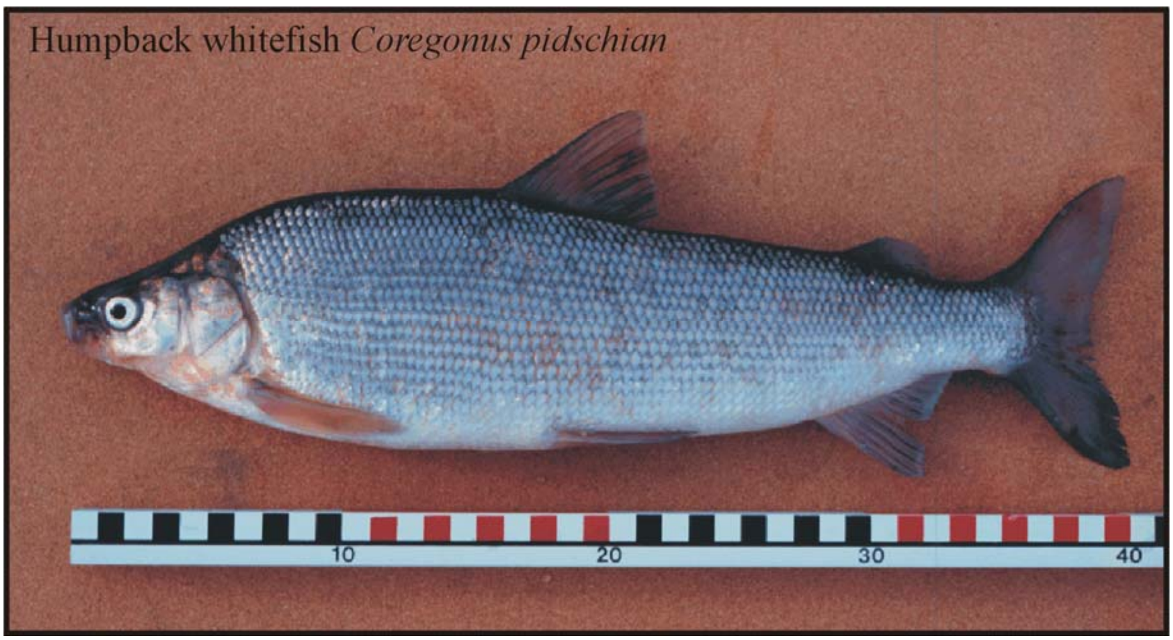
U.S. Fish & Wildlife Service

Humpback Whitefish *Coregonus pidschian* of the Upper Tanana River Drainage

Alaska Fisheries Technical Report Number 90



Fairbanks Fish and Wildlife Field Office
Fairbanks, Alaska
April 2006

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Humpback Whitefish *Coregonus pidschian* of the Upper Tanana River Drainage

Randy J. Brown

Abstract

Humpback whitefish *Coregonus pidschian* are the primary fishery resource in the upper Tanana River drainage. Subsistence users in the region have reported that their catches have been less in recent years than they remembered in the past, suggesting that fish abundance in the region may have declined. Previous fisheries investigations in the region identified that humpback whitefish were present but provided no information on life history, migration, or habitat use that could be used to evaluate local residents' concerns. A multi-year investigation was therefore initiated. It proceeded in a step-wise fashion through several stages beginning with systematic sampling to confirm species identification and describe the demographics of the population; then to otolith chemical analyses to determine if the population ranged downstream to marine water; from there to radio telemetry to identify migrations and important habitats; and finally to directed sampling on spawning areas to provide additional demographic information with which to evaluate radio telemetry data. Sampling data revealed that humpback whitefish were the only whitefish species available in the open river and lake systems of the upper Tanana River drainage. Most fish were mature adults. The average age was 6.7 years and ages ranged from 1 to 26 years (n = 153). Otolith chemical analyses of ten fish failed to find the high levels of strontium that would result from a migration to marine water, indicating that the population remained in freshwater. Radio tag relocations from 222 tagged humpback whitefish revealed that most fish followed an annual pattern of migration within the upper drainage that included using: 1) lake habitats for feeding in the spring and early summer; 2) river habitats by mid to late summer for migration to spawning areas; 3) two swiftly-flowing, gravel substrate regions of rivers for spawning; and 4) flat-water, soft-substrate habitats of rivers or open lake systems for overwintering. Radio tag data indicated that most humpback whitefish spawned on sequential years rather than on alternate years. These data provide a basis for guiding fishing practices and development activities in the region to minimize impacts on the fishery and ensure continued productivity. Projects designed to estimate the abundance of humpback whitefish from the two identified stocks could be developed if that information became a priority.

Introduction

Humpback whitefish *Coregonus pidschian* are members of what McPhail and Lindsey (1970) refer to as the humpback whitefish complex of species. It includes three forms in North America; lake whitefish *C. clupeaformis*, Alaska whitefish *C. nelsonii*, and humpback whitefish

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C. pidschian, that are distinguishable only by differences in population level modal gill raker counts on the first gill arch. For the purposes of this study, all three forms are considered to be synonymous.

Humpback whitefish is the major species targeted in subsistence fisheries occurring in and adjacent to the Tetlin National Wildlife Refuge in the upper Tanana River drainage. Most subsistence fishing is done by families from the villages of Northway and Tetlin. Case (1986) estimated the average household harvest in Northway to be 170 kg per year. Similarly, Halpin (1987) estimated the average household harvest in Tetlin to be 258 kg per year. While salmon have been documented in the region, they have never been abundant and are not targeted in the fishery (U.S. Fish and Wildlife Service 1990). Residents in the upper drainage have expressed concerns about possible declines in humpback whitefish populations to Tetlin National Wildlife Refuge personnel directly (Bob Schulz, U.S. Fish and Wildlife Service, personal communication) and to the Eastern Interior Alaska Subsistence Regional Advisory Council as well. The main issue for residents was a perception that humpback whitefish were less abundant than they had been in the past.

All humpback whitefish living within river systems are thought to follow a similar life history pattern. Spawning takes place in the late fall in flowing water over a gravel substrate (Alt 1979). Their eggs are cast into the water column where they drift downstream and sink to the bottom, becoming lodged in the interstitial spaces in the gravel (Scott and Crossman 1973; Morrow 1980). The eggs develop through the winter and larvae hatch in the spring, emerging into the water column as the high flows of spring and early summer fill the waterways (Naesje et al. 1986; Shestakov 1991; Bogdanov et al. 1992). Larvae are carried downstream by the rapidly flowing water to a wide array of chance destinations that include backwaters along the river, off-channel lakes, and estuary regions at river mouths (Shestakov 1992). They become mature after four or five years of growth and prepare to spawn (Alt 1979; Reist and Bond 1988). Beginning in midsummer, they migrate toward upstream spawning sites, during which time they reportedly do not feed (Dodson et al. 1985). Major spawning areas appear to be used each year, so fidelity to natal spawning areas is thought to be high (Hallberg 1989). Following spawning, mature fish retreat downstream to overwintering locations (Alt 1979), and eventually to feeding areas by the following spring. Schmidt et al. (1989) found that overwintering whitefish in the extreme habitats of the Arctic coast of Alaska did little if any feeding regardless of food availability. It is unclear if whitefish in less extreme environments behave similarly. Spawning is generally thought to occur every other year or even less frequently for most whitefish species including humpback whitefish (Reist and Bond 1988; Lambert and Dodson 1990). Reported otolith age estimates range as high as 57 years for lake whitefish (Power 1978). Reist and Bond (1988) proposed that during the fall spawning period there are three main components of whitefish populations: immature fish far downstream of the spawning areas; mature non-spawners also downstream of the spawning areas but not necessarily in the same places as immature fish; and mature spawners in upstream spawning areas. Based on these concepts, we might infer that spawning areas are the extreme upstream limit of a population's range, and the rearing areas for immature fish are the extreme downstream limit.

As this project began, anthropological data (Case 1986; Halpin 1987), as well as more recent communications from residents (Bob Schulz, U.S. Fish and Wildlife Service, personal communication), were available regarding traditional fishing locations for humpback whitefish in the upper Tanana River drainage. Age and size structure, migration patterns, important habitats, and population levels, however, were virtually unknown. There was no basis for evaluating local residents' concerns. Thus, a step-wise research model was developed to gain a comprehensive understanding of the fishery in the upper Tanana River drainage. The research proceeded through four basic stages of investigation that permitted discoveries in the early stages to give direction to later stages. They were:

1) systematic sampling to confirm species identification and describe the demographics of the population (i.e., size composition, age structure, and growth patterns);

2) otolith chemical analyses to determine if the population ranged downstream to marine water;

3) radio telemetry to identify important habitats (i.e., spawning, overwintering, and feeding), migrations, and spawning frequency, and estimate habitat fidelity and annual survival rates; and

4) sampling on spawning areas to confirm spawning activity and describe the length distribution of the mature component of the population.

Once obtained, these data would provide a basis for guiding fishing practices and development activities in the region to minimize impacts on the fishery and ensure continued productivity. Also, projects designed to estimate and interpret the abundance of humpback whitefish could be developed if that information became a priority.

Study Area

The upper Tanana River drainage, in eastern interior Alaska, is a complex region of inter-connected lake systems, sloughs, and rivers (Figure 1). Wetland areas lie at relatively high elevations, from 500 to 600 m above sea level (in this paper the term "wetland" refers to open lake and stream systems in river floodplains). The region experiences a continental climate, with cold winters and warm summers (Brabets et al. 2000). Rivers and lakes generally freeze by mid-October and remain frozen until late April or May. Annual precipitation in the region may total 25 cm or more (U.S. Fish and Wildlife Service 1990).

The Nabesna and Chisana rivers flow north from large glaciers in the Wrangell Mountains immediately to the south (Wiles et al. 2002). Flow from these rivers is turbid during the summer months and clears during the winter. The Tanana River originates at the confluence of the Nabesna and Chisana rivers, and shares their annual cycles of turbidity and clarity. These three major rivers, along with an assortment of lakes, sloughs, and smaller streams in the region, were the water bodies of interest in this study. For the purposes of this investigation, the drainage was stratified into two study areas referred to as the "upper region", which included all river and lake systems upstream of a point midway between Tetlin and Mansfield lakes, and the "lower region", which included all river and lake systems downstream of this point but upstream of the Delta River (Figure 1).

Methods

Systematic Sampling

Systematic sampling was conducted during summer 1998 in four wetland areas in the upper region that were known to be used by local fishers. The main objectives in the sampling component of the project were to confirm species presence in the region, identify population differences such as mean sizes and ages of fish among sample areas, explore the general relationships between fish age and the dynamics of growth and survival based on catch statistics, calculate catch rates to identify differences in relative abundances among sample sites and seasons, and to investigate the incidence of anadromy in the population. The wetland areas were Fish Lake, Kalutna River, Moose Creek, and Tenmile Lake (Figure 2). Samples were collected during four 3-day periods beginning on; July 8, July 14, August 20, and August 26. Monofilament gillnets 16 m long and 2 m deep, with 5 cm stretch mesh were used at all sites. Four sites were selected within each wetland area and one gillnet was set at each site for 4 hours during each sampling period.

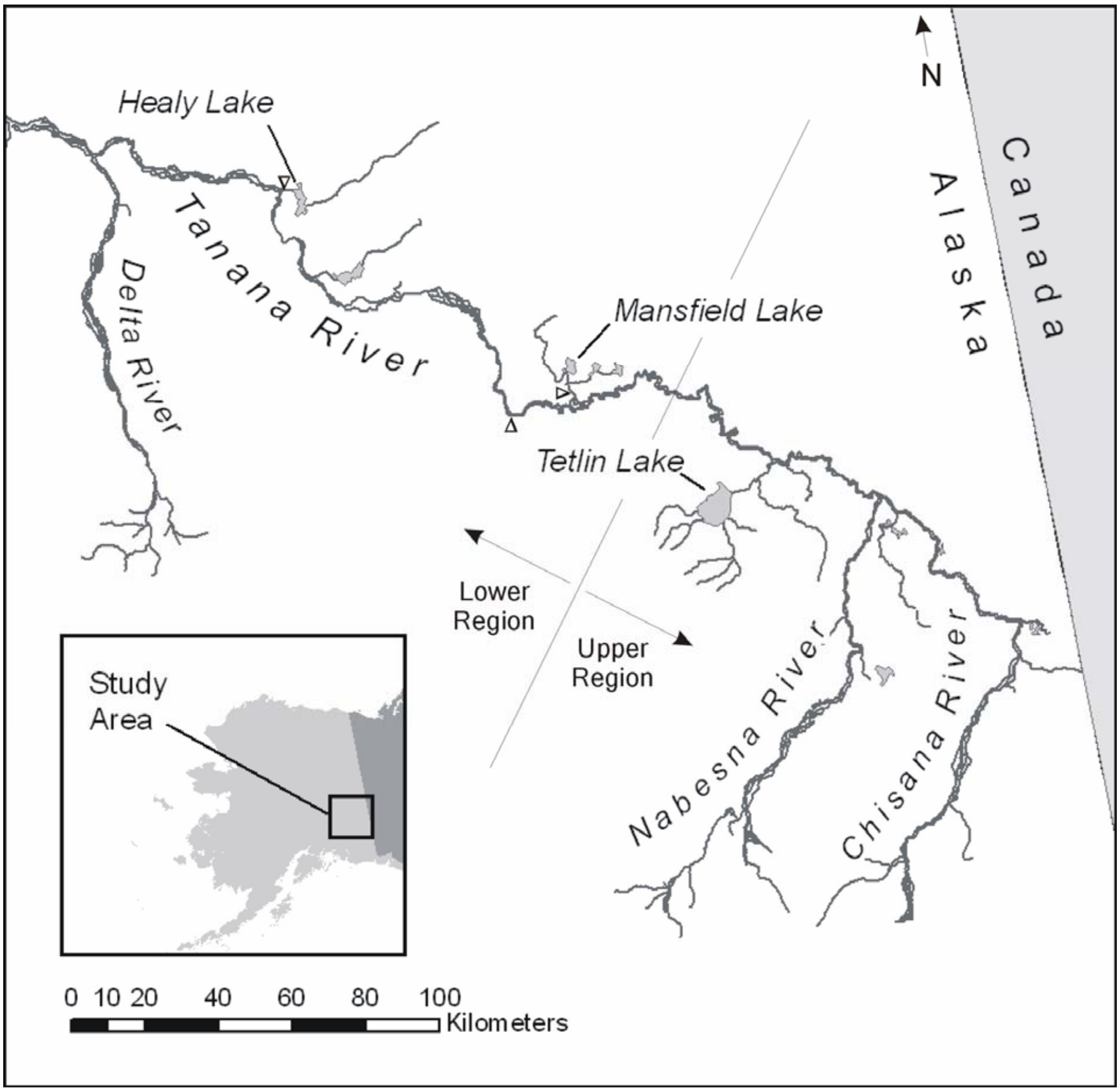

Figure 1. Geographic features in the upper and lower regions of the study area in the Tanana River drainage in eastern interior Alaska. The triangles mark the locations of remote receiving stations that operated during the radio telemetry component of the project.

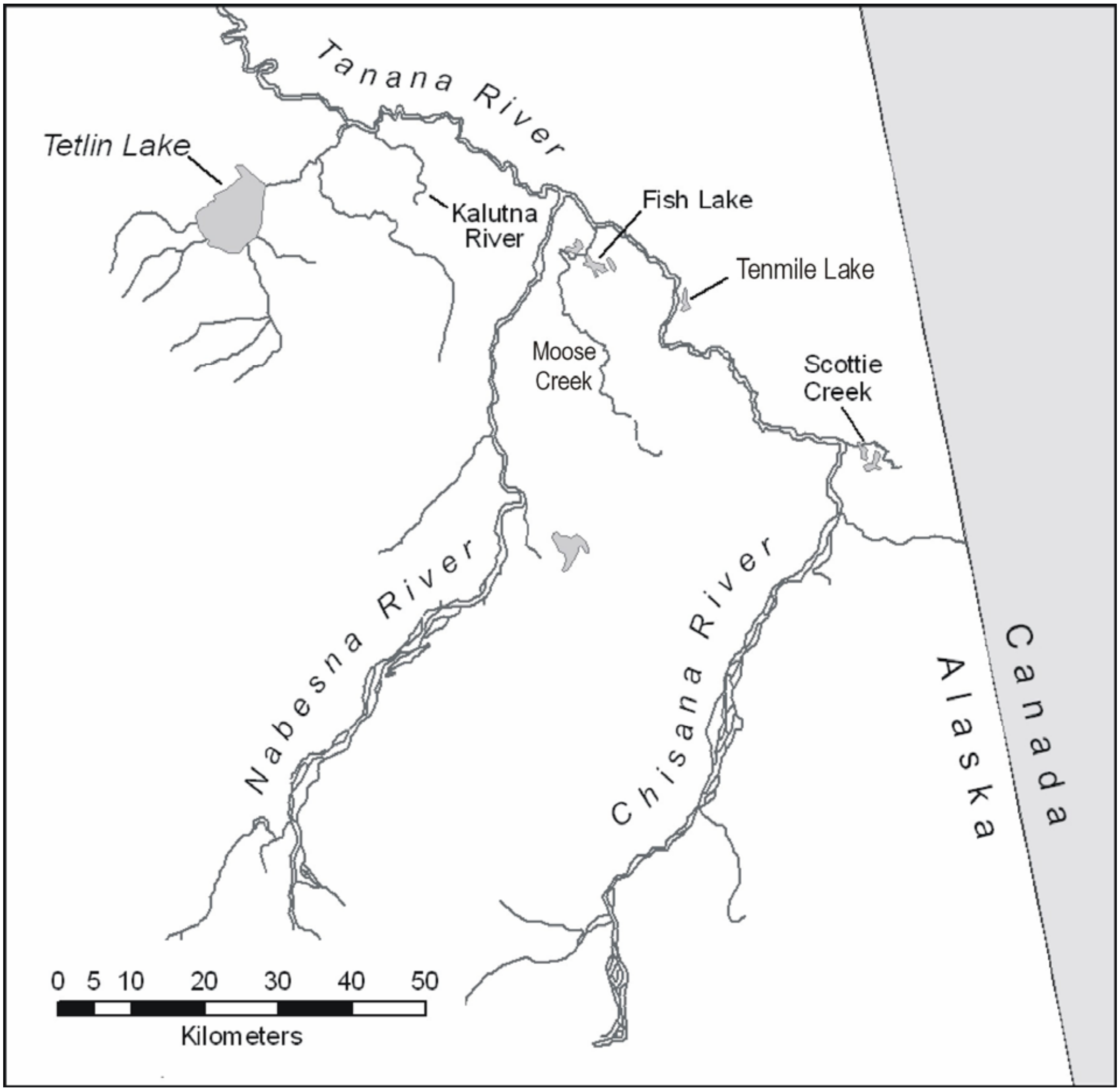

Figure 2. Geographic features in the upper region of the study area in the Tanana River drainage in eastern interior Alaska. Systematic sampling took place in the Kalutna River, Fish Lake, Moose Creek, and Tenmile Lake. Radio tagging in the upper region took place in the Kalutna River, Fish Lake, Tenmile Lake, and Scottie Creek.

All fish captured were identified to species, measured for fork length (length) to the nearest 1 mm, weighed to the nearest 5 g, sexed, and sagital otoliths were collected for aging and otolith chemical examination. Otoliths were thin-sectioned (sectioned) in the transverse plane through the core (Secor et al. 1992), mounted on a glass slide, and polished so that growth increments could be clearly viewed with transmitted light. Each otolith section was approximately 200 µm thick. Sectioned otoliths that were eventually selected for chemical analyses were further polished on a lapidary wheel with 1 µm diamond abrasive. They were coated with a thin layer of conductive carbon in final preparation for analysis. Otolith aging criteria followed the methods and illustrations of Chilton and Beamish (1982) and Howland et al. (2004).

It was thought that if fish in the upper Tanana River drainage were randomly moving from one wetland to another and from wetland to river systems that fish in all sample areas would be similar. Alternatively, if fish sorted themselves in some manner within localized habitats there could be size and age structuring among sample areas. Data were therefore compared between wetland sample areas using an ANOVA F test. Null hypotheses were that mean lengths, weights, and ages of fish were equal among wetland sample areas versus alternative hypotheses that they were different. Significant differences were based on $\alpha = 0.05$. Upon significant F test results, follow-up analyses using Tukey's multiple comparisons procedure were performed to determine the wetland area with the longest, heaviest, and oldest fish in residence, using an experiment-wise error rate of $\alpha = 0.05$. Catch rates for each sample period in each sample site were expressed as the number of fish captured per 16 m net per hour of fishing effort (CPUE). General trends in CPUE among sample sites and over the course of the summer are presented and discussed.

Catch at age data can be used to describe survival and mortality rates of fish populations (Hilborn and Walters 1992). In basic form, catch at age analysis assumes that: 1) fish within a population recruit to a capture program at some age, which is usually taken to be the mode of an age-frequency plot; 2) all fish from that age and greater are equally vulnerable to the capture method; and 3) cohorts recruit at the same or similar levels of abundance. The decline in catch-frequency that is usually observed for successive age classes following the mode is therefore considered to be the result of mortality acting on the cohorts. If the assumptions are met, annual survival rates can be calculated based on the progressive decline in abundance of fish with age. Perhaps the most problematic assumption in this study is that cohort strength remains similar from year to year. This assumption can be tested and violations can be accounted for by sampling a population over multiple years, essentially tracking individual cohorts through two or more years (Robson and Chapman 1961; Hilborn and Walters 1992). In this study, however, only one year of age-associated sampling was conducted. Resulting survival rates calculated from these data are presented and compared with other similar studies in the literature (Mills and Beamish 1980; Mills et al. 2004) and with estimates obtained by other means within this study.

Robson and Chapman (1961) presented statistical methods of calculating annual survival rate and estimation error for fish populations based on age frequency data, or catch curves, from fish capture events. Their methods have been used by other scientists studying lake whitefish populations (Mills and Beamish 1980; Mills et al. 2004), and were utilized in this study as well. Survival estimates were calculated from age frequency data between the ages of 5 (the mode of the age frequency histogram) and 15 years (data were sparse beyond age 15).

Otolith Chemistry

Fish otoliths are composed primarily of calcium carbonate. They grow continually throughout a fish's life as dissolved material in the body fluids precipitate on the outer surface (Campana 1999). Marine water has a relatively high concentration of strontium (Sr) ions in solution compared to freshwater (Martin and Meybeck 1979; de Villiers 1999). As a result, the material that precipitates on fish otoliths when they are in marine water is highly enriched with Sr compared to material precipitated when they are in freshwater (Campana 1999). Areas of enhanced Sr in fish otoliths can be identified with an electron microprobe (Campana et al. 1997), and these areas provide evidence of fish migrations to marine water.

A random subsample of 10 humpback whitefish otoliths collected in the upper Tanana River were selected for otolith chemical analyses in an effort to detect fish that had been to marine water. The objective was not to estimate the proportion of anadromous versus freshwater components of the population, rather, to detect anadromous fish. The sampling problem was therefore one of detection probability, which required fewer samples than proportion estimation. Specifically stated the problem was: what is the probability of selecting at least one anadromous fish in a random sample of 10 if the actual proportion of anadromous fish in the population is 0.5? This probability was calculated based on the binomial probability distribution, using a range of sample sizes and a range of actual proportion values (Figure 3). With a sample size of 10, for example, there was a 97% probability of selecting at least one anadromous fish when the actual proportion of anadromous fish in the population was 0.3. A sample size of 10 was judged to be an adequate sample size for the investigation.

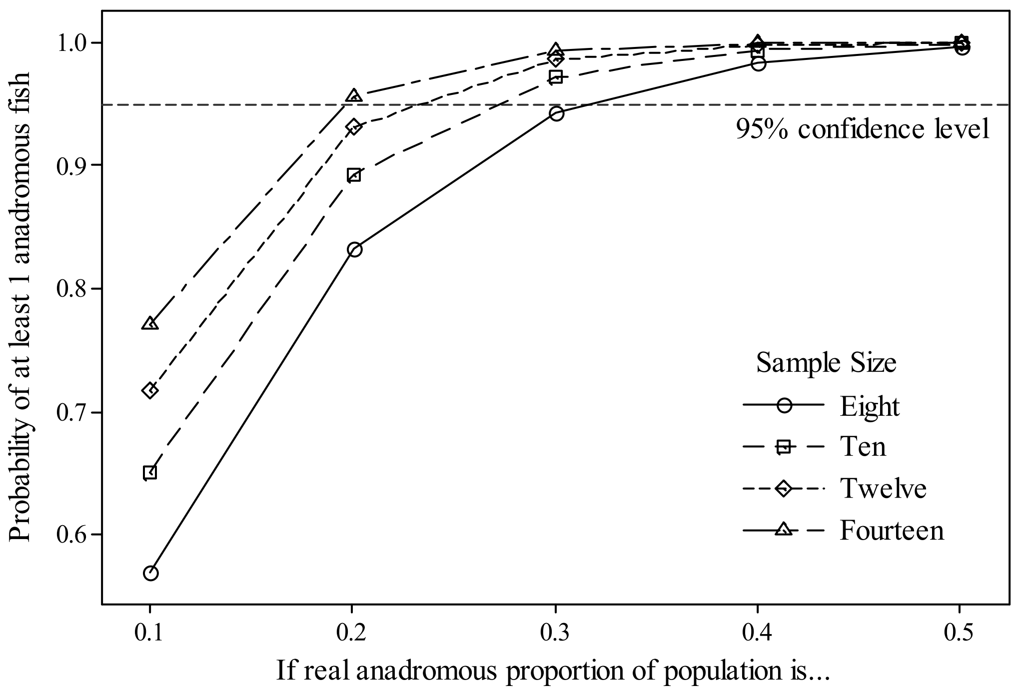

Figure 3. Plot of the probability of detection of at least one anadromous fish in a given size sample with a selection of hypothesized anadromous proportions in a population.

A wavelength-dispersive electron microprobe was used for chemical analyses of otoliths in this study. The technology functions by bombarding points on a sample surface with a focused beam of electrons. Atoms within the material are ionized by the electron beam and emit x-rays unique to each element. Spectrometers are tuned to count the x-rays from elements of interest, in this case, Sr. The x-ray counts at each sample point are proportional to the elemental concentration in the material (Potts 1987; Reed 1997; Goldstein et al. 2003).

Strontium x-ray counts were collected from a series of points along a core (precipitated during the first year of life) to margin (precipitated just prior to the fish's death) transect for each otolith. The electron beam used for this procedure was 5 µm in diameter and was operated at an accelerating voltage of 15 kilo-electron-volts, and a nominal current of 20 nano-amperes. Center-to-center distance between transect points was approximately 8 µm and the penetration depth of the beam was about 3 µm (Gunn et al. 1992). X-ray counts were collected for 25 s at each point. Strontium x-ray counts were converted to estimates of Sr ppm concentration based on a regression equation relating the two measures, similar to the process described by Howland et al. (2001).

Classification of upper Tanana River humpback whitefish as freshwater resident or anadromous life history forms was accomplished empirically by comparing their otolith Sr distribution graphs with those of known life history fish. This qualitative technique was used effectively by Babaluk et al. (1997) in an investigation of the anadromous behavior of Arctic char *Salvelinus alpinus* in a northern Canadian lake. Strontium graphs of twenty known life history salmonid fish (10 freshwater resident and 10 anadromous) were prepared for comparison. All known life history fish were of a size common for mature individuals, and each was collected in habitats and circumstances that guaranteed they actually belonged in the life history category in which they were placed. Known freshwater fish included Dolly Varden *S. malma*, Arctic grayling *Thymallus arcticus*, lake trout *S. namaycush*, steelhead *O. mykiss* (broodstock from a hatchery that wasn't ever released), inconnu *Stenodus leucichthys*, broad whitefish *C. nasus*, lake whitefish, humpback whitefish, least cisco *C. sardinella*, and round whitefish *Prosopium cylindraceum*. Known anadromous fish included coho salmon *O. kisutch*, sockeye salmon *O. nerka*, steelhead, Dolly Varden, inconnu, broad whitefish, humpback whitefish, least cisco, Bering cisco *C. laurettae*, and Arctic cisco *C. autumnalis*. Strontium graphs of known freshwater fish had low point-to-point variability and low concentration levels of Sr compared to those of known anadromous fish, which had low levels of Sr in their cores, reflecting their freshwater natal environments, and areas where Sr concentration levels rose precipitously, reflecting periods of time spent in marine water.

Radio Telemetry

Two hundred twenty-two radio transmitters were deployed on Tanana River humpback whitefish between 2000 and 2003 to identify major patterns of migration, migration distances, and seasonal habitat use. Humpback whitefish were captured for tagging during the early summer feeding season in six different wetland areas; four in the upper region of the study area and two in the lower region. In the upper region, transmitters were deployed in the Kalutna River in 2000, Fish and Tenmile lakes in 2001, and Scottie Creek and a second deployment in Tenmile Lake in 2002. These upper region tagging areas were within 100 km of the confluence of the Nabesna and Chisana rivers. In the lower region, transmitters were deployed at Mansfield and Healy lakes in 2003. These lakes were located approximately 180 and 330 km downstream, respectively, from the confluence of the Nabesna and Chisana rivers (Figure 1).

Radio transmitters operated in the 150 MHz range during the first year and for administrative reasons were changed to the 162 MHz range for all subsequent deployments. There were as many as 16 transmitters on each frequency at any one time, but they were digitally coded for unique identification. The transmitters weighed about 9 g in the air, and were approximately 5 cm long and 1 cm in diameter. They were each equipped with a whip antenna about 42 cm long. The transmitters were programmed for two different activity schedules. Most (n = 190) were programmed to turn on at the time of surgery and transmit every 3 s for 24 weeks, go dormant for 16 weeks during the winter, and then begin transmitting again until the batteries expired. They lasted for approximately 13 months, providing a full year-long record of seasonal movements. A smaller group of transmitters (*n* = 32) deployed during 2002 in the second Tenmile Lake tagging event, were programmed to transmit for 2-week periods during late September (spawning period), late January (overwintering period), and late May (spring feeding period) for 2 years. These provided information on annual fidelity to important habitats and spawning frequency of tagged fish.

Monofilament gillnets with 5 cm stretch mesh webbing were utilized for fish capture. Approximately 5 m of netting was set and constantly monitored until a fish struck the net, at which time the fish was disentangled, placed into a tub of water, and evaluated for tagging. Fish appearing to be unhurt by capture were considered to be suitable candidates for tagging.

Candidate fish were anesthetized and prepared for surgery immediately following capture. They were placed directly into a clove oil anesthetic solution as described by Anderson et al. (1997). Clove oil was diluted in solution to a concentration of 20 mg/L during the first tagging season in 2000, and was increased to 25 mg/L for all subsequent work. Both of these anesthesia solutions were lower in concentration than Anderson et al. (1997) reported using with rainbow trout *O. mykiss*. Fish were considered to be fully anesthetized when they lost equilibrium, rolled over, and became non-responsive to stimulation. Anesthetized fish were measured to the nearest 10 mm and weighed to the nearest 10 g prior to surgery.

Radio transmitters were surgically implanted in candidate fish as outlined by Winter (1996). Anesthetized fish were placed ventral side up in a padded, V-shaped tagging cradle and provided with a constant stream of water over their gills. Anesthesia solution bathed the gills until the first suture was tied. Fresh water was then used until the surgery was complete. All surgical tools, as well as the radio transmitters themselves, were soaked in a Betadine solution prior to use. Scales were removed from the incision area, anterior to the pelvic fins and just to the fish's left of center. An incision, approximately 2 cm long, was then made through the body wall parallel to the long axis of the fish. A grooved director, a narrow metal device about 10 cm long, was inserted into the fish's body cavity towards the vent. A hypodermic needle 25 cm long was then inserted through the body wall posterior to the pelvic fin, its tip meeting the grooved director inside. The needle was then pushed forward along the grooved director, which protected internal organs from the needle tip, until it emerged from the incision. The transmitter antenna was then threaded into and through the needle, the needle and grooved director were removed, the transmitter was inserted into the body cavity, and the antenna exited the body through the posterior needle hole. The incision was closed with monofilament sutures following a simple interrupted pattern, as recommended by Wagner et al. (2000). Most fish required three stitches for adequate closure. A tissue adhesive compound was applied to the wound line and the suture knots as a final step. Upon completion of surgery, fish were placed into a tub of water to recover. Once upright position was achieved, fish were released. Total time from capture to release ranged from 12 to 18 minutes per fish.

Regular boat and aerial surveys were conducted to locate radio tagged fish. Surveys were repeated at approximately 3 to 4-week intervals while the transmitters were active, and more frequently during the late fall when many of them were expected to be in spawning habitats. Additionally, three fixed receiving stations were established to record the passage of radio tagged fish. One was on the Tanana River about 190 km downstream from the confluence of the

Nabesna and Chisana rivers (Figure 1). This station was active throughout the project. The other two stations were located on the outlet streams of Mansfield and Healy lakes during 2003 and 2004 when transmitters from those areas were active.

Humpback whitefish are known to concentrate in swiftly-flowing, gravel-substrate regions of rivers to spawn in the late fall (Alt 1979; Fleming 1996). The presence of radio-tagged fish in these types of habitats (as indicated by the presence of visible riffles and gravel bars in the river bed) in late September and early October indicated probable spawning habitats. Fish present in spawning habitats were classified as "spawners", and those that remained through the fall in feeding lakes or in flat-water, soft-substrate habitats (as indicated by the absence of riffles or visible gravel bars and the presence of mud or silt banks in the river bed) were classified as "nonspawners".

Fish were judged to be alive if they moved 2 km or more between aerial surveys. Position data from several aerial surveys of transmitters known to be immobile found that the assigned positions were always within 1 km of the actual position. In a similar manner, Fleming (1996) found that his mean aerial survey location error, based on 139 position estimates of known location transmitters, was 1.04 km. It was important to err on the conservative side when evaluating a fish's status, so a position change of 2 km between surveys was selected as indicating movement, and therefore life. It was possible that fish moving less than 2 km from a previous location were also alive, particularly in some of the small wetland systems of the region, but the determination could not be made based on observed movement in those situations. Known mortalities were those fish that were harvested or where predation was verified, as when a transmitter was tracked to a bald eagle *Haliaeetus leucocephalus* nest.

Overwintering and feeding habitats were identified based on fish locations during early and late winter (transmitters were inactive between mid-November and late March), and early summer respectively. Most transmitters (n = 190) were designed to be active for 13 months, which included two annual feeding seasons, the year in which they were tagged and the year following tagging. Annual survival rates for each tagging group individually and for all groups combined were the proportion of tagged fish known to be alive in the spring following tagging. Fidelity rates were the proportion of fish known to have survived for one year following tagging that returned to the same wetland system in which they were tagged. Confidence intervals for annual survival and feeding habitat fidelity rates were estimated based on the binomial probability distribution (Thompson 1992).

It is the currently accepted perspective that whitefish species, including humpback whitefish, practice a spawning routine where they may spawn one year and skip the next one or more years until they accumulate enough energy reserves to spawn again (Reist and Bond 1988; Lambert and Dodson 1990). Lambert and Dodson (1990) refer to this routine as "skip-spawning". If this is true, then we could expect about half or less of the mature population to be present in spawning areas each fall, and none two years in a row. If, however, some fish do spawn on sequential years, then a larger proportion of the population would be in spawning areas each fall. The incidence of sequential year spawning was evaluated in two ways. In the first case, a 1-tailed test of the null hypothesis that the proportion of tagged fish from each sample group was ≤ 0.5, versus the alternative hypothesis that the proportion was >0.5, was evaluated with a binomial, one-sample, proportion test. Significant differences were based on $\alpha = 0.05$. In the second case, a sample (n = 32) of long-duration transmitters was deployed specifically to determine if any humpback whitefish were present in spawning areas during two successive years. Fish tagged with long-duration transmitters were followed through two full annual cycles of spawning, overwintering, and feeding periods. Annual survival and feeding habitat fidelity data from long-duration transmitters were combined with those from the shorter duration transmitters.

Nabesna River Spawning Area Survey

A suspected spawning area in the Nabesna River was visited in late September of 2001 and 2002 to verify that humpback whitefish present in the area were in spawning condition, and to determine if non-spawning fish were also present. The goal was to capture and evaluate the spawning condition of at least 200 humpback whitefish. A 90 m beach seine with 3 m depth and 1 cm stretch-mesh size was used for capture. Sampling sites were selected based on the presence of radio-tagged fish in the vicinity and a suitable streambed for setting a beach seine. Beach seines were pulled at five sites that were widely distributed within the suspected spawning area.

When humpback whitefish approach spawning time, a number of detectable physiological changes occur. The testes of males swell and turn from a reddish color to white. The swelling is minor relative to body size, so the body does not become swollen or distended. Distinct tubercles, or bumps, develop on scales along the lateral sides of spawning condition males, as well as across their heads (McPhail and Lindsey 1970; Vladykov 1970). When spawning males are handled, milt flows from the vent (Snyder 1983). The egg masses of females expand greatly within the body cavity, becoming as much as 15% or more of the total body mass (Bond and Erickson 1985; Clark and Bernard 1988). Females in this condition are referred to as gravid, and the body cavity appears to be highly distended or swollen. When spawning females are handled, eggs flow freely from the vent (Snyder 1983). Females in spawning condition also develop breeding tubercles, but they are not as distinct as those on the males (McPhail and Lindsey 1970; Vladykov 1970). The presence and distinctiveness of tubercles, flowing milt or eggs, and normal or distended body form were used to determine the spawning condition and sex of each fish. Nine fish were injured during capture and were sacrificed to confirm external determinations and all others were released unharmed. A sub-sample of fish was measured to the nearest 1 cm. A Kolmogorov-Smirnov goodness of fit procedure (Zar 1999) was used to test the null hypothesis that the length distribution of the samples collected during the summer in feeding habitats was not different than the length distribution of the samples collected during the fall in spawning habitat.

Results

Systematic Sampling

Two hundred and seventy-five humpback whitefish were captured during the sampling events in 1998; no other whitefish species were encountered. The sample consisted of 39% female and 61% male. Mean length, weight, and age were 402 mm (range 303 to 545 mm), 803 g (range 240 to 1,800 g), and 6.7 years (range 1 to 26 years) respectively. Highly significant ANOVA F tests ($P < 0.001$) of length, weight, and age data indicated there were differences between sample sites. Follow-up analyses with Tukey's multiple comparisons procedure revealed that humpback whitefish in Tenmile Lake were significantly longer, heavier, and older than they were in the other sampling sites (P = 0.011 in all cases) (Figure 4). The mean length of humpback whitefish in Tenmile Lake was 449 mm, compared to 393-396 mm for Fish Lake, Kalutna River, and Moose Creek samples. The mean weight of humpback whitefish in Tenmile Lake was 1,256 g, compared to 732-759 g for Fish Lake, Kalutna River, and Moose Creek samples. The mean age of humpback whitefish in Tenmile Lake was 10 years, compared to 6 years or less for Fish Lake, Kalutna River, and Moose Creek samples. When analyzed separately from Tenmile Lake samples, the lengths (P = 0.716), weights (P = 0.612), and ages (P = 0.465) of fish from Fish Lake, Kalutna River, and Moose Creek were similar to each other.

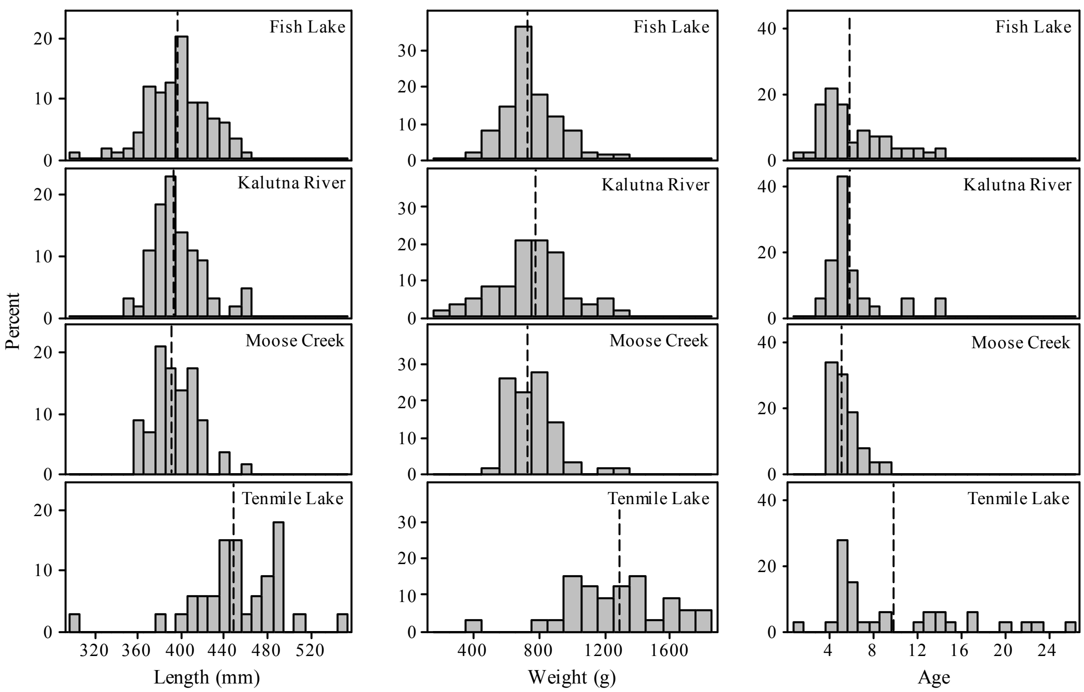

Figure 4. Length, weight, and age distributions of humpback whitefish sampled in 1998 from four sites in the upper Tanana River drainage. Mean values are indicated by the vertical dashed line in each figure.

The modal age of humpback whitefish from the combined collections was 5 years, and over 80% of the sample fish were between 3 and 9 years of age (Figure 5, middle panel). Length at age boxplots revealed substantial overlap in fish size across age classes (upper panel). Based on these data, a fish 420 mm long, for example, could be a large fish at age-5 or a small fish at age-13 (see dashed line in upper panel). Logistic regressions of age frequency data from age 5 and up illustrating the decline in abundance with age that is due to progressive mortality, and from age length data illustrating the decline of growth rate with age (bottom panel), are similar to a model of the expected population structure for long-lived Arctic lake fish, as presented by Power (1978). The estimated annual survival rate for the population, based on age frequency data (catch curve analysis) between the ages of 5 and 15 years, was 0.69 (95% CI ranged from 0.64 to 0.74).

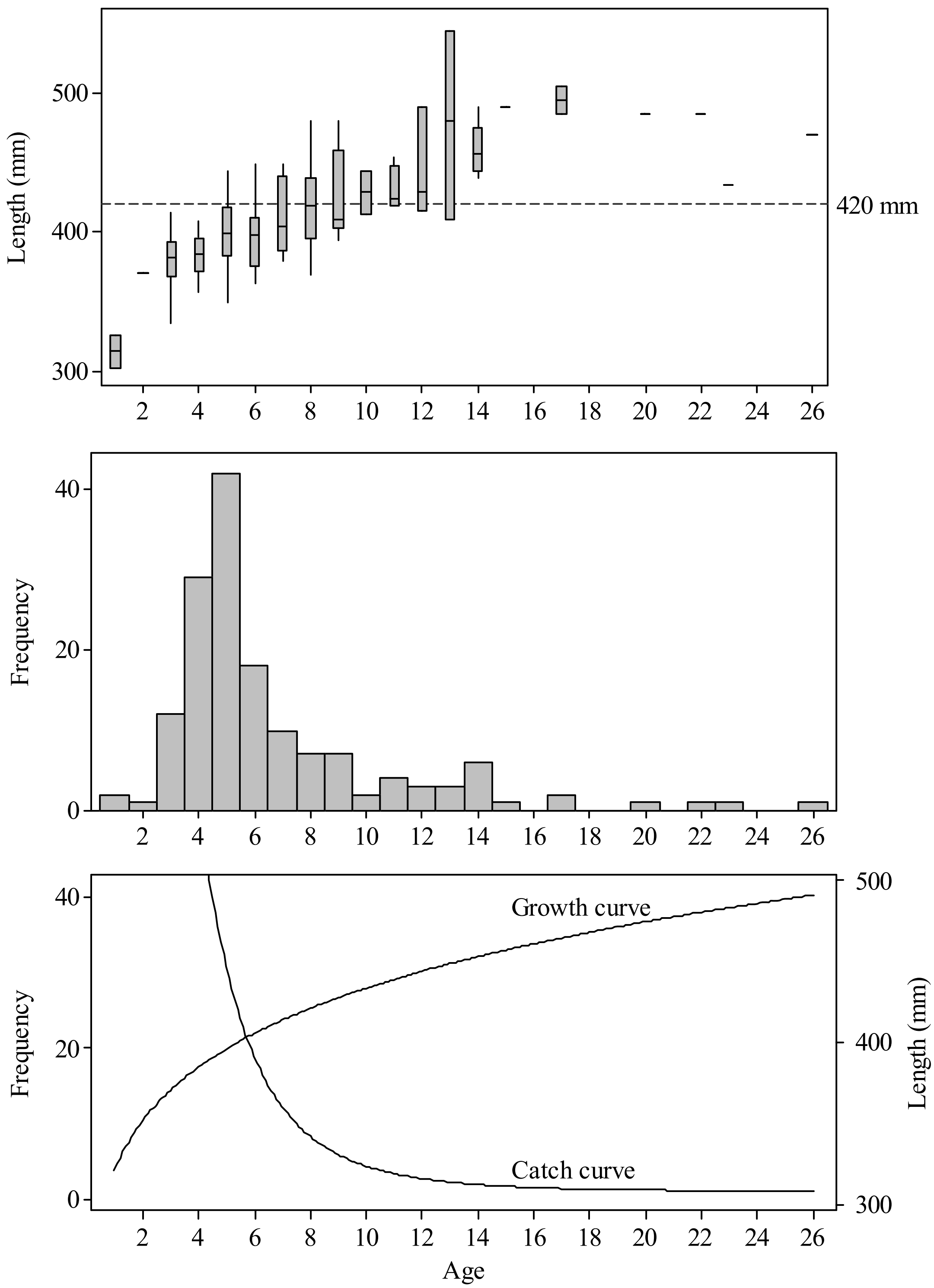

Figure 5. Length at age boxplots (top panel), catch at age histogram (middle panel), and growth (length) and catch (frequency) curves illustrating their general relationships with fish age (bottom panel) based on catch statistics of upper Tanana River drainage humpback whitefish (*n* = 153).

Catch rates varied among sample sites and tended to be greater in July than in August (Figure 6). Fish Lake had the highest catch rates of all, exceeding 3.5 fish per hour per net during the mid-July sampling period. Catch rates in the Kalutna River exceeded 1.6 fish per hour per net during the early July sampling period, and Moose Creek also produced more than 1.6 fish per hour per net during the mid-July sampling period. Fish were caught in Tenmile Lake at a maximum rate of 1.3 fish per hour per net during the early July sample period. When all sampling sites were considered together and a seasonal CPUE was calculated based on the total catch and total net hours fished, it became clear that catch rates were at a maximum during mid-July at 1.58 fish per hour per net (total catch in mid-July was 101 fish), and declined by late August to less than 0.1 fish per hour per net (total catch in late August was 6 fish).

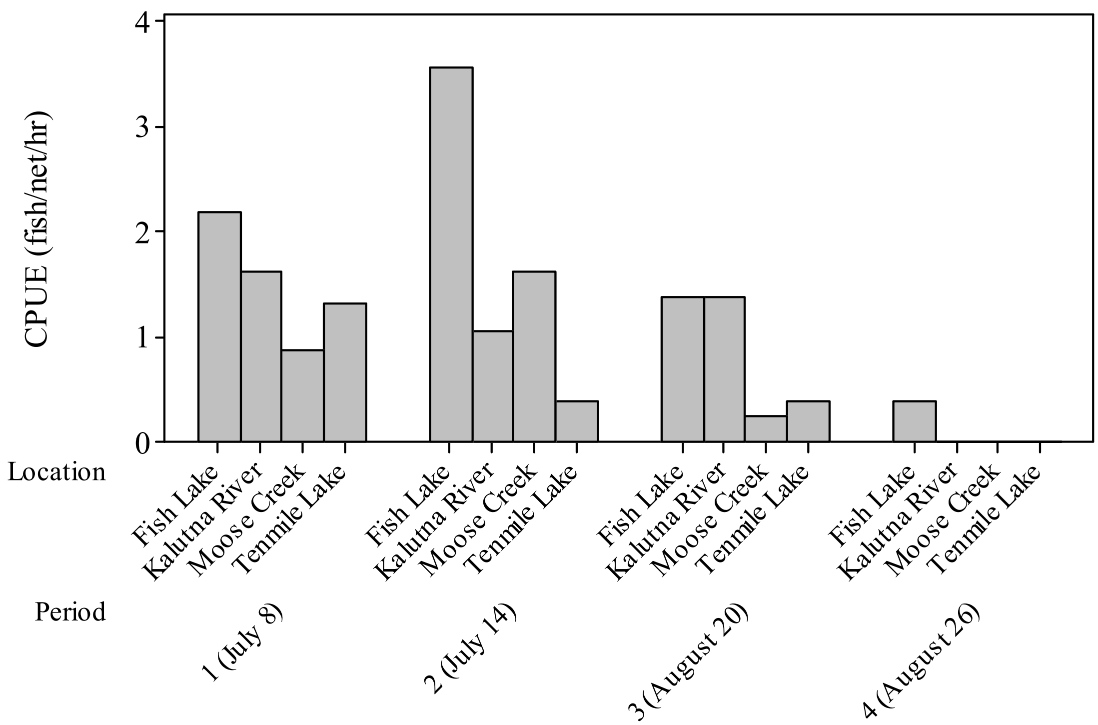

Figure 6. Catch rates expressed as CPUE (fish/net/hr) for the sampling component of the upper Tanana River humpback whitefish study by sample location and time period.

Otolith Chemistry

Otolith Sr distribution was evaluated along core to margin transects for ten humpback whitefish samples collected in the upper Tanana River drainage. Strontium concentration graphs from all ten fish were consistent with those of known freshwater resident fish and did not show the precipitous peaks of Sr concentration seen in the otoliths of known anadromous fish (Figure 7). These data indicate that few if any humpback whitefish from the upper Tanana River populations range downstream to marine environments.

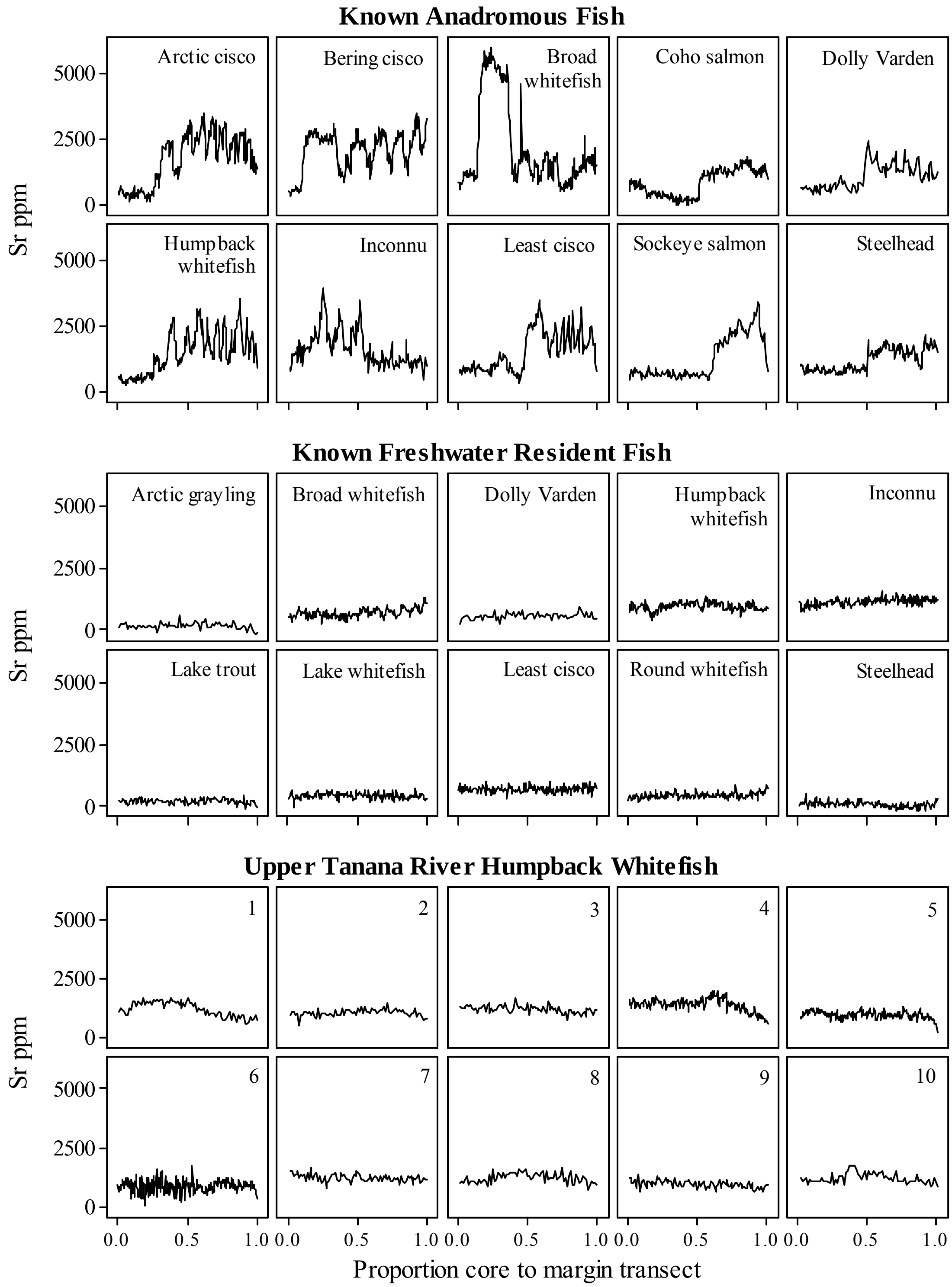

Figure 7. Graphs of otolith Sr concentration along core to margin transects of 10 known anadromous and 10 known freshwater resident salmonid fish of several species, and 10 unknown life history humpback whitefish from the upper Tanana River.

Radio Telemetry

Most radio-tagged humpback whitefish appeared to be mature adults, and only in the Mansfield and Healy lakes tagging events were a substantial number of fish captured that were small enough (length < 36 cm; Alt 1979) that they could be classified as immature. The overall mean length of tagged fish was 429 mm (range 320 to 510 mm) (Table 1). The overall mean weight was 1,060 g (range 390 to 1,800 g). Sex could not be determined by outward appearance in the spring and early summer when the tagging events took place.

Table 1. Radio transmitters deployed, and length and weight statistics from the seven tagging groups (individually and combined) of Tanana River humpback whitefish.

	Sample	Length (mm)		Weight (g)	
Collection	(*n*)	Mean	Range	Mean	Range
Kalutna River	32	435	390 to 510	1,140	850 to 1,660
Fish Lake	31	443	400 to 490	1,100	840 to 1,470
Tenmile Lake (2001)	32	456	390 to 510	1,310	870 to 1,790
Tenmile Lake (2002)	32	456	370 to 510	1,270	750 to 1,800
Scottie Creek	32	419	380 to 450	910	650 to 1,780
Mansfield Lake	34	394	320 to 510	760	390 to 1,580
Healy Lake	29	402	340 to 470	910	540 to 1,480
Total tagged fish	222	429	320 to 510	1,060	390 to 1,800

Fish tagged in the four upper region wetlands, Kalutna River, Fish Lake, Tenmile Lake, and Scottie Creek (Figure 2) were only located in the upper region and none were recorded moving downstream past the remote station on the Tanana River (Figure 1). They moved freely between the wetlands in which they were tagged and the river system. No barriers to movement between these environments were apparent, except perhaps between Tenmile Lake and the Chisana River and Fish Lake and the Chisana River during winter due to dewatering or freezing of the shallow (>0.5 m) outlet streams, however, this was not verified on the ground.

Similar to fish in the upper region of the study area, fish tagged in Healy Lake (Figure 1) had free passage between the lake and the Tanana River. The lake was shallow (≤1 m) except for a channel through which the Healy River flowed (~ 2 m depth). Flow between Healy Lake and the Tanana River appeared to be maintained throughout the year. Radio-tagged fish from Healy Lake were never located farther than 50 km downstream from the lake, but one fish traveled over 300 km upstream into the Nabesna River during the fall.

Mansfield Lake is situated relatively far from the Tanana River and fish passage between the two environments is achieved through Mansfield Creek, a small stream that meanders across the floodplain for about 16 km. Flow rates were low throughout the summer of 2003, the summer in which the tagging event occurred in Mansfield Lake. Beavers *Castor canadensis* took advantage of the low flows that summer and constructed three dams across Mansfield Creek in mid-summer within 2 km of the lake outlet, effectively blocking fish passage. One radio-tagged fish from Mansfield Lake had migrated to the Tanana River in early June, prior to dam construction, but the rest were confined to the lake throughout the late summer and fall. Residents of Tanacross removed the three beaver dams at the end of September, the beginning of spawning season, at which time eight radio-tagged fish exited the lake and migrated into the Tanana River. One fish migrated 140 km downstream and was located near Healy Lake in the late fall, while the others that left the lake stayed near or upstream of the mouth of Mansfield Creek. Two fish migrated into the Nabesna River spawning area in late October, almost three weeks after other radio-tagged fish had moved to overwintering habitats. Due to beaver dams obstructing free passage of Mansfield Lake fish during the summer, their observed habitat use through the seasons is not thought to be what it would have been under normal circumstances, and was therefore not comparable with data from the other wetlands.

General seasonal movement patterns were similar for all of the tagging groups from open wetland systems (Mansfield Lake data excluded). Most radio-tagged fish remained in lake systems throughout the early part of the summer, which is thought to be the primary feeding season for the species (Alt 1979; Schmidt et al. 1989; Lambert and Dodson 1990). Beginning in July there was a steady movement of fish from lake systems to the river, where they initially remained near the outlet streams of their tagging lakes. The Healy Lake receiving station revealed that when radio-tagged fish moved from the lake to the river, they tended to stay in the river for the rest of the summer rather than moving between the two environments on some shorter time frame. By late August fish were migrating to distant flowing water locations and were no longer holding position near their tagging lakes. By late September, spawning season for humpback whitefish (Alt 1979), over 70% of fish were in a small number of swiftly-flowing, gravel-substrate habitats rather than in lake or other flat-water, riverine habitats. Fish stayed in these swiftly-flowing, gravel-substrate habitats through early to mid-October, when they migrated back downstream into flat-water, soft-substrate habitats where they remained through the winter. Over 70% of radio-tagged fish overwintered in flat-water, soft-substrate riverine habitats (Figure 8). Most of the remaining fish overwintered in Tetlin Lake, Healy Lake, and the Scottie Creek wetlands, which are open lake systems that maintain flowing water connections to the Tanana or Chisana River. One fish overwintered in Fish Lake and five fish overwintered in Tenmile Lake, which are suspected to be closed systems during the winter. Some fish overwintered more than 100 km away from their spring feeding habitats. Most fish were located in the same locations in November and April, suggesting very little movement during the winter. Beginning in late April, overwintering fish began migrating back to lake systems for feeding. Almost 80% of radio-tagged fish demonstrated that they were alive one year following tagging by migrating from wintering to feeding habitats. Over 85% of fish known to be alive in the spring, were present in the same wetland areas where they were tagged, indicating a high level of fidelity to familiar feeding habitats.

Fish radio-tagged at the mouth of the Kalutna River were found to use Tetlin Lake for feeding in the spring following tagging. Twenty-seven of 28 fish known to be alive a year following tagging were present in Tetlin Lake, while 1 fish moved to Tenmile Lake. It had been the perception at the time of tagging that Kalutna River fish were part of a feeding population from that site. The telemetry data, however, indicated that they were members of the Tetlin Lake feeding group. Thus, it was hypothesized that Kalutna River fish had migrated from Tetlin Lake to the Tanana River just prior to the radio tagging event. The radio-tagged fish confirmed this hypothesis by migrating from Tetlin Lake out to the Tanana River during the second summer. For these reasons, those fish found in Tetlin Lake during the feeding season in the year following tagging were considered to have exhibited feeding site fidelity.

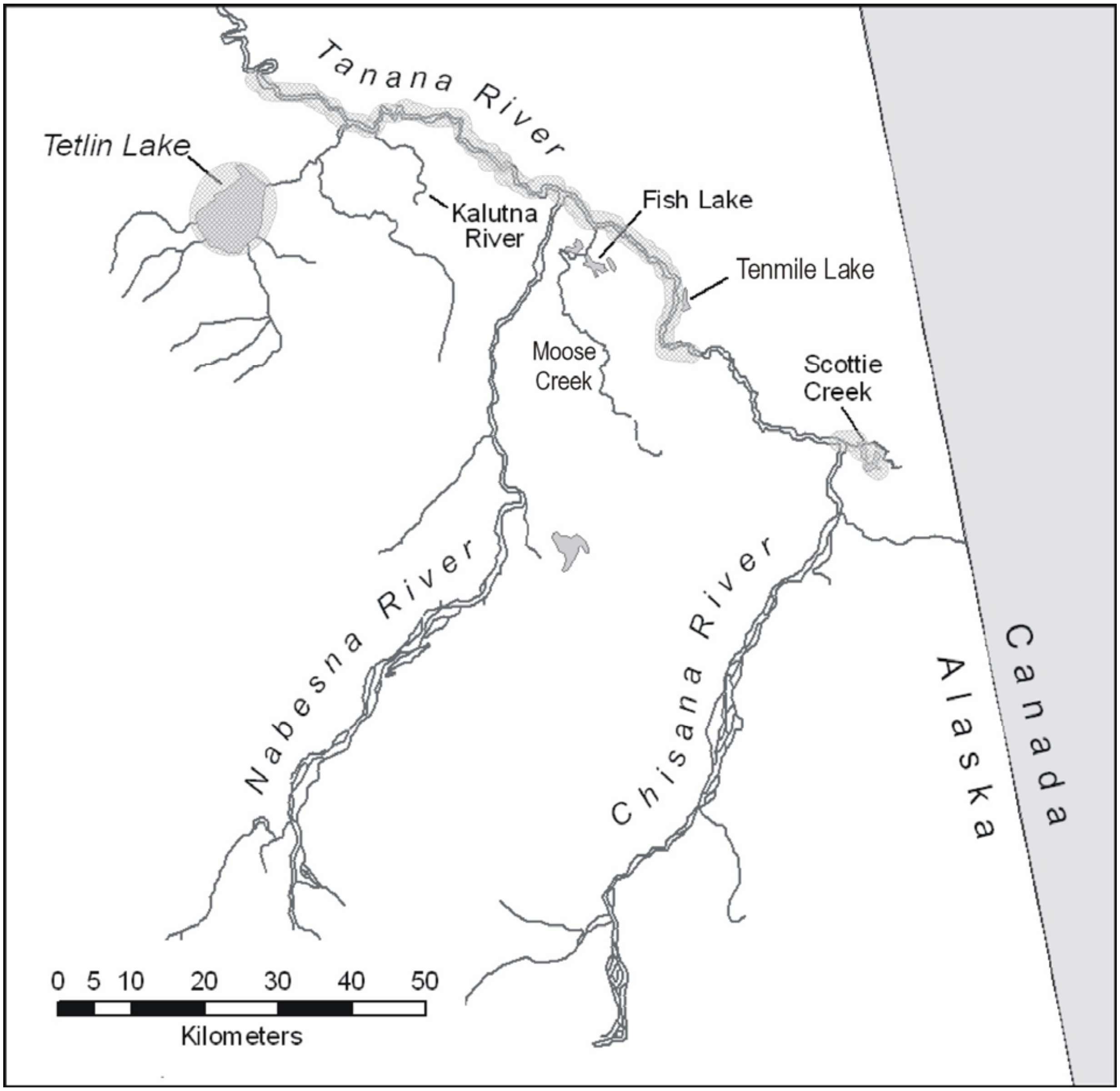

Figure 8. Primary humpback whitefish overwintering areas in the upper region of the study area included flat-water, riverine habitats in the Tanana and Chisana rivers, and in Tetlin Lake and the Scottie Creek wetlands (shaded areas).

The presence of radio-tagged fish in swiftly-flowing, gravel-substrate habitats in late September and early October indicated probable spawning areas. Two such areas were identified in the upper region: one in the Nabesna River encompassing a 20 km reach beginning approximately 15 km upstream from the mouth; and another in the Chisana River encompassing a 30 km reach in the vicinity of Scottie Creek (Figure 9). The proportion of spawners among the tagging groups was significantly greater than 0.5 for four of the groups from the upper region, as well as for the combined total of all radio-tagged fish except those from Mansfield Lake ($Z > 2.8$ and $P < 0.005$ for all significant tests) (Table 2). Two fish from Mansfield Lake and one fish from Healy Lake migrated into the Nabesna River, and none of the fish from these two sites went into the upper Chisana River.

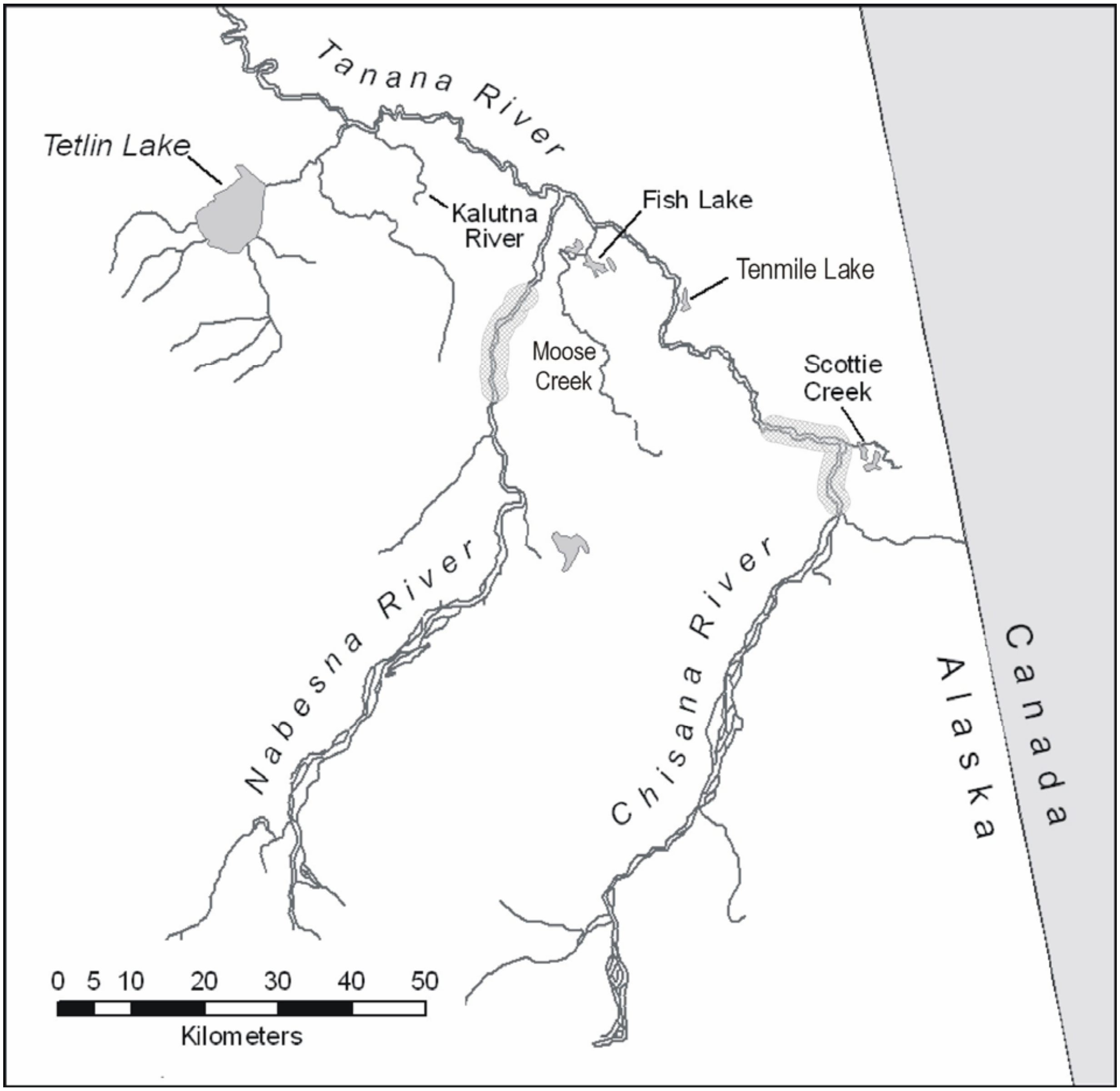

Figure 9. Humpback whitefish spawning areas in the Nabesna and Chisana rivers (shaded areas).

The distribution of radio-tagged fish into the two swiftly-flowing, gravel-substrate reaches of the upper region during spawning season varied for each tagging group (Table 2). More fish from the Kalutna River and Fish Lake groups migrated to the Nabesna River during spawning season than to the Chisana River. By contrast, more fish from the Tenmile Lake and Scottie Creek groups migrated to the Chisana River during spawning season than to the Nabesna River. Fish from Mansfield Lake were prevented from migrating out of the lake during late summer when other radio-tagged fish were migrating to spawning areas. Their observed distribution during spawning season, 25 fish in Mansfield Lake, 1 unaccounted for, 6 in the Tanana River, and 2 fish in swift-flowing, gravel substrate reaches of the Nabesna River, is therefore not thought to be representative of the actual spawning distribution of the group. Fish from Healy Lake appeared to migrate from the lake to several potential spawning habitats: approximately 30 km up the Healy River; the Tanana River near the Healy Lake outlet; in a swiftly flowing braided region of the Tanana River approximately 110 km upstream from Healy Lake; and 350 km upstream to the Nabesna River (Figure 10).

Table 2. Spawning proportion and geographic distribution of radio-tagged humpback whitefish from the seven tagging groups. Sample size is the number of tagged fish minus harvested fish prior to spawning season. Data in this table from the Tenmile Lake 2002 group, which were equipped with 2-year duration transmitters, reflect information from the first season only. Spawning proportions that were significantly greater than 0.5, as determined by the binomial, one-sample, proportion test, are indicated with an asterisk. Confidence intervals were estimated based on the binomial distribution (Thompson 1992).

Tagging sites	Sample size	Spawning proportion (95% CI)	Chisana spawners	Nabesna spawners	Tanana spawners	Healy spawners
Kalutna River	32	0.75* (0.60-0.90)	5	19	0	0
Fish Lake	30	0.80* (0.66-0.94)	10	14	0	0
Tenmile Lake 2001	32	0.81* (0.68-0.95)	16	10	0	0
Tenmile Lake 2002	30	0.83* (0.70-0.97)	17	8	0	0
Scottie Creek	32	0.59 (0.42-0.76)	17	2	0	0
Mansfield Lake	34	0.06 (na)	0	2	0	0
Healy Lake	29	0.45 (0.27-0.63)	0	1	7	5
Combined total except Mansfield Lake	185	0.71* (0.64-0.77)	65	54	7	5

The overall annual survival rate, considering all groups except Mansfield Lake, was 0.77 (Table 3). Survival rates of fish from the different groups ranged from 0.52 (Healy Lake group) to 0.90 (Fish Lake group). Of all radio-tagged fish known to have survived for a full year following tagging, excluding those from Mansfield Lake, 86% were found to have returned to the lake systems in which they were tagged. Fidelity rates of fish from the different groups ranged from 0.61 (Fish Lake) to 0.96 (Kalutna River tagging group). Data from the Mansfield Lake group are presented (Table 3) but were not included in the group calculations. The criteria for determining survival required that a fish had to have moved more than 2 km from a previous position. As such, some relatively sedentary fish could be alive, yet indistinguishable from those that had died. Therefore, annual survival and habitat fidelity rates must be considered as minimum estimates.

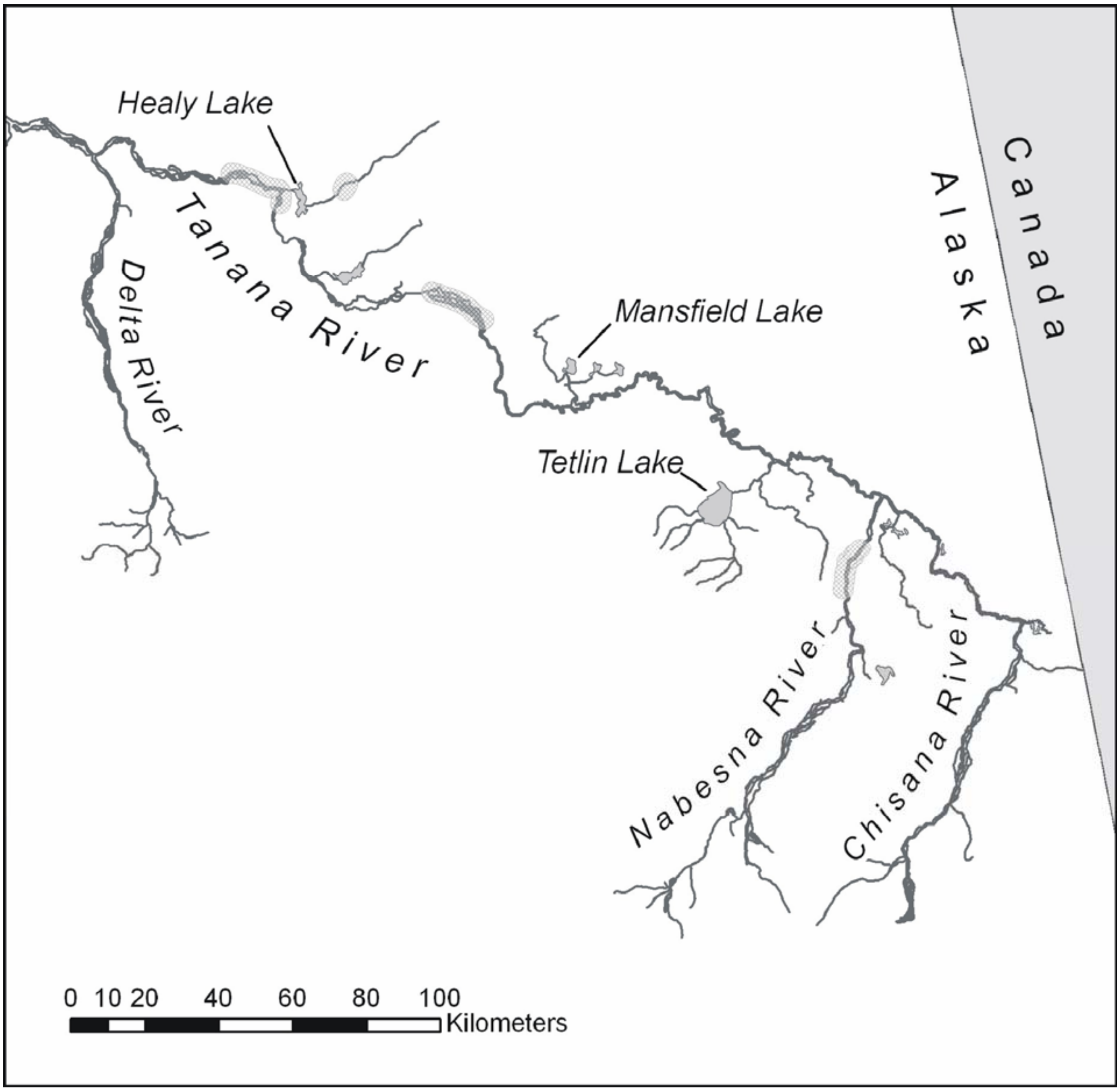

Figure 10. Probable spawning areas used by humpback whitefish from the Healy Lake feeding group (shaded areas).

Long-duration transmitters deployed in Tenmile Lake during the feeding season in late May 2002, revealed that many mature humpback whitefish spawn on successive years. Thirty-two fish were initially tagged and two were harvested later that same summer. The effective sample size during the first spawning season was therefore 30 fish. Of these 30 fish, 25 migrated to previously identified spawning habitats in the Nabesna and Chisana rivers, and the other 5 fish remained in Tenmile Lake or moved to flat-water, soft-substrate regions of the Chisana and Tanana rivers. Following spawning, fish retreated downstream and overwintered in the lower reaches of the Chisana River and the Tanana River. During the feeding season of year 2, 24 of the 25 fish that had spawned on year 1 were known to be alive, and 22 returned to Tenmile Lake to feed. Sixteen of 24 fish that had spawned on year 1 migrated to the same spawning areas again on year 2. None of the fish switched spawning areas.

Table 3. Annual survival and feeding site fidelity rates for groups of radio-tagged humpback whitefish in the upper Tanana River drainage. Data in this table from the Tenmile Lake 2002 group, which were equipped with 2-year duration transmitters, reflect information from the first year only. Confidence intervals were estimated based on the binomial distribution (Thompson 1992).

Tagging groups	Sample size	Known alive at one year	Survival rate (95% CI)	Returned to home lake after 1 year	Feeding site fidelity rate (95% CI)
Kalutna River	32	28	0.88 (0.71-0.96)	27	0.96 (0.90-1.00)
Fish Lake	31	28	0.90 (0.74-0.98)	17	0.61 (0.43-0.79)
Tenmile Lake 2001	32	28	0.88 (0.76-0.99)	24	0.86 (0.73-0.99)
Tenmile Lake 2002	32	24	0.75 (0.57-0.89)	22	0.92 (0.81-1.00)
Scottie Creek	32	22	0.69 (0.53-0.85)	20	0.91 (0.79-1.00)
Mansfield Lake	34	17	0.50 (na)	17	1.00 (na)
Healy Lake	29	15	0.52 (0.34-0.70)	14	0.93 (0.81-1.00)
Combined total except Mansfield Lake	188	145	0.77 (0.70-0.83)	124	0.86 (0.80-0.91)

Fifteen fish equipped with long-duration transmitters were known to have survived through two full years, and 13 of these were located during both winters. Only those 13 fish provided data regarding overwintering site fidelity. During the winter, fish from Tenmile Lake were distributed along approximately 100 km of the Chisana and Tanana rivers, from the mouth of the Tetlin River to a few km upstream from Tenmile Lake, and in the lower few km of Scottie Creek. They were judged to have exhibited overwintering site fidelity if they were located during the second winter within 2 km of where they were located during the first winter. This occurred for 6 of 13 fish. The other seven fish overwintered at sites ranging from 2.6 to 57.2 km apart.

Nabesna River Spawning Area Survey

Beach seines were pulled at five locations in the Nabesna River spawning area in late September 2001 and 2002. The largest single catch was 219 fish, including 215 humpback whitefish, 3 round whitefish, and 1 Arctic grayling. The total catch from the five sets included 430 humpback whitefish, 4 round whitefish, 3 Arctic grayling, and 1 longnose sucker *Catostomus catostomus*. Spawning condition was evaluated for 428 of 430 humpback whitefish examined in the survey; two fish escaped before being fully examined. All but one fish from this sample were judged to be in spawning condition, and the one nonspawning individual was a juvenile fish measuring approximately 150 mm. Sex was determined for 402 humpback whitefish. Of these, 22% were male (n = 88) and 78% were female (n = 314). Length measurements were recorded for 224 humpback whitefish captured in the Nabesna River spawning area. The mean length was 400 mm, the mode was 390 mm, and lengths ranged from 330 mm to 510 mm. Minimum size at maturity, based on the spawning area sample, was 330 mm for females and 340 mm for males. The length distribution of the samples collected in feeding habitats during summer 1998 was similar to the length distribution of the samples collected in spawning habitat during fall 2001 and 2002 (Kolmogorov-Smirnov test statistic D = 0.0659, P = 0.6057) (Figure 11).

The earliest evidence of spawning in the Nabesna River spawning area occurred during the last few days of September. During the 2001 sampling project in the Nabesna River spawning area, which took place on September 28, males leaked milt when handled, eggs could be expressed from gravid females, and a few females were found to be in post-spawning condition. In addition, a gravid female round whitefish captured in the area was found to have consumed what appeared to be a stomach-full of humpback whitefish eggs. During the 2002 sampling project, which took place on September 26 and 27, all males leaked milt when handled, but eggs could not be expressed from any of the females despite the fact that they appeared to be very gravid.

Discussion

Humpback whitefish were the most abundant whitefish species encountered in the open waterways of the upper Tanana River drainage. Three types of sampling occurred during this project: systematic sampling in feeding habitats during the course of the summer; directed sampling to catch fish for the radio-tag component; and beach-seine sampling in spawning habitat during spawning season. Sampling for radio-tagging candidates was directed to a certain number of fish and as soon as the target sample number was attained, the fishing activity stopped. As a result, the radio-tagged sampling procedure was not systematic and did not necessarily represent the overall population of the upper Tanana River drainage. Representative samples of the overall humpback whitefish population are thought to have been obtained from the systematic sampling in feeding habitats and the beach-seine sampling in spawning habitats.

The 5 cm stretch mesh gillnets set in lakes are effective on humpback whitefish ranging in length from about 15 to 50 cm in length, which encompasses all age groups except age 0 and small age 1 individuals. The 1 cm stretch mesh beach-seine used in the fall would have captured fish as small as 10 cm or less, which would have included age 0 individuals if they had been present. It is notable that the length distributions of these two representative sample groups were so similar (Figure 11), suggesting that the samples were drawn from the same population.

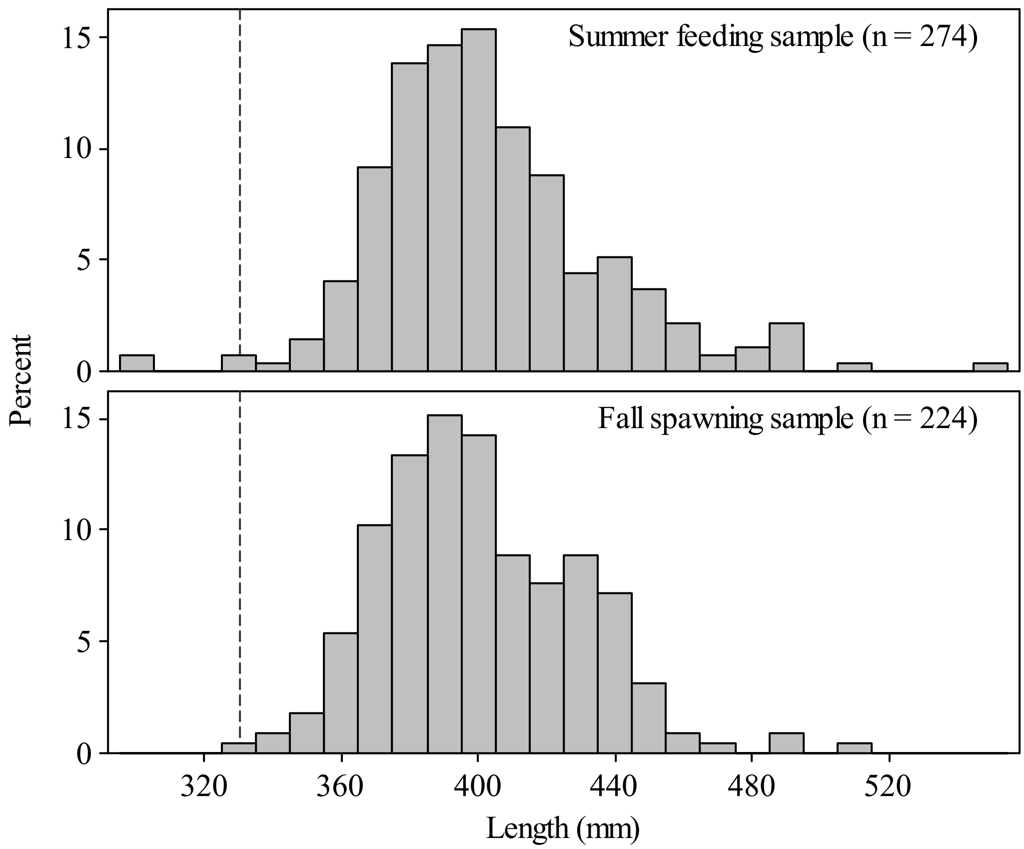

Figure 11. Length distributions of humpback whitefish from the 1998 sampling project, when fish were collected in the summer from feeding habitats in the upper Tanana River drainage, and the 2001-2002 sampling project, when fish were collected in the fall from the Nabesna River spawning area. The dashed vertical line at 330 mm represents the size of the smallest mature humpback whitefish found on the Nabesna River spawning area.

Most humpback whitefish encountered during this project in the upper Tanana River drainage were of a size that would indicate maturity. All the fish represented in the length distribution histogram from the spawning area (Figure 11, lower panel) were in spawning condition, and therefore mature, while maturity of fish sampled in feeding habitats was not specifically investigated. The similarity of length distributions between the feeding and spawning habitat samples indicated that the feeding fish were predominantly mature also. Hilborn and Walters (1992) caution that representative sampling is difficult to achieve because fish of different size or age classes often distribute themselves unequally within the aquatic environment, and are not necessarily equally vulnerable to the capture methods. Nevertheless, it must be assumed that the same downstream larval distribution mechanisms that have been documented for whitefish species in Asian and Scandinavian rivers (Naesje et al. 1986; Shestakov 1991; Bogdanov et al. 1992) are also operating for Alaska whitefish populations. As such, juvenile humpback whitefish were expected to be far downstream from the spawning areas. Additionally, sampling projects conducted in lower drainage or estuarine habitats elsewhere collect reasonable samples of juvenile and mature whitefish (Bond and Erickson 1985; Moulton et al. 1997) suggesting that when juvenile fish are present, they are captured too. All this considered, it is thought that sampling data from the feeding and spawning habitats were representative of the humpback whitefish population in the upper Tanana River drainage, and that the primary demographic group represented was the mature component.

The comparisons of mean lengths, weights, and ages from humpback whitefish collected in the four feeding habitat sampling sites indicated that there was an underlying structure to their geographic distribution. Fish collected in Tenmile Lake were significantly larger and older than those in the other sample collections (Figure 4). Initial theories regarding this phenomenon were that there could be a genetic component to the difference, or that habitat quality was variable leading to differential growth and survival rates. Lindsey (1963) and Fenderson (1964) both documented sympatric populations of lake whitefish with different morphological characteristics, feeding habits, and spawning seasons, so it was reasonable to consider a genetic component to the observed differences among groups. If the observed size and age structure was the result of a habitat factor (i.e., Tenmile Lake was better habitat than other locations), then: A) fish in the region were non-migratory with no opportunity to explore for better habitat; B) fish competed for optimal habitat resulting in the larger, older fish occupying Tenmile Lake and preventing additional recruitment; or C) fish randomly recruit to available feeding habitat and return each year with great consistency. All the feeding sample sites were open systems and few immature fish were encountered in the region. The non-migratory hypothesis was therefore not considered to be realistic. Hughes and Reynolds (1994) found that Arctic grayling compete for preferred positions within rivers resulting in larger, older fish in upstream reaches and smaller, younger fish in downstream reaches. Nothing in the literature, however, suggests that humpback whitefish exhibit similar territorial behavior. It became clear, after the radio telemetry data became available, that the most reasonable explanation for the observed size structuring was the last alternative; that fish randomly recruit to available feeding habitat and return each year with great consistency.

Recent technological advances in radio telemetry technology have resulted in reduced transmitter size and increased operational life. Previous telemetry projects with whitefish species, including inconnu, have focused primarily on development of tagging methods and locating spawning habitats (Chang-Kue and Jessop 1983, 1991; McLeod and Clayton 1993; Howland 1997; Brown 2000; Brown and Eiler 2000; Morris et al. 2000; Underwood 2000). Not long ago transmitters small enough for use with whitefish operated for only a few months, which was adequate for the purpose of locating spawning habitats. But the long-term behavior of whitefish species relative to important seasonal habitats remained essentially a mystery. This project is thought to be the first to explore the migratory behavior of humpback whitefish over the course of a year or more.

Radio telemetry data from the four upper Tanana River drainage wetland systems, Kalutna River, Fish Lake, Tenmile Lake, and Scottie Creek, revealed that all tagging groups contained a mix of individuals from two populations: one spawning in the Nabesna River; the other spawning in the Chisana River (Table 2, Figure 9). Both spawning areas are located at the lower-ends of their respective glacial outwash plains, approximately 100 km downstream from the glacier faces (Wiles et al. 2002), in high gradient, swiftly-flowing, gravel-substrate regions of the rivers. They are separated geographically by approximately 120 river km. A majority of fish tagged in the different feeding groups moved out of the lake systems into the river system in mid to late summer and proceeded to migrate to one or the other of the two spawning areas. Fish tagged in the Kalutna River migrated upstream to reach both spawning areas. Fish tagged in the other groups migrated upstream to reach the Chisana River spawning area, but downstream in the Chisana River to get to the mouth of the Nabesna River, and then upstream to reach the Nabesna River spawning area. Nabesna spawners tagged in the Scottie Creek wetlands had to go downstream approximately 100 km before reaching the mouth of the Nabesna River. The concept of a population of whitefish being distributed in some linear fashion between upstream spawning sites and downstream rearing areas requires some elaboration to account for these findings.

The movement of radio-tagged fish from wetland feeding habitats to the river in mid to late summer is consistent with the CPUE data, which recorded high catch rates in all sampled wetland areas in July that declined precipitously by mid-August (Figure 6). Once they moved into the river, most of the tagged fish remained within about 10 km of their respective lake outlet streams for as much as two or three weeks before beginning to migrate to spawning areas. During their initial period in the river the tagging groups remained geographically segregated from each other. As the migration began in earnest in late August and early September, fish from all groups could be found throughout the river system in the upper drainage. By mid-September, most spawners had arrived in spawning areas. A small number of fish continued to trickle in until late September when the migration to spawning areas was over.

Spawning in the Nabesna River began in late September and appeared to conclude by mid-October. The sampling project showed that most fish in the Nabesna River spawning area were imminently ready to spawn by the end of September, and round whitefish found feeding on eggs on September 28 indicated that some spawning had already begun. Kepler (1973) found Arctic grayling feeding on humpback whitefish eggs as early as September 19 in the Chatanika River spawning area, and similarly concluded that the event marked the beginning of the spawning period for that population. Based on these data, the Chatanika River population appears to initiate spawning almost 10 days earlier than the Nabesna River population, but it is likely that the actual start date is somewhat variable from year to year. Radio-tagged fish remained in spawning areas of the Nabesna and Chisana rivers through the first week of October, when they began to migrate downstream into flat-water, soft-substrate habitats. Almost all radio-tagged spawners had retreated from the spawning areas by mid-October indicating that the spawning period was drawing to a close. Hallberg (1989) proposed that most humpback whitefish in the Chatanika River completed spawning by October 10 based on declining harvest rates in the spear fishery there, and tower counts of out-migrating post-spawners. Bidgood (1974) reported that two lake-spawning, lake whitefish populations he studied in Alberta, Canada, begin spawning a few weeks later in the year than the river-spawning populations discussed above. Additionally, spawning activity extended over several months for the lake-spawning populations rather than the two or three week period observed for the river-spawning populations. Habitat conditions faced by river-spawning populations like the ones examined here, probably limit their spawning opportunities to a relatively brief period at the onset of winter.

The physiological consequences for individuals that prepare to spawn on a given year but are prevented from migrating to desired spawning areas, as undoubtedly occurred for many fish in Mansfield Lake during 2003, are unknown. Only eight fish exited the lake after the beaver dams were removed in late September, and only two of those migrated to the Nabesna River spawning area, arriving after all other radio-tagged fish had already retreated downstream. One would imagine that those two fish would not have migrated to the spawning area so late unless they were able to delay final development to spawning readiness. The other six fish stopped in the Tanana River in soft-substrate riverine areas that were characteristic of overwintering habitat. They remained in those areas throughout the winter. It is not clear if they were unable to delay ripening and gave up the migration short of the spawning area, or were non-spawners that year to begin with. It does not seem reasonable that only 2 of 34 (6%) fish tagged in Mansfield Lake were spawners while 45% to 83% of all the other tagging groups were spawners (Table 2). A substantial number of Mansfield Lake fish probably missed the opportunity to spawn that year. Perhaps events that prevent normal migration, like the beaver dams on the outlet stream to Mansfield Lake, are the genesis of new spawning populations; when ripening fish spawn by default where they must, rather than in their natal reach, provided the default habitat is suitable for egg development and subsequent larval survival. Judging from the small number of spawning areas that have been identified, the alignment of these factors may be a rare occurrence.

Fidelity to natal spawning areas has been assumed for whitefish species, but compelling supportive data are sparse. Underwood (2000) and Taube and Wuttig (1998) conducted simultaneous mark and recapture projects on inconnu spawning populations on the Selawik and Kobuk rivers, respectively, during several years in the mid-1990s. The two rivers lie adjacent to each other in northwest Alaska and inconnu from both rivers rear and overwinter in the same estuary system. Subsequent-year recaptures totaling 35 fish on the Selawik River and 43 fish on the Kobuk River all came from the river in which they were originally tagged. No crossovers occurred. A genetic study of the two inconnu populations revealed distinct stock structuring, indicating that gene flow between the two populations was low (Miller et al. 1998). This study was not designed to determine the natal spawning origins of individual fish, but was able to show that there was fidelity to spawning habitats with no crossovers for the 16 humpback whitefish that were found twice in spawning habitats ($n = 5$ in the Nabesna River and $n = 11$ in the Chisana River). There appears to be spawning site fidelity for humpback whitefish in the upper Tanana River drainage, and these telemetry data indicate that virtually all humpback whitefish in the upper region belong to either the Nabesna or Chisana River populations.

Radio-tagged humpback whitefish exhibited a feeding site fidelity rate of 0.86 (Mansfield Lake data excluded) during the course of this project (Table 3). A majority of radio-tagged fish from all tagging groups returned to the same feeding habitats they had used the previous season. No comparable data for humpback whitefish were found in the literature, but Morris (2003) reported similar feeding site fidelity behavior for radio-tagged broad whitefish in coastal drainages of northern Alaska. The tendency to return to familiar seasonal habitats explains how fish in Tenmile Lake maintain a population of larger, older individuals in an open system with multiple feeding habitats. All feeding habitats were occupied by individuals from both spawning populations. The observed size and age differences between feeding habitat groups (Figure 4) are therefore not a genetic effect and must be a habitat effect coupled with the behavioral trait of habitat fidelity. Habitat effects could be the result of improved feeding and growth opportunities for fish using Tenmile Lake, reduced mortality through improved fitness leading to greater survival, reduced levels of predation or harvest, or a combination of these factors.

Annual survival rates for the upper Tanana River humpback whitefish populations were calculated from age frequency data (catch curve analysis) collected in 1998, and determined empirically using radio telemetry data collected during the years 2000 through 2004. Violations of two of the three assumptions listed previously may have occurred with the age frequency data, but they are not thought to have negated the value of the analyses. In the first case, it is unlikely that annual recruitment is constant, however, there is little evidence in the age frequency histogram (Figure 5, middle panel) that great swings in age class abundance occurred during the age interval examined. In the second case, it is unlikely that all fish age 5 and older were available for capture during the sampling events in 1998. Humpback whitefish mature across a range of ages (Alt 1979), so while many fish in the upper region populations mature at age 4 and recruit to feeding habitats the next summer as age 5 fish, others undoubtedly mature at age 5 and become available for the first time in feeding habitats at age 6. Hence, a greater proportion of age 6 fish in the population were available for capture in feeding habitats of the upper region than of age 5 fish. This capture availability disparity between age categories declines with increasing age, and probably masks a slightly lower survival rate for the youngest age classes. Despite these violations of assumptions, it is notable that the annual survival rate estimates from the age frequency calculations and the radio telemetry methods were similar enough that their 95% confidence intervals overlapped (Table 4). When compared with estimates of annual survival rates from populations of lake whitefish experiencing varying levels of exploitation, the estimates from this study are most similar to those experiencing low levels of exploitation or no exploitation at all (Mills and Beamish 1980; Mills et al. 2004). These analyses support the notion that the populations in the upper Tanana River are not being over-exploited at this time.

Table 4. Annual survival rate estimates from catch curve calculations and radio telemetry data from this study, and from catch curve calculations and mark recapture methods applied to populations of lake whitefish experiencing different levels of exploitation. Catch curve survival rate estimates presented here from other studies include only those using fin-ray aging techniques (see Mills et al. 2004 for details of this issue). Estimates from this study include 95% confidence intervals. Reported values from other studies include the mean values of multiple estimates, the number of populations in the sample, and the range of values reported.

Estimate type	Exploitation level	Annual survival rate
Catch curve (this study)	unknown	0.69 (95% CI: 0.64-0.74)
Radio telemetry (this study)	unknown	0.77 (95% CI: 0.70-0.83)
Catch curve[a]	moderate to high	mean = 0.40 (*n* = 4; range: 0.19-0.50)
Catch curve[a]	low	mean = 0.68 (*n* = 6; range: 0.60-0.75)
Catch curve[b]	unexploited	mean = 0.77 (*n* = 13; range: 0.71-0.85)
Mark recapture[a]	low	0.75 (*n* = 1)
Mark recapture[b]	unexploited	mean = 0.73 (*n* = 2; range: 0.70-0.76)

[a](Mills and Beamish 1980)
[b](Mills et al. 2004)

Lambert and Dodson (1990) studied the energetic requirements of a population of lake whitefish that spawned in a small river in the Hudson Bay region of eastern Canada. Their data indicated that individuals could not obtain enough energy during the brief feeding season each year to support sequential year spawning, and proposed that they spawned every other year instead. This ecological concept is widely considered to be the rule for many northern fish species and leads to the expectation that approximately 50% of mature whitefish populations should be in non-spawning condition each year. Definitive empirical evidence, however, has been elusive primarily because representative samples of widely dispersed populations are difficult or impossible to obtain. As a result, most direct evidence supporting the alternate-year spawning theory is limited to findings of at least some mature fish in non-spawning condition during the fall (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 theory directly, and suggested that repeat spawning might be more prevalent than commonly thought. Other evidence that sequential year spawning might be common among whitefish populations involves recaptures of dart-tagged spawning fish from one year being recaptured on spawning grounds again the next year (Hallberg 1989; Taube and Wuttig 1998; Underwood 2000).

Two sources of radio telemetry data indicate that sequential year spawning is common with humpback whitefish in the upper Tanana River drainage. The most compelling data were that 16 fish equipped with long-term transmitters were present on the spawning areas on two successive years. Sampling during spawning season in the Nabesna River spawning area showed that fish present in the area were preparing to spawn and that no non-spawning mature fish were present. Finding 16 radio-tagged fish in the spawning areas two years in a row was therefore considered to be strong evidence that those fish spawned on two sequential years.

A less direct, but still compelling argument for sequential year spawning was the finding that significantly more than half of the radio-tagged fish were present on spawning areas during the spawning season following tagging (Table 2). Similar to the previous discussion, their presence in the spawning areas during spawning season was considered to be a strong indication that they spawned that season. Biased selection of candidate fish for radio-tagging is a valid argument against these data indicating sequential year spawning but biased selection was not thought to be an issue in this case. Reist and Bond (1988) pointed out that the different demographic components of riverine whitefish populations (i.e., immature fish, mature spawners, mature non-spawners) may occupy distant geographic habitats. Obtaining representative samples of "the population" is therefore difficult or impossible in most cases. The situation with humpback whitefish in the upper Tanana River drainage was different though. The radio telemetry data suggested that the radio-tag samples were representative of the mature component, both spawners and non-spawners, of the population. None of the radio-tagged fish from the upper region tagging areas (Kalutna River, Fish Lake, Tenmile Lake, and Scottie Creek) migrated downstream past the receiving station, indicating that they remained in the upper region. Most (110 out of 130 known to be alive in year 2) radio-tagged fish returned on the second year to the same feeding areas in which they were tagged, and the ones that did not exhibit feeding site fidelity were located in other feeding lakes in the region and not in notably different habitat types or in distant locations. Therefore, virtually all the mature component of the population was present in the feeding habitats during the sampling events for radio-tag candidates. These factors suggested that radio tags were deployed in a representative manner in the mature population. If sequential year spawning did not occur for humpback whitefish, as argued from an energetic perspective by Lambert and Dodson (1990), the spawning proportion should have been statistically ≤0.5. But the spawning proportion was significantly >0.5 for four of the five tagging groups in the upper region, and for the groups combined, indicating that sequential year spawning was a common occurrence. Combined with the direct data provided by the long-term transmitters, it was undeniable evidence that many mature humpback whitefish spawn on sequential years.

Transmitters were deployed in humpback whitefish from Mansfield and Healy lakes to explore the downstream range of feeding groups of mature humpback whitefish from the Nabesna and Chisana rivers' spawning populations. Evidence from the upper four tagging locations; Kalutna River, Fish Lake, Tenmile Lake, and Scottie Creek, indicated that individuals originated only from the Nabesna or Chisana rivers' spawning populations. The beaver dam blockage of the outlet from Mansfield Lake precluded comparable spawning origin data from that system, but it was clear that at least some originated from the Nabesna River spawning population. Healy Lake remained open to the Tanana River throughout the year and their spawning origins became apparent following fall aerial surveys. Only one of 13 spawners from Healy Lake originated from an upper Tanana River drainage spawning area, the Nabesna River, and the other 12 spawners were gathered in two areas of the Tanana River and in the upper Healy River. The site in the upper Healy River was identified by residents of Healy Lake as a traditional late fall fishing site where large numbers of whitefish could be easily speared. Finding five radio-tagged fish at the site during spawning season was a strong indication that it was used for spawning. It is clear that while Nabesna or Chisana River humpback whitefish spawning stocks might be present in Healy Lake, other spawning stocks dominate in the feeding group there. These data indicate that the mature component of the Nabesna and Chisana rivers spawning populations reside primarily in the upper Tanana River drainage, upstream from Healy Lake.

The Healy Lake fish community was unique among the sample areas examined in this study. It was the only lake where least cisco were present and the only lake where immature humpback whitefish were abundant. Least cisco are small (27 to 42 cm mature size; McPhail and Lindsey 1970) pelagic feeding whitefish that are found in many lakes and rivers in the Yukon River drainage. Least cisco have been documented in Jatahmund and Takomahto lakes (U.S. Fish and Wildlife Service 1990), which are located between the Nabesna and Chisana rivers. Populations in those lakes are considered to be closed since they have not been caught in the river system of the upper region. Both immature and mature humpback whitefish and least cisco were present in Healy Lake, which is an open wetland system, indicating that it was used as rearing habitat for young fish and feeding habitat for mature fish. By contrast, the fish community in the open lake systems farther upstream in the Tanana River drainage, where other sampling for this study occurred, consisted almost entirely of mature humpback whitefish with no least cisco present.

Life History Summary

The following is an ontogenetic life history summary for humpback whitefish originating from the spawning populations of the Nabesna and Chisana rivers. It is based primarily on evidence gathered during this study along with general life history information from other studies referred to earlier in this paper. Hypotheses are introduced to explain certain aspects of life history that are not clearly addressed by data gathered during this study or in the literature.

Humpback whitefish spawn during the transition from fall to winter in relatively discrete regions of the Nabesna and Chisana rivers (Figure 9). The eggs develop through the winter and larval fish emerge into the river in the spring. They are taken downstream in the current and are entrained in numerous backwaters and off-channel lakes of the Tanana River. Water level during this period of time certainly plays a role in larval distribution to off-channel habitats, with high water thought to provide greater access than low water. The migration of a radio tagged fish from Healy Lake to the Nabesna River spawning area, a distance of over 300 km along the river, suggests that young humpback whitefish from the Nabesna and Chisana rivers spawning areas are distributed downstream at least that far, and probably considerably farther. Otolith chemistry data (Figure 7), however, indicate that few, if any, reach the ocean, approximately 2,000 km downstream from spawning areas.

After 4 or 5 years of growth, young humpback whitefish mature and migrate upstream to natal spawning areas. They reach spawning areas by fall and participate in their first spawning event soon after. After spawning in the swift current of their natal origins, they retreat downstream into the slower, flat-water regions of the Chisana and Tanana rivers for overwintering (Figure 8). The process for selecting overwintering habitat for first-time spawners is unknown, but presumably they move downstream from spawning habitat until they encounter current conditions that enable them to maintain position with minimal energy expenditure. The presence of other fish may also influence their choice of overwintering locations. Feeding is thought to be minimal during winter.

Fish that have spawned for the first time and survived the winter in the upper Tanana River drainage must locate a suitable feeding habitat in the spring, which for humpback whitefish means lake systems (Alt 1979). This process is not clearly understood, but probably involves upstream migration from overwintering habitats, followed by explorations into peripheral flows that eventually lead them to off-channel lakes. Smell is a powerful sense for fish species in general and for Salmonidae in particular (Moyle and Cech, Jr. 1996). It is hypothesized that humpback whitefish identify off-channel feeding lakes based on the smell of their outflows. If this hypothesis is true, a fish overwintering near the confluence of the Nabesna and Chisana rivers, for example, would be expected to locate upstream feeding habitats such as Fish Lake or Tenmile Lake, and not downstream feeding habitats such as Tetlin Lake. In any case, once a feeding area is located it becomes familiar and fish tend to return to familiar habitats.

Lakes that support large components of humpback whitefish in the upper Tanana River drainage allow feeding fish to reliably enter in the spring to feed and exit in late summer for spawning and overwintering. Lakes that allow fish to enter during high spring flows but prevent fish from leaving later in the summer would interrupt normal annual cycles as identified with radio telemetry in this study. If overwintering was not possible in such systems, all fish trapped within would die. Fish Lake and Tenmile Lake had shallow channels that remained open to fish passage until late summer but appeared to be too shallow for fish passage during the winter. No radio-tagged fish moved between the river and Fish or Tenmile Lake during the winter. Lakes such as Yarger or Eliza, on the northeast side of the Chisana River just downstream from Tenmile Lake, appear to be suitable feeding habitats but the channels between those lakes and the river allow fish passage only during high flows, so fish that entered to feed would risk becoming trapped. Lakes such as these are not likely to maintain large feeding groups of fish like systems that are more consistently open. Streams flow continuously through Tetlin Lake and the Scottie Creek wetland system. Many radio-tagged fish from those lake systems returned during the winter following spawning. A smaller stream flows through Mansfield Lake and beavers were able to block it during summer 2003, preventing fish from leaving. As a result, many fish overwintered in the lake. Aerial survey data collected the following summer revealed that many of those fish had moved more than 2 km from overwintering positions and were thus, shown to have survived the winter. While they may have been prevented from migrating to spawn, they were not all killed in the process. Local residents indicated that there was a traditional fishery that took place in the old village of Mansfield, at the lake outlet, indicating that the feeding group of fish was maintained in the lake, despite the possibility of becoming isolated from the river sometimes. It is possible that people have played a historical role in maintaining the feeding group of humpback whitefish in Mansfield Lake by keeping the outlet stream free of beaver dams for boat access to the lake.

Seasonal habitat fidelity is hypothesized to confer a survival advantage to the species. It would seem that if a fish survived the winter in a particular location, the probability would be good of surviving there again. Similarly, if a fish was successful at feeding through the summer in productive habitat and was able to return to the river by fall, the probability would be good of doing it again the next year. Experimenting with new habitats would be riskier. A fish could never know if overwintering was possible in a particular location without spending a winter there. A fish could never know if a productive feeding lake allowed access back to the river later in the summer without trying it. This habitat fidelity hypothesis suggests that the risk associated with exploring new overwintering and feeding habitats is borne primarily by young fish following their first spawning event. The sampling project in 1998 and the tagging events between 2000 and 2003 were targeting fish already present in feeding habitats. Presumably they had spawned at least once, survived the winter, and found productive feeding habitats. Hence, this study could not address the hypothesis that there was greater risk of mortality for fish during the year following their first spawning event than during later years.

Those fish that survive the winter following first spawning, feed successfully the next summer, and return to the river in the fall are thought to begin a relatively safe annual pattern of life in the upper drainage. They spawn on most years, overwinter in the same or similar location as they did when they first returned as mature fish, and most feed in the same lake system each summer. Their annual cycle may require migrations of 100 to 150 river km between feeding, spawning, and overwintering locations. Their greatest risks in life would be harvest in the regional subsistence fishery and predation by northern pike *Esox lucius*, river otters *Lontra canadensis*, bald eagles, or ospreys *Pandion haliaetus*. The annual survival rates calculated from age frequency data and inferred by radio tagging results (Table 4), suggest that the combined fishery and natural sources of mortality are relatively low for fish that have survived for at least a year following their first spawning event.

Threats to the populations include those that are human caused and those that may occur with climate change. Gravel extraction or other development activities in the spawning areas would probably have a negative impact on the fish populations. Intensive fishing activities targeting spawning or feeding habitats would be expected to reduce population levels as well. During the late fall, most mature humpback whitefish from the Nabesna and Chisana rivers' spawning populations are present in the two spawning areas. This is an inherently risky situation for the fish populations because a directed fishery in those sites could harm large components of the populations. Similarly, almost all mature humpback whitefish in the two populations are present in upper region feeding lakes during the summer. In most cases fish access the lakes through narrow channels that could be blocked with nets. If a net was maintained all summer across the outlet channel of Tenmile Lake, for example, the feeding group of fish using the lake could be depleted in one season. New fish would colonize the lake again but it would take many years to regain the feeding population of large, old fish that it currently supports. Depleting the feeding population of one or two lakes in the region would not imperil the fish populations as a whole, but if many lakes in the region were aggressively fished in this way, region-wide population levels, as well as age and size composition, would undoubtedly be reduced.

Climate change may alter flow patterns in rivers and water levels in lakes in the region, and these changes would have an affect on habitats used by fish. Similar to many other glaciers in Alaska, the Nabesna and Chisana glaciers are retreating (Wiles et al. 2002). The Nabesna Glacier is 70 km long, the largest outlet glacier in the Wrangell Mountains, and has retreated about 3 km during the last 100 years. The Chisana Glacier is 25 km long and has retreated about 1.5 km during the last 100 years. Clearly the sources of water for the Nabesna and Chisana rivers are secure for the foreseeable future, but flow volume could change, possibly altering the habitat qualities of the spawning areas. If seasonal river flow levels in the area were to rise there could be increased access to feeding habitats that are unavailable now and could lead to an increase in region-wide fish abundance if feeding habitat is a limiting factor. Alternatively, if flow levels were to drop then some habitats currently available may become unavailable and could lead to a decline in region-wide fish abundance. World climate appears to be on a warming trend with Arctic regions experiencing the greatest warming effect (Hinzman et al. 2005). This trend will undoubtedly influence flow patterns in the upper Tanana River drainage, but it is not thought to be an immediate threat to humpback whitefish populations.

Recommendations

Habitat Management

The most important and direct action that can be done to preserve humpback whitefish populations in the upper Tanana River drainage is to protect the habitats they use. The spawning areas that were identified in the Nabesna and Chisana rivers are regions with multiple braided channels amid a wide gravel riverbed. Similar braided regions of the Gerstle River near the Alaska Highway crossing, and the Tanana River near Fairbanks are actively mined for gravel. The spawning areas should be protected from gravel mining operations and other projects that would disturb the riverbed. Movement of heavy equipment during winter should be routed around the spawning areas to avoid altering flow patterns during the egg development period. Development projects that would impede fish passage between lake and river systems should be avoided. Projects involving dikes, culverts, or bridges could change natural flow patterns in river channels or water levels in lakes. Projects such as these should be carefully evaluated and efforts should be made to preserve the natural conditions that currently exist in the region.

Fishing Strategies

Fishing activities could be directed to ensure the preservation of the two spawning stocks and to prevent excessive harvests of specific feeding groups. For example, fish migrating along the Tanana, Nabesna, and Chisana rivers during late summer and fall are in peak physical condition following feeding season and prior to spawning season. They come from both spawning stocks and from multiple feeding groups. Fishing with gillnets or fishwheels in the rivers in late summer and fall would provide fish of the highest food quality during the year, and would spread the harvest over both stocks and all feeding groups. Fishing in the river early in the summer would be less productive than in the late summer and fall, since most fish would be feeding in lakes at that time. Fishing in lakes or in lake-outlet streams would target fish from both spawning populations, but from a single feeding group. It is unlikely that there would be a problem with fishing activities within a lake or at a lake-outlet stream if fishing were conducted during periodic intervals during the summer. But if fishing were continuous throughout the summer the feeding group could be depleted, and fishing in the lake in subsequent years would not be very productive until more fish recruited to the lake again. This generalization regarding lake fishing effects on the lake feeding groups would probably be more noticeable in small feeding lakes in the region such as Fish and Tenmile lakes (about 3 to 4 km across the longest dimension), and would take longer to notice in large feeding lakes such as Tetlin Lake (about 12 km across the longest dimension). Fishing in the spawning areas during the late fall may be very productive, but it would entail the greatest degree of risk to the populations among all the fishing options discussed. Most of the mature population is thought to be present in those relatively small geographic areas at that time, so a modest fishing operation could harvest a significant fraction of the total spawning population at that time. It would be safest to avoid fishing on the spawning areas in the fall. During winter, humpback whitefish from both spawning stocks and all feeding groups are widely distributed along the major rivers and open lake systems in the upper region. Fishing under the ice would therefore be low risk to the populations. Fish captured during the winter would be in their poorest condition of the year, most having just expended a large fraction of their energy stores during spawning. Winter fishing would be less productive than during the summer because most fish remain stationary throughout the winter. In summary, fishing in lakes or in lake-outlet streams would be productive during early and mid-summer, but continuous fishing in a specific lake could deplete the feeding group. Fishing in the rivers would be most productive from mid-summer through the fall, and fish would be in optimal physical condition during that time. The harvest would be distributed across both spawning stocks and all feeding populations so risk would be minimal. Fishing in spawning areas during the fall would be productive, but would entail the greatest risk to the spawning populations. Fishing in winter under the ice would be less productive than at other times, but the risk to the populations would be low.

Future Fisheries Studies, Abundance Estimates

Humpback whitefish spawning areas are the most discrete habitats that are important to the populations. A spawning area is the one place where all members of the population originate and where all return to spawn. It is the one place where a humpback whitefish population can be sampled in a stock specific manner, permitting stock assessment research. As such, spawning area locations are extremely important. In this study two major spawning areas were located in the upper region of the study area, in the Nabesna River and the Chisana River. Healy Lake fish were apparently using three other spawning areas as well. Spawning activity was only verified with a fall sampling program in the Nabesna River spawning area, but should be similarly verified in the other sites too.

Currently there is no information regarding humpback whitefish abundance in the two upper region spawning populations. Nor is there any information on the abundance of fish in feeding groups. Abundance estimates of the humpback whitefish spawning population in the Chatanika River were obtained with mark recapture techniques for several years in the late 1980's and early 1990's. The spawning population varied between a high estimate of 41,211 fish in 1988 to a low estimate of 12,700 fish in 1994 (Timmons 1990; Fleming 1999). There is no reason to expect that spawning population abundances in the Nabesna or Chisana rivers should be similar to that in the Chatanika River, but they may be in the same order of magnitude (i.e., tens of thousands) and would probably experience similar levels of variation in abundance over time.

Whitefish Lake is a large shallow lake in the Kuskokwim River drainage in western Alaska. It is similar in size and depth to Tetlin Lake and is open to the Kuskokwim River by way of an outlet stream. Three whitefish species; humpback whitefish, broad whitefish, and least cisco, utilize the lake during the spring and summer for feeding. The U. S. Fish and Wildlife Service (USFWS) and the Kuskokwim Native Association have operated a weir on the outlet stream for several years beginning in 2001, and have counted as many as 30,000 humpback whitefish leaving the lake during the summer and fall (Harper et al. in review). There is no reason to expect that the Tetlin Lake feeding group population should be similar to that in Whitefish Lake, but it may be in the same order of magnitude (i.e., tens of thousands). Presumably, smaller lake systems such as Fish and Tenmile lakes would have fewer fish in their feeding groups than large lake systems like Tetlin Lake.

Obtaining humpback whitefish spawning or feeding group population estimates would be costly and time consuming, but could be accomplished in the upper Tanana River with the current understanding of migration and habitat use. It must be understood, though, that effective harvest management strategies, based on the annual abundance of spawning fish, have not been developed for whitefish species like they have for many populations of Pacific salmon *Oncorhynchus* spp. Essentially, the problem would be one of determining how many fish would be required on the spawning areas each year to maintain a given level of harvest. If the combined Nabesna and Chisana rivers spawning populations, for example, were 50,000 fish, could 10,000 fish, 20% of the spawning population, be harvested annually without depleting the stocks? At this time there is no information available to guide a decision such as this. In the Chatanika River, a management plan was developed that established an arbitrary minimum abundance level of 10,000 spawning humpback whitefish to allow the fishery (Fleming 1999). Essentially, the population declined to near this level by the early 1990's, the fishery was closed in 1991, and it has not been reopened since. Spawning area harvests of humpback whitefish ranged between 2,500 and 4,500 (9% to 22% of the spawning population estimates) between 1986 and 1989 (Timmons 1990; Fleming 1999), however, the fishery is not thought to be the sole cause of the population decline. Age structure analyses of the population revealed weak age classes, suggesting cohort failures prior to gaining spawning maturity.

It is recommended that if humpback whitefish spawning population abundance estimates become a priority in the future, they should be collected for a minimum of 6 years (the mode of the age distribution was 5 years (Figure 5), so 6 years would presumably extend through a complete generation) and 10 years would be better, to gain an understanding of annual variability. Additionally, an effort should be made to collect simultaneous, complimentary harvest data. These two data sources would permit an empirical assessment of harvest rates (i.e., the harvested fraction of the spawning population), which could lead to harvest guidelines for a given spawning population.

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