LIFE HISTORY AND SPAWNING MOVEMENTS OF

BROAD WHITEFISH IN THE MIDDLE YUKON RIVER

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A

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Abstract

Broad whitefish *Coregonus nasus* have long been an important subsistence resource across its Arctic and sub-Arctic range. Despite its regional importance, little is known about the life history and ecology of this species. This research illuminates fundamental life-history information through the use of catch-per-unit-effort (CPUE) run timing, gonadosomatic index (GSI), radio telemetry, and aging and microchemical analysis of otoliths. From 2001 to 2006, fishwheels were used to capture individuals 1,200 km upstream from the mouth of the Yukon River. CPUE data indicated a consistent increase in daily fish numbers through mid-September. The GSI showed an increasing gonad weight over the sampling period, indicating preparation for spawning. Thirty-one of 41 radio-tagged fish were tracked to a 260 km long spawning area centered 350 km upstream of the tagging site. Thirteen of 17 fish found in the spawning area in 2003 overwintered nearby. Ages of 79 individuals ranged from 5 to 16 years (mean age = 10; median age = 9). Microchemical analysis showed amphidromy in 10 of 12 individuals by examining otolith strontium (Sr) concentrations. This information indicates that the broad whitefish captured in this study were mature, migrating to a spawning/overwintering area, and have a complex amphidromous life history.

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Acknowledgments

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Introduction

This study was conducted to expand our knowledge of broad whitefish *Coregonus nasus* life history in the Yukon River. In Alaska, broad whitefish are one of eight species in three genera (*Stenodus* [1 species], *Coregonus* [5 species], *Prosopiun* [2 species]) commonly known as whitefish. Whitefishes are found throughout Alaska, with their largest distribution north of the Alaska Range. Although whitefish are locally important for human and dog food, their limited commercial value has left them low on the priority list for research, except where large-scale construction or hydrocarbon and mineral exploration requires an environmental impact statement. For this study, we used a variety of techniques to look at the lifetime and seasonal movements of broad whitefish migrating past Rampart Rapids, 1,200 km upriver in Yukon River from the Bering Sea.

Taxonomy and world distribution

Pallus first described the broad whitefish in 1776 based on specimens collected from the Bay of Ob in Arctic Russia (Berg 1962). The first record of broad whitefish in North America was from Milner under the name *C. kennicottii* in 1883 (Scott and Crossman 1973). The broad whitefish is classified as Order Salmoniformes, Family Salmonidae, Subfamily Coregoninae, and Species *Coregonus nasus* (Fishbase 2009). The species is characterized as robust, thick, or heavily built, and the profile of the head is short, not concave, while the snout is blunt and "sheep-like" (Figure 1; Lindsey 1962; McPhail and Lindsey 1970).

Broad whitefish are widely distributed above 60º north latitude. The species ranges across the Arctic from the Perry River in western Nunavut, Canada, westward through Alaska's North Slope rivers, to the giant rivers of central Russia, and as far west as the Pechora River on the western slopes of the Ural Mountains in Russia. Their range also extends into Bering Sea tributaries as far south as the Kuskokwim River on the Alaskan coast and to the Penzhina River

Figure 1. A broad whitefish from the Rampart Rapids sampling site. Scale bar in cm.

on the Sea of Okhotsk in Siberia (Lindsey 1962; Mecklenburg et al. 2002).The movements of broad whitefish are not restricted to freshwater habitats as they are often captured in nearshore marine waters adjacent to the mouths of these rivers (Crawford 1979; Martin et al. 1987; Reist and Bond 1988; Chang-Kue and Jessop 1992).

Life history

Broad whitefish have been aged using three different hard structures (i.e., scales, otoliths, and fin rays), and age estimate results have been markedly different depending on the structure used for aging. Reported ages using scales rarely exceed 15 years (Popov 1975; Chang-Kue and Jessop 1992; Shestakov 2001). Alt (1976), also using scales, reported maximum ages ranging from 8 to 11 years for five populations of broad whitefish in Alaska. However, Bond and Erickson (1985) showed that scales underestimated the age of broad whitefish, most dramatically in fish over 13 years of age. In an extreme case, the discrepancy between scale and otolith ages for one fish was 14 years. The oldest fish in Bond and Erickson's (1985) study was estimated to be age 35. Treble and Tallman (1997), also using otoliths, found a maximum age of 30 years for broad whitefish in their study of the population in the Mackenzie River delta, Canada. Based on these results, it appears that broad whitefish are capable of living for at least 30 years.

Broad whitefish vary widely in length and weight depending on their habitat. They are reported by Berg (1962) to have an average length of 45 cm and average weight of 2 kg in Russia and, likewise, in North America by Scott and Crossman (1973). Berg (1962) reported broad whitefish as large as 86 cm from the Ob' River and 16 kg from the Kolyma River, large river drainages in the Russian Arctic. Alt's (1976) study of five populations of broad whitefish in Alaska revealed an average maximum length of 55 cm, with the largest fish coming from the Minto Flats area on the Tanana River at 64 cm. The largest reported Alaskan specimen was 67 cm from the Colville River at Umiat (Alt and Kogl 1973).

Many aspects of broad whitefish reproductive and early life-stage behavior are unknown, but some basic characteristics have been described in Canada and Russia and inferences can be made from studies of other species in Europe. Pre-spawning movements have been documented for mature broad whitefish, presumably because this is when subsistence and commercial fisheries target these fish. Spawning takes place in the fall near or after ice-up, making sampling difficult (Chang-Kue and Jessop 1983; Prasolov 1989; Shestakov 2001). The preferred spawning habitat is in flowing waters over sand or gravel substrates (Chang-Kue and Jessop 1983; Treble and Tallman 1997; Shestakov 2001). The eggs are broadcast into the water column, where they are fertilized, sink to the bottom, and become entrained in the interstitial spaces of the substrate. The eggs incubate over the winter, hatch in the spring, and their emergence into the water column coincides with the spring freshet, which disperses the larvae downstream (Naesje et al. 1986; Shestakov 1991). The exact timing of emergence of broad whitefish is unknown, but Naesje et al. (1986) found larval cisco *C. albula* and whitefish *C. larvaretus* emerging into the water column just after ice out in a Norwegian river. This spring dispersal mechanism distributes larval broad whitefish into a wide array of floodplain lakes, sloughs, side channels, and estuary habitats downstream from the spawning location (Shestakov 1992). Fixed-net and seining data from the Anadyr River in eastern Siberia indicated that post-spawners and juveniles moved into floodplain lakes and oxbows to feed with the rise in waters of spring freshet (Shestakov 2001). Similar patterns of reproduction, development, and dispersal into rearing habitats are thought to occur in the Yukon River

Otolith microchemistry has become an important tool for examining fish life history and discriminating among stocks in recent years (Babaluk et al. 1997; Tzeng et al. 1997; Brown 2000; Zimmerman 2005; Brown et al. 2007). The wavelength-dispersive electron microprobe (WD-EP) permits analysis of otolith chemistry, providing evidence of migration of individuals over their entire lifespan. By comparing the quantities of different elements in the mineral-protein matrix of the otoliths, a lifetime chronology of habitat usage can be determined. In this study, our interest was whether this population of broad whitefish has used estuarine habitat during their life, and the element chosen to indicate this habitat usage was strontium (Sr). Strontium occurs in concentrations between one and two orders of magnitude higher in marine waters than fresh waters and varies proportionally to salinity (Secor et al.1995). It has been shown in the laboratory that salinity influences the chemical composition of otoliths, and there is a significant change in Sr concentrations in the otolith from fresh water with increasing salinity (Fowler et al. 1995; Secor et al. 1995; Farrell and Campana 1996; Zimmerman 2005). A gradient of Sr concentration occurs in the mixing zone of river deltas and, at some point, the marine Sr become detectable above the fresh water levels.

Yukon River broad whitefish

Broad whitefish occur throughout many of the major tributaries of the Yukon River drainage in Alaska and Canada. However, there have been no systematic sampling studies to determine their distribution within the drainage. This species has been found in Canada in both the Porcupine and Yukon rivers, and in tributaries draining both the north and south sides of the Yukon Flats. There appears to be a spawning migration into the upper Koyukuk River (Andersen et al. 2004). They are present in other large tributaries of the Yukon River, including the Nowitna, Innoko, and Chandalar rivers, and broad whitefish have been found in the Tanana River drainage as far upstream as the mouth of the

Chena River. The villages along the lower Yukon River also catch broad whitefish in subsistence fisheries (Crawford 1979) and in a small commercial fishery. There are also many records of broad whitefish occurrence in agency documents as anecdotal components within other studies. As a result, the lack of specific knowledge about the distribution and population status limits the effectiveness of any management program for this species.

Broad whitefish migrations have not been investigated in the Yukon River drainage. Radio and anchor tagging studies in the Mackenzie River have shown that mature broad whitefish make extensive upstream spawning migrations in the late summer and fall (Babaluk et al. 1997; Chang-Kue and Jessop 1997). Data from fisheries studies in the Arctic rivers of Russia are consistent with what has been found in Canada (Prasolov 1989; Shestakov 2001). Similar migrations of mature broad whitefish preparing to spawn are also thought to occur in the Yukon River. Post-spawning migrations are unknown in the Yukon River, but in the Mackenzie River system, post-spawners retreat from the spawning areas in the Peel, Arctic Red, and mainstem Mackenzie rivers to the Mackenzie River delta to overwinter (Chang-Kue and Jessop 1983, 1997). It is presumed that broad whitefish in the Yukon River retreat to overwintering areas following spawning like other coregonids in the system (Brown 2000). Movements of these fish in the spring and summer before the spawning migration, along with the migration patterns of juvenile and non-spawning individuals, are undocumented in the Yukon River.

Recent improvements in radio-telemetry equipment have greatly expanded the use of these devices in fisheries work. The decrease in transmitter size and the increase in battery lifespan have allowed fisheries biologists to use them on species that have not been studied previously. In the past, biologists have also lost valuable information when tagged fish moved out of their perceived home range (Alt 1975, 1986). To avoid this problem, satellite-linked remote receiving stations have been developed to reduce the aerial survey area by partitioning the river into its tributaries and the mainstem, thereby allowing tracking efforts to be concentrated (Eiler 1995).

Currently, there are two fisheries for broad whitefish in the Yukon River drainage, a rural subsistence fishery for human and dog food, which occurs throughout the drainage, and a commercial fishery that began in 2005 near the mouth of the river. The subsistence fishery is unrestricted and the commercial fishery is bound by an upper catch limit of 4,500 kg of coregonids, although Bering ciscoes *C. laurettae* are currently the primary species sought in the fishery (ADF&G 2008a). Most commonly, broad whitefish are harvested on the Yukon River at two times during the year: 1) in late summer and fall using gill nets and as bycatch in the salmon fishery (mature fish heading to spawning grounds); and 2) an under-the-ice gill-net fishery in the spring (targeting immature and non-spawning adults). Villages, such as Allakaket on the Koyukuk River (Andersen et al. 2004) and Arctic Village on the East Fork of the Chandalar River (Adams et al. 2005), that do not experience sizeable salmon harvests, are more dependent on their whitefish fishery, including broad whitefish, than those villages along the mainstem Yukon River. These villages target broad whitefish throughout the year in lakes where summer feeding occurs, as well as in rivers (Andersen et al. 2004; Adams et al. 2005). In these fisheries, the reporting criteria for whitefish species is to list inconnu *Stenodus leucichthys* separately and combine all others into either “large” or “small” whitefish reporting categories (ADF&G 2008a; USF&WS 2008), meaning that species-specific harvest data are largely absent.

It is hoped that the information revealed by this study will be considered by fisheries and land managers when making decisions along the Yukon River and its tributaries and in regards to land-use issues especially near or above any spawning area(s). My objectives were to: (1) collect size (i.e., length and weight) and age data, determine run timing using video catch-per-unit-effort (CPUE) counts for broad whitefish moving past the study site, and establish whether these fish were undergoing a spawning migration by examining the gonadosomatic index; (2) locate the spawning area and identify overwintering habitat using radio-telemetry methods; and (3) determine if broad whitefish passing the study site were amphidromous by looking for an elevated Strontium (Sr) micro-chemical signature in their otoliths using an electron microprobe.

Methods

Study Site

The Yukon River in Alaska is a 2,250-km corridor used by migrating Pacific salmon *Oncorhynchus spp.* and whitefishes Coregoninae. The climate at the tagging site, Rampart Rapids (65.34332 N, 151.05758 W), 1,200 km upstream from the Yukon River mouth, is described as continental sub-arctic. River ice begins forming in October, with an average first ice date of October 10 in Tanana, 60 km downstream of the tagging site. A “safe man” (approximately 7.5 cm in depth) ice cover occurs on average by November 10 (NWS 2008). The average breakup at Tanana occurs by May 10 (NWS 2009). There are no barriers to movement such as waterfalls or dams along the mainstem Yukon River in Alaska. Substrate along the 450 km of river between the Rampart Rapids study site and the spawning area of other whitefish, identified by Brown (2000), ranges from bedrock and large cobble at the Rampart Rapids site to silt, sand, and gravel on the spawning grounds (Figure 2).

Figure 2. Major tributaries of the Yukon River. The arrow indicates the sampling site at Rampart Rapids 1,200 km from the mouth. The remote receiving stations that divide the Yukon River drainage into its tributaries are also shown.

Sampling

Data were compiled between 1998 and 2006 from broad whitefish sampled incidentally from the subsistence fishery for the purposes of calculating a gonadosomatic index (GSI), determining the size and age structure of the population, for deployment of radio transmitters for tracking purposes, and for CPUE analyses. As a result, sample sizes varied for GSI, age structure, and length and weight distributions. Data collection began each year in mid-June and was completed by mid-September, with the exact starting and ending dates determined by river and weather conditions. All fish were captured using fishwheels (wheels), mechanical dip nets that use the river's current to push paddles and baskets to scoop fish from the water. Fish were lifted from the river in the baskets and were funneled into a live box beside the wheel. The capture wheels were modified from those normally used on this section of the Yukon River with the addition of padding on the chute, netting instead of wire on the sides and bottom of the baskets, and a reduction in rotational speed to minimize harm to captured fish (Zuray 2009).

Age, length, weight, and feeding

Broad whitefish were collected for the purpose of creating age, length, and weight distributions and a GSI for the population. Fork lengths were measured to the nearest 1 cm and weights were recorded to the nearest 0.01 kg. Sagittal otoliths were collected for aging purposes. Otoliths were extracted using one of two methods; either a dorsal bifurcation of the skull from the back of the head through the entire skull or by a horizontal cut above the eye to the back of the skull. The otoliths were cleaned with water and stored dry in envelopes. Otoliths were individually mounted to glass slides using thermal glue and transversely sectioned to approximately 0.3 mm and read using transmitted light (Secor et al. 1992). The sex ratio of the sample was biased toward females because during GSI development, fish that looked to be females were selectively sampled.

Similarity in the length distribution of males and females was compared with a Kolmogorov-Smirnov test. It has been reported that coregonids fast while on their spawning migration (Prasolov 1989; Brown 2000), so broad whitefish collected for aging and GSI estimation also had their stomachs examined for general feeding condition. These fish were classified as feeding or fasting based on the presence or absence of food, respectively.

Reproductive biology

The data for the GSI was produced by weighing each female broad whitefish, then removing and weighing both ovaries. The GSI was calculated as (ovary weight ⁄ whole body weight) •100 (Bond and Erickson 1985). These results gave total ovary weight as a percentage of whole body weight and were examined over time to determine the temporal nature of spawning preparation. Increasing GSI values over time indicated that fish were preparing to spawn (Snyder 1983). Male broad whitefish were not used in the GSI evaluations because the gonad weight of male coregonids changes little relative to females as they prepare to spawn (Lambert and Dodson 1990). As a result, it is more difficult to classify male fish as spawners or non-spawners.

Run timing

Run-timing data was expressed in terms of CPUE, with one unit of effort defined as one wheel running for 24 h. These data were collected using a video camera mounted on the chute of the fishwheel with a door-triggered switch to save frames of video from a buffer before the switch was tripped (Daum 2005). These counts began in June of each sampling year when the fishwheel became operational and continued until mid-September when fishing was terminated. The daily counts (relative abundance) were graphed by number of broad whitefish captured per wheel day.

Radio telemetry

The surgical technique used for this study has been successfully used with humpback whitefish *C. pidschian* (Brown 2006; McDermid et al. 2007) and broad whitefish (Morris 2000). It has been adapted from various sources, including Anderson (1997), Winter (1996), Morris (2000), and detailed in Brown (2006). Transmitter size was determined from size data collected at the study site in previous years; the transmitters weighed 9 g, were 5 cm long, and had a diameter of 1 cm. Transmitters were deployed in 2002 between August 29 and September 2 in an attempt to cover the peak of the run as determined by CPUE data the previous two years (Daum 2005). An attempt was also made that year to implant transmitters into an equal number of males and females; this transmitter distribution was implemented to identify dramatic differences in the behavior between the sexes if they occurred.

In 2003, the main focus in deploying transmitters was to distribute them over a large portion of the spawning migration. The objective was to determine if individuals with different run timing used different spawning areas. Implantation began on September 1 and concluded on September 15. Transmitters were distributed over this two-week period, and were implanted every day except for November 3 and 8 when no suitable fish were caught and on November 7 and 14, which were Sundays when there was no fishing. The goal was to deploy one transmitter each day on the first two days and last two days, two transmitters on the third, fourth, seventh, and eighth days, and three transmitters on the fifth and sixth days of sampling. During the 2003 deployment, fish were selected for implantation by being the next available fish suitable for tagging, with no regard to sex of the fish because there was no discernable difference in the destination of either sex from the 2002 deployment.

During the 2002 field season, 20 continuously broadcasting, digitally coded transmitters were deployed. These transmitters were detectible by fixed-location tracking stations along the river that were maintained by the National Oceanographic & Atmospheric Administration (NOAA) and the Alaska Department of Fish & Game (ADF&G) and by aerial tracking flights. A tracking station 11 km upstream from the tagging site would verify upstream movement following tagging, and another 150 km downstream documented any downstream migration. The tracking stations sent data to a satellite on an hourly basis (Eiler et al 2006).

Transmitters for the 2003 season were duty-cycle programmed, digitally coded transmitters with similar weight and dimensions as those used in 2002, but were not compatible with the remote-tracking stations. The duty-cycle program was for nine hours on, 15 hours off, seven days a week. With this programming cycle, the battery life was extended to 635 d, which encompassed two spawning seasons, allowing some information to be collected regarding spawning periodicity. Brown (2000) reported that inconnu with esophageal and external transmitters initially moved downstream after tagging. In order to evaluate this movement for broad whitefish with surgically implanted transmitters, weekly boat tracking was conducted in both 2002 and 2003 for a distance of approximately 10 km downstream of the tagging site.

A series of aerial survey flights were conducted each fall, initially starting at the tagging site and proceeding upstream, and later focusing on the upstream reaches where tagged fish had migrated. During late October and November, the expected spawning period (Chang-Kue and Jessop 1992), the surveys were conducted bi-monthly, weather permitting. The spawning area was identified based on tagged fish located in an upstream region in the general area of other tagged broad whitefish.

Otolith chemistry

Otoliths of six male and six female broad whitefish were randomly selected for microchemical analysis from the 78 samples used for aging. Sample size was determined using the same logic as in Brown (2006); the probability of detecting an anadromous fish in this sample (12 fish) was greater than 95% if the real proportion of anadromy in the population is 0.3. Each otolith was then inspected for flaws and large cracks or scratches, which would interfere with the electron beam. If an otolith was found unacceptable, the next sample of that gender was inspected. After polishing with 3μm alumina grit on a glass plate, otoliths were polished further with 1μm diamond grit on a lapidary wheel. The otoliths were carbon coated and analyzed using the electron microprobe at the UAF Advanced Instrumentation Laboratory (Fairbanks, Alaska).

The path of the electron beam was determined by picking a starting point in the core of the otolith then picking another point at the margin to make one straight line or by connecting a series of lines that covered all of the growth rings while avoiding anomalies in the otolith that would deflect or otherwise alter the electron beam. Electron-beam conditions were set at 15 KeV, 20 nA, with a beam diameter of 5 μm, point spacing of 8 μm, and a count time of 25 seconds per point. The detection limit of the WD-EP for Sr under these conditions was approximately 320 mg/kg (Brown et al. 2007).

The microprobe collected and counted Sr x-rays that were emitted by the electron bombardment. Strontium replaces calcium (Ca) in the mineral-protein matrix of the otolith due to its chemical similarity to Ca (Secor et al. 1995; Brown 2000). The determination of the fish's life-history classification was made based on two types of assessment; a visual comparison of Sr x-ray graphs of unknown life-history fish with similar graphs from fish known to be either freshwater resident or amphidromous as illustrated by Babaluk et al. (1997), and numerically, based on two empirically determined critical values. First, the Sr x-ray counts per second were converted to mg/kg using a regression equation presented in Brown et al. (2007):

$$Sr(mg/kg) = -2637 + 1709\ Sr(counts \bullet s^{-1} \bullet nA^{-1}).$$

A transect's maximum Sr concentration was the first of the two critical points in the determination of amphidromy. The other critical point was an index of the coefficient of variation (CVI) of the Sr x-ray counts of the individual core-to-margin transects (Brown et al. 2007). This was calculated as:

$$CVI = (\text{actual CV of Sr x-ray counts}) \bullet (\text{expected CV of Sr X-ray counts})^{-1};$$

$$CV = SD \bullet mean^{-1} \bullet 100.$$

This index allowed comparison of how different the actual CV was from the expected CV; i.e., if the Sr concentration was homogeneous across the entire otolith. The expected CVI if Sr concentration was homogeneous would be one and taking into account differences in seasonal uptake of Sr and drainage concentration differences, this number was expected to be slightly higher than one. Brown et al. (2007) determined that fish with a known life history could be divided into freshwater resident and amphidromous categories when maximum Sr concentration in mg/kg was plotted against CVI using the critical points of two for CVI and 1,700 mg/kg of Sr. Fish with CVI's less than two and maximum Sr less then 1,700 mg/kg all had a known freshwater life history. Likewise, fish with maximum Sr and CVI values greater than these critical points had known marine water exposure in their life history. Figure 3 shows Sr concentration histograms of known freshwater and anadromous fishes. These are the criteria used to

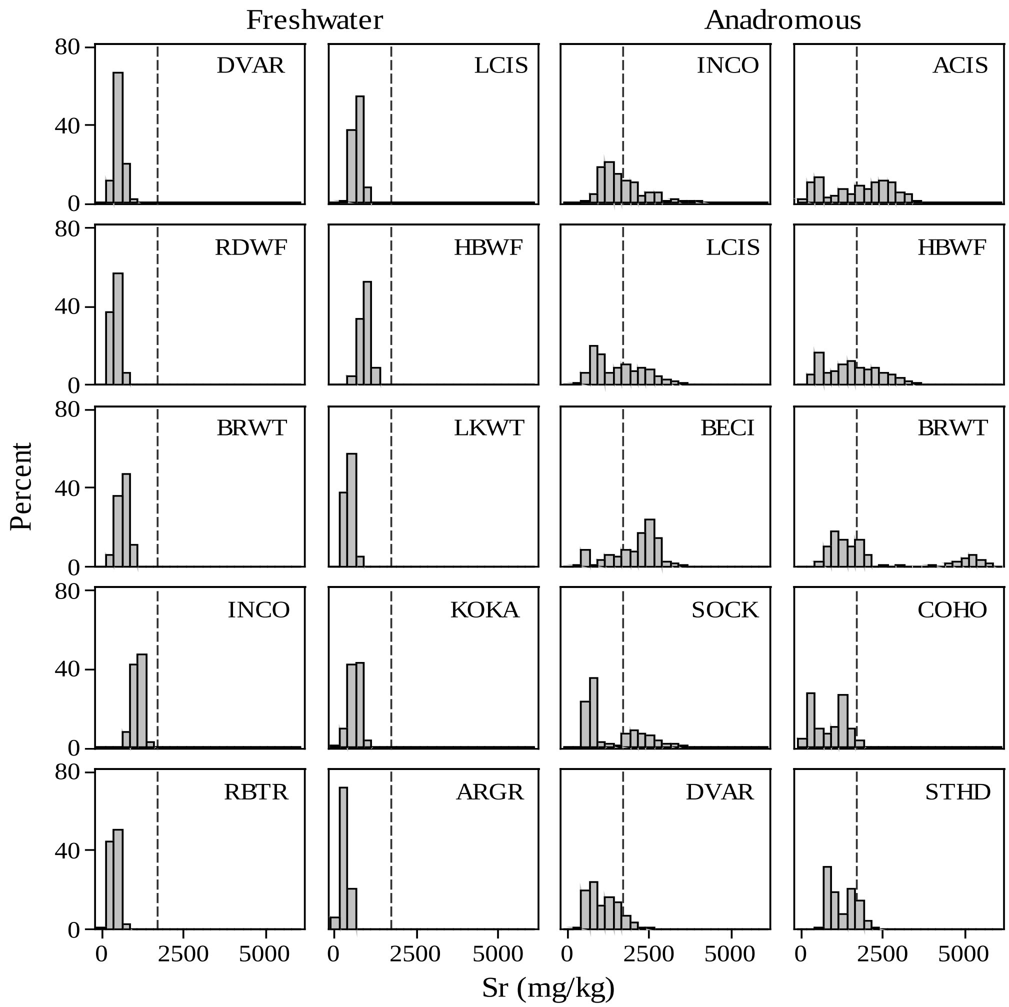

Figure 3. Strontium concentration histograms of a core to margin transect of 10 freshwater and 10 anadromous salmonid species. Abbreviations freshwater top to bottom; Dolly Varden *Salvelinus malma*, least cisco *Coregonus sardinella*, round whitefish *Prosopium cylindraceum*, humpback whitefish *C. pidschian*, broad whitefish, lake whitefish *C. clupeaformis* inconnu *Stenodus leucichthys*, kokanee *Oncorhynchus nerka*, rainbow trout *O. mykiss*, Arctic grayling *Thymallus arcticus*; anadromous, inconnu, Arctic cisco *C. autumnalis*, least cisco, humpback whitefish, Bering cisco *C. laurettae*, broad whitefish, sockeye salmon *O. nerka*, coho salmon *O. kisutch*, Dolly Varden, steelhead *O. mykiss*; from Brown et al. 2007.

show use of estuarine habitats. Growth annuli, corresponding to age in years, can be apportioned to the Sr transect and provide an annual examination of the life history of the individual.

Results

Sampling

One hundred and nineteen broad whitefish were sampled to obtain length and weight data. Of these fish, 85 were female and 34 were male. Seventy-eight (59 female, 19 male) of these fish had their sagittal otoliths removed for age estimation and 27 of these females were used to calculate a GSI. The larger proportion of females in the sample was due to the selection of fish that appeared to be female when sampling for the GSI. The remaining data were collected from individuals captured as part of the radio-telemetry portion of this study and were not aged or used in the development of the GSI.

Age, length, and weight distributions, and feeding

All broad whitefish in the sample appeared to be mature individuals preparing to spawn based on the age and length distributions and GSI data. Table 1 shows the median and range for age length and weight by sex and for the mixed population. Length-at-age and age-frequency distributions are shown in Figure 4. A large proportion (62%) of the sample population was represented by fish ages 6 to 10. The length-frequency histogram in Figure 5 shows that 90% of the sample population was between 49 and 61 cm. Only two females were found to have food in their stomach at the time of capture; however, it appeared to be only silt. All other broad whitefish examined in this analysis were fasting.

GSI, maturity assessment, minimum age, and length at maturity

The GSI was constructed using data from 27 female broad whitefish collected between August 8 and September 6, 2001. When examined over time, a trend of

Table 1. Age, length, and weight data; values given as median and ranges.

	Age (years)	Length (cm)	Weight (kg)
Males	9 (6 – 16)	54.5 (48 – 62)	2.30 (1.60 – 3.00)
Females	9 (5 – 16)	54.0 (39 – 64)	2.23 (0.72 – 3.43)
Males and Females	9 (5 – 16)	54.0 (39 – 64)	2.25 (0.72 – 3.43)

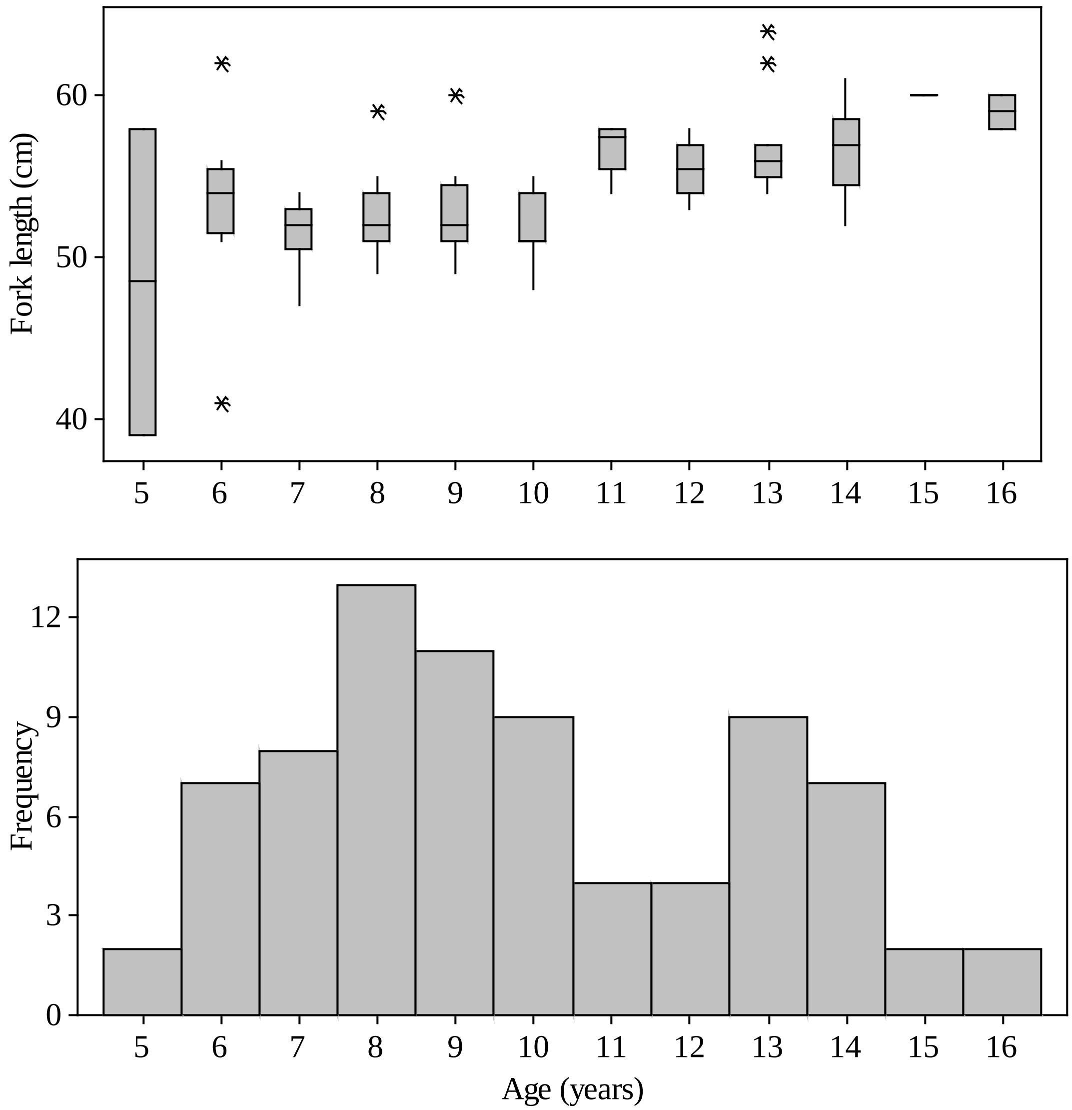

Figure 4. Length-at-age distribution plot (top panel) and age-frequency histogram (lower panel) n=78. The box plot (at top) includes median line, interquartile range box, whiskers that encompass more than 95% of data points and outliers shown as stars.

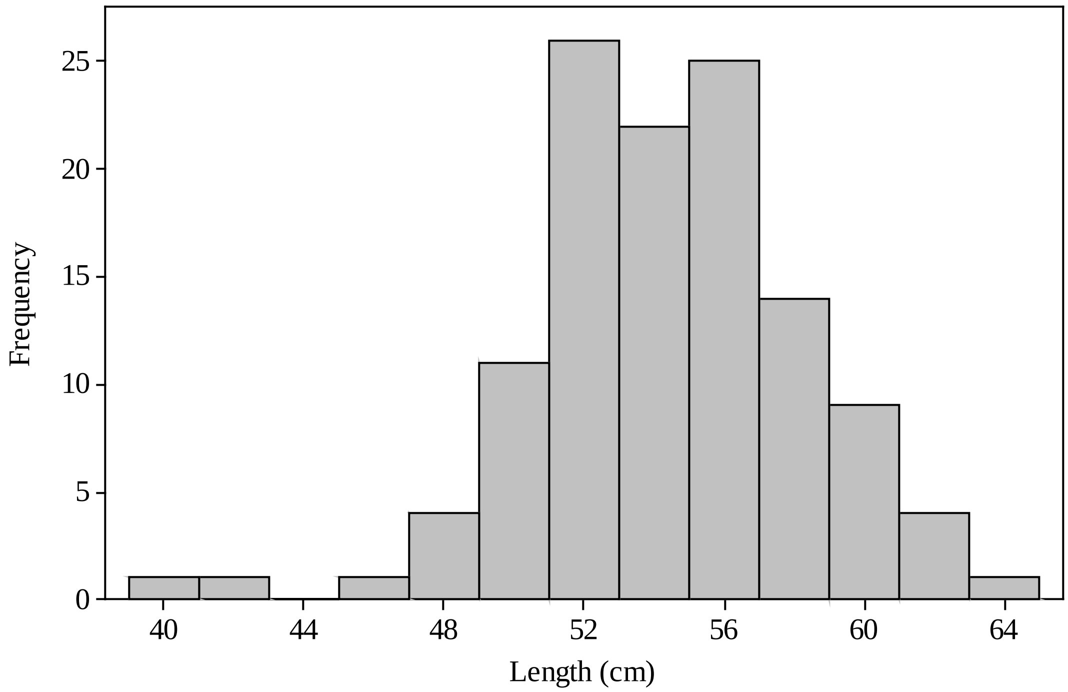

Figure 5. Mixed sex length-frequency histogram for 119 broad whitefish.

steadily increasing GSI was revealed which indicated these fish were preparing to spawn (Figure 6). The GSI by length and age showed that all females sampled were above the GSI of three that Bond and Erickson (1985) gave as the maturity point for female broad whitefish in July and August (Figure 7). The youngest and smallest female in the sample was age 5 and 39 cm. While this fish was smaller and younger than most estimates of minimum size and age at maturity (Alt 1976; Bond and Erickson 1985; Prasolov 1989; Chang-Kue and Jessop 1992), its GSI value of 18% established that it was mature and preparing to spawn.

Run timing

Six years of run-timing data were collected from video monitoring of the fishwheels used to capture broad whitefish for this project (Figure 8). Broad whitefish began to appear in the catch as early as mid-June, but consistent catches of five to 10 individuals daily occurred near August 15 each year. The run continued to increase in the first weeks of September with catches as large as 42 individuals per day. Run size began to decline after the second week of September, but sampling stopped at that point because the fishwheels began collecting ice with the colder air and water temperatures of late fall, making it dangerous to continue operations.

Radio telemetry

Forty-one radio transmitters (20 in 2002 and 21 in 2003) were implanted into broad whitefish, ranging in size from 46 to 61 cm. During the 2002 field season, there were nine males and 11 females implanted with transmitters, while in 2003 six males and 15 females were implanted with transmitters. No discernible difference was found between the destination of males and females along the river in either year.

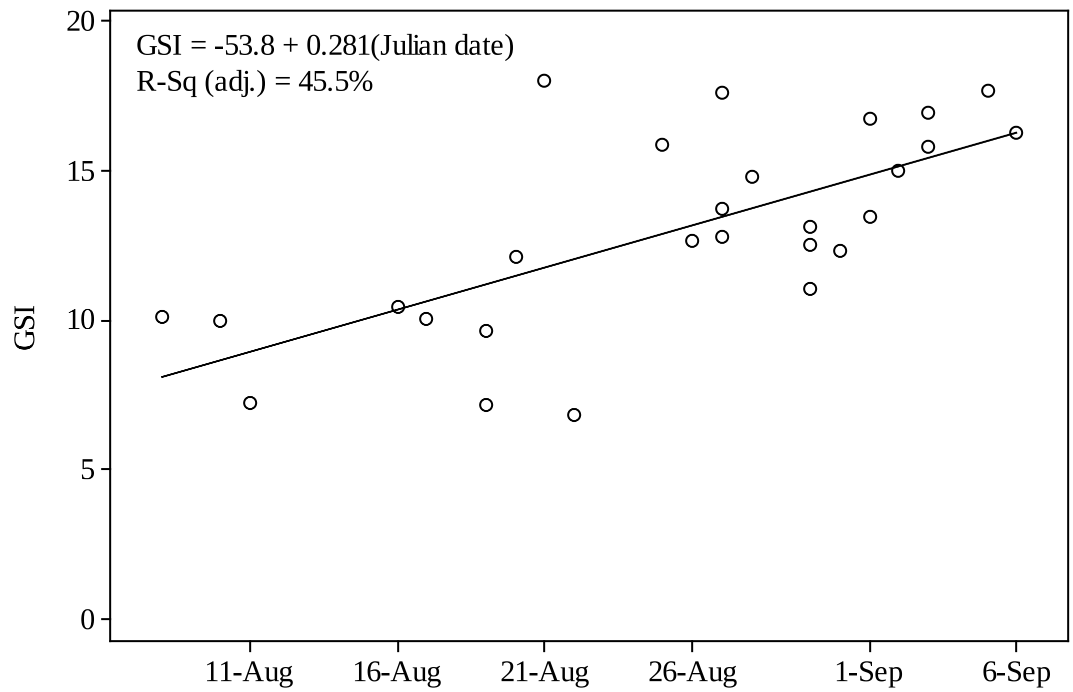

Figure 6. Gonadosomatic Index (GSI) for females by date. Julian dates (day of year) were used for trend-line calculation. The positive slope of the trend line shows an increase in GSI with time indicating preparation for spawning.

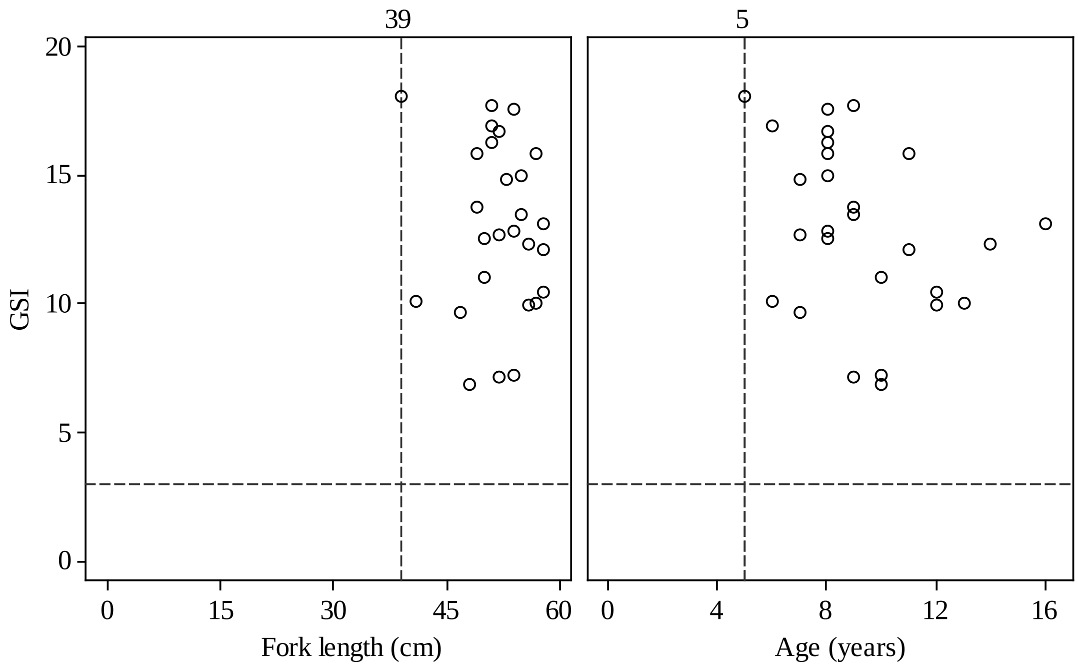

Figure 7. GSI by length (left panel) and age (right panel). The dashed horizontal line denotes a GSI of 3, the critical point for maturity cited by Bond and Erickson (1985) for mature females in late summer. The dashed vertical line denotes the youngest and smallest mature female, here the same fish.

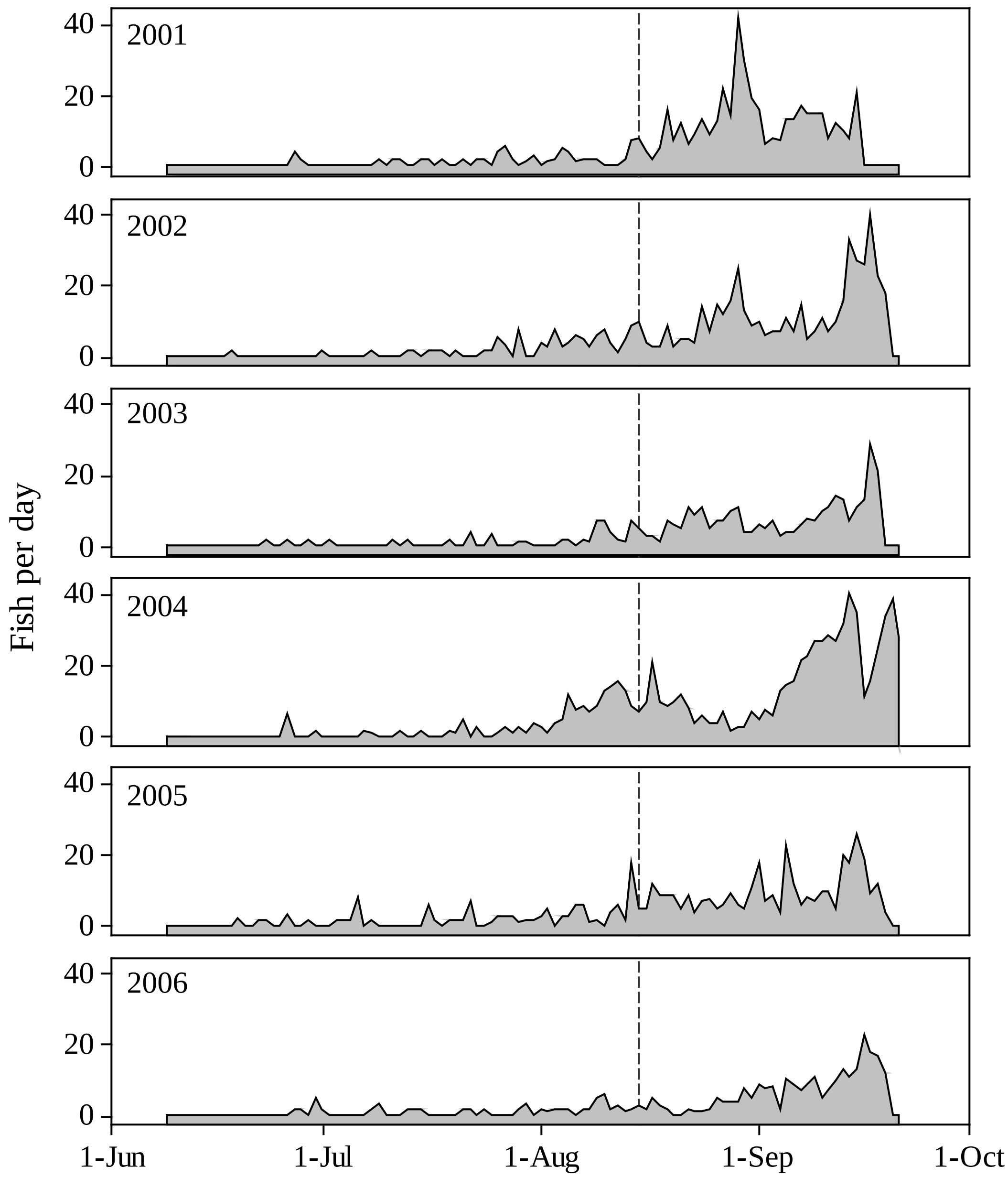

Figure 8. CPUE graphs for 2001 through 2006. In all six CPUE graphs shown above, a steady increase in the daily number of broad whitefish occurs on or about August 15 (dashed line). The run continues after the sampling operation ends as catches decline which is not evident in the plots.

Boat tracking conducted both years indicated that all fish held in slow water within 5 km downstream from the tagging site for one to several days before resuming their upstream migrations.

In 2002, it took an average of 322 hours for fish to recover from surgery and reach the Raven's Ridge receiving station 11 km upstream from the tagging site (Figure 2). The maximum recovery time was 667 hours and the minimum recovery time was 80 hours. Three of the 20 fish tagged in 2002 were not recorded at the Raven's Ridge station. These fish may have been injured during capture or tag implantation, or simply may have been missed by the station because one of these three fish was located approximately 11 km upstream of Steven's Village during an aerial survey on December 3. The other two fish were never found outside the tagging area, but had moved within the area between boat tracking sessions, indicating that they had recovered from the surgery. Tagged fish were located upstream of the receiving station by aerial surveys conducted from the end of September through December 2002. Of the 17 fish recorded passing Raven's Ridge, three individuals were not relocated upstream by aerial survey. A total of 15 fish were located at least once upstream from Raven's Ridge. This was the only station to record broad whitefish passage, which indicated that the tagged fish were somewhere along the mainstem Yukon River between this station and Circle, located 1,760 km from the Bering Sea (Figure 2). The fish appeared to remain along a large stretch of the Yukon River extending approximately 260 km downstream from the confluence of the Porcupine River. There was movement of the implanted fish within this stretch of river from one survey to the next, but the fish seemed to stay within this area through the last survey on December 3, 2002 (Figure 9). Broad whitefish migrated to a region of the Yukon Flats with wide, braided channels, old established islands that have large mature white spruce *Picea glauca*, cottonwood *Populus balsamifera*, and birch *Betula papyrifera* trees, and

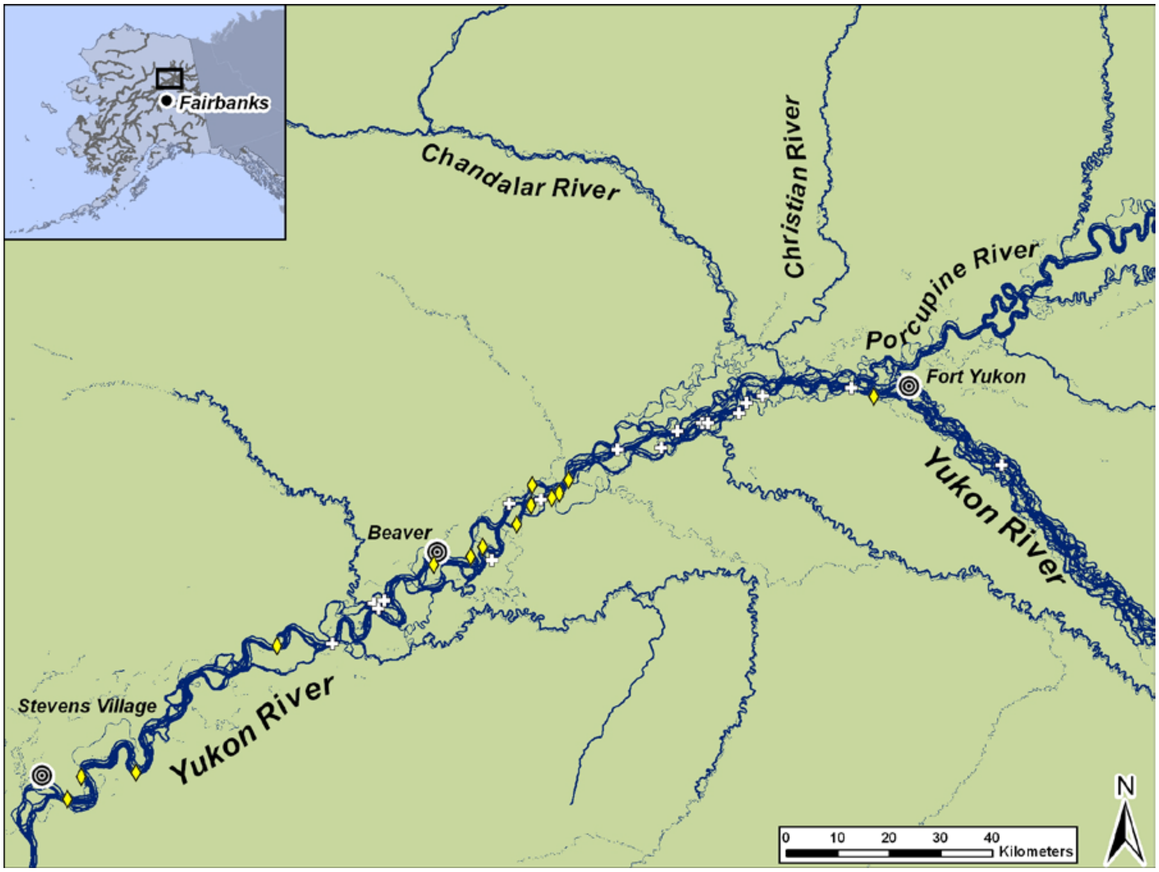

Figure 9. Farthest upstream movements of radio-tagged fish. Fish location denoted by diamonds for the 2002 season and crosses for the 2003 season.

substrate that ranged from silt to cobble (Figure 10). A U.S. Geological Survey gauging station near Steven's Village, at the lower end of this region, reported current speeds of approximately 1.4 m/s in September (Brabets et al. 2000), but no measurements were made on the spawning grounds.

The transmitters deployed in 2003 were not compatible with the satellite-linked receiving stations, so no estimate of recovery time was possible. The implanted fish were found concentrated along the same stretch of the mainstem Yukon River, with one fish venturing approximately 26 km upstream of Fort Yukon (Figure 9). A total of 17 of the 21 fish implanted in 2003 were located at least once during aerial surveys of the Yukon Flats region.

Considering both tagging years, 31 of the 41 tagged fish were located at least once by aerial surveys on the suspected spawning grounds, a success rate of 75%. Of the other ten fish: 1) four fish (two from each year) were never located outside of the tagging area by the remote stations or aerial survey; 2) three fish from 2002 were recorded migrating by the receiving station at Raven's Ridge, but were not located by aerial survey or any other station; and 3) one fish from the 2003 tagging was suspected to be a mortality because it remained immobile for four months 5 km downstream of the tagging site. The last two fish were not located on the spawning grounds. Their farthest upstream movements were 140 km upstream from the tagging site. One of these fish was located on October 16 in this area and then relocated 230 km downstream of the tagging site on December 11 while surveying for another group of tagged fish on the same frequency. The 31 fish that resumed migrations were located, in some cases four or five times, in the mainstem Yukon River in two loose groups distributed along a 260-km reach within the Yukon Flats. One group was found downstream

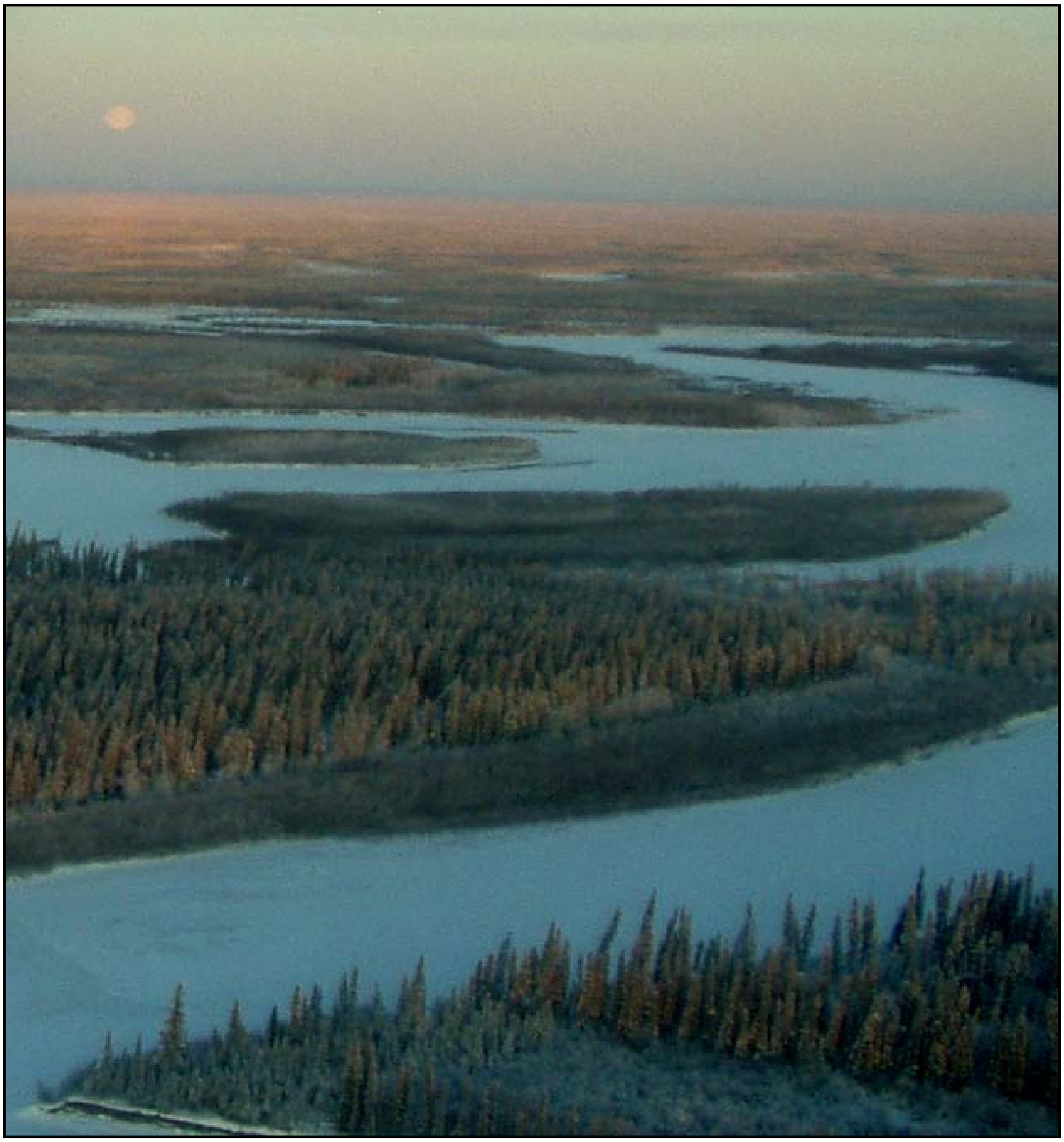

Figure 10. View upstream of the broad whitefish spawning grounds on the Yukon River.

from the confluence of the Chandalar River (9 fish) and the other group was found upstream from the village of Beaver (12 fish). The other ten fish were more widely distributed along the river between Fort Yukon and Steven's Village -three were upstream of the Chandalar group and seven were downstream of the Beaver group. Of the 31 individuals described as successful, 21 (67%) were located in the 150-km reach between the Chandalar River and the village of Beaver. Although no ground-truthing was possible because of river conditions in early winter, the presence of over 50% of the implanted fish tagged on two successive years in the same area indicated that it is a major spawning location for broad whitefish.

A survey on April 20, 2004, located 13 fish, all between Fort Yukon and Steven's Village. The April positions for 12 of the fish ranged from less than 1 km to 32 km downstream from their December 11 survey positions, with one fish moving 20 km upstream (Figure 11.). The April 20 survey documented that at least some broad whitefish were overwintering in the Yukon Flats following spawning. Presumably, these fish would migrate to feeding habitats following spring ice breakup. A September 28, 2004 survey was conducted to determine if any fish that had spawned in 2003 were again present on the spawning grounds in 2004. Only one fish was located and it was not in riverine spawning habitat. Rather, it was in Shovun Lake, which is a connected lake system in the Christian River drainage, 33 km north east of the mouth of the Chandalar River (Figure 11).

Otolith chemistry

Of the 12 otoliths selected for microchemical analysis, 10 showed evidence of marine influence. The graphs in Figure 12 illustrate Sr concentrations along a core to margin microprobe transect. The dashed line at 1,700 mg/kg indicates an empirical critical point for classifying amphidromy. These graphs show that Sr is taken up periodically over the life of the individual with peaks greater than

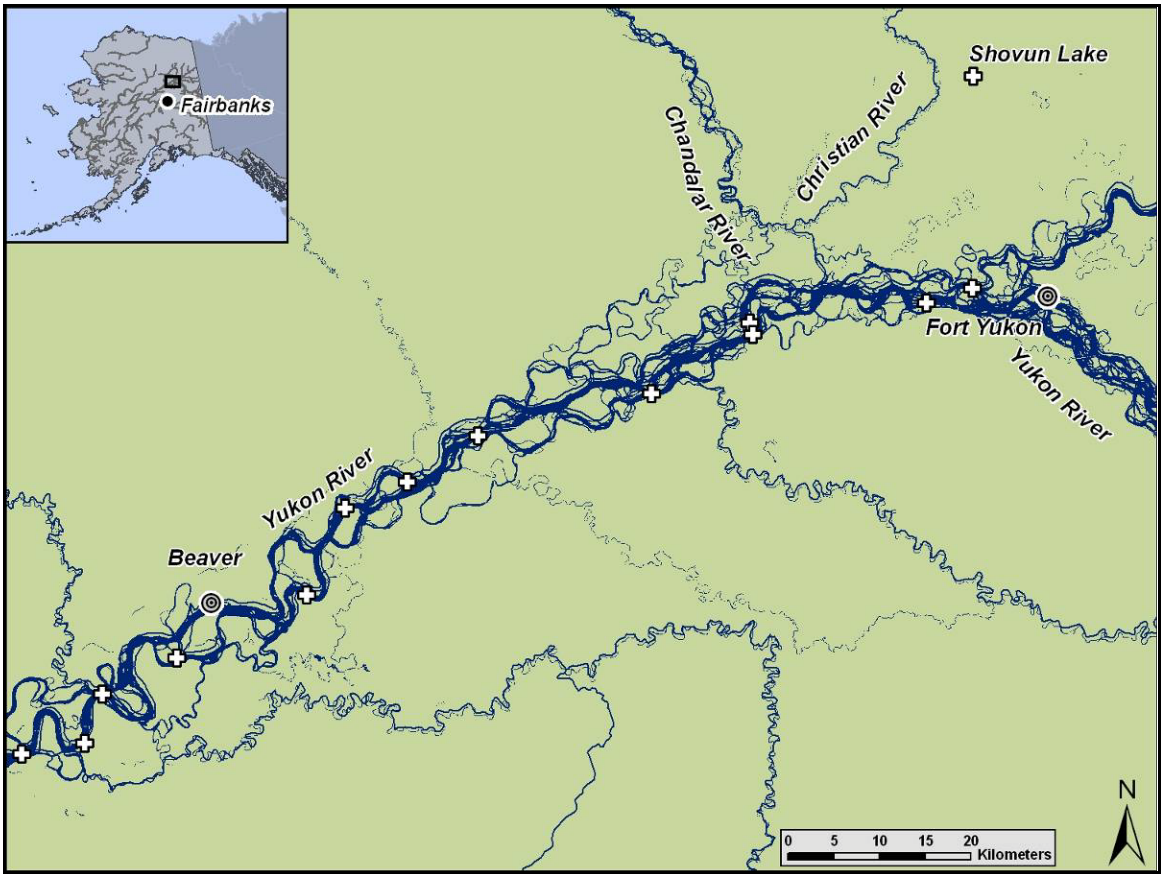

Figure 11. Overwintering locations for 13 of 17 radio-tagged fish from 2003. Also shown is a fish located in Shovun Lake during a September 2004 survey.

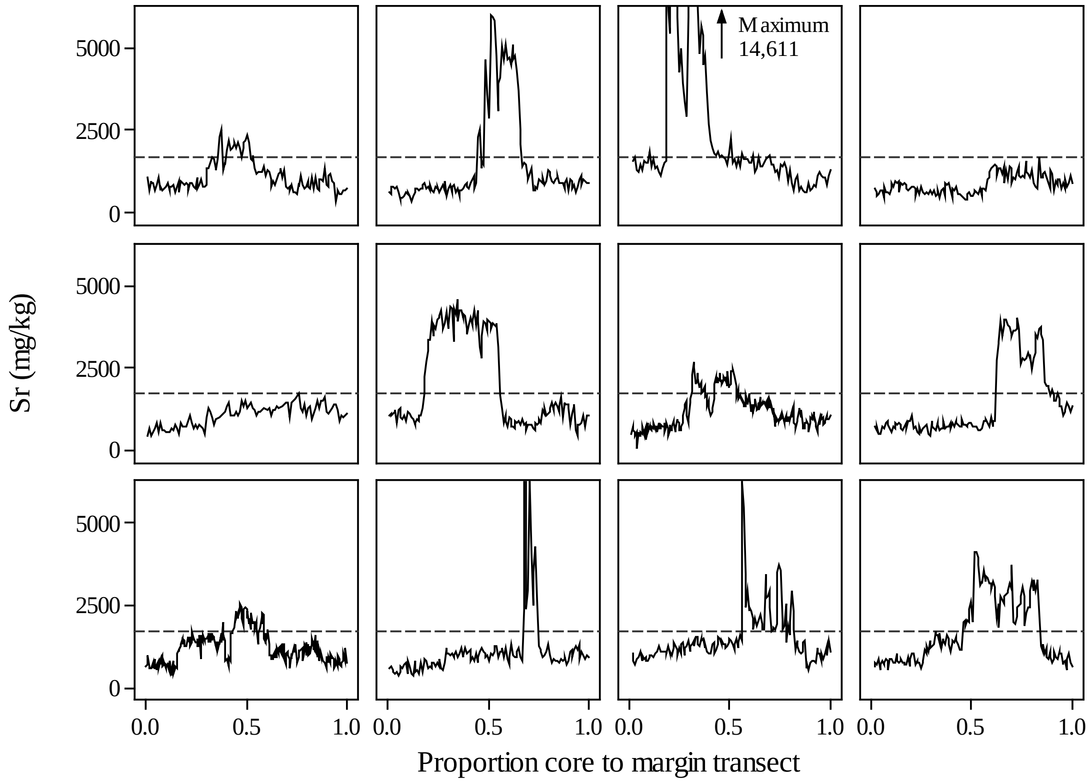

Figure 12. Core to margin Strontium (Sr) graphs. The dashed line indicates the 1,700 mg/kg critical point for anadromy.

1,700 mg/kg, indicating estuarine habitat use. Strontium concentration histograms in Figure 13 allow for a better interpretation of whether an individual has spent time in estuarine habitats. Although the individuals in row 1, column 4 and row 2, column 1 have points above the 1,700 mg/kg line, we consider them non-anadromous.

This pattern is not uncommon in coregonids with a known freshwater life history and is similar to the inconnu from Great Slave Lake shown in Figure 3. The individuals that were shown to be using the estuarine habitat consisted of six females ranging in age from 7 to 11 and four males ranging in age from 8 to 13. The two individuals that did not use the estuarine habitat were males, one age 8 and the other 9. Figures 14 and 15 illustrate the relationship between the annuli in the optical image and the bands of high Sr concentration in the map and peaks of the transect graph.

Discussion

This study was undertaken to better understand the life history of broad whitefish in the Yukon River by (1) studying size, age, and maturity to characterize demography, (2) documenting seasonal migrations with radio telemetry to identify important habitats, (3) using otolith microchemistry to look at lifetime migration patterns between freshwater and marine environments, and (4) consolidating information from unpublished and multi-species reports. Information revealed by this research has shown similarities between broad whitefish and other coregonids, particularly inconnu, humpback whitefish, and Bering cisco, that are captured concurrently at the Rampart Rapids study site (Brown 2000; Daum 2005; Brown et al. 2007). These similarities include: (1) these species make long migrations up the Yukon River from estuarine habitats; (2) they are mature individuals preparing to spawn; and (3) they are a long-lived species that make multiple spawning migrations over their life span.

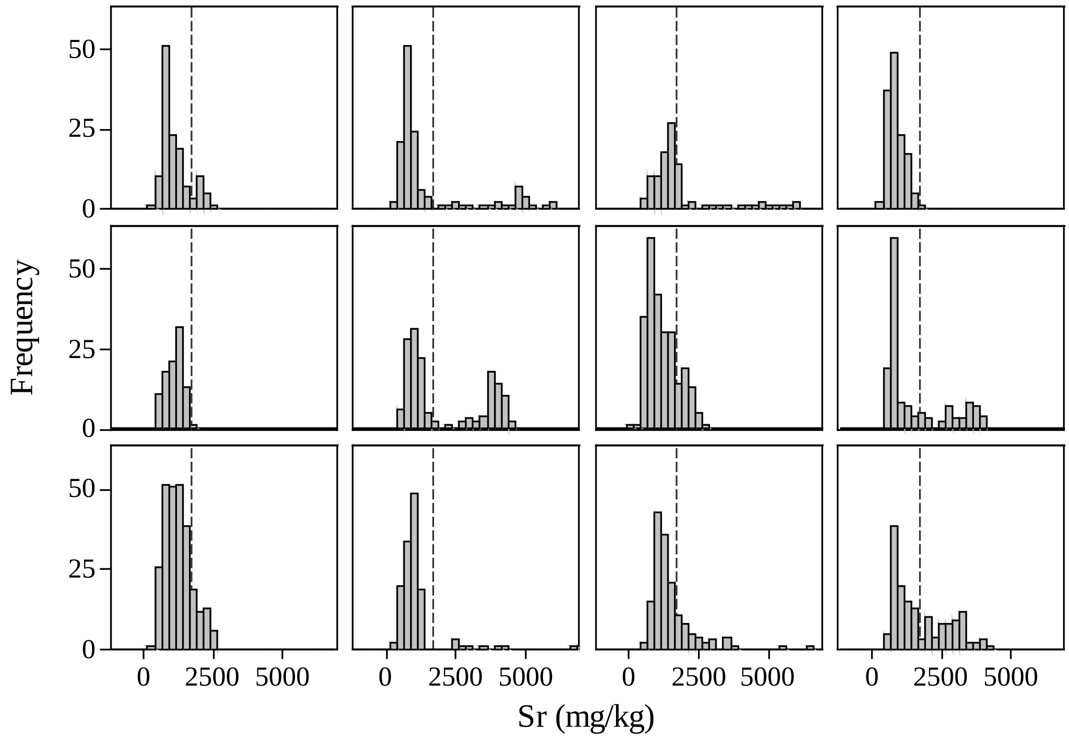

Figure 13. Strontium (Sr) concentration (mg/kg) histograms for otoliths in Figure 12.

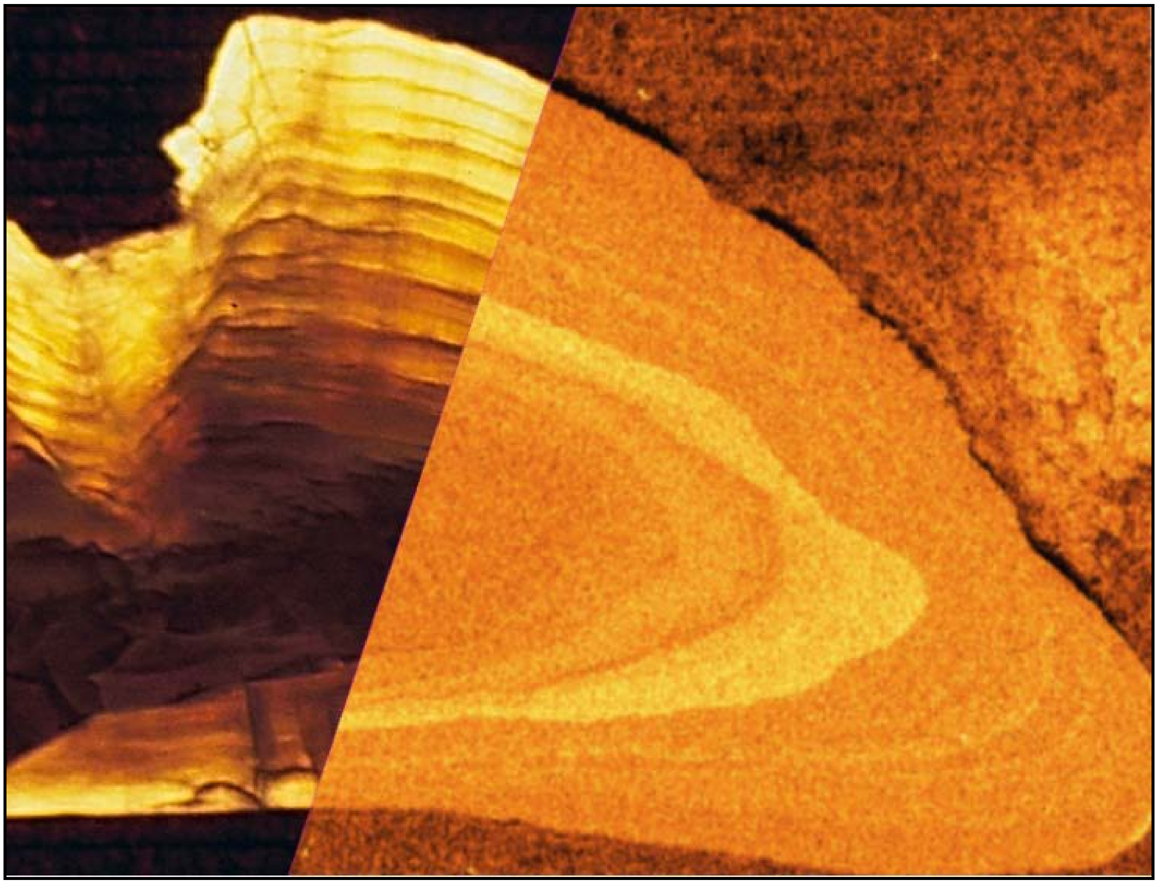

Figure 14. Composite opitical image and Sr map of an otolith. This shows the age annuli on the left and a Sr map on the right. In the Sr map, the lighter the color the higher the Sr concentration. The division between the two is approximately the micro-probe transect graph illustrated in Figure 15.

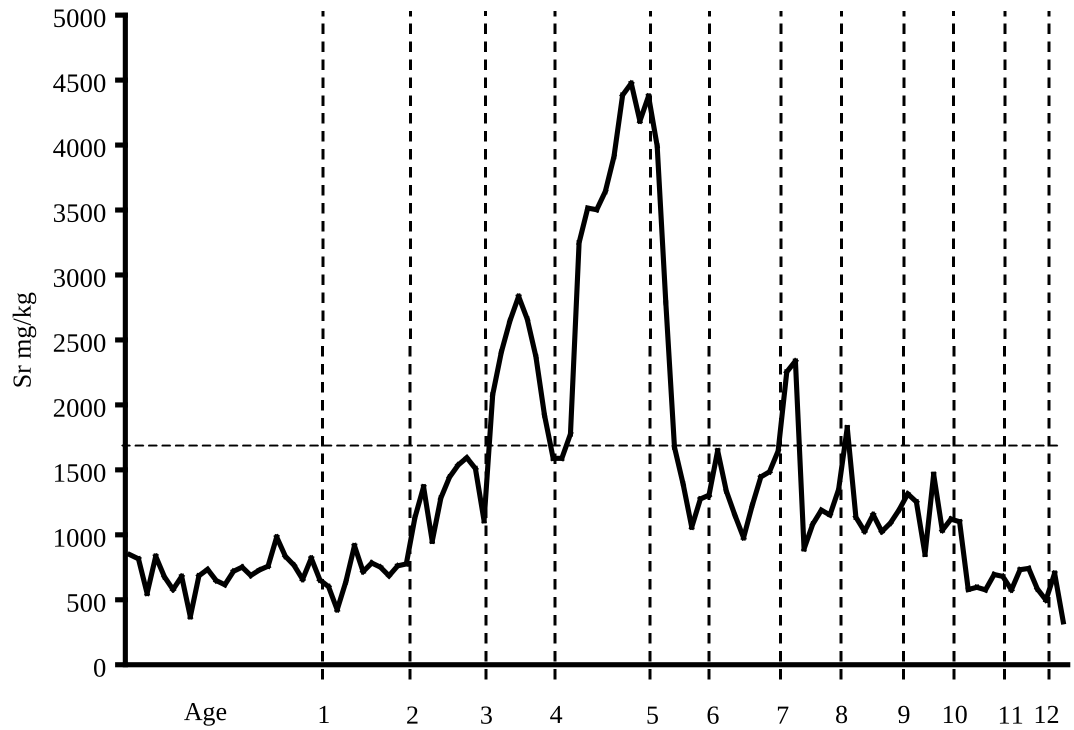

Figure 15. Strontium core to margin transect of the otolith in Figure 14. Age annuli (dashed vertical lines) and the 1,700 mg/kg amphidromy critical point (dashed horizontal line) are indicated. The large peak between ages 4 and 5 corresponds to the bright band in the Sr map in Figure 14.

Age and Length Composition

The otoliths for the age-composition examinations were collected primarily from GSI sampling, which resulted in a female bias to the sample. However, when the age distribution of males was compared to females, there were similar trends. For example, ages 7 through 10 comprised 52.6% of the male population and 52.5% of the female population. Likewise, ages 11 and 12 were comprised of 10.4% males and 10.1% females, which led to the conclusion that the sample was representative of the population. This similarity in distribution was also evident when the length distributions of males and females were compared, which showed that size distributions were similar. Because of the small sample size of males collected in this study, the estimated age at first spawning is less certain than for females. Chang-Kue and Jessop (1992) indicated that male and female broad whitefish mature at age 7 (Table 2), while studies of other species of coregonids indicate that males typically mature before females (Alt 1976; Terble and Tallmen 1997; Brown 2004; VanGerwen-Toyne et al. 2008). Age of mass maturity, when 50% of an age group is mature, was not calculated because all females in my samples were mature fish, as evidenced from the GSI data. Males in the sample were assumed to be mature because of their association with mature females. In the aforementioned studies, ages for mass maturity of broad whitefish were 6 or 7 for males and 7 or 8 for females. The youngest individuals in this study were two females aged at age 5. In contrast, the youngest male collected was age 6. The mixed sex age-frequency histogram showed a bimodal distribution, where ages 11 and 12 had poor representation and ages 13 and 14 had good representation in the sample. Age-frequency histograms in studies of broad whitefish or other coregonids using otolith ages are frequently unimodal, with the majority of the population between ages 7 to 13 for broad whitefish (Brown 2000; Howland et al. 2004; Brown 2006; VanGerwen-Toyne et al 2008) and ages 4 to 8 for humpback whitefish (Brown 2006). In this study, 48% of the population fell between ages 6 and 10 and 20% were

Table 2. Comparison of broad whitefish in 11 systems across their range.

River	Reference	Age at maturity (years)	Sample size	Migration distance (km)	Spawning period	Overwintering
Yukon	This study	5-6 [2]	78	1,450-1700	Late November	Near spawning site
Anadyr River	Shestakov (2001)	6-7 [1]		≥1200	Early November	
Arctic Red River	Tallman et al. (2002)	5-6 [2]	603	350-450		
Mackenzie River	Reist and Bond (1988)	7		>500	Early November	Downstream of spawning site
Ob' River	Prasolov (1989)	7-8 [1]		≈ 800	Late October	Downstream of spawning site
Peel River	VanGerwen-Toyen et al. (2008)	5-6 [2]	2942	>500	Late October	Downstream of spawning site
Prudhoe Bay	Gallaway et al. (1997); Morris (2000)	9		>275	Early November	Downstream of spawning site
Selawik River	Brown (2004)	7-8 [2]	114	>400	Early November	
Tanama River	Popov (1975)	7-8 [1]		>500		
Travaillant Lake	Tallman et al. (2002)	5-6 [1]	746	5-12		
Tuktoyaktuk Peninsula	Change-Kue and Jessop (1983; 1992)	7 [1]	2433,	>700	Early November	Downstream of spawning site

Aging method 1= scales, 2 = otoliths

contained in ages 13 and 14. The large portion of the population in the older age groups suggests that there may be fluctuations in recruitment into the spawning population influenced by either environmental shifts or variations in the intensity of exploitation by humans or other predators. Brown (2004) suggested several possible explanations for similar variation in the distribution observed in his study of the Selawik River Delta; including unusually high predation, high water events at critical points in the life cycle, low winter flow combined with low winter temperatures, and storms effecting dispersal of juveniles. Coregonids of all species are often harvested in greater numbers in years with low salmon returns (Andersen et al. 2004). However, the overall age distribution of this population does not stray markedly from patterns revealed in other studies of broad whitefish, even though the youngest fish in this spawning population appears to be one or two years younger than individuals of spawning populations at higher latitudes (Prasolov 1989; Treble and Tallman 1997; Babaluk et al. 2001).

Based on length-at-age data of the broad whitefish sampled in this project, there was a difference of 9 cm or more between the largest and smallest fish for six of the 12 age groups, with a maximum of 21 cm at age 6. This observed variation in length-at-age may be an indication of differences in the quality of feeding areas. Fish passing the study site at the Rampart Rapids on the Yukon River were captured during a spawning migration and presumably came from a variety of different feeding areas. Research on the downstream distribution and migration of larval and juvenile coregonids has shown that passive movement of larval coregonid fishes downstream and into floodplain lakes was correlated with the magnitude of freshet flow (Naesje et al. 1986; Shestakov 1991, 1992). As flows subsided, the juveniles not washed into floodplain lakes actively moved into lakes connected to the main river to access feeding areas. Shestakov (1992) indicated that in one year of his study, spring freshet flows were low and the distribution of juveniles in floodplain lakes was lower than in other years. For humpback whitefish in the upper Tanana River, Brown (2006) found that humpback whitefish from four feeding area tagging sites were nearly equally distributed between the two spawning areas in the region. However, fish from one feeding area were older, longer, and heavier than those from the other three sites. The author concluded that fish from the two spawning areas were randomly recruited to feeding areas of different quality and that they had high fidelity to these feeding sites. Speculation on specific destinations of the offspring of this population is outside the scope of this study, but they certainly include suitable habitats between the spawning areas in the Yukon Flats to estuarine waters at the river mouth. It is likely that the quality of feeding and rearing areas was variable, which would lead to differences in growth rates and the age at first spawning.

Gonadosomatic Index

The GSI pattern revealed that broad whitefish captured in the late summer and fall at the study site were preparing to spawn. A consistent increase in GSI was observed over the sampling period and it was expected to continue to increase as spawning time drew closer. Expanding the sampling period would have allowed for a more accurate prediction of the timing of spawning, but river conditions at that season become increasingly hazardous with slush and pan ice beginning to flow by early October. When these GSI estimates were compared to similar data from studies completed in the Mackenzie River and its tributaries, similar patterns were observed. However, those patterns were shifted earlier in the season in the Mackenzie River, presumably due to differences in water temperature (Bond and Erickson 1985; VanGerwen-Toyne et al. 2008). Using freeze-up and break-up dates in these two river systems, it would appear that average water temperatures in the Yukon River are warmer than in the Mackenzie River (Pavelsky and Smith 2004; NWS 2009).

Run Timing

The run-timing data spanned six years and was collected from a fishwheel video monitoring project run in conjunction with a fall chum salmon *O. keta* monitoring study (Daum 2005). These data showed that broad whitefish began to enter the catch in late June and July, with the majority of the run appearing in September. However, our sampling efforts did not catch the end of the run due to declining air temperatures that made running the fishwheels dangerous as a result of ice build up on the raft and baskets. It is likely that the run continued to pass the capture site through October because radio-tagged fish did not arrive in the spawning area until late October or early November. The late run timing affords spawning broad whitefish some protection from exploitation because river conditions at that time of year limit fishing effort. Similar to the comparison of this population and studies from higher latitudes with regard to seasonal maturity rate, run timing is likely influenced by water temperature as well, possibly accounting for the later run timing for this population than has been reported in other studies (Reist and Bond 1988; VanGerwen-Toyne et al. 2008). In systems with good light transmittance, photoperiod could play a role in determining spawning timing. However, in the turbid glacial flow of the Yukon River, light penetration is limited to the top few cm until the river freezes, which reduces sediment inputs from glaciers and bank erosion (Brabets et al. 2000).

Radio Telemetry

Of the 41 broad whitefish implanted with radio transmitters, 31 were located on the spawning grounds. The spawning grounds began 190 km upstream from the tagging site and extended 290 km upstream along the mainstem Yukon River in the Yukon Flats, based on farthest upstream locations. Implanted fish were distributed unevenly along this reach with two loose groups near the middle with a space of about 15 km between, one fish 30 km upstream of the others, and the others scattered throughout the reach. Finding such a large proportion of implanted fish from two consecutive tagging years along the same reach indicated the importance of this area for spawning broad whitefish.

The telemetry portion of this study not only delineated the likely spawning region for this population, but also that the same area was used as overwintering habitat. How long these fish remained in the area is unknown, but it was likely that they move during or just after the ice breakup to take advantage of increased flows that accompany spring freshets to access off-channel feeding lakes. Shestakov (1992) reported that juvenile broad whitefish in the Anadyr River in eastern Russia use the high water of May and June to move into feeding lakes downstream from the spawning grounds. It is possible that adults exhibit fidelity to these lakes as was documented by Brown (2006) for humpback whitefish in the upper Tanana River. The overwintering strategy of these fish is different from what has been reported for broad whitefish in the Mackenzie River by Chang-Kue and Jessop (1983; Table 2) or for inconnu in the Yukon River by Brown (2000), the only other coregonid species radio tagged at the same study site. Chang-Kue and Jessop (1983) offered mid-November as the beginning of the post-spawning downstream migration of their tagged broad whitefish from spawning to delta areas of the Mackenzie River. The battery life of the transmitters in their study, however, was only 90 d, which did not allow them to follow their fish into spring. Brown (2000) found that inconnu that spawned in early October would retreat from their spawning area in the upper reaches of the Yukon Flats and migrate downstream past the Raven’s Ridge station beginning in mid-October. This different overwintering area is likely due to the channel configuration and current speed in the inconnu spawning area approximately 100 km upstream from the broad whitefish spawning area, which has shallow braided channels and current that is much faster than where broad whitefish in this study spawned. Broad whitefish spawned in older, more established channels that had deep pool habitat that does not freeze to the bottom during the winter.

There may also be advantages to the overwintering strategy exhibited by broad whitefish. One of the fish that overwintered on the spawning grounds was relocated in Shovun Lake off the Christian River, a tributary of the Chandalar River approximately 75 river kilometers (rkm) from its last location on the spawning grounds. The topography and hydrology of this area would indicate that this migration may be much more direct during high water such as a spring freshet. A difference of only 5 m separates the elevation of Shovun Lake and the Chandalar River at the confluence of the Christian River over a straight-line distance of 27 km. In addition, the Christian River can more accurately be described as a pearled stream, with numerous lakes of various sizes along its course. During the spring freshet, this area may become one large lake, facilitating easy movement along its course. Because this lake is upstream from the spawning area, some possible explanations for how or why this fish moved to this location are: 1) as a juvenile, it was washed into the area during a flood event and, as an adult, it had fidelity to the site; 2) the fish was trying to locate a better feeding site; or 3) as put forth by Brown (2006), adult whitefish after first spawning randomly move into feeding areas and, if they succeed in feeding, overwintering, and migrate back to the spawning area, they have fidelity to that feeding area. The movements of mature broad whitefish in the Yukon River during and after the spawning run revealed the importance of the Yukon Flats spawning area and highlighted some differences in the life history of this population compared with other high-latitude populations of broad whitefish such as those on the lower Mackenzie River. For example, many fish in the Yukon River population remained in upstream reaches for overwintering, while individuals in the Mackenzie River apparently migrated downstream from their spawning area to the delta following spawning. Also, the distance of migration appear to be nearly three times as far in the Yukon River, 1,500 to 1,700 km compared to 350 to 400 km in the Mackenzie River (Table 2). The distance to feeding areas may have also affected their overwintering strategy. This population appeared to remain in freshwater habitat after maturity, while some Mackenzie River broad whitefish use the estuary and migrate to freshwater systems beyond the estuary along the Tuktoyaktuk Peninsula (Bond and Erickson 1985; Chang-kue and Jessop 1992)

Otolith Microchemistry

The microchemical analysis of the 12 individuals indicated that there was a high incidence of amphidromy in this population and provided some details on the frequency of individual movements between estuarine and freshwater habitats through their life spans. The peaks in Sr, indicating use of estuarine habitat, in the core to margin transect graphs in Figure 12 show similar patterns to the aged Sr transect graph in Figure 15. This would suggest that broad whitefish slowly move down to the estuary, feeding along the way for up to three years. Brown et al. (2007) identified three of the seven populations in his study in which no amphidromous individuals were detected. These populations were all greater than 1,700 km from the mouth of the Yukon River. These data demonstrate that broad whitefish populations in the Yukon River drainage do not require estuarine habitats to attain maturity. Alt (1976), working with scale ages, found the highest growth rates and youngest age-at-maturity of five populations of broad whitefish from Alaska to be in the Porcupine River, which was identified by Brown et al. (2007) as a non-amphidromous population. Otoliths from Brown et al. (2007) found similar high growth rates in the Porcupine River. Detailed comparative studies of ecology, growth rates, age-at-maturity, and other life-history attributes of amphidromous and non-amphidromous populations are needed to better understand the energetic requirements of broad whitefish.

Of the ten fish found to be amphidromous, all individuals showed peaks in Sr concentration along the mid portion of the core to margin transect, then a decline in Sr concentrations returning to freshwater levels. This is illustrated in the composite optical/Sr map (Figure 14) and the associated core to margin Sr concentration graph (Figure 15) of the same otolith. Between ages 3 and 8, this individual made repeated trips to estuarine waters and then ceased using this habitat, as evidenced by the return of Sr levels below the 1,700 mg/kg critical point after age 8. This suggests that once these fish reach sexual maturity, they are able to acquire sufficient resources to sustain somatic and reproductive demands in freshwater habitats without returning to estuarine habitats. Brown (2006) hypothesized that humpback whitefish in the upper Tanana River prospect for feeding habitats upstream from their overwintering habitat after their first spawning by using olfaction to guide them. The exact odor, whether it is other fish of their own species, food, or water chemistry, is unknown. Fish that find a suitable feeding habitat with dependable access develop fidelity to that feeding lake. Going elsewhere has greater risk because it is unknown if access to the river will be available at low water levels, which are not unusual in late summer. In this study, one radio-tagged fish spawned in the Yukon River near the mouth of the Chandalar River, overwintered in the same vicinity, and then was found in September 2004 in Shovun Lake, approximately 75 rkm upstream from its overwintering area. It was unlikely, given the late date, that this fish would spawn that year. Treble and Tallman (1997) noted an alternate year spawning strategy in the Mackenzie River. Likewise Bond and Erickson (1985) found a similar spawning strategy in tributaries of the Tuktoyaktuk Peninsula, Northwest Territories, Canada. Tallman et al. (2002) found a low occurrence of resting adults in both amphidromous (from the Arctic Red River) and potamodromous (from Travaillant Lake) populations, 8% and 9%, respectively. Even though the true age and life history of this fish is unknown, the fact that this female was tagged migrating upstream, did not return downstream after overwintering on the spawning grounds, and was not on the spawning grounds in 2004 illustrates the complex life history of this species.

This research provides the most comprehensive examination of the life history of broad whitefish in the Yukon River to date. The Yukon River is unique among the large rivers of the Arctic/sub-Arctic region in that it occupies a narrow band of latitude flowing east to west. Most other major rivers of this region flow south to north, providing for a different flow regime, with the mouths breaking up after the headwaters and likely freezing up in reverse (Pavelsky and Smith 2004). In contrast, the Yukon River breaks up and freezes somewhat uniformly along its length, with an average breakup date for its entire 2,250 km length within Alaska of May 11, ranging from May 5 at Eagle to May 18 at Mountain Village (NWS 2009). A comparison of the behaviors of the broad whitefish in the Yukon River with those in these other river systems is shown in Table 2. The differences in age at maturity and behavior could be attributed to the differences in climate and hydrological régime of the system in which they live.

There is little or no data from Russia on the extent of amphidromy in broad whitefish, but research has been conducted in the Mackenzie River system in Canada. Tallman (2002) described differences in amphidromous and potamodromous populations of broad whitefish in the Mackenzie River and nearby Travaillant Lake, which is connected to the Mackenzie River. Those amphidromous populations traveled only 350 to 450 km, compared to 1,400 to 1,650 km for the fish in this study (Table 2). Brown et al. (2007) found amphidromous broad whitefish at four of the seven sampling sites in the Yukon River drainage, including fish in this study. They found amphidromous broad whitefish in two major tributaries, the Koyukuk and Tanana rivers (1,600 km and 1,300 km from the sea, respectively), as well as in the upper reaches of the Yukon Flats above the upper limit of migration of radio-tagged broad whitefish from this study. Three of their sampling sites were upstream from the broad whitefish spawning area identified in my study. These locations included the upper Yukon River (2,000 km from the sea), the Porcupine River (2,000 km from the sea), and the Chandalar River (1,800 km from the sea), none of which have a physical barrier to fish migration. No amphidromous individuals were detected in those distant upstream sites. Brown et al. (2007) were unsure whether it was the distance from the sea or the suitability of spawning habitat that limited the apparent upstream distribution of amphidromous fish into the drainage. Two possible explanations for the occurrence of amphidromous and non-amphidromous fish in the same system are: 1) there are spawning areas that consist entirely of non-amphidromous fish that have not yet been located; or 2) a portion of the offspring from spawning areas with both amphidromous and non-amphidromous individuals make their way into populations comprised solely of non-amphidromous individuals.

Brown's (2000) research firmly established that coregonids routinely made long migrations within the Yukon River corridor. Previous studies in the Yukon River by Alt (1976, 1986) and Alt and Kogl (1973), although not explicitly stated, treated coregonids other than inconnu as local residents, not moving far from where they were observed. Brown (2000) was able to ground-truth the presence of spawning inconnu by targeting radio-tagged individuals with beach seines. In the process, he also found spawning humpback whitefish and Bering cisco. As a result, broad whitefish were the only species that was passing the Rampart Rapids study site with an undetermined spawning destination. Spawning movements for broad whitefish have been documented on the Alatna and Kanuti rivers and the mainstem Koyukuk River (Brown and Severin 2009). Brown (2004, Brown et al. 2007) also determined that whitefish captured in the Selawik and Koyukuk rivers used estuarine habitats during a portion of their life history. Outside of Alaska, spawning movements and estuarine habitat use have been documented in the Mackenzie River drainage and coastal waters near the Mackenzie River mouth (Chang-Kue and Jessop 1983; Bond and Erickson 1985;

Reist and Bond 1988; Chang-Kue and Jessop 1992, 1997; Treble and Tallman 1997; Babaluk et al. 2001; Tallman et al. 2002; VanGerwen-Toyne 2008), as well as along the northern coast of Alaska (Morris 2000).

As in Brown's (2000) study with inconnu, otolith microchemistry and radio telemetry were used to illuminate lifelong and seasonal movements of Yukon River broad whitefish. Other information identified in my study includes the confirmation that this population was preparing to spawn, the age composition of mature fish, and the timing of the spawning migration. Broad whitefish moving past the Rampart Rapids in late August and September were migrating to a spawning reach between 1,400 and 1,650 km upstream from the Bering Sea. Fish began arriving at the spawning area in October and most likely spawned during early November. Many of the spawning fish overwinter in the spawning area. After hatching in the spring, the juveniles reached the estuary by age 2 or 3 and moved between fresh and marine waters each year until they reach maturity at 6 or 7 years of age. Otolith microchemistry data indicated that after reaching maturity, broad whitefish migrate upstream in the fall to spawn and recruit to feeding areas in freshwater habitats the following summer. Despite this information, there is more to learn about juvenile rearing habitats prior to reaching the estuary and feeding habitats of adults that remain in fresh water after reaching sexual maturity. To explore the questions raised by my study, it will be necessary to expand sampling and telemetry efforts in the Yukon River drainage and in potential feeding areas to estimate the proportion of non-amphidromous individuals and to identify other spawning areas, especially those with high proportions of non-amphidromus fish. These future evaluations will help to clarify the downstream distribution of non-amphidromous populations, summer feeding distribution of amphidromous populations, and spawning origins for the non- amphidromous populations that appear to exist upstream from the Yukon Flats, more than 1,700 km from the Bering Sea.

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