MIGRATORY PATTERNS OF YUKON RIVER INCONNU AS DETERMINED WITH OTOLITH MICROCHEMISTRY AND RADIO TELEMETRY

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By
Randy J. Brown, B.S.

Fairbanks, Alaska
May 2000

Abstract

Migratory patterns of Yukon River inconnu *Stenodus leucichthys* were evaluated using otolith aging and microchemical techniques and radio telemetry. Research was conducted each fall between 1997 and 1999, on inconnu captured at a study site 1,200 river km from the Bering Sea. Biological data were collected to establish maturity and spawning condition. Sagittal otoliths were analyzed optically to determine age distribution, and microchemically to determine amphidromy. Inconnu were tagged with radio transmitters and located in upstream spawning destinations. Inconnu captured at the study site were uniformly large, mature fish preparing to spawn. Age estimates ranged from 7 to 28 years. Microchemical analyses suggested that the population was amphidromous rather than freshwater only. Preliminary testing of radio transmitter attachment methods showed that the internal method (pushed through the esophagus into the stomach) was superior to the external method (attached behind the dorsal fin) for use with migrating inconnu. Most radio-tagged inconnu were located during their spawning time in a common region of the Yukon River. Inconnu captured at the study site each fall were mature fish engaged in a spawning migration that originated in the lower Yukon River or associated estuary regions, and continued towards a common spawning destination in the Yukon River, approximately 1,700 river km from the sea.

Table of Contents

List of Tables

List of Figures

Introduction

Inconnu *Stenodus leucichthys* are large whitefish (Figure 1) found in both Asia and North America (Berg 1962; Scott and Crossman 1973). Specimens exceeding 100 cm in length and 15 kg in weight are not uncommon, and much larger individuals have been recorded (Alt 1969; Scott and Crossman 1973). Their current taxonomic placement within the bony fishes class is: Order: Salmoniformes; Family: Salmonidae; Subfamily: Coregoninae; Genus: Stenodus; Species: *Stenodus leucichthys* (American Fisheries Society 1991; Moyle and Cech, Jr. 1996). Two subspecies are recognized, *S. l. leucichthys*, isolated in the Caspian Sea drainage of western Asia, and the more broadly distributed *S. l. nelma*, inhabiting Asian and North American river systems flowing into Arctic Ocean and Bering Sea waters (Scott and Crossman 1973).

FIGURE 1.—Inconnu Stenodus leucichthys are large whitefish in the Family: Salmonidae, Subfamily: Coregoninae.

Inconnu are capable of traveling widely within their home drainages during their lives, which may span two decades or more (Alt 1987; Howland 1997). They spawn in the fall, broadcasting their eggs into flowing freshwater over a gravel substrate (Morrow 1980). Fertilized eggs settle to the bottom, hatching several months later. Larvae emerge in the spring when rising water levels distribute them downstream (Reist and Bond 1988; Shestakov 1991). Juveniles feed on a wide variety of invertebrates initially, but soon become piscivorous, feeding almost exclusively on fish for the duration of their lives (Fuller 1955; Alt 1965). Inconnu are commonly found feeding in marine waters near the mouths of their natal rivers (Petrova 1976; Alt 1987; Reist and Bond 1988), a migratory behavior known as amphidromy, a specialized form of diadromy in which a fish migrates between fresh and saltwater for reasons including, but not restricted to, spawning (McDowall 1988). However, amphidromy is not obligatory, and non-amphidromous populations have been described in some locations (Petrova 1976; Alt 1987; Howland 1997). Following several years of growth, inconnu become sexually mature and take part in upstream spawning migrations every two or more years till death (Alt 1987; Reist and Bond 1988).

The Yukon River, in northwest North America, harbors a substantial population of inconnu. They are present from near-shore marine waters near its mouth to more than 2,500 km upstream, and in many of its tributary rivers (Scott and Crossman 1973; Morrow 1980; Martin et al. 1987). Spawning locations have been identified in the Koyukuk and Tanana river drainages, major tributaries to the Yukon, and are suspected in several other areas as well (Alt 1987). Despite our knowledge of basic inconnu life history and their distribution in the Yukon River drainage, uncertainty persists regarding specific movement patterns along the river. For example, it is unclear whether an inconnu captured 1,000 km from the sea is an amphidromous fish migrating to some distant, upstream site, a non-migratory fish remaining in a localized region of the river, or a non-amphidromous, migratory fish at some point along its range. This uncertainty, coupled with unknown spawning and rearing locations, complicates any attempt to effectively manage the fishery.

Currently, inconnu are harvested throughout their range on the river. Sport fishers harvest a limited number each year (Mills 1989, 1994) and are restricted by regulation to a certain number of fish per day. A much larger number are taken directly or incidentally during net or fishwheel fisheries (Crawford 1978; Alt 1987) that are not regulated for inconnu. The movement patterns of inconnu along the river must be understood to develop a meaningful and effective management strategy for the fishery, if it is deemed necessary.

This thesis describes an inconnu migration study conducted between 1997 and 1999. It focuses on inconnu captured approximately 1,200 km upstream from the mouth of the Yukon River (Figure 2) during August and September. The main objectives of the study were to determine if they were migrating from marine environments near the river's mouth, and to locate their spawning destinations. Otolith microchemical techniques were used to determine whether fish were coming from marine environments, and radio telemetry was used to accomplish the spawning destination work. Prior to the two migration components of the study, the maturity and spawning condition of inconnu at the study site were evaluated using biological data gathered from harvested inconnu.

The thesis is organized into chapters, each chapter describing a different component of the study. Since different background information and methodology were required for each component, the chapters are designed to stand alone. Each has an introduction, methods, results and discussion section. The final chapter, a summary conclusion section, synthesizes the results from all components of the project together. A general introduction and a single references section bracket the body of the thesis.

Study Area

The Yukon River flows more than 3,000 km from its headwaters in northern British Columbia to its mouth on the Bering Sea in western Alaska. It drains an area of

FIGURE 2.—Study site on the Yukon River in Alaska, located 1,200 river km from the Bering Sea.

approximately 855,000 km^2. The study site is located 1,200 river km from the sea at approximately 65^{0}20' N latitude and 151^{0}03' W longitude at an elevation of 67 m (Figure 2). Near the study site, the river can be over 1 km wide and 15 m deep, and flows from 8 to 12 km per hour. Due to the glacial origins of some tributaries, the water is silty during the summer, but clears during the winter. The region experiences a continental climate with long, cold winters and brief, warm summers. The river generally freezes by late October or November and the ice remains until late April or May of the following year.

Biological Sampling

Introduction

Inconnu can be captured throughout the summer season at the study site. However, their apparent abundance, as determined by local fishers' informal catch-rate assessment, is relatively low early in the summer, and increases as the fall approaches. This pattern of variable abundance suggests that a population of inconnu may be moving past, or moving into, the study site each fall. Alt (1987) contends that a migration to upstream spawning areas does occur in that area of the river each fall, although precise spawning locations have not been identified. Additionally, it is unclear whether captured fish represent a single spawning stock with a common life history, or multiple stocks with variable life histories.

Inconnu engaged in spawning migrations exhibit certain detectable biological indicators of their condition. In general, the gonads of seasonal spawning fish become enlarged as spawning time approaches, increasing the ratio of egg to body mass (Snyder 1983). A gonadosomatic index (GSI) is created when this ratio is measured for many fish in a population and plotted over a period of time. Howland (1997) demonstrated the utility of the procedure for inconnu when she documented an increasing GSI trend in female inconnu preparing to spawn in the Mackenzie River drainage. The feeding condition of inconnu can potentially reveal their intentions also. Alt (1969) reported that pre-spawning inconnu fasted for several weeks or months prior to spawning. Evaluating the GSI trend and feeding condition of inconnu captured at the study site would provide two sources of supportive or refutatory evidence concerning their spawning condition.

This component of the study describes the basic inconnu sampling operation at the study site. The primary objective was to compile a GSI trend chart and to assess the feeding condition of sampled inconnu to determine whether it was reasonable to assume that a spawning migration was occurring. Secondary objectives were to describe captured inconnu according to length and weight distribution, to determine the sex ratio of sampled fish, and to evaluate whether the sex of whole fish could be reliably determined by external examination.

Methods

Local fishers from the area near the study site provided inconnu from their catches for sampling. Upon delivery, fish were placed in a cold-water bath ($<5^0$C) until processed, usually within 12 hours. A total of 266 fish were sampled between July 22 and September 20, 1997. Fishing effort was not uniform over the time period, so access to fish for sampling was not continuous, and sample numbers do not directly reflect their abundance in the river. However, there was no attempt to preferentially sample or segregate the catch by size or sex. As a result, the sample is assumed to be roughly representative of the population. The fork length (length) of each fish was recorded to the nearest 1 cm. Whole fish were then placed on a digital platform scale, and weights were recorded to the nearest 10 g. Egg skeins from female fish were similarly weighed and recorded. The feeding condition of each fish was evaluated by examination of the stomach. Food was either present or absent. Prior to evisceration, the sex of each fish was predicted, based solely on the relative distention of the belly, by the two to three samplers present. Following evisceration, the true sex was recorded and the accuracy of the prediction was noted. Finally, sagittal otoliths were collected from each fish for aging and otolith microchemical work. Details of this procedure are discussed in the next chapter (Otolith Aging and Microchemical Analyses). Inconnu carcasses were ultimately prepared for drying and returned to the local fishers after the sampling was completed.

Sampling data were used to create charts displaying information about the population of inconnu present at the study site. A GSI trend chart was prepared, with values calculated as egg weight percentage of the whole body weight [(egg weight /whole body weight)(100); Snyder 1983]. GSI values were analyzed against the Julian date of fish capture, and plotted against the calendar date. The null hypothesis was that the slope of the regression line fitted to the GSI data was equal to zero. This would happen if no enlargement of gonads occurred over time, and would indicate that spawning was an unlikely objective for the sampled fish. Lengths of female and male inconnu were compared with a median test, and a chart displaying length distribution by sex was prepared. Weights of female and male inconnu were similarly compared with a median test. The weights of sampled inconnu were plotted against their lengths to demonstrate the relationship between the two measures.

Results

Two hundred and sixty-six inconnu were sampled at the study site. Of these, 110 were females and 156 were males, a ratio of approximately 0.7 to 1. Gonadosomatic index trend data were collected from 108 of the females. All females examined appeared to be gravid, each possessing great skeins of eggs filling the gut cavity (Figure 3). The percent egg mass of sampled inconnu rose from about 11% in late July to about 23% in mid-September (Figure 4). A linear regression of the data against the Julian date of capture revealed a positive slope that was significantly different than zero ($P < 0.001$). The R^2 value was 50%, suggesting that the date of capture explained approximately half of the observed variation in GSI values. When GSI values were regressed against Julian date and fish weight the R^2 value rose to 61%, revealing that fish weight was also a significant contributing factor to GSI variation ($P < 0.001$).

FIGURE 3.—Eviscerated female inconnu harvested at the study site. The relatively large volume of eggs was typical of all female inconnu sampled during the 1997 study season.

All inconnu sampled appeared to be relatively large, mature adults. Median lengths and weights of sampled female inconnu were significantly greater than those of males ($P < 0.001$ in both cases). The median length of females was 80 cm (range 71-103 cm) compared to 72 cm (61-85 cm) for males (Figure 5). The median weight of females was 5,485 g (range 3680-13,680 g) compared to 3,840 g (2,210-6,690 g) for males. Weight was highly correlated with length for both female and male inconnu (R^2 female = 87%; R^2 male = 88%). However, female weight increased at a significantly greater rate than male weight with increasing length ($P < 0.001$; Figure 6).

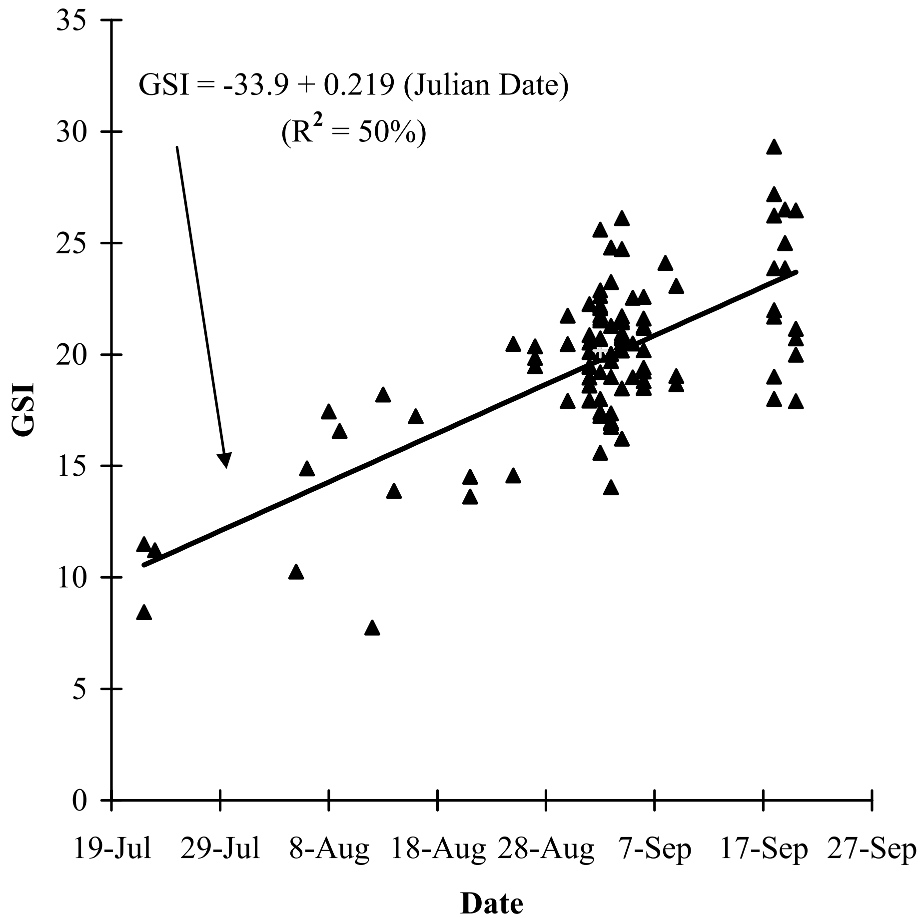

FIGURE 4.—GSI trend chart showing an increase in GSI values over time. The least squares line of best fit for the data, along with the regression equation, are presented. The positive slope (0.219) is significantly different than zero ($P < 0.001$). The R2 value of 50%, suggests that the date of capture explains approximately 50% of the observed variation in GSI values. (The regression equation was calculated using Julian date rather than calendar date. July 19 is Julian date 200, and September 27 is Julian date 270.)

Of the 266 inconnu sampled during the project, only two had food in their stomachs. In one, the contents could not be identified. In the other, however, it was clear that a juvenile longnose sucker *Catostomus catostomus* had been consumed. The stomachs of all other sampled inconnu were empty.

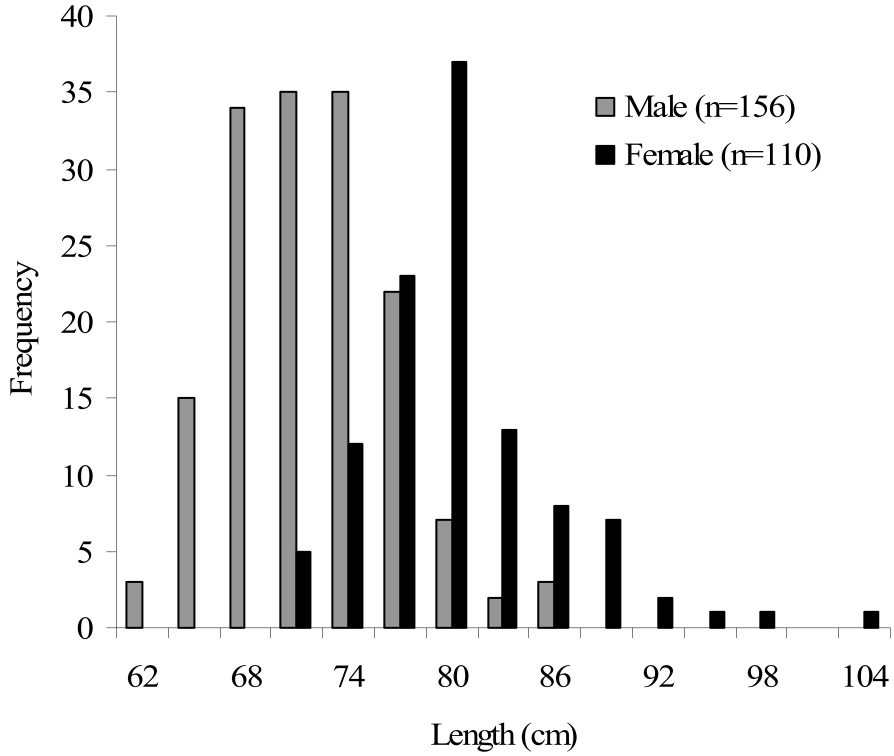

FIGURE 5.—Length distributions of male and female inconnu sampled at the study site, showing clearly that smaller fish were predominantly male, and larger fish were predominantly female. Length data was organized in 3 cm length groups for the figure.

Whole fish were sexed with great accuracy during the sampling study. Of the 266 fish sampled, 264 were predicted correctly by unanimous consent of the two or three samplers present. Neither eggs nor milt could be expressed from any fish by abdominal palpation. Two fish had external features that were ambiguous, and there was disagreement among the samplers as to the sex of these fish.

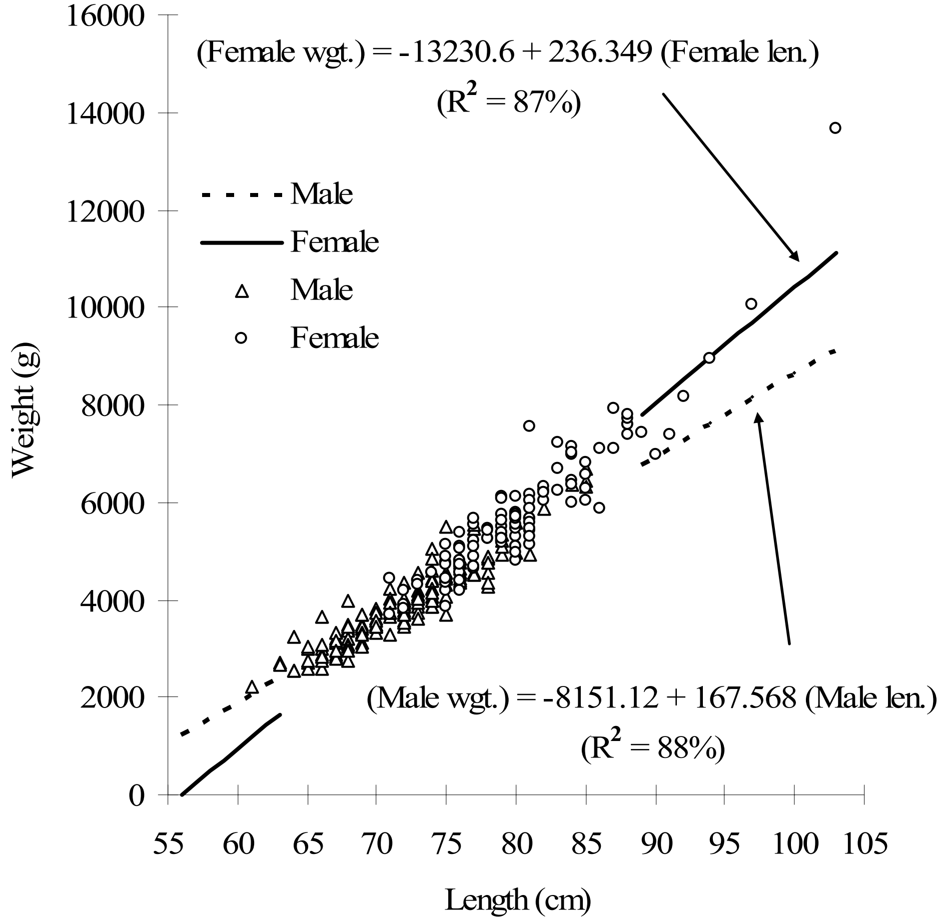

FIGURE 6.—Male and female weight versus length scatterplot, with associated least squares regression lines from the respective data. It is clear that small fish are predominantly male and large fish are predominantly female. The high R2 values for both fitted lines suggest that most of the variation observed in weight can be directly explained by length.

Discussion

Both the GSI trend (Figure 4) and the feeding condition data provide supportive evidence for the notion that a spawning migration occurs at the study site in the fall. The gravid appearance of all females (Figure 3), and the absence of immature fish further support the notion, and additionally suggest that all sampled inconnu were members of a spawning population, and not a mixture of spawning and non-spawning fish. The data fail to provide information about whether sampled fish were from a common spawning stock or from multiple stocks. Similarly, the direction of migration along the river cannot be determined. This information must be obtained in other ways.

The demonstrated ability to distinguish female from male inconnu without eviscerating them has potential utility for tagging projects, allowing sex-specific patterns of movement to be evaluated. Strange (1996) contends that the ability to distinguish between the sexes by external examination is contingent upon the examined population being mature and preparing to spawn. In support of this contention, the only distinctive factor between female and male inconnu in this study was the distention of the belly for females, and the lack of it for males. Researchers considering the practice with populations of inconnu whose spawning condition is unknown, or where pre-spawning and non-spawning inconnu coexist, must proceed cautiously to avoid erroneous interpretation of sex-specific movement data.

The distinctly shifted length distribution of female and male inconnu in the sample (Figure 5) is similar to that reported by Taube (1996) for inconnu on the Kobuk River in northwest Alaska. It is clear from Taube's (1996) data that Kobuk River fish attain larger average sizes than those sampled at the Yukon River study site, a phenomenon Alt (1969) reports as well.

Otolith Aging and Microchemical Analyses

Introduction

Otoliths are mineral structures that lie within endolymphatic hollows associated with the semi-circular canal network near the brain in teleost fish (Platt and Popper 1981). They function in hearing and balance, and are composed primarily of calcium carbonate amid a proteinaceous matrix (Degens et al. 1969). They grow throughout a fish's life as material precipitates on the outer surface, and are generally considered to be insoluble (Campana and Neilson 1985). In many species, growth increments, similar to tree rings, are apparent both on daily intervals for juvenile fish (Campana and Neilson 1985), and on annual intervals for adults (McFarlane and Beamish 1995). Three pairs of otoliths are found in most fish species. The largest pair, sagittae, is commonly used for producing age estimates for a wide variety of fish species (Chilton and Beamish 1982).

Inconnu have traditionally been aged by counting annuli on their scales (Alt 1969; Taube 1996; Underwood et al. 1998), although Howland (1997) recently explored the utility of using otoliths. Scale aging techniques are non-lethal and have a long history of use (Chilton and Beamish 1982), but the structures are vulnerable to resorption and have been shown to consistently underestimate the ages of older specimens of long-lived fishes when compared to otolith age estimates (Barnes and Power 1984; Welch et al. 1993; Lowerre-Barbieri et al. 1994). Consistent with this generalization, Howland (1997) reports inconnu age estimates from otoliths in excess of 30 years in the Mackenzie River drainage, while maximum age estimates from scales have not exceeded 23 years (Alt 1969; Taube 1996; Underwood et al. 1998). Despite the fact that growth increments on inconnu aging structures have not been validated at this time, otoliths were used in this study to produce age estimates.

In recent years, fisheries scientists have used trace element distribution within growth increments in otoliths to describe life history events and patterns of movement of many fishes. Interpretations of these studies have been based on the assumption that the environmental conditions a fish experiences (salinity, temperature, contamination) are major determinants of the chemical composition of otoliths (Secor 1992; Babaluk et al. 1997; Tzeng et al. 1997). Laboratory experiments suggest that this is a valid assumption (Mugiya and Tanaka 1995; Secor et al. 1995; Farrell and Campana 1996). While great potential exists for examining a wide range of elemental markers that may confirm a fish's presence or absence in a given location or habitat (Severin et al. 1995; Thorrold et al. 1998), the clearest results in the discipline have been the documentation of fish movements between fresh and saltwater by examination of otolith strontium (Sr) distribution (Secor 1992; Babaluk et al. 1997; Tzeng et al. 1997), a procedure used successfully by Howland (1997) on Mackenzie River inconnu.

Strontium is a 2+ ion in solution and precipitates in otoliths, replacing calcium (Ca) ions in the mineral matrix, in direct proportion to its concentration in water (Radtke 1989; Fowler et al. 1995; Secor et al. 1995). Strontium concentration in water varies with salinity (Dietrich et al. 1980; Wells 1997), with ocean water worldwide relatively stable at about 8.1 ppm (Lide 1990), and freshwater systems variable, but generally close to 0.1 ppm (Rosenthal et al. 1970). Diadromous behavior places fish in both fresh and saltwater. Strontium distribution patterns within otoliths are expected to vary accordingly.

Electron microprobe technology can be used to examine the Sr distribution in fish otoliths (Campana et al. 1997; Reed 1997). The electron microprobe functions by bombarding selected points on an otolith with a finely focused beam of electrons. Atoms struck by the beam emit x-rays of a wavelength characteristic to the element. Spectrometers, tuned to element-specific wavelengths, count emitted x-rays. The x-ray counts at each sample site are roughly proportional to the number of atoms present. The concentration of Sr in the otoliths of diadromous fish varies widely along a core-to-margin transect, while in otoliths of non-diadromous fish it varies little (Babaluk et al. 1997). Plotting Sr x-ray counts from transects across otoliths produces a fish's lifetime record of saltwater and freshwater movements. Superimposing visible growth increments upon such a plot reveals year-by-year movements.

This chapter describes an otolith aging and microchemical study of Yukon River inconnu. The main objectives were to produce age estimates for sampled fish, and to use otolith microchemical techniques to test Alt's (1987) contention that inconnu found in the late summer and fall at the study site are from an amphidromous stock. The establishment of evaluative criteria upon which to judge the unknown life history sample fish was a required preliminary step to the otolith microchemical work. It involved the examination of otoliths from known amphidromous and freshwater-only inconnu. Additionally, the Sr concentration in Yukon River water was tested to verify that it was actually much less than in ocean water, a critical condition for the validity of the procedure. Secondary objectives were to examine lifetime patterns of movement for selected inconnu between fresh and saltwater, as indicated by Sr distribution across otoliths.

Methods

Sagittal otoliths (otoliths) were collected from 266 inconnu sampled at the study site in the fall of 1997. The basic capture and handling methods are detailed in the previous chapter (Biological Sampling). This section continues, detailing otolith removal procedures and methodology used for aging, microchemical analyses, and other associated activities. Each inconnu head was severed from the body just behind the gill plates. The top of the head, from the dorsal margin of the gill plates to the dorsal margin of the orbits, was removed with a sharp knife. The brain, exposed with this action, was moved, revealing the otoliths lying beneath. Both otoliths were then removed with a forceps. Secor et al. (1991) refers to this technique as the "open-the-hatch method" (p. 15). The otoliths were cleaned by gently rubbing them between a finger and thumb in water until all blood and other tissue fell away. They were then placed in a labeled coin envelope and stored dry.

Dried inconnu otoliths were thin-sectioned (sectioned) and polished in preparation for microscopic viewing and microprobe analysis. One otolith from each fish was ground on a diamond grinding wheel in the transverse plane through the core (Secor et al. 1991), mounted on a glass slide with thermoplastic glue and polished with 3 micron aluminum oxide abrasive powder for optical viewing. Each otolith section was approximately 100 microns thick. Otoliths selected for microprobe analysis were further polished with 1 micron and 0.25 micron diamond abrasives. Preparation was completed with the application of a 30-nm layer of conductive carbon.

Viewing of sectioned otoliths for aging was done with a dark-field (double polarizing filters), transmitted light, compound microscope. With this equipment, opaque zones appeared dark, and translucent (hyaline) zones appeared light. Annuli identification criteria followed basic descriptions by Chilton and Beamish (1982) and illustrations by Haas and Recksiek (1995). However, the specific interface between age-0 growth and age-1 growth, essentially the first annulus, was determined by referencing known-age juvenile otoliths from an in-progress, related study of broad whitefish *Coregonus nasus* (Figure 7; unpublished data). The otoliths of these closely related species are similar in outward appearance and in their patterns of opaque and translucent zones when sectioned. Both the inconnu in this study and the broad whitefish in the related study were harvested in the mid to late summer, so the stage of otolith deposition was expected to be similar. The age-1 annulus was considered to be the interface between the first translucent zone and the second opaque zone, the first opaque zone being the core region. A translucent margin was not counted as an additional year, while an opaque margin was. Age distribution charts of male and female inconnu are presented, and age estimates were associated with length data (see previous chapter, Biological Sampling) to produce sex-specific, age-length keys (Devries and Frie 1996).

Twelve of the 266, sectioned otoliths were selected for microchemical analyses using a stratified, random sampling procedure. Inconnu were stratified into four age groups: 9-

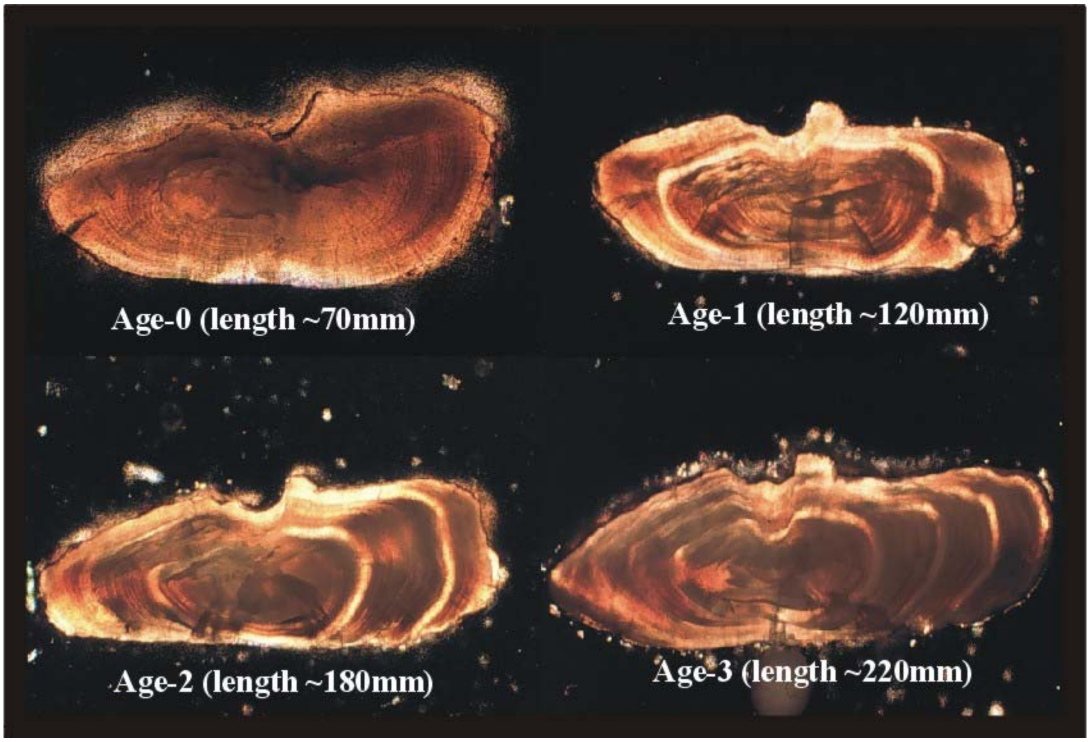

FIGURE 7.—Sectioned otoliths from known-age juvenile broad whitefish. The pattern of opaque and translucent regions were used as references to assist in aging inconnu in the present study. The lengths referred to in the figure are approximate fork lengths of sampled broad whitefish.

11 years; 12-14 years; 15-19 years; and those 20 years and older. The possibility of sex-specific patterns of movement demanded that equal numbers of male and female fish be selected. The greater potential for obtaining long-term movement information from older fish than from younger fish influenced the selection distribution among age groups. Two fish, a male and a female, were selected from both the 9-11 year group and the 15 to 19 year group, and four fish, two males and two females were selected from both the 12-14 year group and the 20 year plus group. Candidates for microchemical analyses were chosen randomly from within these age and sex groups. Selected individuals were then evaluated based on the clarity of the otolith growth increment marks. Those with indistinct growth increments or obscured regions were rejected.

The otoliths of four other inconnu with known life histories were subjected to otolith microchemical analyses to establish standard Sr x-ray distribution patterns from which to judge the unknowns. Two mature inconnu from both freshwater-only and amphidromous life histories were chosen. Freshwater-only inconnu were from the Great Slave Lake in northern Canada (Howland 1997). Amphidromous inconnu were collected from the northern mouth of the Yukon River, where brackish water is known to exist (Martin et al. 1987).

A Cameca SX-50 electron microprobe equipped with wavelength dispersive x-ray spectrometers was used for microchemical analyses. Linear transects across the specimens, from the core region (precipitated during the first year of life) to the margin (precipitated when the fish was older), were made with a 6 micron diameter, 15 kilo-electron volt, 20 nano-ampere beam. Center-to-center distance between transect points was approximately 10 microns. Counts were collected for 25 s at each point. Strontium x-ray graphs (Sr graphs) were created from the data. They were plotted as Sr x-ray counts versus transect points. Annual growth increments crossed by transects were indicated by vertical lines on the Sr graphs of unknown life history subjects.

Strontium x-ray maps (Sr maps) provided graphic images of Sr distribution across entire regions of otoliths. Strontium maps were created by sampling otolith sections in a grid pattern with points approximately 9 microns apart. Each point, analogous to a pixel on a computer screen, was examined with a 6 micron diameter, 15 kilo-electron volt, 200 nano-ampere beam, for 0.1 s. Strontium maps were composed of over 60,000 individual points, and revealed banded patterns of elemental distribution across otolith sections. High concentration regions in Sr maps (indicating that a fish was in saltwater) are bright yellow, while low concentration regions (indicating that the fish was in freshwater) are dark orange. In this study, Sr maps were used primarily to evaluate interpretation of patterns within Sr graphs. They also revealed subtle patterns of Sr distribution that were obscured or unclear for various reasons in the Sr graphs.

The Sr concentration in Yukon River water was tested at two different seasons of the year. Water samples were collected in early April 1998, when the river was ice covered and the water was clear, and in early September 1998, when the river was free of ice and turbid. Samples of unfiltered water, for determining total Sr concentration, and of water passed through a 0.63 micron filter to remove suspended solids for determining dissolved Sr concentration. Samples were collected from the surface layer in mid-river locations. They were sent to a professional contaminates analysis laboratory that determined Sr concentrations using inductively coupled plasma emission spectroscopy, an analytical method capable of detecting Sr in water at concentrations as low as 0.001 ppm.

Results

At least one otolith from each of the 266 sampled inconnu was prepared for age analysis. Most were readable (Figure 8), but a few were obscured and required the alternate otoliths to be prepared as well. The median age of females was 11 years, and for males, 10 years. Females ranged between 7 and 28 years of age, while males ranged between 7 and 23 years of age. Age at length varied for female and male inconnu. For example, female inconnu 80 cm in length varied between 9 and 16 years of age (Table 1). Similarly, male inconnu 72 cm in length varied between 8 and 12 years of age (Table 2).

Strontium concentration in Yukon River water fell within the expected range (Rosenthal et al. 1970). In April, when the river was clear, total and dissolved Sr concentrations were similar, at approximately 0.164 ppm. In September, when the river was turbid, the total Sr concentration was greater than dissolved, showing that some Sr was carried in the suspended silt. Total Sr concentration was approximately 0.141 ppm and dissolved Sr concentration was approximately 0.125 ppm. At greater than 100 times detection

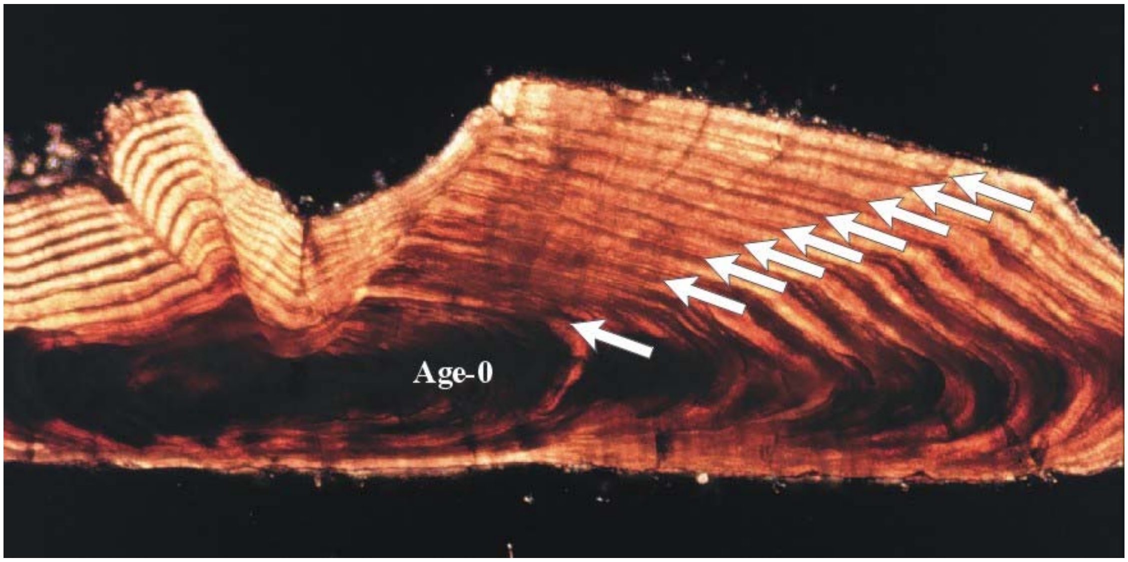

FIGURE 8.—Sectioned otolith from a young inconnu harvested at the study site in 1997, demonstrating the aging method used in this study. Note the similarity of the core region in this figure (labeled Age-0) with the image of the age-0 broad whitefish otolith section (Figure 7). The arrows mark nine annuli. The translucent margin, beyond the ninth annuli, is not interpreted as another year.

limit for the analytical procedure, the error in measurement was considered by the testing laboratory to be small, certainly less than 10%.

Strontium graphs from the otoliths of freshwater-only and amphidromous inconnu revealed distinctly different patterns of Sr distribution. One Sr graph of each is presented here. The Sr graph from the freshwater-only inconnu (Figure 9a) shows a relatively constant low level of Sr x-ray counts across the core to margin transect. By contrast, the Sr graph from the amphidromous inconnu (Figure 9b) displays several large peaks of high Sr x-ray counts across its transect path.

A measure of the variability expected from machine counting error would be helpful for interpretation of Sr graphs, allowing random counting errors to be distinguished from real differences in Sr concentration. Strontium x-ray counts from electron microprobe

TABLE 1.—Female inconnu age-length key. Length is fork length to the nearest cm. In the columns with multiple ages represented, the first number is the number of fish in the cell, the numbers in parentheses are the actual ages of fish in the cell.

Length	Number	Sample Allocation Per Age Group											
Group	**in Sample**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16-19**	**20-23**	**24-28**
71	**2**			2									
72	**3**				1	1	1						
73	**2**			1		1							
74	**1**					1							
75	**9**			1	4	3	1						
76	**11**	1			4	5	1						
77	**8**				5	2	1						
78	**4**			1		1	1		1				
79	**12**			1	2	4	3	2					
80	**14**			1	1	5	3	3			1(16)		
81	**11**		1	1	1	4	3	1					
82	**4**				1	1	1	1					
83	**3**					1		1			1(18)		
84	**6**					1	3		1	1			
85	**4**					1	2				1(16)		
86	**2**					1			1				
87	**2**					1	1						
88	**5**									2	3(16,16,16)		
89	**1**											1(20)	
90	**1**											1(21)	
91	**1**											1(21)	
92	**1**												1(28)
94	**1**											1(23)	
97	**1**												1(27)
103	**1**												1(27)
Total	**110**	**1**	**1**	**8**	**19**	**33**	**21**	**8**	**3**	**3**	**6**	**4**	**3**

TABLE 2.—Male inconnu age-length key. Length is fork length to the nearest cm. In the columns with multiple ages represented, the first number is the number of fish in the cell, the numbers in parentheses are the actual ages of fish in the cell.

Length Group	Number in Sample	Sample Allocation Per Age Group										
		7	8	9	10	11	12	13	14	15	16-19	20-23
61	**1**		1									
63	**2**	1	1									
64	**3**		1	2								
65	**5**	4	1									
66	**7**	2	2	2		1						
67	**12**	1	5	5		1						
68	**11**	1	4	1	5							
69	**11**		2	4	3	2						
70	**12**		2	1	6	2	1					
71	**7**	1		2	2	1	1					
72	**16**		1	3	6	2	4					
73	**10**		1	2	3	3			1			
74	**16**			2	5	3	1	2	1		2(17,17)	
75	**9**				3	2	2	1				1(23)
76	**10**				4	2	3	1				
77	**5**			1		2	1					1(21)
78	**7**				2	2		1		1	1(18)	
79	**4**						1			2	1(19)	
80	**2**						1				1(17)	
81	**1**										1(19)	
82	**1**										1(16)	
84	**1**										1(16)	
85	**3**								1		1(19)	1(23)
Total	**156**	**10**	**21**	**25**	**39**	**23**	**15**	**5**	**3**	**3**	**9**	**3**

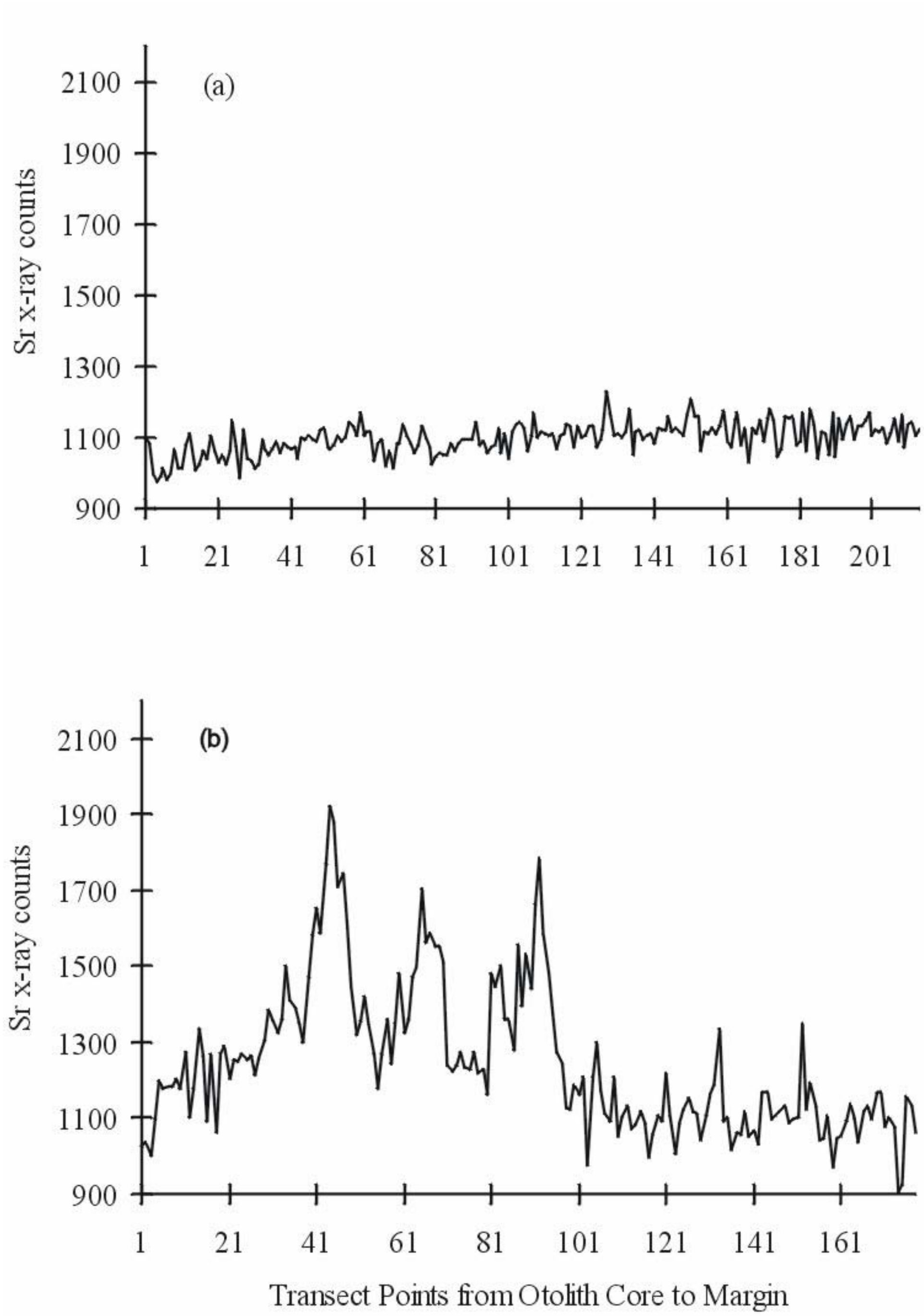

FIGURE 9.—Strontium graphs of known freshwater inconnu from the Great Slave Lake region of Northwest Territories (a), and known amphidromous inconnu from the mouth of the Yukon River in western Alaska (b). Note the extreme spikes of Sr x-ray counts in the Sr graph of the amphidromous inconnu (b) compared to the relatively constant low level of Sr x-ray counts in the Sr graph of the freshwater inconnu (a).

analyses of a homogeneous material have an error that follows a Poisson distribution, whereby the square root of the mean is equal to 1 standard error (Reed 1997). To illustrate the Poisson distributed error as it relates to otolith Sr analyses, lines representing the mean value (1,097) and 1.96 standard deviations (1.96 times the square root of 1,097) on either side of the mean (1,162 and 1,032) have been added to the Sr graph of the freshwater inconnu, initially presented in Figure 9a (Figure 10). These upper and lower bounds encompass the range of values where 95% of the data would be expected to fall if repeated trials were conducted on a homogeneous material. There are 214 data points in this data set. In a perfect Poisson distribution, 5% of the points, 11 in this case, would fall above or below these lines. In reality, 33 points lie outside the lines, suggesting that the distribution of Sr x-ray counts was the result of more than just counting error and that Sr concentration was not constant across the otolith despite the fact that the fish did not travel to saltwater.

Electron microprobe analyses of all 12 inconnu otoliths in this study revealed signs of amphidromy. Six representative Sr graphs are presented here, 3 from female inconnu (Figure 11) and 3 from male inconnu (Figure 12). The Sr graphs for all sample inconnu showed large peaks of Sr x-ray counts similar to the Sr graph of the amphidromous inconnu (Figure 9b), and in contrast to the relatively constant, low level of Sr x-ray counts seen in the Sr graph of the freshwater-only inconnu (Figure 9a). All fish had similar, low core levels of Sr abundance (Figures 11 and 12), roughly varying between 950 and 1,200 x-ray counts per point. The first Sr spike (Figures 11 and 12, arrows), the indicator of movement into an enriched saline environment, occurred before the age-1 annulus for 11 inconnu, and before the age-2 annulus for 1 inconnu (Sr graph not presented). Maximum levels of Sr abundance varied for each fish, ranging from a low of near 1,500 x-ray counts (Figures 11b and 12b) to a high approaching 2,200 x-ray counts (Figure 11a).

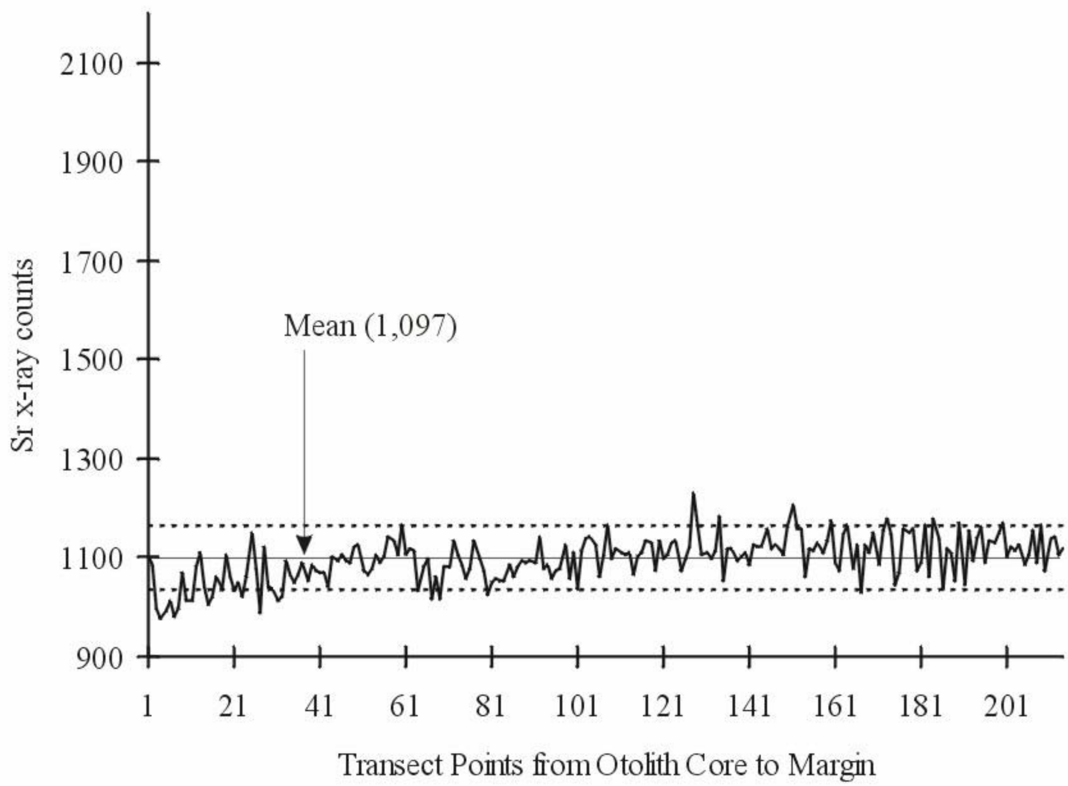

FIGURE 10.—Strontium distribution across the otolith of a freshwater inconnu with the mean value and 1.96 standard deviations either side of the mean value marked. Note that few points fall outside the 1.96 standard deviation bounds. Machine error alone would produce variability in which 95% of the data points would fall within these bounds when the otolith Sr concentration was the same everywhere.

Strontium maps of inconnu otoliths provided graphic evidence of the banded pattern of Sr distribution associated with visible growth increments. Two representative Sr maps are presented here, chosen for their distinctive patterns and the interpretive benefits gained from them. The first, a Sr map associated with the Sr graph in Figure 11a, reveals that small and closely associated peaks on Sr graphs, are real, and representative of distinct bands of Sr enriched material in the otolith mineral (Figure 13). The second, a Sr map associated with the Sr graph in Figure 11c, compares Sr distribution with

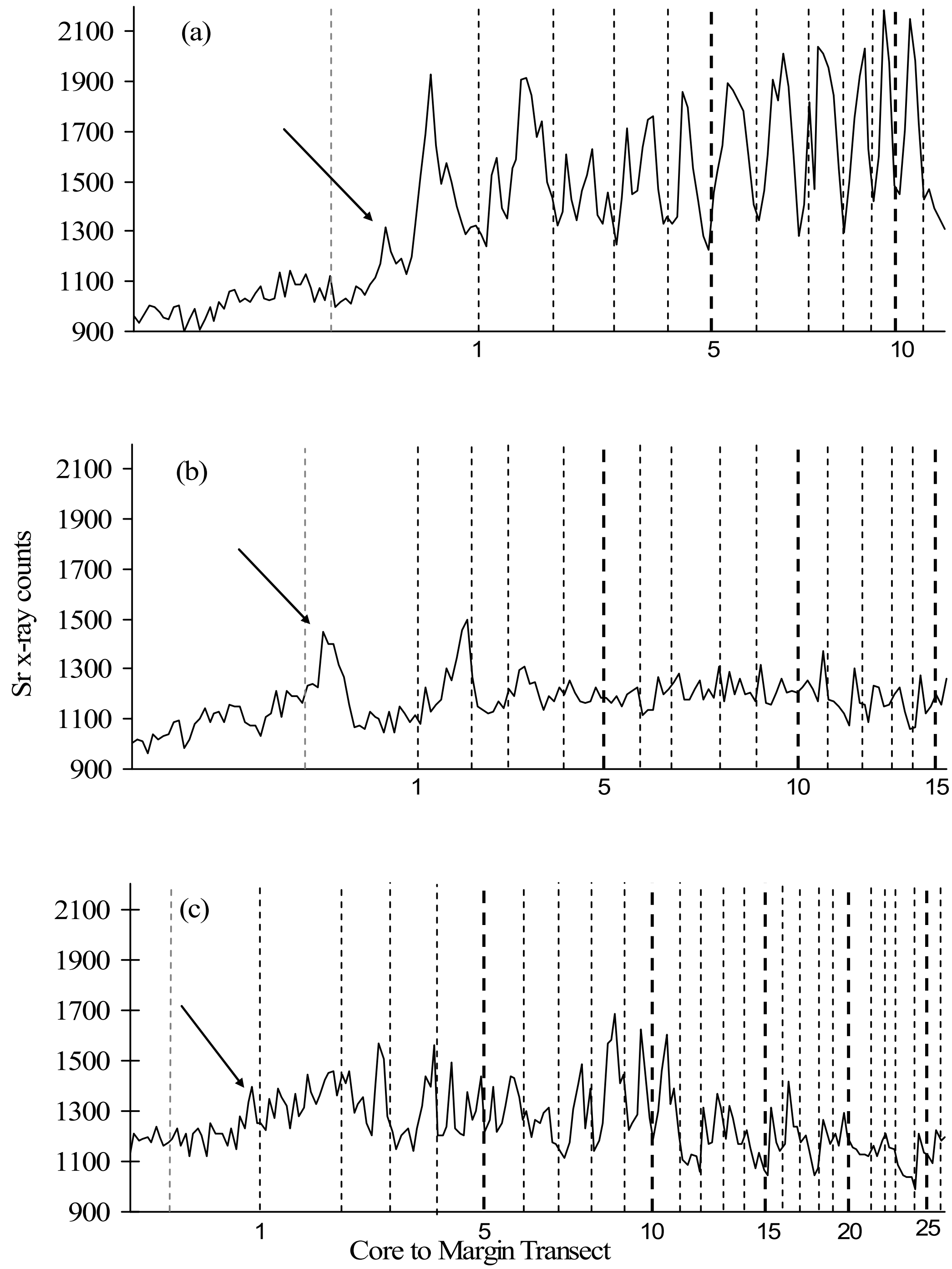

FIGURE 11.—Strontium distribution across otoliths of three female inconnu (a, b, c). The core is to the left, the margin is to the right. Arrows indicate first movement into saltwater. Vertical lines represent the locations where the transects crossed visible annuli.

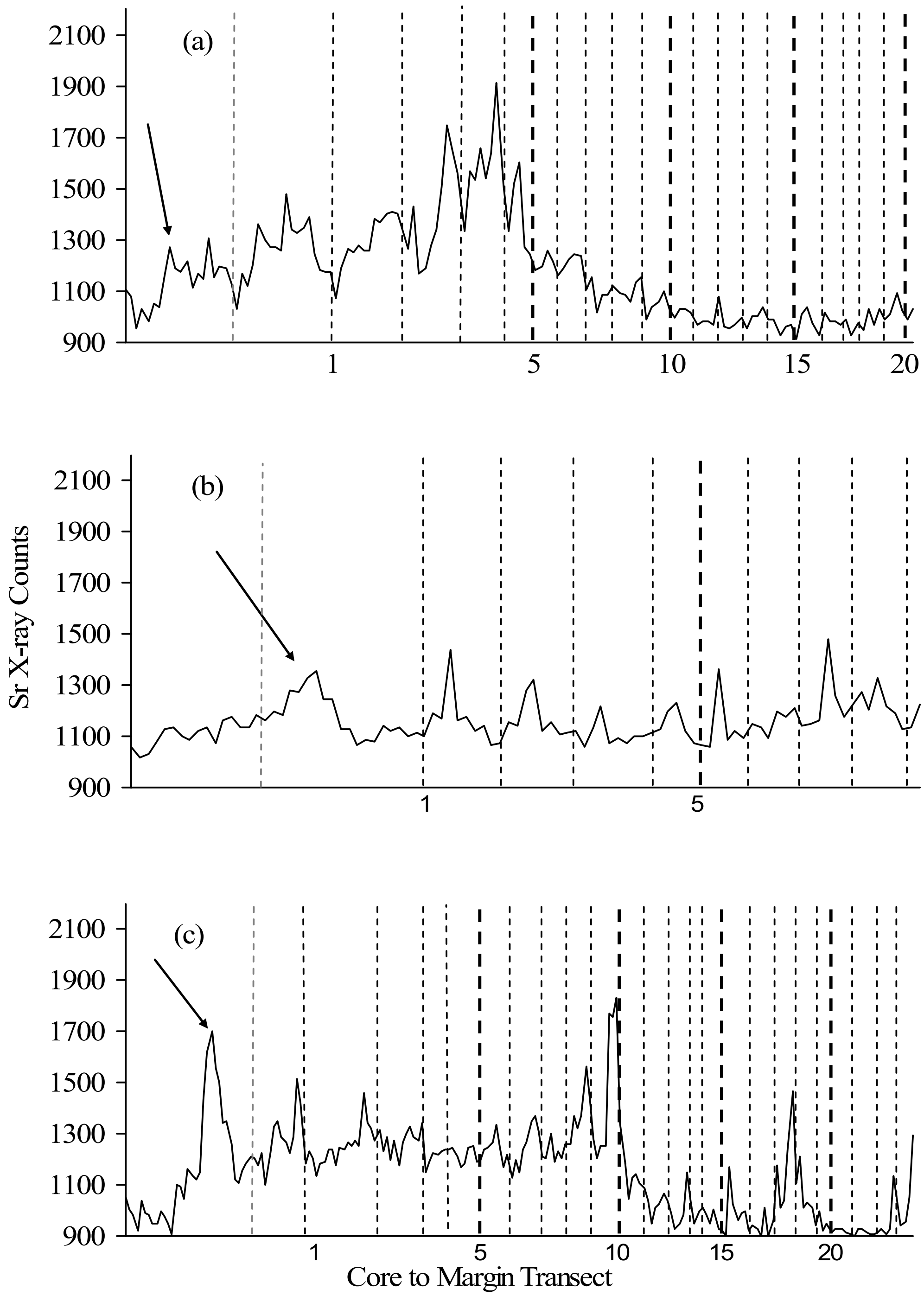

FIGURE 12.—Strontium distribution across otoliths of three male inconnu (a, b, c). The core is to the left, the margin is to the right. Arrows indicate first movement into saltwater. Vertical lines represent the locations where the transects crossed visible annuli.

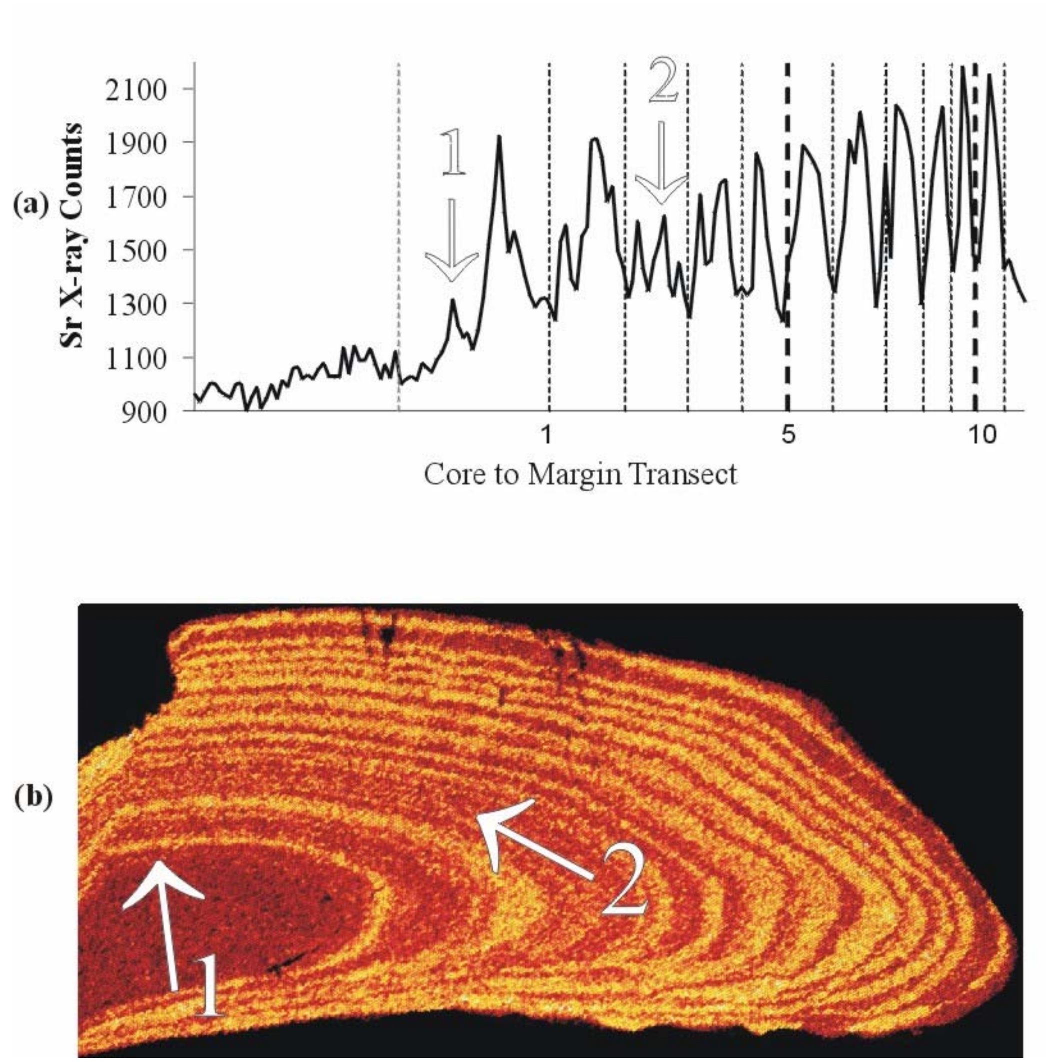

FIGURE 13.—A comparison of the Sr graph, initially presented in Figure 11a (a), with the Sr map (b) of the same otolith. Note the presence of an enriched band (yellow region) of Sr in the Sr map (b) associated with peak 1 from the Sr graph (a). Also note the multiple bands of enriched Sr on the Sr map (b) at arrow 2, associated with the peaks at arrow 2 on the Sr graph (a).

(a)

(b)

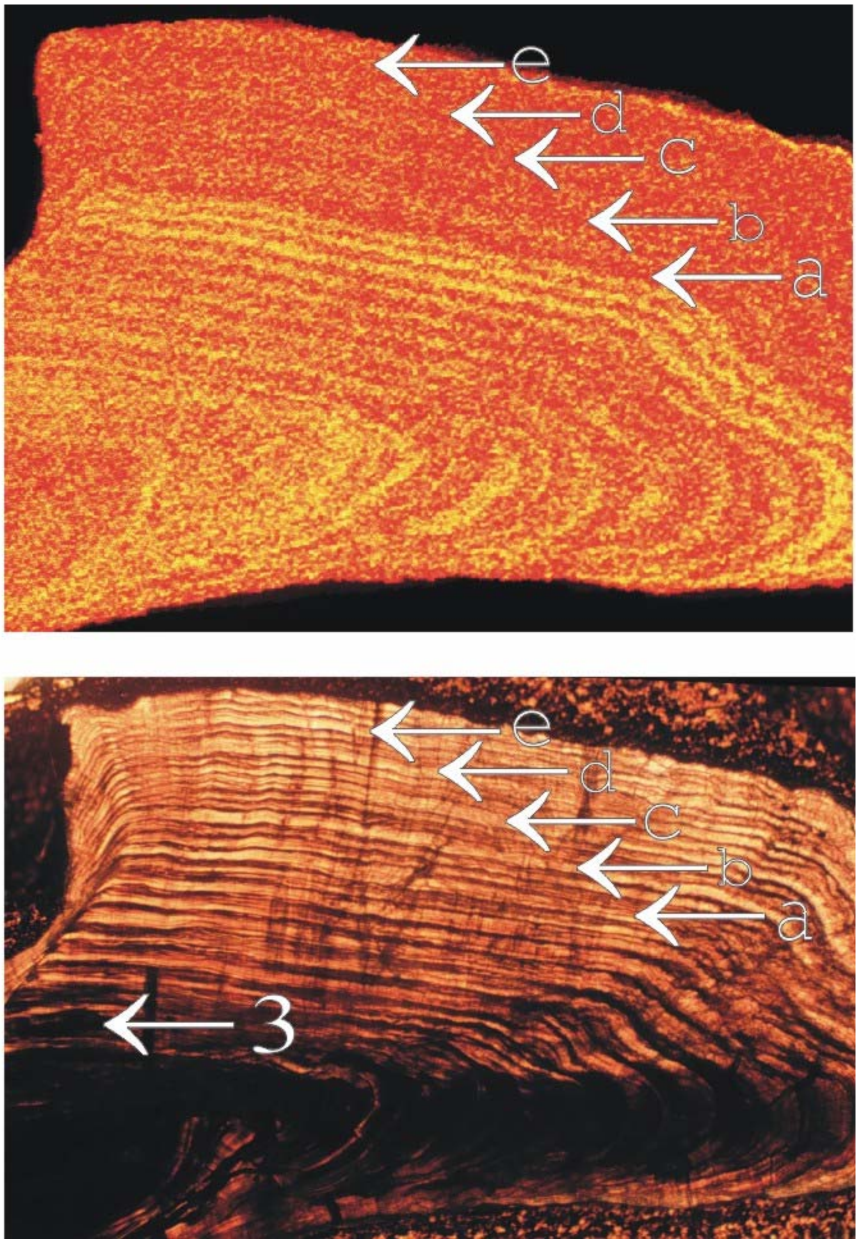

FIGURE 14.—Strontium map (a) and optical image (b) from the otolith used to create the Sr graph presented in Figure 11c. Note the faint orange bands in the outer region of the x-ray map high-lighted by the arrows (a-e), and their associated placement in the optical image as high-lighted by the outer arrows (a-e). In the optical image it is clear that those bands, associated with the fish's presence in freshwater, begin after annuli 11, and are separated by 3 annuli in each case. (Early annuli are difficult to see in this image (b), so annulus 3 is identified as a reference.)

Discussion

visible growth increments in the optical image of the otolith (Figure 14). Both images distinctively support the Sr distribution patterns seen in their associated Sr graphs.

Discussion

Otolith age analyses provided some interesting perspectives on the inconnu captured at the study site. The age distribution of female inconnu was shifted somewhat to the older age classes relative to that of male inconnu. This phenomenon follows Alt's (1973) generalization that females in a population are, on average, older than males. Maximum age estimates of female and male inconnu captured at the study site were considerably greater than Alt (1973) estimated, but are comparable to those reported by Howland (1997) on the Mackenzie River. The difference may be attributable to the aging structure, scales for Alt (1973) and otoliths for Howland (1997) and for the current study. If assumptions are made that the samples collected for this study were roughly representative of the population, and that sampled fish were uniformly in spawning condition (Biological Sampling chapter), then it follows that the youngest few age classes were predominantly first-time spawners. Thus, it could be inferred that a small number of precocious inconnu mature at 7 or 8 years of age. For most, however, maturity comes somewhat later, at 9 to perhaps 11 or 12 years of age, with females delayed one or more years than males. The reduced abundance of older male and female inconnu suggests that multiple spawning events occur for a relatively small proportion of the population.

Microchemical analysis of fish otoliths to evaluate diadromous behavior lies firmly on the principle of a low concentration of Sr in freshwater and a high concentration of Sr in saltwater. Physical oceanographers have determined that the proportional chemical composition of ocean water everywhere is nearly identical, with absolute concentrations of elements varying directly with salinity (Dietrich et al. 1980; Wells 1997). However, freshwater concentrations of dissolved salts, including Sr, are variable and influenced by watershed geology, precipitation, and evaporation (Wetzel and Likens 1991). The few records available for freshwater systems in Alaska and neighboring Canada indicate that Sr concentrations are low relative to saltwater, as expected (Likens and Johnson 1968; Snyder-Conn and Lubinski 1993; Babaluk and Reist 1996). Chemical testing of Yukon River water near the sampling site showed that Sr concentration levels were low there as well, and verified a critical principle upon which this work was based.

Strontium graphs appear to be very noisy, with Sr x-ray counts varying from point-to-point. This variability complicates interpretation of diadromous movement patterns. Knowing that a particular peak really indicates a fish movement into saltwater and not random, point-to-point variation, requires some background information. Two procedures were presented in this study, clarifying interpretation and providing a means with which to assess Sr graphs with some confidence. The first was an empirical demonstration of the error inherent in the analytical method using the Sr graph of the freshwater-only inconnu from the Great Slave Lake (Figure 10). The second presented graphical evidence in the form of a Sr map (Figure 13) that clarified interpretation of the associated Sr graph, and established a numerical criterion for determining saltwater movement of inconnu from a Sr graph.

The observed variation in Sr x-ray counts, illustrated in Figure 10, were slightly greater than the expected variation from counting error alone for repeated trials on a homogeneous material. While the otolith from the freshwater-only inconnu may have had extremely low compositional variability, it is unrealistic to expect a natural otolith to be chemically identical, from point-to-point, across a core-to-margin transect. Factors such as temperature (Radtke 1989; Radtke et al. 1990; Fowler et al. 1995; Secor et al. 1995) and metabolic condition (Sadovy and Severin 1992, 1994; Tzeng 1996; Tzeng et al. 1997) are known to have minor influences on otolith Sr concentrations, and may explain the imperfect distribution of Sr x-ray counts in Figure 10. In any case, it should be clear that variability of about 150 or so Sr x-ray counts between points (given the microprobe operating conditions used in this study) should not be interpreted as a change in saline environments. By extension, differences much greater than 150 counts can confidently be attributed to a change in saline environment. Obviously, there is a gray area in between, in which interpretation would be difficult.

The Sr map in Figure 13b, shows that the small initial peak seen in its associated Sr graph (Figure 13a, arrow 1), at approximately 1,300 x-ray counts, represents the transect crossing a distinct, thin band of enriched Sr arcing across the otolith near the large core region in the lower left (Figure 13b, arrow 1) and not random counting error. This assessment supports the conclusions from Figure 10, that a difference in Sr x-ray counts of greater than 150 can be interpreted as an indication of movement into saltwater. In this case there is an increase from an average of approximately 1,050 Sr x-ray counts to a peak of 1,300 Sr x-ray counts, a rise of over 200. Essentially, these procedures have calibrated Sr x-ray counts for inconnu in freshwater, at roughly between 950 and 1,200 x-ray counts (given the microprobe operating conditions used in this study), and established the validity of interpreting an initial rise to about 1,300 Sr x-ray counts as an indicator of fish movement into saltwater.

Much more life history and movement information can be deduced from Sr maps of otoliths. Three small peaks are seen in between the second and third annuli on the Sr graph in Figure 13a (arrow 2). These peaks suggest three distinct movements between fresh and saltwater during that year. The difference between Sr x-ray counts in high and low points in this area exceed 200, supporting the interpretation of the peaks as multiple movements between fresh and saltwater, and not random counting errors. The Sr map of the otolith (Figure 13b) reveals 3 distinct, thin, yellow bands of enriched Sr associated with the 3 peaks (arrow 2). It is clear that the inconnu did, in fact, make repeated trips between fresh and saltwater that year.

Another informative Sr map is presented in Figure 14a. It is particularly interesting when compared with its associated optical image (Figure 14b). The outer region of the Sr map (Figure 14a) contains five faint, orange bands (arrows a - e), regions of low Sr concentration, indicating freshwater residence. Between the orange bands are broader yellow regions indicating that the fish was consistently present in an enhanced salinity environment during those time intervals. The first of the orange bands (arrow a) follows the age-11 annulus in the optical image (Figure 14b, arrow a). Similarly, arrows b, c, d, and e in the optical image (Figure 14b) show the positions of the corresponding orange bands from the Sr map (Figure 14a, arrows b, c, d, and e) in relation to the annuli. Three annuli separate each orange band. Spawning for Yukon River inconnu, involves an extensive freshwater migration, taking as long as several months to complete (Alt 1969). If otolith growth continues during the migration, and there is no evidence to the contrary at this point, there should be a layer of low Sr material applied to the otolith. The regularly spaced, orange bands in the outer region of this Sr map (Figure 14a, arrows a - e) may represent spawning events, beginning at age 11, with 3-year intervals between events. The years between spawning events seem to be spent primarily in brackish water, as indicated by the consistent low-level Sr enhancement between the orange bands (Figure 14a). If this interpretation is correct, this fish was captured on its sixth spawning migration, at 26 years of age. Consistent with this interpretation, the fish was a large, gravid female (103 cm length, 13,670 g weight) when harvested at the study site in September 1997.

Variation in maximum Sr x-ray counts among inconnu (Figures 11 and 12) suggests that some favor more saline waters than others. Inconnu are found throughout the lower-river and near-shore waters near the mouth of the Yukon River (Crawford 1978; Martin et al. 1987) as well as in Norton Sound coastal environments north of the Yukon River mouth. It may seem reasonable to attempt calibration of Sr x-ray counts to marine salinity levels to further describe inconnu movements in near-shore waters, but there are serious complications hampering this objective.

It is generally understood that inconnu restrict their marine movements to brackish water with salinity somewhat less than full-strength ocean water (Berg 1962; Alt 1969; Reist and Bond 1988). As a result, once leaving the Yukon River, they would be expected to frequent an intermediate salinity environment. However, the marine environment near the mouth of the Yukon River is highly variable. Vertical and horizontal salinity gradients have been documented there (Martin et al. 1987). The locations of these gradients are unstable, changing on a continuous basis due to winds, tides and river flow levels. Given these conditions, a fish could venture into a high salinity area to feed, retreating to a low salinity area to rest, on a daily or shorter time scale. The Sr enhancement in the otolith of such a fish, as revealed by Sr x-ray counts, may be somewhere in the middle of what could be expected from living in a constant environment at either salinity extreme. Therefore, calibration of Sr x-ray counts in otolith material to specific salinities within estuary waters is probably not possible.

Radio Telemetry

Introduction

Radio telemetry has been used with great effect to describe migrations and localized movements of many fish species in recent years. Conceivably, the technology could be used with inconnu at the study site to locate their spawning destinations. However, previous attempts to use radio telemetry to locate inconnu spawning areas in the region were inconclusive (Alt 1975, 1986), failing even to provide compelling evidence of a prevailing direction of travel along the river. Upstream movement was assumed based on the behavior of other documented spawning migrations of inconnu (Taube 1996; Howland 1997; Underwood et al. 1998). Radio telemetry technologies and techniques have advanced in recent years, and their successful use with other inconnu populations suggested that they could now be used on Yukon River inconnu to find their spawning destinations.

Radio telemetry studies on inconnu in North America have used three basic tagging methods; external (attached beside the dorsal fin), internal (pushed through the esophagus into the stomach), and surgical (placed into the body cavity). Alt (1975, 1986) used all three methods in the Yukon River. Canadian researchers used external and internal tags in the Mackenzie River drainage in northwest Canada (McLeod et al. 1985; Tallman et al. 1996; Howland 1997). Underwood et al. (1998) used internal and surgical tags in the Selawik River in northwest Alaska. Capture methods, use of anesthetics, holding times following tagging, habitats, and time of year varied among projects.

An assumption common to all tagging projects is that tagged fish are not adversely affected by the capture, handling and tagging process, and that they behave like untagged fish once released. Inferences from fish movements will be flawed if this assumption is violated. Experiments that have tested the effects of different tagging methods indicate that there are differences in behavior and swimming performance in some species (McCleave and Stred 1975; Haynes 1978; Lewis and Muntz 1984; Mellas and Haynes 1985). Variable, sometimes poor, performances of inconnu in past radio telemetry projects (Alt 1975, 1986; McLeod et al. 1985; Tallman et al. 1996; Howland 1997; Underwood et al. 1998) suggest that the species is sensitive to handling and tagging, and that behavioral assumptions have occasionally been violated. However, lack of controlled conditions between projects prevents a rigorous comparison of the effectiveness of different transmitter application methods. As a result, the most appropriate transmitter for use in this study was unclear.

Underwood et al. (1998) used the surgical method of transmitter application on inconnu with reasonable success. However, Winter (1996) cautions that gravid female fish are not ideal candidates for surgically implanted transmitters. He further explains that fish with surgically implanted transmitters often require a lengthy recovery period before their behavior returns to normal. The results of the basic sampling component of this study (Biological Sampling chapter) indicate that inconnu at the study site have spawning intentions, and therefore may not have time for recovery and subsequent movement to possibly distant spawning destinations. For these reasons, the surgical transmitter attachment method was rejected for use in this study.

Both internal and external transmitter attachment methods appeared to be attractive options. Both could be quickly applied. Internal transmitters could probably provide data about inconnu movements for a few months at most, considering that fish may expel the transmitters when they resume eating following spawning. By contrast, external transmitters could potentially provide data on multiyear movements. No wound would be required for internal transmitter application, and no hydrodynamic effect upon swimming was expected. Two wires must be passed through the dorsal musculature to mount external transmitters, and hydrodynamic effects of these transmitters upon inconnu swimming performance in the swiftly flowing Yukon River were possible, but unknown. Both methods could potentially be used to discover the spawning destinations of inconnu captured at the study site.

This chapter describes three field seasons of radio telemetry work with Yukon River inconnu. The project began in the late summer of 1997 and concluded in the early winter of 1999. The purpose was to locate the spawning destinations of mature inconnu captured in the late summer and fall at the study site (Figure 2). The first year of work was primarily dedicated to testing the behavioral and performance effects upon inconnu, of two transmitter attachment methods. The second year was dedicated to using the information gained during the first year to locate the spawning destinations of radio-tagged inconnu. The third year was dedicated to confirming the previous year's results by repeating the telemetry work, followed by a site visit to suspected spawning locations to document the presence of untagged inconnu in spawning condition. In addition, migration rates were calculated and post-spawning movement patterns were described.

Methods

1997: First year of the project

Twelve external and 13 internal radio transmitters were applied to inconnu during 1997. Candidate fish were captured in fishwheels equipped with padded chutes and live-boxes. Immediately following capture, they were placed in a neoprene cradle submersed in a water-filled tub, tagged and released. The tags were deployed at a maximum rate of three per day during the tagging period, from August 21 to September 6. Only female inconnu were used in the experiment to eliminate the possibility of sex-specific behavior differences and to standardize spawning condition; all females examined were preparing to spawn, while male condition could not be determined. A minimum length of 75 cm was required for candidate fish. Anesthetics were not used.

External and internal radio transmitters were identical in function and transmitted in the frequency range between 150 and 154 MHz. Each transmitter was equipped with a motion sensor and activity monitor that indicated if the fish was currently moving, had moved within the previous 8 hours, or had remained inactive for the previous 8 hours. They were 5 cm in length and had antennas 30 cm long. The two transmitter types were alternately deployed throughout the tagging period.

External transmitters weighed 30 g and were of a balanced-weight design (Lewis and Muntz 1984), intended to distribute the weight evenly between the right and left sides of the fish. They consisted of two small batteries positioned on opposite sides of the dorsal fin that were linked to the electronic component of the tag behind the fin (Figure 15a). They were anchored to the fish with two wires passing through the dorsal musculature (Winter 1996). The capture and application procedure for external transmitters took approximately 5 minutes for each fish.

Internal transmitters weighed 25 g, were cylindrical in shape and 2 cm in diameter (Figure 15b). They were gently pushed through the mouth and esophagus into the stomach with a plastic tube (Eiler et al. 1992). Inconnu tagged internally also carried a numbered anchor tag placed at the base of the dorsal fin for identification purposes in case of recapture, a procedure not required for those receiving external transmitters. The capture and application procedure for internal transmitters took approximately 3 minutes for each fish.

Radio-tagged fish were located with remote radio receiving stations (stations; Figure 16; Eiler 1995), and by aerial and boat surveys. Two stations located 11 km upstream from the study site (henceforth, collectively referred to as “station 1”), recorded upstream and subsequent downstream movements. A third station was located about 839 km from the mouth of the Yukon River, 361 km downstream from the study site. Aerial surveys of the Yukon River drainage upstream of the study site were conducted on September 26 and 27, prior to spawning, and on October 7, when spawning was thought to be occurring (Morrow 1980). The surveys covered the Yukon River and large tributaries from the study site to more than 600 km upstream. Survey aircraft flew at 500 to 700 m elevation at approximately 90 knots. Boat surveys, ranging as far as 60 km downstream from the tagging site, were conducted to evaluate immediate tagging response. Fish locations and times were plotted on 1:250,000 scale topographic maps of the region.

Four criteria were used to evaluate the performance of inconnu from the two experimental groups. A Chi-squared test of differences in probabilities (Conover 1999) was used to compare the proportion of fish from each group that resumed upstream migration following tagging. Mann-Whitney tests (Conover 1999) were used to compare delays between tagging and resumption of migration, travel rates and the distances moved upstream from the tagging site for the two groups. Delays between tagging and resumption of migration were calculated as the elapsed time between

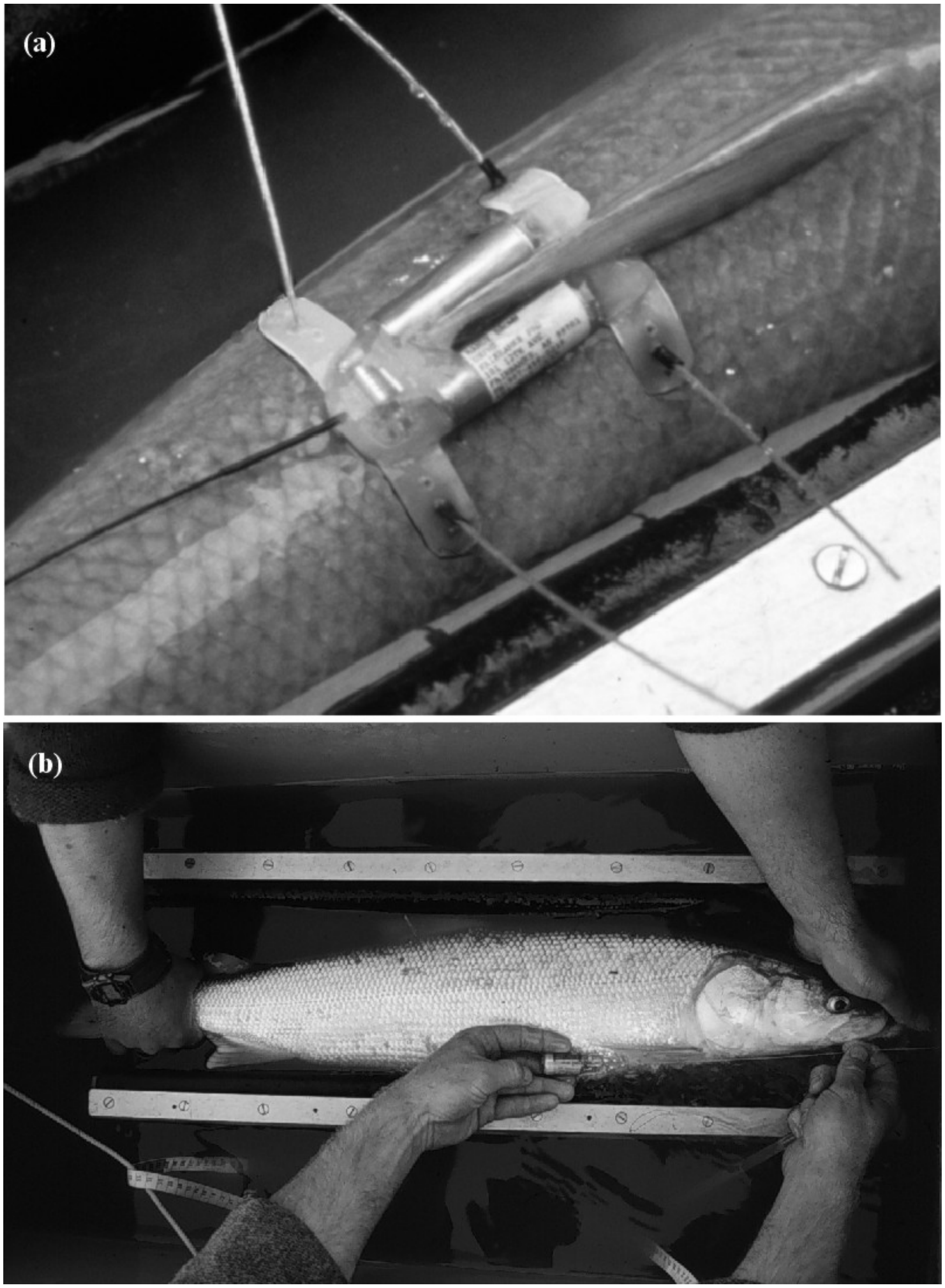

FIGURE 15.—External (a) and internal (b) radio transmitters used with inconnu on the Yukon River. Note that the dorsal fin is bracketed by the external transmitter's twin batteries (a). An additional crimp fitting will be applied to the upper left wire, and all four wires will be trimmed close before release. The internal transmitter (b) is being held beside a candidate fish prior to insertion.

FIGURE 16.—Remote radio receiving station located on a high bluff over the Yukon River, 11 km upstream of the study site. This station, and others like it, recorded the passage of radio-tagged inconnu moving along the river.

tagging and upstream migration past station 1. Travel rates were calculated from distance and elapsed time between station 1 and the September aerial survey locations. The actual calculations utilize the hour in which the fish was identified at a particular location. Reported rates were standardized to km/d. October aerial survey locations were used as the distance traveled upstream. All tests used a 95% significance level.

1998 and 1999: Second and third years of the project

A total of 60 internal radio transmitters were applied to inconnu at the study site during the 1998 and 1999 field seasons. In 1998, 35 transmitters were deployed between August 25 and September 10. They were applied to 27 female and 8 male inconnu that ranged in length from 74 to 92 cm. In 1999, 25 transmitters were deployed between August 25 and September 4. They were applied to 16 female and 9 male inconnu that ranged in length from 69 to 97 cm. The internal transmitter specifications were identical to those described in the previous section.

The tagging procedures followed for most inconnu during 1998 and 1999 were identical to those described in the previous section for internal radio transmitters. A modification of the tagging procedures was implemented for 6 of 25 radio-tagged inconnu during the 1999 tagging event. Instead of being taken at the time of capture, tagged and released immediately, the 6 selected fish were detained in the live-box of the fishwheel with other fish for 1 to 5 hours before release. This procedural modification was enacted because there was an interest in applying radio transmitters to inconnu captured at other locations on the river, where the probability of tagging inconnu at the time of capture was low. If inconnu were to be tagged at other sites, they would probably be taken from live-boxes, having been captured and held for some period of time prior to tagging and release. The procedure was intended to simulate those conditions. While the design was not rigorous enough to fully evaluate the behavior and performance effects of detaining inconnu, the procedure was intended as a preliminary examination of possible gross effects.

Similar to the 1997 field season, inconnu with radio transmitters were recorded moving past stations and were located during aerial and boat surveys. In addition to the stations that were present during 1997, 11 km upstream and 361 km downstream of the study site, five others were operational in the upper river in 1998 and 1999. The locations and distances from the study site of the additional stations are as follows: the Chandalar River, 400 km upstream; the Sheenjek River, 505 km upstream; the Porcupine River, 585 km upstream; the Black River, 545 km upstream; and the Yukon River, 560 km upstream (Figure 17). The aerial surveys, in conjunction with the stations, provided coverage of possible migration destinations.

Aerial surveys of the Yukon River drainage, upstream of the tagging site, were conducted on October 5 and 13, 1998, during the expected spawning time, and on September 28, 1999, just prior to the expected spawning time (Morrow 1980). Survey aircraft flew at 500 to 700 m elevation at approximately 90 knots. Locations and times were plotted on 1:250,000 scale topographic maps of the region.

Boat surveys were conducted only on October 7, 1999, to locate and attempt recapture of radio-tagged inconnu on suspected spawning grounds. Beach seine hauls targeted relocated inconnu, assuming that untagged fish, if present, would be found in association with tagged fish. A 90 m seine net was used. The net hung approximately 3 m deep and had a stretched mesh size of 5 cm. Captured fish were counted, identified to species, sex, and spawning condition (as determined by external examination and the presence of flowing milt or eggs), and released.

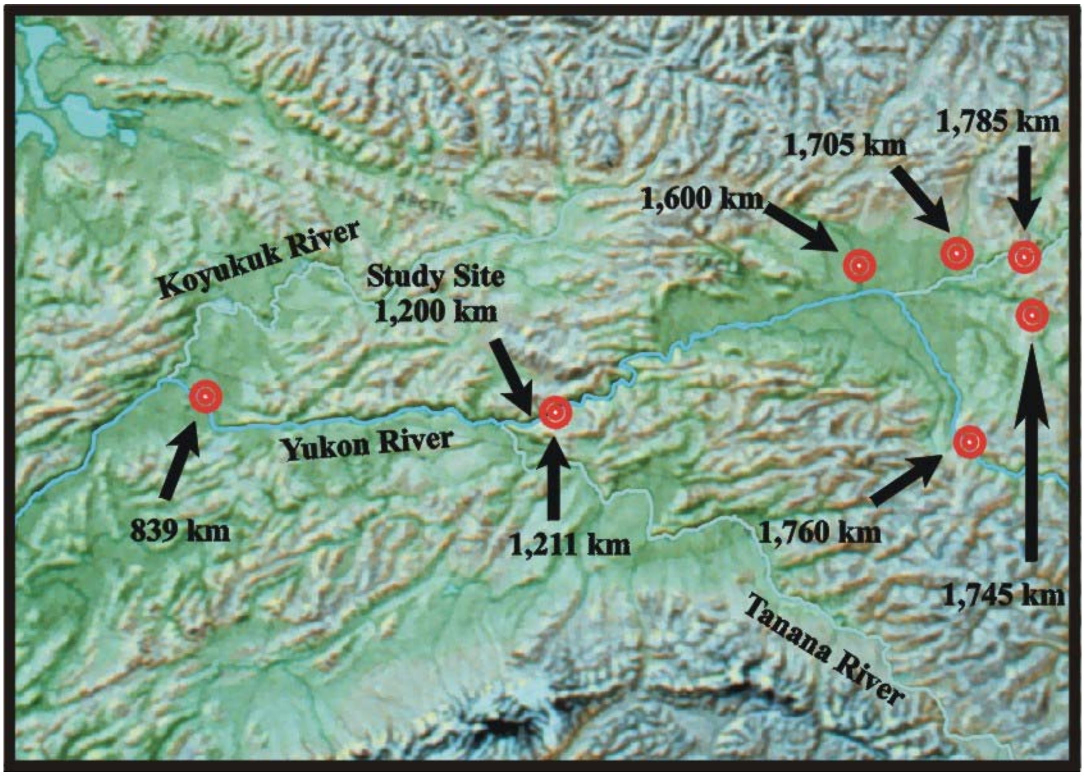

FIGURE 17.—Locations of remote radio receiving stations in the Yukon River drainage. Distances are from the mouth of the river. The downstream station is at river km 839. Station 1 is at river km 1,211, just upstream of the study site. Stations in the upper river are as follows: Chandalar River at 1,600 km; Sheenjek River at 1,705 km; Porcupine River at 1,785 km; Black River at 1,745 km; and Yukon River at 1,760 km. During the 1997 season, only station 1 and the downstream station were in place. During the 1998 and 1999 seasons all stations were operational.

Position and time data from the tagging event, station output, and aerial survey locations were the basis for all interpretations about behavior, movements, timing of movements, and migration rates. The proportion of tagged fish resuming migration and the delay time between tagging and resumption of migration were calculated from tagging data, and data collected at station 1. Maximum upstream movements were estimated based on locations obtained by aerial surveys and data from upstream stations. Downstream migration rates were calculated based on records from station 1 and the downstream station. The actual calculations utilize the hour in which the fish was identified at a particular location. Reported rates were standardized to km/d.

Results

1997: First year of the project

A total of 25 radio transmitters were successfully applied to mature, female inconnu in 1997. Initially, all fish in both experimental groups moved downstream from the tagging site. A few fish moved only 1 to 2 km, but most moved to a backwater area of the river approximately 15 km downstream. Eleven fish failed to resume upstream migration. Instead, they moved downstream over a period of weeks until they were beyond the boat survey range. A total of 14 fish were recorded moving upstream past station 1. All but one of these fish were subsequently relocated by aerial surveys in late September and early October. All relocations were in the Yukon River rather than in tributaries. Ten of the 14 fish that moved upstream were recorded moving downstream past station 1 between mid-October and mid-November.

The two experimental groups of inconnu performed differently for three of four test criteria. A significantly greater proportion of fish with internal transmitters moved upstream ($P = 0.028$), 10 of 13 fish compared to 4 of 12 fish with external transmitters (Table 3). Fish with internal transmitters were delayed following tagging for a significantly shorter period of time ($P = 0.0401$), with a median value of 8.6 days compared to 21.3 days for fish with external transmitters (Table 3). Ten fish were located during the September aerial surveys, six with internal transmitters and four with external transmitters. Fish with internal transmitters traveled upstream at a faster median rate, 27 km/d, than fish with external transmitters, 20 km/d, but the difference was not significant (Table 3). All fish located in September were relocated farther upstream in October, 11 or 12 days later. They moved an average of 159 km between surveys, ranging from 92 km to 259 km. Thirteen fish (10 from the September surveys and 3 others) were located during the October aerial survey, 9 with internal transmitters and 4 with external transmitters. Fish with internal transmitters traveled significantly farther (P = 0.0069), with a median distance of 470 km beyond the tagging site, compared to 367 km for fish with external transmitters (Table 3). The ranges of the two experimental groups did not overlap.

TABLE 3.—Performance results for inconnu tagged with external and internal radio transmitters (number of sample fish in parentheses).

Sample Characteristic	Transmitter Application Method		Significant Difference
	External	Internal	
Number of fish released	12	13	NA
Proportion resuming migration	0.33 (4)	0.77 (10)	Yes
Median delay time (d)	21.3 (4)	8.6 (10)	Yes
Median travel rate (km/d)	20 (4)	27 (6)	No
Median distance traveled (km)	367 (4)	470 (9)	Yes

Actual lengths of tagged inconnu ranged from 75 cm to 100 cm. Despite the attempted randomness of the selection process, the median lengths of fish in the two experimental groups were significantly different (external=83 cm; internal=80 cm; P=0.0216). Despite this length discrepancy between groups, fish length could not be correlated to the success or failure of fish to resume migration. The median length for fish that resumed migration was 80 cm (n=14), compared to 82 cm for those that failed to resume migration (n=11). These values were not significantly different.

Downstream migration was recorded by station 1 beginning on October 14, 1997. By October 26, 9 fish had moved past station 1. Another fish was detected moving downstream on November 13, 1997. Two fish were recorded moving past the downstream station in 1997, one on October 23, and the other on November 19.

1998: Second year of the project

In 1998, all 35 radio-tagged inconnu resumed migration following tagging. Median delay time was 128 hours, about 5.3 d. The swiftest recovery was effected in 21 hours (2 fish accomplished this feat), while the slowest was 360 hours, about 15 d (Figure 18). The individual that was delayed 360 hours was a male that had been recaptured twice in the tagging fishwheel-- once 5 days after tagging, and again 11 days after tagging. No other inconnu with radio transmitters were recaptured in either the tagging fishwheel or in the personal use fishery upstream of the tagging site during 1998.

All 35 inconnu were located during the October 5, 1998 aerial survey. All were in the Yukon River, from 430 to 540 km upstream of the study site (Figure 19), with a median position of 470 km, revealing a slight downstream distribution within this range. However, radio-tagged inconnu were found throughout the 110 km long region with no distinct areas of concentration apparent.

During the October 13, 1998 aerial survey, restricted to the region between 400 km and 560 km upstream of the study site, only 14 inconnu were located. Most were at or downstream of their October 5 positions. Only two fish were slightly upstream (10 km or less) of their previous positions. Their distribution ranged from 425 km to 540 km upstream of the study site, with a median position of 467 km.

The stations in the upper river never recorded the passage of any inconnu. Of particular interest was data from the Yukon River station, located 560 km upstream of the study site, as all of the radio-tagged inconnu ascended that fork of the drainage. That station

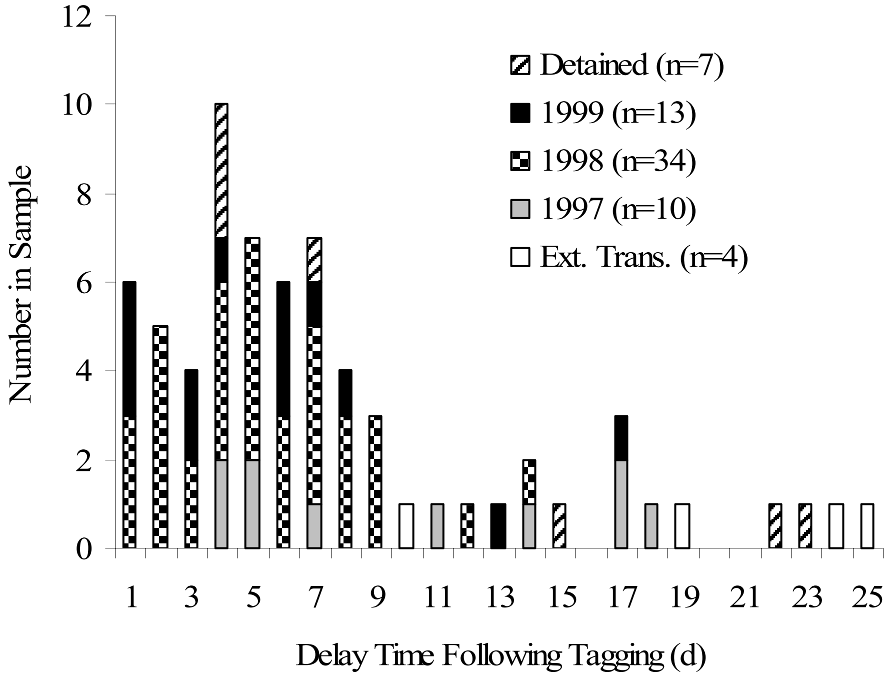

FIGURE 18.—Delay time between tagging and resumption of upstream migration for 64 internally tagged inconnu and 4 externally tagged inconnu during the 3 years of the radio telemetry project. (Only 62 of the internally tagged inconnu were considered to have been successful, as 2 fish that went upstream were either never located again, or were thought to have been harvested.) Delay times were calculated to the hour, but have been rounded to the nearest day for presentation. The detained group includes one fish tagged in 1998 that was recaptured and thus detained, as well as six fish from the 1999 season. All fish in the groups labeled by year (1997, 1998, 1999) were internally tagged inconnu released immediately following capture and tagging.

was located 20 km upstream of the nearest inconnu position determined from the aerial surveys, yet no signal was recorded there.

Downstream migration was recorded by station 1 beginning on October 10, 1998. By October 24, 22 fish had moved past. Between October 17 and 29, 16 fish were recorded moving past the downstream station. Only 11 of 16 inconnu recorded by the

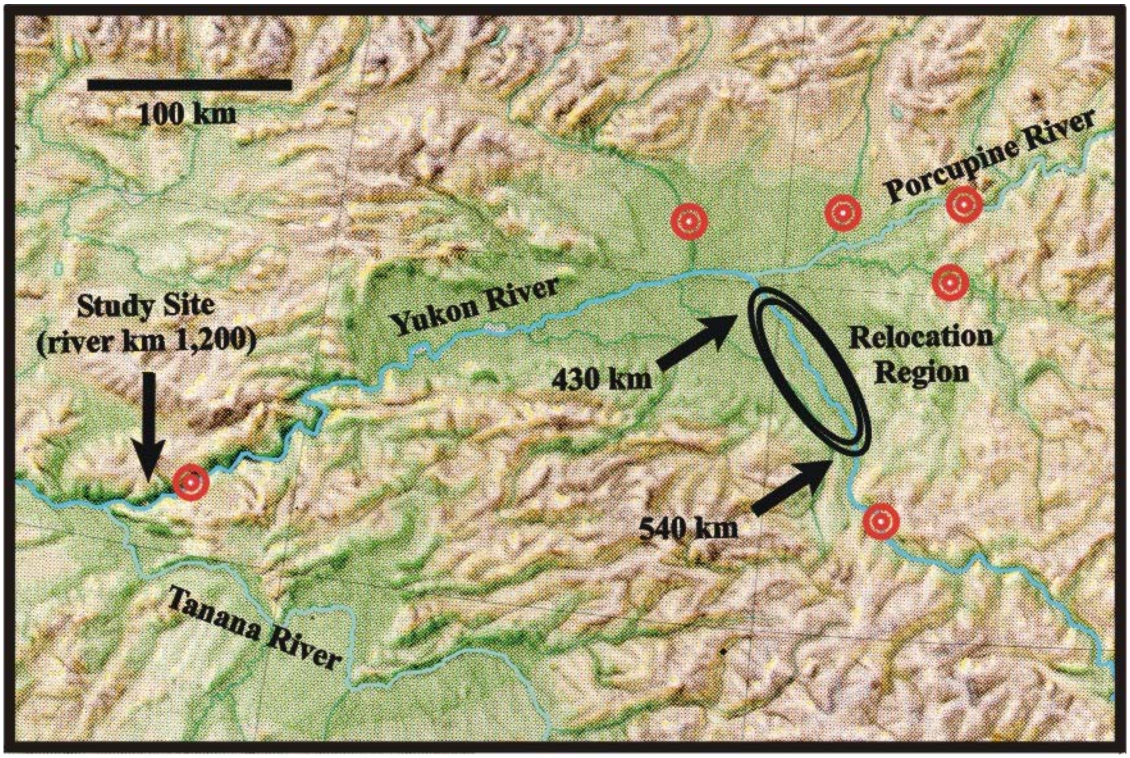

FIGURE 19.—Primary relocation region of radio-tagged inconnu upstream of the study site. During 3 years of study, 62 inconnu with internal tags moved upstream following tagging. Fifty-seven of these fish were located during spawning season, early October, in the relocation region between 430 km and 540 km upstream of the study site (1,630 km to 1,740 km from the Bering Sea) in the mainstem of the Yukon River. Boat tracking and seine sampling during October, 1999, took place between 470 km and 520 km upstream of the study site, in the upstream half of the relocation region.

downstream station, were also recorded by station 1. Thus, a minimum of five fish passed station 1 undetected while migrating downstream.

1999: Third year of the project

The radio telemetry results from the 1999 season were more complicated than those from 1998. Nineteen of 25 radio-tagged inconnu resumed migration following tagging.

Of the 6 inconnu that failed to resume migration, 1 was from the detained group, and 5 were from the immediate release group. The 19 inconnu that resumed migration were composed of 5 that had been detained by design, 1 that had been recaptured twice in the tagging fishwheel and thus, had experienced unplanned detainment, and 13 from the immediate release group.

As in past years, delay times between tagging and resumption of migration for individual fish varied widely. Median delay time when all 19 migrating inconnu were considered was 133 hrs, about 5.5 d. When the 13 inconnu that experienced no detainment at the fishwheels were considered independently, the median delay time dropped to 98 hrs, about 4.1 d. The 6 inconnu that were detained during tagging or recapture had a median delay time of 145 hrs, about 6.0 d. Considering all 19 inconnu, the shortest delay time was 25 hours, while the longest was 562 hours, about 23.4 d (Figure 18).

Fifteen inconnu were located during the September 28, 1999 aerial survey. Thirteen were in a region of the Yukon River, from 435 km to 495 km upstream of the study site, with a median position of 478 km (Figure 19). The other two inconnu were located upstream of station 1 in the Yukon River, one 200 km and the other 350 km upstream of the study site. The fish at the 200 km distance had experienced a long delay following tagging (23.4 d) and had resumed migration on September 23, just 5 d prior to the survey. That fish had traveled at 36 km/d during the interval. An additional inconnu experienced a similarly long delay following tagging (22.2 d) and resumed migration on September 25. It was not located on the September 28 aerial survey, but had probably not entered the survey area by that time. The transmitter of one radio-tagged inconnu was received at station 1 from initial contact on September 6, until well into the winter of 1999. In all likelihood, the fish was harvested by one of several local fishers maintaining fish-camps within radio reception range of the station. Two radio-tagged inconnu that resumed migration and were expected to have been present in the area surveyed, were unaccounted for in the upper river, but were recorded moving downstream past station 1 later in the fall. Similar to 1998, there was no indication that any radio-tagged inconnu moved upstream of the stations in the upper river.

The boat survey and associated seine sampling of the Yukon River (Figure 20) occurred between 470 km and 520 km upstream of the study site, within an area that was the apparent destination of some radio-tagged inconnu. Five inconnu were located during the survey, and four seine hauls were conducted in close proximity to the located inconnu. Fifteen inconnu, 5 females (including one radio-tagged fish) and 10 males, were captured by seine. All were large, mature fish in spawning condition. Milt was easily expressed from all males. Eggs flowed freely from two females, but not from the other three. It was clear that spawning time was imminent, yet none of the captured inconnu appeared to have spawned at that time. In addition to inconnu, 25 Bering cisco *Coregonus lauretus* and 3 humpback whitefish *C. pidscian* were also captured by seine. All were in a state of spawning readiness, similar to the inconnu.

Downstream migration was recorded by station 1 beginning on October 9, 1999. By October 25, 18 fish had moved past station 1. Five of these fish were subsequently detected by the downstream station a few days later.

Migration Rates

Upstream migration rates were obtained for 25 radio-tagged inconnu, 10 during 1997, and 15 during 1999. Aerial surveys were flown too late during 1998 to get reliable figures, as the fish had already reached spawning destinations prior to the flights. The upstream migration rate data from 1997 includes four externally tagged fish and six internally tagged fish**.** Median upstream migration rates were similar for the two study years, 26 km/d for 1997, and 21 km/d for 1999. The range of migration rates was

FIGURE 20.—Seine sampling on October 7, 1999, in the apparent spawning destination of radio-tagged inconnu. A 90 m net, anchored to shore at one end, was set in an area where a radio-tagged inconnu had been located (a). Riley Morris releases a large female inconnu captured in the set (b).

similar for the two years as well, from a low near 16 km/d, to a high of 30 km/d in 1997 and 36 km/d in 1999.

Downstream movements of 18 radio-tagged inconnu were recorded by station 1 and by the downstream station, allowing downstream migration rates to be calculated. Of the 18 fish, 2 were from 1997, 11 were from 1998, and 5 were from 1999. The median downstream migration rate was 95 km/d, and ranged from a low of 57 km/d to a high of 160 km/d.

Downstream migration rates based on aerial survey locations in the suspected spawning area were avoided because of uncertainty about starting times of downstream movements. None-the-less, one inconnu located during the October 13, 1998 aerial survey, 450 km upstream of the study site, was subsequently recorded moving past the downstream station on October 17 (its passage was missed by station 1), resulting in an extreme migration rate of 197 km/d over the 811 km distance. Because it is unclear exactly when this fish began moving downstream, this figure must be considered a minimum estimate.

Discussion

1997: First year of the project

Past studies of inconnu indicate that both mortality of tagged fish and the loss of tags are factors requiring consideration. Alt (1975) captured inconnu with fishwheels for his radio telemetry project in 1974, and felt that the capture method may have caused mortality. McLeod et al. (1985) reported that some inconnu with internal tags seemed to have regurgitated them shortly after being released. In the experimental component of this study, both mortality and tag loss were evaluated by tracking fish with a boat following tagging. All fish were located and their movements were mapped over a period of about 2 weeks following tagging. During this period of time there was no evidence that any fish in either group died. Nor was there any evidence of regurgitation. All fish were recorded moving to new locations between surveys, and many responded by swimming away when the tracking boat approached.

This experiment clearly showed that inconnu with external tags performed differently than those with internal tags. Given this difference, the conclusion is inescapable that at least one group violated the assumption of equivalent behavior between tagged and untagged fish. It was assumed that the group with a larger proportion resuming upstream migration, with a shorter delay time, and a more distant destination, was less affected by the transmitters and the tagging process, and behaved more similar to untagged fish, than the other group. Therefore, the internal tagging method was selected over the external tagging method for use with migrating inconnu.

1998 and 1999: Second and third years of the project

A total of 60 internal transmitters were applied during the second and third years of the radio telemetry study, with an overall success rate of 53/60, or 88%. Success is defined in this situation as tagged fish that resumed migration following tagging and were either located in the upper river during fall aerial surveys, or recorded migrating downstream by station 1 following probable spawning. The high success rate observed with internally tagged inconnu lends support to the conclusions from the radio telemetry experiment conducted in 1997.

The successful use of internal transmitters in this study does not mean they are the best choice for inconnu in all situations. Inconnu engaged in spawning migrations forgo feeding, presumably for several months prior to and following spawning (Alt 1969). During this period of time, the transmitter seems to occupy the stomach without consequence, allowing apparently normal behavior to occur and tracking to be accomplished. It is unknown whether inconnu disgorge or otherwise rid themselves of the transmitters at some later date. Mellas and Haynes (1985) found that rainbow trout *Oncorhynchus gairdineri* were able to eat even with internal transmitters in their stomachs, so it may be possible for inconnu to do likewise. However, considering that mature inconnu consume relatively large fish as their major food items (Fuller 1955; Alt 1965), it seems unlikely that a transmitter could remain in place with the antenna extended if the host fish were actively feeding. Pending an experimental evaluation of the long-term function of internal transmitters on inconnu, it would be prudent to use them only to study inconnu movements associated with spawning.

During the three years of this study, a great majority of internally tagged inconnu migrated upstream from the study site a distance of 425 km and 540 km and remained in the mainstem Yukon River (Figure 21). They were present in that location during their spawning season, in early October (Morrow 1980). A total of 73 internal transmitters were applied during the 3 years with a success rate was 62/73, or 85%. Fifty-seven of the 62 successful fish (92%) were located in the previously described stretch of river.

This gathering behavior, exhibited on 3 successive years, indicates that the site is an important spawning area. The visit to the site by boat, and the successful seine net sampling at various locations in the area, virtually eliminates any doubt regarding the area's importance as a spawning destination. The presence of spawning Bering cisco and humpback whitefish in the area further suggests that the environmental qualities that make that region of the Yukon River attractive and presumably productive for spawning inconnu, also make it attractive for other spawning coregonids. Further study of this region of river is warranted.

Downstream migration timing was similar for all three years of the study. It appears that by mid to late October spawning activities conclude, and post-spawning inconnu rapidly migrate to the lower-river and brackish water environments. The failure of the

FIGURE 21.—The view from an airplane flying about 500 m above a braided region of the Yukon River in the upper reaches of the Yukon Flats. This typifies the entire110 km long region in which radio-tagged inconnu were located during their spawning season. (Photo by Ted Heuer, Yukon Flats National Wildlife Refuge)

stations to record the downstream movement of all radio-tagged inconnu known to have moved past, leaves a measure of uncertainty about how widespread the post-spawning movement really is. It is possible that some proportion of the population remain in the upper-river for some unknown period of time.

Conclusion

Movement patterns of returning adult Pacific salmon *Oncorhynchus spp.* are relatively simple to describe using catch data. They are absent from freshwater systems, and then they arrive, being caught progressively farther upstream with time. By contrast, inconnu movement patterns on the Yukon River are difficult to interpret from catch data. Inconnu seem to be present during most of the year throughout the drainage (Alt 1969, 1987; Crawford 1978). Evidence of major migrations from the lower river, from increasing and decreasing catch rates along the river, would be difficult to gather, and even if possible, has not been documented. As a result, migrations of inconnu along the Yukon River have been largely invisible to humankind.

The three major components of this study, however, have shown that a major migration of inconnu occurs each year along the river. The biological sampling and aging components of this study revealed that inconnu captured in the fall at the study site were primarily or entirely mature adults preparing to spawn. The otolith microchemical analyses provided compelling evidence that most or all inconnu had experienced saltwater during their lives. And finally, the radio telemetry component of the study revealed their spawning destination as a highly braided region of Yukon River mainstem in the upper reaches of the Yukon Flats (Figure 21). The Yukon River inconnu life history story, as revealed by this study, can be summarized as follows. Each year, mature inconnu migrate from the lower river, or beyond, upstream into the Yukon Flats, a total distance of approximately 1,700 km. They arrive by late September or early October prepared to spawn. By mid-October, most inconnu have completed spawning and have begun a rapid, downstream migration to the lower river.

It must be understood that this synthesis speaks to the behavior of inconnu captured during August and September at the study site, approximately 1,200 river km from the sea. Inconnu are also captured at this site in the spring and summer and may be part of the same stock of fish, or perhaps not. In all likelihood, there are many different spawning stocks with unique migratory patterns, co-existing along the river.

Otolith microchemistry is an emerging science that can reveal many, previously unknowable life history parameters of fish. Its intended use in this study was simply to determine if sampled inconnu had been to sea. The actual information was much more detailed, revealing lifetime movement patterns between fresh and saltwater environments. Where before, uncertainty prevailed regarding movement patterns of these fish, now there is a clear picture of vast migrations, complex movements in and near marine environments, and individual variability. The discipline promises to reveal the hidden life histories of many other diadromous fishes during the coming years.

A fundamental quality of technical research, and in fact, of most areas of human inquiry, is that for every question answered, more are developed. This study has been no different. Many basic questions arise about fish biology and migration. For example, are other coregonids captured at the study site also amphidromous and engaged in spawning migrations? What is the migratory behavior of inconnu found in the Yukon River farther upstream than the study fish moved? Major ecological questions may be fewer, but perhaps more fundamental to understanding the migratory patterns observed. For example, what qualities of the identified spawning region of the Yukon River are so attractive and productive for inconnu and presumably for other coregonids? Is the area chosen because of inherent environmental qualities? Or, is it simply that the juveniles are distributed downstream in the river, by a fluke of geography, to an environment in which feeding and survival are maximized? These and many more questions may be pondered and possibly addressed through scientific study at some point in the future, further expanding our understanding of the Yukon River, and the fishes that inhabit the drainage.

Acknowledgments

Primary technical, logistical and financial support for this project came from the U. S. Fish and Wildlife Service, Fairbanks Fishery Resource Office. John Eiler of the National Marine Fisheries Service provided critical support for the radio telemetry component of the project. John Burr of the Alaska Department of Fish and Game inspired the project in the beginning, and provided technical and material support as well. The Yukon Flats National Wildlife Refuge provided funding for aerial telemetry surveys. The Koyukuk/Nowitna National Wildlife Refuge maintained a radio receiving station. Dr. James Reynolds and the late Dr. Jacqueline LaPerriere of the University of Alaska Fairbanks, Cooperative Fish and Wildlife Research Unit, provided invaluable technical advise during the planning stage, and as the project evolved. Dr. Ron Barry of the University of Alaska Fairbanks, advised on statistical matters. Dr. Ken Severin of the University of Alaska Fairbanks, opened his laboratory for use and provided critical support for the otolith aging and microchemical component of the project. U.S. Fish and Wildlife Service pilots, Mike Vivion and Dave Sowards, flew the aerial surveys. Fisherman, Stan Zuray, kept the fishwheels turning. Others that directly assisted with the project include James Akaran, Pete Anselmo, Charlie Campbell, Bill Carter, Laurel Devaney, Judy Gordon, Kim Howland, Ted Heuer, John Jozifek, Thomas McDonough, Jeff Melegari, Jon Moreland, Bill Morris, Riley Morris, Keith Mueller, Sandy Murley, Mike Spindler, and Jessica Tilley. Many others, too many to list, provided indirect support, of one sort or another, during the course of the project.

References

Alt, K. T. 1965. Food habits of inconnu in Alaska. Transactions of the American Fisheries Society, 94(3): 272-274.

----------. 1969. Taxonomy and ecology of the inconnu *Stenodus leucichthys nelma*, in Alaska. University of Alaska Fairbanks, Biological Paper Number 12, Fairbanks, Alaska.

----------. 1973. Annual progress report for a life history study of sheefish and whitefish in Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Volume 14, Juneau, Alaska.

----------. 1975. Annual performance report for a life history study of sheefish and whitefish in Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Volume 16, Juneau, Alaska..

----------. 1986. Annual performance report for interior whitefish program. Pages 45-56 *in* M.R. Doxey, J.E. Hallberg, and K.T. Alt, authors. Interior trout, salmon, and whitefish studies. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Volume 27, Juneau, Alaska.

----------. 1987. Review of inconnu *Stenodus leucichthys* studies in Alaska. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Fishery Manuscript Number 3, Juneau, Alaska.

American Fisheries Society. 1991. Common and scientific names of fishes from the United States and Canada, 5th edition. American Fisheries Society, Special Publication Number 20, Bethesda, Maryland.

Babaluk, J. A., and J. D. Reist. 1996. The use of strontium distribution in Dolly Varden and Arctic char otoliths from Ivvavik National Park for determining life history and stock differences. Department of Fisheries and Oceans, A Preliminary Report Prepared for Parks Canada, Winnipeg, Manitoba.

Babaluk, J. A., and seven coauthors. 1997. Evidence for non-anadromous behaviour of Arctic charr (*Salvelinus alpinus*) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada, based on scanning proton microprobe analysis of otolith strontium distribution. Arctic 50(3): 224-233.

Barnes, M. A., and G. Power. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. Environmental Biology of Fishes, 10: 297-299.

Berg, L. S. 1962. Freshwater fishes of the U.S.S.R. and adjacent countries. Originally Published in Russian in 1948, Translated and Republished by Israel Program for Scientific Translations, Jerusalem, Israel.

Campana, S. E., and J. D. Neilson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Science, 42: 1014-1032.

Campana, S. E., and 18 coauthors. 1997. Comparison of accuracy, precision, and sensitivity in elemental assays of fish otoliths using the electron microprobe, proton-induced x-ray emission, and laser ablation inductively coupled plasma mass spectrometry. Canadian Journal of Fisheries and Aquatic Science, 54: 2068-2079.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Department of Fisheries and Oceans, Canadian Special Publication of Fisheries and Aquatic Sciences 60, Ottawa, Ontario.

Conover, W. J. 1999. Practical nonparametric statistics, 3d edition. John Wiley & Sons, Inc., New York.

Crawford, D. 1978. Lower Yukon River sheefish study, October 1977-June 1978. Alaska Department of Fish and Game, Sheefish Investigation Number 9, Anchorage, Alaska.

Degens, E. T., W. G. Deuser, and R. L. Haedrich. 1969. Molecular structure and composition of fish otoliths. Marine Biology, 2(2): 105-113.

Devries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483-512, *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Dietrich, G., K. Kalle, W. Krauss, and G. Siedler. 1980. General oceanography, an introduction, 2d edition. John Wiley & Sons, New York.

Eiler, J. H. 1995. A remote satellite-linked tracking system for studying Pacific salmon with radio telemetry. Transactions of the American Fisheries Society 124:184-193.

Eiler, J. H., B. D. Nelson, and R. F. Bradshaw. 1992. Riverine spawning by sockeye salmon in the Taku River, Alaska and British Columbia. Transactions of the American Fisheries Society 121: 701-708.

Farrell, J., and S. E. Campana. 1996. Regulation of calcium and strontium deposition on the otoliths of juvenile tilapia, *Oreochromis niloticus*. Comparative Biochemical Physiology, 115A(2): 103-109.

Fowler, A. J., S. E. Campana, C. M. Jones, and S. R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. Canadian Journal of Fisheries and Aquatic Science, 52: 1431-1441.

Fuller, W. A. 1955. The inconnu (*Stenodus leucichthys mackenziei*) in Great Slave Lake and adjoining waters. Journal of the Fisheries Research Board of Canada, 12(5): 768-780.

Haas, R. E., and C. W. Recksiek. 1995. Age verification of winter flounder in Narragansett Bay. Transactions of the American Fisheries Society, 124: 103-111.

Haynes, J. M. 1978. Movement and habitat studies of Chinook salmon and white sturgeon. Doctoral dissertation. University of Minnesota, Minneapolis, Minnesota.

Howland, K. L. 1997. Migration patterns of freshwater and anadromous inconnu, *Stenodus leucichthys*, within the Mackenzie River system. Master's thesis. University of Alberta, Edmonton, Alberta.

Lewis, A. E., and W. R. A. Muntz. 1984. The effects of external ultrasonic tagging on the swimming performance of rainbow trout, *Salmo gairdneri* Richardson. Journal of Fish Biology 25: 577-585.

Lide, D. R., editor. 1990. CRC handbook of chemistry and physics. CRC Press, Inc. USA.

Likens, G. E., and P. L. Johnson. 1968. A limnological reconnaissance in interior Alaska. U.S. Army Cold Regions Research and Engineering Laboratory, Research Report 239, Hanover, New Hampshire.

Lowerre-Barbieri, S. K., M. E. Chittenden Jr., and C. M. Jones. 1994. A comparison of a validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional scale method. Fishery Bulletin, 92: 555-568.

Martin, D. J., C. Whitmus, L. Hachmeister, E. Volk, and S. Schroder. 1987. Distribution and seasonal abundance of juvenile salmon and other fishes in the Yukon River delta. U.S. Department of Commerce, NOAA, OCSEAP Final Report 63: 123-277.

McCleave, J. D., and K. A. Stred. 1975. Effect of dummy telemetry transmitters on stamina of Atlantic salmon (*Salmo salar*) smolts. Journal of the Fisheries Research Board of Canada, 32:559-563.

McDowall, R. M. 1988. Diadromy in fishes: migrations between freshwater and marine environments. Timber Press. Portland, Oregon.

McFarlane, G. A., and R. J. Beamish. 1995. Validation of the otolith cross-section method of age determination for sablefish (*Anoplopoma fimbria*) using oxytetracycline. Pages 319-330, *in* D.H. Secor, J.M. Dean, and S.E. Campana, editors, Recent developments in fish otolith research. University of South Carolina Press, Columbia, South Carolina.

Mcleod, C., and 13 coauthors. 1985. Fall fish spawning habitat survey, 1983-1985. Department of Fisheries and Oceans, RL&L/EMA Slave River Joint Venture, Edmonton, Alberta.

Mellas, E. J., and J. M. Haynes. 1985. Swimming performance and behavior of rainbow trout (*Salmo gairdneri*) and white perch (*Morone americana*): effects of attaching telemetry transmitters. Canadian Journal of Fisheries and Aquatic Science, 42:488-493.

Mills, M. J. 1989. Alaska statewide sport fish harvest report (1988). Alaska Department of Fish and Game. Fishery Data Series No. 122, Juneau, Alaska.

----------. 1994. Harvest, catch, and participation in Alaska sport fisheries during 1993. Alaska Department of Fish and Game. Fishery Data Series No. 94-28, Anchorage, Alaska.

Morrow, J. E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage, Alaska.

Moyle, P. B., and J. J. Cech, Jr. 1996. Fishes, an introduction to ichthyology, 3d edition. Prentice Hall, Upper Saddle River, New Jersey.

Mugiya, Y., and S. Tanaka. 1995. Incorporation of water-borne strontium into otoliths and its turnover in the goldfish *Carassius auratus*: effects of strontium concentrations, temperature, and 17β-estradiol. Fisheries Science, 61(1): 29-35.

Petrova, N. A. 1976. The biology of the inconnu, Stenodus leucichthys nelma, from the Irtysh River basin. Journal of Ichthyology, 16(1): 17-27.

Platt, C., and A. N. Popper. 1981. Fine structure and function of the ear. Pages 3-36, *in* W.N. Tavolga, A.N. Popper, and R.R. Fay, editors. Hearing and sound communication in fishes. Springer-Verlag, New York.

Radtke, R. L. 1989. Strontium-calcium concentration ratios in fish otoliths as environmental indicators. Comparative Biochemical Physiology, 92A(2): 189-193.

Radtke, R. L., D. W. Townsend, S. D. Folsom, and M. A. Morrison. 1990. Strontium: calcium concentration ratios in otoliths of herring larvae as indicators of environmental histories. Environmental Biology of Fishes, 27: 51-61.

Reed, S. J. B. 1997. Electron microprobe analysis, 2d edition. Cambridge University Press, Cambridge, Massachusetts.

Reist, J. D., and W. A. Bond. 1988. Life history characteristics of migratory coregonids of the lower Mackenzie River, Northwest Territories, Canada. Finnish Fisheries Research, 9: 133-144.

Rosenthal, H. L., M. M. Eves, and O. A. Cochran. 1970. Common strontium of mineralized tissues from marine and sweet water animals. Comparative Biochemistry and Physiology, 32: 445-450.

Sadovy, Y., and K. P. Severin. 1992. Trace elements in biogenic aragonite: correlation of body growth rate and strontium levels in the otoliths of the white grunt, *Haemulon plumieri* (Pisces: Haemulidae). Bulletin of Marine Science, 50(2): 237-257.

----------. 1994. Elemental patterns in red hind *(Epinephelus guttaltus*) otoliths from Bermuda and Puerto Rico reflect growth rate, not temperature. Canadian Journal of Fisheries and Aquatic Science, 51: 133-141.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa, Ontario.

Secor, D. H. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Norone saxatilis*. Fishery Bulletin, 90:798-806.

Secor, D. H., J. M. Dean, and E. H. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute, and the Belle W. Baruch Institute for Marine Biology and Coastal Research, Technical Publication Number 1991-01, Palo Alto, California.

Secor, D. H., A. Henderson-Arzapalo, and P. M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? Journal of Experimental Marine Biology and Ecology, 192: 15-33.

Severin, K. P., J. Carrol, and B. L. Norcross. 1995. Electron microprobe analysis of juvenile walleye Pollock, *Theragra chalcogramma*, otoliths from Alaska: a pilot stock separation study. Environmental Biology of Fishes, 43: 269-283.

Shestakov, A.V. 1991. Preliminary data on the dynamics of the downstream migration of coregonid larvae in the Anadyr River. Journal of Ichthyology, 31(3): 65-74.

Snyder, D. E. 1983. Fish eggs and larvae. Pages 165-197, *in* L. A. Nielsen, D. L. Johnson, and S. S. Lampton, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Snyder-Conn, E., and M. Lubinski. 1993. Contaminant and water quality baseline data for the Arctic National Wildlife Refuge, Alaska, 1988-1989, volume 2, raw data. U.S. Fish and Wildlife Service, Ecological Services, Technical Report NAES-TR-93-03, Fairbanks, Alaska.

Strange, R. J. 1996. Field examination of fishes. Pages 433-446 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2d edition. American Fisheries Society, Bethesda, Maryland.

Tallman, R. F., W. M. Tonn, and K. J. Howland. 1996. Migration of inconnu (*Stenodus leucichthys*) and burbot (*Lota lota*), Slave River and Great Slave Lake, June 1994 to July 1995. Northern River Basins Study, Project Report Number 117, Edmonton, Alberta.

Taube, T. T. 1996. Abundance and composition of sheefish in the Kobuk River, 1994-1995. Alaska Department of Fish and Game, Fishery Manuscript No. 96-2, Anchorage, Alaska.

Thorrold, S. R., C. M. Jones, P. K. Swart, T. E. Targett. 1998. Accurate classification of juvenile weakfish *Cynoscion regalis* to estuarine nursery areas based on chemical signatures in otoliths. Marine Ecology Progress Series, 173: 253-265.

Tzeng, W. 1996. Effects of salinity and ontogenetic movements on strontium:calcium ratios in the otoliths of the Japanese eel, *Anguilla japonica* Temminck and Schlegel. Journal of Experimental Marine Biology and Ecology, 199: 111-122.

Tzeng, W., K. P. Severin, and H. Wickstrom. 1997. Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. Marine Ecology Progress Series, 149: 73-81.

Underwood, T. J., K. Whitten, and K. Secor. 1998. Population characteristics of spawning inconnu (sheefish) in the Selawik River, Alaska, 1993-1996, final report. U.S. Fish and Wildlife Service, Fairbanks Fishery Resource Office, Alaska Fisheries Technical Report Number 49, Fairbanks, Alaska.

Welch, T. J., M. J. Van Den Avyle, R. K. Betsill, and E. M. Driebe. 1993. Precision and relative accuracy of striped bass age estimates from otoliths, scales, and anal fin rays and spines. North American Journal of Fisheries Management, 13: 616-620.

Wells, N. 1997. The atmosphere and ocean: a physical introduction, 2d edition. John Wiley and Sons, New York.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analyses, 2d edition. Springer-Verlag, New York.

Winter, J. 1996. Advances in underwater biotelemetry. Pages 555-590 *in* B.R. Murphy, and D.W. Willis, editors. Fisheries techniques, 2d edition. American Fisheries Society, Bethesda, Maryland.