Abstract—Recent research demonstrated significantly lower growth and survival of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) during odd-numbered years of their second or third years at sea (1975, 1977, etc.), a trend that was opposite that of Asian pink salmon (*O. gorbuscha*) abundance. Here we evaluated seasonal growth trends of Kvichak and Egegik river sockeye salmon (Bristol Bay stocks) during even- and odd-numbered years at sea by measuring scale circuli increments within each growth zone of each major salmon age group between 1955 and 2000. First year scale growth was not significantly different between odd- and even-numbered years, but peak growth of age-2. smolts was significantly higher than age-1. smolts. Total second and third year scale growth of salmon was significantly lower during odd- than during even-numbered years. However, reduced scale growth in odd-numbered years began after peak growth in spring and continued through summer and fall even though most pink salmon had left the high seas by late July (10–18% growth reduction in odd *vs.* even years). The alternating odd and even year growth pattern was consistent before and after the 1977 ocean regime shift. During 1977–2000, when salmon abundance was relatively great, sockeye salmon growth was high during specific seasons compared with that during 1955–1976, that is to say, immediately after entry to Bristol Bay, after peak growth in the first year, during the middle of the second growing season, and during spring of the third season. Growth after the spring peak in the third year at sea was relatively low during 1977–2000. We hypothesize that high consumption rates of prey by pink salmon during spring through mid-July of odd-numbered years, coupled with declining zooplankton biomass during summer and potentially cyclic abundances of squid and other prey, contributed to reduced prey availability and therefore reduced growth of Bristol Bay sockeye salmon during late spring through fall of odd-numbered years.

Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift

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Competition among Pacific salmon (*Oncorhynchus* spp.) for food resources in the North Pacific Ocean and Bering Sea is a potentially important mechanism affecting salmon growth and population dynamics. Reduced growth at sea may lead to delayed maturation (Rogers, 1987), lower reproductive potential (Groot and Margolis, 1991), or greater risk of predation (Juanes, 1994).

Density-dependent growth in the ocean has been observed among sockeye (*O. nerka*), pink (*O. gorbuscha*), and chum salmon (*O. keta*), which are the most abundant species among Pacific salmon (Rogers[1]; Eggers et al.[2]). Density-dependent growth may occur during early marine life (Peterman, 1984) or during the homeward migration period when the potential for high growth rate (Ishida et al., 1998) may be influenced by high concentrations of salmon (Rogers and Ruggerone, 1993).

Since the early 1970s, salmon abundance in the North Pacific Ocean has increased, whereas body size for many populations of all salmon species has declined (Bigler et al., 1996). However, greater abundance of adult sockeye salmon returning to Bristol Bay, Alaska, was associated with increased growth during the first and second years at sea, followed by relatively low growth during the third year at sea, and greater adult size at a given abundance (Ruggerone et al.,

[1] Rogers, D. E. 2001. Estimates of annual salmon runs from the North Pacific, 1951–2001. Report SAFS-UW-0115, 11 p. School of Aquatic Sciences, Univ. Washington, Seattle, WA.

[2] Eggers, D. M, J. Irvine, M. Fukawaki, and V. Karpenko. 2003. Catch trends and status of North Pacific salmon. Doc. no. 723, 34 p. North Pacific Anadromous Fisheries Commission (NPAFC), 889 Pender Street, Vancouver, Canada.

2002). Increased growth of Bristol Bay sockeye salmon during the first two years at sea was associated with greater adult returns, but high abundance apparently led to increased competition and reduced growth during the third year.

The potential for competition for food between Asian pink salmon and Bristol Bay sockeye salmon stocks is great in the North Pacific Ocean and Bering Sea. Trophic level, diet, and feeding behavior of pink salmon overlap significantly with sockeye salmon (Welch and Parsons, 1993; Davis et al., 2000; Kaeriyama et al., 2004). Asian pink salmon are highly abundant, averaging approximately 162 million adults in odd-numbered years and 104 million adults in even-numbered years, 1955 to 2000 (Rogers[1]). Bristol Bay sockeye salmon and Asian pink salmon overlap in the central North Pacific Ocean and the Bering Sea. Greatest overlap is with pink salmon from the eastern Kamchatka Peninsula and Sakhalin Island (French et al., 1976; Takagi et al., 1981; Myers et al.[3]), which are especially abundant, as shown by average harvests of 79,000 metric tons (t) in odd-numbered years and 33,000 t in even-numbered years, 1955–99 (Sinyakov, 1998; Anonymous[4]).

Evidence for competition between Asian pink and Bristol Bay sockeye salmon was provided in a recent investigation by Ruggerone et al. (2003). During 1955–97, annual sockeye salmon scale growth during the second and third years at sea was significantly reduced during odd- compared to even-numbered years. Adult sockeye salmon length was relatively low when sockeye salmon overlapped with abundant odd-year pink salmon during the year prior to homeward migration. Furthermore, smolt-to-adult survival of Bristol Bay sockeye salmon was significantly lower when they encountered odd-year pink salmon during the second year at sea. However, Bristol Bay sockeye salmon encountered relatively few pink salmon during their first year at sea and no competition effect was observed during this early marine period.

In our study we examined the seasonal growth of Bristol Bay sockeye salmon scales in an effort to determine the approximate timing and duration of reduced growth during odd-numbered years at sea that was observed by Ruggerone et al. (2003). Scale circuli increments and annuli are correlated with salmon body size (Clutter and Whitesel, 1956; Fukuwaka and Kaeriyama, 1997; Fukuwaka, 1998). We compared seasonal scale growth before and after 1977 to examine seasonal growth trends associated with the twofold increase in Bristol Bay sockeye salmon abundance and the 1977

ocean regime shift (Rogers, 1984; Beamish and Bouillon, 1993; Rogers[1]). We also examined the hypothesis that seasonal growth during the second growing season was dependent on previous marine growth (Aydin, 2000). These hypotheses were tested by using scales from Kvichak River and Egegik River sockeye salmon, which averaged approximately 16 million fish per year or approximately 57% of the annual sockeye salmon run to Bristol Bay, 1955–2000.

Methods

For our study, we used scales from four age groups of Kvichak River sockeye salmon and three age groups of Egegik River sockeye salmon collected from the late 1950s through 2000 (Fig. 1). Adult salmon scales were obtained from the Alaska Department of Fish and Game (ADFG) archive in Anchorage, Alaska, and from the School of Aquatic and Fishery Sciences, University of Washington. Scales have been collected annually for measuring and quantifying age composition for management of the fisheries in Alaska. We selected scales from salmon sampled in the Kvichak and Egegik rivers rather than in the ocean fisheries to reduce the possibility of mixed stocks in the scale collection. Scale collections from the Kvichak River began in 1955, whereas collections from Egegik River began in 1960. Major freshwater and ocean age groups from Kvichak (ages 1.2, 1.3, 2.2, 2.3) and Egegik (ages 1.3, 2.2, 2.3) sockeye salmon were measured. Age was designated by European notation, i.e. the number of winters spent in freshwater before going to sea (1 winter=age-1. or two winters=age-2.) followed by the number of winters spent at sea (two winters=age-.2 or 3 winters=age-.3.). Nearly all Bristol Bay sockeye salmon mature after spending two or three winters at sea.

Scales were selected for measurement in this study only when 1) we agreed with the age determination previously made by ADFG, 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. We measured up to 50 scales per year, representing equal numbers of male and female salmon from each age group within each stock.

Scale measurements followed procedures described by Davis et al. (1990) and Hagen et al.[5] After selecting a scale for measurement, the scale was scanned from a microfiche reader and its image was stored as a high resolution digital file. High resolution (3352×4425 pixels) allowed the entire scale to be viewed and provided enough pixels to be seen between narrow circuli

[3] Myers, K. W., K. Y. Aydin, R. V. Walker, S. Fowler, and M. L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. Report FRI-UW-9614, 159 p. School of Aquatic and Fishery Sciences, Univ. Washington, Seattle, WA

[4] Anonymous. 2002. Biostatistical information on salmon catches, escapement, outmigrants number, and enhancement production in Russia in 2001. Doc. no. 646, 14 p. NPAFC, 889 Pender Street, Vancouver, Canada.

[5] Hagen, P. T., D. S. Oxman, and B. A. Agler. 2001. Developing and deploying a high resolution imaging approach for scale analysis. Doc. 567, 11 p. North Pacific Anadromous Fish Commision, 889 Pender Street, Vancouver, Canada.
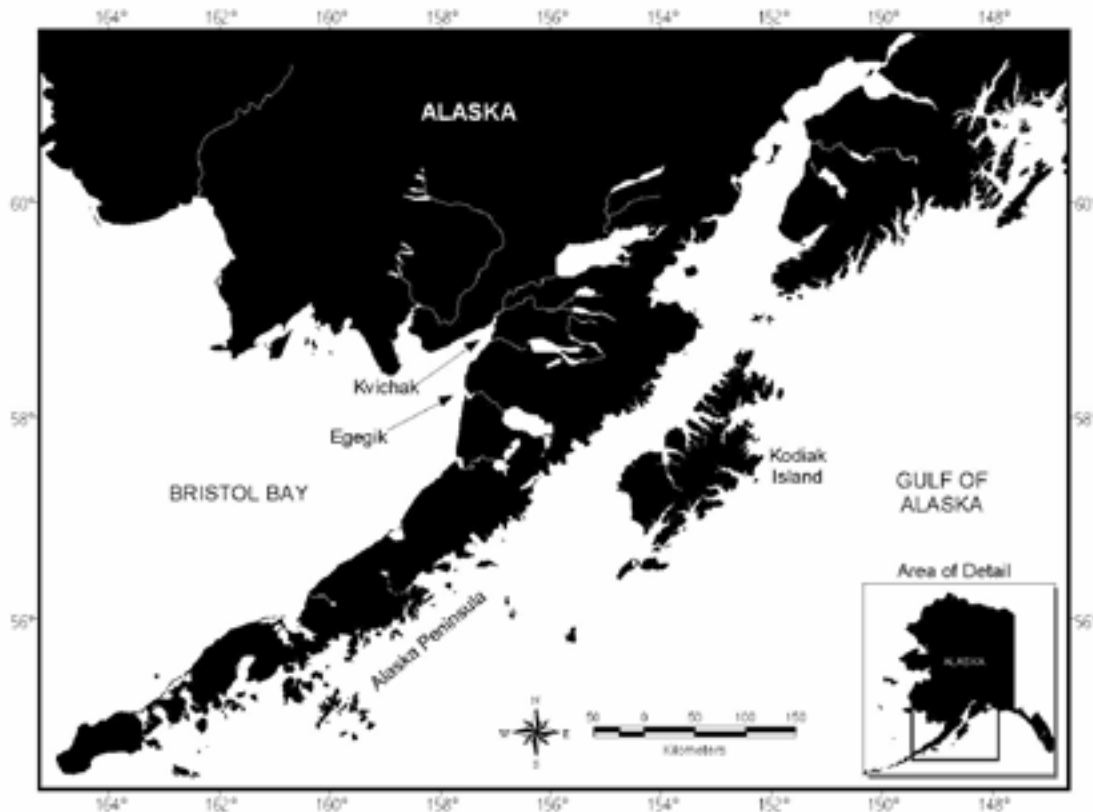
Figure 1
Map of Bristol Bay, Alaska, and the location of the Kvichak and Egegik river systems.

to ensure accurate measurements of circuli spacing. The digital image was loaded in Optimas 6.5 (Media Cybernetics, Inc., Silver Spring, MD) image processing software to collect measurement data with a customized program. The scale image was displayed on a digital LCD flat panel tablet. The scale measurement axis was determined by a perpendicular line drawn from a line intersecting each end of the first saltwater annulus. Distance (mm) between circuli was measured within each growth zone (i.e., from the scale focus to the outer edge of the first freshwater (FW1) annulus, between the first and second freshwater (FW2) annuli, within the spring plus (FWPL) growth zone, within each annual saltwater (SW1, SW2, SW3) growth zone, and from the last ocean annulus to the edge of the scale (i.e., the saltwater plus [SWPL] growth zone).

Data analysis

Mean scale circuli increments (distance between adjacent circuli pairs) of each age group and stock were calculated for each year when 10 or more scales were available. Typically, 40 to 50 scales of each age group and stock were measured in a given year. To facilitate evaluation of trends between odd- and even-numbered years at sea, scale circuli measurements were described in terms of the odd- or even-numbered year when the salmon entered the ocean. Thus, a salmon smolt entering the Bering Sea during an even-numbered year interacted with abundant odd-year Asian pink salmon during its second growing season (SW2) and less abundant even-year pink salmon during its third year, if it remained at sea. The number of circuli pairs considered in our analysis differed by growth zone, ranging from 22 circuli (SW1) to 20 circuli (SW2) to 15 circuli (SW3) in order to represent the majority of salmon. Analyses of seasonal scale growth trends were based on the mean of annual mean scale circuli increments, percentage change in scale circuli increments during odd- versus even-numbered years, and percentage change in odd- and even-year growth during periods before and after the 1977 ocean regime shift. A two-sample *t*-test was used to test for differences between odd- and even-numbered year scale growth at each circuli pair. Correlation was used to determine whether an individual's growth during the second growing season was related to previous growth at sea.

Results

First year (SW1) growth of ocean age-3 sockeye salmon

Kvichak and Egegik river sockeye salmon scale growth (distance between adjacent circuli) increased rapidly
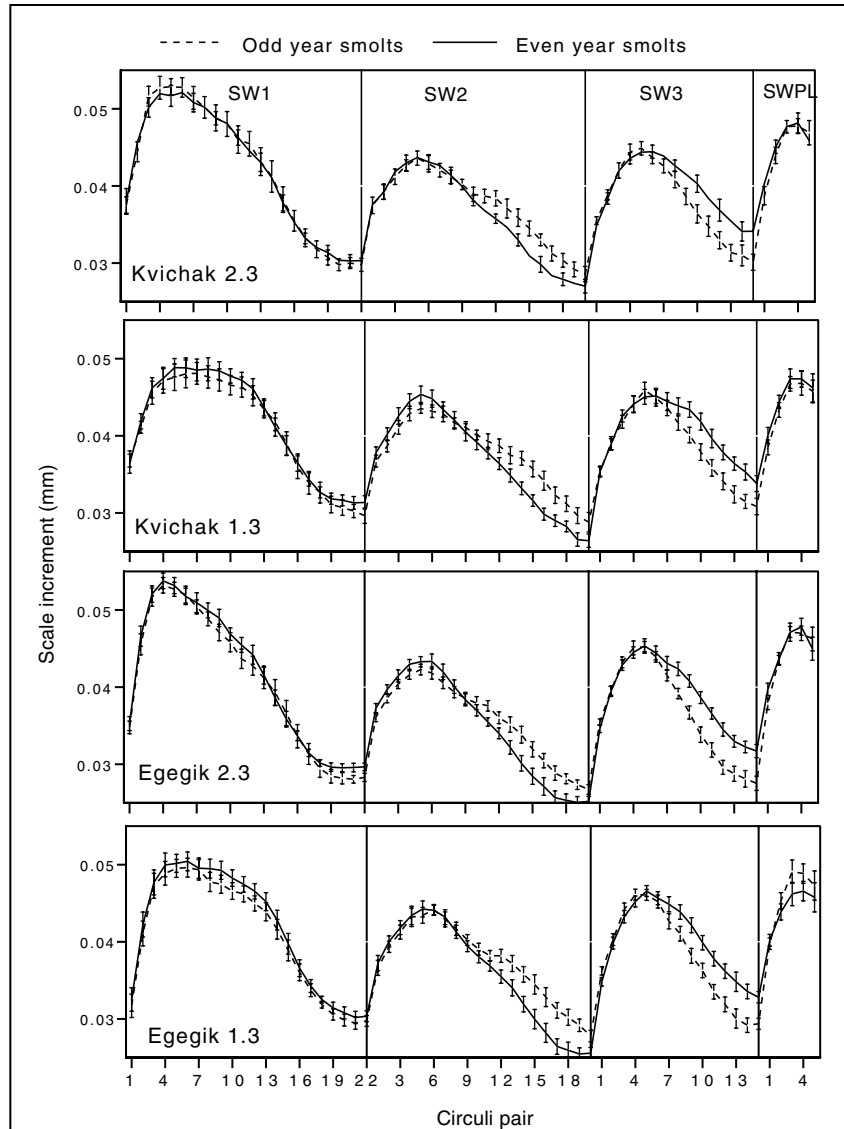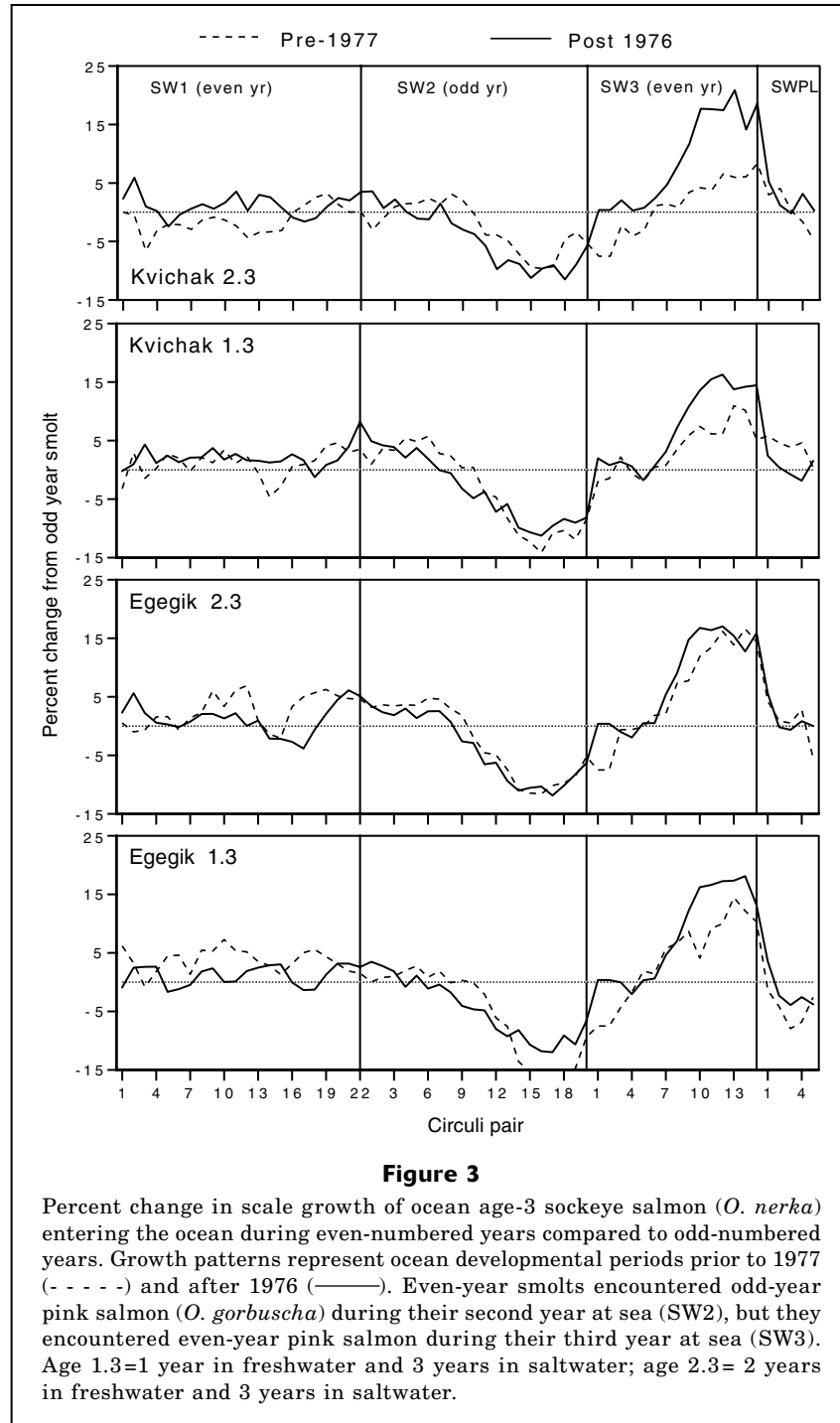
Figure 2

Average seasonal scale growth for Kvichak and Egegik ocean age-3 sockeye salmon (*Oncorhynchus nerka*) that entered the ocean as smolts during odd (- - - - -) and even (———) numbered years, 1952–2000. Growth of salmon spending one (age 1.3) and two years (age 2.3) in freshwater are shown separately. Circuli pair ordering restarts at the beginning of each new growing season (SW1, SW2, SW3, SWPL). 95% confidence intervals (CIs) are shown at each measurement.

after the fish entered Bristol Bay during May and early June, reaching peak growth near the fifth circuli (Fig. 2). Thereafter, growth declined steadily to a minimum at the first ocean annulus (circuli 18–22).

Peak scale growth of age-2. smolts was significantly greater compared with that of age-1. smolts for both Kvichak (df=79, t=5.757, P<0.001) and Egegik salmon (df=73, t=4.667, P<0.001). During the first eight circuli, age-2. smolts averaged 6.5% greater growth than age-1. smolts. Thereafter (circuli 11–20), growth of age-2. smolts declined more rapidly and averaged 2.3% (Kvichak) to 6.1% (Egegik) less than growth of age-1. smolts.

Within the SW1 growth period, no statistically significant difference in circuli growth was detected between smolts entering the ocean during odd- and even-numbered years (P>0.05). However, there was a trend for greater growth among even-year smolts in some

Figure 3

Percent change in scale growth of ocean age-3 sockeye salmon (*O. nerka*) entering the ocean during even-numbered years compared to odd-numbered years. Growth patterns represent ocean developmental periods prior to 1977 (- - - - -) and after 1976 (———). Even-year smolts encountered odd-year pink salmon (*O. gorbuscha*) during their second year at sea (SW2), but they encountered even-year pink salmon during their third year at sea (SW3). Age 1.3=1 year in freshwater and 3 years in saltwater; age 2.3= 2 years in freshwater and 3 years in saltwater.

portions of SW1, including the annulus (circuli 18–22) and immediately after peak growth (circuli 7 to 13) (Figs. 2 and 3).

SW1 growth of both even- and odd-year smolts tended to be greater after the 1977 climate shift than prior to this period, except for the last few circuli (Fig. 4). The greatest difference in growth between these two periods occurred immediately after entry into Bristol Bay (circuli 1–3) and during the last part of the SW1 growth period (circuli 13–19). This bimodal pattern of growth between the two periods was somewhat consistent among both stocks and freshwater age groups. However, Kvichak age 2.3 salmon experienced especially high early marine growth that was 17% greater, on average, after 1976. Following peak scale growth in spring, Egegik age 1.3 sockeye salmon experienced a
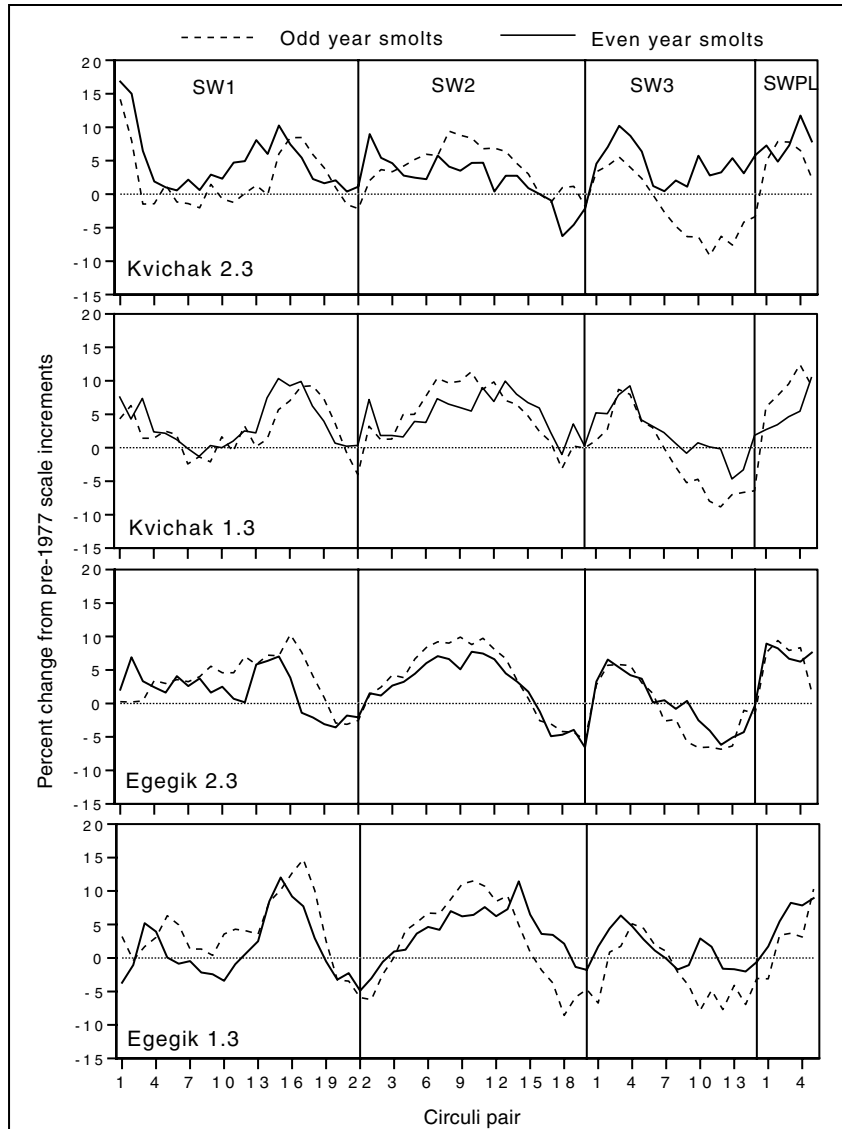
Figure 4

Percent change in scale growth of ocean age-3 sockeye salmon (*O. nerka*) entering the ocean during 1977–97 from those entering the ocean during 1952–76. Growth patterns represent smolts entering the ocean during odd- (- - - - -) and even-numbered years (———). Even-year smolts encounter odd-year pink salmon (*O. gorbuscha*) during their second year at sea (SW2), but they encountered even-year pink salmon during the their third year at sea (SW3).

15% increase in growth after 1976. In contrast, growth near the winter annulus (circuli 20–22) was up to 5% lower after the 1977 climate shift.

Second year (SW2) growth of ocean age-3 sockeye salmon

At the beginning of the second growing season (SW2), when Bristol Bay sockeye salmon are farthest south in the North Pacific Ocean (French et al., 1976), scale growth of both stocks and age groups increased rapidly, but the rate of increase was 59% less than that of SW1 and 37% less than SW3 growth (Fig. 2). Peak growth occurred near circuli 5 or 6 and it averaged 15% lower than that of SW1 growth.

During their second year at sea, even-year sockeye smolts inhabited the North Pacific and Bering Sea when Asian pink salmon were abundant in offshore waters

Table 1

Summary of two sample *t*-tests for evaluating the circuli number at which sockeye scale growth began to differ between odd-versus even-numbered years of the second and third seasons at sea. Between-year differences in circuli growth were greater after the circuli number shown in this table. No consistent pattern of differences between odd- and even-numbered years was observed during the first season at sea. Age "1.2" is a fish that has spent one year in fresh water and two years in salt water. SW2=2 years in saltwater.

Age	Ocean period	Stock	Circuli no.	df	*t*-value	*P* (two tailed)
1.2	SW2	Kvichak	C11	43	2.412	0.020
2.2	SW2	Kvichak	C11	44	3.283	0.002
2.2	SW2	Egegik	C11	39	3.434	0.001
1.3	SW2	Kvichak	C12	42	3.068	0.004
	SW3	Kvichak	C8	42	3.126	0.003
1.3	SW2	Egegik	C11	38	2.140	0.038
	SW3	Egegik	C7	38	2.527	0.016
2.3	SW2	Kvichak	C11	43	2.711	0.010
	SW3	Kvichak	C8	43	2.384	0.022
2.3	SW2	Egegik	C11	39	3.061	0.004
	SW3	Egegik	C7	39	2.728	0.010

(i.e., during odd-numbered years). Initial scale growth prior to the SW2 peak in spring was the same between odd- and even-numbered years, although there was a tendency for greater growth following the SW1 annulus of even-year smolts (Fig. 3). Immediately after peak growth near circuli 11, scale growth of even-year smolts became significantly less than that of odd-year smolts (Table 1). The growth differential continued through the end of the SW2 growing season and it reached a maximum reduction of –10% to –18% near circuli 14 to 18 (Fig. 3). This pattern was consistent before and after the 1977 climate shift and among each stock and age group. The reduced growth of even-year smolts during SW2 corresponded with high abundance of pink salmon in the central North Pacific Ocean during odd-numbered years.

Scale growth during SW2 of both odd- and even-year smolts tended to be greater after the 1977 climate shift (Fig. 4), a period when abundance of Bristol Bay sockeye salmon and Asian pink salmon was great. This pattern was consistent among both age groups of Kvichak and Egegik River sockeye salmon. Greatest growth differential between the two periods (up to 10%) occurred just after peak growth (circuli 5 to 15), a pattern that differed markedly from both SW1 and SW3. In contrast to the relatively large increase in growth shown in the central portion of SW2 after 1977, growth at the beginning of SW2 was similar during both periods and growth at the end of SW2 was relatively low after the climate shift.

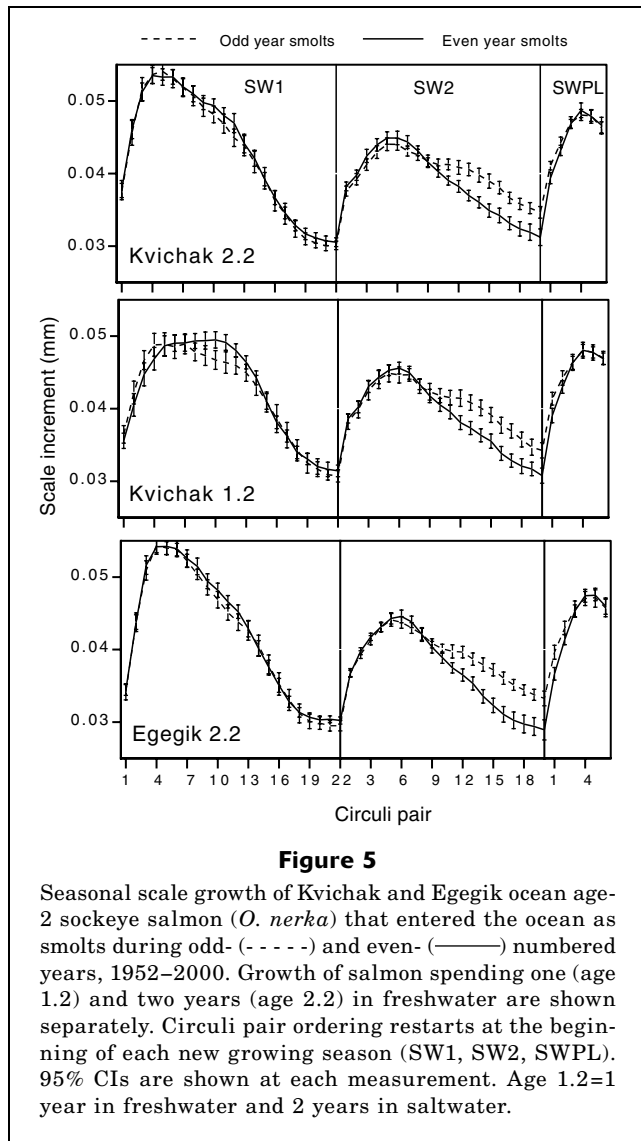### Third year (SW3) growth of ocean age-3 sockeye salmon

Scale growth at the beginning of the third year at sea increased rapidly, peaked near circuli 5–6, then declined steadily through the year (Fig. 2). Peak growth during SW3 was intermediate to the relatively high peak growth during SW1 and relatively low peak growth during SW2.

During their third year at sea, even-year sockeye smolts inhabited the North Pacific and Bering Sea when relatively few Asian pink salmon were in offshore waters (i.e., even-numbered years). Prior to peak growth, SW3 growth of even-year smolts was similar or below that of odd-year smolts (Fig. 3), a pattern that continued from the previous season. Immediately following the peak, growth of even-year smolts significantly increased in relation to odd-year smolts (Table 1), and growth remained relatively high throughout the remaining season (Fig. 2). Growth of even-year smolts was approximately 5% to 15% greater than that of odd-year smolts from circuli 8 to the annulus (Fig. 3). Differences in growth during even- versus odd-numbered years tended to be greater after 1976 when both pink and sockeye salmon were relatively abundant.

Peak SW3 scale growth was up to 10% greater after the mid-1970 regime shift during both odd- and even-numbered years (Fig. 4). However, after the peak growing season, scale growth was typically lower after 1976. The relatively low growth after 1976 was especially pronounced among odd-year smolts that inhabited the ocean during odd-numbered years when Asian pink salmon were abundant in offshore waters. Scale growth of odd-year smolts during SW3 was as much as 10% lower than that prior to 1977.

Scale growth during both SW3 and SW2 were significantly reduced during odd-numbered years at sea (Table 1). However, SW3 scale growth during odd- versus even-years diverged immediately after the peak, whereas

Figure 5

Seasonal scale growth of Kvichak and Egegik ocean age-2 sockeye salmon (*O. nerka*) that entered the ocean as smolts during odd- (- - - - -) and even- (———) numbered years, 1952–2000. Growth of salmon spending one (age 1.2) and two years (age 2.2) in freshwater are shown separately. Circuli pair ordering restarts at the beginning of each new growing season (SW1, SW2, SWPL). 95% CIs are shown at each measurement. Age 1.2=1 year in freshwater and 2 years in saltwater.

Figure 6

Percent change in scale growth between ocean age-2 sockeye salmon (*O. nerka*) entering the ocean during even years and those entering during odd-numbered years. Growth patterns represent ocean rearing periods prior to 1977 (- - - - -) and after 1976 (———). Even-year smolts encountered odd-year pink salmon (*O. gorbuscha*) during the second year at sea (SW2).

growth during SW2 diverged two or three circuli after the peak (Fig. 2). Late season growth of even-year smolts during SW3 was greater than late season growth during SW1 and SW2, whereas growth of odd-year smolts during SW3 was intermediate to SW1 and SW2 growth. These relatively large, older fish experienced a longer growing season, especially during even-numbered years, when few pink salmon were present.

Growth during homeward migration (SWPL) of ocean age-3 sockeye salmon

The peak return of sockeye salmon to Bristol Bay occurs near 3 July. Scale growth during the homeward migration peaked at circuli 3 and 4, then declined (Fig. 2). Peak growth was less than that of SW1, but greater than SW2 and SW3 growth. No growth difference was detected between odd- and even-year migrants during
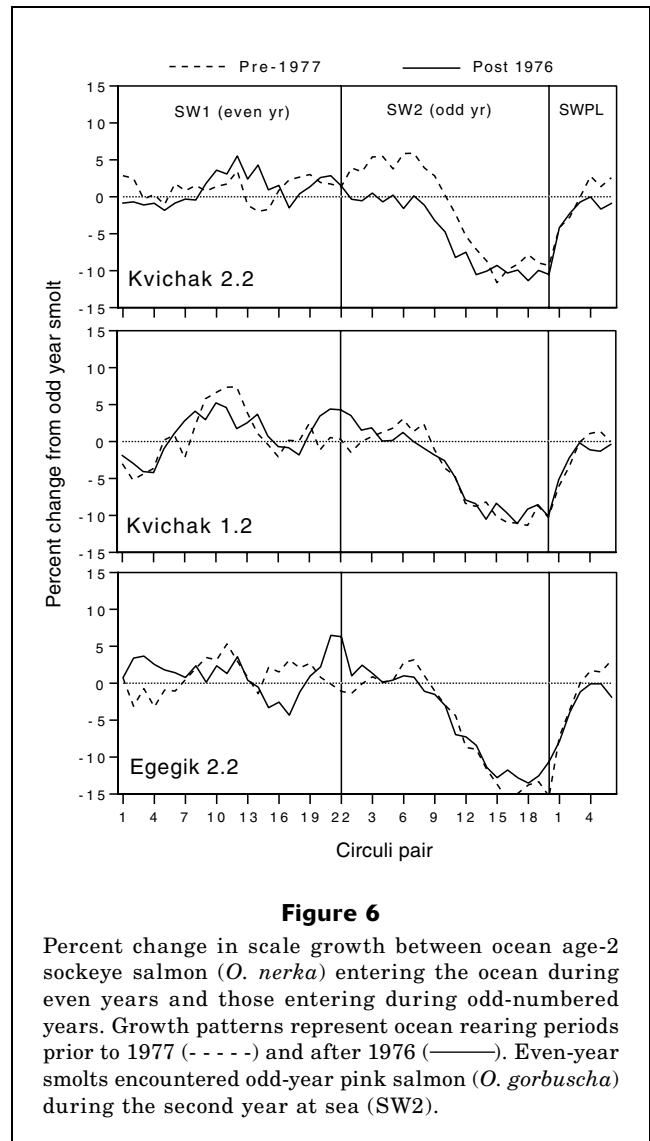
the period of homeward migration. Spring growth after 1976 was 5–10% greater than that during the earlier time period (Fig. 4).

First year ocean (SW1) growth of ocean age-2 sockeye salmon

Scale growth patterns of ocean age-2 Kvichak and Egegik sockeye salmon were remarkably similar to that of ocean age-3 sockeye, especially among those having the same freshwater age (Fig. 5). Sockeye salmon that had spent two winters in freshwater had significantly greater SW1 peak growth compared with those spending one winter in freshwater (Kvichak stock: df=85, t=6.772, P<0.001). Growth of age-2. smolts during the first eight circuli averaged 9% higher compared to age-1. smolts. However, as with ocean age-3 salmon, postpeak growth of age-2 smolts averaged 3.5% less than that of age-1.

smolts. Growth of even- and odd-year smolts during the first growing season was not significantly different but even-year smolts tended to have somewhat greater growth immediately following peak growth (circuli 7–13) and at the end of the growing season (circuli 19–22) (Fig. 6).

SW1 growth was markedly greater after 1976 when salmon abundance was relatively high compared with the growth during 1952–1976 (Fig. 7). Greater growth during the recent time period was most pronounced immediately after entry to Bristol Bay and after peak growth (circuli 13–18), but it was relatively low at the end of the growing season (circuli 20–22). These patterns were generally consistent between odd- and even-year smolt years.

Second year (SW2) growth of ocean age-2 sockeye salmon

SW2 scale growth patterns of ocean age-2 sockeye salmon were similar to SW2 patterns of ocean age-3 sockeye salmon. Scale growth of odd- and even-year smolts was similar until scale growth of even-year smolts significantly declined approximately three circuli after peak growth (Fig. 5, Table 1). Lower growth of even-year smolts continued to the end of the growing season. Scale growth of even-year migrants during their second year at sea was approximately 10% to 15% less than that of odd-year migrants (Fig. 6). Low growth of even-year migrants was associated with odd-numbered years at sea—a trend that was observed among SW2 and SW3 growth periods of ocean age-3 sockeye salmon.

Scale growth during SW2 was greater after 1976 when salmon abundance was relatively high compared with the growth before 1977, especially during the middle of the growing season (Fig. 7). However, after 1976, growth near the end of the growing season (circuli 17–20) tended to be below average. These patterns were consistent among the two stocks and three age groups.

Late season growth of ocean age-2 sockeye salmon during the second year at sea differed from that of ocean age-3 sockeye salmon (Figs. 2 and 5). Growth after circuli 8 of SW2 was significantly greater among ocean age-2 compared with ocean age-3 sockeye salmon (df=283, t=12.81, P<0.001), averaging 11% greater growth.

Growth during homeward migration (SWPL) of ocean age-2 sockeye salmon

Scale growth of ocean age-2 sockeye salmon during the homeward migration peaked at circuli 4, then declined. Prior to peak growth, even-year migrants experienced approximately 5% less growth than odd-year migrants, a pattern that was similar prior to and after the climate shift (Fig. 6). Low initial growth during SWPL appeared to be a continuation of relatively low growth during SW2. No difference in peak growth between odd- and even-years was apparent. Growth tended to be higher after the mid-1970s (Fig. 7).
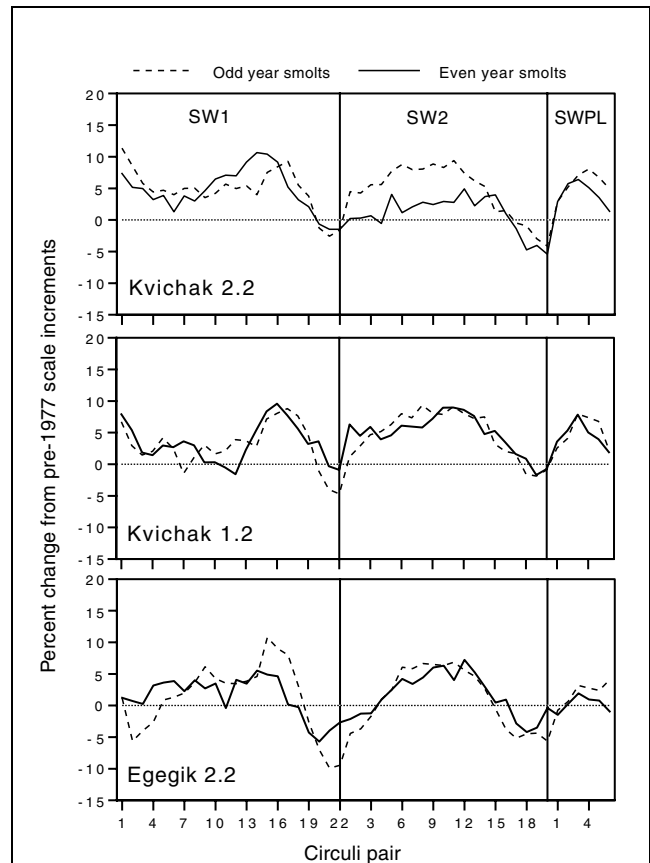

Figure 7

Percent change in ocean age-2 sockeye salmon (*O. nerka*) scale growth entering ocean during 1977 to 1998 compared with 1952–1976. Growth patterns represent smolts entering ocean during odd- (- - - - -) and even-numbered years (———). Even-year smolts encountered odd-year pink salmon (*O. gorbuscha*) during the second year at sea (SW2).

Relationship between early marine and late SW2 scale growth

We examined correlations between early marine scale (SW1 growth through the first eight circuli of SW2) and late SW2 growth (circuli 11 to annulus), corresponding with periods before and after the divergent scale growth pattern observed between odd- and even-numbered years. Negative correlations between early marine and late SW2 scale growth were observed among each stock and age group, before and after the 1977 regime shift, and among fish inhabiting the ocean during odd- or even-numbered years (Table 2). Only one of the 28 correlations (Egegik age-2.2, early period, odd SW2 year) was statistically insignificant. Thus, individual sockeye salmon that experienced somewhat low growth during early marine life tended to have somewhat high growth during later portions of their second year at sea, regardless of whether they competed with pink salmon. The strength of the

Table 2

Correlation between early marine scale growth (SW1 through SW2, circuli 1–8) and SW2 scale growth after growth difference in odd and even numbered years (SW2, circuli 11 to annulus). Measurements based on individual fish (n). Correlation coefficient and statistical significance are shown for each age group and stock during early (pre-1977) and recent (post-1976) periods for odd- and even-numbered years at sea. SW2=2 years in saltwater.

Age	Stock	Period	SW2 year	r	n	F-value	P-value
1.2	Kvichak	Early	Even	−0.11	408	5.18	<0.025
		Early	Odd	−0.20	429	18.20	<0.001
		Recent	Even	−0.22	550	27.84	<0.001
		Recent	Odd	−0.24	596	36.07	<0.001
2.2	Kvichak	Early	Even	−0.14	592	12.17	<0.001
		Early	Odd	−0.14	523	10.16	<0.002
		Recent	Even	−0.31	549	56.23	<0.001
		Recent	Odd	−0.17	568	16.78	<0.001
2.2	Egegik	Early	Even	−0.14	428	8.61	<0.004
		Early	Odd	−0.06	441	1.33	0.249
		Recent	Even	−0.14	551	10.21	<0.002
		Recent	Odd	−0.09	599	4.81	<0.030
1.3	Kvichak	Early	Even	−0.15	270	6.53	<0.020
		Early	Odd	−0.15	333	7.50	<0.010
		Recent	Even	−0.35	517	71.18	<0.001
		Recent	Odd	−0.20	504	21.89	<0.001
1.3	Egigik	Early	Even	−0.15	191	4.32	<0.040
		Early	Odd	−0.22	210	10.51	<0.002
		Recent	Even	−0.23	453	24.67	<0.001
		Recent	Odd	−0.27	479	38.60	<0.001
2.3	Kvichak	Early	Even	−0.15	347	7.78	<0.010
		Early	Odd	−0.16	376	10.12	<0.002
		Recent	Even	−0.24	438	25.86	<0.001
		Recent	Odd	−0.18	407	13.38	<0.001
2.3	Egegik	Early	Even	−0.16	460	12.35	<0.001
		Early	Odd	−0.23	416	23.94	<0.001
		Recent	Even	−0.18	546	17.94	<0.001
		Recent	Odd	−0.17	543	16.11	<0.001

correlations was low, but the consistent pattern among stocks, age groups, and time periods indicates that the negative correlations were not spurious.

Discussion

Previous research documented reduced annual scale growth of Nushagak Bay (Bristol Bay) sockeye salmon during odd-numbered years of their second and third years at sea (Ruggerone et al., 2003). The primary finding of our investigation was that salmon scale growth reduction during odd-numbered years did not occur throughout the second and third years at sea. During the second year at sea, scale growth reduction began three to five circuli after peak scale growth. During the third year at sea, scale growth reduction began immediately after peak growth. This finding was consistent among all

age groups of both Kvichak and Egegik sockeye salmon prior to and after the mid-1970s regime shift that led to greater sockeye salmon abundance. Comparison of seasonal scale growth patterns before and after the regime shift indicated that the recent period of high sockeye salmon abundance was associated with relatively high growth 1) immediately after entry to Bristol Bay, 2) after peak scale growth during the first growing season, 3) during the middle of the second growing season, and 4) during the third spring but followed by below average growth during the remaining summer and fall.

Timing of peak scale growth and differences in scale growth between odd- and even-numbered years

The approximate time period of peak scale growth can be estimated from previous studies of salmon circuli formation at sea and timing of peak prey production. Bilton

and Ludwig (1966) reported that sockeye salmon in the Gulf of Alaska tended to form annuli during December and January, whereas salmon sampled farther west in the relatively cold waters below the Aleutian Islands appeared to form annuli during March (Birman, 1960). For example, sockeye salmon collected from the eastern range of Bristol Bay sockeye salmon in the Gulf of Alaska (e.g., 152–160°W) averaged 1.2 circuli beyond the winter annulus during January and 3.6 circuli in April. We observed peak circuli growth of Kvichak and Egegik sockeye salmon to occur near circuli 5 to 6 (all ages), indicating that peak scale growth occurred from approximately early May to mid-June. This finding is consistent with scale growth in the year of homeward migration when Bristol Bay sockeye salmon averaged approximately 1 to 2 circuli after peak circuli growth before reaching Bristol Bay, on average, during the first week in July. The estimated date of peak scale growth is also consistent with observations of peak biomass of zooplankton in the Gulf of Alaska and Bering Sea, which typically occurs during May or June (Brodeur et al., 1996; Coyle et al., 1996; Mackas et al., 1998; Mackas and Tsuda, 1999). However, Ishida et al. (1998) reported that salmon growth was greatest between June and July, a period apparently later than peak scale growth and peak zooplankton biomass. Furthermore, scale growth may lag behind body growth (Bilton, 1975). Based on these observations, the observed divergence in scale growth between odd- and even-numbered years likely began after zooplankton biomass declined and during a period of high potential body growth of salmon.

Differences in SW2 scale growth between odd- and even-numbered years at sea began three to five circuli after peak growth, rather than immediately after the peak as shown among fish during their third year at sea (SW3). Because younger salmon begin circuli formation earlier in winter than do older salmon (Bilton and Ludwig, 1966; Martinson and Helle, 2000), it is likely that the differences in time of SW2 scale growth was only slightly later than that scale growth during SW3. The reason for the somewhat later differences between odd and even years of younger sockeye salmon might relate to the degree of diet overlap with pink salmon. In the central North Pacific Ocean and Bering Sea, pink salmon in their second growing season have greater diet overlap with larger sockeye salmon (Davis, 2003), such as sockeye salmon in their third season at sea. Thus, competition for prey may be greatest between pink salmon and the larger, older sockeye salmon, leading to earlier growth differences between the SW3 than the SW2 growth period. Alternatively, this pattern may reflect differences in the distribution of age-2 and age-3 sockeye salmon: age-3 salmon maybe distributed farther west where overlap with Asian pink salmon is greater.

Interactions with pink salmon and prey

Spatial and temporal overlap between Asian pink salmon and Bristol Bay sockeye salmon are important factors that affect the degree of competition. Little or no overlap occurs between these stocks during the first growing season (SW1) and there are typically small numbers of pink salmon originating from Bristol Bay (Rogers[1]). Little sampling has occurred during winter (Myers[6]), but data collected during fall and spring indicate that some overlap between Asian pink salmon and Bristol Bay sockeye begins in the central North Pacific Ocean during winter (French et al., 1976; Takagi et al., 1981; Myers et al.[3]). The degree of overlap likely increases into spring when both species reach their southernmost distribution, which is somewhat farther south for pink salmon. As the temperature begins to increase, both species migrate northwest—pink salmon leading the migration. Both species enter the Bering Sea but many Bristol Bay salmon and some Asian pink salmon remain in the North Pacific Ocean. In June, some Asian pink salmon leave the high seas for coastal areas, whereas others remain offshore through July (Myers et al.[3]; Azumaya and Ishida, 2000). During odd-numbered years, pink salmon are more broadly distributed on the high seas and catch per effort in the Bering Sea remains high through at least mid-July (up to 400 fish per 30 tans (1.5 km) of gill net) compared with that during even-numbered years (Azumaya and Ishida, 2000). Catch per effort of pink salmon during July is somewhat lower in the central North Pacific Ocean. Most pink salmon in the Bering Sea likely originate from the eastern Kamchatka Peninsula, which supports a major Asian population that is dominated by odd-year pink salmon. Thus, the period of overlap between Asian pink salmon and Bristol Bay sockeye salmon is from approximately winter through July and greatest overlap likely occurs during late spring through at least mid-July.

The relatively slow growth of sockeye salmon scales during odd-numbered years at sea began in the period of overlap with pink salmon and continued for months after pink salmon left the high seas. This finding indicates that prey availability was reduced for months after most pink salmon left the high seas. Sugimoto and Tadokoro (1997) examined zooplankton biomass during June and July, 1950–81 and concluded that Asian pink salmon caused the observed alternating pattern of zooplankton biomass in the central North Pacific Ocean and the eastern Bering Sea. Shiomoto et al. (1997) examined macrozooplankton biomass in the central North Pacific Ocean during 1985–94 and also concluded that Asian pink salmon, especially those from the eastern Kamchatka Peninsula, reduced the biomass of macrozooplankton. Shiomoto et al. (1997) noted that lower zooplankton biomass was still apparent in the central North Pacific Ocean after many pink salmon had migrated into the Bering Sea. These findings support the hypothesis that predation by pink salmon altered zooplankton biomass from spring through at least July.

[6] Myers, K. 1996. Survey on overwintering salmonids in the North Pacific Ocean: Kaiyo Maru, 5 January–29 January 1996. Report FRI-UW-9607, 54 p. Univ. Washington, Seattle, WA.

Timing of peak zooplankton biomass occurs later in the year in northern regions, but zooplankton biomass typically declines during summer and fall (Batten et al., 2003). Declining zooplankton biomass in epipelagic waters is related, in part, to the ontogenetic migration to deep waters of some major zooplankton species, such as *Neocalanus* spp. (Mackas and Tsuda, 1999). Declining zooplankton biomass during summer likely enhanced the effect of competition exerted by pink salmon during odd-numbered years. July through at least September is a period of high potential salmon growth (Ishida et al., 1998); therefore sockeye salmon may be especially influenced by prey reduction during this period. During early spring, when scale growth of sockeye salmon was great and did not differ between odd- and even-numbered years, prey availability was apparently sufficient to minimize the effects of competition. Walker et al. (1998) reported that density-dependent growth of Asian pink salmon occurred after late June—a finding that is consistent with our study.

The transition from foraging on zooplankton to foraging on squid for both pink and sockeye salmon may also contribute to the alternating-year pattern of sockeye salmon growth. Aydin (2000) suggested that pink and sockeye salmon may begin to feed intensively on micronekton squid after reaching sufficient size during their second growing season. Pink salmon reportedly begin feeding on squid during spring, whereas sockeye salmon may not begin to feed on squid until summer because sockeye salmon are smaller. During odd-numbered years, pink salmon may have reduced the availability of squid to sockeye salmon and influenced the observed differences in scale growth after spring. In support of this hypothesis, sampling of sockeye and pink salmon during a recent 10-year period in the Bering Sea (June and July) indicated a 58% reduction among sockeye salmon and 32% reduction among pink salmon in the weight of squid consumed during odd- compared to even-numbered years (Davis, 2003). Few annual estimates of squid abundance are available, but Sobolevsky (1996) estimated that epipelagic squid biomass in the western Bering Sea was approximately five times greater in an even-year (1990) than in an odd-year (1989). Population dynamics and life history of squid are not well known (Nesis, 1997; Brodeur et al., 1999), but their apparent one- or two-year life history, in conjunction with predation by pink salmon, may lead to an alternating-year pattern of squid abundance that re-enforces the alternating-year pattern of sockeye salmon growth.

Ruggerone et al. (2003) reported that Bristol Bay sockeye salmon that inhabited the ocean in odd-numbered years of their second year at sea experienced lower smolt-to-adult survival compared with sockeye salmon that were present during even-numbered years. Lower survival was believed to be related to competition with Asian pink salmon. Our findings suggest that this mortality was likely related to reduced growth during late spring through fall, rather than during the first winter. We hypothesize that reduced sockeye

salmon growth during the second year at sea led to lower energy reserves and to greater mortality during the second winter, but predation on smaller salmon may also be an important factor (Nagasawa, 1998). Bioenergetic modeling of salmon by Aydin (2000) indicated the greatest difference between the need for prey and prey availability is during winter. Nagasawa (2000) reported exceptionally low prey availability and corresponding low lipid content for salmon in the North Pacific Ocean during winter. Ishida et al. (1998) examined salmon on the high seas and determined that condition factor of all salmon species was lowest during late winter. Beamish and Mahnken (2001) provided evidence that relatively low growth of salmon during summer and fall can lead to significant growth-related mortality during the first winter at sea. Growth-related mortality appears to occur among Bristol Bay sockeye salmon in response to competition with pink salmon, but this competition-related mortality primarily occurs during the second winter at sea.

Bristol Bay sockeye salmon are broadly distributed across the North Pacific Ocean and Bering Sea. They occur in several oceanographic regions in which dominant prey may vary (e.g., the Bering Sea [euphausiids, squid, fish], subarctic current [squid], ridge domain [small zooplankton], the Alaska stream [small zooplankton, squid, fish], and the coastal domain [fish, euphausiids]) (Pearcy et al., 1988; Aydin, 2000). The alternating-year pattern of scale growth was persistent among adult Kvichak and Egegik sockeye salmon of all age groups returning to Bristol Bay even though many of these fish likely inhabited different ocean habitats. Thus, the observed scale growth pattern is either highly persistent in most of these ocean habitats or it is especially important in certain key regions inhabited by Bristol Bay sockeye salmon.

Salmon growth in relation to the regime shift of the mid-1970s

Several studies indicate that a significant change in the species assemblage of the North Pacific Ocean began near 1977 and concurrent with a dramatic shift in physical oceanic regimes (Francis et al., 1998; Anderson and Piatt, 1999). Pacific salmon abundance, including Bristol Bay sockeye salmon, more than doubled after this period (Rogers[1]). Zooplankton and squid biomass have appeared to increase substantially, especially in coastal regions, since the mid-1970s (Brodeur and Ware, 1992; Brodeur et al., 1996). Furthermore, Mackas et al. (1998) reported that the period of maximum zooplankton biomass shifted one or two months earlier after the mid-1970s. In comparison, seasonal scale growth of Kvichak and Egegik sockeye salmon during the first and second years at sea tended to be high after the regime shift. This pattern was also observed in annual scale measurements of sockeye salmon (Ruggerone et al., 2002). Spring scale growth of sockeye salmon after the regime shift was relatively high immediately after entry of sockeye salmon into Bristol Bay and during

their third year at sea, but spring growth was relatively low during the second year. Growth during the second year was relatively high during summer, a pattern that was different from SW1 and SW3 growth. Seasonal scale growth patterns of sockeye salmon indicate that the response of salmon to the 1977 ocean regime shift varied with age and season but that the greater growth during early marine life was associated with greater adult returns. The shift in seasonal growth patterns of sockeye salmon likely reflected their opportunistic forging behavior and the changes in prey species abundances caused by climate change (Kaeriyama et al, 2004).

Greater growth of sockeye salmon when they initially entered the Bering Sea after the 1977 ocean regime shift may reflect differences in seaward migration patterns. Prior to the 1977 regime shift, juvenile sockeye salmon were observed in a narrow band that extended from the shore along the Alaska Peninsula to as far as 50 km offshore (Straty, 1981; Hartt and Dell, 1986). However, recent survey results indicate that juvenile sockeye salmon are broadly distributed in the eastern Bering Sea from the Alaska Peninsula to north of 58°N and that the highest catch rates occur beyond 50 km offshore (Farley et al.[7]). Zooplankton are more abundant in offshore, deeper waters of Bristol Bay than within near shore waters (Straty, 1981; Napp et al., 2002), indicating that the recent northerly seaward migration patterns of juvenile sockeye salmon may place them in areas of higher prey densities and lead to higher early marine growth rates.

Sockeye salmon scale growth during the third year of growth (SW3) was relatively low after 1977, indicating that density-dependent growth was most apparent during this late life stage when mortality is likely relatively low (Ruggerone et al., 2002). Our study indicated the reduced SW3 growth after the 1977 regime shift occurred after peak spring growth, indicating that interspecific competition was most apparent during summer and fall. During the spring homeward migration (SWPL) period, scale growth was above average after 1977. Age-specific size of adult sockeye salmon returning to Bristol Bay was density dependent, but size at a given density was greater after 1977 (Rogers and Ruggerone, 1993; Ruggerone et al., 2003).

[7] Farley, E. V., Jr., R. E. Haight, C. M. Guthrie, and J. E. Pohl. 2000. Eastern Bering Sea (Bristol Bay) coastal research on juvenile salmon, August 2000. Doc. 499, 18 p. North Pacific Anadromous Fish Commission, 889 Pender Street, Vancouver, Canada.

Farley, E.V., Jr., C.M. Guthrie, S. Katakura, and M. Koval. 2001. Eastern Bering Sea (Bristol Bay) coastal research on juvenile salmon, August 2001. Doc. 560, 19 p. NPAFC, 889 Pender Street, Vancouver, Canada.

Farley, E.V., Jr., B.W. Wing, A. Middleton, J. Pohl, L. Hulbert, M. Trudel, J. Moss, T. Hamilton, E. Parks, C. Lagoudakis, and D. McCallum. 2002. Eastern Bering Sea (BASIS) Coastal Research (August–2002) on Juvenile Salmon. Doc. 678, 27 p. NPAFC, 889 Pender Street, Vancouver, Canada.

Salmon survival and scale growth

Biologists have suggested that rapid growth early in life can lead to greater growth in subsequent periods because larger animals have a greater variety of prey and prey size available to them (Pearcy et al., 1999). Aydin (2000) hypothesized that rapidly growing salmon in their first year at sea would more quickly reach a threshold size for feeding on abundant, energy-rich micronekton squid, leading to even greater growth in their second year. However, comparison of early marine scale growth (SW1 through SW2, circuli 8) with late season SW2 growth of individual Kvichak and Egegik sockeye salmon indicated a negative rather than positive relationship. Individual salmon having relatively great early marine scale growth tended to experience reduced scale growth during the later portion of their second year when sockeye salmon reach the size needed to readily consume larger prey such as squid. This finding reflects the growth of sockeye salmon survivors and not those that died at sea. Thus, we interpret this counterintuitive finding as an indication that slow growing sockeye salmon during late SW2 survived primarily when their early marine growth was relatively high. Salmon that experienced both low early marine growth and low SW2 growth apparently did not survive and were not represented in the scale collection. These observations do not necessarily reject the hypothesis that high early marine growth leads to high subsequent growth. In fact, other analyses of sockeye scales indicate spring growth is positively correlated with fall growth within a given year (G. Ruggerone, unpubl. data).

Effect of freshwater age on seasonal scale growth

Scale growth during the first year at sea was different among salmon spending one versus two winters in freshwater. Early SW1 scale growth of sockeye salmon spending two winters in freshwater (age-2.) was significantly greater than that of salmon spending only one winter in freshwater. This trend might reflect differences in migration timing or size (or both) of age-2 versus age-1 smolts. Age-2 smolts are approximately 17 mm longer than age-1 smolts and most age-2 smolts enter marine waters before age-1 smolts (Crawford and West[8]). After peak growth in spring, scale growth of age-1. smolts exceeded that of age-2. smolts. The different early marine growth patterns of age-1. and age-2. smolts did not appear to significantly affect the size of the fish at the end of the growing season. For example, during 1958–72, age-2.1 sockeye salmon sampled immediately south of the Aleutian Islands were 25 mm longer than age-1.1 sockeye salmon (French et al., 1976). The size difference between age-2. and age-1. smolts declined to 8 mm during the second growing season.

[8] Crawford, D. L., and F. W. West. 2001. Bristol Bay sockeye salmon smolt studies for 2000. Reg. Info. Rept. 2A01-12, 164 p. Alaska Dept. Fish Game, 333 Raspberry Road, Anchorage, AK.

Difference in growth by ocean age

Barber and Walker (1988) reported that peak SW2 scale growth for Bristol Bay sockeye salmon (Ugashik stock) was less than peak growth during SW1 and SW3. They suggested that this trend reflected lower prey availability for sockeye salmon in the North Pacific Ocean than in the Bering Sea (Mackas and Tsuda, 1999). But Bristol Bay sockeye salmon also develop in the Bering Sea during their second growing season (French et al., 1976; Myers et al.[3]). Kvichak and Egegik sockeye salmon scales, 1955–2000, exhibited relatively low growth throughout SW2 year compared to SW1 and SW3 years. We suggest that low SW2 growth may also be related to the inability of sockeye salmon to efficiently capture large prey (Aydin, 2000) and to a lower bioenergetic efficiency when consuming smaller prey. Salmon in their third year at sea may experience greater prey availability and capture efficiency because they are larger.

Late season growth of ocean age-2 sockeye salmon during SW2 was significantly greater than that of ocean age-3 sockeye salmon. This finding indicates that the greater size-at-age of ocean age-2 sockeye salmon compared to ocean age-3 sockeye salmon at the end of the second growing season (French et al., 1976) may be largely related to increased growth during the later portion of the second growing season at sea.

Conclusions

Seasonal scale growth patterns of Kvichak and Egegik sockeye salmon exhibited significant differences in SW2 and SW3 scale growth during odd- versus even-numbered years. Differences in scale growth did not begin until after peak scale growth and difference began somewhat later for younger SW2 sockeye salmon. The persistence of this pattern over the past 45 years may be caused by pink salmon, especially those from eastern Kamchatka that are highly abundant during odd-numbered years. During odd-numbered years, pink salmon reduced prey abundance prior to migrating to coastal areas in June and July (Shiomoto et al., 1997; Sugimoto and Tadokoro, 1997). This prey reduction, coupled with declining abundance and ontogenetic vertical migrations of some zooplankton (Mackas and Tsuda, 1999), appears to have influenced (reduced) growth of sockeye salmon from early summer through fall of odd-numbered years. We hypothesize that the alternating odd- and even-year growth pattern of sockeye salmon may be re-enforced by the one- or two-year life cycle of prey, such as squid, whose abundance may be out-of-phase with the two-year cycle of pink salmon. These data, coupled with previous findings of reduced smolt-to-adult survival of sockeye salmon that interacted with odd-year pink salmon during the second year at sea (Ruggerone et al., 2003), indicate that reduced growth of salmon during the second year at sea can lead to measurable salmon mortality. Sockeye mortality associated with pink salmon likely occurs during winter when demand for prey by salmon exceeds the low availability of prey (Aydin, 2000), but it may also occur in response to size-selective predation. Our study indicates that salmon growth and survival are influenced by complex food web interactions, which are likely to significantly shift under various scenarios of climate change that affect temperature, CO_2, and phytoplankton community structure of the Bering Sea (Hare et al.[9]).

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