

Morphological Variability among Spawning Populations of Bering Cisco *Coregonus laurettae*

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Bering Cisco *Coregonus laurettae* is an anadromous coregonine species known almost exclusively from northwestern North America and with only three documented spawning populations, all in Alaska. Previous studies of Bering Cisco phenotypic variation examined individuals collected primarily in coastal rearing habitats where population affiliation was not known. Here we compare meristic counts and morphometric ratios of pre-spawning adults among the three known populations: one each in the Yukon, Kuskokwim, and Susitna rivers in Alaska. We also compare meristic data with those previously reported for this species. Populations in the Yukon and Kuskokwim rivers were very similar, while the population in the Susitna River was significantly divergent for certain meristic counts and morphometric ratios. Our findings are consistent with recent genetic analyses that found the Susitna River population to be the most divergent of the three populations. While the Yukon and Kuskokwim river populations survived the Wisconsin Ice Age in the Beringian Refugium, the Susitna River population colonized the drainage following ice retreat sometime in the last few thousand years. The population's divergence from the source population in the Yukon or Kuskokwim river could be due to a founder effect or adaptation to different environmental conditions.

BERING Cisco *Coregonus laurettae* is an anadromous North American coregonine species with a terminal mouth and non-pigmented ventral fins (Fig. 1; Bean, 1881; McPhail, 1966). Bean (1881) described the species initially and named it after his wife, Lauretta. Bering Cisco and North American Arctic Cisco *C. autumnalis* were considered to be synonymous and classified in numerous ways including *C. laurettae* (Bean, 1881), *Leucichthys laurettae* (Dymond, 1943), and *C. autumnalis* (Walters, 1955) until meristic analyses of samples from across their coastal range yielded evidence for recognition of two valid forms in North America (McPhail, 1966). These two forms were differentiated most clearly by the number of gill rakers on the lower limb of the first gill arch. Bering Cisco had 21 to 25 gill rakers on the lower limb of the first gill arch and were present in the Yukon River and coastal waters from the western Beaufort Sea south across western Alaska and in the Gulf of Alaska, while Arctic Cisco had 26 to 30 gill rakers on the lower limb of the first gill arch and were present in the Mackenzie River and coastal waters of the Beaufort Sea. The ranges of these two forms intersected in the western Beaufort Sea. Genetic evidence provided further support for McPhail's (1966) assessment that Bering Cisco and Arctic Cisco were valid species. Arctic Cisco in North America was synonymous with the Arctic Cisco in Asia, and Bering Cisco was the low gill raker form in western Alaska (Bickham et al., 1997; Turgeon and Bernatchez, 2003; Politov et al., 2004).

Spawning populations of Bering Cisco have been documented in the Yukon and Kuskokwim rivers in western Alaska (Alt, 1973; Brown and Daum, 2015), and the Susitna River in southcentral Alaska (Fig. 2; Alaska Department of Fish and Game [ADFG], 1983). To date, no spawning populations have been recorded in Asian rivers (Shestakov, 1991; Chereshnev, 1993; Chereshnev et al., 2002). Sampling and migration data within the Yukon, Kuskokwim, and Susitna river drainages indicate that Bering Cisco migrating to spawn avoid tributaries and spawn in turbid, heavily braided, main-stem habitats (Alt, 1973; ADFG, 1983; Brown

et al., 2007; Brown and Daum, 2015; M. Thalhauser, ADFG, pers. comm.). Despite sampling efforts in many other river systems in Alaska and eastern Asia, only these three spawning populations of Bering Cisco are known.

Bering Ciscos have been documented in lagoons, estuaries, and river mouths from the western Beaufort Sea in northern Alaska to Cook Inlet in the North Pacific Ocean (Fig. 2). Within the western Beaufort Sea, they have been captured in the Colville River estuary and near the community of Utqiagvik, also known as Barrow (McPhail, 1966; Bickam et al., 1997; Padilla et al., 2016). Within the Chukchi Sea, they have been captured in the Kuk Lagoon (Padilla et al., 2016), several locations within Kotzebue Sound (Alt, 1973; Georgette and Shiedt, 2005), and from the mouth of the Chegitun' River on the Asian coast northwest of the Bering Strait (Chereshnev, 1984). Within the Bering Sea, they have been captured in Grantley Harbor (Alt, 1973), Safety Sound, Golovnin Lagoon, the Koyuk River mouth, the Unalakleet River mouth, offshore in Norton Sound (Wolotira et al., 1979), the Yukon River mouth (Martin et al., 1987; Padilla et al., 2016), Scammon Bay (Runfola, 2011), Hooper Bay (Stickney, 1984), the Aphrewn River estuary (Brown and Eiler, 2005), and Kuskokwim Bay (Stickney, 1984). Limited records exist from Bristol Bay (McPhail, 1966; McPhail and Lindsey, 1970; Padilla et al., 2016). In coastal waters of the North Pacific Ocean, Bering Cisco have been identified in northern Cook Inlet (McPhail, 1966; Blackburn, 1977), in southwest Cook Inlet (Blackburn et al., 1980), and at a tide-water weir at Mortensen's Creek at the far southwest Alaska Peninsula (Hildreth and Dion, 2006). These records indicate that Bering Cisco use a wide range of coastal habitats that may be great distances from their natal rivers.

McPhail (1966) examined material collected primarily in coastal sampling activities around Alaska without information on spawning origins or life history that is currently available. The purpose of this study was to improve our understanding of population level diversity of Bering Cisco by comparing meristic counts and morphometric ratios of

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Fig. 1. Bering Cisco *Coregonus laurettae* is an anadromous North American coregonine species with a terminal mouth and non-pigmented ventral fins.

pre-spawning individuals from the three known spawning populations: one each in the Yukon, Kuskokwim, and Susitna rivers in Alaska (Alt, 1973; ADFG, 1983; Brown and Daum, 2015; Padilla et al., 2016). We then examine our population specific data in context with McPhail's (1966) original findings and more recent genetic analyses (Russ, 2015).

MATERIALS AND METHODS

Sample collections.—Whole fish samples of Bering Cisco were collected from the Yukon, Kuskokwim, and Susitna river drainages in Alaska (Fig. 2; Table 1). All fish were collected in their spawning areas or while migrating to their spawning areas near the onset of spawning. Due to the timing and location of these sampling events, we consider all sampled fish to be pre-spawning adults. Bering Ciscos were identified based on their distinctive terminal mouths and pale ventral fins (Fig. 1), which are diagnostic traits among the coregonines present in the three drainages (McPhail and Lindsey, 1970; Mecklenburg et al., 2002). Most Bering Ciscos in the Yukon River were captured in a fish wheel that was non-selective across the size range of the species (see Brown et al., 2012). The remaining five fish of that sample were captured with a small mesh gillnet. Bering Ciscos in the Kuskokwim River were aggregated in the spawning area and were all captured with a small mesh beach seine. Most Bering Ciscos in the Susitna River were aggregated in the spawning area and were captured using electrofishing techniques. The remaining six fish of that sample were captured in a fish wheel downstream from the spawning area. Captured fish were immediately frozen and kept in that condition until processed in the lab. Meristic and morphometric data from these samples of known population provenance provide the foundation for this work. Voucher specimens and tissue samples from each population were archived in the fish collection at the University of Alaska Museum in Fairbanks, Alaska. Information on these samples can be accessed at http://arctos.database.museum/saved/Coregonus_laurettae_2010_AK.

Age data.—Sagittal otoliths were extracted from sample Bering Ciscos for ageing. Otoliths were thin-sectioned in the transverse plane through the core (Secor et al., 1992) and examined under a compound microscope with transmitted light. Annuli were identified based on descriptions and figures in Chilton and Beamish (1982). Brown et al. (2012)

presented data suggesting that the median age of mature male Bering Cisco was less than that of mature females. Therefore, we initially tested null hypotheses that median ages of males and females were equal within each sample group. Age data from males and females were pooled when test results were nonsignificant. We then tested the null hypothesis that the median age of mature Bering Ciscos was equal among the three sample groups.

Meristic counts.—Counts of fin rays, scales, gill rakers, branchiostegal bones, and vertebrae followed the methods of Hubbs and Lagler (1958). Fin-ray counts were made from the dorsal fin, left side pectoral fin, left side pelvic fin, and anal fin. Lateral line scales were counted and scale rows were counted above and below the lateral line (LL). Gill rakers

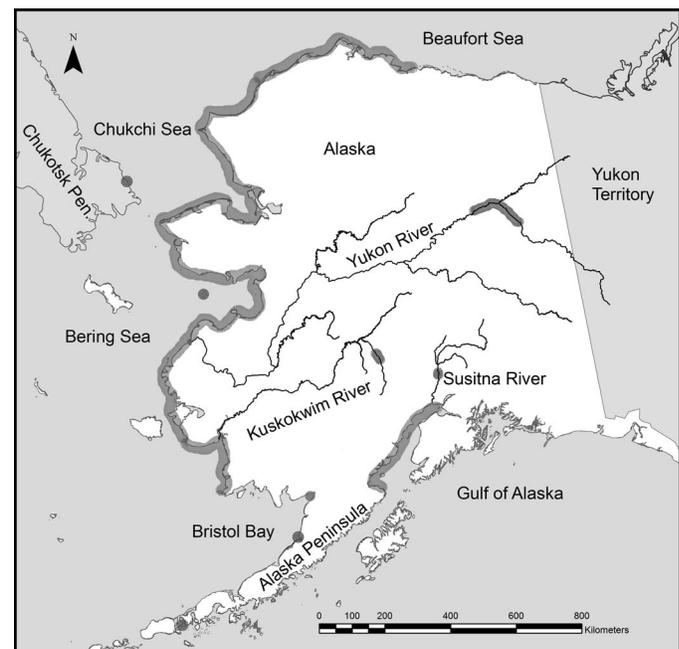


Fig. 2. Samples were collected from pre-spawning Bering Cisco at or approaching the three known spawning areas located in main-stem reaches (shaded) of the Yukon, Kuskokwim, and Susitna rivers in Alaska. Documented marine distribution is indicated by shaded coastal areas in western and northern Alaska, northern Gulf of Alaska, and isolated occurrences on the Alaska Peninsula, Bristol Bay, and eastern Chukotsk Peninsula.

Table 1. Bering Cisco sample collection data including drainage, sample location, latitude and longitude (WGS84 datum), river km (rkm), collection year, and sample size (*n*).

Drainage, location	Latitude	Longitude	rkm	Year	<i>n</i>
Yukon River					
Eagle Rapids	64.8072	-141.1764	2,000	1992	5
Rapids	65.3387	-151.0656	1,176	2010	37
Kuskokwim River					
South Fork	62.8694	-154.0174	990	2010	39
Susitna River					
Susitna Station	61.5468	-150.5165	42	2010	6
Sunshine Station	62.1055	-150.0859	130	2006	1
				2009	10
				2010	20
				2011	3

were counted from the first arch on the left side and partitioned as lower limb count, upper limb count, and total count. Branchiostegal bones were similarly counted from the left side. Vertebrae were counted from whole fish x-rays viewed on a light table. These count data were analyzed without transformation.

Morphometric measurements.—Point to point lengths were measured using calipers and recorded for each fish examined. Fork length (FL) was recorded to the nearest 1 mm. Whole body weight was recorded to the nearest 1 g. Head length (HL), snout to dorsal end of opercular opening (Snout–D Opercular O), snout to pectoral-fin origin (Snout–Pectoral FO), snout to dorsal-fin origin (Snout–Dorsal FO), snout to pelvic-fin origin (Snout–Pelvic FO), snout to anal-fin origin (Snout–Anal FO), snout to adipose-fin origin (Snout–Adipose FO), dorsal-fin base, dorsal-fin length, dorsal-fin origin to pelvic-fin origin (Dorsal FO–Pelvic FO), dorsal-fin origin to pectoral-fin origin (Dorsal FO–Pectoral FO), dorsal-fin origin to anal-fin origin (Dorsal FO–Anal FO), dorsal-fin origin to adipose-fin origin (Dorsal FO–Adipose FO), pectoral-fin base, pectoral-fin length, pelvic-fin base, pelvic-fin length, pelvic-fin origin to pectoral-fin origin (Pelvic FO–Pectoral FO), anal-fin base, anal-fin length, anal-fin origin to adipose-fin origin (Anal FO–Adipose FO), anal-fin origin to pelvic-fin origin (Anal FO–Pelvic FO), caudal peduncle width (W), caudal peduncle depth (D), body depth, head depth, snout to anterior eye margin (Snout–A Eye margin), eye diameter, interorbital distance, upper jaw length, and lower jaw length were measured according to Hubbs and Lagler (1958) to the nearest 0.01 mm. Partial body and partial head measurements were analyzed as proportions of FL or HL.

Analyses.—Null hypotheses of equality among the three sample groups for meristic or morphometric parameters were tested using ANOVA or Kruskal-Wallis procedures as appropriate for data distributions (Zar, 1999). If hypotheses of equality could not be rejected at the 95% level of confidence, no further analyses were required. However, if initial hypotheses of equality were rejected, paired tests were conducted to rank significantly different sample groups. Differences were considered to be significant at a 95% family level of confidence using either the Tukey multiple comparisons method or a non-parametric alternative of adjusting the individual contrast α -level to reduce the probability of type-1 error (Zar, 1999; Verhoeven et al., 2005). Because we compared parameter values among three sample groups for

almost all hypothesis tests, our minimum Bonferroni adjusted α -level for individual contrasts was $\alpha = 0.05/3 = 0.017$.

Additionally, we tested similar hypotheses of equality for two meristic parameters among the three sample groups of Bering Cisco in this study and the Bering Cisco and Arctic Cisco sample groups examined by McPhail (1966). We tested the null hypothesis that mean lower limb gill raker counts were similar among the five sample groups. In the event of a rejection of the null hypotheses of equality, a Tukey multiple comparisons procedure would be performed to rank significantly different sample groups (Zar, 1999).

Comparisons between lateral line counts of Bering Cisco in this study and McPhail's (1966) Bering Cisco data were conducted with a Chi-square test using a modification of the scale number categories presented by McPhail (1966). He used a histogram with seven bins each spanning 3-counts to illustrate the count variation he observed but did not present a list of actual counts. We, therefore, combined the two lowest and two highest bins to achieve adequate sample numbers per scale count category for analysis (Conover, 1999). We tested the null hypothesis that proportional distribution of scale counts among the five length bins was similar among sample groups.

Two principal components analyses (PCA) were conducted, one using meristic count data and the other using morphometric ratios, to visualize variation among our three sample groups in two dimensions and to identify the most influential parameters (Jolliffe, 1986; Abdi and Williams, 2010). Our dataset had a small number of cells with missing or obviously incorrect values, eight in the meristic dataset (0.6% of cells) and eight in the morphometric dataset (0.2% of cells), with no individual fish missing more than one cell value. Rather than censor the large amount of other data accompanying the missing or incorrect values, we substituted cell values obtained with a non-parametric multiple imputation procedure (Josse and Husson, 2012).

RESULTS

Overview.—Female Bering Ciscos were longer and heavier than males in all three sample groups, and fish from the Yukon River tended to be larger than those from the Kuskokwim and Susitna rivers (Table 2). Median ages of males and females were similar within sample groups so age data were pooled. Median age of Yukon and Kuskokwim river fish was five years, while fish from the Susitna River were significantly younger at four years. The range of ages in each of our sample groups were reasonably similar, but the minimum age of maturity of sampled fish from the Susitna River was three years, while from the Yukon and Kuskokwim rivers it was four years.

Meristics.—Table 3 summarizes observed meristic trait variation within and among the three Bering Cisco sample groups in this study. Meristics from the Yukon and Kuskokwim River samples were similar for all parameters. Mean vertebrae count of Susitna River samples was significantly less than those from the Yukon or Kuskokwim rivers. Mean dorsal-fin ray and branchiostegal bone counts from Susitna River samples were significantly lower than those from the Kuskokwim River but were similar to those from the Yukon River. Similarly, mean values for scale row counts above and below the lateral line were significantly greater for Susitna River samples than for those from the Yukon or Kuskokwim

Table 2. Descriptive data from Bering Cisco sample groups from the Yukon, Kuskokwim, and Susitna rivers in Alaska. The F- or H-statistic from initial ANOVA or Kruskal-Wallis tests of each parameter is presented with zero to three asterisks to indicate the resulting level of significance: $P > 0.05$, $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$, and $P \leq 0.001$, respectively. Data for each sample group include mean (standard deviation) for length and weight parameters for females (F) and males (M) separately, and median (range) for the age parameter, plus sample size, and statistical grouping letter. Sample group means or medians that do not share a statistical grouping letter were significantly different.

Descriptive data	Statistic	Yukon	Kuskokwim	Susitna
Fork length (mm), F	$F_{2,40} = 15.32^{***}$	362 (20) 20 A	339 (19) 10 B	322 (23) 13 B
Fork length (mm), M	$F_{2,75} = 21.44^{***}$	337 (27) 22 A	330 (19) 29 A	301 (18) 27 B
Weight (g), F	$F_{2,40} = 7.03^{**}$	572 (97) 20 A	427 (75) 10 B	502 (124) 13 AB
Weight (g), M	$F_{2,75} = 7.52^{***}$	431 (99) 22 A	372 (58) 29 B	352 (64) 27 B
Age (y)	$H_2 = 13.39^{**}$	5 (4–10) 40 A	5 (4–12) 37 A	4 (3–11) 35 B

rivers. A principal component analysis of these meristic data, leaving out total gill raker count because it was the sum of the lower and upper limb counts, revealed a distinct positive separation of Susitna River samples from Yukon and Kuskokwim River samples. The separation is most strongly influenced by counts of scale rows above and below the lateral line and upper and lower limb gill rakers in Principal Component (PC) 1 and by counts of fin rays and branchiostegal bones in PC 2 (Fig. 3).

Morphometrics.—Table 4 summarizes measured morphometric trait variation within and among the three Bering Cisco sample groups in this study. In parallel to results based on meristic evidence, Susitna River samples consistently exhibited equal or greater morphometric ratio values than samples from either the Yukon or Kuskokwim rivers. Mean FL of males from the Susitna River was significantly less than for males from the Yukon or Kuskokwim rivers, and mean FL of females from the Susitna River was significantly less than for females from the Yukon River (Table 2). Because FL is the denominator in most of the morphometric ratios, these results suggest that fish from the Susitna River have a relatively thicker body than those from the Yukon or Kuskokwim rivers. A principal component analysis of morphometric data provides some support for this suggestion revealing a positive separation of Susitna River samples from those in the Yukon and Kuskokwim rivers, influenced most strongly in PC 1 by body depth ratios: body depth/fork length, (adipose-fin origin to anal-fin origin)/fork length, (dorsal-fin origin to pelvic-fin origin)/fork length, and (dorsal-fin origin to anal-fin origin)/fork length (Fig. 4). The relatively subtle

separation of Yukon and Kuskokwim river sample groups is influenced most strongly in PC 2 by fin length to body length ratios (i.e., pelvic-fin length/fork length) and segments of body length to fork length ratios (i.e., [snout to anal-fin origin]/fork length).

Lower limb gill raker counts.—Null hypotheses that mean lower limb gill raker counts were similar among Arctic and Bering Cisco sample groups presented by McPhail (1966) and Bering Cisco from the Yukon, Kuskokwim, and Susitna river sample groups in this study were rejected overall ($F_{4,248} = 328.98$, $P < 0.001$), and for all except one subsequent paired contrasts at a 95% family level of confidence. In paired contrasts, the null hypothesis that mean lower limb gill raker counts of Bering Cisco from the Yukon and Kuskokwim river sample groups were equal could not be rejected. As expected, McPhail's (1966) Arctic Cisco ($n = 76$) had the greatest mean value at 27.7 (range = 26.0–30.0). Bering Cisco from the Susitna River ($n = 40$) had the second largest mean at 24.1 (range = 21.0–27.0). McPhail's (1966) Bering Cisco ($n = 56$) had the third largest mean at 23.0 (range = 21.0–25.0). Our combined western Alaska samples, including fish from the Yukon and Kuskokwim rivers ($n = 81$), had the lowest mean value at 22.1 (range = 20.0–24.0; Fig. 5).

Lateral line scale counts.—We tested the null hypothesis that lateral line scale counts were similar for McPhail's (1966) Bering Cisco sample group ($n = 33$) and the combined samples in this study ($n = 104$). Lateral line scale counts among sample groups in our study were found to be statistically similar (Table 3; Fig. 6) so they were pooled for

Table 3. Meristic counts for Bering Cisco sample groups from the Yukon, Kuskokwim, Susitna rivers in Alaska. The F-statistic from initial ANOVA tests of each parameter is presented with zero to three asterisks to indicate the resulting level of significance; $P > 0.05$, $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$, and $P \leq 0.001$, respectively. Data for each sample group include mean, (range), sample size, and statistical grouping letter. Sample group means that do not share a statistical grouping letter were significantly different.

Meristic parameter	F-statistic	Yukon	Kuskokwim	Susitna
Dorsal-fin rays	$F_{2,102} = 3.66^*$	14.2 (11–16) 37 AB	14.6 (13–17) 39 A	14.1 (13–15) 29 B
Pectoral-fin rays	$F_{2,102} = 0.59$	16.3 (14–17) 37 A	16.5 (14–18) 39 A	16.5 (15–19) 29 A
Pelvic-fin rays	$F_{2,102} = 0.34$	12.1 (11–14) 37 A	12.1 (10–14) 39 A	12.2 (10–14) 29 A
Anal-fin rays	$F_{2,102} = 2.53$	14.0 (12–16) 37 A	14.4 (12–16) 39 A	14.3 (12–16) 29 A
Lateral line scales	$F_{2,101} = 2.27$	84.3 (76–91) 37 A	85.0 (79–93) 38 A	86.1 (78–93) 29 A
Scale rows above LL	$F_{2,102} = 19.24^{***}$	9.9 (8–11) 37 B	9.8 (9–11) 39 B	10.9 (9–13) 29 A
Scale rows below LL	$F_{2,102} = 17.67^{***}$	9.5 (8–10) 37 B	9.3 (8–12) 39 B	10.3 (9–12) 29 A
Gill rakers (lower limb)	$F_{2,118} = 48.29^{***}$	22.2 (20–24) 42 B	22.1 (20–24) 39 B	24.1 (21–27) 40 A
Gill rakers (upper limb)	$F_{2,113} = 11.82^{***}$	12.7 (12–14) 37 B	12.6 (10–15) 39 B	13.5 (12–15) 40 A
Gill rakers (total)	$F_{2,113} = 40.66^{***}$	34.9 (33–38) 37 B	34.6 (30–38) 39 B	37.6 (34–40) 40 A
Branchiostegal bones	$F_{2,101} = 3.10^*$	9.3 (8–10) 37 AB	9.5 (9–11) 39 A	9.1 (8–11) 28 B
Vertebrae	$F_{2,96} = 18.23^{***}$	62.9 (59–65) 35 A	62.8 (61–65) 37 A	61.1 (59–64) 27 B

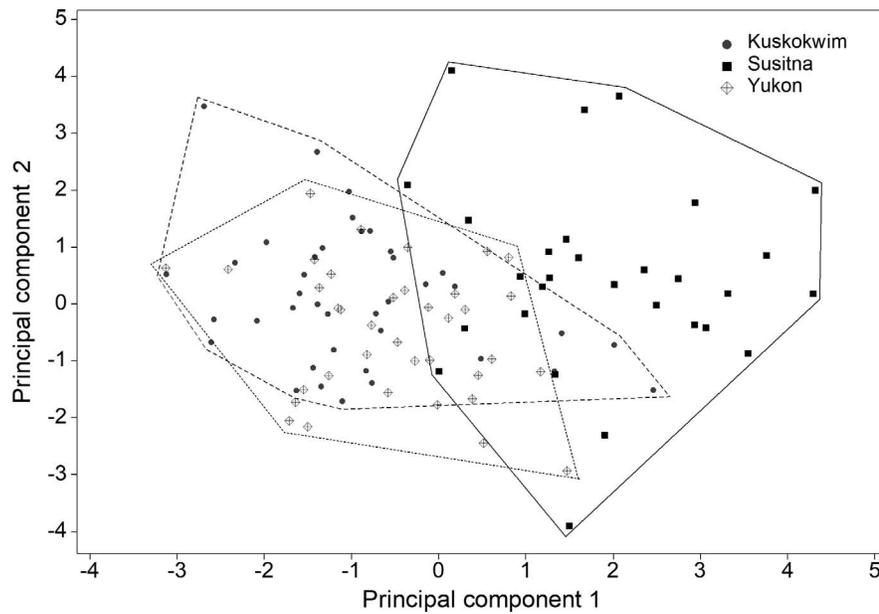


Fig. 3. Scatterplot of the Bering Cisco meristic data scores from the first two principal components illustrating the relatively close intermingling of Yukon and Kuskokwim river samples compared to the distinct separation to the right of the Susitna River samples.

the comparison with McPhail's (1966) data using a Chi-square test. The null hypothesis of similar proportional distribution of counts among five bins could not be rejected ($\chi^2 = 0.992$, $df = 4$, $P = 0.911$).

DISCUSSION

Our analyses yielded evidence of incipient morphological differentiation among spawning populations of Bering Cisco. Yukon and Kuskokwim river populations were more similar

Table 4. Morphometric ratios for Bering Cisco sample groups from populations in the Yukon, Kuskokwim, and Susitna rivers in Alaska. The F-statistic from initial ANOVA tests of each parameter is presented with zero to three asterisks to indicate the resulting level of significance: $P > 0.05$, $0.05 \geq P > 0.01$, $0.01 \geq P > 0.001$, and $P \leq 0.001$, respectively. Data for each sample group include mean, (standard deviation), sample size, and statistical grouping letter. Sample group means that do not share a statistical grouping letter were significantly different.

Morphometric ratios	F-statistic	Yukon	Kuskokwim	Susitna
Head length/FL	$F_{2,102} = 0.64$	0.203 (0.008) 37 A	0.202 (0.006) 39 A	0.204 (0.006) 29 A
(Snout–D Opercular O)/FL	$F_{2,102} = 1.00$	0.147 (0.006) 37 A	0.147 (0.005) 39 A	0.149 (0.006) 29 A
(Snout–Pectoral FO)/FL	$F_{2,102} = 0.88$	0.204 (0.011) 37 A	0.205 (0.008) 39 A	0.202 (0.009) 29 A
(Snout–Dorsal FO)/FL	$F_{2,102} = 19.98^{***}$	0.425 (0.009) 37 A	0.411 (0.010) 39 B	0.423 (0.012) 29 A
(Snout–Pelvic FO)/FL	$F_{2,102} = 7.27^{***}$	0.473 (0.012) 37 A	0.460 (0.019) 39 B	0.462 (0.015) 29 B
(Snout–Anal FO)/FL	$F_{2,101} = 9.47^{***}$	0.693 (0.012) 36 A	0.679 (0.014) 39 B	0.685 (0.016) 29 AB
(Snout–Adipose FO)/FL	$F_{2,102} = 3.13^*$	0.758 (0.017) 37 A	0.750 (0.020) 39 A	0.760 (0.011) 29 A
Dorsal-fin base/FL	$F_{2,102} = 10.04^{***}$	0.120 (0.006) 37 B	0.127 (0.007) 39 A	0.121 (0.007) 29 B
Dorsal fin length/FL	$F_{2,102} = 1.65$	0.123 (0.031) 37 A	0.129 (0.024) 39 A	0.136 (0.032) 29 A
(Dorsal FO–Pelvic FO)/FL	$F_{2,101} = 21.90^{***}$	0.201 (0.011) 36 B	0.198 (0.015) 39 B	0.219 (0.015) 29 A
(Dorsal FO–Pectoral FO)/FL	$F_{2,102} = 21.17^{***}$	0.277 (0.012) 37 A	0.266 (0.009) 39 B	0.283 (0.010) 29 A
(Dorsal FO–Anal FO)/FL	$F_{2,102} = 9.39^{***}$	0.332 (0.010) 37 B	0.327 (0.010) 39 B	0.338 (0.012) 29 A
(Dorsal FO–Adipose FO)/FL	$F_{2,102} = 1.32$	0.353 (0.010) 37 A	0.356 (0.010) 39 A	0.357 (0.012) 29 A
Pectoral-fin base/FL	$F_{2,100} = 17.59^{***}$	0.037 (0.003) 36 B	0.039 (0.003) 39 A	0.041 (0.002) 28 A
Pectoral fin length/FL	$F_{2,101} = 3.44^*$	0.148 (0.009) 37 B	0.150 (0.010) 38 AB	0.154 (0.009) 29 A
Pelvic-fin base/FL	$F_{2,101} = 13.65^{***}$	0.042 (0.004) 37 B	0.047 (0.005) 38 A	0.048 (0.005) 29 A
Pelvic fin length/FL	$F_{2,102} = 9.80^{***}$	0.132 (0.008) 37 B	0.138 (0.010) 39 A	0.142 (0.009) 29 A
(Pelvic FO–Pectoral FO)/FL	$F_{2,102} = 4.99^{**}$	0.277 (0.012) 37 A	0.267 (0.013) 39 B	0.271 (0.016) 29 AB
Anal-fin base/FL	$F_{2,102} = 46.02^{***}$	0.105 (0.006) 37 B	0.116 (0.005) 39 A	0.119 (0.007) 29 A
Anal fin length/FL	$F_{2,101} = 5.02^{**}$	0.095 (0.016) 37 B	0.097 (0.015) 39 B	0.107 (0.016) 28 A
(Anal FO–Adipose FO)/FL	$F_{2,102} = 48.93^{***}$	0.152 (0.006) 37 B	0.154 (0.008) 39 B	0.168 (0.007) 29 A
(Anal FO–Pelvic FO)/FL	$F_{2,102} = 2.12$	0.235 (0.014) 37 A	0.234 (0.010) 39 A	0.240 (0.013) 29 A
Caudal peduncle W/FL	$F_{2,102} = 9.93^{***}$	0.041 (0.004) 37 B	0.039 (0.006) 39 B	0.045 (0.007) 29 A
Caudal peduncle D/FL	$F_{2,102} = 14.29^{***}$	0.071 (0.003) 37 B	0.070 (0.005) 39 B	0.075 (0.003) 29 A
Body depth/FL	$F_{2,102} = 17.85^{***}$	0.206 (0.016) 37 B	0.205 (0.014) 39 B	0.225 (0.016) 29 A
Head depth/HL	$F_{2,101} = 1.25$	0.616 (0.027) 37 A	0.623 (0.045) 38 A	0.631 (0.036) 29 A
(Snout–A Eye margin)/HL	$F_{2,102} = 0.87$	0.228 (0.022) 37 A	0.230 (0.021) 39 A	0.223 (0.021) 29 A
Eye diameter/HL	$F_{2,102} = 2.80$	0.203 (0.024) 37 A	0.213 (0.020) 39 A	0.201 (0.026) 29 A
Interorbital distance/HL	$F_{2,102} = 4.23^*$	0.294 (0.018) 37 A	0.280 (0.024) 39 B	0.287 (0.023) 29 AB
Upper jaw length/HL	$F_{2,102} = 0.23$	0.338 (0.013) 37 A	0.339 (0.013) 39 A	0.339 (0.015) 29 A
Lower jaw length/HL	$F_{2,102} = 3.76^*$	0.411 (0.038) 37 AB	0.427 (0.026) 39 A	0.408 (0.032) 29 B

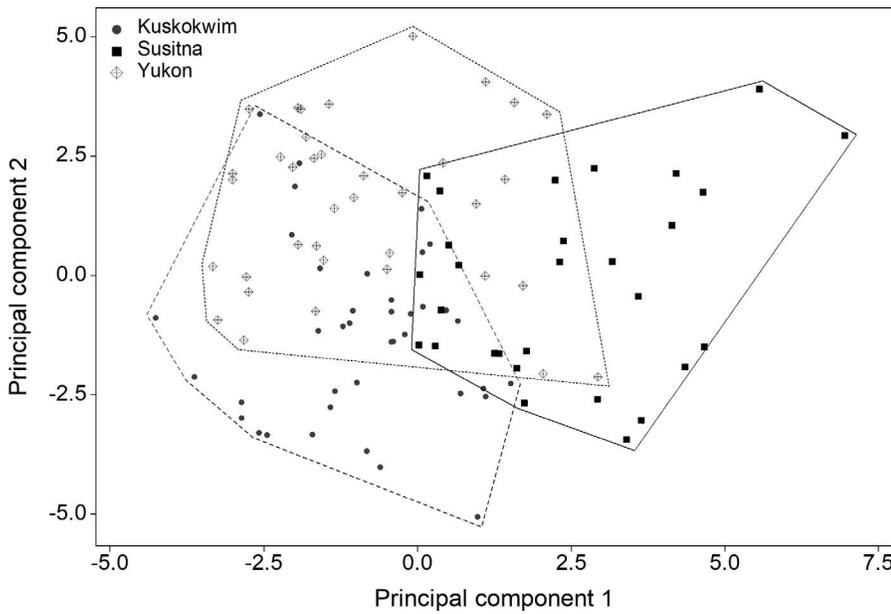


Fig. 4. Scatterplot of Bering Cisco morphometric data scores from the first two principal components illustrating a central area of intersection with clear variation in centers of distribution among the Yukon (upper left), Kuskokwim (lower left), and Susitna (right) river samples.

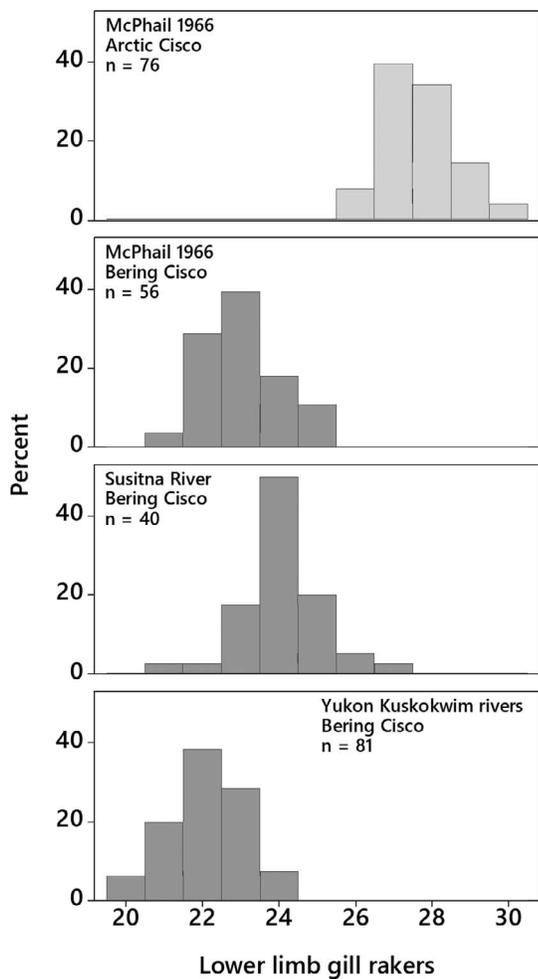


Fig. 5. Histograms of lower limb gill raker counts among Arctic and Bering Cisco collections presented by McPhail (1966), Bering Cisco from the Susitna River, and Bering Cisco from western Alaska, including the Yukon and Kuskokwim river sample groups pooled because they had equal means and distributions.

to each other than to the Susitna River population. A recent population genetics study of structure and patterns of gene flow among these three populations came to similar conclusions (Russ, 2015). Genetically, the Yukon and Kuskokwim river populations were distinct but more similar to each other than either was to the Susitna River population. Further, the Yukon and Kuskokwim river populations had similarly high measures of allelic richness and heterozygos-

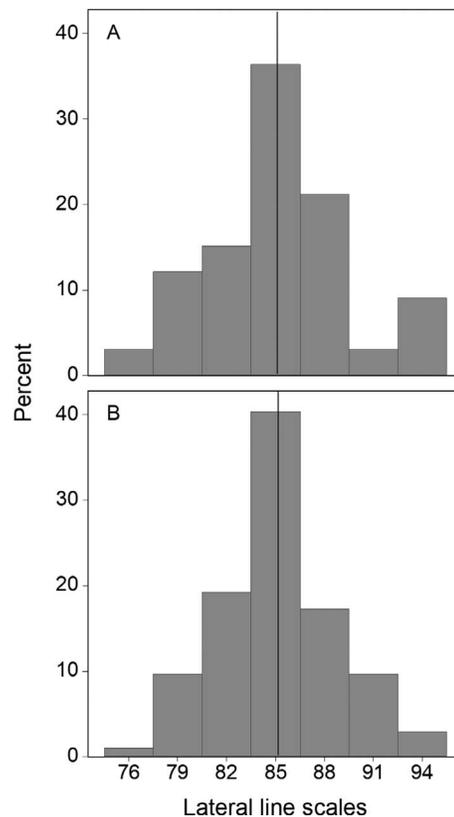


Fig. 6. Histograms of the pooled lateral line scale counts from the three Bering Cisco sample groups in this study (A, $n = 104$, mean = 85.1) and Bering Cisco data presented by McPhail (1966; B, $n = 33$, mean = 85.2). Mean values are indicated with vertical lines.

ity, while the Susitna River population had significantly lower measures of each. The genetic evidence also supported a symmetrically low rate of gene flow between the Yukon and Kuskokwim rivers and negligible connectivity between these and the Susitna River population. The pattern of genetic differences among populations is consistent with the meristic and morphometric variation we examined and report here. Consideration for the evidence of phenotypic and genotypic differentiation among the only three known, geographically distant spawning aggregations of Bering Cisco should inform future strategies for management of this species.

During the Wisconsin glacialiation (70,000–12,000 years before present), the Yukon and Kuskokwim river drainages were mostly unglaciated, sea level reached 100 m lower than at present, an extensive land bridge was exposed between North America and Asia, a continuous region of massive glacialiation flowed from the arc of mountains ringing the Gulf of Alaska far out onto what is now the continental shelf, and the Susitna River valley was entirely bound in ice (Hopkins, 1973; Briner and Kaufman, 2008). Lindsey and McPhail (1986) describe the unglaciated Yukon and Kuskokwim rivers as major northern refugia for fishes that subsequently recolonized the southern drainages once the ice retreated, which is thought to have happened sometime during the last 10,000 years. Ancestral populations of Bering Cisco likely survived the Wisconsin glacialiation in the Yukon River and perhaps the Kuskokwim River as well. Lindsey and McPhail (1986) contended that for saltwater-intolerant species, post-glacial colonization of the southern drainages by fishes from the Yukon River refugium would have occurred via headwater transfer. Bering Cisco are saltwater tolerant, as evidenced by their extensive coastal rearing distribution (Padilla et al., 2016), and may have colonized the Susitna River by either ocean or headwater transfer routes. By whatever route they used, it is clear that a founder population of Bering Cisco colonized the Susitna River sometime during the last few thousand years and appears to now be isolated from the source population in the Yukon or Kuskokwim river.

Lower limb gill raker count comparisons.—Number of lower limb gill rakers is a distinguishing feature of Bering Cisco (McPhail, 1966). Our finding that mean gill raker counts on all three associated parameters were significantly greater for Susitna River samples than for those from the Yukon and Kuskokwim rivers is particularly interesting. The divergent lower limb gill raker counts between the pooled samples from the Yukon and Kuskokwim rivers and McPhail's (1966) collection can be explained given the significantly greater values from the Susitna River samples (Table 3; Fig. 5). McPhail (1966) collected samples around the north and west coasts of Alaska, along the Yukon River, and in Cook Inlet. Padilla et al. (2016) reported that a large majority of rearing Bering Cisco from the western Beaufort Sea to the Alaska Peninsula were members of the Yukon River population. Given the large number of sampling sites in western Alaska relative to Cook Inlet, McPhail's (1966) collection was most likely dominated by individuals from the Yukon River population with smaller numbers from the Kuskokwim and Susitna river populations. McPhail (1966) was not explicit on the number of samples from each region, but even a small number of Susitna River samples in a larger collection of Yukon and Kuskokwim river samples could have shifted the mean lower limb gill raker count significantly to the positive, which is what we observed here.

A more interesting matter involves the shift for the Susitna River population to a greater number of gill rakers, assuming a source population less than 10,000 years ago with similar gill raker counts to the current western Alaska populations. The shallow habitats in the eastern Bering and Chukchi seas, where most Yukon and Kuskokwim river Bering Cisco rear (Alt, 1983; Padilla et al., 2016), appear to be a distinctly different environment than that used by Susitna River Bering Cisco in Cook Inlet (Blackburn et al., 1980). Lindsey (1981) reviewed numerous cases in which a normally demersal coregonine species in a lake, for example, differentiated into sympatric demersal and pelagic forms in the absence of a typically pelagic species occupying that niche. In those cases, the pelagic form would differentiate from the demersal form and develop greater numbers of gill rakers that were longer and thinner as an adaptation to pelagic foraging. It seems plausible that the shift to a greater number of gill rakers for the Susitna River Bering Cisco population was an adaptation to a different foraging environment in Cook Inlet relative to the eastern Bering Sea. Alternatively, a small founder population and subsequent demographic dynamics may have locked the gill raker phenotype characterizing Susitna River populations as a historical accident.

Scale rows above and below the lateral line.—Bering Cisco from the Susitna River sample group averaged two scale rows more mid-body, one above the lateral line and one below the lateral line, than those from the Yukon or Kuskokwim rivers (Table 3). This meristic quality, combined with a smaller average FL, appears to have had a significant positive influence on morphometric ratios dealing with body depth, as identified earlier (Table 4). It is not clear if this deviation from the parent populations occurred as a response to new environmental qualities following colonization of the Susitna River or a simple founder effect. One potentially influential environmental difference between the three populations is upstream migration distance to spawning destinations, which are approximately 1,600 km up the Yukon River (Brown and Daum, 2015), 950 km up the Kuskokwim River (Alt, 1973; M. Thalhauser, ADFG, pers. comm.), and 120 km up the Susitna River (ADFG, 1983). Fish swimming speed is primarily a function of body length and the frequency of tail beats (Videler and Wardle, 1991). It is not clear if the slightly longer and slimmer body morphology of the Yukon and Kuskokwim river populations would confer a selective advantage over the shorter and stouter body morphology of the Susitna River population when the energetic demands of upstream migration are high, while being less advantageous when the energetic demands are comparatively low.

DATA ACCESSIBILITY

Supplemental material is available at <http://www.copeiajournal.org/cg-17-702>.

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