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Yukon River Bering Cisco: A Biological Analysis of the Spawning Population

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ABSTRACT. Bering cisco *Coregonus laurettae* is an anadromous coregonine endemic to three rivers in Alaska: the Yukon River and the Kuskokwim River, which flow to the Bering Sea, and the Susitna River that flows to Cook Inlet. Recent research on Bering cisco was initiated in response to a commercial fishery that began in 2005 at the mouth of the Yukon River and operated for 15 years. Biological data were collected across their range in the Yukon River, but no comprehensive analyses have been published. Here we use these data to conduct basic analytical procedures to gain a better understanding of the biology of the species. Specifically, we identify migration timing, reproductive details, age and growth patterns, and survival. The spawning migration passed a test fish wheel located 1176 km from the sea was present throughout the summer but was strongest from mid-July to mid-August. Spawning took place in October in a braided main-stem reach between 1600 km and 1700 km from the sea. Ovaries of pre-spawning females grew over the summer to as much as 40% of whole-body weight at spawning time. Minimum age at maturity was age three, and few individuals attained an age of 10 years or more. Bering cisco did not feed during the spawning migration. The species grew rapidly for four to six years and exhibited minimal growth after that. Annual survival was estimated to be 61%. Those that survived spawning migrated back to sea to feed and prepare for another spawning event. The data we present here offer new insights into the biology of this extraordinary species, which is truly unique among Alaska coregonines.

Keywords: Bering cisco; *Coregonus laurettae*; Alaska; Yukon River; spawning migration

RÉSUMÉ. Le cisco de Béring *Coregonus laurettae* est une espèce anadrome de la famille des corégones, endémique de trois cours d'eau en Alaska, soit les fleuves Yukon et Kuskokwim, qui se jettent dans la mer de Béring, et la rivière Susitna, qui se déverse dans le Cook Inlet. Des recherches récentes sur le cisco de Béring ont été entreprises en réponse à une pêche commerciale qui a débuté en 2005 à l'embouchure du fleuve Yukon, pêche qui s'est poursuivie pendant 15 ans. Des données biologiques ont été recueillies sur l'ensemble de son aire de répartition dans le fleuve Yukon, mais aucune analyse exhaustive n'a été publiée. Ici, nous utilisons ces données pour effectuer des procédures de base afin de mieux comprendre la biologie de cette espèce. Plus précisément, nous déterminons le moment de la migration, les détails de reproduction, les schémas d'âge et de croissance ainsi que la survie de l'espèce. La migration de frai, observée à l'aide d'un tourniquet à poisson situé à 1 176 km de la mer, a eu lieu tout au long de l'été, mais a été plus intense de la mi-juillet à la mi-août. Le frai a eu lieu en octobre dans un tronçon tressé du cours principal, situé entre 1 600 et 1 700 km de la mer. Avant le frai, les ovaires des femelles ont grossi au cours de l'été pour atteindre jusqu'à 40 % du poids total du corps au moment du frai. L'âge minimum de maturité était de trois ans, et peu d'individus ont atteint l'âge de 10 ans ou plus. Le cisco de Béring ne s'est pas nourri pendant la migration de frai. L'espèce grandit rapidement pendant quatre à six ans, puis sa croissance est minime par la suite. Le taux de survie annuel a été estimé à 61 %. Ceux qui survivent au frai retournent en mer pour se nourrir et se préparer à un autre frai. Les données que nous présentons ici apportent un nouvel éclairage sur la biologie de cette espèce extraordinaire, qui est vraiment unique parmi les corégones de l'Alaska.

Mots-clés : cisco de Béring; *Coregonus laurettae*; Alaska; fleuve Yukon; migration de frai

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INTRODUCTION

Bering cisco *Coregonus laurettae* is an anadromous North American species in the family Salmonidae, subfamily Coregoninae (McPhail, 1966; Mecklenburg et al., 2002). Bering cisco are endemic in three spawning populations, one each in the Yukon and Kuskokwim Rivers, which flow to the Bering Sea in western Alaska, and the Susitna River, which flows to Cook Inlet in south-central Alaska (Alt, 1973; Russ, 2015; Padilla et al., 2016; Brown and Lopez, 2018). We focus on the Yukon River population because it is subject to long-term subsistence fisheries

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and one commercial fishery. That commercial fishery, located at the mouth of the river, began in 2005 and was operational for 15 years (Albert, 2019); it provided frozen Bering cisco to a smoked fish market in New York City (Fabricant, 2008), with mean annual harvests of almost 24,000 fish. When the fishery began, there were several biological aspects of Yukon River Bering cisco that were poorly understood, including the timing of the spawning migration, the spawning destination, age and growth patterns, reproductive details, age at maturity, feeding periods, and survival. To gain a better understanding of these biological features of the species, several research programs were initiated. While the research was conducted in response to the commercial fishery, and fishery managers may benefit from our findings, this manuscript focuses on the biology of Yukon River Bering cisco, and not on fisheries management.

Yukon River Bering cisco spawn in freshwater in October (Brown and Daum, 2012; Albert, 2019). During spawning, Bering cisco broadcast eggs and milt into flowing water over gravel as water temperature declines to 5˚C or colder during the transition from summer to winter (McPhail and Lindsey, 1970). Coregonine species are known to have negatively buoyant and non-adhesive eggs (Hart, 1930; Anras et al., 1999; Gerken, 2009; Teletchea et al., 2009). As such, we assume that fertilized eggs of Bering cisco drift to the substrate and become entrained in crevices in the gravel and cobble, where they incubate during winter.

Fecundity of Yukon River Bering cisco has been estimated to be from 20,000 – 34,000 eggs per female (Dillinger, 1989). Egg diameters were reported to be as much as 1.7 mm during the spawning migration (Dillinger, 1989) but would probably expand to 2 mm diameter upon completion of vitellogeneses, just prior to spawning (Teletchea et al., 2009).

Newly hatched Yukon River Bering cisco are known to move downstream in the spring or early summer to the Yukon River Delta (Martin et al.,1987). Similar movements have been described for the closely related Arctic cisco *C. autumnalis* in the Mackenzie River in northwestern Canada (Reist and Bond, 1988; Fechhelm et al., 2007). The young fish then disperse widely as they forage along coastal areas from the Alaska Peninsula in the south, to the western Beaufort Sea in the north (McPhail, 1966; Alt, 1973; Bickham et al., 1997; Padilla et al., 2016). Bering cisco are thought to occupy estuary environments during winter in western and northern Alaska, which is a strategy common to Arctic cisco in the southern Beaufort Sea (Gallaway et al., 1983; Fechhelm et al., 2007; Moulton et al., 2010; Zimmerman et al., 2013; Carey et al., 2021).

To address unknown features of Bering cisco biology, several research initiatives were launched. Previous and contemporary studies of subsistence harvests indicated substantial use of the species among communities in the Yukon River Delta (Stickney, 1984; Runfola, 2011; Runfola et al., 2018; Padilla and Harding Scurr, 2025). Brown and Daum (2015) conducted a radio telemetry investigation to identify spawning destinations in the drainage. Destinations were located primarily within the upper Yukon Flats, an extensive braided region approximately 1600 km to 1700 km upstream from the mouth of the Yukon River (rkm; Fig. 1; see Froese et al., 2005 for a detailed description of the unique geology of the spawning reach). Fish captured in the commercial fishery at the mouth of the Yukon River were found to be almost exclusively members of the Yukon River population, with few if any from the Kuskokwim River population (Padilla et al., 2015; Russ, 2015).

These research efforts culminated in a two-year (2016 and 2017) mark and recapture study to estimate the spawning population in the spawning area of the upper Yukon Flats (Albert, 2019). The estimated abundance of spawning Bering cisco in 2016 was 387,326 (SE = 37,200), and in 2017, abundance was 387,042 (SE = 42,181). In addition to these and other investigations of Yukon River Bering cisco, recent demographic sampling activities have also taken place along the river and in the estuary. These biological sampling data have not been previously analyzed or published.

In this manuscript we conduct original analyses of these Yukon River Bering cisco demographic data to describe: 1) the timing of the spawning migration up the Yukon River; 2) fasting periods; 3) seasonal variation in gonadosomatic indices (GSI) of females; 4) length distributions of non-spawning and pre-spawning females and males; 5) the proportion of females among all Bering cisco present in the upper Yukon Flats spawning area; 6) age of maturity based on age data from Bering cisco preparing to spawn; 7) annual survival using age data and catch-curve analyses; 8) condition of two demographic groups using whole-body weight-at-length analyses; and 9) growth patterns of males and females with length-at-age data. Ultimately, these data and analyses provide an improved understanding of the biology of the endemic Yukon River Bering cisco population.

MATERIALS AND METHODS

The Yukon River is the largest drainage in Alaska and the fifth largest drainage by area in North America (Revenga et al., 1998). It flows more than 3200 km from its headwaters in Canada to its mouth at the Bering Sea, approximately 2000 km of which is in Alaska (Brabets et al., 2000; Fig. 1). The river is turbid during the summer, when glaciers are flowing strong, and becomes clear during the winter. The Yukon River basin lies within the continental climate zone, with cold winters and warm summers (Shulski and Wendler, 2007). Water temperature in the river ranges from greater than 20˚C during warm summer periods (Brabets et al., 2000; von Biela et al., 2000) and as low as 1˚C during winter, when the river may be covered with ice for as much as six months of the year (Brabets and Walvoord, 2009).

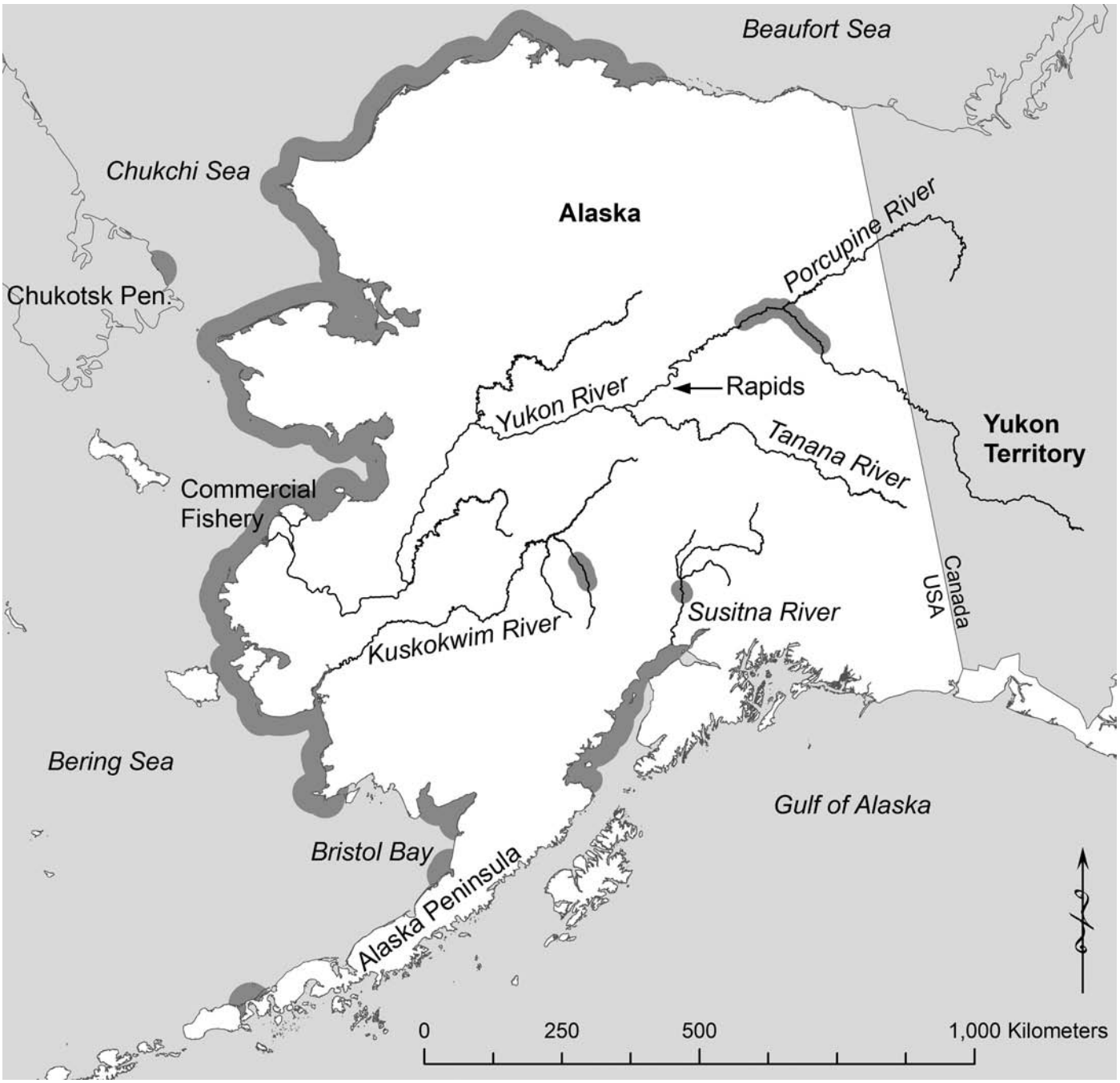


FIG. 1. Map of Alaska highlighting geographic features relating to Bering cisco distribution in general, the location of the Bering cisco fishery at the mouth of the Yukon River, the spawning migration monitoring site at Rapids, (approximate rkm 1176), and the core region of the spawning area in the upper Yukon Flats, a 125 km braided reach upstream from the mouth of the Porcupine River at approximate rkm 1600. The known coastal distribution of Bering cisco is indicated with shading, and the known spawning areas in the South Fork Kuskokwim and Susitna rivers are similarly shaded.

The Yukon River Delta is a sprawling estuary with several large distributaries that separate from the main channel as far as 170 km upstream from the sea and meander across the broad, flat delta. Maximum channel depth in the Yukon River increases towards the delta (Brabets et al., 2000). For example, deep channels have been measured at 9 m where the river leaves the Yukon Flats, about 1400 km from the sea; in the south channel of the delta, the largest distributary, which passes about two thirds of the total flow of the Yukon River, the depth has been measured at up to 30 m (McDowell et al., 1987; Thorsteinson et al., 1989; Brabets et al., 2000). Tidal amplitude can be as high as 1 m at times, but is more commonly 0.5 m or less in the lower reaches of the major channels. This dynamic estuary environment is thought to be where much of the growth and development of Bering cisco takes place.

Within the Yukon River, Bering cisco avoid tributaries and migrate along the main stem from the estuary in the Bering Sea to a major spawning area in the heavily braided upper reaches of the Yukon Flats (Alt, 1973; Brown et al.,

TABLE 1. Basic details of Bering cisco sample collections used in this manuscript, including: time period identifying years in which the sample collections began and ended; general locations of collections, along with the approximate rkm; spawning condition of sampled fish, resting or preparing to spawn, based on female GSI data; and number of female and male samples collected at each location.

Time period	Location (~rkm)	Resting/Spawning	Female	Male
2003–15	Yukon Estuary (0)	Resting	2236	2297
1998–2013	Rapids (1176)	Spawning	774	534
2000–19	Yukon Flats (1650)	Spawning	521	511
1992–2018	Border: USCan (2000)	Spawning	29	42

2007; Brown and Daum, 2015). A small fraction of the annual spawning population migrates farther upstream to unknown spawning destinations in the Canadian part of the drainage (deGraaf, 1981; Edge, 1991; Brown et al., 2007; Brown and Daum, 2015).

We sampled entire collections of Bering cisco, or, in cases where the entire collection could not be sampled, we randomly selected samples. Thus, we randomly selected collections of non-spawning (resting or immature) individuals captured in the commercial fishery at the mouth of the Yukon River from 2006–15 (n = 4543). We sampled all Bering cisco captured in collections from pre-spawning individuals from 1998–2013 (n = 1308) from a test fishery at a narrow reach of the river called Rapids (Fig. 1). Likewise, we sampled all Bering cisco collected from the spawning area in the upper Yukon Flats from 2000–19 (n = 1032) from collections that used gill nets and beach seines, and during the mark and recapture experiments in 2016 and 2017. However, we collected a random sample of 150 females and 150 males during the recapture event. All Bering cisco were sampled from collections from the U.S.–Canada border area from 1992–2018 (n = 71; Table 1).

Sampling data included fork length (FL) to the nearest 1 mm. Sex was determined by internal examination of gonads for individuals that were sacrificed. In the spawning area, female and male Bering cisco had distinctive body forms allowing sex to be identified based on external visual examination (Fig. 2; Albert, 2019). A random subset of sampled fish were sacrificed and weighed, and visual sex assignment was 100% verified by subsequent internal examination. Whole body weight was measured to the nearest 10 g, and for females, ovary weight was measured to the nearest 1 g. Sagittal otoliths were collected for aging and stored in labeled paper envelopes for later processing in the laboratory.

Migration timing data for Bering cisco were collected for 12 years, 2001–12, from a video-equipped fish wheel located at Rapids (Daum, 2005). The fish wheel was originally used to monitor runs of Pacific salmon (*Oncorhynchus* spp.), but the video system enabled other species captured in the fish wheel to be observed and counted as well (Brown et al., 2012). We used daily catch data (Bering cisco per day) from the Rapids test fishery to create daily interval plots across the open water season to visualize periods of weak and strong passage through the years.

We calculated GSI as (ovary weight/whole-body weight × 100; Snyder, 1983). Calculated in this way, GSI is the percent of whole-body weight composed of ovary tissue. We used GSI values to verify the spawning condition of female Bering cisco at five distinct seasons and life history phases: 1) while occupying the estuary near the mouth of the Yukon River when they were harvested during the fall commercial fishery; 2) during a mid-winter sampling program in the lower river, upstream from the delta; 3) during the summer, in upstream areas in the Yukon River while engaged in their spawning migration; 4) in the fall, when sampled in spawning habitats in the upper Yukon Flats (Brown and Daum, 2012; Albert, 2019); and 5) when captured in fall near the U.S.–Canada border, about 270 km upstream from the upper Yukon Flats. We used a polynomial regression function to create a curved regression equation to fit these data and illustrate the increase in GSI values over the course of the year (Pope and Kruse, 2007). We calculated the relationship as:

$$\mathrm{Log}_{10}(\mathrm{GSI}) = \beta_0 - \beta_1(\mathrm{Log}_{10} J) + \beta_2(\mathrm{Log}_{10} J)^2$$

and present it in normal units with a scatter plot of our GSI data (n = 1342) by day of the year (J). While the function was calculated as the day of the year, we adjusted the x-axis to present associated calendar dates in our results and make it easier for readers to place events by month.

We compared mean fork lengths among four sample groups of Bering cisco: female and male non-spawners and female and male pre-spawners. For this we used ANOVA procedures with the Games-Howell post-hoc method of ranking the four groups from largest (A) to smallest (D). Different letters were used to indicate significantly different mean lengths based on $\alpha = 0.05$.

We calculated proportional abundance of pre-spawning female Bering cisco, among all Bering cisco on the spawning area, using data from mark and recapture abundance projects conducted during 2016 and 2017 (Albert, 2019). During both years, within the marking and subsequent recapturing components of the project, we sampled the entire 125 km reach of the upper Yukon Flats spawning area using boat electrofishing methods. The sex of captured fish used in the mark recapture projects were identified based on the greatly enlarged bodies of gravid females as compared with the relatively slim bodies of males (Fig. 2). Each day during the second event, we randomly selected and sacrificed 15 fish classified as females based on our gravid versus slim body shape index, and similarly, 15 males. The second event required 10 days



FIG. 2. Pre-spawning male and female Bering cisco captured in the upper Yukon Flats spawning area, illustrating their distinctive body forms. Scale bars are in cm.

of sampling work with the electrofishing boats. As a result, we identified and sacrificed 150 females, all of which were clearly gravid prior to selecting, and 150 males, all of which were clearly slim in body form. We estimated the annual proportion of females in the spawning aggregations using sex-stratified abundance estimates calculated for each annual mark-recapture experiment (Albert, 2019).

Sagittal otoliths were collected from the commercial fishery (ADFG, 2006; Padilla et al., 2015), the test fish wheel, and spawning area sampling programs (Albert, 2019) for aging. Consistent with basic preparation and aging methods described and illustrated by Chilton and Beamish (1982) and Secor et al. (1992), otoliths were thin sectioned in the transverse plane and viewed with transmitted, polarized light using a compound microscope. Using this viewing method, narrow opaque growth increments, which we considered to be annuli, appeared as dark lines arcing across the otolith surface (Fig. 3). Otolith preparation and aging was conducted by the authors, who have considerable background experience aging coregonine and other species. Aging was usually conducted independently, but if an otolith was difficult to age, as a small fraction were, we discussed the matter together and either came to consensus, prepared the second otolith to see if it was readable, or rejected the age sample entirely. Age at maturity was based on age data collected from samples of Bering cisco preparing to spawn in the upper Yukon Flats spawning area.

Age frequency histograms were prepared to illustrate patterns in recruitment and subsequent age cohort declines (Robson and Chapman, 1961, Dunn et al., 2002; Smith et al., 2012). Annual survival for the population(s) was estimated for a pooled sample of aged male and female Bering cisco from the upper Yukon Flats spawning area. Additionally, we estimated annual survival for females and males separately to examine potential sex-specific differences in survival. We compared survival estimates and associated standard errors of females and males using a *T*-test with $\alpha = 0.05$. Survival estimates were based on the catch-curve method detailed by Robson and Chapman (1961), in which

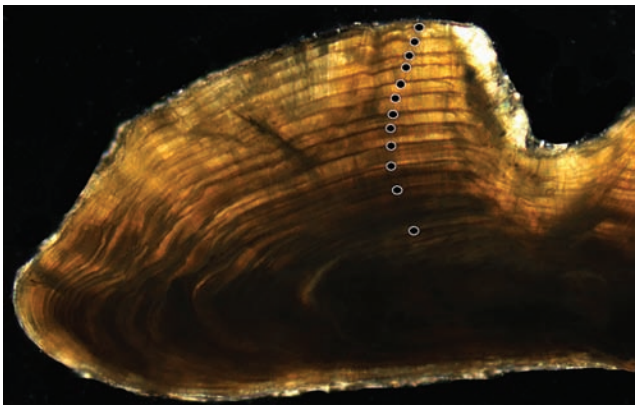


FIG. 3. Image of the thin-sectioned otolith of an age-12 Bering cisco, with circles marking visible annuli.

estimated annual survival can be considered as an average survival of the population (Dunn et al., 2002; Smith et al., 2012). The age of full recruitment was assumed to be the statistical mode plus one year. Age groups up to (but not including) the first age at which catch was zero were included in survival analyses. We did not consider age data from the commercial fishery to be suitable for survival estimates for three reasons: (1) a large fraction of that collection was immature, (2) members of other cohorts were engaged in a spawning migration, and (3) the commercial fishery collection was potentially biased because those Bering cisco were captured with gillnets. We do, however, present the age histogram from the commercial fishery collections and discuss notable differences in age structure between those preparing to spawn in the upper reaches of the Yukon Flats and those collected in the Yukon River Delta.

Whole-body weight-at-length relationships were used to characterize and compare the condition of: 1) non-spawning females captured in the commercial fishery at the mouth of the Yukon River during late fall; and 2) pre-spawning females sampled in the upper Yukon Flats in fall as they prepared to spawn. Condition differences were investigated using a pooled sample of these two datasets to compare mean studentized residual values of a least-squared linear regression of Log_{10} transformed weight and length data (Fechhelm et al., 1996; Pope and Kruse, 2007). Our null hypothesis was that weight-at-length among the two groups of females would be similar. Our alternative hypothesis was that weight-at-length among the two groups would be significantly different at $\alpha = 0.05$ or less. We tested our hypotheses by comparing mean studentized residuals among the two collections with a t-test. We illustrated differences between the two datasets by preparing least-squared linear regressions of log-transformed weight and length data for each dataset independently, and then presented those least-squared linear regressions together in normal units, which are curved functions arcing through a scatterplot of data.

Growth of Yukon River Bering cisco was modeled using the von Bertalanffy growth equation (Chen et al. 1992; Isely and Grabowski 2007) represented by the formula $l^t = L_\infty (1 - e^{-K(t-t_0)}$, where l^t is the length at time t, L_∞ is the asymptotic mean length, K is an estimate of the Brody growth coefficient, and t_0 is a time coefficient where length theoretically equals zero. A three variable equation was iteratively fit to our data using the von Bertalanffy growth model in the Minitab statistical software program (https://www.minitab.com/en-us//). The t_0 parameters were calculated based on modeled L_∞ and K parameters for both females and males. Length and age data suitable for these analyses included female (n = 1580) and male (n = 1536) Bering cisco from samples of non-spawning and pre-spawning individuals in the Yukon River. Separate von Bertalanffy growth curves were modeled and illustrated for female and male Bering cisco.

RESULTS

Bering cisco migrating to spawn in the upper Yukon Flats were present at Rapids through the entire summer. The test fish wheel began turning by mid-June or earlier each year and would continue turning until late September. While Bering cisco were present in the catch throughout the summer, their abundance was usually greatest from mid-July through mid-August, when daily catches of Bering cisco averaged between 100 and 150 fish per day, before declining to low levels by late August and September, when daily catches averaged 25 fish per day or less (Fig. 4). Alt (1973) reported the presence of pre-spawning Bering cisco in mid-June at the mouth of the Porcupine River, which is at the lower end of the Bering cisco spawning area in the upper Yukon Flats (Fig. 1). He suggested that they had either overwintered in the Yukon River or started the spawning migration early. The overwintering option would have to include a winter spent fasting, and, despite this, readiness to spawn in the fall. No Bering cisco to date has ever been reported feeding upstream from the Yukon River Delta or coastal habitats (Alt, 1973; Dillinger, 1989; this study). By contrast, Bering cisco are routinely reported to feed in estuary habitats (Alt, 1973; Brown and Eiler, 2005; Runfola, 2011). A more plausible explanation than overwintering in the Yukon River is that some fraction of pre-spawning Bering cisco begin the spawning migration early in the year, under the river ice. Brown and Daum (2015) reported average upstream migration rates of 13 radio-tagged Bering cisco at 13.1 km/day (range = 8.5–21.0 km/day) between two remote receiving stations 605 km apart along the Yukon River. Assuming an average of 13.1 km/day is representative of the broader population, it would require about 90 days to migrate from estuary habitats at the Bering Sea to Rapids (rkm 1176), and about 126 days to migrate from the sea to the spawning area in the upper Yukon Flats (approximate rkm 1650). These data suggest that Bering cisco encountered in the Rapids test fishery in June began their spawning migration under ice in March, and those that Alt (1973) encountered in the middle reaches

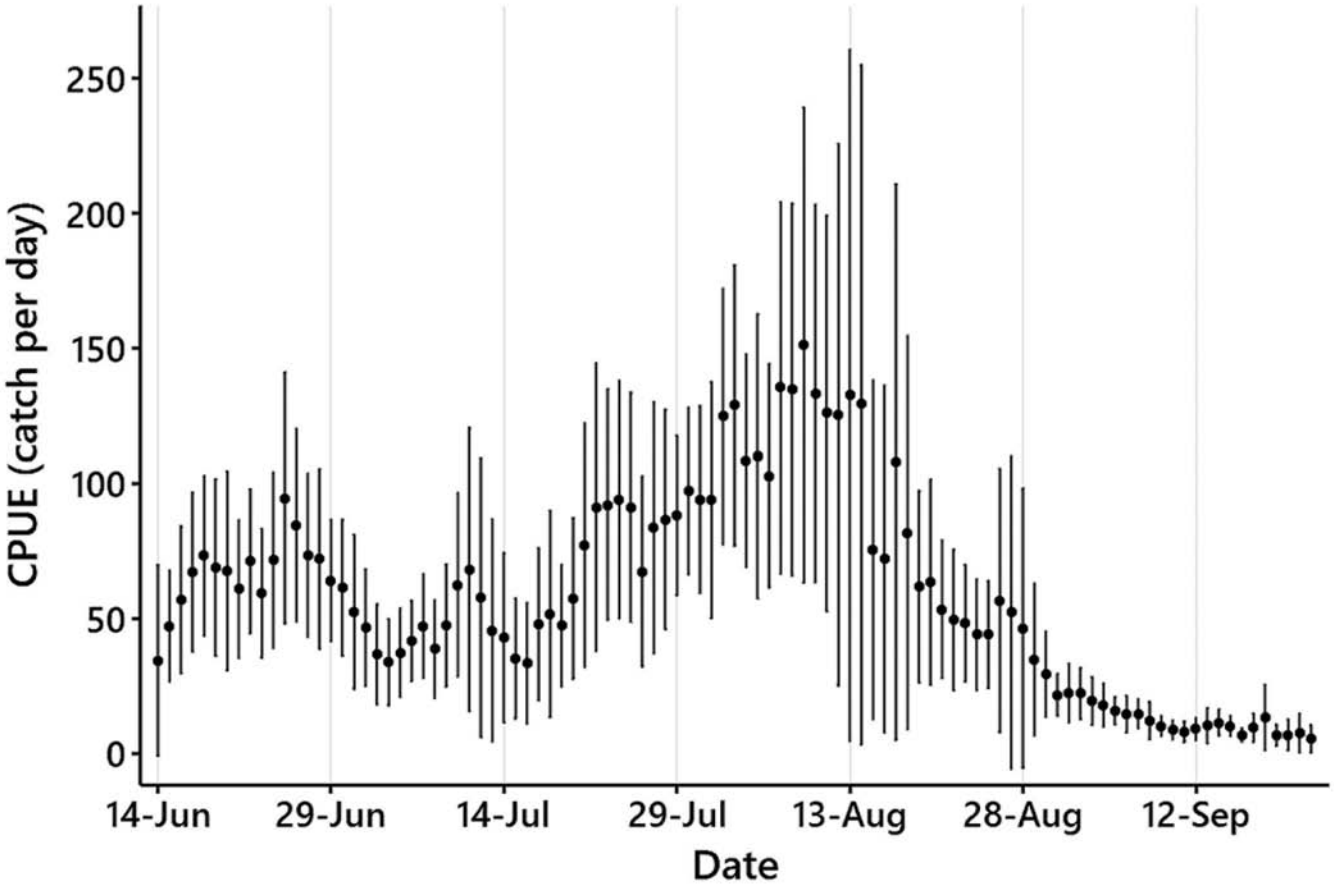


FIG. 4. Interval plots of mean catch per unit effort (CPUE) for catch of Bering cisco per day by date (with 95% confidence intervals) of Bering cisco captured at the Rapids test fish wheel at rkm 1176 of the main stem Yukon River, 2001 – 12.

of the spawning area in mid-June began their spawning migration in February. Those that were present at Rapids in early- to mid-June would be expected to arrive in the spawning reach in mid-summer and remain there until spawning begins in early- to mid-October.

Sampling from the test fishery at Rapids during the summer and in the spawning area during September and October revealed that all Bering cisco in the upper river were mature and preparing to spawn (Brown et al., 2012). None were feeding, and the GSI values of females as they approached spawning time were elevated to as much as 40% of whole-body weight (Fig. 5). In contrast, all female Bering cisco sampled in estuary habitats in late fall had GSI values of about 3% or less of whole-body weight, indicating that they were either immature or mature but in a resting state and not preparing to spawn. The sample group from under ice in January, approximately 135 km upstream from the sea, (see Fig. 5) is thought to be a group of fish that had started the upstream migration under ice and moved towards spawning habitats later in the year.

Length distributions of female and male Bering cisco preparing to spawn in the upper river were significantly larger on average than non-spawning females and males captured in the commercial fishery (Fig. 6). Mean FL of pre-spawning females (381 mm, *SE* = 0.713) and males (345 mm, *SE* = 0.718) were significantly greater than for non-spawning females (355 mm, *SE* = 0.504) and males (333 mm, *SE* = 0.453). Mean lengths of pre-spawning males were significantly greater than non-spawning males. It was not surprising that pre-spawning females and males were longer on average than the non-spawning females and males captured in the commercial fishery. Only mature individuals preparing to spawn were present in the upper river, including the spawning area. Length distribution data indicate that some younger and immature female and male Bering cisco were captured in the fishery, shifting those length distributions slightly smaller.

In 2016, 10,338 Bering cisco were captured, and sex was recorded during tagging and subsequent recapture activities. Similarly, in 2017, 14,870 Bering cisco were captured, and sex was recorded. Using sex-stratified abundance estimates calculated separately for 2016 and 2017, females accounted for 25.5% (SE = 0.04%) and 36% (SE = 5.6%), respectively, of the estimated Yukon Flats spawning population. The preponderance of males in the spawning area during both years of the mark and recapture abundance projects in the upper Yukon Flats spawning area (Albert, 2019) suggests sex-specific survival or sex-specific spawning frequency. Other collections of pre-spawning Bering cisco in spawning areas took place in the Susitna

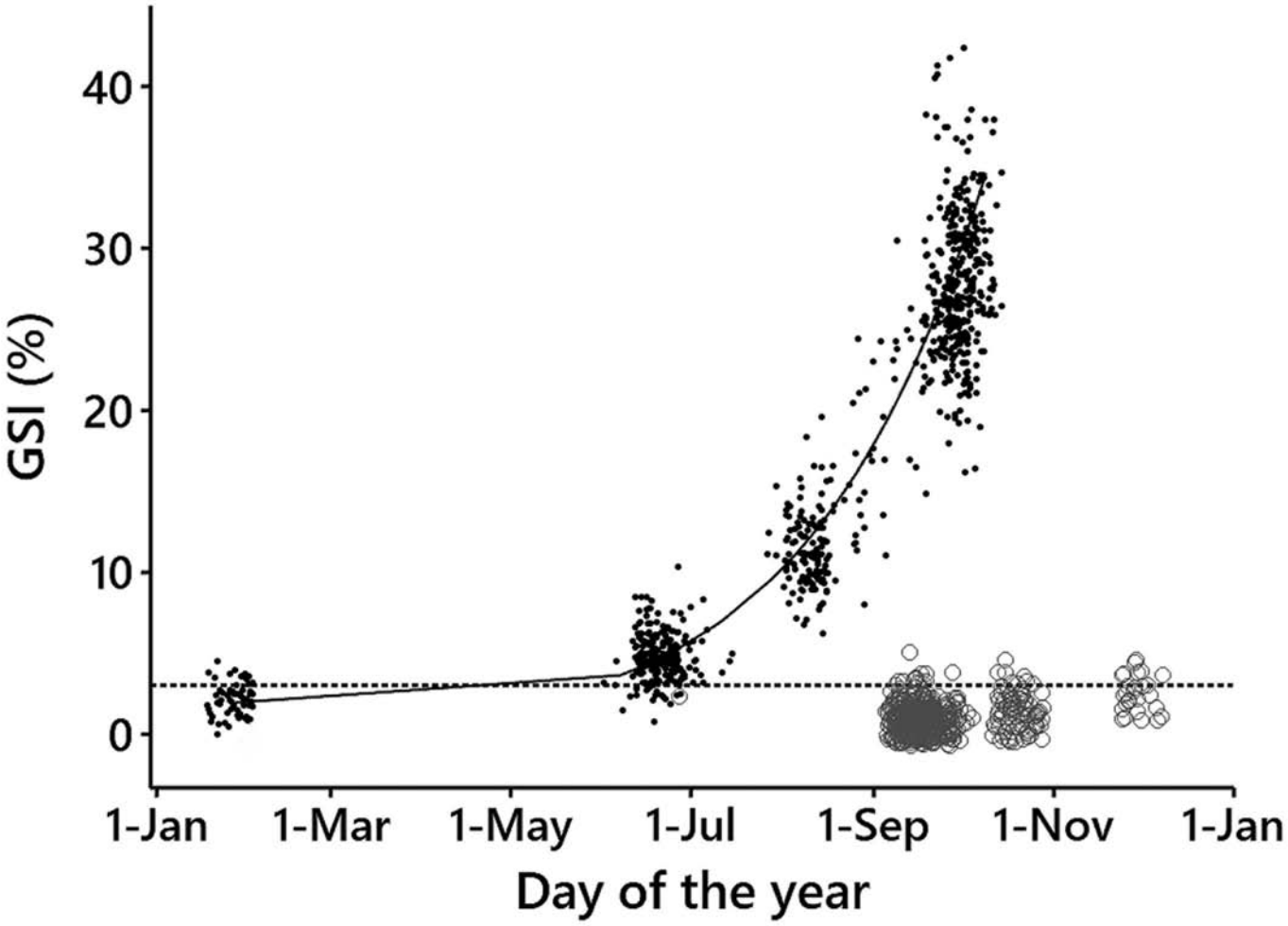


FIG. 5. Gonadosomatic indices (GSI) for collections from non-spawning fish captured in the commercial fishery at the mouth of the Yukon River during the period between September and December (open circles near or below the dashed reference line at GSI = 3, a value that non-spawning females rarely exceed. GSI data from the spawning migration in riverine environments (filled black circles) include a small collection in late January approximately 130 km upstream from the sea. We believe this group was in the early stages of migration, preparing to spawn later that year. Collections further upstream in the river include a late June–early July collection at Rapids of Bering cisco that were migrating to the spawning area further upstream in the upper Yukon Flats in early-to-mid-October. The polynomial equation that best fit spawning migration GSI data was: $Log_{10}(GSI) = 10.93 - 12.41*Log_{10}(day\ of\ year) + 3.495*Log_{10}(day\ of\ year)^2$; $R^2 = 93.05\%$. While function was calculated as day of year, for ease of understanding we adjusted the x-axis to present associated calendar dates.

River in 1981 and 1982 (ADFG, 1983). Biologists used boat electrofishing techniques to capture Bering cisco in the spawning reach, approximate rkm 125 (ADFG, 1983). The authors did not report the number of fish they captured, but they reported male to female ratios of 1:1 in 1981 and 1.4:1 (42% female) in 1982. Other researchers working with coregonine species have reported significantly different proportions of females and males in spawning areas. The predominance of females or males in spawning areas varies widely among studies and coregonine species. Female predominance has been observed in several studies (Bunnell, et al., 2006; Marjomaki, et al., 2023), as well as in studies predominantly observing males (Van Oosten and Hile, 1947; Howland et al., 2000). Occasionally, females and males have been reported to be near parity in spawning aggregations (Normandeau, 1969; Harper et al., 2012). Additionally, annual trends have been observed to alternate between female and male predominance in Humpback Whitefish (*Coregonus pidschian*) spawning areas (Brown and Shink, 2020). We hypothesize that the low observed proportion of spawning females in this study is most likely a result of spawning less frequently than males.

Minimum age at maturity for Bering cisco was age three (Fig. 7) for both males and females (Fig. 8). Age-three individuals made up a small fraction of sampled Bering cisco preparing to spawn. A much larger component was age four, and age-five fish represented the mode in almost all annual collections in the spawning area. Considering the guidance provided by Robson and Chapman (1961) and Smith et al. (2012) on interpreting catch curves, all Bering cisco should be mature by age six, the first age class following the modal age. Maximum age was 14 years, and only one of over 3000 individuals we aged survived that long.

The combined annual survival of pre-spawning female and male Bering cisco (n = 1587), across multiyear collections was estimated to be (s) = 0.61, SE = 0.008 (Fig. 7). Analyzed separately, the annual survival of females (n = 843; s_f = 0.653; SE = 0.010) was significantly

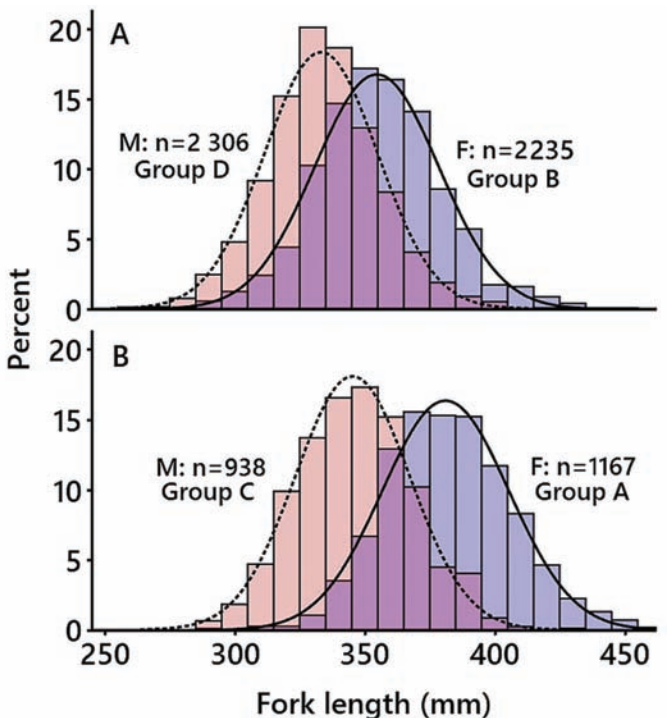


FIG. 6. Fork length histograms of female (F) and male (M) Bering cisco collected from non-spawning fish in the Yukon River Delta (A), and from fish preparing to spawn in the upper Yukon Flats (B). Games-Howell statistical grouping letters are indicated for the four groups, with different letters indicating significant differences.

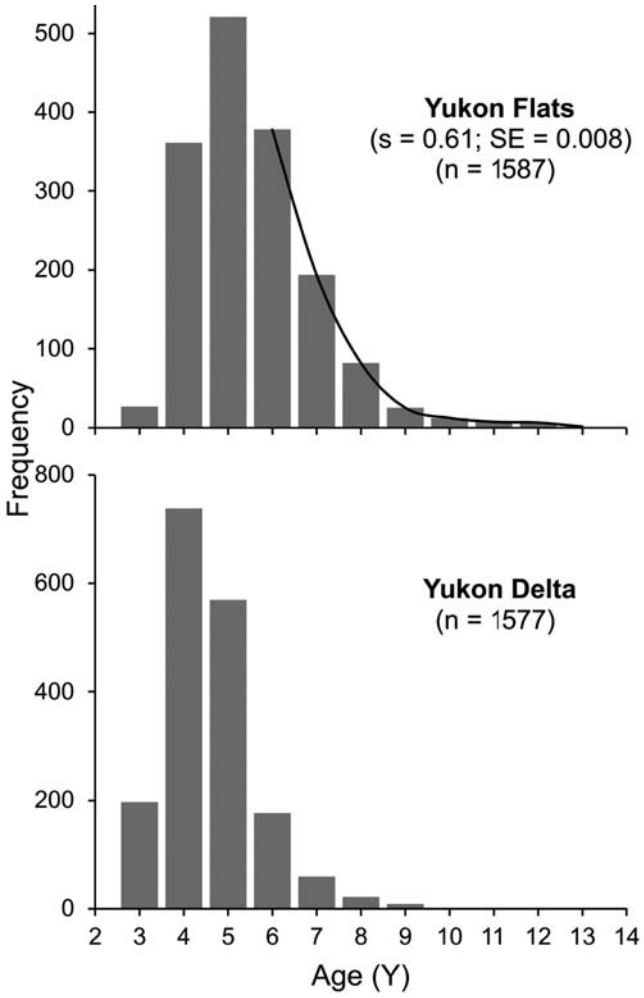


FIG. 7. Catch-curve survival estimate from a large, multi-year collection of mature pre-spawning Bering cisco from the Yukon Flats spawning population (n = 1587). The curved line arcing down the right side of the age distribution mode illustrates long-term average mortality following full recruitment to the spawning population at age six. Estimated annual survival rate of the mature population was s = 0.61, SE = 0.008. Yukon River Delta age data, including a large fraction of immature fish primarily age three and four, are presented for comparison.

greater (T = 6.83; DF = 1453; $p < 0.001$) than the annual survival of males (n = 744; s_m = 0.549; SE = 0.012; Fig. 8). Prior to aging and tagging studies, researchers were not certain that Bering cisco in the upper Yukon Flats survived spawning. However, the age and catch curve data analysis clearly demonstrates that about 61% of all mature Bering cisco survive from one year to the next. Additionally, some Bering cisco tagged during the mark and recapture project in the spawning area were subsequently reported to have been captured alive in coastal communities the following summer, verifying their post-spawning survival.

Sample data used for weight-at-length analyses included 533 non-spawning female Bering cisco harvested in the commercial fishery, and 334 pre-spawning females collected from the spawning area. Our analyses indicated that non-spawning females from the coastal collection were significantly heavier at length than those preparing to spawn in the upper Yukon Flats spawning area (T = 2.7889; DF = 863; $p < 0.0054$; Fig. 9). We suspect that reduced weight at length observed for the pre-spawning samples can be interpreted as the energetic cost of the 1650 km spawning migration, which is accomplished without feeding. In contrast, the non-spawning individuals are most likely those fish that are busy accumulating stored energy, such as lipids (Fraley et al., 2021), in preparation for an upcoming spawning migration. As such, they should be approaching the best condition of their lives.

Asymptotic maximum length of female Bering cisco (L_∞ = 391.1; SE = 1.6) was significantly greater (T = 2.7889; DF = 863; $p < 0.0054$) than for males (L_∞ = 359.8; SE = 1.5; Table 2). Growth parameter estimates of females (K = 0.550; SE = 0.0192) and males (K = 0.594; SE = 0.0268), however, were not significantly different (T = –1.33; DF = 2798; p = 0.182). Growth curves fit to length-at-age data for females and males (Fig. 10) illustrate rapid growth to age four to six, and by age six, growth slows noticeably as they approach their respective L_∞ values. Individuals age six and older are very close to their respective L_∞ values and probably focus almost entirely on accumulating energy to support a future spawning event. We suspect that it would be unlikely for post-spawning Bering cisco to spawn again the next year, given the lateness of their spawning (early to mid-October) and return migration to the sea, and the likely early timing of the onset of the next year's migration. It seems much more likely that post-spawning Bering cisco would require a year or more of foraging in rich marine and estuarine habitats before they would be ready for another spawning migration.

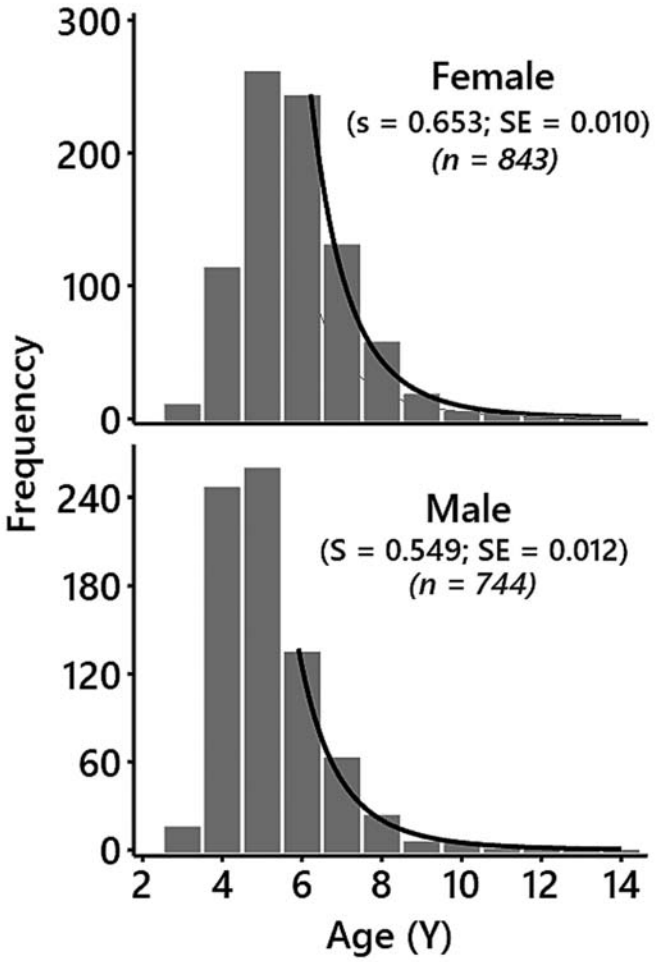


FIG. 8. Catch curve survival estimates of pre-spawning Bering cisco females and males sampled in the upper Yukon Flats spawning area.

DISCUSSION

Gallaway et al. (1983) published a paper suggesting that Arctic cisco found in the Colville River Delta in northern Alaska and nearby coastal areas of the southern Beaufort Sea might be natal to the Mackenzie River in northwest Canada, about 700 km in coastal marine water to the east. At the time, the idea seemed unlikely and perhaps impossible. How could such a small coregonine fish make that ocean journey to the west as small juveniles, and to the east as mature fish preparing to spawn? But Gallaway et al. (1983) made their case in the paper that the other coregonine species found in the Colville River Delta, least cisco *C. sardinella*, humpback whitefish *C. pidschian*, and broad whitefish *C. nasus*, could be sampled in the fall and early winter, and many would present biological evidence, similar to what we have presented here, indicating that they were preparing to spawn or had recently spawned. Arctic cisco in the Colville River, however, did not show any signs of spawning, even though juvenile Arctic cisco are present in the Colville River Delta every summer. It bothered them that they couldn't find biological evidence that Arctic cisco were spawning in the Colville River like the other coregonine species present there. They believed that Arctic cisco had to be fundamentally different than the other coregonine species. About five years later, Reist and Bond (1988) published an important paper on the life histories of coregonine species in the Mackenzie River. They classified Arctic cisco as being more tolerant of saltwater than the other coregonine species that tended to restrict their movements to the brackish water environments of estuaries, rather than marine water.

Additionally, Gallaway et al. (1983) knew that Arctic cisco made spawning migrations up the Mackenzie River. They proposed that juvenile Arctic cisco emerged into the Mackenzie River Delta in the spring and early summer and somehow made their way along coastal waters to the west. Since that time, there have been many investigations that followed Gallaway et al. (1983), never contradicting the basic premise, but rather, adding many new details supporting the nature of the biological system of Arctic cisco in the southern Beaufort Sea (Fechhelm et al., 2007; Moulton et al., 2010; Zimmerman et al., 2013).

Subsistence and commercial fisheries targeting coregonine species have operated in the Colville River for many years (Gallaway et al., 1983; Fechhelm et al., 2007; Moulton et al., 2010). Arctic cisco has been the preferred species for most people because of the high fat content and good flavor (Gallaway et al., 1983). Similarly, in the case of the Yukon River, Bering cisco has been the preferred species for those who live in communities along the coast (Runfola, 2011; Stickney, 1984) and for the commercial fishery that catered to the New York market. The migratory distances in marine environments for some Bering cisco, however, are much greater than the migration of Mackenzie River Arctic cisco occupying the Colville River. Yukon River Bering cisco occupy rearing and foraging habitats as distant as the south side of the Alaska Peninsula, which is approximately 1000 km along the coast from the Yukon River Delta. The distance from the Yukon River Delta to the Colville River Delta, where Yukon River Bering cisco mix during winter with Arctic cisco (Bickham et al., 1997; Padilla et al., 2016) is approximately 1700 km along the coast. The known migration distances in marine waters indicate that Bering cisco is a fully anadromous species, as defined by Gross et al. (1988) and McDowall (2001).

Coregonine fishes share qualities with both freshwater species, which remain in lakes or rivers throughout life (Lindsey and Kratt, 1982; Lindsey, 1983; Howland et al., 2000), and amphidromous species (McDowall, 2007), which spawn in freshwater, but move or migrate to salt water to forage and grow, then return to freshwater to continue to feed and grow before ultimately spawning in freshwater (Brown et al. 2007, 2025). Yet coregonine fishes are neither. At the same time, it is rare to find coregonine species that have the qualities of fully anadromous species that spawns in freshwater, moves or migrates to sea as a young fish to take advantage of the abundant food resources there, and then remains in saltwater foraging and growing, until it eventually matures and migrates back

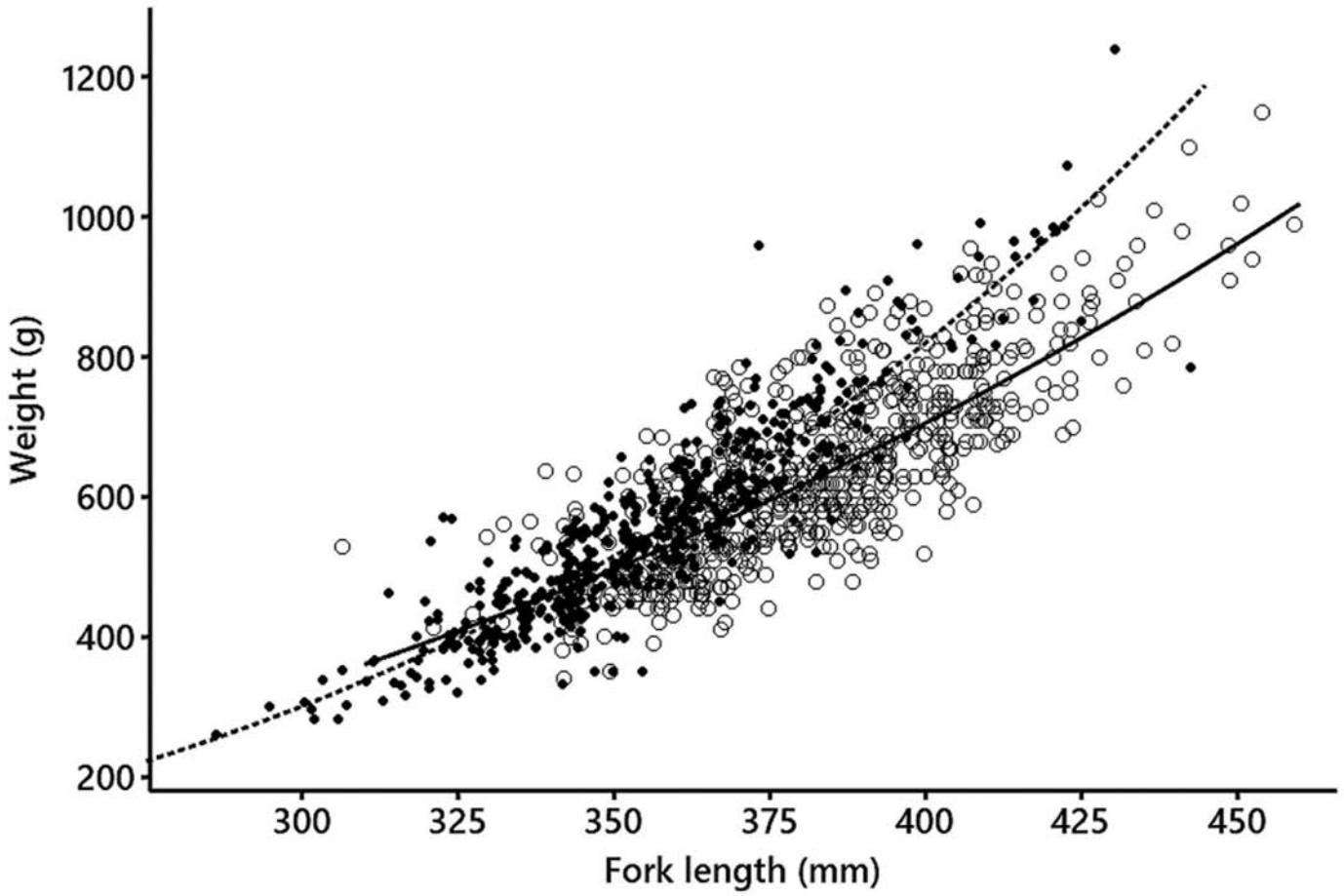


FIG. 9. Whole body weight (Wt) at length (FL) scatterplots of pre-spawning females captured in the spawning area (n = 334; open circles and black line fit to data using the equation $Log_{10}[Wt] = -10.641 + 2.855 \times Log_{10}[FL]$ and presented in normal units). Non-spawning females captured during late fall in the commercial fishery at the mouth of the Yukon River (n = 533; black circles and dashed line fit to data using the equation $Log_{10}[Wt] = -12.773 + 3.245 \times Log_{10}[FL]$ and presented in normal units). Data indicate that the non-spawning group was, on average, heavier at length than the pre-spawning group.

TABLE 2. Parameter estimates and other details of von Bertalanffy growth curves for female and male Bering cisco.

Sex	n	L∞ (SE)	K (SE)	t0
Female	1580	391.06 (1.638)	0.550 (0.019)	–0.040
Male	1535	359.75 (1.514)	0.594 (0.027)	–0.265

into freshwater specifically to spawn, but not to feed (Gross et al., 1988; McDowall, 2001). The data we presented here indicate that Yukon River Bering cisco follow this anadromous strategy very closely.

FUTURE RESEARCH

While we have elaborated here on several different aspects of Bering cisco biology within the Yukon River drainage, most of their lives are spent in coastal habitats and estuaries from the Alaska Peninsula in the south to the western Beaufort Sea in the north (McPhail, 1966; Alt, 1973; Padilla et al., 2016). Young Bering cisco almost certainly follow a similar life history pattern to Arctic cisco, migrating with ocean currents from the natal river to estuaries and river mouths that can be distant from the natal river (Fechhelm et al., 2007; Moulton et al., 2010). The Alaska current through the Bering and Chukchi Seas runs north along the western Alaska coast and into the Arctic Ocean (Woodgate and Aagaard, 2005; Irving et al., 2009). Therefore, we might expect most young Bering cisco would move north with the current from the Yukon River to find rearing habitats. Padilla et al. (2016) demonstrated that Bering cisco from the Yukon River population were, in fact, widely distributed in rearing habitats across western and northwest Alaska, both south and north of the Yukon River Delta.

An interesting yet unstudied aspect of their marine life is the return migration from rearing habitats to the Yukon River estuary after maturity is attained and where they prepare for a spawning migration. We suspect that Bering cisco in distant rearing habitats would almost certainly have to migrate to the Yukon River during the summer prior to their first spawning migration. Salmonids, including Bering cisco, do not have antifreeze compounds in their body fluids (Fletcher et al., 1988; Irving et al., 2009). As such, they would have to remain in the estuary rearing habitats they occupy during winter until sea ice

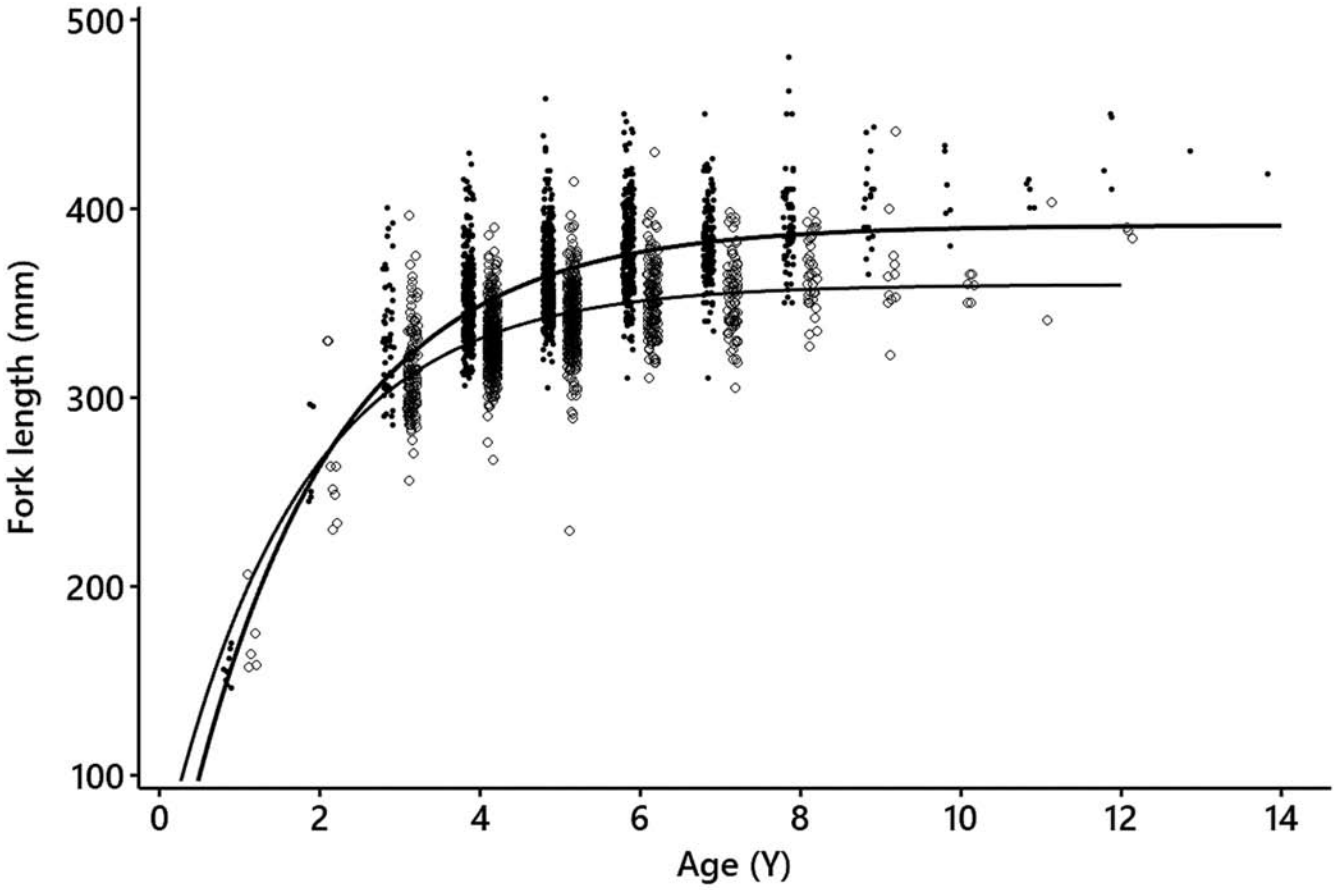


FIG. 10. von Bertalanffy growth curves for female (filled circles and upper curved regression line) and male (open circles and lower curved regression line).

breaks up and the sea warms sufficiently to allow them to return to the Yukon River.

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