

Evidence for Bottom-Up Effects on Pink and Chum Salmon Abundance and the Consequences for Other Salmon Species

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Total abundances of adult pink, chum, and sockeye salmon returning from the North Pacific Ocean have been at a high level since the ocean regime shift in 1976-77, but increasing abundances were not synchronous among all species and regions (Ruggerone et al. 2010). The large increase in total chum salmon abundance was due to significant increases in hatchery production that offset stable or declining regional abundances of wild chum salmon. Total abundance of hatchery chum salmon began to exceed total abundance of wild chum salmon in the mid-1980s. Regions where hatchery pink and/or chum salmon abundances significantly exceeded wild salmon abundance include Japan, Prince William Sound, and Southeast Alaska. Increased marking and monitoring of hatchery salmon by management agencies would allow more accurate measures of abundance and productivity of wild salmon.

Abundance of wild pink salmon has been exceptional, averaging approximately 4.2 to 5.6 times more adult fish than wild sockeye and chum salmon, respectively (Ruggerone et al. 2010). Pink salmon represent nearly 70%, on average, of all wild adult salmon returning from the ocean. The exceptional abundance of pink salmon appears to be related to their unique life history, which seems to be especially suited to ocean conditions since the 1976/77 regime shift. Pink salmon fry spend little time in freshwater after emergence from redds, and they migrate quickly through the estuary; therefore, juvenile pink salmon may experience less impact relative to other salmonids in estuarine habitats degraded by human activities. The early entry of pink salmon fry into coastal marine waters relative to most other salmon species may be conducive to growth and survival during the recent period when ocean temperature and productivity tended to be higher and earlier relative to that prior to the mid-1970s (Brodeur and Ware 1992; Ruggerone and Goetz 2004).

Rapid growth is important for pink salmon, which have the highest early marine growth rates of salmon (Ricker 1976; Brett 1979). Rapid growth of pink salmon is accomplished by continuous feeding at rates that maintain a full stomach at high prey densities (Godin 1981). Moss et al. (2005), using stock-specific scale growth from immature pink salmon captured at sea versus scale growth of these returning adults, demonstrated that larger and faster-growing pink salmon experienced higher survival.

Few long time series of salmon growth at sea exist, especially for pink salmon. However, early marine scale growth of Alaska sockeye salmon was consistently above average following the mid-1970s ocean regime shift (Ruggerone et al. 2007), suggesting rapid early marine growth of sockeye salmon (and presumably pink salmon) contributed to greater survival and abundance after the regime shift. Total abundance of Alaska sockeye salmon since 1955 was positively correlated with their scale growth during the first two years at sea. Given that the diet of sockeye and pink salmon overlap considerably in the ocean (Davis et al. 2005; Myers et al. 2009), it is likely that pink salmon growth also increased after the mid-1970s regime shift (Walker et al. 1998). Evidence suggests that bottom-up (growth-related) processes associated with ocean regime shifts and seasonal ocean conditions strongly influence wild salmon abundance. However, greater abundance of salmon has led to density-dependent growth, which is more apparent and detectable during late life stages when growth-related mortality is less (Ruggerone et al. 2007).

Salmon Interactions at Sea

Although productivity of the ocean is a primary driver of salmon survival and abundance, evidence indicates salmon interactions at sea can be significant. Salmon migrate long distances at sea and interact with other salmon originating from distant regions; therefore, high regional abundances of salmon may have adverse impacts on salmon from other regions. These interactions are difficult to evaluate because there are numerous potentially confounding factors (see below). Nevertheless, the interaction between Bristol Bay sockeye salmon and Asian pink salmon is one example of this previously unknown interaction (Ruggerone et al. 2003). Additionally, recent evidence suggests that the high abundance of Asian chum

salmon, which originate primarily from hatcheries, adversely affects the survival, age-at-maturation, and adult length-at-age of chum salmon from Norton Sound in northern Alaska (Ruggerone et al. 2011). Although abundance of Norton Sound chum salmon is low, these salmon are highly important to people for subsistence.

Pink Salmon Effects on Fraser Sockeye Salmon

The great abundance of pink salmon has consequences for other species of salmon (Ruggerone and Nielsen 2004, 2009) as well as marine birds (Toge et al. 2011). Using sockeye salmon data provided by the Pacific Salmon Commission, we found that high abundances of pink salmon adversely influenced the growth, age-at-maturation, and survival of Fraser River, British Columbia, sockeye salmon.

The mean productivity of 16 Fraser River sockeye salmon populations during brood years 1961 to 2005 was inversely correlated with abundance of North American pink salmon ($r = -0.60$; Fig. 1). Productivity was defined as the residual from the stock-specific Ricker recruitment curve (Peterman et al. 1998). The relationship shows two modest outliers corresponding with brood years 2003 and 2005, i.e., adult returns in 2007 and 2009. The unusually low 2009 sockeye salmon return surprised managers and led to ongoing investigations (Peterman et al. 2010; www.cohencommission.ca/en/). The low returns in 2007 and 2009 were consistent with alternating-year abundances of pink salmon, but the relationship (Fig. 1) suggests that other factor(s) also contributed to these low sockeye returns. In 2010, sockeye salmon abundance was high, as expected from the alternating-year pattern of pink salmon abundance, but stock-specific productivity of the 2010 return has yet to be reported by the Pacific Salmon Commission. Since 1979, sockeye salmon productivity from odd-numbered brood years has been significantly lower than productivity from even-numbered years. Most sockeye salmon produced by odd-numbered broods mature four years later in odd-numbered years. The unusual sockeye returns in recent years are consistent with interactions with pink salmon, although some other factor(s) also affected survival.

Evidence indicates that growth of Fraser River sockeye was a key factor influencing their survival in relation to pink salmon. Adult length-at-age of Fraser sockeye salmon was significantly smaller during odd-year returns. Adult length-at-age was inversely related to abundance of adult sockeye and pink salmon.

Growth at sea also affected age-at-maturation of Fraser River sockeye salmon, which was delayed among odd-year broods compared with even-year broods. Age-at-maturation was positively correlated with abundance of pink salmon in North America ($r = 0.69$, Fig. 2a), suggesting that higher abundance of pink salmon led to reduced sockeye growth and delayed maturation. Productivity of Fraser River sockeye salmon (mean of 16 populations) was inversely correlated with age-at-maturation of the broods since 1961

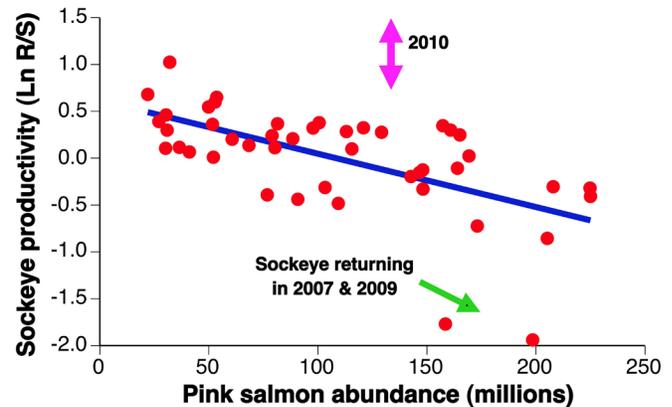


Fig. 1. Relationship between mean productivity of 16 Fraser River sockeye stocks (brood years 1961-2005) and abundance of pink salmon returning to North America (southern British Columbia, Southeast Alaska, Prince William Sound, Kodiak stocks) during the year of adult sockeye return, i.e., brood year plus four years. Productivity of the 2003 and 2005 broods was consistent with the pink salmon hypothesis, but other factors impacted these broods. The vertical arrow indicates the likely range in productivity of the 2006 brood year that produced an abundant sockeye return in 2010 following apparently favorable ocean conditions. Productivity is the residual from the stock-specific Ricker recruitment curve. Sockeye salmon data provided by the Pacific Salmon Commission.

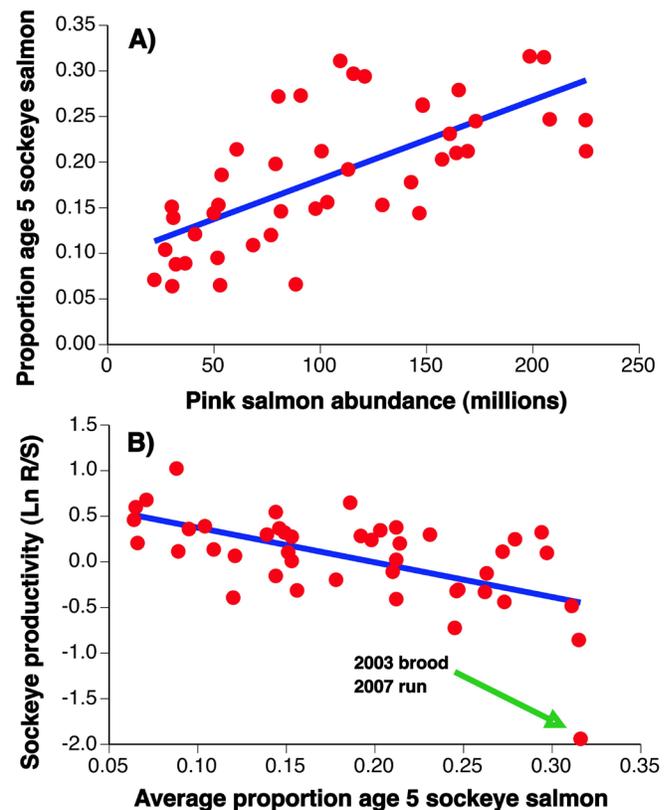


Fig. 2. Relationship between the mean proportion of age-5 Fraser River, British Columbia, sockeye salmon in the brood year return (mean of 16 stocks) and the abundance of North American pink salmon (A), and the relationship between Fraser River sockeye salmon productivity and the mean proportion of age-5 Fraser sockeye salmon in the adult brood year return (B).

($r = -0.58$; Fig. 2b). These findings suggest that growth of sockeye salmon was reduced by high pink salmon abundance, and high pink salmon abundance contributed to delayed maturation and lower survival of Fraser River sockeye salmon. Delayed maturation is an important mechanism in which reduced growth can contribute to lower survival of salmon. This analysis indicates mortality can be high during late marine life in addition to high mortality during early marine life. The growing evidence for bottom-up control of salmon survival and abundance and for competition over prey highlights the need to better understand interactions between and among species of salmon at sea. Additional effort is needed to identify the time period(s) of species interaction (Beamish et al. 2010).

Pink Salmon Effects on Bristol Bay Sockeye Salmon

Evidence based on Alaskan sockeye salmon smolt survival, adult returns, and ocean growth indicates there is competition with abundant Asian pink salmon stocks (Ruggerone et al. 2003, 2005). Information was reported at the 2011 NPAFC workshop (Wertheimer and Farley, this report) that suggested smolt-to-adult survival of Bristol Bay sockeye salmon was not inversely correlated with abundance of Asian pink salmon. While preparing the 2003 manuscript, we also found no strong correlation between smolt-to-adult survival of Bristol Bay sockeye salmon and Asian pink salmon abundance, but we also recognized there were multiple reasons why correlation analysis failed to document a relationship. Therefore, Ruggerone et al. (2003) and subsequent manuscripts used several more robust approaches to test the pink salmon hypothesis as further discussed below.

We identified six reasons why correlation analyses did not detect a negative relationship between survival of Bristol Bay sockeye salmon and Asian pink salmon abundance:

- (1) Ocean productivity is a major factor driving pink and sockeye salmon production and both Asian pink and Bristol Bay sockeye salmon responded similarly to ocean conditions in recent decades (Ruggerone et al. 2010);
- (2) The interaction between Bristol Bay sockeye salmon and Asian pink salmon begins during the second year at sea (Ruggerone et al. 2003, 2005). Time of this interaction is important because significant and highly variable mortality of salmon occurs during the first year at sea and, therefore, prior to the pink salmon interaction. We do not consider pink salmon interaction to be the primary factor driving sockeye salmon survival, but there is considerable evidence that this interaction is an important factor;
- (3) There is undoubtedly significant measurement error in Bristol Bay smolt-to-adult survival rates and error in total pink salmon abundance estimates and inconsistent error from year to year would weaken a correlation;
- (4) Pink and sockeye salmon distribution at sea varies from year to year, and this influences the degree of interaction independent of total abundance;
- (5) Analyzing relationships involving only the total abundance of Asian pink salmon may not reveal correlations because there are year-to-year stock-specific migration patterns and abundances of pink and sockeye salmon. As indicated by overlap in known ocean ranges from high seas tagging experiments (Myers et al. 1996), the primary Asian pink salmon stock that interacts with Bristol Bay sockeye salmon is that from Eastern Kamchatka, but pink salmon from other regions of Asia and North America are also abundant and could interact with Bristol Bay sockeye salmon. It is noteworthy that the dominant odd-year line of pink salmon returning to western Kamchatka switched to even-year dominance (most apparent beginning in 1994) following the tremendous spawning escapement in 1983 (Bugaev 2002; Ruggerone and Nielsen 2009). Year-to-year variation in stock-specific abundances and the degree of overlap in ocean distribution with Bristol Bay sockeye salmon would inhibit correlation;
- (6) Cyclic abundances of pink salmon may create annual cycles in abundances of their prey, which in turn influence the feeding rate of sockeye and pink salmon (Ruggerone et al. 2005).

According to Farley et al. (2011), Bristol Bay post-smolts during 2002-2007 had higher energy density in even-numbered years and this likely contributed to somewhat higher adult returns and survival from even-year smolt migrations rather than lower survival, which is expected when post-smolt sockeye interact with abundant pink salmon during the following odd-numbered year. Higher energy density in even-numbered years corresponded with lower abundance of post-smolt sockeye salmon, leading Farley et al. (2011) to suggest that energy content of sockeye salmon was density-dependent. Therefore, in relation to Asian pink salmon, high energy density of sockeye salmon near the end of the first growing season of even-numbered years may have offset negative effects that could have occurred during subsequent years when they began to overlap with pink salmon. Farley et al. (2011) also produced confidence intervals for their post-smolt abundance and survival estimates, indicating high uncertainty in the estimates in some years. Uncertainty was higher in even-numbered years, e.g., the 95% CI for abundance and survival in 2006 was 27.2-139.5 million post-smolts and 9.6-95.9% survival, respectively. Correlation between post-smolt abundance near the end of the first year at sea and the corresponding adult return was weak ($r = 0.14$) and non-significant ($p = 0.79$).

Therefore, rather than comparing sockeye survival directly with pink salmon abundance trends, Ruggerone et al. (2003) examined the effects of pink salmon on survival and abundance of Bristol Bay sockeye salmon using two approaches: (1)

comparison of smolt survival rates by odd- versus even-years of smolt migration, and (2) stock-specific adult returns by odd- versus even-years of smolt migration across a 21-year time period. These two independent approaches are more robust to assumptions required by correlation analysis and are consistent with the fact that pink salmon are approximately 39 times more abundant in the central Bering Sea during July of odd- versus even-numbered years based on sampling at sea (Davis et al. 2005; Myers et al. 2009). Sockeye salmon smolts migrating in even-numbered years averaged 46% to 26% lower survival, depending on smolt age, than odd-year migrants. Scale growth analyses demonstrated that even-year migrants were influenced by abundant odd-year pink salmon immediately after peak growth in spring of their second year at sea (Ruggerone et al. 2005). Furthermore, 22% fewer adult salmon returned from even-year smolt migrations during 1977-1997, based on age-specific returns to each Bristol Bay watershed (Ruggerone et al. 2003; Ruggerone and Nielsen 2004, 2009).

Finally, it is important to note that adult length-at-age and annual scale growth of Bristol Bay sockeye salmon were negatively correlated with Asian and/or eastern Kamchatka pink salmon abundance since the 1950s (Ruggerone et al. 2003, 2007; Ruggerone and Nielsen 2004). Total prey consumption and quality of prey declined more in sockeye than pink salmon during odd- versus even-numbered years (Davis et al. 2005). The density-dependent growth relationships and diet analyses were consistent with alternating-year patterns of sockeye smolt survival and adult abundance and the fact that salmon survival is strongly influenced by growth at sea (Moss et al. 2005). Mean salmon size measurements provide more robust values compared with survival estimates and size measurements are less prone to measurement error.

In summary, we are not surprised by a lack of correlation between survival of Bristol Bay sockeye salmon and abundance of Asian pink salmon. This relationship can be confounded by numerous factors. Nevertheless, multiple lines of evidence indicate that pink salmon affect the growth and abundance of Bristol Bay sockeye salmon, and new analyses indicate pink salmon also affect growth, age-at-maturation, and abundance of Fraser River sockeye salmon.

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