

Environmental controls of phenology of high-latitude Chinook salmon populations of the Yukon River, North America, with application to fishery management

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Phenologies of a number of anadromous fish species have been demonstrated to vary in concert with environmental factors that change with global warming, such as water and air temperatures. Anadromous fishery managers will need advice from models of phenology, or migratory timing, as functions of environmental factors in those harvest areas where annual migratory timing can vary sharply. Such models are also necessary to advise fishery managers on how and when global warming projections of the IPCC model ensemble should be factored into regulatory decisions. Specifically, we demonstrate that the annual timing of marine exit of Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) at 63°N 165°W for 1961–2009 varied in close concert with modelled sea surface temperature, air temperature, and sea ice cover. The best linear model for 1961–2009 combines sea surface and air temperatures to explain 59% of the annual variability in migratory timing (ice cover is available only for 1970–2009). Changes in phenology of high-latitude Chinook salmon are expected in response to global warming. As average temperatures increase, the frequency of earlier migrations is expected to increase, making management of the fishery more challenging.

Keywords: air temperature, anadromous, Chinook salmon, climate change, fishery management, IPCC climate forecasts, migratory timing, NCEP reanalysis, phenology, sea surface temperature, sea ice cover, Yukon River.

Introduction

The timing of occurrence of anadromous fish species, such as Pacific salmon (*Oncorhynchus* spp.), Atlantic salmon (*Salmo salar*), American shad (*Alosa sapidissima*), and alewives (*Alosa pseudoharengus*), at specific locations during the life cycle, also known as phenology, has been reported to vary in concert with environmental conditions, such as air and water temperature, and river flow (Leggett, 1977; Mundy, 1982; Blackburn, 1987; Quinn and Adams, 1996; Hodgson *et al.*, 2006; Keefer *et al.*, 2008; Anderson and Beer, 2009; Ellis and Vokoun, 2009). Relationships between timing of salmon migrations and marine hydrographic features have been described for a number of salmon species (Fujii, 1975; Leggett, 1977; Nishiyama, 1977; Ueno, 1992). Nishiyama (1977) explained delays in timing of spawning migrations of eastern Bering Sea (Bristol Bay) sockeye salmon (*Oncorhynchus nerka*) with the temporal duration of frontal boundaries that were hypothesized to form barriers to migration. More recent work on the relationship between ocean conditions and freshwater timing of Bristol Bay sockeye salmon (Hodgson *et al.*, 2006) is not directly comparable with the work of Nishiyama, which focused on ocean conditions on smaller spatial scales. Hodgson *et al.* (2006) used large-scale geographic averages of monthly sea surface temperatures (SSTs) from April to peak freshwater migration (July), which might not be related

consistently to the stability of fronts in the Aleutian Island passes described by Nishiyama (1977).

Because management of fisheries for anadromous species is based on expected time of arrival in harvest areas, it is essential to identify environmental conditions that influence timing to implement effective management measures (Mundy, 1982; Quinn and Adams, 1996; Cooke *et al.*, 2004; Keefer *et al.*, 2008; Anderson and Beer, 2009). Similarly, understanding the influence of trends in environmental conditions projected by the Intergovernmental Panel on Climate Change (IPCC, 2007) on phenology of anadromous species would allow fishery regulators to develop appropriate adaptive management strategies.

Climate change in northern latitudes is expected to be particularly acute. Arctic surface air temperatures have warmed at twice the global rate (Anisimov *et al.*, 2007). Much of the Yukon River watershed has experienced a substantial warming trend in air temperatures since 1950 (Sagarin and Micheli, 2001). Given the covariation between spring air temperatures and timing of returning adult Chinook salmon in the lower Yukon River (Mundy, 1982), a warming climate would be expected to change the migratory timing. Predicting how migratory timing and fishery management would change under a global warming scenario requires development of mechanistic understandings (Cooke *et al.*, 2008) of how the

environmental factors interact with the biology of Chinook salmon to effect changes in migratory timing.

Retrospective studies might also assist in designing the coordinated field and laboratory studies that are ultimately necessary to identify and test the cause-and-effect relationships among environmental variables and the underlying physiological mechanisms of migration. Opportunities for retrospective study of environmental control of phenology in anadromous species over a very wide range of years and latitudes are available for Pacific salmon because of collection of observations of maturing adults at long-established sites by fishery management agencies throughout the species' geographic range. The long time-series of annual observations allow quantitative descriptions over periods of decades of the annual variations in timing of maturing Pacific salmon and the correlations between the variations in phenology and environmental factors (Fujii, 1975; Nishiyama, 1977; Mundy, 1982; Blackburn, 1987; Quinn and Adams, 1996; Hodgson *et al.*, 2006; Keefer *et al.*, 2008; Anderson and Beer, 2009).

The long time-series (1961–present) of salmon observations available from the Yukon River delta and the more recent availability of long time-series of marine ice from satellite observations and SSTs from the National Climate Environmental Modeling Project (NCEP) model reanalysis (see Kalnay *et al.*, 1996) provide an opportunity for retrospective study. For the high-latitude Chinook salmon populations of the Yukon River (Alaska, USA, Yukon Territories and British Columbia, Canada, 60–68°N), large fluctuations in annual timing of marine exit into the lower river make it particularly important for fishery managers to understand the degree to which environmental factors could be used to predict annual timing (Mundy, 1982). Making choices of time- and space-scales for the environmental variables requires a hypothesis regarding their roles in determining the timing of marine exit for Yukon River Chinook salmon.

The following hypothesis explains which environmental variables should be analysed in conjunction with Yukon Chinook salmon timing information, and it guides selection of the time- and space-scales over which the environmental variables are analysed to explain the specific phenology of interest, i.e. the timing of marine exit. In our hypothesis, the stability of the water column in a marine staging area near the river mouth controls the timing of marine exit in two ways. First, a stable water column keeps the turbid freshwater plume of the Yukon River distinct from the relatively clear and saline waters of the Bering Sea. The distinct and persistent salinity front presents a barrier that osmotically incompetent individuals cannot cross; in addition, it might increase the time necessary to achieve osmotic competence by limiting exposure of migrants farther offshore in the staging area to brackish waters. Second, a stable water column prevents establishment of the horizontal gradients and other hydrographic patterns of olfactory cues (olfactants) and salinity that guide osmotically competent individuals into the river, increasing the amount of time needed for marine exit, by making it harder for individuals to find the river. Environmental conditions that favour water-column stability, such as persistent and extensive ice cover and the associated low sea surface and air temperatures, would therefore be associated with a later timing of marine exit. The time- and space-scales for the environmental variables are determined by the schedule and locations of marine migration for maturing salmon in our hypothesis. According to the hypothesis, Yukon River Chinook salmon start moving from the shelf-

break area in the Bering Sea at the end of March to accumulate in a marine staging area between St Lawrence Island and the Yukon River delta in April and May (Figure 1). The initiation of marine exit happens between the end of May and the middle of June. The actual timing of the start of marine exit each year depends primarily on conditions related to water-column stability. Once marine exit has been initiated, the progression of the migration as observed in the lower river is determined primarily by the marine and estuarine environmental conditions experienced by the migrants before the initiation of the migration.

The hypothesis was developed by reference to published literature, reviewed below, the historical biological and fishery records compiled by the Alaska Department of Fish and Game from which the data presented are drawn, and from our own experiences in contributing to the management of the fishery. A brief description of the biology and river sets the stage for our analysis. A comprehensive description of the Yukon River watershed and its salmon and fisheries is found in Krueger and Zimmerman (2009). In an average year, maturing Chinook salmon start to exit the Bering Sea at 62–63°N at the end of May, with catches increasing until the expected midpoint of the migration on 21 June and declining thereafter (Mundy, 1982). The migration is effectively at an end in the lower river by mid-July, but a few Chinook may be caught as late as the first half of September (Mundy, 1982; Evenson *et al.*, 2009). The many different spawning populations, or stocks, appear to be relatively homogeneous with respect to migratory timing in the lower river, although there is a tendency for upper river populations to dominate the earliest catches (Templin *et al.*, 2005).

The Yukon River's Chinook salmon are composed of semi-discrete spawning aggregates, utilizing mainstream and tributary spawning areas as far as 3058 km from the river mouth (Evenson *et al.*, 2009). Depending on the genetic method used, Yukon Chinook are broadly organized geographically into three populations (spawning aggregates or stocks) along the axis of the main river; lower, middle, and upper or Canadian (see Figure 6 in Utter *et al.*, 2009).

The management of the fisheries in the lower river, Area Y-1, is critical to the success of conservation efforts for Chinook in the entire watershed (Evenson *et al.*, 2009) and timing information is critical to the success of the management of the fishery (Mundy, 1982). Timing information can help managers avoid the conservation problems created when the fishery catch information from an early migration of low to average abundance is mistaken for larger than average abundance, resulting in overharvesting and the subsequent loss of expected harvest allocations to fisheries upriver. Should the frequency of early migrations increase in response to climate change, the challenges of preventing overharvesting would therefore increase.

Methods

Although ~3000 daily observations of Chinook salmon migration are available for future analysis, this exploratory work focuses on two annual statistics, the 15th (FIFDJ) and 50th (MDJ) percentiles of the cumulative daily observations of catch per unit effort (cpue). The abbreviation MDJ is used for the 50th percentile, because it is also known as the annual median date of the migration. The cpue observations come from two different types of fishery: a commercial fishery (1961–1979) and a test fishery (1980–2009). The percentiles of catch per boat hour from the commercial fishery of lower Yukon area 1 (Y-1) for 1961–1979

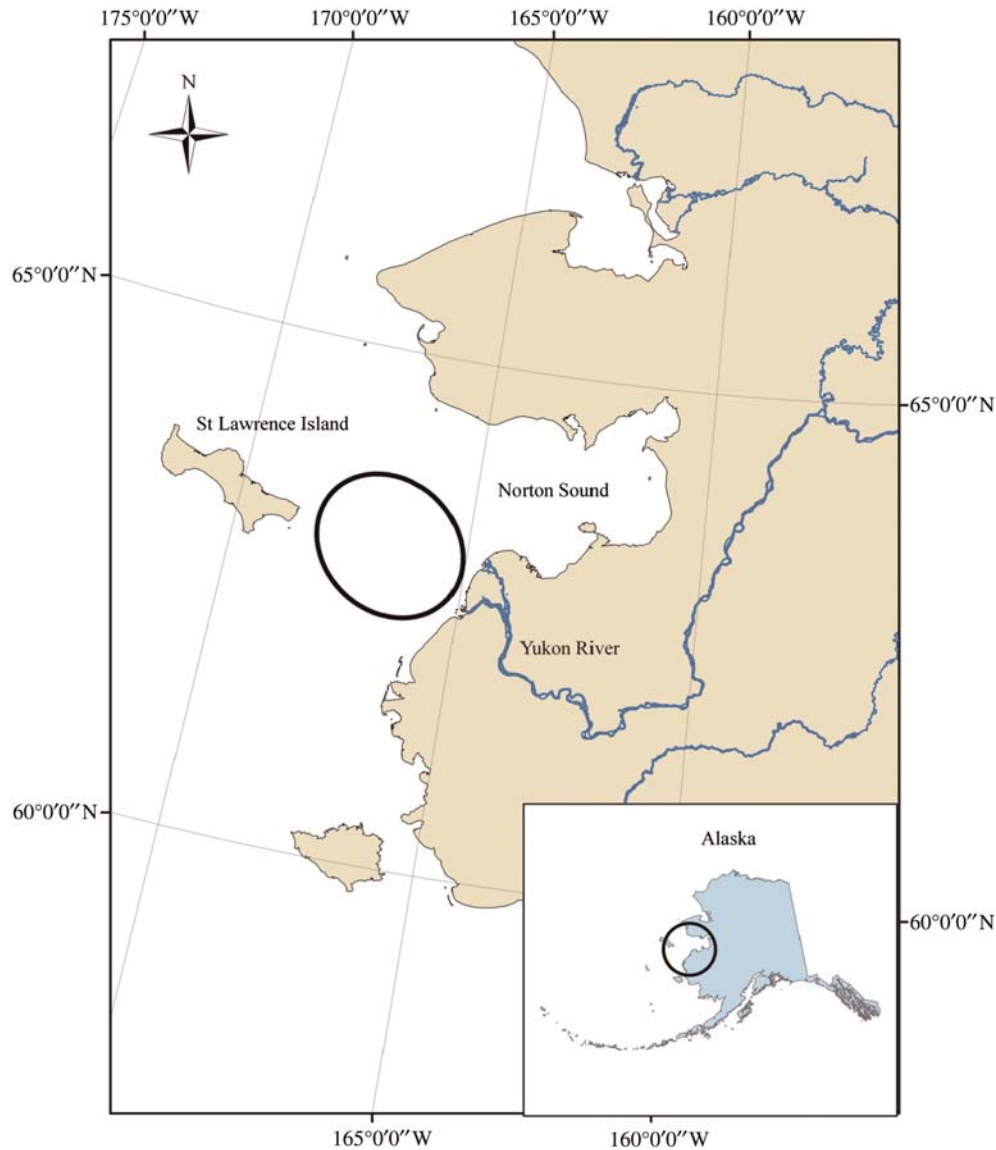


Figure 1. General location of the nominal staging area (oval) on a map displaying the Yukon River delta, St Lawrence Island and vicinity, with an inset map of Alaska.

are from the original Alaska Department of Fish and Game database of commercial and test fishing observations on which the analysis of Mundy (1982) was based. The percentiles of catch per hundred fathoms per hour for 1980–2009 are based on the combined daily cpue of gillnet test fisheries at Big Eddy and Middle Mouth (Alaska Department of Fish and Game). The test fishery at Big Eddy is located in Y-1 on the southernmost of the river’s three main channels, 37 km from the river mouth at 62.7°N 164.5°W. The Middle Mouth test fishery is located in Y-1 on the middle channel, above its confluence with the northernmost channel, 32.2 km from the river mouth (62.8°N 163.9°W). Cpue for the test fisheries for 1981–2009 was obtained from the ADF&G database. The test fisheries sample the Chinook salmon migrations on the delta continuously from late May to 15 July. The commercial catch data for 1961–1979 were chosen for this study rather than the data of an earlier test fishery at Flat Island (see Mundy, 1982), because the location of commercial fishing is more comparable with the locations of Big Eddy and

Middle Mouth, and because the Flat Island test fishery sampled the migration of only the southern channel near the estuary. Although commercial fishing did not happen on every date of the migratory period during 1961–1979, interpolation for missing values (see Hodgson *et al.*, 2006) was investigated and deemed unnecessary for two reasons. First, MDJ computed from the linearly interpolated cpue data did not differ appreciably from the medians based on non-interpolated cpue, because commercial fishing happened at regular intervals and on most dates in most years. The number of dates in June per year for 1961–1979 with non-zero cpue ranged from 13 to 24 (median 19, mean 18.7, standard deviation 3.45). Second, the MDJ based on the cpue of the commercial fishery for 1961–1979 (mean 20.40, variance 21.73) did not differ significantly from the MDJ based on the cpue of the combined test fisheries for 1980–2009 (mean 20.83, variance 22.72) in a single-factor ANOVA ($F = 0.097$; $p = 0.757$). Note that the daily catches were not de-tided for this analysis.

The marine environmental factors were taken from the marine location and time-frame in which Chinook salmon are presumed to be before exiting the marine environment, here called the nominal (marine) staging area. The location of the nominal staging area is next to the approximate location of the plume of Yukon River water entering the Bering Sea, roughly 62–64°N by 165–169°W, but the actual locations of the salmon over time before marine exit have not been measured. Direct measurements of the vertical density structure of the Bering Sea in the nominal staging area are lacking (see Danielson and Kowalik, 2005); proxies were therefore used. April mean air temperatures (AMATC) as used by Mundy (1982) were taken from a land-based weather station next to the nominal staging area at 64.5°N 165.4°W (US National Weather Service, Nome, Alaska) for 1961–2009. AMATC is related to SST, wind-driven mixing of the water column, and the percentage ice cover, and it was the environmental factor earlier demonstrated by Mundy (1982) to be related to timing of Chinook salmon in area Y-1.

Daily SSTs for the location 63.1°N 165.5°W for 1961–2009 were derived from the NCEP reanalysis model by N. Bond (NOAA Pacific Marine Environmental Laboratory, Seattle, WA, USA). The model SST refers to the estimated temperature of the surface of the ice when present and the SST when ice is absent. Monthly modelled mean SSTs for May (MSSTC) were computed as arithmetic means of the daily modelled SSTs. May was selected rather than April as the time when most migrants would be within or in proximity to the nominal staging area (Figure 1).

The average daily proportion of ice cover from 20 March to 1 June for the most nominal staging area (62–63°N by 166–169°W) over the period 1970–2009 (PICE) was computed by Jinlun Zhang (Applied Physics Laboratory, University of Washington, Seattle, WA, USA) using satellite ice concentration data from the National Snow and Ice Data Center (NSIDC). The period between the vernal equinox (20 March in most years) and the end of May was chosen as the period between the nominal start of the migration from the Bering Sea shelf and the start of marine exit when salmon are accumulating and milling about in the staging area.

To standardize terms for reporting and discussing results, annual migrations with MDJ < 20 June are defined as early and those with MDJ > 22 June are defined as late. Migration seasons with AMATC < -7.1°C are defined as cool, and warm migration seasons are defined as those with MSSTC > 0.40°C before 1970 and those with PICE < 0.56 thereafter.

Regression and correlation analyses (Microsoft Excel © Analysis ToolPak) were used to examine the consistency of the hypothesis with the observations. For the statistical analysis, the hypothesis holds that the response variables, MDJ and FIFDJ, are linear functions of the explanatory environmental variables (AMATC, MSSTC, and PICE) that represent the stability of the water column in the nominal staging area. Pairwise correlations of year and all possible combinations of the year and the explanatory and response variables measure the strength of linear time-trends, identify colinearity among explanatory variables, and illustrate the strength of association among all variables. A significant correlation (significance probability $p < 0.05$) with year indicates a linear time-trend. In order for the Yukon data to be consistent with the hypothesis, the response variables have to be significant linear functions of the explanatory variables.

Results

The average phenology of Chinook salmon on the Yukon River delta has not changed appreciably since it was first examined by Mundy (1982). The MDJ and FIFDJ are 14 June and 21 June, respectively (Table 1). The range limits of FIFDJ are 5 June–23 June, and the MDJ occurred as early as 10 June and as late as 30 June in the years 1961–2009 (Table 1; Figure 2). During this period, AMATC averaged -7.1°C, with a maximum of -1.7°C and a minimum of -17.1°C (Table 1). MSSTC averaged slightly below zero (-0.234°C; range limits from -3.8 to 2.8°C; Table 1). The average PICE was 0.56, with a low of 0.23 and a high of 0.78 (Table 1).

A slight, but statistically significant, warming time-trend ($r = 0.290$, $p = 0.043$, first row Table 2) is evident in AMATC (1961–2009); however, no significant linear time-trend is evident for the other explanatory (AMATC, MSSTC, and PICE) or response (FIFDJ and MDJ) variables (first row Table 2). Explanatory variables were all correlated significantly with each other (Table 2), which indicates that the relationships between response and explanatory variables have substantial colinearity and multicollinearity. Although the explanatory variables are all correlated highly significantly with the response variables (Table 2), MSSTC has the largest absolute correlation coefficients with both response variables (Table 2).

Table 1. Mean, standard deviation (s.d.), maximum and minimum of response timing variables, date in June of the 50th percentile of cpue (MDJ), and date in June of 15th percentile of cpue (FIFDJ), and explanatory variables, May mean daily SST °C (MSSTC), April mean air temperatures °C (AMATC), 1961–2009, and average daily proportion ice cover, 20 March–1 June, PICE, 1970–2009.

Parameter	Response		Explanatory		
	MDJ	FIFDJ	MSSTC	AMATC	PICE
Mean	20.65	13.69	-0.23	-7.10	0.562
s.d.	4.68	4.84	1.65	3.31	0.154
Maximum	30	23	2.78	-1.67	0.784
Minimum	10	5	-3.83	-17.06	0.231

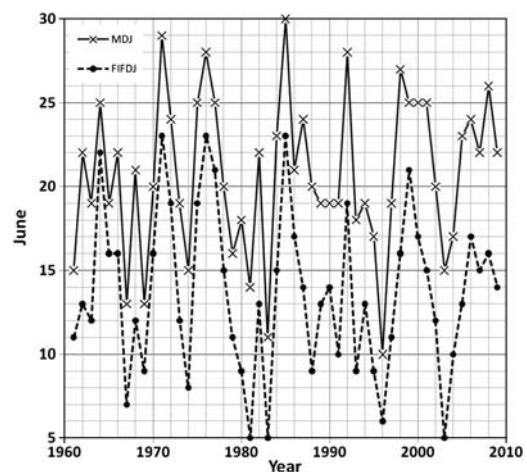


Figure 2. Dates in June of the 15th (FIFDJ) and 50th (MDJ) percentiles of Chinook salmon cpue from commercial (1961–1979) and test fisheries (1980–2009) in the lower Yukon River, Alaska, USA.

Table 2. Product-moment correlation coefficients, *r*, between variables and year.

Variable	MDJ	AMATC	PICE	MSSTC	FIFDJ
Year	0.126 ^{n.s.}	0.290*	-0.269 ^{n.s.}	-0.151 ^{n.s.}	0.090 ^{n.s.}
MDJ	1.000	-0.590	0.660	-0.728	0.891
AMATC	-	1.000	-0.704	0.519	-0.683
PICE	-	-	1.000	-0.659	0.685
MSSTC	-	-	-	1.000	-0.689

Correlations have significance probabilities of *p* < 0.001, except where noted.

**p* < 0.05; ^{n.s.}*p* > 0.05.

Earlier spring warming, as measured by the explanatory variables, was associated with earlier migration of Chinook salmon (Table 2; Figures 3a–c). MSSTC was correlated most strongly with timing (MDJ and FIFDJ; Table 2), followed by PICE and AMATC. During the study period, there were more cool (23) than warm (17) migration seasons and there were fewer late (17) than early (21) migrations. Below average MSSTC was associated with all the late migrations (17/17), whereas an above average MSSTC was associated with all but two of the early migrations (19/21). The response variables display significant bivariate correlations with all the explanatory variables (Table 2), with significance of the *F*-values of the linear relationships all being <0.001 (not presented). Squaring the *r*-values of Table 2, AMATC explains 35 and 47% of the annual variability in MDJ and FIFDJ, respectively (see also trend lines, Figure 3a). MSSTC explains 53 and 47% of annual variability in MDJ and FIFDJ, respectively (see also trend lines, Figure 3b). PICE explains 44 and 47% of the annual variability in MDJ and FIFDJ, respectively (see also trend lines, Figure 3c).

The forecast models were examined using the multiple correlation coefficient (MULTR), adjusted coefficient of determination (ARSQ), the standard error (s.e.), and significance of *F* (*p*; Table 3). When the multiple coefficient of determination was adjusted for the number of variables in the equation (ARSQ, Table 3), all explanatory variables together explained 56% of the variability in MDJ and 59% of the variability in FIFDJ, respectively (ARSQ as a percentage, Table 3). The best and most parsimonious combination of timing predictors was air and SST, which explained 57% of the variability in MDJ [see Equation (1)] and 60% of the annual variation in FIFDJ, respectively [see Equation (2) and Table 3].

$$\text{MDJ} = (-0.410)\text{AMATC} + (-1.638)\text{MSSTC} + 17.357. \quad (1)$$

$$\text{FIFDJ} = (-0.649)\text{AMATC} + (-1.342)\text{MSSTC} + 8.748. \quad (2)$$

Both Equations (1) and (2) fitted the data well (see Figure 4a and b), with the model of FIFDJ [Equation (2)] having the best overall performance for maximizing MULTR and ARSQ and minimizing s.e. (Table 3; Figure 4b). Significance probability values for the MDJ regression coefficients were 0.011 and 3.93×10^{-06} for AMATC and MSSTC, respectively. Probability values for the FIFDJ regression coefficients were 1.28×10^{-04} and 8.73×10^{-05} for AMATC and MSSTC, respectively. The multicollinearity that was expected from the correlations between explanatory variables (Table 2) was evident from the relatively small differences between the ARSQ values of the multivariate models (Table 3).

The MDJ of the 1998 migration was not modelled well by Equation (1) (Figure 4a, large solid triangle). The 1998 model

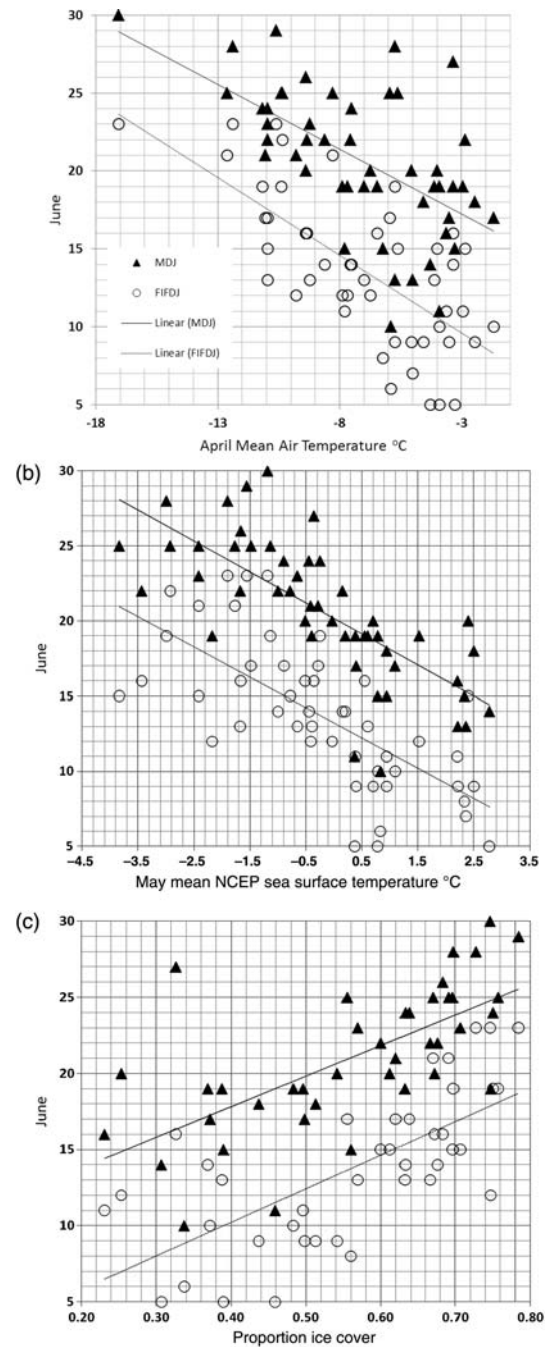


Figure 3. Dates in June of the 15th (FIFDJ; open circles) and 50th (MDJ; solid triangles) percentiles of Chinook salmon cpue (1961–2009) vs. (a) AMATC, (b) MSSTC, and (c) PICE.

value indicated an earlier-than-average migration; however, the actual migration actually happened 7.7 days later. Two other predictions of annual median dates had residuals of a week or more (1983 and 1996; Figure 4a, large solid triangles). However, the migrations were modelled correctly as earlier than average, although the model was not able to capture the magnitude of the actual MDJ in these years. The best model of FIFDJ [Equation (2)] was better able to capture the early timing of the migration in 1998, having a residual of only 4.6 days (Figure 4b). Predictions of FIFDJ by Equation (2) in 1983 and 1996 had the largest observed residuals for this model, 5.8 and

Table 3. Multiple regression and analysis of variance statistics in order of correlation for median date in June (MDJ) and date in June of 15th percentile (FIFDJ) as functions of May mean SST °C (MSSTC), April mean air temperatures °C (AMATC), 1961–2009, and average proportion ice cover, 20 March–1 June, PICE, 1970–2009.

Parameter	MULTR	ARSQ	s.e.	n	p
MDJ					
PICE and AMATC	0.715	0.484	3.39	40	1.81×10^{-06}
MSSTC	0.728	0.520	3.24	49	3.06×10^{-09}
MSSTC and PICE	0.754	0.545	3.18	40	1.77×10^{-07}
MSSTC and AMATC	0.769	0.574	3.05	49	1.12×10^{-09}
MSSTC and PICE and AMATC	0.772	0.563	3.12	40	3.07×10^{-07}
FIFDJ					
MSSTC	0.689	0.463	3.54	49	4.45×10^{-08}
MSSTC and PICE	0.741	0.525	3.43	40	3.98×10^{-07}
PICE and AMATC	0.747	0.534	3.39	40	2.72×10^{-07}
MSSTC and AMATC	0.787	0.603	3.05	49	2.25×10^{-10}
MSSTC and PICE and AMATC	0.791	0.594	3.17	40	8.32×10^{-08}

Multiple correlation coefficient (MULTR), adjusted coefficient of determination (ARSQ), standard error (s.e.), sample size (n), and significance of F (p).

5.5 days, respectively; these were nonetheless smaller than the residuals of the corresponding predictions of MDJ for these years by Equation (1).

Discussion

Although the effects of global warming on the environmental factors in the limited geographic localities of this study (air and model SSTs and proportion ice cover) are not so far readily apparent, the strength of environmental control of marine exit timing by covariates of temperature makes it reasonably certain that marine exit timing of Yukon Chinook will track climate change. Our data and analysis are consistent with the hypothesis of control of the timing of marine exit by factors related to water-column stability in a nearshore marine staging area. However, the specifics of the hypothesis could not be tested by our results, because of lack of ambient measures of environmental conditions. The hypothesis is supported by observations in the literature, which are presented below to explain it more fully and to develop its content.

For salmon preparing to exit the sea, migratory behaviour and sexual maturation are ultimately controlled by endocrine processes initiated and influenced by the photoperiod (reviewed in Cooperman *et al.*, 2010). In March, Yukon River Chinook salmon are located on feeding grounds along the continental shelf break of the Bering Sea within a relatively narrow range of longitudes, roughly 55–59°N (see Figure 15, Myers *et al.*, 2009). As a stock-specific response to increasing photoperiod (Gilhousen, 1960; Quinn, 1982; Hasler and Scholz, 1983), the individual Chinook in our hypothesis start to leave the shelf break area after the vernal equinox to gather in a nominal marine staging area between St Lawrence Island and the Yukon River delta, 62–63°N by 166–169°W (Figure 1). Historically, models of Pacific salmon migration have assumed that the timings of adults, as observed in freshwater, are influenced by variations in temperatures, currents, and other environmental variables over the big geographic areas between the river and the oceanic feeding areas (Gilhousen, 1960; Quinn, 1982; Blackbourn, 1987; Hodgson *et al.*, 2006; Keefer *et al.*, 2008; Anderson and Beer, 2009), but

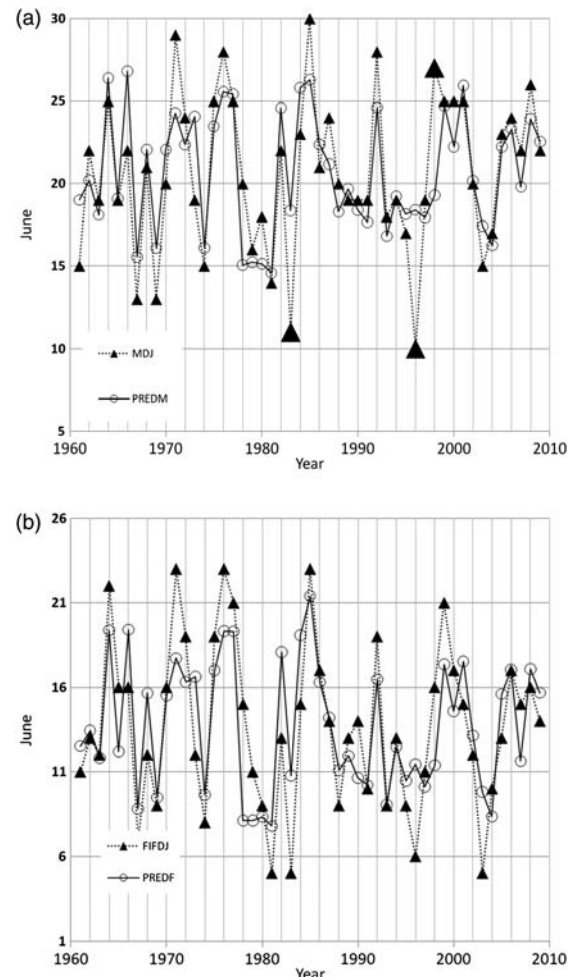


Figure 4. (a) Observed 50th percentile (MDJ; solid triangles) of Chinook salmon migration and predicted MDJ (PREDM; open circles) from Equation (1) for 1961–2009. Observed MDJ in years denoted by (three) large triangles have predictions with residuals larger than a week. (b) Observed 15th percentile (FIFDJ; solid triangles) of Chinook salmon migration and predicted FIFDJ (PREDF; open circles) from Equation (2) for 1961–2009. Note that none of the residuals is greater than or equal to a week.

conditions in the ocean environment outside the nominal staging area were not included in our hypothesis. All Chinook stocks in our hypothesis pooled, or accumulated, in the nominal staging area for a variable amount of time before marine exit, thereby reducing or eliminating the influence of environmental factors experienced before reaching the staging area and eliminating the need to account for average distance from the river of origin at the start of homeward migration.

Control of marine exit by environmental factors related to water-column stability is supported by observations of Atlantic salmon movements and fine-scale vertical hydrographic features in nearshore areas (Westerberg, 1982; Døving *et al.*, 1985). In a field experiment, the movements of maturing salmon with and without intact sense of smell were compared with the ambient fine-scale vertical hydrographic structure in coastal marine waters. Differences in behaviour between the two groups were inferred to result from the differing ability to navigate towards freshwater using olfactory discrimination of differences in

concentrations of odours (olfactants) between small horizontal layers of the water column. An analysis of vertical movements of sockeye salmon approaching freshwater entry revealed that they most frequently swam near the depth of the steepest horizontal gradients in temperature, but did not do so exclusively (Quinn and terHart, 1987; Quinn *et al.*, 1989). Although vertical movements of sockeye in coastal marine waters corresponded to the vertical distribution of temperature and salinity, horizontal movements were not explained fully by temperature and salinity, pointing to other, unmeasured environmental factors as navigational cues (Quinn *et al.*, 1989). Pauses, or pooling, of salmon migration in estuaries before entering freshwater for periods of the range of observed median dates of timing in this study (20 d), and longer, have been noted by multiple authors (Mundy *et al.*, 1993; Olson and Quinn, 1993; Cooke *et al.*, 2004). Cooke *et al.* (2008) reported preliminary results that early freshwater entry for late-run Fraser River sockeye salmon is correlated with the degree of coastal mixing, here termed water-column stability. Pooling of Chinook salmon in the Columbia River estuary was advanced to explain in part the influence of river flow and water temperature on variations in timing of maturing adult salmon (Keefer *et al.*, 2008).

The often-observed pooling of salmon near river mouths might be explained by the need for a period of exposure to brackish water before freshwater entry to allow osmoregulatory physiological mechanisms to adapt to freshwater. Physiological salinity sensors that allow salmon and other fish species to respond to changes in ambient salinity have been identified at the molecular level (calcium-sensing receptor proteins, CaRs; Nearing *et al.*, 2002). The sensors mediate the change to osmotic competency by responding to alternating changes in ionic strengths of sodium, calcium, and magnesium in ambient waters (Nearing *et al.*, 2002). In our hypothesis, the potential for marine exit of an individual maturing adult salmon is facilitated by exposure to patches or pockets of brackish water of varying salinities created by wind-driven mixing of the water column in the marine staging area.

Salmon arriving in the marine staging areas early in the maturation process do not move into the river immediately, because they are not yet capable of maintaining osmotic balance in freshwater, as explained above (see also Cooperman *et al.*, 2010), and because they might not get sufficient guidance from olfactory cues (Hasler and Scholz, 1983; Ueda *et al.*, 1998) and horizontal salinity gradients (Quinn *et al.*, 1989), depending on the stability of the water column. Once they have progressed to the point of being osmotically competent, Chinook salmon continue to accumulate in the staging areas in the absence of horizontal gradients in olfactory and salinity cues sufficient to guide them into the river.

The hydrographic structure of the water column in the nominal staging area is hypothesized to be very different in warm and cold years, because it is largely controlled by ice extent and duration. As the ice melts in spring, the shelf waters in the northern Bering Sea start the transition into a stratified two-layer system, with cold, dense water subject to tidal mixing on the bottom and warmer, lighter water subject to wind-driven mixing on the top (Danielson and Kowalik, 2005). Tidal mixing was assumed to be negligible for determining ambient temperature–salinity conditions for salmon, which are in the surface waters. According to our hypothesis, the migration is delayed in cold years, because the time required to become ready physiologically to enter freshwater is increased by lack of alternating exposures to cells of

brackish and marine waters. Conversely, in a warm year, propagation of cells of brackish water offshore over broad areas following a period of strong wind-driven mixing is hypothesized to accelerate the migration. Water-column mixing is also hypothesized to accelerate the migration in warm years by providing the fine-scale vertical hydrographic structure to aid salmon navigation, by detecting vertical differences in concentrations of olfactants, temperature, and salinity, as hypothesized earlier by Westerberg (1982). The durations of alternating periods of fine-scale vertical hydrographic structure followed by establishment of larger scale horizontal hydrographic structure (see Quinn *et al.*, 1989) are hypothesized ultimately to explain much of the variability in timing of migration in warm years.

Some warm springs have produced notably late migrations (1998, 2000); however, cool springs have produced only one substantially early migration (1961), which circumstance is explained by the hypothesis. The late migrations that occasionally happen in warm years are explained in the hypothesis by a lower frequency and intensity of wind-driven mixing of the estuary and nearshore marine waters. The rarity of early migrations in cold years over a 49-year period of observation provides strong support for the hypothesis. Consequently, warming of the waters of the staging area is likely to make the timing of marine exit more variable, because the timing would become more dependent on wind events. The combination of the increased risk of overharvesting imposed by early migrations and the uncertainty imposed by an increased influence of wind events in warm springs would make fishery management under global warming much more challenging.

The definitions of “cool” and “warm” are based on proxies for the physical variables that are hypothesized to control the timing of marine exit; these definitions might therefore be imprecise. The proxies are clearly sufficient to characterize “cool” environments that produce late migrations, but might not be as appropriate to define the conditions that produce exclusively early migrations.

Regardless of the hypothesis that guided their selection, the explanatory variables provide managers a reasonably reliable forecast of whether the migration will be early or late, if not of the magnitude of the deviation from average. For example, although the migration of 1998 was estimated by Equation (1) to occur slightly early on 19 June, information on MSSTC considered alone indicated that the migration would most likely be late. All 17 of the observed late migrations happened following below average MSSTC (-0.234°C) and MSSTC in 1998 was below average (-0.36°C). Nonetheless, below average MSSTC has also been followed by two slightly early migrations (1989; 19 June and 1973; 19 June) and by seven average migrations. Only 2 of the 17 migrations following below average PICE were late (1998; 0.326 and 2000; 0.555) and both migrations followed below average MSSTC. Therefore, an empirical timing forecast rule is that an earlier than average migration will happen whenever MSSTC is above average and PICE is below average. Further development of empirical forecast rules identifying early migrations promises to be particularly important, because management of early migrations is so challenging for managers. As noted earlier, authorizing harvesting early in the season, before preseason abundance estimates can be verified, runs a high risk of overharvesting (Evenson *et al.*, 2009). The risk of overharvesting might be reduced or eliminated if the migratory timing could be verified independently of harvest data (Mundy, 1982).

Although statistically significant, the simple linear model of migratory behaviour as a function of air and SSTs, Equations (1) and (2), did not explain ~40% of the interannual variability in timing, because of an inability to control for other likely sources of variability. One likely source of variability is the lack of measures of the physical ambient (subsurface) conditions. The explanatory variables, ice cover, and air and SSTs are approximate measures of ambient temperature and salinity levels in the staging area. Direct measures of historical ambient physical conditions do not exist (Danielson and Kowalik, 2005). Although other oceanographic model reanalyses might provide estimates of ambient conditions, uncertainty regarding the actual location of the salmon in the nearshore marine environment and the ambient physical conditions in those locations will invariably introduce substantial uncertainty into our predictions. Direct measures of fish location in relation to fine-scale hydrographic structure using a combination of ultrasonic fish tags and oceanographic instruments developed and applied to Atlantic salmon by Westerberg (1982), as later applied to Pacific salmon by Quinn and terHart (1987), might be possible in warm years; however, the presence of ice requires developing and applying new approaches for Yukon River Chinook.

Another source of variability not currently accounted for in our models stems from the method of estimating the response variable, i.e. percentiles of cpue. Cumulative daily percentiles of annual cpue are approximate measures of the relative magnitudes of the daily number of Chinook salmon passing the sampling localities at Big Eddy and Middle Mouth. One basic assumption of any net sampling is that cpue is proportional to the number of fish available to the fishing gear and that the proportionality remains stable in time and space, so that it can be taken as a constant, known as catchability (Quinn and DeRiso, 1999). Catchability is the fraction of the population removed by a unit of effort in a unit of time.

Changes in catchability during the course of a migratory season are a source of uncertainty in the timing predictions of our models; however, interannual changes in catchability are not. Gillnets are size-selective, so interannual changes in the average size composition of the Chinook populations (Evenson *et al.*, 2009) could change the annual catchability. Factors such as the changing hydrology of the river at the fishing sites, differing materials used to manufacture the gillnets, and the differing fishing skills of the crews employed are likely to change the annual catchability over a 49-year period.

Other possible sources of uncertainty in our model predictions are (i) genetic differences among stocks (spawning populations), (ii) within stock genetic differences, and (iii) variability in freshwater factors, such as river flow (Anderson and Beer, 2009). The relevance to our model of variability inherent in the phenotypic expression of genetic differences in migratory behaviour by individuals within a stock depends on whether or not those genetic attributes are actually expressed at the sampling sites. In our hypothesis, the environmental (physical) factors have approximately the same effect on the physiology of the timing of marine exit of all individuals in all stocks. Nonetheless, as the migrations proceed upriver, the cumulative effects of physical conditions in different parts of the watershed and the expression of genetically based stock-specific differences in migratory behaviour influence the observed timing. Should the multiple populations (lower, middle, and upper) identified genetically by the sources used by Utter *et al.* (2009) exhibit distinct characteristic timings in the

lower river, as opposed to being well mixed as hypothesized, the percentile estimates of timing would reflect changes resulting from changes in relative abundances of the populations in addition to reflecting the changes related to the explanatory (environmental) variables used here. Based on analysis of a limited number of samples, some differentiation in timing by population possibly happen in the lower river, at least for upper (Canadian) river populations (Templin *et al.*, 2005). Genetic stock identification and application of electronic tagging technologies (Cooke *et al.*, 2008) are essential for reducing the uncertainty of the predictions of timing.

Conclusions

Phenology of Chinook salmon in the lower Yukon River is most likely controlled by environmental factors related to water-column stability during spring that are represented by SST, air temperature, and sea ice cover. The environmental control factors will change as the warming projections of the IPCC model ensemble are realized. Long-term increases in average sea surface and air temperatures and corresponding decreases in spring ice cover in the marine staging areas will result in earlier migrations, on average, with potentially much larger interannual variability in the timing of migration as the incidence of wind-driven mixing of the water column increases. An increased frequency of early migrations and increased influence of wind events would both increase the risk of overharvesting, thereby making management more challenging. During the period of this study (1961–2009), the modelled sea surface and air temperatures and ice cover of the marine staging areas of Norton Sound and the northern Bering Sea did not reflect the warming of the atmosphere apparent in the Yukon River watershed to the west and of the sea surface above the Arctic Circle to the north. The annual median timing of marine exit of Yukon River Chinook salmon remained stable about a long-term mean of 21 June for 1961–2009.

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