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ARTICLE

Spawning Distribution of Bering Ciscoes in the Yukon River

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Abstract
Bering Ciscoes *Coregonus laurettae* are anadromous salmonids with known spawning populations only in the Yukon, Kuskokwim, and Susitna rivers in Alaska. A commercial fishery for the species was recently initiated at the mouth of the Yukon River, inspiring a series of research projects to enhance our understanding of the exploited population. This study was designed to delineate the geographic spawning distribution of Bering Ciscoes in the Yukon River. One hundred radio transmitters per year in 2012 and 2013 were deployed in prespawning Bering Ciscoes at a site located 1,176 km upstream from the sea. A total of 160 fish survived fish wheel capture and tagging, avoided harvest and predation after tagging, and continued migrating upstream to their spawning destinations. Approximately 79% migrated to spawn in the upper Yukon Flats, upstream from the mouth of the Porcupine River, and 21% migrated to spawn in the lower Yukon Flats. Locating the Bering Cisco spawning area, which is almost entirely encompassed by the Yukon Flats National Wildlife Refuge, enhances our ability to protect it from anthropogenic disturbance and enables future biological research on the spawning population.

Conservation of migratory fish in large rivers requires an understanding of habitat use across a species' range and the ability to manage anthropogenic impacts to essential habitats such as migration routes and spawning areas (Gross 1987; Bronmark et al. 2014). Anthropogenic activities known to impact aquatic habitats include the construction of dams (Rosenberg et al. 1997), water withdrawal (Carlson and Muth 1989; Yang et al. 2004), sediment release (Waters 1995), riverbed gravel mining (Brown et al. 1998), and other construction and extraction activities. The Yukon River in Alaska has been sheltered from most major habitat-altering activities because of its remoteness from human population centers; however, a hydroelectric dam was built in 1958 across the main stem upstream from the Alaska–Yukon Territory border (Gordon et al. 1960) and construction of a large hydroelectric dam was considered but rejected at Rampart Canyon in Alaska during the 1960s (USFWS 1964). Mining riverbed gravel, however, is a common method of obtaining fill material for communities along the Yukon River in Alaska (Woodward–Clyde Consultants 1980; Brown et al. 2012a). Disturbing or removing gravel from fish spawning habitats has been shown to reduce spawning success (Fudge and Bodaly 1984; Meng and Müller 1988), which could jeopardize the viability of affected populations. Development activities such as riverbed gravel mining can be managed to avoid impacts on essential habitats of migratory fish only if those habitats have been identified.

Bering Ciscoes *Coregonus laurettae* are anadromous salmonids with known spawning populations only in the Yukon, Kuskokwim, and Susitna rivers in Alaska (McPhail and Lindsey 1970; Alt 1973; Alaska Department of Fish and Game [ADFG] 1983; Brown et al. 2007). Rearing fish are present in coastal habitats of south-central Alaska (Blackburn et al. 1980) and widely distributed in estuaries and lagoons from Kuskokwim Bay north to the western Beaufort Sea in western Alaska (McPhail 1966; Alt 1973; Bickham et al. 1997). Bering Ciscoes have traditionally been harvested in subsistence fisheries throughout their range (Stickney 1984; Georgette and Shiedt 2005; Runfola 2011). The recent establishment of a commercial fishery at the mouth of the Yukon River (Brown et al. 2012a; J.

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Estensen, ADFG, personal communication) represents a distinct change in harvest pattern. Concern over the effects of the commercial fishery on Bering Cisco populations has inspired numerous research projects designed to enhance our understanding of the biology of the species in general and of the Yukon River population in particular.

Historical fish survey data from within the Yukon River indicate that Bering Ciscoes are present only in main-stem habitats and do not migrate into tributary systems (Brown et al. 2012a). Bering Ciscoes are the most numerous of the coregonid species observed in a video-monitored fish wheel at Rapids (Daum 2005; Brown et al. 2012b), which is a narrow, swiftly flowing region of the Yukon River located at river kilometer (rkm) 1,176, as measured from the mouth of the Yukon River (Figure 1). Ripe Bering Ciscoes were reported in the upper reaches of the Yukon Flats in early October (Brown 2000), indicating at least some spawning activity in the area. The species has occasionally been captured farther upstream in the community of Eagle (Brown et al. 2007), near the Alaska–Yukon Territory border, and a single individual was documented in the community of Dawson in Yukon Territory (deGraaf 1981). Compared with fish wheel catches at Rapids (Brown et al. 2012b), the apparent reduction in relative abundance upstream from the Yukon Flats suggests that most Bering Ciscoes migrate to spawn in the uniquely braided habitats of the Yukon Flats, similar to anadromous populations of Inconnus *Stenodus leucichthys* (Brown 2000; Brown and Burr 2012) and Broad Whitefish *C. nasus* (Carter 2010).

Modern radio telemetry technology is a powerful tool for monitoring fish migrations in large rivers and identifying essential habitats such as spawning areas (Adams et al. 2012; McKenzie et al. 2012). In the Yukon River, for example, several major spawning areas for coregonid species, including Inconnus (Brown 2000; Brown and Burr 2012), Broad Whitefish (Carter 2010), and Humpback Whitefish *C. pidschian* (Brown 2006; Dupuis and Sutton 2014) have been identified using radio telemetry methods. The primary objective of this 2-year radio telemetry investigation was to delineate the geographic spawning distribution of Bering Ciscoes in the Yukon River. Secondary objectives included the collection of descriptive data related to spawning timing and migration speeds upstream and downstream along the river.

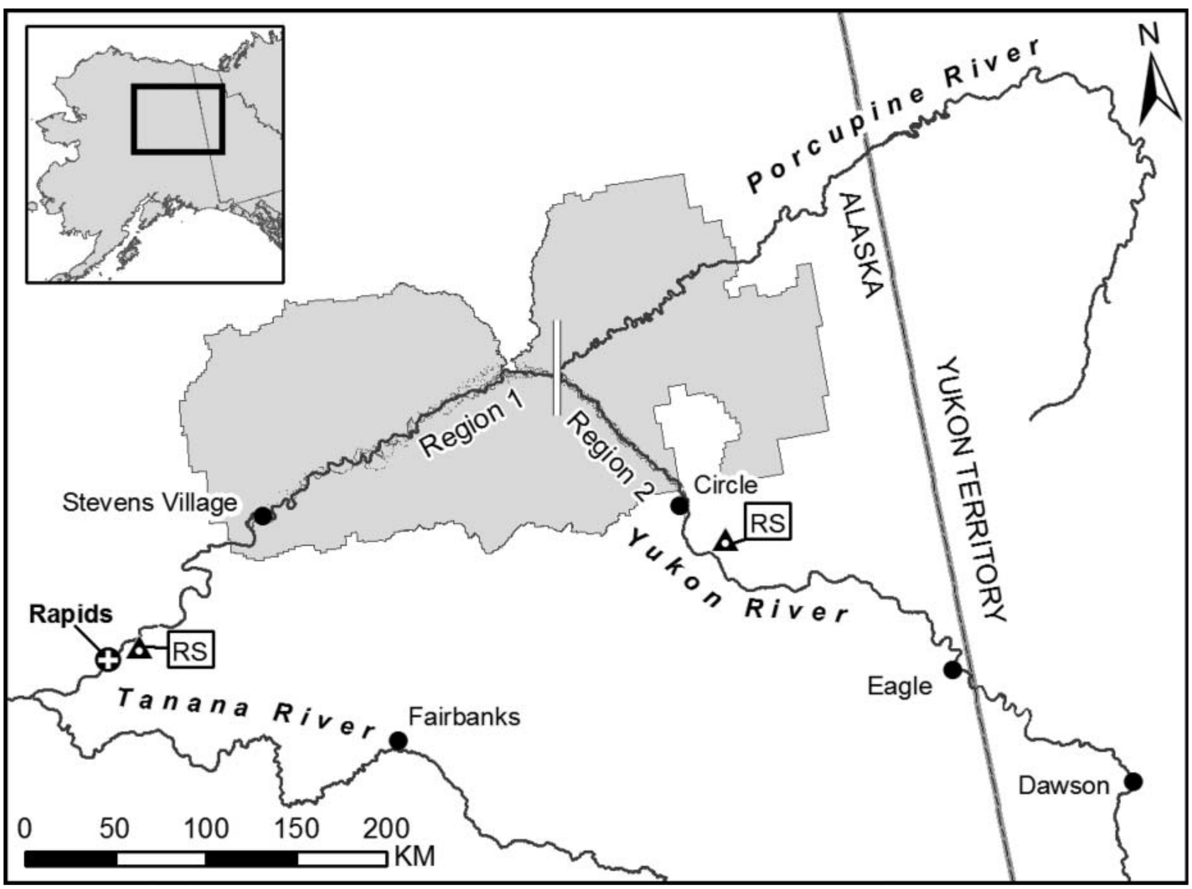

FIGURE 1. The study area within the Yukon River drainage ranged from the tagging site at Rapids (rkm 1,176) to the border crossing between Alaska and Yukon Territory (rkm 2,013). Two radio-receiving stations (RS) were operating along the river during this project: one at rkm 1,186, 10 km upstream from the tagging site, and the other located upstream from the Yukon Flats at rkm 1,791. The border between Regions 1 and 2 is indicated by the vertical white line at the mouth of the Porcupine River. The Yukon Flats National Wildlife Refuge is represented by the shaded polygon.

STUDY AREA

The Yukon River is the largest drainage in Alaska and the fifth largest in North America (Revenga et al. 1998). It drains an area of more than 850,000 km^2, approximately 500,000 km^2 of which is in Alaska (Brabets et al. 2000). It flows more than 3,000 km from its headwaters in northern British Columbia, Canada, to its mouth at the Bering Sea in western Alaska. Average annual flow near the Yukon River mouth is approximately 6,400 m^3/s, although peak flow in early summer averages about 20,000 m^3/s.

This project was focused on a 837-km reach of the central Yukon River drainage that encompassed the Yukon Flats. It ranged from the tagging site at Rapids, rkm 1,176, to the Alaska–Yukon Territory border, rkm 2,013 (Figure 1). The Yukon Flats itself, most of which lies within the Yukon Flats National Wildlife Refuge, includes a 400-km reach of uniquely braided habitat extending from the community of Stevens Village near the downstream end to the community of Circle near the upstream end (Froese et al. 2005). Numerous tributary rivers enter the main stem within the Yukon Flats including the Porcupine River, which is the largest tributary by area in the Yukon River drainage (Brabets et al. 2000).

METHODS

Overview of the project.—This project consisted of two independent summer seasons of radio tagging on the mainstem Yukon River at Rapids, followed by two independent fall seasons of tracking activities to locate upstream spawning destinations and determine spawning timing. Radio tags were surgically implanted in prespawning Bering Ciscoes that were released following surgery and allowed to continue their upstream migration. Two remote radio-receiving stations (stations) were established at sites previously used for basin-wide Pacific Salmon *Oncorhynchus* spp. telemetry studies (Eiler 2012). Upstream and subsequent downstream migrations of radio-tagged fish were monitored with the two stations. Aerial surveys were conducted throughout the study area to identify locations of tagged fish before, during, and after the fall spawning season.

Capture, selection, and tagging.—Bering Ciscoes were captured with a fish wheel operating at Rapids (Figure 1) where relative abundance data have been collected annually since 2001 (Brown et al. 2012b). Previous demographic sampling had established that all Bering Ciscoes at the site were mature, prespawning individuals. There were no selection criteria based on sex or size so all captured Bering Ciscoes were potential candidates for tagging. Fork length (FL) for each selected fish was measured to the nearest 0.5 cm, and sex was identified based on the obvious gravid versus slim body forms of the females and males, respectively. Digitally coded radio transmitters were surgically implanted into candidate fish during each of two summers, 2012 and 2013, using methods considered to be appropriate and effective for salmonid fishes (Winter 1996; Wagner et al. 2000; Jepsen et al. 2002). Tagged fish were released as soon as they exhibited a desire to swim away.

Deployment schedule.—Radio transmitters were deployed in multiple tagging periods during 2012 and 2013. Historical annual profiles of the relative abundance of the spawning migration of Bering Ciscoes at Rapids revealed high interannual variability in the timing of peak values during summer and a distinct decline in relative abundance by mid- to late August as the end of the run passed the site (Brown et al. 2012b). Because predicting timing of peak periods of abundance was not possible, radio tag deployment was systematically scheduled at 2- to 3-week intervals among four 3-d tagging events during 2012 and three 3-d tagging events during 2013.

Relocation data.—Relocations of tagged fish were based on records from the two stations and aerial survey flights of the upper Yukon River drainage in Alaska. The stations were located approximately 10 km upstream from the tagging site (lower station) and 615 km upstream from the tagging site (upper station; Figure 1). The lower station was used to identify all the radio-tagged fish that recovered from surgery; avoided recapture, harvest, and predation; and continued upstream migration. Recovery time was calculated as the time interval between surgery and migration upstream past the lower station. The lower station also provided timing data on postspawning downstream migration. Data from the upper station were used to identify radio-tagged fish that migrated upstream beyond the Yukon Flats towards the community of Eagle and Yukon Territory. Upstream migration rates were calculated from radio-tagged fish recorded at both the lower and upper stations. Five aerial surveys in 2012 and three in 2013 were conducted during late September and October to locate tagged fish within the study area.

Spawning locations and timing.—Migration patterns of individual fish and major congregation areas were used to infer spawning destinations and subsequent spawning timing. Coregonid species exhibit spawning migration patterns of migrating in late summer and fall to upstream spawning destinations where fish congregate, followed by a period of several days or weeks when prespawning fish remain in a spawning area; spawning then occurs relatively synchronously, and postspawning fish migrate back downstream (Reist and Bond 1988; Underwood 2000; Brown 2006; VanGerwen-Toyne et al. 2008). Bering Cisco spawning locations were therefore identified as their final positions in October prior to the postspawning downstream migration. Spawning timing was inferred from downstream migration data collected from the lower station. A Kruskal–Wallis nonparametric rank test (Zar 1999) was used to test the null hypothesis that downstream migration timing, expressed in units of Julian days for statistical analysis, was similar among years. Statistical significance was based on $\alpha = 0.05$ for this and all other analyses in this manuscript.

Spawning distribution.—The Yukon Flats was partitioned for analysis of spawning distribution into two geographic regions (Figure 1) based in part on distinctly different river morphologies, as described by Froese et al. (2005), and in part on the known spawning distributions of Inconnus (Brown 2000; Brown and Burr 2012) and Broad Whitefish (Carter 2010). Region 1 was defined as the Yukon River downstream from the mouth of the Porcupine River, which included a 260-km reach of the Yukon Flats with stable wandering channels and permanent islands (Froese et al. 2005) that encompassed the Broad Whitefish spawning region. Region 2 was defined as the Yukon River upstream from the mouth of the Porcupine River, which included a 180-km reach of the Yukon Flats with extensively braided channels and ephemeral islands (see Froese et al. 2005, their Figure 4) that encompassed the Inconnu spawning region. The spawning location for each Bering Cisco was classified as being in Region 1 or Region 2. Chi-square tests of differences in probabilities (Conover 1999) were used to test null hypotheses that proportional spawning distribution between Regions 1 and 2 was similar among sampling periods within years and similar among years. Data from groups were pooled when test results were nonsignificant. Proportional spawning distribution by region was subsequently estimated based on the binomial distribution.

RESULTS

Tagging and Recovery

Two hundred radio transmitters were surgically implanted in prespawning Bering Ciscoes during 2012 (n = 100) and 2013 (n = 100; Table 1). Water temperature during the tagging periods varied slightly among years averaging 15.8°C (range 15.0–17.0°C) in 2012 and 17.2°C (range 16.5–18.0°C) in 2013. Female Bering Ciscoes dominated the annual samples in both 2012 (64%) and 2013 (62%). Mean FL of females (39 cm, SE = 0.20 cm, n = 126) was greater than for males (35 cm, SE = 0.24 cm, n = 71); a pattern that was consistent between years and with previous sampling data (Brown et al. 2012b). Recovery success averaged 0.80 overall and was slightly greater in 2012 (0.83) than in 2013 (0.77). Recovery times averaged 13.6 d (SE = 0.72 d) and were slightly shorter in 2012 (mean = 12.7 d, SE = 0.96 d) than in 2013 (mean = 14.7 d, SE = 1.06 d). Altogether, 160 out of 200 radio-tagged Bering Ciscoes (80%) recovered from capture and tagging; avoided harvest, recapture, and predation; and continued migrating upstream to their spawning destinations.

Spawning Distribution

Radio-tagged Bering Ciscoes that continued upstream migration to spawning destinations were distributed almost entirely within Regions 1 and 2 of the Yukon Flats (Table 1). Thirteen fish migrated upstream past the upper station but 10 migrated back downstream by early October and only 3 (<2% of the sample) remained upstream to spawn. Additionally, seven fish (three in 2012 and four in 2013) migrated upstream past the lower station but were not subsequently located farther upstream, so their spawning destinations were not identified. The proportional distribution of tagged fish between spawning regions were similar between deployment periods in 2012 (χ^2 = 5.356, df = 3, P = 0.148) and 2013 (χ^2 = 0.301, df = 2, P = 0.860). Annual groups (pooled deployment periods within years) were also similarly distributed among spawning regions (χ^2 = 0.085, df = 1, P = 0.771). Using pooled data from both years, the estimated proportion of Bering Ciscoes spawning in Region 1 was 0.209 (95% confidence interval [CI] = 0.148–0.282) and in Region 2 was 0.791 (95% CI = 0.718–0.852).

TABLE 1. Tagging, recovery, and spawning destination details for the Yukon River Bering Cisco radiotelemetry project during 2012 and 2013. Data include sample period dates, the number of fish tagged, the number of tagged fish that recovered and continued migrating upstream, the recovery rate, and spawning destinations by deployment periods, by years, and for the project as a whole.

Year	Period	Dates	Tagged	Recovered	Rate	Region 1	Region 2	Unknown
2012	One	Jun 19–21	25	24	0.96	2	22	0
	Two	Jul 10–12	24	21	0.88	4	16	1
	Three	Jul 24–26	17	15	0.88	2	11	2
	Four	Aug 7–9	34	23	0.68	8	15	0
	Total		100	83	0.83	16	64	3
2013	One	Jun 25–27	35	23	0.66	4	17	2
	Two	Jul 9–11	40	38	0.95	8	29	1
	Three	Jul 23–25	25	16	0.64	4	11	1
	Total		100	77	0.77	16	57	4
2012 and 2013			200	160	0.80	32	121	7

Migration Rates

Migration rates upstream prior to spawning and downstream after spawning were available for small samples of fish. The mean upstream migration rate of 13 individuals was 13.1 km/d and ranged from 8.5 to 21.0 km/d over the 605-km distance between stations. Migration rates of two fish recorded migrating downstream past both stations were 44.8 and 50.6 km/d. These small samples of migration rates provide a hint of what might be common for the species.

Spawning Timing

Fourteen radio-tagged Bering Ciscoes in 2012 and 58 in 2013 were recorded migrating downstream past the lower station after spawning. Downstream migration timing in 2012 (median = October 24, range October 14 to November 1) and 2013 (median = October 21, range October 13–27) were similar (H = 3.04, df = 1, P = 0.081). Most Bering Ciscoes spawned in Region 2, approximately 500 km upstream from the lower station. The downstream migration from that region to the lower station would require about 10 d at the rates reported above, assuming the two values collected were reasonably representative. From these data we inferred that most spawning took place during the second and third weeks of October, which is consistent with previous sampling data from the Yukon Flats (Brown 2000).

DISCUSSION

Spawning Distribution

The results presented here provide strong evidence that nearly all Yukon River Bering Ciscoes spawn within the Yukon Flats, a unique geographic region encompassed by the Yukon Flats National Wildlife Refuge (Figure 1). Long-term protection from development activities that would alter substrate or change flow patterns in this area is now possible. Such protection would also benefit other migratory species spawning in the main-stem channels of the Yukon Flats.

Froese et al. (2005) described morphological qualities of the middle Yukon River from the White River mouth in Yukon Territory, approximately 106 km upstream from Dawson, to the Dalton Highway Bridge in Interior Alaska, a 1000-km reach that included the Yukon Flats. The Yukon River upstream and downstream from the Yukon Flats averages approximately 0.5 km wide, the riverbed is composed of 8–16 m of gravel over bedrock, the channel is stable and sinuous, and some permanent islands are present. The river widens to as much as 6 km as it transitions to the upper Yukon Flats near the community of Circle. The Yukon Flats upstream from the Porcupine River, our Region 2, is described as being strongly braided with numerous ephemeral islands. Downstream from the Porcupine River, our Region 1, very sinuous channels become more stable again and islands become more permanent. The riverbed throughout the Yukon Flats is composed of about 30 m of gravel over at least 350 m of fine lake sediment. The interface between the lacustrine sediment and the fluvial gravel is approximately 3 million years old indicating great temporal stability of the riverbed. These habitat qualities are unique within the Yukon River drainage.

The habitat qualities that make the Yukon Flats so attractive to spawning Bering Ciscoes and other coregonid species have not been specifically identified, but they must enhance the survival and development of the eggs that reside in the substrate through the winter. Coregonid species broadcast negatively buoyant, nonadhesive eggs over gravel without nest preparation (McPhail and Lindsey 1970; Teletchea et al. 2009). The eggs sink to the substrate and become entrained in cracks and crevices, which not only protects the eggs from predation (Hart 1930; Letichevskiy 1981) but also allows contact with surface or subsurface water, essential for respiration (Fudge and Bodaly 1984). Coregonid eggs reside in the substrate through the winter and hatch, emerge, and move downstream during the high-flow period in spring (Shestakov 1991; Bogdanov et al. 1992; Næsje et al. 1995). Habitat qualities within the Yukon Flats appear to be ideal for this process.

This study focused on a main-stem reach upstream from rkm 1,176 and did not investigate the possibility of spawning aggregations of Bering Ciscoes farther downstream, although the possibility is thought to be unlikely. The most compelling arguments against the presence of downstream spawning areas are the strikingly similar morphological characteristics of other Bering Cisco spawning areas with that of the Yukon Flats, and the absence of any downstream habitat regions similar to the Yukon Flats. Spawning areas of Bering Ciscoes in the Susitna River were documented in a braided main-stem reach having a similar morphology to the Yukon Flats but at a much smaller scale (ADFG 1983). Similarly, preliminary results from a radio-tagging project in the Kuskokwim River indicate that Bering Ciscoes in that drainage migrate to spawn in a highly braided reach of the glacial South Fork Kuskokwim River (M. Thalhauser, ADFG, personal communication). The morphological similarity of the known spawning destinations of these three Bering Cisco populations suggests a strong habitat association and argues against the presence of spawning areas for Bering Ciscoes in the Yukon River downstream from our study area.

Upstream Migration

Upstream migration rates of 13 Bering Cisco averaged 13.1 km/d, which is substantially slower than some of the larger salmonids such as Inconnus (22 km/d; Brown and Burr 2012), Chum Salmon *O. keta* (40 km/d; J. Eiler, National Marine Fisheries Service, personal communication), and Chinook Salmon *O. tshawytscha* (51 km/d; Eiler et al. 2014). At the average migration rate reported here, the spawning migration of Bering Ciscoes from the sea to the Yukon Flats, about

1,600 km, would require about 122 d. Prespawning Bering Ciscoes are present at Rapids in mid-June each year when the fish wheel is deployed (Brown et al. 2012b), but it isn't clear when the earliest migrants arrive there. Considering these data, we speculate that the annual spawning migration begins at the mouth of the Yukon River under ice as early as mid-March or perhaps earlier. Similar to other coregonid fishes, Bering Ciscoes fast during the extended spawning migration (R. J. Brown, unpublished data) and draw energy from stored nutrients. The significant energy reserves required for migration undoubtedly factor into the preferred status of Bering Ciscoes in coastal subsistence and commercial food fisheries (Runfola 2011; Brown et al. 2012a).

Downstream Migration

The minimum age of mature Bering Ciscoes in the Yukon River is 4 years, and few exceed 8 years of age (Brown et al. 2012b). Because of this limited age distribution, it was hypothesized that few individuals spawned more than once, and we were unable to determine whether postspawning Bering Ciscoes migrated downstream to the sea or died near the spawning grounds, similar to Pacific Salmon. Our downstream migration data indicated that at least some postspawning Bering Ciscoes migrate downstream. The number of downstream migrants recorded at the lower station varied considerably between 2012 ($n = 14$) and 2013 ($n = 58$) suggesting that either fewer fish migrated downstream after spawning in 2012 than in 2013 or that detection probability at the station differed among years. A better understanding of postspawning migratory behavior and associated mortality rates would enhance management of the species.

Sex Bias of the Sample

The proportional dominance of females in both annual samples in this study was a curious phenomenon. Female dominance in various species of Cisco *Coregonus* spp. has been identified previously for populations in the Laurentian Great Lakes. Pratt and Chong (2012), for example, reported female proportions of four species of deepwater Cisco in Lake Superior from 0.59 to 0.77. TeWinkel et al. (2002) documented long-term variation in the annual female proportion of Bloaters *C. hoyi* in Lake Michigan from 0.35 to more than 0.80. In that case, the authors contended that males suffered greater mortality as young fish, such that after poor recruitment years, older females became dominant. Brown (1970) reported extreme female dominance of Bloaters in Lake Michigan during the 1960s ranging from 0.94 to 0.97. Our annual values of 0.64 and 0.62 are modest by comparison. Future research on the factors leading to female dominance in the spawning population could reveal useful information on sex-specific mortality.

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