U.S. Fish & Wildlife Service

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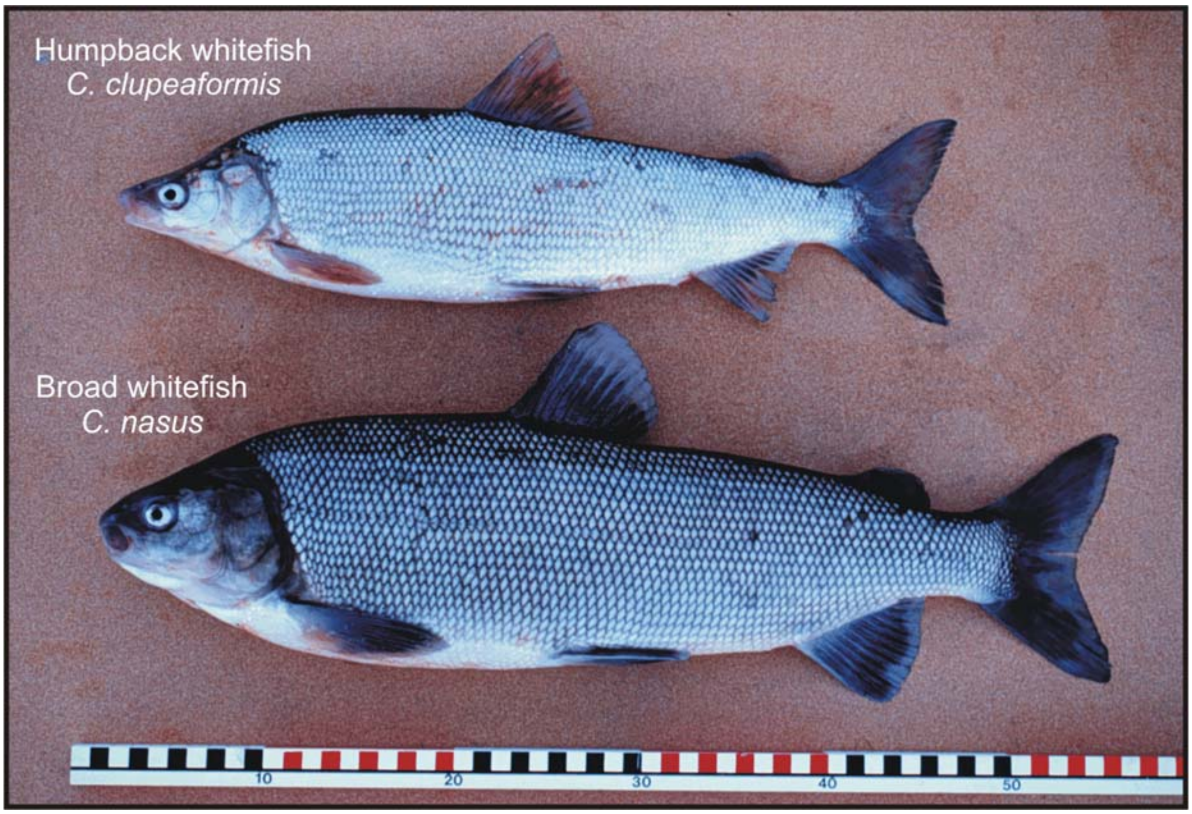
Alaska Fisheries Technical Report Number 104



Fairbanks Fish and Wildlife Field Office
Fairbanks, Alaska
August 2009

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Distributions and Demographics of Whitefish Species in the Upper Koyukuk River Drainage, Alaska, with Emphasis on Seasonal Migrations and Important Habitats of Broad Whitefish and Humpback Whitefish

Randy J. Brown

Abstract

Five whitefish species have been identified in the upper Koyukuk River drainage in the northern interior of Alaska. They include inconnu *Stenodus leucichthys* (sheefish), broad whitefish *Coregonus nasus*, humpback whitefish *C. clupeaformis*, least cisco *C. sardinella*, and round whitefish *Prosopium cylindraceum*. Whitefish species are important components of the regional subsistence economy where they make up more than 85% of the non-salmon fish harvests drainage-wide. They are harvested in many of the rivers and lakes of the upper Koyukuk River drainage during all seasons of the year. Tagging and otolith chemistry studies have shown that anadromy is a common life history strategy for most whitefish species in the upper Koyukuk River drainage. Sampling data and traditional knowledge accounts suggest that the Alatna River is a spawning destination for several species. Despite this wealth of general knowledge, neither species distribution within the upper Koyukuk River drainage nor the demographics of whitefish populations in the region have been documented. Spawning habitats other than the Alatna River have not been identified and seasonal migrations among lake and riverine habitats in the region are poorly understood. In this study, six lake and river habitat regions were sampled during spring and fall to describe the geographic distribution of species in the upper Koyukuk River drainage and to document the demographic qualities of sampled fish. Broad whitefish and humpback whitefish, the two primary species taken in local fisheries, were radio tagged in two tributary drainages to identify their spawning, overwintering, and feeding habitats, and to describe their seasonal migrations among these habitats. Whitefish of all species except round whitefish were found to be predominantly mature individuals. Immature fish were very uncommon. Inconnu were only encountered in fall and early winter in the main-stem Koyukuk and Alatna rivers. Broad whitefish were encountered in most sampled habitats but were only common in main-stem Koyukuk and Alatna River habitats during late fall and winter, and in Kanuti River lake habitats during summer. Humpback whitefish were common in all sampled habitats. Least cisco were encountered in all sampled habitats but were only common in main-stem Koyukuk and Alatna River habitats during fall, and in Kanuti River lake habitats during summer. Most broad whitefish and humpback whitefish overwintered in river rather than lake habitats. Sampling and radio telemetry data confirmed that all four of these species used spawning habitats in the Alatna River, which appeared to be the only spawning habitat used by inconnu and broad whitefish. Additional humpback whitefish spawning habitats were identified with radio telemetry in the Kanuti and South Fork Koyukuk rivers and least cisco were found spawning with humpback whitefish in the Kanuti River. These sampling and radio telemetry data suggest that after broad whitefish and humpback whitefish migrate from downstream rearing habitats to the upper Koyukuk River drainage to spawn, they remain in the upper drainage, feeding in lakes during summer, spawning in gravel-substrate river habitats during late fall, and overwintering primarily in rivers.

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Introduction

Six whitefish species (Family: Salmonidae, Subfamily: Coregoninae) are present in the Yukon River drainage in Alaska, five of which have been documented in the Koyukuk River drainage, a major tributary of the Yukon River (Brown et al. 2007; Figure 1). Inconnu *Stenodus leucichthys* (sheefish), broad whitefish *Coregonus nasus*, and humpback whitefish *C. clupeaformis* (the taxonomy of humpback whitefish follows the recommendations of McDermid et al. 2007) are relatively large (1 kg or greater mature weight) and are actively sought in subsistence fisheries in the region (Andersen et al. 2004). Least cisco *C. sardinella* and round whitefish *Prosopium cylindraceum* are relatively small (~0.3-1.0 kg mature weight) and are minor components of the fishery. Bering cisco *C. laurettae* are present in the Yukon River drainage (Alt 1973) but are thought to remain in main-stem habitats and have not been identified in tributary systems (Brown et al. 2007).

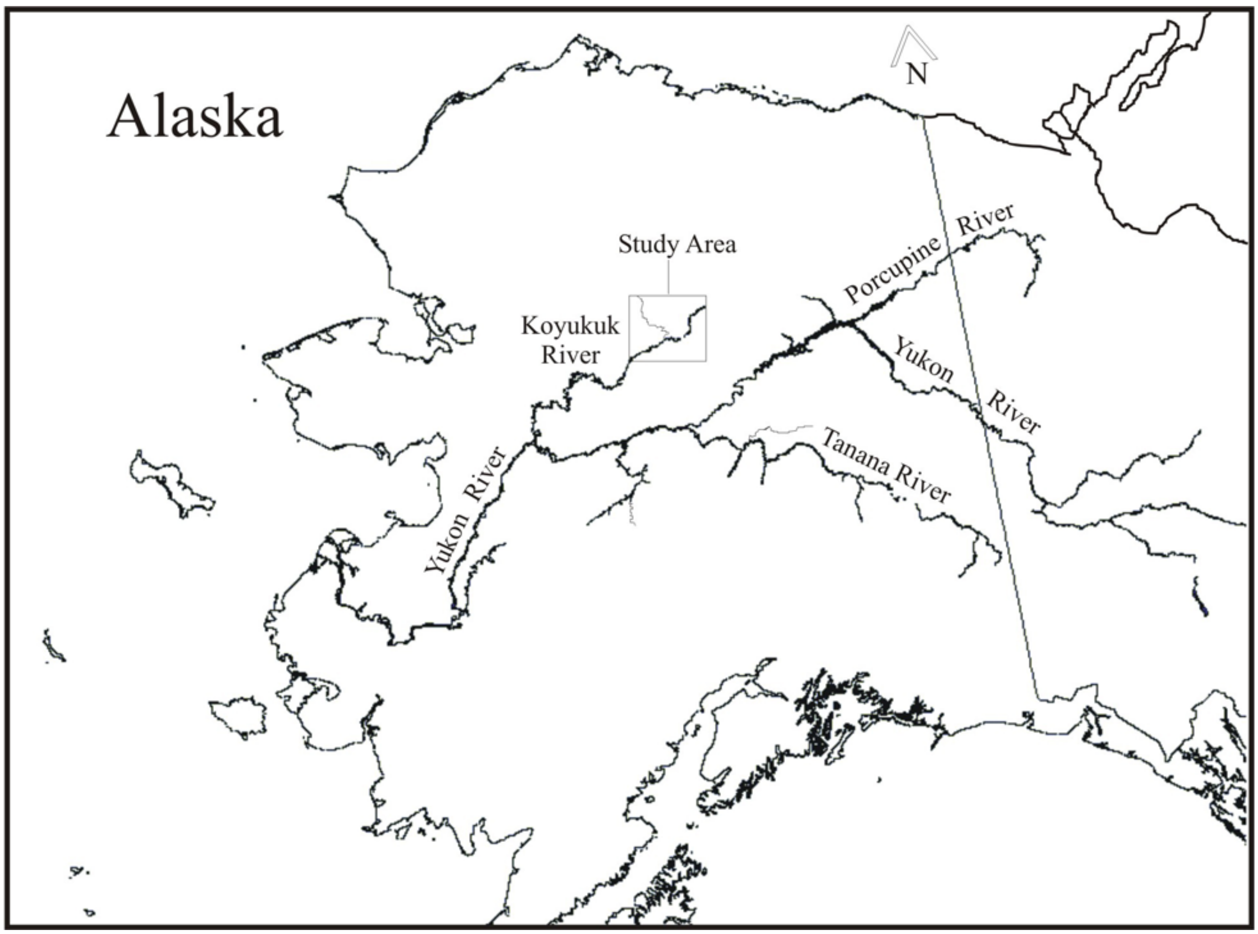

Figure 1. The Yukon River and its major tributaries in Alaska. Field activities for this project took place in the upper Koyukuk River drainage in northern interior Alaska.

Salmon *Oncorhynchus* spp. spawning migrations into the upper Koyukuk River drainage are not as strong or dependable as they are along the Yukon River mainstem (Hayes et al. 2008). As a result, residents of the region depend heavily on whitefish resources for human and dog food (Marcotte and Haynes 1985; Andersen et al. 2004). Andersen et al. (2004) reported Koyukuk drainage harvests during 2002 of approximately 11,000 kg each of broad whitefish (about 6,500 fish) and humpback whitefish (about 8,000 fish), which represented more than 57% of all non-salmon species harvested by weight. It was further explained that fishing effort in the region was compensatory in that when salmon were more available, fewer whitefish were sought, and when salmon were less available, more whitefish were sought. The historical background provided by Andersen et al. (2004) suggested that whitefish have always been an important food source for people in the upper Koyukuk River drainage.

Riverine whitefish species share many life history characteristics. They spawn in the fall, broadcasting their eggs in flowing water over a gravel substrate (McPhail and Lindsey 1970; Morrow 1980). The eggs develop during the winter and larvae emerge into the water column in the spring just as the winter snow melts and river flow rises (Naesje et al. 1986; Shestakov 1991; Bogdanov et al. 1992). The emerging larvae are distributed downstream into a wide range of feeding habitats that include off-channel ponds, sloughs, and estuaries (Shestakov 1992). Immature whitefish rear for several years in these habitats until maturity, at which time they migrate back upstream to spawn (Reist and Bond 1988). In general, whitefish survive spawning and some species may live for 30 years or more, spawning multiple times.

Important habitats required to sustain whitefish populations include spawning, rearing, feeding, and overwintering. Spawning habitats are considered to be the most critical for Yukon River populations because they are singular geographic regions, often occupying a reach only a few km long, where a large fraction of a population concentrates each fall. By contrast, there are many locations used for rearing, feeding, and overwintering that are distributed over the entire range of the population (e.g., Brown 2000, 2006). Disturbing a spawning area by mining the gravel substrate, for example, could destroy a population (Meng and Müller 1988; Brown et al. 1998), while disturbing a rearing channel, feeding lake, or overwintering reach used by members of the population might impact those individuals but would not destroy the entire population.

Tagging and otolith chemistry studies have shown that four whitefish species found in the upper Koyukuk River drainage rear in habitats as far away as the mouth of the Yukon River, approximately 1,600 km downstream. Alt (1977) tagged inconnu in the Yukon delta and recaptured some of them in the Alatna River, demonstrating that there was a migration between the two sites. Based on a maturity assessment, Alt (1970) determined that inconnu migrated to the Alatna River to spawn. Brown et al. (2007) analyzed otolith strontium (Sr) levels in samples of inconnu, broad whitefish, humpback whitefish, and least cisco captured in the upper Koyukuk River drainage. Elevated Sr levels in the otoliths of many of the sampled fish indicated that anadromy was a common strategy for all four species. Most inconnu, broad whitefish, and humpback whitefish, and some least cisco that were tested had reared in marine water. These data clearly established that these populations ranged widely though the drainage.

Andersen et al. (2004) surveyed fishing families in Koyukuk River communities as far upstream as the paired communities of Bettles and Evansville (Figure 2). All communities downstream from Bettles and Evansville reported substantial harvests of whitefish species while Bettles and Evansville did not. It was further suggested that the few whitefish that were reported in Bettles and Evansville may have been captured downstream or in other drainage systems because whitefish other than round whitefish were not known to occur that far upstream. It was clear from these reports that whitefish spawning habitats were downstream from the communities of Bettles and Evansville.

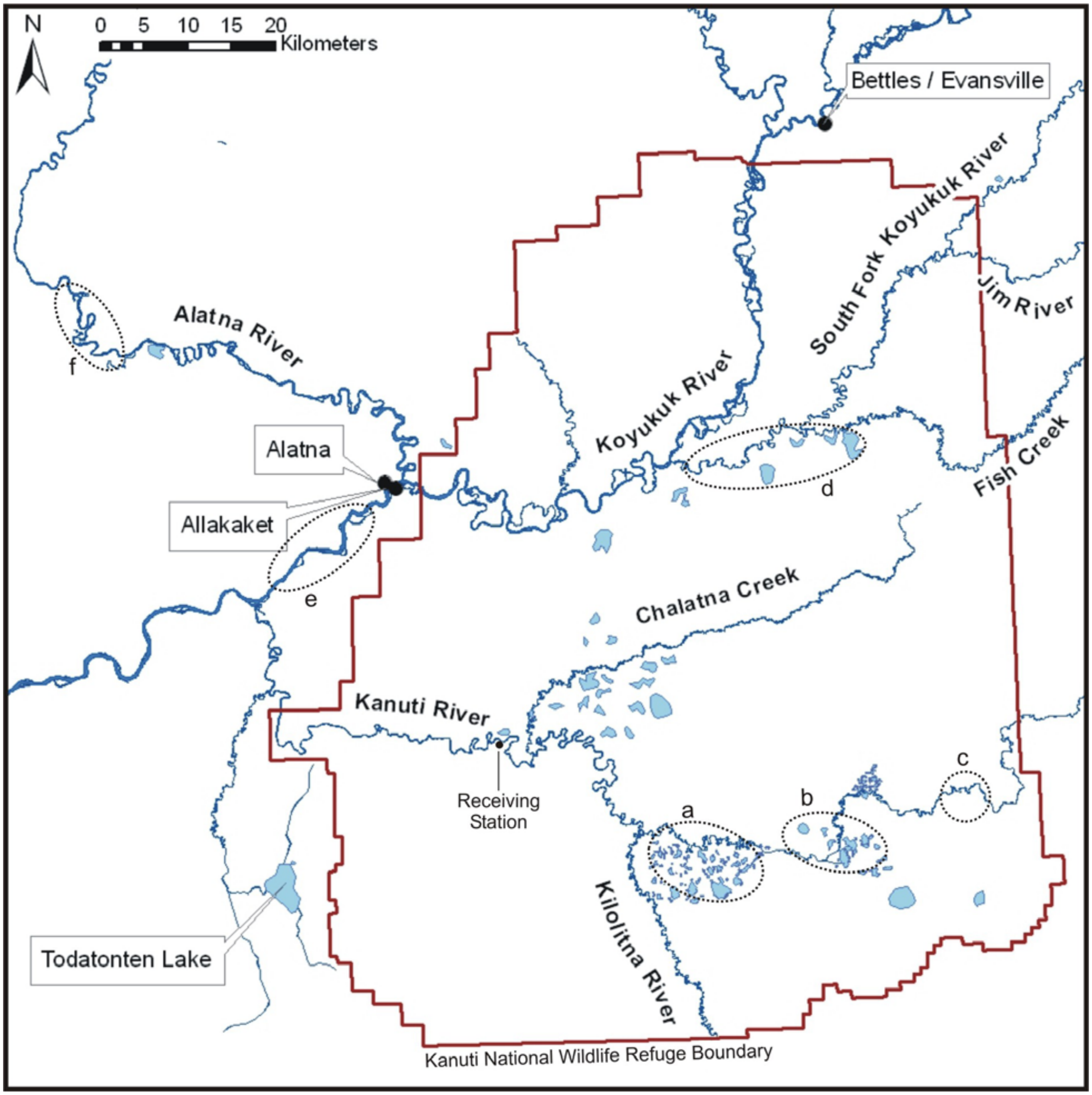

Figure 2. The study area within the upper Koyukuk River drainage with major tributaries, communities, and other landscape features identified. Sampling and radio tagging activities took place in lake and river habitats indicated with dashed ellipses. Spring sampling took place in the Kanuti and Mud lakes regions of the upper Kanuti River (ellipses a and b; 2003), and in lakes of the South Fork Koyukuk River (ellipse d; 2003), while fall sampling took place in the upper Kanuti River (ellipse c; 2005), the main-stem Koyukuk River (ellipse e; 2003), and in the spawning region of the Alatna River (ellipse f; 2003). Radio tagging took place in the Kanuti and Mud lakes regions (ellipses a and b; spring 2004), in lakes of the South Fork Koyukuk River (ellipse d; spring 2005), and in the upper Kanuti River (ellipse c; fall 2005).

Alt (1977) had previously identified inconnu spawning habitat approximately 80 km up the Alatna River, a major tributary of the Koyukuk River downstream from Bettles and Evansville. Residents of Allakaket have traditionally used beach seines to harvest large numbers of whitefish of several species at fall fishing sites on the Alatna River (Andersen et al. 2004; Andersen 2007), which are in the inconnu spawning area identified by Alt (1977). Females of all species harvested during the fall fishery were reportedly heavy with eggs (Andersen 2007) indicating they were preparing to spawn. These sampling and harvest data indicated that the Alatna River was a major spawning destination for whitefish species in the upper Koyukuk River drainage.

Whitefish species also occur in the Kanuti and South Fork Koyukuk River drainages (Glesne 1986), where traditional subsistence fisheries take place during the spring and summer (Andersen 2007) when whitefish species are typically feeding (Alt 1979; Reist and Bond 1988; Brown 2006). Prior to this investigation, neither species distribution among tributaries of the upper Koyukuk River nor demographic composition of whitefish in the region had been described. Additionally, aside from the whitefish spawning area in the Alatna River, no other spawning habitats had been identified.

This study was conducted to improve our understanding of whitefish species in the upper Koyukuk River region. Primary objectives were to describe the geographic distributions and demographic qualities of whitefish sampled in a selection of lake and river habitats of the upper Koyukuk River drainage, and to locate spawning habitats for broad whitefish and humpback whitefish, the major non-salmon species harvested by residents in the region (Andersen et al. 2004). Secondary objectives were to identify feeding and overwintering habitats used by broad whitefish and humpback whitefish and to describe the timing of their seasonal migrations among habitats. With this information, whitefish populations could be monitored, which could lead to effective harvest management, and essential habitats and migratory routes could be protected from disturbance due to development activities.

Study Area

The Koyukuk River is a major tributary of the Yukon River in the northern interior of Alaska (Figure 1). It drains an area of approximately 91,000 km^2, with an average annual discharge of 770 $m^3 \cdot s^{-1}$, which is approximately 12% of the discharge from the entire Yukon River (Brabets et al. 2000). The Koyukuk River drainage lies within the boreal forest ecological region (Hultén 1968) and experiences a continental climate (Shulski and Wendler 2007). Annual temperature extremes may range from -50°C or colder in the winter to +30°C or warmer in the summer. Annual precipitation is generally between 20 and 40 cm. Freezing temperatures prevail in the drainage from October through April and rivers and lakes are generally ice-free from late May through September.

Activities associated with this project were focused on the lakes and rivers of the Kanuti National Wildlife Refuge (NWR) and nearby drainages (Figure 2). The Kanuti NWR encompasses over 5,000 km^2 in the middle Koyukuk River drainage, including substantial lowland regions of the Kanuti and South Fork Koyukuk rivers (USFWS 1993). Lowlands in the Kanuti River extend for approximately 50 km in an east-west direction, from the Mud Lakes area (Figure 2, ellipse b) to the mouth of Chalatna Creek, and approximately 50 km in a north-south direction, from upper Chalatna Creek to the lower reaches of the Kilolitna River. It is a region of slow, meandering, soft-substrate river channels with numerous lakes, many of which are seasonally connected to the river. Most of the lakes in the Kanuti River flats are shallow thaw ponds from 1- to 3-m deep (Glesne 1986; USFWS 1993). Lowlands in the South Fork Koyukuk River (Figure 2, ellipse d) encompass a smaller area, extending approximately 25 km in an east-west direction and 15 km in a north-south direction. The rivers flow swiftly over gravel and sand substrate through these lowlands and many of the connected lake systems are oxbow lakes. The

Alatna River lies outside the Kanuti NWR but figures prominently in the life histories of whitefish species (Alt 1977) and traditional fisheries (Andersen et al. 2004; Andersen 2007) in the region. The Alatna River flows swiftly over gravel and sand substrate with comparatively few connected lakes within the lower 150 km. The main-stem Koyukuk River provides a conduit for fish to move among the regional lakes and rivers and to other aquatic systems.

Methods

Distribution and demographic sampling

Whitefish species were sampled between 2003 and 2005 in lake and oxbow habitats of the Kanuti and South Fork Koyukuk River drainages during spring, and in the mainstem Koyukuk River between the mouths of the Kanuti and Alatna rivers, and in the upper Kanuti River during fall (Figure 2). Sampling was conducted with monofilament gillnets and with small mesh beach seines. Gillnets were 15 m long and 2 m deep. Individual gillnets were hung with either 5- or 10-cm stretch-mesh web, and both were fished in all sampling locations. Based on net selectivity models developed for Pacific salmon and whitefish species in the Yukon River (Bromaghin 2005), these two mesh sizes were considered to be optimal for fish ranging from about 20–50 cm fork length. These nets were therefore capable of capturing both juvenile and mature size individuals of all whitefish species; mature inconnu being an exception. Spring sampling was systematic in that many lake and oxbow habitats were sampled in the South Fork Koyukuk (n = 17) and Kanuti River (n = 19) drainages in an effort to identify all species and demographic groups present. The purpose of fall sampling in the main-stem Koyukuk and upper Kanuti rivers was to identify all species that were migrating upstream to spawn or were present in spawning habitats, and to verify maturity and spawning condition of captured fish. In addition to directed sampling activities, a limited number of samples were obtained by request from the subsistence fishery on the Alatna River during late fall to verify species harvested. The Alatna River samples consisted of 15 heads (from behind the gill plates forward) of each recognizable whitefish form harvested.

All fish captured were identified to species, measured to the nearest 0.5 cm fork length (length), weighed whole to the nearest 1 g for fish <1,000 g total weight and to the nearest 10 g for fish ≥1,000 g total weight. The egg skeins of females were weighed to the nearest 1 g. Egg skeins of female whitefish preparing to spawn increase in mass beginning in mid-summer and are dramatically larger than those of non-spawning females by fall (Lambert and Dodson 1990) (Figure 3). A gonadosomatic index calculated as:

$$\text{GSI} = (\text{egg weight} \cdot \text{whole body weight}^{-1}) \cdot 100,$$

was used to classify fall-caught female fish as either non-spawning (GSI <3) or preparing to spawn (GSI >3), based on criteria presented by Brown (2004). Whitefish species migrating to spawn are usually reported to be fasting rather than feeding (Alt 1969; Lambert and Dodson 1990; Brown 2000). Feeding condition can therefore be an indicator of spawning condition in fall-caught fish. The stomach of each male fish was examined and the feeding status was determined based on the presence (feeding) or absence (fasting) of food. Minimum ages at maturity have been reported for certain northern whitefish populations (e.g., Reist and Bond (1988) for species in the lower Mackenzie River and Brown (2000, 2004) for Yukon River inconnu and species in the Selawik River delta, respectively). Assuming similar development towards maturity for species in the upper Koyukuk River, these data can be used to determine the likely demographics of sampled fish based on age. Because some whitefish species are capable of living for 30 years or more, otoliths or fin rays are required for aging (Mills and Beamish 1980; Barnes and Power 1984; Howland et al. 2004). Sampled fish were sacrificed in this investigation so otoliths were collected for aging purposes. In preparation for age analyses, otoliths were thin-sectioned (sectioned) in the transverse plane through the core and mounted on a glass slide for microscopic viewing. Each otolith section was approximately 200 μm thick, and growth increments could be clearly viewed with transmitted light (Figure 4). Annuli identification criteria followed descriptions and illustrations in Chilton and Beamish (1982). These data, as detailed above, were used to describe the demographic composition of whitefish species from the upper Koyukuk River drainage.

Figure 3. Eggs skeins of female whitefish preparing to spawn (upper skeins) are dramatically larger in the fall than those of females that are not preparing to spawn (lower skeins). Scale bar is in cm.

Additional length, weight, and age samples were available from other sources as well. Length and weight data were collected from all fish involved in the radio telemetry component of the project, however, none of those fish were sacrificed so sex, age, and feeding condition data were not available. Samples of fish heads from four whitefish species harvested in the late fall subsistence fishery in the Alatna River were collected for species verification, age analyses, and maturity assessments. These samples provided species and age data only. In all, over 330 whitefish of five species were examined.

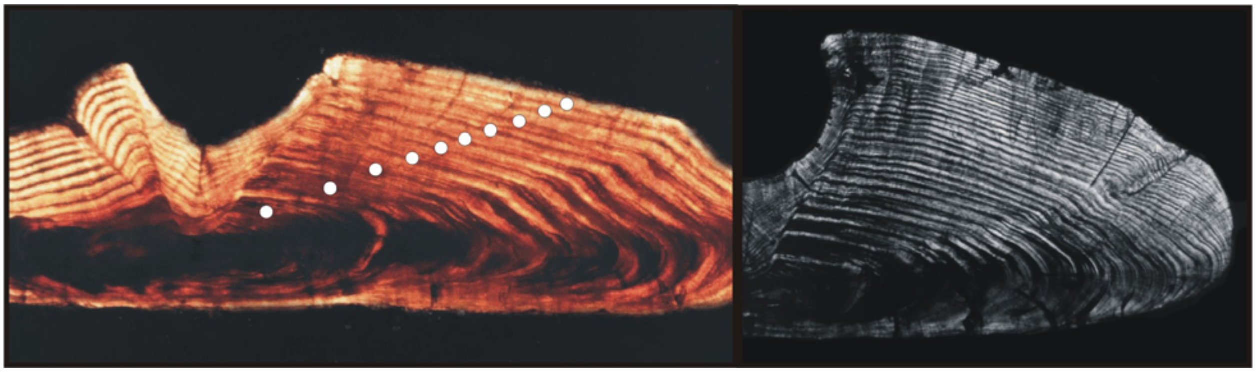

Figure 4. Otolith images illustrating the aging method used in this study. On the left is the otolith from an age-10 fish with white spots marking annuli. On the right is an image from an age-32 fish.

Radio telemetry

Broad whitefish and humpback whitefish were captured for tagging in lake and oxbow habitat in the upper Kanuti River drainage and in the lower South Fork Koyukuk River (Figure 2). Local residents, as reported by Andersen et al. (2004) and Andersen (2007), have identified both regions as important fishing areas for whitefish. Monofilament gill nets with 5-cm stretch mesh webbing and small mesh (2.5-cm stretch mesh) beach seines were utilized for fish capture. The gill nets were set and constantly monitored until fish became entangled, at which time they were removed, placed into a tub of water, and evaluated for tagging. The beach seine was only used in gravel substrate riverine habitats.

Mature fish were sought for tagging because the primary objective of the study was to identify spawning areas. Minimum length criteria were employed to maximize the probability of selecting mature candidates for tagging. Mature broad whitefish as small as 39 cm in length have been reported in the Mackenzie River delta (Tallman et al. 2002). In the Selawik and Yukon River drainages in Alaska, however, mature broad whitefish were reported to be at least 45 cm long (Alt 1976; Brown 2004). Mature humpback whitefish sampled from two populations within the Yukon River drainage were both reported to be at least 33 cm long (Fleming 1996; Brown 2006). Minimum length criteria for radio tagging candidates were therefore 45 cm for broad whitefish and 33 cm for humpback whitefish.

Radio transmitters were surgically implanted in broad whitefish and humpback whitefish during 2004 and 2005 using methods detailed by Brown (2006). Numerous aerial surveys were conducted to locate radio-tagged fish during the fall spawning period (late September and October), during the winter (November through April), and during the spring feeding season (May and June) during the 13 or 18 month life-spans of each group of transmitters. Location analyses were conducted with each fish to determine if sufficient movement had occurred between locations to know with certainty that fish were alive from one season to the next. Brown (2006) and Fleming (1996) evaluated the error of positions assigned during aerial surveys by obtaining repeat locations of stationary transmitters with known locations. Both investigations found that nearly all assigned positions were less than 1 km from known positions. Brown (2006) proposed that a difference of 2 km between aerial survey positions was a sufficient distance to be certain that fish movement had occurred, and thus, that a fish was alive between aerial surveys. In this study, survival was accepted if a fish had moved at least 2 km from a previous location. In addition to aerial survey data, a stationary receiver located on the

Kanuti River (see Figure 2) recorded the time and identification of fish migrating downstream and upstream past the site.

Most radio-tagged fish were captured in off-channel lake and oxbow habitats in the Kanuti and South Fork Koyukuk rivers during their spring feeding season. Tracking data from these fish during fall revealed spawning locations used by the feeding groups. Identification of spawning areas was based on late fall aggregations of radio-tagged fish in swiftly-flowing, gravel substrate regions of rivers, as characterized by McPhail and Lindsey (1970), Scott and Crossman (1973), and Morrow (1980). Previous fall sampling activities have shown that whitefish present in spawning habitats are virtually all preparing to spawn (e.g., Alt 1969; Brown 2000, 2006; Hander et al. 2008). The presence of radio-tagged fish in spawning habitats was therefore considered to be evidence of spawning.

Spawning proportion was estimated based on the binomial distribution as the number of tagged fish judged to have migrated to spawning habitats divided by the number of tagged fish known to be alive at that time. Overwintering habitats were identified based on fish locations during January and February. The proportion of fish exhibiting fidelity to feeding habitats was estimated based on the binomial distribution as the number of tagged fish that returned to the same lakes used the previous summer divided by the number of tagged fish known to be alive at that time. Most radio transmitters were programmed to last for 13 months, but, those deployed in the South Fork Koyukuk River during spring 2005 were programmed to transmit for approximately 18 months, which encompassed two spawning seasons. The proportion of fish spawning during two successive spawning seasons was estimated based on the binomial distribution as the number of tagged fish present in the spawning area on both years divided by the number of tagged fish that were present in the spawning area during the first year that were known to be alive during the second year. The proportion of fish surviving a full year following tagging was estimated based on the binomial distribution as the number of tagged fish known to be alive a year following tagging versus the total number of tagged fish. A small number of humpback whitefish were tagged during fall 2005 in a spawning area that was discovered in 2004 in the upper Kanuti River. Tracking data from these fish revealed their overwintering locations and feeding habitat distributions the next spring.

Confidence limits for binomial proportional estimates, at the $\alpha = 0.05$ level of precision, were determined using an iterative process such that the proportion of fish observed in an event was as close as possible to the upper 0.025 proportion of a low probability distribution without exceeding it, and as close as possible to the lower 0.025 proportion of a high probability distribution without going below it (e.g., Hander et al. 2008). Binomial probabilities were considered to two decimal places. Binomial probability distributions were calculated following Zar (1999) as:

$$P(X) = \frac{n!}{X!(n-X)!} p^X q^{n-X} ,$$

where: n = the number of fish in the sample,
X = the number of fish possessing quality 1,
$(n - X)$ = the number of fish possessing quality 2,
p = the probability of X,
$q = (1 - p)$, and
$P(X)$ = the estimated probability of selecting X fish in a sample of size n.

Qualities 1 and 2 were binomial pairs such as spawners versus non-spawners, those exhibiting fidelity to feeding habitats versus those not exhibiting fidelity, or those known to have spawned during two successive years versus those that that did not.

Results

Distribution and demographic sampling

Five whitefish species and two individuals of a hybrid form were captured during sampling activities in the upper Koyukuk River drainage between 2003 and 2005 (Table 1). Inconnu were only encountered in the mainstem Alatna River during late fall. Numerous broad whitefish were encountered in river-connected lake habitats in the Kanuti River drainage and in the mainstem Koyukuk and Alatna rivers. Broad whitefish were comparatively rare in the South Fork Koyukuk River drainage where only a single individual was encountered during two spring sampling events in the drainage. Humpback whitefish were common or abundant in all sampled habitats. Least cisco were common or abundant in all sampled habitats except in the South Fork Koyukuk River drainage, where they were comparatively rare. Round whitefish are reportedly captured at times during subsistence fishing activities in the upper Koyukuk River drainage, but never in large numbers (Andersen 2007). Only two were captured in sampling activities during this project, one each in the Kanuti and South Fork Koyukuk River drainages (Table 1). Two hybrid fish were captured in the Kanuti River during spring. Alt (1971) documented this hybrid form in the Chatanika River in another region of the Yukon River drainage. He proposed, based on general appearance, meristic counts, and morphological measurements, that it was a cross between inconnu and humpback whitefish. No Bering cisco were captured.

Table 1. Whitefish species captured during sampling activities between 2003 and 2005 in the Koyukuk, Alatna, Kanuti, and South Fork Koyukuk rivers. Samples from the Alatna River were requested from and provided by subsistence fishers from the village of Allakaket.

Species	Koyukuk	Alatna	Kanuti	South Fork	Total
Inconnu	0	15	0	0	15
Broad whitefish	0	15	22	1	38
Humpback whitefish	24	30	79	46	179
Least cisco	17	15	60	8	100
Round whitefish	0	0	1	1	2

Length and weight data were collected from broad whitefish (n = 23), humpback whitefish (n = 149), and least cisco (n = 85). Median length and weight of broad whitefish were 52.0 cm and 1,810 g, respectively (Figure 5). The sample ranged from 46.0 cm to 61.5 cm in length and 1,320 g to 3,220 g in weight, which are size ranges consistent with a mature demographic group (Alt 1976; Brown 2004). Median length and weight of humpback whitefish were 43.5 cm and 960 g respectively. The sample ranged from 22.5 cm to 54.0 cm in length and 130 g to 2,050 g in weight. Three of 149 sampled humpback whitefish were <33.0 cm length and were considered to be immature based on minimum size of maturity data presented by Fleming (1996) and Brown (2006). All other humpback whitefish were ≥33.0 cm length and were considered to be mature. Median length and weight of least cisco were 33.5 cm and 380 g respectively. The sample ranged from 21.0 cm to 40.0 cm in length and 82 g to 830 g in weight. The smallest mature least ciscos in the Chatanika (Fleming 1996) and Selawik River (Brown 2004) populations were reported to be approximately 27.0 cm. Six of 85 sampled least cisco were <27.0 cm and were considered to be immature. All other least cisco were ≥27.0 cm in length and were considered to be mature. These data suggest that the upper Koyukuk River drainage is predominantly populated by mature broad whitefish, humpback whitefish, and least cisco and that immature fish are rare in the region.

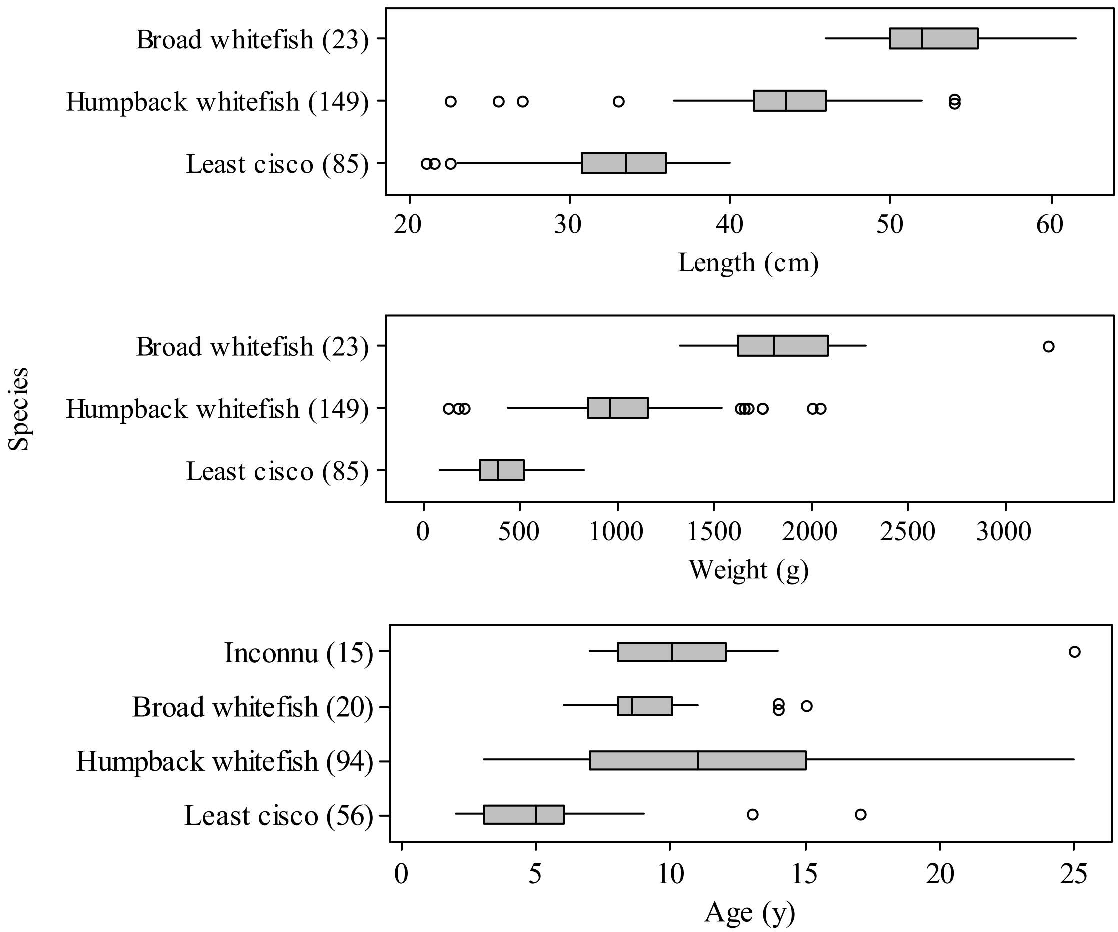

Figure 5. Length, weight, and age distributions of whitefish species sampled in the upper Koyukuk River drainage. Sample sizes are indicated in parentheses. Boxplots include median line, interquartile range box, whiskers that encompass more than 95% of data points, and outliers.

Age data were collected for 185 whitefish of four species in the upper Koyukuk River drainage. Inconnu samples (n = 15) were all obtained from the fall subsistence fishery in the Alatna River. They were captured while migrating to spawn in the late fall. Inconnu ranged from age 7 to age 25 with a median age of 10 years, an age distribution consistent with the mature demographic group (Reist and Bond 1988; Brown 2000). Broad whitefish (n = 20) were also mature fish, most (n = 15) being captured while migrating to spawn up the Alatna River in the late fall and the others (n = 5) being >45 cm in length. Broad whitefish ranged from age 6 to age 15 with a median age of 8.5 years, also consistent with a mature demographic group (Reist and Bond 1988; Brown 2004). Humpback whitefish (*n* = 94) ranged from age 3 to age 25 with a median age of 11 years. Least cisco (*n* = 56) ranged from age 2 to age 17 with a median age of 5 years. A small number of humpback whitefish and least cisco were thought to be immature based on minimum length of maturity criteria, as discussed earlier, but the majority of fish were classified as being mature based on minimum length and age at maturity data (Fleming 1996; Brown 2004, 2006).

Gonadosomatic indices were calculated for females and feeding condition was evaluated for males and females for spring and fall-sampled groups of humpback whitefish and least cisco. Gonadosomatic indices of spring-sampled female humpback whitefish (*n* = 17) and least cisco (*n* = 14) were uniformly <3, as expected for all demographic groups at that time of year (Figure 6). Gonadosomatic indices of all fall-sampled humpback whitefish (*n* = 10) and all except one fall-sampled least cisco (*n* = 8) were >3. All male and female spring-sampled humpback whitefish (*n* = 40) and all except one spring-sampled least cisco (*n* = 25) were feeding, while all fall-sampled humpback whitefish (*n* = 24) and least cisco (*n* = 22) were fasting. These data indicate that fish are actively feeding in lake and oxbow habitats during spring and that mature fish preparing to spawn predominate in the main-stem Koyukuk River during fall.

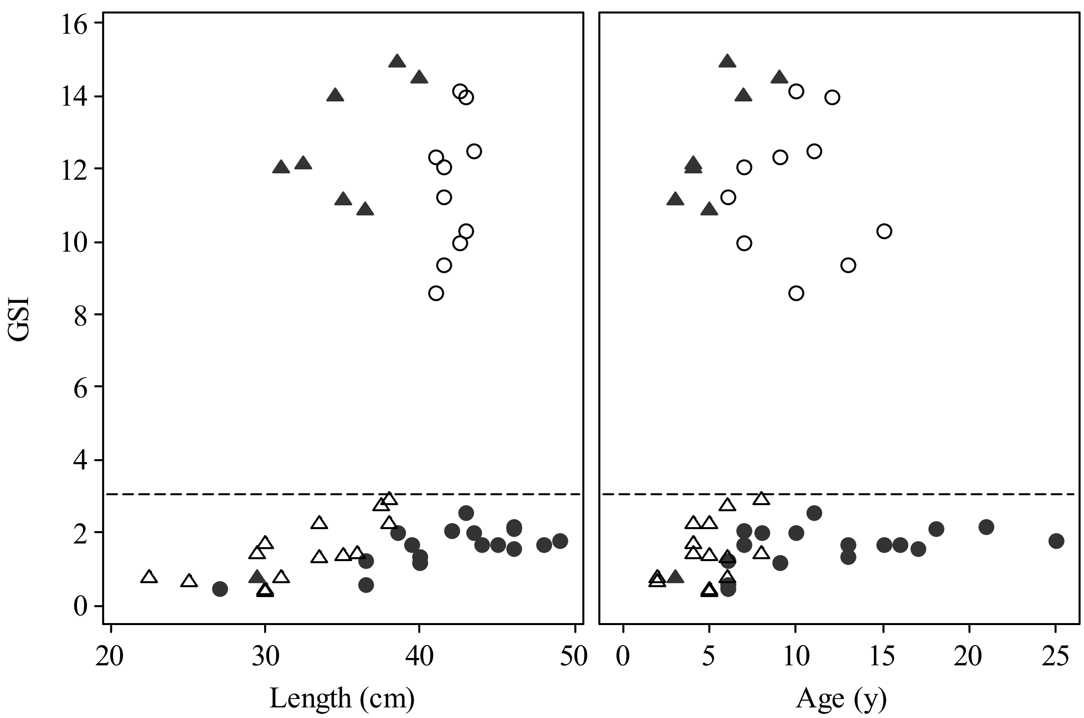

Figure 6. Gonadosomatic indices of humpback whitefish (spring = ●; fall = ○) and least cisco (spring = △; fall = ▲) plotted against length and age. All spring sampled fish had GSI values less than three (indicated with dashed lines). All fall-sampled humpback whitefish were mature and preparing to spawn. All except one fall-sampled least cisco were also mature and preparing to spawn.

Radio telemetry

One hundred two radio tags were deployed on broad whitefish and humpback whitefish in the upper Koyukuk River drainage during 2004 and 2005 (Table 2). Broad whitefish were tagged in lake and oxbow habitats in the upper Kanuti River in May 2004 (*n* = 17). Humpback whitefish were tagged in lake and oxbow habitats in the upper Kanuti River drainage in May 2004 (*n* = 32), in the lower South Fork Koyukuk River drainage in May 2005 (*n* = 32), and in a spawning region of the upper Kanuti River in September 2005 (*n* = 21). Natal spawning origins were not known for any fish tagged in May. All humpback whitefish tagged in the spawning region of the upper Kanuti River during September, however, were in spawning condition as evidenced by their gravid appearance and the presence of pearl tubercles (McPhail and Lindsey 1970; Vladykov 1970), which are only present on whitefish preparing to spawn (Figure 7).

Table 2. Summary details of radio tagging activities in the upper Koyukuk River drainage.

Tagging location	Species	Year	Season	*N*	Duration
Kanuti River Flats	Humpback whitefish	2004	Spring	32	13 months
Kanuti River Flats	Broad whitefish	2004	Spring	17	13 months
South Fork Koyukuk River	Humpback whitefish	2005	Spring	32	18 months
Upper Kanuti River	Humpback whitefish	2005	Fall	21	13 months

Figure 7. Pearl tubercles (white bumps on scales and head) on a humpback whitefish preparing to spawn.

Broad whitefish tagged in May 2004 in the Kanuti River dispersed during the early summer among several lakes in the drainage with stream connections to the river. They remained in these lakes throughout the summer, presumably feeding. At least 15 of the 17 tagged broad whitefish in 2004 were known to be alive in late September. Only one of these broad whitefish migrated to the Alatna River to spawn (Figure 8) in late September and October, where it remained through the winter. Five others migrated out of the Kanuti River into the Koyukuk River between the mouths of the Kanuti and Alatna rivers, where they remained during the winter. Eight of the 15 broad whitefish known to be alive in the late fall, remained in lakes in the upper Kanuti River throughout the fall and winter. Many of the broad whitefish that overwintered in lakes did not move enough the next spring to be certain they had survived the winter. It is possible that they died during the winter. All of the broad whitefish that overwintered in rivers (one in the lower Alatna River, one in the upper Kanuti River, and five in the Koyukuk River) survived the winter and returned by late May to the same lakes in the upper Kanuti River to feed the next spring. Upstream migration rates of five broad whitefish returning to the upper Kanuti River in spring were calculated based on time and distance intervals between their recorded passage past the stationary receiver, which recorded the time from a fixed location, and a spring aerial survey, which identified a time and a location elsewhere along the river. The average upstream migration rate for broad whitefish returning into the upper Kanuti River was almost 20 $km \cdot d^{-1}$ ($n = 5$, range: 15-24 $km \cdot d^{-1}$). In all, 9 of 17 tagged fish were known to have survived a full year following tagging, which represents a minimum annual survival rate of 0.53 (95% CI = 0.33 to 0.77). Several other broad whitefish were repeatedly located within lakes and may also have been alive, but if so, they failed to move far enough to be certain.

Sixty-four humpback whitefish were tagged in May 2004 and 2005 in lakes and oxbows of the upper Kanuti and South Fork Koyukuk rivers. Tagged fish dispersed during the early summer among several lake systems with stream connections where they presumably fed through most of the summer. At least 30 of the 32 tagged humpback whitefish in the Kanuti River, and 27 of 32 in the South Fork Koyukuk River were known to be alive in late September. Twenty-two humpback whitefish from the Kanuti River (73% of those known to be alive) and 20 humpback whitefish from the South Fork Koyukuk River (74% of those known to be alive) migrated during the late summer and fall to discrete upstream reaches of flowing water over gravel. General habitat qualities in these reaches were consistent with previous descriptions of whitefish spawning habitat (e.g., Alt 1969; McPhail and Lindsey 1970; Brown 2006) and were interpreted as such. Based on these data, the annual spawning proportion of humpback whitefish in the upper Koyukuk River drainage was estimated to be 0.74 (95% CI = 0.63-0.83) (Table 3). Kanuti River humpback whitefish migrated to two spawning areas; the Alatna River ($n = 12$) in a 30 km reach between 75 and 105 km upstream from the mouth, and the upper Kanuti River ($n = 10$) in a 10 km reach between 230 and 240 km upstream from the mouth (Figure 8). South Fork Koyukuk River humpback whitefish migrated to a braided reach in the South Fork Koyukuk River between the mouths of Fish Creek and the Jim River ($n = 20$) where there appeared to be two concentrated spawning reaches; a lower reach about 5 km long, an upper reach about 12 km long, and a 20 km reach in between that was apparently unused for spawning. Considering the South Fork Koyukuk River spawning habitats as one site, three distinct spawning reaches were identified in the upper Koyukuk River drainage.

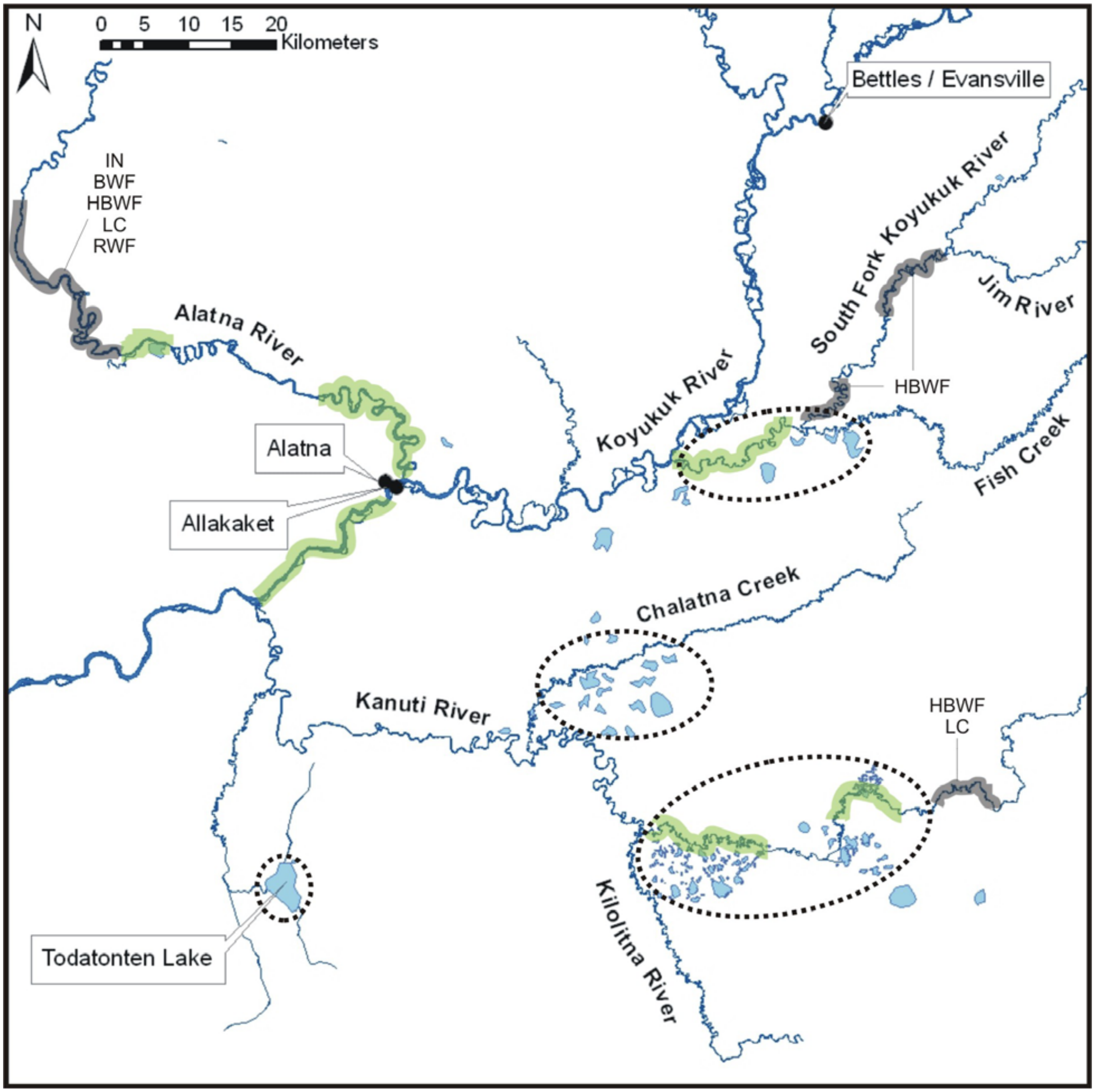

Figure 8. Whitefish spawning reaches (dark shaded regions), major overwintering habitats (light shaded regions), and lake and oxbow feeding habitats (within dashed ellipses) that were identified through sampling and radio telemetry studies in the upper Koyukuk River drainage. Spawning habitat in the upper Alatna River is used by inconnu (IN), broad whitefish (BWF), humpback whitefish (HBWF), least cisco (LC), and round whitefish (RWF), in the upper Kanuti River by humpback whitefish and least cisco, and in the South Fork Koyukuk River by humpback whitefish.

Most radio-tagged humpback whitefish overwintered in riverine habitats, including all those that spawned in the fall and most of those that did not spawn. This included 25 of 28 fish from the Kanuti River group that were known to be alive in winter, an estimated proportion of 0.89 (95% CI = 0.77-0.97), and 19 of 24 fish from the South Fork Koyukuk River group that were known to be alive in winter, an estimated proportion of 0.86 (95% CI = 0.77-0.92). Humpback whitefish tagged in the Kanuti River overwintered in the Alatna, Koyukuk, and Kanuti rivers, while those tagged in the South Fork Koyukuk River overwintered almost exclusively in the South Fork

Koyukuk River (Figure 8), with only one fish known to have migrated out to the main-stem Koyukuk River to overwinter. Humpback whitefish from the Kanuti River group that had overwintered in the Koyukuk or Alatna rivers, migrated back into the upper Kanuti River during May, as indicated by stationary receiver and aerial survey records. The average upstream migration rate for humpback whitefish returning into the upper Kanuti River was approximately 15 $km \cdot d^{-1}$ (n = 13, range: 5-28 $km \cdot d^{-1}$). Fish that overwintered in the upper Kanuti or South Fork Koyukuk River also migrated back into lake habitats during spring, although the timing records were not as complete as for those that migrated past the stationary receiver.

Table 3. Estimated spawning proportions, annual survival rates, and feeding site fidelity proportions of humpback whitefish based on spring season tagging events in feeding habitats of the upper Kanuti and South Fork Koyukuk rivers, individually and combined, and from the upper Tanana River for comparison (95% confidence intervals are indicated in parentheses).

Tagging group	Spawning proportion	Annual survival	Feeding site fidelity
Kanuti	0.73 (0.58-0.87)	0.63 (0.47-0.78)	0.95 (0.84-0.99)
South Fork	0.74 (0.58-0.88)	0.59 (0.44-0.76)	0.89 (0.74-0.99)
Combined	0.74 (0.63-0.83)	0.61 (0.50-0.72)	0.92 (0.83-0.98)
Tanana[a]	0.71 (0.64-0.77)	0.77 (0.70-0.83)	0.86 (0.80-0.91)

[a] data from Brown (2006)

In all, 20 of 32 tagged humpback whitefish from the Kanuti River group (63%), and 19 of 32 tagged humpback whitefish from the South Fork Koyukuk River group (59%) were known to have survived a full year following tagging. Based on these data, the minimum annual survival rate was estimated to be 0.61 (95% CI = 0.50-0.72) (Table 3). Of the 39 tagged humpback whitefish known to be alive in the spring, 36 returned to the same lakes where they had been feeding the previous year, which represented a minimum feeding site fidelity proportion of 0.92 (95% CI = 0.83-0.98). Considering only humpback whitefish from the South Fork Koyukuk River group, whose transmitters were programmed for extended operation, 12 of 20 humpback whitefish that had spawned during fall 2005 were known to be alive during fall 2006. Eight of the 12 surviving humpback whitefish were again located in the spawning reach, indicating a sequential year spawning proportion of 0.67 (95% CI = 0.43-0.90), while the other four remained in feeding habitats during the fall and then migrated out to the lower reaches of the South Fork Koyukuk River for the winter.

Twenty-one humpback whitefish were tagged in early September 2005 in the spawning region in the upper Kanuti River, which had been identified in fall 2004 (Figure 8). Pearl tubercles (Vladykov 1970) were apparent on all humpback whitefish captured at the site (Figure 7), which confirmed that the reach was being used for spawning. Least cisco in spawning condition were also captured at the site, indicating that the spawning area was being used by at least two whitefish species. All 21 tagged humpback whitefish remained in the spawning reach until late September or early October. Fifteen of 21 fish were located during winter, all in riverine habitat. Of these 15, 7 fish had migrated out to the Koyukuk River, approximately 235 km downstream, while eight fish overwintered in the upper Kanuti River. Seventeen fish were located in lake feeding habitats the following June. These included Todatonten Lake, the outflow of which drains into the lower Kanuti River, connected lake systems in the Chalatna Creek drainage, and a network of lake systems in the upper Kanuti River (Figure 8). These data indicate that humpback whitefish spawning in the upper Kanuti River disperse into many feeding habitats within the drainage.

Discussion

Whitefish sampling data from the upper Koyukuk River drainage clearly indicated that almost all inconnu, broad whitefish, humpback whitefish, and least cisco were mature individuals. Brown (2006) reported similar findings for humpback whitefish in the upper Tanana River wetlands. He inferred from sampling and otolith chemistry data that larvae from those populations dispersed to downstream rearing areas shy of the Yukon River estuary where they remained for several years until they matured and returned to spawn. In the upper Koyukuk River, anadromous individuals of all four species were identified based on otolith chemistry analyses (Brown et al. 2007), which established that the populations were distributed to salt water at the Yukon River mouth or beyond, at least 1,600 km downstream. Downstream distribution of whitefish larvae during spring has been documented with directed sampling studies in the Yukon River in Canada (Bradford et al. 2008), in a Norwegian drainage (Naesje et al. 1986), and in two Russian drainages (Shestakov 1991; Bogdanov et al. 1992). In addition, Martin et al. (1987) conducted an extensive fish sampling program in the Yukon River delta and reported that juvenile whitefish of several species were a major component of their catches. In their summary of whitefish life history characteristics in the Mackenzie River drainage, Reist and Bond (1988) indicated that most species segregated by demographic groups along the river, with juveniles being most closely associated with delta and coastal environments (i.e., Chang-Kue and Jessop 1992) and mature fish migrating into upstream reaches for spawning and possibly feeding (i.e., Chang-Kue and Jessop 1983; VanGerwen-Toyne et al. 2008). Our sampling data indicating a preponderance of mature fish in the upper Koyukuk River drainage are consistent with these other literature sources.

Known whitefish spawning areas have been characterized as having substrate composed predominantly of cobble, gravel, or sand (Alt 1969, 1977; Brown 2000, 2006). Spawning areas for humpback whitefish have been documented in suitable habitats in flowing water (Alt 1979; Brown 2006) and in lakes (Anras et al. 1999). Distinct migrations from summer feeding areas to fall spawning areas have been recognized for several whitefish species in numerous drainage systems. Examples include broad whitefish in the main-stem of the Mackenzie River in northern Canada (Chang-Kue and Jessop 1983), lake cisco *C. artedii* and lake whitefish *C. clupeaformis* in the Eastmain River, a Hudson Bay drainage in eastern Canada (Lambert and Dodson 1990), least cisco and humpback whitefish in the Chatanika River, a tributary of the Tanana River in Alaska (Timmons 1991), inconnu in the Slave and Arctic Red rivers in the Mackenzie River drainage (Howland 1997), inconnu in the main-stem Yukon River (Brown 2000), broad whitefish in the Anadyr River in eastern Russia (Shestakov 2001), and inconnu, Arctic cisco *C. autumnalis*, broad whitefish, lake whitefish, and least cisco in the Peel River, a tributary of the Mackenzie River (VanGerwen-Toyne et al. 2008). Similar migrations between summer feeding and fall spawning habitats are thought to occur for all riverine populations.

Three whitefish spawning destinations have been identified in the upper Koyukuk River drainage based on migration behavior of radio-tagged broad whitefish and humpback whitefish, together with biological sampling data, past literature (Alt 1977), and traditional knowledge accounts (Andersen 2007). The distinct migrations of many radio-tagged fish from lake habitats where they had been feeding during the spring and summer, to gravel substrate, riverine habitats in the fall, were consistent with spawning migrations documented elsewhere, as discussed earlier. The ages and sizes of sampled fish in the region were consistent with a mature demographic group (Figure 5). The high GSI values of fall-sampled least cisco and humpback whitefish indicated that a spawning migration was taking place in the main-stem Koyukuk River (Figure 6). Female whitefish harvested in the Alatna River during the fall subsistence fishery, as documented by Andersen (2007), were reportedly heavy with eggs indicating they were prepared to spawn. Alt (1970, 1977) had previously identified a reach of the Alatna River in the vicinity of Siruk Creek, approximately 75-80 km upstream from the mouth, as a major spawning destination for inconnu based on tagging, sampling, and aerial survey data. The 12 humpback whitefish and 1 broad whitefish that migrated from lake habitats in the upper Kanuti River to the Alatna River stopped in this same reach (Figure 8), remained there through the late fall, and then moved into the lower Alatna River or out into the Koyukuk River for the winter. Pearl tubercles (Vladykov 1970) (Figure 7) were present on humpback whitefish and least cisco sampled in the upper Kanuti River in fall 2005, at the gravel substrate reach identified as the migration destination of 10 radio-tagged humpback whitefish in fall 2004, confirming that the reach was a spawning destination. The identification of the spawning reaches in the South Fork Koyukuk River is currently based on migration timing and behavior of 20 mature-sized, radio-tagged humpback whitefish. The Alatna River spawning area appears to be the only one in the upper Koyukuk River drainage that supports all four whitefish species examined in this investigation, and possibly round whitefish too.

Broad whitefish were not abundant in the spring anywhere in the upper Koyukuk River drainage. Only 17 radio tags were deployed in the upper Kanuti River drainage in spring 2004. While numerous tagged fish migrated among lake feeding systems in the upper Kanuti River during the spring and summer, and six migrated more than 170 km downstream to the Koyukuk River or farther, only one tagged broad whitefish migrated into recognizable spawning habitat in the Alatna River. Alatna River harvest data from local fishers indicated that broad whitefish were routinely captured during late fall beach seine and early winter under-ice gillnet fisheries (Andersen 2007), verifying that the drainage is a spawning destination for broad whitefish. While these may be interesting findings, they are not substantial enough to allow large-scale inferences about broad whitefish migration and habitat use patterns in the upper Koyukuk River drainage.

Based on a study of energetic requirements for spawning lake cisco and lake whitefish, Lambert and Dodson (1990) concluded that individuals could not obtain enough energy during the brief feeding season each year to support sequential year spawning, suggesting that these species spawned once every two or more years once mature. This ecological concept is generally considered to be valid for most whitefish populations, which leads to the expectation that no more than 50% of mature fish in whitefish populations should be in spawning condition each year (e.g., Moulton et al. 1997). While it may be possible to sample a population in a representative manner to test this hypothesis when it is bound in a lake system (e.g., Johnson 1976; Power 1978; Mills et al. 1995; Wang et al. 2008), it is much more complicated in an open river system where demographic groups are often widely dispersed geographically (Reist and Bond 1988; Brown et al. 2007). As a result, most direct evidence supporting the alternate-year spawning hypothesis is limited to findings of at least some mature fish in non-spawning condition during the fall (e.g., Moulton et al. 1997; Brown 2004). Reist and Bond (1988) were not able to account for sufficient numbers of non-spawning, mature components of Mackenzie River whitefish species to support the alternate-year spawning hypothesis directly, and suggested that sequential year spawning might be more prevalent than commonly thought. Recent radio telemetry work with humpback whitefish in the upper Tanana River (Brown 2006) and with inconnu in the Selawik River (Hander et al. 2008) have shown that sequential year spawning commonly occurs for at least some populations.

Two sources of telemetry data from this study indicate that sequential year spawning is common for humpback whitefish populations in the upper Koyukuk River drainage. In the first case, radio telemetry data from the South Fork Koyukuk River tagging group provided direct evidence that 67% (8 of 12) of surviving tagged fish that had spawned during the fall of year one spawned again during the fall of year two. In the second case, the spawning proportion of spring-tagged humpback whitefish from the Kanuti and South Fork Koyukuk River groups was 0.74 (95% CI = 0.63-0.83) (Table 3), significantly greater than 0.50, the maximum level expected if sequential year spawning did not occur. Brown (2006), using these same two methods with humpback whitefish in the upper Tanana River drainage, found that 67% (16 of 24) of surviving tagged fish that had spawned during year one also spawned during year two, and that the spawning proportion of 185 spring-tagged fish was 0.71 (95% CI = 0.64-0.77), both very similar values to those from this investigation (Table 3). These data suggest that sequential year spawning may be common for humpback whitefish populations throughout the Yukon River drainage.

Because the environmental conditions required for development of whitefish eggs and subsequent dispersal of larvae are thought to be very similar among species, they often share spawning habitats. For example, Brown (2000) found inconnu, humpback whitefish, and Bering cisco when he sampled the inconnu spawning region in the upper reaches of the Yukon Flats. Humpback whitefish, least cisco, inconnu, and round whitefish share the spawning habitat on the Chatanika River, a tributary of the Tanana River in interior Alaska, which is thought to be the cause of hybridization events (Alt 1971). The Alatna River spawning reach appears to support spawning populations of five whitefish species including inconnu, broad whitefish, humpback whitefish, least cisco, and possibly round whitefish (Alt 1977; Andersen 2007) (Figure 8). The Kanuti River spawning reach is definitely used by humpback whitefish and least cisco. Sampling has not been conducted in the humpback whitefish spawning reaches identified in the South Fork Koyukuk River (Figure 8) to determine if additional species spawn there as well. Sampling and radio telemetry data suggest that inconnu and broad whitefish in the upper Koyukuk River drainage spawn only in the Alatna River, which appears to be the most important whitefish spawning location in the drainage.

Radio telemetry and sampling data from both spring and fall seasons indicate that once humpback whitefish mature and return from distant downstream rearing areas to their upper Koyukuk River spawning origins they tend to occupy local habitats from that time on. Brown et al. (2007) reported that 10 of 12 humpback whitefish they sampled from the upper Koyukuk River drainage had lived for a period of time in marine water prior to capture. It follows that a substantial fraction of the humpback whitefish populations rear in very distant locations, a deduction that is supported by the sampling data presented earlier demonstrating a preponderance of mature fish in the upper Koyukuk River drainage. Whitefish rearing in marine environments must migrate a minimum of 1,600 km upstream to reach upper Koyukuk River drainage spawning destinations, which is undoubtedly an energetically costly migration (Lambert and Dodson 1990). Spring-tagged humpback whitefish from the Kanuti and South Fork Koyukuk River drainages exhibited a combined feeding site fidelity proportion of 0.92 (Table 3) indicating that very few individuals prospect for new feeding habitats once they initially find one. Seventeen of the original 21 humpback whitefish tagged in the Kanuti River spawning reach were located during the following feeding season in lake systems within the

Kanuti River drainage (Figure 8), again suggesting that most individuals from a spawning population occupy local rather than distant habitats once they return to spawn. Brown (2006) maintained a stationary receiver on the Tanana River 190 km downstream from radio-tagging activities in the upper Tanana River. He found that only 1 of 193 humpback whitefish tagged in the upper Tanana River migrated downstream past the stationary receiver. Similar to demographic findings presented above, humpback whitefish populations in the Tanana River drainage were predominantly mature individuals. Brown (2006) proposed that humpback whitefish recruited to the upper Tanana River drainage when they became mature and migrated to their origins to spawn. Humpback whitefish in the upper Tanana River drainage appeared to follow an annual cycle within the local region of feeding in lakes during spring and summer, spawning in one of two identified spawning reaches during fall, and overwintering primarily in rivers but also in some lakes. Humpback whitefish (and perhaps broad whitefish and least cisco) in the upper Koyukuk River drainage appear to be following the same annual and lifetime patterns as humpback whitefish from the Tanana River drainage. By occupying local habitats rather than returning to distant downstream feeding and overwintering habitats following their first spawning event, whitefish dramatically reduce the energetic costs associated with subsequent spawning. Presumably, this behavior would lead to more frequent spawning events, greater probability of survival (by avoiding long migrations along the river system), and increased lifetime fecundity, all of which would be beneficial for the respective populations.

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