

## Pink and Sockeye Salmon Interactions at Sea and Their Influence on Forecast Error of Bristol Bay Sockeye Salmon

Gregory T. Ruggerone<sup>1</sup>, Beverly A. Agler<sup>2</sup>, Brendan M. Connors<sup>3</sup>, Edward V. Farley, Jr.<sup>4</sup>, James R. Irvine<sup>5</sup>, Lorna I. Wilson<sup>2</sup>, and Ellen M. Yasumiishi<sup>4</sup>

<sup>1</sup>Natural Resources Consultants, Inc., 4039 21<sup>st</sup> Avenue West, Suite 404, Seattle, WA 98199, USA

<sup>2</sup>Alaska Department of Fish and Game, Mark, Tag and Age Laboratory,  
10107 Bentwood Place, Juneau, AK 99801, USA

<sup>3</sup>ESSA Technologies, 2695 Granville Street, Vancouver, BC V6H 3H4, Canada

<sup>4</sup>Auke Bay Laboratories, Alaska Fisheries Science Center, NMFS, NOAA,  
17109 Point Lena Loop Road, Juneau, AK 99801, USA

<sup>5</sup>Fisheries and Oceans Canada, Pacific Biological Station,  
3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada

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**Abstract:** Total sockeye abundance in Alaska tends to be positively correlated with North Pacific pink salmon abundance, leading to questions about the importance of competition at sea between these two species. We examined annual scale growth of Bristol Bay sockeye salmon at sea and quantified forecast error of Bristol Bay sockeye stocks over the past 40 years to test the hypothesis that competition with pink salmon reduces the growth and survival of sockeye salmon. Sockeye growth during the second and third years at sea exhibited a strong alternating-year pattern and was negatively correlated with pink salmon abundance from eastern Kamchatka and central Alaska. In addition, forecast error of sockeye stocks from southeastern Bristol Bay (Kvichak, Naknek, Egegik, and Ugashik) exhibited an alternating-year pattern suggesting competition with pink salmon also affected survival. After standardizing forecast error relative to adjacent years, forecasts in even-years were too high and forecasts in odd-years were too low, likely reflecting competition with pink salmon during the year prior to the return year. Sockeye salmon from northwestern Bristol Bay (Wood River) exhibited weaker growth and forecast error relationships with pink salmon abundance, which is consistent with their more easterly distribution at sea. Sockeye scale growth during the first year at sea was not related to pink salmon abundance, as expected, and the observed greater growth during this early marine period in recent decades likely contributed to the greater abundance of Bristol Bay salmon. These findings highlight sockeye growth and survival dynamics that cannot be explained by physical oceanographic patterns and support the hypothesis that competition with pink salmon adversely affects the growth and survival of Bristol Bay sockeye salmon.

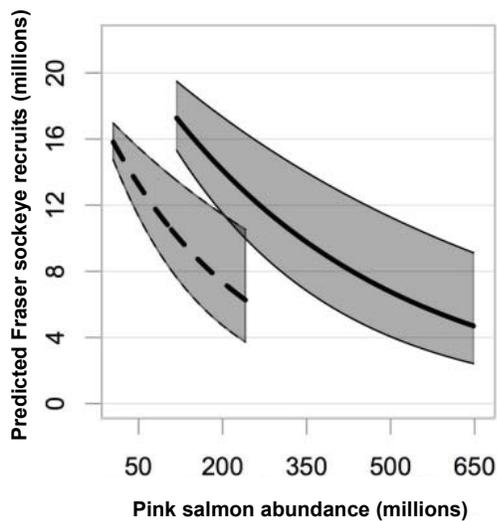
**Keywords:** Bristol Bay, Fraser River, sockeye, pink salmon, forecast, competition, food web, density dependence

### INTRODUCTION

To evaluate whether declines in Fraser River sockeye salmon survival occurred across a broader area than the Fraser watershed, Peterman and Dorner (2012) examined the productivity of 64 sockeye salmon populations spanning 17 regions from Puget Sound, Washington, to western Alaska. Sockeye spanning a large multi-regional area, from Puget Sound through British Columbia and into Southeast Alaska, were characterized by declining productivity since the early 1980s. In contrast, the productivity of sockeye populations in central and western Alaska was either stable or increasing

over time. Peterman and Dorner (2012) concluded that future research into the factors driving broad-scale variability in sockeye dynamics should focus on mechanisms that operate at large, multi-regional spatial scales encompassing the two regions of correlated sockeye productivity patterns.

Competition at sea with increasingly abundant pink salmon is one possible large-scale process that could contribute to the pattern described above. Ruggerone and Connors (2015) tested the hypothesis that competition at sea with pink salmon contributed to declines in productivity among the 36 sockeye populations spanning the large southern area identified by Peterman and Dorner



**Fig. 1.** Predicted Fraser River adult sockeye recruits ( $\pm 2$  SE) as a function of pink salmon abundance returning to North America (dashed line) or to both North America and Asia (bold line). Other variables in the model, such as sockeye spawning abundances and sea surface temperature, were held at mean values. See Ruggerone and Connors (2015) for modeling methods and results.

(2012). They found that sockeye productivity was negatively correlated with the combined abundance of pink salmon from Asia and North America as well as the abundance of pink salmon from only North America. Also, sockeye length-at-age was negatively correlated with pink salmon abundance, whereas sockeye age-at-maturity was positively correlated with pink salmon abundance. Evidence supported the hypothesis that the interaction primarily occurred during the second year at sea rather than the first year at sea (but see McKinnell and Reichardt 2012). Furthermore, sockeye productivity, growth, and maturation exhibited alternating-year patterns consistent with the hypothesis that increasing pink salmon abundance leads to increased competition for food. Statistical modeling predicted that an increase in North Pacific pink salmon abundance from 200 to 400 million fish resulted in a 39% decline in the recruitment of Fraser River sockeye salmon. The investigators did not provide a prediction for the effect of North American pink salmon on Fraser sockeye salmon. However, using modeling results from the original investigation, a 50 to 250 million increase in pink salmon abundance from North America only is predicted to result in a 56% decline in Fraser sockeye recruitment. This suggests that the per capita effect of North American pink salmon was approximately 1.4x greater than that of pink salmon from both Asia and North America (Fig. 1). Most hatchery pink salmon are produced in Alaska, and approximately 50 million adult pink salmon returned to hatcheries in North America each year from 2000 to 2010 (primarily Prince William Sound and Kodiak; Ruggerone and Irvine 2015). The predicted decline in Fraser sockeye recruitment from an increase of 50 million pink salmon (150 to 200 mil-

lion) salmon was 18% (or 1.83 million sockeye salmon), assuming an equal effect of pink salmon from each region of North America.

In contrast with sockeye populations in the southern half of their range, Peterman and Dorner (2012) showed that sockeye productivity in western and central Alaska was either stable or increasing. The overall abundance of these stocks tended to be positively correlated with the abundance of North Pacific pink salmon (Ruggerone et al. 2010), which begs the question: how can sockeye abundance in western and central Alaska be positively correlated with pink salmon when sockeye abundance in southern areas is negatively correlated with pink salmon abundance? First, it has been hypothesized that high abundance and survival of salmon in general is largely due to favorable early marine conditions (e.g., Mueter et al. 2002; Beamish et al. 2004; Farley et al. 2007; Stachura et al. 2014). In support of this hypothesis, sockeye abundance in Alaska (all regions combined) was positively correlated with growth of Bristol Bay (Bering Sea) and Chignik (Alaska Peninsula; Gulf of Alaska) sockeye salmon during their first and second years at sea (Ruggerone et al. 2007). Likewise, survival of pink salmon was linked to favorable growth during early marine life (Moss et al. 2005). This evidence suggests that favorable ocean conditions during early marine life enhanced survival and consequently adult abundances of both sockeye and pink salmon. Second, research also indicated that Asian pink salmon affect the growth and survival of Bristol Bay sockeye salmon in western Alaska during their second and third years at sea, but not during the first year at sea (Fig. 2; Ruggerone et al. 2003, 2005; Ruggerone and Nielsen 2004). Therefore, for northern sockeye populations such as those in Bristol Bay, the evidence suggests that both early marine conditions and competition between pink and sockeye salmon in the 2<sup>nd</sup> and 3<sup>rd</sup> years at sea influenced marine survival and adult sockeye salmon abundances. In contrast, declining sockeye salmon productivity in the southern area over the past two decades may be related to both unfavorable ocean conditions during early marine life (Rensel et al. 2010; Beamish et al. 2012; Thomson et al. 2012; McKinnell et al. 2014), and competition with abundant pink salmon beginning in the second year at sea (Ruggerone and Connors 2015), perhaps compounded by changing ocean productivity (Nielsen and Ruggerone 2009; Irvine and Akenhead 2013).

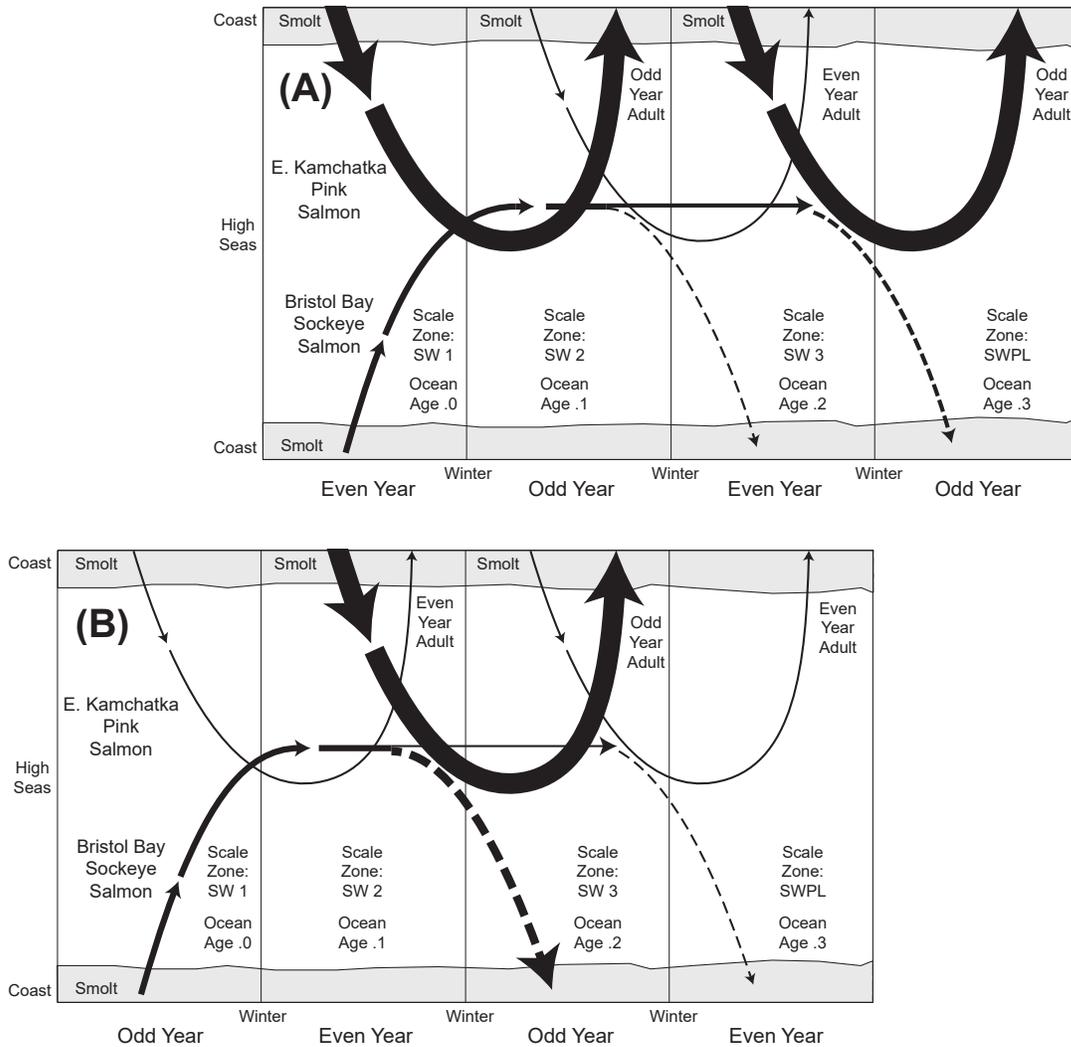
The goal of this paper is to further evaluate the evidence for competition between Bristol Bay sockeye salmon and pink salmon originating from Russia and central Alaska. Our objectives involve the testing of four hypotheses: (1) scale growth of Bristol Bay sockeye salmon stocks exhibit alternating-year patterns consistent with patterns of competition with pink salmon, (2) scale growth of Bristol Bay sockeye stocks during the second and third years at sea, but not the first, are negatively correlated with the abundance of pink salmon, (3) forecast error of Bristol Bay sockeye salmon is related to the alternating-year pattern of pink salmon

abundance, and (4) evidence for hypotheses 1–3 is strongest for sockeye salmon having the greatest geographic overlap with pink salmon stocks that exhibit strong alternating-year patterns of abundance. Distribution at sea of sockeye salmon from northwestern Bristol Bay (e.g., Wood River; Fig. 3) is east of stocks originating in southwestern Bristol Bay (e.g., Kvichak, Naknek, Egegik, Ugashik) (Rogers 1988; Habicht et al. 2010). This results in less overlap with Russian pink salmon that exhibit strong alternating-year patterns of abundance, such as those from eastern Kamchatka.

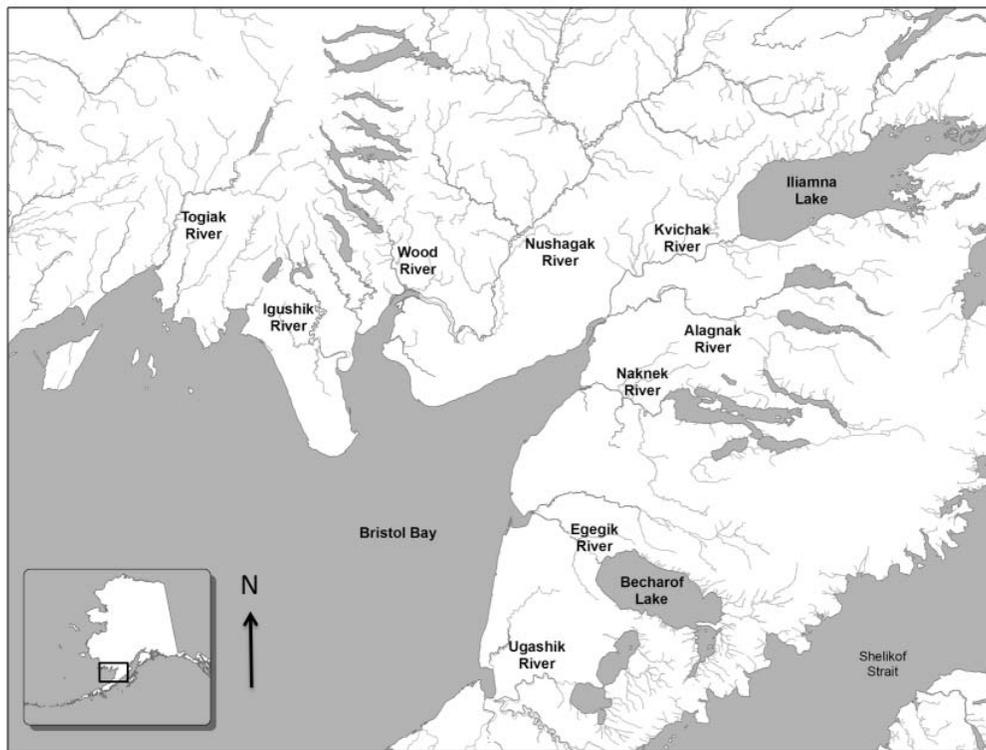
**MATERIALS AND METHODS**

**Sockeye Scale Measurements and Analyses**

Scales collected from adult sockeye salmon that returned to the river to spawn were used to characterize annual growth during the first, second, and third years at sea from 1965 to 2009. Scales were measured from four southeastern Bristol Bay sockeye stocks: Kvichak, Naknek, Egegik, and Ugashik, and one northwestern Bristol Bay stock: Wood River (Fig. 3). The goal was to measure 50 scales (equal male and female salmon) from each of the



**Fig. 2.** Diagram of temporal overlap between Asian pink salmon and Bristol Bay sockeye salmon based on seasonal scale growth patterns (Ruggerone et al. 2005). (A) Sockeye salmon smolts entering the ocean during even-numbered years first encounter abundant odd-year pink salmon (bold solid line) during the first winter at sea and the second growing season, i.e., primarily during SW2, leading to reduced growth and abundance of maturing age-x.2 sockeye salmon in even-numbered return years (thin dashed line). (B) Sockeye salmon smolts entering the ocean during odd-numbered years do not encounter abundant odd-year pink salmon until their second winter at sea and the third growing season, i.e., during SW3, leading to relatively greater growth and abundance of maturing age-x.2 sockeye salmon in odd-numbered return years (bold dashed line). Odd-even abundance patterns of age-x.3 sockeye salmon are less distinct, as described in the text and Fig. 9. Sockeye scale growth (SWPL zone) indicates little interaction between Asian pink salmon and maturing sockeye salmon presumably because maturing sockeye salmon are distributed farther north during fall, winter, and spring compared with immature sockeye salmon (French et al. 1976). Period of overlap between pink and immature sockeye salmon is from approximately winter through July, but the effect of interaction may continue until prey populations recover. Redrawn from Ruggerone et al. (2003).



**Fig. 3.** Map of Bristol Bay and the eight sockeye salmon stocks considered in this investigation. Southeastern stocks include Naknek, Kvichak, Egegik, and Ugashik. Northwestern stocks include Wood River and smaller stocks (Nushagak, Igushik, and Togiak) not individually considered here.

four dominant age groups (1.2, 2.2, 1.3, 2.3), where the first digit represents the number of winters in fresh water and the second digit represents the number of winters at sea. Thus, up to 200 scales were measured per year per stock, and up to 1,000 scales were measured per year for all stocks combined.

Scale measurements were made by the Alaska Department of Fish and Game (ADF&G) Mark, Tag, and Age Lab following procedures described in Hagen et al. (2001) and Ruggerone et al. (2007). Scales were selected for measurement only when: (1) we agreed with the age determination previously made by ADF&G; (2) the scale shape indicated that the scale was removed from the “preferred area” (Koo 1962); and (3) circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis. The scale measurement axis was determined by a perpendicular line drawn from a line intersecting each end of the first saltwater annulus. Scale measurements included both circuli and annuli measurements within each growth zone in fresh water and the ocean but only annual growth during each of two or three years at sea are reported. Overall, 32,957 sockeye scales were measured. A few age groups in a given year contained fewer than 10 scales and were excluded from the analyses. Sufficient high quality scales were not available for Egegik age-1.2 and Ugashik age-2.3 sockeye salmon because these age groups were relatively rare for these stocks.

Median annual scale growth at sea was calculated for each year and stock and then normalized to the mean of the southeastern Bristol Bay sockeye salmon stocks, 1965–2009, to facilitate comparison of Wood River and southeastern Bristol Bay sockeye scale growth. A Model II two-factor ANOVA (factors: odd/even year, stock) was used to test for scale growth differences related to these factors during each year at sea. A Model II ANOVA was used to reduce degrees of freedom in the F-statistic and the likelihood of rejecting the null hypothesis as a result of large sample size (Zar 1996). Autocorrelation in annual median scale growth was quantified to test whether there was an alternating year pattern that was consistent with autocorrelation in pink salmon abundance. Only lag 1 and lag 2 partial autocorrelation was presented because the strength of autocorrelation declined rapidly after lag 2. Partial autocorrelation was shown at lag 2 because it describes autocorrelation after accounting for lag 1 autocorrelation. Ordinary least squares linear regression was used to test whether median annual scale growth was negatively correlated with pink salmon abundance after the dependent and independent values were detrended to remove linear time trends. Diagnostic tests, including serial autocorrelation of model residuals and plots of residuals on predicted values, were conducted to evaluate model assumptions. Analysis of covariance was used to test whether the relationships between annual median sockeye growth and pink

salmon abundance were of a similar magnitude and direction between the Wood River and southeastern Bristol Bay sockeye salmon stocks. This test helped to evaluate whether Wood River sockeye, which are distributed farther east in the North Pacific Ocean, might exhibit less competition with Asian pink salmon.

### Salmon Stock Data

Annual numerical abundances of adult pink salmon by region of the North Pacific were available from Ruggerone and Irvine (2015). The abundance of pink salmon from the eastern Kamchatka region was used as the primary index of potential pink salmon competitors with Bristol Bay sockeye salmon because the eastern Kamchatka stock is very large and appears to have the greatest degree of overlap with Bristol Bay sockeye salmon among large Asian and North American stocks (Takagi et al. 1981; Myers et al. 1996). Additionally, we compared sockeye growth with the combined abundances of pink salmon from central Alaska (southern Alaska Peninsula, Kodiak, Cook Inlet, Prince William Sound) and Eastern Kamchatka because the distribution of Bristol Bay sockeye salmon also overlaps these North American stocks to some extent.

### Forecast Error of Bristol Bay Sockeye Salmon

Pre-season forecasts of sockeye salmon abundance (catch plus spawning escapement) as estimated by the ADF&G were tabulated by dominant age group and watershed from 1968 to 2010 (e.g., Pennoyer 1970; Baker et al. 2009). Dominant age groups included age-1.2, age-2.2, age-1.3, and age-2.3 salmon. Age-specific abundances of adult sockeye salmon returning to each watershed in Bristol Bay were provided by the ADF&G (T. Baker, tim.baker@alaska.gov, pers. comm.). These adult return data included estimates of Bristol Bay sockeye salmon harvested outside of the Bristol Bay management area. Forecast error ( $e$ ) was calculated as:

$$e_{i,t} = \hat{R}_{i,t} - R_{i,t}, \quad (1)$$

where  $\hat{R}$  is the forecasted run size (i.e., pre-fisher abundance),  $R$  is the observed run size and  $e$  is the forecast error for stock  $i$  in year  $t$ . We also calculated forecast error relative to error during the previous and following years as a means to examine whether there was an alternating-year pattern of forecast error:

$$\text{Relative } e_{i,t} = e_{i,t} - \left( \frac{e_{i,t-1} + e_{i,t+1}}{2} \right), \quad (2)$$

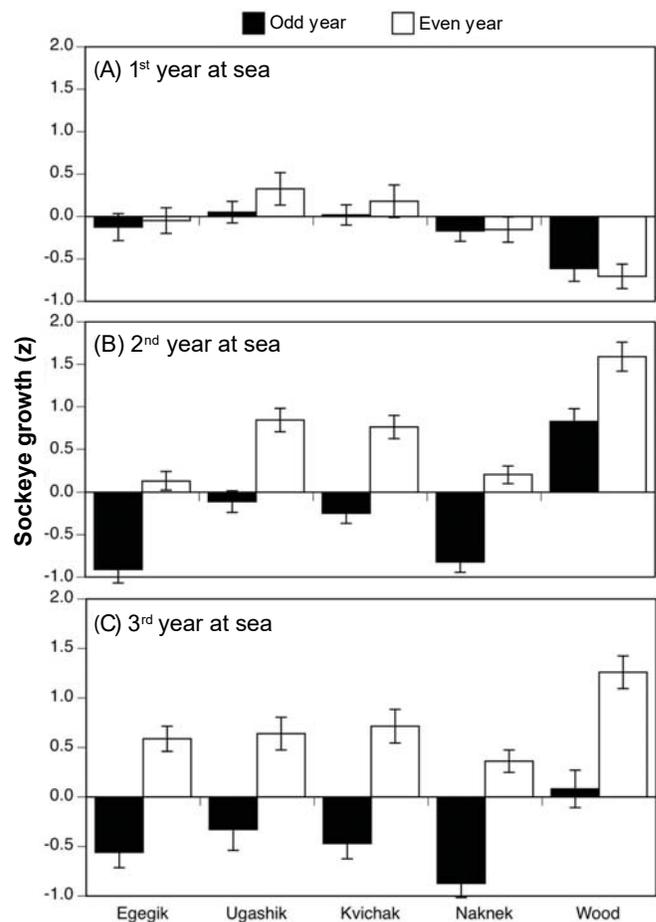
where relative error for population  $i$  in year  $t$  is the forecast error minus the average of the forecast error in the preceding and following year. This approach removed the autocorrelation associated with forecast error that stemmed in part from under-forecasting of sockeye runs following the ocean regime shift in the mid-1970s (Ruggerone and Baker 2011).

## RESULTS

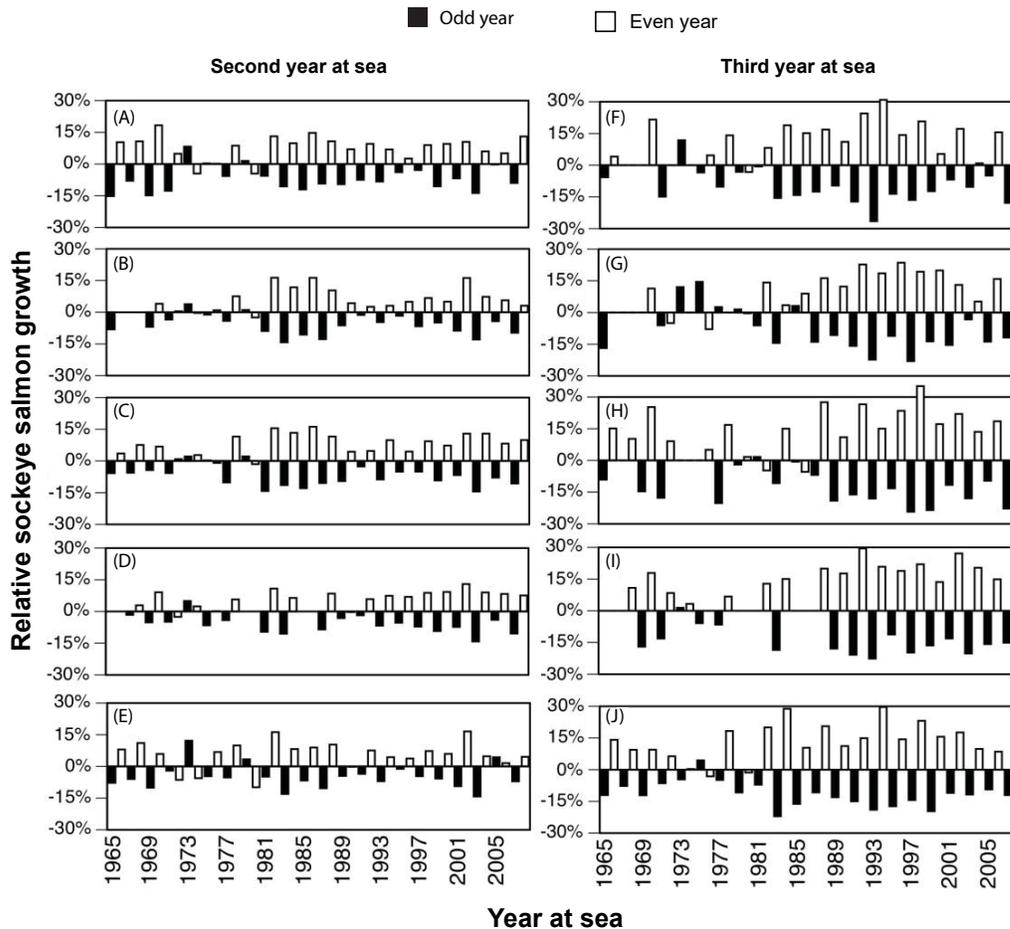
### Alternating-year Patterns in Sockeye Growth

Second (two factor ANOVA:  $df = 1, 4; F = 355; P < 0.001$ ) and third year ( $df = 1, 4; F = 657; P < 0.001$ ) scale growth of sockeye salmon was significantly less during odd-numbered years, but there was no evidence of a difference in growth between odd- and even-years during the first year at sea (Fig. 4,  $df = 1, 4; F = 1.99; P > 0.05$ ). This pattern supported the hypothesis that maturing pink salmon, which are most abundant in odd-numbered years, compete with sockeye salmon for food.

Growth varied by sockeye salmon stock during each year at sea (Fig. 4;  $df = 1, 4; F \geq 22.6; P < 0.02$ ). During the first year at sea, Wood River sockeye growth was significantly less than each of the four southeastern stocks



**Fig. 4.** Comparison of mean ( $\pm 1$  SE) of annual median scale growth of sockeye salmon originating from each of five watersheds in Bristol Bay, Alaska, during odd- versus even-numbered years of the first (A), second (B), and third years (C) in the ocean. Scale growth values were normalized to mean growth of the southeastern stocks (Egegik, Ugashik, Kvichak, and Naknek) to facilitate comparison with Wood River sockeye growth, 1965–2009.



**Fig. 5.** Annual mean scale growth of sockeye salmon during each year at sea as a percentage of mean growth during the previous and following years at sea, 1965–2008: Egegik (A, F), Ugashik (B, G), Kvichak (C, H), Naknek (D, I), and Wood River (E, J). Growth during odd-numbered years is shown in black bars and growth in even-numbered years is shown in white bars to highlight the pattern of higher than average growth in even versus odd years.

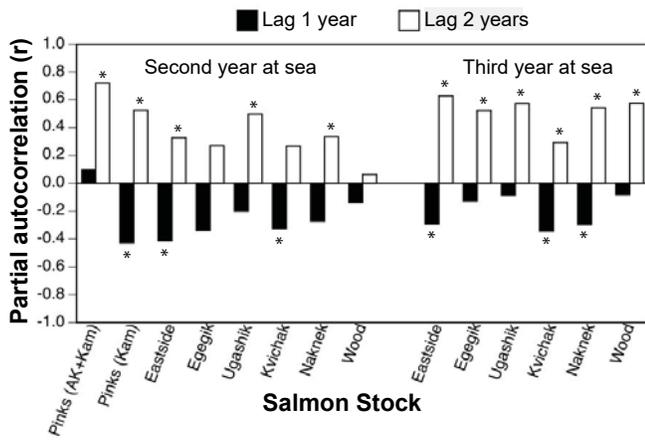
( $P < 0.01$ ). However, during the second and third year at sea, growth of Wood River sockeye salmon was significantly greater than each of the four southeastern stocks ( $P < 0.005$ ). The interaction term (stock  $\times$  odd-even year) was non-significant for growth during each year at sea ( $P > 0.05$ ), indicating the odd-even pattern was consistent among the five stocks.

Lower scale growth during odd-numbered years compared with adjacent even-numbered years was observed in nearly all years for each of the five Bristol Bay sockeye stocks from 1965 to 2008 (Fig. 5). Odd-year growth during the second year at sea averaged  $6.2\% \pm 0.2\%$  (SE) less than adjacent even-year growth. During the third year at sea, odd-year growth averaged  $10\% \pm 0.4\%$  less than adjacent even-year growth. In odd-numbered years, annual growth was up to 15% or 24% less than growth in adjacent even-number years for second and third years at sea, respectively. For all stocks, the alternating-year pattern of sockeye growth was somewhat less consistent during the 1970s compared with subsequent years (Fig. 5).

### Partial Autocorrelation of Pink Salmon Abundance and Sockeye Growth

Autocorrelation of eastern Kamchatka pink salmon abundance during 1965 to 2009 was negative at lag 1 ( $r = -0.4$ ,  $P < 0.01$ ) and partial autocorrelation was positive at lag 2 ( $r = 0.5$ ,  $P < 0.01$ ), reflecting the alternating-year abundance pattern of this major pink salmon stock (Fig. 6). Pink salmon abundance was relatively high during odd-numbered years and low during even-numbered years at sea, resulting in the negative autocorrelation at lag 1 and positive partial autocorrelation at lag 2. The somewhat stronger partial autocorrelation at lag 2 than lag 1 presumably reflects the stronger effect of parent abundance than the potential negative interaction between broodlines of pink salmon. Partial autocorrelation of total pink salmon from central Alaska and eastern Kamchatka was positive at lag 2 ( $P < 0.01$ ) but non-significant at lag 1 ( $P > 0.05$ ).

Growth of each sockeye stock displayed consistent patterns of autocorrelation during the second and third years at sea, reflecting their alternating-year growth patterns (Fig. 6). Consistent with the hypothesis that competition with eastern



**Fig. 6.** Partial autocorrelation of median annual sockeye salmon scale growth at lags one-year and two-years during the second and third years at sea (1965–2009). Partial autocorrelation of pink salmon abundances from eastern Kamchatka (Kam) and from central Alaska plus eastern Kamchatka (AK+Kam) are shown for comparison. Partial autocorrelation and autocorrelation are identical at lag 1. Statistically significant values are identified (\* $P < 0.05$ ).

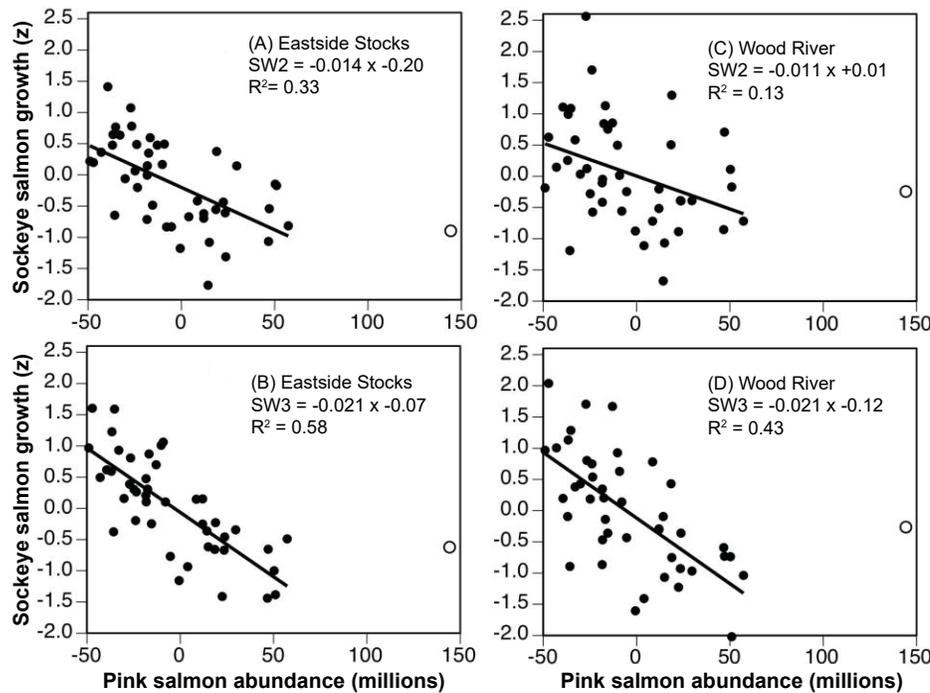
Kamchatka pink salmon reduces sockeye growth, autocorrelation of sockeye growth was negative at lag 1 and partial autocorrelation was positive at lag 2. The magnitude of lag 2 partial autocorrelations was typically greater (avg.  $r = 0.29$  to  $0.52$ ) than lag 1 autocorrelations (avg.  $r = -0.28$  to  $-0.20$ ) for sockeye in their second and third years at sea, respec-

tively (Fig. 6). This pattern of larger magnitude lag 2 partial autocorrelation was also observed in eastern Kamchatka and central Alaska pink salmon, reflecting the fixed two-year life cycle of pink salmon. Growth of Wood River sockeye salmon exhibited less lag 1 and lag 2 partial autocorrelation ( $P > 0.05$ ) than growth of each southeastern Bristol Bay stock during the second year at sea, but this difference was less apparent during the third year at sea.

In contrast to these patterns, growth of each sockeye stock during the first year at sea displayed positive autocorrelation at lag 1 ( $P < 0.05$ ), and none of five stocks exhibited significant partial autocorrelation at lag 2 ( $P > 0.05$ ). Thus, growth during the first year at sea did not reflect potential interaction with pink salmon, as expected (Fig. 4A). Instead, the positive serial autocorrelation reflected increased early marine growth over time, especially after the mid-1970s (Ruggerone et al. 2007).

**Negative Correlation of Sockeye Growth and Pink Salmon Abundance**

Detrended median annual scale growth of southeastern sockeye salmon stocks during the second and third years at sea was negatively correlated with the abundance of eastern Kamchatka pink salmon during 1965 to 2008 ( $P < 0.001$ ). Approximately 33% and 58% of the annual variability in southeastern Bristol Bay salmon scale growth was explained by pink salmon abundance during the second and third years at sea, respectively (Fig. 7). Likewise, median annual



**Fig. 7.** Linear regression of median annual detrended, normalized growth in the 2<sup>nd</sup> (A, C) and 3<sup>rd</sup> (B, D) year at sea for southeastern Bristol Bay stocks (A, B) and Wood River sockeye salmon (C, D) in relation to detrended eastern Kamchatka pink salmon abundance, 1965–2008. Values in 2009 are shown (open circle) but not included in the regression because pink salmon abundance was exceptional. Average pink salmon abundance during 1965–2009 was 43 million fish.

growth of Wood River sockeye salmon stocks during the second and third years at sea was negatively correlated with the abundance of eastern Kamchatka pink salmon during 1965 to 2008 (SW2:  $P < 0.016$ ; SW3:  $P < 0.001$ ). Approximately 13% and 43% of the annual variability in Wood River scale growth was explained by pink salmon abundance during the second and third years at sea, respectively (Fig. 7). Serial autocorrelation of the model residuals was non-significant for all stocks and ocean ages ( $P > 0.05$ ). Examination of model residuals plotted on predicted values did not reveal patterns, indicating no need for data transformations or alternative models. Analysis of covariance indicated that the detrended southeastern and Wood River regressions on eastern Kamchatka pink salmon were coincident for ocean ages -2 and -3; there was no statistical difference in the slopes or intercepts (Fig. 7,  $P > 0.05$ ). Regressions performed using raw rather than detrended scale growth and pink salmon abundance led to the same findings: sockeye growth declined with increasing abundance of pink salmon ( $P < 0.05$ ) and serial autocorrelation of the model residuals was non-significant ( $P > 0.05$ ). Analysis of covariance using raw data also indicated that the slopes of the southeastern and Wood River regressions were coincident ( $P > 0.05$ ), but growth of Wood River sockeye salmon was greater than growth of southeastern Bristol Bay stocks at each abundance level of eastern Kamchatka pink salmon during the second and third years at sea ( $P < 0.001$ ). The finding of greater growth of Wood River sockeye salmon is consistent with the ANOVA presented above (Fig. 4).

Scale growth of Bristol Bay sockeye salmon was also compared with the combined abundances of pink salmon returning to central Alaska and eastern Kamchatka. During the second year at sea, detrended scale growth of southeastern Bristol Bay ( $R^2 = 0.18$ ) and Wood River ( $R^2 = 0.12$ ) sockeye salmon were negatively correlated with detrended abundance of central Alaska and eastern Kamchatka pink salmon ( $P < 0.05$ ). During the third year at sea, the negative correlations ( $P < 0.001$ ) were stronger for both southeastern Bristol Bay ( $R^2 = 0.48$ ) and Wood River sockeye salmon ( $R^2 = 0.37$ ).

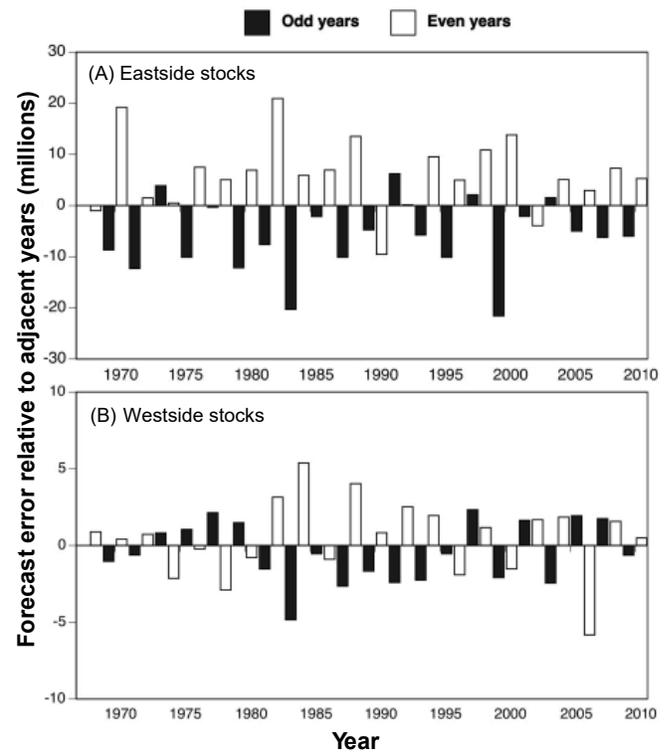
### Forecast Error of Bristol Bay Sockeye Salmon

Forecast error of southeastern Bristol Bay sockeye salmon (Kvichak, Naknek, Egegik, and Ugashik stocks) relative to adjacent years was positive during even-numbered years (avg. 6.1 million fish per year), and negative during odd-numbered years (avg. -6.3 million fish per year), 1968–2010 (Fig. 8). A positive forecast error occurs when the pre-season forecast is too high relative to the observed run. After standardizing forecast error relative to adjacent years, forecasts in even-numbered years were too high in 86% of the years, whereas forecasts in odd-numbered years were too low in 81% of the years. This finding is consistent with the observation that abundant odd-year pink salmon compete with sockeye salmon during the year prior to their

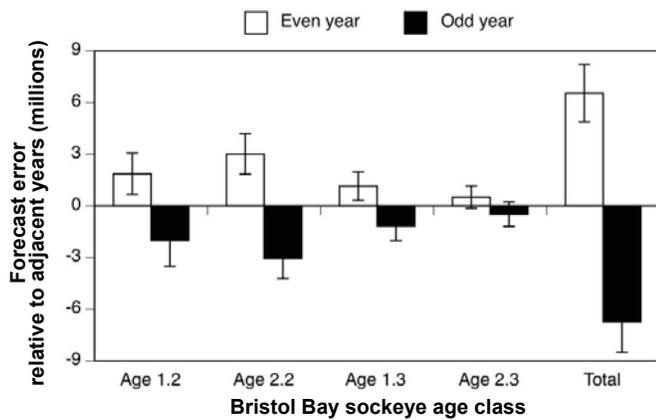
return to Bristol Bay (Fig. 2). In other words, high positive forecast error in even-year runs reflects potential competition with abundant pink salmon in the previous odd-numbered year. In even-numbered years, forecasts of southeastern Bristol Bay sockeye salmon tended to be too high.

Relative forecast error of northwestern Bristol Bay sockeye salmon (Wood River, Nushagak, Igushik, and Toigiak stocks combined) was positive during even-years (avg. 0.48 million fish per year) and negative during odd-years (avg. -0.48 million fish per year), but this pattern was not as consistent nor as strong as it was for the southeastern stocks (Fig. 8). After standardizing forecast error relative to adjacent years, forecasts in even-numbered years exceeded zero in 64% of the years, whereas forecasts in odd-numbered years were below zero in 62% of the years.

The alternating-year pattern in forecast error was not consistent among ocean age-2 and -3 sockeye salmon. For all stocks combined, relative forecast error of ocean age-2 sockeye salmon was 1.9–3.0 million ( $\pm 1.2$  million) fish too high in even-numbered years (Fig. 9), or approximately 30% too high, on average. In contrast, relative forecast error in even-numbered years of ocean age-3 sockeye salmon was only 0.5–1.2 million ( $\pm 0.8$  million) fish too high, or 13% too high. The lower relative forecast error of ocean age-3 sockeye salmon likely reflected their interaction with



**Fig. 8.** Annual relative forecast error of southeastern (A) and northwestern (B) Bristol Bay sockeye salmon abundance (millions of fish) relative to mean error in the previous and following years. Northwestern stocks include Wood River and the smaller stocks shown in Fig. 2. Positive values indicate that the pre-season forecast was larger than the observed abundance.



**Fig. 9.** Mean forecast error ( $\pm 1$  SE) of Bristol Bay sockeye salmon abundance by age group (millions of fish) relative to mean error in the previous and following years.

pink salmon during both even- and odd-numbered years; ocean age-2 sockeye salmon only interact with pink salmon during their second year at sea, based on scale growth measurements (Fig. 2; Ruggerone et al. 2005).

## DISCUSSION

### Sockeye Growth

Growth of all five major Bristol Bay sockeye salmon stocks during the second and third years at sea exhibited a strong alternating-year pattern that is consistent with the hypothesis that sockeye salmon compete with abundant pink salmon for food on the high seas. From 1965 to 2009, sockeye growth at sea was low during odd-numbered years when pink salmon abundance was high (Irvine et al. 2014), whereas sockeye growth was high in even-numbered years when pink salmon abundance was low. Evidence for competition was further supported by the significant positive partial autocorrelation at lag two-years of eastern Kamchatka and central Alaska pink salmon abundance and scale growth of all five sockeye stocks during the third year at sea and three of five stocks during the second year at sea. Autocorrelation of pink salmon abundance and sockeye growth was stronger at lag two-years compared with lag one-year, as expected because pink salmon have a fixed two-year life cycle. Both the lag one-year autocorrelation of eastern Kamchatka pink salmon abundance and the lag one-year autocorrelation of sockeye growth were negative, as predicted by the competition hypothesis. Lastly, detrended scale growth of Bristol Bay sockeye salmon was negatively correlated with the detrended abundances of pink salmon originating from eastern Kamchatka and from central Alaska/eastern Kamchatka during the 44-year period. The natural experimental control provided by the alternating-year abundance pattern of pink salmon, the negative correlation between sockeye growth

and pink salmon abundance, the high diet overlap of the two species (Davis et al. 2005), and the observed 36% reduction in sockeye stomach fullness during odd-numbered years at sea (Davis 2003) provide strong support for the competition hypothesis.

### Sockeye Salmon Forecast Error

Salmon forecasts in Alaska contribute to pre-season and early-season management of the fisheries and to pre-season planning by the salmon industry (Munro 2015). Salmon forecasts do not consider potential effects of pink salmon on the abundance of other salmon species. However, we found that the forecast error of Bristol Bay sockeye salmon from 1968 to 2010, especially those from southeastern Bristol Bay, exhibited an alternating-year pattern that is consistent with the growth of sockeye salmon in relation to competition with pink salmon. The forecast error pattern is also consistent with the alternating-year pattern observed in sockeye smolt-to-adult survival and adult returns from smolt migrations (Ruggerone et al. 2003). The forecast error pattern largely stems from interactions with pink salmon during the previous full year at sea rather than the year of return because relatively few pink salmon inhabit the southeastern Bering Sea (Ruggerone et al. 2010) and because sockeye scale growth during the homeward migration period did not reveal an alternating-year pattern (Ruggerone et al. 2005). Therefore, during even-numbered years of sockeye return, Bristol Bay sockeye interacted with abundant odd-year pink salmon during the previous year; whereas, during odd-numbered years of return, sockeye interacted with relatively few pink salmon. Sockeye forecasts tended to be too high in even-numbered return years and too low in odd-numbered return years. For example, in 2015, the pre-season inshore Bristol Bay sockeye forecast was exceptionally large—approximately 52 million sockeye salmon—yet the observed run was even larger (58 million fish; ADF&G 2015). This single observation is consistent with the findings presented here and with the dramatic decline in the abundance of eastern Kamchatka pink salmon beginning in 2013 (Klovach et al. 2014, 2015).

The strength of the alternating-year forecast error pattern varied with ocean age of sockeye salmon. The pattern was relatively weak for ocean age-3 sockeye and strong for ocean age-2 sockeye salmon. This pattern reflects interaction with both even- and odd-year abundances of pink salmon by ocean age-3 sockeye and interaction with only even- or odd-year pink salmon by ocean age-2 sockeye salmon (Fig. 2). The somewhat lower than expected return of ocean age-3 sockeye salmon in even-numbered years likely reflects the complex effects of growth at sea on both maturation and survival. For example, Bristol Bay and Fraser River sockeye salmon delayed maturation when encountering numerous pink salmon during their second year at sea of odd-numbered years (Ruggerone and Baker 2011; Ruggerone and Connors 2015).

## Southeastern versus Northwestern Sockeye Patterns in Relation to Pink Salmon

Studies of Bristol Bay sockeye migration and distribution at sea, including genetic stock identification analyses, indicate that northwestern stocks are distributed farther east in the ocean than southeastern stocks (Rogers 1988; Habicht et al. 2010; Seeb et al. 2011), suggesting that northwestern stocks overlapped less with Asian pink salmon, including eastern Kamchatka pink salmon. For example, based on the protracted smolt emigration through a series of five nursery lakes, the average timing of Wood River smolts at the outer boundary of Bristol Bay was estimated to be 10 weeks behind that of Egegik and Ugashik sockeye salmon (Rogers 1988).

Our findings support the hypothesis that Wood River sockeye salmon, a large northwestern Bristol Bay stock, interact less with Asian pink salmon than the southeastern sockeye stocks. During the first year at sea, Wood River scale growth was significantly less than that of southeastern sockeye stocks, reflecting the protracted entry of Wood River smolts into the Bering Sea and less time to grow in the ocean. However, during the second and third years at sea, scale growth of Wood River sockeye salmon was greater than that for southeastern sockeye stocks, presumably reflecting a more easterly marine distribution compared with southeastern sockeye stocks (Habicht et al. 2010) and so reduced overlap with abundant Asian pink salmon. Greater growth during the second and third years at sea may reflect less competition of northwestern stocks with Asian pink salmon, as also suggested by weaker autocorrelation of scale growth and weaker forecast error in relation to pink salmon. Although Asian pink salmon may have less effect on Wood River sockeye salmon than on southeastern stocks, all sockeye stocks exhibited negative relationships with pink salmon abundance, including pink salmon from central Alaska. However, we found no evidence that Wood River sockeye salmon were more strongly influenced by pink salmon from central Alaska. Correlations between sockeye growth and the combined abundances of pink salmon from eastern Kamchatka and central Alaska tended to be weaker than those involving only eastern Kamchatka pink salmon.

### Pink Salmon Effects and Prey Life History

The life history of key prey shared by pink and sockeye salmon likely contributes to the strong alternating-year patterns shown in this and other studies (Ruggerone and Connors 2015). Pink salmon appear to influence the standing crop of macrozooplankton and create an alternating-year pattern in their biomass (Shiomoto et al. 1997; Sugimoto and Tadokoro 1997). These macrozooplankton are also consumed by sockeye salmon. Squid, such as *Berryteuthis anonychus*, are an exceptionally important prey of both pink and sockeye salmon in some regions, and squid abundance in pink and sockeye diets is reduced in odd-numbered years

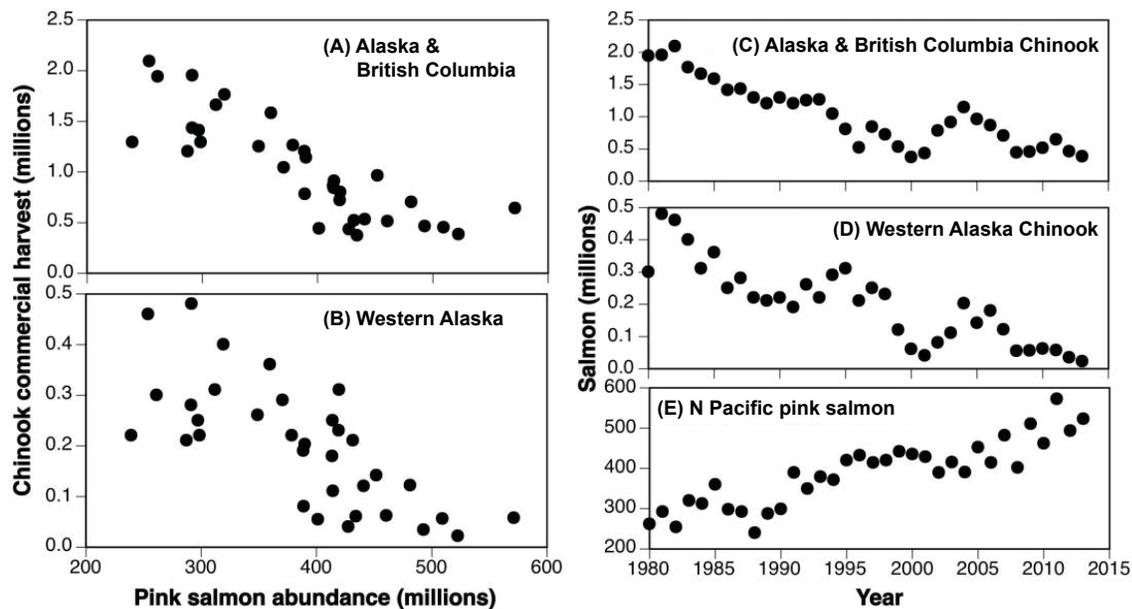
when pink salmon are abundant (Kaeriyama et al. 2004; Davis et al. 2003, 2005; Aydin et al. 2005). These squid (*B. anonychus*) exhibit a two-year life cycle and so it has been hypothesized that predation by pink salmon may be a key factor controlling squid abundance (Arkhipkin et al. 1996; Jorgensen 2011). Predation by pink salmon on prey with biennial life histories (Tsuda et al. 2004) may enhance the alternating-year pattern of prey abundance, leading to the alternating-year pattern of sockeye salmon growth, productivity, and age-at-maturation.

Sockeye scale growth analyses indicated that the effect of pink salmon on sockeye growth was greater during their third compared with second year at sea. This finding may reflect more intense predation on higher trophic level prey, such as squid that exhibit a biennial pattern, compared with zooplankton that are consumed more frequently by smaller salmon (Davis 2003). Greater growth-related mortality of sockeye salmon during the second compared with third year at sea may also contribute to the observed pattern (Ruggerone et al. 2007).

## CONCLUSION

The growth and forecast error analyses presented here are consistent with, and build upon, previous investigations into competition between Bristol Bay sockeye stocks and pink salmon at sea (Ruggerone et al. 2003; Nielsen and Ruggerone 2009). They are also consistent with an investigation of Russian sockeye growth in relation to pink salmon abundance (Bugaev et al. 2001), and recent analyses of 36 sockeye populations ranging from Puget Sound through British Columbia and into Southeast Alaska (Ruggerone and Connors 2015). Collectively, these studies support the hypothesis that pink and sockeye salmon compete for food on the high seas, leading to reduced growth, survival, and abundance of sockeye salmon, and increased age-at-maturity. In Alaska, favorable marine conditions since the mid-1970s, as indicated by greater growth during early marine life (Ruggerone et al. 2007), have likely masked the effects of competition on sockeye survival. In contrast, abundances of sockeye salmon in the southern region, including the Fraser River, have declined because marine conditions during early life appear to have been unfavorable and increasing abundance of pink salmon has led to greater competition for food on the high seas.

The evidence for food competition suggests that the high abundance of pink salmon in recent decades has significantly influenced the epipelagic food web of the North Pacific Ocean. It seems highly unlikely that physical oceanographic conditions in the ocean could produce the strong alternating-year patterns observed in sockeye salmon across much of their range. Given this evidence for a strong effect of pink salmon on the food web, it is noteworthy that Chinook salmon abundance has declined throughout Alaska and British Columbia, and length-at-age



**Fig. 10.** Commercial harvest of Chinook salmon in (A) Alaska and British Columbia and (B) western Alaska (1980 to 2013) in relation to adult pink salmon abundance in the North Pacific Ocean. Similar relationships were produced if pink salmon from only North America were used. Chinook salmon harvest and pink salmon abundance trends over time are shown in plots C, D, and E. Pink salmon abundance was the three-year mean abundance corresponding to the year of Chinook harvest and the two previous years when Chinook may have potentially interacted with pink salmon in the ocean. Western Alaska includes Bristol Bay, Kuskokwim, Yukon, and Unalakleet Chinook salmon. Commercial Chinook catch estimates for Alaska and British Columbia were from NPAFC catch records (e.g., Irvine et al. 2012). Commercial Chinook harvest statistics reflect management decisions in recent years to greatly reduce harvest rates. Hatchery Chinook salmon produced in Alaska (Vercessi 2014) were subtracted from the total commercial Chinook catch estimates.

of many Alaskan Chinook populations has declined over time (Lewis et al. 2015). Analysis of the Chinook salmon diet in the central Bering Sea revealed a 56% reduction in stomach fullness and a 68% reduction in weight of fish and squid consumed during odd- versus even-numbered years, 1991–2000 (Davis 2003). Furthermore, the commercial catch of Chinook salmon in western Alaska and throughout Alaska and British Columbia have been negatively correlated with pink salmon abundance since 1980 (Fig. 10), leading to an intriguing and important question: could pink salmon play a role in the decline of Chinook salmon in Alaska and British Columbia?

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