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Documentation of Annual Spawning Migrations of Anadromous Coregonid Fishes in a Large River using Maturity Indices, Length and Age Analyses, and CPUE

Randy J. Brown[1,*], David W. Daum[1], Stanley J. Zuray[2], and William K. Carter III[1]

with 8 figures and 1 table

Abstract: Coregonid fishes contribute to major food fisheries throughout the Yukon River drainage in northwest North America. Research and management activities related to these coregonid fishes, however, have been minimal because of the commercial and international focus on Pacific salmon *Oncorhynchus* spp. populations that share the drainage. We studied five coregonid species at a fish-wheel sampling site 1,200 km from the Bering Sea. They were inconnu *Stenodus leucichthys*, broad whitefish *Coregonus nasus*, humpback whitefish *C. clupeaformis*, least cisco *C. sardinella*, and Bering cisco *C. laurettae*. Otolith chemistry studies have shown that anadromy is a common or prevailing life history strategy for all five species at our fish-wheel sampling site. Radio telemetry studies revealed major spawning habitats for four species in the Yukon Flats, an extensive braided region of the river 1,600 to 1,700 km upstream from the Bering Sea. The objectives of this study were to document the demographic qualities of migrating coregonids at the fish-wheel sampling site and to define seasonal periods of relative abundance based on daily catch rates. Maturity indices indicated that nearly all fish were mature and preparing to spawn. Minimum lengths and ages of maturity ranged from low values of 23 cm and 2 years for least cisco, to high values of 58 cm and 7 years for inconnu. A video system on the sampling fish wheel provided seven years of species-specific catch rate data that we used to identify the timing of seasonal spawning migrations for all species except least cisco.

Keywords: Yukon River, Stenodus, Coregonus, spawning, migration

Introduction

Six coregonid species are commonly recognized in the Yukon River drainage in Alaska: inconnu *Stenodus leucichthys*, broad whitefish *Coregonus nasus*, humpback whitefish *C. clupeaformis*, least cisco *C. sardinella*, Bering cisco *C. laurettae*, and round whitefish *Pro-*

Authors' addresses:
[1] U.S. Fish and Wildlife Service, Fairbanks FWFO, 101 12th Ave., Room 110, Fairbanks, Alaska 99701, USA.
[2] Rapids Research Center, Box 172, Tanana, Alaska 99777, USA.
* Corresponding author, e-mail: randy_j_brown@fws.gov

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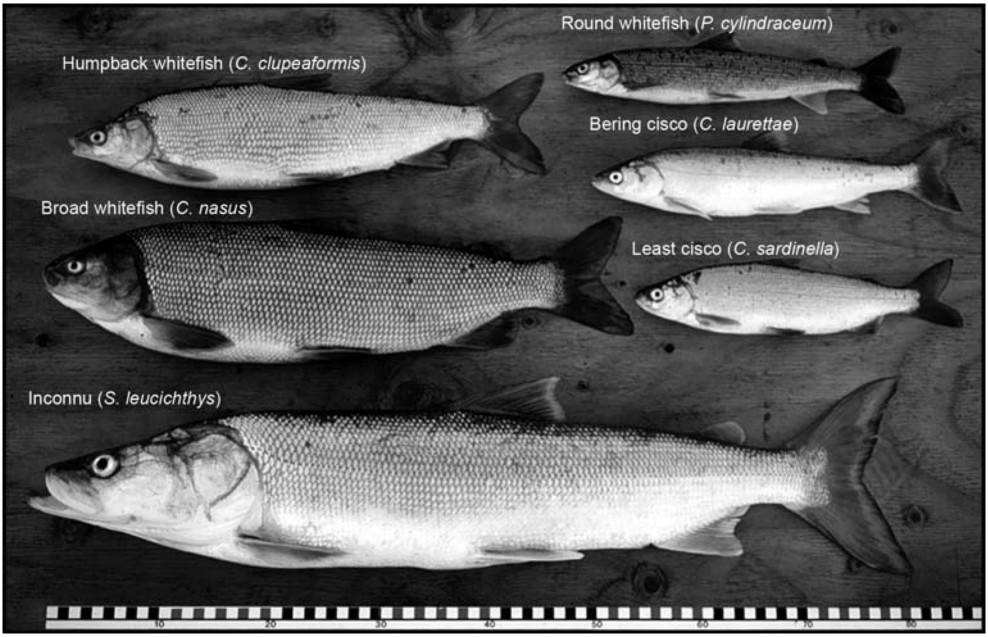

Fig. 1. Six coregonid species commonly recognized in the Yukon River drainage in Alaska: inconnu *Stenodus leucichthys*, broad whitefish *Coregonus nasus*, humpback whitefish *C. clupeaformis*, least cisco *C. sardinella*, Bering cisco *C. laurettae*, and round whitefish *Prosopium cylindracium*. The scale bar is in cm.

sopium cylindracium (Fig. 1). Pygmy whitefish *P. coulterii* are present in some lakes in the upper drainage in Canada but have not been identified in the Alaska portion of the drainage (Lindsey & Franzin 1972). The '*Coregonus clupeaformis* complex' of species, as described by McPhail & Lindsey (1970), includes three forms: *C. clupeaformis*, *C. pidschian*, and *C. nelsonii*, the last two of which are reportedly present in the Yukon River drainage in Alaska (Morrow 1980). Specific identification of these three forms, however, is virtually impossible in environments where they occur together. As a result, Alt (1979) recommended that all members of the complex in Alaska be referred to as *C. pidschian*. In a more recent genetics analysis of these three similar forms across North America, McDermid et al. (2007) concluded that the complex should be considered a single species, *C. clupeaformis*, and that they should be differentiated at the subspecies level. In this manuscript, we retain the common descriptive name of humpback whitefish, per McPhail & Lindsey (1970), and follow the species recommendation of McDermid et al. (2007), *C. clupeaformis*.

Coregonid species are extensively harvested for human and dog food throughout the Yukon River drainage (Brase & Hamner 2003; Andersen et al. 2004; Brown et al. 2005), yet there have been few attempts to monitor or manage these fisheries. In part, this is because coregonid populations in open river systems are very widely dispersed and often segregated demographically among habitats (Reist & Bond 1988), and also because fisheries management activities in the drainage have historically been focused on Pacific salmon species *Oncorhynchus* spp., which support commercial and personal food fisheries in Alaska and

Yukon Territory (Hayes et al. 2008). Harvest records of coregonid fishes rarely identify them to species, with the exception of inconnu. In most cases where harvests of non-salmon species are reported, the coregonid species are simply grouped together as 'whitefish', or 'large whitefish' and 'small whitefish' (Brase & Hamner 2003; Hayes et al. 2008). Some recent anthropological studies of rural fishing practices have identified coregonid harvests to species (Andersen et al. 2004; Brown et al. 2005), which improves the usefulness of these data.

Commercial coregonid fisheries have occasionally been permitted in the Yukon River drainage (Hayes et al. 2008), but have been primarily for local markets and for relatively short duration. A more recent commercial coregonid fishery was initiated in the lower Yukon River in fall 2005 and has taken place annually since then. Coregonids from this fishery are marketed in New York City. Initially, all coregonid species were targeted, but the fishery has recently focused on Bering and least cisco. The fishery has been limited to an annual harvest of about 4,500 kg due to the lack of population data for these species. A much larger allocation has been requested, suggesting that the fishery could expand. Concern over the effects of this fishery has generated calls from fisheries managers and rural communities for improved understanding of these resources.

The focus of previous research into migrations of coregonid species in the Alaska portion of the Yukon River drainage has been primarily on inconnu (Alt 1977; Brown 2000), with more localized studies directed toward other species (Fleming 1996; Brown 2006). Alt (1977) used anchor tagging methods to document inconnu migrating widely within the drainage between estuarine rearing and feeding habitats to upstream spawning destinations. Brown (2000) used radio telemetry techniques to identify a major inconnu spawning region in the upper reaches of the Yukon Flats, 1,700 km from the sea. A similar radio telemetry project with broad whitefish (currently in progress) indicated that the Yukon Flats is their spawning destination too, although in a region approximately 100 km downstream from inconnu spawning habitat (B. Carter, unpublished data). Fleming (1996), working with least cisco and humpback whitefish, and Brown (2006), working with humpback whitefish, examined small-scale migrations (<300 km) within specific tributary systems. More recently, Brown et al. (2007) investigated upstream migrations of anadromous coregonids in the drainage by conducting otolith chemistry analyses on samples from a number of main-stem and tributary sites between 1,200 and 2,000 km from the Bering Sea. They found that anadromous coregonids of five species were migrating from 1,600 to 2,000 km upstream to spawn, indicating that populations of these species ranged widely in the drainage. Coregonid harvests in the lower river were clearly composed of multiple populations precluding population assessments from those harvests. This investigation was initiated to improve our understanding of the demographic qualities and timing of the anadromous coregonid migrations in the mainstem Yukon River, 1,200 km from the sea, which could lead to the development of monitoring or assessment programs for these coregonid populations.

Methods

Demographics

Coregonid fish examined in this study were harvested with fish wheels from the main-stem Yukon River, approximately 1,200 km from the Bering Sea (Fig. 2). The fish wheels captured fish of many species ranging in length from <20 cm to >100 cm. Representative subsamples of coregonid fishes were opportunistically collected from local harvests between 1997 and 2003. We assumed the catch of each species was representative of the population in the river at that location and time. Each coregonid fish was identified to species and measured for fork length (length) to the nearest cm. Sex was determined by opening the body with a ventral cut and identifying male or female gonads. Periodically through the season, subsampled individuals from the catch were weighed whole to the nearest 10 g. Ovaries were removed from females and eggs were then weighed to the nearest 10 g for egg masses ≥100 g and to the nearest 1 g for egg masses <100 g to determine maturity and spawning readiness of females. Sagittal otoliths were extracted for aging.

Spawning maturity and readiness were determined based on critical gonadosomatic index (GSI) values of female fish. Gonadosomatic index values were calculated as egg weight percentage of the whole body weight following the methods of Snyder (1983): $GSI = (\text{egg weight} \cdot \text{whole body weight}^{-1}) \cdot 100$. The eggs of non-spawning coregonids remain small throughout the summer and fall (Lambert & Dodson 1990; Brown 2004), while those of fish preparing to spawn increase rapidly from GSI values less than three in June to values as great as 20 or more by the fall spawning period (Petrova 1976; Bond &

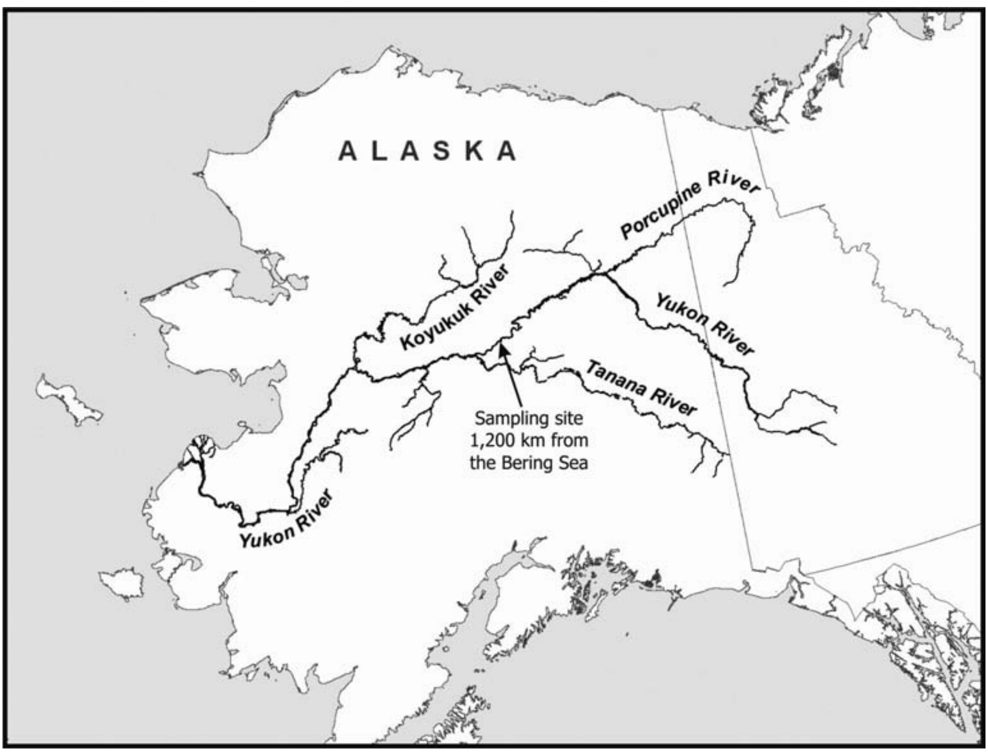

Fig. 2. The Yukon River drainage in Alaska and Canada with major tributaries and sampling site location indicated.

Erickson 1985; VanGerwen-Toyne et al. 2008). Female fish with GSI values greater than three in the late summer and fall were considered to be mature and preparing to spawn. The smallest mature fish of each species was considered to be a good estimate of the minimum length of maturity. Length distributions of the catches were tabulated and illustrated with boxplots.

One otolith from each fish was sectioned in the transverse plane and mounted on a glass slide with thermoplastic glue for aging (Secor et al. 1992). Each section was approximately 200 µm thick, which permitted growth increments to be viewed with transmitted light. Fish age was determined based on the descriptions and illustrations in Chilton & Beamish (1982). The youngest mature fish of each species was considered to be a good estimate of the minimum age of maturity. Age distributions of mature fish were tabulated by species and illustrated with boxplots.

Migration timing and run strength

One fish wheel in the sampling region was operated every day from about mid-June to late September between the years 2001 to 2007 to obtain relative abundance data for Pacific salmon species. Holding captured fish for periodic counting events in submerged boxes mounted to fish wheels has been shown to negatively impact their subsequent migrations following release (Bromaghin et al. 2007). To reduce these impacts on chum salmon *O. keta* and other species captured in the sampling fish wheel, a video system was developed to collect images of every fish during capture, precluding the need to hold them for later examination (Daum 2005). The video images were of sufficient quality to identify all captured fish to the species level. As a result, the relative abundances of coregonid species passing through the sampling fish wheel were recorded and tabulated.

The sampling fish wheel was run for approximately 14 hours each day during June and July of each year and for 24 hours each day during August and September to obtain catch-per-unit-effort (CPUE) data. All catch data were standardized to captures per 24-hour sampling period. Species-specific CPUE data for coregonid fishes were plotted against the Julian date for each of the seven years of the project to illustrate seasonal trends in relative abundance. Periods of high relative abundance were assumed to indicate the occurrence of substantial migrations past the sampling site. The date of the highest CPUE value for each species for the year was considered to be the peak of each species' annual migration. Cumulative CPUE data, the sum of daily CPUE values for each year, were tabulated for each species. The strengths and weaknesses of cumulative CPUE data for assessing variation in annual run strength were considered.

Results

Demographics

Six coregonid species were captured at the Yukon River sampling site during this project. Round whitefish were rare and were not considered further. Least cisco were present but never abundant. Inconnu, broad whitefish, humpback whitefish, and Bering cisco were present and seasonally abundant.

Gonadosomatic index values were calculated for 108 inconnu, 27 broad whitefish, 32 humpback whitefish, 36 least cisco, and 103 Bering cisco. Gonadosomatic index values progressively increased throughout the summer with the highest values, which approached 20 or greater, occurring in September (Fig. 3). With the exception of a Bering cisco sampled in June, all sampled fish identified as female had GSI values greater than three, indicating they were mature and preparing to spawn. Very small inconnu, broad whitefish, humpback whitefish, and least cisco were rarely encountered, were considered to be immature, and could not

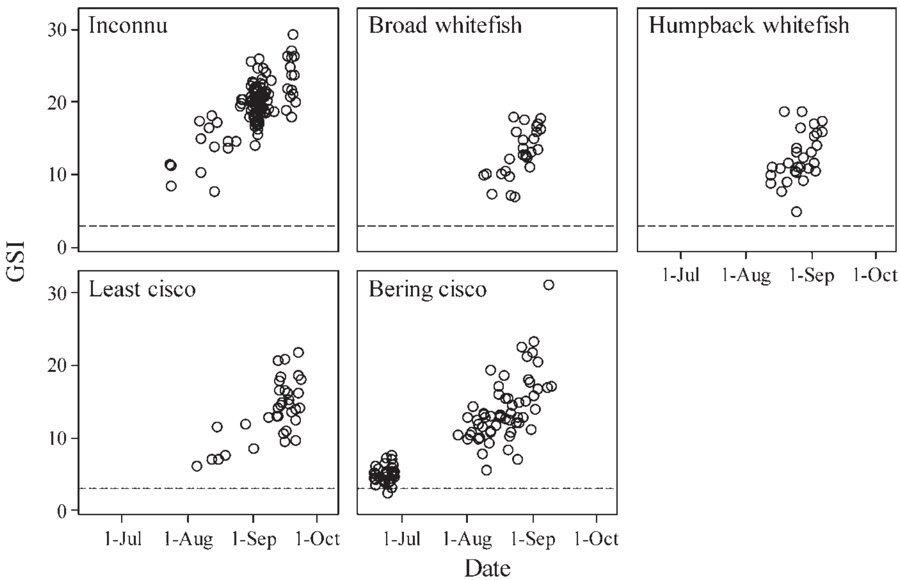

Fig. 3. Gonadosomatic indices for five coregonid species sampled in the Yukon River 1,200 km from the sea. In late summer and fall, non-spawning fish have GSI values <3 (dashed lines) and all mature fish preparing to spawn have GSI values >3. These plots indicate that sampled fish were mature and preparing to spawn.

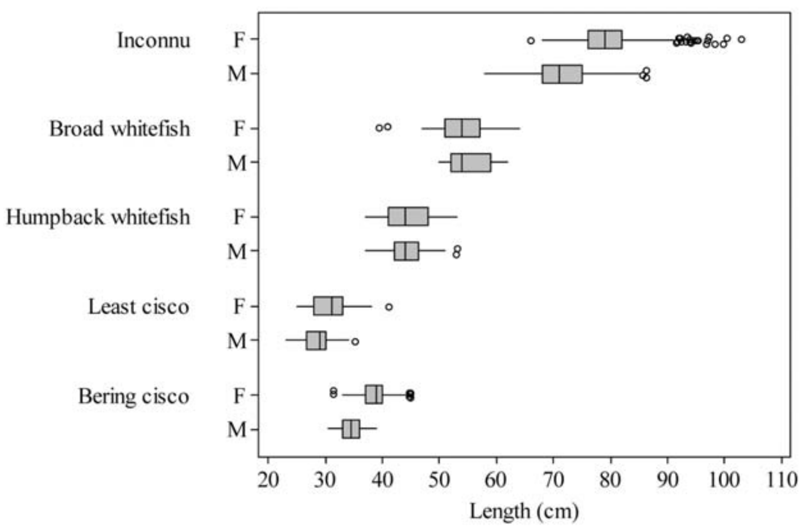

Fig. 4. Length distributions of mature coregonid fishes sampled in the Yukon River 1,200 km from the sea. Female (F) and male (M) components of these samples are displayed separately to highlight sex-related differences. All boxplots in this paper include median line, interquartile range box, whiskers encompassing more than 95% of data points, and outliers.

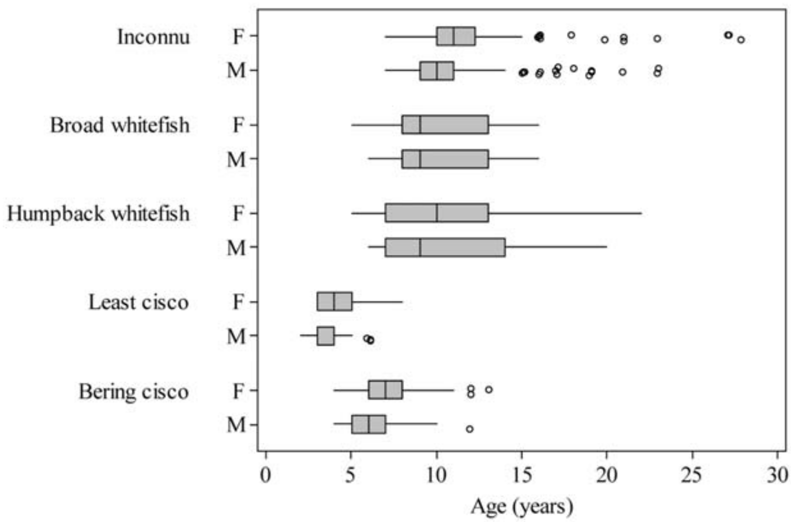

Fig. 5. Age distributions of mature coregonid fishes sampled in the Yukon River 1,200 km from the sea. Female (F) and male (M) components of these samples are displayed separately to highlight sex related differences. (Note: the first quartile and the median value of male least cisco are both 3 years.)

Table 1. Demographic and peak migration timing data for coregonid species in the fish wheel catch at the sampling site during the summers of 2001 through 2007. Minimum length and age at maturity data for females (F) only are empirical data from GSI maturity assessments. Sample length and age ranges for female and male (M) fish include the larger sample of examined fish that were judged to be mature based on their association with known mature females. Sample sizes are indicated as parenthetical subscripts by sex. Reported minimum ages at maturity for Mackenzie River coregonid species are presented for comparison. The average peak run date for four coregonid species includes the standard deviation (SD) as an indicator of the annual variability observed during the seven years of data collection.

Category	**Inconnu**	**Broad whitefish**	**Humpback whitefish**	**Least cisco**	**Bering cisco**
Minimum length at maturity (cm)	$F_{(108)}$ 71	$F_{(27)}$ 39	$F_{(32)}$ 38	$F_{(36)}$ 25	$F_{(103)}$ 31
Minimum age at maturity (year)	$F_{(108)}$ 7	$F_{(27)}$ 5	$F_{(28)}$ 6	$F_{(29)}$ 3	$F_{(78)}$ 5
Sample length range (cm)	$F_{(682)}$ 66–103 $M_{(818)}$ 58–86	$F_{(59)}$ 39–64 $M_{(19)}$ 50–62	$F_{(43)}$ 37–53 $M_{(30)}$ 37–53	$F_{(42)}$ 25–41 $M_{(45)}$ 23–35	$F_{(131)}$ 31–45 $M_{(65)}$ 31–39
Sample age range (year)	$F_{(110)}$ 7–28 $M_{(156)}$ 7–23	$F_{(59)}$ 5–16 $M_{(19)}$ 6–16	$F_{(39)}$ 5–22 $M_{(26)}$ 6–20	$F_{(36)}$ 3–8 $M_{(40)}$ 2–6	$F_{(105)}$ 4–13 $M_{(57)}$ 4–12
Minimum age at maturity (year) for Mackenzie River species[1]	6	7	7	4	6[2]
Average peak run date (SD)	Sept. 3 (5.6 d)	Sept. 14 (7.0 d)	Aug. 31 (19.9 d)	NA	July 21 (19.2 d)

[1] from Reist & Bond (1988)

[2] Arctic cisco in the Mackenzie River are considered to be analogous to Bering cisco in the Yukon River

be identified to sex. All Bering cisco had distinct gonad development and were considered to be mature. Males associated with the mature females were assumed to be mature also. Minimum lengths and ages of mature female coregonids, based on elevated GSI values, ranged from 71 cm and 7 years for inconnu, 39 cm and 5 years for broad whitefish, 38 cm and 6 years for humpback whitefish, 25 cm and 3 years for least cisco, and 31 cm and 5 years for Bering cisco (Fig. 4 and 5; Table 1). Length and age ranges of all female and male fish sampled at the site were lowest for least cisco and greatest for inconnu.

Migration timing and run strength

Distinct periods of relatively high abundance and scarcity were evident for inconnu, broad whitefish, humpback whitefish, and Bering cisco (Fig. 6 and 7). Least cisco was never captured in sufficient number for CPUE analysis. Patterns of relative abundance for inconnu were the most seasonally distinct, consistently increasing from an occasional capture each day during June and July to as much as 80 or more per day by the second half of August (Fig. 6). Inconnu abundance usually peaked in early September and declined later in September. Sampling activities were terminated each year due to freezing conditions before the inconnu run was complete. Broad whitefish arrived later than other species, becoming relatively abundant in late August and September. Peak passage rates of as many as 40 fish per day occurred just prior to the termination of sampling activities in late September most years. It is likely that most of the broad whitefish run passed after sampling activities terminated each year. Humpback whitefish exhibited less consistent seasonality than inconnu or broad whitefish, with major peaks of abundance occurring in the first half of August during some years (peak values exceeding 60 fish per day). Humpback whitefish were almost absent in the catch during 2007 and few were captured in 2003 and 2006. It was clear from the late season presence of humpback whitefish in the catch that the run continued to some extent after sampling activities terminated each year. Bering cisco were present at relatively high abundance during the longest seasonal period each year, with two or more periods of relatively high abundance and declines during all years except 2007, when there was a single period of very high abundance. Bering cisco were present in the fish wheel catches when sampling activities began each year in June, sometimes at >100 fish per day, indicating that an early component of the run preceded sampling activities. Catches declined to very low values by early September indicating that the run was essentially over before sampling activities terminated each year.

Cumulative CPUE data revealed the magnitude of annual variability in relative abundance for inconnu, broad whitefish, humpback whitefish, and Bering cisco (Fig. 8). Bering cisco were the most abundant coregonid species in the catch every year, with a cumulative CPUE averaging 5,652 fish. The relative abundances of broad whitefish and humpback whitefish in the catch were very similar in magnitude and trend, with cumulative CPUE averages of 439 and 566 respectively. Their annual patterns of high and low abundance in the catch are virtually identical (Fig. 8). Cumulative CPUE data for inconnu varied considerably among years but did not follow the same pattern of annual abundance in the catch as broad whitefish and humpback whitefish. In 2004, for example, the relative abundance of inconnu in the catch was relatively low, but was greatest among sample years for broad whitefish and humpback whitefish. Cumulative CPUE values for inconnu, broad whitefish, and humpback whitefish

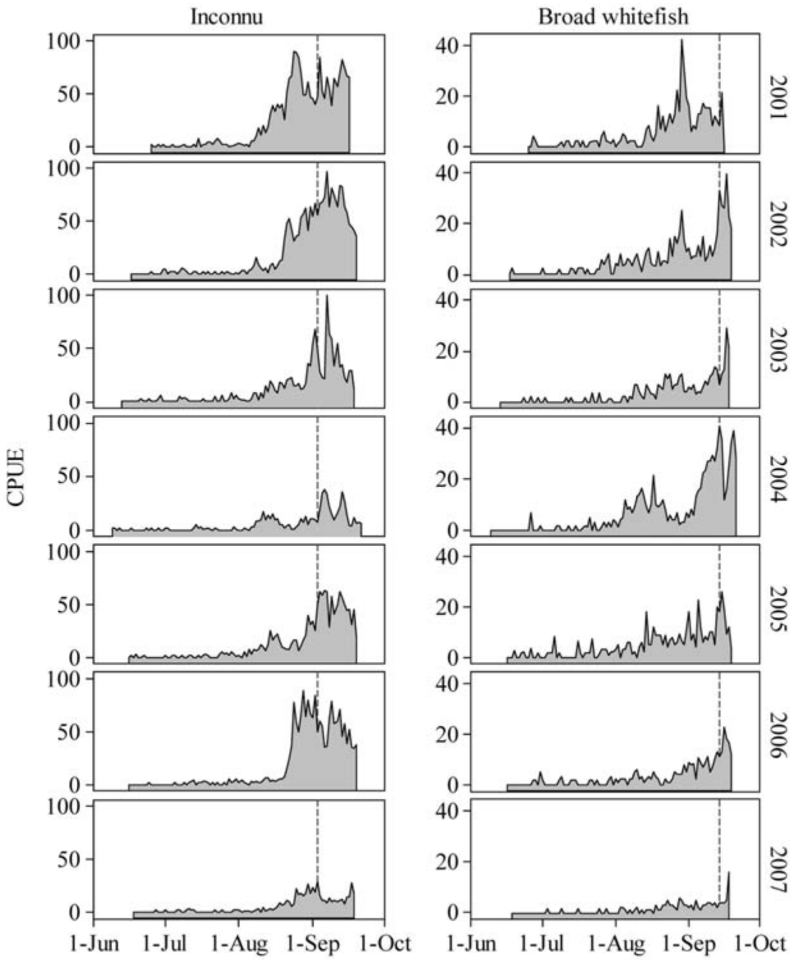

Fig. 6. Relative abundance (CPUE) of inconnu and broad whitefish in the fish wheel catch at the sampling site during the summers of 2001 through 2007. Reference lines indicate the average peak run times during the seven years of data collection.

were at their lowest levels in 2007. In contrast, the cumulative CPUE value for Bering cisco was at its highest level in 2007. These data suggest that if cumulative CPUE values reflect actual variations in run strength, then the factors influencing run strength must be different among species.

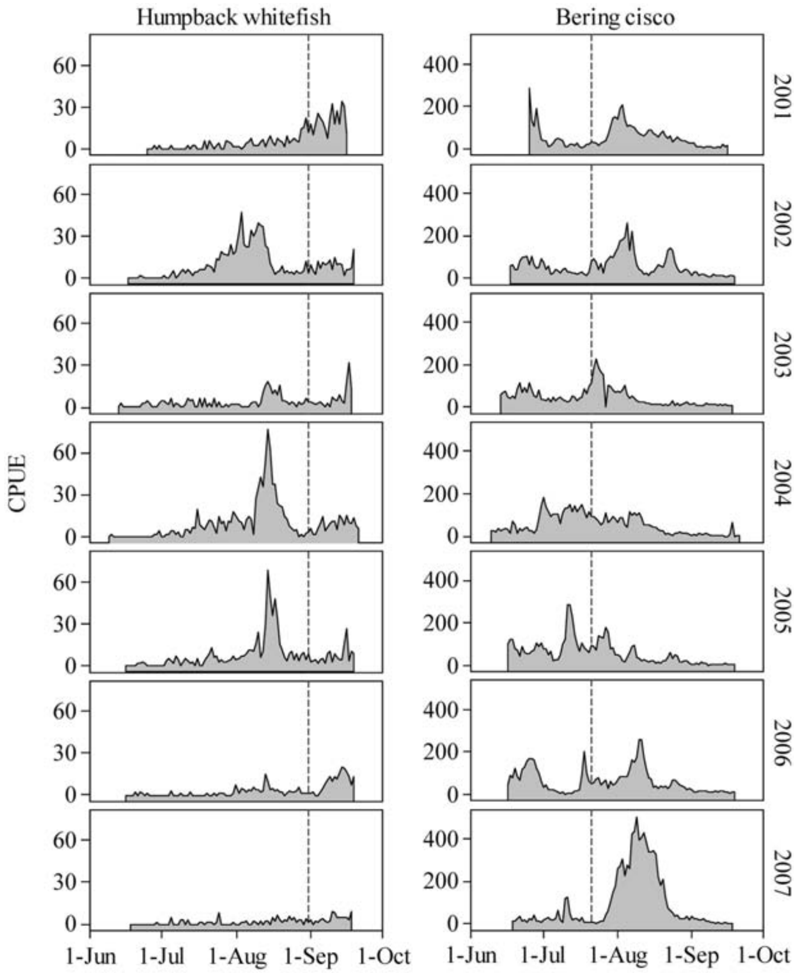

Fig. 7. Relative abundance (CPUE) of humpback whitefish and Bering cisco in the fish wheel catch at the sampling site during the summers of 2001 through 2007. Reference lines indicate the average peak run times during the seven years of data collection.

Discussion

Demographics

Almost all coregonid fishes captured during the summer season at our sampling site were mature and preparing to spawn. Juvenile inconnu, broad whitefish, humpback whitefish, and least cisco were encountered occasionally but had not developed identifiable gonads so sex could not be determined. All individuals that could be identified as female, based on the weighed or observed presence of large skeins of eggs, were preparing to spawn. Pre-spawn-

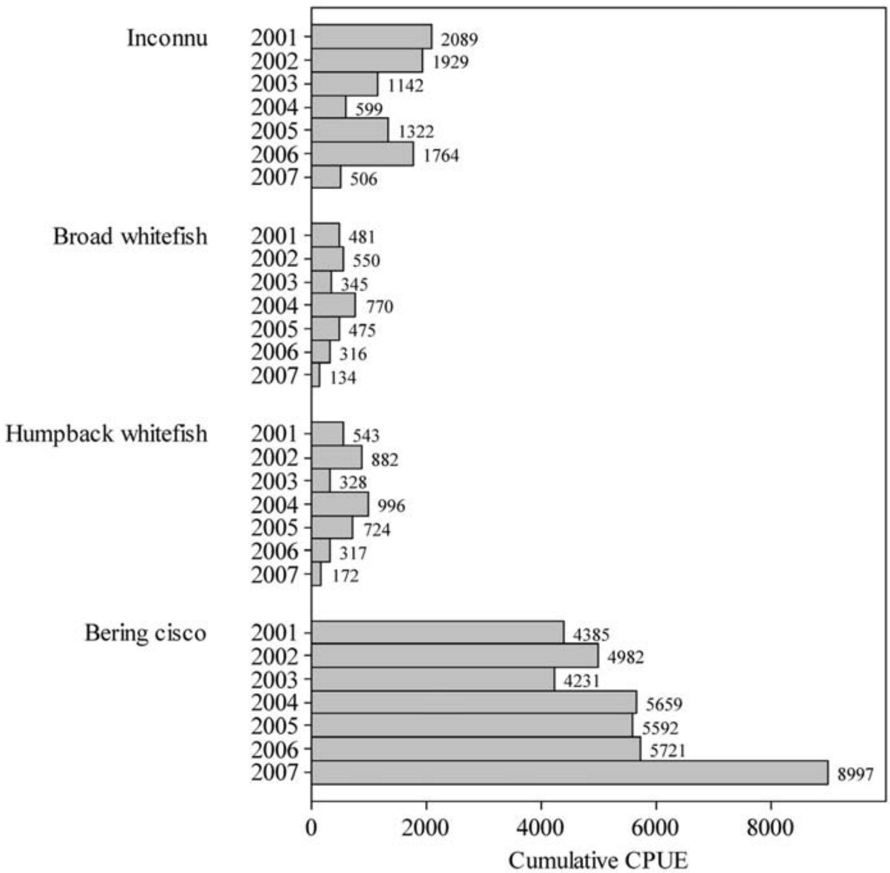

Fig. 8. Cumulative annual CPUE data (values to the right of each bar) for four coregonid species in the catch at the fish wheel sampling site during the summers of 2001 through 2007.

ing coregonids have reportedly been the primary demographic group sampled from other large rivers as well. Howland (1997), sampling inconnu in the Arctic Red and Slave rivers in the Mackenzie River drainage in northern Canada, and VanGerwen-Toyne et al. (2008), sampling several coregonid species in the Peel River (another tributary of the Mackenzie River), reported that nearly all fish that they examined were preparing to spawn. Alt (1969) observed that only mature inconnu preparing to spawn migrated upstream beyond the delta region in the Kobuk River in northwest Alaska. Similarly, Reist & Bond (1988), in their review of life history characteristics of Mackenzie River coregonids, indicated that fish preparing to spawn began migrating to upstream spawning areas early in the summer, distancing themselves from juvenile and non-spawning mature fish that remained in lower drainage or estuarine feeding habitats. The Yukon River is very turbid during the open water season when our fish wheel was operated (Brabets et al. 2000). Presumably, feeding and rearing fish occupy habitats more conducive to foraging during this time period leaving mature, pre-spawning fish as the dominant demographic group in the turbid main stem.

Spawning migrations of coregonid species in the Yukon River have been reported previously in the vicinity of our sampling site. During sampling activities in fall 1974, Alt (1979) examined inconnu, broad whitefish, humpback whitefish, and Bering cisco that he believed were preparing to spawn. Alt (1977) inferred that inconnu made a spawning migration up the Yukon River into the Yukon Flats based on sampling and tag recovery data but was not able to determine their actual destination. Brown (2000) expanded on Alt's (1977) work and documented the spawning readiness of inconnu at the sampling site using GSI data and used radio telemetry to identify their spawning destination in the upper reaches of the Yukon Flats, approximately 1,700 km from the sea (Brown 2000). During fall sampling in the inconnu spawning region, we found that spawning humpback whitefish and Bering cisco were also present. A similar radio telemetry study with broad whitefish is currently in progress in the Yukon River. Based on preliminary results, this species spawns in a region of the Yukon Flats approximately 100 km downstream from the inconnu spawning reach (B. Carter, unpublished data). Brown et al. (2007) evaluated the incidence of anadromy among the five coregonid species at the fish wheel sampling site by analyzing otolith strontium levels and found that anadromy was common to prevalent depending on the species. Together these data provide clear evidence of spawning migrations of five anadromous coregonid species past our sampling site, 1,200 km from the Bering Sea.

The minimum ages at maturity for Yukon River coregonid species (Table 1) are within one or two years of most reports for the same or similar species in other systems. Reist & Bond (1988) reviewed life history characteristics of migratory coregonids in the lower Mackenzie River drainage, a similar large river environment to the Yukon River, and provided estimates of minimum ages of maturity for the same suite of coregonid forms as we examined in this study (for this comparison we consider Arctic cisco *C. autumnalis* in the Mackenzie River to be analogous to Bering cisco in the Yukon River; McPhail 1966). Reist & Bond (1988) reported a minimum age of maturity for inconnu of six years, while in the Yukon River we found a minimum age of seven years for both female and male inconnu. Minimum ages of maturity for all other species common to both river systems were lower in the Yukon River by one or two years, perhaps reflecting the latitudinal differences between the two systems.

Migration timing and run strength

Distinct periods of relatively high and low abundance were apparent in the multi-year CPUE figures for inconnu, broad whitefish, humpback whitefish, and Bering cisco (Fig. 6 and 7). Annual migrations of inconnu appeared to occur with the most consistent timing beginning in mid-August and showing signs of decline in September when sampling terminated each year. The average peak run date of September 3 (Table 1) is therefore considered to be a meaningful date for this species. A major component of the broad whitefish migration apparently passes the sampling site after the sampling project terminates each year (Fig. 6), which is consistent with the later spawning period of broad whitefish as documented by Chang-Kue & Jessop (1983) in the Mackenzie River and by B. Carter (unpublished data) in the Yukon River. As a result, the calculated average peak run date of September 14 is thought to be a poor descriptor for this species. The migration timing of humpback whitefish appears to be irregular, possibly bimodal, and may continue for some period of time after sampling is terminated each year

(Fig. 7). The calculated average peak run date of August 31 for humpback whitefish is, therefore, considered to be a poor descriptor for this species. The Bering cisco migration begins at the fish-wheel sampling site prior to the June start-up dates for the sampling. Alt (1973) captured Bering cisco at various sites in the Yukon River up to 1,600 km from the sea in June 1971 and 1972. He suggested that the presence of mature Bering cisco so far upstream in the drainage in June indicated either that this species overwintered in the river or had a very rapid upstream migration from the sea. Our failure to capture non-spawning Bering cisco leads us to believe that those captured early in the season begin migration each spring before the river ice is gone. The Bering cisco migration timing was irregular and multimodal during most years, so the average peak run date of July 21 (Table 1) is a poor descriptor for the species. Reist & Bond (1988) speculated that the extended summer migration of mature Arctic cisco in the Mackenzie River, as documented by Stein et al. (1973), may have resulted from the wide geographic distribution of fish rearing in nearshore marine waters from the Colville River delta in the west (Fechhelm et al. 2007) to the Anderson River delta in the east (Bond & Erickson 1992). Presumably, fish rearing nearby enter the river earlier than those rearing far from the Mackenzie River mouth. We believe an analogous situation occurs for Yukon River Bering cisco. In western Alaska, they are known to spawn only in the Yukon and Kuskokwim rivers (Alt 1973), yet they are found rearing in brackish lagoons and other nearshore waters from the southern coast of Kuskokwim Bay (LaVine et al. 2007) north to the Colville River delta (Bickham et al. 1997). It seems reasonable to assume that the extended migration timing with multiple modes of peak abundance observed most years at our fish-wheel sampling site (Fig. 7) reflects the different marine migration distances required from the widely dispersed rearing aggregations.

Stein et al. (1973) reported on fish sampling operations at multiple sites in the Mackenzie River drainage in northern Canada. They used standardized multi-mesh gillnets and presented their migration timing data for coregonid and other fish species as monthly averages of daily catch rates. As a result, their CPUE data are not directly comparable to data presented here. By sampling multiple sites at different distances from the sea, however, they were able to identify seasonal trends in relative abundances of coregonid fishes relative to their distances from the sea. Coregonid migrations peaked earlier in the season close to the sea and later in the season farther from the sea, the expected pattern from a directed upstream migration. The single sampling site for this investigation was approximately 1,200 km upstream from the Bering Sea, where many or most of the coregonid fish rear (Brown et al. 2007). Many fish continue their migration another 400 to 500 km past the fish-wheel sampling site to spawn (Brown 2000; B. Carter, unpublished data). As a result, the migration timing described in our paper is relevant to this sampling site only and would be expected to shift somewhat earlier downstream and somewhat later upstream.

Interpretation of abundance indices requires the assumption that CPUE data and actual fish abundance levels are positively correlated (Flynn & Hilborn 2004). At a gross level (one or two inconnu per day versus 80 to 100 per day) this assumption is very easy to accept. At progressively finer levels, however, actual differences in fish abundance become less certain. It is clear that the annual migration timing of coregonid species presented in our paper is validly inferred from gross differences in daily CPUE. Attempting to compare run strengths among years or between species, however, using a run strength indicator such as cumulative CPUE (Fig. 8) would be a mistake without additional information validating the analysis.

Flynn & Hilborn (2004) used a cumulative CPUE index of sockeye salmon *O. nerka* returning to Bristol Bay to forecast run strength to the region. Their index was based on standardized sampling data from multiple locations with a long history of cumulative CPUE and on subsequent run strength data from the spawning escapement projects in the region. Initially a linear relationship between the cumulative CPUE and regional run strength was modeled without considering additional factors, but a series of forecast failures illustrated its limitations. Flynn & Hilborn (2004) added two factors to the model in an effort to improve its forecast effectiveness: age composition of the returning fish and air temperature from a nearby weather recording station. These additional factors, along with a more complex mathematical model, improved the forecast accuracy of the cumulative CPUE index. Others who have used cumulative CPUE indices to monitor fish abundance or forecast fish run strength have also considered environmental factors such as wind speed, temperature, river flow level, or tide stage (Molyneaux 1994; Hurst et al. 2004; Newland & Bue 2007).

We presented our cumulative CPUE data (Fig. 8) as a record of annual variation in catch, but are not ready to accept that they faithfully reflect annual variation in run strength or population abundance. We have no historical record of actual abundance of any coregonid species with which to develop a model relationship. We suspect that river flow levels and water temperature could influence capture efficiency, but are unable to describe these effects without complementary abundance data. Additionally, an unknown fraction of the annual broad whitefish and humpback whitefish runs probably pass after our sampling is terminated each September, and an unknown fraction of the Bering cisco run probably pass before the sampling project starts each June. A low cumulative CPUE value for broad whitefish, for example, could result from a poor run, a late run, an unusual fall flood affecting capture efficiency, or other factors we have not considered. Also, because northern coregonid species are iteroparous with unknown spawning frequencies (Reist & Bond 1988; Lambert & Dodson 1990), annual run strength could be relatively low simply because a large fraction of the population were not spawning that year. Daily CPUE data presented here appear to be effective at identifying the timing of annual spawning migrations of coregonid species at the fish-wheel sample site, but more background work will be required before cumulative CPUE data can be used to infer variation in population abundance among years.

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