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ARTICLE

Migration Trends of Sockeye Salmon at the Northern Edge of Their Distribution

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Abstract
Climate change is affecting arctic and subarctic ecosystems, and anadromous fish such as Pacific salmon *Oncorhynchus* spp. are particularly susceptible due to the physiological challenge of spawning migrations. Predicting how migratory timing will change under Arctic warming scenarios requires an understanding of how environmental factors drive salmon migrations. Multiple mechanisms exist by which environmental conditions may influence migrating salmon, including altered migration cues from the ocean and natal river. We explored relationships between interannual variability and annual migration timing (2003–2014) of Sockeye Salmon *O. nerka* in a subarctic watershed with environmental conditions at broad, intermediate, and local spatial scales. Low numbers of Sockeye Salmon have returned to this high-latitude watershed in recent years, and run size has been a dominant influence on the migration duration and the midpoint date of the run. The duration of the migration upriver varied by as much as 25 d across years, and shorter run durations were associated with smaller run sizes. The duration of the migration was also extended with warmer sea surface temperatures in the staging area and lower values of the North Pacific Index. The midpoint date of the total run was earlier when the run size was larger, whereas the midpoint date was delayed during years in which river temperatures warmed earlier in the season. Documenting factors related to the migration of Sockeye Salmon near the northern limit of their range provides insights into the determinants of salmon migrations and suggests processes that could be important for determining future changes in arctic and subarctic ecosystems.

Climate warming is having measurable effects on freshwater ecosystems by altering the physical environment, with some of the most pronounced changes occurring in arctic and subarctic regions (Schindler and Rogers 2009; Williamson et al. 2009). Conservation concerns over the potential consequences of the altered physical environment on salmonid populations are growing. Improving our understanding of how environmental conditions can affect salmon life history by influencing the timing of adult salmon migration into freshwater for reproduction is a primary research need (Juanes et al.

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2004; Crozier et al. 2011; Hinch et al. 2012; Kovach et al. 2015). The timing of freshwater entry for reproduction is a life history trait that can influence all life history stages and often differs among salmon populations because of strong local adaptation to heterogeneous environmental conditions, including climatic variation (Crozier et al. 2011; Kovach et al. 2015).

An examination of trends and interannual variation in migration timing with respect to environmental conditions can reveal migration cues that, if sensitive to climate change, could have implications for population and ecosystem dynamics. Variation in migration timing influences population dynamics, as migration timing constrains the conditions experienced in the river and on the spawning grounds, thus impacting spawning success (Rand et al. 2006). Shifts and interannual variation in migration timing influence ecosystems by making the timing of acquiring salmon resources more difficult to predict for salmon consumers, including commercial and recreational fisheries (Hodgson et al. 2006; Mundy and Evenson 2011; Kovach et al. 2015). Currently, we lack empirical data on environmental drivers of interannual variation in migration timing in high-latitude ecosystems (Kovach et al. 2015).

Sockeye Salmon *Oncorhynchus nerka* are ecologically and economically important throughout their range. After 1–3 years in the ocean, adult Sockeye Salmon return to their natal rivers in midsummer, cease feeding, and begin a physiologically taxing upriver migration to spawn (Burgner 1991; Schindler and Rogers 2009; Hinch et al. 2012). The migration of salmon through the ocean to their natal river is under strong genetic control and likely triggered by population-specific responses to photoperiod (Hodgson et al. 2006 and references therein). In addition, migration timing is strongly heritable, with low plasticity (Quinn and Adams 1996; Quinn et al. 2007; Crozier et al. 2008, 2011). However, the phenological step of entering freshwater can be altered considerably in some years, as demonstrated by Sockeye Salmon arriving more than 10 d earlier into the Columbia River (Crozier et al. 2011). Other populations of Sockeye Salmon have been observed migrating into freshwater later than they did historically, likely due to warmer temperatures (Kovach et al. 2015).

Multiple mechanisms exist by which ocean and freshwater conditions may influence migrating salmon, thereby creating interannual variability in freshwater entry (Quinn and Adams 1996; Cooke et al. 2004; Crozier et al. 2011; Kovach et al. 2015). Broad-scale ocean conditions may influence migration timing by determining the energy state of adults when they enter freshwater (Kovach et al. 2015). For instance, Cooke et al. (2004) postulated that fish with lower energy would migrate earlier. The Pacific Decadal Oscillation (PDO) is an index of oceanwide temperature conditions that could have relationships with the energy level of fish. As defined by Mantua et al. (1997), the PDO is "the leading principal component of North Pacific monthly sea surface temperature (SST) that represents Pacific climatic variability and correlates with changes in northeast Pacific marine ecosystems." Delayed timing of Sockeye Salmon migrations in southeast Alaska has been correlated with positive PDO values (Kovach et al. 2015). For Alaska, the PDO also represents other large-scale patterns of SST, such as the El Niño–Southern Oscillation (Downton and Miller 1998; Keefer et al. 2008). The North Pacific Index (NPI) also integrates broad-scale conditions over the ocean and is derived from variations in atmospheric surface level pressure that influence wind patterns, storms, and ocean productivity (Trenberth and Hurrell 1994; Crozier et al. 2011). Ocean conditions represented by the NPI could affect the energy level of fish when they are staging for freshwater entry. Ocean conditions, particularly temperature, influence the location of the fish across the ocean and thus the distance remaining to the natal stream, which in turn affects the timing of freshwater entry (Blackbourne 1987; Hodgson et al. 2006).

While salmon stage in the ocean before entering their natal river, SST and the extent of sea ice in the staging area may influence the start of the freshwater migration (Mundy and Evenson 2011). In the staging area, SST is representative of the wind-driven, mixed layer of the water column (Mundy and Evenson 2011). Similarly, sea ice extent is an environmental condition that favors water column stability when present. Water column stability creates a barrier with freshwater mixing in the staging area, limiting exposure to brackish water and thereby delaying migration by reducing olfactory and salinity cues that help guide individuals into the river (Mundy and Evenson 2011). Furthermore, migration timing can be related to freshwater temperatures and flows by stimulating initiation of migration, by affecting travel rates, or by delaying passage due to unsuitable conditions (Gilhousen 1990; Quinn et al. 1997; Hodgson et al. 2006). In the Fraser River, British Columbia, high flows are often associated with later migratory timing, as higher flows are harder to swim against, whereas warmer river temperatures often lead to earlier migration to avoid increasingly adverse swimming conditions (Hodgson and Quinn 2002; Hodgson et al. 2006).

In addition to environmental cues, characteristics of the Sockeye Salmon run itself may influence trends and interannual variability in migration timing. The size of the annual run may influence migration timing simply due to the number of fish that need to pass through the river system. A shorter run duration would be expected when there are fewer returning fish in a given year. However, run size may also alter timing, as group size could influence the ability to migrate in the ocean and through the river (Berdahl et al. 2016). An optimal-sized group could influence migration timing by enhanced navigation ability and gradient tracking through collective behavior (Berdahl et al. 2016). Variation in life history patterns of freshwater and ocean residence times (e.g., 1 year in freshwater and 2 years in the ocean; 1 year in freshwater and 3 years in the ocean; etc.) of fish that return in a given year may also influence timing by affecting run size. Age-classes of Sockeye Salmon have been found to differ in their timing of river entry, a pattern that is likely related to energetic condition (Newell et al. 2007; Katinic et al. 2017).

Exploring whether and how environmental conditions are linked to migration timing of Sockeye Salmon and potentially drive interannual variability near the northern limits of their range will provide additional perspectives on the determinants of Sockeye Salmon population dynamics and will inform conservation efforts working to anticipate anthropogenic impacts. Identifying the drivers of the population will explain current conditions and help to anticipate future conditions in an environment that is rapidly changing. Furthermore, understanding the determinants of populations at the northern limit will assist in anticipating the processes that are important for populations undergoing range expansion, as is anticipated for salmonids (Logerwell et al. 2015). Regionally, salmon populations respond similarly to climatic variables, but studies on Sockeye Salmon in the high latitudes are lacking (Mundy and Evenson 2011; Kovach et al. 2015). The Pilgrim River, Alaska (Figure 1), provides a tractable high-latitude system for study, as there is one population of Sockeye Salmon with a short migration and no commercial harvest or hatchery influence. Commercial harvest can have a strong selective effect on populations (Kendall and Quinn 2009; Kendall et al. 2009), as can hatcheries (Ford et al. 2006). The presence of one Sockeye Salmon population suggests that the Pilgrim River would not benefit from the portfolio effect seen in other Sockeye Salmon watersheds (Schindler et al. 2010). Moreover, these Sockeye Salmon may be more responsive to environmental conditions than to genetic determinants because of their short migration distance (Hodgson et al. 2006). The number of returning adult Sockeye Salmon varied dramatically across the years of this study (Keith 2016), further indicating that this population is sensitive to environmental and/or anthropogenic drivers.

Predicting how migratory timing will change under global warming scenarios requires developing an understanding of how environmental factors interact with salmon migrations (Cooke et al. 2008; Mundy and Evenson 2011; Kovach et al. 2015). We explored relationships between the river entry timing of returning Sockeye Salmon spawners and the PDO, NPI, SST, sea ice extent, river temperature, and river height. These environmental variables reflect climatic drivers operating at broad, intermediate, and local spatial scales (Kovach et al. 2015). We used the expected schedule and location of spawning adults (Mundy and Evenson 2011) to determine the temporal and spatial scales for environmental variables. We also considered characteristics of the Sockeye Salmon migration, including run size and the proportion of fish that spent 2 years in the ocean before returning to the river.

METHODS

*Study area.—*We examined Sockeye Salmon returning to the Pilgrim River (65.196°N, 165.409°W), Port Clarence District, near Nome, Alaska. Sockeye Salmon migrate from winter grounds in the Bering Sea and Gulf of Alaska, along the coast through Norton Sound, and up to the mouth of the Pilgrim River outside Port Clarence (Figure 1). We expected salmon to be staging in the ocean outside of the Pilgrim River during late May through June. The initiation of freshwater entry begins in late June or early July. The river distance from the mouth to the spawning grounds at Salmon Lake is approximately 180 km, with an elevation gain of 150 m. In addition to Sockeye Salmon, other salmon returning to the Pilgrim River include Chum Salmon *O. keta*, Pink Salmon *O. gorbuscha*, Coho Salmon *O. kisutch*, and a limited number of Chinook Salmon *O. tshawytscha*. Year-round residents include Arctic Grayling *Thymallus arcticus*, whitefish *Coregonus* spp., Burbot *Lota lota*, and Northern Pike *Esox lucius*. Anadromous Dolly Varden *Salvelinus malma* also occur in the watershed.

*Sockeye Salmon run timing.—*To determine whether adult Sockeye Salmon have shifted their return timing through the Pilgrim River, we used daily counts of Sockeye Salmon collected at a fish weir from 2003 to 2014 (Keith 2016). The fish weir was located midway between the mouth of the river and the spawning grounds and was operated during the summer by the Norton Sound Economic Development Corporation with assistance from the Alaska Department of Fish and Game (Figure 1). The fish weir was operated from ice-out in late June until early September. Sockeye Salmon begin passing through the weir at the end of June or early July and finish by late August, resulting in a run that lasts about 50 d. The weir trap was monitored 24 h per day and checked hourly. All fish were counted, and a random subset of Sockeye Salmon (n = 5–20 fish per day) was sampled for length (most years) and age (determined from a scale sample).

*Ocean conditions.—*We used the PDO and NPI from January through June to represent the oceanwide conditions Sockeye Salmon experience leading up to their freshwater spawning migration. Monthly mean PDO values for January–June (Joint Institute for the Study of the Atmosphere and Ocean [JISAO]; jisao.washington.edu/pdo/) were averaged to obtain an index for each year from 2003 to 2014. The NPI values (Hurrell 2016) were similarly averaged. We examined the PDO and NPI from January through freshwater entry to explore the influence of oceanwide conditions on the energy level of returning Sockeye Salmon and thus migration timing. The timing of the large-scale ocean conditions is similar to that described by Crozier et al. (2011) and Kovach et al. (2015).

Daily sea ice concentration estimates for 2003–2014, derived from the 25-km-pixel resolution Special Sensor Microwave Imager/Sounder and Special Sensor Microwave/Imager (Cavalieri et al. 1996; http://nsidc.org/data/nsidc-005),

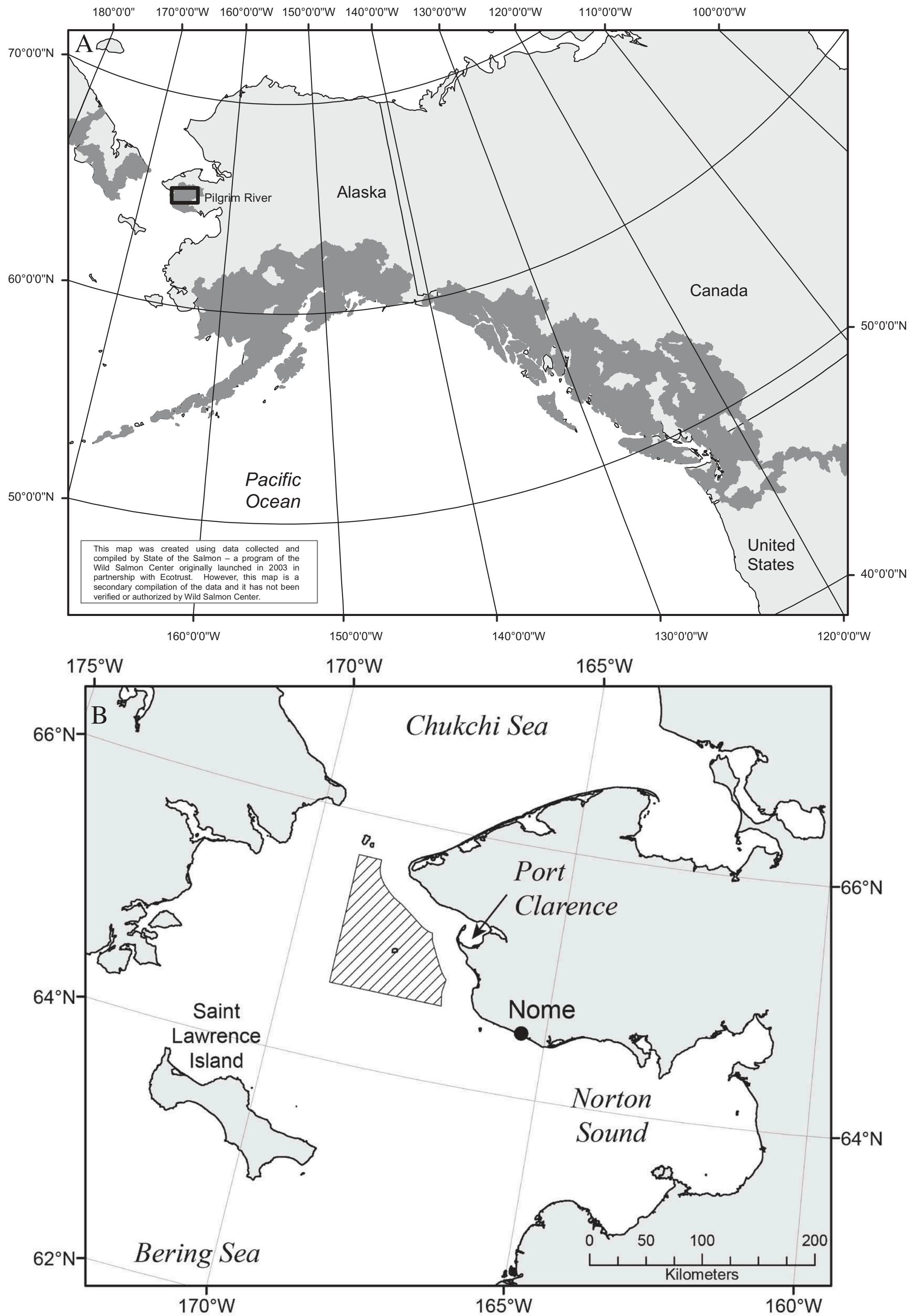

FIGURE 1. Maps of the **(A)** distribution of Sockeye Salmon in North America and Asia, **(B)** staging area of Pilgrim River (Alaska) Sockeye Salmon, and **(C)** spawning migration of Sockeye Salmon in the Pilgrim River. Latitude and longitude lines are depicted in panels (A) and (B).

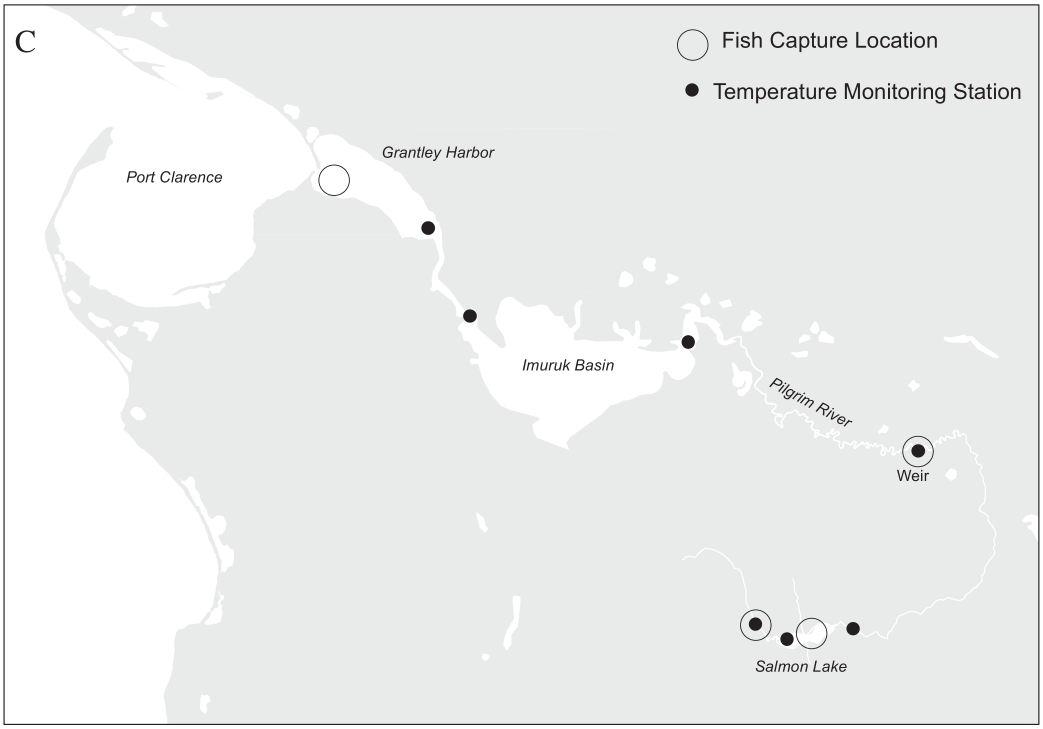

FIGURE 1. Continued.

were obtained for the ocean region outside the mouth of the Pilgrim River (Figure 1). Higher-resolution (6.25-km-pixel resolution) sea ice data exist for the region from the Advanced Microwave Scanning Radiometer (AMSR)–Earth Observing System and from the AMSR-2 (Spreen et al. 2008; http://www.iup.uni-bremen.de:8084/amsr2/index.html); however, the AMSR data have a temporal gap, and we further found the daily ice estimates in our study area to be similar between the high- and low-resolution data. We calculated the median ice value among all 25-km-pixels for each day, and we then averaged the medians for each month annually. Daily SST data were acquired with 0.08789-degree-pixel resolution (www.remss.com; Figure 1) and were summarized in the same manner as the sea ice data. We expected sea ice extent to influence water column stability and to have the highest interannual variability in May. We examined SST for April–June as a measure of water column stability and migration signals during the period we expected salmon to be staging for freshwater entry (Mundy and Evenson 2011).

River conditions.—River temperature and river height were measured in situ during July and August from 2003 to 2014 at the weir site (Figure 1). River temperature and river height were measured in the morning (0800 hours) and evening (2000 hours), and we averaged them to represent the daily value. We used the date of maximum river temperature to compare patterns of river temperatures among years. To represent river flow, we determined the date of the peak river height for each year (Crozier et al. 2011). To compare among years, river height data were only available for July from day of year (DOY) 185 to DOY 211.

Analysis.—We examined several milestones of the Sockeye Salmon migration, including the dates by which 1% (DOY1), 50% (DOY50), and 99% (DOY99) of the annual total run had passed the weir each year. Duration of the run was defined as DOY99 minus DOY1. We also determined the annual run size for each year and the proportion of the run consisting of fish that spent 2 years in the ocean (2-ocean fish), combining fish that spent 1–2 years in freshwater and 2 years in the ocean. The number of Pilgrim River Sockeye Salmon that spend 2 years in the ocean is highly variable across years. We examined trends in migration timing across years and compared ocean and river conditions through time by using linear regression (Hodgson et al. 2006). We also examined trends in characteristics of the Sockeye Salmon run, including run size and 2-ocean fish.

Next, we evaluated the relative contribution of the ocean and river predictors along with run characteristics by using Akaike's information criterion corrected for small sample sizes (AIC_c). The AIC_c is a maximum likelihood estimate of the Kullback–Leibler information criterion with which estimation and model selection can be combined under the framework of optimization (Burnham and Anderson 1998). We examined migration timing by comparing a global model exploring changes in duration and DOY50 with predictor variables that reflect climatic drivers operating at broad, intermediate, and local spatial scales (Kovach et al. 2015). We chose one ocean predictor (broad scale), one staging area predictor (intermediate scale), and two in-river predictors (local scale). The maximum value of the correlations between predictor variables used in model sets was $r < 0.61$ (Table 1). We used a liberal cutoff given the exploratory goals of our analysis. The NPI and PDO are strongly correlated, as are sea ice and SST, thus representing similar information in the models. The NPI was chosen instead of PDO and sea ice was chosen instead of SST to reduce correlations between predictor variables in model subsets comparing predictors from the broad, intermediate, and local spatial scales. We included both the date of maximum river temperature and the date of peak river height because they are not correlated. We also included run size as a characteristic of the Sockeye Salmon run. To test alternate models, we examined all combinations of variables while using no more than three covariates per model, similar to Crozier et al. (2011). Predictors were included in an equal number of models, and the relative importance of predictors was assessed across all models (Arnold 2010). We compared model-averaged coefficients, predictor weights, and predictor ranks to evaluate the relative contributions of predictor variables (Arnold 2010). Analysis was conducted using the package "MuMIn" (Barton 2016) in R statistical software (R Core Team 2016).

RESULTS

Run Timing across Years

Sockeye Salmon migration timing changed over time (Figure 2A). The DOY1 ranged from 180 to 191 and trended later ($r^2 = 0.317$, $P = 0.056$) during 2003–2014. In contrast, DOY99 trended earlier ($r^2 = 0.415$, $P = 0.02$) and ranged from 215 to 233. The trend in DOY50 was not statistically significant ($r^2 = 0.23$, $P = 0.11$). The trends in DOY1 and DOY99 led to a significantly shorter duration of the migration run ($r^2 = 0.589$, $P = 0.0035$; Figure 2B).

Ocean and River Conditions across Years

Neither the PDO ($r^2 = 0.19$, $P = 0.15$) nor the NPI had significant trends through time (Figure 3A, B). The PDO and NPI were correlated with each other, and PDO was also related to the date of peak river height (Table 1). Both sea ice extent and SST in the staging areas decreased with time and were highly correlated with each other (Figure 3C, D; Table 1). In contrast, the in-river conditions of temperature and flow patterns exhibited no trend through time and were not correlated (Figure 3E, F; Table 1). River temperature averaged 12.1°C and ranged from 7°C to 16.75°C across all years. The date of maximum river temperature ranged from DOY 186 to DOY 208, whereas the date of peak river height ranged from DOY 185 to DOY 211 across years.

Characteristics of the Sockeye Salmon Migration across Years

The number of Sockeye Salmon passing the Pilgrim River weir ranged from 85,417 in 2004 to 953 in 2009, with a strong decreasing trend across years ($r^2 = 0.65$, $P = 0.002$; Figure 3). The proportion of 2-ocean fish among returning Sockeye Salmon ranged from 1% to 65% but did not vary with time (Figure 3). The proportion of 2-ocean fish was highly correlated with the PDO and the NPI (Table 1).

Model Comparison

In predicting the duration of the migration, run size was the most important variable, with the largest model coefficient and predictor weight (Table 2). Larger run sizes were related to a longer run duration (Figure 4A). Warmer water temperatures (SSTs) in the staging area were also associated with a longer duration of the migration, but the model coefficient and predictor weight for SST indicated less influence than run size (Table 2; Figure 4). The NPI also contributed to explaining trends in the duration of the migration but had a smaller model coefficient and lower predictor weight than the highest-ranked predictors (Table 2). Increasing NPI was related to a shorter run duration (Figure 4C). The date of peak river height and the date of maximum temperature had minor contributions in explaining the run duration.

Run size was also the most important factor in the model predicting interannual variability of DOY50, with a large model coefficient and high predictor weight (Table 2). Larger run sizes led to earlier dates when 50% of the total run had commenced freshwater migration (Figure 5A). In-river conditions were also important for explaining interannual variability in DOY50; specifically, the date of maximum river temperature had a large model coefficient and a high predictor weight (Table 2). The earlier in the summer that the maximum temperature occurred, the later in the year the DOY50 of the run occurred (Figure 5B). No other variables had large coefficients or predictor weights across models predicting DOY50.

DISCUSSION

Migration timing of Sockeye Salmon differed among years in 2003–2014, with a trend toward a later start and an earlier end and therefore a shorter overall duration of the run. Changes in migration timing have been documented for salmonids in other systems. For example, Sockeye Salmon presently migrate up the Columbia River, Washington–Oregon, 10.3 d earlier than they did in the 1940s (Crozier et al. 2011). In contrast, Sockeye Salmon in southeast Alaska migrate into freshwater later (average = 0.16 d/year) than they did historically and also display a longer run duration (Kovach et al. 2015). Changes in Sockeye Salmon across their range highlight that salmon populations are undergoing a variety of rapid evolutionary and behavioral changes in the timing of freshwater entry for reproduction (Crozier et al. 2011; Kovach et al. 2012). Quantification of regional differences and environmental relationships across different latitudes is insightful for local

TABLE 1. Correlations (r) between environmental variables, including the Pacific Decadal Oscillation (PDO), North Pacific Index (NPI), sea ice extent in the Sockeye Salmon staging area (Ice), sea surface temperature (SST) in the staging area, date of maximum temperature in the Pilgrim River (River temp), and day of peak river height (River height). In addition, correlations between each environmental variable and the size of the Sockeye Salmon run or the proportion of individuals in the run that spent 2 years in the ocean (2-ocean) are presented. Dashes indicate a comparison between the same variable.

Variable	PDO	NPI	Ice	SST	River temp	River height	Run size	2-ocean	Year
PDO	–	–0.675	–0.313	0.342	0.203	–0.710	0.534	0.792	–0.443
NPI		–	0.500	–0.616	–0.269	0.446	–0.337	–0.646	0.292
Ice			–	–0.817	–0.067	0.162	–0.372	–0.485	0.573
SST				–	0.193	–0.344	0.603	0.409	–0.580
River temp					–	–0.168	0.324	0.275	–0.205
River height						–	–0.605	–0.282	0.524
Run size							–	0.503	–0.807
2-ocean								–	–0.350
Year									–

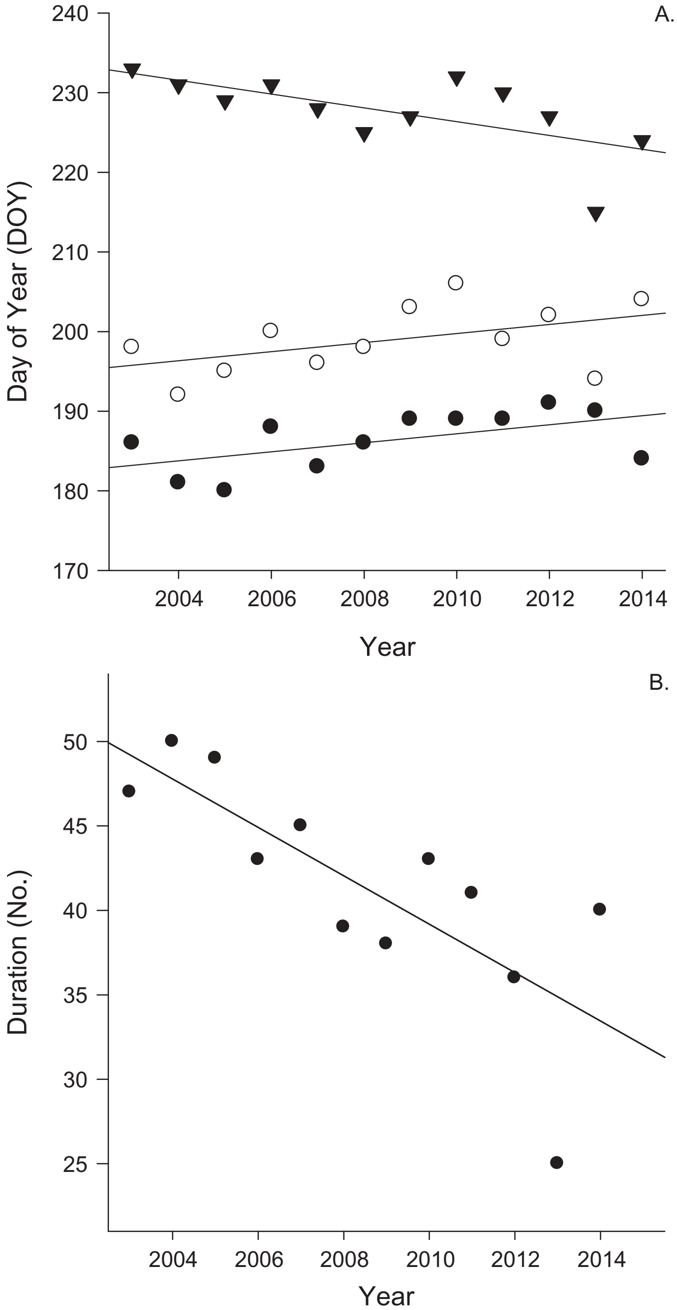

FIGURE 2. **(A)** Sockeye Salmon migration timing milestones, including the day of year (DOY) by which 1% (black shaded circles), 50% (open circles), and 99% (black shaded triangles) of the annual total run had passed the Pilgrim River weir; and **(B)** duration of the migration in the Pilgrim River across years.

TABLE 2. Coefficients of model averages, predictor weights, and predictor ranks across all model subsets explaining the duration of the Sockeye Salmon migration and the date (day of year) by which 50% of the annual total run had passed the Pilgrim River weir (DOY50). The predictor variables include the North Pacific Index (NPI), sea surface temperature (SST) in the staging area, the date of maximum river temperature (River temp), the day of peak river height (River height), and the size of the Sockeye Salmon run.

Predictors	Coefficient	Weight	Rank
Migration run duration			
Run size	2.28	0.55	1
SST	1.48	0.39	2
NPI	–0.70	0.25	3
River height	–0.22	0.12	4
River temp	–0.12	0.1	5
DOY50			
Run size	–2.28	0.82	1
River temp	–1.07	0.53	2
SST	0.01	0.1	3
River height	–0.02	0.08	4
NPI	–0.11	0.07	5

fisheries management and conservation planning. Moreover, understanding the drivers of the population will help to anticipate future impacts from environmental changes and to forecast potential range expansion (Logerwell et al. 2015).

Run size was the primary characteristic related to the migration timing of Sockeye Salmon at the northern edge of their distribution. In the Pilgrim River, run size varied greatly among years and had a strong relationship to the run duration and the midpoint of the run. A decreasing trend in migration duration across study years was underpinned by decreasing run size. The midpoint of the run was reached earlier when the run size was larger. In contrast, an index of population size was unimportant in explaining variation in migration for Sockeye Salmon in the Columbia River, and no trend was found for the population size over a 60-year period from 1950 to 2010 (Crozier et al. 2011). Although run size represents the number of individuals returning to freshwater for spawning and a longer run duration may simply be related to the numbers of fish that ultimately enter the river, run size also raises questions about how group size might affect behavior. As was discussed and reviewed by Berdahl et al. (2016), larger group sizes of migrating salmon can enhance navigation ability and gradient tracking through collective behavior, thereby speeding up freshwater entry. Larger group sizes may increase the rate of homing through the open ocean to natal streams by the benefit of collective navigation, which minimizes errors in individual directional estimates. Similarly, larger groups enhance the ability to sense and respond to complex environmental gradients (e.g., identifying estuaries) by pooling individual estimates and assessing a larger spatial area. Berdahl et al. (2016) also pointed out that in-river navigation may be improved by gradient tracking from larger group sizes in addition to predator avoidance and hydrodynamics. The benefit of collective gradient tracking would be most apparent in complex river systems such as the Pilgrim River, which contains interconnected lakes, high sinuosity, and complex channel connections in its lower section.

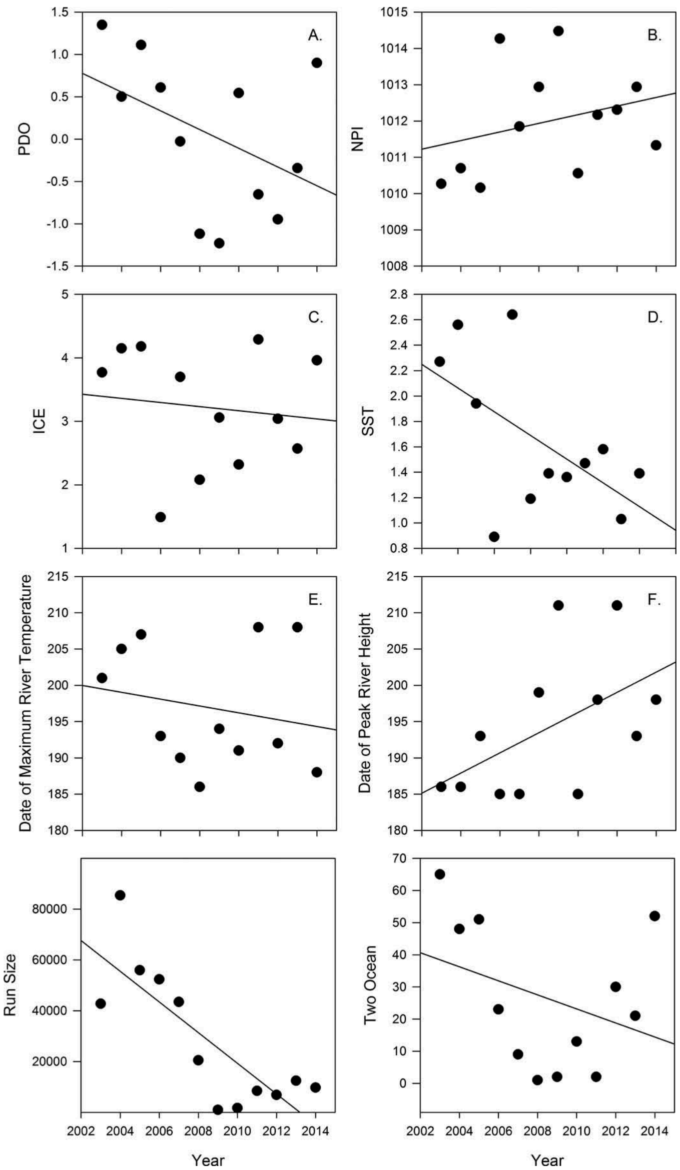

FIGURE 3. Ocean and river variables examined, including the **(A)** Pacific Decadal Oscillation (PDO), **(B)** North Pacific Index (NPI), **(C)** sea ice extent (ICE) in the Sockeye Salmon staging area, **(D)** sea surface temperature (SST) in the staging area, **(E)** date of maximum river temperature, and **(F)** date of peak river height across years. Characteristics of the Sockeye Salmon run (run size and the proportion of fish that spent 2 years in the ocean [two ocean]) are also plotted across years (bottom panels).

Despite the Pilgrim River's location at the northern edge of the Sockeye Salmon's distribution, the NPI was associated with the duration of the migration, suggesting that broad-scale ocean conditions may influence the timing of freshwater entry at high latitudes. We lack information on the specific pelagic location of Sockeye Salmon from the Pilgrim River during the ocean phase of their life history; however, we suspected that environmental conditions represented by the NPI may be influencing the location of fish across the ocean, therefore affecting the distance and time to

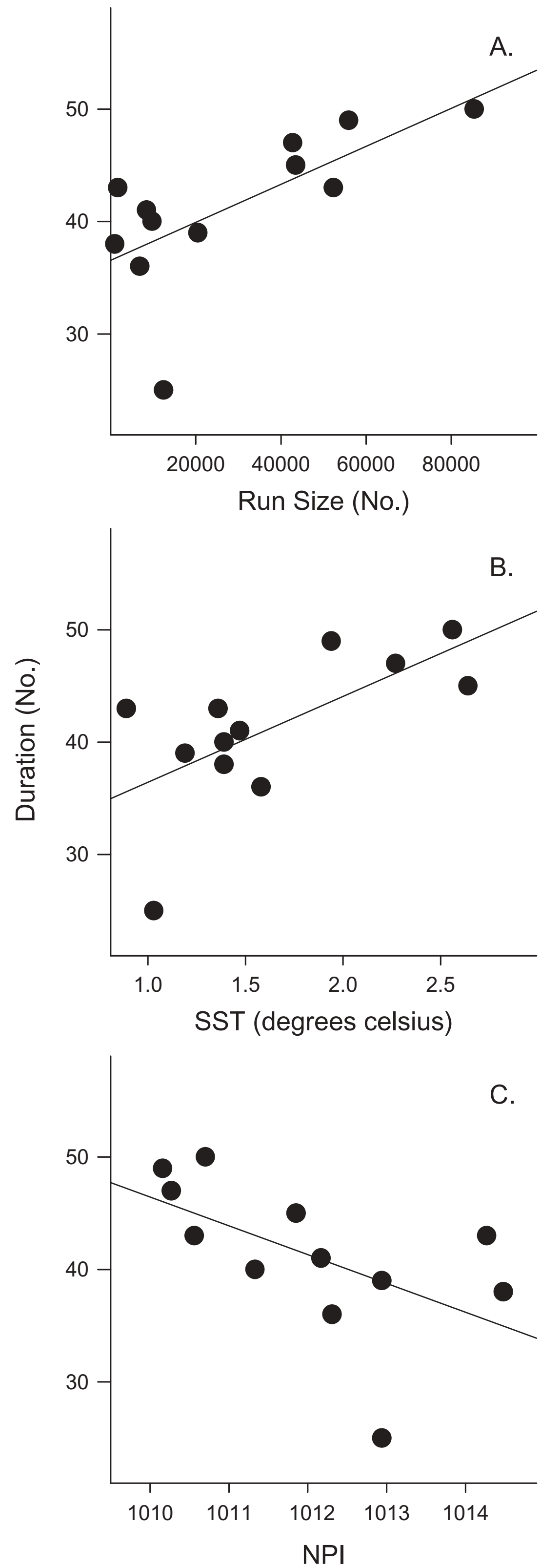

FIGURE 4. Relationship between the duration (number of days) of the Sockeye Salmon migration and **(A)** run size, **(B)** sea surface temperature (SST) in the staging area, and **(C)** the North Pacific Index (NPI).

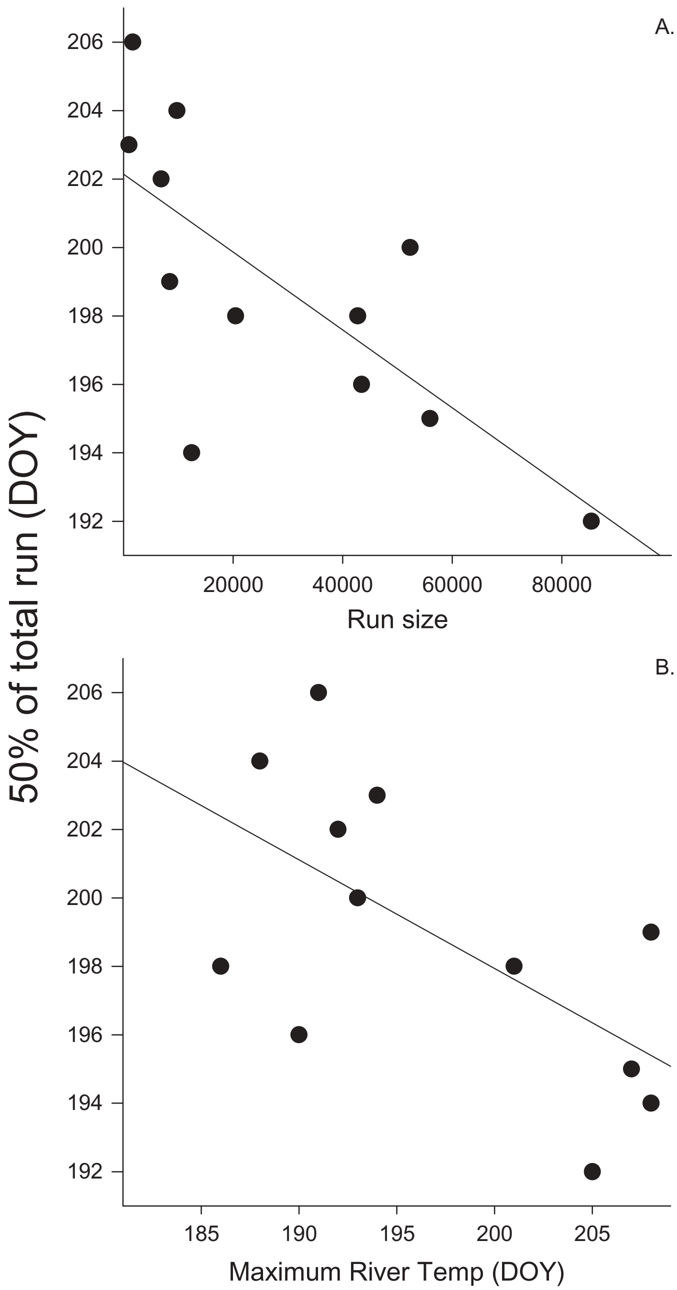

FIGURE 5. Relationship between the date (day of year [DOY]) by which 50% of the annual total Sockeye Salmon run had passed the Pilgrim River weir and **(A)** run size or **(B)** date of maximum river temperature.

return to their natal stream. Blackbourne (1987) suggested that Sockeye Salmon are distributed according to ocean temperatures and that the distance back to the natal river will depend on the pattern of temperature across the ocean (Hodgson et al. 2006). The NPI would then be related to the start of freshwater entry and would influence the run duration. Large-scale ocean conditions that affect the condition of the fish when they arrive at the staging area are also likely to influence freshwater entry (Cooke et al. 2004). If the mechanism is energetic condition of the fish, then the relationship between the NPI and Sockeye Salmon entry into the Pilgrim River suggests that lower NPI values result in lower energy condition of the fish and thus earlier freshwater entry and a longer run duration. Supporting the notion that the NPI influences the condition of Sockeye Salmon, both of the ocean variables (NPI and PDO) had a strong correlation with the proportion of 2-ocean fish. Salmonids in other systems have been linked to these large-scale factors; for example, the PDO influenced Sockeye Salmon and Chinook Salmon migration to the Columbia River (Keefer et al. 2008; Crozier et al. 2011). However, although large-scale factors have been related to run timing, they are often not the strongest predictors if the functional mechanisms involve in-river conditions that are linked to the PDO through storms and river discharges (Keefer et al. 2008).

The SST in the staging area was an important intermediate-scale factor associated with the timing of freshwater entry for Pilgrim River Sockeye Salmon. The SST in early spring has been suggested as a signal that triggers the migration and affects the rates of migration, the schedule of fish maturation, and when salmon enter natal rivers (Myers et al. 2007). Differences in SST in the staging area accord with the ideas of Mundy and Evenson (2011) that interannual variation of environmental conditions in the staging area indicates water column stability and represents the strength of the freshwater signal to initiate upstream migrations. Run duration was longer when SST was warmer in the staging area, as warmer SSTs lead to an earlier start to the migration, thus extending the duration of the run. Interestingly, the SST in the staging area has been getting cooler through time. Sockeye Salmon in southeast Alaska also migrate earlier with warmer SSTs (Kovach et al. 2015). Strong correlations were found between the SST in the staging area and the run timing of Chinook Salmon into the Columbia River, but the direction of the relationship differed among populations within the basin (Keefer et al. 2008).

River conditions influenced interannual variability of the Sockeye Salmon migration in the Pilgrim River. The timing of maximum temperature was related to the midpoint of the run: warm temperature earlier in the migration was related to a later midpoint date, suggesting that earlier maximum temperatures reduce migration speed. The fact that the date of maximum river temperature influenced interannual variation in the run's midpoint also suggests that higher temperatures are energetically costly. River temperature has been influential in the timing of Sockeye Salmon migration in other systems (e.g., Quinn et al. 1997; Cooke et al. 2004; Hodgson et al. 2006), and Sockeye Salmon appear to time their migration to avoid warm in-river temperatures throughout the majority of their range (Hodgson and Quinn 2002). A relationship between temperature patterns and a migration milestone suggests that a more detailed analysis of river temperature influences on migrating Sockeye Salmon in the Pilgrim River would be insightful, especially because the greatest effects of climate warming are occurring at higher latitudes and Sockeye Salmon are likely adapted to the temperatures of the Pilgrim River.

The timing of adult salmon migration into freshwater for reproduction is a critically important life history trait that can influence all life history stages (Crozier et al. 2011; Kovach et al. 2015). Migration timing is an adaptation to long-term average conditions, such as the temperature, flow, and spawning date needs of offspring (Hodgson and Quinn 2002). Identifying the determinants of migration trends and interannual variability in migration timing at the northern edge of the Sockeye Salmon's range helps to anticipate which environmental variables may impact this species in the future. Currently, run size is the primary determinant of Sockeye Salmon migration timing in the Pilgrim River, and an important next step is to tease apart whether changes in migration timing have a feedback on the population size. Identifying the importance of ocean conditions and temperature in the staging area provides another factor that could inform in-season management. For instance, a shorter duration of the migration would reduce opportunities for subsistence harvest. The importance of river temperature highlights the sensitivity of this system and emphasizes that future decisions on human activities within the watershed will need to assess any impacts on river temperature.

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