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Trends in Length, Weight, and Age of Humpback Whitefish in the Tetlin National Wildlife Refuge, Upper Tanana River Drainage, over a 20-Year Time Period

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Cover Photo: Close-up profile of a Humpback Whitefish *Coregonus pidschian*.

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Randy J. Brown and Katie G. Shink

Abstract

Humpback Whitefish *Coregonus pidschian* is an important subsistence fishery resource for local communities within the upper Tanana River drainage. Community members have expressed concerns to Tetlin National Wildlife Refuge (NWR) staff on perceived declines in size and abundance of Humpback Whitefish in the area. To address these concerns, a study was conducted to evaluate demographic changes in local spawning populations of Humpback Whitefish over a 20-year time period. We compared length distributions, weight at length statistics, survival, and growth of Humpback Whitefish using data collected during two time periods separated by about two decades. The results of this study indicate that present-day Humpback Whitefish are, on average, 16 mm (approximately 4%) smaller, slightly heavier at length, exhibit slower growth, and attain smaller maximum sizes than fish sampled 20 years ago. Despite declining in size in recent years, Humpback Whitefish are currently experiencing greater survival than those 20 years ago. These results support local concerns that Humpback Whitefish appear to be getting smaller, but greater survival indicates that abundance is relatively stable or increasing over time. We hypothesize that late in life density-dependent effects and (or) changing environmental conditions may be influencing size and growth dynamics of these populations. To further evaluate the relationships between high survival, environmental conditions, and growth, it is recommended that otolith growth chronologies be developed and analyzed to determine if regional environmental changes may be influencing the different growth patterns we observed here. In addition, these types of sampling events and analyses are recommended every 10–15 years to develop a longer record of population variation for this important subsistence resource.

Introduction

Humpback Whitefish *Coregonus pidschian* is the major species targeted in subsistence fisheries occurring in and adjacent to the Tetlin National Wildlife Refuge (NWR) in the upper Tanana River drainage. Most subsistence fishing is done by families from the communities of Northway and Tetlin. Case (1986) estimated the average household harvest in Northway was 170 kg per year. Similarly, Halpin (1987) estimated the average household harvest in Tetlin was 258 kg per year. While salmon have been documented in the region, they have never been abundant and are not targeted in the fishery (U.S. Fish and Wildlife Service 1990).

Two spawning populations of Humpback Whitefish have been identified in the Tetlin National Wildlife Refuge, upper Tanana River drainage (Brown 2006). Spawning areas were located in braided regions of the Nabesna River, upstream from the community of Northway, and in the Chisana River in the vicinity of Scottie Creek. Every year, mature Humpback Whitefish congregate in large numbers to spawn in these areas during late September and early October. As

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water temperature declines with approaching winter, spawning fish broadcast eggs and milt into the flowing water where eggs are fertilized and then sink to the bottom and lodge in the gravel substrate (Hart 1930; Teletchea et al. 2009). The eggs incubate in the gravel through the winter, hatch in late winter or spring, and larvae emerge into the river during high flows associated with snowmelt in the spring (Shestakov 1991; Næsje et al. 1995; Bogdanov and Bogdanova 2012). The larval fish are swept away by the current to rearing areas that may be far downstream. Some Humpback Whitefish populations in the Yukon River drainage that spawn as far as 1,700 km upstream from the sea are known to rear in the estuary at the mouth of the Yukon River (Brown et al. 2007). The upper Tanana River spawning areas are over 2,000 km upstream from the sea and these populations do not appear to disperse that far downstream. When young fish mature several years later, they migrate back upstream to their natal origins and spawn in the Nabesna or Chisana rivers. Following spawning, mature Humpback Whitefish remain in the upper Tanana River, overwintering primarily in main-stem reaches of the lower Chisana River and in the Tanana River (Brown 2006). Some also overwinter in Tetlin Lake and some of the deeper lakes in the lower Scottie Creek drainage. With increased spring flows Humpback Whitefish migrate into a wide range of wetland streams and lakes in the upper Tanana River to feed through the summer in these productive habitats. By late summer and early fall feeding fish leave the wetland streams and lakes and move to the large rivers again. Those preparing to spawn migrate to their spawning areas in the Nabesna and Chisana rivers and may wait there for several weeks before spawning. Approximately 70% of mature Humpback Whitefish in the upper Tanana River are thought to spawn each year. Because of this dynamic life history, almost all Humpback Whitefish encountered in the upper Tanana River drainage are mature (Brown 2006).

Residents in the upper Tanana River drainage have recently expressed concerns to Tetlin NWR personnel that Humpback Whitefish appear to be smaller and less abundant than they have been in the past. While spawning habitats and seasonal migrations are thought to be temporally stable, length, weight, and age data can vary over time in response to changing environmental conditions or exploitation levels. In response to residents' concerns, we began a monitoring program to provide quantitative mechanisms to evaluate possible changes in size structure, age, growth, and survival of the Humpback Whitefish populations in the region. We used historical length, weight, and age data originally collected in the late 1990s and early 2000s (Brown 2006) as benchmarks to compare with current data. In turn, these datasets may be used as benchmarks for future studies to monitor and quantify changes over longer periods of time. In this study, we tested null hypotheses that various biological parameters associated with length, weight, and age of Humpback Whitefish in the upper Tanana River drainage are similar now to what they were about 20 years ago.

Study Area

The upper Tanana River drainage in eastern interior Alaska is a complex region of interconnected lake systems, sloughs, and rivers (Figure 1). The region experiences a continental climate, with long cold winters and warm summers (Shulski and Wendler 2007). Annual precipitation in the region averages about 24 cm. Wetland areas occur at relatively high elevations, from 500 to 800 m above sea level, and include many river connected lake and stream systems within the extensive regional floodplains (Glesne et al. 2011). The Nabesna and Chisana rivers are the largest tributaries in the upper Tanana River drainage, flowing north from large glaciers in the Wrangell Mountains immediately to the south (Wiles et al. 2002). Flow from these rivers is turbid during the summer months and clears during the winter (Brabets et al. 2000). The Tanana River originates at the confluence of the Nabesna and Chisana rivers, and shares their annual cycles of turbidity and clarity. Rivers and lakes generally begin freezing by mid-October and remain frozen until late April or May. These three major rivers, along with an assortment of lakes, sloughs, and smaller streams in the region, are the habitats occupied by these Humpback Whitefish populations.

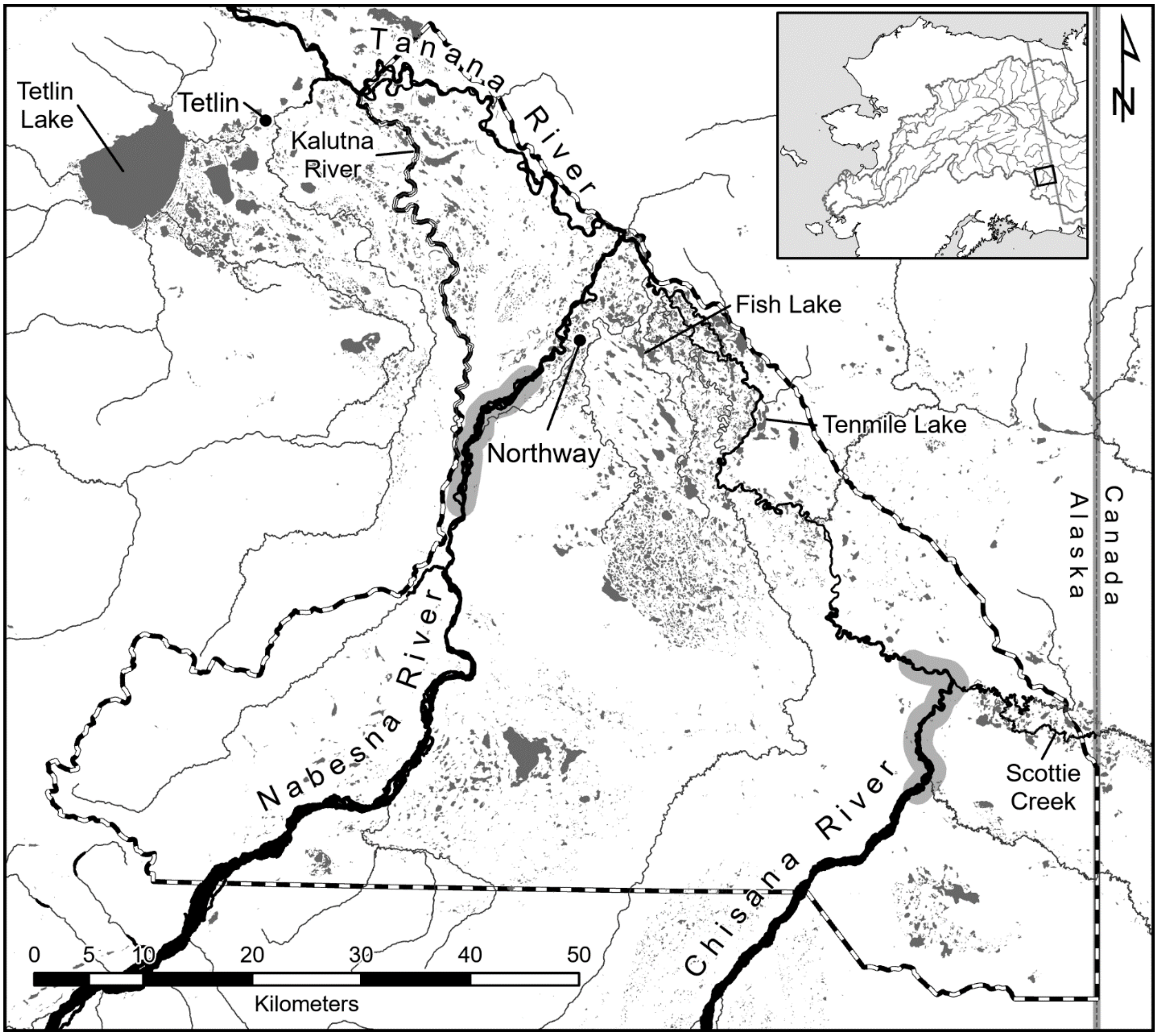

Figure 1. The Tetlin National Wildlife Refuge (dashed boarder) in the upper Tanana River drainage in eastern Alaska, including major rivers, streams, lakes, and wetland systems, and the communities of Northway and Tetlin. Shaded areas represent approximate locations of Humpback Whitefish spawning reaches in the Nabesna and Chisana rivers.

Methods

Overview

To address the fishery concerns of residents in the upper Tanana River drainage, we conducted several analytical tests comparing length, weight, age, and sex data from Humpback Whitefish collected from two time periods. Data collected during the early time period (1998 and 2002; Brown 2006) were compared with similar data collected about 20 years later (2018 and 2019). In 1998 a systematic sampling program was conducted in several sloughs, streams, and lakes in the upper Tanana River drainage during four temporal periods in July and August. Fish were captured with small-mesh gillnets (50 mm stretch-mesh) capable of entangling fish across a wide range of sizes. Samples of fish preparing to spawn were captured with a small-mesh (25 mm stretch-mesh) beach seine in the Nabesna (2002 and 2018) and Chisana (2019) River spawning areas in late September, a season when all spawners within a population are present. During the recent sampling events we sought sample sizes of 200 fish or more to allow parameter and proportion estimates with 95% confidence intervals of about ± 7% of the estimate (Bromaghin 1993), allowing detection of population changes as small as 10% or less. To avoid sampling bias associated with subsampling catches (Hansen et al. 2007), we attempted to sample all fish captured in discreet seine hauls until our 200 fish minimum objective was attained. However, we considered the possibility of very large seine catches. In such an event, we planned to fill a tote capable of holding approximately 150 Humpback Whitefish using large dip nets to subsample multiple fish from various areas of the seine, without pulling the seine too close to shore. Remaining fish could then be released unharmed. These four collections of Humpback Whitefish are considered to be unbiased samples of the fish populations that were present at the times and places of sampling.

Aging of long-lived fish such as Humpback Whitefish generally requires the use of otoliths (Power 1978; Brown et al. 2012), so fish were sacrificed if age data were collected. For every fish, we recorded sex and fork length (FL) to the nearest 5 mm or less. For samples in 1998, 2018, and 2019 we also collected whole body weight to the nearest 10 grams and the head was removed and otoliths collected for aging (Secor et al. 1992). For samples collected in 2018 and 2019, female fish were opened so that egg skeins could be weighed to the nearest 5 grams. The ratio of egg to whole body weight (gonadosomatic index or GSI; Snyder 1983) provides a useful, quantitative index of spawning condition (Brown et al. 2012). We coordinated and worked with residents of the communities of Northway and Tetlin during the recent sampling events to make sure sacrificed fish were put on ice and distributed to community members after sampling had been completed. Data from separate sampling events were then pooled into early (1998 and 2002) and late (2018 and 2019) time periods for subsequent analyses.

Fork length distributions

Fork lengths from the early and late time periods were compared using two analytical methods: (1) a two-sample *t*-test of the null hypothesis that mean FL from the pooled late samples was similar to mean FL from the pooled early samples (Zar 1999); and (2) a two-sample Smirnov test (Conover 1999) of the null hypothesis that length distributions of the two data sets were similar across the full range of lengths. If fish from the later time period were not as large as fish from the early time period, we would observe a significantly smaller mean FL from the pooled late sample, and a FL distribution that was more heavily weighted to the smaller part of the FL range.

Weight-length relationships

Analyzing the weight of fish at 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 samples collected in the upper Tanana River drainage. The equation was algebraically reconfigured to $\log10(W) = \log10\alpha + \beta(\log10(L))$ and calculated as a least-squares linear regression where the $\log10\alpha$ 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. To compare weight and FL relationships between the early and late datasets, we pooled all data in a single power function and compared mean values of standardized residuals (Fechhelm et al. 1995; Pope and Kruse 2007; Brown 2008). Outlier points can disproportionally influence slope and intercept parameters and may not be representative of weight-length relationships of the broader population. Following the methods of Fechhelm et al. (1995), we initially conducted analyses with each of the three data sets with both length and weight, 1998, 2018, and 2019, and censored data points with standardized residuals >3 or <-3.

We then calculated the power function using all weight and FL data together. We used an ANOVA to test the null hypothesis that the mean value of standardized residuals from the pooled 2018 and 2019 collections was similar to that from the 1998 collection. With this analysis, if Humpback Whitefish in the later collections weighed less at a given FL than those in the earlier collection they would have a smaller mean standardized residual.

Aging samples and age distribution

Humpback Whitefish were sampled for aging during two distinct time period; the early period in 1998, and the later period during 2018 and 2019. Brown (2006) originally sampled Humpback Whitefish from several different wetland feeding habitats in the upper Tanana River drainage, but only fish sampled in 1998 were aged. Age data from 1998 were originally available from n = 153 fish subsampled from the larger collection. The dataset was recently expanded to include an additional 93 fish from that collection, increasing the total aged sample from 1998 to n = 246. This sample was a mix of fish from the two spawning populations. Samples were later collected from spawning aggregations in the Nabesna (2018) and Chisana (2019) rivers, which were population specific samples.

Otoliths were ground into thin transverse sections in preparation for aging (Secor et al. 1992). Sectioned otoliths were viewed with transmitted light on a compound microscope. Annuli were identified and counted as described and illustrated by Chilton and Beamish (1982). Age distributions of long-lived fishes such as Humpback Whitefish are commonly skewed to the right (Morin et al. 1982; Mills et al. 2004; Sutton and Edenfield 2012). Because of the non-normal distribution, we used a Kruskal-Wallace nonparametric rank test of the null hypothesis that the age distribution from fish collected in the late period were similar to the age distribution of fish collected in the early period.

Annual survival estimates

Age structure data such as these can be used to estimate the annual survival rate of a population based on the understanding that the mode of the distribution is the age at which most fish recruit to the spawning population. Subsequent declines in frequency with increasing age are the result of progressive mortality over time (Robson and Chapman 1961; Hilborn and Walters 1992). This analysis is most effective for populations in which production and subsequent recruitment are reasonably stable from year to year. Brown (2006) argued that this was a reasonable assumption based on multiple sources of information. He used Robson and Chapman's (1961) method and estimated annual survival from the original 1998 sample to be S_O = 0.69 with a 95% CI from 0.64–0.74, which was consistent with a population experiencing low exploitation. We similarly estimated annual survival from the expanded early sample and the pooled late sample and used a two-sample t-test of the null hypothesis that annual survival in the late time period was equal to annual survival in the early time period (Zar 1999). If the current annual survival is less than annual survival of 20 years ago, whether because of an increase in natural mortality or an increase in exploitation level, we should see a reduction in the proportion of older fish in the age distribution and a steeper catch curve.

Growth

Length at age data can be used to describe growth over time using von Bertalanffy's growth equation $L_t = L_\infty(1-e^{(-K(t-t_o))})$, where L_t is the FL at time t, L_∞ is the fitted value of maximum FL in the population, K is Brody's growth coefficient, and t_o is the hypothetical age when FL = 0 (Chen et al. 1992; Isely and Grabowski 2007). To estimate which values of L_∞, K, and t_o best describe length at age data from Humpback Whitefish samples collected in early and late time periods, a total of eight growth models were iteratively fit using the *FSA* (Ogle et al. 2019) and *nlstools* (Baty et al. 2015) packages within the statistical program R (R Core Team 2019). The full model allowed each parameter to vary for both time periods, while the null model assumed identical parameters for both early and late collections. Remaining models allowed either one or two parameters to vary while the remaining parameter(s) were held constant. To compare model fit, pairwise comparisons of model performance were conducted using ANOVA and all models were ranked using AIC. Final growth equations were plotted to visualize growth patterns for sampled fish from each time period. If fish are not getting as large as they were previously, we should see a smaller value of L_∞ for samples collected in the later period. If fish are still getting as large but growing slower, than we should see similar values of L_∞ but a smaller value of K for samples collected in the later period.

Results

Overview

On September 24, 2018, we set a beach seine twice in the core region of the Nabesna River Humpback Whitefish spawning area and captured 223 Humpback Whitefish (Table 1), one Arctic Grayling *Thymallus arcticus*, and four Round Whitefish *Prosopium cylindraceum*. All Humpback Whitefish had breeding tubercles indicating that they were preparing to spawn (Vladykov 1970). Milt could be expressed from many males when handled but eggs were still bound in skeins at the time of sampling for almost all females and could not be expressed from the fish when handled, indicating that spawning time was still at least a few days away. Of the 223 fish captured, 151 were female (68%) and 72 were male (32%). The predominance of females was also observed in the 2002 sampling data from the Nabesna River spawning area where sex was determined for 393 fish, 310 were females (79%) and 83 were males (21%).

Table 1. Sample sizes of data collected on Humpback Whitefish, in relation to total number of fish (*N*) captured during a sampling event, in the upper Tanana River drainage from 1998–2019. Feeding samples were collected during July and August in foraging habitats and were a mix of individuals from Nabesna and Chisana River spawning populations. Spawning samples collected in late September in the Nabesna (2002 and 2018) and the Chisana (2019) River spawning areas were individuals from a single spawning population.

Year	Period	Demographics	FL	Wt	Sex	Age	*N*
1998	Early	Feeding	274	270	269	246	275
2002	Early	Spawning	215	0	393	0	396
2018	Late	Spawning	223	223	223	223	223
2019	Late	Spawning	217	217	217	215	217

A beach seine was set four times in the core region of the Chisana River Humpback Whitefish spawning area September 27–29, 2019. A total of 217 Humpback Whitefish (Table 1) and >50 Longnose Suckers *Catostomus catostomus* were captured. All but one Humpback Whitefish had breeding tubercles indicating that nearly all fish were preparing to spawn (Vladykov 1970). Milt and eggs could not be easily expressed from most fish when handled, suggesting spawning was at least a few days away. Of the 217 fish captured, 137 were male (63%) and 80 were female (37%). The proportion of female fish was considerably lower than proportions observed during sampling events on the Nabesna River spawning grounds in 2002 and 2018.

Gonadosomatic index

The GSI of female Humpback Whitefish collected from the spawning areas in the Nabesna and Chisana rivers indicated that all except one were preparing to spawn. Non-spawning females have GSI values that almost never exceed 0.03 (Brown et al. 2012). A single non-spawning female was collected on the Chisana River spawning area with no breeding tubercles and a GSI value of 0.01. All other females had breeding tubercles and GSI values much greater than 0.03. The mean GSI value from Nabesna River females (0.192, SE = 0.003, n = 148) was significantly greater than for Chisana River females (0.163, SE = 0.004, n = 77; t_{223} = 5.63, P < 0.001).

Fork length distributions

Mean FL of Humpback Whitefish from the early (n = 489) and late (n = 440) time period was 401.0 mm (SE = 1.41) and 384.8 mm (SE = 1.39), respectively (Figure 2). A t-test of the null hypothesis that mean values of the two collections were similar was rejected at α = 0.05 (t_{927} = 8.15, P < 0.001). The FL distributions clearly illustrated fish ≥450 mm FL are poorly represented in the late sample, only 2.7%, when compared to the early sample at 6.5%. The Smirnov test of similar distributions was based on the maximum difference between the two cumulative distribution functions, which occurred at a FL of 375 mm (Figure 3). The two-sample Smirnov test failed to support the null hypothesis that the two distributions were similar (D_{MAX} = 0.227, P < 0.001). The α = 0.05 critical point for D, given our sample sizes and using the large sample approximation, was w_p = 0.089 (Conover 1999). These two corroborating methods of testing hypotheses related to length, indicate that Humpback Whitefish are now, on average, 16 mm smaller than they were 20 years ago.

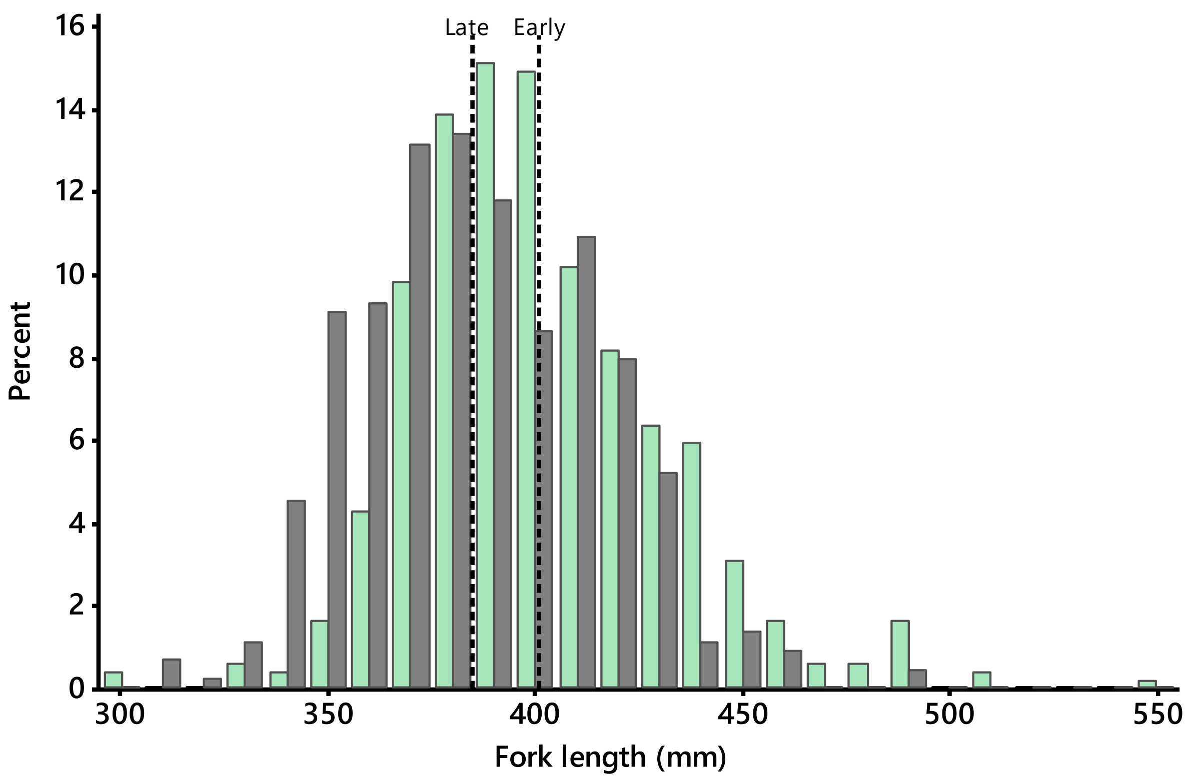

Figure 2. Fork length distributions of Humpback Whitefish from early (light green bars) and late (dark gray bars) time periods. Mean FL for the early (*n* = 489) and late (*n* = 440) collections (vertical dashed lines) were 401.0 mm (SE = 1.41) and 384.8 mm (SE = 1.39), respectively.

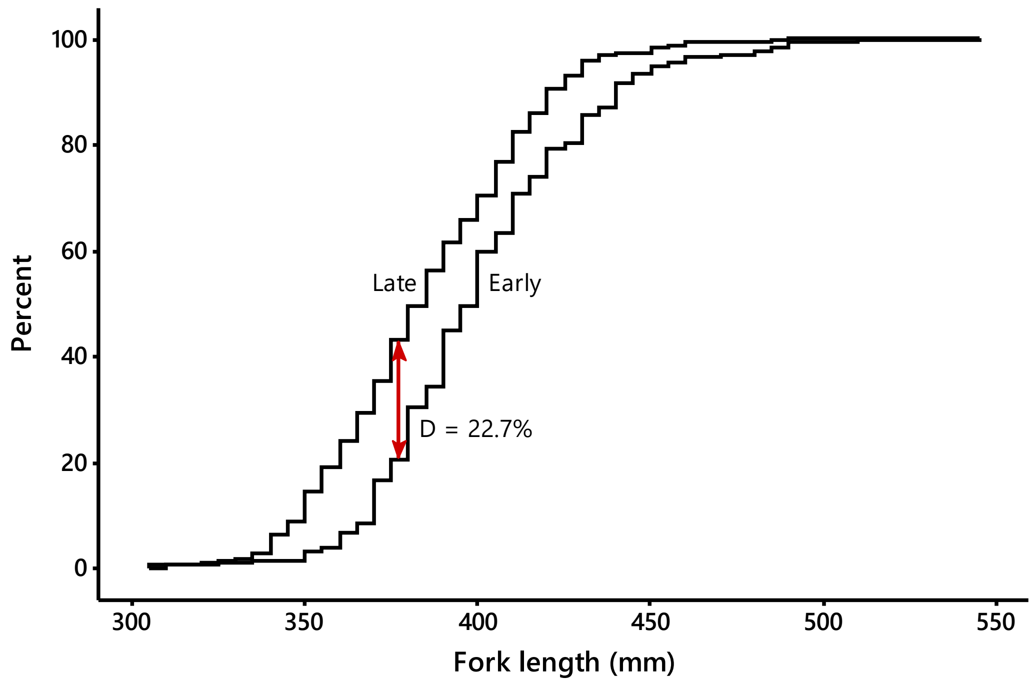

Figure 3. Cumulative distribution functions of Humpback Whitefish FL from early and late time periods. The Smirnov statistic of similar distributions was based on the maximum difference between the two functions, which occurred at a fork length of 375 mm (red arrow).

Weight-length relationships

Initial least squares linear regressions of the weight-length power function of each collection individually revealed a total of seven individuals (1% of the dataset) from the early (n = 4) and late (n = 3) collections had standardized residuals >3 SD above or below the mean. These seven data points were censored and a pooled linear regression was calculated. An ANOVA comparing mean standardized residuals of the early (mean = -0.1662, SE = 0.0754) and late (mean = 0.1013, SE = 0.0391) collections in this pooled regression revealed subtle but significant differences (F_{701} = 12.00, P = 0.001), indicating that fish in the earlier collection weighed slightly less overall at a given length than fish in the later collection (Figure 4). Linear regressions of weight at length were conducted for each time period separately to illustrate the subtle differences in weight-length relationships and estimate separate power functions for the early (W = 0.0000035*($L^{3.206}$)) and late (W = 0.0000315*($L^{2.8446}$)) time periods.

Age distributions

The median ages of Humpback Whitefish samples collected in 2018 (n = 223; median age = 9; age range = 4–21) and 2019 (n = 215; median age = 10; age range = 3–22) were not significantly different (Kruskal-Wallis χ^2 = 0.42, P = 0.519). This pooled collection was considered to represent the most recent age distribution. A comparison of median ages from the early (n = 246; median age = 6; age range = 2–26) and the pooled late (n = 438; median age = 9; age range = 3–22) periods were significantly different (Kruskal-Wallis χ^2 = 114.23, P < 0.001). While the early collection included the oldest fish of the group at age 26, the age histograms of the two collections revealed that the early samples declined more precipitously on the right side of the mode than the late samples (Figure 5), indicating a lower survival rate experienced by fish collected about 20 years ago.

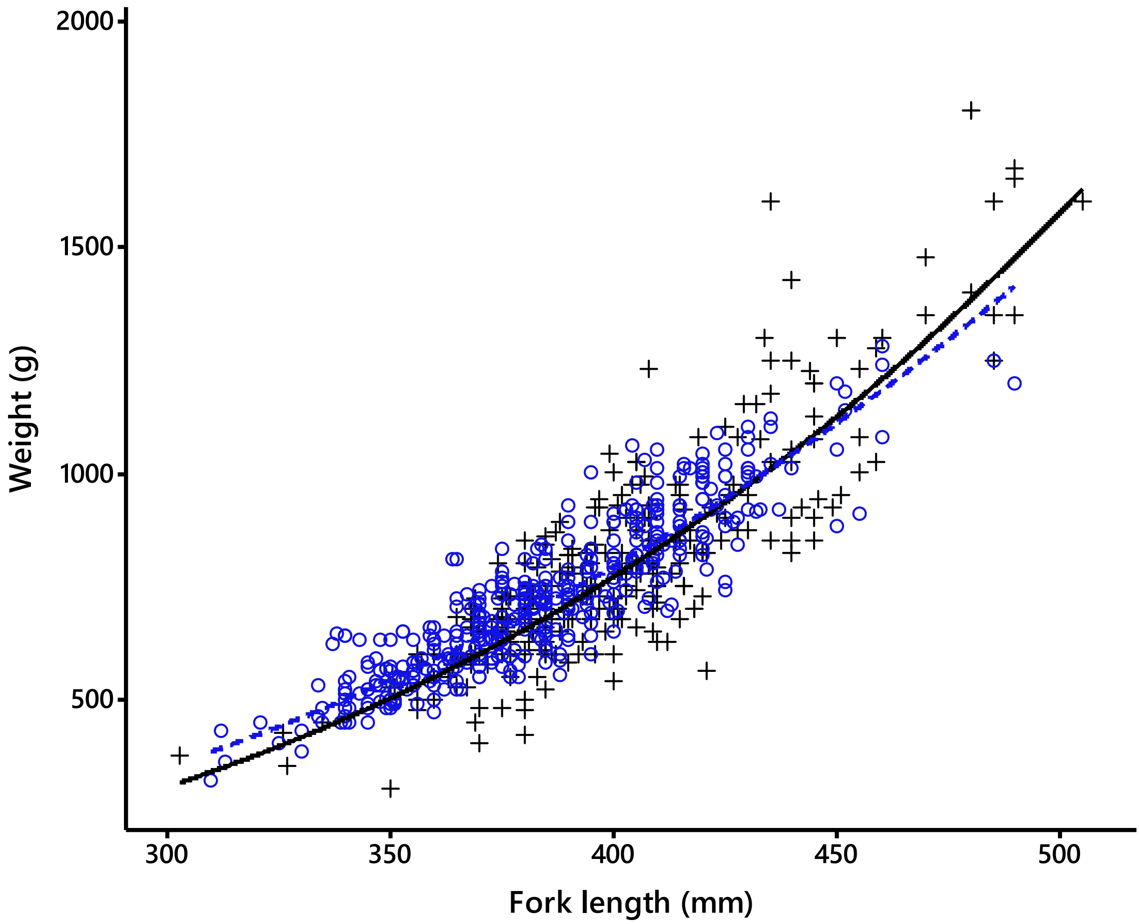

Figure 4. Weight at length regression for Humpback Whitefish from the early collection in 1998 (*n* = 266; black line and crosses) and the pooled later collection (blue dashed line and circles) from 2018 (*n* = 223) and 2019 (*n* = 214).

Annual survival estimates

We used Robson and Chapman's (1961) catch curve method to estimate annual survival for the early (S_E = 0.692, 95% CI = 0.656–0.729) and late (S_L= 0.787, 95% CI = 0.767–0.806) sample groups (Figure 5). These estimates indicated that fish captured in the later period had significantly greater annual survival than fish captured 20 years ago (t_{309} = -4.47, $P < 0.001$). Both groups, however, experienced survival rates consistent with populations experiencing low exploitation (Mills and Beamish 1980; Mills et al. 2004).

Growth

We used our age and FL data to calculate von Bertalanffy growth functions (Chen et al. 1992; Isely and Grabowski 2007) for the early and late sample groups. Pairwise model comparisons and AIC ranking indicated growth of Humpback Whitefish was best described by separate values of L_∞, K, and t_o for each sample group. Fork length (mm) at age was best fit for the early collection (*n* = 245) with the growth equation: $FL = 539.8721*(1-e^{(-0.0566*(age+17.5367))})$. For the late collection (*n* = 438), fork length at age was best fit with the growth equation: $FL = 418.9438*(1-e(^{-0.1918*(age+4.5339)}))$. Notably, the maximum average size of Humpback Whitefish in the early sample group (L_∞ = 539.872 mm; SE = 49.402) was greater than the late sample group (L_∞ = 418.944 mm; SE = 5.460). The growth coefficients that best fit these early and late datasets were K_E = 0.0566 (SE = 0.023) and K_L = 0.1918 (SE = 0.0.033), respectively. These results indicate that fish collected 20 years ago attained greater length at age and greater maximum sizes, but reached them at slower rates, when compared to fish collected in recent sampling events (Figure 6).

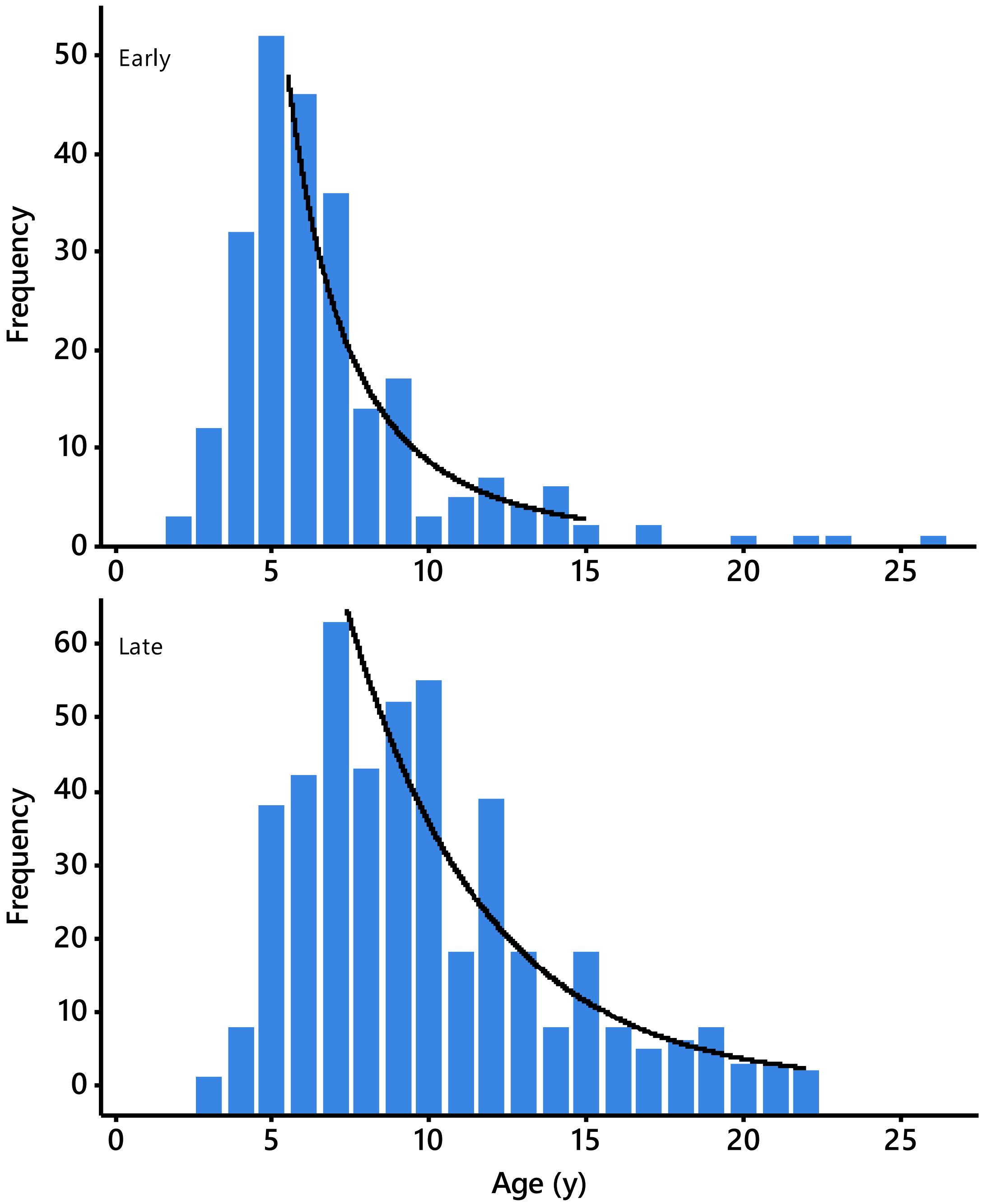

Figure 5. Age histograms from samples collected in the early (*n* = 246) and late (*n* = 438) time periods. Annual survival was estimated to be S_E = 0.692 for the early time period and S_L = 0.787 for the late time period. The declining curves (dark lines) for each data set illustrate average mortality over time following full recruitment.

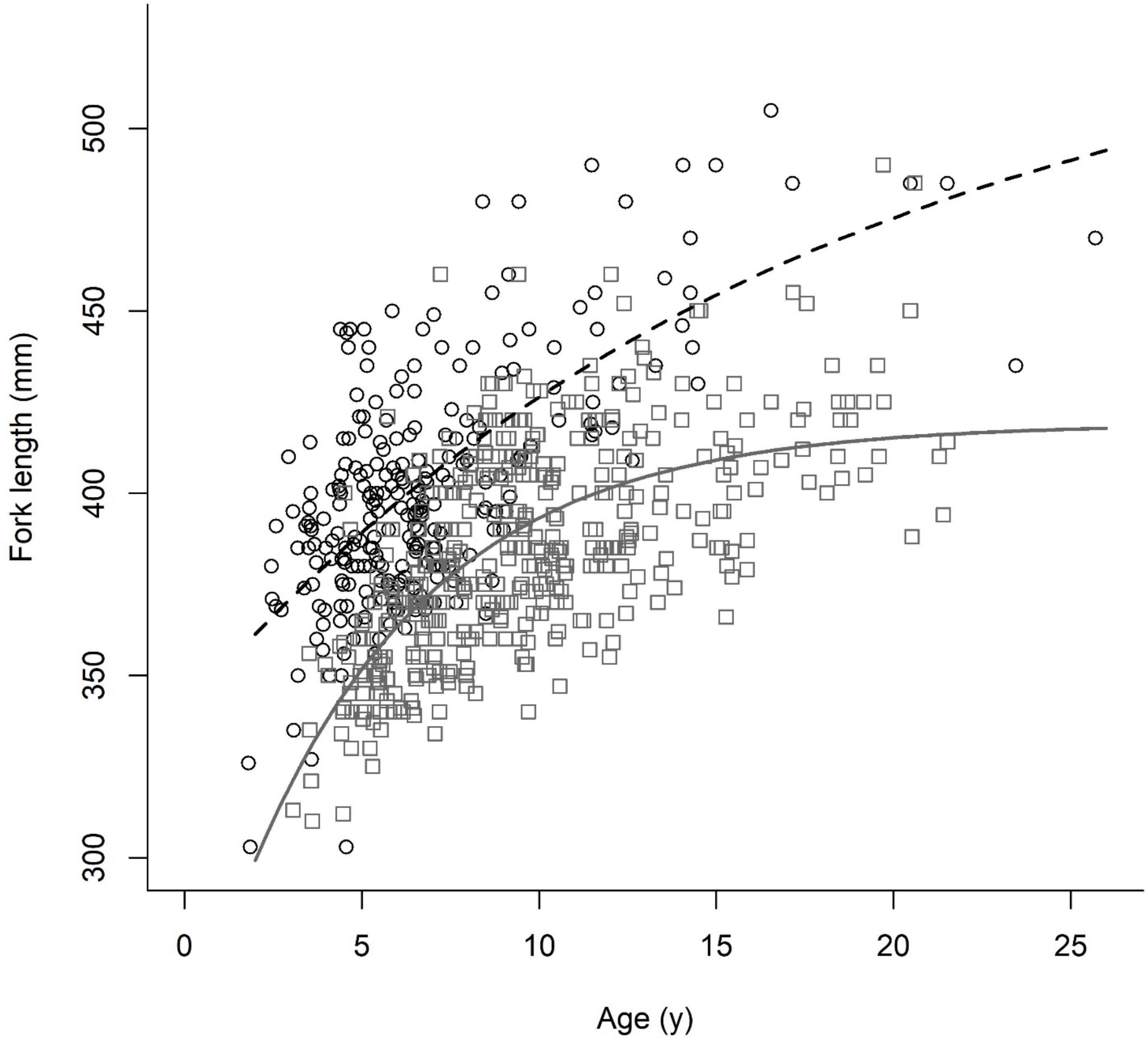

Figure 6. Von Bertalanffy growth curves for the early (*n* = 245; black circles and dashed line) and late (*n* = 438; gray squares and solid line) collections.

Discussion

People from the communities of Northway and Tetlin expressed concerns recently regarding perceived declines in size and abundance of Humpback Whitefish, an important subsistence resource in the region (Robinson et al. 2009; Godduhn and Kostick 2016). To address these concerns, a comparative study was conducted to evaluate changes in length, weight, and age that may have taken place since the last major sampling events about 20 years ago. Samples were originally collected in feeding habitats in 1998 and from the Nabesna River spawning population in 2002. We subsequently collected additional samples in 2018 and 2019 from spawning populations in the Nabesna and Chisana rivers, respectively. Because of unique features of Humpback Whitefish life history in the terminal reaches of the upper Tanana River drainage, as detailed earlier, we consider these sample groups representative of the regional populations during these early and late time periods.

Our data indicate that present-day Humpback Whitefish are smaller, on average, than when sampled 20 years ago. However, the difference in mean size of Humpback Whitefish between the two time periods, about 16 mm or 4% of average length, is not thought to be a particularly important biological issue for a fish of this size. A mean size difference of just under 20 mm was reported for a spawning population of Humpback Whitefish from samples collected a decade apart in the Chatanika River in the lower Tanana River drainage (Fleming 1999; Sutton and Edenfield 2012). That population was similarly experiencing low levels of exploitation at the time due to newly established harvest regulations that were more restrictive than before (Brase 2008), suggesting the size difference observed in this study may be within measures of natural variation for regional populations of Humpback Whitefish. We might be more concerned if we observed a size difference of between 50 and 100 mm because size declines of this magnitude have previously been attributed to largely unregulated fishing and high exploitation rates of Humpback Whitefish in Alaska (Fleming 1999). For example, the difference in mean size of Humpback Whitefish before (mean FL = 392 mm; Hallberg 1988) and after (mean FL = 445 mm; Sutton and Edenfield 2012) restrictive harvest regulations were established was just over 50 mm. This comparison illustrates how high exploitation rates in minimally regulated fisheries can impact size of Humpback Whitefish beyond the range of natural variation. These previous studies and our results suggest that the differences in mean size of Humpback Whitefish in the upper Tanana River drainage are within the range of variation we could expect from natural processes. However, if this declining size trend continues over the coming decades it may become more of a concern.

High survival rate estimates of Humpback Whitefish in the upper Tanana River drainage indicate that exploitation and natural mortality are relatively low. This was illustrated in the age histograms from the early and late sampling periods, in which a much larger component of older individuals, ≥15 years of age, was apparent (Figure 5). In addition, neither age histogram suggested brood year failures during either time period, which indicates relatively stable annual recruitment over the course of about four decades. Survival and recruitment patterns observed in this study are consistent with other populations of Lake Whitefish *C. clupeaformis* and Lake Trout *Salvelinus namaycush* experiencing low exploitation (Mills and Beamish 1980; Mills et al. 2002, 2004). Differences in annual survival estimates between the two time periods may be within the range of natural variation experienced by Humpback Whitefish in the region. For example, distinct sampling efforts within the Chatanika River, Alaska, produced annual survival estimates of 69% and 85% for a local population of Humpback Whitefish (Fleming 1994; Sutton and Edenfield 2012). However, differences in annual survival estimates between the two time periods may also reflect a decline in local fishing effort. Although Humpback Whitefish continue to be an important subsistence resource for nearby communities (Robinson et al. 2009), recent harvest surveys indicate that annual mean household harvest of whitefish in Northway has declined from 170 kg to 124 kg (Case 1986; Godduhn and Kostick 2016). Thus, it seems unlikely that excessive fishing pressure or existing sources of natural mortality are significantly impacting the abundance of Humpback Whitefish in the upper Tanana River drainage at this time.

Length at age data for Humpback Whitefish within the upper Tanana River drainage indicate that in years prior to the 1998 collection, fish were larger at a given age, a growth trend that persisted through life, when compared to later collections (Figure 6). This change in growth over time is consistent with concerns expressed that present-day Humpback Whitefish are smaller than in the past. The patterns observed in our data (i.e., high survival, steady recruitment, and decreased size and growth) resemble those of a population experiencing density dependence, where competition for limited resources limits growth (Jensen 1981; Lorenzen and Enberg 2002). Adult biomass has often been identified as a growth-regulating mechanism in coregonid populations (Healy 1980; Klein 1992; Mills et al. 1995; Mayr 2001). Increased intraspecific competition for limited food and habitat resources restricts growth potential for members of a population during periods of high survival and stable environmental conditions. Habitat size can also impact the degree to which populations are regulated by late in life density dependence, with more pronounced effects observed in populations that occupy habitats with limited capacity such as lakes (Andersen et al. 2017). Few, if any, Humpback Whitefish in the upper Tanana River drainage are anadromous (Brown et al. 2007), increasing the concentration of individuals within a limited number of feeding areas (Brown 2006). Humpback Whitefish exhibit relatively high fidelity to specific feeding areas, a behavior that reduces dispersal opportunities to find more productive feeding habitat. As more individuals recruit to the population, without the compensatory effects of mortality, greater numbers of fish are competing for food within the geographically limited system in the upper Tanana River drainage. Food availability may disproportionally affect the body condition of larger fish that need additional resources to maintain weight. Late in life density-dependent effects can be offset by reducing population density, generally achieved with increased fishing effort (Healy 1980; Mills et al. 1995). Given the observed characteristics, it seems plausible that late in life density dependence could be a mechanism regulating the growth of Humpback Whitefish in the region.

A second potential cause of growth declines of Humpback Whitefish populations within the upper Tanana River drainage may be changing environmental conditions. It is recognized that environmental conditions are changing more rapidly in Alaska when compared to more southerly areas of North America (Chapin et al. 2014). Residents of upper Tanana River communities have hypothesized that increased sedimentation in some traditional fishing areas, such as the Mark Creek–Fish Lake area near the community of Northway, has reduced habitat quality and food availability for Humpback Whitefish (Robinson et al. 2009). If environmental conditions were affecting habitat suitability and prey availability of Humpback Whitefish, fish would likely experience increased competition and decreased growth rates (length at age) compared to the earlier time period. However, identifying the relationship between climate and growth is increasingly difficult to assess due to confounding effects of age and growth in long-lived fishes (Black et al. 2005). Similar to other coregonid fishes, Humpback Whitefish experience several years of rapid growth early in life after which growth declines and eventually plateaus as fish become older, as illustrated by Power (1978). Growth-increment chronologies using otoliths (i.e., measuring widths of annual otolith growth rings) is a validated method that has been successfully used to document the growth response of fish to annually variable environmental conditions (Black et al. 2005, 2013; Matta et al. 2010). To better understand the degree to which climate has affected the growth of Humpback Whitefish in the upper Tanana River drainage, we recommend using similar methods to evaluate differences in growth between the two time periods. This additional analysis may help to clarify the relationships between high survival, environmental conditions, and growth.

Recommendations

There does not appear to be an immediate concern regarding the status of Humpback Whitefish populations in the upper Tanana River drainage. We see no evidence of overexploitation of these populations in the upper Tanana River drainage. Observed changes in length structure and growth patterns between sampling events, however, suggest that these populations vary naturally in response to harvest practices and environmental variation. We recommend that sampling events be conducted every 10–15 years, if possible, to create a multi-decade record of demographic variation for these Humpback Whitefish populations in the Nabesna and Chisana rivers. Additional or more frequent sampling events may contribute to a more refined understanding of natural variability in growth and recruitment of these two spawning populations. More extensive population work, perhaps even abundance estimates, might be appropriate if future sampling events indicate marked decreases in survival or growth. We hypothesize that the decrease in average length overall and length at age observed between our early and late samples may be due to density dependent effects or less productive environmental conditions, both of which could result in increased competition for resources. We recommend an additional set of analyses using otolith growth chronologies to better understand the role of environmental conditions on growth of Humpback Whitefish. This analysis can be conducted using existing archived otoliths and does not require additional sampling efforts.

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References

Andersen, K. H., N. S. Jacobsen, T. Jansen, and J. E. Beyer. 2017. When in life does density dependence occur in fish populations? Fish and Fisheries 18:656–667.

Baty, F., C. Ritz, S. Charles, M. Brutsche, J-P Flandrois, and M-L Delignette-Muller. 2015. A Toolbox for Nonlinear Regression in R: The Package nlstools. Journal of Statistical Software 66:1–21.

Black, B. A., G. W. Boehlert, and M. M. Yoklavich. 2005. Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. Canadian Journal of Fisheries and Aquatic Sciences 62:2277–2284.

Black, B. A., V. R. von Biela, C. E. Zimmerman, and R. J. Brown. 2013. Lake Trout otolith chronologies as multidecadal indicators of high-latitude freshwater ecosystems. Polar Biology 36:147–153.

Bogdanov, V. D., and E. N. Bogdanova. 2012. Ecological aspects of larval drift in coregonids with long migration routes. Russian Journal of Ecology 43:315–322.

Brabets, T. P., B. Wang, and R. H. Meade. 2000. Environmental and hydrologic overview of the Yukon River basin, Alaska and Canada. U.S. Geological Survey, Water-Resources Investigations Report 99-4204.

Brase, A. L. J. 2008. Fishery management report for recreational fisheries in the lower Tanana River Management Area, 2006. Alaska Department of Fish and Game, Division of Sport Fish, Fishery Management Report No. 08-27, Anchorage.

Bromaghin, J. F. 1993. Sample size determination for interval estimation of multinomial probabilities. The American Statistician 47:203-206.

Brown, R. J. 2006. Humpback Whitefish *Coregonus pidschian* of the upper Tanana River drainage. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report Number 90, Fairbanks.

Brown, R. J. 2008. Life history and demographic characteristics of Arctic Cisco, Dolly Varden, and other fish species in the Barter Island region of northern Alaska. U.S. Fish and Wildlife Service, Alaska Fisheries Technical Report Number 101, Fairbanks.

Brown, R. J., N. Bickford, and K. Severin. 2007. Otolith trace element chemistry as an indicator of anadromy in Yukon River drainage coregonine fishes. Transactions of the American Fisheries Society 136:678–690.

Brown, R. J., C. Brown, N. M. Braem, W. K. Carter III, N. Legere, and L. Slayton. 2012. Whitefish biology, distribution, and fisheries in the Yukon and Kuskokwim River drainages in Alaska: a synthesis of available information. U.S. Fish and Wildlife Service, Alaska Fisheries Data Series 2012-4, Fairbanks.

Case, M. 1986. Wild resource use in Northway, Alaska. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper No. 132, Fairbanks.

Chapin, F. S. I., S. F. Trainor, P. Cochran, H. Huntington, C. J. Markon, M. McCammon, A. D. McGuire, and M. Serreze. 2014. Alaska. Pages 514–536 *in* J. M. Melillo, T. Richmond, and G. W. Yohe, editors. Climate change impacts in the United States: the third National Climate Assessment. U. S. Global Change Research Program, Washington D. C.

Chen, Y., D. A. Jackson, and H. H. Harvey. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Canadian Journal of Fisheries and Aquatic Sciences 49:1228–1235.

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

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

Fechhelm, R. G., W. B. Griffiths, W. J. Wilson, B. J. Gallaway, and J. D. Bryan. 1995. Intra- and inter-seasonal changes in the relative condition and proximate body composition of Broad Whitefish from the Prudhoe Bay region of Alaska. Transactions of the American Fisheries Society 124:508–519.

Fleming, D. F. 1994. Stock assessment and relative age validation of Humpback Whitefish and Least Cisco in the Chatanika River during 1993. Alaska Department of Fish and Game, Division of Sport Fish, Fishery Data Series No. 94-41, Anchorage.

Fleming, D. F. 1999. Stock monitoring of whitefish in the Chatanika River during 1998. Alaska Department of Fish and Game, Division of Sport Fish, Fishery Data Series No. 99-18, Anchorage.

Glesne, R. S., W. K. Carter, and D. W. Daum. 2011. Lake habitat and fish surveys on interior Alaska National Wildlife Refuges, 1984–1986. U.S. Fish and Wildlife Service, Alaska Fisheries Data Series Number 2011-12, Fairbanks, Alaska.

Godduhn, A. R., and M. L. Kostick. 2016. Harvest and use of wild resources in Northway, Alaska, 2014, with special attention to nonsalmon fish. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper No. 421, Fairbanks.

Hallberg, J. E. 1988. Abundance and size composition of Chatanika River Least Cisco and Humpback Whitefish with estimates of exploitation by recreational fishermen. Alaska Department of Fish and Game, Division of Sport Fish, Fishery Data Series No. 61, Juneau.

Halpin, L. 1987. Living off the land: contemporary subsistence in Tetlin, Alaska. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper No. 149, Fairbanks.

Hansen, M. J., T. D. Beard, Jr., and D. B. Hayes. 2007. Sampling and experimental design. Pages 51–120 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Hart, J. L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (Mitchill), in the Bay of Quinte, Ontario. Contributions to Canadian Biology and Fisheries VI:167–214.

Healy, M. C. 1980. Growth and recruitment in experimentally exploited Lake Whitefish (*Coregonus clupeaformis*) populations. Canadian Journal of Fisheries and Aquatic Sciences 37:255–267.

Hilborn R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics & uncertainty. Chapman and Hall, New York.

Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187–228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Jensen, A. L. 1981. Population regulation in Lake Whitefish, *Coregonus clupeaformis* (Mitchill). Journal of Fish Biology 19:557–573.

Klein, M. 1992. Effect of exploitation on growth, age-structure, and recruitment of an underfished population of European Whitefish. Polish Archives of Hydrobiology 39:807–815.

Lorenzen, K, and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London B 269:49–54.

Matta, M. E., B. A. Black, and T. K. Wilderbuer. 2010. Climate-driven synchrony in otolith growth-increment chronologies for three Bering Sea flatfish species. Marine Ecology Progress Series 413:137–145.

Mayr, C. 2001. The influence of population density on growth of whitefish (*Coregonus laveretus* L.) in four prealpine lakes. Limnologica 31: 53–60.

Mills, K. H., and R. J. Beamish. 1980. Comparison of fin-ray and scale age determinations for Lake Whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. Canadian Journal of Fisheries and Aquatic Sciences 37:534–544.

Mills, K. H., S. M. Chalanchuk, and D. J. Allan. 2002. Abundance, annual survival, and recruitment of unexploited Lake Charr, *Salvelinus namaychush*, populations at the experimental lakes area, northwestern Ontario. Environmental Biology of Fishes 64:281–292.

Mills, K. H., S. M. Chalanchuk, D. J. Allan, and L. C. Mohr. 1995. Responses of Lake Whitefish (*Coregonus clupeaformis*) to exploitation at the experimental lakes area, northwestern Ontario. Archive for Hydrobiology 46:361–368.

Mills, K. H., E. C. Gyselman, S. M. Chalanchuk, and D. J. Allan. 2004. Growth, annual survival, age and length frequencies for unexploited Lake Whitefish populations. Annales Zoologici Fennici 41:263–270.

Morin, R., J. J. Dodson, and G. Power. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), Lake Whitefish (*C. clupeaformis*), and Round Whitefish (*Prosopium cylindraceum*) populations of eastern James-Hudson Bay. Canadian Journal of Fisheries and Aquatic Sciences 39:958–967.

Næsje, T. F., B. Jonsson, and J. Skurdal. 1995. Spring flood: a primary cue for hatching of river spawning Coregoninae. Canadian Journal of Fisheries and Aquatic Sciences 52:2190–2196.

Ogle, D. H., P. Wheeler, and A. Dinno. 2019. FSA: Fisheries Stock Analysis. R package version 0.8.25.

Pope, K. L., and C. G. Kruse. 2007. Condition. Pages 423–471 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Power, G. 1978. Fish population structure in Arctic lakes. Journal of the Fisheries Research Board of Canada 35:53–59.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Robinson, M., P. Morrow, and D. Northway. 2009. Gender, knowledge, and environmental change related to Humpback Whitefish in interior Alaska. Pages 109–128 *in* J. Kafarowski, editor. Gender, Culture, and Northern Fisheries. Canadian Circumpolar Institute, Edmonton, Alberta.

Robson, D. S., and D. G. Chapman. 1961. Catch curves and mortality rates. Transactions of the American Fisheries Society 90:181–189.

Secor, D. H., J. M. Dean, and E. H. Laban. 1992. Otolith removal and preparation for microstructural examination. Pages 19–57 *in* D. K. Stevenson, and S. E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

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

Shulski, M., and G. Wendler. 2007. The climate of Alaska. University of Alaska Press, Fairbanks.

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

Sutton, T. M., and L. E. Edenfield. 2012. Stock characteristics of Humpback Whitefish and Least Cisco in the Chatanika River, Alaska. Arctic 65:67–75.

Teletchea, F., A. Fostier, E. Kamler, J.-N. Gardeur, P.-Y. Le Bail, B. Jalabert, and P. Fontaine. 2009. Comparative analysis of reproductive traits in 65 freshwater fish species: application to the domestication of new fish species. Reviews in Fish Biology and Fisheries 19:403–430.

U.S. Fish and Wildlife Service. 1990. Fishery management plan Tetlin National Wildlife Refuge. Fairbanks Fishery Resource Office, Fairbanks, Alaska.

Vladykov, V. D. 1970. Pearl tubercles and certain cranial peculiarities useful in the taxonomy of coregonid genera. Pages 167-193 *in* C. C. Lindsey and C. S. Woods, (editors). Biology of coregonid fishes. University of Manitoba Press, Winnipeg.

Wiles, G. C., G. C. Jacoby, N. K. Davi, and R. P. McAllister. 2002. Late Holocene glacier fluctuations in the Wrangell Mountains, Alaska. Geological Society of America Bulletin 114:896–908.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.