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ARTICLE

Seasonal Movements and Habitat Use of Potamodromous Rainbow Trout Across a Complex Alaska Riverscape

Kevin M. Fraley* 

School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Post Office Box 757220, Fairbanks, Alaska 99775, USA

Jeffrey A. Falke

U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Post Office Box 757020, Fairbanks, Alaska 99775, USA

Richard Yanusz and Sam Ivey

Alaska Department of Fish and Game, Sport Fish Division, 1800 Glenn Highway, Suite 2, Palmer, Alaska 99645, USA

Abstract

Potamodromous Rainbow Trout *Oncorhynchus mykiss* are an important ecological and recreational resource in freshwater ecosystems of Alaska, and increased human development, hydroelectric projects, and reduced escapement of Chinook Salmon *Oncorhynchus tshawytscha* may threaten their populations. We used aerial and on-the-ground telemetry tracking, a digital landscape model, and resource selection functions to characterize seasonal movements and habitat use of 232 adult (>400 mm FL) Rainbow Trout across the complex, large (31,221 km²) Susitna River basin of south-central Alaska during 2003–2004 and 2013–2014. We found that fish overwintered in main-stem habitats near tributary mouths from November to April. After ice-out in May, fish ascended tributaries up to 51 km to spawn and afterward moved downstream to lower tributary reaches, assumedly to intercept egg and flesh subsidies provided by spawning salmonids in July and August. Fish transitioned back to main-stem overwintering habitats at the onset of autumn when salmonid spawning waned. Fidelity to tributaries where fish were initially tagged varied across seasons but was high (>0.75) in three out of four drainages. Model-averaged resource selection functions suggested that Rainbow Trout habitat use varied seasonally; fish selected low-gradient, sinuous, main-stem stream reaches in the winter, reaches with suitably sized substrate during spawning, larger reaches during the feeding season prior to the arrival of spawning salmonids, and reaches with high Chinook Salmon spawning habitat potential following the arrival of adult fish. We found little difference in movement patterns between males and females among a subset of fish for which sex was determined using genetic analysis. As most Rainbow Trout undertake extensive movements within and among tributaries and make use of a variety of seasonal habitats to complete their life histories, it will be critical to take a basinwide approach to their management (i.e., habitat protection and angling bag limits) in light of anticipated land-use changes.

Most fishes utilize a variety of habitats to complete their life histories and undertake movements (travel among different habitat types) or migrations (predictable round-trip movements undertaken by a majority of a population) of variable lengths on a periodic or seasonal basis (Alerstam et al. 2003; Dingle and

Drake 2007). For example, fishes often select areas with adequate food and protection from predators and harsh environmental conditions (Beck et al. 2001). Adult life stages may move seasonally among habitats that maximize energy intake (feeding zones), areas that are suitable for successful

*Corresponding author: kmfraley@alaska.edu
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reproduction (reproductive or spawning zones), and habitats that minimize exposure to predators or harsh environmental conditions (refugia or overwintering zones; Northcote 1978; Schlosser and Angermeier 1995; Lucas et al. 2001). Access to and availability of such complementary habitats has been shown to positively influence recruitment and survival of stream fishes (White and Rahel 2008; Falke et al. 2013). Complex life histories and the use of multiple habitat types through ontogeny are characteristic of salmonid fishes, and in adults, seasonal movements among habitats following an annual or biennial cycle are common (Northcote 1997). Quantifying the locations of these seasonal habitats, and the connections among them, is critical for species management, particularly when habitats extend across multiple jurisdictions or management entities (Temby et al. 2015).

Within fish populations, movement patterns vary from uniform short-distance dispersal to directional long-range travel (Gowan et al. 1994; Rodriguez 2010). Examples include long-distance (10–1,000 km) migrations between salt- and freshwater habitats (diadromy) and more localized movements (1–10 km) among freshwater habitats (potamodromy; Northcote 1997). Potamodromy has been observed in many species of the subfamily Salmoninae, including in Rainbow Trout *Oncorhynchus mykiss* (Meka et al. 2003; Schwanke and Hubert 2003). In salmonids, movement patterns vary among populations, life stages, and seasons, and movements are often triggered by environmental cues, such as changes in photoperiod, flow, turbidity, or temperature (Hilderbrand and Kershner 2000; Mellina et al. 2005). In stream fishes it is common to observe a leptokurtic pattern in which the majority of a population makes short movements away from core habitat areas with a smaller proportion of individuals moving long distances (Gowan et al. 1994; Skalski and Gilliam 2000; Radinger and Wolter 2014). To date, the study of movement patterns in stream fishes has been limited to specific life history stages (e.g., spawning migrations), yet less is known regarding patterns over multiple life history stages or seasons when the impetus for movement (e.g., spawn, rear, or take refuge) may vary considerably.

The habitat use and movement patterns within a species or population of fish may differ between sexes (Pusey 1987; Perrin and Mazalov 2000). In freshwater nonanadromous salmonids, females generally have higher energetic demands relative to males owing to the cost of egg production (Koizumi et al. 2006). By comparison, sperm production in males requires relatively little energy (Hutchings and Gerber 2002). However, males often spend more energy competing for females, which can offset the differential energy cost of producing gametes (Jonsson et al. 1991; Cano et al. 2008). As a result of these differences, females may spend more time in feeding habitats where they exhibit risky behaviors to maximize energy input, make shorter spawning movements to minimize energy expenditure resulting in smaller home ranges, or display infrequent reproductive events (e.g., skipped spawning) owing to high caloric thresholds (Hutchings and Gerber 2002).

Conversely, males may spend less time feeding, have larger home ranges, undertake longer exploratory movements and reproductive migrations, or have more frequent reproductive efforts. In nonanadromous salmonids, a male-biased strategy is often observed in which opportunistic males may range far and wide in search of food or mates (Hutchings and Gerber 2002; Olsen et al. 2006), although there are exceptions to this pattern (Koizumi et al. 2006). Consequently, nonanadromous salmonid movements and habitat use may vary by sex, although there is a paucity of studies on this topic in the literature (Hutchings and Gerber 2002; Koizumi et al. 2006).

Even in Alaska, typically considered to contain relatively pristine ecosystems, the management of highly mobile stream fish populations, such as potamodromous Rainbow Trout, is complicated owing to the uncertainty resulting from potential anthropogenic impacts and climate change (Prowse et al. 2006). Additionally, Rainbow Trout are highly sought after as sport fish throughout their native range in western North America, where fishing pressure can be heavy in drainages that are easily accessible by road (Bartlett and Hansen 2000; Jennings et al. 2011). Moreover, in basins where Rainbow Trout and other Pacific salmon *Oncorhynchus* spp. co-occur, Rainbow Trout populations may be highly dependent on food sources derived from spawning Pacific salmon (e.g., eggs and decomposing flesh) to meet energetic demands through periods of low food availability (winter months; Scheuerell et al. 2007; Ruff et al. 2011). Because in recent years some runs of Chinook Salmon *Oncorhynchus tshawytscha* in the upper Cook Inlet have not met escapement goals (Munro and Volk 2014), Rainbow Trout populations that depend on these subsidies may be negatively impacted. In addition, land development (increasing in Alaska) may put pressure on populations owing to increased sedimentation, thinning of riparian zones, increased sportfishing pressure, and altered flow and temperature regimes and loss of habitat connectivity from installation of culverts and hydropower dams (MSBSHP 2013; AEA 2015; American Fisheries Society Western Division, 2015 policy letter to K. D. Rose, Secretary of the Federal Energy Regulatory Commission, on the proposed Susitna–Watana Hydropower project). As a result, a better understanding of seasonal habitat use and movements of potamodromous Rainbow Trout is warranted.

In light of these possible threats, our overall goal was to gain a better understanding of the movements and habitat utilization of an Alaska population of native potamodromous Rainbow Trout to provide information to better protect these economically and ecologically important fish. Our analyses were based on fish location and movement data collected through radiotelemetry, characterization of broad-scale physical and biological characteristics of seasonal habitats calculated from a digital landscape model, and genetic sex identification for a subset of tagged fish. Our specific objectives were to (1) characterize movement patterns by fish within and among main-stem and tributary streams, (2) quantify how these movements varied seasonally and

between sexes, and (3) identify important seasonal habitats across a complex Alaskan riverscape.

METHODS

Study area.—The Susitna River basin (31,221 km²) consists of a large network of glacial and clear-water streams in south-central Alaska that originate in the Alaska Range and Talkeetna Mountains and ultimately form the 482-km Susitna River (Figure 1; Barrick et al. 1983), which drains into the upper Cook Inlet of the Gulf of Alaska. The Susitna River is the 15th largest river in the United States in terms of discharge (Kammerer 1990). The basin is home to large, economically and ecologically important native populations of potamodromous Rainbow Trout. Future anthropogenic land development (expected to double within the next 50 years; Schick 2006) in the Matanuska–Susitna region as well as the proposed Susitna–Watana Hydropower Project (AEA 2015) may affect Rainbow Trout, Arctic Grayling *Thymallus arcticus*, and Pacific salmon in the Susitna basin (MSBSHP 2013). For this study, Rainbow Trout were tagged in the drainages of four westward flowing tributaries of the middle and lower Susitna River basin originating in the Talkeetna Mountains (Figure 1): one with glacial influence, the Kashwitna River (61°

59'7"N, 149°50'57"W), and three runoff-fed streams, Willow Creek (61°46'44"N, 150°9'5"W), Montana Creek (62°6'18"N, 150°3'48"W), and Chuniilna (Clear) Creek (62°22'15"N, 150°0'59"W). Kashwitna River fish were predominantly tagged in the clear-water North Fork, but the remainder of the Kashwitna drainage is heavily influenced by glacial melt. Discharge and turbidity in the Susitna River are highest in June and July at the peak of glacial melt and lowest when flow contribution from glacial melt recedes during fall and early winter. Discharge patterns differ among tributaries, with peaks occurring during snowmelt runoff in May and June and following frequent precipitation events in August and September. Lotic habitats in the Susitna River basin are typically ice-covered from October to April, although open-water leads may occur in areas with swift current or groundwater upwelling. The Susitna River and its tributaries have similar thermal regimes (annual range of 0–14°C), with the lowest temperatures in winter and a peak in midsummer.

The Susitna River basin contains substantial spawning populations of Chinook Salmon (the fourth largest run in the state of Alaska; Hasbrouck and Edmundson 2007), Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, Sockeye Salmon *O. nerka*, and Coho Salmon *O. kisutch*. These salmon, in addition to Rainbow Trout, are the targets of a popular sport fishery (Oslund et al. 2013). Angling for Rainbow Trout in the Susitna River basin is mostly catch and release, and fish may be subjected to heavy pressure from fly fishermen during summer months (June to September). For example, in 2010 the estimated total catch of Rainbow Trout by recreational anglers in the lower basin was 60,770 fish, with 2,260 harvested across 122,235 angler-days (Jennings et al. 2011).

Fish capture and tagging.—Adult Rainbow Trout (>400 mm FL) were captured in 2003 in the four tributaries and only in Willow Creek in 2013 and 2014 via fly-rod-and-reel angling methods. Capture efforts occurred in the late summer to early fall in lower tributary reaches. Fish eligible for surgery were landed quickly with a net and immersed in an anesthetic bath until stage 3–4 anesthesia was attained (Summerfelt and Smith 1990). In 2003 spearmint oil was used as an anesthetic (Yanusz 2009), in 2013 clove oil was used, and in 2014 AQUI-S 20E (AQUI-S New Zealand, Wellington, New Zealand) was employed per collection permit stipulations. Fish with visible injuries or those showing signs of lethargy and exhaustion were rejected as surgical candidates and immediately released. Anesthetized fish were placed ventral-side up in a moist neoprene-lined cradle for surgery. A crew member continuously delivered anesthetic and oxygenated water to the fish's gills with a turkey baster and monitored rapidity of gill movements and movement of the fish for the duration of the surgery. A separate crew member conducted the surgery, first making a small 2-cm incision 1–2 cm off the mid-ventral line about 3–4 cm anterior of the pelvic girdle with a scalpel sterilized in Betadine solution. A grooved rod was then inserted into the incision and towards the posterior of the fish. Next, a hollow 16-gauge needle was inserted

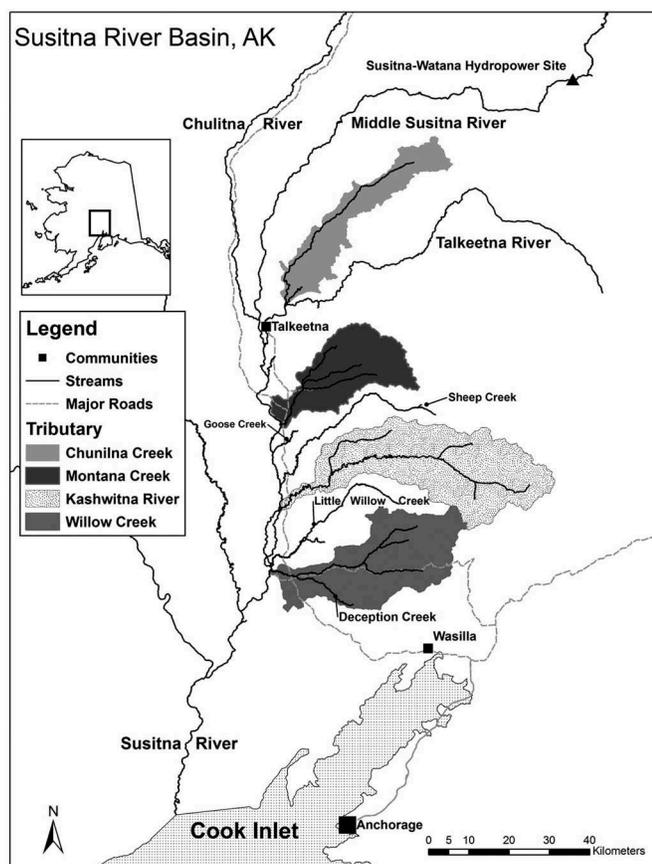


FIGURE 1. Study area location in the Susitna River basin, Alaska. The shaded polygons denote tributaries where Rainbow Trout were tagged.

into the fish just behind the pelvic girdle and directed along the grooved rod until the tip reached the incision (Ross and Kleiner 1982). The antenna wire of a radio transmitter (F1835C in 2013 and 2014: 17 mm × 44 mm, 14 g, battery life capacity 483 d; FI830 in 2003: 12 mm × 53 mm, 11 g, battery life capacity 340 d; Advanced Telemetry Systems, Isanti, Minnesota) was then threaded through the fish via the hollow needle. A radio tag was inserted, bottom first, into the incision site while using the transmitter wire to help position the tag in the fish. After the tag was inserted into the body cavity, the incision was closed with three to four 3–0 PDS monofilament absorbable sutures about 3.2 mm apart. After suturing, the wound was dried with sterile gauze and a few drops of Vetbond surgical glue were applied. Vetbond takes about 10 s to dry, at which time mucous from an adjacent area of the fish was smeared onto the wound to facilitate healing. After each fish recovered from surgery in an aerated basin of fresh river water, a right pelvic fin clip was taken for genetic sex identification (2013 and 2014 fish only) and a numbered Floy FD-94 T-bar anchor tag was implanted at the base of the dorsal fin as an external identifier. Individuals were visually examined and the presence of any physical deformities likely caused by angling (e.g., hooking scars including lacerations, jaw deformities, damaged mandibles, and dysfunctional eyes) was noted. Fully recovered fish were released into a pool or other low-velocity habitat near the site of capture. Surgical tools were sterilized in an iodine–povidine solution and rinsed with a saline solution between each surgery.

Fish tracking.—Monthly fixed-wing aerial surveys were conducted from October 2003 to October 2004 and January to December 2014 during which locations of radio-tagged Rainbow Trout were identified using an Advanced Telemetry Systems model R4500C telemetry receiver. Flights were exhaustive and covered the majority of the lower Susitna River basin main stem and tributaries from upper Chunilna Creek in the north to Cook Inlet in the south (Figure 1). We assumed that tagged fish did not leave the study area or go out to sea based on extensive exploratory tracking outside of the study area, as well as a review of the literature that confirmed that Rainbow Trout in the Susitna River have never been observed to exhibit anadromy (Eaton and Adams 1995; Behnke 2002). Weekly ground tracking of fish along Willow and Deception creeks substituted for aerial tracking during July and August 2014 when no flight surveys were flown. Ground tracking was undertaken via raft and on foot, and an Advanced Telemetry Systems model R4500C telemetry receiver attached to a Yagi antenna was used to pinpoint and record fish locations (Fraley 2015). Transmitter identification number, latitude, longitude, signal strength, and presence or absence of a mortality code were recorded for all surveys. Exact fish locations for each survey were determined based on the highest signal strength reported by the telemetry receiver. Fish mortality (including unquantified transmitter expulsion or failure) was classified by either a mortality signal given off by an inactive radio transmitter (internal tag motion sensor,

triggered by 24 h or more of inaction) or by failure to locate the fish after two or more surveys of the study area. Posttagging (i.e., initial) mortality or tag expulsion was assumed when a transmitter gave repeated mortality signals or permanently disappeared from the study area during the first two telemetry surveys after tagging (see Appendix for additional information on mortality).

Genetic sex identification.—Pelvic fin clips were taken from each radio-tagged Rainbow Trout captured in Willow Creek in 2013–2014 and stored in 95% ethanol. The DNA was isolated in the laboratory using a DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) and electrophoresed to verify success of extraction. Genomic DNA was used as a template in PCR reactions using primers *OmyY1 F* (5'-GTTTCATATGCCAGGCTCAAC-3') and *OmyY1 R* (5'-CGATTAGAAAGGCCTGCTTG-3') following methods of Brunelli et al. (2008). Primers targeting salmonid mitochondrial genome fragments were used as a DNA quality control. All PCR products were dyed and examined using agarose gel electrophoresis. The resulting bands (viewed under UV light) were examined to determine the sex of each fish. Samples exhibiting horizontal bands at 792 base pair length were designated as a male and those without bands at this location as female. Fin clips were also taken from three known female Rainbow Trout from the Alaska Department of Fish and Game's Ruth Burnett Sport Fish Hatchery in Fairbanks, Alaska, and three known male Rainbow Trout from the Montana Fish, Wildlife, and Parks' Murray Springs Trout Hatchery near Eureka, Montana, to serve as controls and verify the accuracy of the sex identification analysis. Each sample was processed two to three times to ensure precision of the analysis. A simple binomial test was employed to determine if the observed sex ratio departed from 1:1.

Fish locations, movement, and tributary fidelity.—Based on 2004 and 2014 data, individual Rainbow Trout locations assessed via aerial telemetry were determined to be accurate within 500 m based on a comparison of GPS locations from aerial tracking with known on-the-ground points from stationary telemetry tags (R. Yanusz and K. M. Fraley, unpublished data). Fish locations were imported into a geographical information system (GIS) using ArcMap (version 10.1; Environmental Systems Research Institute, Redmond, California) and snapped to the nearest stream polyline in a digital landscape model parameterized for the Matanuska–Susitna River basin (NetMap; Benda et al. 2007). The NetMap model generates a synthetic digital stream network layer from a remotely sensed digital elevation model (DEM) based on flow accumulation and channel delineation algorithms (described in Clarke et al. 2008). The result is a network of 50–200-m stream reaches linked to the surrounding landscape and attributed with geomorphic characteristics (e.g., gradient, stream width, drainage area). The Matanuska–Susitna River basin DEM was based on synthetic aperture radar (5-m resolution) and light detection and ranging (<1-m resolution) imagery. We used NetMap

instead of the National Hydrography Dataset (USGS 2013) for the state of Alaska because the current Alaska National Hydrography Dataset is low quality relative to data available for the contiguous USA (e.g., coarser scale, misrepresented flow lines, disconnected and omitted streams). We aggregated the 50–200-m NetMap digital stream reaches to 500-m reaches (to match aerial survey accuracy) to which we assigned fish locations.

We defined fidelity to tributary of capture as the proportion of fish that remained in the tributary of capture relative to those that were located in a different tributary at any time during a single season (Northcote 1997). We identified discrete seasons, including overwintering, spawning, and feeding seasons, based on general life history information for Rainbow Trout in Alaska (Bartlett and Hansen 2000; Yanusz 2009) as follows: the overwintering season was October through early May when Susitna River basin streams are ice covered, the spawning season was immediately following ice-out in mid-May to the cessation of spawning activities in early June, and the feeding season was the open-water season from June to September. We split the feeding season into two seasons (early and late feeding) to investigate the potential difference in fish movement and habitat use before and after the arrival of spawning salmonids (Hasbrouck and Edmundson 2007). The overwintering season was not included in fidelity to tributary of capture because the majority of fish occupied the main-stem Susitna or Talkeetna rivers during this time, and thus were not associated with any particular tributary (see Results). The proportion of complex movements, defined as movements by a fish among multiple tributaries or movement away from the home tributary over multiple seasons (i.e., not a there-and-back journey), was also calculated for each tributary and year (2004 or 2014). An example of a complex movement would be a fish tagged in Tributary A moving to Tributary B during the spawning season, then moving to Tributary C for the early feeding season, and returning to Tributary A during the late feeding season. An example of a noncomplex movement would be a fish tagged in Tributary A that moved to Tributary B during the spawning season but then returned to Tributary A during the early and late feeding seasons.

Interseasonal movement (ISM) distances (network distance between an individual fish's averaged location each season in kilometers) were measured in ArcMap for each tributary, season, and year (Meka et al. 2003). Total annual movements (TAMs; km) were calculated by summing the ISM distances for individual fish that were determined to be alive from the overwintering season through late feeding season for each tributary and year and were averaged for each tributary (Schwanke and Thalhauser 2011). The distance from the confluence of the tributary of capture (DFC; km) was calculated for all individual fish locations by season, year, and tributary (Meka et al. 2003).

Data analysis.—We compared Rainbow Trout TAM, ISM, and DFC among the four tributaries, 2 years (2004 and 2014),

and four seasons (overwintering, spawning, early and late feeding) and by sex using two-factor analysis of variance (ANOVA). If significant differences were detected by the ANOVA, we used Tukey's honestly significant difference post hoc test for multiple comparisons. To address the potential for bias induced by nonnormality of data we compared results of the ANOVA with those from a randomized permutation test (Manly 2006) based on the same main effects. Results of the permutation test were identical to the two-factor ANOVA. Based on those results, we felt justified that proceeding with the ANOVA analysis would not substantially influence the interpretation of our results.

We used resource selection functions (RSFs; Manly et al. 2002; Johnson et al. 2006; Lele 2009) to quantify Susitna River basin Rainbow Trout habitat selection during the overwintering, spawning, early feeding, and late feeding seasons. The RSF approach determines resource selection by comparing the characteristics of used locations (i.e., seasonal habitats) to those of available ones based on weighted distribution theory (Johnson et al. 2006) and an exponential resource selection function (Manly et al. 2002). We limited the study extent (i.e., set of "available" stream reaches) to reaches with an upstream drainage area >12.5 km² as no Rainbow Trout were ever observed in smaller streams.

Covariates used in the RSF analysis were reach-scale attributes derived from the synthetic stream layer continuously across the study extent. Attribute values from 50–200-m reaches were summarized (i.e., averaged) every 500 m to best match the accuracy of assigning telemetry locations. Animal location accuracy is an important consideration when producing and evaluating RSF models (Morehouse and Boyce 2013). We chose five attributes to represent physical and biological processes that potentially affect the distribution of Rainbow Trout within and among seasons. We assumed these modelled attributes were generally applicable to the Susitna River basin because they were based on similar large river networks within the native range of Rainbow Trout (e.g., the Pacific Northwest). The first attribute, channel gradient (GRAD; %) was calculated based on the underlying DEM (Clarke et al. 2008). We predicted that gradient would be important over all seasons owing to the propensity for fish to seek areas of optimal flow, food, and dissolved oxygen availability for refugia, spawning, and rearing (Cram et al. 2013; Laliberte et al. 2014).

The second attribute, sinuosity (SINU; unitless), is a ratio of the magnitude of meandering of a stream across its floodplain. Sinuosity was calculated using a channel path length equal to 40 times the channel width (Rosgen 1994). Increased sinuosity typically results in higher aquatic habitat complexity and is indicative of a stream channel unaltered by human development (Fausch and Northcote 1992). Thus, sinuosity is likely important for Rainbow Trout habitat selection over all seasons.

We also chose mean annual flow (MAF; 1,000 m³/s) as a relative measure of stream size (Clarke et al. 2008). This

metric was calculated based on an equation for south-central Alaska (Brabets 1996) as follows:

$$\text{MAF} = (1.025 \times A^{0.024} \times P^{1.186}) / 1,000$$

where P is the mean annual precipitation (mm) and A is the upstream drainage area (km^2). The MAF was converted to units of $1,000 \text{ m}^3/\text{s}$ to force model-averaged parameters to be informative. Flow is likely important to Rainbow Trout across seasons as they seek out areas with velocity that minimizes energy expenditure but adequately delivers drifting food items to juveniles and adults and dissolved oxygen to eggs (Bisson et al. 1988).

We included a binary variable to represent the presence of adequate spawning substrates (D50; mm) for the spawning season. This metric was calculated based on bed shear stress: the depth–slope product using channel gradient, bank-full flow depth, and water density. The relationship between bed shear stress and D50 was taken from a regional model for the Pacific Northwest (Buffington et al. 2004). We developed a binary predictor to represent reaches that were suitable (1; D50 = 15–25 mm) and unsuitable (0; all other values of D50) for Rainbow Trout spawning based on reported D50 values that fell within the 25th–75th percentiles from 10 populations (Kondolf and Wolman 1993). Substrate size is known to be important for spawning salmonids because substrate that is too fine is less likely to allow dissolved oxygen and wastes to be delivered or removed from interstitial spaces, where eggs are deposited.

Finally, we included a measure of Chinook Salmon spawning habitat potential as a candidate predictor of Rainbow Trout use during the late feeding season (CHINIP). This metric was based on a habitat intrinsic potential model methodology developed by Burnett et al. (2007) and parametrized for spawning Chinook Salmon in the Columbia River basin (Busch et al. 2011). We used the Columbia River basin intrinsic potential model because no model is yet available for our study area. We hypothesized that reaches with high CHINIP are likely selected for by Rainbow Trout during the late feeding season because they are known to seek out salmonid spawning areas to take advantage of food subsidies (e.g., eggs and flesh; Bartlett and Hansen 2000; Fraley 2015).

We used an exponential logistic RSF (Lele and Keim 2006; Lele et al. 2012) to compare environmental conditions in used stream reaches (i.e., where Rainbow Trout were detected using radiotelemetry and known to be present) with those in available reaches drawn at random from the study area extent under 99 bootstrap iterations. The RSF models were constructed in Program R (R Development Core Team 2012) using the ResourceSelection package (Lele 2009; Lele et al. 2014). The RSF approach uses random sampling of the used–available habitat database from a weighted distribution to generate a maximum likelihood estimate of the probability of use for

each habitat factor (Lele 2009; Kowal et al. 2014; Gagné et al. 2015). Predictors were examined for collinearity based on the variance inflation factor. Covariates with a variance inflation factor > 5 were not included in the models (Montgomery et al. 2012).

We used an information-theoretic approach to select the best model predicting Rainbow Trout seasonal habitat selection, given the data (Burnham and Anderson 2002). Candidate models were built separately for each season, based on the following sets of predictors and based on the hypotheses presented above: overwintering (channel gradient, sinuosity, MAF), spawning (channel gradient, sinuosity, MAF, D50), early feeding (channel gradient, sinuosity, MAF), and late feeding (channel gradient, sinuosity, MAF, CHINIP). All possible combinations of variables were considered for each seasonal model. The top model for each season was selected based on scores for the Akaike information criterion corrected for small sample size (AIC_c); those with the lowest AIC_c were considered top models. Model fit for top models was assessed based on the Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000). In order to address model uncertainty, we averaged parameter estimates over models with Akaike weights (w_i) ≥ 0.05 and reported the relative importance of each covariate included in the confidence model set (Barton 2012).

RESULTS

Fish Capture and Tagging

A total of 37 adult Rainbow Trout were captured and tagged in 2003 during 12–13 angling days in each of the four tributaries, with an additional 45 and 39 fish tagged in Willow Creek in 2013 and 2014, respectively (Total $N = 232$; Table 1). The percentage of fish with hooking scars ranged from 10.8% in the Kashwitna River in 2003 to 71.8% in Willow Creek in 2014 (Table 1). Hooking scars were assumed to be caused by catch-and-release sport angling and included deformity and laceration of the upper and lower jaws or operculum and noticeable cross bite. Fish lengths were similar across tributaries and years (mean FL = 483 mm, SD = 56.4; Table 1). Information on posttagging and annual mortality of tagged fish is presented in the appendix.

Genetic Sex Identification

All but two Rainbow Trout from Willow Creek in 2013 and 2014 were successfully assigned to a sex. The DNA was denatured for one of the unknown fish, likely due to decomposition in a faulty storage vial, and the other fish was released before taking a fin clip in order to minimize additional stress after observing the fish was exhausted and sluggish postsurgery. Results of the analysis found that there were 16 males and 27 females tagged in 2013 and 12 males and 27 females in 2014. Thus, the observed sex ratio was significantly female

TABLE 1. Summary of radio-tagged Rainbow Trout in the Susitna River basin, Alaska, by tributary and year. The number of fish tagged (*N*), the mean, minimum (Min), maximum (Max), and standard deviation (SD) of fork length (mm), the percentage of fish with hooking scars (HS), and the number of fish that survived tagging and gave one or more live signals (Live) are shown.

Year	Tributary	<i>N</i>	Fork length				HS	Live
			Mean	Min	Max	SD		
2003	Kashwitna	37	476.05	407	648	53.73	10.8	31
2003	Montana	37	488.76	405	610	58.41	43.2	25
2003	Chunilna	37	492.70	408	670	60.07	13.5	28
2003	Willow	37	519.03	425	674	65.96	24.3	30
2013	Willow	45	459.82	401	545	38.44	42.2	21
2014	Willow	39	470.23	405	660	48.24	71.8	24

biased (65.9% female, 34.1% male overall; binomial test) with a female to male ratio of roughly 8:5 in 2013 and 11:5 in 2014.

Fish Locations, Seasonal Movement, and Tributary Fidelity

Twenty-one aerial telemetry surveys of the Susitna River basin were conducted during the study period (*N* = 11 in 2004; *N* = 10 in 2014). A total of 1,272 fish locations were recorded for Rainbow Trout that survived tagging and gave one or more live signals (Table 2). Fish were detected in the main-stem Susitna, Talkeetna, and Chulitna rivers and in tributary drainages, including Willow Creek, Little Willow Creek, Kashwitna River, Sheep Creek, Goose Creek, Montana Creek, and Chunilna Creek (Figure 1). Fidelity to stream of capture ranged from 33.3% of fish in the Kashwitna River during the spawning season to 100% in Willow Creek in 2014 during the late feeding season (Table 2). Complex movements were observed in 9.5–11.7% of fish from Willow, Montana, and Chunilna creeks, whereas 22.7% of the Kashwitna River fish exhibited complex movements.

We found that Rainbow Trout moved long distances (up to 218.5 km, the longest individual TAM), and those movements differed by season and tributary. Total annual movements were not significantly different among Rainbow Trout tagged in

Willow, Montana, and Chunilna creeks (Tukey's honestly significant difference; mean = 42 km, SE = 37.90, all $P > 0.62$), but fish tagged in the Kashwitna River traveled significantly farther (mean = 105.1 km, SE = 52.87, $P < 0.001$; Figure 2). The shortest annual movement observed was 4.5 km (2004 Montana Creek), whereas the longest was 218.5 km for a fish from the Kashwitna River. Similar to TAM, ISM was significantly different only for fish tagged in the Kashwitna River (mean = 28.5 km, SE = 19.73, $P = 0.006$) and did not differ for those tagged in other tributaries (mean = 16.5 km, SE = 18.30, all $P > 0.05$). Interseasonal movement was significantly different among all seasons (overwintering, spawning, early feeding, and late feeding) when pooled across tributaries (all $P < 0.03$; Figure 3a). Fish made the longest ISMs between overwintering and spawning seasons (mean = 28.5 km, SE = 18.53), and the shortest ISM distances were between early and late feeding season habitats (mean = 8 km, SE = 13.56). Individuals remained closer to their respective tributary confluences during the overwintering season (mean DFC = 1.8 km downstream, SE = 17.25) than during spawning (mean DFC = 19.0 km, SE = 18.1; Figure 3b). There was a significant interaction between tributary and season (ANOVA: $F = 2.52$, $df = 12$, $P = 0.003$), suggesting that fish from different tributaries show slightly different patterns in DFC over seasons. This interaction was driven by Kashwitna River fish spawning and feeding farther upstream of the tributary confluence compared with other subpopulations (likely because these fish typically spend time in the North Fork of the Kashwitna River).

Willow Creek 2013–2014 Sex Bias

Posttagging mortality and tag rejection rates of 2013–2014 Willow Creek Rainbow Trout were higher for females (2013 = 65.4%, 2014 = 37%) than for males (2013 = 37.5%, 2014 = 25%) in both years. Although no significant differences were found between sexes in mean TAM (ANOVA: $F = 0.13$, $df = 1$, $P = 0.73$), ISM ($F = 0.11$, $df = 1$, $P = 0.74$), or DFC ($F = 0.01$, $df = 1$, $P = 0.93$), there was a significant interaction between sex and season in DFC. This interaction indicated that males spawned farther from, but reared closer to, confluences compared with females ($F = 2.92$, $df = 4$, $P = 0.02$).

TABLE 2. Proportion of Rainbow Trout showing fidelity to their tributary of capture, by tributary and year, with sample size in parentheses. Complex movements were defined as movements between multiple tributaries or multiple seasons spent away from the tributary of capture. Willow 2013–2014 includes fish tagged in both years for all but the complex movements section, for which only fish tagged in 2013 were included.

Season	Tributary				
	Willow 2004	Kashwitna	Montana	Chunilna	Willow 2013–2014
Spawning	0.78 (27)	0.33 (27)	0.87 (23)	0.89 (28)	0.75 (20)
Early feeding	0.81 (21)	0.68 (22)	0.89 (18)	0.96 (26)	0.94 (17)
Late feeding	0.86 (21)	0.72 (18)	0.88 (17)	0.94 (16)	1.00 (38)
Complex movements	0.10 (21)	0.23 (22)	0.11 (18)	0.12 (26)	0.12 (17)

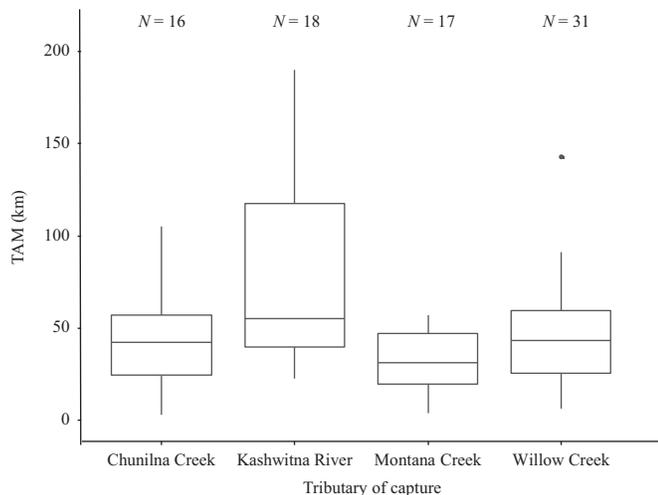


FIGURE 2. Total annual movement (TAM; km) of radio-tagged Rainbow Trout from the Susitna River basin, Alaska, by tributary of capture. The box dimensions represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, the solid lines inside the boxes are the medians, and the dot indicates an outlier.

Habitat Use

All variance inflation factor values were < 5 ; therefore, all covariates were included in respective seasonal RSF models. Across seasons, predicted values from each top model for Rainbow Trout resource selection closely fit the observed values (all Hosmer–Lemeshow goodness-of-fit P -values < 0.05). The top models selected for overwintering Rainbow Trout resource selection (Table 3) suggested that the likelihood of overwintering habitat use increased (+) with SINU and MAF and decreased (–) with GRAD (Table 4). The best-supported models for Rainbow Trout spawning habitat use indicated that use was affected by SINU (+), D50 (+), GRAD (–), and MAF (+). However, unconditional confidence intervals for GRAD and MAF overlapped zero (Table 4). For the early feeding season, the top models of Rainbow Trout habitat selection included MAF (+), GRAD (–), and SINU (–), with confidence intervals for GRAD and SINU overlapping zero. Finally, the top models for the late feeding season included CHINIP (+), GRAD (+), SINU (+), and MAF (–). The confidence interval for MAF overlapped zero.

DISCUSSION

Our research showed that potamodromous Rainbow Trout within a complex, glacially influenced river basin moved long distances and occasionally utilized multiple tributaries within and among seasons. Intertributary movements suggest an intermittently connected basinwide population with heterogeneity in movements. Habitat use by fish varied across seasons, with individuals selecting stream reaches with characteristics supporting refuge from harsh conditions overwinter, spawning in the spring, and feeding over the summer months. In general,

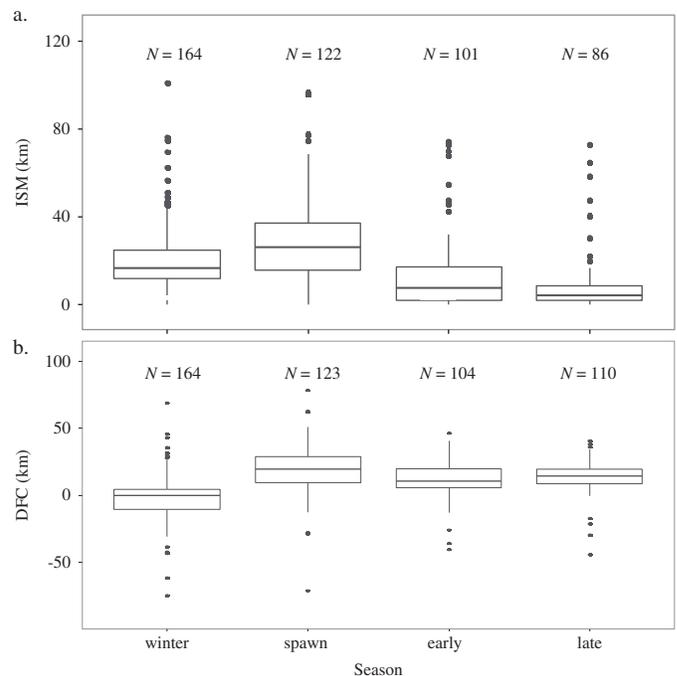


FIGURE 3. (a) Interseasonal movement (ISM; km) and (b) distance from the tributary confluence (DFC; km) of radio-tagged Rainbow Trout from the Susitna River basin, Alaska, among seasons and pooled over the tributary of capture. Season abbreviations are as follows: winter = overwintering season, spawn = spawning season, early = early feeding season, and late = late feeding season. The box dimensions represent the 25th and 75th percentiles, the whiskers show the 10th and 90th percentiles, the lines inside the boxes are the medians, and the dots indicate outliers.

individuals exhibited a previously undocumented seasonal movement pattern in which they overwintered in glacially influenced main-stem reaches during the long ice-covered season from October to May, moved into upper reaches of clear-water tributaries during the spawning season from mid-May to early June, and remained in tributaries to feed from mid-June through September. Movements varied in distance among seasons, with the longest average ISM between overwintering and spawning habitats.

Seasonal Habitat Use and Movements

During the overwintering season (September through May), Rainbow Trout almost exclusively used main-stem Susitna and Talkeetna River habitats with lower gradient and higher sinuosity and MAF. Exceptions to this include 22.6% of the fish tagged in the Kashwitna River that remained within the tributary and 17.9% of the fish tagged in Chunilna Creek that overwintered in a stream–lake system within the tributary. However, these alternative locations likely provided refuge similar to main-stem habitats (Northcote 1997; Meka et al. 2003). Fish likely chose habitats with lower gradient and higher sinuosity and MAF

TABLE 3. Summary of model selection statistics for the top seasonal resource selection models for Rainbow Trout from the Susitna River basin, Alaska (Akaike weight [w_i] > 0.05). Abbreviations are as follows: N = the number of observations included in each model, L-L = the log-likelihood, ΔAIC_c = the difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model, and K = the number of parameters, including the intercept and residual variance. Parameters are abbreviated as follows: GRAD = gradient (%), SINU = sinuosity, MAF = mean annual flow (m^3/s), D50 = median substrate size suitability for Rainbow Trout spawning, and CHINIP = Chinook Salmon spawning intrinsic potential.

Season	Model	N	L-L	AIC_c	ΔAIC_c	w_i	K
Overwinter	GRAD, SINU, MAF (global model)	622	-5,905.33	11,816.7	0.00	0.92	3
	GRAD, SINU		-5,908.75	11,821.5	4.83	0.08	2
Spawning	SINU, D50	201	-1,920.09	3,844.2	0.00	0.48	2
	SINU, D50, GRAD		-1,919.83	3,845.8	1.55	0.22	3
	SINU, D50, MAF		-1,919.93	3,846.0	1.75	0.20	3
	SINU, D50, GRAD, MAF (global model)		-1,919.72	3,847.6	3.41	0.09	4
Early feeding	GRAD, MAF	170	-1,631.68	3,267.4	0.00	0.53	2
	GRAD, MAF, SINU (global model)		-1,631.66	3,269.5	2.04	0.19	3
	MAF		-1,633.72	3,269.5	2.04	0.19	1
	MAF, SINU		-1,633.67	3,271.4	3.99	0.07	2
Late feeding	CHINIP, GRAD, SINU	149	-1,417.9	2,842.0	0.00	0.26	3
	CHINIP, GRAD		-1,419.0	2,842.2	0.16	0.24	2
	CHINIP, GRAD, MAF		-1,418.7	2,843.5	1.46	0.13	3
	CHINIP, GRAD, SINU, MAF (global model)		-1,417.7	2,843.6	1.58	0.12	4
	CHINIP		-1,421.1	2,844.3	2.27	0.08	1
	CHINIP, SINU		-1,420.1	2,844.3	2.28	0.08	2

because minimizing movement and choosing suitable habitat (optimal temperatures, high-volume reaches without bedfast ice; Brown and Mackay 1995) in order to conserve energy during the long, harsh overwintering season is critical to fish survival (Smith and Griffith 1994). Rainbow Trout use of main-stem rather than tributary habitats in the Susitna River basin is similar to what has been observed in other salmonids

(Jakober et al. 1998; Brown et al. 2001) and is likely tied to flow, temperature selection, and available cover (Smith and Griffith 1994). About half of the tagged fish remained in close proximity (< 10 km; 54.9%) to the confluence of their tributary of capture, but a sizeable proportion (45.1%) moved longer distances up- or downstream along the main-stem rivers. This individual variation in movement may be

TABLE 4. Model-averaged parameter estimates, relative variable importance, and lower and upper 95% confidence limits (CLs) for covariates predicting seasonal resource selection of potamodromous Rainbow Trout in the Susitna River basin, Alaska. Estimates are derived from the confidence set of models with $w_i > 0.05$ (Table 3).

Season	Covariate	Parameter estimate	Relative importance	Lower 95% CL	Upper 95% CL
Overwinter	Gradient	-0.06 ± 0.03	1.00	-0.12	> -0.01
	Sinuosity	1.13 ± 0.08	1.00	0.99	1.26
	Mean annual flow	0.69 ± < 0.30	0.92	0.10	1.28
Spawning	Substrate	0.72 ± 0.15	1.00	0.43	1.01
	Sinuosity	0.84 ± 0.15	1.00	0.52	1.16
	Gradient	-0.02 ± 0.02	0.31	-0.07	0.02
Early feeding	Mean annual flow	0.29 ± 0.56	0.29	-0.70	1.28
	Mean annual flow	1.31 ± 0.31	1.00	0.71	1.92
	Gradient	-0.08 ± 0.06	0.73	-0.19	0.03
Late feeding	Sinuosity	-0.01 ± 0.28	0.27	-0.55	0.52
	Chinook Salmon spawning intrinsic potential	3.12 ± 0.73	1.00	1.64	4.60
	Gradient	0.11 ± 0.04	0.85	0.02	0.21
	Sinuosity	0.39 ± 0.19	0.43	< 0.01	0.78
	Mean annual flow	-0.50 ± 0.78	0.33	-1.91	0.91

due to density dependence or random exploratory movements by highly mobile individuals (e.g., staying allows a fish to be closer to spawning habitats, but habitats near tributary mouths may have a high density of conspecifics; Gowan et al. 1994; Skalski and Gilliam 2000; Radinger and Wolter 2014). However, it is difficult to infer the drivers behind the choice of an individual fish to remain near the tributary mouth or to move away with only position and movement data and no available information describing competitive interactions or food resources during winter.

During the spawning season (mid-May to early June), stream reaches predicted to contain optimally sized spawning substrates (15–25 mm), higher sinuosity, larger MAFs, and lower gradients were selected by Rainbow Trout. Substrate size is important for spawning salmonid habitat because the size of particles dictates the ability for dissolved oxygen to flow through interstitial space to embedded eggs and alevin and for waste (e.g., CO₂) to be carried away (Olsson and Persson 1988; Kondolf and Wolman 1993; Falke et al. 2013). Flow and gradient are likely important to Rainbow Trout year-round, as evidenced by the inclusion of these variables in the top RSF models for each season. Fish seek out habitats with velocities that minimize energy expenditure but adequately deliver drifting food items to juveniles and adults (Bisson et al. 1988; Cram et al. 2013). Tributary fidelity was lowest for all the tributaries during the spawning season, suggesting possible intertributary mating within the Susitna River basin. While this would need to be confirmed through further genetic analysis, intertributary mating was observed in three Rainbow Trout tagged in Willow Creek in 2013 (Fraley 2015). Movements were longest between overwintering and spawning habitats, likely because reaches with geomorphic attributes that promote adequate spawning substrate size and upwellings are located farther away from the main stem up smaller tributaries (an example of habitat complementation; White and Rahel 2008; Falke et al. 2013).

Habitat selection during the early feeding season (before the arrival of spawning salmonids, mid-June to mid-July) included reaches with lower gradient and sinuosity and higher flows. Flow was the only covariate with a confidence interval not overlapping zero, and as previously mentioned, is likely important for fish during all seasons. The lack of strong habitat selection observed during this season is undoubtedly a result of a generalist feeding strategy that Rainbow Trout are known to employ postspawning in which they opportunistically feed on aquatic and terrestrial invertebrates, out-migrating juvenile salmonids, and even small mammals (Scheuerell et al. 2007; Lisi et al. 2014). Relative to subsidies provided by spawning salmonids, these food sources are not necessarily concentrated in particular stream reaches within a drainage, so Rainbow Trout are distributed more widely and habitat use is more likely to be driven by intraspecific competition rather than physical habitat characteristics (Hughes 1998; Alanärä et al.

2001). Movements between spawning and early feeding habitats were the second shortest, on average, indicating that spawning and feeding habitats were in closer proximity than spawning and overwintering habitats. This may be due to fish attempting to conserve energy after engaging in energetically demanding spawning activity during the previous weeks.

During the late feeding season (after the arrival of spawning salmonids, late July through early September), Rainbow Trout were more likely to select smaller, sinuous, high-gradient stream reaches with high Chinook Salmon spawning habitat potential (intrinsic potential). This was likely owing to the propensity for Rainbow Trout to concentrate near spawning salmonid aggregations to gorge on drifting eggs and sloughed salmonid flesh to maximize energy intake critical for overwinter survival (Bartlett and Hansen 2000). This phenomenon is also seen in other regions of Alaska, where observed diets of Rainbow Trout and Dolly Varden *Salvelinus malma* have been comprised of up to 80–90% Pacific salmon eggs and flesh during this season (Eastman 1996; Scheuerell et al. 2007; Rinella et al. 2011; Armstrong and Bond 2013). Pacific salmon eggs are estimated to contain roughly 4,500 cal/g of wet weight (although the measure of this value is highly variable within and among species), which is approximately 15% higher than aquatic or terrestrial invertebrates (Eastman 1996; Armstrong 2010). Flesh contains less energy than both eggs and invertebrate prey (only 645 cal/g wet weight; Eastman 1996), but it is abundant and easy to ingest. Interestingly, fidelity to tributary of capture was highest in most tributaries during the late feeding season, perhaps owing to the high abundance of salmonid-derived food. It is possible that Rainbow Trout showed higher fidelity simply because these areas were where they had been captured the previous year (Sell et al. 2014), yet in a related analysis we found that they selected for habitats with the presence of spawning salmonids (Fraley 2015). Fish were more likely to return to the tributary of capture to feed than to spawn, suggesting that feeding habitats within a tributary are highly abundant and not density limited, whereas spawning habitats are less abundant and may be density limited. During this season Rainbow Trout follow the food source of highest abundance and caloric content, and their habitat use is well predicted by characteristics that describe high-quality salmonid spawning habitat potential (i.e., CHINIP).

We assumed that the variables with which we parameterized our Rainbow Trout RSF models and which were derived from existing models and developed for similar rivers in the Pacific Northwest were applicable to our study area in Alaska. Moreover, although coarsely measured, we assumed these variables to be biologically meaningful although they do not capture fine-scale microhabitat use. As such, we believe our approach was adequate for stream networks in Alaska, including the Susitna River basin.

Sex Bias

We found no evidence of sex-biased annual or interseasonal movements in the 2013–2014 Willow Creek Rainbow Trout sample, contrary to our hypothesis and findings from other salmonids (e.g., Neville et al. 2006). However, there was a significant difference in abundance between males and females. This may be a result of sampling bias rather than a true reflection of the population. Males were found to exhibit a lower prevalence of hooking scars than females, which could indicate males are less susceptible to angling and might explain the skewed sex ratio. If the population truly is female biased as we observed, this would be similar to some other populations of steelhead (anadromous Rainbow Trout) along the West Coast of the USA (56–76% female; Ohms et al. 2013). It is unclear why the sex ratio may be biased towards females in the nonanadromous Susitna River basin population, but it may suggest that males have higher mortality rates than females in early life stages since juvenile *O. mykiss* are thought to exhibit a 1:1 ratio (Ohms et al. 2013) or that more females skip spawning each year leading to an (closer to) equal sex ratio on the spawning grounds.

Implications

Rainbow Trout are an important native sport fish in the Susitna River basin and are carefully managed to maintain healthy populations. The results of this study show that Rainbow Trout use a wide variety of habitats throughout the Susitna River basin during different seasons and that there is evidence for a basinwide metapopulation (Falke and Fausch 2010). A metapopulation typically consists of habitat patches that harbor local populations (i.e., tributaries), and dispersal and movement between these patches reduce the risk of extinction of any local population by allowing recolonization following disturbance events or years of no recruitment. Thus, the Kashwitna River subpopulation may be an important vector of gene flow in the basin owing to the prevalence of long-distance and out-of-tributary movements by fish from this drainage (average TAM, ISM, and DFC were significantly higher). However, we cannot conclude that gene flow is actually occurring without capturing or observing migrants from this tributary during the spawning season. High tributary fidelity in Willow, Montana, and Chuniilna creeks suggests that there is an abundance of quality seasonal habitats available for Rainbow Trout in these drainages.

Owing to potential metapopulation dynamics in the Susitna River basin, it is critical to manage Rainbow Trout at a basin-wide scale and maintain riverscape connectivity in order to account for the migratory nature of these fish. The Alaska Department of Fish and Game Rainbow Trout management approach has evolved over the last several decades, with recent emphasis on conservative harvest limits and catch-and-release angling in order to promote healthy populations and trophy fisheries (Bartlett and Hansen 2000). The effect of heavy catch-and-release angling, as evidenced by the presence

of hooking scars on about one-third of all captured fish, may increase stress, cause exhaustion, and result in higher risk of mortality (although fish with hooking scars in our study were not found to have significantly higher rates of mortality; see Appendix).

Additionally, the dependence of Rainbow Trout on salmonid-derived food items to gain adequate energy to survive winter highlights the importance of maintaining healthy Susitna River salmonid runs (Scheuerell et al. 2007). This is particularly important because Chinook Salmon runs have not met escapement goals in the upper Cook Inlet in several recent years (Munro and Volk 2014). Also, the majority of Rainbow Trout from our study occupied main-stem and slough habitats of the middle and lower Susitna River during the lengthy overwintering period. Thus, we conclude that it is necessary to identify the importance of channel size and the number of slough habitats before any changes are made that would reduce the preferred winter habitat. It will be vital to manage the Susitna River basin Rainbow Trout populations at a broad scale in light of anticipated land-use changes.

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ORCID

Kevin M. Fraley  <http://orcid.org/0000-0001-5068-5616>

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Appendix: Sources of Mortality of Radio-Tagged Rainbow Trout

Logistic models explaining initial posttagging mortality or tag expulsion were constructed in R (R Development Core Team 2012), with model covariates including tagging year (2003 and 2013–2014), fork length (mm), tributary (Chunilna Creek, Montana Creek, Kashwitna River, Willow Creek), and presence of hooking scars. The AIC_c model selection was used to identify the top models (AIC_c weight > 0.05; Table A.1), and top models were averaged using the $AIC_{cmodavg}$ package to generate 95% confidence intervals for levels of each parameter (Table A.2).

The cumulative mortality of telemetry-tagged fish was similar across the tributaries of capture and between 2004 and 2014

samples (see Figure A.1). Annual mortality could not be assessed for the Willow Creek sample tagged in 2014 because fish were not tracked for an entire year. Annual mortality ranged from 51% in the 2004 Kashwitna River Rainbow Trout to 75% in the 2013 Willow Creek fish. Initial posttagging mortality or tag rejection was observed in 16.2% of the 2004 Kashwitna sample and in 54.5% of the 2013 Willow Creek sample, and correlations were analyzed for $N = 232$ fish from all tributaries and all years using logistic regression models (Table A.1). Top models from AIC_c model selection (AIC_c weight > 0.05) included “year,” “tributary,” “hooking scars,” and “fork length” as potential predictors of initial mortality or tag rejection; however, only the “year”

TABLE A.1. Summary of logistic model selection statistics explaining initial posttagging mortality or tag expulsion for Susitna River basin Rainbow Trout. Covariates include the tagging year, fork length (mm), tributary (Chunilna Creek, Montana Creek, Kashwitna River, Willow Creek), and presence of hooking scars (yes or no). There were 232 fish that were included in this analysis. Abbreviations are as follows: L-L = the log-likelihood; ΔAIC_c = the difference in the corrected Akaike information criterion (AIC_c) value for a particular model compared with the top-ranked model; K = the number of parameters, including the intercept and residual variance; and w_i = Akaike weight.

Model	L-L	AIC_c	ΔAIC_c	w_i	K
Year	-137.41	278.87	0.00	0.48	2
Year, hooking scars	-137.21	280.52	1.66	0.21	3
Year, fork length	-137.36	280.83	1.96	0.18	3
Year, tributary	-135.87	282.00	3.13	0.10	5
Year, tributary, hooking scars, fork length (global model)	-135.34	285.17	6.30	0.02	7
Tributary	-139.55	287.28	8.42	0.01	4
Tributary, fork length	-139.41	289.08	10.21	<0.01	5
Tributary, hooking scars	-139.54	289.34	10.47	<0.01	5
Hooking scars	-142.73	289.51	10.64	<0.01	2
Fork length	-142.75	289.55	10.68	<0.01	2
Hooking scars, fork length	-142.58	291.27	12.40	<0.01	3

TABLE A.2. Standardized model-averaged parameter estimates, unconditional standard errors (SE), and 95% confidence limits (CLs) for covariates predicting initial posttagging mortality or tag expulsion for Susitna River basin Rainbow Trout. Estimates are derived from the top models examined in Table A.1 with $w_i > 0.05$ (year, tributary; global; year; and tributary models).

Covariate	Parameter estimate	SE	Lower 95% CL	Upper 95% CL
Year	0.10	0.03	0.04	0.16
Hooking scars	-0.20	0.33	-0.84	0.44
Fork length	0.00	0.00	-0.01	0.01
Chunilna Creek (intercept)	-194.70	63.05	-318.28	-71.13
Montana Creek	0.40	0.52	-0.62	1.42
Kashwitna River	-0.51	0.59	-1.66	0.65
Willow Creek	-0.29	0.56	-1.39	0.81

covariate and the Chunilna Creek sample had 95% confidence intervals that did not overlap zero (Table A.2). “Year” was likely a significant factor in posttagging mortality or tag rejection

because of a higher initial mortality rate in the 2013 Willow Creek sample. It is unknown why Chunilna Creek fish had different initial mortality than the other tributaries.

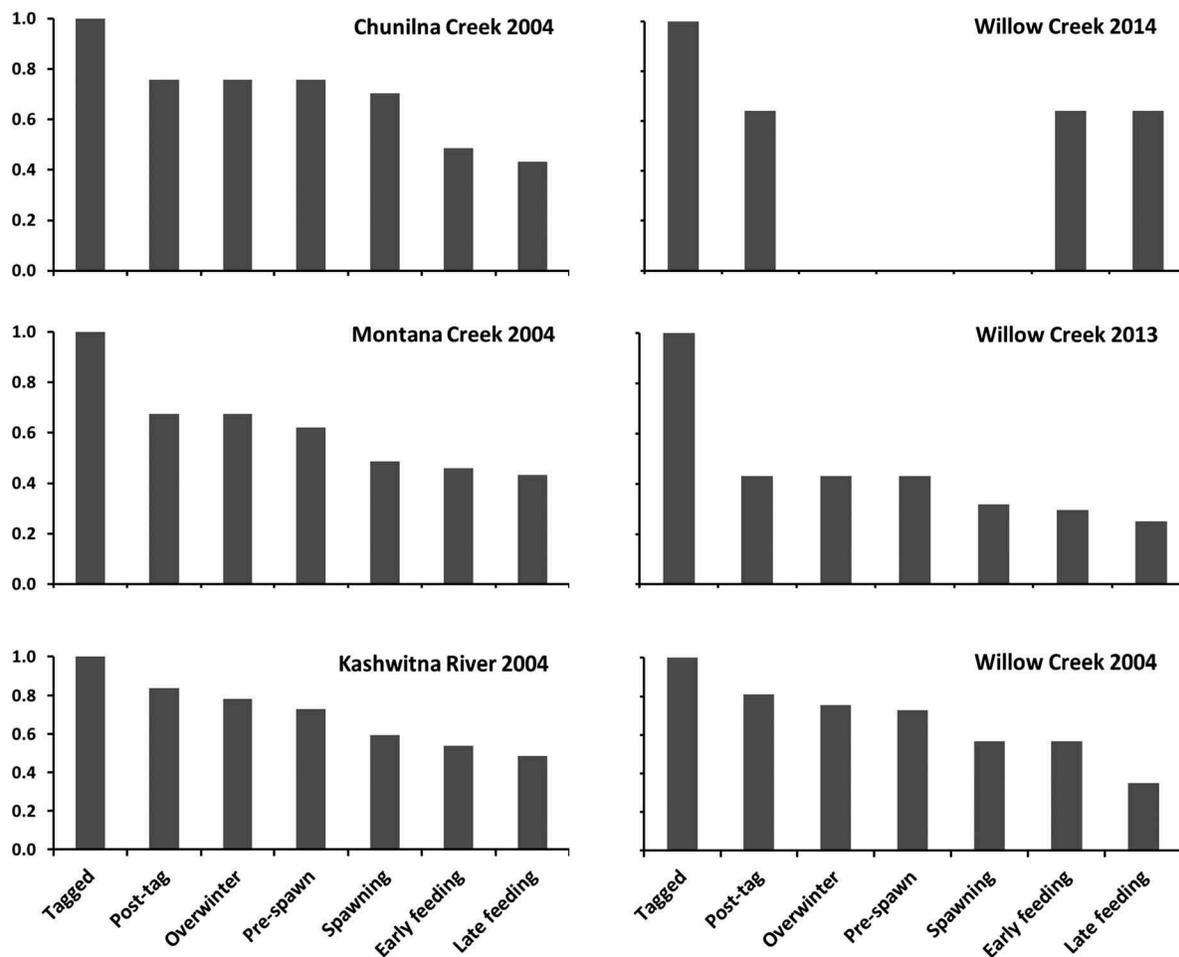


FIGURE A.1. Annual survival of radio-tagged Rainbow Trout from Chunilna Creek in 2004 ($N = 37$), Willow Creek in 2014 ($N = 39$), Montana Creek in 2004 ($N = 37$), Willow Creek in 2013 ($N = 44$), Kashwitna River in 2004 ($N = 37$), and Willow Creek in 2004 ($N = 37$). The asterisk indicates that fish were tagged in Willow Creek in 2014 during the early and late feeding seasons, thus mortality information for overwintering, prespawning, and spawning seasons is not available.

Annual cumulative mortality of Rainbow Trout tagged for this project (51–75%) was similar to other Rainbow Trout telemetry studies in Alaska. Other projects on the Gulkana River (central Alaska), Alagnak River (southwestern Alaska), and the Aniak River (western Alaska) found annual mortality from 35.1% to 71.2% (Schwanke 2002; Meka et al. 2003; Fleming 2004; Schwanke and Thalhauser 2011). In surgically implanted tagging studies, it is difficult to identify sources of perceived mortality in the sample because fish are not visually observed. In the Susitna River basin, natural mortality likely accounted for a significant proportion of the total mortality and may have included predation, starvation, senescence, harsh environmental conditions, and accidents. Predation was observed in dramatic fashion in Willow Creek when a 2013-tagged fish that was observed alive was tracked a week later to the nest of a bald eagle *Haliaeetus leucocephalus* ~0.5 km inland from Willow Creek. Additionally, the lack of food, long duration, harsh temperatures, and dynamic river ice conditions during the overwintering season in the main-stem Susitna and Talkeetna rivers, where fish overwinter, may have contributed to annual mortality. Postspawning deaths were also prevalent, particularly in Willow Creek in 2014 where 33.3% ($N = 12$) of fish that spawned died afterwards, likely due to physically stressful redd building, intrasexual competition, and redd defense during which Rainbow Trout typically do not feed.

Human harvest may also play a role in mortality in the Susitna River basin. Rainbow Trout angling is catch and release only in Montana Creek, Willow Creek, and the Kashwitna River above the Parks Highway Bridge. Other Susitna tributaries (including Kashwitna and ChuniIna creeks) allow harvest of two fish per day, although there is an annual limit of only two fish greater than 20 inches per angler. Both legal and illicit harvest of adult fish occurs. Legal harvest of Rainbow Trout in the Susitna River basin averaged 2,032 fish/year from 2000 to 2010 (Jennings et al. 2011). Illegal harvest was reported by anglers in the Susitna River basin and was observed firsthand by our crew in Willow Creek in 2014 (an angler killed and retained a Rainbow Trout > 400 mm in our presence), although the prevalence and magnitude of this is unknown. Furthermore, a 2013 Willow Creek fish expired under circumstances that may have been an instance of illegal human harvest. One week after being confirmed alive in Little Willow Creek, the bare telemetry tag from the fish was found lying on a sandbar along Deception Creek, with only human footprints nearby (no carcass or bird or bear activity in the vicinity). Finally, initial mortality (16–54%) contributed to total

mortality, although it is unknown what proportion of post-surgery mortality was due to tag rejection or true mortality. Tag rejection, or the expulsion of a surgically implanted tag by the fish, has been documented previously, and a laboratory study found that tag expulsion occurred in up to 25% of internally tagged Rainbow Trout (Ivasauskas et al. 2012). Tag expulsion typically occurs 25–35 d after surgery, and fish that expelled tags exhibited a 100% survival rate in a lab study. Surgical procedure, surgical skill, and water temperature likely influence postsurgery mortality and tag rejection. The sample of fish tagged in 2013 in Willow Creek had higher posttagging mortality compared with other years and tributaries, likely due to warmer water temperatures causing higher stress in fish undergoing surgery and the crew's burgeoning surgical aptitude. Posttagging mortality and tag rejection was found to be different between tagging years and tributaries (ChuniIna Creek had lower mortality than others), but fish fork length and the presence or absence of hooking scars was not different between fish that survived and those that expired.

APPENDIX REFERENCES

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