

Evidence for competitive dominance of Pink salmon (*Oncorhynchus gorbuscha*) over other Salmonids in the North Pacific Ocean

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Abstract

Relatively little is known about fish species interactions in offshore areas of the world's oceans because adequate experimental controls are typically unavailable in such vast areas. However, pink salmon (*Oncorhynchus gorbuscha*) are numerous and have an alternating-year pattern of abundance that provides a natural experimental control to test for interspecific competition in the North Pacific Ocean and Bering Sea. Since a number of studies have recently examined pink salmon interactions with other salmon, we reviewed them in an effort to describe patterns of interaction over broad regions of the ocean. Research consistently indicated that pink salmon significantly altered prey abundance of other salmon species (e.g., zooplankton, squid), leading to altered diet, reduced total prey consumption and growth, delayed maturation, and reduced survival, depending on species and locale. Reduced survival was observed in chum salmon (*O. keta*) and Chinook salmon (*O. tshawytscha*) originating from Puget Sound and in Bristol Bay sockeye salmon (*O. nerka*). Growth of pink salmon was not measurably affected by other salmon species, but their growth was sometimes inversely related to their own abundance. In all marine studies, pink salmon affected other species through exploitation of prey resources rather than interference. Interspecific competition was observed in nearshore and offshore waters of the North Pacific Ocean and Bering Sea, and one study

documented competition between species originating from different continents. Climate change had variable effects on competition. In the North Pacific Ocean, competition was observed before and after the ocean regime shift in 1977 that significantly altered abundances of many marine species, whereas a study in the Pacific Northwest reported a shift from predation- to competition-based mortality in response to the 1982/1983 El Niño. Key traits of pink salmon that influenced competition with other salmonids included great abundance, high consumption rates and rapid growth, degree of diet overlap or consumption of lower trophic level prey, and early migration timing into the ocean. The consistent pattern of findings from multiple regions of the ocean provides evidence that interspecific competition can significantly influence salmon population dynamics and that pink salmon may be the dominant competitor among salmon in marine waters.

Introduction

Pink salmon (*Oncorhynchus gorbuscha*) are unique among Pacific salmon in many ways, but a key characteristic is their invariable two-year life cycle that leads to genetically distinct stocks that can differ significantly in abundance during odd- versus even-numbered years. Large alternating-year abundances of pink salmon are most apparent at the northern and southern range of the species, including the Pacific Northwest and the Russian Far East. Pink salmon grow rapidly and they are the most abundant species of Pacific salmon (Heard, 1991), therefore they have potential to significantly affect other salmon species in the ocean.

The alternating-year pattern of pink salmon abundance provides a unique natural experimental control to test for interactions between pink salmon and other species of salmon in the ocean. The natural experimental control provided by the alternating-year abundance of pink salmon is important because environmental variables in the ocean are often correlated and salmon species often respond similarly to environmental conditions. For example, all species of salmon in northern regions increased significantly after the 1977 ocean regime shift (Rogers, 1984; Beamish and Bouillon, 1993; Mantua et al., 1997). Such correlations confound attempts to evaluate the nature and importance of species interactions, such as competition, as a mechanism that regulates population abundance in offshore marine communities. Competition has been widely described in terrestrial, freshwater, and some marine communities (Schoener, 1983; Bertness et al., 2001) and some scientists have assumed that interspecific competition may influence abun-

dances of offshore marine fish populations (Cushing, 1975; National Research Council, 1999), whereas others have downplayed its importance in regulating these populations (Sinclair, 1988). Quantification of species interactions is important given the growing desire to manage marine fisheries using the concept of ecosystem management (National Research Council, 1999). This is especially important for Pacific salmon because up to five billion juvenile salmon are released from hatcheries each year (Mahnken et al., 1998), often in regions where natural salmon populations are depressed, and concern has been raised about the capacity of the ocean to support these salmon (Pearcy et al., 1999).

A number of recent investigations have utilized the natural experimental control provided by pink salmon to examine interactions between pink and other species of salmon. We reviewed these studies in an effort to document patterns of species interactions and to evaluate whether interspecific competition is an important mechanism influencing salmon population dynamics in marine waters. Since competition often involves a shortage of prey resources, we were particularly interested in competitive interactions before and after periods of climate change.

Findings

Pink salmon abundance and distribution

Pink salmon are the most abundant species of Pacific salmon, representing approximately 58% of all anadromous Pacific salmon (Rogers, 2001). Abundance of adult pink salmon in the North Pacific Ocean averaged approximately 156 million

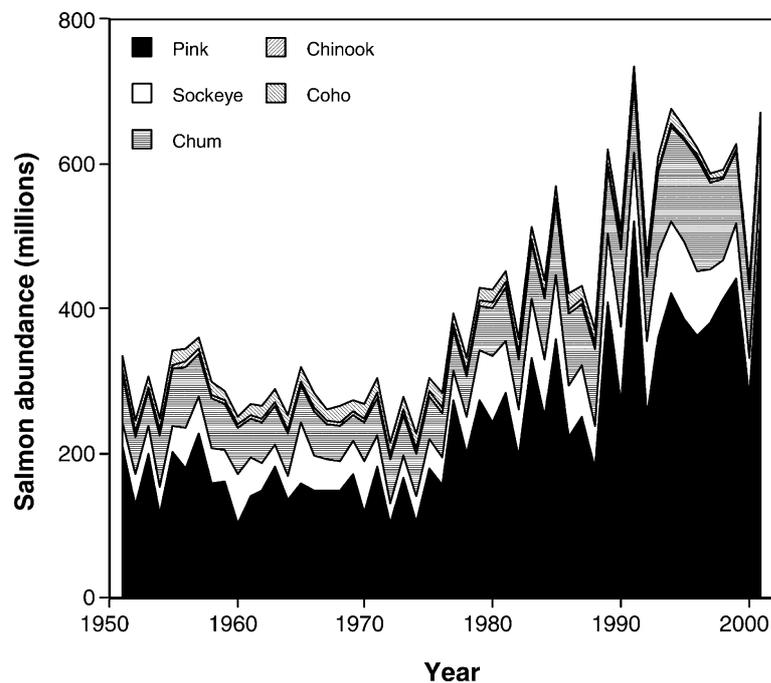


Figure 1. Time series of adult Pacific salmon abundance in Asia and North America, 1951–2001 (Rogers 1987, 2001).

fish per year during 1951–1976, increasing to 323 million fish per year during 1977–2001 (Figure 1). Asian pink salmon represented approximately 56% of the total adult return of pink salmon. In Asia, large runs of pink salmon originated from the Kamchatka Peninsula and Sakhalin Islands, whereas in North America most pink salmon originated from Kodiak Island, Alaska, south to the Fraser River in British Columbia (Heard, 1991).

Large pink salmon populations dominated by odd-year adults are located primarily at the northern and southern range of pink salmon, such as the eastern Kamchatka Peninsula and the Strait of Georgia/Puget Sound. Catch of eastern Kamchatka pink salmon is approximately 380% greater during odd- compared with even-numbered years, i.e., average 5 million fish in even-years versus 24 million fish in odd-years (Sinyakov, 1998). More than 99% of runs in Puget Sound and southern British Columbia (Fraser River) occur during odd-numbered years. Western Kamchatka historically produced primarily odd-year pink salmon runs, but the dominant run abruptly switched to even years after 1983 (Bugaev, 2002). The southeastern Bering Sea

produces relatively small runs that are dominant during even-numbered years. Regions in the central portion of the pink salmon range in North America (southeastern and central Alaska and northern British Columbia) tend to produce large pink runs in both odd- and even-numbered years.

Juvenile pink salmon enter coastal marine waters in early spring after minimal feeding in freshwater, then disperse counter-clockwise along the coast and into the North Pacific Ocean or Bering Sea (Heard, 1991). Ocean migration patterns and distribution of regional pink salmon assemblages have been described from extensive high seas tagging and sampling (Takagi, 1981; Myers et al., 1996). In general, pink salmon disperse broadly across marine waters and may travel up to approximately 7400 km during their 14–16 month stay. For example, pink salmon originating from eastern Kamchatka have the eastern-most distribution of Asian stocks, extending eastward to approximately 155°W (south of Alaskan Peninsula) and south to approximately 44°N. Pink salmon from Washington and British Columbia migrate north into the Gulf of Alaska (up to ~58°N) and westward to approximately 148°W. Thus, pink salmon

disperse broadly into the ocean, but they have little overlap with distant populations. Pink salmon, like other salmon species, typically occupy the upper 30 m of the water column (Heard, 1991).

Sockeye and pink salmon interactions

Diet overlap and prey availability

Pink and sockeye (*O. nerka*) salmon are opportunistic foragers that have similar diets in offshore marine waters (Davis et al., 2000; Kaeriyama et al., 2000, 2004). Their diet includes prey from

several trophic levels, including zooplankton and micronekton such as squid and small fishes. Stable isotope analyses demonstrated that the trophic position of pink and sockeye is similar (Welch and Parsons, 1993; Kaeriyama et al., 2004), as expected from diet data. However, during the second season at sea, pink salmon may begin foraging on larger prey, such as squid, at an earlier date in spring compared with sockeye salmon (Aydin, 2000).

Field research in the central North Pacific Ocean recently demonstrated that zooplankton

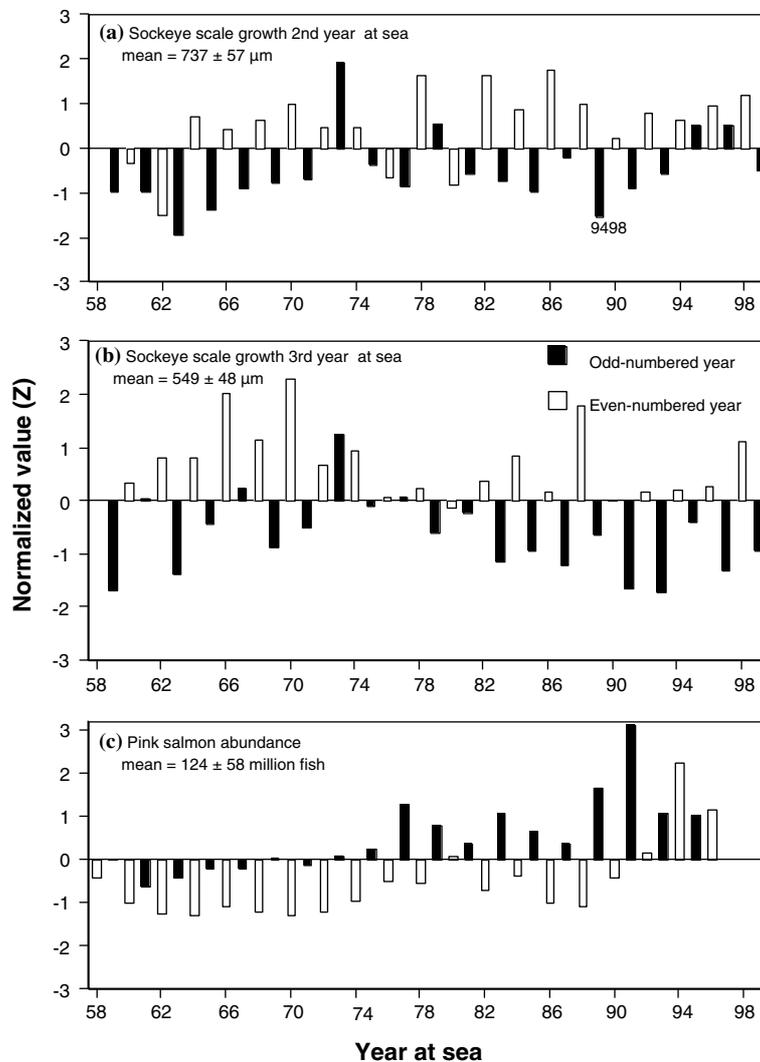


Figure 2. Bristol Bay (Egegik stock) sockeye salmon growth during the second (a) and the third growing seasons at sea (b) and the corresponding abundance of maturing Asian pink salmon (c), 1958–1999. Open bars are even years at sea, and closed bars are odd years at sea. Values are normalized, i.e., standard deviations above and below the long-term mean. Revised from Ruggerone et al. (2003) using a different stock of Bristol Bay salmon.

biomass was significantly reduced during June and July of odd-numbered years (Sugimoto and Tadokoro, 1997; Shiomoto et al., 1997). These researchers concluded that Asian pink salmon, which are abundant during odd-numbered years, had reduced zooplankton abundance over this large region. Sano (1963) reported that prey consumption of both pink and sockeye salmon in the western Pacific Ocean during May through August, 1955–1962, significantly declined during odd-numbered years, corresponding to years when Asian pink salmon were most abundant. The reduction in total prey weight (primarily squid and euphausiids by both species) consumed by sockeye salmon during odd-numbered years (61% reduction) was greater than that of pink salmon (52% reduction). During 1991–2000, stomach contents of pink and sockeye salmon collected in the central Bering Sea declined 24 and 36%, respectively, during odd-numbered years (high pink salmon abundance) (Davis, 2003; Ruggerone et al., 2003). However, two key prey of both species (squid and fish) declined more in sockeye salmon (27% reduction) than in pink salmon (7% reduction), suggesting pink salmon were more efficient at exploiting key prey.

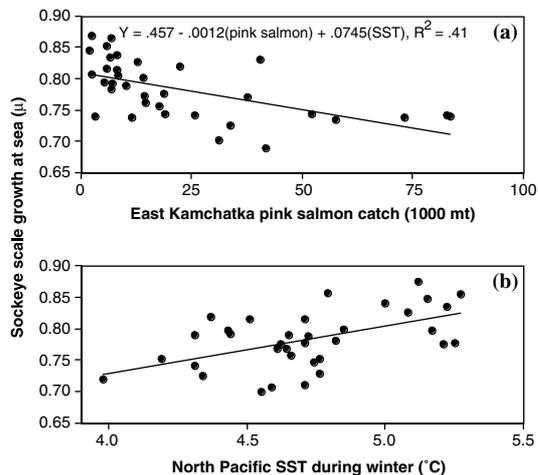


Figure 3. Multi-variate analysis showing the partial effects (Larsen and McCleary, 1972) of pink salmon abundance (A) and winter sea surface temperature (SST; B) on second-year scale growth of Bristol Bay sockeye salmon, 1966–2000. Sockeye scale growth (μ) = $0.457 - 0.0012$ (pink salmon catch) + 0.0745 (temperature); $R^2 = 0.41$, overall $P < 0.001$, P (pink salmon catch) < 0.001 , P (SST) < 0.002 ; P (autocorrelation of residuals at lags 1–10) > 0.05 . Ruggerone, unpublished data.

Bristol Bay, Alaska

Ruggerone et al. (2003) provided evidence that Asian pink salmon, primarily those from the eastern Kamchatka Peninsula, reduced the growth and survival of Bristol Bay, Alaska, sockeye salmon. Annual sockeye salmon scale patterns, 1955–2000, exhibited an alternating-year pattern of growth during the second and third years at sea that was opposite that of Asian pink salmon abundance, which was 56% greater in odd-numbered years (Figure 2). Sockeye growth during the first growing season at sea was not reduced because overlap with Asian pink salmon did not begin until the second season at sea and relatively few pink salmon originate in Bristol Bay. Ruggerone and Nielsen conducted a multi-variate regression analysis and found that scale growth of Bristol Bay sockeye during the second year at sea, 1966–2000, was negatively associated with harvests of eastern Kamchatka pink salmon ($P < 0.001$), but positively associated with winter sea surface temperature in the North Pacific Ocean ($P < 0.002$; Figure 3). This finding suggests pink salmon abundance influenced year-to-year variation in sockeye salmon growth whereas sea-surface temperature influenced the long-term trend in early marine growth shown in Figure 2.

Age-specific length of adult sockeye salmon returning to Bristol Bay, 1958–2000, was inversely

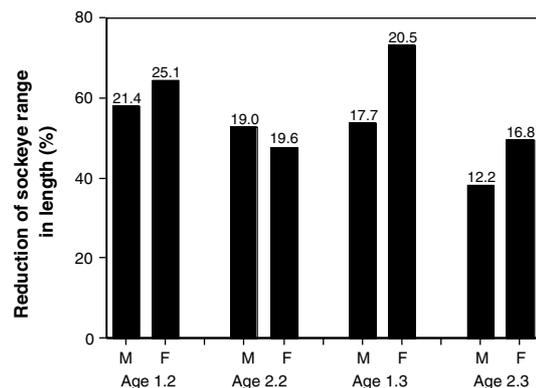


Figure 4. Effect of maximum Asian pink salmon abundance on the observed range in Bristol Bay sockeye lengths during 1958–2000. Maximum effect of Asian pink salmon abundance based on sockeye length change when pink salmon abundance increase from zero to 300 million pink salmon. Estimates based on empirical models of sockeye length (age and sex) presented by Ruggerone et al. (2003). Values at top of each bar are the estimated reduction in sockeye length (mm) associated with maximum pink salmon run.

related to Asian pink salmon abundance during the year prior to homeward migration (Ruggerone et al., 2003). This pattern was consistent among all four major age groups and both sexes of sockeye salmon. Pink salmon tended to have the greatest effect on growth of younger age groups (e.g., ages 1.2 and 2.2) and female salmon. Using the empirical relationships between sockeye length and pink salmon abundance described by Ruggerone et al. (2003), we calculated the maximum potential effect of Asian pink salmon on sockeye length (i.e., sockeye length during maximum versus zero pink abundance) using the approach described by Bugaev et al. (2001). A change from zero to maximum Asian pink salmon abundance may account for up to approximately 38–73% of the observed range in mean Bristol Bay sockeye length, depending on age and sex (Figure 4). Although these analyses demonstrated pink salmon could exert a significant effect on size of Bristol Bay sockeye salmon, the multi-variate analyses indicated that intraspecific competition during the homeward migration had a greater effect on sockeye salmon size.

Ruggerone et al. (2005) examined seasonal scale growth patterns of Bristol Bay sockeye salmon in relation to pink salmon abundance during 1955–2000. They demonstrated that the reduction in salmon growth observed during the second and third years at sea (Figure 2) began immediately after peak prey availability in spring and continued to the end of the growing season, well after pink salmon had left the high seas. The researchers noted that prey population dynamics that influenced the observed alternating-year pattern in sockeye growth are poorly understood. They hypothesized that high consumption rates of pink salmon during spring through mid-July of odd-numbered years, coupled with declining zooplankton biomass during summer (Mackas and Tsuda, 1999; Batten et al., 2003) and potentially cyclic abundances of squid (Sobolevsky, 1996; Nesis, 1997), contributed to reduced prey availability and to reduced growth of Bristol Bay sockeye salmon during spring through fall of odd-numbered years.

A key finding of recent pink/sockeye interaction research was that reduced growth of Bristol Bay sockeye salmon during odd-numbered years was associated with a significant reduction in smolt-to-adult survival during 1977–1997 (Ruggerone et al., 2003).

This analysis was based on annual estimates of salmon smolts that migrated to sea during odd- versus even-numbered years and subsequent age-specific returns of adult salmon. On average, smolt survival declined 35% (from 18.6 ± 3.1 (SE) to $12.1 \pm 2.5\%$ survival) when they entered Bristol Bay in even-numbered years and competed with Asian pink salmon during their second year at sea (odd-numbered year). Younger age-1.2 sockeye salmon experienced the greatest reduction in survival (59%), age-1.3 and age-2.2 experienced intermediate reduction in survival (30%), and the older age-2.3 salmon experienced the least reduction in survival (19%) when interacting with Asian pink salmon during their second season at sea. Some of the reduction in ocean age-2 sockeye salmon may be explained by delayed maturation associated with reduced growth, but analyses demonstrated that overall mortality was greater when sockeye interacted with abundant pink salmon during their second season at sea. It was hypothesized that reduced growth during spring through fall of the second growing season at sea led to greater mortality during winter when demand for prey can exceed prey availability (Nagasawa, 2000; Beamish and Mahnken, 2001; Ruggerone et al., 2005).

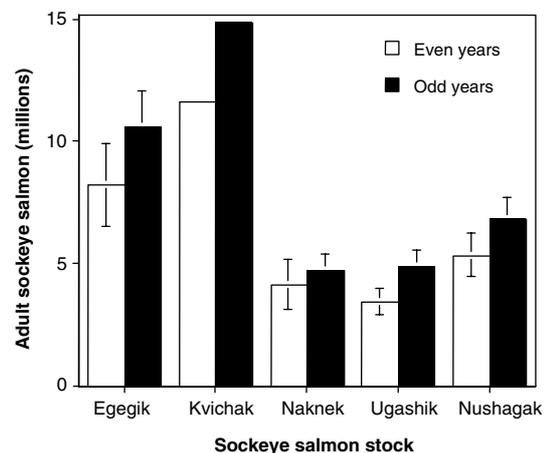


Figure 5. Comparison of adult Bristol Bay sockeye salmon stocks returning from smolts entering the ocean during odd- versus even-numbered years (means \pm 1 SE), 1977–1997 (updated from Ruggerone et al., 2003). Sockeye salmon entering ocean during even-numbered years began their interaction with relatively abundant odd-year pink salmon during first winter at sea. Adult returns of Kvichak salmon is strongly influenced by the five-year spawning cycle, therefore the mean reduction from other stocks (22%) was applied to Kvichak returns.

The findings of the smolt-to-adult survival analysis were further supported by an analysis of age-specific adult sockeye salmon returns to Bristol Bay. This analysis included stocks that did not have annual smolt enumeration programs. Adult returns were compared based on whether they entered the Bering Sea as smolts during odd- versus even-numbered years. Adult returns of four major sockeye salmon stocks declined 22% (from 6.76 ± 0.59 to 5.29 ± 0.62 million fish per stock), on average, during 1977–1997, when they competed with abundant odd-year pink salmon during their second season at sea (Ruggerone et al., 2003). This effect represented a cumulative loss of 59 million adult sockeye salmon, excluding the Kvichak River stock whose returns are strongly influenced by a five-year spawning cycle. In light of previous findings that most salmon mortality at sea occurs during early marine life (Pearcy, 1992), it is noteworthy that the analyses of Bristol Bay adult sockeye return data and smolt-to-adult survival data indicate significant mortality also occurred during the second year at sea.

The Kvichak sockeye salmon stock is a major component of the Bristol Bay salmon population and survival of Kvichak smolts was significantly reduced when they interacted with odd-year pink salmon (Ruggerone et al., 2003). Therefore, we applied the average reduction in adult returns to Bristol Bay (22%) to the average adult return of Kvichak salmon (average 13.25 million salmon per year) in order to calculate the cumulative total loss of Bristol Bay sockeye salmon. This analysis indicated approximately 32.8 million fewer adult Kvichak sockeye salmon returned to Bristol Bay when interacting with odd-year pink salmon during their second season at sea, 1977–1997. The total reduction in Bristol Bay sockeye salmon abundance associated with odd-year Asian pink salmon was approximately 91.8 million fish during 1977–1997 (Figure 5). Thus, Asian pink salmon abundance, including the 380% increase in eastern Kamchatka pink salmon abundance between even- and odd-numbered years, was associated with a 35% reduction in sockeye smolt-to-adult survival and a 22% reduction in adult returns.

Prior to the ocean regime shift in 1977, no effect of competition on Bristol Bay sockeye abundance was detected from an analyses of adult returns even though growth reduction was observed (Ruggerone et al., 2003). Harris (1989) noted that

many Bristol Bay salmon were harvested on the high seas during this early period and were not counted in Bristol Bay catch statistics. Thus, it is possible that catches of salmon on the high seas by international fisheries confounded the analysis prior to 1977.

Kamchatka, Russia

Asian pink salmon have been shown to have a significant adverse effect on the growth of Russian sockeye salmon (Krogus 1964, 1967; Bugaev et al., 2001). Bugaev et al. (2001) examined age and sex-specific mature body weights of Ozernaya River sockeye salmon (eastern Kamchatka Peninsula), 1970–1994, and found that weight of sockeye salmon was inversely related to abundances of local eastern and western Kamchatka pink and sockeye salmon. They estimated that an increase in Kamchatka pink salmon from zero fish to average abundance (~75 million fish) would cause a 20% reduction in sockeye body weight, whereas an increase from zero fish to the peak observed pink salmon run (~170 million fish) could reduce body weight of some sockeye age groups up to 50%. Although the relationships were weak, Bugaev et al. (2001) suggested that on a per capita basis sockeye salmon had a greater effect on sockeye weight than pink salmon, but that pink salmon ultimately had a greater effect on sockeye salmon because pink salmon were much more abundant.

Krogus (1967) examined annual scale patterns of sockeye salmon collected from the Ozernaya River, 1945–1957, and reported scale growth at sea was inversely related to pink salmon abundance. He hypothesized that competition for food was greatest during mid-summer and thereafter when prey availability was less. This hypothesis was recently substantiated by analyses of seasonal scale growth patterns of Bristol Bay sockeye salmon in which growth reduction began immediately after peak scale growth in spring (Ruggerone et al., 2005). However, the alternating-year growth pattern of Ozernaya sockeye salmon was not consistent for all age groups of salmon, leading Krogus to suggest sockeye migration patterns varied among the groups. Although somewhat speculative, he further suggested that increased high seas fishing effort on pink salmon during the study period led to greater growth of sockeye salmon as a

result of less competition. Similar findings of interactions with pink salmon were found for Lake Dalnee (eastern Kamchatka Peninsula) sockeye salmon (Krogius, 1964).

Bugaev and Dubynin (2000) examined a variety of factors potentially affecting the abundance of adult Ozernaya River sockeye salmon, 1976–1998, and hypothesized that Kamchatka pink salmon negatively influenced sockeye abundance. More recently, Bugaev (2002) commented on the potential relationship between an 88% increase in Asian sockeye salmon abundance and the sudden collapse in 1985 of odd-year pink salmon runs in western Kamchatka (97% reduction from approximately 60 million pink salmon during 1975–1983). The pink salmon collapse appeared to be influenced by the exceptionally large spawning escapement and overcrowded spawning grounds in 1983 (~110 million spawners). Since 1983, even-year pink salmon runs to western Kamchatka increased substantially to approximately 61 million salmon per year and odd-year runs declined to less than two million fish per year. In eastern Kamchatka during this same period, odd-year runs of pink salmon increased from approximately 40 to 72 million salmon whereas even-year runs increased only slightly from 11 to 15 million salmon. Annual Kamchatka pink salmon abundance increased approximately 5% from 1976–1983 to 1984–1998. Bugaev hypothesized that the recent de-synchronization of the western and eastern Kamchatka pink salmon runs led to greater growth and survival of Kamchatka sockeye salmon because Kamchatka pink salmon are presently spread between both odd- and even-year lines rather than concentrated in the odd-year line.

In contrast to the hypothesis suggested by Bugaev, there is evidence that the significant shift in Kamchatka pink salmon abundance may have influenced the recent decline of Bristol Bay sockeye salmon that began with the 1991 brood year. Abundance of eastside Bristol Bay salmon (Kvichak, Naknek, Egegik, Ugashik stocks) declined 48% during brood years 1991–1998 compared with those in 1973–1990 (Ruggerone, unpublished analysis). Coincidentally, the 1991 brood year produced age-1 smolts that entered Bristol Bay in 1993 and competed with Asian pink salmon in 1994, the year that marked the beginning of rela-

tively large runs of both odd- and even-year pink salmon. Instead of competing primarily with odd-year pink runs, eastside Bristol Bay sockeye salmon have been competing with continuously large Kamchatka pink salmon runs since the early 1990s. In contrast with eastside Bristol Bay salmon, westside Bristol Bay sockeye salmon (Nushagak District, Togiak stocks), whose ocean distribution is further east and overlaps less with Asian pink salmon (Rogers, 1987; Myers, 1997), increased slightly in abundance (17% increase). Further research is necessary to determine the validity of these hypotheses.

British Columbia

In contrast to the aforementioned studies, Peterman (1982) reported that smolt-to-adult survival of Babine Lake (British Columbia) sockeye salmon was positively correlated with the abundance of pink salmon fry entering the ocean with juvenile sockeye salmon, 1961–1978. He hypothesized that juvenile pink salmon, which were similar in size to sockeye smolts in marine waters, may have swamped predators. However, sockeye salmon survival was also inversely related to adult pink salmon abundance, suggesting adult pink salmon might be a potential predator or possibly a competitor species. No data were collected from the marine waters to test these competing hypotheses.

Chum and pink salmon interactions

Diet overlap and prey availability

Pink and chum salmon (*O. keta*) have similar life histories during early marine life and both species can be highly abundant. Pink salmon enter marine waters after minimal feeding or rearing in fresh and estuarine waters, whereas chum salmon feed briefly on freshwater and estuarine prey before entering nearshore marine areas (Healey, 1980; Heard, 1991). Chum salmon tend to enter nearshore marine areas after pink salmon, but both species rear in nearshore waters for weeks to months before moving offshore. In the Pacific Northwest, large and small mixed-species schools of chum and pink salmon have been observed (Heard, 1991). Juvenile pink and chum salmon are opportunistic foragers and their diet can be similar

in coastal waters (Kaczynski et al., 1973; Beacham and Starr, 1982; Duffy, 2003).

Diet of chum salmon can be altered by pink salmon in offshore marine waters. Sano (1963) reported that total prey weight consumed by chum salmon in the Western North Pacific Ocean during May through August, 1955–1962, was approximately 27% lower during odd-numbered years when pink salmon were abundant. Ivankov and Andreyev (1971) reported that feeding rates of immature chum salmon near the Kuril Islands were lower in years of high juvenile pink salmon abundance. Tadokoro et al. (1996) examined the diet of pink and chum salmon from the Bering Sea and central North Pacific Ocean during June and July and reported that dominant prey of chum salmon changed from gelatinous zooplankton (pteropods, appendicularians, jellyfishes, etc) in 1991 when numerous pink salmon were present to

crustaceans (euphausiids, copepods, amphipods, etc.) and some micronekton (squid and fish) in 1992 when few pink salmon were present. Local biomass of crustaceans in 1991 was inversely related to catch per effort of pink salmon, further indicating pink salmon reduced prey availability. In 1992, crustacean biomass was inversely related to chum salmon abundance, indicating intraspecific competition was also important. Other researchers have documented a shift in the diet of chum toward less nutritional prey in years of high pink salmon abundance (Salo, 1991). On the high seas, chum salmon appear to minimize competition with pink and sockeye salmon by consuming gelatinous zooplankton that are seldom consumed by other salmon (Welch and Parsons, 1993; Azuma, 1995).

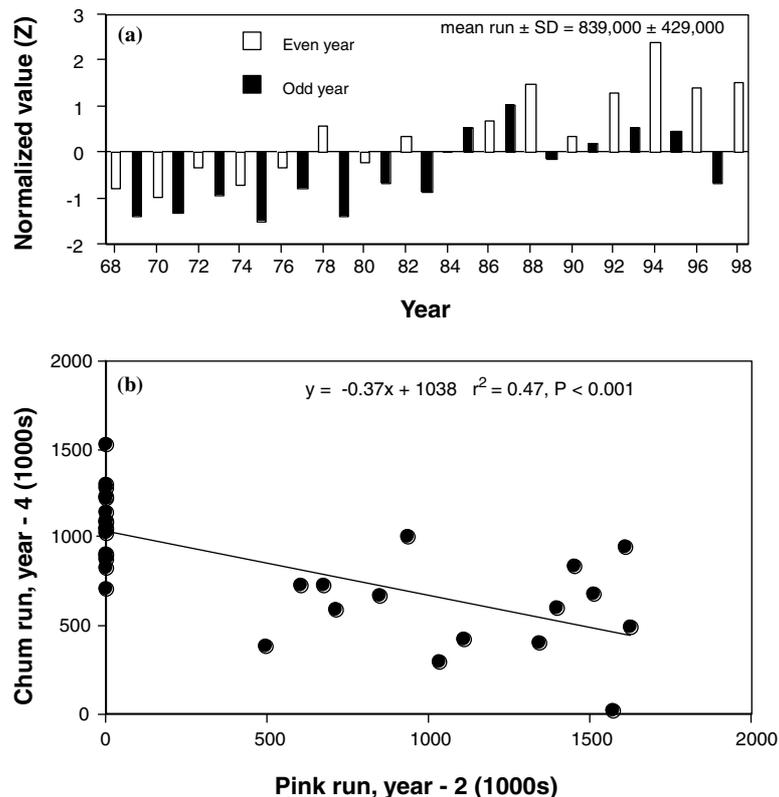


Figure 6. Time series of normalized Puget Sound chum runs during even- (few pink salmon) versus odd-numbered years, 1968–1998 (a), and the relationship between standardized Puget Sound chum and pink salmon runs (b). Chum and pink salmon runs standardized to the level in 1979 (time series mid-point) because both runs increased over time. Pink and chum runs lagged back in time to parent spawning year, i.e., four years for chum salmon (Gallagher, 1979) and two years for pink salmon. Run size data provided by J. Packer, Washington Department Fish and Wildlife, Olympia, WA.

Pacific Northwest

Phillips and Barraclough (1978) reported that chum salmon fry in the Strait of Georgia near the Fraser River estuary were larger in 1967 and 1969 (when pink salmon fry abundance was low) compared with those in 1966 and 1968 (when pink salmon fry were abundant), indicating consumption of prey by chum fry was reduced by pink salmon. Pratt (1974) reported that adult chum salmon in Puget Sound, 1954–1970, were smaller when they returned with the abundant odd-year pink salmon. Thus, during odd-numbered years in the Pacific Northwest, growth of juvenile chum salmon was greater (few juvenile pink salmon present), whereas size of adult chum salmon was less (numerous adult pink salmon present).

In Puget Sound and the Fraser River, large odd-year runs of adult pink salmon produce large numbers of pink salmon fry that enter marine waters in even-numbered years. Adult abundance, productivity (return per spawner), and survival of chum salmon is reportedly lower when juvenile chum salmon enter Puget Sound and Strait of Georgia in even-numbered years with numerous juvenile pink salmon (Gallagher, 1979; Beacham and Starr, 1982; Salo, 1991; Fresh, 1997). For example, during 1968–1998, adult chum salmon returns to Puget Sound exhibited an alternating-year pattern and their abundance was inversely correlated with pink salmon abundance (Figure 6). Beacham and Starr (1982) reported that fry-to-adult survival of Fraser River chum salmon declined 44% (from 1.53 to 0.85% survival) when they entered marine waters in even-numbered years with numerous juvenile pink salmon, 1961–1979. Beacham and Starr (1982) also reported that survival of chum salmon was greater when the median downstream migration timing of chum fry was earlier relative to pink salmon. Early migration timing appeared to reduce competition with pink salmon, thereby enhancing survival.

The odd/even year cycle of chum salmon abundance in the Pacific Northwest is maintained, in part, by a regular alteration in the age-at-maturity that appears to be an evolutionary response to competition with pink salmon (Gallagher, 1979; Smoker, 1984). In Puget Sound, odd-year broods of chum salmon, which produce fry that compete with numerous pink salmon fry, mature at a 50:50 ratio of age-3 and age-4 adult salmon (Salo, 1991). In contrast, even-year

broods, whose fry experience little competition, produce approximately 35% age-3 and 65% age-4 chum salmon. Chum salmon returning to the Fraser River also exhibit this pattern of maturation. This unique pattern of maturation by chum salmon, along with a reduction in survival of odd-year broods, led to a greater number of adult chum salmon returning during even-numbered years. Progeny of these adults experienced less competition with pink salmon and greater survival.

Smoker (1984) used a simulation modeling approach to examine whether the alternating age of maturation of Puget Sound chum salmon was related to environmental versus genetic factors. He concluded that age-at-maturation was highly heritable and that genetic factors led to the alternating pattern of maturity in response to competition with odd-year pink salmon. This finding suggests competition may have been a significant factor for many generations, leading to a genetically influenced pattern of maturation that reduced competition. A key assumption in this analysis was that differences in age and size of chum salmon originating from odd- versus even- brood years led to little interbreeding between the two brood lines. It is noteworthy that the alternating-year pattern of chum salmon abundance was consistent before and after the 1982/1983 El Niño event that appeared to mark a shift in the interaction between pink salmon and Puget Sound Chinook salmon (see below). This consistency might reflect the influence of genetics on altering age-at-maturation as suggested by Smoker. “Alternatively, greater survival of even-year brood chum salmon in response to pink salmon and greater intraspecific competition among chum salmon at older life stages might have led to delayed maturation and the observed alternating-year pattern of chum run size.”

No pink salmon are produced along the Oregon and Washington coasts, yet chum salmon stocks exhibit an alternating-year pattern of run size and age at maturity (Salo, 1991). For example, our updated analysis indicated chum salmon abundance in the Columbia River was 50% greater during even- compared with odd-numbered years, 1960–2000 ($df = 1, 39$; $F = 4.88$, $P = 0.033$; data source: ODFW/WDFW, 2002). The cyclic pattern of chum abundance was consistent throughout the 40-year period and did not change in response to climate patterns. The pat-

tern of chum salmon abundance, which is consistent with Puget Sound and Fraser River chum salmon populations, might be explained by either a lingering genetic effect (Smoker, 1984) established when pink salmon were possibly abundant in this area or by competition with pink salmon in the ocean after chum salmon migrate north. Further research is needed to isolate the cause of this pattern of abundance in chum salmon along the Oregon and Washington coasts.

Kamchatka, Russia

Sinyakov and Ostroumov (1998) evaluated the return per spawner of northeast Kamchatka pink salmon, 1957–1993, as a means to predict adult returns of chum salmon to this region. They suggested that interspecific competition between pink and chum salmon was much less important than intraspecific competition and that environmental factors during spawning, downstream migration, and marine periods similarly affected pink and chum salmon. The researchers did not evaluate alternating-year age-at-maturation.

North Pacific Ocean

The shift in the diet of chum salmon in the North Pacific Ocean in response to pink salmon (see previous discussion) may affect growth of chum salmon. Walker and Myers (1998) examined scale growth of chum salmon collected south of the Aleutian Islands and concluded that chum growth during their third year at sea was inversely related to both Asian pink and chum salmon abundances. The inverse correlation between chum scale growth and Asian pink salmon abundance was observed before and after the 1977 regime shift. Competition with Asian pink salmon was not apparent during the first two years at sea.

Azumaya and Ishida (2000) examined the density and distribution of chum salmon in relation to pink salmon density in the North Pacific and Bering Sea using monthly gill net operations, 1972–1998. They reported that the distribution patterns of chum salmon in offshore waters shifted between even- and odd-numbered years and was opposite that of pink salmon density. Chum salmon were concentrated to the west in even-numbered years and were relatively abundant in the Bering Sea (i.e., years of low Asian pink salmon abundance in this region). During odd-numbered

years, when pink salmon were abundant in the Bering Sea, density of chum salmon declined in the Bering Sea and increased in the eastern North Pacific Ocean. In contrast to findings of other studies, Azumaya and Ishida (2000) reported that age-specific growth of chum and pink salmon (change in mean length from year to year) was not related to the density of the other species, but growth was dependent on abundance of conspecifics. The authors suggested that growth of chum salmon was indirectly influenced by pink salmon because pink salmon altered the distribution of chum salmon, leading to high densities of chum salmon in specific ocean regions and density-dependent growth.

Laboratory study

Beacham (1993) conducted a laboratory study in order to evaluate competition between pink and chum salmon fry in a controlled environment. In contrast to the aforementioned studies, he found that mean weight and survival of chum salmon did not decline in response to increasing density of pink salmon. Instead, weight of pink and chum fry declined in response to increasing density of chum salmon. The results of this experiment may have been influenced by relatively large size of chum salmon (50% larger than pink salmon) and the low daily growth of pink salmon in the aquaria under monoculture and multiple species conditions. This experiment highlighted the influence of body size on species interactions.

Chinook and pink salmon interactions

Diet overlap

Juvenile and immature Chinook salmon (*O. tshawytscha*) are opportunistic in their prey selection, but they tend to feed on higher trophic level prey at earlier life stages compared with pink salmon, based on diet (Brodeur, 1990) and stable isotope analyses (Welch and Parsons, 1993; Kaeriyama et al., 2004). Some diet overlap exists between juvenile pink and Chinook salmon that recently enter marine waters, but it is much less than that between pink and chum salmon (Healey, 1980, 1991; Duffy, 2003). In the Pacific Northwest, the size of juvenile pink and subyearling Chinook salmon do not differ significantly at the time chinook enter marine waters since pink fry have been growing in marine areas for weeks to months.

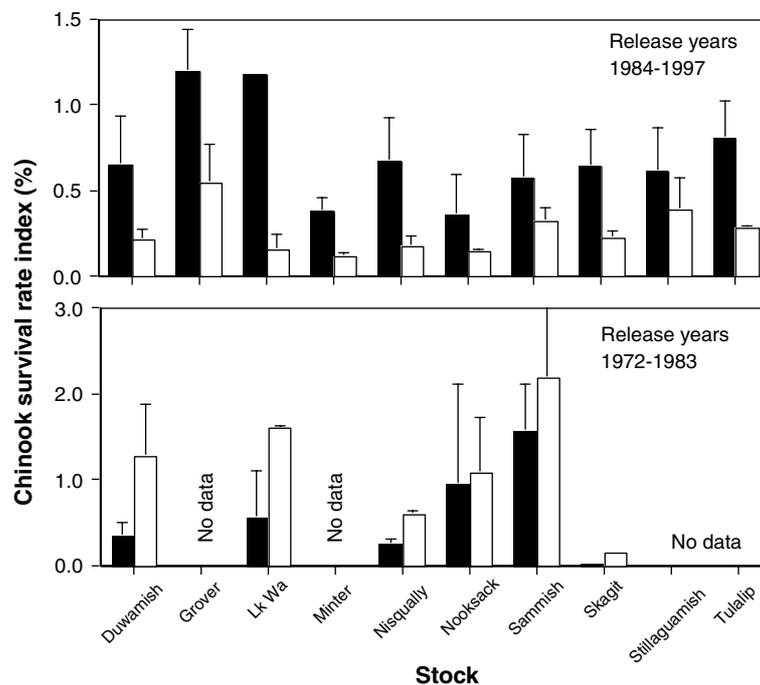


Figure 7. Release to recovery survival of coded-wire-tagged subyearling chinook salmon released into 10 Puget Sound watersheds during odd (■) and even (□) numbered years. Survival analysis split into periods before (lower graph) and after the 1982/1983 El Nino (upper graph), which led to significant changes in the marine environment (Pearcy, 1992). Values are mean + 1 standard error. Figure reproduced from Ruggerson and Goetz (2004) by permission.

Pacific Northwest

In the Pacific Northwest, where adult pink salmon are highly abundant in odd-numbered years, the release of 53.5 million coded-wire-tag (CWT) Chinook salmon was used to examine potential competition between subyearling pink and Chinook salmon (Ruggerson and Goetz, 2004). Coded-wire-tagged subyearling Chinook salmon released into streams and entering Puget Sound during even-numbered years experienced 62% lower survival than those entering the sea during odd-numbered years, 1984–1997 (Figure 7). This pattern was consistent for 10 Puget Sound stocks (range: 36–86% survival reduction depending on stock) and three lower mainland British Columbia stocks near the Fraser River (45–61% survival reduction). Analysis of age-specific recovery rates of Chinook salmon indicated that lower survival from even-year releases was established during the first year at sea. Furthermore, Chinook salmon entering Puget Sound and the eastern Strait of Georgia with numerous juvenile pink salmon in even-numbered years experienced significantly reduced growth during the first year at sea (aver-

age 17 mm reduction among survivors) and delayed maturation (average 12% increase in age-4 and older salmon). In contrast, few pink salmon originate from streams along coastal Washington and lower Vancouver Island and survival of tagged Chinook salmon released into these streams (9 stocks) did not vary between even- and odd-numbered years ($P > 0.05$). The lack of an alternating-year pattern in coastal stocks and the observation that growth and survival of Chinook salmon were reduced during the first year at sea indicates survival and growth were primarily influenced in Puget Sound and the lower Strait of Georgia.

The survival pattern of Puget Sound Chinook salmon in relation to pink salmon appeared to be influenced by climate-induced changes in the marine environment. During 1972–1983 and immediately prior to the exceptional 1982/1983 El Nino (Pearcy, 1992), the odd/even year survival pattern of Puget Sound Chinook salmon tended to be opposite that during 1984–1997 (Ruggerson and Goetz, 2004; Figure 7). Prior to the 1982/1983 El Nino, sea surface temperatures along the coast

were relatively cool, upwelling was more frequent, prey availability was greater, and Puget Sound Chinook salmon experienced relatively high survival when they entered Puget Sound with numerous juvenile pink salmon. The researchers provided evidence that salmon predators and prey in the Puget Sound region were much more abundant during 1972–1983. They hypothesized that prior to the 1982/1983 El Niño, growth of juvenile Chinook salmon was relatively high and pink salmon provided a buffer to abundant predators rather than competition for prey.

The investigation of pink and Chinook salmon interactions in the Puget Sound region provided evidence that climate can alter predator-prey interactions and competition between species (Ruggerone and Goetz, 2004). From 1972–1983 to 1984–1997, Chinook survival in Puget Sound declined 50%, juvenile herring (Chinook prey) and piscivorous seabird abundance declined substantially (PSWQAT, 2002), but pink salmon abundance nearly doubled. A factor contributing to competition and the inverse relationship between pink and Chinook salmon was believed to be the observed earlier peak zooplankton production during the recent period (Bornhold, 1999) that favored early-arriving juvenile pink salmon over Chinook salmon. Ruggerone and Goetz (2004) suggested that the primary mortality source for Chinook salmon switched from predators to competitors in response to climate change and associated changes of marine species in the Puget Sound region.

Kamchatka, Russia

Grachev (1967) analyzed annual and seasonal scale patterns of stream-type Chinook salmon returning to the Kamchatka River, Russia, 1935–1955. The translated manuscript indicated that scale growth was inversely related to pink salmon abundance during the first and second growing seasons at sea, but not during subsequent years. Growth of juvenile Chinook salmon in their first ocean year was less during even-numbered years, corresponding with abundant juvenile pink salmon produced by the dominant odd-year broods (Sinyakov 1998). During the second year at sea, chinook growth was reportedly greater during odd-numbered years, a trend that was opposite that observed in Bristol Bay sockeye salmon (Ruggerone et al., 2003) and opposite that of

Chinook salmon captured in the central Bering Sea during the 1990s (K. Myers, unpublished data, University of Washington, personal communication). Although there were some inconsistencies in the translated manuscript, the findings suggest Kamchatka Chinook salmon may be distributed westward of most Asian pink salmon during their second growing season.

Coho and pink salmon interactions

Coho salmon (*O. kisutch*) feed at a higher trophic level (e.g., fishes and squid) than pink salmon during the first season at sea, but diet overlap increases during the second season as pink salmon switch to larger prey such as fish and squid (Brodeur, 1990; Ogura et al., 1991). Stable isotope ratios suggested some overlap in the trophic level of pink and coho salmon (Welch and Parsons, 1993; Kaeriyama et al., 2004). Consistent with the observation of diet overlap during the second growing season, Ogura et al. (1991) reported that final year growth rates of coho salmon were lower in years of high pink salmon abundance (odd-numbered years) in the western North Pacific Ocean. We are aware of no other studies that examined interactions between pink and coho salmon in the marine environment.

Intraspecific competition

Pink salmon are highly abundant and their rapid migration and dispersal as fry from streams through the estuary and into nearshore marine waters may be a mechanism to minimize intraspecific competition during early life. In offshore waters of the Bering Sea and central North Pacific Ocean, reduced consumption of prey and alteration of diet has been documented during odd-numbered years when pink salmon abundance is great (Tadokoro et al., 1996; Davis, 2003). Walker and Myers (1998) examined scale growth of pink salmon collected south of the Aleutian Islands and found second year scale growth was density-dependent prior to the 1977 climate shift when zooplankton and pink salmon abundance was less (Brodeur and Ware, 1992; Mantua et al., 1997). After 1977, when salmon abundance and prey production was relatively great, Walker and Myers found that both first and second year growth were positively correlated with pink salmon abundance.

This analysis included both even- and odd-year lines of pink salmon, which may have confounded density-dependent relationships. After excluding the genetically distinct and smaller even-year pink salmon (see below), Azumaya and Ishida (2000) demonstrated that size of odd-year pink salmon in the Bering Sea was inversely related to their abundance during 1973–1997. We examined average weight of odd-year adult pink salmon in Puget Sound, 1959–1999, and found that their weight was inversely related to total abundance of pink salmon returning to the Fraser River and Puget Sound ($n = 21$, $P = 0.013$, $R^2 = 0.28$).

The relationship between pink salmon growth and density may be confounded by the unique genetic characteristic of odd- versus even-year pink salmon, which are genetically distinct (Heard, 1991). For example, Azumaya and Ishida (2000) documented that length of pink salmon in the Bering Sea during July was significantly greater during odd-numbered years when pink salmon were highly abundant compared with length in even-numbered years (few smaller-sized pink salmon were captured in even years). These authors attributed greater size of odd-year pink salmon to genetic factors. Heard (1991) reviewed adult size of pink salmon from North America and concluded that the odd-year line of pink salmon tended to be larger than the even-year line. This pattern was consistent in areas where odd-year pink salmon were dominant (e.g., Puget Sound) and in areas where both odd- and even-year pink salmon were relatively abundant (e.g., central and northern British Columbia). In contrast, in some areas of Russia, pink salmon size was inversely related to abundance (Heard, 1991).

Birman (1976) argued that the two-year life cycle of abundance shown by pink salmon and other salmon species in Russia was related to a variety of factors other than interspecific competition. Birman (1976) suggested that abundances of zooplankton and salmon in the North Pacific Ocean was related, in part, to two-year cycles in ocean currents and wind, which in turn were influenced by a two year solar cycle. He also suggested that a two-year cycle in river flows influenced pink and chum salmon in the Amur River, Russia, and interactions between seaward migrating juvenile salmon and returning adults maintained two-year cycles of abundance. We are not

aware of other studies that support Birman's ideas on two-year cycles in the North Pacific Ocean.

The genetically distinct odd- and even-year lines of pink salmon can lead to significantly different levels of abundance that is maintained, in part, by the invariable two-year life cycle of pink salmon. Ricker (1962) and Heard (1991) reviewed possible mechanisms that might lead to dominance of one line. Potential mechanisms included compensatory mortality where small populations suffer disproportionately greater mortality, compensatory fishing, cannibalism of adults on juvenile pink salmon, fouling of the spawning grounds by dead eggs produced by the dominant line, and food competition. Ultimately, Ricker could find no strong evidence for any single mechanism and suggested that multiple factors likely interact to develop and maintain dominance. It is noteworthy that considerable attempts to establish or enhance off-year lines of pink salmon through supplementation have failed (Heard, 1991). It is also noteworthy that the off-year line in western Kamchatka rebounded immediately following the collapse of the dominant odd-year line in response to significant over-crowding of the spawning grounds (Bugaev, 2002). These findings suggest that the odd-year line was somehow suppressing the even-year line, but not by fouling of the spawning grounds or cannibalism. Intraspecific competition remains a possible mechanism leading to dominant pink salmon cycles, possibly by influencing cyclic patterns in production of prey species at critical early life stages (Ruggerone et al., 2005).

Interactions with pink salmon in freshwater

Juvenile pink salmon spend little time in freshwater habitats prior to migrating to sea (Heard, 1991), therefore effects of competition with other species in fresh water is likely negligible. However, as described below, several studies indicate pink salmon benefit other salmon species, primarily by providing an important source of food.

A variety of studies have documented significant predation on pink salmon as they migrate down river to marine waters (Heard, 1991). Coho salmon, steelhead (*O. mykiss*), cutthroat trout (*O. clarki clarki*), and char (*Salvelinus* spp.) are key predators that benefit from the abundance of pink salmon fry. Pink salmon fry are also consumed by other salmonids in nearshore marine waters.

In the Skagit River, Washington, the adult return per spawner of coho salmon was positively correlated with pink salmon spawners co-occurring with subyearling life stage coho salmon (Michael, 1995). Juvenile coho salmon reportedly consumed pink salmon eggs and flesh of carcasses, leading to greater growth and survival.

In the Keogh River, British Columbia, steelhead smolt abundance and size were positively correlated with the abundance of spawning pink salmon during the previous fall (Ward and Slaney, 1988). During the fall, steelhead parr fed intensively on dislodged pink salmon eggs and possibly carcasses, leading to enhanced growth and survival in freshwater. Steelhead survival at sea was positively correlated with smolt size, suggesting that consumption of pink salmon in streams also had a beneficial effect on survival at sea.

Pink salmon typically spawn prior to most other species of Pacific salmon, therefore their redds may be subjected to superimposition by other salmon spawning in the same reaches. Gallagher (1979), who documented lower returns of Puget Sound chum salmon that competed with juvenile pink salmon in marine waters, provided evidence that pink salmon returns declined with increasing abundances of chum salmon on the spawning grounds. Other than interactions involving predation, this is one example where pink salmon were adversely affected by other Pacific salmon.

Discussion

Interspecific competition has long been thought to be one of the more important processes determining the structure of natural communities, and many studies have documented competition in terrestrial, freshwater, and marine communities (Schoener, 1983; Bertness et al., 2001; Chase et al., 2002). Still, the role of interspecific competition in structuring populations has been controversial, largely because many factors may influence populations and because "ghosts of competition past" may or may not have been important in partitioning of species niches and reducing competition during the current period. The variety of studies presented here utilized the natural experimental control provided by alternating-year abundances of pink salmon to show that prey abundance, diet, growth, and survival of salmon varied inversely to pink salmon

abundance. These studies provide evidence that competition can be an important process in offshore marine waters where the lack of experimental controls and vast area occupied by migratory species often inhibit evaluation of interspecific competition (Cushing, 1975; Sinclair, 1988).

The variety of studies from the North Pacific Ocean, Bering Sea, and adjoining coastal waters indicates pink salmon influenced each species of salmon by reducing availability of prey. Chum and sockeye salmon experienced lower prey availability, reduced food consumption and growth, and lower survival in years when pink salmon were abundant (e.g., Salo, 1991; Ruggerone et al., 2003). Puget Sound Chinook salmon experienced reduced growth and survival when pink salmon were abundant (Ruggerone et al., 2004), and one study indicated growth of coho salmon on the high seas was reduced during years of high pink salmon abundance (Ogura et al., 1991). In the North Pacific Ocean, consumption of key prey changed more in sockeye and chum salmon than in pink salmon when abundance of pink salmon was great (Salo, 1991; Tadokoro et al., 1996; Davis, 2003), suggesting that pink salmon were efficient foragers. We are not aware of studies indicating other salmon species adversely affect pink salmon in marine waters through competitive interactions, although a laboratory study suggested growth of pink salmon fry declined in the presence of large chum salmon (Beacham, 1993). The consistency in findings presented here suggests that pink salmon may be the dominant competitor among salmonids in the North Pacific Ocean.

Competitor characteristics of pink salmon

The ability of pink salmon to affect other salmonids stems from their great abundance, rapid growth, high feeding rates, and their unique life history (LeBrasseur and Parker, 1964; Heard, 1991). Pink salmon enter the marine waters, such as Puget Sound, before many other subyearling salmon and begin foraging on small, lower trophic level invertebrates (Healey, 1980). This life history trait enables pink salmon to avoid competition in freshwater and estuarine areas while allowing access to marine prey before most other salmon. Subyearling Chinook and chum salmon tend to follow pink salmon from nearshore to epipelagic habitats and they experience reduced prey avail-

ability or growth in years of high pink salmon abundance (Salo, 1991; Ruggerone and Goetz, 2004). In the North Pacific Ocean, sockeye salmon from Bristol Bay appear to follow pink salmon as both species migrate northwest during spring (Myers et al., 1996), leading to reduced growth of sockeye salmon. In spring of their second season at sea, pink salmon appear to begin exploiting large prey, such as squid, earlier in the season compared with smaller sockeye salmon (Aydin, 2000). Pink salmon also appear to exploit key prey more efficiently than sockeye and chum salmon (Tadokoro et al., 1996; Davis, 2003). Thus, pink salmon compete with other species by directly altering prey availability of other salmon or indirectly by feeding on smaller prey and altering food web dynamics.

Climate change and competition

Competition between pink and other salmon species was observed before and after the 1977 ocean regime shift, suggesting the influence of competition can transcend recent climatic events. Competition was observed before and after 1977 among Bristol Bay and Russian sockeye salmon (Krogus, 1967; Bugaev et al., 2001; Ruggerone et al., 2005) and chum salmon in the North Pacific Ocean and Puget Sound (Sano, 1963; Tadokoro et al., 1996; Salo, 1991). However, in the Puget Sound region, coded-wire-tag data indicated mortality of chinook salmon switched from predation-based to competition-based mortality in response to the 1982/1983 El Niño that influenced predator, competitor, and prey abundances (Ruggerone and Goetz, 2004). Thus, competition can be an important factor affecting salmon populations in multiple climatic regimes or, in some cases, it may only occur during periods of low prey reduction.

Climate has a long-term effect on salmon populations, as indicated by the 1977 ocean regime shift that led to substantial increases in abundances of all salmon species in northern regions (Rogers 1984, Mantua et al., 1997; Figure 1). If population trends of salmon species are positively correlated, how can competition be an important factor regulating salmon populations in the marine environment? We propose that the answer lies in the temporal and spatial scales of competition and other factors that influence salmon abundance. Although mechanisms leading to greater salmon

abundance after 1977 are not well known, greater prey production during early marine life may have been a key factor (Brodeur and Ware, 1992; Ruggerone et al., 2002). Apparently all species of salmon benefited by this change because they are opportunistic foragers and their diets are often similar (Welch and Parsons, 1993; Kaeriyama et al., 2004). However, the rapid increase in salmon after 1977 led to food limitations, as indicated by studies of intraspecific competition effects on salmon growth at sea (Bigler et al., 1996; Rogers and Ruggerone, 1993). Thus, while climate change enhanced salmon survival during a critical life stage of salmon, prey availability at some life stages was limited and competition continued to influence growth and survival of salmon. The finding of competitive dominance of pink salmon across multiple climate regimes seems to be somewhat unique in the ecological literature because other studies suggest climate change may alter competition and favor one species over the other (Skud, 1982; Jiang and Kulczycki, 2004).

Management implications

The finding that interspecific competition in marine waters can affect salmon population levels has important implications for management of salmon harvests and hatcheries. Competition is a function of species abundances and salmon hatcheries have released up to five billion salmon per year into the North Pacific Ocean in order to enhance or maintain harvests (Mahnken et al., 1998). In some regions, such as the Pacific Northwest, numerous hatchery salmon are released into streams with depressed native salmon runs. Although interactions between hatchery and native salmon have rarely been directly studied in marine waters (Levin et al., 2001), concerns have been raised about effects of competition (Bigler et al., 1996; Percy et al., 1999). These concerns have raised the controversial question of whether hatchery salmon production should be allocated among countries (Joyner, 1975; Heard, 1998), but actions are unlikely without more data indicating competition can limit population abundances.

Competition from conspecific salmon can be greater than that from other species because niche overlap is greater among conspecific salmon (Azumaya and Ishida, 2000; Bugaev et al., 2001; Ruggerone et al., 2003). Studies of intra-

specific competition, however, typically lack the experimental control, such as that offered by cyclic pink salmon abundances, needed to evaluate the effects of competition on population levels. Effects of intraspecific competition are typically based on changes in growth or habitat utilization. Given the greater per capita effect of intraspecific competition, our review of interspecific competition provides evidence that intraspecific competition may significantly influence salmon growth and survival, especially when numerous hatchery fish are released into the environment during periods of low prey production (Achord et al., 2003).

Future research

Mechanisms linking pink salmon to reduced growth and/or survival of other salmon is not well known in some regions. For example, in Puget Sound, where Chinook salmon exhibited a strong alternating-year pattern of growth and survival that was opposite pink salmon abundance, juvenile Chinook salmon feed more on larger and higher trophic level prey compared with juvenile pink salmon, and the linkage between pink and Chinook salmon was not obvious (Ruggerone and Goetz, 2004). The researchers suggested that pink salmon might indirectly reduce availability of Chinook salmon prey by altering food web dynamics. Although diet of salmon has been frequently examined, food web dynamics supporting foraging salmon are not well known because salmon continually change habitats and prey preferences as they grow and because prey population dynamics are rarely studied.

In Alaska, Bristol Bay sockeye salmon exhibited a strong alternating-year pattern in growth at sea from 1955 to 2000 (Ruggerone et al., 2003). This pattern was persistent even though sockeye are broadly distributed and forage in ocean regions having different dominant prey species (Aydin, 2000). Examination of seasonal sockeye scale growth indicated growth reduction began after peak growth in spring and continued well after pink salmon had migrated to coastal waters (Ruggerone et al., 2005). These researchers hypothesized that two-year life cycles of key prey, in conjunction with predation by cyclic pink salmon, may help maintain cyclic patterns in prey

abundances and the observed cyclic patterns of salmon growth and survival.

Observations of competition between pink salmon and other salmon were facilitated by alternating-year patterns of pink salmon abundance. These observations suggest new hypotheses about food web dynamics, life history patterns of prey species, and mechanisms in which climate change influences species assemblages in the ocean. In addition to the natural experimental control provided by the alternating-year pattern of pink salmon abundance, Pacific salmon provide a unique research tool because they migrate across large expanses of the North Pacific Ocean, then return to natal streams where data can be readily gathered on their seasonal growth at sea, survival and abundance. These characteristics of salmon and relatively long time series of data for some salmon stocks provide opportunities to investigate relationships among physical oceanographic and climatic conditions, community structure and population dynamics, and anthropogenic activities that affect fish and fisheries. Studies should attempt to incorporate the natural experimental control provided by alternating-year abundances of pink salmon.

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