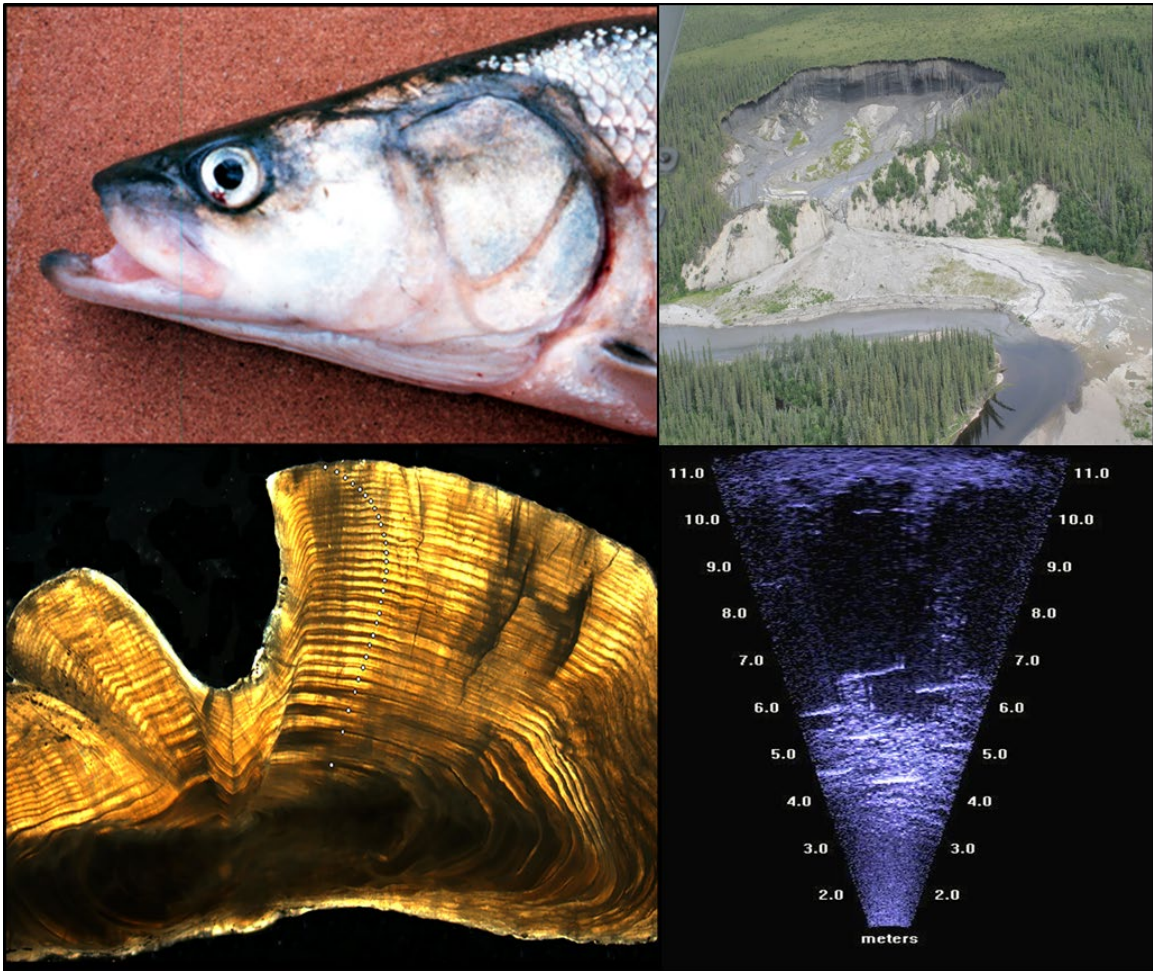


Selawik River Inconnu Age Structure Evaluation and Spawning Population Abundance, Selawik National Wildlife Refuge

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Cover photos are of an Inconnu (top left) with the distinctive protruding lower jaw, the Selawik River permafrost thaw slump in 2009 (top right), an Inconnu otolith section with white dots indicating age increments (bottom left), and a computer screen capture of Inconnu passing from right to left through the ensonified area of the dual frequency identification sonar.

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Selawik River Inconnu Age Structure Evaluation and Spawning Population Abundance, Selawik National Wildlife Refuge

Raymond F. Hander, Randy J. Brown, and William K. Carter, III

Abstract

In 2004 a large permafrost thaw slump began emitting substantial volumes of fine sediment into the Selawik River upstream from the Inconnu *Stenodus leucichthys* spawning area. Following this event, the once clear-flowing river ran turbid for about nine summers before the thaw slump stabilized and ceased emitting sediment. To determine if sediment input had a negative effect on egg survival and subsequent recruitment, we investigated: 1) age structure to identify the strength of cohorts from years before and after the thaw slump started; and 2) documented annual abundance of spawning inconnu to provide corroborative evidence of potential recruitment failure. For comparison, we obtained similar age structure data from Inconnu preparing to spawn in the Kobuk River, a neighboring drainage without a thaw slump. From 2011 to 2018, otoliths (aging), fork length, and weight samples were collected from 200 spawning Inconnu from the Selawik River. A similar but more variable number of samples were collected from Kobuk River Inconnu. Mean fork lengths of males in the Selawik River were greater than in the Kobuk River for most years, but males in the Kobuk River were heavier at a given length than in the Selawik River. Growth and length at age, was identical for the two populations. Mature Inconnu ages ranged from 9 to 34 in the Selawik River and 8 to 40 in the Kobuk River. Age histograms for both populations indicated variation in recruitment patterns. For both populations, intermittent periods of high recruitment were followed by periods of low recruitment. A large recruitment event occurred synchronously for both populations from 2015 to 2018. Abundance of spawning Inconnu in the Selawik River ranged from about 16,000 to 25,000 during the study but no correlation between abundance and recruitment was detected. During 2018, recruitment to the Selawik River spawning population was possible from up to five cohorts from years in which the slump was active, ages 9–13. Only the age-12 and 13 cohorts, spawned in 2005 and 2004, respectively, were represented from the Selawik River, albeit weakly. Ages 11–13 were more strongly represented from the Kobuk River. Because these cohorts from the thaw slump time period were in the early region of the ascending limb of the recruitment curve, the data did not establish that the thaw slump has affected recruitment. A subsequent age collection is recommended in 5 years to confirm this finding.

Introduction

Inconnu (Sheefish) *Stenodus leucichthys* is a large, long-lived, iteroparous, coregonid fish found in several Arctic and sub-Arctic waters of Asia and North America (McPhail and Lindsey 1970; Scott and Crossman 1973). In the Kotzebue Sound region of northwest Alaska, two spawning populations have been identified, one in the upper Kobuk River (Alt 1969) and the other in the

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upper Selawik River within the Selawik National Wildlife Refuge (Refuge; Underwood 2000; Figure 1). The United States Congress identified Inconnu as a species of special interest in the Refuge, which was established in the Alaska National Interest Lands Conservation Act (ANILCA; USFWS 1993). In ANILCA, Congress mandated that Inconnu be maintained in their natural diversity and that opportunities for subsistence use continue. Inconnu is one of the most important food fishes in the Kotzebue region where 20,000 or more are harvested each year in subsistence, sport, and commercial fisheries (Georgette and Loon 1990; Taube and Wuttig 1998; Savereide 2002; Braem et al. 2018).

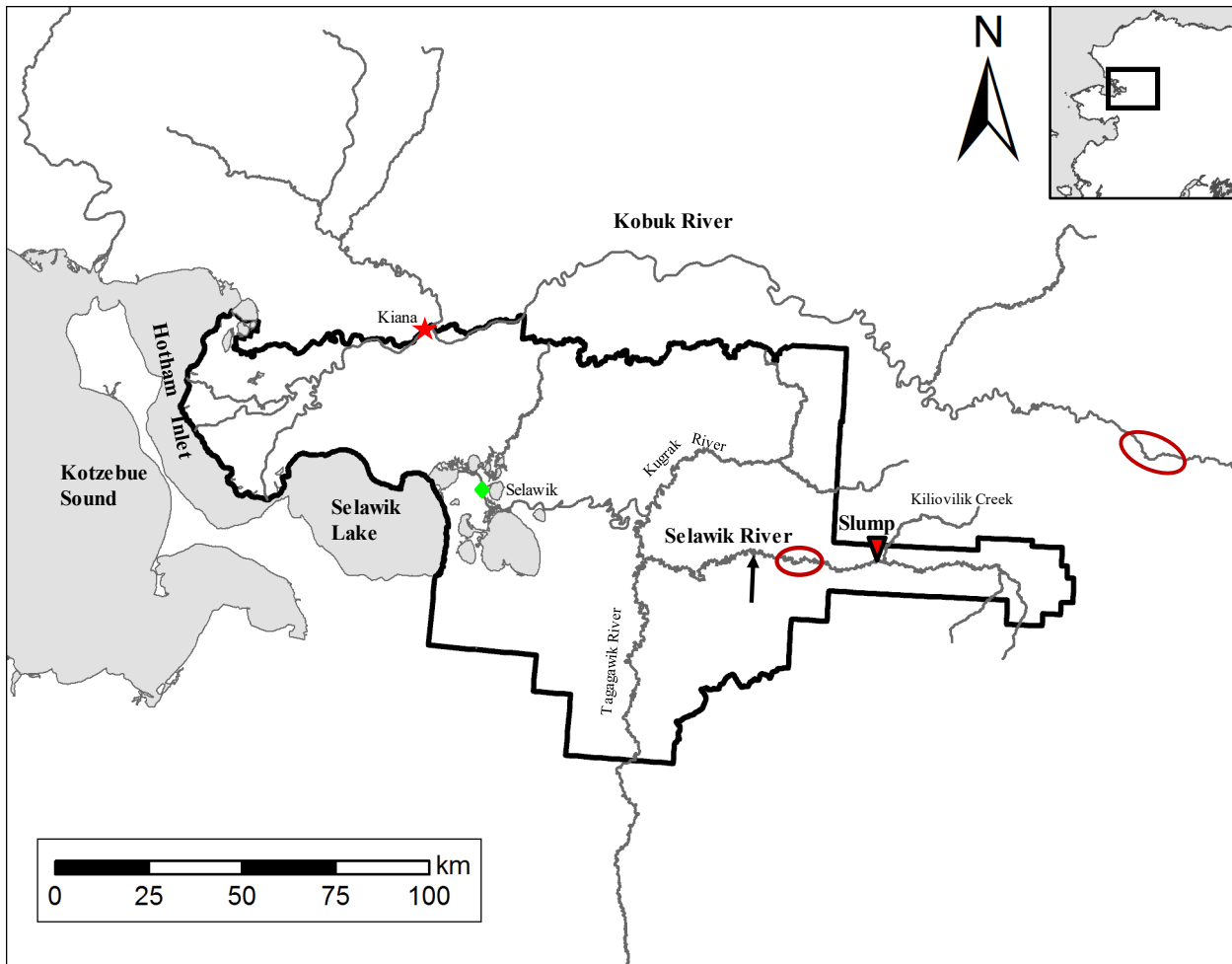


Figure 1.—Inconnu habitat in eastern Kotzebue Sound with major features indicated. The Selawik National Wildlife Refuge is outlined in bold with the Selawik community at the green diamond. The locations of the Selawik and Kobuk River Inconnu spawning areas are indicated with the red ellipses, the permafrost thaw slump is indicated with the red triangle near the mouth of Kiliovilik Creek, and the black arrow points out the sonar site. The red star locates Kiana, which is near the ADF&G Chum Salmon test fishery site where Kobuk River Inconnu samples originate.

Inconnu from the Kobuk and Selawik River populations in northwest Alaska live their entire life-cycle within those rivers and the associated estuary in eastern Kotzebue Sound, including Hotham Inlet and Selawik Lake. Mature Inconnu preparing to spawn begin a slow migration up either the Kobuk River or Selawik River in early to mid-summer, initially feeding in the lower reaches with non-spawning fish and arriving at spawning areas by late summer or fall (Alt 1969; Underwood 2000). Non-spawning adults and immature Inconnu remain in the lower reaches of the rivers and estuary systems. By early September, Inconnu complete their migration to

upstream spawning areas, where they remain until late September to early October when spawning takes place. Eggs are broadcast over gravel and cobble substrate (Alt 1969; Gerken 2009). The fertilized eggs are non-adhesive and negatively buoyant, so they drift downstream and settle into the interstitial spaces in the substrate where they incubate through the winter (Teletchea et al. 2009). Following spawning, adult Inconnu migrate downstream to the estuary to overwinter (Underwood 2000; Savereide and Huang 2016). Eggs are thought to hatch in the late winter or spring and larvae are then carried downstream to lake and estuary rearing areas during the spring runoff (Shestakov 1991; Bogdanov et al. 1992; Naesje et al. 1995). Thus, the two Inconnu populations in northwest Alaska share rearing, overwintering, and feeding habitats while using the unique habitat qualities of their respective natal drainages for spawning and egg development.

During the summer of 2004, a large retrogressive permafrost thaw slump (slump) began emitting fine sediment into the Selawik River approximately 50 rkm upstream from the only known Inconnu spawning area (Figure 1; Underwood 2000; Hander et al. 2008). Previous to 2004, the Selawik River flowed clear through the spawning area, a 12 rkm reach of gravel and cobble substrate (Underwood 2000). From approximately 2004 to 2011 the Selawik River flowed turbid through the spawning area during the summer months and at times the gravel bars in the spawning area became layered in fine sediment and mud. As of 2012, more than 580,000 m³ of sediment had thawed with approximately two-thirds of that volume mobilized into the Selawik River (Jensen et al. 2014). Over the summers of 2009–2011, measured turbidity at the slump outflow averaged 34 times greater than a reference site upstream from the slump, and turbidity near the Inconnu spawning area was about 11 times greater than at the reference site (Calhoun 2012). Turbid water conditions have been observed at the mouth of the Tagagawik River, 150 rkm downstream from the slump (Figure 2), but were rarely observed in the lower Selawik River, 100 rkm farther downstream. From these observations we can deduce that the sediment released by the slump has been progressively and steadily deposited onto the riverbed. A September 2016 site visit to the slump and 2018 aerial images revealed that it has stabilized and its floor and deposition fan have been almost completely vegetated with grasses and shrubs (Figure 3). Sediment emission from the slump now appears to be negligible although during heavy rain or high discharge sediment may erode into the Selawik River from the toe of the deposition fan.



Figure 2.—Aerial views of the permafrost thaw slump in the upper Selawik River drainage and its erosion progression 2004–2012 (left image), and at the confluence of the Selawik and Tagagawik rivers in 2006 (right image), approximately 150 rkm downstream from the slump, illustrating the persistence of the turbid flow.

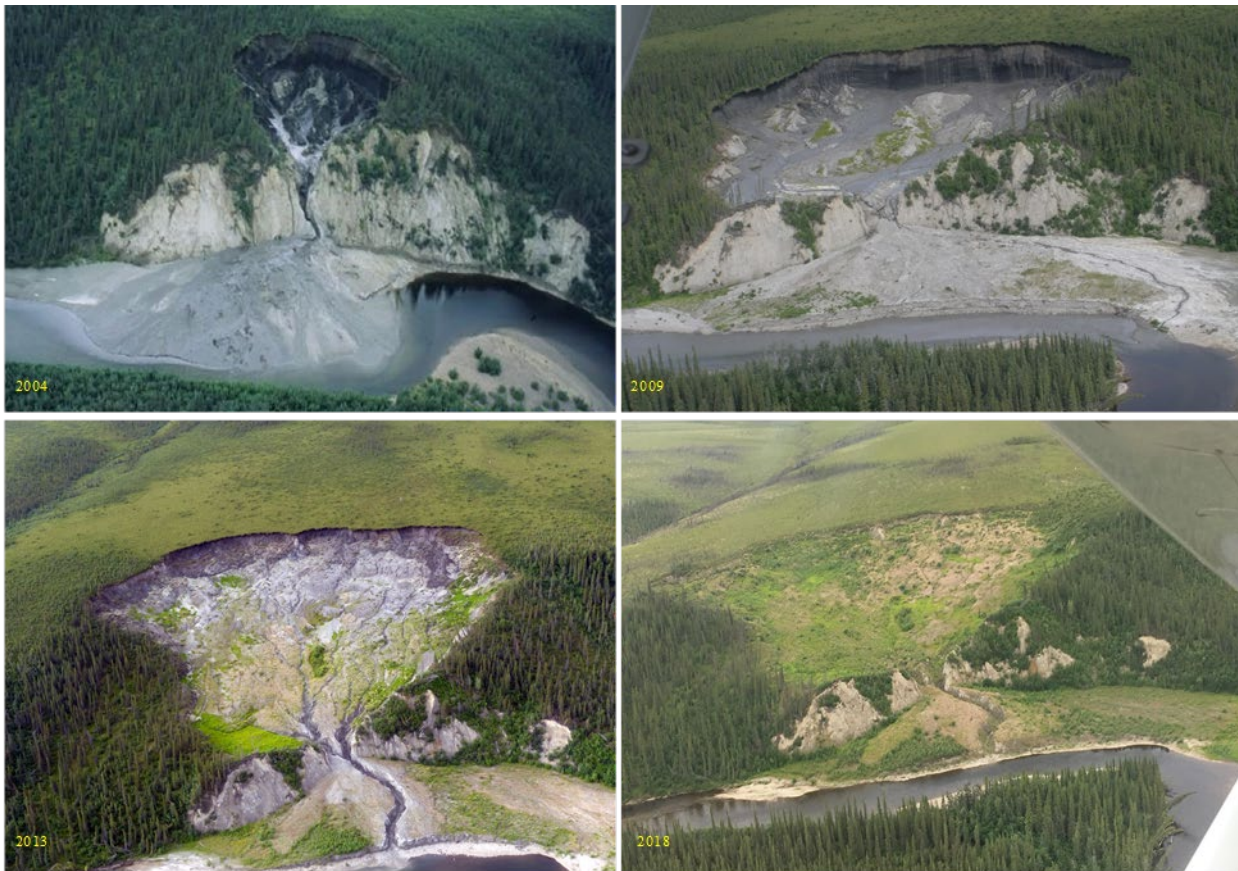


Figure 3.—Aerial views of the permafrost thaw slump's growth and maturation. Note the gradual loss of the headwall height (slump's vertical perimeter wall), the onset of vegetation by 2009 and subsequent reduction of thaw related discharge from the slump by 2018.

It is well documented that turbidity, whether human or natural caused, and the associated sedimentation of stream bottoms have had profound negative effects on stream spawning fishes (Waters 1995; Wood and Armitage 1997; Birtwell 1999). Stream sedimentation can have three basic effects on spawning habitat: 1) sediments can penetrate gravel substrates and restrict interstitial flow; 2) it can fill the substrate's interstitial spaces and change it to a smooth rather than rough surface; and 3) it can cover eggs that settle into interstitial spaces (Chapman 1988; Birtwell 1999). Chapman (1988) provided a comprehensive review of the effects of sedimentation on salmonid egg development and explained that there was an inverse relationship between fine sediment concentrations and interstitial flow. Reducing interstitial flow reduces dissolved oxygen levels available to eggs, and leads to reduced egg survival. For example, Birtwell (1999) reported that survival of Chinook Salmon *Oncorhynchus tshawytscha* eggs declined from about 90% to <35% when fine sediment concentrations in the substrate increased from 10% to 40%. Fudge and Bodaly (1984) investigated egg survival in Lake Whitefish *Coregonus clupeaformis* spawning habitats that were experiencing elevated sediment deposition and found more than 10 times greater survival in control samples than in samples from habitats experiencing sedimentation. They contended that direct exposure to flowing or upwelling water was required to facilitate egg respiration. When the eggs were covered by fine sediment or when interstitial flow was reduced, egg survival declined dramatically (Fudge and Bodaly 1984).

We observed that sediment input from the slump was reduced once freezing temperatures prevailed in the fall when spawning occurred and suspect that eggs are not being covered by sediment. However, given the magnitude of sediment input from the slump (Figure 2), it is almost certain that there was sediment deposition in porous substrate restricting interstitial flow.

A change to smoother substrate from sedimentation causes eggs to be carried to suboptimal habitats that may put them at greater risk to predation.

Gravel and cobble substrate provides protection for eggs against predation by other fishes, which can be substantial (Hart 1930; Alt 1969; Letichevskiy 1981). Based on observations of exposed gravel bars in the spawning area it is likely that the substrate within the Selawik River became smoother as more sediment filled the cracks and crevices. This would have reduced its capacity to hold and shelter eggs. Inconnu are broadcast spawners and do not prepare redds for egg deposition, hence they have no mechanism to clean the substrate of sediments. We therefore believe that a change to smoother substrate is the mechanism most likely to reduce egg survival in the Selawik River.

We predicted that if egg survival was dramatically reduced because of sedimentation of the spawning substrate, then there would be a proportional reduction or elimination of recruitment for affected age classes relative to unaffected age classes and a subsequent reduction in spawning population abundance. There could be two basic sources of recruitment failure; one caused by a failure of egg development on the spawning area, which should affect only the Selawik River Inconnu population, and the other from environmental or predation affects in the shared rearing and overwintering habitat, which would affect both the Selawik and Kobuk River Inconnu populations (Smith et al. 2015). Multiple years of age distribution data were used to test the null hypothesis that there was no difference in recruitment of Selawik River Inconnu to the spawning population for cohorts that were spawned pre- and post-slump, versus the alternative hypothesis that there was a significant decline in recruitment for cohorts spawned after the start of the slump.

If a recruitment failure were unique to the Selawik River population, it would indicate a problem on the Selawik River spawning area. If recruitment failure occurred on a single cohort only, it would be unlikely to have been caused by sedimentation of the spawning gravel. Because Inconnu are considered to be age-0 during their first summer, an age-10 fish would come from a brood year that spawned 11 years previously (see Appendix Table A.1). If egg development failed in 2004, the first year of the slump, recruitment failure should be noticed in the 2015 season for individuals maturing at age-10. If sedimentation of the spawning gravel were more gradual and the effects on egg development less complete, recruitment failure or decline would take longer to detect. A simultaneous decline in spawning population abundance would distinguish between a partial recruitment failure and a sampling anomaly. Age distribution data obtained prior to 2015 would establish an unaffected (pre-2004 cohort) baseline.

The primary objectives of our study were to: 1) collect age structure data from male Inconnu from the Selawik and Kobuk River spawning populations 2011–2018; 2) identify recruitment events based on a series of non-parametric statistical tests of annual age distribution samples; 3) determine the spawning population abundance of Selawik River Inconnu in 2011–2018; and 4) infer a slump effect or no slump effect based on results of age structure tests and spawning population abundance data.

Study Area

The Selawik River drainage lies primarily within the Refuge in northwest Alaska. The main stem of the river flows from east to west along or adjacent to the latitude line of the Arctic Circle (Latitude 66.5569°) through a wide tundra valley for approximately 300 rkm, 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 Refuge experiences a maritime climate during the ice-free periods of the year (late May to early October) and transitions to more of a continental climate during the winter months (Shulski and Wendler 2007). Average high temperatures during mid-summer are about 15°C and average low temperatures during mid-winter are about -23°C. The average annual precipitation is approximately 25 cm. The Refuge is located in a discontinuous permafrost zone in the Selawik and Kobuk River watersheds (Jorgenson et al. 2008) with permafrost overlain by subarctic tundra vegetation or taiga occupying the majority of the area (USFWS 2011).

Sampling for this study was conducted on the Selawik River upstream from the Tagagawik River (Figure 1). The river in this area meanders through the valley in a series of pools and runs with an abundance of woody debris. The Inconnu spawning area where fish sampling took place was in the vicinity of Ingruksukruk Creek (Figure 1; Underwood 2000) and the substrate there was primarily gravel and cobble. A dual-frequency identification sonar (DIDSON) was operated downstream from the spawning area where the substrate was primarily gravel and sand (Figure 1).

Methods

Overview

This project involved several components that together established a baseline of indicators of possible impacts of the Selawik River slump on egg survival and eventual recruitment to the Inconnu spawning population. First, we collected a series of annual age, length, and weight data from spawning Inconnu from both spawning populations. The Kobuk River population served as an unaffected paired sample for comparison, so we compared body condition (i.e., weight at length; Pope and Kruse 2007) and growth (i.e., length at age, Isely and Grabowski 2007) from the two populations to support this assumption. Second, we collected annual counts of spawning Inconnu within the Selawik River to assess annual patterns in recruitment. Together, these components provided an analytical framework for evaluating the impacts of the slump on the Selawik River Inconnu population.

Sampling and otolith collection

From 2011 to 2018 male Inconnu were sampled during September from the Selawik River spawning area, approximately 210 rkm upstream from Selawik Lake. Male and female Inconnu were sampled during July and August in the Kobuk River near the community of Kiana, approximately 100 rkm upstream from Hotham Inlet. We used Bromaghin's (1993) statistical methods for determining appropriate sample sizes for estimating multinomial proportions at various levels of precision and accuracy. A sample size of 200 individuals provided proportion estimates of two different age classification levels to within 7% or less of their actual values at $\alpha = 0.05$. Inconnu on the Selawik River were captured by angling, which was shown to produce similar length distributions to those captured with beach seines during a previous mark-recapture project (Hander et al. 2008). The first 200 male Inconnu captured were sacrificed for age analysis. Kobuk River Inconnu were captured using drift gillnets with 14.9 cm stretch mesh webbing (Menard and Kent 2010). While gillnets are selective for fish size (Bromaghin 2005), the net was a standard size for large Chum Salmon, which are similar in circumference to mature male Inconnu, so we assumed that the gillnet was non-selective for that demographic group.

Each Inconnu captured was measured for fork length (FL) to the nearest 5 mm or less, weighed whole to the nearest 100 g, egg skeins of females were weighed to the nearest 10 g, and sagittal otoliths were retrieved from the head of each fish, rinsed clean, and stored dry in a coin envelope for later aging. Inconnu carcasses from the Selawik River collection were transported downstream to the village of Selawik where they were distributed to residents and Inconnu carcasses from the Kobuk River collection were offered to residents of Kiana or Noorvik.

Otolith preparation and aging

Age analysis took place at the U.S. Fish and Wildlife Service laboratory in Fairbanks, Alaska. One otolith from each fish was thin-sectioned in the transverse plane through the core and mounted on a glass slide using thermal glue (Secor et al. 1992). Each section was approximately 0.3-mm thick and annuli were viewed with a compound microscope using polarized transmitted light. Annuli were identified and counted based on descriptions and illustrations in Chilton and Beamish (1982). Because egg incubation takes place during the winter following spawning, and the first annuli is produced during the first winter as a fish, Inconnu brood age in years was therefore the number of annuli plus one.

Feeding status and gonadosomatic index

The Kobuk River collection project was downstream from the spawning area and non-spawning Inconnu could potentially be sampled there. We tested our assumption that spawning fish were the predominant demographic group in the sample by examining captured fish for two indicators of spawning preparation. First, stomach fullness was evaluated for every captured fish, because Inconnu are known to cease feeding during their spawning migrations (Alt 1969; Brown 2000; Esse 2011). Second, a gonadosomatic index ($GSI = [\text{egg weight}/\text{whole body weight}] * 100$) was created for all female Inconnu because non-spawning females rarely have GSI values greater than 3% (Brown et al. 2007, 2012a). Therefore, fish without food in their stomachs and females with elevated GSI indices would provide support for our assumption of sampling the Kobuk River spawning population.

Female proportion of spawning sample

From 2011 to 2018 Inconnu were captured in the Selawik River spawning area and externally examined to classify individuals as either male or female, a sex assignment method found to be reliable in the fall season with fish preparing to spawn (Brown 2000). Those classified as females were counted and immediately released unless badly injured during capture. Hander et al. (2008) found that a sample obtained using angling methods produced similar length distributions and sex composition to a sample obtained using beach seines, so we assumed that our angling samples were representative of the annual spawning populations. We estimated female proportion with exact 95% CIs, as discussed by Conover (1999), in annual spawning samples including those from 2004 and 2005 (Hander et al. 2008). We then estimated an overall weighted average following methods detailed by Taylor (1997).

Length comparisons

Length, weight, and age data from male Inconnu from the Selawik and Kobuk River spawning populations were used to test hypotheses related to length distributions and growth. Male Inconnu were more abundant and used to avoid sacrificing egg bearing females. Annual mean FL data for male Inconnu from the Selawik and Kobuk River populations were initially

compared with a series of two sample *t*-tests of the null hypothesis that mean FLs were similar within annual collections for the two populations. Statistical comparisons in this manuscript were considered to be significant at $\alpha = 0.05$. All statistical analyses were conducted using Minitab statistical software version 18.1. To reduce the probability of Type 1 errors when conducting multiple statistical tests, we applied false discovery rate control in these analyses, as described by Verhoeven et al. (2005). One-way ANOVA procedures were subsequently conducted to test null hypotheses that mean FL of annual samples within the Selawik River population were similar, and annual samples within the Kobuk River population were similar as well. If hypotheses of equality could not be rejected, no further analyses were required. However, if initial hypotheses of equality were rejected, paired contrasts using Tukey's multiple comparisons method were conducted to rank significantly different sample groups. The primary reason for conducting these analyses was to collect corroborative evidence for a recruitment event if one was observed. If one of these spawning populations was infused with a large number of new recruits, the mean age would decline and, because older Inconnu tend to be larger than younger Inconnu (Brown 2000; Tallman and Howland 2017), the mean FL would be expected to decline as well.

Weight and FL analysis

Analyzing the weight of fish given FL provides an index of physical condition (Pope and Kruse 2007). We used the standard power function $W = \alpha L^\beta$ to describe and illustrate the relationship between weight (W) and FL (L) for Inconnu samples collected from spawning populations in the Selawik and Kobuk rivers, with all years pooled. The equation was algebraically reconfigured to $\log_{10}(W) = \log_{10}\alpha + \beta(\log_{10}(L))$ and calculated as a least-squares linear regression where the $\log_{10}\alpha$ parameter was the Y-intercept and the β parameter was the slope of the regression describing the curvature of the relationship when presented in normal units. We compared weight and FL relationships between males from the two populations, and females that were predominantly from the Kobuk River population, by pooling all data in a single power function and comparing mean values of standardized residuals (Fechhelm et al. 1995; Pope and Kruse 2007; Brown 2008). We used an ANOVA to test the null hypothesis that mean values of standardized residuals for the three groups were similar versus the alternative hypothesis that at least one was significantly different. An initial significant result would be followed by a series of paired contrasts using Tukey's honestly significant difference (HSD) method of multiple comparisons with an adjusted family error rate. With this analysis, if individuals from one population weighed less at a given FL than those in the other population they would have a significantly smaller mean standardized residual value.

Growth

We reasoned that given their common rearing environment, individuals in the two neighboring populations should exhibit similar growth rates. We used a von Bertalanffy growth model, $L_t = L_\infty * (1 - e^{(-K*(t-t_0)})}$ (Chen et al. 1992; Isely and Grabowski 2007), to estimate growth parameters L_∞ , the asymptotic length, and K, the Brody growth coefficient, for males from both populations. We estimated these parameters using an iterative process for solving nonlinear regression functions. We used an analytical process to compare growth models for the two groups that is analogous to one described by Zar (1999) for comparing two regression lines. We first conducted a two sample *t*-test of the null hypothesis that estimates of L_∞ were similar for the two populations versus the alternative hypothesis that they were significantly different. If similar, we conducted another two sample *t*-test of the null hypothesis that estimates of K were similar for the two populations. If population specific growth parameters were found to be similar, data would be pooled for a descriptive presentation of growth patterns for male Inconnu in northwest

Alaska. Growth patterns of female Inconnu from the Kobuk River population were similarly analyzed to illustrate the growth differences between males and females.

Age structure analysis

Age data from the Selawik and Kobuk River Inconnu populations were used to test two related hypotheses. In the first case, we reasoned that both populations experienced a common rearing and overwintering environment in Selawik Lake and Hotham Inlet (Alt 1977; Underwood 2000; Smith et al. 2015). Additionally, if both populations were similarly distributed throughout this estuarine environment they would also experience similar rates of natural and fishing mortality. Therefore, we hypothesized the annual age distribution of the two spawning populations would be similar in the absence of some factor that affected one of the populations but not the other. We used a Kruskal-Wallis nonparametric rank test (Zar 1999) of the null hypothesis that median ages from both populations during all 8 years of the project were similar, versus the alternative hypothesis that at least one median age was different. Upon a significant result, we tested a series of eight null hypotheses that median ages of the two populations were similar within annual collections versus the alternative hypotheses that they were different. False discovery rate control was also used in these analyses (Verhoeven et al. 2005).

In the second case, we considered proportional changes of young and old components of the two spawning populations. The young component contained the first few year classes of recently recruited individuals in each spawning population, essentially the ascending limb of the age distribution. The older component included individuals in the descending limb of the age distribution and beyond that we assumed had spawned previously and experienced multiple years of additional natural and fishery-related mortality. The actual cut-point age separating young and old components of the spawning populations was defined by our data because no large scale aging studies with otoliths had previously been conducted with these populations. A significant recruitment event would be expected to increase the proportion of young fish with a corresponding decline of the older portion of the spawning population. Alternatively, one or more years of recruitment failure would result in the persistence of the older portion of the spawning population. Recruitment synchrony between populations would support our assumption of a common environment effect. Asynchrony would suggest river-specific effects such as greater fishing mortality for the Kobuk River population or a slump effect for the Selawik River population. Both events would reduce the older component relative to the younger within each system. We used a Chi-square (χ^2) test of the null hypothesis that the annual proportional compositions of the young and old components of the two spawning populations were similar throughout the 8-year time period versus the alternative hypothesis that at least one sample group was different. Upon a significant outcome, a series of χ^2 tests of null hypotheses that proportional compositions of young and old components of the two spawning populations were similar within annual collections. False discovery rate control was also used in these analyses (Verhoeven et al. 2005).

Inconnu abundance

To provide a count of post-spawning Inconnu in the Selawik River, we used a Dual Frequency Identification Sonar (DIDSON), an imaging sonar system (Belcher et al. 2001; Burwen et al. 2010). The sonar site was at 66.5000°, -158.4355° and used from 2011 to 2018 (Figure 4). The site had characteristics considered optimal for effective sonar operation that included: 1) it was located downstream of known spawning activity; 2) was a single river channel; 3) had a gradually sloping bottom without sudden inflections; 4) had no structure or debris that could

impede fish detection; and 5) had a uniform non-turbulent flow that did not support milling behavior (adapted from Melegari 2019).



Figure 4.—Selawik River sonar site with an inset aerial view.

The sonar was operated at 1.8 MHz (high frequency) for observations less than 12 m from the transducer and 1.1 MHz (low frequency) for distances up to 30 m (Burwen et al. 2007). A partial weir was constructed approximately 1 m upstream from the sonar to direct downstream migrating fish through the sonar beam. Fish passage and migration timing data were collected 24 hours per day in 20-minute sample periods. These 20-minute files were saved to an external hard drive. The sonar software used for analysis was DIDSON V5.26.22 (Sound Metrics Corporation, Bellevue, Washington). Sonar data were later processed by using the Echogram and Source Image features of the standard DIDSON software package to count all fish images identified as downstream migrating Inconnu, providing a census of the annual spawning population.

Species identification is a critical component of any sonar counting operation (Burwen et al. 2010; Pipal et al. 2012). The Selawik River and associated lakes support numerous populations of anadromous and resident fish species. However, Inconnu is the largest fish species present in the Selawik River during the late fall, and the only large and abundant species that has been captured in the vicinity of the spawning area (USFWS 1993; Hander et al. 2008). The minimum length of mature male Inconnu during an extensive sampling program during 2004 and 2005 was 59 cm FL (Hander et al. 2008). Spawning Humpback Whitefish *Coregonus pidschian* are present each fall in the same area as Inconnu (Brown 2013), although maximum size of the species is approximately 10 cm smaller than the minimum size of spawning Inconnu (Brown 2004; Hander et al. 2008). Maximum size of Broad Whitefish *C. nasus* approach the minimum size of spawning Inconnu but the species is rarely encountered in the upper Selawik River. In 2011 and

2013, Humpback Whitefish, Broad Whitefish, and Inconnu captured at the sonar site were tethered and observed with sonar imaging at varying frequencies and distances from the transducer to qualitatively equate size, shape and swimming characteristics between species. In this study, we classified all downstream migrating sonar targets >59 cm FL as Inconnu in the Selawik River, which was similar to the threshold length of >60 cm FL used by Esse (2011) in the Sulukna River, a tributary of the Yukon River.

Equipment maintenance, adjustment, and technical malfunctions resulted in some missing portions of hourly counts. Different methodologies were used to make up for missed counts based on the amount of time missed. Partial hourly counts (≥ 15 and < 60 min) were standardized to 1h, using

$$E_h = (60 / M_c) \cdot C_h,$$

where E_h = estimated hourly downriver count for hour h ,

M_c = number of minutes of the hour that were counted, and

C_h = downriver count during the sampled time in hour h .

Counts for hours with <15 minutes were discarded and treated as missing hours. When counting was suspended for more than 60 minutes, data for the missing time period were interpolated by averaging counts from the same time period on the day before and the day after the missed hourly count using:

$$E_d = (E_b + E_a)/2,$$

where E_d = downriver fish count for missing time period d ,

E_b = downriver count from the same time period of the previous day, and

E_a = downriver count from the same time period of the next day.

Results

Feeding status and gonadosomatic index

Our assumption that Inconnu sampled in the lower Kobuk River were preparing to spawn was confirmed. No food was found in the stomachs of fish sampled in either river, which is consistent with Inconnu spawning migration. The GSI values from Kobuk River females collected 2011–2018 ($n = 314$) revealed that all were >3% (GSI range 3.4–21.0) and increased through the season consistent with data from known spawners in other drainages (Figure 5). Gonadosomatic indices are not particularly effective for assessing the spawning readiness in males during summer because the seasonal change in gonad mass between non-spawning and spawning Inconnu and other coregonid species can be an order of magnitude less for males than for females (Lambert and Dodson 1990). However, the fact that no fish were feeding and all females were preparing to spawn provided a measure of confidence in our use of the Kobuk River samples as representative of annual spawning populations from the Kobuk River.

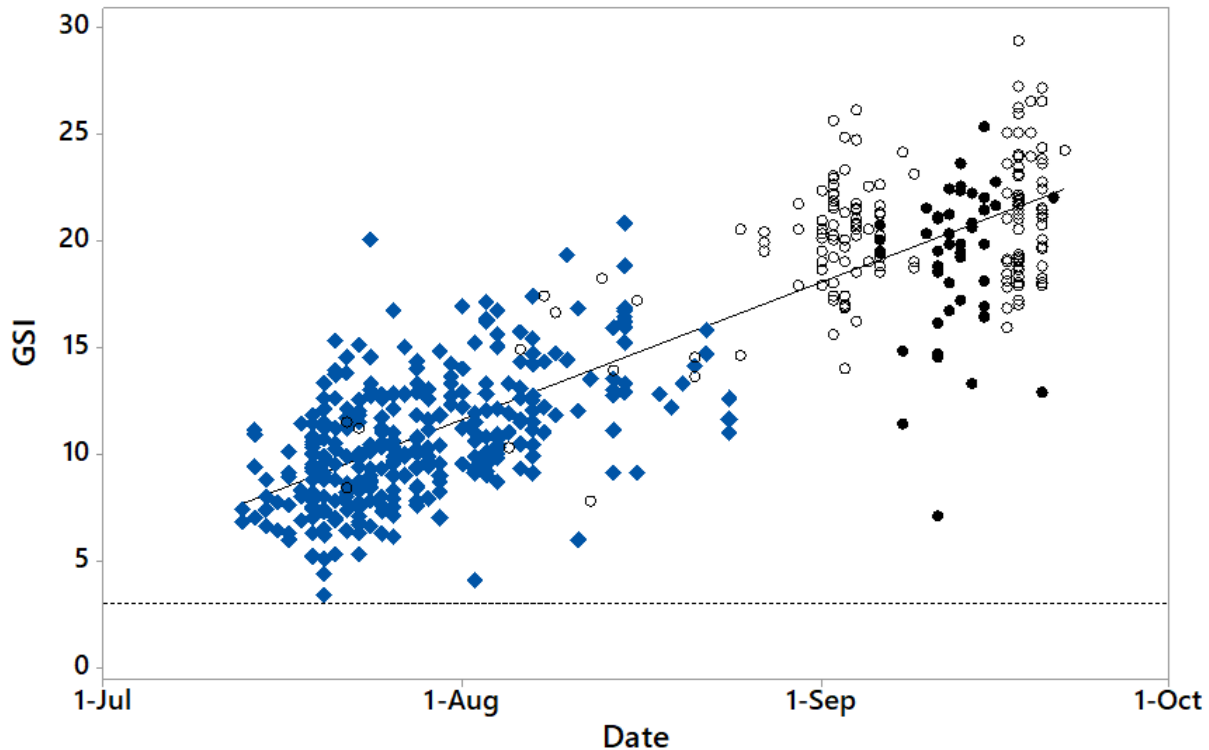


Figure 5.—Gonadosomatic index [$GSI = (\text{egg weight} / \text{whole body weight}) * 100$] of female Inconnu from the Kobuk (blue diamonds; $n = 314$) and Selawik (black circles; $n = 45$) River populations, 2011–2018. For comparison, GSI data from Yukon River populations (open circles; $n = 156$; Brown 2000; McKenna et al. 2015) are included. Samples from the Selawik and Yukon rivers were from Inconnu that were known to be preparing to spawn. The Kobuk River samples were collected in the lower Kobuk River and we were initially uncertain whether they were preparing to spawning or resting fish. The reference line at $GSI = 3$ indicates the level at which non-spawning fish rarely exceed.

Female proportion of spawning sample

The proportion of females in sampled Inconnu from the Selawik River varied annually from 0.21 (95% CI = 0.185–0.241) in 2004 to 0.42 (95% CI = 0.365–0.473) in 2012 (Figure 6). The weighted mean proportion of females when considering all 10 sample years was estimated to be 0.28 (SE = 0.007). The consistency of these data suggest that males normally outnumber females in the spawning areas.

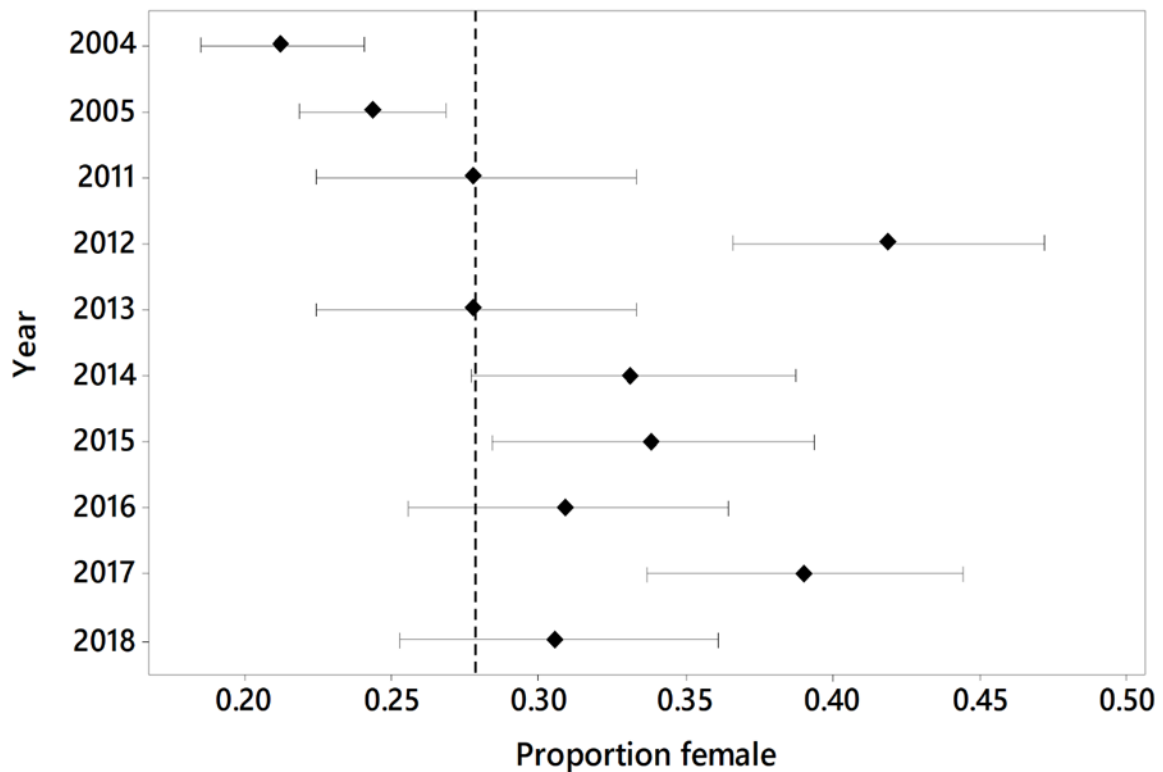


Figure 6.—Proportion female with 95% CI for 10 different years of sampling the Inconnu spawning population on the Selawik River. The weighted mean proportion female was approximately 0.28 (vertical dashed line).

Length comparisons

T-tests of null hypotheses that mean FL of male Inconnu for the eight pairs of annual collections from the Selawik and Kobuk River spawning populations were rejected for all paired contrasts (Figure 7). Mean FL of Kobuk River Inconnu was significantly greater than of Selawik River Inconnu only for the 2011 sample year ($t_{355} = 2.14$, $P = 0.033$). Selawik River Inconnu had greater mean FL for all subsequent annual collections ($P < 0.001$). Within the Selawik River population samples, mean FLs were similar 2011–2015, followed by significant declines in 2016 and 2017 and a slight rebound in 2018 ($F_{7,1548} = 11.62$, $P < 0.001$). By contrast, mean FLs of the Kobuk River population samples revealed significant and steady declines throughout the time series ($F_{7,1053} = 29.56$, $P < 0.001$).

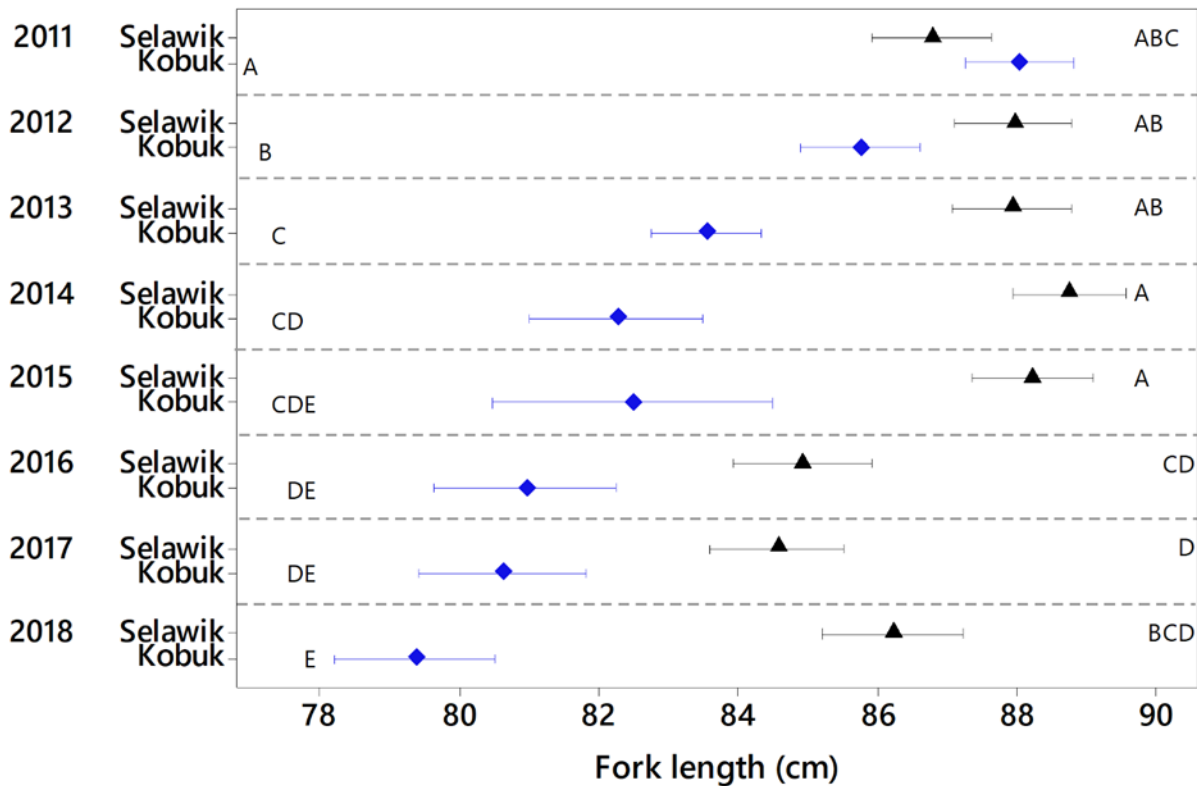


Figure 7.—Interval plot of mean FL with 95% confidence intervals for mature male Inconnu from the annual collections of Selawik and Kobuk River spawning populations. Comparison of mean FL among the eight annual samples of the Selawik River population, with grouping letters displayed on the right margin of the figure, and of the Kobuk River population, with grouping letters displayed on the left margin of the figure. Groups with shared letters were similar, otherwise they were significantly different.

Weight and FL analysis

Initial least squares linear regressions of $\log_{10}(W) = \log_{10}\alpha + \beta(\log_{10}(L))$ for three groups of Inconnu separately: male Inconnu from the Selawik River population; male Inconnu from the Kobuk River population; and female Inconnu that were predominantly (87%) from the Kobuk River population. These three analyses resulted in a small fraction (~5%) of standardized residuals beyond three SD from the predicted lines. These outlying data points can have high influence on regression slope and intercept parameters and they were not considered representative of the weight and length relationships of the general population. In a manner similar to Fechhelm et al. (1995), outlier data points with standardized residuals >3 and <-3 were removed from the data set. Least-squares linear regressions were recalculated to establish the following mathematical relationships between weight and length for: Selawik River males ($W = 0.0073 * L^{3.032}$), Kobuk River males ($W = 0.0083 * L^{3.036}$); and females ($W = 0.0460 * L^{2.663}$). We then conducted a single least-squares linear regression with data from all three groups pooled. The null hypothesis of similarity of mean standardized residuals from the three groups was rejected ($F_{2,2892} = 775.34, P < 0.001$). Subsequent comparisons among groups using Tukey’s HSD method revealed that females were significantly heavier at length than either group of males and that males from the Kobuk River population were significantly heavier at length than males from the Selawik River population (Figure 8).

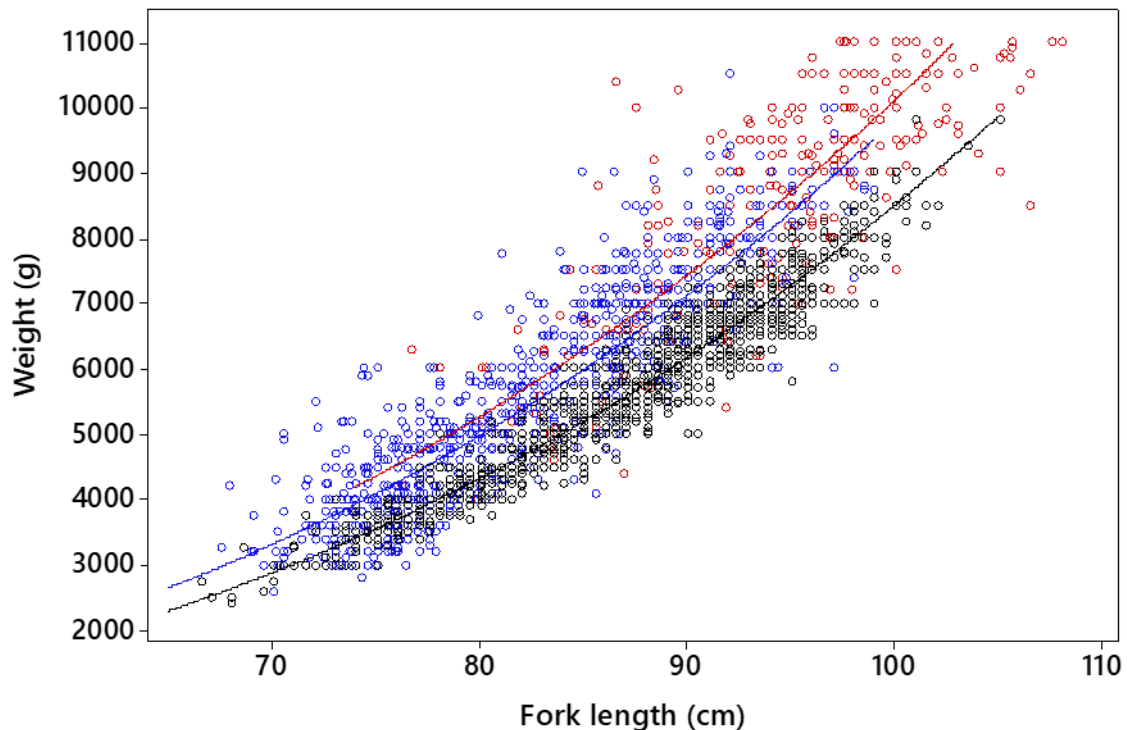


Figure 8.—The relationship between Inconnu weight at length plot for males from the Selawik ($n = 1,543$; black circles and prediction line) and Kobuk ($n = 1,029$; blue circles and prediction line) River spawning populations, and for perspective, female Inconnu ($n = 323$; red circles and prediction line) predominantly from the Kobuk River population. The largest females in the sample were over 113 cm FL and 16,000 g but we limited this figure to highlight the range of values common to males.

Age data and analyses

During sampling years 2011–2018, 2,991 mature Inconnu were sampled from the Selawik ($n = 1,607$) and Kobuk ($n = 1,384$) River spawning populations. Otoliths were prepared for viewing and ages were obtained (Figure 9). From the 2,982 fish from this sample, most were easily readable, and only 9 were unable to be aged ($<0.5\%$). Ages ranged 9–34 years in the Selawik River population and 8–40 years in the Kobuk River population.

Length at age data were used to test the null hypothesis that male Inconnu from the Selawik River population grow similarly to those from the Kobuk River population. Von Bertalanffy growth models were calculated for both groups separately and the null hypothesis that estimates of L_{∞} for the Selawik ($L_{\infty} = 99.18$, $SE = 1.17$) and Kobuk ($L_{\infty} = 97.69$, $SE = 1.92$) River populations were similar could not be rejected ($t_{1897} = 0.66$, $P = 0.509$). A subsequent test of the null hypothesis that estimates of the Brody growth coefficients for the Selawik ($K = 0.0834$, $SE = 0.0079$) and Kobuk ($K = 0.0759$, $SE = 0.0107$) River populations were similar could also not be rejected ($t_{2194} = 0.56$, $P = 0.573$). We concluded the two populations exhibit similar growth patterns. Length at age data for male Inconnu from both populations were therefore pooled to create a descriptive growth model for male Inconnu for the region (Figure 10).

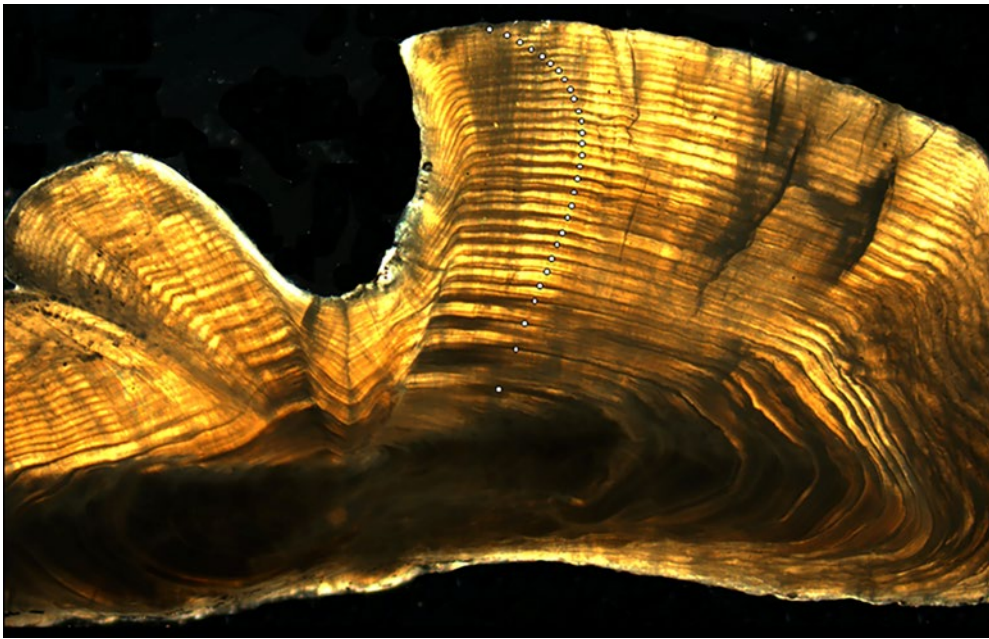


Figure 9.—Image of a sectioned Inconnu otolith viewed with transmitted light in dark-field mode using a compound microscope. Twenty-nine annuli are indicated with white spots arcing across the ventral part of the otolith from the core (lower center) to the margin.

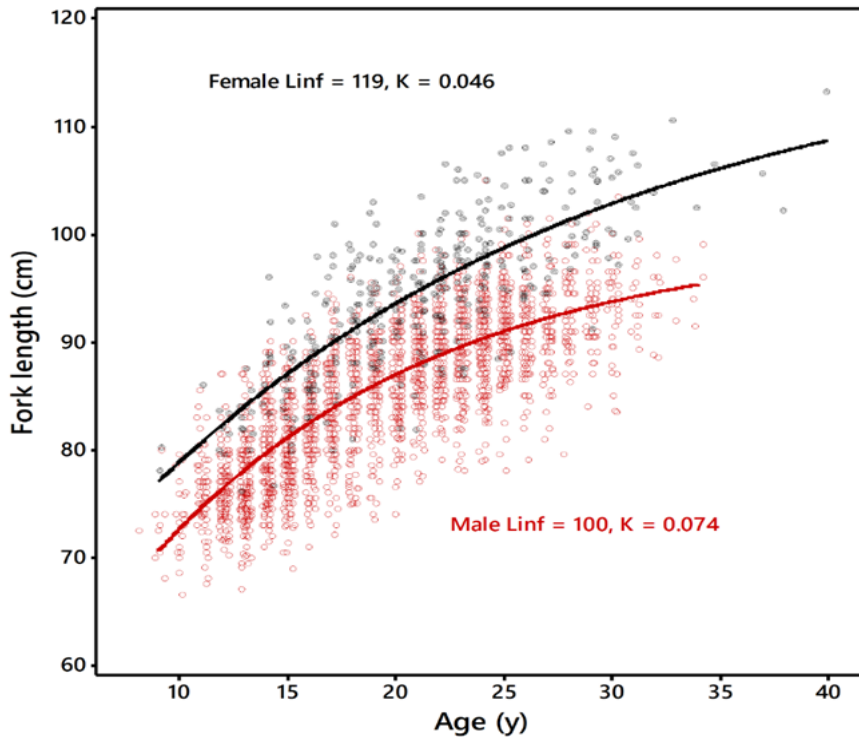


Figure 10.—von Bertalanffy growth curves for mature male (red circles and line; $n = 2,656$) and female (black circles and line; $n = 371$) Inconnu from the Selawik and Kobuk River spawning populations. Fork length at age was best fit for male Inconnu with the growth equation: $FL \text{ (cm)} = 100.02 * (1 - e^{(-0.074 * (\text{age} + 7.4095))})$. The Brody growth coefficient that best fit the male data was $K_m = 0.074$. Fork length at age was best fit for female Inconnu with the growth equation: $FL \text{ (cm)} = 118.69 * (1 - e^{(-0.046 * (\text{age} + 13.7248))})$. The Brody growth coefficient that best fit the female data was $K_f = 0.046$.

The final equation for males was $FL \text{ (cm)} = 100.02 * (1 - e^{-(0.074 * (\text{age} + 7.41))})$. In addition, a sufficient number of female Inconnu were sampled for length and age over the years ($n = 371$) to calculate a growth model to illustrate the growth differences among sexes. As expected, the L_{∞} value for females was much greater than for males ($L_{\infty} = 118.69$, $SE = 6.58$) and the Brody growth coefficient was considerably lower ($K = 0.046$, $SE = 0.0126$). The female growth equation was $FL \text{ (cm)} = 118.69 * (1 - e^{-(0.046 * (\text{age} + 13.7248))})$.

Median ages of eight annual samples from both the Selawik and Kobuk River spawning populations, a total of 16 groups, were significantly different overall ($H_{15} = 138.48$, $P < 0.001$). Subsequent paired contrasts revealed similar median ages for the two populations in the years 2011, 2015, and 2016, and significantly different median ages during the years 2012–2014, 2017, and 2018 (Figure 11). The median age of the Selawik River population was greater than that of the Kobuk River population during all years in which median ages were significantly different.

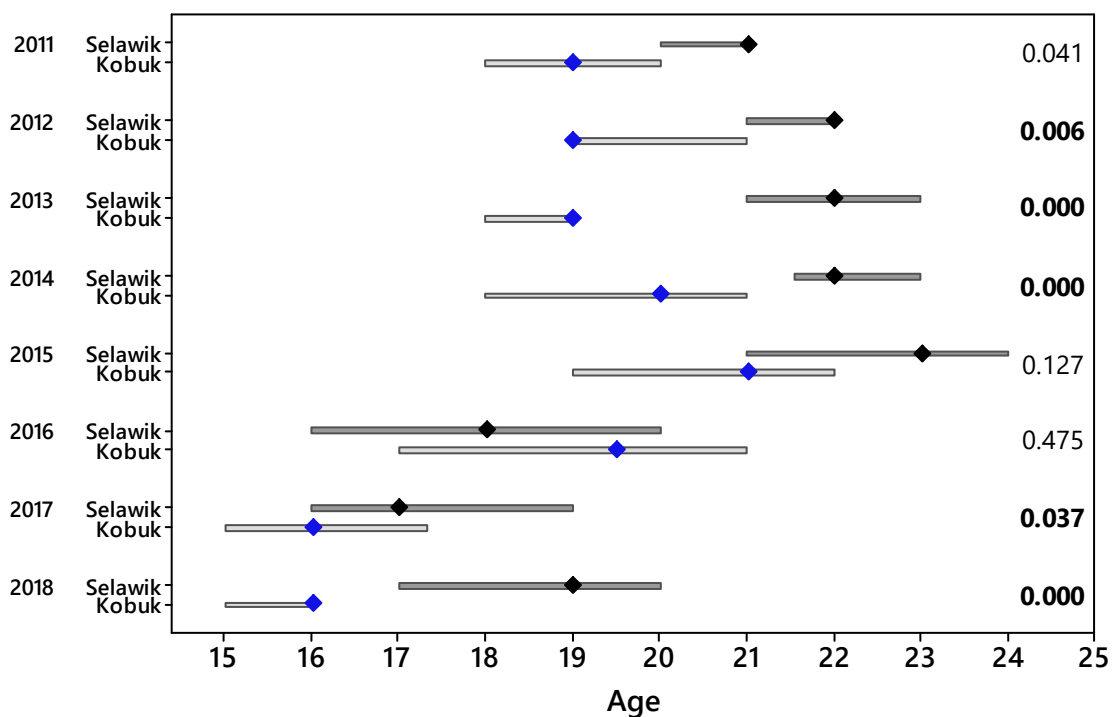


Figure 11.—Plots of annual median age with 95% CIs for Selawik (dark shaded boxes-black diamonds) and Kobuk (light shaded boxes-blue diamonds) River Inconnu populations during the years 2011–2018. P -values from paired contrasts with Kruskal-Wallis nonparametric test procedures are presented on the right, with bold values indicating significantly different median ages following the application of false discovery rate control (Verhoeven et al. 2005).

Age samples from the Selawik and Kobuk River Inconnu spawning populations indicated maturity was attained for most fish between age-12 and age-15, with a small number of individuals maturing as young as age-9 (Figure 12). We therefore established our cut-point between recent recruits and older cohorts between the ages of 15 and 16. The null hypothesis that the proportional compositions of the young (≤ 15 years of age) and old (> 15 years of age) demographic components were similar throughout the 8-year time period for both populations was rejected ($\chi^2 = 195.498$, $DF = 15$, $P < 0.001$). Within annual collections of the

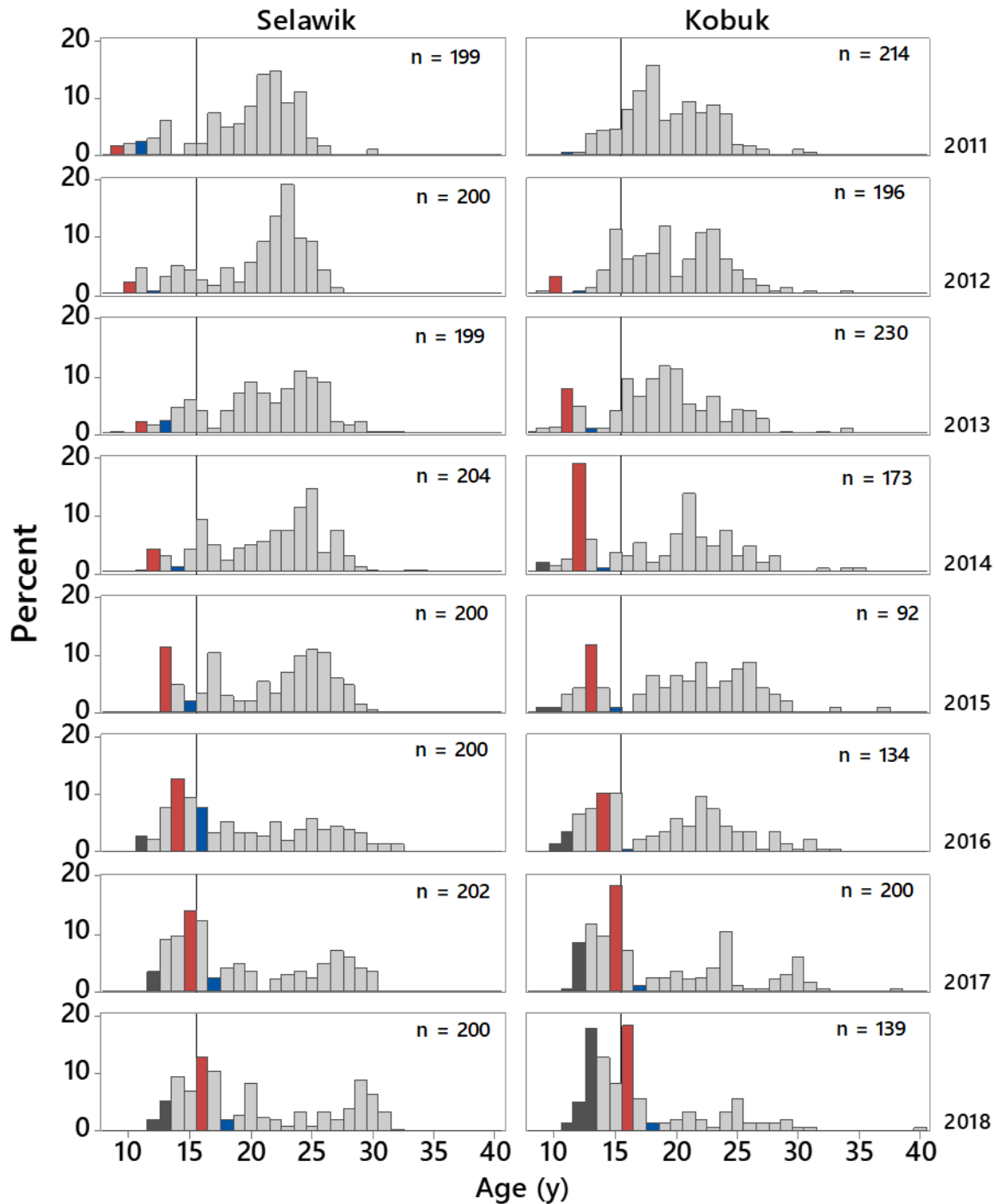


Figure 12.—Age histograms of mature Selawik River (left) and Kobuk River (right) Inconnu during 2011–2018 illustrating major age structure features. The vertical solid reference lines delineate the classification boundary between the recently recruited group that are 15 years of age and younger from the older group that are greater than 15 years of age. Note the observed shift to the right over time of strong (e.g., red bars) and weak (e.g., blue bars) age classes in both populations and the proportional decline of older cohorts as new recruits emerge. Selawik and Kobuk River samples show reasonably similar recruitment patterns although the Selawik River sample appears to have a weaker post-slump component at this time (dark shaded bars; these cohorts shown in the Kobuk River for comparison).

Selawik and Kobuk River populations, the null hypotheses could not be rejected for the years 2011–2013, 2015, and 2016, but null hypothesis were rejected for the years 2014, 2017, and 2018 (Table 1). A plot of the proportional composition of the young component of the two populations by sample year clearly distinguishes between the years of similarity and differences among populations (Figure 13).

Table 1.—Results of paired annual Chi-square tests of null hypotheses that the proportional composition of recent recruits ≤ 15 years of age (Young; number of fish and proportion [Prop] of annual sample) and older spawning Inconnu > 15 years of age (Old) in the Selawik and Kobuk rivers were similar each year. *P*-values are presented on the right, with bold values indicating significant outcomes following the application of false discovery rate control (Verhoeven et al. 2005).

Year	Population	Young (Prop)	Old (Prop)	Total	χ^2 (DF)	<i>P</i> -value
2011	Selawik	34 (0.17)	165 (0.83)	199	0.996 (1)	0.318
	Kobuk	29 (0.14)	185 (0.86)	214		
	Total	63 (0.15)	350 (0.85)	413		
2012	Selawik	38 (0.19)	162 (0.81)	200	0.124 (1)	0.725
	Kobuk	40 (0.20)	156 (0.80)	196		
	Total	78 (0.20)	318 (0.80)	396		
2013	Selawik	34 (0.17)	165 (0.83)	199	0.988 (1)	0.320
	Kobuk	48 (0.21)	182 (0.79)	230		
	Total	82 (0.19)	347 (0.81)	429		
2014	Selawik	25 (0.12)	179 (0.88)	204	25.807 (1)	<0.001
	Kobuk	59 (0.34)	114 (0.66)	173		
	Total	84 (0.22)	293 (0.78)	377		
2015	Selawik	37 (0.19)	163 (0.81)	200	2.835 (1)	0.092
	Kobuk	25 (0.27)	67 (0.73)	92		
	Total	62 (0.21)	230 (0.79)	292		
2016	Selawik	72 (0.36)	130 (0.64)	202	0.745 (1)	0.388
	Kobuk	54 (0.40)	80 (0.60)	134		
	Total	126 (0.38)	210 (0.62)	336		
2017	Selawik	72 (0.36)	128 (0.64)	200	6.916 (1)	0.009
	Kobuk	98 (0.49)	102 (0.51)	200		
	Total	170 (0.43)	230 (0.57)	400		
2018	Selawik	48 (0.24)	152 (0.76)	200	18.011 (1)	<0.001
	Kobuk	64 (0.46)	75 (0.54)	139		
	Total	112 (0.33)	227 (0.67)	339		

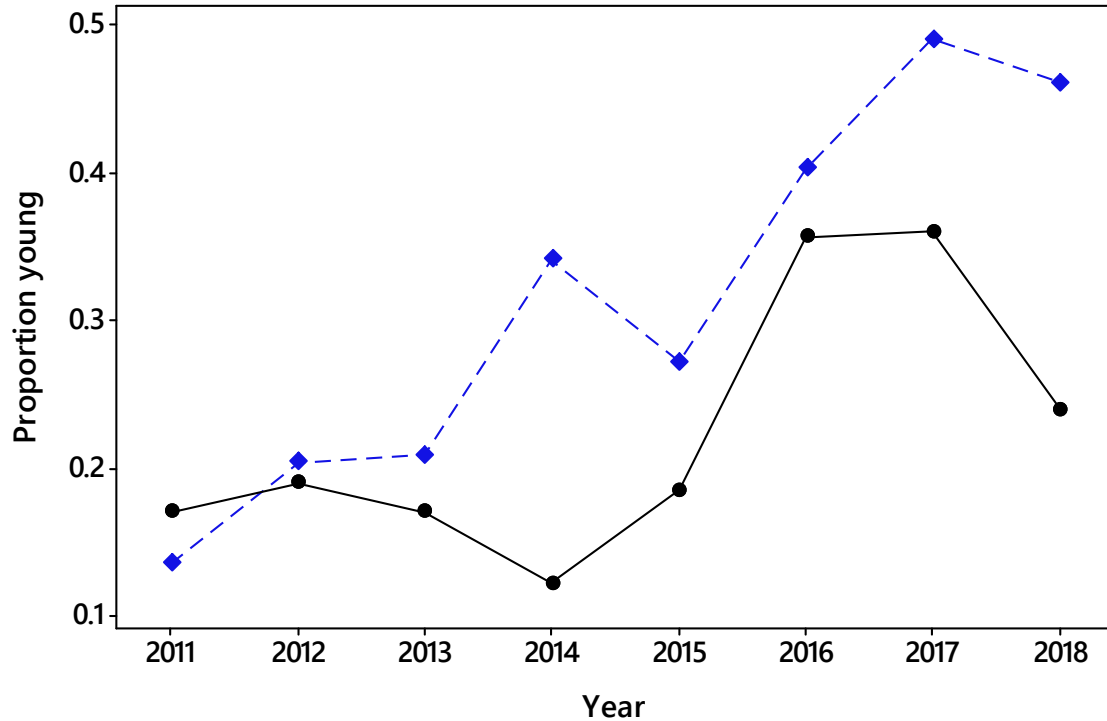


Figure 13.—Scatterplot of proportion of young (≤ 15 years old) Inconnu in annual spawning population samples from the Selawik (black circles and solid line) and Kobuk (blue diamonds and dashed line) rivers during the time period 2011–2018. A major recruitment event was apparent during 2016 and 2017 for both populations (see Figure 12). The first signs of the recruitment event took place in 2014 for the Kobuk River population and appears to have reached a maximum in 2017 for both populations.

Abundance and post-spawning migration timing

Sonar counts of spawning Inconnu in the Selawik River were obtained for 6 of 8 years. The sonar counting project began operations most years by September 25th and continued during most years through October 10th, which encompassed nearly all of the post-spawning migration (Figure 14). River freezing conditions halted sonar operations on October 5, 2014, near the beginning of the migration making those data unusable. High stream discharge in 2016 forced operation into low frequency mode at greater than 30 m distance producing unusable data because the image resolution was insufficient to distinguish between Inconnu and co-migrating Humpback Whitefish. Annual abundance of spawning Inconnu ranged from 16,600 in 2012 to 24,900 in 2013 (Figure 15). No significant correlation was detected between the proportion of young new recruits in the spawning population and the abundance of spawning Inconnu (Figure 16; Pearson’s $r = -0.123$, $P = 0.817$). Selawik River Inconnu consistently exhibited a nocturnal migration pattern with the majority of downstream migrating fish passing between 2100 and 0800 hours (approximate civil twilight for October 1, 2017, at Selawik, Alaska; Figure 17; USNO 2019).

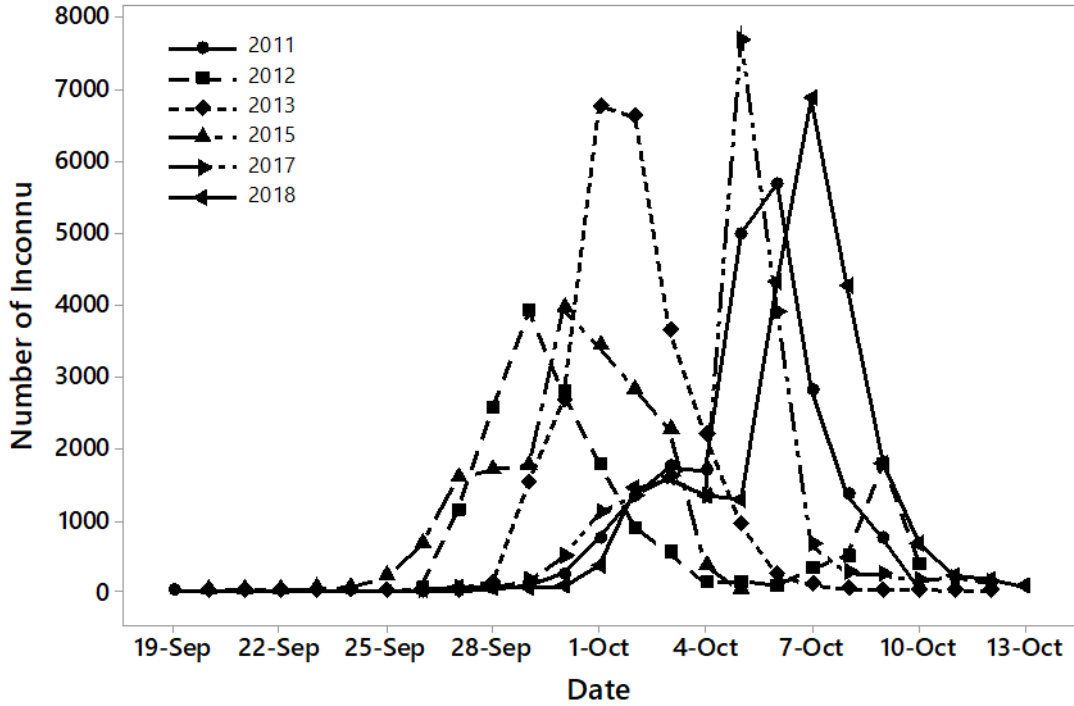


Figure 14.—Daily downstream sonar passage of post-spawning Selawik River Inconnu from 2011–2018. The mean peak migration date was October 3.

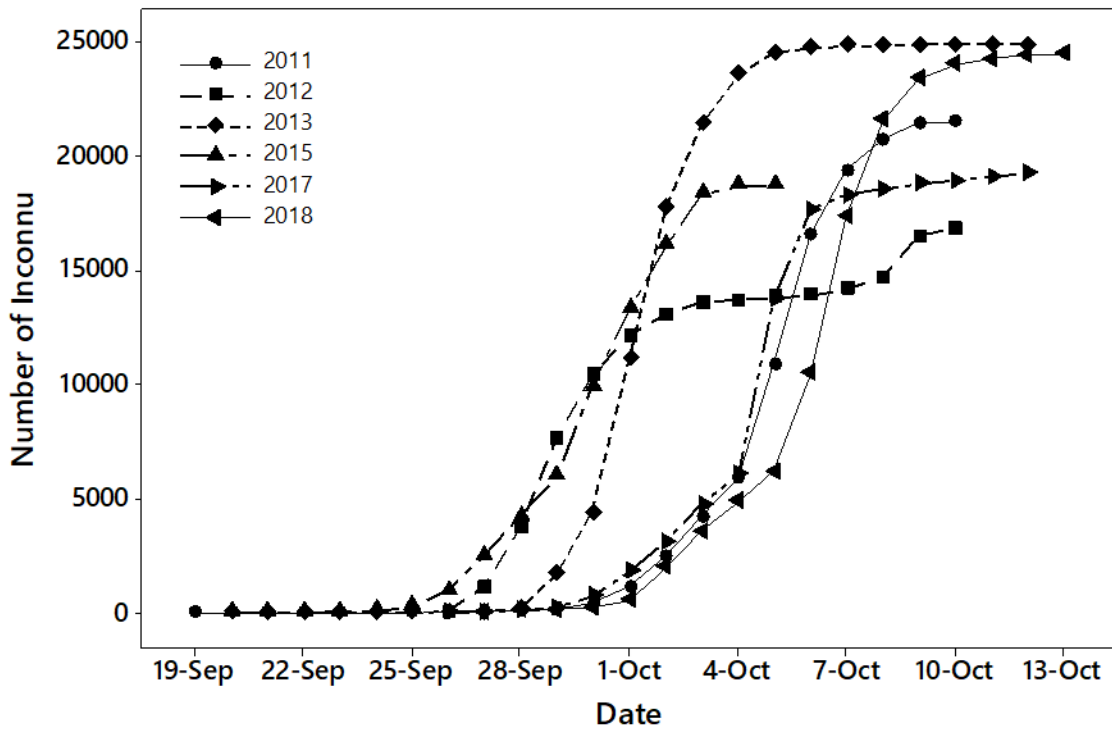


Figure 15.—Cumulative daily downstream sonar passage of Selawik River Inconnu during 6 years of successful operation between 2011 and 2018.

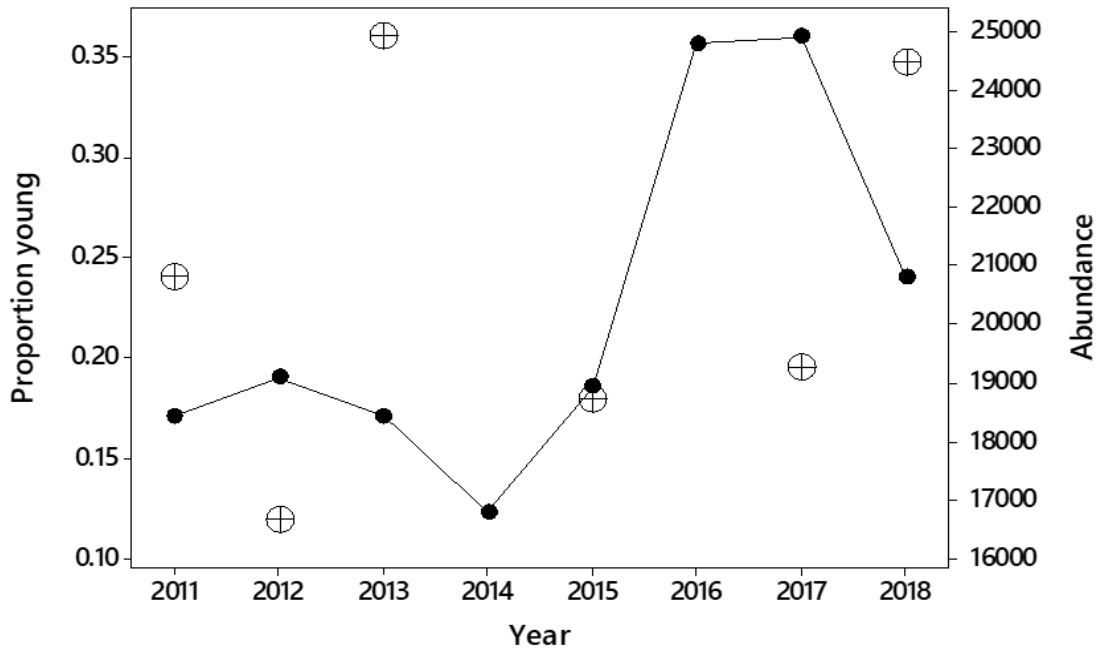


Figure 16.—Scatterplot of proportion young recruits in the Selawik River spawning population by year (black circles with connect line) and abundance of the Selawik River spawning population (open circles with cross). No significant correlation was apparent between the two measures during the 6 years in which both types of data were available (Pearson’s $r = -0.123$, $P = 0.817$).

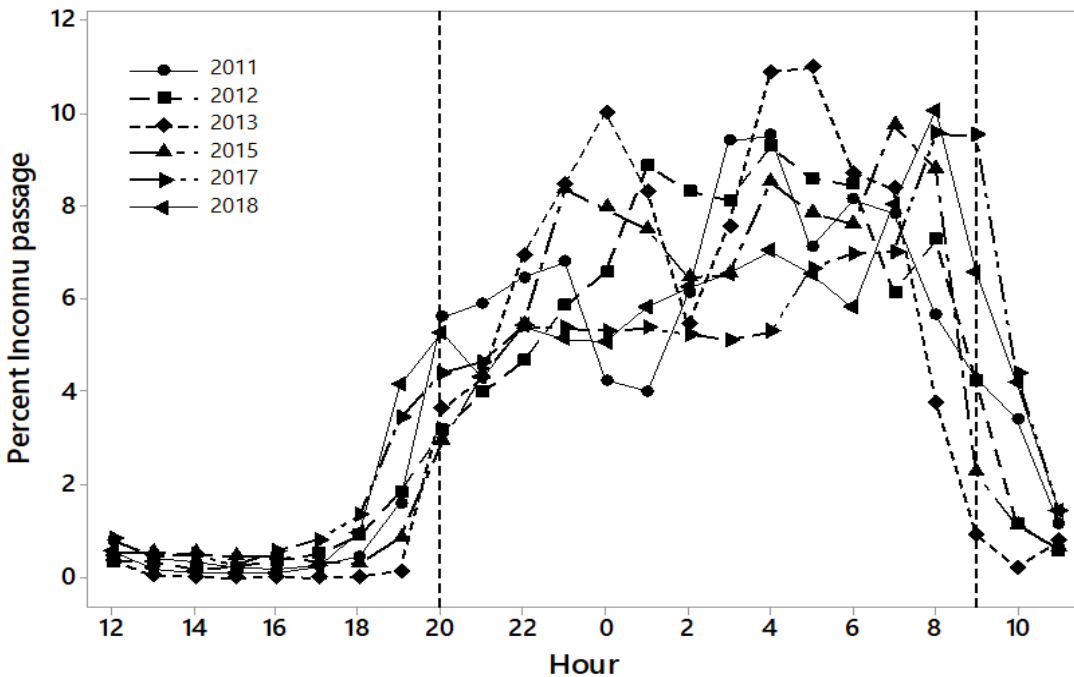


Figure 17.—Nocturnal migration timing pattern of post-spawning Inconnu from the Selawik River. This graph depicts the percent of Inconnu that passed the sonar during a particular hour for the duration of the respective year’s sonar deployment. For example, in 2013 during the 0400 hour approximately 11% of the Inconnu run passed the sonar. The vertical dashed bars reference approximate civil twilight for October 1.

Discussion

Overview

Chronic sediment release from the slump in the upper Selawik River, and subsequent deposition in the Inconnu spawning area downstream, raised concern about potential negative effects to the population and the subsistence users that depend on it. In response to these concerns we compiled biological data from the Selawik River Inconnu population and from its neighboring population in the Kobuk River for comparison. These biological data allowed us to analyze maturity and spawning readiness, body condition, length distribution, age structure, growth, and recruitment dynamics in both populations, and annual spawner abundance for the Selawik River population only. The primary goal of our research was to use these data to infer if the slump had an effect on recruitment for Selawik River Inconnu. Because most Inconnu from populations in the Selawik and Kobuk rivers appear to mature between 10 and 15 years of age (Figure 12), several years older than other populations (Brown 2000; Howland 2005; Esse 2011), our sample does not yet include a sufficient number of age classes from post-slump cohorts to infer whether or not the slump affected recruitment. However, these data do provide the background necessary to make a determination following the collection of another age sample in a few years when additional post-slump cohorts would be expected in the mature population.

Female proportion of spawning sample

The finding that the spawning population of Inconnu in the Selawik River is dominated by males was first documented from a mark-recapture project in 2004 and 2005 (Hander et al. 2008). The proportion female in the spawning population was 0.21 in 2004 and 0.24 in 2005 (Figure 6). We continued to observe the same pattern during this project with an overall annual average proportion female from all 10 sampling years of 0.28 (range 0.21–0.42). Others have documented similar findings from spawning populations sampled in the upper Yukon Flats (0.41, SE = 0.03, $n = 1$ year; Brown 2000), the Sulukna River (0.41, SE = 0.03, $n = 1$ year; Esse 2011), the Alatna River (0.28, SE = 0.03, $n = 1$ year; McKenna et al. 2015), and the Peel River (mean = 0.37, range = 0.29–0.46, $n = 5$ year; VanGerwen-Toyne et al. 2008). Savereide and Huang (2016) conducted a large-scale, multi-year, radio telemetry program with mature Inconnu from the Kobuk River spawning population. While they did not specifically estimate female proportion in the spawning population, they did find that annual survival was high (0.88–0.91) and that females returned to spawn about half as often as males, a situation that results in a male dominated spawning population. These data suggest this phenomenon is common for all populations of spawning Inconnu.

Weight and fork length analysis

Our analysis of body condition among our samples of male Inconnu preparing to spawn in the Selawik and Kobuk rivers, and female Inconnu preparing to spawn primarily in the Kobuk River, revealed that females were significantly heavier at length than males, as expected, and that males from the Kobuk River population were significantly heavier at length than males from the Selawik River population, which we did not expect (Figure 8). Sexual dimorphism in Inconnu has been demonstrated for numerous populations including those in the Kobuk (Alt 1969), Selawik (Hander et al 2008), Yukon (Brown et al. 2012b), Sulukna (Esse 2011), and Peel rivers (VanGerwen-Toyne et al. 2008), with females being larger and heavier on average than males. These data are consistent with the previous studies and demonstrate that females tend to be heavier at a given length than males, which is related to sex-specific differences in body form. It

was unclear why males from the two populations should differ so markedly in body condition when length at age was found to be equivalent (Figure 10). Mature fish from both populations are known to occupy similar estuarine habitats (Alt 1977; Underwood 2000; Smith et al. 2015) and would be expected to experience similar foraging opportunities. It is possible, however, that the observed difference in condition can be explained by energetics given the seasonal difference of the two sampling events and their geographic positions relative to the respective spawning areas. The Kobuk River samples were collected in July and August in the lower Kobuk River in the early stages of the spawning migration, approximately 340 rkm downstream of the spawning area near the mouth of the Pah River (Savereide and Huang 2016). In contrast, the Selawik River samples were collected in mid-September within the spawning area about two weeks prior to spawning. Inconnu sampled in the Kobuk River were in peak condition as they began their spawning migration while fish sampled in the Selawik River had been fasting for two or three months and had expended energy migrating approximately 210 rkm upstream to their spawning area. We hypothesize that the observed differences in condition for mature males from the two populations (Figure 7) represent the energetic costs of the spawning migration.

Growth

In addition to being heavier at length than males, female Inconnu also attain greater fork length at age than males as well (Figure 10). This growth pattern was also documented for Inconnu in the Mackenzie River drainage (Howland 2005). An important conclusion of these growth analyses is that Inconnu continue to grow throughout life, although the rate of growth slows down with age (Howland 2005). Older fish are therefore larger on average than younger fish. As such, mean FL of a spawning population would be positively correlated with median age, which we observe most clearly with the Selawik River samples (Figures 7 and 11).

Mean length comparisons

With the exception of the 2011 annual collection, the male Inconnu sample from the Kobuk River population had a significantly smaller mean FL than from the Selawik River population (Figure 7). Additionally, annual mean FL declined steadily through our time series for the Kobuk River population, while the Selawik River population remained stable 2011–2015 and then declined sharply 2016–2018, years in which a distinct recruitment event was apparent for both populations (Figure 12). The recruitment event was building prior to 2016, more obvious for the Kobuk River population than the Selawik River population, but was not pronounced enough in the Selawik River population to effect the annual mean FL until 2016 (Figure 7). The mean FL differences observed between the Kobuk and Selawik River populations are thought to be a result of the much greater harvest that takes place in the Kobuk River (Braem et al. 2018). Additionally, harvest on the Kobuk River is primarily on mature fish migrating upstream to spawn (Georgette and Loon 1990; Taube and Wuttig 1998), while most of the Selawik River harvest occurs near the community of Selawik in the lower river and Selawik Lake where both populations are present (Alt 1977; Underwood 2000; Smith et al. 2015). The differential exploitation rates for the two populations results in the older age classes in the Kobuk River population being depleted more quickly than in the Selawik River population, leading to a reduction in mean FL (Figure 7) and median age (Figure 11), and a more profound decline in the older component of the age structure histogram once a recruitment event begins (Figure 12).

Age data and analyses

Our data indicated that most Selawik and Kobuk River Inconnu matured between age 12 and 15 (Figure 12) with a small number of precocious individuals maturing as young as age 9 and 10. Otolith aged samples from other spawning populations mature considerably younger with most fish gaining maturity at about age-10 and the most precocious fish by age-7 or younger (Brown 2000; Howland 2005; Esse 2011; McKenna et al. 2015). The consequence of a greater age of maturity is that it requires more time for cohorts spawned in 2004 or later to recruit to the spawning population (Appendix Table A.1). Theoretically, the 2018 sample should have included recruits from five cohorts potentially influenced by the slump (ages 9–13; Figure 12). However, only ages 12 and 13 were represented relatively weakly in the Selawik River sample and ages 11–13 are represented more strongly in the Kobuk River sample. No age-9 or age-10 cohorts were represented in either population sample in 2018.

Age distributions of both populations reveal periods of one or more years in which recruitment was strong followed by years in which recruitment was weak (Figure 12). These periods of strong and weak recruitment are not perfectly synchronous between the two populations, but areas of similarity are present. For example, the age-16 cohort in the 2018 sample, was noticeably strong for both populations beginning several years previously (Figure 12, red bars). Similarly, the age-18 cohort in the 2018 sample was noticeably weak through time for both populations (Figure 12, blue bars). The reason for this variable recruitment is not clear. We hypothesize that weather events such as high flows during the spawning season could interfere with the spawning activity of adults or cause broadcast eggs to settle in suboptimal habitat. Underwood (2000), for example, described a situation in which numerous radio-tagged Inconnu preparing to spawn in the Selawik River left the river during a high flow event just prior to the spawning season and did not return. These types of drainage-specific affects could influence cohort strength of one population and not the other. Weather events, predation, or competition for limited resources occurring after a cohort hatched and descended to the estuary system would be expected to influence survival for both populations (Ricker 1954). Our age distributions suggest that drainage-specific and common environment processes are both occurring.

Recruitment and abundance of spawning Inconnu

Our assumption that we would observe a positive correlation between a recruitment event and the abundance of spawning Inconnu appeared to be incorrect (Figure 16). The reasoning was consistent with current theory of fish population structure in a relatively constant recruitment environment, as described by Robson and Chapman (1961) and Hilborn and Walters (1992). Immature fish experience high natural mortality and low fishing mortality prior to recruiting to the mature demographic group. Mature fish of all ages experience relatively low natural mortality and similar fishing mortality through life. These conditions result in greater numbers of recently recruited individuals than those that have experienced multiple years of natural mortality and exploitation. This situation results in classic right-skewed age frequency histograms (Power 1978; Muir et al. 2008; Tallman and Howland 2017). Our sample of mature Inconnu in the Selawik River, however, are the spawning fraction of the mature population and the non-spawning fraction are in the estuary. Recent long-term radio telemetry studies on Inconnu in the Kuskokwim (Stuby 2018), Yukon (Brown and Burr 2012), and Kobuk (Savereide and Huang 2016) rivers have shown that spawning frequency for individual fish ranges from annually to once every 4 or 5 years with no consensus on the proportion of the mature population that might be spawning in any given year. If the annual proportion spawning was relatively constant over time, we should observe a positive correlation between the occurrence of a recruitment event and

the abundance of spawning Inconnu. That we do not observe this correlation indicates that the annual proportion of mature Inconnu spawning varies widely from year to year.

Recommendations

The effects of sediment deposition, if any, on the Selawik River Inconnu spawning population may not be readily evident because of the few years of young recruits, including post-slump age classes, which have entered the spawning population as of 2018. It is recommended that an age collection occur in 2023 on the Selawik and Kobuk rivers, thus allowing the current young recruits to be fully established in the spawning populations and to determine if there are changes to the Selawik River population age structure that align with slump activity.

The geologic history and permafrost distribution in the Selawik River basin predisposes it to thermokarst disturbance. The abrupt increase in the extent and rate of permafrost degradation has significant ecological implications for tundra ecosystems. (Jorgenson et al. 2006). Along the Selawik River corridor there is ample evidence of active erosion from elevated banks. Observational analysis of the slump in 2007 compared to pre-slump high altitude aerial imagery (K. Yoshikawa (unpublished); Brooks 1988) indicated that the slump had encroached on a historic slump scar (Figure 18). We recommend observation of the Selawik River corridor for other permafrost failure features that may directly affect fish populations and their habitat and use this study's age data as a basis to detect relative changes in the spawning population age structure.

This study contributed spawning population age structure, growth, and recruitment variability characteristics for Selawik and Kobuk river Inconnu, as well as abundance data for Selawik River spawners that are critical components for resource management applications. Ongoing sonar operations on the Kobuk River, by the Fairbanks ADF&G Sport Fish Division, are collecting abundance data for a more complete regional spawner abundance picture. Contemporary and regular region-wide harvest estimates are also needed for estimation of exploitation rates. Alaska Department of Fish and Game's Kotzebue District has the largest subsistence salmon fishery in the state that lacks an annual harvest assessment program (Braem et al. 2018). The most recent Kotzebue District subsistence fish harvest survey including whitefishes was 2012–2014 (Braem et al. 2018).

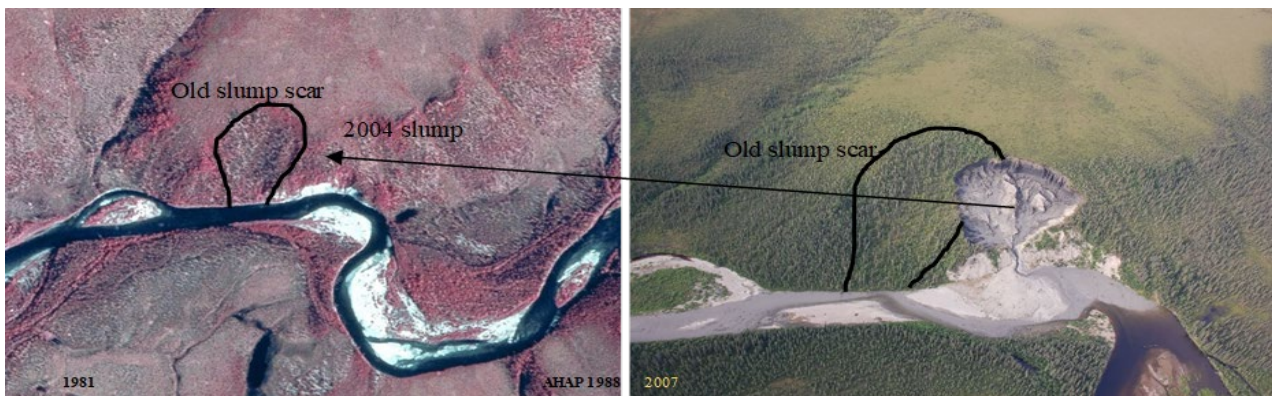


Figure 18.—Comparison of a historic slump scar identified by K. Yoshikawa (unpublished) and encroachment on to the scar by the current slump. The historic slump may have predisposed the current slump's activity.

Authors Note

Near the completion of this manuscript we discovered that the slump began thawing again, growing laterally, and delivering unknown amounts of sediment into the Selawik River (Figure 19). Remote sensing imagery from mid-July 2019 revealed recent growth features and low level aerial reconnaissance and photography in mid-October 2019 confirmed the slump's renewed activity.



Figure 19.—An October 17, 2019, slump reconnaissance photograph. Note the newly exposed perimeter headwall bearing ice-rich soil that thawed and flowed down through a new outlet chute just downstream of the original outlet. The right-hand third of the slump persisted as evidenced by the established vegetation on the original slump floor. See Figure 4 for a comparison to the slump's condition in July 2018.

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Figure 20.—From left to right, Selawik, Alaska residents Frank “Sonny” Berry, Jr. (Selawik National Wildlife Refuge), Patrick Foster, Sr., and Ingram Clark. Integral team members contributing to valuable Selawik River area knowledge and Inconnu otolith collection.

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Appendix Table A.1.—Brood year specific ages and expected research year at maturity for a selection of pre-slump and post-slump brood years. Minimum age at maturity is thought to be 9 years. Age classes expected to be mature on a given research year are in bold. The shaded region in the lower right represents the age classes that could potentially be affected by the thaw slump.

Research Year	Brood year specific ages and expected research year at maturity										
	Pre-slump brood years				Post-slump brood years						
	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
2004	3	2	1	0							
2005	4	3	2	1	0						
2006	5	4	3	2	1	0					
2007	6	5	4	3	2	1	0				
2008	7	6	5	4	3	2	1	0			
2009	8	7	6	5	4	3	2	1	0		
2010	9	8	7	6	5	4	3	2	1	0	
2011	10	9	8	7	6	5	4	3	2	1	0
2012	11	10	9	8	7	6	5	4	3	2	1
2013	12	11	10	9	8	7	6	5	4	3	2
2014	13	12	11	10	9	8	7	6	5	4	3
2015	14	13	12	11	10	9	8	7	6	5	4
2016	15	14	13	12	11	10	9	8	7	6	5
2017	16	15	14	13	12	11	10	9	8	7	6
2018	17	16	15	14	13	12	11	10	9	8	7
2019	18	17	16	15	14	13	12	11	10	9	8
2020	19	18	17	16	15	14	13	12	11	10	9
2021	20	19	18	17	16	15	14	13	12	11	10
2022	21	20	19	18	17	16	15	14	13	12	11
2023	22	21	20	19	18	17	16	15	14	13	12
2024	23	22	21	20	19	18	17	16	15	14	13
2025	24	23	22	21	20	19	18	17	16	15	14
2026	25	24	23	22	21	20	19	18	17	16	15