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Executive Summary

The U. S. Minerals Management Service (MMS), now the Bureau of Ocean Energy Management (BOEM), defined specific questions concerning Arctic cisco in the Colville River, Alaska, based on a community workshop held in Nuiqsut and requested that the U.S. Geological Survey implement a study developing and applying scientific tools and techniques to address those questions (see below Problem Statement and Justification**)**. We used genetics, otolith chemical composition, otolith microstructure, stable isotope analyses, and stomach content analyses to assess population structure, movements, growth patterns, environmental influences on growth, and trophic dynamics of Arctic cisco from the Colville River subsistence fishery. We found support for the Mackenzie hypothesis, which suggests that Arctic cisco found in Alaskan rivers originate from the Mackenzie River, Canada. Using 11 microsatellite loci and the ATPase 6 mitochondrial gene, we found no evidence of genetic differentiation among Arctic cisco collected from the Colville River and five putative Mackenzie River spawning populations (Arctic Red, Peel, Mountain, Carcajou and Great Bear rivers; $P > 0.19$ in all comparisons). Model-based clustering methods also supported genetic admixture between sample collections from the Colville River and Mackenzie River basin. Otolith microchemistry (Sr/Ca ratios) confirmed repeated, annual movements of Arctic cisco between low-salinity habitats in winter and marine waters in summer. Harvest data supported the hypotheses that salinity affects the distribution of sub-adults within the Colville River and that wind patterns affect recruitment of Arctic cisco to the Colville River. Annual increments evident in otolith microstructure were measured to build retrospective growth histories for each individual. Over the last three decades, significant interannual variability was present in the patterns of growth between cohorts, as evident by difference among growth curve parameters, and specifically young-of-the-year (YOY) growth. There was evidence of a long term increase in YOY growth over time and growth was correlated with monthly averages of the Arctic Oscillation index, air temperature, east wind speed, sea ice concentration, and river discharge with and without time lags. Lagged correlations between Arctic cisco growth and environmental parameters suggested underlying mechanisms mediated by prey species. Strong correlations with river discharge suggested that the food web may incorporate a terrestrial carbon source delivered through river discharge. Stable isotope analysis of YOY Arctic cisco muscle tissue did support a reliance on terrestrial carbon sources for marine captured fish and stomach content analysis identified several zooplankton prey species known to mature slowly (longer than 1 growing season) that could explain the lagged relationship between environmental parameters and fish growth. This project used analytical techniques to confirm two previous hypotheses: 1. Colville

River Arctic cisco are part of a large panmictic population originating in the Mackenzie River, Canada, and 2. Arctic cisco make annual migrations to marine waters each summer. Moreover, correlates with YOY growth, stable isotope, and diet results link a vertebrate consumer to oceanographic processes and terrestrial inputs in the Beaufort Sea, broadening our understanding biological oceanography in the Arctic. With an improved understanding of Arctic cisco ecology, BOEM has an increased capacity to anticipate potential influences of development on Arctic cisco. This work resulted in four peer-reviewed publications that provide wider dissemination of this valuable information:

Ramey, A., S.L. Graziano, and J.L. Nielsen. 2008. Isolation and characterization of eight microsatellite loci from the Arctic cisco, *Coregonus autumnalis.* Molecular Ecology Resources. 8:357-359

von Biela, V.R., C.E. Zimmerman, and L.L. Moulton. 2011. Long-term increases in young-of-the-year growth of Arctic cisco (*Coregonus autumnalis*) and environmental influences. Journal of Fish Biology 78:39-56.

von Biela, V.R., C.E. Zimmerman, B.R. Cohn, and J.M. Welker. 2013. Terrestrial and marine trophic pathways support young-of-year growth in a nearshore Arctic fish. Polar Biology 36(1):137-146.

Zimmerman, C.E., A.M. Ramey, S.M. Turner, F.J. Mueter, S.M. Murphy, and J.L. Nielsen. 2013. Genetics, recruitment, and migration patterns of Arctic cisco (*Coregonus autumnalis*) in the Colville River, Alaska and Mackenzie River, Canada. Polar Biology. 36:1543-1555.

Contents

Problem statement and justification

Arctic cisco or Qaaktaq (*Coregonus autumnalis*) are an important subsistence resource for the village of Nuiqsut, Alaska. Subsistence users have expressed concern over declines in harvests and size of Arctic cisco from the Colville River (Fig. 1.1). Issues concerning population of origin, life history and recruitment variation over time, and changes in migration and diet of Arctic cisco ranked high in a list of critical research elements developed by the local community in a workshop hosted by MMS in Nuiqsut, November 18-20, 2003 (MBC 2004, Report MMS 2004-003). Six questions specific to Arctic cisco in the Colville River were identified by MMS to be addressed in this study:

1) Can we assign Arctic cisco from the Colville River back to a population of origin with high confidence? (Chapter 2)
2) Can we define genetic relationships among Colville and Mackenzie rivers' Arctic cisco populations? (Chapter 2)
3) Are there year-to-year genetic variations among Arctic cisco recruiting to the Colville River? (Chapter 2)
4) Has growth in Arctic cisco decreased over recent time? (Chapter 3)
5) Have migration routes to and from coastal habitats changed in Arctic cisco?
6) Can growth inferred from otoliths be used as an indicator of changes in diet over time?

Chapter 1: Age and Length Distributions of Arctic cisco from the Colville and Mackenzie rivers

INTRODUCTION

The subsistence fishery of Arctic cisco in the Colville River, Alaska, is thought to be composed entirely of juveniles from tributaries of the Mackenzie River in Canada. Arctic cisco are thought to make the long-distance movement from Canada to Alaska during their first summer of life and return to Canada during the summer prior to the first spawning in the fall (Craig 1989, Fechhelm and Griffiths 1990). If Arctic cisco in the Colville River are juveniles from individuals spawning in Mackenzie River tributaries, fish captured in the Colville River should be younger and smaller than those captured swimming upstream in tributaries of the Mackenzie River during the late summer on their spawning migration.

MATERIALS AND METHODS

Otoliths were collected from Arctic cisco captured in the subsistence gill net fishery at Nuiqsut on the Colville River (Fig. 1.1). Nets are typically 76-mm (stretched and measured knot-to-knot) mesh multifilament gillnets and range in length from 18 to 30 meters (Murphy et al. 2007). At least thirty otoliths per year were collected from fish captured in 17 of the 21 years from 1986 to 2007 (otoliths were not collected in 1989, 2002, 2003 and 2004). A total of 819 otoliths were collected from the Colville River

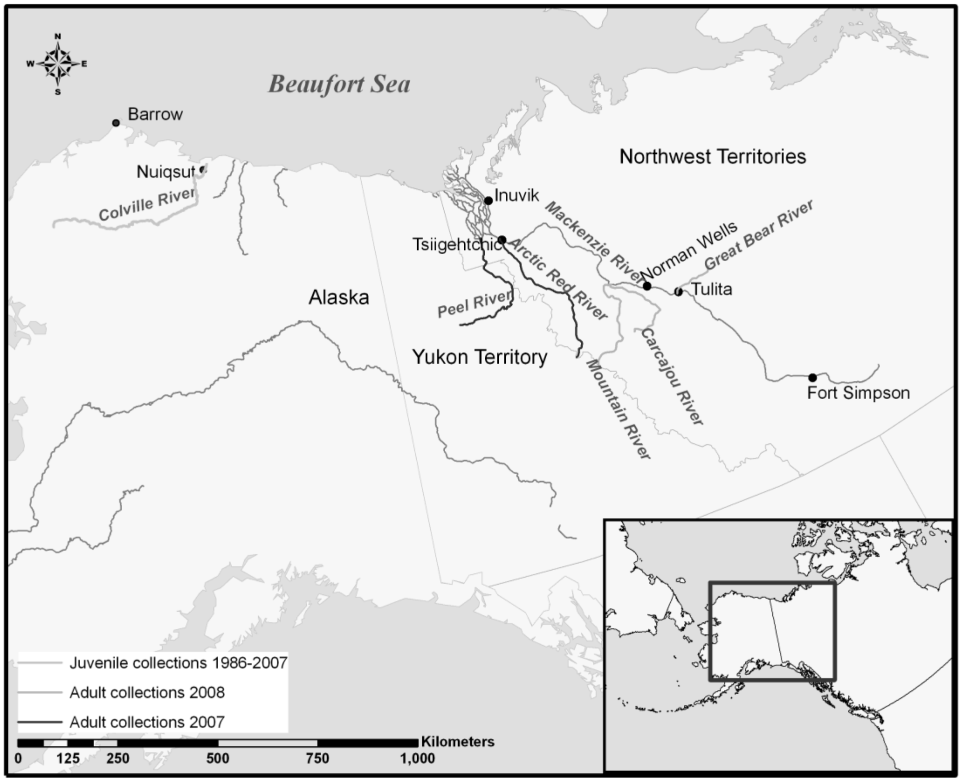

Fig. 1.1: Map showing collection locations for Arctic cisco from the Colville and Mackenzie rivers.

fishery and fish length was known for 408 individuals. Sex was not determined for juvenile fish. Adult Arctic cisco were collected from five tributaries of the Mackenzie River, Northwest Territories, Canada: Arctic Red River (n = 60), and Peel River (n = 54) in 2007; Great Bear River (n = 55), Carcajou River (n = 52), and Mountain River (n = 59) in 2008. At the Mackenzie River sites, individuals were also captured with 76-mm stretched mesh monofilament gill nets. Sex was determined for adult fish based on the presence of eggs or milt.

Otoliths were removed from fish, cleaned, dried, and stored in vials. Otoliths were embedded in Epothin epoxy (Buehler Ltd.), sectioned on a transverse plane through the nucleus with a low-speed wafering saw, and affixed to glass slides with cyanoacrylate glue. After drying, slides were ground using 1200-grit sandpaper. Digital images of each otolith were captured at a magnification of 40x on a black background with reflected light using a digital camera attached to a dissection microscope. Each individual was assigned an age by counting the translucent zones. Otolith ageing has been indirectly validated through the agreement with length frequency analyses of young Arctic cisco (age-0 to age-2, Underwood et al., 1995; Fechhelm et al,. 2007).

Age distributions were compared among Mackenzie River tributaries using a non-parametric Friedman's test so sex could be included as an additional variable (SAS Proc FREQ). If age distributions among fish sampled at each Mackenzie tributary were similar then the age distribution from all Mackenzie tributary fish were be compared in a two-sample Wilcoxon text with the age distribution of Colville River Arctic cisco. In the event that age distributions do differ among Mackenzie River tributary Arctic cisco, and additional Komogorov-Smirnov test was preformed including the Colville River Arctic cisco.

Length distributions were also compared among fish captured in Mackenzie River tributaries using a mixed model so that sex could be included as a covariant. If age distributions among fish captured in Mackenzie River tributaries were similar, then the lengths of all fish captured in Mackenzie River tributaries were pooled for comparison to fish captured in the Colville River using a two-sample t-test. Sexual dimorphism could not be similarly assessed in juvenile fish from the Colville River and therefore were pooled.

RESULTS

Age distributions among fish captured in Mackenzie River did not differ by tributary or sex ($P >$ 0.05; Fig. 1.2). The age distribution of fish captured in the Mackenzie River tributaries was significantly older than those captured in the Colville River (Wilcoxon two-sample test statistic = 249067; two sided P <0.0001; Fig. 1.3). The mean age of fish captured in the Mackenzie River tributaries was nearly 10 years old, compared to just 6 years old in the Colville River.

Length distributions did not differ among fish captured in Mackenzie River tributaries, but did differ by sex with females being larger than males (Tributary F=2.2, P > 0.05; Sex F = 73.44, P < 0.0001; Fig. 1.4 and 1.7). The length of fish captured in the Mackenzie River tributaries was longer than Arctic cisco captured in the Colville River (two-sample t-test F=242.94, *P* < 0.0001). The mean length of fish captured in Mackenzie River tributaries was 364 mm compared to only 296mm for fish captured in the Colville River.

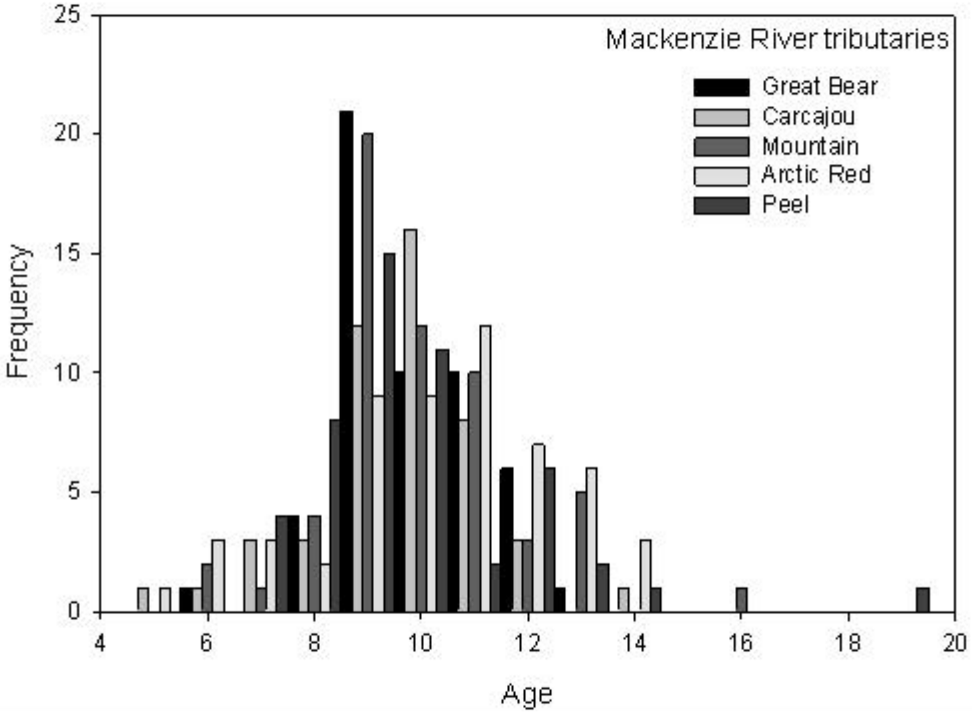

Fig. 1.2: Age distributions of Arctic cisco captured in Mackenzie River tributaries.

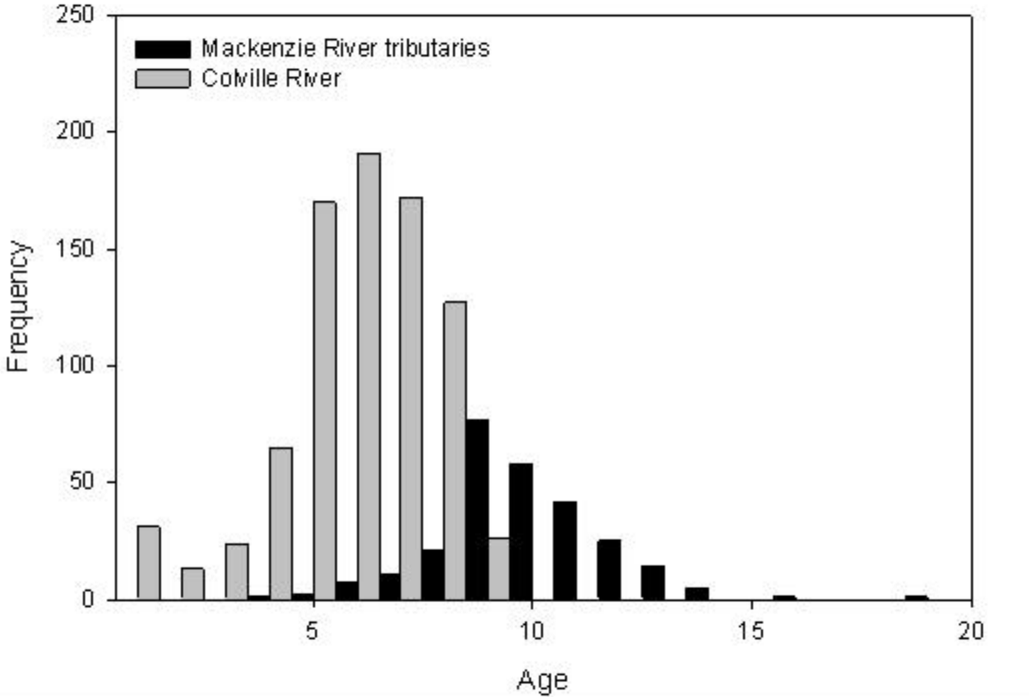

Fig. 1.3: Age distributions of Arctic cisco captured in the Mackenzie River tributaries and Colville River.

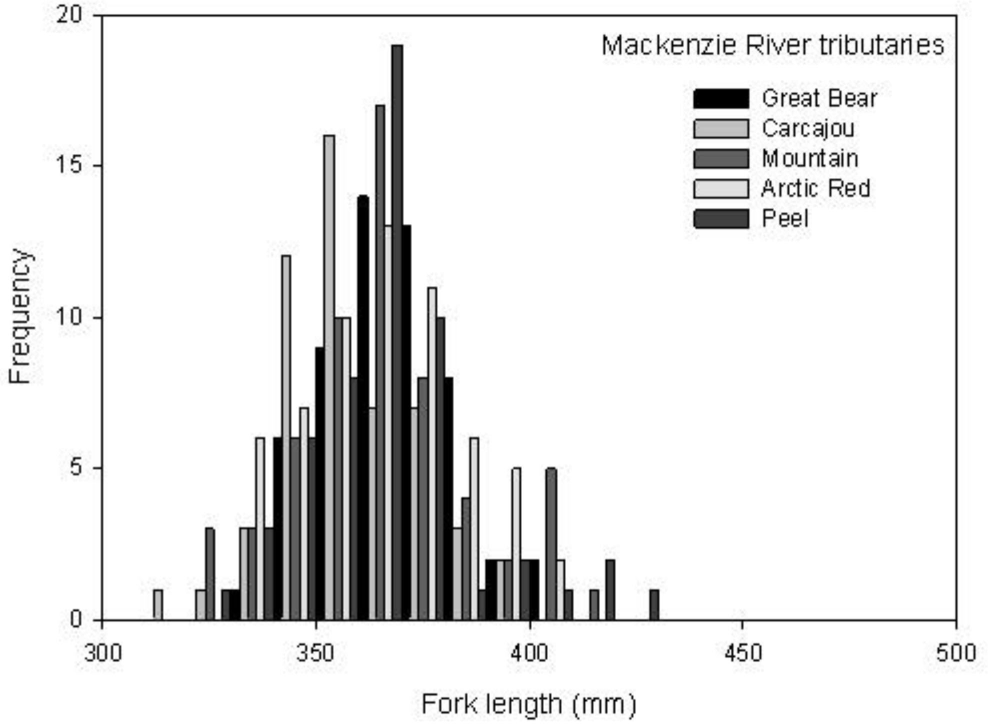

Fig. 1.4: Length distribution of Arctic cisco captured in Mackenzie River tributaries.

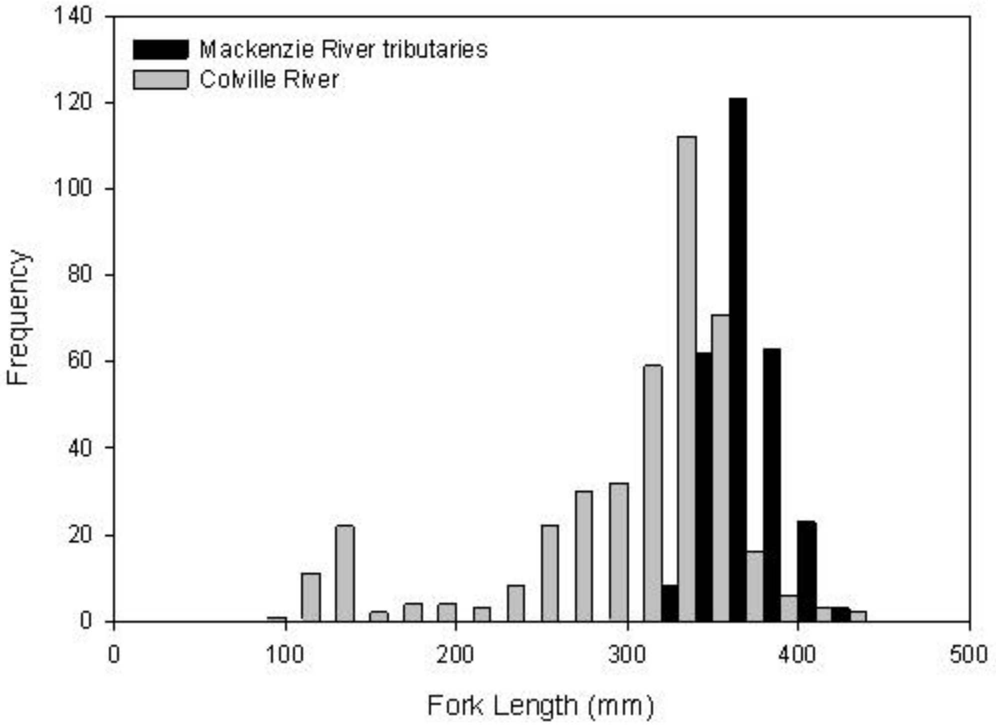

Fig. 1.5: Length distribution of Arctic cisco captured in Mackenzie River tributaries and the Colville River.

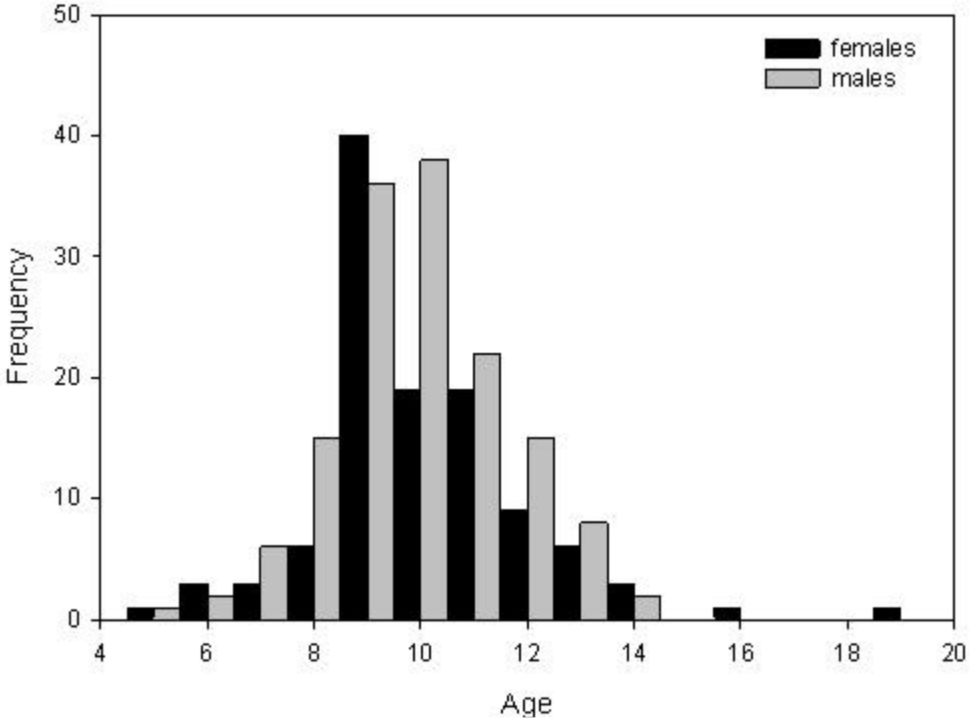

Fig. 1.6: Age distributions by sex for fish captured in Mackenzie River tributaries.

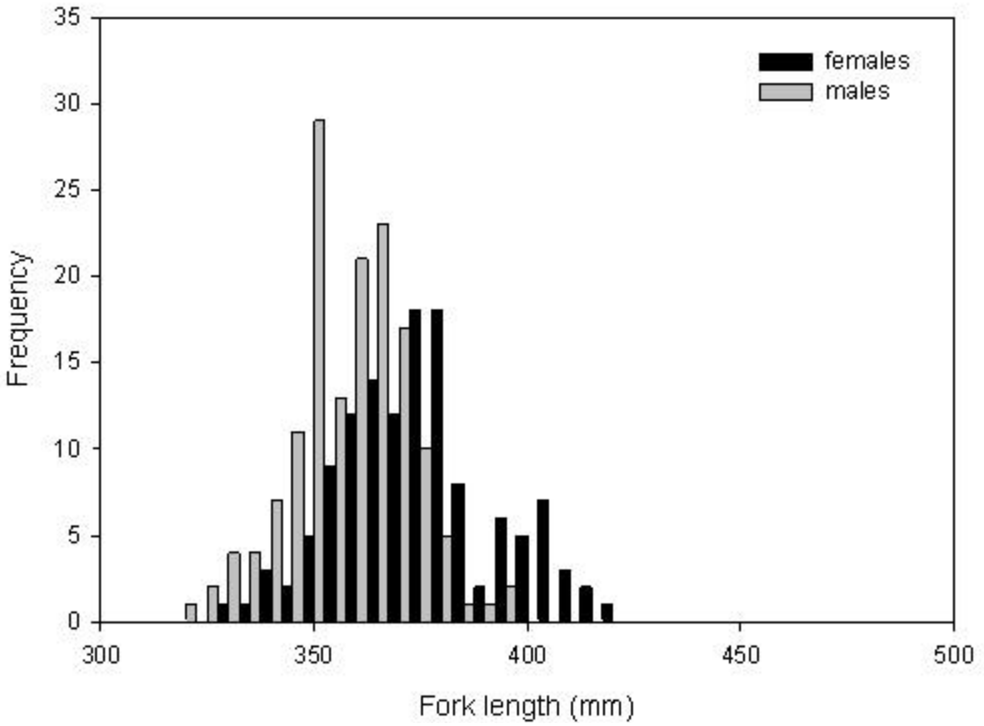

Fig. 1.7: Length distributions by sex for fish captured in Mackenzie River tributaries.

DISCUSSION

Arctic cisco captured in the Colville River were significantly younger and smaller than those captured in the tributaries of the Mackenzie River, as expected if Colville River Arctic cisco are the progeny of individuals from Mackenzie River tributaries. Similar age and length distributions among fish captured in Mackenzie River tributaries suggests similar environmental conditions and life history strategies among fish returning to the Mackenzie River basin. There was also evidence of slight sexual dimorphism between adult Arctic cisco, with females being larger than males despite similar age distributions. Female Arctic cisco may be larger than males because larger size is often favored due to increases in fecundity with size (Parker 1992). Overall, differences in the age and length distributions of fish captured in the Colville and Mackenzie Rivers agrees with other data provided in the following chapters.

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Chapter 2: Genetics, recruitment, and migration patterns of *Coregonus autumnalis* in the Colville River, Alaska and Mackenzie River, Canada

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INTRODUCTION

Arctic cisco (*Coregonus autumnalis*) is an important cultural and subsistence resource in Alaska and Canada (Reist and Bond 1988; Gallaway et al. 1989). For example, in Alaska an annual subsistence fishery occurs in the Colville River as fish gather to overwinter in brackish waters of the Colville River Delta (Fig. 1). In addition to the Colville River, Arctic cisco overwinter in the Sagavanirktok River (Fig. 1) but are not believed to spawn in any Alaska rivers (Craig 1984; Moulton 1989; Morales et al. 1993). Rather, Arctic cisco in Alaskan waters are thought to originate from spawning aggregations found over 650 km to the east in the Mackenzie River, Canada (Fig. 1), the only documented spawning population in North America (Moulton 1989; Fechhelm et al. 2007). This proposed scenario, in which Arctic cisco caught in Alaskan rivers are the progeny of Arctic cisco spawning in Canada has been called the "Mackenzie hypothesis" (Gallaway et al. 1983; Bickham et al. 1989; Morales et al. 1993).

According to the Mackenzie hypothesis it is assumed that age-0 fish emerge from spawning habitats in the Mackenzie River and are flushed or move downstream into ice-free waters of the Mackenzie River delta (Craig 1989). It is assumed that some age-0 fish, that are abundant in delta channels during their first summer (Reist and Bond 1988; Fechhelm et al. 2007) are transported westward in the Beaufort Sea by wind driven currents. Recruitment of Arctic cisco is controlled by wind speed and strength (Fechhelm and Griffiths 1990) and strong easterly winds result in higher abundance of Arctic cisco in coastal Alaskan waters and rivers, whereas lower recruitment occurs when westerly winds prevail (Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990; Schmidt et al. 1991; Colonell and Gallaway 1997). Once in Alaskan waters, Arctic cisco are assumed to make annual migrations between summer feeding habitats in the Beaufort Sea and overwintering habitats in river deltas (Craig 1989). Between the ages of 6 – 8 years, Arctic cisco are thought to reach sexual maturity and return to the Mackenzie River system to spawn.

While predominately based on observed relationships between recruitment patterns into Alaskan rivers and wind speed and direction, the Mackenzie hypothesis has also been examined using genetic tools. Previous investigations using DNA restriction site analysis and allozymes did not find evidence for genetic differentiation between collections of Arctic cisco from the Colville River and Mackenzie River basin, a finding that supports the Mackenzie hypothesis (Bickham et al. 1989; Morales et al. 1993). There is limited evidence, however, for genetic differentiation among sample collections of Arctic cisco from Mackenzie River tributaries (Bickham et al. 1989; Lockwood and Bickham 1991) and between collections from the Mackenzie River and Beaufort Sea near Point Barrow (Morales et al. 1993), findings that do not support the Mackenzie hypothesis. In addition, studies of age structure support the Mackenzie hypothesis. Arctic cisco are iteroparous (Reist and Bond 1988) and reported to live up to 19 years (Bond and Erickson 1997), but fish older than age-8 are rare in Alaskan waters (Murphy et al. 2007). Presumably, after the first spawning event, Arctic cisco remain within the Mackenzie River and delta and make annual migrations to feed at sea but do not return to rivers in Alaska. If there were local spawning populations in Alaska, it is assumed that fish older than age-8 would be more common.

While the Mackenzie hypothesis remains the most plausible and accepted explanation of recruitment of Arctic cisco to Alaska, we conducted this study to reexamine the Mackenzie hypothesis for three reasons. First, in spite of all the evidence to the contrary, both local residents and some scientists continue to ask if some recruitment of Arctic cisco could originate from local Alaska spawning populations or from Asia (MBC Applied Environmental Sciences

2004). Second, methodological advances in genetic analyses warranted a reassessment using new techniques. Third, and most important, climatic and oceanographic changes during the last decade have resulted in diminished sea ice, warming, and changes in northern wind and atmospheric circulation patterns (Overland et al. 2008, 2010). Given the critical role that temperature and wind play in the early life history and recruitment of Arctic cisco in Alaska (von Biela et al. 2011, 2013), a reassessment of the Mackenzie hypothesis, including recruitment and wind data that expands previous studies and includes data from the recent warm period (Overland et al. 2008), was warranted to better understand how changes in climate may affect this important subsistence resource.

In this study, we revisit the Mackenzie hypothesis using several lines of investigation. First, we use newer genetic analyses including microsatellite markers and mitochondrial DNA (mtDNA) sequence data to test for differentiation among collections of Arctic cisco from the Colville River and five tributaries of the Mackenzie River. Second, we reexamine the link between wind conditions in the Beaufort Sea, recruitment of Arctic cisco to the Colville River region, and subsequent harvest in the Colville River area using new data. Third, we examine the relation between recruitment during their first winter and age structure of Arctic cisco to confirm that a lack of recruitment of age-0 fish results in missing age-classes in subsequent fall migrations as proposed by Fechhelm and Griffiths (1990). Fourth, we compare the age composition of Arctic cisco in the Colville River fishery to those collected from the Peel River, a tributary of the lower Mackenzie River to determine if there are differences consistent with the Mackenzie hypothesis. Finally, we examine patterns of strontium in otoliths of Arctic cisco to test the migration chronology of Arctic cisco that was proposed by Craig (1989). Strontium is substituted for otolith calcium in levels reflecting the concentration of strontium in the environment, which is generally greater in seawater than freshwater. Strontium-to-calcium ratios (Sr/Ca), therefore, can be used to trace the movement of fish among environments of different salinity (Campana 1999; Zimmerman et al. 2003; Brown et al. 2007). Combining these lines of inquiry, we provide a new test of the Mackenzie hypothesis in light of new methods of analysis and longer time series to improve our understanding of how this important resource may respond to future climate and development scenarios.

MATERIALS AND METHODS

Genetic Sample Collections

Arctic cisco were collected from the subsistence fishery on the Colville River near the village of Nuiqsut in 2005, 2006, and 2007 (n = 86, 176, and 136, respectively) (Fig. 1). Mature fish were also collected in late summer from five tributaries of the lower Mackenzie River where Arctic cisco are presumed to spawn: the Arctic Red (n = 60), and Peel (n = 54) rivers in 2007 and the Great Bear (n = 55), Carcajou (n = 52), and Mountain (n = 59) rivers in 2008 (Fig. 1). Arctic cisco were caught using monofilament gill nets at all collection locations.

DNA extraction and microsatellite amplification

Genomic DNA was extracted from fin, gill, or muscle tissue using the DNeasy Tissue Kit (Qiagen, Valencia, CA) or Purgene DNA Extraction Kit (Gentra Systems Inc., Minneapolis, MN) following the manufacturer's protocols. Sixteen microsatellite loci were identified as nuclear genetic markers to assess population structure of Arctic cisco including: seven microsatellite loci originally isolated from congenerics (*Cisco-90*, *Cisco-157*, *Cisco-181*, *Cocl-Lav4*, *Cocl-Lav6*, *Cocl-Lav8*, and *LGL BWF2*; Patton et al. 1997; Turgeon et al. 1999; Rogers et al. 2004), three previously published microsatellite loci developed from Arctic cisco (*Aut135*,

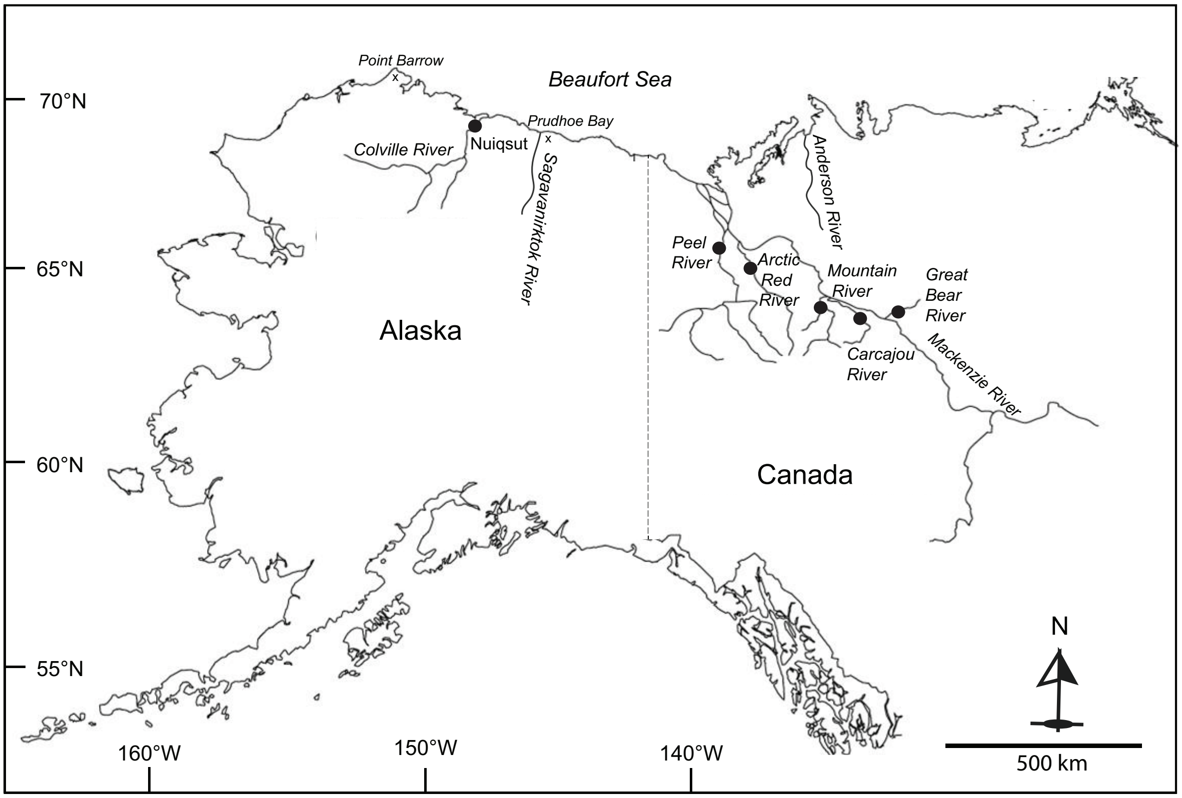

Figure 2.1. Genetic sample collection locations (black circles) for Arctic cisco from the Colville River and Mackenzie Rivers, 2005-2007.

Aut139 and *Aut151*; Ramey et al., 2008), two unpublished loci developed from Arctic cisco for this study (*Aut134* and *Aut189*, Table 2.1), and four unpublished microsatellite loci taken from GenBank (*Bom3c*, *Bom17c*, *Bom21c*, and *Bom22b*). Five microsatellite loci (*Aut135*, *Bom21c*, *Cisco-90*, *Cocl-Lav6* and *Cocl-Lav8*) were subsequently excluded from our panel after preliminary analyses because of low allelic polymorphism (< 4 alleles per locus).

Microsatellite loci were amplified using PCR in 10 μL volumes containing 4 – 50 ng of genomic DNA, 10 mM Tris-HCl (pH 8.3), 1.5 mM $MgCl_2$, 50 mM KCl, 0.01% gelatin, 0.01% NP-40, 0.01% Triton X-100, 3.7 – 4.0 μM each unlabeled primers, 0.1 – 0.3 μM labeled tail primer, 2 mM each dNTP and 0.3 – 0.5 U of Taq DNA polymerase. Reactions were carried out in MJ Research (BIORAD, Hercules, CA) or MWG thermocyclers (MWG Biotech Inc., Huntsville, AL) with an initial denaturation time of 2 min at 94°C followed by variable thermoprofiles (Table 2.1) and a final 10 min elongation step at 72°C. PCR products were separated on 6% polyacrylamide gels using a LI-COR Model IR2 automated fluorescent DNA sequencer (Lincoln, NE). Forward primers were either directly fluorescently labeled to visualize alleles (*Bom3c*, *Bom17c*, *Bom22b*, *LGL BWF2*, *Cisco-151*, *Cisco-181*, and *Cocl-Lav4*) or were synthesized with universal tails on the 5' ends and visualized by adding fluorescently labeled complementary tailed sequences to the PCR reaction (*Aut134*, *Aut139, Aut151*, and *Aut189*). Size standards were created by determining allele sizes for specific samples at each locus relative to the M13 phage single nucleotide ladder and these samples were then used in subsequent gels. To verify allele sizes across all loci for quality control, a minimum of 10% of all samples were independently amplified and scored. GeneImagIR v4.05 (Lincoln, NE) software was used to assign allele scores.

Mitochondrial DNA sequencing

A 594 base pair (bp) fragment of the mitochondrial ATP synthase VI subunit gene (ATPase 6) was sequenced for a subsample of 372 Arctic cisco (Colville River, n = 258; lower Mackenzie River system, n = 114) using previously published primers (H9208 and L8558; Giuffra et al. 1994). The ATPase 6 gene was selected for use in the current study as it has been used in previous genetic investigations of North American ciscoes (Turgeon and Bernatchez 2001, 2003). Primers were modified on the 5' ends with a universal M13F(-29) or M13R tail (Oetting et al. 1995). Mitochondrial DNA (mtDNA) was amplified using a MJ Research thermocycler using PCR conditions as follows: initial denaturation at 94 ºC for 1 min followed by 35 cycles of

Table 2.1. Eleven microsatellite loci with original citation, annealing temperatures (T_A), A = number of alleles, A_R = allelic richness, H_o = observed heterozygosity, H_e = expected heterozygosity, and the GenBank accession number for each locus used to assess genetic structure of Arctic cisco.

Locus	Reference	T_A (°C)	A	A_R	H_o	H_e	Accession #
_Aut134_*[†a]	this study	52	29	28.992	0.772	0.831	EU603399
_Aut139_*[†]	Ramey et al. 2008	50	47	46.803	0.871	0.877	EF192595
_Aut151_*[‡]	Ramey et al. 2008	50	33	33.000	0.886	0.875	EF192596
_Aut189_*[‡b]	this study	52	38	37.946	0.778	0.782	EU603400
Bom3c[†c]	unpublished	55	38	37.896	0.905	0.907	AY507115
Bom17c[†d]	unpublished	50	21	20.951	0.817	0.815	AY507114
Bom22b[†e]	unpublished	55	17	16.911	0.572	0.563	AY507121
Cisco-157[†]	Turgeon et al. 1999	55	23	22.947	0.795	0.792	N/A
Cisco-181[‡]	Turgeon et al. 1999	57	32	31.929	0.931	0.946	N/A
Cocl-Lav4[†]	Rogers et al. 2004	52	21	20.933	0.579	0.580	AY453197
LGL BWF2[†]	Patton et al. 1997	52	15	14.946	0.609	0.595	N/A

*PCR profiles consisted of 30-40 cycles of 15s denaturation, 15s annealing, and 30s extension, all other loci had a PCR profile of 30s, 30s, 60s respectively. [†] indicates loci that went through 30 cycles of PCR, and [‡] indicates 40 cycles [a] F: TCATGAAATCACACACCC R: CTCACGCATCACACACC [b] F: TTATACTGCATGGTGC R: GCCTGGCTCAATTTGT [c] F: GTGGACTGCTGCTTTGTTG R: GCTGTATCTTTAACCTCCC, [d] F: GGCAACAGACAGAAATAAG R: TATGTCACAAGGGGCAGTG, [e] F: GGATGCCTTCTTGATGCTT, R: CATTTATCAGCCTCTCAGCC

94 ºC for 1 min, 62 ºC for 1 min, and 72 ºC for 1 min ending with a final elongation step at 72 ºC for 10 min. Sequencing reactions were conducted using a simultaneous bi-directional sequencing kit (Epicentere technologies, Madison, Wisconsin) and fluorescently labeled primers. The sequencing reaction was conducted using a RoboCycler ® thermocycler (Stratagene, La Jolla, CA) with the following conditions: initial denaturation at 92 ºC for 2 min followed by 30 cycles of 92 ºC for 30 s, 60 ºC for 30 s and 70 ºC for 1 min. Sequences were visualized on a LI-COR Long ReadIR 4200 automated sequence using a 5.5% acrylamide gel. Sequence data were aligned and proofed using AlignIR software (LI-COR, Lincoln, NE). Nucleotide positions for sequences amplified from Arctic cisco were confirmed by alignment with the published sequence for the complete mtDNA genome of European whitefish (*C. lavaretus*) (Miya and Nishida 2000; GenBank accession no. AB034824).

Population genetic statistics

Microsatellite allelic size ranges, total number of alleles (A), and observed and expected heterozygosity (H_o and H_e, respectively) were generated by locus and by population using FSTAT v2.9.3 (Goudet 2001). The average number of alleles was calculated using GENALEX (Peakall and Smouse 2006). Average allelic richness by population, allelic richness by locus, and private allelic richness across 11 nuclear loci were calculated using HP-RARE 1.0 (Kalinowski 2005), which uses the rarefaction procedure to account for variable sample sizes. An exact test for Hardy-Weinberg equilibrium (HWE) was done by locus using ARLEQUIN v3.01 (Excoffier et al. 2005) with a Bonferroni correction (Sokal and Rolhf 1995; $k = 11$ loci, $\alpha = 0.05 / 11$ or 0.0045). ARLEQUIN v3.01 was used to test for pairwise linkage disequilibrium between all possible pairs of loci with a Bonferroni correction ($k = 55$ comparisons, $\alpha = 0.05 / 55$

or 0.0009). Samples were divided into sample collections by location and year (n = 8) and major river systems (Colville and Mackenzie rivers) to examine population structure. Pairwise F_{ST} comparisons between all sample collection pairs and major river systems were calculated using Arlequin v3.01 and a Bonferroni correction was applied ($\alpha = 0.0017$ k = 28; $\alpha = 0.0167$ k = 3; $\alpha = 0.025$ k = 2, respectively). An analysis of molecular variance (AMOVA) using ARLEQUIN v3.01 was conducted to quantify genetic variability and estimate its distribution among sampling collections (between years for the Colville samples and tributaries for the Mackenzie) and major river systems (Colville and Mackenzie).

The frequency of mtDNA haplotypes, haplotype diversity, and nucleotide diversity were calculated using ARLEQUIN v3.01 and NETWORK version 4.5.1.6 (Fluxus Technology Ltd. 2009; http://www.flexus-engineering.com/sharepub.htm) was used to generate a median joining network (Bandelt et al. 1999) of mtDNA haplotypes. ARLEQUIN 3.01 was used to calculate pairwise F_{ST} comparisons of haplotype frequencies between Arctic cisco from the Colville River and the Mackenzie River system.

Model-based clustering analysis

Allele frequencies for microsatellite loci were used to probabilistically assign genotypes to populations or clusters using STRUCTURE v2.3.1 (Pritchard et al. 2000). Two sets of analyses were conducted: one using genotypic data for all samples collected from the Colville River and Mackenzie River system (n = 678) and a second using only data derived from samples collected from five tributaries of the lower Mackenzie River system where Arctic cisco are presumed to spawn (n = 280). The number of populations or clusters (K) was assessed for values of K from 1 to 10 for the analysis of genotypic data for all sample collections combined (e.g., the possibility of up to ten ‘source populations’ was explored). Values of K from 1 to 5 were assessed for genotypic data derived from samples collected from the lower Mackenzie River system (e.g., structuring among five tributaries was explored). Five replicate model runs were conducted for each assumed value of K using the admixture model with correlated allele frequencies for 100,000 Markov chain Monte Carlo repetitions after a burn-in of 10,000. The mean natural log probability of sample genotypes clustering to K populations for five replicates was used to calculate the posterior probability for each value of K. The highest penalized posterior probability of K, where mean natural log likelihoods for each value of K were penalized by one-half of their variance, was inferred to be the most likely number of clusters or populations among sample genotypes (Hubisz et al. 2009).

Retrospective analyses of catch data

Recruitment of Arctic cisco to the Colville River region, catch rates of young-of-year fish during summer surveys in the Prudhoe Bay region, historical harvest data for the commercial and subsistence fall fishery, and environmental data compiled by Murphy et al. (2007) were examined. First, a recruitment index was constructed by standardizing log-transformed catch-per-unit-effort (CPUE) in Prudhoe Bay during summer (days-of-year 200 – 258) for age-0, age-1, and age-2 Arctic cisco, and then averaging the age-specific indices corresponding to a given cohort. Thus, an improved recruitment estimate was obtained for each cohort or year class based on catch rates at three ages sampled in three consecutive summers. The main environmental indicator to link recruitment to wind conditions in the Beaufort Sea was an annual index of average easterly wind speed for the period from July 1 to August 31 at the Deadhorse airport located at Prudhoe Bay (Murphy et al. 2007). The recruitment index was modeled as a function of easterly winds using a linear model with a threshold. Residuals from the model were used as an index of recruitment anomalies to examine the effect of climate conditions (i.e., near-shore temperature, ice conditions; Murphy et al. 2007) on anomalous recruitment using correlations and linear regression analyses.

Second, we examined harvest rates as indices of recruitment to the fishery. We examined estimates of age-specific catch rates (ages 5-8) for both the commercial and subsistence fishery. To test whether catch rates of 5, 6, 7, and 8-year old fish are related to variability in recruitment 5-8 years earlier we computed Pearson's product moment correlations between the available time series of catch rates at each age and the recruitment time series at the appropriate lag. R version 2.12.2 (R Development Core Team 2011) was used for all statistical analyses.

Chronology of migration

Nine otoliths, collected in 1986 (n = 3), 1995 (n = 3) and 2005 (n = 3), were examined in this study. Otoliths were provided by L. Moulton of MJM Research (Lopez Island, Washington) and were drawn from an archive of otoliths collected from subsistence fisheries in the Colville River (von Biela et al. 2011). Prior to preparation for age and microchemical analysis, otoliths were rinsed in deionized water, air dried, and weighed. Each otolith was embedded in thermoplastic cement on a glass slide, ground in the sagittal plane, and polished. Individual otoliths were mounted sulcus side down and ground with 2000-grit wet-dry sandpaper on a glass plate to the level of the nucleus. The slide was then warmed on a hotplate and the otolith flipped with the sulcus side up. The otolith was again ground using 2000-grit wet-dry sandpaper until the primordia were exposed, polished with 12000-grit polishing cloth, and finally, polished with a slurry of 0.05 μm alumina and deionized water. Analysis of otolith Sr and Ca followed the methods of Zimmerman and Nielsen (2003) and Zimmerman (2005).

Otoliths were mounted on a petrographic slide (Donohoe and Zimmerman 2010), which was then rinsed with deionized water, air dried, and coated with a 40-nm carbon layer. Based on annual banding patterns, the fish examined ranged in age from 5 to 8 years old. Elemental analysis was conducted with a JEOL 8900 Electron Microprobe at the U.S. Geological Survey, Menlo Park, California. A 15-kV, 50-nA, 10-μm-diameter beam was used for all analyses. Strontianite and calcite were used as standards for Sr and Ca, respectively. Each element was analyzed simultaneously and a counting time of 40 s was used to maximize precision. A transect of points from the core to the edge of the otolith was sampled with a spacing of 14 to 25 μm between sampling points for each otolith. Sr/Ca ratios (molar) were plotted and annuli were superimposed on these figures to describe the chronology of migration for each fish. Based on daily ring count, the mean number of days represented by a 10-μm-diameter sample point in these otoliths ranged from 5 days during the first year of life to over 30 days in years 6 through 8.

RESULTS

Microsatellites

Eleven microsatellite loci were used to genotype a total of 678 arctic cisco from Alaska and Canada (http://link.springer.com/content/esm/art:10.1007/s00300-013-1372-y/file/MediaObjects/300_2013_1372_MOESM1_ESM.xls). The number of microsatellite alleles (A) ranged from 15 (*LGL BWF2*) to 47 (*Aut139*; Table 2.1), with a mean $A = 28.55$. All microsatellite loci conformed to HWE when collections were combined. When sampling groups were analyzed individually, two loci deviated significantly from HWE in one sample collection each after Bonferroni correction (Aut139 in the Great Bear River collection had lower observed heterozygosity than expected, $P < 0.0001$; and Bom17c in the Colville 2006 collection had higher observed heterozygosity than expected, $P = 0.0034$). There was no evidence of inbreeding; global $F_{\mathrm{IS}} = 0.007$. No linkage disequilibrium was detected between loci for all collections combined. When sampling groups were analyzed individually, one pair of loci in the Colville 2007 sample collection showed significant evidence of linkage after Bonferroni correction ($P = 0.0002$). Allelic richness was similar for fish in the Colville River (average A_R = 23.99) and Mackenzie River (average A_R = 23.45) (Table 2.2). Private allele richness was 4.10 for fish in the Colville River and 3.56 for fish from the Mackenzie River system. Average observed and expected heterozygosity across all loci were 0.774 and 0.778, respectively. No statistically significant pairwise F_{ST} differences were detected between sample collections ($P \geq 0.126$) (Table 2.3) or major river drainages ($P = 0.477$). AMOVA results show that over 99.94% of the allelic variation was found within individuals. The highest posterior probability (1.00) as determined using model-based clustering analyses occurred when K = 1 for genotypic data for all sample collections of Arctic cisco combined (Table 2.4) and when only genotypic data from the Mackenzie River system were considered (Table 2.4).

Mitochondrial DNA

Nineteen mtDNA haplotypes and 29 variable nucleotide positions were identified from the amplification and sequencing of a 594 bp fragment of ATPase 6 gene from 372 samples (Fig. 2.2; Table 2.5). Haplotype diversity among the 19 Arctic cisco haplotypes (AMN) was 0.414 ± 0.030 and nucleotide diversity averaged across all positions equaled 0.0011 ± 0.0009. Fish from the Colville River and Mackenzie River tributaries shared the five most common haplotypes (AMN001, AMN002, AMN006, AMN007 and AMN012). Colville River samples had 12 unique haplotypes found at low frequencies (1-2 fish each; < 1%) including two highly divergent haplotypes (AMN009 and AMN015). Two haplotypes found at low frequency (1 fish each) in the Arctic Red River sample collection (AMN010 and AMN011) were not identified in Colville

River samples. No statistically significant difference was detected in haplotype frequencies for Arctic cisco from the Colville and Mackenzie rivers using pairwise F_{ST} comparison ($P = 0.678$).

Table 2.2. Population-specific descriptive statistics for eleven microsatellite loci of Arctic cisco collected from the Colville River and the Mackenzie River system, 2005-2008.

	n	Average *A*	Average A_R	Private allelic richness	H_o	H_e
Mackenzie River	280	23.455	23.45	3.56	0.775	0.777
Arctic Red	60	15.455	14.62	0.63	0.765	0.759
Great Bear	55	15.909	15.58	0.74	0.769	0.779
Carcajou	52	15.182	15.18	0.70	0.804	0.790
Mountain	59	14.364	13.83	0.12	0.767	0.767
Peel	54	14.727	14.54	1.16	0.771	0.763
Colville River	398	25.727	23.99	4.10	0.773	0.779
Colville 2005	86	16.818	14.45	0.74	0.787	0.774
Colville 2006	176	21.273	15.13	0.68	0.778	0.779
Colville 2007	136	20.545	15.41	1.01	0.767	0.767

n= number of individuals in each population, average *A* = number of alleles per locus, average A_R = allelic richness, private allelic richness was calculated across 11 loci, H_o = observed heterozygosity, and H_e = expected heterozygosity.

Table 2.3. Pairwise $\boldsymbol{F}_{\mathbf{ST}}$ values for eleven microsatellite loci in collection of Arctic cisco. No pairwise comparisons were significantly different ($P \geq 0.126$ for all comparisons).

	Arctic Red	Great Bear	Carcajou	Mountain	Peel	Colville 2005	Colville 2006
Colville 2007	0.00061	-0.00144	-0.00070	0.00129	-0.00032	0.00052	0.00037
Colville 2006	0.00006	0.00054	-0.00053	0.00082	0.00100	-0.00122	
Colville 2005	0.00005	0.00095	-0.00189	-0.00070	-0.00012		
Peel	-0.00081	0.00026	-0.00012	0.00042			
Mountain	-0.00070	0.00232	0.00048				
Carcajou	0.00047	0.00036					
Great Bear	0.00064						

Table 2.4. The number of populations or clusters (K) inferred from model-based clustering analyses using the admixture ancestry model and correlated allele frequencies for *C. Autumnalis* genotypes derived from the Colville River and the Mackenzie River system. Each value for Ln Pr(X│K) is the mean of five STRUCTURE simulations using a burnin of 10,000 and 100,000 Markov chain Monte Carlo repetitions. The posterior probabilites [Pr(K)] are given for each assumed number of clusters.

	K	Ln Pr(X│K)	Pr(K)
Colville River and Mackenzie River system			
	1	-31033.7	1.00000
	2	-31056.0	0.00000
	3	-31186.0	0.00000
	4	-31441.2	0.00000
	5	-31703.7	0.00000
	6	-31816.8	0.00000
	7	-32382.9	0.00000
	8	-33319.6	0.00000
	9	-33420.7	0.00000
	10	-33394.8	0.00000
Mackenzie River system only			
	1	-12795.9	0.26894
	2	-12795.0	0.73106
	3	-12873.6	0.00000
	4	-12961.3	0.00000
	5	-12955.2	0.00000

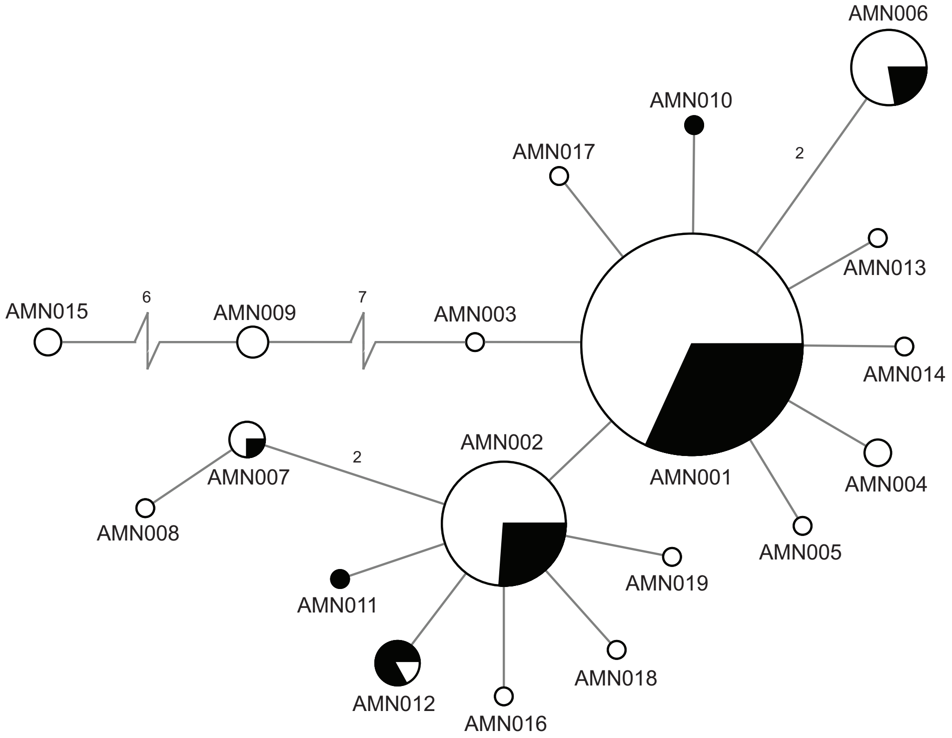

Figure 2.2. Minimum spanning network for mitochondrial DNA ATP synthase VI subunit gene haplotypes detected from putative Arctic cisco. Circles are drawn proportional to the frequency at which haplotypes were observed. Shading represents the sample location from which haplotypes originated: white (Colville River) and black (lower Mackenzie River system). A single mutation separates nodes unless indicated by number. Lines separating nodes are drawn to scale unless indicated by a break.

Retrospective Recruitment Patterns

Retrospective analysis of recruitment confirmed previous research (Fechhelm et al. 2007) showing a correlation between year-class strength of Arctic cisco in the Colville River and wind conditions. Recruitment was best described by a linear model with a threshold below which wind speed did not affect recruitment ($r^2 = 0.70$, $F = 54.3$, $P < 0.001$) (Fig. 2.3). This implies that year-class recruitment failures occur in years with average July-August winds from the west

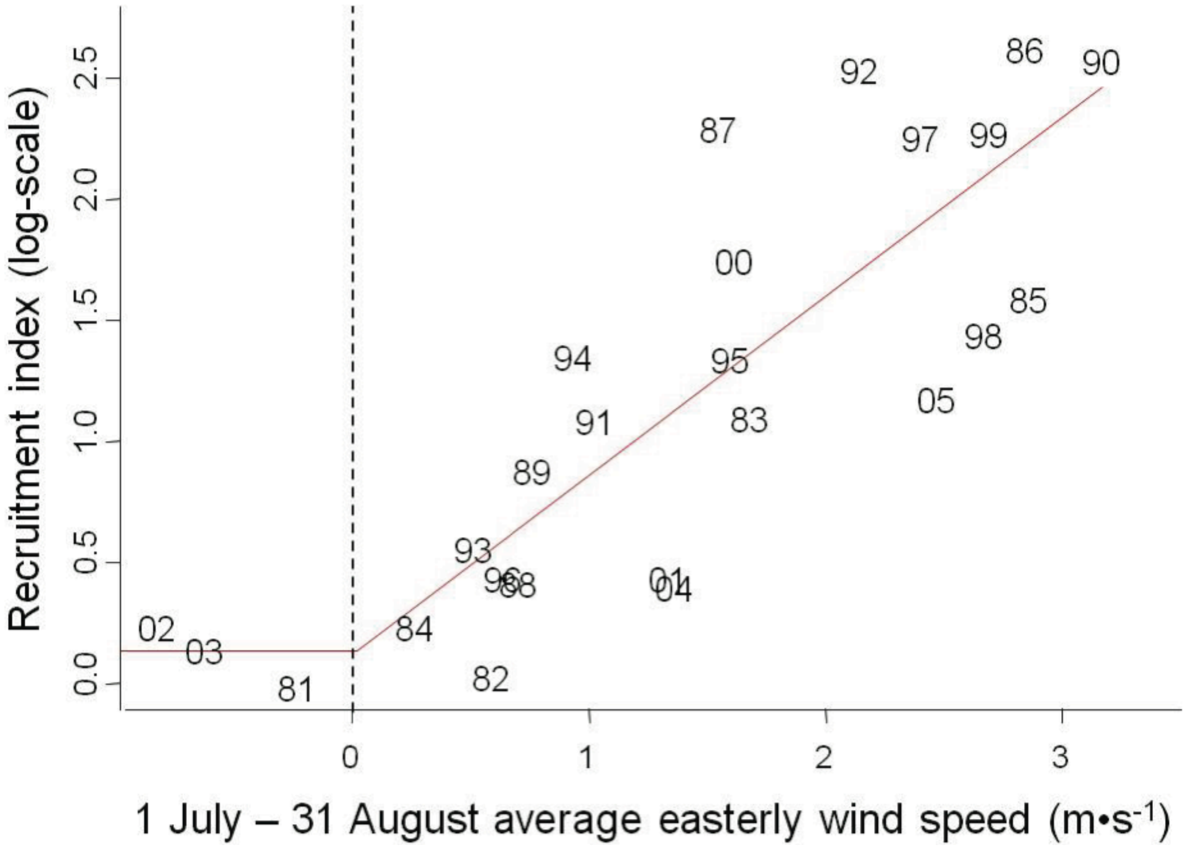

Figure 2.3. Relationship between average easterly wind speeds (m/s) and Arctic cisco recruitment index for the Colville River, Alaska, 1981-2005. The numbers on the plot indicate the recruitment class.

and that recruitment increases linearly with the strength of easterly winds. Strong recruitment translated into elevated catch rates in the Colville River fishery 5-8 years later, with significant correlations ($P < 0.05$) between age-specific CPUE and the combined recruitment index ranging from 0.73 (age 7) to 0.86 (age 5) for commercial CPUE and from 0.60 (age 8) to 0.80 (age 6) for subsistence CPUE.

Recruitment anomalies (i.e., residuals from the best-fit model) suggest that after accounting for the effects of wind, recruitment was anomalously low in the early 1980s, increased in the mid-1980s, and declined significantly since then with below-average recruitment in recent years (Fig. 2.4). No significant effects of climate conditions (near-shore temperatures or ice conditions) during early ocean life on these recruitment anomalies were found; thus, the variation in these anomalies remains unexplained.

Age composition of Arctic cisco in the Colville River, estimated from aged samples obtained in the fishery between 1985 and 2004, ranged from 4 to 9 (mean 5.9). Arctic cisco captured in the Peel River in 1998 and 2002, ranged in age from 5 to 19 (mean 10.7; VanGerwen-Toyne et al. 2008). Fish captured in the Peel River were, therefore, older on average than Arctic cisco found in the Colville River.

Chronology of migration

Movement among different salinity environments for the nine Arctic cisco examined by otolith analysis in this study (Fig. 5) followed the life history model of seasonal movements between nearshore and coastal environments first presented by Gallaway et al. (1983) and Craig (1989). During the first year of life, otolith Sr/Ca ratios were low as juvenile fish presumably hatched and migrated downstream in their natal river and then increased as they entered saltwater and migrated west along the coast. Each year thereafter, otolith Sr/Ca ratios oscillated between lower and higher values indicating that fish moved between marine waters of high salinity during summer to areas of fresher or brackish waters to overwinter. Sr/Ca values associated with the first and second winter were often as low as Sr/Ca values associated with young-of-the-year freshwater residence (e.g., Fig. 5f and 5h) indicating that some Arctic cisco overwintered in freshwater in their first years.

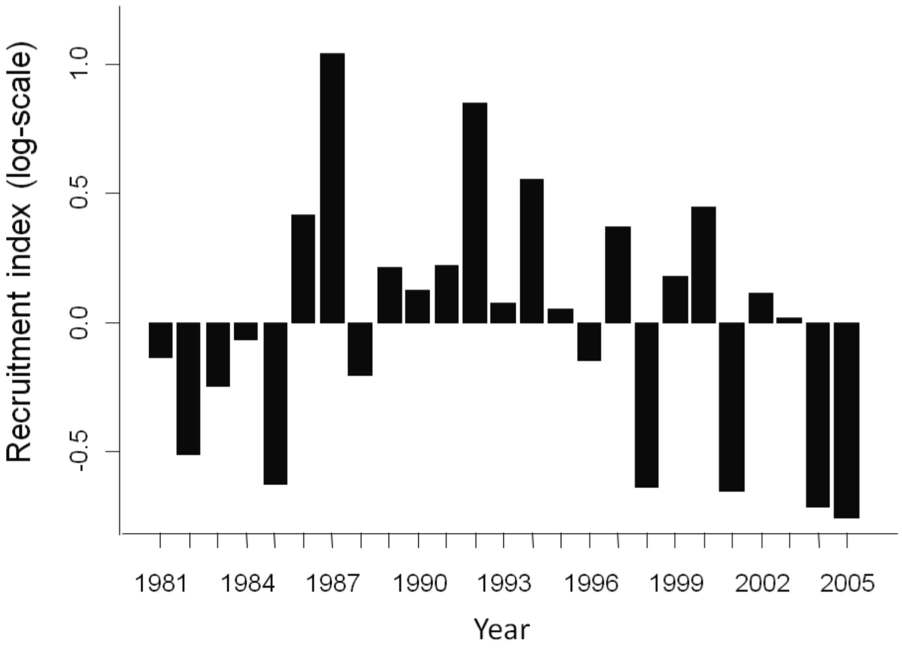

Figure 2.4. Recruitment anomalies (*i.e.*, residuals from the best-fit model) after accounting for the effects of wind given by year, Arctic cisco, Colville River, Alaska, 1981-2005.

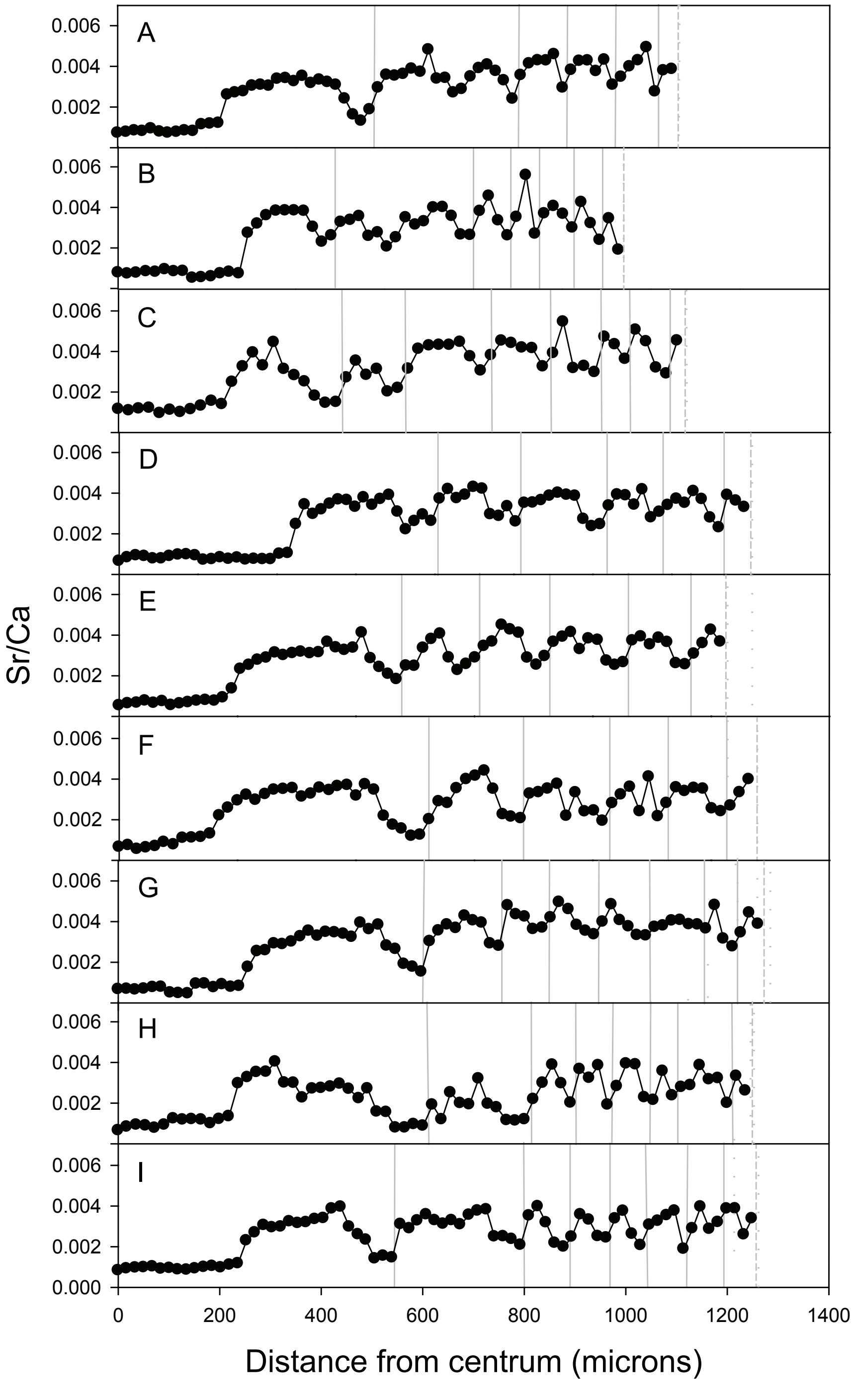

Figure 2.5. Transects of otolith Sr/Ca, beginning in the otolith core and ending at the edge of the otolith for Arctic cisco captured in the Colville River, Alaska in 1986, 1995, and 2005. The dashed line indicates the location of the otolith edge, and the solid grey lines indicate location of annuli, which corresponds to the transition from winter to spring.

DISCUSSION

Based on our reanalysis of genetics and recruitment, we find no evidence to refute the Mackenzie hypothesis. No genetic differentiation was detected between sample collections of Arctic cisco from the Colville River and the Mackenzie River system. Furthermore, no evidence for structuring was found using genotypic data derived from sample collections from tributaries of the lower Mackenzie River system. Recruitment of Arctic cisco to Alaska continues to be correlated to wind patterns and year class recruitment failures occur in years dominated by westerly winds, indicating that recent broad-scale changes to atmospheric circulation patterns have not changed sufficiently to preclude recruitment of Arctic cisco to Alaska. Further, Arctic cisco sampled from the Colville River appear to make repeated, annual migrations between low and higher salinity habitats in support of proposed models of Arctic cisco movement patterns.

Genetic analyses were conducted to assess population structure among sample collections of Arctic cisco from the Colville River and tributaries of the Mackenzie River. No statistically significant genetic differences were found between sample collections of fish from the two watersheds. Global F_{IS} across all sample locations and years was low (0.007) suggesting minimal levels of inbreeding in Arctic cisco, adding additional support for a single large interbreeding population. Furthermore, model-based structuring methods support a single admixed population when considering genotypic data from all sample collections. Collectively, these genetic data do not refute the Mackenzie hypothesis and instead support the conclusion of previous investigations that fish spawning in the Mackenzie River are the source population of Arctic cisco recruited into overwintering habitats within the Colville River (Bickham et al., 1989; Morales et al., 1993).

Genetic analyses of Arctic cisco from the Mackenzie River drainage did not support population differentiation among collections of fish made from putative spawning tributaries using standard population genetic statistics or model-based clustering methods. Thus, we found no support for genetic differences among spawning aggregations of Arctic cisco in the Mackenzie River system, contrary to a previous assessment (Bickham et al. 1989). Our results (i.e., lack of genetic differentiation among tributaries) suggest weak fidelity of Arctic cisco to natal streams for spawning within the lower Mackenzie River watershed.

Two highly divergent mtDNA haplotypes (AMN009 and AMN015) were found at low frequencies among the Colville River sample collections. These haplotypes could be from interspecific hybrids (Bernatchez and Dodson 1991; Bickham et al. 1997; Rogers et al. 2001) or from fish mis-identified to species at the time of collection. Schlei et al. (2008) examined eight species of North American coregonids using DNA barcoding and, of the 49 individuals analyzed, one fish morphometrically identified as a Bering cisco (*Coregonus laurettae*) was subsequently identified as an Arctic cisco using molecular techniques. Bering cisco are occasionally caught in the Colville River but not the Mackenzie River and were once considered to be conspecific with Arctic cisco (McPhail 1966).

Approximately 70% of the variation in recruitment of juvenile Arctic cisco to Alaskan waters was determined by the strength of easterly winds during summer (July – August), leading to variations in catch rates in the fishery 5-8 years later. This supports the hypothesis that Arctic cisco captured in Alaska originate from the east and, presumably from the Mackenzie River. Analysis of age structure further supports the hypothesis that Arctic cisco only rear in Alaska rivers and coastal waters until they reach maturity and return to the Mackenzie River. If local populations were established in Alaska rivers, we would have expected to capture fish of older ages as we saw in Mackenzie River tributaries.

The chronology of migration between freshwater and saltwater for Arctic cisco generally follows the conceptual model proposed by Gallaway et al. (1983) and Craig (1989) based on otolith microchemistry; although, it appears that Arctic cisco may be overwintering in lower salinity habitats during their first winters at sea. For example, at ages two and three (Fig. 5b) otolith Sr/Ca ratios decline to values similar to those observed in presumed freshwater rearing during the first year of life in the river suggesting some fish overwintered in low salinity habitats. Previous capture data indicate that Arctic cisco overwinter in areas of moderate salinity (~5 ppt) (Schmidt et al. 1989).

Otolith Sr/Ca ratios measured in Arctic cisco were greater than those reported for other Salmonines. For example, molar ratios of otolith Sr/Ca measured in this study ranged from 0.0005 to 0.0056 while a range of 0.0009 to 0.0034 was reported for several salmonids exposed to salinities ranging from freshwater (salinity = 0 psu) to full seawater (salinity = 33 psu; Zimmerman 2005). It is unclear why otolith Sr/Ca ratios can be so much higher in Arctic cisco, but variation among species can result from different physiological pathways and filters (Campana 1999) and different responses to interactions among environmental variables (Elsdon and Gillanders 2003, 2004). Otolith Sr/Ca ratios associated with overwinter periods increased with fish age, indicating that older fish overwinter in higher salinity habitats. Because otolith growth slows as fish age, however, the temporal resolution of the 10-µm-diameter electron beam used to measure Sr/Ca ratios also decreases with the age of the fish. As a result, measurement points taken in the first years of life discriminate salinity over a range of only a few days, a time period that is likely to reflect occupation of a salinity-specific habitat. In contrast, measurements taken during age-8 cover a mean of 35 days and, thus, are more likely to integrate movement among different salinity habitats. This variation in temporal resolution among ages makes it more difficult to establish overwinter salinities at older ages. Otolith analyses indicated that Arctic cisco reside in brackish waters throughout the winter leading to additional questions about their overwintering physiology. It is not clear if fish experience yearly re-smoltification and undergo physiological changes necessary for fresh/salt water adaptation in their fall and spring transitions to and from the Beaufort Sea (see similar life history traits described in anadromous Arctic char *Salvelinus alpinus* by Aas-Hansen et al. 2005).

Climate conditions in the Arctic have undergone significant changes, particularly during the last 20 years (Walsh 2008; Overland et al. 2008; 2010). These changes include increased warming (Overland et al. 2008) and increased storminess and shifts in atmospheric circulation patterns (Overland et al. 2010). In spite of these changes, Arctic cisco recruitment patterns are still best described by the Mackenzie hypothesis. How Arctic cisco populations respond to future changes remains a critical question. Murphy et al. (2007) found weak effects of spring and summer temperature conditions on overwinter survival of Arctic cisco, suggesting that survival of young-of-the-year and sub-adults was reduced during summers with above-average temperatures. Similarly, von Biela et al. (2011) found that young-of-the-year growth rates of Arctic cisco were strongly positively related to temperature and river flow. Ultimately, Arctic cisco growth, survival, and recruitment dynamics are closely related to a set of environmental variables that are likely to change dramatically over the next 50 to 100 years. Continued monitoring and assessment of existing theory is needed to ensure continued conservation of this important subsistence resource.

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Chapter 3: Long-term increases in young-of-the-year growth of Arctic cisco *Coregonus autumnalis* and environmental influences

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INTRODUCTION

Climate change effects on Arctic freshwater and nearshore ecosystems are expected to result in changes to temperature, hydrology, ice regimes, biogeochemical processes, trophic structure and food web interactions, primary and secondary productivity, and the distribution of species (Wrona *et al.,* 2006). How any single species or population responds to these changes will likely vary among locations and depend on the life history and range of habitats used (Reist *et al.,* 2006a). Diadromous species that spawn in freshwaters and feed in marine waters integrate climate change effects across freshwater, estuarine, and marine habitats and, thus, the total impact is expected to be significant (Reist *et al.,* 2006a).

The current understanding of population level change in Arctic species has been hindered by a lack of long-term data and a poor understanding of Arctic ecology in the spring and winter months (Reist *et al.,* 2006a,b; Wrona *et al.,* 2006). Fish otoliths collected for ageing represent a potential source of long-term annual growth rate data that integrate year-round conditions. Growth rates of individuals have long been used across plant and animal taxa to monitor population health and understand ecosystem change (Sebens, 1987) and are typically linked to demographic rates and changes in population abundance through increases in survival and reproduction of larger individuals (Reiss, 1989; Roff, 1992). Otoliths collected from Arctic cisco *Coregonus autumnalis* (Pallas) captured in the Colville River, Alaska, subsistence fishery from 1986 to 2007 were used to assess change in growth among years and environmental correlates of growth. The goal of this study was to test for long-term shifts in first year growth of *C. autumnalis* based on otolith growth increments and conduct exploratory analyses to infer the potential underlying cause of changes in first year growth.

In Alaska, *C. autumnalis* make long-distance movements from spawning to rearing locations and smaller-scale annual marine migrations between feeding and over-wintering habitats. *C. autumnalis* captured in Alaska waters are the progeny of fish that spawn in tributaries of the Mackenzie River, Canada (Craig, 1989; Fechhelm & Griffiths, 1990). Spawning and hatching success has not been extensively studied in Canada, but hatching is thought to coincide with spring freshet and river break-up as it does with other coregonids (Naesje et al. 1986; Naesje et al. 1995; Urpanen et al. 2005). After hatching, *C. autumnalis* migrate downstream and out of the Mackenzie River delta where they are swept west to the Colville River delta by nearshore wind-driven currents, a migration thought to last about 35 days on average(Gallaway *et al.,* 1983; Fechhelm & Griffiths 1990; Dillinger *et al.,* 1992; Colonell & Gallaway, 1997). Several studies have supported the wind-driven migration model that requires average wind speeds of 5 km/h during the open water season for a successful recruitment to Alaska, with increasing speeds resulting in stronger recruitment years (Fechhelm et al., 2007). YOY *C. autumnalis* are generally thought to migrate in a nearshore band of brackish water, but have been found in good condition as far as 15-km offshore (Jarvela and Thorsteinson, 1999). Each winter, the Colville River freezes as nearshore sea ice forms and *C. autumnalis* enter deepwater river habitats to overwinter. A lack of deepwater habitats in other North Slope drainages, including the Sagavanirktok River, is thought to limit overwintering habitat to the Colville and Mackenzie rivers (Fechhelm *et al.,* 2007). During summer (mid-June to early September), fish return to the Beaufort Sea for summer feeding migrations. At age six to nine, *C. autumnalis* migrate back to Mackenzie River tributaries to spawn in mid-September to early October (Gallaway *et al.,* 1983; Moulton *et al.,* 1989). Migration of YOY fish to Alaska is perhaps the most well understood life history stage of *C. autumnalis*. The migration has been well studied because juvenile *C. autumnalis* returning to the Colville River in the fall provide an important subsistence resource for the residents of the Alaskan Arctic Coastal Plain (George & Kovalsky, 1986). Recently, wide variation in catch rates of *C. autumnalis* has lead to concern among subsistence users (Gallaway *et al.,* 1983). Further, traditional knowledge, based on long-term observations, suggests that fish size-at-age and abundance have decreased and subsistence users are concerned about the productivity of *C. autumnalis* populations.

Changes in climate could alter growth rates and fish size. Temperature has been positively correlated with growth in *C. autumnalis* through direct influences on metabolism (Griffiths et al., 1992). Other environmental variables may indirectly influence growth by altering regional productivity at lower trophic levels. Based on the current understanding of oceanography in the nearshore Beaufort Sea, increased primary productivity is associated with stronger east (upwelling favourable) winds, reduced summer sea ice concentrations and associated increases in light penetration, and increased terrestrial carbon inputs associated with the discharge of the Mackenzie River (Carmack and Macdonald, 2002; Dunton *et al.,* 2006). Several authors have hypothesized that long-term increases in temperature and decreases in sea ice will lead to a more productive Arctic, but caution that species specifically adapted to Arctic conditions could be negatively influenced (Reist *et al.,* 2006a, Wrona *et al.,* 2006, Pabi et al., 2008). To assess the long-term response of an Arctic species to changing climate at an annual scale, a YOY growth chronology of *C. autumnalis* captured between 1986 and 2007 was constructed. Otolith growth was used as a proxy for fish growth. YOY growth was expected to be influence by long-term climatic shifts in several environmental indicators. YOY growth was selected over growth of other ages because fish typically respond most strongly to environmental variability during their early life history (Sogard, 1997). To assess the possible underlying mechanisms responsible for anticipated changes in YOY growth, exploratory regression analyses were conducted using the Arctic Oscillation index, temperature, east wind speed, sea ice concentration, and river discharge.

MATERIALS AND METHODS

Otoliths were collected from *C. autumnalis* captured in the subsistence gill net fishery at Nuiqsut on the Colville River (Fig. 3.1). Nets are typically 76-mm (stretched and measured knot-to-knot) mesh multifilament gillnets and range in length from 18 to 30 meters (Murphy *et al.,* 2007). At least thirty otoliths per year were collected from fish captured in 17 of the 21 years from 1986 to 2007 (otoliths were not collected in 1989, 2002, 2003 and 2004). The total number of otoliths available for this study was 819 and fish length was known for 408 individuals (Table 3.1). Otoliths were removed from fish, cleaned, dried, and stored in vials.

Otoliths were embedded in Epothin epoxy (Buehler Ltd.), sectioned on a transverse plane through the nucleus with a low-speed wafering saw, and affixed to glass slides with cyanoacrylate glue. After drying, slides were ground using 1200-grit sandpaper. Digital images of each otolith were captured at a magnification of 40x on a black background with reflected light using a digital camera attached to a dissection microscope. Each individual was assigned an age by counting the translucent zones. Otolith ageing has been indirectly validated through the agreement with length frequency analyses of young *C. autumnalis* (age-0 to age-2, Underwood *et al.*, 1995; Fechhelm *et al,.* 2007). The first annual increment, representing the growth during age-0 and referred to here as YOY growth, was measured using image analysis software. Each YOY growth increment was assigned a calendar year by subtracting the age from the capture year. YOY growth was defined as the distance from the nucleus (which contains the primordia) to the outer edge of the first translucent zone (appears as the narrow dark area with reflected

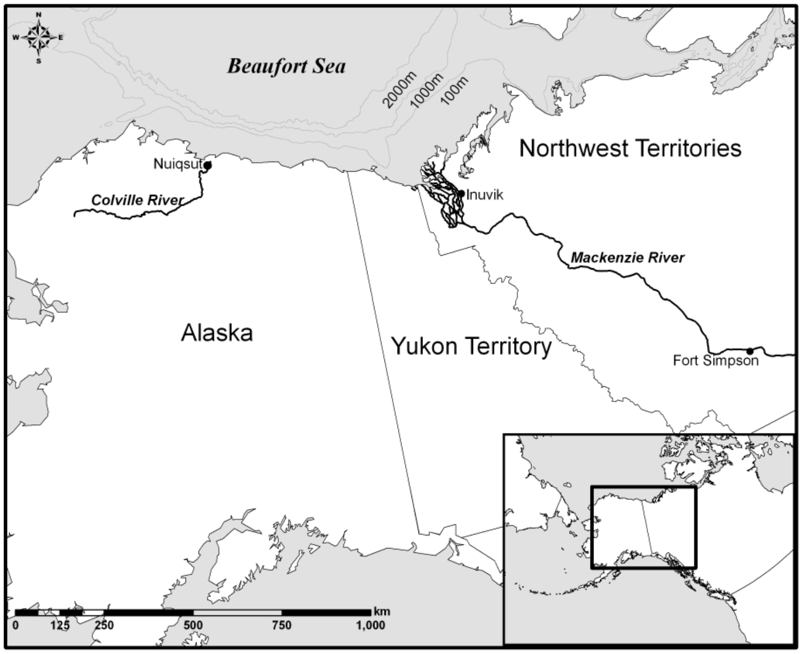

FIG. 3.1. Northern Alaska and Canada study region showing locations of Arctic cisco collections and environmental correlates.

light) along the longest possible radius. The otolith radius was measured as the longest possible distance between the nucleus and the ventral edge of the transverse section (Fig. 3.2).

To confirm that otolith growth was correlated with somatic growth, fish of known fork length were compared to otolith radius using a simple linear regression without a defined intercept (Francis, 1990). The relationship between otolith radius and fish length was not used to back calculate previous fish lengths due to the extra assumptions associated with back calculation (Francis, 1990). Capture age effects were anticipated based on Lee's phenomenon and corrected for by standardizing each YOY growth increment to the average width of YOY growth for all individuals of a given capture age. To determine if this standardization technique successfully controlled for the effect of capture age, the effect of capture age on YOY growth, before and after standardizing, was tested using a one-way analysis of variance. Finally, the standardized YOY growth was tested for autocorrelation using Durbin-Watson's D. All subsequent analyses were performed on standardized YOY growth. Change in YOY growth over time was assessed through linear regression ($P < 0.05$).

TABLE 3.1. Number of otoliths collected from Arctic cisco harvested in the Nuiqsut, Colville River, AK, USA, subsistence fishery, by year. Numbers in parentheses indicate samples that were not included in the analysis.

Year	*YOY Growth Increments*	*Samples Collected*
1978	5	
1979	26	
1980	53	
1981	5	
1982	7	
1983	15	
1984	12	
1985	57	
1986	63	27
1987	74	49
1988	18	29
1989	27	
1990	77	56
1991	20	124
1992	30	32
1993	16	32
1994	39	28
1995	20	34
1996	8	26
1997	21	27
1998	43	27
1999	104	30
2000	30	25
2001	14	28
2002	7	
2003	9	
2004	19	
2005		45
2006		74
2007		126
Total	**819**	**819**

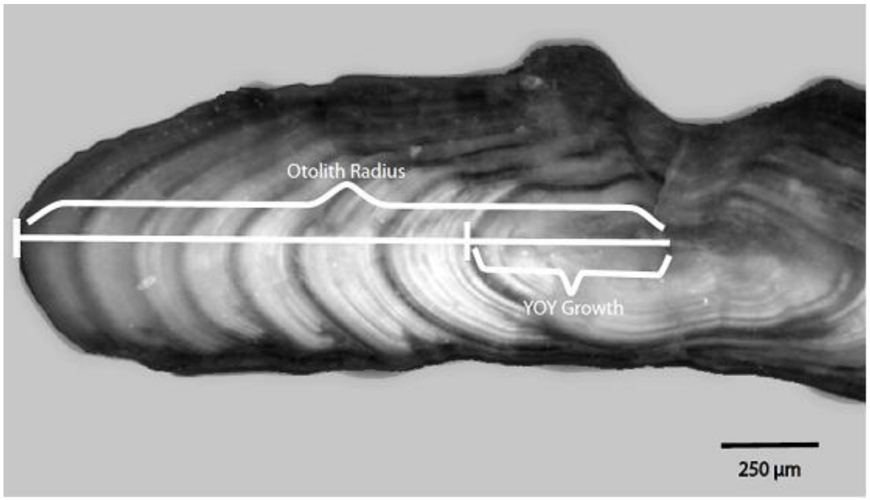

FIG. 3.2. Photomicrogaph of transverse section of an Arctic cisco otolith. Measurement axis is the line going down the longitude of the otolith, and YOY growth and otolith radius with hashes.

Density dependence was also assessed by comparing the total catch per unit effort (CPUE) of a year class (combining data from all ages at capture across several sampling years) in the Colville River subsistence fishery to YOY growth (Moulton & Seavey, 2003; L. Moulton, unpublished data). Fishing year CPUEs were estimated based on daily catch and effort data for 76-mm mesh nets and standardized to net length. One unit of fish effort was defined as one net fished for one day and standardized to net length. In each fishing year, catch data was partitioned by year class based on age distributions. Age distributions were estimated by ageing otoliths from a subsample of fish captured in the fishery each year (typically >100 individuals). The cumulative catch rates of a year class across several fishing years was used as an index of density, or the year class CPUE (Moulton & Seavey, 2003).

Environmental covariates included monthly Arctic Oscillation (AO) index as a broad measure of environmental variation, as well as monthly mean air temperature, east wind speed, sea ice concentration, and river discharge as local environmental indicators. All environmental covariates were compared to YOY growth with and without time lags to test for direct influences on growth or indirect influence. Lags of up to two years were used to account for long generation times in many potential prey species (Hirche & Bohrer, 1987; Prokopowicz & Fortier, 2002). Months were arranged in water years, 1 October – 30 September, rather than calendar years to follow the hydrological cycle. The winter AO is a non-seasonal pattern of sea-level pressure in the Arctic, similar to the North Atlantic Oscillation, which may impact ecosystems through changes in ocean currents, temperatures, ice cover, and precipitation (Thompson and Wallace, 1998). Water temperature was not available for this time series in the Beaufort Sea, Mackenzie or Colville rivers, so air temperature recorded at Inuvik, Northwest Territories at the mouth of the Mackenzie River was used as a proxy for water temperature (Station 2202570, Environment Canada). Mean monthly east wind speed (wind direction 45-135°) were calculated based on hourly wind data from Barrow, Alaska (Station 500546, National Climatic Data Center). Easterly winds during the open water season (June-October) are upwelling favourable, drawing deep nutrient water to the shelf and stimulating productivity (Carmack and Macdonald, 2002). Mean monthly sea ice concentrations were calculated from estimates of daily sea ice concentrations based on a 25-km resolution passive microwave satellite imagery for the Beaufort Sea Shelf from Amundsen Gulf, Northwest Territories, to Barrow, Alaska, excluding a 25-km coastal buffer to avoid spurious ice estimates in pixels with land (Cavalieri *et al.,* 1996; Cavalieri *et al,* 1999; National Snow and Ice Data Center, 1979-2004). Mean monthly river discharge rate (m^3s^{-1}) was compared to growth. Mackenzie River discharge may influence YOY *C. autumnalis* directly with little or no time lag (e.g., within season changes in salinity or water temperature) or indirectly with a time lag based on the relationship between fluvial inputs and nearshore productivity in the Arctic (Salen-Picard *et al.,* 2002; Carmack *et al.,* 2006; Dunton *et al.,* 2006; Forest *et al.,* 2008; Holmes *et al.,* 2008). The oceanography of the Beaufort Sea is strongly influenced by the Mackenzie River, even throughout the winter since headwaters extend 1,000s of kilometers south into the temperate zone (McNamara *et al.,* 1998; Walker & Hudson, 2003; Holmes *et al.,* 2008). River discharge was measured at Ft. Simpson by the Water Survey of Canada (Station 10GC001). The Ft. Simpson site was chosen over other Mackenzie River locations for this measurement because only one main channel is present at this point.

YOY growth was correlated to a given environmental parameter using linear regression weighted by sample size of individuals in each cohort. Given the lack of precise phenological information on the life history of the study species and the environment, changes in growth were correlated to an environmental parameter in each month of the year. This exploratory analysis resulted in multiple independent linear regressions and increased the likelihood of type-1 error or spurious correlations. Bonferroni corrections were not implemented because they can be over conservative (increase type II error; Cabin & Mitchell, 2000). However, exact P values were reported when $0 .05 > P > 0.0001$ to assess significance and results were interpreted based on the expectation that important environmental variables and seasons would be significant in more than one test (i.e., the same relation would be significant across many months or the same month would be significant across multiple environmental variables).

RESULTS

Most individuals were between 310 and 350mm at capture (Fig. 3.3) and five to eight years old (Fig. 3.4). There was a significant positive relation between otolith radius and fork length for individuals of known length (slope = 3.67; $r^2 = 0.84$, $P < 0.0001$, Fig. 3.5). An effect of capture age was detected on YOY growth increment using an ANOVA ($F = 8.58$; $P < 0.0001$) and was corrected by standardizing each YOY growth increment to the average for the capture age ($F = 0.0$; ANOVA; $P > 0.05$). There was little evidence of 1st order autocorrelation in the time series of YOY growth (autocorrelation = -0.080; Durbin-Watson's D = 2.066). Standardized YOY growth increased over time (Fig. 3.6; linear regression; slope = 0.00540; $P = 0.0083$; $r^2 = 0.29$). CPUE was not related to YOY growth (Fig. 3.7; linear regression; slope = 0.00206; $P=0.0539$; $r^2 = 0.11$).

All environmental variables correlated with growth with and without time lags (Table 3.2, Fig. 3.8). In general, correlations with growth across all variables were more prevalent with time lags of one and two years. YOY growth was positively related to the AO in March with a lag of two years and during the current year's winter. Similarly, the strongest relationship between temperature and YOY growth occurred in March with a two-year lag, along with other months throughout the previous and current years. The speed of east winds in Barrow was positively correlated with growth in the open water months of July and August with a lag of two years. Growth was negatively correlated with sea ice concentration for several spring, summer and fall months with a one year lag (April – May and July – October). Mackenzie River discharge correlated positively with growth in eight with a two-year lag (October and December – June). River discharge was also positively correlated to YOY growth during April of the current year.

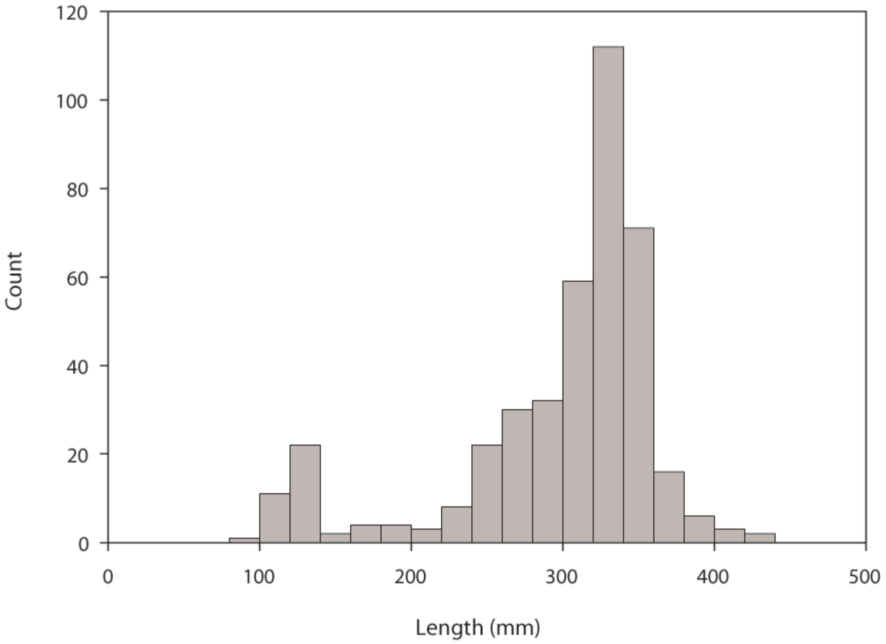

FIG. 3.3. The length frequency distribution of Arctic cisco captured in the Colville River, Alaska, USA.

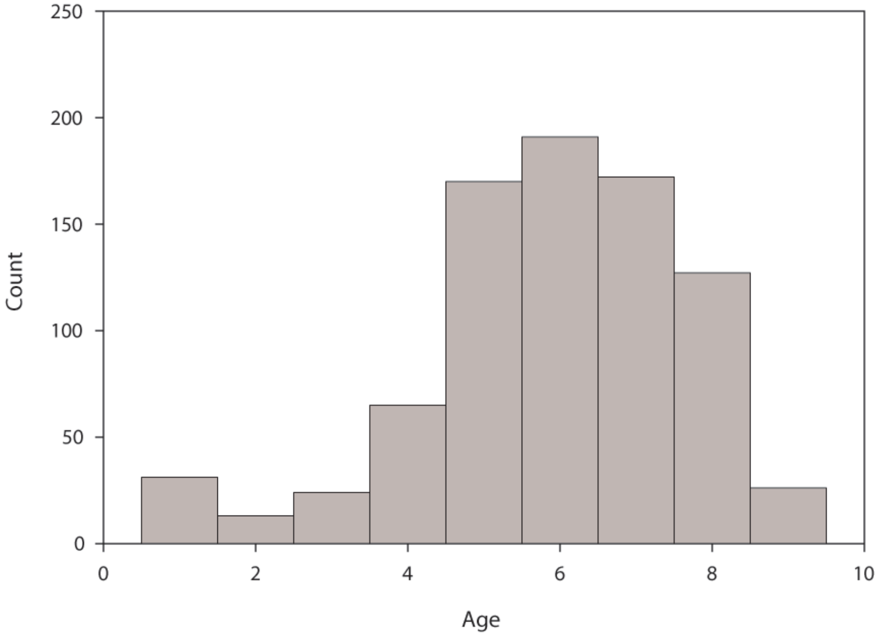

FIG. 3.4. The age frequency distribution of Arctic cisco captured in the Colville River, Alaska, USA.

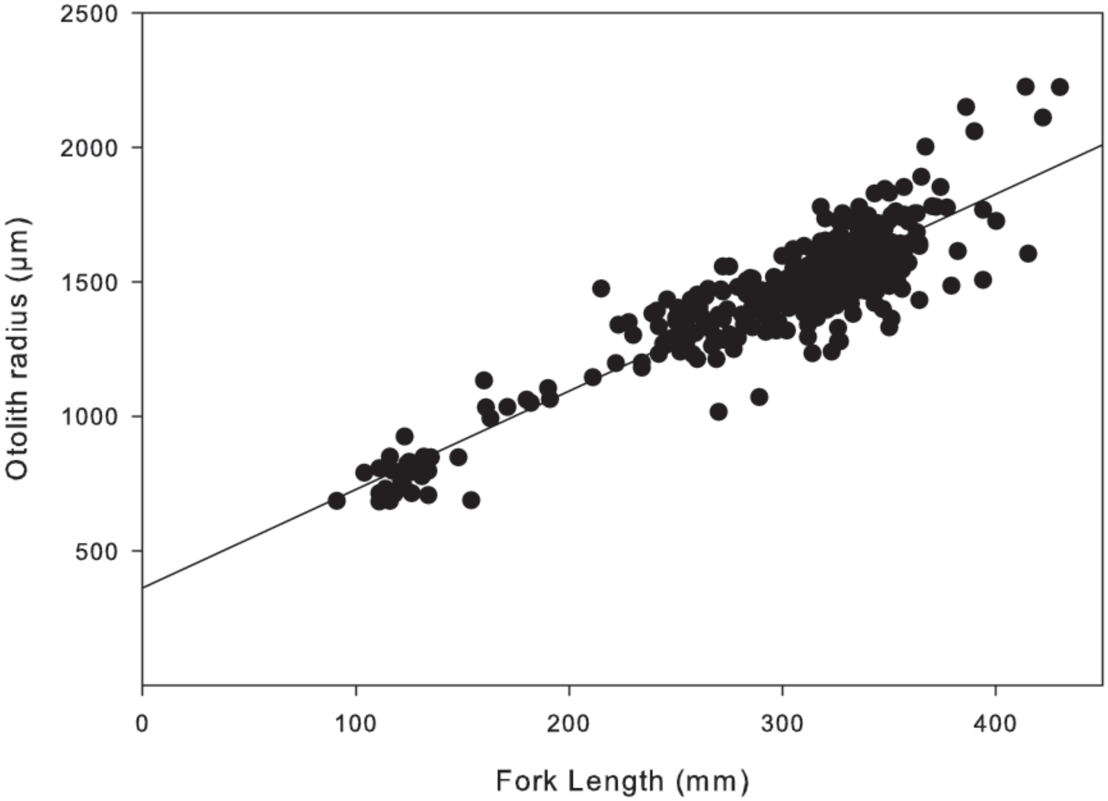

FIG. 3.5. Linear regression of fish length and otolith radius for fish of known length and captured in the Colville River, Alaska, USA (1986-2007).

DISCUSSION

The growth of YOY *C. autumnalis* increased from 1978 to 2004 (Fig. 3.6). Increases in YOY growth over time could be due to changes in conditions that increase the daily rate of growth, cause earlier hatching, or both. Because hatching of coregonids is typically associated with spring ice break-up, an event that has shifted less than week over the last 100 years with an abrupt transition in the mid-1970s, prior to the earliest records in this study (Naesje *et al.,* 1986; Naesje *et al*., 1995; Magnuson *et al*., 2000; Urpanen *et al.,* 2005), the hatch date of Mackenzie River *C. autumnalis* was assumed to be similar across the YOY growth time series. Increases in growth correlated strongly with increased summer east wind speeds lagged by two years, decreases in sea ice concentration during the previous year, and increases in the Mackenzie River discharge with a two-year lag. The changes in growth rates and environmental variables correspond to a regime shift in the Pacific Ocean and Beaufort Sea in the late 1980s (Hare & Mantua, 2000).

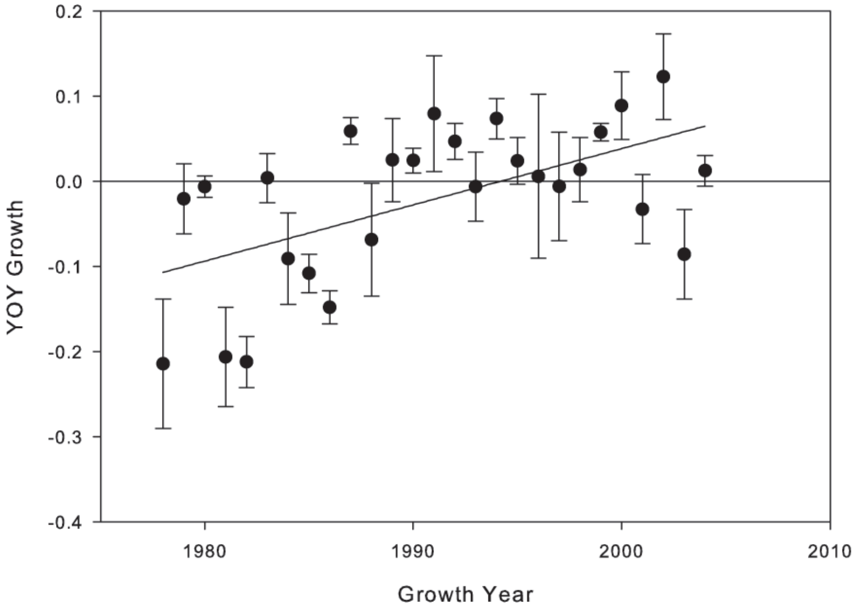

FIG. 3.6. Mean young-of-the-year (YOY) increment size for the entire available growth record (1978-2004) of Arctic cisco captured in the Colville River, Alaska, USA.

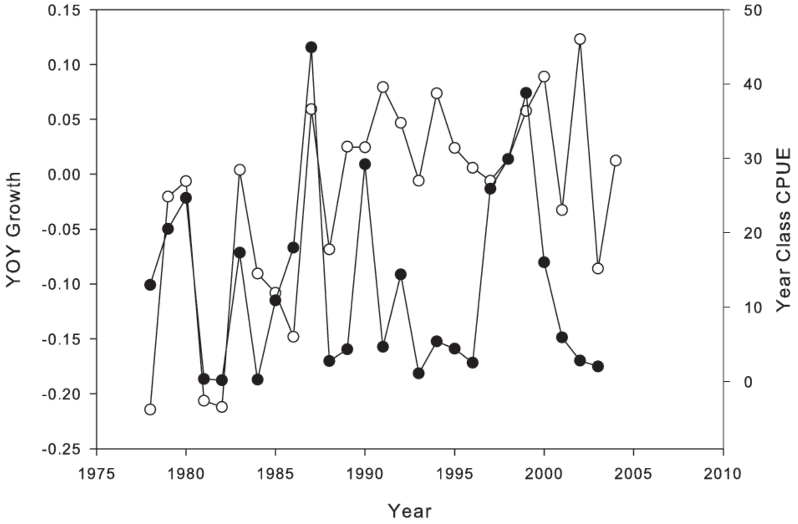

FIG. 3.7. Line graph of mean young-of-the-year growth (YOY growth, ○) and year class catch per unit effort (CPUE, ●) for fish captured in the Colville River subsistence fishery. Linear regression found no significant relationship.

TABLE 3.2. The coefficient of determination (r^2) and *P* value for each correlate to young-of-the-year growth of Arctic cisco.

Environmental Covariate	**Lag**	**Month**	**r^2**	***P***
Arctic Oscillation	2 year	March	0.22	0.0085
	None	December	0.17	0.0200
Temperature	2 year	October	0.15	0.0487
		March	0.58	<0.0001
	1 year	December	0.27	0.0089
		February	0.16	0.0412
		July	0.19	0.0275
	None	July	0.15	0.0450
East Wind Speed				
	2 year	March	0.26	0.0045
		July	0.28	0.0035
		August	0.24	0.0062
	1 year	February	0.17	0.0193
		March	0.22	0.0091
		July	0.13	0.0385
	None	November	0.32	0.0016
		January	0.34	0.0011
		June	0.14	0.0335
Sea Ice Concentration	2 year	January	0.26	0.0081
	1 year	November	0.17	0.0283
		April	0.14	0.0432
		May	0.24	0.0104
		July	0.24	0.0098
		August	0.31	0.0036
		September	0.29	0.0048
	None	October	0.25	0.0086
		February	0.21	0.0169
River Discharge	2 year	October	0.23	0.0071
		December	0.31	0.0014
		January	0.50	<0.0001
		February	0.45	<0.0001
		March	0.40	0.0003
		April	0.37	0.0005
		May	0.35	0.0007
		June	0.13	0.0367
	None	April	0.16	0.0210

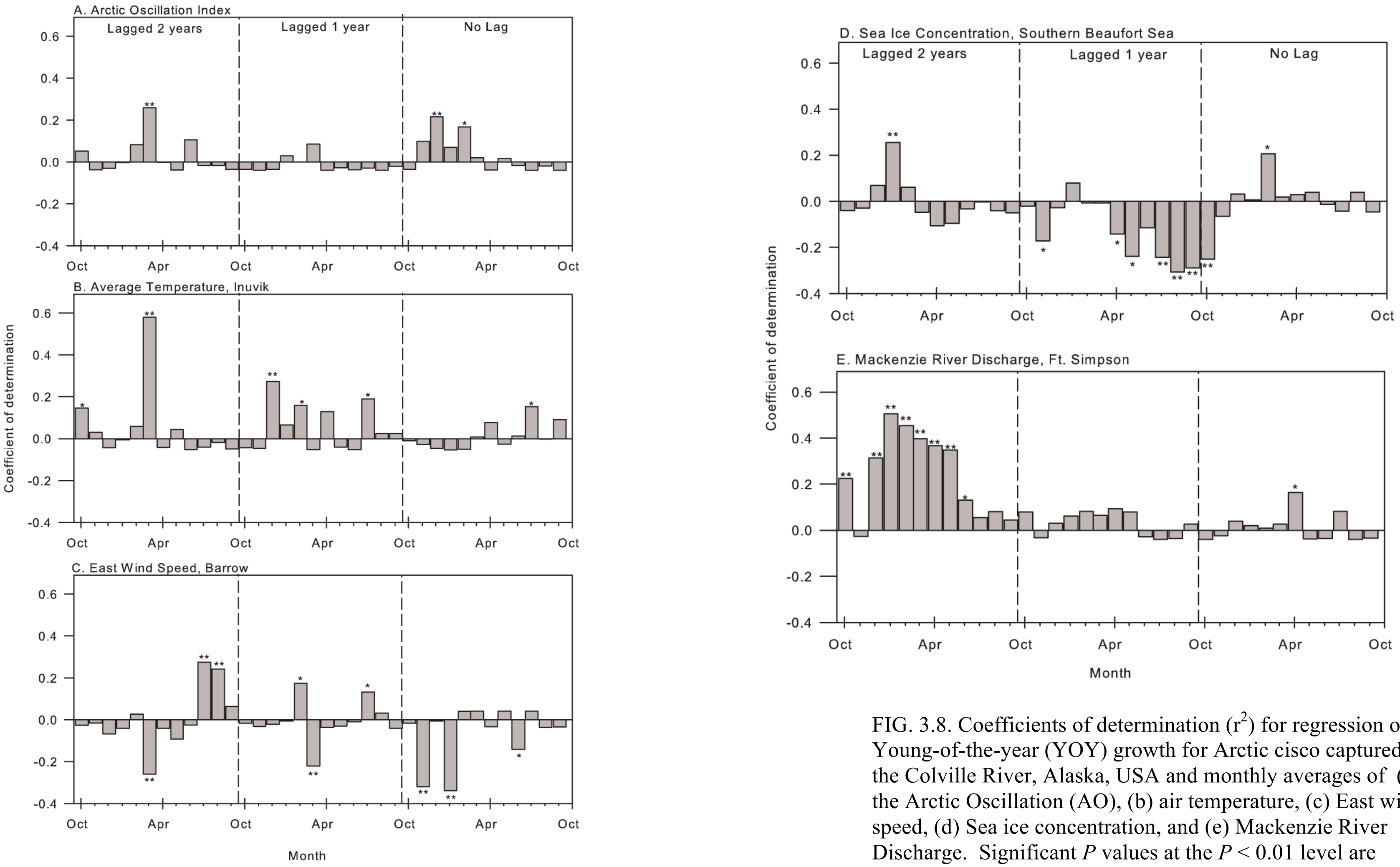

FIG. 3.8. Coefficients of determination (r^2) for regression of Young-of-the-year (YOY) growth for Arctic cisco captured in the Colville River, Alaska, USA and monthly averages of (a) the Arctic Oscillation (AO), (b) air temperature, (c) East wind speed, (d) Sea ice concentration, and (e) Mackenzie River Discharge. Significant *P* values at the $P < 0.01$ level are indicated by ** and * at the $P < 0.05$ level.

Arctic Oscillation, temperature, east wind speed, sea ice concentration, and river discharge were statistically related to YOY growth, but varied greatly in the persistence of relationships and predictive power (Fig. 3.8). Arctic Oscillation was least often correlated with growth and the correlations had relatively low predictive power [Fig. 3.8(a)]. Low predicative power of this variable is not surprising, as AO is an index of sea level pressure that would influence individual fish only indirectly through many parameters, such as wind, currents, precipitation, sea-surface temperature, and sea-ice that are all strongly correlated with AO (Thompson & Wallace, 1998). All significant AO correlations occurred during the fall and winter months, the months during which long-term climate signals are strongest in AO (Thompson & Wallace, 1998). In addition, the correlations did not occur in isolation; the lagged correlation in March was synchronous with correlations in temperature, east wind speed, and discharge. Overall, the correlations between the monthly AO and YOY growth provided evidence that growth could be responding to climatic signals and suggests that stronger correlations can be uncovered when growth is compared to regional indicators of the Beaufort Sea.

Warmer temperatures were associated with increases in YOY growth, with and without time lags [Fig. 3.8(b)]. Many of the correlations between YOY growth and temperature could be spurious, as predictive power and *P* values were often low and months with significant correlations did not group together [Fig. 3.8(b)]. The best supported correlation between temperature and YOY growth was in March with a two-year lag as indicated by high predictive power, low *P*-value, and synchronous correlations with other predictive variables. Given the strong relationship between temperature and growth documented in numerous studies (Rogers & Ruggerone, 1993; Neilson & Geen, 1984; LeBreton & Beamish, 2000) and previous studies showing that *C. autumnalis* preferred and grew more rapidly in the upper limits of the natural summer temperature range (11 – 16 ºC; Fechhelm *et al.,* 1983; Griffiths *et al.,* 1992; Fechhelm *et al.,* 1997), stronger unlagged correlations between YOY growth and temperature were expected. Although Murphy *et al.* (2007) found strong correlations between summer air temperatures and sea surface temperatures, the weak correlations between YOY growth and temperature could indicate that air temperature is a poor proxy for water temperature experienced by YOY fish or that other factors influencing productivity were more limiting to growth.

Stronger east winds, reduced sea ice concentration, and Mackenzie River discharge were each strongly related to increases in YOY growth with time lags of one or two years [Fig. 3.8(c-e)]. These lagged correlations suggests that the processes underlying the correlations are biologically mediated through lower trophic levels, rather than the result of a more immediate temperature or salinity influences on *C. autumnalis* physiology. Stronger east winds during July and August with a two year lag were related to increased YOY growth [Fig. 3.8(c)]. East winds bring deeper nutrient rich waters onto the Beaufort Sea shelf and likely enhance productivity at lower trophic levels (Carmack and Macdonald, 2002). East winds also promote mixing by driving freshwater from the Mackenzie River plume offshore and westward (Dunton *et al.,* 2006). Several other correlations were present, but they did not persist and some correlations occurred in winter when wind cannot influence oceanography due to the presence of sea ice.

Reduced sea ice concentration in the southern Beaufort Sea over the previous year (April - May and July - October) consistently correlated with increased YOY growth [Fig. 3.8(d)]. Carmack and Macdonald (2002) predicted that reductions in sea ice associated with climate warming would result in increased phytoplankton production through the availability of nutrients and light, and decreased ice algae production in the Beaufort Sea. Across the circumpolar Arctic, reduced sea ice has been correlated with increased primary production (Arrigo *et al.,* 2008). The negative correlation between sea ice concentrations and YOY growth suggests that increased phytoplankton production at the base of the pelagic food web increases prey availability or quality the following year. There is no evidence that reduced ice-algae production negatively influences *C. autumnalis* growth, but reduced ice-algae production may be more important in benthic communities.

Mackenzie River discharge was the most consistent and predictive explanatory variable for YOY growth, with significant relationships in most months when lagged by two years [Fig. 3.8(e)]. The high predictive power and consistency of the correlations suggests a relation between river discharge and YOY growth. River discharge may influence productivity in the Beaufort Sea more than other oceanographic features, such as upwelling, because nearshore upwelling is limited by freshwater stratification and fluvial inputs contain large concentrations of biologically available carbon necessary for phytoplankton blooms (Macdonald *et al.,* 1987; Emmerton *et al.,* 2008; Holmes *et al.,* 2008;).

The Canadian Beaufort Sea shelf is described as an open estuary with the Mackenzie River dominating the physical oceanography in terms of salinity, temperature, and production (Carmack & Macdonald, 2002). Unlike other North American Arctic rivers, the headwaters of the Mackenzie extend in to the temperate zone and the river continues to discharge freshwater on to the shelf through the winter, when other Arctic rivers cease to flow and marine waters intrude the delta. Due to the sea ice dam or stamukhi, the water reaching the Mackenzie River delta and nearshore throughout the winter months does not mix or disperse into the Beaufort Sea and forms a seasonal freshwater lake just outside the river mouth, called Lake Herlinveaux (Carmack & Macdonald, 2002). In spring, discharge increases to a flood and the large amount of relatively warm river water melts the sea ice and the freshwater once contained in Lake Herlinveaux and spring discharge water spread out over the shelf and stratify the water column, allowing the phytoplankton bloom to occur (Carmack & Macdonald, 2002; Dunton *et al.,* 2006). If increases in the amount of freshwater stored in Lake Herlinveaux over the winter and the magnitude of the spring flood could increase the amount of dissolved organic carbon (DOC) and other nutrients (Largier, 1993; Schell *et al.,* 1998; Dunton *et al.,* 2006; Holmes *et al.,* 2008) or intensify the spring bloom by expanding water column stratification (Carmack & Macdonald, 2002; Dunton *et al.,* 2006) it could explain why river discharge correlated with YOY growth in so many months. River discharge has been shown to influence nearshore primary productivity and higher trophic levels with similar time lags in other regions (Kerr & Ryder, 1992; Largier, 1993; Salen-Picard *et al.,* 2002; Wells *et al.,* 2008).

Environmental variables were more often correlated with growth in YOY *C. autumnalis* when lagged by at least one year. The influence of environmental variables on *C. autumnalis* growth appears to occur over time scales longer than a given season or within a year. The presence of time lags indicates a bottom-up and trophically mediated mechanism and the length of the lags suggests that some component of the trophic pathway requires more than one growing season. *C. autumnalis* juveniles feed predominately on herbivorous zooplankton, particularly copepods and juvenile mysids (Knutzen *et al.,* 1990). Zooplankton species adapted to Arctic growing conditions often take several years to develop and may be responsible for the lagged correlations between environmental variables and YOY growth.

An ongoing diet study has found *Pseudocalanus minutus* (Krøyer, 1845) and *Calanus hyperboreus* (Krøyer 1838) to be key prey items in YOY *C. autumnalis*, with the importance of *C. hyperboreous* increasing and *P. minutus* decreasing with fish size during the first year (von Biela *et al*., unpublished). Studies of zooplankton across the nearshore Beaufort Sea also identified *P.minutus and C. hyperboreous* as common species by biomass (Horner & Murphy*,* 1985; Hopkey *et al.,* 1994a-c). *C. hyperboreus* has a multiyear life history of two to four years, at similar latitudes, and *P. minutus* requires one full year for development (Hirche & Bohrer, 1987; Torke 2001). It is possible that the abundance of these prey resources could be responding to trends in primary production and account for the lags in the relations between east wind speed, sea ice concentration, or river discharge and YOY growth. *C. hyperboreus* could be a preferred prey resource due to their high lipid density (Hirche & Bohrer, 1987; Prokopowicz & Fortier, 2002). Unlike many of the other zooplankton species in more southern latitudes, *C. hyperboreus* has specifically adapted to the short Arctic growing season by storing energy dense lipid during the productive Arctic summer and entering diapause to conserve these fuels through much of the winter (Hirche & Bohrer, 1987; Prokopowicz & Fortier, 2002). At the end of the summer the lipid content of *C. hyperboreus* can reach 74% of dry weight (Bradstreet & Cross, 1982). Due to the high lipid content of and abundance, *C. hypberboreus* plays a central role in the Arctic food web as a major prey item of bowhead whales *Balaena mysticetus* L. and Arctic cod *Boreogadus saida* (Lepeckin, 1774) (Lowry *et al*., 1980; Bradstreet & Cross, 1982).

There was no evidence of density dependence influencing the YOY growth record. The relation between YOY growth and CPUE suggested a positive trend, if any, through the 1980s

(Fig. 3.7). Such a trend would suggest that strong recruitment years, with more individuals, were associated with better growth and is opposite of the expectation under density dependence. However, this study was not designed to determine the influence of density dependence on growth in *C. autumnalis* populations; the analysis only indicates that it is not necessary to standardized growth to density before assessing the possible environmental covariates. Density dependence may not have been detected because only individuals that successfully recruited to the subsistence fishery were sampled and typically individuals influenced by density dependence have increase mortality and reduced fishery recruitment.

The long-term increase in YOY *C. autumnalis* growth rates, suggests that even exclusively Arctic species may benefit from increases in pelagic productivity. An increase in productivity could influence fish growth by increasing availability of a prey species that has always been exploited or switching to a new prey source, or both. Future research should assess the possible mechanism relating sea ice concentration and river discharge to productivity at upper trophic levels. Taking advantage of increases in productivity is likely easier for trophic generalists, as opposed to specialists. A better understanding of trophic ecology and a population's capacity to exploit changing prey species may prove useful for predicting the ultimate impact of climate change on some species.

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concerning *C. autumnalis* and this study. Any use of trade names or products is for descriptive purposes only and does not imply endorsement of the U. S. Government.

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Chapter 4: Terrestrial and marine trophic pathways support young-of-year growth in a nearshore Arctic fish

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INTRODUCTION

River discharge supplies nearshore marine communities with a carbon source that may influence ecosystem and fish production (Caddy 2000; Salen-Picard et al. 2002; Darnaude 2005; Dunton et al. 2006; Wrona et al. 2006; Vinagre et al. 2011b). The influence of terrestrial carbon on ecosystems and fisheries has been most extensively examined in relatively warm, eutrophic seas such as the Gulf of Mexico and Mediterranean Sea (Caddy 2000; Salen-Picard et al. 2002; Schlacher et al. 2008). In cool, oligotrophic Arctic seas, terrestrial carbon may also play an important role in production and understanding the current fate of terrestrial carbon in Arctic ecosystems is useful for predicting shifts as carbon dynamics are altered under climate change (Wrona et al. 2006; Dunton et al. 2012).

Arctic seas are generally oligotrophic and seasonally receive large amounts of organic carbon from rivers (Dittmar and Kattner 2003; Emmerton et al. 2008; Holmes et al. 2008). Carbon exported during the spring freshet is more biologically available than previously thought due to limited microbial use during the cold, short residence time in rivers and flood plains (Dittmar and Kattner 2003; Holmes et al. 2008). Recently, the presence of terrestrial carbon in the Beaufort Sea food web was confirmed across several taxa of benthic invertebrates using carbon isotope ratios (Dunton et al. 2006; 2012). Fewer nearshore fish species have been sampled and generally show less terrestrial carbon use (Kline et al. 1998; Dunton et al. 2006; 2012).

A lack of terrestrial carbon use was particularly surprising among anadromous and amphidromous fish associated with the band of brackish nearshore water, such as Arctic cisco (*Coregonus autumnalis*) (Craig 1989; Jarvela and Thorsteinson 1999). Differences in carbon sources by life stage have been noted for other species (Darnaude 2005) and the possibility that more Beaufort Sea fish species rely on terrestrial carbon at sea exists. To date sampling has not included young-of-year (YOY) fish, a critical life stage when fish grow rapidly reaching 25 - 40% of adult length (von Biela et al. 2011).

Arctic cisco are the focal species of an active and culturally important subsistence fishery in a region without commercial fishing (Fechhelm et al. 2007). Juveniles forage in the nearshore Beaufort Sea in Canadian and Alaskan waters, but spawning likely occurs throughout the Mackenzie River drainage, Northwest Territories, Canada, with some juveniles migrating to Alaska shortly after hatching (Craig 1989; Fechhelm and Griffiths 1990; Zimmerman et al. submitted). Terrestrial carbon use during the YOY life stage has been implied by significant correlations between YOY growth and river discharge (von Biela et al. 2011).

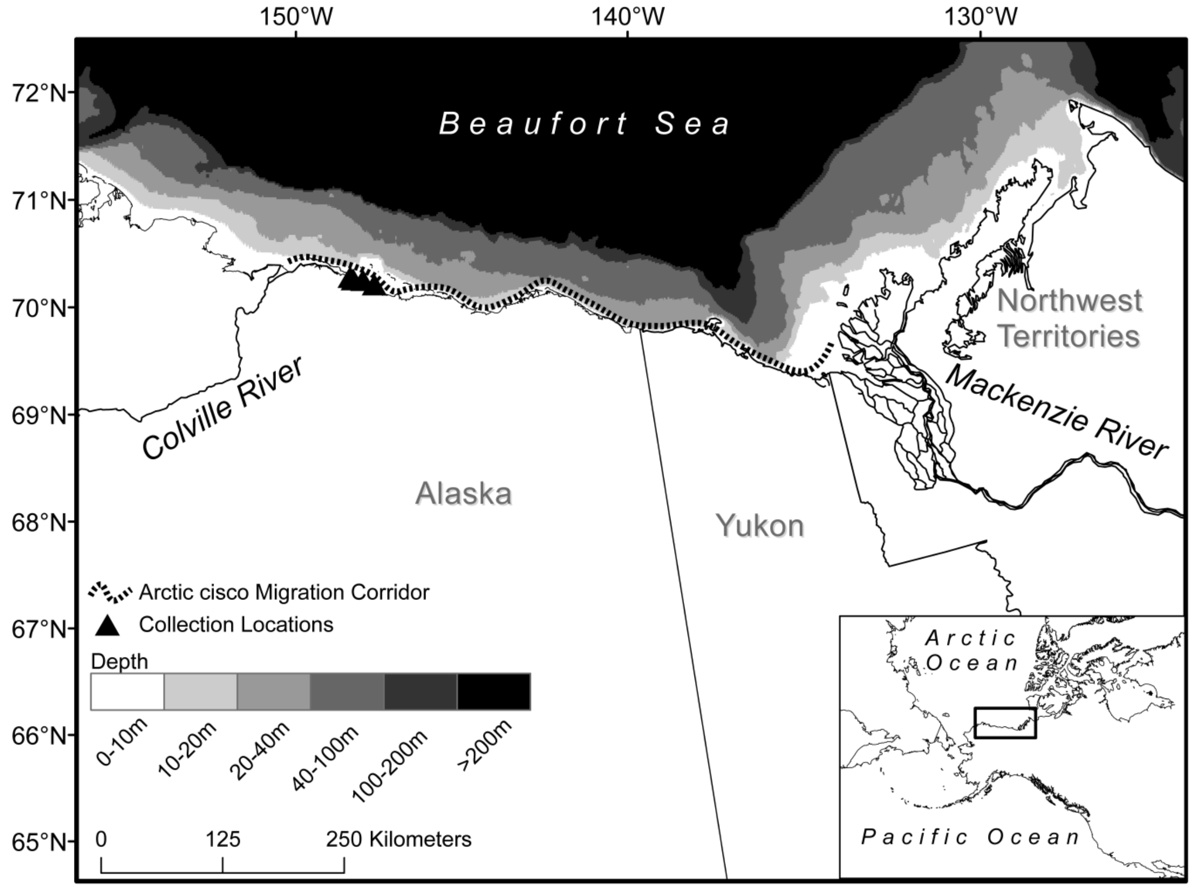

Fig. 4.1 Map of Arctic cisco collection locations near Prudhoe Bay, Alaska, and the YOY migration corridor in the nearshore Beaufort Sea

Here we examine the food web structure of YOY Arctic cisco using stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) to assess carbon and nitrogen sources and stomach content analysis to identify key prey species. We hypothesized that the $\delta^{13}C$ and $\delta^{15}N$ values of YOY Arctic cisco would reflect a reliance on terrestrially derived carbon as opposed to a more immediate and complete reliance on marine derived carbon (Kline et al. 1998; Darnaude 2005; Vinagre et al. 2011b). In addition, we hypothesized that stomach content analysis would identify species with life cycles of >1 year that could be responsible for the length of the lagged correlation between river discharge and YOY growth as demonstrated by von Biela et al. (2011).

MATERIALS AND METHODS

All YOY Arctic cisco were collected in August 2009 during annual monitoring of the YOY migration near Prudhoe Bay, Alaska, using nearshore fyke nets in water depths of ≤2m (sites 214, 218, 220 and 230 from Fig. 4.1 in Fechhelm et al. 1999; Fig. 4.1) . Arctic cisco were classified as YOY if fork length was <90 mm (Fechhelm et al. 2007). Fish were immediately frozen at capture and shipped to the USGS Alaska Science Center in Anchorage. Fish were thawed and fork length was measured to the nearest millimeter. An epaxial muscle sample was removed from each fish and frozen for stable isotope analysis. The cardiac and pyloric sections of the stomach were removed and weighed before and after stomach content removal to the nearest 0.001g. All prey items were fixed in 10% formalin for several weeks and later preserved in a 70% ethanol solution. Prey items were identified to the lowest taxonomic level possible and counted under a dissection microscope. For each taxonomic group a voucher specimen was collected for reference.

Epaxial muscle samples were freeze dried and subsampled for stable isotope analysis at the University of Alaska Anchorage, ENRI Stable Isotope Laboratory. Each sample was analyzed for $\delta^{13}C$ (ratio of $^{13}C/^{12}C$) and $\delta^{15}N$ (ratio of $^{15}N/^{14}N$) using a Costech 4010 Elemental analyzer (Costech Analytical, Valencia, CA) interfaced with a Thermo-Finnigan Delta Plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Electron Corp., Waltham, MA). Stable isotope ratios were reported using standard delta notation. Lipids were not extracted prior to analysis as Arctic cisco muscle has minimal lipid content (<5%) and terrestrial and marine nutrient sources have sufficiently different end members so that lipid correction is not critical to interpretation (Post et al. 2007; Logan et al. 2008; Tomy et al. 2009). Differences in stable isotope ratios among fish from difference length classes are likely independent of body size *per se* and reflect shifts in diet (Vinagre et al. 2011a).

Stable isotope values were interpreted using terrestrial and marine carbon end member values for suspended particulate organic matter (SPOM) and benthic particulate organic matter (BPOM) from terrestrial (river) and marine (shelf) ecosystems in the eastern Beaufort Sea and typical literature fractionation coefficients. In this system, the $\delta^{13}C$ of marine SPOM is enriched compared to terrestrial SPOM, but BPOM is similar between sources (Dunton et al. 2012). Nitrogen isotopes ($\delta^{15}N$) also differ between marine and terrestrial producers with nitrogen ratios of marine producers exceeding those of terrestrial producers (Dunton et al. 2006). Carbon fractionation was assumed to be ~1‰, nitrogen fractionation was assumed to be ~3.4‰ (Vander Zanden and Rasmussen 2001; Post 2002; Dunton et al. 2012) and a trophic level of 3 (i.e., secondary consumer) for YOY Arctic cisco was anticipated based on a diet of zooplankton (Dunton et al. 2012). Under these assumptions predicted isotope ratios for secondary consumers were calculated and compared to isotope ratios of YOY Arctic cisco.

Table 4.1: Wet weights of each prey type used to calculate the relative contribution of each prey type by mass.

Prey Type	Wet Weight (mg)	Source	Source Species
Acartia	0.05	Bogorov 1959	*A. longiremis*
Calanus	2.38	Scott et al. 2000	*C. glacialis* stage V
	6.44		*C. hyperboreus* stage V
Eurytemora	0.05	Hopkey et al. 1994	*E. herdmani*
Gammarus	0.80	Hopkey et al. 1994	*G. wilkitzkii*
Harpacticoid	0.04	This study	
Metridia	0.90	Gronvik and Hopkins 1984	*M. longa*
Mysis	6.39	Hopkey et al. 1994	*M. littoralis*
Pseudocalanus	0.08	Bogorov 1959	*P. elongatus*

Key prey types were defined as any prey type that occurred in at least 10% of samples. Prey composition was described by the relative abundance of each key prey type and the relative mass of each key prey type. The average wet weight for each species was based on literature values or calculated from a stomach that held only 1 prey type and used to calculate the relative contribution by mass (Table 4.1). The relative abundance and mass of each prey type was compared among length classes using a one-way analysis of variance (ANOVA) with an arcsine transformation for proportions and post-hoc pairwise two-sample t-tests. Stable isotope ratios were not obtained for zooplankton prey types because they may have been influenced by preservation and gut contents (Feuchtmayr and Grey 2003). All fish were categorized into 10mm length bins for analysis of stable isotope ratios and stomach contents. Each stable isotope ratio was compared among length groups using an ANOVA with a significance of $P < 0.05$ and post-hoc pairwise t-tests between groups. Stable isotope ratios were also compared between the largest YOY fish here and values reported in Dunton et al. (2012) for age 1+ Arctic cisco using a t-test.

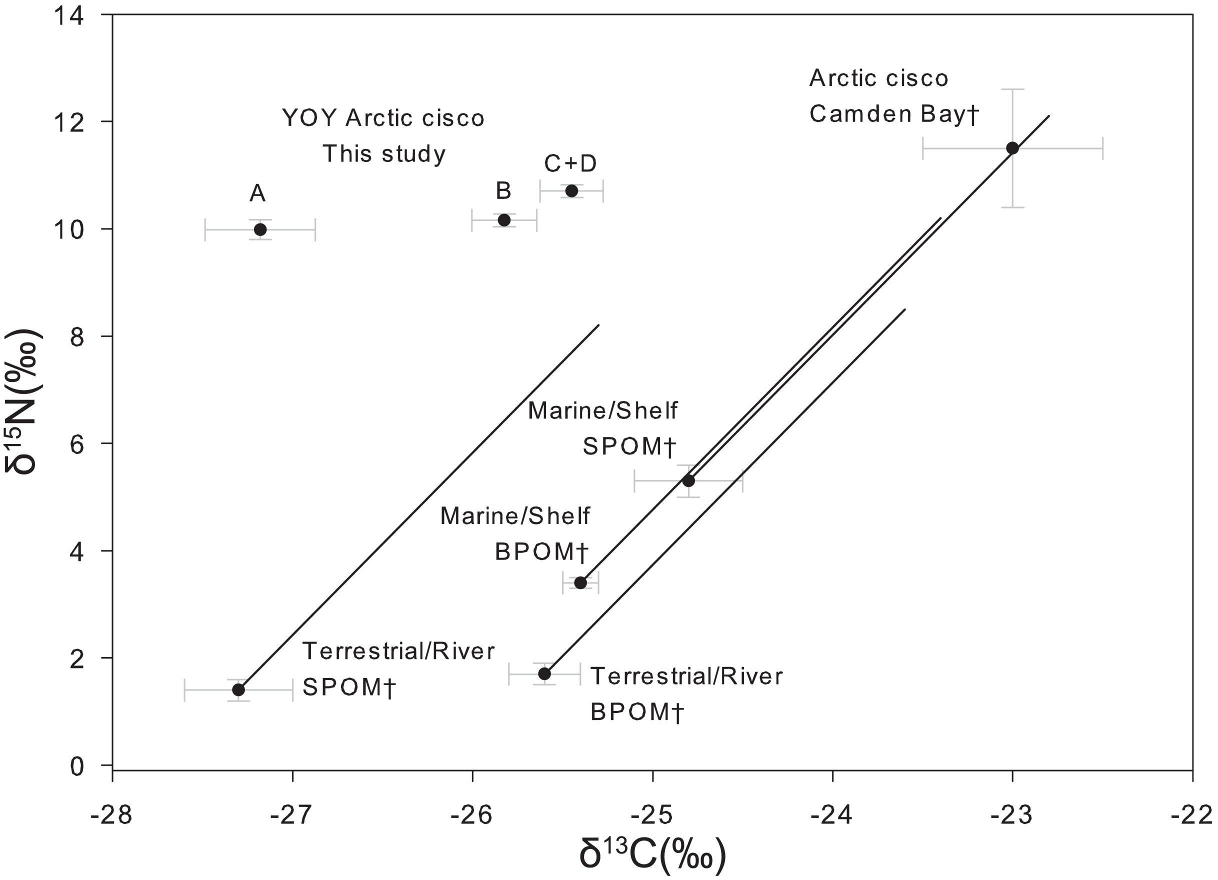

Fig. 4.2 Carbon and nitrogen stable isotope values of YOY Arctic cisco captured in Prudhoe Bay, Alaska, by length classes plotted with published end member benthic particulate organic matter (BPOM) and suspended particulate organic matter (SPOM) values from the Beaufort Sea and values from age 1+ Arctic cisco. Solid black mixing lines begin at each organic matter source and terminate at the predicted value for a secondary consumer assuming isotope fractionations of 3.4‰ and 1.0‰ per trophic level for nitrogen and carbon, respectively. Length classes are denoted as follows: A. Fish <50mm fork length, B. Fish 50-59mm fork length, C. Fish 60-69mm fork length, D. Fish 70-79mm fork length. Individuals from length class C and D did not differ significant in their carbon or nitrogen values and were grouped together in this plot. Symbol denotes data source †Dunton et al. 2012. Error bars denote standard error.

RESULTS

A total of 84 YOY Arctic cisco were captured and ranged in fork length from 37mm to 79mm. Individuals were divided into four length classes: <50mm (n = 5), 50-59mm (n=43), 60-69mm (n=24), and 70-79mm (n=12). Both carbon and nitrogen stable isotope values differed by length class (Carbon F = 3.60, df=3, *P* < 0.05; Nitrogen F = 3.90, df=3, *P* < 0.05; Fig. 4.2; Table 4.2). Fish from the smallest length class (FL <50mm) had significantly depleted $\delta^{13}C$ with a mean of -27.3‰ compared to -25.7‰ for all individuals $\geq$50mm (*P* < 0.05). Overall, the $\delta^{13}C$ values of YOY Arctic cisco indicate that terrestrial SPOM was the most likely carbon source (Fig. 4.2).

The $\delta^{15}N$ values were also lower in smaller fish, with the 50-59 mm length class averaging 10.2‰ compared to 10.7‰ in the 60-69 mm length class and 10.8‰ in the 70-79mm length class. The $\delta^{15}N$ values of the <50mm length class were not significantly different from any other class and had an average of 10.2‰. Compared to published values of $\delta^{13}C$ and $\delta^{15}N$ from older age 1+ Arctic cisco reported in Dunton et al. (2012), carbon was significantly depleted (t = 3.37, P <0.05) and nitrogen was similar (t = 1.82, P >0.05) in larger YOY fish (60-79mm). Isotope values for fish from each length class were plotted with terrestrial and marine SPOM and BPOM sources from published studies and predicted values for secondary consumers reliant on each source (Fig. 4.2).

Diet items were most often identified to genus as species level identification was not always possible. Prey groups represented in at least 10% of samples were *Pseudocalanus* (76%), *Calanus* (49%), *Eurytemora* (76%), *Acartia* (54%), *Metridia* (19%), *Mysis* (26%), Harpacticoids (30%), and Gammarids (18%). Although nematodes were present in 64% of fish

Table 4.2: Nitrogen and carbon isotope ratios (mean±standard error) of young-of-year (YOY) Arctic cisco captured in Prudhoe Bay, Alaska, by length classes.

YOY Arctic cisco	n	δ^{15}N (‰)	δ^{13}C (‰)
<50 mm	5	10.2±0.1	-27.3±0.4
50-59 mm	43	10.2±0.1	-25.8±0.2
60-69mm	24	10.7±0.2	-25.4±0.2
70-79mm	12	10.8±0.2	-25.5±0.3

stomachs in low numbers (average of 1.7 nematodes/stomach), they were not considered a prey item because they were likely parasitic (Stewart and Bernier 1999).

More than half of the *Calanus* prey items were identified to species (62%) and showed a nearly equal ratio between the frequency of *C. hyperboreus* (52%) and *C. glacialis* (48%). An equal ratio was assumed to calculate an average wet weight for the *Calanus* prey category in combination with literature values for each species. Other prey items that occurred in less than 10% of samples were: Diptera (9%), *Oncaea spp.* (4%), *Centropages abdominalis* (4%), *Oithona spp.* (2%), isopods (1%), *Heterorhabdus tanneri* (1%), and *Tortanus discaudatus* (1%).

Diet differed by length class with larger fish consuming a greater proportion of *Calanus* and *Mysis* prey by number and mass compared to smaller fish. The relative number of *Calanus* prey items was higher for fish in the 70-79mm length class compared to fish in either the <50mm and 50-59mm length classes (F = 3.05, df=3, *P* <0.05, Fig. 4.3). By mass, a higher proportion of *Calanus* prey were consumed by fish in the 70-79mm and 60-69mm length classes compared to either the 50-59mm and <50mm length classes (F = 7.09, df=3, *P* < 0.001, Fig. 4.4). The proportion of *Mysis* prey by mass was higher among fish from the 70-79mm length class compared to all other length classes (F = 3.20, df=3, *P* <0.05, Fig. 4.4).

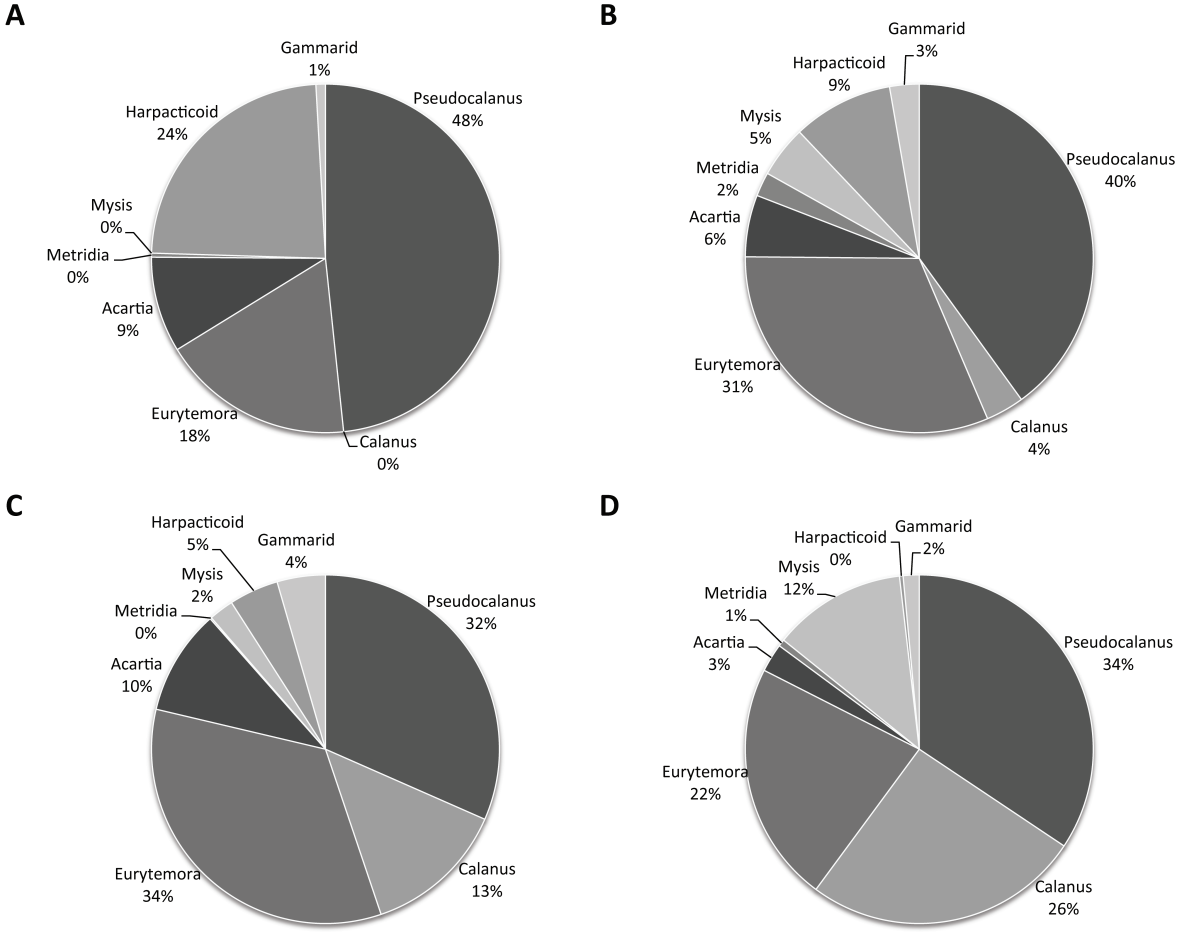

Fig. 4.3 The relative numeric composition of key diet items in YOY Arctic cisco in four length classes: A. Fish <50mm fork length, B. Fish 50-59mm fork length, C. Fish 60-69mm fork length, D. Fish 70-79mm fork length. The relative number of *Calanus* prey items was higher for fish in the 70-79mm length class compared to fish in either the <50mm and 50-59mm length classes (F = 3.05, df=3, $P < 0.05$)

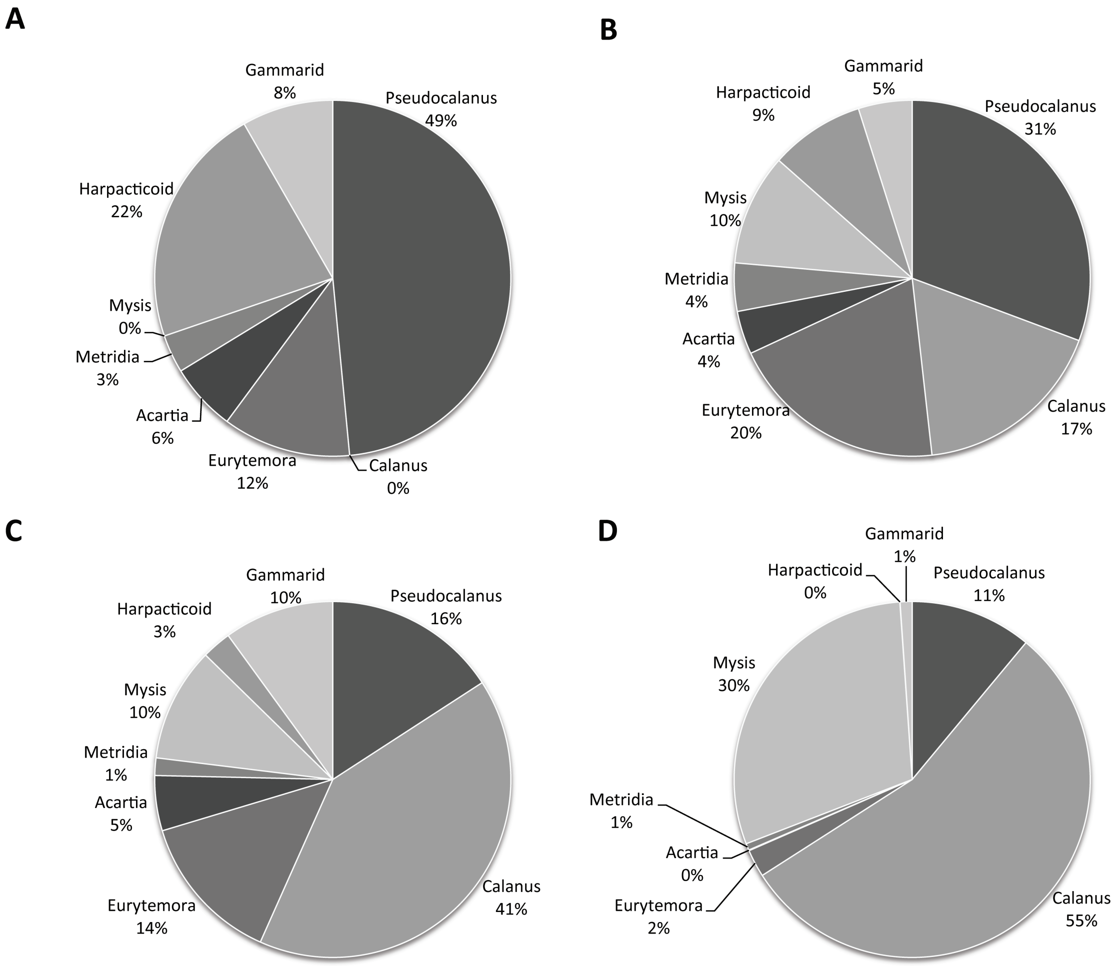

Fig. 4.4 The relative composition by mass of key diet items in YOY Arctic cisco in four length classes: A. Fish <50mm fork length, B. Fish 50-59mm fork length, C. Fish 60-69mm fork length, D. Fish 70-79mm fork length. By mass, a higher proportion of *Calanus* prey were consumed by fish in the 70-79mm and 60-69mm length classes compared to either the 50-59mm and <50mm length classes (F = 7.09, df=3, $P < 0.001$). The proportion of *Mysis* prey by mass was higher among fish from the 70-79mm length class compared to all other length classes (F = 3.20, df=3, $P < 0.05$)

DISCUSSION

In contrast to other studies with older Arctic cisco using marine carbon sources, YOY Arctic cisco in this study used terrestrial carbon sources that are obtained through a mixture of neritic and offshore zooplankton prey (Kline et al. 1998; Dunton et al. 2006; 2012). The $\delta^{13}C$ values from most YOY Arctic cisco were in the expected range of a secondary consumer relying on terrestrial suspended carbon sources (SPOM), but not marine sources (Fig. 4.2). Isotope values showed a tendency for the smaller fish to rely more heavily on terrestrial carbon sources and feed at a slightly lower trophic level, but there was evidence of terrestrial carbon use in fish of all length classes (Table 4.2; Fig. 4.2). Carbon isotope values of the smallest fish (<50mm) were more depleted than expected for a secondary consumer using any of the potential carbon sources examined here, but still the terrestrial SPOM source was the most likely carbon source.

Terrestrial carbon has previously been recognized for its importance in the nearshore Beaufort Sea food web and other nearshore areas (Carmack and Mcdonald 2002; Darnaude 2005; Dunton et al. 2006; Vinagre et al. 2011b; Vinagre et al. 2011c; Dunton et al. 2012). When combined with an understanding of low *in situ* marine production in the Beaufort Sea, the presence of terrestrial carbon sources in many species suggests that nearshore production is dependent on allochthonous terrestrial inputs from river discharge and coastal erosion (Dunton et al. 2006). Arctic cisco, and other species that use terrestrial carbon, can be influenced by terrestrial processes even while at sea if river discharge controls carbon export from coastal plains, foothills, and headwater regions (Holmes et al. 2008; Vinagre et al. 2011c). Changing climates may also influence terrestrial carbon inputs and nearshore marine production by altering the timing and magnitude of river discharge and erosion rates. Interannual differences in YOY Arctic cisco growth has been strongly correlated with Mackenzie River discharge over the last several decades and the results from this study provide evidence of the underlying mechanism leading to these observed correlations (von Biela et al. 2011).

Other fish species also show variation in carbon source with life stage or feeding location (Darnaude 2005; Dunton et al. 2006; Vinagre et al. 2011b). Near the Rhone River, France, Darnaude (2005) found shifts in carbon sources between juvenile and adult flatfish due to differences in diet and depth distribution with age. Yellow sole (*Buglossidium luteum*) adults primarily use terrestrial carbon and juveniles primarily use marine carbon, while the pattern is opposite in sand sole (*Pegusa lascaris*). Near the Tagus River, Portugal, some fish species exhibit a gradient in carbon sources with fish captured closer to the river using more terrestrial carbon than fish captured further from the river (Vinagre et al. 2011b). In the Beaufort Sea, Dunton et al. (2006) found Arctic cod (*Boreogadus saida*) captured in lagoons use more terrestrial carbon compared to those captured on the open coastal shelf. Future research should address the influence of river discharge and terrestrial carbon availability on life history traits of marine and anadromous fish living in river influenced marine habitats.

Nitrogen isotope values should be interpreted with more caution than carbon isotope values in this study. Nitrogen end member values may vary more widely across seasons, the fractionation values for nitrogen are known to have wider variability, and differences due to nitrogen source can be confounded with differences in trophic level (Kling et al. 1992; Post 2002; Vizzini and Mazzola 2003; Tamelander et al. 2009; Dunton et al. 2012). The $\delta^{15}N$ values of YOY Arctic cisco, however, were within 3.4‰ or one trophic level of the expected value for a secondary consumer of terrestrial SPOM and similar to those of age 1+ Arctic cisco (Kline et al. 1998; Dunton et al. 2012; Fig. 4.2).

Terrestrial isotope signatures of YOY Arctic cisco likely reflect recent foraging in the Beaufort Sea, rather than past freshwater residency after hatching. In general, YOY fish are known to have much faster carbon turn-over compared to adults due to their rapid growth rates. In a whole lake manipulation of $\delta^{13}C$, the half-life of carbon isotopes ranged from 8 to 18 days for YOY bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and yellow perch (*Perca flavescens*) compared to more than 100 days for adults (Weidel et al. 2011). Even among adults, Perga and Gerdeaux (2005) found that the stable isotope composition of whitefish (*C. laveretus*) muscle tissue reflected the food consumed during the growing season regardless of collection date. At the time of capture, YOY Arctic cisco had likely been in nearshore waters for a month or more and spent little time in freshwater after hatching. Migration time to Prudhoe Bay from the Mackenzie River delta has been estimated at 35 days (Gallaway et al. 1983; Fechhelm and Griffiths 1990; Dillinger et al. 1992; Colonell and Gallaway 1997). Hatch dates are thought to coincide with spring freshet and are quickly followed by down-stream migration as in other coregonids (Naesje et al. 1986; Naesje et al. 1995; Urpanen et al. 2005). Given the quick turnover rates for stable isotopes in YOY fish, long migration in nearshore water, and short freshwater residency it is likely that isotope signatures only reflect nearshore foraging.

Diet composition of YOY Arctic cisco depended on fish length. The proportion of *Calanus* and *Mysis* prey items increased with length class. *Calanus* prey was not found in the stomachs of the smallest fish (<50mm) and gradually increased to 26% of prey items and 55% of prey mass in the largest fish sampled (70-79 mm). In the largest fish *Calanus* were the second most numerically dominate prey class and primary prey class by mass (Fig. 4.3 and 4). Similarly, *Mysis* prey did not occur in the stomach of the smallest fish sampled (<50mm), but accounted for 12% of prey items and 30% of prey mass in the largest fish sampled (70-79mm)

(Fig. 4.3 and 4.4). There were no statistically significant declines in prey species with increasing length class, but the contribution of *Pseduocalanus* and Harpacticoid prey items tended to decrease with fish length (Fig. 4.3 and 4.4).

Differences in diet composition by fish of different size can be driven by extrinsic or intrinsic factors. If fish of different length classes live in separate microhabitats within the nearshore Beaufort Sea, different encounter rates could exist for individual prey groups and the differences would be extrinsic. These fish, however, were all captured in the same nearshore fyke nets and there was no evidence of separation by size at capture. An intrinsic limitation is the most likely mechanism leading to difference in prey composition by fish length class. Smaller YOY Arctic cisco are likely unable to consume the larger *Calanus* and *Mysis* prey due to gape limitations and might also have reduced abilities to detect or capture larger prey (Bremigan and Stein 1994; Romare et al. 1999). The *Calanus* and *Mysis* prey were by far the largest species consumed by YOY Arctic cisco in this study (Table 4.1).

Many prey groups identified in this study were consistent with past zooplankton distribution studies in nearshore Arctic waters. Two *Mysis* species, *M. litoralis* and *M. relicta,* are common epibenthic species in the nearshore brackish waters that have been suggested as important prey items for nearshore fish communities (Jarvela and Thorsteinson 1999) and are known to have longer life cycles (1, 2, or even 4 years; reviewed in Audzijonytė and Väinölä 2005). *Pseudocalanus, Eurytemora*, *Acartia*, and Harpacticoid prey items have previously been identified in nearshore zooplankton studies within the Beaufort Sea and specifically within the low salinity waters of the Mackenzie River plume and Prudhoe Bay (Horner and Murphy 1985; Walkusz et al. 2010). Any of these nearshore prey items could be providing a conduit for terrestrial carbon to YOY Arctic cisco.

Calanus in the diet of YOY Arctic cisco were inconsistent with their typical distribution in offshore marine waters. Although *Calanus* species are not characteristic of nearshore brackish waters where YOY Arctic cisco are typically found, they do occur at low densities in nearshore waters (Horner and Murphy 1985; Walkusz et al. 2010). Our sampling is unable to determine whether *Calanus* species became available to YOY Arctic cisco in nearshore waters or if Arctic cisco were able to move offshore to forage for *Calanus.* It is more likely that *Calanus* prey became available in the nearshore waters since nearshore *Mysis* prey were found in the same stomachs and all fish were captured nearshore. Of the YOY Arctic cisco consuming *Mysis* prey, nearly all (91%) consumed *Calanus* prey as well. It is unlikely that YOY Arctic cisco moved offshore to forage on *Calanus* prey and later returned to the nearshore to forage on *Mysis* prey prior to nearshore capture. Summer storms could bring *Calanus* prey into nearshore waters in greater numbers or YOY Arctic cisco may preferentially select *Calanus* prey for their large body size and high lipid densities that can reach 74% of dry weight at the end of the summer (Bradstreet and Cross 1982; Hirche 1997; Scott et al. 2000; Peterson et al. 2002; Prokopowicz and Fortier 2002; Dunton et al. 2012). The large body size and high lipid densities of *Calanus* prey are made possibly by a longer life cycle of several years (2 or 3 years for *C. glacialis* in the Beaufort Sea and 2 to 4 years for *C. hyperboreus*) and represents an adaptation to the short Arctic growing season where individuals use resources gathered over several summers to attain larger size and ultimately higher fecundity (Hirche 1997; Wold et al. 2011).

We have previously suggested that YOY Arctic cisco may rely on longer lived copepods, like *Calanus spp.,* and that the life cycle of these copepods would account for the one and two years lags present in the relationships between YOY Arctic cisco growth and environmental predictors of production (von Biela et al. 2011). Here we have shown that YOY Arctic cisco do forage on long-lived *Calanus* copepods and Mysids. Further study is required to determine if YOY Arctic cisco preferentially select these larger, longer lived prey items and if they are consistently present in YOY Arctic cisco diets across years and throughout the Beaufort Sea.

Here we have demonstrated that Arctic cisco lie at a cross roads between terrestrial and marine ecosystems and are vulnerable to change in either system. Arctic cisco and other nearshore fish could be important indicators for the Beaufort Sea in the face of a changing climate and increased development. Future climate predictions for the Beaufort Sea were recently summarized by Walkusz et al. (2010) and include increased Mackenzie River discharge from increasing precipitation and thawing permafrost (Carmack and Macdonald 2002). Under this scenario, a resulting increase in nutrients and decreases in light penetration is anticipated (Wrona et al. 2006; Retamal et al. 2008). In the event that light does not become limiting to production, changes in the phenology and increases in the magnitude of phytoplankton production may lead to the replacement of large copepods, like *Calanus,* by smaller copepods (Uye 1994). Substituting large lipid-rich species, with lower quality prey may have cascading effects for Beaufort Sea food webs. A similar process has already been identified in the Bering Sea under the Oscillating Control Hypothesis, where warm years are associated with decreased production of large zooplankton and reduced survival of young pollock (*Theragra chalcogramma*) (Hunt et al. 2011). Our study of Arctic cisco may also provide insight to other high profile Arctic species such as bowhead whales *Balaena mysticetus* L. and Arctic cod which also feed heavily on *Calanus* and *Mysis* prey items (Lowry and Burns 1979; Bradstreet and Cross 1982).

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