10 and a Bonferroni correction of 1/27 (Table S1), providing evidence of no relationship between the depths and temperatures recorded for the fish. The significant correlation (0.08 for an Upper Yukon fish) was low and positive, indicating a weak relationship of higher temperatures and deeper depths. Similar to reach Y2, most of the correlations (70%) were negative, indicating that higher temperatures experienced by the fish may be weakly associated with shallower depths.

DISCUSSION

Radio-archival tags provided site-specific information on the swimming depth of Chinook Salmon returning to the Yukon River basin and the thermal conditions experienced by the fish during the upriver migration. These data provide a baseline for comparing past conditions and migratory patterns with those of subsequent returns in this and other river drainages and are of particular interest in relation to the changing climatic patterns. The ability to track the fish to their final destination substantially enhanced recovery efforts. Spawning ground recoveries accounted for 45% of the tags deployed during the study compared to 26% recovered in local fisheries. The combined recovery rate during this study (>71%) was considerably higher than recovery rates that have been reported for most archival tag studies (Eiler et al. 2022b). The ability to obtain larger samples and more representative results is a major advantage for addressing many of the issues currently facing resource managers and local communities.

Swimming depth

All of the tagged fish exhibited a similar swimming pattern during the upriver migration, characterized by continuous and highly variable fluctuations in depth. This pattern was observed throughout the basin from the lower main stem to the upper headwaters. Although our study did not include depth information downstream of Russian Mission, data from several archival tags deployed on Chinook Salmon in the Bering Sea and recovered 70–150 km upstream from the Yukon River mouth showed the same variable pattern after the fish entered the river, with depth ranging from near the surface to 28 m (Walker and Myers 2009).

Interpreting this pattern is complicated by the lack of fine-scale and lateral positioning information. This limitation made it difficult to determine how swimming depth related to the depth and geomorphology of the river. Chinook Salmon are strong swimmers and are capable of moving vertically through the water column, but this behavior would be metabolically costly if exhibited over long periods of time. The most likely explanation is that the fish were following the contours of the river bottom. Salmon generally swim along the shoreline during their upriver migration to avoid faster-moving water farther out in the channel (Quinn 2018), although Hughes (2004) speculated that larger fish may swim farther offshore in deeper water despite the faster current to reduce the energy costs associated with wave drag. Based on conversations with Yukon River gill-net fishermen, Chinook Salmon are usually caught in the lower portion of their nets, even when fishing in relatively shallow nearshore eddies. Catches would be spaced more randomly throughout the net if the fish were swimming at variable depths within the water column, further suggesting that they were traveling near the river bottom. Sonar information collected near Eagle, Alaska, also suggests that Chinook Salmon tend to be bottom oriented on both sides of the main stem (Carroll et al. 2007).

The general geomorphology of the river lends credence to this interpretation. In most free-flowing rivers (i.e., those not confined by natural features or man-made structures), the deepest part of the channel shifts back and forth between alternate sides of the river due to current-generated erosion and deposition along the opposing banks (Church 2006). Chinook Salmon traveling near the river bottom as they move upstream along the shoreline would regularly transition from shallow to deeper stretches of river, which would account for the variable depths exhibited by the fish. Johnson et al. (2007) reported that Columbia River Chinook Salmon tended to remain on one side of the river during the spawning migration, which would accentuate this pattern. Limited boat tracking upriver of the Russian Mission tagging site indicated that radio-tagged Chinook Salmon often moved into nearshore eddies, where the reverse flow would reduce the current encountered by the fish while still keeping them in close contact with the main river (Eiler et al. 2015). This behavior would further account for the shallow depths that were periodically exhibited by the fish as they moved upstream.

Similar swimming depths were observed for fish moving through the same section of river regardless of their final destination. Average depth within the lower main stem was comparable for both Upper Yukon and Tanana stocks during all 3 years of the study, with Upper Yukon fish swimming somewhat deeper on average, particularly in reaches Y2 and Y3. The shallower depths displayed by Tanana fish farther upriver may reflect increased bank orientation as they approached the Yukon–Tanana River confluence and prepared to leave the main stem. Innoko River fish traveling through reach Y1 were in close proximity to their terminal tributary, and the shallower depths observed for these fish may also reflect bank orientation as they approached the tributary mouth. Between-year differences in depth were minimal for both Upper Yukon fish and Tanana fish. Comparisons among the other regional stocks were limited by the small number of fish tracked to these areas. Swimming depth did not appear to be influenced by the time of day during the upriver migration or after fish entered their terminal tributary, likely due to the bottom-oriented swimming pattern.

As expected, swimming depth became progressively less as the fish moved upriver into shallower reaches of the basin. However, periodic spikes were observed in middle and upper reaches of the main stem, revealing the presence of relatively deep areas within the riverbed. Similar observations were made for multiple fish moving through the same general location (Eiler et al. 2022b). The fish did not appear to linger in these areas. For example, the fish illustrated in Figure 4 displayed this pattern upstream of the Ruby tracking station (243 h after release), spending <20 min within an area with an average depth of 19 m. Depths during the previous and subsequent 24 h averaged 6.1 and 4.9 m, respectively. Temperatures associated with the deeper depths averaged 21.9°C, which was comparable to the average temperatures recorded 24 h before (21.2°C) and after (20.9°C) this period.

Thermal conditions during the upriver migration

Annual and regional patterns

The thermal conditions encountered by the fish varied during the 3 years of the study. Water temperatures were generally warmer in 2004. This tendency was particularly evident in the lower main stem, where thermal conditions were frequently >18°C and periodically exceeded 21°C. Lower main-stem temperatures did not exceed 20°C during 2002–2003 and were typically below 19°C. However, this interannual pattern was not consistent throughout the basin. Upper Yukon fish encountered cooler temperatures downstream of the Yukon–White River confluence (reach Y6) during 2004 compared to 2002–2003, when conditions were more variable and periodically exceeded 18°C.

Cooler temperatures were encountered by the fish after leaving the main stem. Fish entering the Tanana River experienced a pronounced decline in temperature, particularly during 2003, when minimum temperatures were considerably lower. Fish entering other main-stem tributaries also experienced progressively cooler temperatures as they traveled farther upstream from the confluence. Although Tanana tributaries were generally cooler in 2003 than in 2004, this pattern was less evident in the Upper Yukon. Insufficient information is available for 2002 and among the other regional stocks to make between-year comparisons.

The factors that influence thermal conditions in large river basins are complex and often are not fully understood. Annual and regional differences likely reflect the hydrology of a particular watershed as well as the atmospheric conditions within the area. For example, river temperatures in glacial drainages are dependent on snow accumulation during the previous winter, spring precipitation, solar radiation, and summer temperatures, with rapid melting and greater runoff associated with warmer weather, resulting in lower water temperatures (Brabets et al. 2000). The White River is glacial, and the cooler main-stem temperatures downstream of the Yukon–White River confluence during 2004 were likely related to warmer atmospheric conditions and increased glacial runoff within the watershed. Glacial runoff in the Tanana River watershed, combined with cold groundwater from the Chena and Salcha rivers (Brabets et al. 2000), likely contributed to the consistently cooler temperatures encountered by fish in the Tanana River. Conversely, warmer temperatures in the lower main stem were likely influenced by the absence of glaciers as well as by the lower elevation and river gradient that characterize the region (Brabets et al. 2000).

Thermal conditions in terminal tributaries were generally cooler. A pronounced diel pattern was also observed as fish left the main stem and neared spawning areas, with water temperatures declining from early evening to early morning and increasing during daylight hours. Swimming depth did not exhibit a diel pattern during this period, with fish observed at varying depths throughout the day. This dichotomy suggests that the diel pattern in temperature likely relates to warmer ambient temperatures and increased solar radiation during daylight hours. The depths recorded for fish on the spawning grounds were relatively shallow compared to those in main-stem reaches, ranging from <1 to 3–5 m, and water temperature is likely influenced to a greater extent by these factors.

Effects of temperature during the spawning migration

Temperature is often considered the preeminent factor when assessing the impact of the environment on aquatic organisms (Brett 1971; Fry 1971). Metabolic rate increases as temperatures rise, which affects all biological processes and requires a greater expenditure of energy for life systems to function. Higher temperatures also reduce oxygen levels in the water, making it more difficult for fish to breathe (Brett 1972). These effects are particularly critical for salmon during the spawning migration due to the increased energy and oxygen demands associated with sustained upriver movements as well as the dependence on stored energy reserves.

Elevated temperatures in rivers used by Pacific salmon and the potential impact on these populations have become a major concern. Until recently, this issue was focused primarily on conditions in southern drainages (from California to southern British Columbia). However, it has become increasingly important in northern rivers as well. Mass mortality and reduced productivity in Alaskan rivers during 2019 have been attributed to a record heat wave and drought during the summer (Jones et al. 2020; Westley 2020; von Biela et al. 2022). Although the conditions associated with this event were considered extreme, a general warming trend within the region has been apparent for some time (Walsh et al. 2011; Carey et al. 2017), and numerous forecasts predict that this trend will continue in the foreseeable future (Vavrus et al. 2012; Hodson et al. 2013). If so, water temperature will likely have an escalating impact on northern populations of salmon.

In addition to increased mortality, other adverse effects, ranging from reduced stamina and swimming speed to pronounced shifts in run timing, have been attributed to increasing temperatures during the spawning migration (Supplemental Information 1 available in the online version of this article). Although many of these factors are ostensibly sublethal, the additive and collateral effects may be sufficient to jeopardize both the survival and the reproductive success of the fish. The delayed response by the fish may also confound efforts to determine the underlying causes. Since the late 1990s, water temperatures in the Yukon River basin have frequently exceeded 18°C during summer (when adult Chinook Salmon are migrating upriver), periodically ranging as high as 20°C (von Biela et al. 2020). These conditions coincide with the dramatic decline in Chinook Salmon abundance, but the limited environmental information available prior to this period makes it difficult to determine the extent that temperature has been a contributing factor.

Recent efforts have been made to assess the impact of temperature on Chinook Salmon during the spawning migration. Based on sampling during 2016–2017, over half of the returning adults in the Yukon River basin exhibited clinical signs of heat stress, although the proportion varied by year and location (von Biela et al. 2020). Studies have also attempted to determine the effect of "sublethal" temperatures on the fish. von Biela et al. (2020) observed no mortality among adult Chinook Salmon that were captured in the lower Yukon River and held for several hours at 18°C, whereas 44% mortality was observed for those held at 21°C. The fish that survived the 21°C treatment were not lethargic and were similar in appearance and behavior to those held at 18°C. However, other studies suggest that prolonged exposure to high but presumably sublethal temperatures may have a profound effect on both survival and spawning success. Berman (1990) reported that nearly all of the adult Chinook Salmon that were exposed to a temperature of 19°C over several weeks died, whereas no mortality was observed for fish that were held at 14°C. Prolonged exposure to elevated temperatures during the migration has also been linked to depleted energy reserves, prespawning mortality, and a reduction in the size and number of viable eggs (Pankhurst and King 2010; Martin et al. 2015; Bowerman et al. 2018). Bowen et al. (2020) reported that elevated temperatures had a broad effect on Chinook Salmon physiology and potentially disrupted both basic and more specialized cellular functions, with a wider range of adverse effects observed at 21°C than at 18°C.

The temperatures encountered by Yukon River Chinook Salmon during our study often exceeded 18°C, particularly during 2004, when temperatures in excess of 20°C were frequently observed in the lower main stem. Disease was also a concern during this period. Since the late 1990s, the parasite *Ichthyophonus* has been reported in Yukon River Chinook Salmon, with elevated infection rates during 2002–2004 (Zuray et al. 2012). Higher temperatures have been associated with accelerated progression and increased severity of disease in salmonids (Wedemeyer 1996; Kocan et al. 2009), and Kocan et al. (2004) suggested that *Ichthyophonus*-infected Chinook Salmon destined for the Tanana and Upper Yukon may have succumbed to the parasite while nearing their terminal spawning areas.

In spite of the prolonged exposure to warmer conditions in 2004 and the increased prevalence of *Ichthyophonus* during the 3 years of our study, the fish did not exhibit migratory patterns that would suggest a negative response. Most were either tracked to terminal spawning areas or harvested in local fisheries. Only a small percentage (<4%) of the fish in 2004 were last located in nonterminal reaches of the main stem (where the status of the fish was difficult to determine and potentially represented individuals that died while in transit to their final destination), which was comparable to the proportions in 2002 and 2003 when conditions were cooler. Similar results were observed during the 2002–2004 basinwide telemetry study, when large numbers of radio-tagged Chinook Salmon (i.e., several thousand) were tracked upriver. The proportion of fish that were last located in nonterminal reaches was small and comparable among years, and there is evidence that at least a portion of these fish were harvested (but not reported) in local fisheries (Eiler et al. 2014). Elevated mortality was not observed downstream of terminal spawning tributaries, where shallower depths enhanced efforts to locate the radio-tagged fish. Stock composition estimates for the returns were also similar among years, suggesting that differences in temperature had little if any effect on the basinwide distribution of the fish.

Prolonged exposure to elevated temperatures during the spawning migration has been linked to prespawning mortality in salmon (Bowerman et al. 2018; von Biela et al. 2022). The proportion of fish that successfully spawned during our study is unknown due to the variable condition of the fish when recovered on the spawning grounds, ranging from live individuals to dead fish in advanced stages of decomposition. All of the dead fish that could be examined had spawned, suggesting that prespawning mortality was not prevalent. Future efforts to synchronize recovery efforts with the status of the fish would help to address this question. Subsequent carcass sampling of untagged fish in the Yukon River basin suggested that prespawning mortality of female Chinook Salmon is minimal, although partial spawning has been reported (Hamazaki et al. 2013; Twardek et al. 2021).

Delayed movements and thermal refugia

When exposed to adverse river conditions, salmon will sometimes alter their migratory behavior, delaying upriver movements and holding in coldwater refugia along the migratory route (Supplemental Information 1). In addition to reducing exposure to warmer temperatures, coldwater sites may also provide an opportunity for the fish to conserve energy prior to resuming upriver movements. Bardach and Bjorklund (1957) reported that freshwater fish are capable of detecting temperature changes as small as 0.05°C, and suggested that the ability to take advantage of even small differences in temperature could result in significant reductions in the basal metabolic rate. Keefer et al. (2018) reported that temperatures in thermal refugia along the Columbia River ranged from 2°C to 10°C colder than temperatures in the migratory corridor, which would represent a substantial energetic advantage for fish holding over an extended period (Plumb 2018).

The fish in our study did not appear to seek out and use thermal refugia. Discrete periods of sustained exposure to colder temperatures were not observed, and the continuous and highly variable fluctuations in swimming depth suggest that fish were actively moving upriver and not holding in localized areas. Migration rates would be considerably slower if fish were holding for extended periods, but as previously mentioned, the movements of the fish were relatively rapid and comparable among the 3 years of the study.

It is not known whether the continuous upriver movements of the fish represent a lack of thermal refugia or reflect the intrinsic behavior of the fish. The large volume of water and degree of mixing within the main stem may limit the availability of coldwater sites along the migratory route. However, salmon typically exhibit movement patterns that enable them to complete their migration and arrive on spawning grounds when local conditions are favorable. Yukon River Chinook Salmon have a relatively compressed run timing (~6 weeks) and must travel considerable distances to reach their final destination (Eiler et al. 2014); hence, the inherent need to arrive within a limited period of time may outweigh the negative effects imposed by suboptimal temperatures.

Spawning ground temperatures

Water temperatures in spawning areas used by Chinook Salmon typically range from 2.2°C to 18.9°C, with conditions <13°C generally considered optimal (McCullough 1999; EPA 2003). Temperatures above this level have been linked to lower fertilization rates, increased developmental abnormalities, and reduced embryo survival (McCullough 1999; Richter and Kolmes 2005). Thermal conditions in Tanana tributaries were mostly below 13°C during 2002–2003, whereas temperatures in other regional tributaries (as well as those in Tanana tributaries during 2004) were often near or above this level.

Exposure to warmer temperatures was compounded by the diel pattern exhibited by the fish as they approached and entered terminal tributaries, with temperatures often <13°C at night but above this threshold during the day. This pattern was evident across regions and stocks, including fish returning to Tanana River tributaries in 2003 (i.e., when temperatures were generally cooler), and suggests that temporal differences in temperature during spawning may increase the vulnerability of the fish to adverse effects. Although average daily temperature is commonly used to assess river conditions, this metric does not reflect diel patterns and may be misleading when assessing conditions in terminal spawning areas by underreporting the exposure of the fish to suboptimal conditions.

Cumulative effects of temperature

Considering the impact of elevated temperatures on salmon in other river drainages, the fish during our study were resilient in their response to the warmer temperatures encountered during 2004. However, fully assessing the impact of warmer conditions on reproductive success (including the number of viable eggs produced and egg-to-fry survival) is a major challenge and was beyond the scope of this study. Eliason et al. (2011) suggested that salmon returns are capable of acclimating over time to gradual increases in temperature. However, the relatively rapid increases in temperature currently being reported may exceed the capacity of these fish to adapt, and the continued warming trend forecasted for the region may compromise salmon returns in northern rivers.

Sullivan et al. (2000) reported that lethal and sublethal effects of temperature on migrating salmon depend on both the duration and severity of the exposure. Several authors have also suggested that the effects of temperature are cumulative and potentially influence both reproductive success and survival (Golden 1978; Elliott 1981; McCullough 1999). If so, upper-river stocks in the Yukon River basin would be particularly vulnerable to future increases in temperature due to the extended distances traveled and the prolonged exposure to warmer conditions in main-stem reaches. Lower-river stocks may also be at greater risk due to the lack of glaciers and the lower elevation and river gradient that characterize terminal tributaries in this section of the basin. Assessment efforts that target these stocks could provide useful indices for evaluating the impact of elevated temperatures on the entire return.

Water temperatures in the Yukon River were generally warmer in 2004 than in 2002–2003, but this pattern was not consistent throughout the basin. Several reaches in the upper basin were actually cooler in 2004 than in the two previous years. Although the effects of temperature on the fish may be cumulative, it would be useful to determine whether subsequent exposure to more favorable conditions (e.g., reaches with lower temperatures, thermal refugia) enables the fish to recover from the adverse conditions previously encountered.

CONCLUSIONS

The current warming trend occurring throughout the northern Pacific is predicted to continue into the foreseeable future. Although the long-term effects of this trend are not fully understood, the impact on Pacific salmon may become increasingly severe. Considerable demands are placed on adult salmon during the spawning migration even when conditions are optimal. Unfavorable conditions during this period have the potential to amplify these demands and adversely affect the returns. A wide range of negative effects has been linked to elevated water temperatures during the spawning migration, and understanding the migratory patterns of the fish in relation to the environmental conditions encountered can help in assessing the impact and managing the returns.

Radio-archival tags provided site-specific information on the movements of Yukon River Chinook Salmon and the thermal conditions experienced by the fish during the spawning migration. These data, in conjunction with information from a concurrent radiotelemetry study, provide a baseline for comparing past conditions and migratory patterns with those of present and future returns. The swimming patterns of the fish were characterized by continuous and highly variable fluctuations in depth throughout the upriver migration. This pattern, along with anecdotal information, suggests that the fish were swimming along the contours of the riverbed and is consistent with the premise that Chinook Salmon are primarily bottom oriented as they move upriver.

The temperatures encountered by the fish often exceeded 18°C (the threshold typically associated with adverse effects), particularly during 2004, when conditions in excess of 20°C were frequently observed in the lower main stem. Although altered behavior and adverse effects have been reported for Chinook Salmon in other river drainages under similar conditions, the fish in our study did not exhibit migratory patterns that would suggest a negative response, as most individuals were tracked to terminal spawning areas or harvested in local fisheries. Although temperatures in terminal tributaries were often near or above the upper range usually considered optimal for spawning (13°C), signs of prespawning mortality were not observed and the general behavior and appearance of the fish were similar among years. A pronounced diel pattern was observed as the fish approached their spawning grounds, and assessments based on average daily temperature may not adequately reflect exposure to suboptimal conditions.

Based on the thermal patterns observed, lower-river and upper-basin salmon may be particularly vulnerable to future increases in temperature. Assessment efforts that target these stocks could provide useful indices for evaluating the impact on the entire return. Additional information on the cumulative effects of temperature during the return is also needed to better evaluate the impact of prolonged exposure to elevated temperatures.

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CONFLICT OF INTEREST

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

Data available at https://www.fisheries.noaa.gov/inport/item/67520.

ETHICS STATEMENT

Fish were handled according to the methods described in the American Fisheries Society's *Guidelines for the Use of Fishes in Research* (https://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf). The methods and procedures used were reviewed and approved by the Joint Technical Committee of the U.S.–Canada Yukon River Panel, and conform to National Marine Fisheries Service standards.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.