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Comparison of Inconnu Spawning Abundance Estimates in the Selawik River, 1995, 2004, and 2005, Selawik National Wildlife Refuge

Raymond F. Hander, Randy J. Brown, and Tevis J. Underwood

Abstract

Selawik River inconnu (sheefish) *Stenodus leucichthys* were sampled during the 2004 and 2005 spawning migrations using mark-recapture techniques to estimate the current abundance of the spawning population and compare it with the abundance in 1995. The 2004 and 2005 marking events were from mid-July to mid-August and the recapture events were from late August to mid-September. During the marking events, fish were primarily captured with beach seines due to turbid water conditions caused by a large permafrost thaw slump in the upper Selawik River drainage. Water clarity improved with the onset of autumn freezing, so fish were captured with hook and line during the recapture events. The estimated abundance of spawning inconnu for 2004 and 2005 was 23,652 (95% CI = 13,383 – 33,920) and 46,324 (95% CI = 25,069 – 67,580), respectively. The estimated abundance of spawning inconnu in 1995 was 5,990 (95% CI = 4,098 – 7,882), indicating that the spawning population expanded significantly during the 10 year interval. This population expansion is thought to be the result of an episodic recruitment event of young inconnu into the spawning population.

Introduction

Inconnu (sheefish) *Stenodus leucichthys* are large, long-lived, piscivorous whitefish found in many Arctic and sub-Arctic waters of Asia and North America (Alt 1969; Scott and Crossman 1973; Morrow 1980). They are one of the most important food fishes in the Kotzebue region of Northwest Alaska, where 20,000 or more are harvested each year in subsistence, sport, and commercial fisheries (Taube 1997; Savereide 2002; Georgette and Loon 1990; Georgette and Koster 2005; Georgette and Shiedt 2005). Two spawning populations have been identified in the region, one in the upper Kobuk River (Alt 1969) and the other in the upper Selawik River (Underwood et al. 1998; Figure 1). No other spawning populations are thought to exist in the region. The United States Congress identified inconnu as a species of special interest in the Selawik National Wildlife Refuge (Refuge), which they established in the Alaska National Interest Lands Conservation Act (ANILCA) in 1980 (USFWS 1993). In ANILCA, Congress mandated that sheefish be maintained in their natural diversity and that opportunities for subsistence use be maintained. The spawning area of the Selawik River population lies entirely within Refuge lands and is therefore a population of special interest.

Inconnu from the Kobuk and Selawik River populations live their entire life-cycle within that river and estuary system in northwest Alaska. They overwinter in the Selawik Lake, Hotham

Authors: Raymond Hander and Randy Brown are fisheries biologists with the U.S. Fish and Wildlife Service. They can be contacted at Fairbanks Fish and Wildlife Field Office, 101 12th Ave., Room 110, Fairbanks, AK 99701 or ray_hander@fws.gov and randy_j_brown@fws.gov. Tevis Underwood is an Assistant Refuge Manager for the Arctic National Wildlife Refuge. He can be contacted at Arctic National Wildlife Refuge, 101 12th Ave., Room 236, Fairbanks, AK 99701 or tevis_underwood@fws.gov.

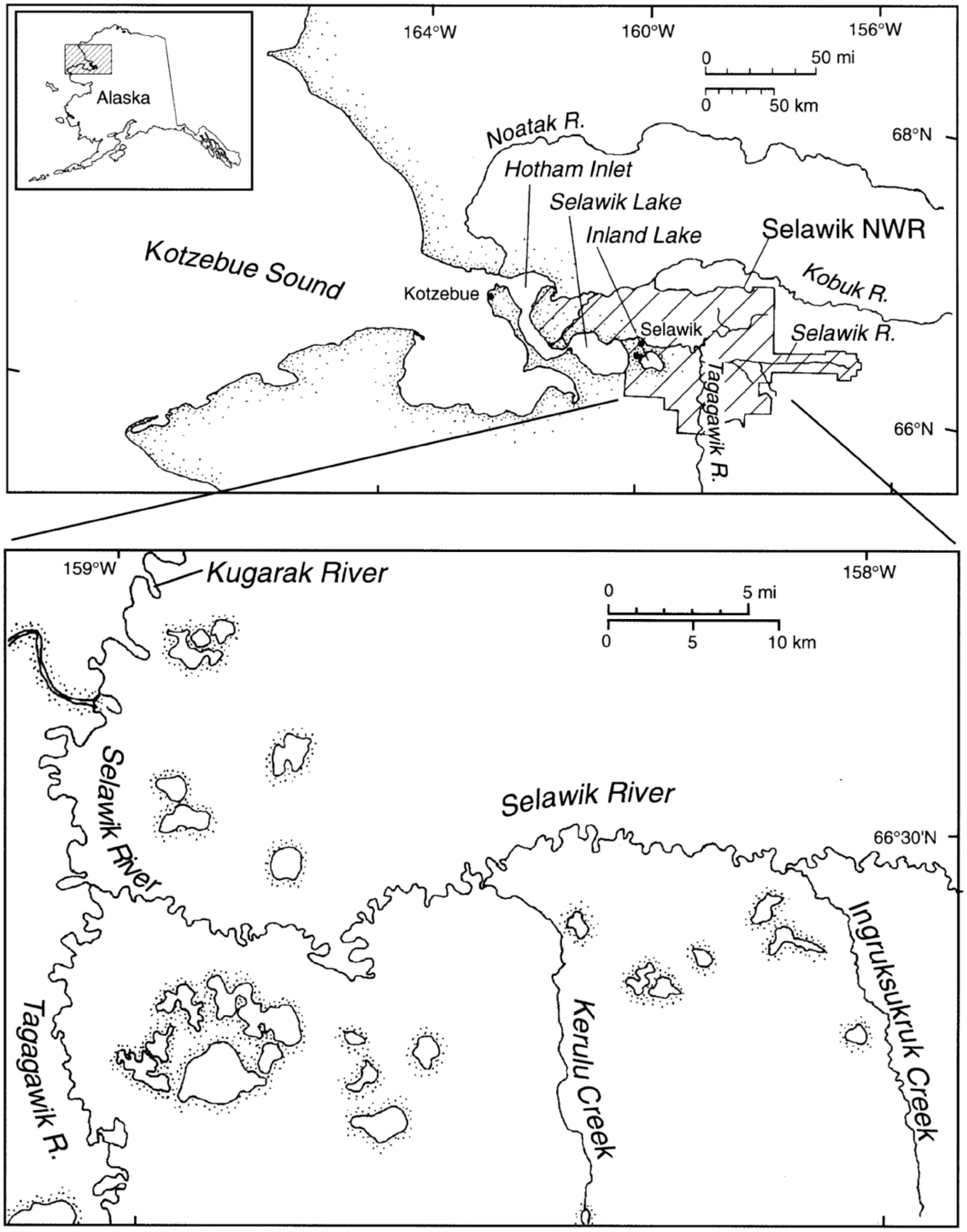

Figure 1. The Kotzebue region and Selawik National Wildlife Refuge (top), and a closer view of the study region in the upper Selawik River drainage (bottom).

Inlet, and other associated waterways (Alt 1969, 1973) (Figure 1). Tagged fish from both the Selawik and Kobuk rivers have been recaptured as far seaward as the village of Kotzebue, where the brackish water of Hotham Inlet meets the marine water of Kotzebue Sound (Taube 1996, 1997; Underwood et al. 1998, 2000). They tolerate brackish environments but cannot survive the cold temperatures of fully marine water in the winter, which approaches –2°C under ice cover (Black 1957; U.S. Navy Hydrographic Office 1958; DeVries and Cheng 2005). Both populations are thus confined to the aquatic habitats to the freshwater side of the brackish-marine divide near the village of Kotzebue. Most inconnu mature by 8 to 12 years of age and are capable of living for 30 years or more (Brown 2000; Howland 1997; Howland et al. 2004). With ice break-up, mature inconnu begin a slow spawning migration up either the Kobuk or Selawik rivers, initially feeding in the lower reaches with nonspawning fish during the early summer, and arriving at spawning areas in the upper reaches by late summer or fall. Nonspawning adults and immature inconnu remain in the lower reaches of the rivers and estuary systems (Alt 1969). By early September, inconnu complete their migration to upstream spawning areas, where they remain until late September or early October when spawning takes place. Eggs are broadcast over gravel and cobble substrate. The fertilized eggs settle into the interstitial spaces in the substrate and develop through the winter. Post-spawning inconnu leave the area immediately, returning to the large lake systems and estuaries for overwintering (Underwood 2000). Eggs are thought to hatch in the late winter or spring and larvae are carried downstream with the high waters of spring (Shestakov 1991; Bogdanov et al. 1992; Naesje et al. 1986). Tag return data (Taube and Wuttig 1998; Underwood 2000) and genetic analysis (Miller et al. 1998) indicate that inconnu exhibit spawning fidelity to their river of origin.

Mature inconnu were thought to need one or more years following a spawning event to accumulate sufficient energy reserves to spawn again, resulting in skip-year spawning behavior (Alt 1969; Reist and Bond 1988; Lambert and Dodson 1990). Both Taube (1997) and Underwood (2000), however, suggested that some sequential-year spawning may occur in the Kobuk and Selawik River inconnu populations based on sequential-year captures of fish. Taube and Wuttig (1998) estimated that almost 10% of inconnu present in the Kobuk River spawning area during 1997 were also present during 1996. The prevalence of sequential-year spawning, however, has not been rigorously examined.

The relationship between inconnu spawning population size and the production of young fish is of great interest, particularly given the substantial harvests in the Kotzebue region. Spawning population estimates in the mid-1990s suggested that 30,000 to 40,000 fish spawned in the Kobuk River population (Taube 1996, 1997; Taube and Wuttig 1998) and 3,000 to 7,000 fish spawned in the Selawik River population (Underwood et al. 1998). Long-term variation in spawning population size has not been studied anywhere and is strictly a matter of speculation about the importance relative to overall population dynamics. In 2004, the U. S. Fish and Wildlife Service (USFWS) began a two-year study to estimate the abundance of spawning inconnu in the Selawik River and determine long-term trends in population levels by comparing current estimates with those from the previous study (Underwood et al. 1998). We limited our comparisons to the results from the 1995 season because of its similarity in procedure and operation to the current work. The primary objectives of our study were to: 1) estimate the abundance of spawning inconnu; 2) identify trends in population levels between 1995 and 2004 to 2005; 3) test the hypothesis that the size structure of the population of spawning inconnu in the Selawik River in 2004 and 2005 was similar to that in 1995; and, 4) document the occurrence and model the rate of sequential-year spawning using radio-telemetry and mark-recapture techniques.

Study Area

The Selawik River drainage lies primarily within the Refuge in northwest Alaska. The mainstem of the river flows from east to west through a wide tundra valley for approximately 300 km, terminating in Selawik Lake (Figure 1). Two major tributaries join the Selawik River; the

Tagagawik River flowing from the south, and the Kugarak River flowing from the north. The region has a maritime climate during the ice-free periods of the year (late May to early October) and transitions to an Arctic climate during the winter months. Seasonal temperature extremes range from about 34°C in the summer to -50°C in the winter. Annual precipitation usually falls between 38 and 51 cm (USFWS 1993).

Sampling for the study was conducted on the Selawik River upstream from the Tagagawik River (Figure 1, bottom). The river in this area meanders through the valley in a series of pools and runs with an abundance of woody debris. The substrate in the region where the marking event took place, in the vicinity of Kerulu Creek, was primarily mud and sand. In the region where the recapture event took place, in the vicinity of Ingruksukruk Creek, the substrate was primarily gravel and cobble.

The Selawik River is normally clear. However, in the spring of 2004, a large permafrost thaw slump (slump) occurred in the upper drainage about 80 km upstream from the marking area (Figure 2) and emitted a heavy sediment load into the river, inundating the Selawik River with highly turbid water. At times during the project, the turbid flow extended as far as the mouth of the river, approximately 260 km downstream of the slump. Late in the season, when freezing temperatures became common and the slump emitted less sediment, water clarity improved.

Figure 2. Aerial views of the permafrost thaw slump in the upper Selawik River drainage during summer 2006, and at the confluence of the Selawik and Tagagawik rivers, approximately 150 km downstream from the slump, illustrating the persistence of the turbid flow.

Methods

Study Design and Basic Project Details

The abundance of spawning inconnu on the Selawik River was estimated in 2004 and 2005 with two-event mark-recapture experiments using the Bailey estimator (Seber 2002). The marking event (Event I) occurred from 7 July through 19 August in the vicinity of Kerulu Creek, a 21 km long reach of river about 25 km downstream of the spawning area. The spawning area was defined with radiotelemetry in earlier experiments to extend across a 12 km reach of the Selawik River in the vicinity of Ingruksukruk Creek (Underwood et al. 1998; Figure 1). The recapture event (Event II) occurred from 28 August through 15 September across the full range of the spawning reach. The population was considered to be closed, with Event I occurring during migration from Selawik Lake and Hotham Inlet feeding habitats to the upstream spawning area, and Event II occurring when the annual spawning population was expected to be in the spawning area. Sampling during Event II occurred with replacement to be consistent with the earlier work by Underwood (2000). Mortality between events was considered to be negligible because Event I occurred during immigration to the spawning area where Event II occurred, and the elapsed time between Events I and II was small. Therefore, the abundance estimate was considered to be valid for the time and location of Event II.

Sampling activities during Events I and II were distributed across the entire geographic ranges of the respective regions. In most cases, sampling of a specific site occurred no more frequently than once every three days. Not all sample sites were equally productive, nor were all productive sites always productive; therefore, effort was adaptive to sampling success. For example, if few or no fish were captured at a specific site within a short period of time, the six person sample crew would move to a new location. In contrast, if fish were being readily captured at a specific site the crew would continue sampling there through the day or until capture rates dropped. As a result, the geographic distribution of overall effort, tag deployment during Event I, and fish examined during Event II were clumped within the respective sampling regions rather than being evenly distributed among all possible sites.

Data Collection and Tagging Procedures

Captured inconnu were restrained in a hinged and padded fish cradle for data collection and tagging. Data, including location, date of capture, capture method, time of capture, sex (male, female, or unknown), tag number, fork length (length; measured to the nearest cm), time of release, status of capture (new fish in Event I and II, Event I recapture, or Event II recapture), crew initials, and comments, were recorded on field data sheets. Additionally, inconnu were examined for prior anchor tags or anchor tag scars, fin clips, and visual implant tags from the 1994 to 1996 study. These data were also recorded on field data sheets. Anchor tags were inserted near the base of the dorsal fin to facilitate locking between interneural bones. Anchor tags were white in 2004 and green in 2005. The tip of the left pelvic fin (approximately one-third of the entire fin) was clipped as a secondary mark in 2004 and 2005, and all fish examined during Event II were examined for the secondary mark to identify tag loss if it occurred. During 2005, marked inconnu encountered from 2004 had their right pelvic fin clipped so that an individual fish could be identified from secondary marks as having been encountered in 2004 and 2005.

Data Analysis

Similar, but not identical procedures to those described above were followed during the earlier spawning population projects conducted by Underwood et al. (1998). The most important difference, and the only one that complicated comparisons across years, was that the population estimates in the earlier studies were limited to fish across the length range of the recaptured sample only (Event II). The length stratification or partition approach has routinely been used when fish across a wide range of lengths are present and the capture method is only effective for a subsample of the population, or when the study is focused on a particular demographic group identifiable by length (e.g., DeCicco 1999; Roach and McIntyre 1999; Schwanke and Bernard 2005). In such cases the resulting population estimates may be stratified across length classes or limited to a particular length group within the population (Seber 2002). The limited range of lengths in the samples of recaptured inconnu in the earlier work was originally thought to indicate sampling bias and estimates of the spawning population during those years were conservatively limited to fish between 75 and 111 cm fork length (Underwood et al. 1998). It is now our perception that all fish available for capture during Event I were pre-spawning inconnu migrating to the spawning area, and that the capture methods employed in both Events I and II were equally effective across the entire length range of inconnu present. The apparent sampling bias observed in the earlier studies (Underwood et al. 1998) is thought, instead, to be a sample size issue. A small random sample of recaptured fish would not be expected to have the same length range as a much larger sample of marked fish. Therefore, we did not partition the population based on the length ranges of recaptured fish in the current studies, and we reanalyzed data from 1995 without partitioning for comparison.

Our primary goal was to estimate the abundance of spawning inconnu within ±25% of the real value at a 0.95 level of confidence. The spawning population in 1995 was estimated to be between 3,690 and 7,274 fish (Underwood et al. 1998). We assumed that if the current population was approximately 10,000 fish, assuming a modest increase over the 1995 level, the sample requirements to achieve desired accuracy and precision goals would be about 1,600 fish handled during Events I and II combined (Robson and Regier 1964).

Temporal Recapture Probabilities

Two types of temporal data were evaluated with Chi-squared tests for differences in recapture probabilities, as detailed by Conover (1999). In the first case, we considered whether the time of tagging during Event I, early or late, influenced a fish's presence or catchability in the spawning habitat during Event II. If so, the probability of recapturing fish from the two time periods would be different and could represent a violation of the assumption of a closed population (Seber 2002) if, for example, early tagged fish were less likely to continue their migration to the spawning area than later tagged fish. We tested the null hypothesis that the number of recaptured fish in Event II originating from early and late categories of Event I were proportionally equal versus the alternative hypothesis that they were different. Significant differences were based on $\alpha = 0.05$. The early season interval extended from the start of Event I to the day in which half of all marked fish were accounted for. The late season interval extended from the day after half of all marked fish were accounted for to the end of Event 1. Recaptured fish from Event II were assigned to either early or late season categories based on the date of original tagging. Data for this test were the number of fish tagged in the early and late season categories of Event I and the number of recaptured fish from each category.

In the second test of temporal differences in recapture probabilities, we considered whether the time of examination during Event II, early or late, affected the ratio of recaptured fish in the examined population. If so, then the assumptions of uniform mixing of marked and unmarked fish during Event II and equal capture probability of marked and unmarked fish (Seber 2002) could be violated. We tested the null hypothesis that the numbers of recaptured fish in early and late categories of Event II were proportionally equal versus the alternative hypothesis that they were different. Significant differences were based on $\alpha = 0.05$. The early season interval extended from the start of Event II to the day in which half of all examined fish were accounted for. The late season interval extended from the day after half of all examined fish were accounted for to the end of Event II. Recaptured fish from Event II were assigned to either early or late season categories based on the date of recapture. Data for this test were the number of fish examined in the early and late season categories of Event II and the number of recaptured fish in each category.

Length Distribution

Fish marked during Event I were captured primarily with beach seines and fish examined during Event II were captured primarily with hook and line. Because we used two different methods of fish capture, we assumed that capture during Event I did not generally affect the catchability of fish during Event II. To test whether there were any length-related effects of capture on the probability of being recaptured, length distributions of marked fish from Event I were compared with length distributions of recaptured fish during Event II using a Kolmogorov-Smirnov (KS) test of the equality of distributions, as detailed by Conover (1999). If all marked fish from Event I were available for capture during Event II, and recaptured fish during Event II were random samples of the marked fish present in the spawning area, then the KS test of the length distributions of the two sample groups should be similar. We tested the null hypothesis that there would be no difference in the length distributions of the two groups, versus the alternative hypothesis that they would be different. Significant differences were based on $\alpha = 0.05$. Rejection of the null hypothesis would indicate a violation of one or more assumptions necessary for an unbiased estimate of the spawning population.

Radiotelemetry

Radiotelemetry was employed during the 2005 project to reexamine the geographic bounds of the Selawik River spawning area and to test the hypothesis that some inconnu spawn during sequential years. Thirty radio transmitters were surgically implanted into inconnu during Event I following the basic methods detailed in Brown (2006). The transmitters were designed to transmit during three seasons of each year including fall spawning period, winter, and spring feeding period for five years. This schedule allowed multiple spawning events to be recorded. Radio transmitters were deployed in male and female inconnu between 21 July and 18 August 2005 at a maximum rate of three per day. Boat surveys during Event II were used to verify the presence of radio-tagged fish in the spawning area and to direct sampling efforts. Aerial surveys during the late September spawning period 2005 were used to define the current geographic bounds of the spawning area. Aerial surveys of the spawning area during the spring 2006 feeding period were conducted to determine if any radio-tagged inconnu had died in the spawning area in fall 2005, and aerial surveys in late September 2006 were conducted to identify any inconnu that were present on the spawning area during two sequential years.

Statistical Analysis

The abundance of spawning inconnu in the Selawik River was estimated from Seber (2002) as:

$$\hat{N} = \frac{n_1(n_2+1)}{(m_2+1)} \qquad 1$$

where:

$\hat{N}$ = estimated number of spawning inconnu
n_1 = number of fish marked during Event I
n_2 = number of fish examined during Event II
m_2 = the subsample of n_1 that were recaptured during Event II.

The variance of $\hat{N}$ was estimated as:

$$\hat{v}\left(\hat{N}\right) = \frac{n_1^2(n_2+1)(n_2-m_2)}{(m_2+1)^2(m_2+2)} \qquad 2$$

The resulting 95% confidence interval was calculated as:

$$(95\%\ \mathrm{CI}) = \hat{N} \pm 1.96\sqrt{\hat{v}} \qquad 3$$

The accuracy of $\hat{N}$, as discussed by Robson and Regier (1964), was calculated as:

$$Accuracy\left(\hat{N}\right) = \left(\frac{1.96\sqrt{\hat{v}}}{\hat{N}}\right)x\left(100\right) \qquad 4$$

We used the goodness-of-fit method of comparing two populations (Seber 2002) to test the null hypothesis that there was no change in the Selawik River spawning population between any two years in which spawning populations were estimated. The test statistic was calculated as:

$$Z = \frac{\hat{N}_a - \hat{N}_b}{\sqrt{\hat{v}\left(\hat{N}_a\right) + \hat{v}\left(\hat{N}_b\right)}} \qquad 5$$

Where:

Z = the test statistic

$\hat{N}_a$ = the spawning population estimate from population 'a'

$\hat{N}_b$ = the spawning population estimate from population 'b'

$\hat{v}\left(\hat{N}_a\right)$ = the variance of $\hat{N}_a$

$\hat{v}\left(\hat{N}_b\right)$ = the variance of $\hat{N}_b$.

The null hypothesis was rejected at critical values $Z \geq 1.96$ or $Z \leq -1.96$, corresponding to $\alpha \leq 0.05$.

Length Composition

Inconnu length data were used to characterize the spawning population during 2004 and 2005, and to compare the recent length distributions with those from the earlier studies. For each of the three study years (1995, 2004, and 2005), length distributions from Event I were compared with length distributions from recaptures in Event II and from all fish examined in Event II using an exact KS test as implemented in StatXact version 6.1 (Cytel 2003). Nonsignificant test results for comparisons of the length distributions from Event I and recaptures in Event II, and from all fish in Events I and II would indicate no sampling bias in either event. In this case, data were pooled to represent the length composition of spawning inconnu for the year. Nonsignificant test results for comparisons of the length distributions from Event I and recaptures in Event II, and significant test results for comparisons of the length distributions from all fish in Events I and II would indicate sampling bias during Event I (Seber 2002). In this case length distribution data from Event II only, were selected to represent the length composition of spawning inconnu for the year. Kolmogorov-Smirnov tests were also conducted between pairs of annual length distributions of spawning inconnu to test the null hypothesis that they were similar among years.

Length data were compiled into six different 10-cm categories to evaluate the length composition of spawning inconnu. Based on the range of lengths observed in 1995 (Underwood et al. 1998), appropriate categories were determined to be: <70 cm, 70 to <80 cm, 80 to <90 cm, 90 to <100 cm, 100 to <110 cm, and ≥110 cm. Estimates of the proportional length compositions within categories were calculated from Cochran (1977) as:

$$\hat{p}_j = \frac{n_j}{n} \qquad 6$$

where:

$\hat{p}_j$ = the estimated proportion of inconnu within the jth category

n_j = the number of sampled inconnu in the jth category

n = the total number of inconnu sampled.

An estimate of the variance of each $\hat{p}_j$ was calculated as:

$$\hat{v}\left(\hat{p}_j\right) = \frac{\hat{p}_j\left(1-\hat{p}_j\right)}{n-1} \qquad 7$$

The estimated abundance of spawning inconnu within each category in the population was calculated as:

$$\hat{N}_j = \hat{p}_j \hat{N} \qquad 8$$

where:

$\hat{N}_j$ = the estimated number of spawning inconnu in the jth length category

$\hat{N}$ = the spawning population estimate.

The variance of $\hat{N}_j$ was calculated from Goodman (1960) as:

$$\hat{v}\left(\hat{N}_j\right) = \hat{v}\left(\hat{p}_j\hat{N}\right) = \left(\hat{p}_j\right)^2\left(\hat{v}\left[\hat{N}\right]\right) + \left(\hat{N}\right)^2\left(\hat{v}\left[\hat{p}_j\right]\right) - \left(\hat{v}\left[\hat{p}_j\right]\right)\left(\hat{v}\left[\hat{N}\right]\right) \qquad 9$$

Sex Ratio

As inconnu approach spawning, they stop eating and the eggs of females begin expanding during the process of vitellogenesis. During this time, external morphologies of male and female inconnu become distinct and are used to estimate the sex of individual fish. Brown (2000) reported that all but 2 of 266 inconnu sampled from the Yukon River inconnu spawning migration during August and September were correctly classified to sex prior to evisceration. Sex ratios of the spawning populations of inconnu were estimated during 2004 and 2005 using data from Event II only because sex-specific morphology was less distinct during Event I. Proportional estimates and associated variances were calculated using equations (6) and (7) above.

Sequential-year Spawning

The rate of sequential-year spawning of Selawik River inconnu was explored with radiotelemetry data collected during two sequential spawning seasons, as discussed earlier, and mark-recapture data from 2004 and 2005. The approach with radiotelemetry was directed at locating radio-tagged inconnu in spawning habitat during two sequential spawning seasons. Alt (1969), who sampled Kobuk River inconnu in their spawning habitat, Brown (2000), who sampled the fall spawning migration of Yukon River inconnu downstream from their spawning habitat, and Howland (1997), who sampled spawning migrations of inconnu in the Slave and Arctic Red rivers in the Mackenzie River drainage, reported that only fish preparing to spawn were present. Based on these findings, it was assumed that a fish's presence in spawning habitat during spawning season indicated its intention to spawn. The number of radio-tagged inconnu present on the spawning area during 2005 and 2006 was considered to be a binomial random variable. The probability of an inconnu spawning on sequential years was estimated across a range of annual survival rates that were thought to be reasonable (0.60 to 0.90).

The number of radio-tagged fish on the spawning area in 2005 was considered to be the original sample. This number was multiplied by the upper and lower bounds of the survival rate being considered (0.60 to 0.90) to obtain the range of radio-tagged fish likely to be alive in 2006. The probability of an observed number of fish spawning on two sequential years was considered to be at the upper bound of a lower probability of occurrence, or at the lower bound of a greater probability of occurrence. Binomial probability curves were prepared using an iterative process with Minitab statistical software such that the number of fish observed on the spawning area on two successive years was as close as possible to the upper 95% CI of a low probability curve without exceeding it, and as close as possible to the lower 95% CI of a high probability curve without going below it. Binomial probabilities were considered to two decimal places. The probability of a fish spawning on two successive years was thought to lie within the range of these low and high probabilities for both low and high survival rates.

The mark-recapture approach to evaluate sequential-year spawning (sys) was a modified two-event mark-recapture study with the objective of estimating the number of fish marked during year 1 (2004) that were present again in spawning habitat on year 2 (2005). All fish marked during Events I and II in year 1 were considered to be the marked population for the sequential-year spawning study (Event I $_{sys}$). All fish examined during Events I and II in year 2 were considered to be the examined population (Event II $_{sys}$) and were sampled with replacement. Inconnu were examined for primary and secondary marks to ensure that tag loss during the year-long interval between Event I $_{sys}$ and Event II $_{sys}$ was not a problem. We conducted a KS test of the null hypothesis that the length distributions of fish marked during Event I $_{sys}$ and fish recaptured during Event II $_{sys}$ were similar. The lengths at the time of tagging were used for fish recaptured during Event II $_{sys}$ to avoid length bias caused by annual growth. A significant difference between these length distributions would indicate size selectivity in one or both sampling events, precluding further analysis. The population estimate for year 2 was obtained from fish marked and recaptured during 2005 only, as described earlier. An algebraic reconfiguration of equation (1) above isolated the unknown number of fish tagged during Event I $_{sys}$ and present during Event II $_{sys}$ on one side of the equation as follows:

$$\hat{n}_{1,2} = \frac{\hat{N}_2(m_{1,2}+1)}{(n_2+1)} \qquad 10$$

where:

$\hat{n}_{1,2}$ = the estimated number of fish tagged during year 1 that were present on the spawning area again during year 2

$\hat{N}_2$ = the estimated abundance of spawning inconnu during year 2

$m_{1,2}$ = the number of fish tagged during year 1 that were recaptured during year 2

n_2 = the number of fish examined during year 2 (includes all fish from Events I and II).

The proportion of inconnu present in spawning habitat on two sequential years was considered across a range of annual survival rates with the equation:

$$\hat{P}_{1,2} = \frac{\hat{n}_{1,2}}{S_A n_1} \qquad 11$$

where:

$\hat{P}_{1,2}$ = the estimated proportion of inconnu spawning on two sequential years

n_1 = number of fish tagged in year 1 (2004), includes all tagged fish from Events I and II

S_A = annual survival rate.

The variability associated with $\hat{n}_{1,2}$ and $\hat{P}_{1,2}$ was modeled across ranges of values for $\hat{N}_2$ (the standard 95% CI) and S_A (0.60 to 0.90) to gain an understanding of possible rates of repeat spawning given the available mark-recapture data.

Results

Basic Project Details

Mark-recapture projects for Selawik River inconnu proceeded as planned during 2004 and 2005 (Table 1). There were no major interruptions to the project like the high-water events in 1994 and 1996 (Underwood et al. 1998). The river was very turbid during Event I in 2004 and 2005 (Figure 2), requiring the use of beach seines as the primary gear for fish capture, and much less turbid during Event II in both years, permitting the use of hook and line sampling methods. A total of 1,459 inconnu in 2004, and 1,882 in 2005 were examined during Events I and II combined, and there was no evidence of tag loss in either year. A total of 918 fish were examined during 1995.

Table 1. Dates and sampling results for Events I and II during the 1995, 2004, and 2005 project years.

Sampling data		1995	2004	2005
Event I	Dates of operation	7/17–8/31	7/13–8/14	7/07–8/19
	Marked fish	546	441	627
Event II	Dates of operation	9/05–9/22	8/28–9/15	8/29–9/14
	Examined fish	372	1,018	1,255
	Recaptured fish	33	18	16
$n_1 + n_2$		918	1,459	1,882

Temporal recapture probabilities

There were no time-related effects on the probability of recapture during the two years of this project or in 1995. The null hypothesis could not be rejected for any of the Chi-squared test of temporal recapture probabilities (Table 2). These data are consistent with our assumptions that tagged fish are members of a closed population that are present in spawning habitat during Event II and that they are uniformly mixed with unmarked fish (see Appendix A for an *a posteriori* assessment of all mark-recapture assumptions discussed by Seber 2002).

Table 2. Dates, sampling data, and results of Chi-squared tests for temporal effects on the probability of recapture related to the time of marking during Event I and the time of examination during Event II for the 1995, 2004, and 2005 project years.

		Event I Temporal Data		Event II Temporal Data	
Year	Data type	Early	Late	Early	Late
1995	Time period	7/17–7/27	7/28–8/31	9/05–9/11	9/12–9/22
	Marked/Examined fish	282	264	196	176
	Recaptures	17	16	15	18
	Chi-squared results	$T_1 = 0.000$, $P = 0.988$		$T_1 = 0.636$, $P = 0.425$	
2004	Time period	7/13–7/23	7/24–8/14	8/28–9/08	9/09–9/15
	Marked/Examined fish	226	215	518	500
	Recaptures	10	8	8	10
	Chi-squared results	$T_1 = 0.129$, $P = 0.720$		$T_1 = 0.293$, $P = 0.588$	
2005	Time period	7/07–8/06	8/07–8/19	8/29–9/06	9/07–9/14
	Marked/Examined fish	325	302	772	483
	Recaptures*	6	9	10	6
	Chi-squared results	$T_1 = 0.821$, $P = 0.365$		$T_1 = 0.006$, $P = 0.936$	

*The discrepancy in total number of recaptures between Events I and II in 2005 was the result of a radio-tag recapture that could not be specifically identified. As a result, it could not be classified as early or late tagged for the Event I temporal test. Its recapture date was known so it could be classified for the Event II temporal test. The Chi-squared test was conducted with the radio-tagged fish being tagged early and late and neither option resulted in a significant outcome.

Length Distribution

Kolmogorov-Smirnov tests of the similarity of length distributions of inconnu marked during Event I and recaptured during Event II for the years 1995, 2004, and 2005 were all nonsignificant (Figure 3). Kolmogorov-Smirnov tests of the similarity of length distributions of inconnu marked during Event I and examined during Event II revealed significant differences between the two groups in 2004 ($P < 0.0001$), but not in 1995 or 2005 (Figure 4). Length data from Events I and II were pooled for length composition analyses except in 2004, when only length data from Event II were used.

Radiotelemetry

Radio tags were deployed in 30 pre-spawning inconnu during Event I in 2005 of which 26 migrated upstream into the spawning area prior to Event II. Four radio-tagged fish were not located during the spawning season, despite extensive boat and aerial surveys. Two of these four fish were located in the spawning area during spawning season 2006, indicating that the surgeries may have distracted them from spawning in the Selawik River in 2005. The geographic distribution of radio-tagged fish during the 2005 spawning season was very similar to the distribution identified in 1995 by Underwood et al. (1998). Repeat locations of radio-tagged fish during September revealed movement among pools within the spawning area on a regular basis. For instance, individual fish found in the upper reaches of the spawning reach one day, might be found in the lower reaches on another day. This behavior was also noted by Underwood et al. (1998). The geographic bounds of the spawning area appeared to remain consistent across years and the telemetry data verified that the sampling area during Event II was appropriate (Figure 5).

Spawning Population Estimates

The Selawik River inconnu spawning population was estimated to be 5,990 in 1995 (reevaluated without length partitioning), 23,652 in 2004, and 46,324 in 2005 (Table 3; Figure 6). Spawning population estimates in 2004 and 2005 were both significantly greater than in 1995 (Z = 3.32, P = 0.001 and Z = 3.70, P = 0.0002 respectively), but the population estimates in 2004 and 2005 were not significantly different at the 95% confidence level (Z = 1.88, P = 0.0602).

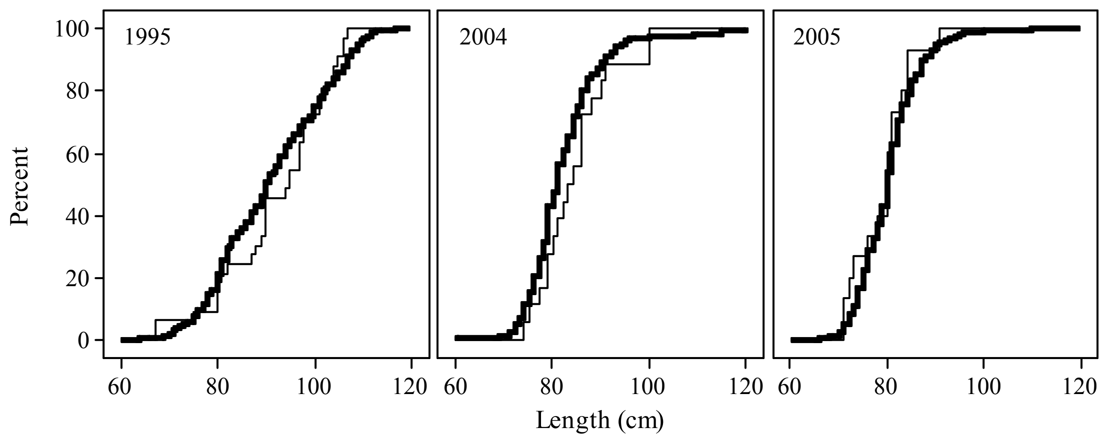

Figure 3. Cumulative length distributions of marked (heavy lines) and recaptured inconnu (light lines) for the years 1995, 2004, and 2005 of the Selawik River inconnu spawning population project. Kolmogorov-Smirnov tests found them to be similar for all three years.

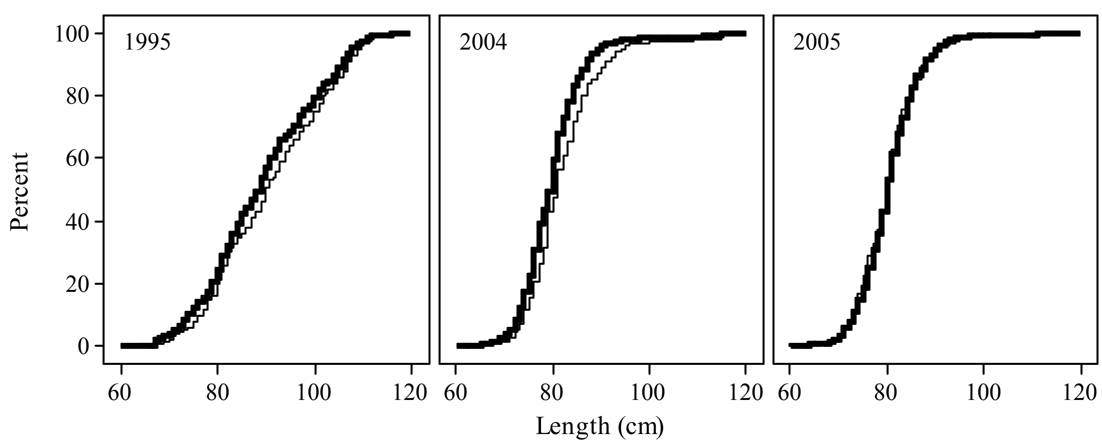

Figure 4. Cumulative length distributions of all Selawik inconnu collected during the marking (heavy lines) and recapture (light lines) events during 1995, 2004, and 2005. Kolmogorov-Smirnov tests found them to be similar in 1995 and 2005 and significantly different in 2004 (*P*<0.0001).

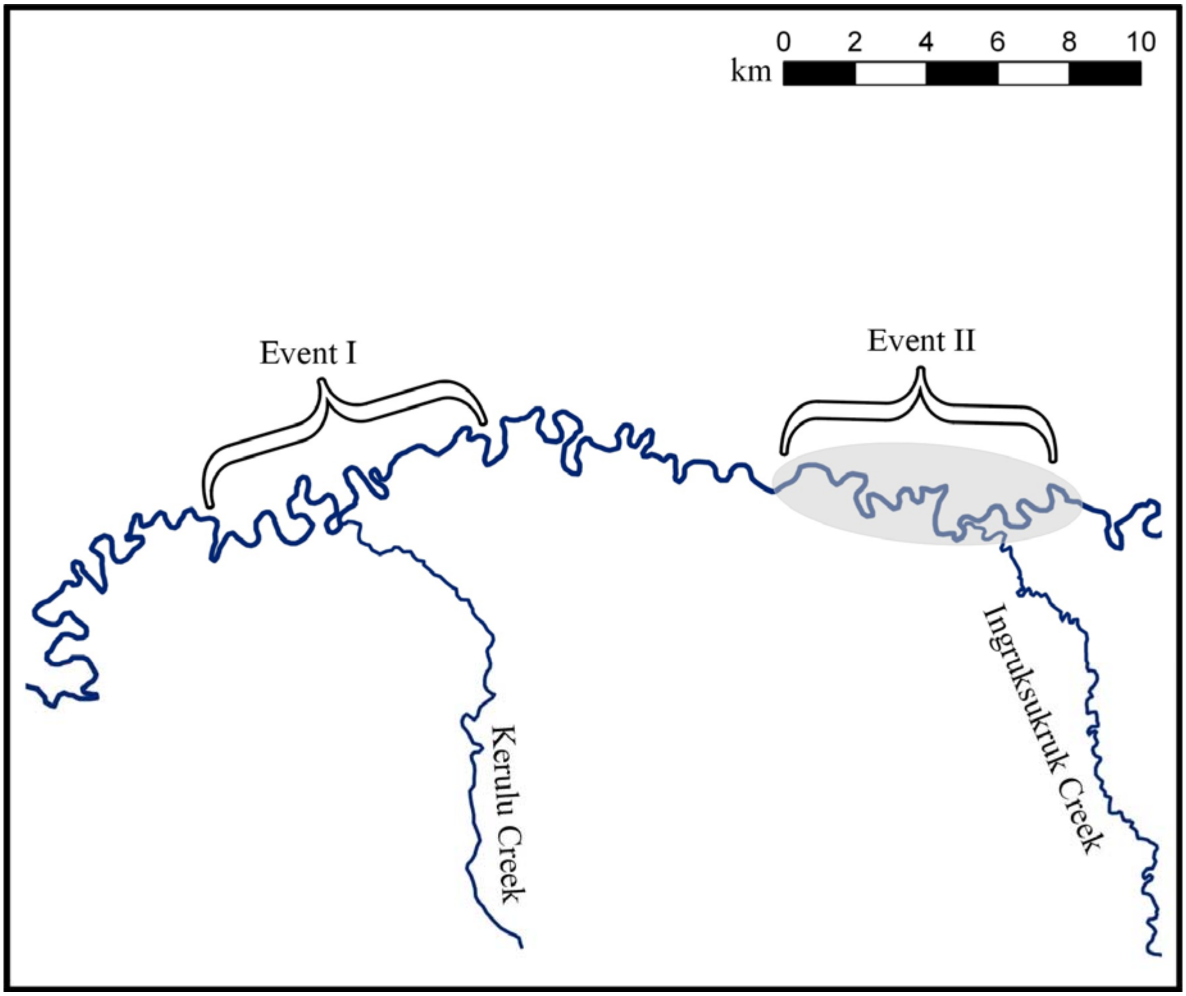

Figure 5. The locations of Events I and II in the upper Selawik River drainage during the inconnu spawning population abundance projects, and the major concentration region of radio-tagged inconnu during Event II, just prior to spawning time (shaded region).

Table 3. Selawik inconnu spawning population estimates $(\hat{N})$ and 95% CI's for the years 1995, 2004, and 2005. Included are the number of fish marked in Event I (n_1), the number of fish examined in Event II (n_2), the number of recaptured fish in Event II (m_2), and the accuracy of the estimate at the 95% level of confidence.

Year	n_1	n_2	m_2	$\hat{N}$	95% CI	$Accuracy(\hat{N})$
1995	546	372	33	5,990	4,098 – 7,882	32%
2004	441	1,018	18	23,652	13,383 – 33,920	43%
2005	627	1,255	16	46,324	25,069 – 67,580	46%

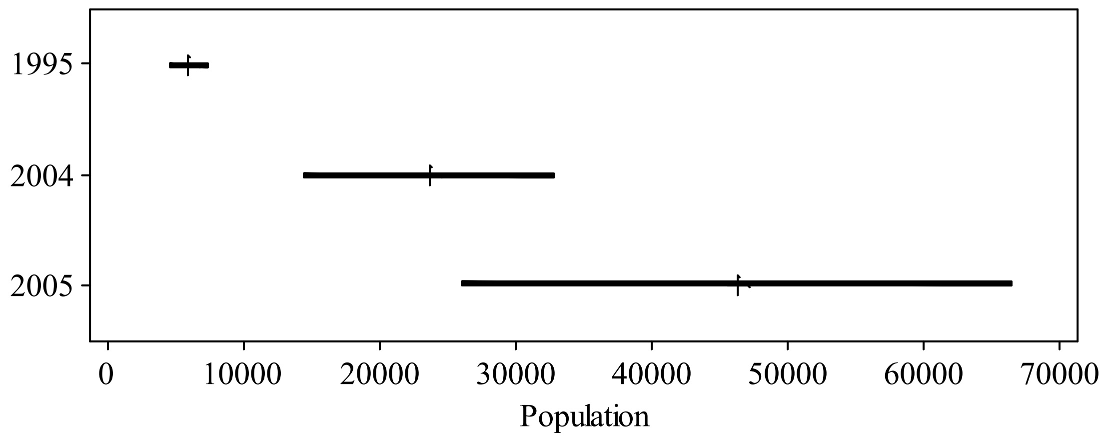

Figure 6. Spawning population estimates with 95% CI's for inconnu on the Selawik River in 1995, 2004, and 2005.

Length Composition and Sex Ratio

Length histograms of spawning inconnu from the Selawik River during 1995, 2004, and 2005 illustrated a dramatically reduced proportional representation of larger fish over the 10-year period (Figure 7). For example, in 1995 approximately 26.2% of all sampled fish were ≥100 cm, compared to about 1.3% in 2004 and 0.6% in 2005. Mean lengths of male (78.2 cm) and female (87.4 cm) inconnu, pooled respectively from 2004 and 2005, were significantly different (ANOVA, $P < 0.001$), with females averaging almost 10 cm longer than males. Male inconnu ranged in length from 59 to 100 cm, and females from 68 to 120 cm. The spawning population was dominated by male inconnu in both 2004 (79%) and 2005 (76%). The decline from 79% to 76% from 2004 to 2005 was numerically significant ($Z = 2.337$, $P = 0.019$), but given the small percentage difference and the possibility of sex classification errors (Brown 2000) it is not thought to be biologically significant. Length histograms from three inconnu spawning populations from which sex-specific length data were collected (Kobuk River data from Alt 1969; unpublished Yukon River data from R. Brown) illustrate that the smaller length classes were dominated by male inconnu, and the larger length classes were dominated by females (Figure 8). Length data from 1995, 2004, and 2005, and sex ratio data from 2004 and 2005 were used to allocate the respective population estimates into six, 10-cm length categories (Figure 9).

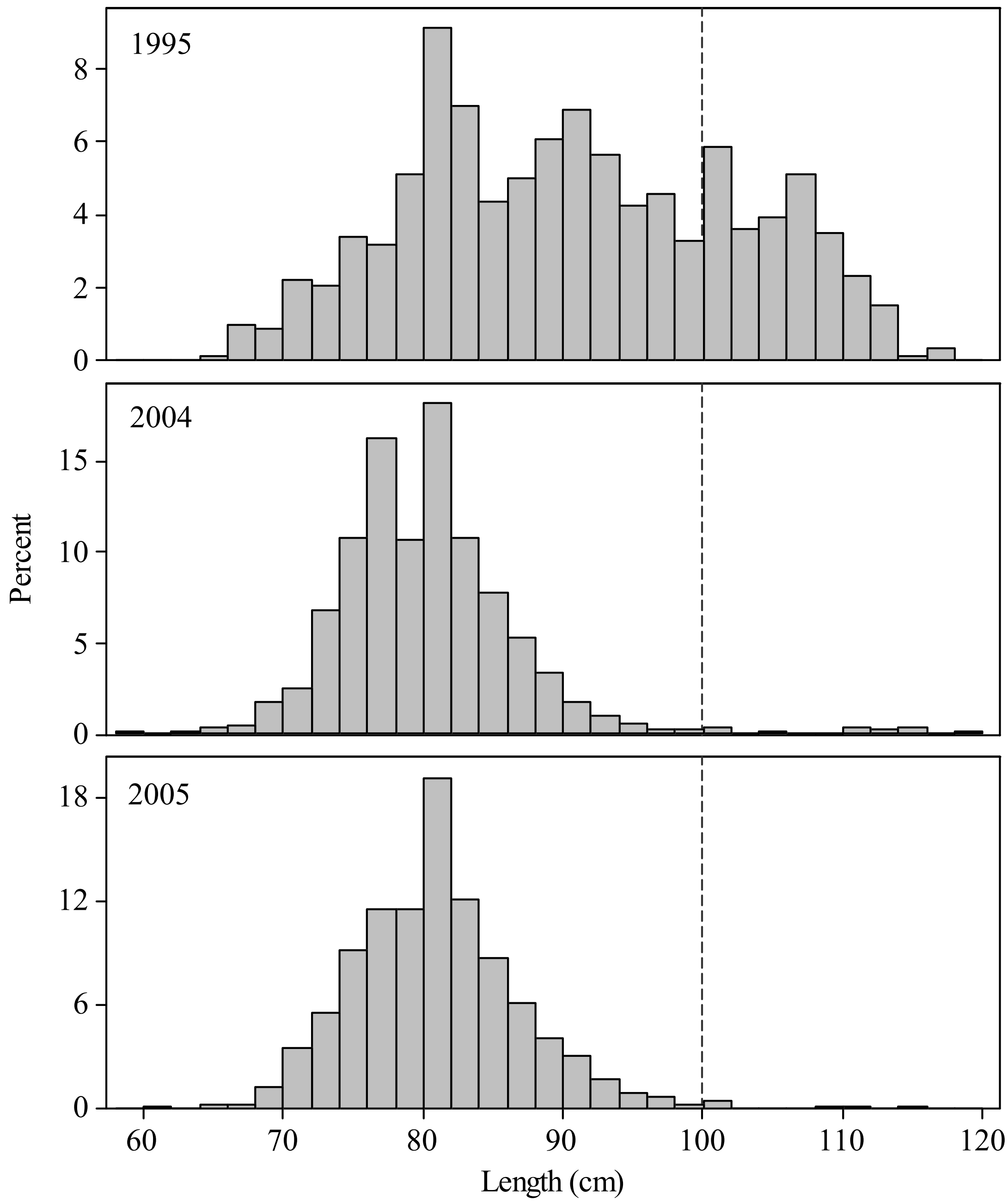

Figure 7. Length distributions of spawning inconnu from the Selawik River during 1995, 2004, and 2005, illustrating the reduced proportional representation of larger fish over the 10-year period. In 1995, for example, approximately 26.2% of all sampled fish were ≥100 cm (vertical dashed line), compared to about 1.3% in 2004, and 0.6% in 2005.

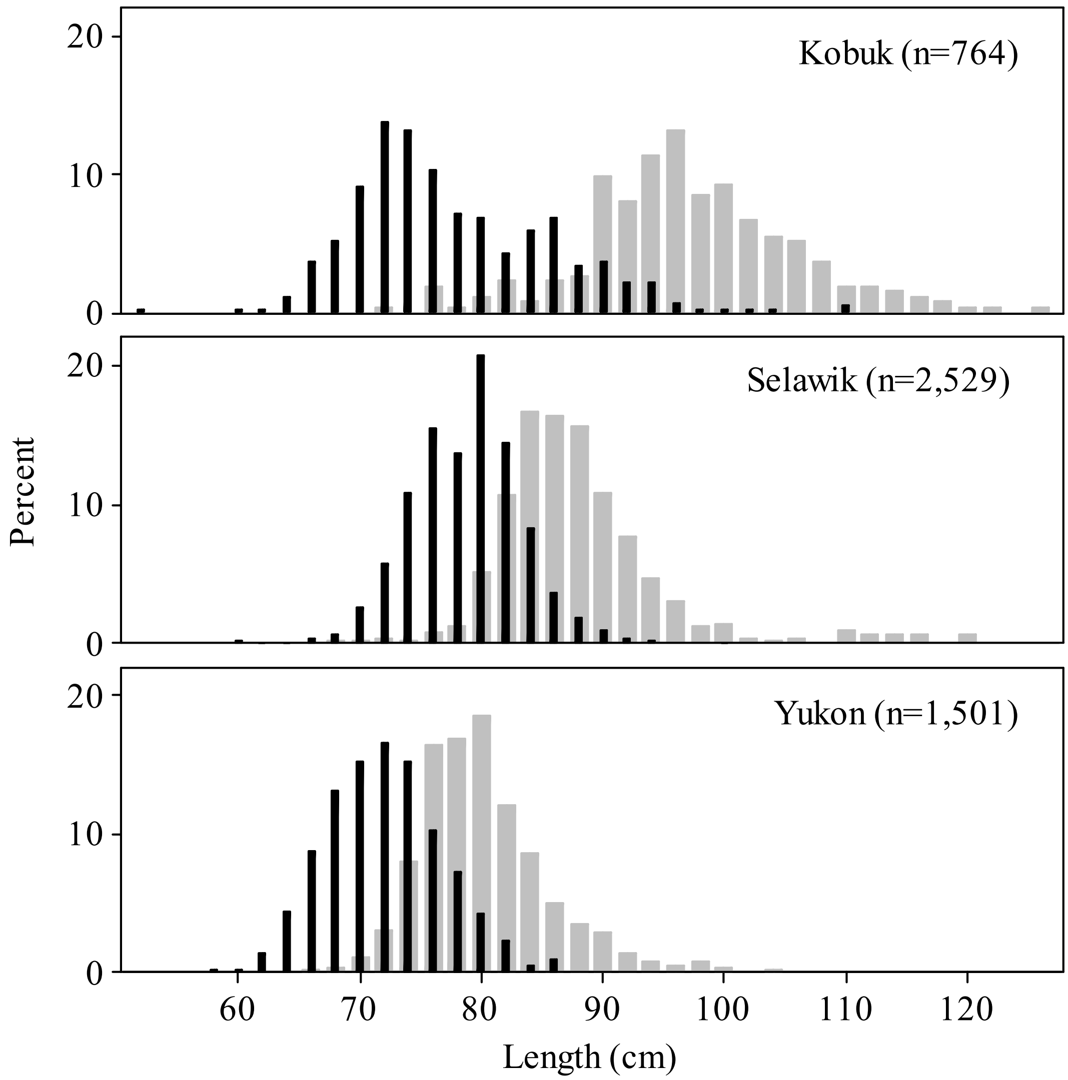

Figure 8. Length histograms of male (narrow, dark bars) and female (wide, light bars) inconnu from spawning populations on the Kobuk, Selawik, and Yukon rivers, illustrating the tendency for mature females to be larger than mature males.

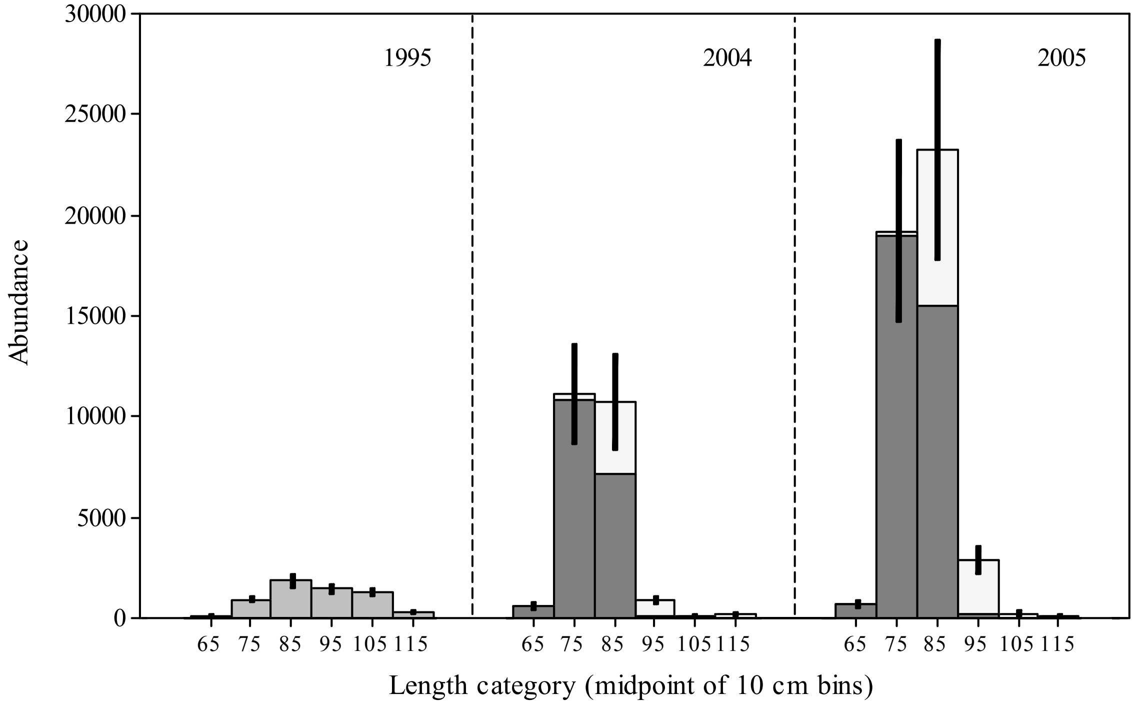

Figure 9. Length composition of the Selawik River inconnu spawning population based on sample length distributions and population estimates for 1995, 2004, and 2005. Length groups are indicated as midpoints of 10 cm bins. The relative abundance of male (dark bars) and female (light bars) inconnu within length classes is indicated for the years 2004 and 2005. Solid vertical lines indicate ±1 SE of respective length category estimates.

Estimates of Sequential-year Spawning

Twenty-six radio-tagged inconnu were present on the Selawik River spawning area during spawning season in 2005, and nine were again present in 2006. No radio-tagged fish were present during the June 2006 aerial survey, indicating that the nine inconnu present during spawning season 2006 had moved from the area in 2005 and returned again. Considering annual survival within the range of 0.60 to 0.90, from 16 to 23 of the original 26 radio-tagged fish were expected to be alive in 2006. Binomial probability curves suggested that spawning on sequential years would occur at a rate between 0.36 to 0.80 if annual survival were 0.60, and between 0.26 to 0.58 if annual survival were 0.90 (Figure 10).

During 2004, anchor tags were deployed on inconnu preparing to spawn in the upper Selawik River (n = 1,459), and a sub-sample of these fish were recaptured in 2005 (n = 40). Kolmogorov-Smirnov tests of the similarity of length distributions between 2004 marked fish during Event I, Event II, and Events I and II combined, with their respective recaptured groups in 2005 were all nonsignificant (P = 0.869, 0.794, and 0.526 respectively) (Figure 11). A Chi-squared test of differences in probabilities between the numbers of marked and recaptured inconnu from Events I (marked in 2004: 441, recaptured in 2005: 15) and II (marked in 2004: 1,018, recaptured in 2005: 25) respectively, was similarly nonsignificant (T_1 = 0.973, P = 0.324). These two tests of inequality are consistent with our assumption that the recaptured component was a random sample of the marked population. The proportion of inconnu in the population that spawn on sequential years based on these mark-recapture data were modeled across the range of the standard 95% confidence interval for the spawning population estimate in 2005 (Table 3) and annual survival rates ranging from 0.60 to 0.90 (Figure 12). Based on this approach, it was estimated that Selawik River inconnu spawn during sequential years at a rate somewhere between 0.40 and 1.00. High population levels and low annual survival produced sequential-year spawning rates in excess of 1.00, an impossible situation. It is likely that sequential-year spawning rates lie in the intersection of the ranges of rates determined directly with radiotelemetry and with the mark-recapture model, between 0.40 and 0.80 (Figure 13). The likelihood of environmental and sex-related effects on spawning frequency would probably result in variable annual rates of sequential-year spawning.

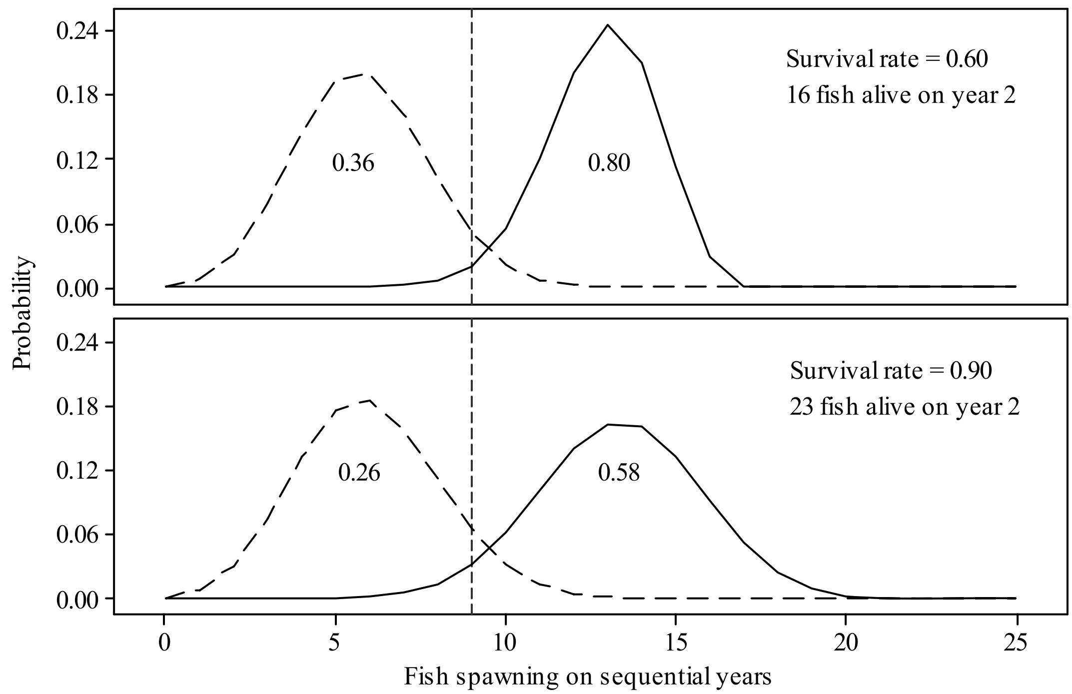

Figure 10. Binomial probability curves illustrating the range of likely rates of occurrence of sequential-year spawning at two levels of annual survival given the observation of nine radio-tagged fish (center line) on the spawning area on two sequential years.

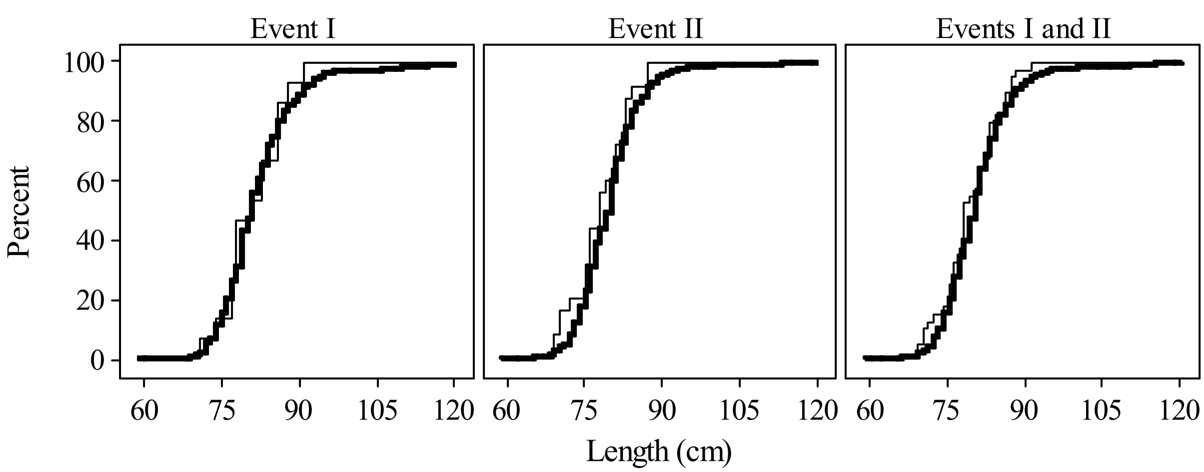

Figure 11. Cumulative length distributions of inconnu marked during 2004 during Event I, Event II, and Events I and II combined (heavy lines), and their respective recaptured groups during 2005 (light lines). Kolmogorov-Smirnov tests indicated that all three pairs of length data were similarly distributed (*P* = 0.869, 0.794, and 0.526 respectively).

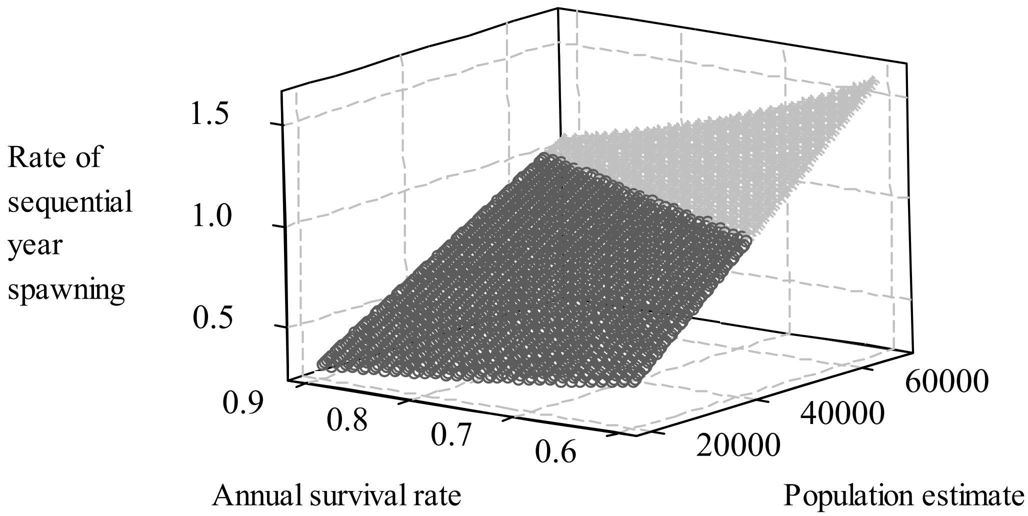

Figure 12. Three dimensional plot illustrating the influence of annual survival rate and the inconnu spawning population estimate on estimates of the rate of sequential-year spawning based on recaptures of tagged fish from 2004 in 2005. The lighter region of the surface represents combinations of population estimates and annual survival rates that result in rates of sequential-year spawning that are >1.0, which are not possible.

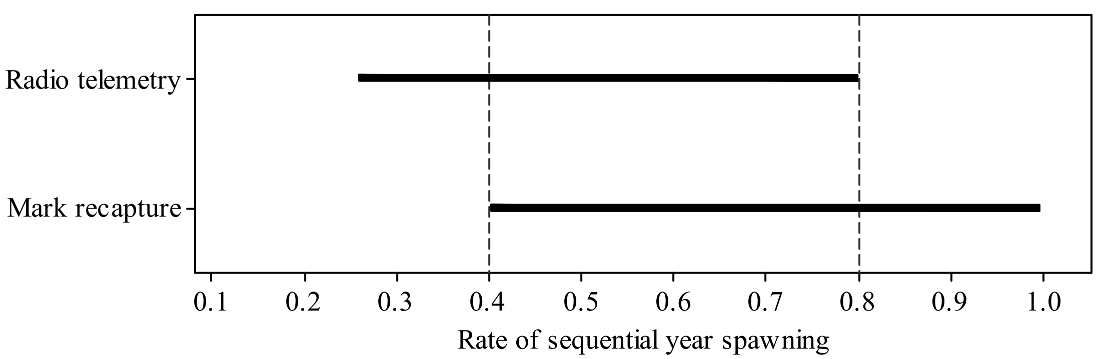

Figure 13. Ranges of possible rates of sequential-year spawning based on radiotelemetry and mark-recapture data. It may be that the actual rate lies somewhere within the intersection of these two ranges, between 0.40 and 0.80.

Discussion

Spawning Population Estimates

The Selawik River inconnu spawning population estimates during 2004 and 2005 represented a significant increase relative to 1995 levels (Table 3; Figure 6). These estimates are similar to those of the Kobuk River during the mid 1990s (Taube and Wuttig 1998), which was always thought to maintain the largest share of the regional inconnu population. It is not known if the Kobuk River spawning population has experienced a similar increase. DeCicco (2006) suggested that inconnu populations may be subject to episodic recruitment events, probably influenced by environmental conditions. The increase in the spawning population along with the strong observed shift in length distribution towards smaller fish (Figure 7), are consistent with this suggestion.

Management

A combination of harvest management, stock assessment, and habitat protection are thought to be the best way to assure long-term preservation of the Kotzebue region inconnu stocks. Mature and immature fish from the Kobuk and Selawik River spawning populations are harvested in the Selawik Lake and Hotham Inlet fisheries, which take place during all seasons of the year (Alt 1969; Taube 1997; Underwood et al. 1998; Savereide 2002). Kohler et al. (2005) suggested that the mixed stock and demographic nature of the fishery in the region made inconnu stocks vulnerable to overharvest. Current fishery management consists of a commercial harvest quota of 11,340 kg of inconnu, a sport fishing limit of 10 inconnu per day in the region (except for the upper Kobuk and Selawik rivers, where the limit is 2 inconnu per day), and subsistence harvest is unrestricted, although, there are net length and mesh size restrictions. This management strategy appears to be conservative given the observed increase in the Selawik River inconnu spawning population.

The majority of the regional annual inconnu harvest comes from the winter mixed stock fishery with no current means to determine individual stock contributions. The preliminary genetics work of Miller et al. (1998) suggested that mixed stock analysis could be used to clarify the geographic distribution of the two stocks in the region and estimate their respective contributions to the fisheries. The spawning area in the upper Selawik River has been geographically defined with radio telemetry and the habitat will be protected from human disturbance as directed by the U.S. Congress in the ANILCA (USFWS 1993). The spawning area in the upper Kobuk River has been generally defined with sampling (Alt 1969; Taube 1996, 1997; Taube and Wuttig 1998) and will be more clearly defined during the next few years during a planned radio telemetry project with spawning inconnu in that drainage. Presumably that habitat can then be specifically protected as well. Regional harvest assessments together with estimates or indices of spawning abundances and recruitment levels would be valuable as well, although, economical methods to obtain these data on an annual basis have not been developed yet.

A permafrost thaw slump located approximately 50 km upstream from the inconnu spawning area began to emit large amounts of silt into the river in the spring of 2004 (Figure 2; Hander and Olson 2007). The slump continues to erode during the open water season and it is likely to continue for an unknown period of time. The slump could potentially impact the spawning success of Selawik River inconnu by clogging interstitial spaces in the gravel and cobble substrate where fertilized eggs are thought to settle and develop through the winter (Waters 1995). Physical habitat requirements for inconnu egg development have not been studied, but, a change in substrate type is likely to change egg development and survival rates. Any impact to Selawik River inconnu population may not be known until those cohorts reach maturity and return to spawn, at about 8 to 12 years of age (Brown 2000; Howland 1997). It is recommended that the thaw slump be monitored and its impact on the Selawik River inconnu spawning population be studied.

Length Distribution

Length composition analyses between 1995, and 2004 and 2005, showed a dramatic proportional increase of the smaller length classes that were composed primarily of males. These smaller fish account for the major portion of the current spawning population. Other researchers working in the Selawik and Kobuk rivers have not encountered length distributions that indicated such a disproportionate number of smaller fish (Alt 1969, 1987; Taube 1996, 1997; Taube and Wuttig 1998; Underwood 2000), suggesting that we witnessed a significant event. Male inconnu mature earlier than females (Alt 1969; Brown 2000). If the population expansion was due primarily to early maturing males (Figure 9), then the spawning population should continue increasing as the female component of the burgeoning young population recruit to the spawning population over the next few years. Female inconnu grow larger than males (Figure 8) and should eventually increase the proportion of larger fish that are currently overshadowed by the apparent influx of smaller length classes. If the spawning population was sampled for length and sex every year for the next few years, we predict that the sex ratio would become closer to parity, and the length distribution would swell towards the larger length classes with a relative moderation of the smaller length classes, becoming more similar to the length distribution observed in 1995 (Figure 7). Monitoring length distribution information will be important for future management to help determine proportional contributions of spawning male and female inconnu.

Spawning Frequency

It was apparent that sequential-year spawning was occurring at a greater rate than observed in other studies from the Selawik and Kobuk Rivers. It was assumed that the spawning frequency of inconnu, and other coregonid species, is two or more years (Scott and Crossman 1973; Reist and Bond 1988). The “skip-spawning” concept came from both sampling and energetics perspectives. Fall season observations of individuals that were of a size or age indicating maturity, but were not preparing to spawn, have demonstrated that at least some mature individuals do not spawn every year (Alt 1969; Moulton et al. 1997; Brown 2004). Representative sampling of entire populations to estimate the spawning fraction of the mature component directly have not been conducted in open systems, largely because coregonid populations disperse over large geographic regions and demographic groups segregate into different habitats (Reist and Bond 1988). Lambert and Dodson (1990) studied the energetic costs of freshwater migration of two anadromous coregonid species and concluded that those species could not accumulate enough energy over the course of a year to support spawning on an annual basis. However, various sampling and mark-recapture data with coregonid species suggest that sequential-year spawning occurs at an unknown rate for many species, including inconnu. Hallberg (1989), for example, documented numerous tagged humpback whitefish *Coregonus pidschian* and least cisco *Coregonus sardinella* on the Chatanika River spawning area during two successive spawning seasons. Brown (2006), used radiotelemetry to estimate a sequential-year spawning rate of 0.71 (95% CI: 0.64 to 0.77) for mature humpback whitefish in the upper Tanana River in Alaska. Underwood (2000) documented recaptures of many tagged inconnu in the upper Selawik River a year following tagging, leading him to speculate that some level of sequential-year spawning was occurring. Similarly, Taube and Wuttig (1998) reported recaptures of tagged inconnu in the upper Kobuk River a year following tagging and estimated that approximately 9.6% of the spawning population in 1997 was also present in 1996. This represented a sequential-year spawning rate, by simple ratio calculation, of about 0.08. Our estimates of 0.40 to 0.80 (Figure 13) are comparable to those reported by Brown (2006) for humpback whitefish. While these data demonstrate that significant sequential-year spawning is occurring, annual and sex-specific variability must be better understood before they are routinely applied to monitoring or management efforts.

Accuracy

The initial goal of this project was to estimate the Selawik River inconnu spawning population during 2004 and 2005 within 25% of the real value 95% of the time. To achieve this level of accuracy and precision, a level that Seber (2002) contends is appropriate for accurate management applications, requires the examination of sufficient numbers of fish during Events I and II combined, and this number varies according to the number of fish in the population. Robson and Regier (1964) developed formulae and tables designed so that researchers could quickly determine appropriate combinations of n_1 and n_2 for their purposes. Population levels, however, are unknown prior to project operations, so one uses the best information available to predict the number of fish likely to be present. In this case, we considered it probable that the population could approach or exceed the upper bounds of the confidence interval of the previous work (Underwood 2000) and used 10,000 fish as a possible number. Our point estimates during 2004 and 2005 were substantially greater than this, making our sampling and tagging efforts insufficient to achieve the desired level of accuracy. To achieve the desired level of accuracy given the estimated population levels in 2004 and 2005, would have required total annual samples ($n_1 + n_2$) of approximately 2,800 and 3,000 respectively. Our estimates were within 50% of the real value at a 95% confidence level (Table 3), which Seber (2002) contends is adequate when a rough idea of population size is needed. The consequence of reduced accuracy, however, is that differences between population levels must be very large to detect (Figure 6), as was illustrated by our inability to confidently state that the spawning populations in 2004 and 2005 were statistically different.

Acknowledgements

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Appendix A. *Two-event mark-recapture assumptions for use with the Bailey estimator.*

Seber (2002) listed six assumptions that must be true, in whole or in part, for a Petersen type mark-recapture population estimate to be valid. We believe these assumptions were met in 1995, 2004, and 2005. Following is a discussion related to each of the assumptions and the evidence and logic that were used to justify their acceptance.

1. It was assumed that the population was closed. Because we were interested in a specific demographic group within the population, mature spawners, we either had to recognize the spawning component among spawning and nonspawning components, which was not considered possible, or design the sampling events so only the spawning component was available. Based on maturity sampling conducted by Alt (1969), Howland (1997), and Brown (2000) on other spawning populations, it was thought that the spawning component was the only demographic group present in the upper Selawik River drainage during Events I and II. All lines of evidence we have examined in this study; the radiotelemetry work, our failure to identify any temporal influence on recapture probabilities during early and late seasons of Events I and II (Table 2), and the overall similarity of length distributions between Events I and II (Figures 3 and 4), support the maturity sampling work and were consistent with this assumption being true.

2. It was assumed that all fish had the same probability of capture during Event I, had an equal probability of capture during Event II, or marked and unmarked fish mixed completely between Events I and II (Seber 2002). Because Event I occurred downstream from the spawning area where Event II took place, and the locations of radio-tagged fish during Event II indicated that the population was present in the spawning area at that time, the spawning population must have migrated through the area where Event I took place. A small number of fish may have migrated through prior to Event I, and some may have migrated through after Event I. The capture, lack of temporal effects on recapture probabilities (Table 2), length distribution similarities between Events I and II (Figures 3 and 4), and radiotelemetry data (Figure 5) were all consistent with meeting at least one of the conditions of this assumption.

3. It was assumed that marking did not affect the subsequent catchability of fish. Because the capture methods were different between Events I and II, capture during Event I was not thought to induce any capture-happy or capture-shy behavior during Event II (Seber 2002). The similarity of length distributions between the marked and recaptured populations (Figure 3) argue against any systematic length or sex related effect of capture on the probability of recapture. These data were consistent with meeting this assumption.

4. It was assumed that fish examined during Event II were a simple random sample of all fish present. This assumption was difficult to test directly, but the statistical similarity of length distributions among marked and recaptured fish during 2004 and 2005 (Figure 3) suggest that the recaptured components of Event II were random samples of their respective marked components from Event I. It is thought that if the length distributions of the recaptured fish in Event II were consistent with random sampling from their population, then it is likely that the examined fish during Event II would be a random sample of all fish present. In the absence of any contrary evidence, it is thought that the conditions of this assumption were met.

5. It was assumed that marked inconnu did not lose their marks between Events I and II. All marked fish during 2004 and 2005 received a primary mark consisting of an anchor tag near the dorsal fin and a secondary mark consisting of a distinctive pelvic fin clip. All fish captured were examined for primary and secondary marks. The time interval between Events I and II was

relatively small, so healing or scarring of secondary marks such that they could not be identified was not possible. No evidence of tag loss was observed between Events I and II for either year, which is consistent with meeting the conditions of this assumption.

6. It was assumed that all fish with marks that were captured during Event II were recognized as such and reported. The capture, handling, and data recording procedures during the project involved three people during every capture event. Two people handled the fish in a cradle, observed the fish for marks, reported tag numbers, applied a second secondary mark when previously tagged fish were captured, measured the length, judged the sex, and applied new primary and secondary marks to fish that were not previously tagged. A third person recorded the event in writing. It was thought to be an extremely unlikely event that all three people involved would miss the occurrence of a marked fish. This assumption was therefore considered to be true.