

Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean

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ABSTRACT

The importance of interspecific competition as a mechanism regulating population abundance in offshore marine communities is largely unknown. We evaluated offshore competition between Asian pink salmon and Bristol Bay (Alaska) sockeye salmon, which intermingle in the North Pacific Ocean and Bering Sea, using the unique biennial abundance cycle of Asian pink salmon from 1955 to 2000. Sockeye salmon growth during the second and third growing seasons at sea, as determined by scale measurements, declined significantly in odd-numbered years, corresponding to years when Asian pink salmon are most abundant. Bristol Bay sockeye salmon do not interact with Asian pink salmon during their first summer and fall seasons and no difference in first year scale growth was detected. The interaction with odd-year pink salmon led to significantly smaller size at age of adult sockeye salmon, especially among younger female salmon. Examination of sockeye salmon smolt to adult survival rates during 1977–97 indicated that smolts entering the ocean during even-numbered years and interacting with abundant odd-year pink salmon during the following year experienced 26% (age-2 smolt) to 45% (age-1 smolt) lower survival compared with

smolts migrating during odd-numbered years. Adult sockeye salmon returning to Bristol Bay from even-year smolt migrations were 22% less abundant (reduced by 5.9 million fish per year) compared with returns from odd-year migrations. The greatest reduction in adult returns occurred among adults spending 2 compared with 3 years at sea. Our new evidence for interspecific competition highlights the need for multispecies, international management of salmon production, including salmon released from hatcheries into the ocean.

Key words: Alaska, Bering Sea, Bristol Bay, growth, hatchery, interspecific competition, Kamchatka, management, marine survival, *Oncorhynchus*, Pacific salmon, Russia, scale annuli

INTRODUCTION

The role of interspecific competition in structuring terrestrial, freshwater, coral reef, and marine intertidal communities has been widely investigated (Schoener, 1983; Bertness *et al.*, 2001), but the nature and importance of interspecific competition as a mechanism that regulates population abundance in offshore marine communities is largely unknown. This uncertainty stems from the difficulty in testing competition between species that inhabit broad regions of the world's oceans. Some scientists have assumed that interspecific competition may influence abundances of marine populations (Cushing, 1975; National Research Council, 1999), whereas others have downplayed its importance in regulating populations (Sinclair, 1988).

Intraspecific competition in epipelagic waters of the North Pacific Ocean can lead to density-dependent growth within the highly abundant species of Pacific salmon (*Oncorhynchus* spp.) such as sockeye (*O. nerka*), pink (*O. gorbuscha*) and chum (*O. keta*) salmon (Peterman, 1984; Ishida *et al.*, 1993; Rogers and Ruggerone, 1993; Welch and Parsons, 1993). Pacific salmon are highly migratory and competition may occur between conspecifics originating from distant

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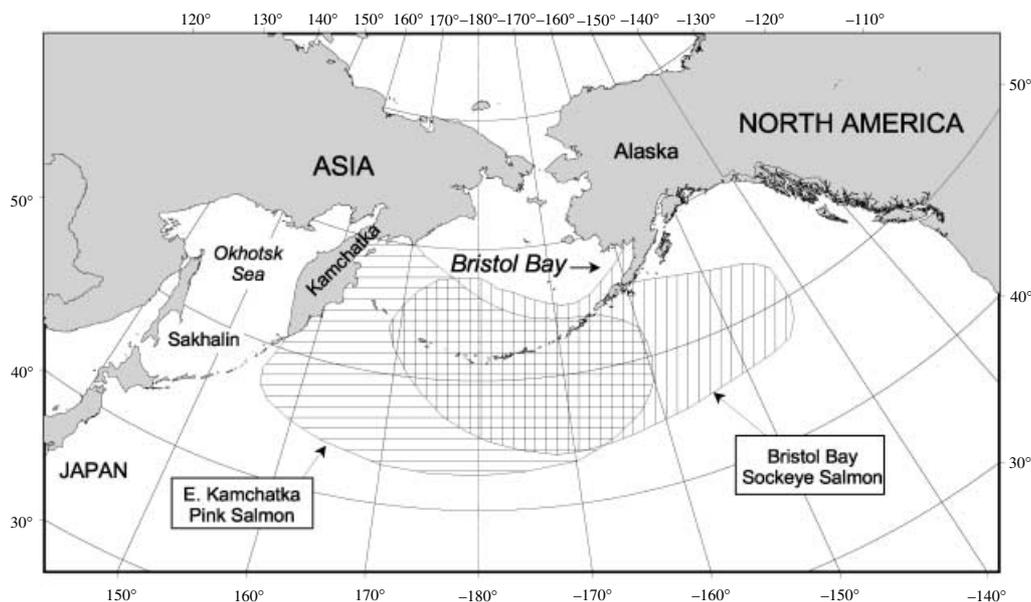
natal rivers (McKinnell, 1995; Pyper and Peterman, 1999). Additionally, several studies have reported evidence of interspecific competition among Pacific salmon leading to reduced growth of the species foraging at the slightly higher trophic level. Asian pink salmon reportedly reduced the length of Russian sockeye salmon (Krogius, 1964; Bugaev *et al.*, 2001) and Asian coho salmon (*O. kisutch*) (Ogura *et al.*, 1991) and altered the diet of Asian chum salmon (Tadokora *et al.*, 1996). These observations of density-dependent growth have led to concerns about salmon carrying capacity in the ocean, especially in the light of increased artificial propagation (Pearcy *et al.*, 1999). However, there is little evidence that competition leads to reduced survival of salmon, although researchers have suggested that pink salmon from Washington and British Columbia may reduce the abundance of chum salmon through competition in nearshore waters (Salo, 1991).

Here we evaluated offshore competition between pink salmon originating from Asia and sockeye salmon originating from Bristol Bay, Alaska, using the unique biennial abundance cycle of Asian pink salmon from 1955 to 2000. Several attributes of Asian pink salmon and Bristol Bay sockeye salmon make them ideal for testing the competition hypothesis. First, pink salmon have a unique 2-year life cycle that can lead to

significant differences in abundance during odd- versus even-numbered years, thereby providing a natural experimental control for environmental conditions that similarly influence both species. Asian pink salmon are most abundant in odd-numbered years, averaging approximately 55% more fish (162 million adults, i.e. catch and spawning abundance) compared with even years (105 million adults) during 1955–2000 (INPFC Secretariat, 1979; Rogers, 1987a, 2001). In comparison, annual pink salmon runs to Alaska are nearly equal during odd- and even-numbered years, and they are less abundant than Asian pink salmon. Furthermore, adult pink salmon distribution is broader in the western and central North Pacific Ocean and Bering Sea in odd-numbered years compared with even-numbered years (Azumaya and Ishida, 2000).

A second attribute that supports tests of the competition hypothesis is that the distribution of Asian pink salmon overlaps that of Bristol Bay sockeye salmon in the North Pacific Ocean and Bering Sea, based on extensive high seas tagging studies since 1956 (French *et al.*, 1976; Takagi *et al.*, 1981; Myers *et al.*, 1996). Pink salmon from eastern Kamchatka migrate the farthest east and have the greatest overlap (Fig. 1), but other Asian stocks also overlap with Bristol Bay sockeye salmon. Overlap in offshore waters begins during winter after the spring seaward migration of

Figure 1. Known range of immature Bristol Bay sockeye salmon and maturing eastern Kamchatka Peninsula pink salmon, based on the international tag recovery database, 1956–95 (French *et al.*, 1976; Takagi *et al.*, 1981; Myers *et al.*, 1996). Area of known overlap is approximately 2 million km² and represents high densities of both species. Actual overlap is probably broader than that shown. Sakhalin and Okhotsk pink salmon migrate to approximately 177°E and overlap with the western distribution of Bristol Bay sockeye salmon.

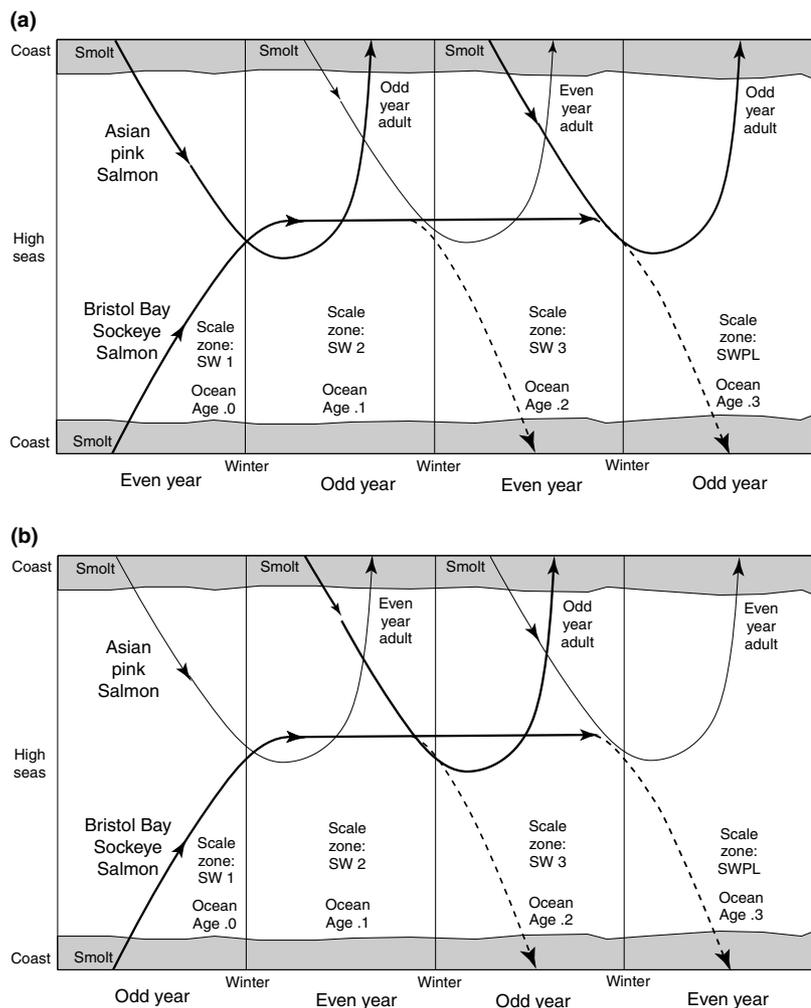


juveniles and continues through July when adult pink salmon return to coastal waters and enter spawning streams (Fig. 2). Pink salmon invariably spend one winter at sea whereas sockeye salmon typically spend two or three. The trophic level, diet, and feeding behaviour of pink salmon overlap significantly with sockeye salmon (Welch and Parsons, 1993; Davis *et al.*, 2000; Kaeriyama *et al.*, 2000). Macrozooplankton abundance in the central North Pacific is lower during odd-numbered years, apparently due to the high abundance of Asian pink salmon in odd years (Shiomoto *et al.*, 1997). Consumption of prey by individual sockeye and pink salmon tends to decline during years when pink salmon are most abundant; however, the decline in the dominant prey may be greater for sockeye salmon than pink salmon (58% versus 31% reduction) (Davis *et al.*, 2000). Pink salmon are the most abundant salmonid, and Asia (Russian Far East) supports the largest pink salmon

runs in the world. Bristol Bay supports the largest sockeye salmon runs in the world. Thus, competition between Asian pink salmon and Bristol Bay sockeye salmon was expected to be greatest during odd-numbered years when Asian pink salmon were most abundant.

To establish the mechanism by which pink salmon might reduce Bristol Bay sockeye salmon survival, we first compared annual scale growth of sockeye salmon at sea and their final adult length in odd- and even-numbered years. A reduction in sockeye salmon growth in offshore waters during odd-numbered years (high pink salmon abundance) would support the hypothesis that competition for food might lead to reduced sockeye salmon survival. The effect of Asian pink salmon on survival of adult sockeye salmon was evaluated by comparing smolt-to-adult survival rates and total adult returns of sockeye salmon resulting from even- versus odd-numbered year smolt migrations.

Figure 2. Diagram of temporal overlap between Asian pink salmon and Bristol Bay sockeye salmon. Sockeye salmon smolts entering the ocean during even-numbered years first encounter abundant odd-year pink salmon (bold line) during the first winter at sea and the second growing season, i.e. primarily during SW2 (a), whereas sockeye salmon smolts entering the ocean during odd-numbered years do not encounter abundant odd-year pink salmon until the second winter at sea and the third growing season, i.e. during SW3 (b). Interaction between Asian pink salmon and maturing sockeye salmon may be minimal because maturing sockeye salmon are distributed farther north during fall, winter and spring compared with immature sockeye salmon (French *et al.*, 1976). Pink salmon spend one winter at sea, whereas most sockeye spend two (age-.2) or three (age-.3) winters at sea. Period of overlap between species is from winter to July, but the effect of interaction may continue until prey populations recover.



Sockeye salmon first interact with Asian pink salmon during the second season (Fig. 2). Therefore, a reduction in survival or abundance of sockeye salmon smolts entering the ocean during even-numbered years would support the hypothesis that Asian pink salmon affect survival of Alaskan sockeye salmon.

MATERIALS AND METHODS

Sockeye salmon scale and adult length measurements

An index of annual Bristol Bay sockeye salmon growth at sea was estimated by measuring distances between scale annuli using the methodology developed by the University of Washington's High Seas Salmon Research Program (Davis *et al.*, 1990; Zimmermann, 1991). Scale annuli measurements are correlated with salmon length (Fukuwaka and Kaeriyama, 1997). Sockeye salmon scales were obtained from commercial harvests of adult fish in Nushagak Bay, a major fishing district within Bristol Bay. Scales of both age-1.3 and age-1.2 sockeye salmon, corresponding to the dominant age groups in this fishing district, were measured at a magnification of 56 \times (age is designated by European notation, i.e. the number of winters spent in freshwater before going to sea, one winter = age-1.x or two winters = age-2.x, followed by the number of winters spent at sea, two winters = age-x.2 or three winters = age-x.3). Sample size was 100 adult salmon scales (equal sex ratio) per year per age group; 1955–97 for age 1.3 and 1955–90 for age 1.2 fish. Average length of adult Bristol Bay sockeye salmon was determined for each sex and age, based on regular sampling of adult returns by the Alaska Department of Fish and Game (ADFG) in each river system during 1958–2000 (Rogers and Ruggerone, 1993).

Salmon abundance and survival statistics

Abundance of Bristol Bay sockeye salmon by age and river system (stock) was obtained from a database previously used to reconstruct annual runs of Pacific salmon throughout their range since 1950 (Rogers, 1987a, 2001). Age-specific adult sockeye salmon returns in a given year were used to estimate adult salmon returns from smolt migrations occurring in odd- versus even-numbered years where even-year smolts interacted with abundant odd-year pink salmon during the second growing season.

Abundances of Asian (Japanese and Russian) pink salmon after 1991 were based on annual estimates of catch and spawning density provided by the North Pacific Anadromous Fish Commission in

documents and statistical yearbooks (NPAFC, 2001). Prior to 1992, abundances of Asian pink salmon were calculated from catch statistics provided by the International North Pacific Fisheries Commission, the Food and Agriculture Organization of the United Nations (FAO), and by the USSR (Fredin *et al.*, 1977; INPFC Secretariat, 1979; Fredin, 1980; Harris 1989), and a 60% harvest rate, which was estimated from catch and spawning abundance statistics in the early 1990s (Rogers, 2001). Commercial catches by Japan on the high seas and inside the Russian 200-mile zone are included in the abundance estimates. These estimates represent an index of Asian pink salmon abundance on the high seas that largely reflects catch trends. Actual harvest rates may have been higher during even-numbered years when pink salmon were less abundant (Semko, 1969), a trend that helped to maintain the dominance of odd-year pink salmon runs.

Sockeye salmon smolt to adult survival rates were based on reported age-specific smolt abundance estimates and subsequent age-specific adult returns (Crawford and West, 2001). Smolt estimates were available for the Kvichak (1977–97), Egegik (1982–97), and Ugashik (1983–97) rivers, all of which enter into Bristol Bay. Earlier years of Kvichak smolt data were not used because they were based on a different sampling methodology and represented a period of lower salmon production.

Statistical analysis

Time series analysis with transfer function models (Liu and Hudak, 1992) was used to develop multivariate relationships between adult sockeye salmon length and the independent variables – Asian pink salmon abundance and Bristol Bay sockeye salmon abundance. An intervention model approach was incorporated to model a level shift during the mid-1970s, as this approach reduced residual error more than incorporation of an autoregressive error term. Model assumptions were examined and validated using autocorrelation, cross correlation and collinearity analyses. Additionally, correlation between sockeye salmon scale growth and pink salmon abundance used the procedure recommended by Pypers and Peterman (1998) to control for type I error resulting from autocorrelation.

Analysis of variance (ANOVA) was used to test for differences in sockeye salmon size, abundance and survival during odd- compared with even-numbered years at sea. An arcsine transformation was applied to sockeye salmon survival estimates.

RESULTS

Pink salmon effects on sockeye salmon growth

Since the mid-1950s, Bristol Bay sockeye salmon scale growth exhibited a distinct alternating year pattern of growth during the year prior to homeward migration (Fig. 3). Scale growth was typically below average during odd-numbered years at sea and above average during even-numbered years for both ocean age-2 and age-3 sockeye salmon. This unique time series of sockeye salmon growth highlights the effect of Asian pink salmon, which exhibit a distinct odd- and even-year pattern of abundance that is opposite to that of sockeye salmon growth (Fig. 3c).

Long-term trends in sockeye salmon growth in relation to pink salmon abundance were also apparent.

During odd-numbered years and, to a lesser extent, in even-numbered years, sockeye salmon scale growth during the third growing season (SW3) decreased after pink salmon abundance increased during the mid-1970s (Fig. 3b), leading to an inverse correlation between sockeye salmon scale growth and pink salmon abundance ($r = -0.59, P < 0.05$). This transition in scale growth corresponds with the mid-1970s North Pacific Ocean 'regime shift' that had a strong effect on climate, sea surface temperature and abundance of marine species (Anderson and Piatt, 1999). The strong response of sockeye salmon growth to pink salmon abundance is further shown by reduced sockeye salmon growth during recent (1992–96, except 1994) even- and odd-numbered years when Asian pink salmon abundance was large compared with earlier years

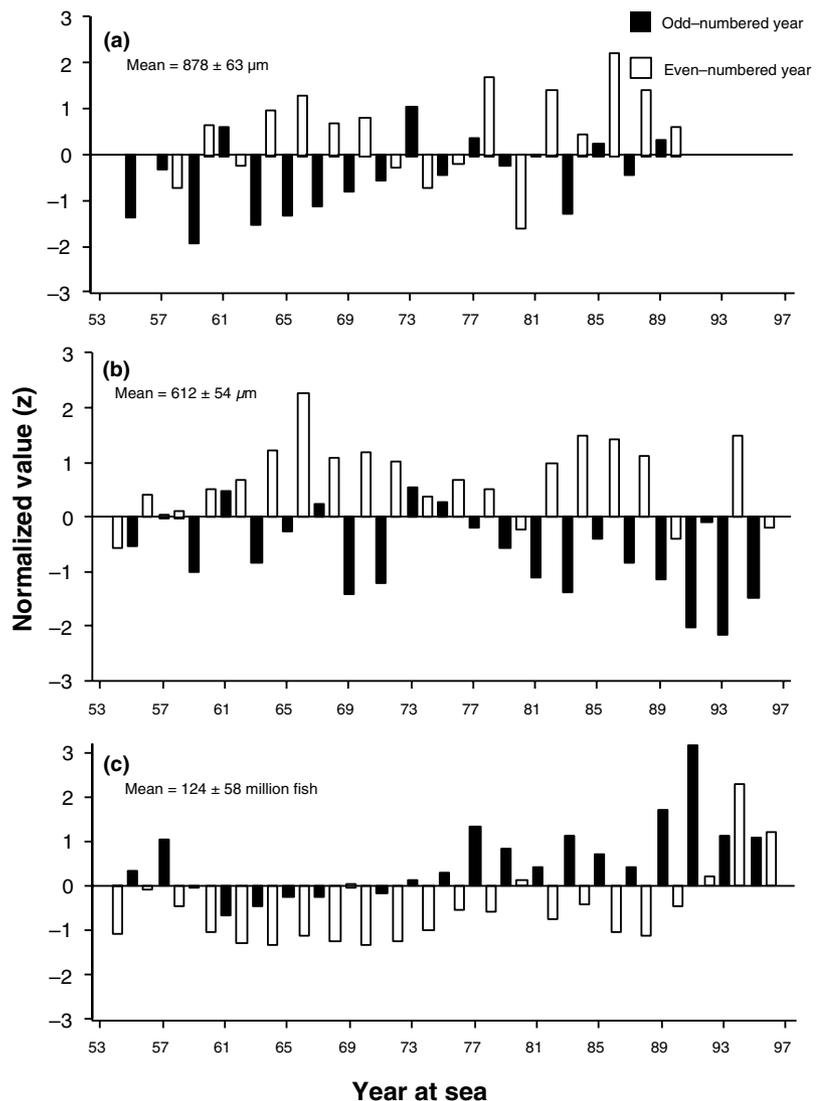


Figure 3. Bristol Bay sockeye salmon growth during the second (a) and the third growing season at sea (b) and the corresponding abundance of maturing Asian pink salmon (c), 1954–96. Growth measurements are based on scales of age-1.2 (a) and age-1.3 (b) sockeye salmon. Age-1.2 scale measurements after 1990 were not available. Open bars are even years at sea, and closed bars are odd years at sea. Values are normalized, i.e. standard deviations above and below the long-term mean.

(Fig. 3). Sockeye salmon scale growth during the second growing season (SW2) was also inversely correlated with pink salmon abundance before and after the mid-1970s ($r = -0.35$, $P < 0.05$), but ocean age-2 growth tended to be greater after the mid-1970s.

Bristol Bay sockeye salmon scale growth was significantly lower during odd-numbered years at sea [i.e. years of high pink salmon abundance; two factor ANOVA (odd/even year, scale zone); age-1.3: $df = 1, 2, 123$; $F = 14.255$; $P < 0.001$; age-1.2: $df = 1, 1, 71$; $F = 4.124$; $P < 0.05$]. Reduced growth during odd-numbered years occurred during both the second [3.7% (age-1.3) to 5.6% (age-1.2) reduction] and third (12.8% reduction) growing seasons ($P < 0.05$). No differences in sockeye salmon scale growth were observed during the first growing season at sea, corresponding to the period when little or no overlap occurs with Asian pink salmon (French *et al.*, 1976; Takagi *et al.*, 1981; Myers *et al.*, 1996). Scale growth during the homeward migration (SWPL) was confounded by resorption of the outer scale margin.

Previous research demonstrated that the length of adult Bristol Bay sockeye salmon was smaller during years when they were abundant, primarily due to intraspecific competition during the spring migration back to Bristol Bay when they concentrate in a relatively small migration corridor and time period (Rogers and Ruggeroni, 1993). Multivariate time series analysis indicated that lengths of adult male and female sockeye salmon (each of four age groups) during 1958–2000 were also inversely related to Asian pink salmon abundance during the previous year

(Table 1). Sockeye salmon length was not related to Asian pink salmon abundance during the year of homeward migration ($P > 0.05$), indicating little interaction with maturing sockeye salmon. Standardized model coefficients indicated that pink salmon abundance affected lengths of female, more than male, sockeye salmon. Maximum percentage reduction in average sockeye salmon length as a result of pink salmon ranged from 1.8% (age-2.3 males) to 4.2% (age-1.2 females), indicating a greater effect on the youngest age group.

Sockeye salmon abundance during the homeward migration period tended to influence final sockeye salmon length more than pink salmon abundance during the previous year. Thus, intraspecific competition had a greater effect on adult salmon length than interspecific competition. Time series analysis indicated a shift in the relationship between final adult length and salmon abundance: beginning with adults returning in 1977, sockeye salmon length was greater at a given abundance of pink and sockeye salmon.

Pink salmon effects on sockeye salmon survival and abundance

Survival was significantly lower for sockeye salmon entering the ocean during even-numbered years [three factor ANOVA (odd/even year, freshwater age, sockeye salmon stock); $df = 1, 1, 2, 89$; $F = 6.208$; $P < 0.02$]. These fish interacted with abundant odd-year Asian pink salmon during the first winter and second growing season at sea, whereas odd-year smolts did not interact with odd-year pink

Table 1. Multivariate time series analysis showing the effect of pink salmon abundance (X3) on lengths (mm) of adult sockeye salmon returning to Bristol Bay (model for each sex and age class), 1958–2000. Asian pink salmon abundance is run size (millions) during the previous year ($t-1$), corresponding to the last year of interaction throughout much of the growing season. Pink salmon abundance during the year of return (t) was not significant ($P > 0.05$), indicating little interaction with maturing sockeye salmon. Other variables in the models are abundance of Bristol Bay (BB) sockeye run (X1; millions) and time period (X2: 0 if 1958–76; 1 if 1977–2000). Age-1.2 level shifts began in 1978. Pink and sockeye salmon run sizes were statistically significant factors for each age group and sex; critical $t_{0.05(2),39} = 2.023$. Standardized model coefficients are shown.

Age	Sex	Multivariate equation	N	R ²	Std model coefficients				t value	
					BB run	Pink Period run	BB run	Pink Period run		
1.3	Male	$L = 594.3 - 0.289(X1) + 6.40(X2) - 0.058(X3_{t-1}) + \epsilon$	43	0.49	-0.619	0.415	-0.492	-4.55	2.75	-3.78
1.3	Female	$L = 571.7 - 0.339(X1) + 8.76(X2) - 0.067(X3_{t-1}) + \epsilon$	43	0.59	-0.710	0.556	-0.551	-5.88	4.14	-4.76
2.3	Male	$L = 596.8 - 0.310(X1) + 6.03(X2) - 0.040(X3_{t-1}) + \epsilon$	43	0.46	-0.697	0.411	-0.355	-5.00	2.65	-2.66
2.3	Female	$L = 578.8 - 0.315(X1) + 8.31(X2) - 0.055(X3_{t-1}) + \epsilon$	43	0.48	-0.715	0.574	-0.485	-4.93	3.54	-3.56
1.2	Male	$L = 524.9 - 0.211(X1) + 6.75(X2) - 0.070(X3_{t-1}) + \epsilon$	43	0.26	-0.340	0.332	-0.467	-2.15	1.84	-3.01
1.2	Female	$L = 508.8 - 0.198(X1) + 9.87(X2) - 0.082(X3_{t-1}) + \epsilon$	43	0.31	-0.362	0.550	-0.593	-2.20	2.94	-3.87
2.2	Male	$L = 538.5 - 0.404(X1) + 14.50(X2) - 0.062(X3_{t-1}) + \epsilon$	43	0.50	-0.712	0.777	-0.433	-5.29	5.19	-3.35
2.2	Female	$L = 523.8 - 0.424(X1) + 14.21(X2) - 0.064(X3_{t-1}) + \epsilon$	43	0.47	-0.704	0.715	-0.419	-5.10	4.66	-3.17

salmon until their third growing season. Lower survival of even-year migrating juveniles occurred in each of the three sockeye salmon populations for which survival data were available. Survival of both freshwater age-1 and age-2 juvenile sockeye salmon was less during even-year migrations, but the reduction was greatest for the smaller and younger age-1 salmon (45% versus 26% reduction) (Fig. 4). Examination of age-specific contributions to the survival rates indicated that the youngest sockeye salmon (age-1.2) experienced the greatest reduction in survival (59%), whereas the oldest age group (age-2.3) was affected the least (19% reduction). Intermediate age groups (age-1.3 and age-2.2) experienced intermediate reductions (30%).

The effect of Asian pink salmon on the abundance of Bristol Bay sockeye salmon was evaluated by comparing adult returns from juvenile sockeye salmon entering the ocean during odd- versus even-numbered years during 1956–76 and 1977–97, corresponding to periods of relatively low and high adult salmon production (Beamish and Bouillon, 1993; Mantua *et al.*, 1997). All major Bristol Bay stocks were analysed

except for the Kvichak stock, which is strongly influenced by a 5-year cycle of spawning density that causes the large 5-year cycle of adult returns. Prior to the mid-1970s regime shift when pink and sockeye salmon were less abundant, no difference was detected in odd- and even-year sockeye salmon abundance ($P > 0.05$). After the mid-1970s, the Bristol Bay sockeye salmon return from juveniles entering the ocean during even-numbered years averaged 1.48 million fewer fish per stock per year or a 22% reduction compared with returns from odd-year juveniles (df 1, 3, 76; $F = 3.97$; $P = 0.049$). The reduction occurred in each of the four stocks (Fig. 5), resulting in 5.9 million fewer sockeye salmon per year returning to Bristol Bay from even-year smolt migrations.

Analysis of age-specific sockeye salmon returns after 1976 indicated 1.04 million fewer ocean age-2 sockeye salmon per Bristol Bay stock per year returned from juveniles entering the ocean during even-numbered years compared with odd-numbered years [two factor ANOVA (sockeye salmon stock, odd/even year), df 1, 3, 76; $F = 8.724$; $P < 0.005$]. The return of ocean age-3 sockeye was not statistically different between odd- and even-numbered years ($P = 0.35$), but fewer age-3 sockeye salmon tended to return

Figure 4. Average smolt to adult survival of freshwater age-1 and age-2 Bristol Bay sockeye salmon entering the ocean during odd versus even years, 1977 to 1997. Even-year smolts first interact with relatively abundant odd-year Asian pink salmon during their first winter and second spring at sea, whereas odd-year juveniles first interact with odd-year pink salmon during their second winter and third spring at sea. Contribution of ocean age-2 and age-3 sockeye salmon to the survival estimates is shown. Estimates represent Kvichak, Egegik and Ugashik sockeye salmon populations, which constitute 67% of the adult Bristol Bay sockeye salmon population since 1978 (on average). Error bars show ± 1 SE.

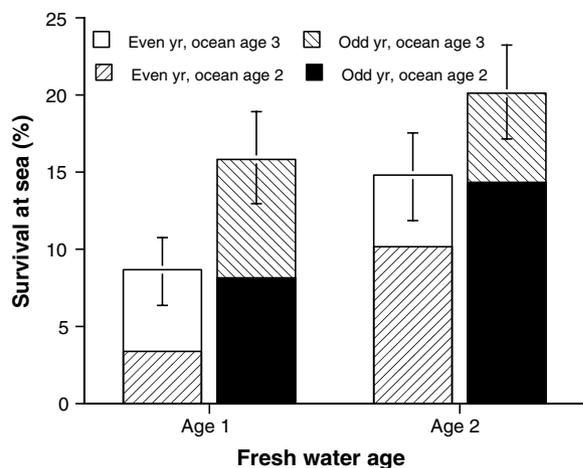
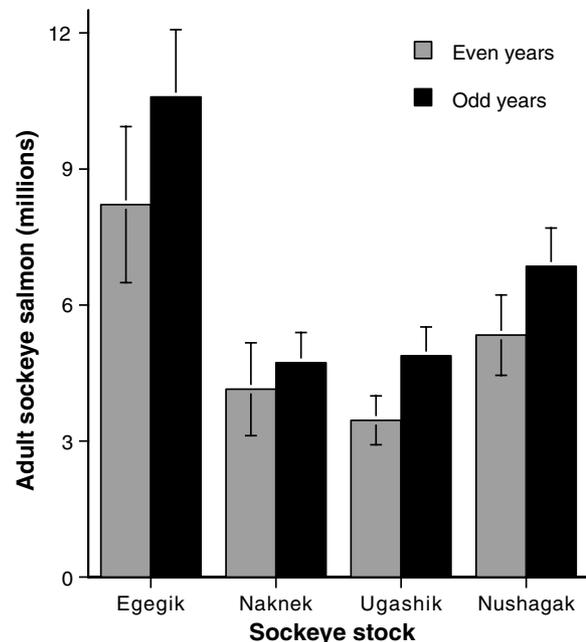


Figure 5. Annual number of adult sockeye salmon returning from juvenile sockeye salmon entering the ocean during odd versus even years (mean ± 1 SE), 1977 to 1997. All major Bristol Bay sockeye salmon stocks are shown except Kvichak (see text).



from juveniles entering the ocean during even-numbered years (average reduction: 0.44 million adults per stock). Ocean age-3 sockeye salmon returns from even-year migrations of juveniles experienced large numbers of pink salmon during their second growing season at sea (SW2 scale zone) but fewer pink salmon during their third season (SW3 scale zone). These results indicate that sockeye salmon abundance was primarily affected during their second growing season at sea.

DISCUSSION

Our analyses show that growth and survival of Bristol Bay sockeye salmon were inversely related to Asian pink salmon abundance, indicating that pelagic marine species can compete and affect population levels over broad regions of the North Pacific Ocean and the Bering Sea. This finding is contrary to the opinion that competition may have little effect on the regulation of populations in the ocean (Sinclair, 1988), a belief founded in part by the difficulty in testing the competition hypothesis. In this study, detection of competition was facilitated by the unique odd/even year cycle of Asian pink salmon abundance. The 2-year cycle is important to the detection of competition because both species appear to respond similarly to decadal-scale cycles, as shown by the significant overall increase in abundance of both species beginning in the mid-1970s (Beamish and Bouillon, 1993). Interspecific competition effects on sockeye salmon growth occurred throughout the 45-year period of investigation, but competition effects on sockeye salmon survival and abundance were most apparent after the mid-1970s when overall survival rates and abundances of both species were relatively high. Further research is needed to evaluate survival prior to the mid-1970s.

The mechanism leading to lower sockeye salmon abundance and survival in this study is reduction in food availability and salmon growth as a result of the relatively high abundance of Asian pink salmon during odd-numbered years. These species are sympatric on the high seas, share similar prey, and Asian pink salmon can reduce prey availability in the central North Pacific Ocean during odd-numbered years (Shiomoto *et al.*, 1997). Size-selective predation on slower growing sockeye salmon by salmon sharks (*Lamna ditropis*) and other large predators is probably a key source of mortality (Nagasawa, 1998). Sockeye salmon is reportedly the dominant prey of salmon sharks in the central North Pacific and Bering Sea, representing up to 40% of their diet.

Other environmental or biological factors cannot explain the observed sockeye salmon abundance pat-

tern exhibited over decades. Bristol Bay sockeye salmon spawning density is largely controlled by the fixed spawning density policy of the ADFG, and it does not vary on a 2-year cycle (two factor ANOVA; odd/even year, stock; $df = 1, 4, 205$; $F = 0.000$; $P > 0.99$). Furthermore, a 2-year cycle originating from fresh-water sources would be inhibited by the variable residence time of sockeye salmon in lakes (either 1 or 2 years), which is partially influenced by growth rate (Burgner, 1991). In marine waters, other species having life history characteristics that might influence the odd/even year pattern observed in Bristol Bay sockeye and Asian pink salmon are not known (Heard, 1991). Predation by returning adult pink salmon on emigrating juvenile sockeye salmon may influence a biennial cycle of sockeye salmon in British Columbia (Peterman, 1982), but pink salmon returning to Bristol Bay are not abundant and they are distributed offshore from juvenile sockeye salmon (Straty, 1981). Abundance of North American pink salmon stocks cannot explain reduced growth and abundance of Bristol Bay sockeye salmon during odd-numbered years as Alaska pink salmon abundance is nearly equal during odd- and even-numbered years, and pink salmon originating from British Columbia and Washington have little overlap with Bristol Bay sockeye salmon (French *et al.*, 1976; Takagi *et al.*, 1981; Myers *et al.*, 1996). Thus, we conclude that Asian pink salmon influenced the growth and survival of Bristol Bay sockeye salmon.

We believe the effect on sockeye salmon abundance and growth shown in this investigation was largely related to the eastern Kamchatka population of pink salmon and secondarily to other Asian pink salmon populations. The international tag recovery database shows that eastern Kamchatka pink salmon have the greatest eastward migration and largest overlap with Bristol Bay sockeye salmon (Fig. 1). From 1955 to 1999 eastern Kamchatka pink salmon were relatively abundant, supporting an average harvest of approximately 24 million fish in odd-numbered years and 5 million fish in even-numbered years (Sinyakov, 1998). The relatively high odd-year abundance of eastern Kamchatka pink salmon has continued throughout the 1990s, whereas even-year abundances of other Asian pink salmon populations increased during the early 1990s. These other Asian pink salmon stocks are also abundant but they overlap with Bristol Bay sockeye salmon to a lesser degree. North American pink salmon from Alaska probably compete with Bristol Bay sockeye salmon but detection of this effect is confounded by the similar odd- and even-year abundances of central and southeast Alaska pink salmon.

Previous researchers have suggested that most salmon mortality occurs during the first few months of marine life (Pearcy, 1992). This study indicated that sockeye salmon abundance was reduced during the second year at sea, corresponding to the period when Bristol Bay sockeye and Asian pink salmon first overlap (French *et al.*, 1976; Takagi *et al.*, 1981; Myers *et al.*, 1996). The salmon interaction probably begins during the first winter at sea of both species when they are primarily located in the central North Pacific (Fig. 2). During spring and early summer, many immature sockeye salmon and maturing Asian pink salmon migrate northwest and enter the central Bering Sea. Many maturing pink salmon coexist with immature sockeye salmon in the Bering Sea until mid-July. Although most pink salmon leave offshore rearing areas by August for coastal spawning streams, the effect of pink salmon probably continues until prey populations increase. Thus, the period of salmon interaction occurs from winter to at least summer.

Sockeye scale growth during the third year at sea was strongly influenced by pink salmon abundance. This reduction in growth, however, did not correspond to a reduction in sockeye salmon abundance. Instead, ocean age-3 sockeye salmon abundance was slightly greater after interacting with odd-year pink salmon in their third year at sea. This suggests that sockeye salmon abundance, in relation to interactions with pink salmon, is established during the second year at sea, but sockeye salmon growth during the third year continues to be influenced by large numbers of pink salmon. Furthermore, these data show that the potential increase of ocean age-3 sockeye salmon, resulting from reduced growth during the second year at sea and delayed maturation (Rogers, 1987b), did not offset reduced returns of ocean age-2 siblings.

The reduction in sockeye salmon scale growth during the second growing season (SW2) was less than that during the third season (SW3). This result may reflect greater overlap between the older ocean age-3 sockeye salmon and Asian pink salmon, and/or size-selective predation on smaller individuals during the second compared with the third year at sea. McKinnell (1995) examined sockeye salmon scale growth patterns and concluded that older salmon from northern British Columbia migrated farther and overlapped to a greater degree with Bristol Bay salmon compared with younger fish. Size-dependent mortality in the present study is supported by the observation that pink salmon had the greatest effect on the youngest sockeye salmon, leading to less differential SW2 scale growth during odd- and even-numbered years. In contrast to annual sockeye salmon scale growth, differential size of

adult sockeye salmon was most apparent among the younger ocean age-2 compared with older ocean age-3 sockeye salmon because ocean age-3 sockeye salmon interact with both odd- and even-year pink salmon populations, whereas ocean age-2 sockeye salmon interact with only one pink salmon population.

Bristol Bay supports one of the most valuable salmon fisheries in the world. During smolt years 1977 to 1997 approximately 59 million fewer sockeye salmon returned to Bristol Bay from even-year compared with odd-year smolt migrations. This reduction represents approximately \$310 million less to sockeye salmon fishermen, based on the average ex-vessel value of Bristol Bay sockeye salmon during 1980–99.

This study indicates that interspecific competition can occur among salmon species originating from different continents that feed in broad regions of the North Pacific Ocean and Bering Sea. Thus, salmon management actions taken in one region can affect species abundance in distant regions. These effects can have significant economic consequences for harvesters of impacted stocks, as indicated by Bristol Bay sockeye salmon, or they may potentially inhibit the recovery of salmon listed under the US Endangered Species Act. Salmon hatcheries have been a primary management tool for maintaining or supplementing salmon harvests in many regions of the North Pacific. Most Asian pink salmon are native, but significant hatchery production occurs in Russia (Sakhalin and Iturup islands) and Japan. During the 1990s, up to 1.6 billion juvenile pink salmon per year were released from hatcheries into the North Pacific Ocean, of which approximately 45% were from Asia (Mahnken *et al.*, 1998). All Bristol Bay sockeye salmon are native. Although the interactions between hatchery pink salmon and native populations of sockeye salmon in the open ocean remain unknown, our results may raise the controversial idea that hatchery salmon production should be allocated among countries (Joyner, 1975; Bigler *et al.*, 1996; Heard, 1998).

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