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Differential north–south response of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) marine growth to ecosystem change in the eastern Bering Sea, 1974–2010

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Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) returns to western Alaska were historically high and variable but recently reached record lows. Understanding the differential influence of climatic and oceanic conditions on the growth of juvenile Chinook salmon in the north and south eastern Bering Sea is key to understanding mechanisms and factors affecting the production dynamics of Chinook salmon from western Alaska and the Arctic. Summer growth was lower and more variable among years for Chinook salmon in the south than the north eastern Bering Sea. Summer growth decreased with a rise in sea temperatures in the north and south and increased with more sea ice coverage and a later time of ice retreat in the south but not in the north. Capelin (*Mallotus villosus*), an important prey for juvenile Chinook salmon in the north and during cold years may link increased growth to cooler sea temperatures. Reduced and more variable summer growth of juvenile Chinook salmon from the eastern Bering Sea with warming may have implications on overwintering survival.

Keywords: Bering Sea, climate, fish, ice, temperature

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) is an important cultural, commercial, and sport fishing species to the people of Alaska. In western Alaska, harvest of adult Chinook salmon from the Yukon and Kuskokwim rivers dropped from around 150 000 in the 1980s and 1990s to around 50 000 in the 2000s (ADF&G Chinook Salmon Research Team, 2013). Although there is an apparent downwards trend in adult returns to both rivers recently, the longer time-series reveals that the productivity residuals from these two rivers showed no consistent temporal pattern prior to the brood (spawning) year 2001 (M. J. Catalano, unpublished data). The State of Alaska, Chinook Initiative 2013 states: "what is not clear from available data is where, when, and how changes in productivity occur. Moreover, available data (harvest and escapement) are insufficient to foresee this downturn and to readily adapt fishery management schemes as it occurred." This uncertainty has led to conservative management by Federal (i.e. groundfish prohibited species catch; subsistence) and State (catch and escapement) governments that reduces catch of Chinook salmon to achieve escapement goals. The reduced catch and uncertainty regarding total returns of Chinook salmon to the Yukon and Kuskokwim river's "threatens the viability of social and

economic systems in Alaska that are highly dependent on Chinook salmon for their cultural value, sustenance, and income" (ADF&G Chinook Salmon Research Team, 2013).

Both the Arctic Yukon Kuskokwim Chinook research plan (Schindler *et al.*, 2013) and State of Alaska Chinook salmon Initiative acknowledge a lack of understanding of basic abundance, rate information, and associated mechanisms impacting survival during key periods of life for Chinook salmon. Environmental impacts on salmon marine survival are greatest during their first year at sea (Beamish and Mahnken, 2001); increased survival is a function of the growth rate, size, and energetic status (fitness) that juvenile salmon attain during their first summer at sea (Farley *et al.*, 2011). In turn, size and energetic status of juvenile salmon is linked to the climate and ocean conditions they encounter (Farley *et al.*, 2009, 2011).

The eastern Bering Sea (EBS) ecosystem, where western Alaska Chinook salmon spend the majority of their marine life history, is undergoing dramatic change owing to warming climate. The Intergovernmental Panel on Climate Change Regional Climate (IPCC) Projections for the EBS suggests that (i) the Arctic is very likely to warm during this century more than the global mean; (ii) warming is projected to be largest in winter and smallest in summer; and (iii) sea ice is very likely to decrease in its extent and thickness (Christensen *et al.*, 2007). Probably the biggest effect on the EBS ecosystems will be the extent, duration during winter, and thickness of sea ice. These characteristics are believed to determine benthic vs. pelagic productivity on the EBS shelf (Hunt *et al.*, 2011), as well as the boundary between Arctic and Subarctic demersal fish communities (Grebmeier *et al.*, 2006).

Biophysical measurements along the EBS shelf have been used to determine the boundary, termed the "North–South Transition Zone" that separates Subarctic and Arctic ecosystems at around 60°N (Stabeno *et al.*, 2012). Furthermore, climate model projections to 2050 for sea ice extent and duration during winter and spring suggest that ice will be less common in May within the north EBS (north of 60°N; NEBS), but will continue to be extensive through April, whereas in the south EBS (south of 60°N; SEBS), extent and duration will be highly variable (Stabeno *et al.*, 2012). Recent evidence of the impact of warming on ecosystem function in the SEBS suggests sustained warming led to a shift to lower quality prey for fish, reduced fish fitness prior to winter, and increased mortality over winter (Coyle *et al.*, 2011; Farley *et al.*, 2011; Hunt *et al.*, 2011; Heintz *et al.*, 2013). Therefore, we must understand the factors impacting critical periods for Yukon and Kuskokwim river Chinook salmon because climate warming will likely lead to greater uncertainty in production dynamics and more conservative management for these important stock.

Fish and oceanographic survey data collected during Bering Arctic Subarctic Integrated Surveys (BASIS; 2002–2018) suggest that juvenile western Alaska Chinook salmon spend their first summer at sea feeding and growing within the relatively shallow regions (<100 m depth) of the EBS shelf off the Yukon and Kuskokwim rivers (Murphy *et al.*, 2009). During this period, larval and juvenile fish including Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), age-0 walleye pollock (*Gadus chalcogrammus*), and other forage fish dominate the diets of juvenile Chinook salmon both north and south of the transition zone; however, age-0 pollock were more prevalent in the diets of juvenile Chinook salmon found south of the transition zone during years with anomalously warm summer sea temperatures (Farley *et al.*, 2009). These Chinook salmon stocks are separated north and south of the transition zone—Yukon River stocks are primarily distributed to the north of the transition zone, whereas Kuskokwim and Central Alaska stocks are primarily distributed to the south (Murphy *et al.*, 2009). The distribution of the Yukon River stocks also varies depending on spring and summer sea temperatures. For instance, juvenile Yukon River Chinook salmon were distributed within Norton Sound (63°N–64°N) and Bering Strait (65°N–66°N) during years with warmer sea temperatures and further south near Nunivak Island (60°N) during years with colder sea temperatures (Murphy *et al.*, 2017). In addition, marine survival for juvenile Yukon River Chinook salmon was lower during years with a northerly distribution (Murphy *et al.*, 2017), suggesting that climate warming may have a negative impact on these juvenile Chinook salmon.

Our objective is to understand how climate and ecosystem function impact growth during the juvenile life stage of Chinook salmon to the north and south of the 60°N transition zone in the EBS. Because year-class strength is determined prior to fall for juvenile Chinook salmon from the Yukon River, we focus our study on factors influencing early marine growth and length. We do so by (i) comparing distributions in early marine (summer) growth between Chinook salmon from the Yukon (north eastern Bering Sea: NEBS) and Kuskokwim (south eastern Bering Sea: SEBS) rivers using the time-series (1974–2010) data on growth measurements on the scales from adult Chinook salmon collected from both rivers; (ii) test the relationship between sea surface temperatures, sea ice indices, zooplankton indices, and summer growth of juvenile Chinook salmon in both regions and prior to and during the recent warm (2002–2006) and cool (2007–2010) stanza. We expect higher and less variable summer growth of Chinook salmon in the north than in the south, a decrease in growth with warming, and an increase in growth with greater sea ice coverage and later sea ice retreat from the south to the north during spring and higher zooplankton production. These hypothesis are specific to the southeast Bering Sea in that warming has recently led to a shift to lower quality prey for fish and reduced fish fitness (Coyle *et al.*, 2011; Farley *et al.*, 2011; Hunt *et al.*, 2011; Heintz *et al.*, 2013).

Study site

The EBS lies in the northern region of the North Pacific Ocean and bound to the south by the Alaska Peninsula and to the north by the Bering Strait (Figure 1). This subarctic sea has a deep basin in the southwest and a broad shallow continental shelf in the north and east. The Yukon River system drains into the NEBS, north of the transition zone, and the Kuskokwim River drains into the SEBS, south of the transition zone. The Yukon River is the fourth largest river in North America and has a length of 3185 km extending into Canada's Yukon Territory and British Columbia, basin area of 855 000 km^2, a discharge of 7000 $m^3 s^{-1}$, and drains into Norton Sound region within the NEBS (Czaya, 1983). The Kuskokwim River is the ninth largest river in the United States and has a length of 1130 km, basin area of 124 319 km^2, a discharge of 1897 $m^3 s^{-1}$ and drains into Kuskokwim Bay (Benke and Cushing, 2011). Seasonal discharge of river water is lowest in May, highest in June, and tapers off during summer (Brabets *et al.*, 2000). Peak outmigration of Chinook salmon smolt from the Yukon and Kuskokwim River occurs during June (Hillgruber *et al.*, 2007; Howard *et al.*, 2017).

Methods

Adult scales

A 37 year time-series of marine summer growth of Chinook salmon during the first year at sea from 1974 to 2010 was inferred

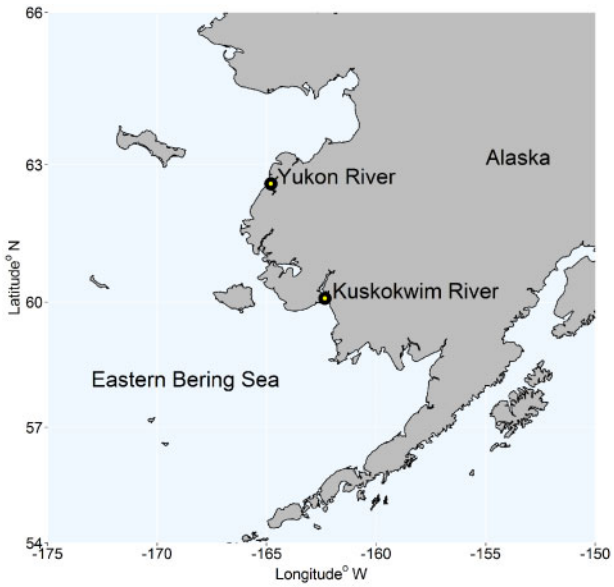

Figure 1. Map showing the rearing habitat for juvenile salmon on the eastern Bering Sea shelf and entrance to the Yukon and Kuskokwim rivers, the origin for the Chinook salmon in our study.

from growth increments measured on scales taken from adult Chinook salmon that returned to the Yukon and Kuskokwim rivers during 1977–2014. Scales were obtained from Alaska Department of Fish and Game (ADF&G) archives and digitized by ADF&G's Mark Tag and Age Lab in Juneau, Alaska. Scales were selected from a study completed by Ruggerone *et al.* (2007), updated through 2009, and scales from 2010 to 2014 run years from a study by Ruggerone and Connors (2015). For the Yukon River, samples were caught with large-mesh (8.5 inch mesh) set gillnets in commercial and/or test fishery harvests in the lower Yukon River. For the Kuskokwim River, scale samples were taken from Chinook salmon caught in commercial and test fisheries near Bethel, which employed a mixture of mesh size gillnets (5.5–6 and 8–8.5 inch); scales were also selected from Chinook salmon caught in weirs on spawning tributaries (Ruggerone *et al.*, 2007). We assumed no effect of gear selectivity on early marine growth rates of these salmon.

As in Ruggerone *et al.* (2007), a target of 50 adult Chinook salmon scales from each of the age groups (1.3 and 1.4) per year were selected for both the Yukon ($n = 3\,483$) and Kuskokwim ($n = 2\,813$) rivers. Age was designated by European notation; that is, *a.b*, where $a =$ the number of winters spent in fresh water (after spending one winter in the gravel), and $b =$ the number of winters spent in the ocean (Koo, 1962). Scale radius measurements were taken from 21 to 284 fish within a year group. Age and sex information was available for each individual fish. Scales were included in the study if there was agreement in the age determination for that fish, if the scale was taken from the preferred position on the fish above the lateral line and below the dorsal fin, and if growth patterns were not obstructed by regeneration or significant resorption (Ruggerone *et al.*, 2007). Scale measurements followed procedures described by Davis *et al.* (1990) and Hagen *et al.* (2001) and were taken from along the longest axis of the scale and marks were made at the location of each circulus, each annulus, and edge of the scale.

Several assumptions were made and assessed for using scale measurements as a proxy for summer growth in length of juvenile salmon. The first assumption made was that the radius of the scale grows in proportion to the growth in body length of the fish and therefor increments along the radius of the scale can represent growth in body length of the fish, as in Dahl (1909) and Clutter and Whitesel (1956). The second assumption made was that circuli, intra-annular rings, formed on the scale on a constant rate during the first year at sea and the distances between circuli estimate growth in length for a particular period during the year (Bilton and Robins, 1971). Bilton and Robins (1971) found that mean circulus spacing was positively correlated with number of days fed for juvenile sockeye salmon reared at constant light and temperature in the lab over 2 months ($r = 0.77$, $n = 12$, p-value < 0.01). Therefore, interannual variation in growth rate because of changes in prey availability is reflected as interannual changes in the spacing of a discrete set of circuli.

These assumptions were assessed through the examination of scales and lengths of juvenile Chinook salmon ($n = 51$) that were captured during BASIS surveys (late August to early October, 2002–2005, 2007) within the EBS (Farley *et al.*, 2007). Scales were taken from the preferred area of the body and mounted on gum cards; body length (mm, snout to fork of the tail) were taken at sea. In the lab, scales on gum cards were pressed onto plastic acetates and scales that showed no signs of regeneration were used in the analyses (Arnold, 1951). These scales were measured from the centre of the focus to the edge of each marine circulus and edge of the scale, and the number of circulus counted. Julian day of capture was recorded. Annual means values were constructed for scale radius, fork length, number of marine circuli, and Julian day of capture. Least squares regression models indicate positive and significant linear relationships between fork length and scale radius for individual fish observations and means grouped by region and year (Figure 2, Table 1). A positive and significant relationship was found between the number of circuli and Julian day sampled at sea, whereas a positive but not statistically significant (p-value $= 0.07$) relationship occurred between the mean annual number of circuli and mean annual Julian day sampled. No significant autocorrelation was detected in the residuals of each model.

Examination of adult scales taken from Chinook salmon returning to the Yukon and Kuskokwim River indicate the minimum number of circuli formed on the scale during the first year at sea was 15, the lowest mean # of circuli in a year was 25. Therefore we used the distance from the 1st saltwater circulus to the 15th saltwater circulus and distance from the 16th to the 25th circulus on the scales of adult Chinook salmon to estimate early summer (mid-June–August) and late summer (September-mid-October) juvenile growth during the 1st summer at sea, respectively, from years 1974 to 2010. Post-summer growth was the distance from the 25th circulus to the last circulus formed during the first year at sea. Smolt length was estimated as the distance from the centre of the focus to the end of the fresh-water growth on the scale. Cumulative scale radius, an index of fork length, was calculated for length at the time of formation of the last fresh-water circulus, the 15th circulus, 25th circulus, and last circulus during the first year at sea. Annual means and 1 *SD* of the means were constructed for each measure.

Sea surface temperature indices

Seasonal means of sea temperature were calculated to match juvenile circulus deposition periods (June–August, September–October) and regions (NEBS, SEBS) for years from 1974 to 2010 (Figure 3).

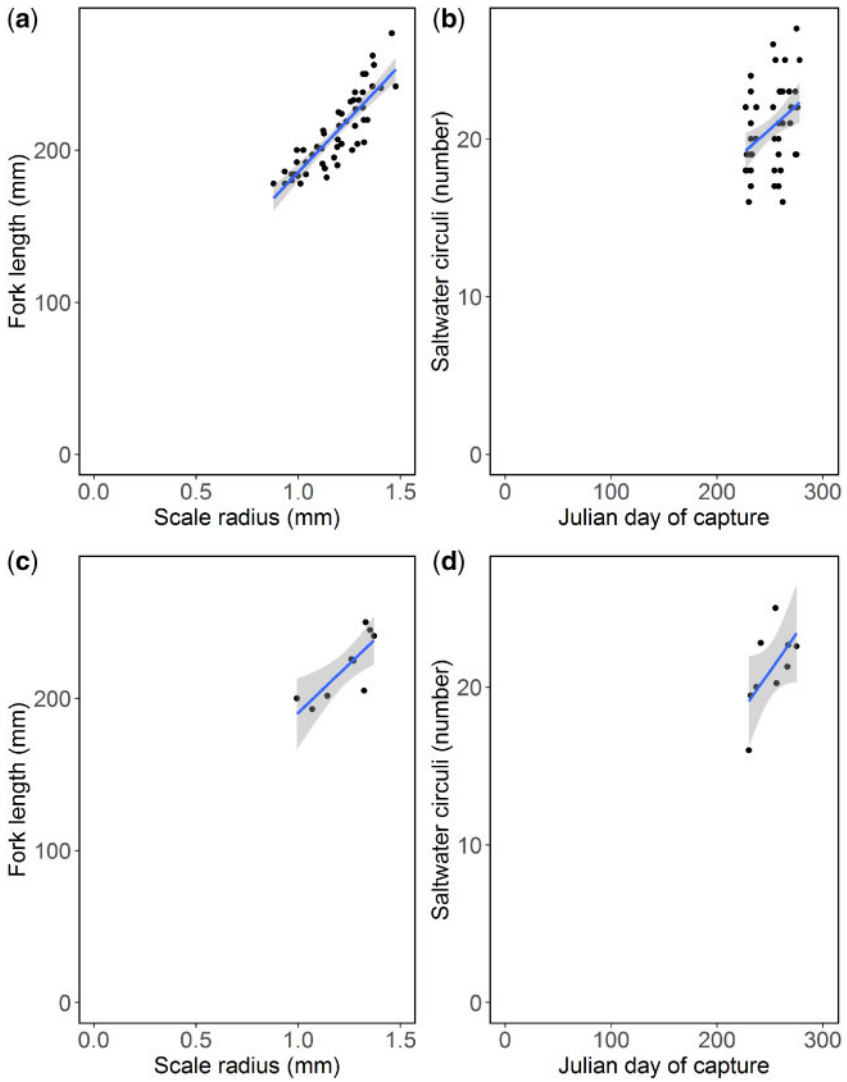

Figure 2. Least squares linear regression relationships relating (a) fork length and scale radius by individual (a) and by region and year group (b), and number of saltwater circuli on the scale and Julian day of capture for individual fish (c) and by region and year grouping (d) for juvenile Chinook salmon sampled with surface trawl gear in the eastern Bering Sea, for years 2002–2005, and 2007.

Table 1. Least squares linear regression model results relating: (i) mean fork length and scale radius of individual fish, (ii) fork length and scale radius by region and year group, (iii) number of circuli and Julian day of capture for individual fish, and (iv) mean number of circuli and mean Julian day of capture by region and year for juvenile Chinook salmon sampled in the eastern Bering Sea, 2002–2005 and 2007.

Variable	Estimate	S.E.	*t*-value	Pr(>|*t*|)	R^2	*F*	*p*
Model 1							
Intercept	45	13	3.32	0.0017	0.76	158	<0.0001
Scale radius	141	11	12.6	<0.0001	–	–	–
Model 2							
Intercept	62	45	1.4	0.208	0.65	13	0.009
Scale radius	128	36	13	0.009	–	–	–
Model 3							
Intercept	3	5	0.55	0.58	0.19	12	0.001
Julian day	0.07	0.02	3.5	0.001	–	–	–
Model 4							
Intercept	−3	12	−0.26	0.80	0.38	4	0.07
Julian day	0.10	0.05	2	0.08	–	–	–

Statistics include model estimates, standard error (S.E.), test statistic (*t*-value), probability of the test statistic (Pr(>*t*)), and model coefficient of determination (R^2), *F*-statistic (*F*), and probability of *F* (*p*).

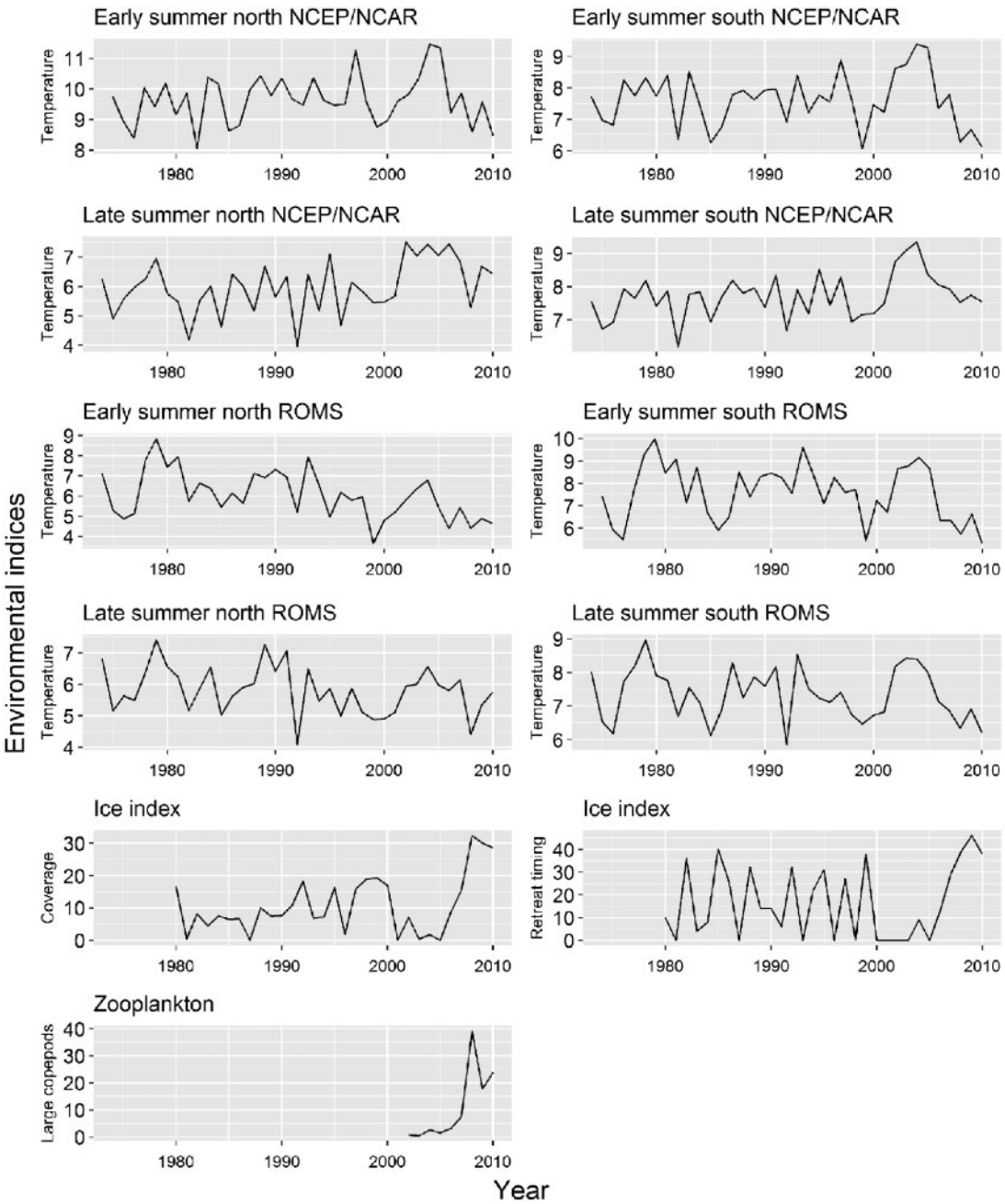

Figure 3. Environmental indices for the north and south eastern Bering Sea, 1974–2010.

First, the NCEP/NCAR reanalysed data were a source of seasonal mean sea surface temperature (SST) values (Kalnay *et al.*, 1996; https://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl, last accessed 14 June 14 2019). Second, the regional ocean modelling system (ROMS) estimates of subsurface (top 20 m of the water column) sea temperatures were available from Hermann *et al.* (2016). This index did not include Bristol Bay. The northern region was defined as from 60.1°N around Nunivak Island to the entrance of the Bering Strait (65°N) and from 172.5°W to 165°W within the inner domain (5–50 m isobath). The southern region was defined as from 57°N to 60°N, west of Cape Newenham (162°W) and within the inner domain (5–50 m isobath).

Sea ice indices

The ice cover index and timing of ice retreat index for the EBS were available from the Bering Climate website that originated in the National Snow and Ice Data Centre (Figure 3; https://www.beringclimate.noaa.gov/data/BCresult.php, last accessed 2 February 2018, last updated 21 August 2016). The ice cover index is the average ice concentration in a 2° × 2° box (56°N–58°N, 163°W–165°W) from 1 January to 31 March, 1980–2010. Small values indicate the lack of or very little ice in the SEBS. The ice retreat index is the number of days after 15 March when the sea ice covers 10% of the 2° × 2° box (56°N–58°N, and 163°W–165°W) in the SEBS. The region of these two indices is in the SEBS in an area occupied by the Chinook salmon leaving the Kuskokwim River.

Large copepod index

The estimated mean density (# per m^3) of large copepods in the southeast Bering Sea during late summer was available from 2002 to 2010 (Eisner and Yasumiishi, 2018). The index consisted of Calanus, Metridia, and Neocalanus copepods, prey for small fish, such as capelin (Andrews *et al.*, 2016).

Diet analysis

Food habit information was collected from juvenile Chinook salmon in the NEBS (≥60°N) and SEBS (<60°N) during the late summer BASIS survey during warm (2004–2006, 2014) and cold (2007–2013) stanzas (Farley *et al.*, 2005). At each sampling station, stomach contents of multiple fish were pooled and gut contents sorted into taxa. We defined taxa as amphipods, capelin, crab, euphausiids, other fish, Pacific herring (*Clupea pallasii*), Pacific sand lance, age-0 pollock, and shrimp.

A stomach content index for each taxa was calculated as the prey weight divided by the predator weight for the pooled samples at each station. We averaged the stomach content index for each taxa among stations by region (NEBS, SEBS) and stanza (cold, warm). The number of stations for north and cold group included 19 in 2007, 10 in 2009, 16 in 2010, 15 in 2011, and 21 in 2013, the north and warm group included 38 in 2004, 17 in 2005, 34 in 2006, and 29 in 2014, and the south and warm group included 24 in 2004, 24 in 2005, and 4 in 2006.

Statistical analyses

For graphical and statistical analyses, we used R version 3.3 and RStudio version 0.99.89 (RStudio Team, 2015; R Core Team, 2016). An ANOVA test was used to determine the influence of region, age at maturity, sex, and year on annual means of growth variables. Whisker plots were used to show the mean and 1 *SD* of the mean for growth variables by significant groupings. Next, a *t*-test was used to test for differences in mean summer growth between two groups with matching years. The *t*-tests were implemented with the t.test function with the stats package (version 3.0.3) in R. The var.test function (version 3.0.3) was used to test for differences in interannual variability in mean growth between two groups with matching years.

To determine the relationship between growth and environmental indices we used scatterplots and linear regression models at a significance level of $\alpha = 0.05$, adjusted for the number of groupings by applying a Bonferroni correction factor for the number of regression models for each growth variable ($p = 0.05/20 = 0.002$). Correlations were used to examine the relationships among fresh-water scale growth (a proxy for smolt length), summer growth, and total length (fresh water plus summer growth).

Results

Growth differences

ANOVA test results indicated a significant effect of age on early and late summer growth for the SEBS and NEBS Chinook salmon (Table 2). Differences in growth between sexes was found for the early summer growth of NEBS Chinook salmon, but owing to small samples sizes and the visual appearance of similar growth pattern in Figure 4, we combined sexes.

Early summer growth was higher for Chinook salmon in the NEBS than in the SEBS (Figure 4, Table 3). Age 1.3 Chinook salmon had more early summer growth than age 1.4 Chinook salmon in the NEBS, but were not different between ages in the SEBS. Results of the *t*-tests indicated that growth differences were greater between regions than between ages within a region (Table 3).

Table 2. ANOVA for the effect of sex and age on early summer (C1–C15) and late summer (C16–C25) scale growth (mm) of Chinook salmon during the first year at sea in the south (SEBS) and north (NEBS) eastern Bering Sea regions, 1974–2010.

Source of variation	df	SS	MS	*F*	*p*-value
NEBS C1–C15					
Sex	1	0.320	0.3196	42.487	<0.001
Age	1	0.051	0.0509	6.772	0.0093
Residuals	3 480	26.179	0.0075	–	–
SEBS C1–C15					
Sex	1	0.002	0.00246	0.322	0.5702
Age	1	0.043	0.04253	5.573	0.0183
Residuals	2 810	21.448	0.00763	–	–
NEBS C16–C25					
Sex	1	0.01	0.0078	0.773	0.379
Age	1	1.59	1.5931	157.583	<0.001
Residuals	3 480	35.18	0.0101	–	–
SEBS C16–C25					
Sex	1	0.000	0.00039	0.043	0.835
Age	1	0.225	0.22503	24.861	<0.001
Residuals	2 810	25.435	0.00905		

Statistics include degrees of freedom (df), sum of squares (SS), mean sum of squares (MS), *F*-statistics (*F*), and probability of *F* (*p*-value).

Late summer growth was higher for 1.3 and 1.4 SEBS Chinook salmon than age 1.4 NEBS Chinook salmon (Table 3, Figure 5). Results of the *t*-tests indicated that growth differences were greater between ages within a region than between regions (Table 3). By region, late summer growth was higher for the age 1.3 fish and lower for the age 1.4 fish within each region.

Interannual variability in early summer growth was higher for SEBS Chinook salmon than NEBS Chinook salmon (Table 4). Specifically, early summer growth was more variable interannually for the SEBS ages 1.3 and 1.4 Chinook salmon than the age 1.4 NEBS Chinook salmon. No significant difference was detected in the interannual variability in late summer growth among region and age groups or between age groups within a region.

Smolt lengths as indicated by fresh-water scale growth were significantly greater by 0.02 mm for Chinook salmon in the NEBS (males: mean = 0.44 mm, females: mean = 0.44 mm) than in the SEBS (mean = 0.42 mm) as indicated by *t*-tests, but only differed by 4%. Summer growth was positively correlated with fresh-water scale growth for male ($r = 0.61$, $p < 0.001$) and female ($r = 0.48$, $p = 0.002$) Chinook salmon in the NEBS but not for Chinook salmon in the SEBS ($r = 0.16$, $p = 0.35$).

Mean number of circuli formed on the scales during the first year at sea varied from 24 to 34 for the NEBS and SEBS Chinook salmon (Figure 6). Chinook salmon in the SEBS tended to have more circuli than in the NEBS. An increase in the number of circuli was detected during the recent warm stanza relative to the cool stanza.

Cumulative scale radius, a proxy for fish length, shows stable fresh-water growth among groups and over time (Figure 7). The greatest amount of growth occurred during the early summer

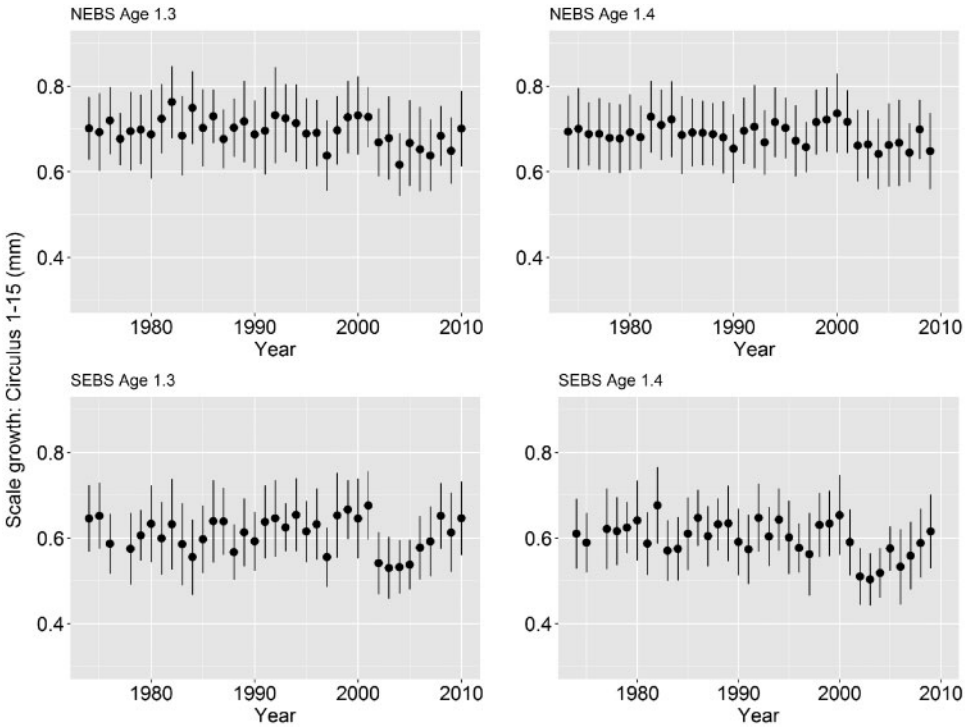

Figure 4. Means and 1 *SD* of the means (whiskers) for early summer (June–August) growth of Chinook salmon during the first year at sea in the north (NEBS) and south (SEBS) eastern Bering Sea from 1974 to 2010. Growth was estimated as the distance from the 1st to the 15th circulus on scales of age 1.3 and 1.4 adult Chinook salmon that returned to the Yukon and Kuskokwim rivers.

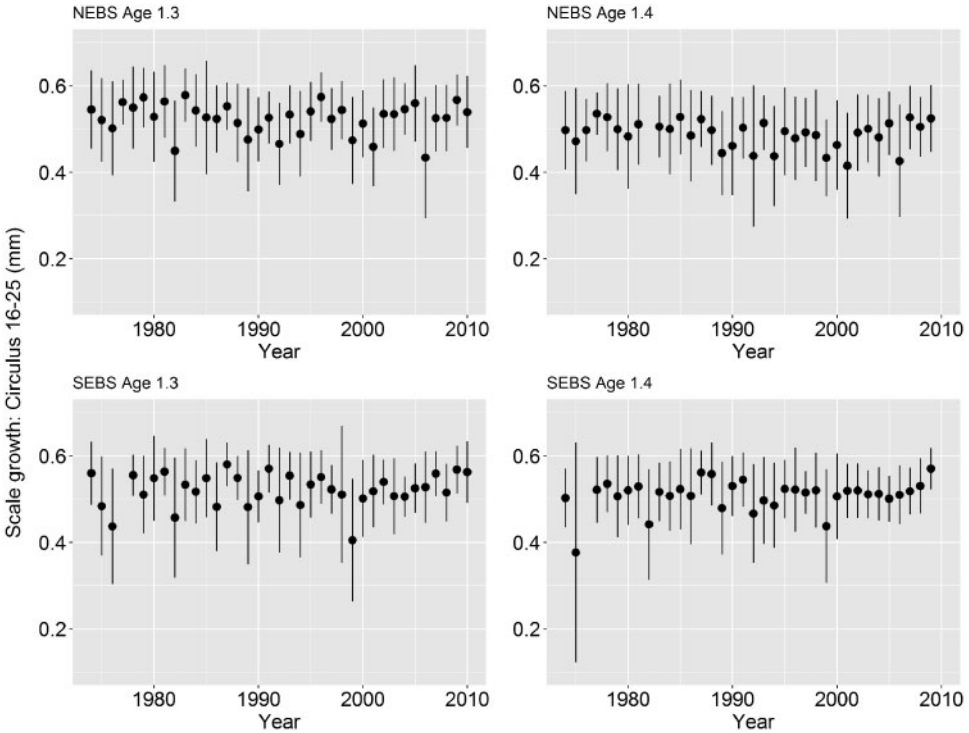

Figure 5. Means and 1 *SD* of the means (whiskers) for late summer (September–October) growth of Chinook salmon during the first year at sea in the north (NEBS) and south (SEBS) eastern Bering Sea from 1974 to 2010. Growth was estimated as the distance from the 16th to the 25th circulus on scales of age 1.3 and 1.4 adult Chinook salmon that returned to the Yukon and Kuskokwim rivers.

Table 3. Results for differences in means of the annual means of early summer (C1–C15) and late summer (C16–C25) scale growth (mm) of Chinook salmon during the first year at sea in the south (SEBS) and north (NEBS) eastern Bering Sea regions, 1974–2010.

Variable/comparison	Difference	*t*	df	*p*-value
C1–C15				
NEBS 1.3 vs. NEBS 1.4	0.008	2.3	35	0.030
SEBS 1.3 vs. SEBS 1.4	0.011	1.9	33	0.060
NEBS 1.3 vs. SEBS 1.3	0.086	13.7	35	<0.001
NEBS 1.4 vs. SEBS 1.4	0.089	15.8	34	<0.001
NEBS 1.3 vs. SEBS 1.4	0.096	17.6	34	<0.001
NEBS 1.4 vs. SEBS 1.3	0.079	14.4	34	<0.001
C16–C25				
NEBS 1.3 vs. NEBS 1.4	0.039	10.9	35	<0.001
SEBS 1.3 vs. SEBS 1.4	0.014	3.0	33	0.005
NEBS 1.3 vs. SEBS 1.3	0.002	0.4	35	0.721
NEBS 1.4 vs. SEBS 1.4	−0.025	−4.2	34	<0.001
NEBS 1.3 vs. SEBS 1.4	0.016	2.3	34	0.020
NEBS 1.4 vs. SEBS 1.3	−0.037	−6.6	34	<0.001

Statistics include the difference, *t*-statistic (*t*), degrees of freedom (df), and probability of *t* (*p*-value).

Table 4. Results for differences in variance of the annual means of early summer (C1–C15) and late summer (C16–C25) scale growth of Chinook salmon during the first year at sea in the south (SEBS) and north (NEBS) eastern Bering Sea regions, 1974–2010.

Variable/comparison	Variance ratio and *F*	*p*-value
C1–C15		
NEBS 1.3 vs. NEBS 1.4	1.680	0.128
SEBS 1.3 vs. SEBS 1.4	0.983	0.959
NEBS 1.3 vs. SEBS 1.3	0.601	0.134
NEBS 1.4 vs. SEBS 1.4	0.352	0.003
NEBS 1.3 vs. SEBS 1.4	0.591	0.123
NEBS 1.4 vs. SEBS 1.3	0.358	0.003
C16–C25		
NEBS 1.3 vs. NEBS 1.4	0.979	0.948
SEBS 1.3 vs. SEBS 1.4	1.158	0.671
NEBS 1.3 vs. SEBS 1.3	0.862	0.658
NEBS 1.4 vs. SEBS 1.4	1.019	0.957
NEBS 1.3 vs. SEBS1.4	0.999	0.992
NEBS 1.4 vs. SEBS 1.3	0.880	0.708

Statistics include the difference in variances, *F*-statistic (*F*), and probability of *F* (*p*-value).

period. A reduction in growth during the early and late summer periods occurred in 2002. The trend in total scale radius during the first year at sea was also stable because of the increase in post-summer growth during warm years.

Growth and environmental indices

Table 5 shows results of the linear regression models relating scale growth and radius measurements to environmental indices for 1974–2001 and 2002–2010. During 1974–2001, late summer and post-late summer scale growth and radius were significantly and positively related to sea temperature for the SEBS Chinook salmon, but not NEBS Chinook salmon, except for a positive relationship between sea temperature and post-late summer growth of age 1.3 NEBS Chinook salmon. Early summer growth and scale radius were not related to environmental indices during this period.

During 2002–2010, early summer scale growth of Chinook salmon was significantly related to environmental indices for age 1.3 SEBS Chinook salmon, but not for age 1.4 SEBS, age 1.3 NEBS, and 1.4 NEBS Chinook salmon (Figure 8, Table 5). Early summer growth and scale radius of age 1.3 SEBS Chinook salmon was negatively and significantly related to sea temperature and positively and significantly related to sea ice indices and zooplankton densities (Figures 8 and 9). In addition, early summer scale radius of age 1.4 NEBS Chinook salmon was significantly and negatively related to sea temperature (Figure 9). Post-summer growth was positively and significantly related to sea temperature for age 1.3 SEBS Chinook salmon. No significant relationships were found between environmental indices and late summer growth, late summer scale radius, and total scale radius to the end of the last circulus formed during the first year at sea.

Juvenile Chinook salmon diets

Proportion of prey taxa in the stomachs of juvenile Chinook salmon in the EBS varied by region and stanza (Figure 10). Sand lance and pollock were more prevalent during the warm stanzas than the cold stanza. Capelin were more prevalent in the diets of juvenile Chinook salmon during the cold stanzas than the warm stanzas. Capelin, crab, herring, and other fish were more prevalent in diets of Chinook salmon in the NEBS than in the SEBS.

Discussion

Our retrospective analysis of the juvenile Chinook salmon marine summer growth in the EBS showed: (i) greater and less variable early summer growth in the NEBS and lower and more variable early summer growth in the SEBS, (ii) early summer growth was clearly more related to sea temperature, sea ice, and large copepod densities in the SEBS than in the NEBS, and (iii) early summer growth more strongly related to environmental indices during the recent warm and cold stanzas (2002–2010) than 1974–2001. Our results indicate that warming sea temperatures and loss of sea ice was related to slower summer growth of juvenile Chinook salmon in the EBS, especially in the SEBS. The negative effects of warming on growth rates is in contrast to many previous studies (e.g. Thresher *et al.*, 2007; Rindorf *et al.*, 2008; Baudron *et al.*, 2014). Species in the northern regions of their distribution typically have increased growth rates with warming. However, the juvenile Chinook salmon in our study had increased growth rates in response to cooler sea temperatures and more ice-associated availability of lipid-rich prey rather than metabolic increases because of warming. We found an indirect effect of temperature and sea ice on the growth rates of Chinook salmon acting primarily on the abundance of their prey (capelin) and prey (large copepods) of capelin.

Our results showing that early summer growth of Chinook salmon was less variable among years in the NEBS than the SEBS may be because of the more consistent occurrence of sea ice and ice-associated phytoplankton blooms in the NEBS than the SEBS (Sigler *et al.*, 2016). Sea ice does not always extend into the SEBS leading to latitudinal differences in productivity, especially during low ice and warm years (Stabeno *et al.*, 2012). The timing and southern extent of sea ice is important in determining the amount and location of biological productivity and lipid-rich prey available for fish, mammals, and birds in the EBS (Sigler *et al.*, 2011, 2016; Stabeno *et al.*, 2012). In the NEBS, sea ice arrives earlier in the year, has higher concentrations, occurs more

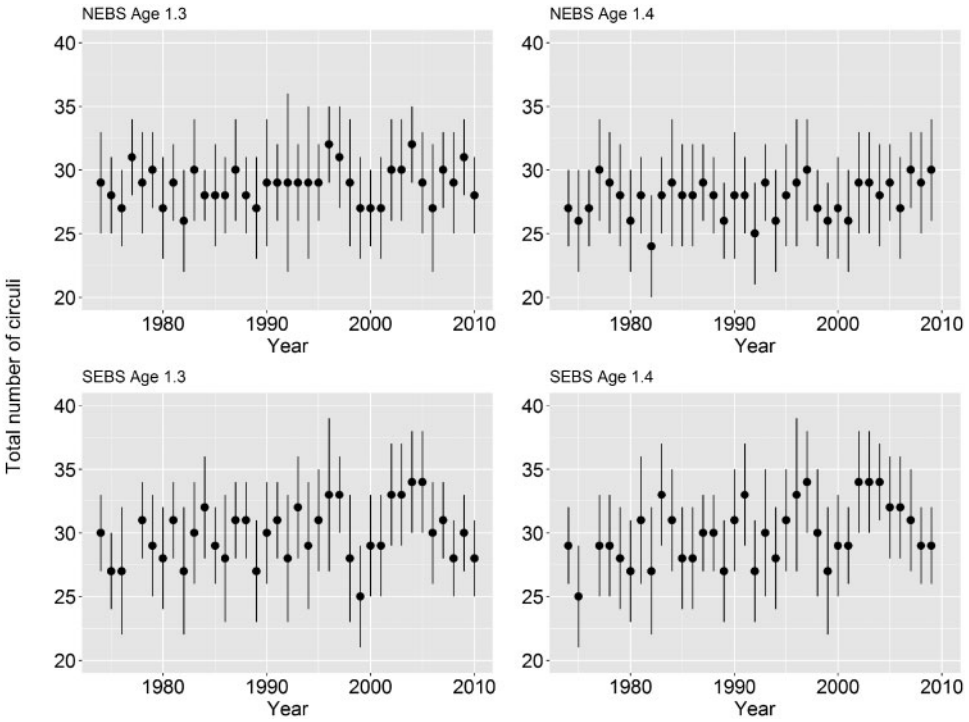

Figure 6. Means and 1 *SD* of the means for the total number of circuli on the scale of Chinook salmon during the first year at sea in the north (NEBS) and south (SEBS) eastern Bering Sea from 1974 to 2010. Circuli were estimated from the scales of age 1.3 and 1.4 adult Chinook salmon that returned to the Yukon and Kuskokwim rivers.

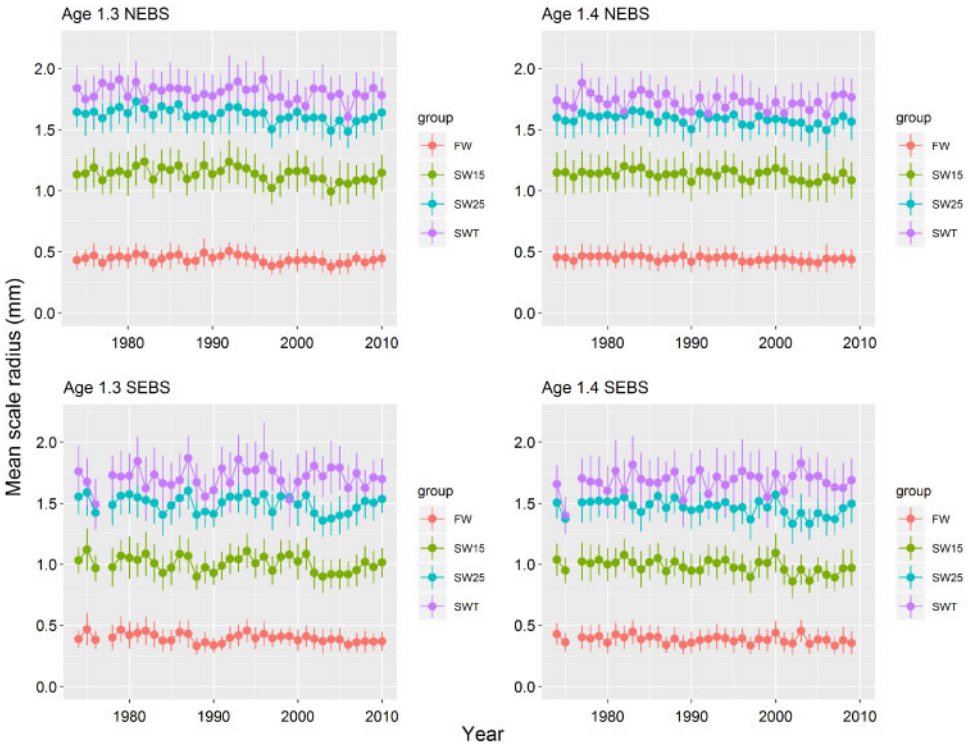

Figure 7. Mean and 1 *SD* of the mean of scale radius measurements of Chinook salmon for the first year at sea in the north (NEBS) and south (SEBS) eastern Bering Sea from 1974 to 2010. Scale radius was estimated from age 1.3 and age 1.4 adult Chinook salmon that returned to the Yukon and Kuskokwim rivers. Distances include from the centre of the scale to the end of fresh-water growth (FW), 15th circulus (SW15), 25th circulus (SW25), and last circulus (SWT) on the scale.

Table 5. Significant ($\alpha \leq 0.002$) predictor variables in least squares linear regression models relating environmental variables to early summer scale growth (C1–C15), early summer scale radius (SW15), late summer scale growth (C16–C25), late summer scale radius (SW25), post-summer growth (C25-CT), and post-summer scale radius (SWT) of Chinook salmon during the first year at sea in the south (S) and north (N) eastern Bering Sea regions, 1974–2010.

Variable	1974–2001	2002–2010
C1–C15	–	S13: NCEP(−), ROMS(−), IRI(+), ICI(+), ZOOP(+)
C16–C25	S13: NCEP(+), ROMS(+)	–
C25-CT	S13, S14, N13: NCEP(+)	S13: NCEP(+), ROMS(+)
SW15	–	S13: NCEP(−), IRI(+), ICI(+), ZOOP(+)N14: NECP(−)
SW25	S13, S14: NCEP(+), ROMS(+)	–
SWT	S13: NCEP(+), ROMS(+), S14: NCEP(+)	–

Growth was estimates from scale of age 1.3 (13) and 1.4 (14) adult Chinook salmon that returned to the Yukon and Kuskokwim rivers. Indices include sea surface temperature (NCEP), 0–20 m sea temperature (ROMS), ice retreat timing (IRI), ice cover index (ICI), and large copepod densities (ZOOP).

consistently among years, and persists longer through spring than in the SEBS (Stabeno *et al.*, 2012). In addition, Andrews *et al.* (2016) found that the presence of higher quality prey (i.e. capelin) was consistent in the NEBS, even during the more recent warm sea temperature stanzas relative the SEBS. The persistence of high quality prey for juvenile Chinook salmon in the NEBS may explain less variable in growth rates in the NEBS than the SEBS.

We also found that juvenile Chinook salmon in the NEBS grew more during early summer than those in the SEBS. This result may also be related to juvenile Chinook prey. Within the NEBS, juvenile Chinook salmon were distributed farther north and offshore with broader overall distributions during warm years, and distribute farther south and closer to shore during cold years (Murphy *et al.*, 2013). Capelin were also in higher relative abundance in the northern regions than in the southern regions of the NEBS during years with warmer sea temperatures and found throughout the NEBS during cooler years (Andrews *et al.*, 2016). The shift from the south to the north for juvenile Chinook salmon in the NEBS during warmer years may be a response to shifting distributions of their preferred prey (capelin). In the SEBS, the relative abundance of capelin declines dramatically during warm years and whereas capelin increase in abundance within the SEBS during cool years, their overall abundance is less in the SEBS than the NEBS regardless of climate (Andrews *et al.*, 2016).

Our finding that SEBS Chinook salmon had more early summer growth during cold years and less early summer growth during warm years supports the Oscillating Control Hypothesis (Hunt *et al.*, 2011). The hypothesis states that a later timing of sea ice retreat allows for a later ice-associated bloom of phytoplankton at a time when zooplankton nauplii are present and can consume the phytoplankton and in turn provide more lipid-rich prey for forage fish such as capelin. Capelin is an important component of the prey found in juvenile Chinook salmon stomachs in the NEBS (Farley *et al.*, 2009). Capelin are not only more abundant in the EBS during cold years but they also consumed more lipid-rich prey (large copepods) during cold summers than during warm summers in the EBS (Coyle *et al.*, 2011; Andrews *et al.*, 2016). Greater consumption of capelin during the cold stanzas and consumption of lower-energy prey pollock and sand lance during the warm stanza, especially for those juvenile Chinook salmon in the SEBS (see Farley *et al.*, 2009) indicate that the most likely link to high early summer growth for juvenile Chinook salmon is the availability of higher quality prey such as capelin. We linked higher densities of large copepods in the SEBS, high quality prey for capelin, to the higher early summer growth of SEBS Chinook salmon during the recent warm (2002–2006) and cold (2007–2010) stanzas.

Several reasons explain the lack of significant relationship between environmental indices and early summer growth of NEBS Chinook salmon. First, Chinook salmon were larger after leaving fresh water and during summer in the NEBS than in the SEBS. Larger fish can eat more and larger prey, have faster growth rates, and survive longer between meals, increasing survivability. Second, early summer growth of NEBS declined in 2002 and remained low from 2002 to 2010. Third, other mechanism may drive growth rates of fish such as metabolic demands, spatial and temporal overlap with prey, predators, and competitors.

Climate impacts of the recent 2002–2006 warming and 2007–2010 cooling periods in the SEBS were evident in the shift in relationships between environmental indices and growth over time. Early summer growth and size of Chinook salmon was associated with environmental indices during the recent warm and cool period (2002–2010), whereas late summer growth and size of Chinook salmon was more clearly and positively associated with warming prior to 2002–2010. These shifts in relationships indicate changes in processes influencing growth rates of Chinook salmon in the EBS. The 2017–2019 warming and near lack of sea ice during spring in the NEBS (Cornwall, 2019) could impact Chinook salmon growth rates and survival in the NEBS.

Understanding factors influencing growth of juvenile Chinook salmon in the EBS is key to understanding mechanisms factors affecting the production dynamics of Chinook salmon from western Alaska. The abundance of juvenile Chinook salmon sampled during late summer in the NEBS is used to predict adult returns from the same juvenile cohort to the upper Yukon River, 2003–2017 (Murphy *et al.*, 2017). This finding indicates that mortality after September is relatively stable. Therefore, early summer growth and size of juvenile Chinook salmon is likely important in determining year-class survival during the first year at sea, especially during the recent warm and cool stanzas.

Climate model projections indicate an increase in sea temperature and decline in the maximum seasonal fraction of sea ice coverage and fewer years of ice coverage in the SEBS through 2050 (Overland and Wang, 2007). Our results suggest that warming sea temperatures and loss of sea ice during winter and spring will lead to reduced early marine growth and increased variability in size of Yukon and Kuskokwim Chinook salmon. This will likely lead to higher marine mortality, as size of juvenile Chinook salmon is positively related to their survival (Howard *et al.*, 2016). Therefore, we hypothesize that the link between early marine growth and survival for juvenile Chinook salmon in the EBS

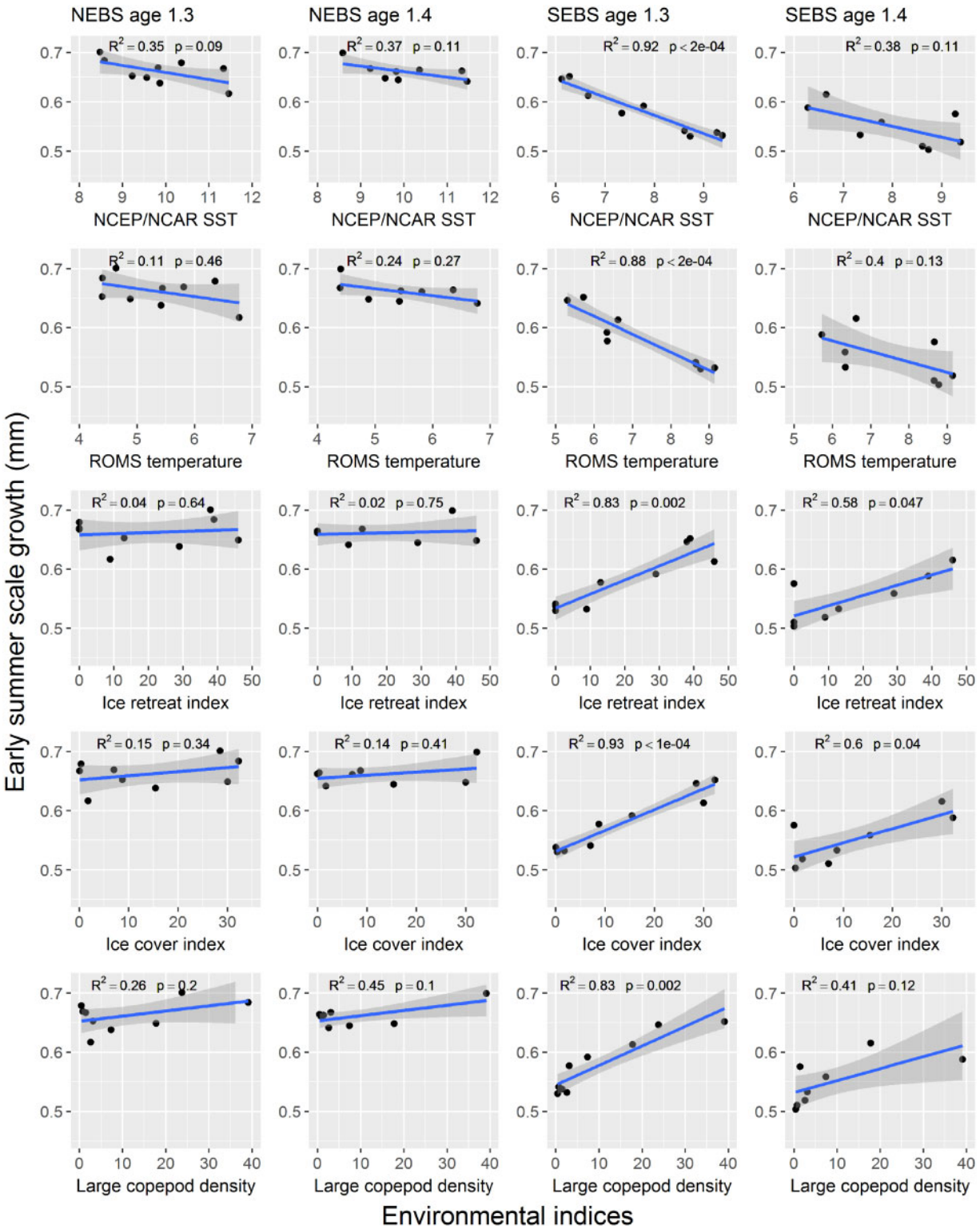

Figure 8. Least squares linear regression relationships relating environmental indices and early summer growth of Chinook salmon during the first year at sea in the north (NEBS) and south (SEBS) eastern Bering Sea from 2002 to 2010. Growth was estimated as the distance from the 1st to the 15th circulus on scales of adult Chinook salmon that returned to the Yukon and Kuskokwim rivers.

is the availability of capelin. Because relative abundance of capelin along the EBS shelf is expected to decline because of warming sea temperatures, we expect continued declines in body size of juvenile Chinook salmon and increased variability in the abundance of adult Chinook salmon returning to western Alaska in the future.

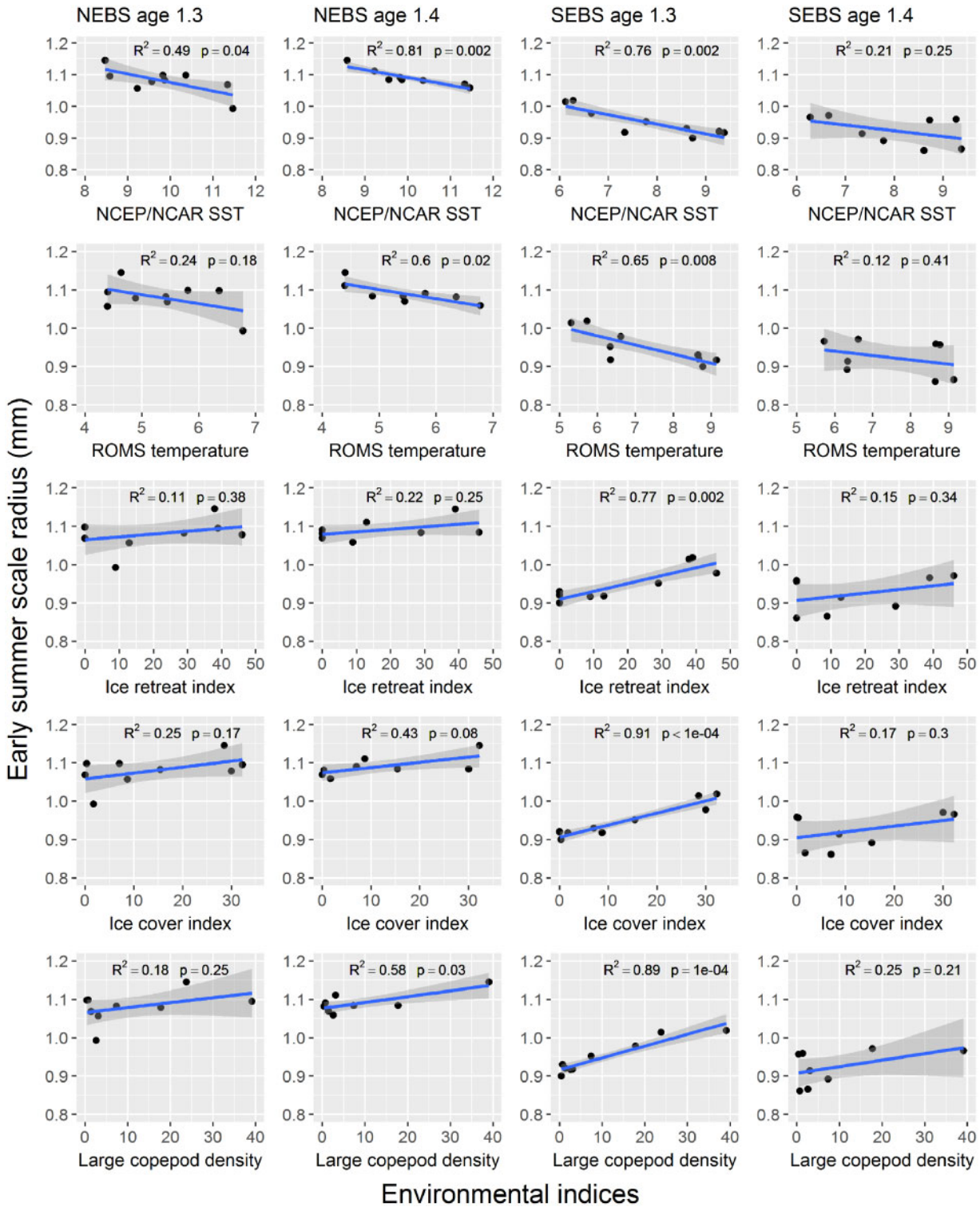

Figure 9. Least squares linear regression relationships relating environmental indices and early summer growth during the first year at sea in the north (NEBS) and south (SEBS) eastern Bering Sea from 2002 to 2010. Scale radius was estimated as the distance from the centre of the scale to the 15th circulus on scales of adult Chinook salmon that returned to the Yukon and Kuskokwim rivers.

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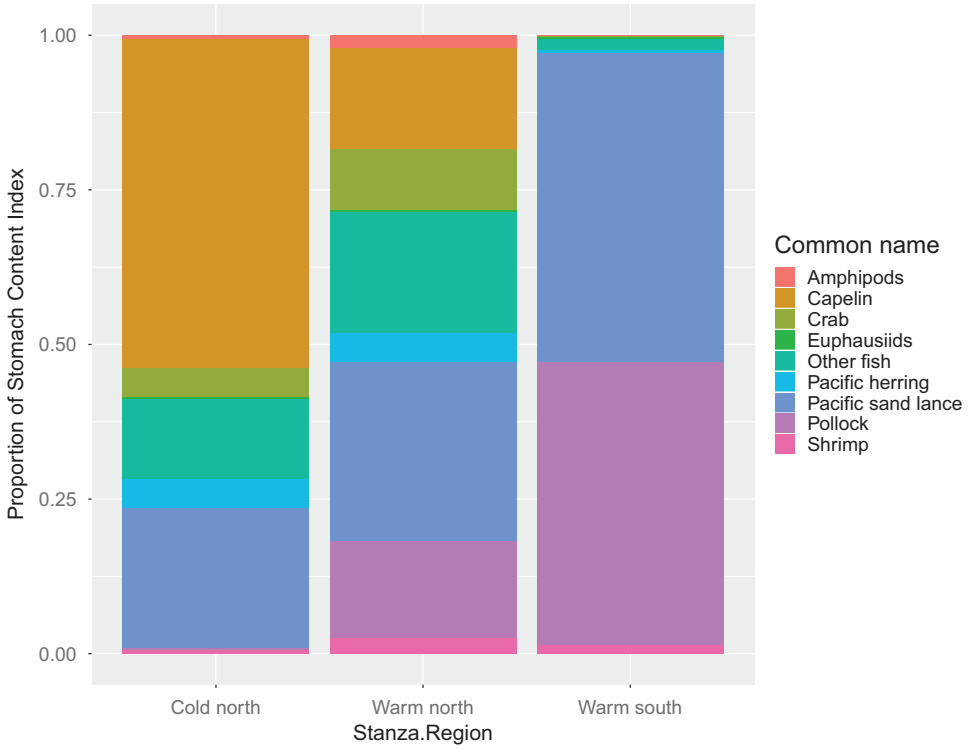

Figure 10. Stomach content index of juvenile Chinook salmon in the south and north eastern Bering Sea during the warm and cool stanzas.

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