Response of Pink salmon to climate warming in the northern Bering Sea

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ABSTRACT

Life-history and life-cycle models of Pink salmon (*Oncorhynchus gorbuscha*) are developed to provide insight into production dynamics of northern Bering Sea Pink salmon. Arctic ecosystems, including freshwater and marine ecosystems in the northern Bering Sea, are warming at a rapid rate. Due to their short, two-year life cycle, Pink salmon are well known to respond rapidly to ecosystem change and can provide unique insight into ecosystem impacts of warming Arctic conditions. Life-cycle models suggest a lack of density-dependence for adult Pink salmon spawners in the Yukon River and potential for some density-dependence for adult Pink salmon spawners in the Norton Sound region. Life-history models identify a positive and significant relationship between the abundance index for juvenile Pink salmon and average Nome air temperature during their freshwater residency (August to June). This relationship supports the notion that warming air temperatures in this region (as a proxy for river and stream temperatures) are contributing to improved freshwater survival or increased capacity of freshwater habitats to support Pink salmon production. Life-history models also identify the number of adult Pink salmon returning to Norton Sound and the Yukon River is significantly related to the juvenile abundance in the northern Bering Sea. This result indicates that much of the variability in survival for northern Bering Sea Pink salmon occurs during early life-history stages and that juvenile abundance is an informative leading indicator of Pink salmon runs to this region.

1. Introduction

The Pacific Arctic Region (PAR), that is, the northern Bering Sea, and the Chukchi Sea to the East Siberian and Beaufort seas, is experiencing significant warming and extremes in seasonal sea ice extent and thickness (Frey et al., 2014; Baker et al., 2020; Danielson et al., 2020). Over the past two decades, record summer sea-ice minima (2007, 2011, 2012; 2017 and 2018) have occurred, and climate models project that the southern Chukchi Sea will be sea-ice free for 5 months (July to November) within a decade or two (Overland et al., 2014). In the northern Bering Sea, sea ice is projected to be less common during May, but will continue to be extensive through April (Stabeno et al., 2012). However, recent events during 2017 and 2018 in the northern Bering Sea indicate that open water in this region during winter is already occurring (Stabeno and Bell, 2019). The presence of sea ice during winter and into spring is known to influence summer bottom temperatures; however, climate models project that the loss of seasonal sea ice during spring and into fall months is currently resulting in, and expected in the future to lead to, increased sea surface temperatures during summer months in both the northern Bering Sea and Chukchi Sea (Wang et al., 2012). In addition, the reduction in seasonal sea ice is likely contributing to increased primary and secondary production (Arrigo and van Dijken, 2011) that could shift the ecosystem to a more pelagic state (Grebmeier et al., 2006).

These shifts in the PAR ecosystem are likely to have large impacts on the ecology of upper trophic level species such as fishes, birds, and mammals (Sigler et al., 2011). For instance, the community structure of some upper trophic level species already show evidence of changes in the Chukchi Sea, such as the shift from predominantly piscivorous seabirds to planktivorous seabirds in recent decades (Gall et al., 2017). Large scale distributional shifts of walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*G. microcephalus*) in response to reduced cold pool extent in the northern Bering Sea were also found (Stevenson and Lauth, 2018). Other ecosystem consequences of continued warming have been described elsewhere, such as the Barents Sea, and include changes in zooplankton community structure as well as shifts in species distributions and relative abundances (Hop and Gjøsæter, 2013; Orlova et al., 2013; Fossheim et al., 2015). Because the upper trophic level species are typically top predators, they must adapt via biological responses to physical forcing and thereby are "sentinels" of ecosystem variability and reorganization (Moore et al., 2014). As such, there will likely be fishes that do better under climate warming and those that may not.

The most common salmon species in the PAR include Pink (*Oncorhynchus gorbuscha*) and Chum (*O. keta*) salmon (Nielsen et al., 2013; Carothers et al., 2013; Stephenson, 2006). Of these two salmon species, Pink salmon are the most abundant in the North Pacific Ocean (Ruggerone and Irvine, 2018) and have the broadest distribution in the PAR from the Yukon River to small steams from Point Hope to Point Barrow (Craig and Haldorson, 1986). Vagrants have also been found upstream in the Mackenzie River to Fort Good Hope, Northwest Territories (Dunmall et al., 2018), as far east in the Canadian western Arctic as Paulatuk, Northwest Territories (Dunmall et al., 2013) and Kugluktuk, Nunavut (Dunmall et al., 2018), and along the east coast of Greenland (Dunmall et al., 2013). Spawning Pink salmon have also been documented along the Chukotka Peninsula coastline from the northern Bering Sea, into the Chukchi Sea and as far east as the Kolyma River (Radchenko et al., 2018).

Pink salmon production around the North Pacific Ocean has increased over the last decade (Radchenko et al., 2018). While some authors have expressed concern that Pink salmon may be exerting top-down control on the food web (Batten et al., 2018) and affecting growth and survival of other species reliant on the marine food web (Ruggerone et al., 2016; Oka et al., 2012; Springer et al., 2018), others have illustrated no evidence of Pink salmon abundance on marine production (Radchenko et al., 2018). While Pink salmon abundance in northern regions of their range is still quite low in relation to stocks farther south, there is evidence that the abundance of some northern stocks is increasing during this period of warming.

Pink salmon have a short 2-year life-cycle that include freshwater and marine environments (Radchenko et al., 2018). Adult Pink salmon in the northern regions return to rivers during July to September and their eggs hatch during late winter and into spring. Fry enter the marine environment during late May through June (Howard et al., 2017) and they spend the summer as juveniles in near coastal regions before migrating offshore into the North Pacific Ocean for the winter. After winter, they migrate back to their natal spawning grounds. The 2-year life-cycle creates separate even and odd year brood lines that do not overlap on spawning grounds (Radchenko et al., 2018).

Conditions in both freshwater and marine environments are important to the survival of Pink salmon. In northern regions of Pink salmon distribution, cold river and stream temperatures in the freshwater environment are believed to limit salmon production (Dunmall et al., 2016); however, continued warming air and stream temperatures, and longer periods of ice-free conditions may benefit salmon survival within this environment (Nielson et al., 2013). Two critical periods in the marine environment are believed to be important to marine survival of salmon. The first critical period is during their early marine residence where rapid growth is believed to reduce predation (Parker, 1968). The second critical period is during their first winter at sea where juvenile salmon that attain sufficient size and energy reserves (lipids) during their first summer at sea have higher probability of survival (Beamish and Mahnken, 2001). Both critical periods are linked to ecosystem function (i.e. optimum sea temperatures for growth, quantity and quality of prey resources) during their first summer at sea as juveniles and there is evidence in the PAR that warmer sea temperatures benefit juvenile Pink salmon early marine growth (Moss et al., 2009; Andrews et al., 2009; Wechter et al., 2017). Thus, the expectation is that Pink salmon in the PAR will respond positively to the rapid warming in both freshwater and marine environments.

To better understand Pink salmon dynamics in this region, we examine the total life-cycle productivity for the Yukon River and Norton Sound area (total number of adult returns per spawner; R/S) based on models that relate abundance estimates for adult returns to the number of spawners two years earlier. We include Nome air temperatures as a proxy for river and stream temperatures and estimates of summer sea surface temperature taken from satellite measurements in the northern Bering Sea in the life-cycle productivity models to explore whether temperature in these environments is affecting production. Next, we use surface trawl survey data to examine early marine life-history periods and conditions in these environments that may impact Pink salmon survival. Juvenile Pink salmon caught during the surface trawl survey are most likely from spawning populations (previous year) in this region (Farley et al., 2005); the juveniles return as adults the following summer to western Alaska rivers. For freshwater and early marine effects, we relate juvenile Pink salmon relative abundance to the total number of spawners to the Yukon River and Norton Sound region and to Nome air temperatures as a proxy for river temperature. Strong positive relationships would suggest that the number of spawners along with warmer freshwater temperatures lead to increased relative abundance of juvenile Pink salmon in the northeastern Bering Sea region. Finally, we examine the relationship between the indices of adult Pink salmon returns to the Yukon River and Norton Sound region with the juvenile Pink salmon relative abundance, body size, and summer sea temperatures from satellite estimates. Strong positive relationships would suggest higher numbers of juveniles along with warmer temperatures and increased size lead to greater numbers of adult Pink salmon the following year.

2. Materials and methods

2.1. Life-cycle models

A time series (1995 to 2018) of adult Pink salmon return indices (harvest and spawners) and spawner indices to the Yukon River and Norton Sound were derived from a number of sources. The time series for the number of Yukon River and Norton Sound region Pink salmon returns are from Estensen et al. (2018) and Menard et al. (2020). For the Yukon River, the number of adult Pink salmon spawners is indexed from estimates of passage past the Pilot Station Sonar in the lower river (JTC, 2019), escapement past the East Fork Andreafsky River weir downstream of the sonar (Conitz, 2019), and total harvest of this species in the Yukon River (Estensen et al., 2018). While some lower river escapement of Pink salmon occur in systems downstream of the East Fork Andreafsky River weir and Pilot Station Sonar, a majority of total number of Pink salmon spawners in the Yukon River is accounted for by these assessment projects. For Norton Sound, the adult Pink salmon spawner index includes rivers that contain weirs or counting towers for more accurate values and have long enough time series to compare with our juvenile Pink salmon abundance index. These include the Eldorado, Snake, Kwiniuk, Nome, and North rivers. The annual indices of total Norton Sound adult Pink salmon returns are the sum of total annual harvest from the Norton Sound area, as most salmon harvest occur in marine waters downstream of spawner assessment projects, plus the sum of annual adult Pink salmon spawners to the index rivers.

Annual mean Nome air temperatures (1995 to 2018; August $_{(t)}$ to June $_{(t+1)}$) where t represents the year of adult Pink salmon spawning, were obtained from the National Weather Service web site: https://w2.weather.gov/climate/xmacis.php?wfo=pafg. The mean August $_{(t)}$ to June $_{(t+1)}$ air temperature represents the period of incubation (adult Pink salmon that entered freshwater streams and rivers to spawn during late July through August of year t) and rearing (over winter to when they leave freshwater as fry to enter the marine environment during late May through June of year t+1) of Pink salmon in northern regions of their distribution. We used the annual mean air temperature as a proxy for stream and river temperatures in the northern Bering Sea region for the Pink salmon production models. Air temperatures have been used to estimate seasonal freshwater stream temperatures (McNyset et al., 2015), however we understand there are caveats given the span of seasons (includes winter) in our use of air temperatures as proxy for stream temperatures in this region.

Annual mean sea surface temperatures (1995 to 2018; SST_{t+1}) within the northeastern Bering Sea, where t represents the year of adult Pink salmon spawning, were estimated using data from satellite sources (NOAA Coral Reef Watch, 2018). Daily SST data were averaged within the northeastern Bering Sea (latitudes 60°N to 65°N; longitudes 166°W to 171°W) for each month. We then averaged the monthly mean sea surface temperatures for June to September for each year to represent sea temperature juvenile Pink salmon would experience during their first summer at sea.

The number of adult Pink salmon that return (R) to the river each year is a function of the number of adult spawners (S) two years prior as well as life-cycle events that occur during freshwater and marine residence. One measure of productivity is to examine the number of adults produced per spawner. Adult Pink salmon return and spawner data for the Yukon River and Norton Sound region are shown in Fig. 1a,b. There is increased variation in return indices at higher spawner index levels for both the Yukon River stocks and Norton Sound region stocks suggesting a multiplicative error structure. To understand between-stock variability in the northern Bering Sea region, we calculated the correlation of $\ln(R/S)$ between the Norton Sound region stock group and the Yukon River stock group to determine whether their productivity is synchronous. To take into account density dependent effects, we included models that relate the number of spawners to the number of adult returns (see Quinn and Deriso, 1999),

(1) $\ln R_{t+2} = a + \gamma \ln S_t + \epsilon$ Cushing Model (Cushing, 1971)

(2) $\ln (R_{t+2}/S_t) = a - \beta S_t$ Ricker Model (Ricker, 1975)

where a is the natural log of the productivity parameter and γ and β are the density-dependence parameters. While the Cushing model includes a density-dependent parameter, this model lacks a peak level of recruitment (Quinn and Deriso, 1999); recruitment continues to increase as spawning level increases. To provide density dependence in the Cushing model, γ must be less than 1. The Cushing model is typically not used for salmon stocks to examine the relationship between the number of returns and spawners due to lack of density dependence at high spawning levels; however, it may be informative for northern river systems experiencing rapid warming with potential for shifts in the underlying capacity of these ecosystems to support higher production. In addition, we included the annual estimates of Nome air temperature, as a proxy for freshwater temperatures, and annual average of sea temperature in the life-cycle models to test whether their inclusion helps explain production dynamics in this region.

A step-wise selection of a linear regression model (S-plus; Insightful Corporation, 2001) was used to determine the most parsimonious life-cycle models that explain production dynamics of Pink salmon in the northern Bering Sea region. In S-plus, the effects of additional terms to the model are determined by comparing the Mallow's C_p statistic estimated by

$$\boldsymbol{C_p = \left(\frac{RSS}{\hat{\sigma}^2}\right) + 2 * p - n}$$

where n is the sample size, $\boldsymbol{\hat{\sigma}^2}$ is the mean square error of the true regression model, RSS is the residual sum of squares and p is the number of parameters in the model, which equals the number of predictors plus 1 if the intercept is included in the model. The stepwise selection process requires an initial model often constructed explicitly as an "intercept-only" model. The step function in S-plus calculates the C_p statistic for the intercept only model as well as those for all reduced and augmented models. If any term has a C_p statistic lower than that of the intercept only model, the term with the lowest C_p statistic is dropped. We also tested the residuals of the most parsimonious models for autocorrelation between consecutive years to see if the other potential factors beyond those in the model could influence adult Pink salmon returns.

2.2. *Life-history models*

The information on juvenile Pink salmon marine ecology in the northern Bering Sea comes from integrated ecosystem surveys conducted during late summer and early fall months of 2003 to 2018 (except 2008) (Fig. 2). For this study, the northern Bering Sea consisted of stations sampled between 60°N to 65°N and juvenile Pink salmon captured in the survey region are assumed to be of wild origin originating from spawning populations within the Norton Sound region and Yukon River. Details on survey design can be found in Murphy et al. (2017). Briefly, juvenile Pink salmon were captured using a model 400/601 rope trawl, made by Cantrawl Pacific Limited of Richmond, British Columbia. The rope trawl was rigged with buoys on the headrope to sample from near surface to approximately 20 to 25 m depth. Sampling stations were generally completed during daylight hours (0730 – 2100, Alaska Daylight Savings Time). All trawl deployments lasted 30 minutes and covered between 2.8 – 4.6 km. A vertical (surface to near bottom depths) conductivity and temperature at depth (CTD) cast was done at each station to measure oceanographic characteristics during the survey. The surveys generally occurred during September; however, there was some variability in start and end dates among years (Table 1). The median year-day for the surface trawl survey during all years (2003 to 2018) was 256 (September 12).

A multi-year distribution map of juvenile Pink salmon in the northern Bering Sea using the standardized catch estimated as:

$$\boldsymbol{C\_std_{i,y} = \frac{C_{i,y}}{E_{i,y}}\overline{E}}$$

where $C_{i,y}$ is the number of juvenile Pink salmon captured at station i during year y, $E_{i,y}$ is the area (km^2) swept by the trawl and $\boldsymbol{\overline{E}}$ is the average effort (km^2) (Murphy et al., 2017). Zero catch boundary conditions were added to land masses, and the prediction surface was estimated with a neighborhood kriging model (Murphy et al., 2017).

Fish captured in the trawl were sorted to species. Subsamples of up to n=50 juvenile Pink salmon were randomly selected, and these fish were measured to fork length (nearest mm) and weighed (nearest gram). Juvenile pink salmon fork length and weight were adjusted to take into account the annual differences in the surface trawl survey median year-day that could influence our interpretation of juvenile Pink salmon size due to differences in size of juveniles that could occur over the course of the survey period. We estimated adjusted length and weight by:

$$\boldsymbol{L_{J,i,y} = \left(YD_{Capture\,j,i,y} - 256\right) * 1.18mm}$$

$$\boldsymbol{W_{j,i,y} = \left(YD_{Capture\,j,i,y} - 256\right) * 0.2g}$$

where $L_{j,i,y}$ and $W_{j,i,y}$ are the length and weight of a juvenile Pink salmon *j* caught at station *i* during year *y*, $YD_{Capture\ j,\ i,\ y}$ is the year-day of capture of the juvenile Pink salmon *j* at station *i* during year *y*, 256 is the median year-day (September 12) for all years (2003 to 2018) of the surface trawl survey, and 1.18 mm and 0.2 g are the estimated daily growth rate in length (Moss et al., 2009) and weight (Grant et al., 2009) for juvenile Pink salmon.

An abundance index of juvenile Pink salmon for the northern Bering Sea was based on catch per unit effort (CPUE, catch per km^2) where the number of juvenile Pink salmon caught at each station was divided by the area swept by the trawl. We used an index of relative abundance and not actual abundance because juvenile Pink salmon captured at the outer regions of our survey may be from stocks other than Yukon River and North Sound (Farley et al., 2005). Area swept by the trawl at each station was determined by multiplying the distance (km) traveled by the horizontal distance (km) of the trawl opening that was measured by net sonar. The distance traveled was estimated using:

$$\boldsymbol{x = \cos^{-1}(\sin(lat_s) * \sin(lat_e) + \cos(lat_s) * \cos(lat_e) * \cos(\Delta \mathrm{lon})) * 6371,}$$

where lat_s is the trawl start latitude position in radians, lat_e is the trawl end latitude position in radians, Δlon is the longitude distance between the start and end trawl positions in radians, and 6371 is the earth radius in km (Murphy et al., 2017).

Mixed-layer depth expansions were applied to the area-swept indices of juvenile Pink salmon to generate an abundance index for juvenile Pink salmon as described in Murphy et al. (2017). Mixed layer depth expansions account for changes in the vertical extent of trawl sampling depths and juvenile habitat over time. Summer sea temperatures below the mixed layer depth in the northern Bering Sea are generally cold (< 2° C), which are not suitable habitat for juvenile salmon (Brett, 1952); therefore, this correction is used to provide a reasonable approximation for the vertical distribution of juvenile salmon in the northern Bering Sea

(Murphy et al., 2017). Oceanographic characteristics from the CTD casts were used to determine the mixed layer depth defined as the depth where seawater density (sigma-theta) increased by 0.10 kg m^{-3} relative to the density at five meters (Danielson et al., 2011). Mixed layer depth was set to 5 m off bottom when the entire water column was vertically mixed. The mixed layer depth adjustments applied to annual relative abundance estimates, θ_y, were estimated by

$$\boldsymbol{\theta_y = \frac{\sum_i M_{i,y} C_{i,y}}{\sum_i C_{i,y}}}$$

where $C_{i,y}$ is the number of juvenile Pink salmon captured at station i during year y, and $M_{i,y}$ is equal to the ratio of mixed-layer depth to trawl depth when trawl depth is shallower than mixed layer depth, and 1.0 when trawl depth is below the mixed-layer depth. The juvenile abundance index for Pink salmon was estimated by multiplying the average ln(CPUE) by θ_y

$$\boldsymbol{N_y = \frac{\sum_i ln(CPUE_{i,y})}{n_y} * \theta_y}$$

where n is the number of stations i sampled during year y.

Life-history models were constructed for northern Bering Sea Pink salmon using multiple sources of data. The models included the juvenile Pink salmon abundance index and adjusted average juvenile weight during the northern Bering Sea surface trawl survey. A subset (2003 to 2018) of Nome air temperatures and summer SSTs described above were used in the life-history models to represent freshwater and early marine conditions for relationships with juvenile Pink salmon relative abundance and adult returns. Annual estimates of adult Pink salmon returns and spawners to the Northern Bering Sea region were developed from a subset of the available annual estimates (2003 to 2018) of adult Pink salmon returns and spawners to the Yukon River and Norton Sound region.

Because the juvenile Pink salmon relative abundance is estimated during September, the life-history model for juvenile abundance incorporates potential freshwater and early marine effects

$\ln$ (juvenile relative abundance $_t$) = $\ln$ (adult spawners$_{(t\text{-}1)}$) + Nome air temp + $\ln$ (adjusted weight $_t$) + SST_t

and includes the number of adult Pink salmon that spawned during the prior year, stream temperature during their freshwater life history stage, adjusted weight of juvenile salmon during year t, and summer sea surface temperatures during year t.

The life-history model relating early marine effects with adult Pink salmon returns

$$\ln(\text{adult returns}_{(t+1)}) = \ln(\text{juvenile relative abundance}_t) + \text{SST}_t + \ln(\text{adjusted weight}_t)$$

examined the relationship between the number of adult Pink salmon returning the following year to the region with juvenile abundance, juvenile weight (condition), and sea temperature in the early marine period. We applied the step-wise variable selection procedure described above to select the most parsimonious life-history models that explain production dynamics of Pink salmon in the northern Bering Sea region.

3. Results

3.1. Life-cycle productivity

The adult Pink salmon return and spawner indices to the Norton Sound region and Yukon River during 1995 to 2018 ranged between a few thousand to several million (Table 2). More adult Pink salmon return during even years than odd years, especially within the Norton Sound region. However, adult returns to the Norton Sound region during the recent odd year of 2017 was much higher (> 2 million) than most of the previous odd years (generally < 1 million except for 2005) within the time series. Overall, productivity ($\ln R/S$) appears higher during the late 1990s and from 2013 to 2015 (Fig. 3). The correlation between Yukon River and Norton Sound region productivity was positive and significant ($r = 0.47$, $p = 0.02$).

The average Nome air temperature (proxy for freshwater temperatures) for the period covering adult Pink salmon spawning, fry emergence and smolt migration to the marine environment was below 0°C during each year (Table 2). Coldest temperatures occurred during 1999, 2009 and 2012 with warmer temperatures occurring during 2003 to 2005 and 2014 to 2016. The summer SSTs covering the period of juvenile Pink salmon residence in the northeastern Bering Sea had similar trends with coolest temperatures during the late 1990s and during 2008 to 2012 and warmer temperatures during the early 2000s and from 2015 to 2017 (Table 2). The correlation between Nome air temperatures and summer SSTs was positive and significant ($r = 0.61$, $p = 0.002$).

The life-cycle model fits and results for the Norton Sound region and Yukon River are shown in Fig. 1a,b and Table 3. For the Yukon River, the most parsimonious Cushing model included the natural log of spawners and summer SST which explained 71% of the variation in the natural log of returning adult Pink salmon. However, the parameter estimate for summer SST is not significant ($p = 0.11$) in the model. The most parsimonious Ricker model included SST, explaining 11% of the variation in adult Pink salmon production to the Yukon River; neither parameter estimates for number of spawners and SST were significant ($p = 0.232$ and 0.124, respectively). For Norton Sound stocks, the most parsimonious Cushing model was one that included the natural log of spawners and summer SST, explaining 77% of the variation in the natural log of adult Pink salmon returns to the region. The most parsimonious Ricker model was one that contained spawners and summer SST, explaining 53% of the variation in the natural log of adult Pink salmon production to the region. No significant autocorrelation between consecutive years is evident in the residuals of the most parsimonious models (Fig. 4 a-c). In addition, the gamma parameter for the Cushing model was 0.66 for Norton Sound stocks and 0.82 for the Yukon River stock suggesting that density-dependence on the spawning grounds may be more evident in the Norton Sound stocks than the Yukon River stocks.

3.2. Early life-history

Juvenile Pink salmon are distributed throughout the northern Bering Sea during late summer months (Fig. 2). The region of highest catch densities occurred within the shallow (< 50 m) coastal habitats from the northern to southern margins of the northern Bering Sea survey area. Observed average size of juvenile Pink salmon varied from 136 to 193 mm (25.7 to 70.8 g) with an average of 164.6 mm (44.8 g) (Table 1). Adjustments for survey timing increased the overall average size of juvenile Pink salmon to 165.6 mm (44.9 g) with the largest differences occurring during 2005 and 2007. Juvenile Pink salmon were generally smaller during 2006, 2009, 2011 and from 2015 to 2018 (Fig. 5a,b). Moreover, the number of larger fish that occurred as outliers to the sample of juvenile Pink salmon was highest during 2007 and 2016 to 2018 (Fig. 5b), years that coincided with warm sea temperatures. Mixed layer depth corrections ranged from a low of 1.00 (<1%) during 2016 to a high of 1.79 (79%) during 2005 with an overall average of 1.22 (22%) to juvenile Pink salmon relative abundance estimates (Table 4). Juvenile Pink salmon relative abundance was high during 2003 to 2007 and again from 2013 to 2018 with lower abundance during 2009 to 2012.

The step-wise model selection statistics to explore life-history events that may impact Pink salmon production in fresh water and the early marine period are shown in Table 5. For the juvenile abundance model, freshwater effects including the number of spawners and Nome air temperatures were significant and explained 55% of the variation in juvenile Pink salmon relative abundance during September (Fig. 6). The step-wise selection process removed summer SST and the natural log of weight, (both represent early marine effects) as these variables did not contribute to the most parsimious model. For the adult return model, the *Cp* values for the natural log of weight and sea temperature during September were lower than the intercept only model, suggesting these variables could be removed. The most parsimonious model (Fig. 7) that included juvenile Pink salmon relative abundance explained 62% of the variation in adult Pink salmon returns to the northern Bering Sea region.

4. Discussion

Our analysis provides new insights into production dynamics of Yukon River and Norton Sound Pink salmon stocks. The best fit life-cycle models suggest that density-dependence on the spawning grounds may be low within the Yukon River but may be present within river systems draining into Norton Sound. We interpret this result to indicate that there may be potential for increased freshwater production especially within the Yukon River. The best fit life-history models suggest that the number of juvenile Pink salmon during September is a function of the number of adult Pink salmon spawners and Nome air temperature, reflecting the importance of freshwater production to overall numbers of juvenile Pink salmon. In addition, juvenile Pink salmon relative abundance during September is a good predictor of the number of adult Pink salmon that return the following year indicating that conditions in fresh water and early marine environments are key to our understanding of Pink salmon production dynamics in this region.

Our analysis of the productivity patterns highlights the synchrony (positive, significant correlation) in temporal variation among Pink salmon stocks in the northeastern Bering Sea. These patterns have been found for Pink salmon stocks across western North America (Malick and Cox, 2016) as well as other salmon stocks that show positive correlation at regional scales (Pyper et al., 2001, 2002, 2005; Peterman et al., 1998; Peterman and Dorner, 2012; Dorner et al., 2017). The synchrony in production suggests shared factors that are affecting Pink salmon stocks throughout the study region. The best fit life-cycle models included summer SSTs indicating the potential importance of sea temperature on Pink salmon production in this region. This result is similar to other analyses of salmon productivity in the Northeast Pacific Ocean (Mueter et al., 2002), illustrating the importance of summer sea temperatures to production of Pink salmon in the northeastern Bering Sea.

The best fit life-history models were those that included the number of spawners, Nome air temperatures and the relative abundance of juvenile Pink salmon. For the juvenile abundance model, we found positive, significant relationships between annual juvenile Pink salmon relative abundance and the number of adult Pink salmon spawners the prior year along with annual average Nome air temperatures. This result supports the hypothesis that warming air temperatures in this region (as a proxy for river and stream temperatures) may be improving freshwater production leading to higher numbers of juvenile Pink salmon in the northern Bering Sea region during summer months. For the adult Pink salmon return model, the number of juvenile Pink salmon in the northern Bering Sea region during late summer predict the number of adults returning the following year. While summer SSTs were not included in these models, we note that there is a significant positive correlation between SSTs and Nome Air temperatures that may indicate that temperature, either fresh water or early marine are important for Pink salmon production in this region.

These relationships suggest a possible connection between changes in fresh water and early marine environments and subsequent adult production. However, the amount of variation in juvenile Pink salmon relative abundance explained by adding adult Pink salmon spawners and Nome air temperatures was less than the amount of variation explained in the adult Pink salmon returns by the juvenile index. This suggests other factors affecting early marine survival of juvenile Pink salmon in the northern Bering Sea during summer months could influence total production or that Nome air temperatures may not fully reflect the freshwater temperature dynamics thereby reducing the influence of juvenile Pink salmon relative abundance.

Although freshwater conditions in the Arctic are known to limit salmon production, it can be difficult to predict how salmon will respond to warming freshwater habitats (Nielson et al., 2013). A case study on projecting effects of climate warming on Atlantic salmon suggested that northern rivers could become more productive with increased colonization success northward and diminished production to river systems in the southern range (Reist et al., 2006).   Density-dependent mortality due to too many spawners on the river, temperature, and stream flows are all factors contributing to fluctuations in freshwater survival (Heard, 1991). In addition, stream habitats with a minimum temperature of 4°C during spawning and temperatures above 2°C during egg incubation were found to benefit establishment of Chum and Pink salmon in high latitude and high elevation watersheds (Dunmall et al., 2016).

Nome air temperatures from August (spawning year) to June the following year were used as a proxy for freshwater stream temperatures in the region. The average air temperature was below 0°C which is most likely colder than stream temperatures, especially during summer months. Limited information on stream temperatures at various locations along the Pilgrim River (north of Nome, Alaska) during the summer months of 2013 to 2016 show that temperatures varied between 8.4°C to 18.7°C (Carey et al., 2019). These temperatures are well above the minimum temperature of 4°C for successful Pink salmon spawning suggested in Dunmall et al. (2016). In addition, some river systems in the Norton Sound region experienced extremely high temperatures during summer 2019 that were believed to contribute to observed adult Pink salmon die offs on the spawning grounds (pers. Comm. Gay Sheffield). Given the nature of rapid warming in the region with respect to the marine ecosystem (Baker et al., 2020; Danielson et al., 2020; Huntington et al., 2020), it is likely that freshwater temperatures during winter and summer months in the Norton Sound and Yukon River drainage are warming enough to both improve survival and to open new areas along rivers and streams for Pink salmon to establish thereby increasing production potential in this region.

Pink salmon returns to this region are typically higher during even years (odd year juvenile Pink salmon brood), but more recently the returns to the Norton Sound region during odd years have also been high. Studies have indicated that embryonic survival of the even-year broodline for British Columbia Pink salmon is higher than the odd-year broodline in a cold (4°C) incubation environment with higher alevin and fry growth observed (Beacham and Murray, 1988). Increasing dominance of odd-year brood lines has been documented with the inference of favorable survival during period of warming freshwater habitats (Irvin et al., 2014). The difference in temperature tolerance between the even and odd-year brood lines has been linked to dispersal after the Pleistocene Era glaciation some 10,000 years ago (Beacham et al., 2012), where even-year broodlines likely survived the glaciation in the northern refugia (Aspinwall, 1974) and the odd-year brood line may have occupied more southern refugia (McPhail and Linsey, 1970). Therefore, warming freshwater habitats in the northern regions may be improving odd-year broodline survival, leading to more adult Pink salmon returning during odd years.

Earlier studies on juvenile Pink salmon marine ecology in the northern Bering Sea found that warmer sea surface temperatures during spring and summer were positively related to their growth (Andrews et al., 2009; Farley et al., 2009; Wechter et al., 2017). Presumably, higher growth rates during their early marine period would reduce size-selective mortality and lead to higher survival for juvenile salmon (Parker, 1968). We found that juvenile Pink salmon adjusted weight and length declined over the course of our time series even though sea temperatures were increasing during the survey period. This result was counter-intuitive as growth rates typically increase with temperature. Dispersal, changes in prey quality and quantity, and migratory patterns of juvenile Pink salmon could be contributing to this apparent negative relationship between size and temperature.

Although juvenile Pink salmon were distributed throughout the northern Bering Sea survey region, the vanguard of their distribution can be under sampled, particularly during warm years. Moss et al. (2009) examined juvenile Pink salmon distribution and size within the northern Bering Sea and Chukchi Sea during 2007. They found that the highest catches of juvenile Pink salmon were in the Chukchi Sea and that these juveniles were larger than those in the northern Bering Sea region. The year 2007 was characterized by exceptionally warm sea temperatures in the Chukchi Sea and significantly increased annual mean water transport through the Bering Strait (Woodgate et al., 2010). Moreover, the water flow from the northern Bering Sea through the Bering Strait and into the Chukchi Sea has increased by 50% over the past two decades (Woodgate et al., 2015). Given that the sea temperatures have been much higher during recent years of our survey period, it is possible that juvenile Pink salmon from the northern Bering Sea region were advected north with the largest fish at the vanguard of the migration through the Bering Strait and into the Chukchi Sea and out of the northern Bering Sea survey area.

The large numbers of juvenile Pink salmon found near the Bering Strait could also be related to higher Pink salmon production in the northern regions of the PAR. Adult Pink salmon have become more prevalent in subsistence catches in the high Arctic particularly during even-numbered years (Dumnall et al., 2013; Dunmall et al., 2018). Further, the large catch of juvenile Pink salmon in the Chukchi Sea during 2007 (Moss et al., 2009) coincided with higher adult returns to the Beaufort Sea coast during 2008 (Dunmall et al., 2013; Dunmall et al., 2018). While Pink salmon appear to be poised to take advantage of warm-water thermal refugia within several watersheds of the Arctic (North American North Slope; Dunmall et al., 2016), it is unknown whether spawning has been successful in this region. Adult Pink salmon returns to the northern regions of the Kamchatka peninsula have recently increased (Klovach et al., 2018) and record returns have occurred during most recent years to Norton Sound rivers (Menard et al., 2018). Farley et al. (2005) speculated that juvenile Pink salmon caught offshore in the northern Bering Sea could be of Russian origin. In addition, Kondzela et al. (2009) found that most of the juvenile Chum salmon caught in the Bering Strait area during 2007 were from Anady-Kanchalan rivers in the northern Kamchatka region. In any case, stock-specific juvenile data for Pink salmon are needed to better understand movement and production dynamics during this time of rapid warming.

The significant correlation between juvenile Pink salmon relative abundance and adult returns the following year suggests that the second critical period has not contributed as much to the annual variation in Pink salmon production to the northern Bering Sea region. The addition of sea surface temperature and weight did not improve our model for adult Pink salmon returns to the northern Bering Sea region. Our result is similar to studies that utilized juvenile salmon abundance indices from surface trawl data to predict adult returns. For example, a stock-specific juvenile Yukon River Chinook salmon index collected in the northern Bering Sea is used to provide management advice for expected run sizes (Murphy et al., 2017). Within southeast Alaska, adult Pink salmon returns are predicted using a juvenile Pink salmon index collected during summer months within Icy Strait (Orsi et al., 2016). Both applications are used to inform management decisions and provide more accurate outlooks than previous models.

Lastly, it is important to note results from the life-cycle models that utilize harvest and spawner data for Pink salmon to the Yukon River and Norton Sound regions are limited by incomplete data. Our estimates of Pink salmon total number of returns and spawners to the Yukon River and Norton Sound region are considered indices of abundance as total accounting of Pink salmon abundance in this region is not currently possible. Total harvest includes stocks not indexed in the spawning escapement and escapement assessment programs are designed to estimate other salmon species and do not fully account for Pink salmon abundance. Productivity values and inferences are presented here to illustrate relative change over time or relationships to environmental parameters, and should not be considered absolute values. Consequently, our interpretation of the results from these models should be considered cautiously. In addition, separate analyses of odd and even year broodlines may be warranted given that they are ecologically and reproductively isolated, suggesting that stock-recruitment relationships may differ between broodlines. The adult return and spawner time series for the region are short, therefore combining the two broodlines allowed a more complete examination of relationships between environmental conditions and indices of productivity in the context of changing climate conditions. Additional analyses into these relationships should be explored in the future, as the extension of time series and collection of new environmental data enable such models.

Continued monitoring of salmon through life-cycle and life-history models will provide insight into how warming Arctic climate conditions are impacting critical periods in salmon production. Our analyses suggest that Pink salmon production in the northeastern Bering Sea is driven by freshwater and early marine habitat dynamics. While we used air temperature as a proxy for stream temperature, broad-scale predictive models of climate change in the Arctic provide little information about feedback processes contributing to local conditions (Nielsen et al., 2013). To explore emerging connections within freshwater habitats, local knowledge regarding stream conditions, salmon abundance and spawning locations will be needed for perspective to current observations. Further monitoring of stream temperatures, flow and ice dynamics will improve our understanding of how climate warming is impacting this important habitat and context to shifts in abundance northward into the high Arctic.

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Fig. 1. Indices of adult Pink salmon spawners and returns (spawners plus harvest) to the Yukon River (a) and Norton Sound region (b). The solid line represents the Cushing model fit and the dashed line represents the Ricker model fit to the spawner and return data.

Fig. 2. Typical station grid (black dots) sampled during late August to September (2003 to 2018; excluding 2008) surface trawl surveys of the Northern Bering Sea. Lines indicate the 50 m and 100 m depth contours. Spatial distribution of juvenile Pink salmon based on catch data (ln CPUE, catch per unit effort, scaled to average effort km^2). Color contours are from the neighborhood kriging prediction surface of ln(CPUE). The map includes locations for Norton Sound region and Yukon River adult Pink salmon escapement index rivers (Snake, Eldorado, Kwiniuk, Yukon, Andreafsky) and the Pilot Station index.

Fig. 3. The natural log of adult Pink salmon returns per spawner for the Yukon River (solid line) and Norton Sound region (dashed line) for brood years 1995 to 2017.

Fig. 4. The autocorrelation functions for residuals of the most parsimonious life-cycle models including the Cushing model for the Yukon River (a), the Cushing model (b) and Ricker model (c) for the Norton Sound region. The dashed lines are the upper and lower bounds for significant autocorrelation.

Fig. 5. Box plots of juvenile Pink salmon adjusted a) length (mm) and b) weight (g) during late August to September 2003 to 2018 (no survey was conducted during 2008) in the northeastern Bering Sea. Length and weight were adjusted to September 12 of each year. The solid horizontal line in the box plot is located at the median of the data, and the upper and lower ends of the box are located at the upper quartile and lower quartile of the data, respectively. The lines extending above and below the box indicate the variability outside the upper and lower quartiles.

Fig. 6. The relationship (dark line) between the natural log of juvenile Pink salmon relative abundance and the natural log of adult Pink salmon spawner index with Nome Air temperature (open circles; 2003 to 2018).

Fig. 7. The relationship (dark line) between the natural log of adult Pink salmon return index to the Yukon River and Norton Sound region and the natural log of the relative abundance of juvenile Pink salmon from the surface trawl surveys (black dots; 2003 to 2018).

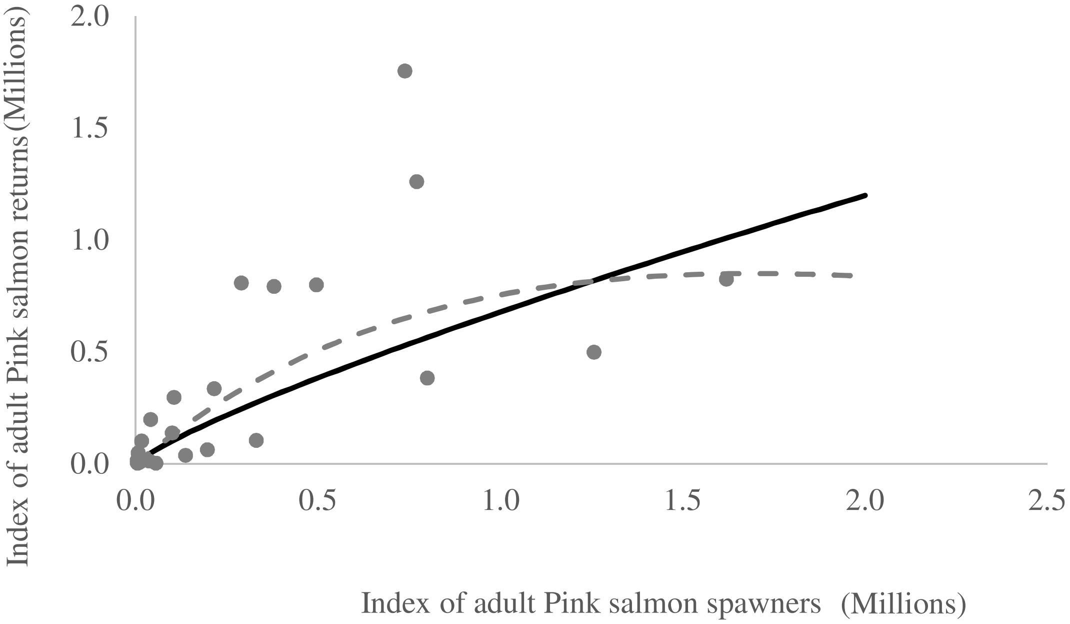


Figure 1a.

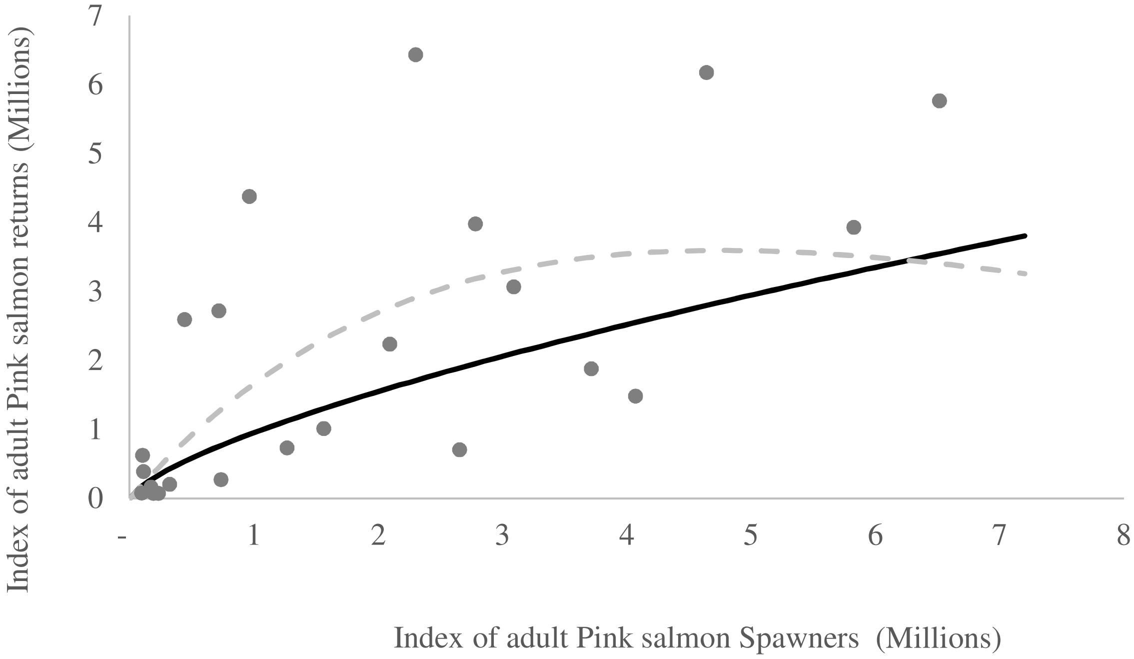


Figure 1b.

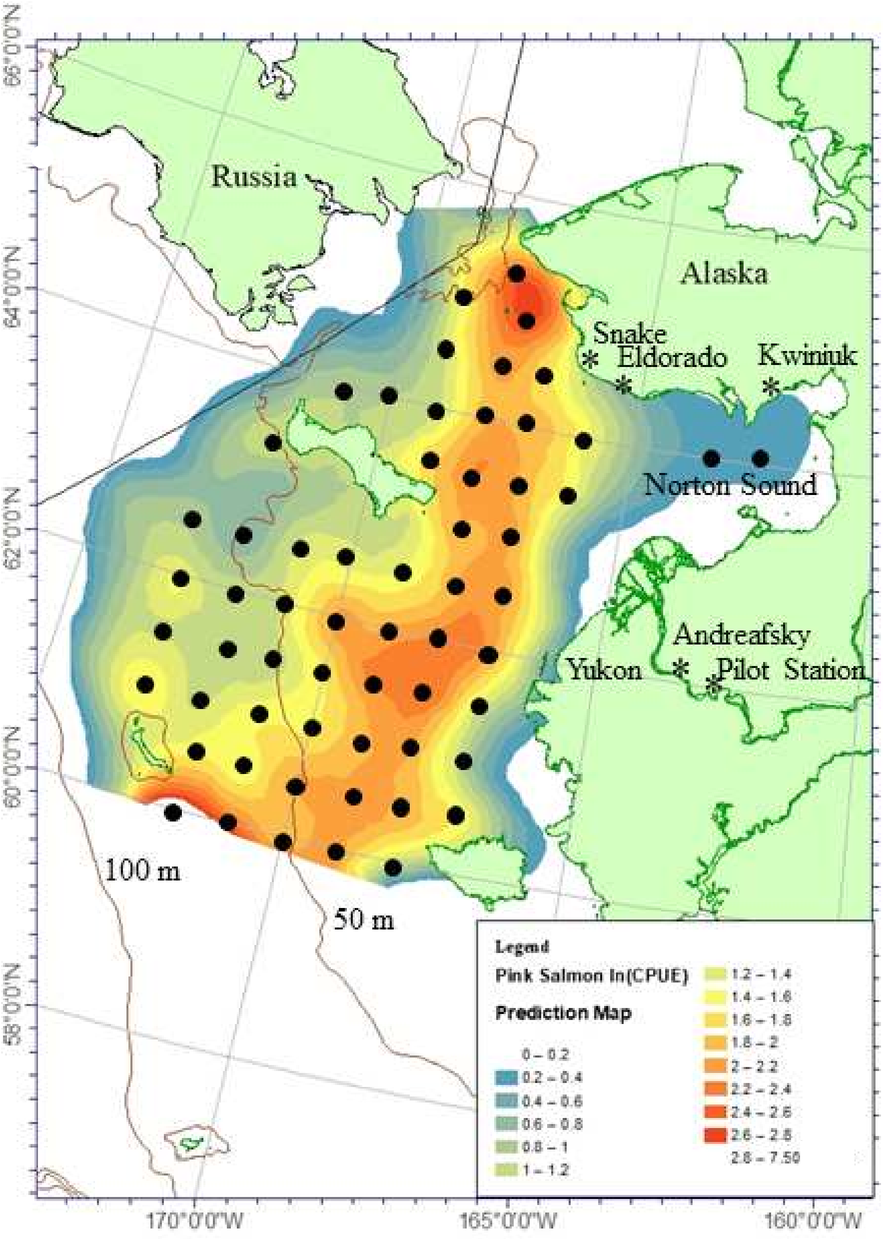

66°0'0"N
64°0'0"N
62°0'0"N
60°0'0"N
58°0'0"N
170°0'0"W
165°0'0"W
160°0'0"W
Russia
Alaska
Snake
Eldorado
Kwiniuk
Norton Sound
Andreafsky
Yukon
Pilot Station
100 m
50 m
Legend
Pink Salmon ln(CPUE)
Prediction Map
0 – 0.2
0.2 – 0.4
0.4 – 0.6
0.6 – 0.8
0.8 – 1
1 – 1.2
1.2 – 1.4
1.4 – 1.6
1.6 – 1.8
1.8 – 2
2 – 2.2
2.2 – 2.4
2.4 – 2.6
2.6 – 2.8
2.8 – 7.50

Figure 2

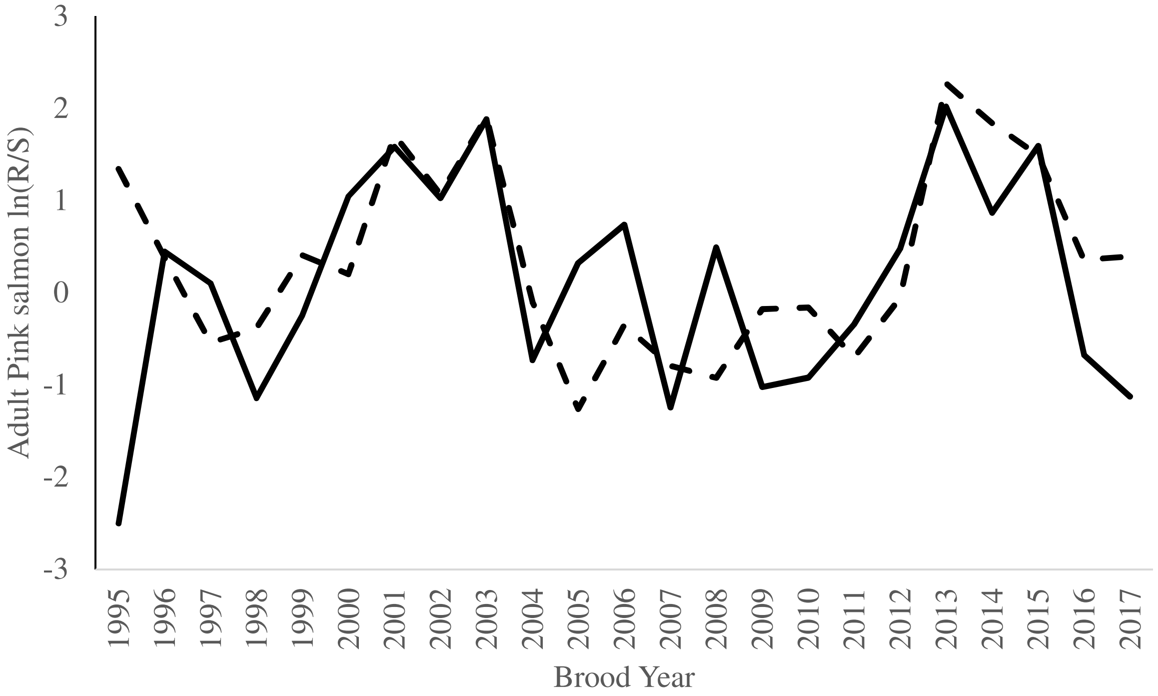

3
2
1
0
-1
-2
-3
Adult Pink salmon ln(R/S)
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
Brood Year

Figure 3

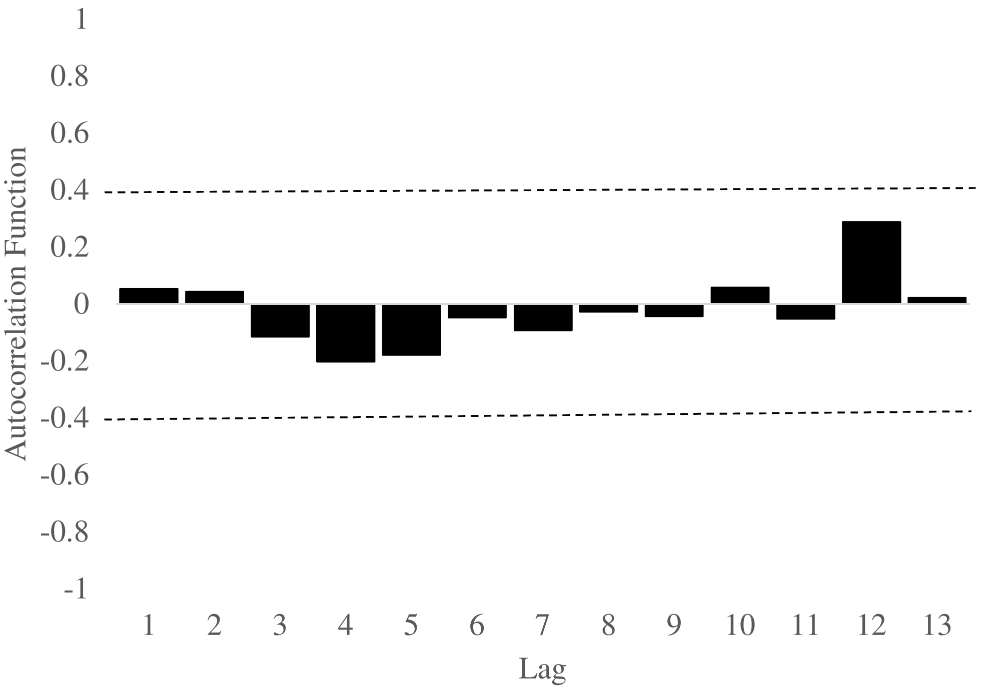


Figure 4a

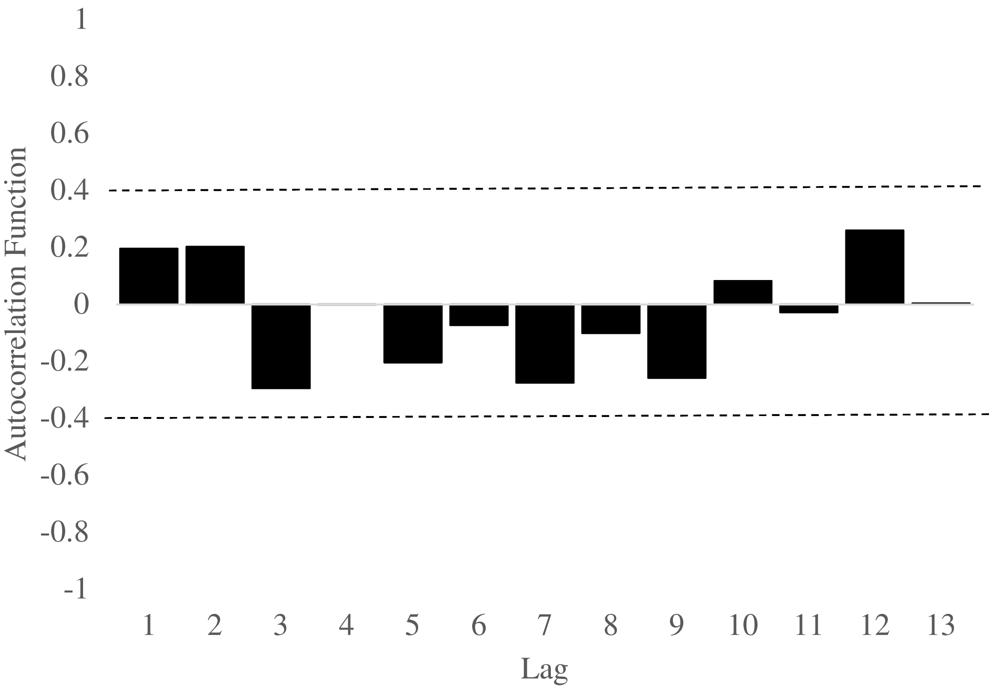


Figure 4b

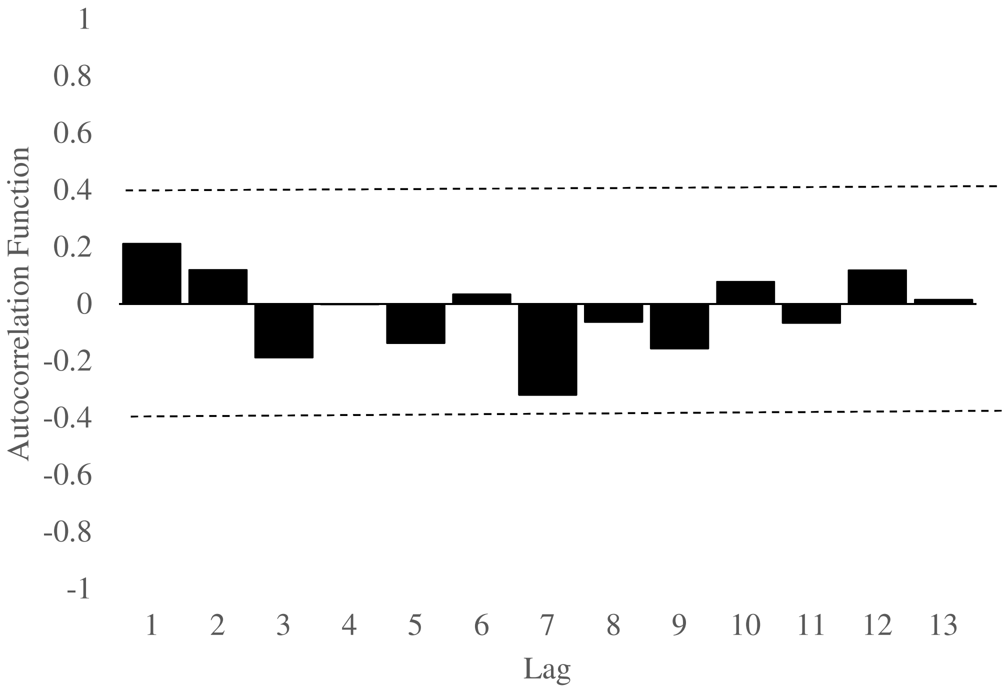

Autocorrelation Function
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
1
2
3
4
5
6
7
8
9
10
11
12
13
Lag

Figure 4c

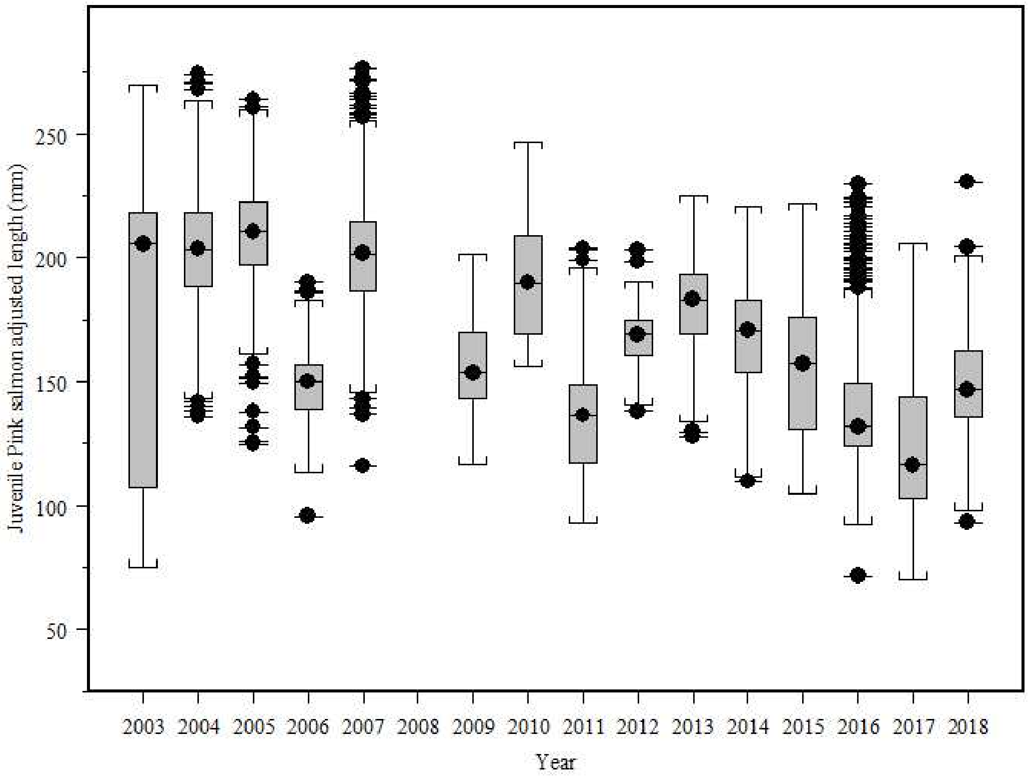
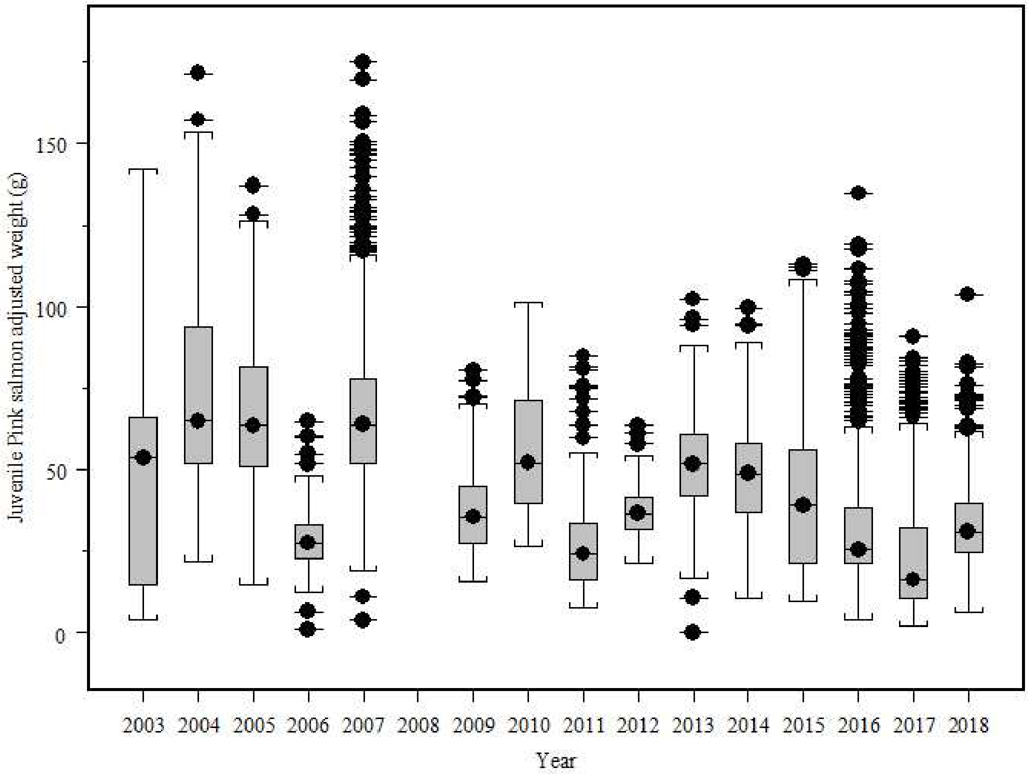
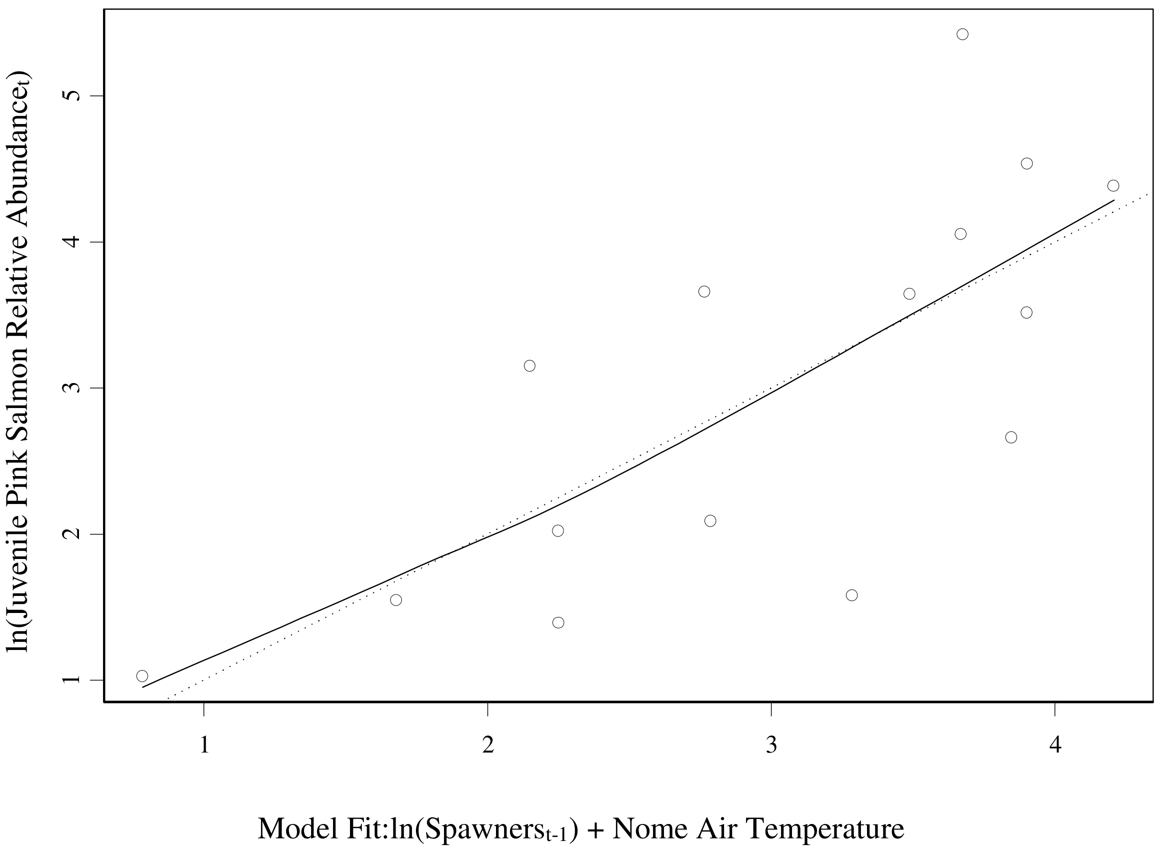

Juvenile Pink salmon adjusted length (mm)
250
200
150
100
50
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year

Figure 5a


Juvenile Pink salmon adjusted weight (g)
0
50
100
150
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year

Figures 5b



ln(Juvenile Pink Salmon Relative Abundance$_t$)
5
4
3
2
1
1
2
3
4
Model Fit:ln(Spawners$_{t-1}$) + Nome Air Temperature

Figure 6

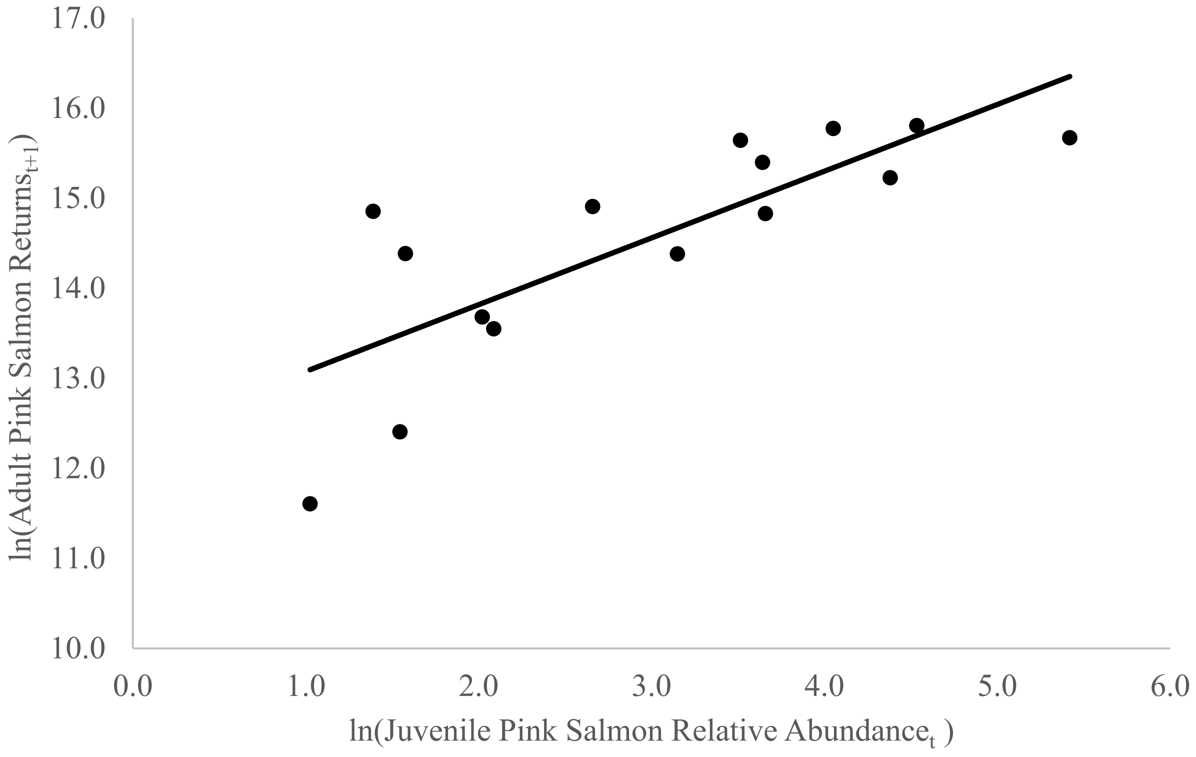

17.0
16.0
15.0
14.0
13.0
12.0
11.0
10.0
0.0
1.0
2.0
3.0
4.0
5.0
6.0
ln(Adult Pink Salmon Returns$_{t+1}$)
ln(Juvenile Pink Salmon Relative Abundance$_t$)

Figure 7.

Table 1. The year, survey timing (start and end day), average date adjustment in days (Adj. days), average observed and adjusted (Adj.) length (L, mm), weight (W, g) and standard error (SE) for the number (N) of juvenile pink salmon sampled in the northeastern Bering Sea during 2003 to 2018. * no survey conducted in the NBS during 2008.

Year	Survey Timing		Adj.	N	L	SE	Adj. L	SE	W	SE	Adj. W	SE
	Start	End	(days)		(mm)		(mm)		(g)		(g)	
2003	21-Aug	8-Oct	8	550	167.0	1.4	176.6	2.4	45.9	1.1	47.5	1.3
2004	10-Sep	30-Sep	8	622	192.6	0.9	202.3	0.9	70.8	1.1	72.5	1.1
2005	17-Sep	3-Oct	16	287	188.6	1.2	207.5	1.3	63.1	1.3	66.4	1.3
2006	31-Aug	19-Sep	-2	353	150.8	0.7	148.5	0.8	29.3	0.4	28.8	0.5
2007	14-Sep	1-Oct	11	1098	186.8	0.5	199.9	0.6	64.4	0.7	66.6	0.7
2009*	30-Aug	13-Sep	-4	365	160.6	0.7	155.7	0.9	38.3	0.6	37.5	0.6
2010	10-Sep	4-Oct	10	189	179.4	1.2	190.9	1.7	54.3	1.3	56.3	1.4
2011	29-Aug	17-Sep	-8	417	145.0	0.9	135.5	1.0	27.9	0.6	26.2	0.6
2012	11-Sep	25-Sep	8	110	157.9	0.9	167.9	1.2	35.4	0.7	37.1	0.7
2013	10-Sep	24-Sep	6	684	174.2	0.5	181.3	0.6	50.6	0.5	51.7	0.5
2014	4-Sep	22-Sep	-1	372	168.7	0.8	167.8	1.0	48.5	0.8	48.3	0.8
2015	2-Sep	16-Sep	-4	983	161.4	0.8	156.2	0.9	42.4	0.7	41.6	0.7
2016	28-Aug	12-Sep	-10	395	153.9	1.2	141.9	1.4	37.3	1.1	35.2	1.2
2017	27-Aug	8-Sep	-9	848	136.4	1.0	125.4	1.0	25.7	0.6	23.9	0.7
2018	3-Sep	15-Sep	-4	1171	152.9	0.5	148.5	0.6	33.4	0.3	32.6	0.3

Table 2. Indices of adult Pink salmon returns and spawners to the Norton Sound region and Yukon River (1995 - 2018), the average Nome Air temperatures (°C, August t to June t+1), and average summer sea surface temperatures during June to September (°C, SST t+1).

Adult	Norton Sound Region		Yukon River		Nome Air	Summer
Year	Returns	Spawners	Returns	Spawners	Temp.	SST
1995	169,496	49,409	55,284	55,137	-4.6	7.2
1996	3,089,682	2,535,593	216,582	214,837	-3.3	6.7
1997	189,439	163,728	4,519	4,301	-3.9	7.5
1998	3,712,761	3,070,848	336,166	330,624	-3.1	6.3
1999	95,302	73,077	4,771	4,716	-5.5	5.7
2000	2,091,074	1,883,867	105,461	104,866	-4.6	6.4
2001	109,878	79,706	3,675	3,666	-2.6	5.7
2002	2,300,537	2,239,565	298,111	289,688	-4.5	7.8
2003	441,387	392,827	17,864	15,673	-1.9	7.8
2004	6,513,682	6,432,486	808,739	799,009	-2.8	9.2
2005	2,652,592	2,594,334	103,255	100,121	-2.6	7.9
2006	5,825,726	5,763,830	384,274	379,366	-5.1	6.5
2007	734,723	708,669	138,492	136,374	-3.3	8.4
2008	4,069,508	3,932,201	793,747	770,035	-4.4	6.6
2009	320,631	275,834	39,225	36,924	-5.4	6.5
2010	1,560,810	1,484,282	1,261,091	1,256,789	-4.7	7.1
2011	231,000	206,127	13,298	10,973	-3.1	6.3
2012	1,265,834	1,013,565	500,227	495,026	-6.2	6.4
2013	102,117	73,928	7,791	6,715	-4.9	7.0
2014	960,447	735,843	799,804	738,121	-1.7	8.2
2015	716,045	626,383	50,632	40,473	-2.0	7.1
2016	4,638,943	4,378,422	1,755,412	1,619,366	-1.1	8.9
2017	2,780,199	2,723,866	199,040	196,573	-2.9	8.9
2018	6,253,239	6,176,411	825,957	785,957	-1.4	9.3

Table 3. Results of the step-wise model selection for Yukon River and Norton Sound region Pink salmon life-cycle models (1995 - 2018). Statistics include C_p, residual standard error (RSS), coefficient of variation (R^2), the mean square error of the true regression model $\hat{\sigma}^2$, parameter estimate (Estimate) and standard error (SE), *t* value of the parameter estimate and significance of the estimate (Prob).

Region	Model	*Cp*	*RSS*	$\hat{\sigma}^2$	Estimate	SE	*t* value	Prob	R^2
Yukon									
	Cushing								
				1.27					0.71
	Intercept Only	1.0	24.2		-0.47	2.07	-0.23	0.821	
	ln(spawners)	42.9	80.1		0.82	0.12	6.80	0.000	
	Summer Sea Surface Temp	1.7	27.6		0.34	0.21	1.69	0.107	
	Ricker								
				1.31					0.11
	Intercept Only	0.5	26.8		-2.44	1.61	-1.52	0.144	
	Summer Sea Surface Temp	1.0	30.1		0.35	0.22	1.60	0.124	
Norton Sound	Cushing								
				0.52					0.77
	Intercept Only	1.4	10.2		1.10	1.59	0.68	0.504	
	ln(spawners)	41.7	32.4		0.66	0.10	6.61	0.000	
	Summer Sea Surface Temp	13.9	17.8		0.54	0.14	3.88	0.001	
	Ricker								

			0.55					0.53
Intercept Only	1.1	10.5		-3.36	1.04	-3.24	0.004	
spawners	9.6	16.3		0.00	0.00	-3.32	0.003	
Summer Sea Surface Temp	14.5	19.0		0.57	0.14	4.02	0.001	

Table 4. Juvenile Pink salmon natural log of the catch per unit effort (CPUE), relative abundance (defined as the natural log of the adjusted CPUE), average sea temperature above the mixed layer depth (°C), and average August$_{t-1}$ to June$_t$ air temperatures (°C) in Nome, Alaska during 2003 to 2018. * no ship board data available for 2008.

Juvenile Year	Mixed Layer Depth Adjustment	ln CPUE	Relative Abundance	Summer SST	Nome Air Temp.
2003	1.78	2.54	4.5	7.8	-1.9
2004	1.46	2.51	3.7	9.2	-2.8
2005	1.79	1.96	3.5	7.9	-2.6
2006	1.20	1.69	2.0	6.5	-5.1
2007	1.18	3.08	3.6	8.4	-3.3
2009*	1.01	1.38	1.4	6.5	-5.4
2010	1.08	1.43	1.5	7.1	-4.7
2011	1.16	1.36	1.6	6.3	-3.1
2012	1.21	0.84	1.0	6.4	-6.2
2013	1.02	3.09	3.1	7.0	-4.9
2014	1.04	2.00	2.1	8.2	-1.7
2015	1.26	4.30	5.4	7.1	-2.0
2016	1.00	2.65	2.7	8.9	-1.1
2017	1.03	3.94	4.1	8.9	-2.9
2018	1.04	4.22	4.4	9.3	-1.4

Table 5. Results of the step-wise model selection for Pink salmon freshwater and early marine life-history events. Statistics include C_p, residual standard error (RSS), the mean square error of the true regression model $\widehat{\sigma}^2$, coefficient of variation (R^2), parameter estimate (Estimate) and standard error (SE), t value of the parameter estimate and significance of the estimate (Prob).

Model	C_p	RSS	$\widehat{\sigma}^2$	Estimate	SE	t value	Prob	R^2
Juvenile Abundance Model								
			0.98					0.55
Intercept Only	17.2	9.8		-9.60	3.50	-2.74	0.018	
ln(spawners)	18.4	14.5		0.35	0.19	1.85	0.090	
Nome Air Temp	25.2	21.3		0.29	0.09	3.26	0.007	
Adult Return Model								
			0.75					0.62
Intercept Only	1.1	8.4		12.3	0.52	23.6	0.000	
Juvenile Index	17.3	22.0		0.74	0.16	4.6	0.000	