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

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Arctic cisco *Coregonus autumnalis* young-of-year (YOY) growth was used as a proxy to examine the long-term response of a high-latitude fish population to changing climate from 1978 to 2004. YOY growth increased over time ($r^2 = 0.29$) and 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. Overall, the most prevalent correlates to YOY growth were sea-ice concentration lagged 1 year (significant correlations in 7 months; $r^2 = 0.14–0.31$) and Mackenzie River discharge lagged 2 years (significant correlations in 8 months; $r^2 = 0.13–0.50$). The results suggest that decreased sea-ice concentrations and increased river discharge fuel primary production and that life cycles of prey species linking increased primary production to fish growth are responsible for the time lag. Oceanographic studies also suggest that sea ice concentration and fluvial inputs from the Mackenzie River are key factors influencing productivity in the Beaufort Sea. Future research should assess the possible mechanism relating sea ice concentration and river discharge to productivity at upper trophic levels. Journal of Fish Biology © 2010 The Fisheries Society of the British Isles
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Key words: Beaufort Sea; climate proxy; Colville River; Mackenzie River; otolith; sea ice.

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 probably vary among locations and depend on the life history and range of habitats used (Reist *et al.*, 2006*a*). Diadromous species that spawn in fresh waters and feed in marine waters integrate climate change effects across freshwater, estuarine and marine habitats and, thus, the total effect is expected to be significant (Reist *et al.*, 2006*a*).

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.*, 2006*a*, *b*; Wrona *et al.*, 2006). Fish

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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 overwintering habitats. *Coregonus autumnalis* captured in Alaskan 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 (Næsje *et al.*, 1986, 1995; Urpanen *et al.*, 2005). After hatching, *C. autumnalis* migrate downstream and out of the Mackenzie Delta where they are swept west to the Colville Delta by nearshore wind-driven currents, a migration thought to last *c*. 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^{-1} 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 & Thorsteinson, 1999). Each winter, the Colville River freezes as nearshore sea ice forms and *C. autumnalis* enter deep-water river habitats to overwinter. A lack of deep-water 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 6 to 9 years, *C. autumnalis* migrate back to Mackenzie River tributaries to spawn in mid-September to early October (Gallaway *et al.*, 1983; Moulton, 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 autumn provide an important subsistence resource for the residents of the Alaskan Arctic Coastal Plain (Fechhelm *et al.*, 2007). Recently, wide variation in catch rates of *C. autumnalis* has led to concern among subsistence users (Gallaway *et al.*, 1983). Further, traditional knowledge, based on long-term observations, suggests that fish condition 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. On the

basis of 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 & 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.*, 2006*a*; 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 influenced 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 gillnet fishery at Nuiqsut on the Colville River (Fig. 1). Nets are typically 76 mm (stretched and measured knot to knot) mesh multifilament gillnets and range in length from 18 to 30 m (Murphy *et al.*, 2007). At least 30 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 (Table I) and fork length (L_F) was known for 408 individuals. Otoliths were removed from fish, cleaned, dried and stored in vials.

Otoliths were embedded in Epothin epoxy (Buehler Ltd; www.buehler.com), 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 ×40 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 L_F-frequency analyses of young *C. autumnalis* (age 0 to 2 years; Fechhelm *et al.*, 2007). The first annual increment, representing the growth during age 0 years 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 primordium) to the outer edge of the first translucent zone (appears as the narrow dark area with reflected 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. 2).

To confirm that otolith growth was correlated with somatic growth, fish of known L_F were compared to otolith radius using a simple linear regression without a defined intercept (Francis, 1990). The relationship between otolith radius and L_F was not used to backcalculate previous L_F due to the extra assumptions associated with backcalculation (Francis, 1990). Capture-age effects were anticipated on the basis of Lee's phenomenon (Lee, 1912) 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
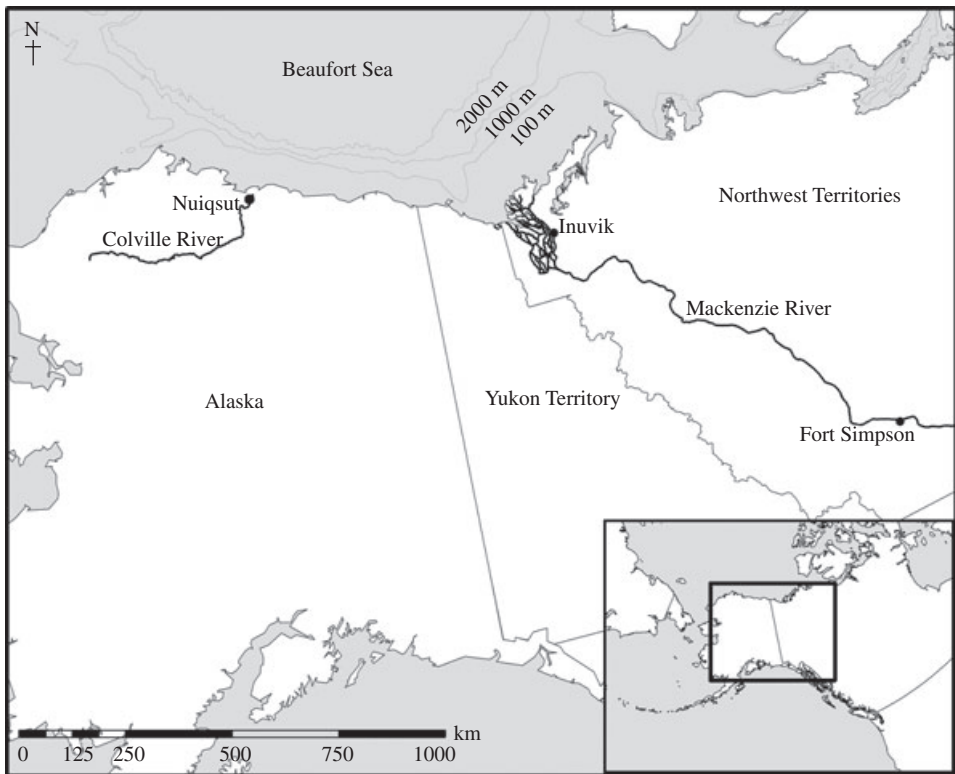
Fɪɢ. 1. Map of *Coregonus autumnalis* range in northern Alaska, U.S.A., and Canada, including the Mackenzie
       River, Beaufort Sea and the collection location in Nuiqsut, Alaska, along the Colville River.

and after standardizing, was tested using a one-way ANOVA. 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 ($P < 0.05$).

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,
unpubl. 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 1 day and standardized to net length. In each fishing year, catch data were
partitioned by year class based on age distributions. Age distributions were estimated by
ageing otoliths from a sub-sample 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 index (AO) as a broad mea-
sure 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 influ-
ences on growth or indirect influence. Lags of up to 2 years were used to account for long gen-
eration times in many potential prey species (Hirche & Bohrer, 1987; Prokopowicz & Fortier,
2002). Months were arranged in water years, 1 October to 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 affect ecosystems

Table I. Number of otoliths collected from *Coregonus autumnalis* harvested in the Nuiqsut, Colville River, AK, U.S.A. subsistence fishery by year

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

YOY, young of year.

through changes in ocean currents, temperatures, ice cover and precipitation (Thompson & 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; www.climate.weatheroffice.gc.ca). 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; www7.ncdc.noaa.gov/CDO/cdo). Easterly winds during the open water season (June to October) are favourable for upwelling, drawing deep nutrient water to the shelf and stimulating productivity (Carmack & 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, 1999). Mean monthly river discharge rate ($m^3 s^{-1}$) was compared to growth. Mackenzie River discharge may influence YOY *C. autumnalis* directly with little or no time lag (*e.g.* within
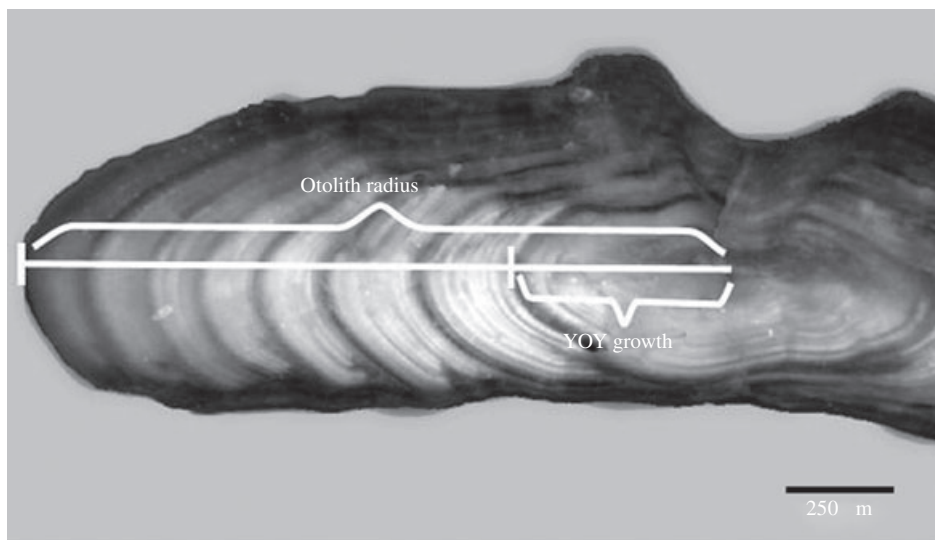
Fig. 2. Photomicrograph of transverse section of a *Coregonus autumnalis* otolith. The axis measure is the line going down the longitude of the otolith; young-of-year (YOY) growth and otolith radius are indicated (⊢).

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 thousands of kilometres south into the temperate zone (McNamara *et al*., 1998; Walker & Hudson, 2003; Holmes *et al*., 2008). River discharge was measured at Fort Simpson by the Water Survey of Canada (Station 10GC001). The Fort Simpson site was chosen over other Mackenzie River locations for this measurement because only one main channel is present at this point.

Young-of-year growth was correlated to a given environmental variable 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 variable in each month of the year. This exploratory analysis resulted in multiple independent linear regressions and increased the likelihood of type I error or spurious correlations. Bonferroni corrections were not implemented because they can be over-conservative (increase type II error; Cabin & Mitchell, 2000). *P*-values were reported 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 350 mm at capture (Fig. 3) and 5 to 8 years old (Fig. 4). There was a significant positive relation between otolith radius and L_F for individuals of known length (slope $= 3 \cdot 67$; $r^2 = 0 \cdot 84$, $P < 0 \cdot 001$; Fig. 5). An effect of capture age was detected on YOY growth increment using an ANOVA ($F_{5,745} = 8 \cdot 58$, $P < 0 \cdot 001$) and was corrected by standardizing each YOY growth increment to the average for the capture age ($F_{5,745} = 0 \cdot 01$, $P > 0 \cdot 05$). There was
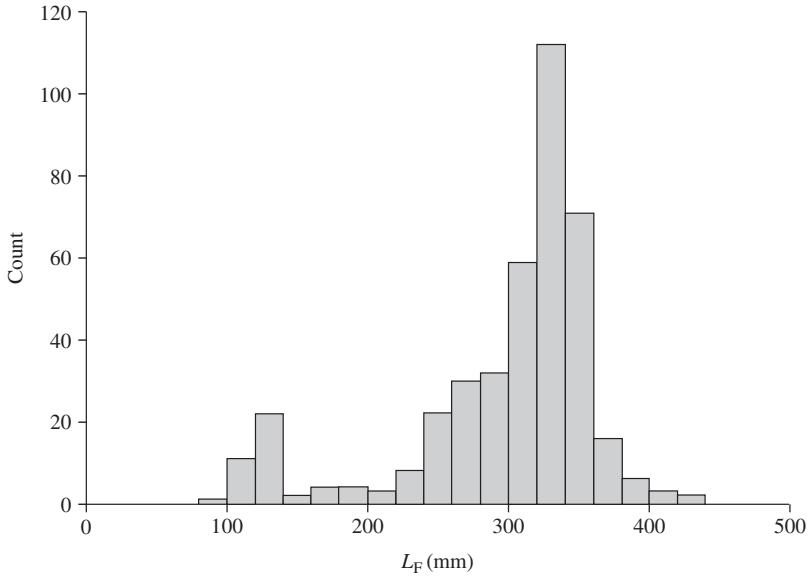
FIG. 3. The fork length (L_F) frequency distribution of *Coregonus autumnalis* captured in the Colville River, AK, U.S.A.

little evidence of first-order autocorrelation in the time series of YOY growth (auto-correlation $= -0.080$; Durbin–Watson's $D = 2.066$). Standardized YOY growth increased over time (Fig. 6; linear regression; slope $= 0.00540$; $r^2 = 0.29$, $P < 0.01$). CPUE was not related to YOY growth (Fig. 7; linear regression; slope $= 0.00206$; $r^2 = 0.11$, $P > 0.05$).
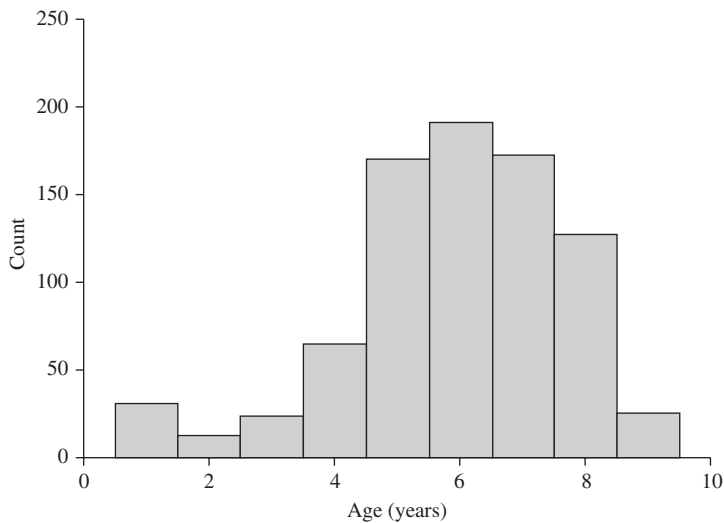

FIG. 4. The age-frequency distribution of *Coregonus autumnalis* captured in the Colville River, AK, U.S.A.
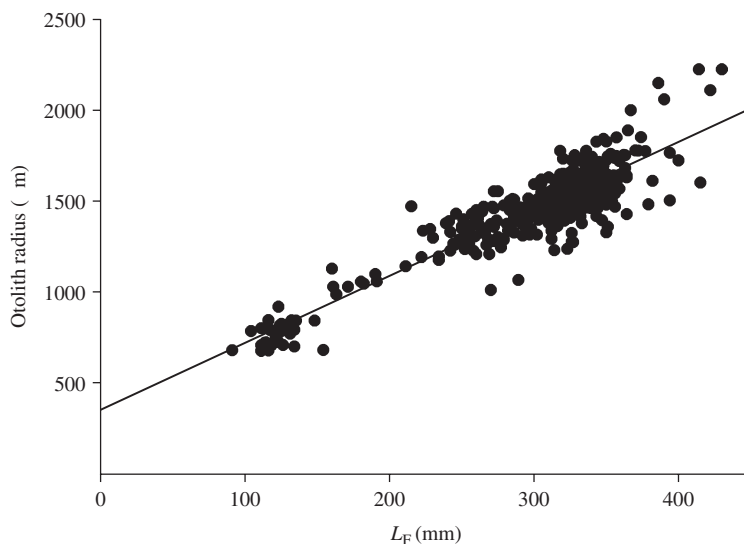
FIG. 5. Linear regression of fork length (L_F) and otolith radius for fish of known L_F and captured in the Colville River, AK, U.S.A. (1986–2007). The curve was fitted by: $y = 3·666x + 360·400$ ($r^2 = 0·84$).

All environmental variables correlated with growth with and without time lags (Table II and Fig. 8). In general, correlations with growth across all variables were more prevalent with time lags of 1 and 2 years. YOY growth was positively related to the AO in March with a lag of 2 years and during the current year's winter. Similarly, the strongest relationship between temperature and YOY growth occurred
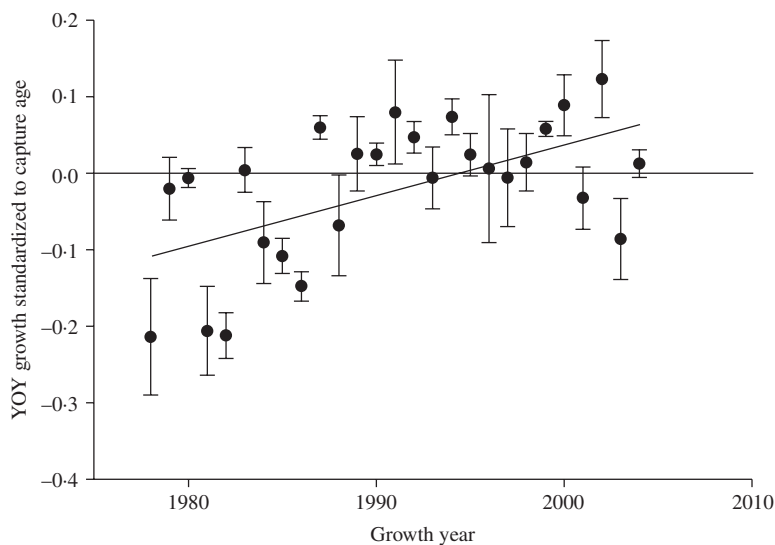

FIG. 6. Mean young-of-the-year (YOY) increment size for the entire available growth record (1978–2004) of *Coregonus autumnalis* captured in the Colville River, AK, U.S.A. The curve was fitted by: $y = 0·007x − 13·170$ ($r^2 = 0·29$).
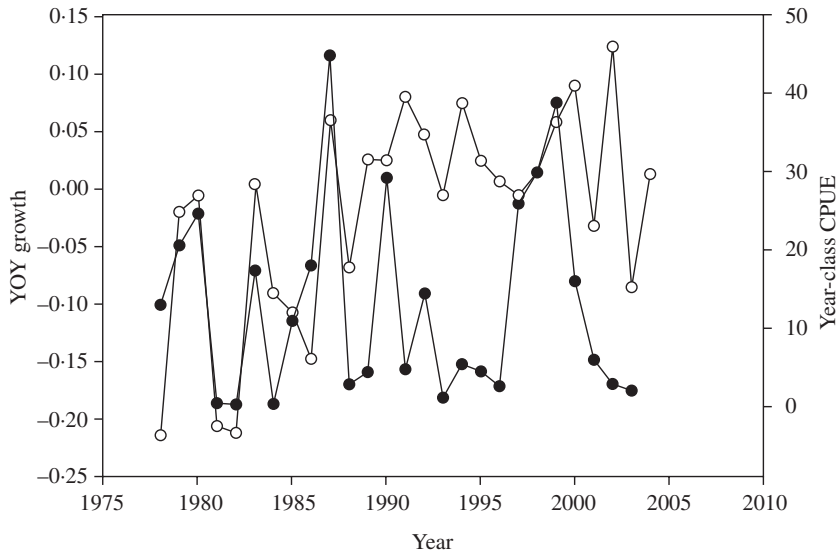
FIG. 7. Graph of mean young-of-the-year growth (YOY growth, ○) and year-class catch per unit effort (CPUE, ●) for fish captured in the Colville River subsistence fishery. There was no significant relationship ($P > 0.05$).

in March with a 2 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 2 years. Growth was negatively correlated with sea-ice concentration for several spring, summer and autumn months with a 1 year lag (April to May and July to October). Mackenzie River discharge correlated positively with growth in eight with a 2 year lag (October and December to June). River discharge was also positively correlated to YOY growth during April of the current year.

DISCUSSION

The growth of YOY *C. autumnalis* increased from 1978 to 2004 (Fig. 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 a week over the last 100 years with an abrupt transition in the mid-1970s, prior to the earliest records in this study (Næsje *et al*., 1986, 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 2 years, decreases in sea-ice concentration during the previous year and increases in the Mackenzie River discharge with a 2 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).

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

Environmental covariate	Lag	Month	r^2	P
Arctic oscillation	2 years	March	0·22	<0·01
	None	December	0·17	<0·05
Temperature	2 years	October	0·15	<0·05
		March	0·58	<0·001
	1 year	December	0·27	<0·01
		February	0·16	<0·05
		July	0·19	<0·05
	None	July	0·15	<0·05
East wind speed				
	2 year	March	0·26	<0·01
		July	0·28	<0·01
		August	0·24	<0·01
	1 year	February	0·17	<0·05
		March	0·22	<0·01
		July	0·13	<0·05
	None	November	0·32	<0·01
		January	0·34	<0·01
		June	0·14	<0·05
Sea-ice concentration	2 year	January	0·26	<0·01
	1 year	November	0·17	<0·05
		April	0·14	<0·05
		May	0·24	<0·05
		July	0·24	<0·01
		August	0·31	<0·01
		September	0·29	<0·01
	None	October	0·25	<0·01
		February	0·21	<0·05
River discharge	2 year	October	0·23	<0·01
		December	0·31	<0·01
		January	0·50	<0·001
		February	0·45	<0·001
		March	0·40	<0·001
		April	0·37	<0·001
		May	0·35	<0·001
		June	0·13	<0·05
	None	April	0·16	<0·05

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. 8). Arctic oscillation was least often correlated with growth and the correlations had relatively low predictive power [Fig. 8(a)]. Low predictive 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 variables, such as wind, currents, precipitation, sea surface temperature and sea ice that are all strongly correlated with AO (Thompson & Wallace, 1998).
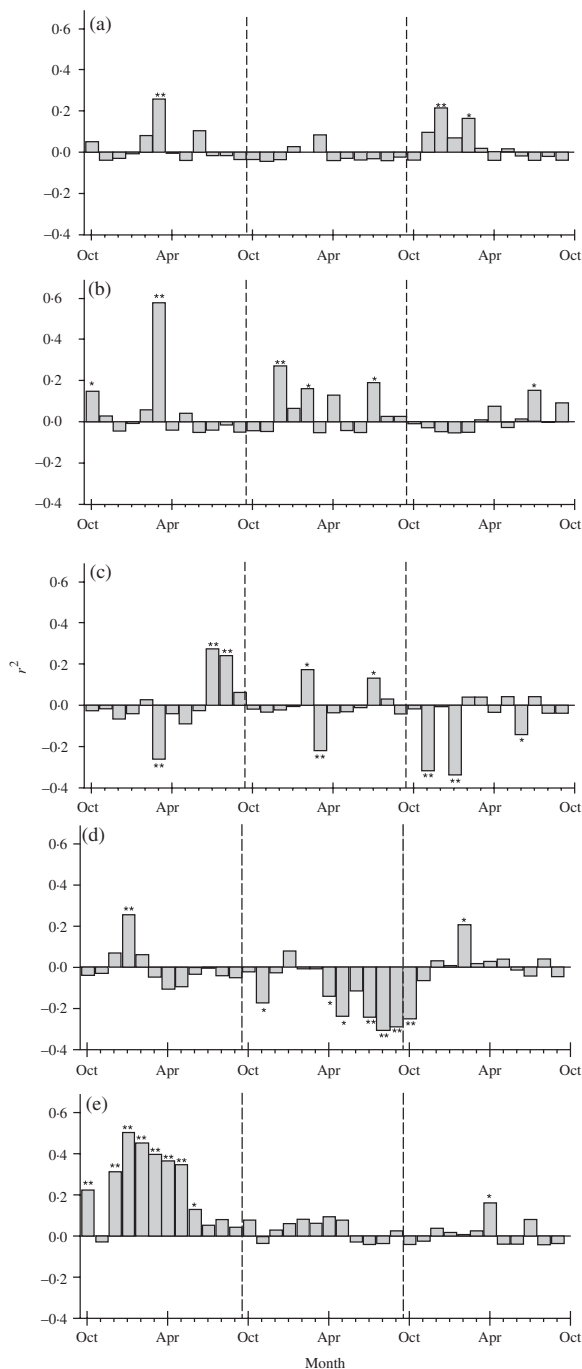
FIG. 8. Coefficients of determination (r^2) for regression of young-of-the-year (YOY) growth for *Coregonus autumnalis* captured in the Colville River, AK, U.S.A. and monthly averages of: (a) the Arctic oscillation (AO), (b) air temperature, (c) east wind speed, (d) sea-ice concentration and (e) Mackenzie River discharge. Broken vertical lines delineate years with the previous two years to the left and the current year on the right. $^{**}P < 0.01$; $^{*}P < 0.05$.

All significant AO correlations occurred during the autumn 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 suggest 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. 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. 8(b)]. The best supported correlation between temperature and YOY growth was in March with a 2 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 (Neilson & Geen, 1985; Rogers & Ruggerone, 1993; 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° C; Fechhelm *et al.*, 1983, 1997; Griffiths *et al.*, 1992), 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 1 or 2 years [Fig. 8(c)–(e)]. These lagged correlations suggest that the processes underlying the correlations are biologically mediated through lower trophic levels rather than the result of more immediate temperature or salinity influences on *C. autumnalis* physiology. Stronger east winds during July and August with a 2 year lag were related to increased YOY growth [Fig. 8(c)]. East winds bring deeper nutrient-rich waters onto the Beaufort Sea shelf and probably enhance productivity at lower trophic levels (Carmack & Macdonald, 2002). East winds also promote mixing by driving fresh water 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 to May and July to October) consistently correlated with increased YOY growth [Fig. 8(d)]. Carmack & 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 relationship in most months when lagged by 2 years [Fig. 8(e)]. The high predictive power and consistency of the correlations suggest a relationship 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 River extend into the temperate zone and the river continues to discharge fresh water 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 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 fresh water 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 fresh water 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 1 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. *Coregonus 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* and *Calanus hyperboreus* to be key prey items in YOY *C. autumnalis*, with the importance of *C. hyperboreus* increasing and *P. minutus* decreasing with fish size during the first year (V. R. von Biela, C. E. Zimmerman, S. E. Burril, B. R. Cohn & J. M. Welker, unpubl.

data). Studies on zooplankton across the nearshore Beaufort Sea also identified *P. minutus and C. hyperboreus* as common species by biomass (Horner & Murphy, 1985; Hopky *et al*., 1994*a*, *b*, *c*). *Calanus hyperboreus* has a life history of 2 to 4 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 relationship between east wind speed, sea-ice concentration or river discharge and YOY growth. *Calanus 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 mass (Bradstreet & Cross, 1982). Due to their high lipid content and abundance, *C. hyperboreus* plays a central role in the Arctic food web as a major prey item of bowhead whales *Balaena mysticetus* and Arctic cod *Boreogadus saida* (Lepechin) (Lowry & Burns, 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. 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. This study was not, however, designed to determine the influence of density dependence on growth in *C. autumnalis* populations; the analysis only indicates that it is unnecessary to standardize 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 increased 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 probably 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 effect of climate change on some species.

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