Board of Fisheries

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Dear Chairman Jensen and Board of Fish Members:

In the interest of understanding the complex topic of Ocean Carrying Capacity (OCC) this document written by two career fisheries research scientists is presented.

High Ocean Biomass of Salmon and Trends in Alaska Salmon in a Changing Climate

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EXECUTIVE SUMMARY

The abundance and biomass of wild and hatchery pink, sockeye, and chum salmon in the North Pcific Ocean has been higher in the past 2.5 decades (1990-2015) than at any time in the 90-year time series. The high biomass has been remarkably consistent from 1990-2015. There has been higher variability in numbers of salmon than in biomass due to the variability in pink salmon abundance. The high sustained abundance and biomass is driven in no small part by historically high abundance of Alaska salmon, and corresponds with the renaissance of Alaska salmon fisheries from their nadir in the 1970s. Statewide commercial catches of salmon were just 22 million fish in 1973; for 1990-2015, statewide catches have averaged 177 million salmon, an eight-fold increase.

This remarkable recovery and historically high abundance of Alaska salmon can be attributed to five major factors: (1) large expanses of relatively pristine and undeveloped habitats; (2) salmon management policies that have evolved since statehood; (3) the elimination of high seas drift-net fisheries; (4) production from large-scale hatchery programs designed and managed to supplement natural production; and (5) favorable environmental conditions associated with the 1977 "regime shift" affecting the ecosystem dynamics of the North Pacific Ocean. Habitat, management, and enhancement set and maintain the productive capacity that responds to marine environmental conditions: ocean "carrying capacity".

Carrying capacity has been defined as the ability of an ecosystem to sustain reproduction and normal functioning of a set of organisms. Ocean carrying capacity for Pacific salmon is not a fixed productivity limit, and the considerable regional and temporal variability in salmon stocks is a response to non-homogeneous ocean conditions. Over the past few decades, conditions in the North Pacific Ocean have

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been generally favorable to Pacific salmon as reflected by the sustained high abundances and catches. However, extremes in survival and production have occurred both temporally and geographically. Survival and year-class strength of salmon is the result of responses to local, regional, and basin scale conditions. Marine conditions vary geographically and temporally within a given year, interannually, and in the context of oceanographic regimes favorable or unfavorable to salmon production.

There are concerns that the high abundance in the North Pacific Ocean, coupled with high variability in stock performances, indicate that carrying capacity is being exceeded, and that competitive interactions are negatively affecting growth and survival. These concerns have been raised for over 20 years. Rather than indicate that carrying capacity has been exceeded, the trend of the past three decades show that the North Pacific Ocean has had the capacity for the recovery and sustained production of wild stocks while supporting the expansion of large-scale enhancement production from Japan (chum salmon) and Alaska (chum and pink salmon).

A proposed mechanism for negative impacts of high abundance of salmon in the ocean is that their feeding capacity alters the biomass of oceanic zooplankton, and in turn the phytoplankton biomass. In this scenario, this “trophic cascade” and alteration of food webs then negatively impacts other species, including coho and Chinook salmon. The record numbers and abundance of Pacific salmon can appear to be an imposing load on the North Pacific Ocean ecosystem. However, assessments of nektonic trophic structure in the Gulf of Alaska and the western North Pacific Ocean indicate that salmon have low to moderate impacts on oceanic food webs, and they respond to, rather than control, changes in ocean productivity.

Pink salmon have been identified as a keystone predator restructuring oceanic food webs to the detriment of other species. Four lines of evidence call this conclusion into question. First, Russian researchers report that in extensive ocean research programs, they have found typically no significant correlations occur among pink salmon growth rate, stock abundance, or zooplankton standing crop. Second, high numbers of pink salmon in the North Pacific Ocean have been associated with record run sizes and continued sustained biomass of salmon, rather than a reversal in these trends when pink salmon abundance increased. Third, pink salmon have shown the greatest variation in abundance among Alaska salmon, especially in response to anomalous ocean conditions. Thus rather than restructuring the food webs, they appear to be the most sensitive to changes in marine conditions. Finally, the high predation pressure of pink salmon in the context of epipelagic food webs is justified because other species, especially chum and sockeye salmon, switch to other, poorer quality prey items when pink salmon are abundant. However, the obvious implication is that these other species will “switch back” to the prey with higher nutritional value when pink salmon are at lower levels of abundance. Because chum and sockeye salmon comprise almost 80% of the oceanic biomass of salmon, salmon predation pressure on the “high value” prey remains relatively constant.

Effects of pink salmon abundance are often used as a proxy for deleterious effects of large-scale enhancement in general. In fact, while pink salmon are the most numerous of the salmon species in the North Pacific Ocean, wild stocks of pink salmon contribute some 85% of the overall abundance.

Density dependent interactions have been identified within and between species of salmon. These interactions have been observed during both periods of low and high abundance. Changes in size, survival and age at maturity have been attributed to these interactions. Despite the existence of competitive interactions in the marine environment, high productivity of Alaska salmon has persisted during this period of high abundance. In general, size declines of pink and chum salmon occurred prior to the 1977 regime shift, and thus are associated with poorer ocean conditions rather than ocean abundance of salmon, and sockeye salmon size has been stable over the past 60+ years.

There is also concern that the high ocean abundance of the big three (pink, chum, and sockeye salmon) negatively impact coho and Chinook salmon in Alaska. For coho salmon, size declines in Southeast Alaska have been linked to pink salmon abundance in the Gulf of Alaska, while in Canada recent size increases in coho salmon have been positively associated with the combined biomass of pinks, chums, and sockeye salmon. The high correlation of run strength between coho and pink salmon in Southeast Alaska is strong evidence that their abundance is driven by similar overall response to shared marine conditions. Density-dependent mechanism other than competition may also play a role in pink salmon/coho salmon dynamics. These include such as predator sheltering of coho salmon juveniles by the more abundant pink salmon juveniles (decreasing predation on coho juveniles), predator aggregation (increasing predation on coho juveniles), and direct predation of coho juveniles and adults on pink salmon juveniles.

Chinook salmon stocks in Alaska have been depressed in recent years due to reduced marine survival, and have declined in size at age for older fish, and age at maturity. These changes are not likely driven by the high abundance of salmon in oceanic habitats. Chinook salmon, by their propensity to utilize deeper depth strata and distribute more broadly on shelf and slope areas during marine residency, are segregated to a large degree from other salmon in their use of ocean habitats with correspondingly different temperatures, prey fields, and predator complexes. Size of Chinook salmon at ocean age 2 has not declined, indicating no density-dependent effect on growth through the first two years at sea. Size declines at older ages are more consistent with selective removal of older, larger fish.

Survival declines of Chinook salmon occurred well into the period of high ocean biomass. There is substantial evidence that much of the variation in Chinook salmon marine survival is due to conditions in the first summer and winter at sea. Changes in the North Pacific ecosystem, such as increased killer whale predation, could introduce more mortality at older ages, and further depress realized survival during periods of poorer environmental conditions for Chinook salmon.

Favorable ocean conditions rather than density-dependent interactions seem to be driving both the high abundance at the basin-scale and the high variability in salmon populations at local and regional scales. Recent climatic and oceanographic events such as the marine heat waves of 2004/2005 and 2014/2015 in the Gulf of Alaska are demonstrative of the intrinsic variability of ocean conditions affecting salmon at local and regional scales. Will density-dependent interactions become increasingly important if and when ocean conditions become less favorable to salmon, with large releases of hatchery fish putting wild stocks in more jeopardy? Or will hatchery fish provide a buffer to sustain fisheries when wild stock productivity is low in response to varying environmental conditions? We conclude the latter, because there is empirical evidence that large releases and returns of hatchery pink salmon in years of both low and high wild stock abundance did not limit the production potential of the wild stocks.

Introduction

The Alaska Board of Fisheries (BOF) was recently petitioned to hold an emergency meeting asking the BOF to amend actions taken in Permit Alteration Requests (PARs) made by the Prince William Sound (PWS) Regional Planning Team and deny the increase in the number of pink salmon eggs taken in 2018 by 20 million eggs. One of the rationales the petitioners used for rescinding the PAR was "… great concern over the biological impacts associated with continued release of very large numbers of hatchery salmon into the North Pacific Ocean, including the Bering Sea and the Gulf of Alaska." To support this concern, the petitioners provided references to record high abundance and biomass of salmon in the North Pacific, as well as possible density-dependent effects of pink salmon on the trophic structure in the North Pacific Ocean and intra-specific and interspecific competition of pink salmon with other species of salmon and seabirds.

The BOF held the emergency meeting on July 17, 2018, and denied the request for rescinding the PAR. The BOF determined there was no need for such an emergency action, and deferred further consideration to the review of the State's salmon enhancement program scheduled for the October 2018 work session. The intention of that review is for members of the BOF to educate themselves about the program and understand the science the enhancement program is predicated on and the current scientific evaluation.

This paper provides a brief, broad overview of the issue of record abundance and biomass of Pacific salmon and the implications for the status of Alaska salmon. We present this overview in six sections. The first is a review of the recent information on abundance of salmon in the North Pacific. The second is an examination of trends in harvest of Alaska salmon, including enhanced production. The third is a discussion of oceanographic conditions and the concept of "carrying capacity" for salmon in the North Pacific. The fourth is a perspective on the relative role of salmon as a component of the North Pacific ecosystem. The fifth looks at intra- and interspecific competition and density dependence among salmon species, and its possible impacts on growth and abundance. The sixth section summarizes our conclusions from this overview.

I. High Abundance and Biomass of Salmon in the North Pacific Ocean

In a recent paper, Ruggerone and Irvine (2018) published an excellent compendium of the available data on numbers and biomass of pink, chum, and sockeye salmon in the North Pacific Ocean over the time period 1925 through 2015. The authors have compiled diverse data sources of harvest, harvest rates, and escapement. They have used reasonable approaches to estimating total salmon escapements by species by region, and to estimate hatchery and wild origins.

They found that the abundance and biomass of pink, sockeye, and chum salmon has been higher in the past 2.5 decades (1990-2015) than at any time in the 90-year time series, averaging 665 million adult salmon each year (1.32 × million metric tons) during 1990–2015 (Figure 1). During 1990–2015, pink salmon dominated adult abundance (67% of total) and biomass (48%), followed by chum salmon (20%, 35%) and sockeye salmon (13%, 17%). When immature salmon biomass was included in the biomass estimates, biomass was dominated by chum salmon (60% of the combined biomass of all three species), followed by pink salmon (22%) and sockeye salmon (18%).

The high biomass has been remarkably consistent over the 1990-2015 time period. There has been higher variability in numbers of salmon than in biomass due to the variability in pink salmon abundance.

Alaska produced approximately 39% of all pink salmon, 22% of chum Salmon, and 69% of sockeye salmon, while Japan and Russia produced most of the remainder. Approximately 60% of chum salmon, 15% of pink salmon, and 4% of sockeye salmon during 1990–2015 were of hatchery origin. Alaska generated 68% and 95% of hatchery pink salmon and sockeye salmon, respectively, while Japan produced 75% of hatchery chum salmon. Salmon abundance in large areas of Alaska (PWS and Southeast Alaska), Russia (Sakhalin and Kuril islands), Japan, and South Korea are dominated by hatchery salmon. During 1990–2015, hatchery salmon represented approximately 40% of the total biomass of adult and immature salmon in the ocean.

In the context of concern for the impacts of hatchery fish on wild salmon and the North Pacific ecosystem, we reiterate three facts about pink salmon noted above. Pink salmon are the most abundant of the species, have the greatest temporal variability in abundance, and are mostly (85%) wild origin (Ruggerone and Irvine 2018). As we will discuss below, the high variability of pink salmon and differences in abundance between odd-year and even-year lines is often used to examine competitive interactions and ecosystem level impacts of salmon in the North Pacific. At the basin-scale, to the extent that such effects may occur, effects of pink salmon are predominately from wild-stock populations rather than from enhanced fish.

II. Trends in Harvest of Alaska Salmon

The high sustained abundance and biomass in the North Pacific Ocean reported by Ruggerone and Irvine (2018) is driven in no small part by historically high abundance of Alaska salmon. It is instructive to put the current levels of salmon harvest into perspective of the 115 year time series of Alaska commercial salmon harvests (Figure 2), to recognize the extent of recovery and extraordinary recent productivity of Alaska salmon. In the early 1970's, Alaska salmon harvests were at their nadir, with statewide catches of all species averaging just 22 million fish in 1973 and 1974 (Figure 2). In the "good old days" of the 1930s, catches sometimes exceeded 100 million. The State of Alaska initiated a number of management actions to address the decline and rebuild production (Clark et al. 2006), with a goal of once again reaching harvests of 100 million salmon. In 1971, the Alaska Legislature established the Division of Fisheries Rehabilitation Enhancement and Development (FRED) within the Alaska Department of Fish and Game (ADF&G) for hatchery development. In 1972, Alaska voters approved an amendment to the state Constitution (Article 8, section 15), providing for an exemption to the "no exclusive right of fishery" clause, enabling limited entry to Alaska's state fisheries and allowing harvest of salmon for broodstock and cost recovery for hatcheries. In 1974, the Alaska Legislature expanded the hatchery program, authorizing private nonprofit (PNP) corporations to operate salmon hatcheries.

Alaska's modern salmon hatchery system started in the 1970s and grew out of depressed fisheries that reached record low harvest levels. At the same time a century old Japanese salmon hatchery system was undergoing dramatic improvements in performance with record high marine survivals of young salmon, increased releases of up to 2 billion juveniles per year, and returns of adult chum salmon ranging from

40 to 60 million fish annually (Kobayashi 1980). These impressive results caught the attention of officials and scientists developing Alaska salmon hatchery program.

Exchanges between Japanese and Alaska scientists, fishermen, and industry helped forge the enhancement strategies and policies in Alaska, resulting in similarities in the two hatchery programs. Similarities include hatcheries operated by private fishermen groups where salmon catches are taxed under a user-pay system to help defray cost of hatchery operations, a focus mostly on pink or chum salmon production, and extensive short-term rearing of pink and chums salmon fry to improve marine survival. However, as reviewed by Heard (2011), there also are significant differences between salmon fisheries, policies, and hatchery operations in the two countries. Commercial salmon fisheries in Japan have been largely dependent on hatcheries while development of hatcheries in Alaska focused on fisheries based on a careful balance between wild and hatchery production (McGee 2004). Some important differences in the two systems include locating Alaska hatcheries on non-anadromous water sources and not on important wild stock river systems, careful selection of brood stocks within a region and restricting use of hatchery brood stocks to specific geographic areas.

Alaska salmon harvests recovered rapidly in the second half of the 1970s, and exceeded 100 million fish by 1980 (Figure 2). With the exception of 1986 (96 million), the statewide catch has been over 100 million salmon annually since 1980. For 1990-2015, harvest has averaged 177 million salmon. After 1980, hatchery production started making up an increasing portion of the harvest. In the last decade (2008-2017), hatchery salmon have composed about 33% of the total commercial harvest, averaging 67 million fish annually (Stopha 2018).

This remarkable recovery and historically high abundance of Alaska salmon can be attributed to five major factors: (1) large expanses of relatively pristine and undeveloped habitats; (2) salmon management policies that have evolved since statehood (Eggers 1992, Clark et al. 2006); (3) the elimination of high seas drift-net fisheries(Clark et al. 2006); (4) production from large-scale hatchery programs designed and managed to supplement natural production (McGee 2004, Stopha 2018); and (5) favorable environmental conditions associated with the 1977 “regime shift” affecting the ecosystem dynamics of the North Pacific Ocean.

III. **Ocean Conditions and Carrying Capacity**

“*Trying to define ocean carrying capacity is like trying to catch a moonbeam in a jar*”. *O. Gritsenko, VINRO, Moscow. Member, NPAFC Committee on Scientific Research and Statistics.*

The recovery of Alaska salmon and the record abundances throughout the North Pacific have been repeatedly linked to changes in ocean conditions characterized as the 1977 regime shift. Warming ocean conditions resulted in striking increases in primary and secondary production (Brodeur and Ware 1992). These changes in temperature and lower-trophic level production were associated with profound changes in species composition of fish and crustaceans (Anderson and Piatt 1999). Salmon as a group benefitted (and are an important component of) these ecosystem level changes, with the dramatic increases in abundance observed around the Pacific rim. The importance of the marine ecosystem to the abundance trends is emphasized by the success of large-scale enhancement systems in both Alaska and

Japan concurrent with the high production of wild stocks from Alaska and Russia. Wild stocks are responding to the effects of climate on both freshwater and marine ecosystems, while variation in hatchery returns for a given level of production is driven entirely by the marine conditions encountered.

Carrying capacity has been defined as the ability of an ecosystem to sustain reproduction and normal functioning of a set of organisms (Farley et al. 2018). For salmon in the ocean, feeding and survival conditions are defined by a complex of physical and biological factors, involving both bottom-up (prey) and top-down (predators) processes (Radchenko et al. 2018). These are dynamic processes, resulting in annual variability in salmon production in the marine environment. The ocean conditions driving these processes vary over both short and long time periods, so that annual variability occurs in the context of "regimes" that can be favorable or unfavorable to salmon (Beamish et al. 1999,2004; Shuntov et al. 2017; Radchenko 2018).

Over the past few decades, "carrying capacity" conditions in the North Pacific Ocean have been generally favorable to Pacific salmon as reflected by the sustained high abundances and catches. However, responses of stocks of Pacific salmon have not been uniform during this period, and extremes in survival and production have occurred both temporally and geographically. Survival and year-class strength of salmon is the result of responses to local, regional, and basin scale conditions, and not a result of a homogeneous ocean carrying capacity (Heard and Wertheimer 2012).

Marine survival of Pacific salmon is more correlated between neighboring populations than with more distant ones (Mueter et al. 2005; Pyper et al. 2005; Sharma 2013), emphasizing the importance of local and regional conditions. The first few months at sea is the period of highest mortality per day for juvenile salmon in the marine environment (Heard 1991; Quinn 2005; Farley et al. 2007, 2018). Variability in mortality during this period can be large, and can be the major driver of year-class strength. An extreme example is the returns of Fraser River sockeye salmon in 2009 and 2010. In 2009, only 1.5 million fish returned, the lowest return since 1947; in 2010, 29 million fish returned, the highest number since 1913. Conditions during the early marine period are considered the primary factor affecting these changes in survival of Fraser River sockeye salmon (Beamish et al. 2012).

Salmon surviving the early marine period are exposed to continued mortality, albeit at a lower rate (Quinn 2005). The first winter at sea has been posited as a critical time period for determining year class strength (Beamish et al. 2004; Moss 2005). Older immature and maturing salmon have much lower mortality rates (Ricker 1976), but these extend over a longer period of time, from 1 year for pink salmon to 5 years for Chinook salmon. Forecasting approaches using juvenile salmon abundance index to predict returns (Wertheimer et al 2017; Murphy et al. 2017) assume that recruitment through the early marine stage has established year-class strength, and that subsequent mortality does not vary substantially from year-to-year. However, Radchenko (2018) reports that cumulative ocean mortality can vary 1.5-2 times. These ocean effects on survival can result in large deviations, positive and negative, from forecasts from juvenile salmon indexes (Figure 3). For 2006, the forecast for Southeast Alaska pink salmon harvest was 35 million fish; the actual harvest was 11 million fish, less than one third of the forecast. In contrast, the pink salmon forecast for 2013 was 53.8 M fish, but the forecast was 43% lower than the actual harvest of 94.7 million fish, the largest harvest since catch records were recorded dating back to 1900 (Figure 3, Figure 4).

These results illustrate that variations in marine survival between different local or regional areas occur in the context of larger basin-scale climatic influences on overall production levels of pink and chum salmon in the GOA. Prevailing basin-scale conditions likely strongly influence environmental factors that favor a higher or lower range or level of potential survival for juvenile salmon from different regions.

The “carrying capacity” encountered by a salmon population is a cumulative effect encompassing different life-history phases. The conditions encountered by the salmon will depend on their geographic origin and their ocean migration patterns, which differ by species and stocks. The ocean is a dynamic environment, with substantial variability throughout the North Pacific basin. In 2013, “carrying capacity” for pink salmon in the Gulf of Alaska (GOA) was high, with strong returns throughout the GOA. Returns in both Southeast Alaska and PWS were at record levels. In contrast, in 2015 pink salmon again returned to PWS in record numbers, while returns in Southeast Alaska were below the 1995-2015 average and below forecasts from juvenile salmon indexes, demonstrative of the regional nature of the response of pink salmon stocks to ocean conditions (nearshore and oceanic).

While the general warming in the North Pacific Ocean has been a feature of the high productivity for salmon (Brodeur and Ware 1992; Mantua et al. 1997; Farley et al. 2018), ocean warming events associated with climate change are occurring with more frequency, often with detrimental impacts on salmon (McKinnell 2017). Recent ocean warming events are associated with the decline of the even-year pink salmon in Southeast Alaska. From 1960 through 2005, there was no clear dominance of even or odd year lines of pink salmon in Southeast Alaska (Figure 4). In the summer of 2005, juvenile pink salmon from SEAK encountered anomalous warm conditions in the Gulf of Alaska (Figure 5). These ocean conditions were associated with the occurrence of neretic fish and invertebrates characteristic of more southern locales, including Humboldt squid, blue shark, Pacific sardine, and pomfret (Wing 2006). The resultant 2006 return was, as noted above, only one-third of forecast, and the lowest since 1988. Even year pink salmon appeared to be recovering relative to the 2006 return, attaining a harvest of 37 million in 2014.

In the winter of 2014/2015, another marine heatwave, aka the warm blob, reached the eastern GOA (DiLrenzo and Mantua 2016). The 2014-brood pink salmon that entered the GOA in 2015 again had poorer than expected survival, attaining only half of the forecast in 2016 (Figure 3). Poor pink salmon returns occurred throughout the Gulf of Alaska in 2016, resulting in a Federal disaster declaration for the fishery. The broad nature of the pink salmon run failure is indicative of shared ocean effects. However, regional and local variability were also apparent. In Southeast Alaska, harvests of pink salmon in the northern area were 20% of the recent 10-year average, whereas in the southern area harvest was 80% of the recent 10-year average. In PWS, much of the catch was supported by fish from Solomon Gulch Hatchery, which was still 50% below forecasts based on average marine survivals. Marine survivals were poorer yet for pink salmon from Prince William Sound Aquaculture Association hatcheries, where returns were less than 20% of forecast (Russell et al. 2017).

The 2005 and 2015 ocean heat waves thus had a broad-scale impact on the carrying capacity for pink salmon in the Gulf of Alaska, with 2015 having a more pervasive impact among regions. Both wild and hatchery fish were affected; the return to SEAK is predominately (> 95%) wild, and the hatchery return to PWS was the lowest since 1993.

It is noteworthy that despite the poor returns of pink salmon, generally the most abundant species in the Alaska harvest, statewide harvest in 2016 was still above 100 million salmon (Figure 2). Variability in abundance numbers throughout the North Pacific reflects high variability in pink salmon, which appear to be the most sensitive salmon species to annual changes in ocean conditions because of their lack of multiple year-classes at sea.

Ruggerone and Irvine (2018) raised the concern that the high abundance of salmon coupled with variability in stock performances indicates that carrying capacity of the North Pacific Ocean for salmon has been reached or exceeded. This is not the first time such concerns have been raised. Various authors over the past 20 years have posited that high abundance of pink, sockeye, and hatchery chum salmon may have exceeded carrying capacity and be negatively affecting or constraining salmon production (e.g., Peterman et al. 1998; Ruggerone et al. 2003; Davis (2003); Sinyakov (2005, cited in Shuntov et al. 2017). In spite of these concerns, abundance and biomass have continued to be high, reaching record levels in recent years (Figure 1).

As Shuntov et al. (2017) noted, ocean carrying capacity for Pacific salmon is not a fixed productivity limit, and the considerable regional and temporal variability in salmon stocks is a response to non-homogeneous ocean conditions. Rather than indicate that carrying capacity has been exceeded, the trend of the past three decades show that the North Pacific Ocean has had the capacity for the recovery and sustained production of wild stocks while supporting the expansion of large-scale enhancement production from Japan (chum salmon) and Alaska (chum and pink salmon). The sky has not yet fallen. This is not to say that the high abundance will persist indefinitely. The shock of the marine heat waves of 2004/2005 and 2014/2015 to Alaska pink salmon demonstrates that carrying capacity can vary within a productive regime, and reminds us that the status of the current production regime is vulnerable to both gradual and abrupt changes driven by a warming climate. Continued warming could result in contraction of the range of Pacific salmon in the North Pacific Ocean (Welch et al. 1998).

IV. **Trophic Position of Salmon in the North Pacific Ecosystem**

A major concern over the high abundance of salmon is that their feeding capacity alters the biomass of oceanic zooplankton, and in turn the phytoplankton biomass (Ruggerone and Irvine 2018; Batten et al., in press). This “trophic cascade” and alteration of the food web has been linked to decline in size and abundance of Alaska Chinook salmon and coho salmon (Ruggerone and Irvine 2018; Shaul and Geiger 2016); growth and diet of salmon (Davis 2003); and declines in seabird nesting success and survival (Springer and Van Vielt 2014; Springer et al. 2018).

Dominance of oceanic food webs by salmon is not consistent with the abundance and biomass of salmon relative to other components of the North Pacific ecosystem, including competitors and prey fields. In the western North Pacific, Shuntov et al. (2017) estimated the nekton biomass was 81.3 million t (from 50 to 100 million t in different years). Pacific salmon accounted for 1–2% of this biomass in the 1980s. Biomass of salmon subsequently increased to the current levels of 4-5 million t, representing 4-8% of total nektonic biomass during the current period of high abundance. During this period, the biomass of the two most abundant fish species within their ranges in the North Pacific, walleye pollock (*Theragra chalcogramma*) and Japanese pilchard (*Sardinops melanostictus*), reached 50 million t each.

In the epipelagic layer, Shuntov et al. (2017) estimated that the mean annual food consumption (plankton and small nekton) by the nektonic fauna varied within 210.4–327.3 million t; in the 0–1000 m layer it ranged from 389.0 to 516.0 million t. The amount of food consumed by salmon was 4–8 million t. The proportion of total nekton ration consumed by salmon in the epipelagic layer was 1% - 15%, depending on oceanic area (Figure 6).

This view of low to moderate impact on epipelagic food webs is consistent with mass-balance modeling of North Pacific ecosystems by Pauley et al. (1996). Pacific salmon and steelhead were estimated to make up 4.6% of the epipelagic fish biomass in the Alaska gyre. If squid are including as competitive nekton for zooplankton production, Pacific salmon made up 3.4% of the nektonic biomass. Estimated salmon biomass was < 1% of the estimated zooplankton biomass.

Similarly, the impacts of juvenile salmon feeding during early marine residency on zooplankton has been found to be relatively low. As noted above, the early marine residency is a period of high and variable mortality which may determine year class strength. Given more limited areal habitat than the coastal zone and ocean basin, this period may represent a potential bottleneck for survival. Orsi et al. (2004) used a bioenergetics model to examine consumption of zooplankton by hatchery and wild chum salmon in Icy Strait, Southeast Alaska. They found that juvenile chum salmon consumed only 0.05% of the zooplankton/km2 in the upper 20-m of the water column, and 0.005% for the integrated water column to 200 m in June and July in 2001. Because juvenile salmon are typically in the upper water column, total standing crop of zooplankton is not likely to be available as forage on a daily basis, but does represent a source for zooplankton abundance in the surface layer through vertical diel migrations. The percentage of available prey consumed by juvenile salmon in the neritic habitat of Icy Strait was less than 0.05% of the available standing stock. Low consumption estimates were also estimated by several other studies. Karpenko (2002) reported that juvenile chum salmon consumed between 0.1 and 1.1% of the total stock of zooplankton in the upper 10 m of Karaginskii Bay, Kamchatka from June to August over a 5-year period. Cooney (1993) estimated juvenile salmon in PWS consumed 0.8–3.2% of the total herbivore production and 3.0–10.0% of the macrozooplankton production. Boldt and Haldorson (2002) reported that juvenile pink salmon near PWS could consume 15–19% of preferred prey taxa such as large calanoid copepods and amphipods if the available standing crop was fixed over a 10-day period; however, on a daily basis, consumption of no taxon exceeded 2% of the standing stock.

Pink salmon have been identified by some authors as the salmon species most affecting oceanic food webs (Ruggerone and Irvine 2018). Surface layer zooplankton indexes have been associated with differences in abundances of odd- and even-year pink salmon stocks (Batten et al. in press). However, there was no directed fish sampling or monitoring of zooplankton below the surface layer (7.5 m) in Batten et al.'s study. Radchenko et al. (2018) reviews studies showing that "as a rule, no significant correlations occur among pink salmon growth rate, stock abundance, or zooplankton standing crop."

A conceptual problem to assigning plankton depletion to pink salmon feeding is prey-switching by salmon species. Pink, chum, and sockeye salmon have substantial overlap in their diets, and the latter two species have been shown to switch to other, "lower-quality" prey when pink salmon are abundant (e.g., Davis 2003). These changes in feeding habit are often used to support the concept of density-dependent interactions with pink salmon and their congeners, e.g., Ruggerone and Connors (2015). However, if other species switch prey in response to high pink salmon abundance, they certainly would switch back to the “higher value” prey when pinks are not as abundant. Chum and sockeye salmon make up on average 78% of the biomass of these three species. As a result, there is more of a constant prey demand among this feeding guild in spite of the high variability in pink salmon abundance in the North Pacific. Rather than shaping the ocean food web, pink salmon appear to be most sensitive to interannual changes in oceanic conditions, resulting in high variability in their numbers, both temporally and geographically.

Competition among species may also be minimized by the distribution of salmon in oceanic habitats. Unlike the schooling behavior characteristic of juvenile salmon and maturing salmon in nearshore and coastal areas, salmon at sea are widely dispersed (Shuntov 2017). This behavior reduces competitive interactions and makes their feeding, growth, and survival in the ocean more density-independent.

The record numbers and abundance of Pacific salmon can appear to be an imposing load on the North Pacific Ocean ecosystem. Four to five million tons of biomass is not a trivial amount. Of this 40% is hatchery origin, primarily chum salmon. Approximately 5 billion hatchery juveniles are released into the North Pacific annually (Figure 7). However, the North Pacific Ocean is a large marine ecosystem, and the numbers are not overwhelming when put into context of total nekton and forage bases. Not all nektonic prey is available to salmon due to depth distribution; Ayedin (2000) concluded local depletion of prey by salmon can occur as salmon school density increases, even if prey is not depleted over large ocean areas. This is an important point in understanding regional differences in changes in size at return.

The sustained high marine abundances of both natural- and hatchery-origin salmon over the past 25 years indicates that the trophic structure has not been altered in some way that inhibits salmon productivity. We agree with the conclusion of Shuntov et al. (2017): “… the role of salmon in the trophic webs of subarctic waters is rather moderate. Therefore, neither pink nor chum salmon can be considered as the species responsible for the large reorganization in ecosystems and the population fluctuations in other common nekton species.”

V. Competition and density dependence versus density independent responses

An intuitive concern with the high abundance of salmon in the context of ocean carrying capacity is that density-dependent competition for limited prey resources may affect growth and survival of salmon populations. Pink, chum, and sockeye salmon have substantial overlap in their diets (Davis 2003, Brodeur et al. 2007) and the latter two species have been shown to switch to other, “lower-quality” prey when pink salmon are abundant (e.g., Davis 2003). High abundance of pink salmon in the Gulf Alaska has been associated with growth and size at return of chum salmon, sockeye salmon, coho salmon, Chinook salmon, and pink salmon themselves (e.g., Agler et al. 2011; Jeffrey et al. 2017; Ruggerone et al. 2003, 2018: Shaul and Geiger 2017; Wertheimer et al. 2004a). Reduced growth can result in lower size-at-age, shifts in age at maturity for species spending multiple years at sea, and reduced fecundity, which can affect productivity of salmon populations. Ruggerone et al. (2003) ascribed large reductions in marine survival of Bristol Bay sockeye salmon to the impact of Asian pink salmon on the sockeye salmon growth at sea. The concern for density-dependent competition is not new; Peterman (1984) found evidence of density-dependent interactions between Fraser River and Bristol Bay sockeye salmon. This was at a time when salmon abundance had not expanded to current levels and when hatchery fish made up a low proportion of the abundance and biomass. As salmon abundance and biomass increases, Aydin (2000) concluded that density-dependent interactions could result in negative feedback loops on prey availability in the ocean ecosystem.

Despite the existence of competitive interactions in the marine environment, high abundance and biomass have not resulted in consistent negative trends in salmon size or productivity. Ruggerone et al. (2018) reported that average size has declined for chum salmon and pink salmon since 1925, but not for sockeye salmon (Figure 8). Most of the size decline for pink and chum salmon occurred prior to 1977, which would suggest that pre-1977 regime change conditions were more important than density dependent interactions. Size of pink salmon and sockeye salmon remained stable during the recent period of high abundance, while chum salmon showed some continued decline. Jeffrey et al. (2017) reported similar results for average sizes of British Columbia pink, chum, and sockeye salmon since 1951. Pink salmon declined initially in size, and then have remained relatively stable since the 1990s at a size that is 20-30% less than in the 1950s and 1960s. There was little change over the time series in the average size of sockeye salmon. Regional differences have certainly been observed. For example, Wertheimer et al. (2004) found evidence of size declines in PWS pink salmon in relation to pink salmon abundance in the GOA, while. Shaul and Geiger (2017) reported that pink salmon size has increased in Southeast Alaska in recent years.

Helle et al. (2007) found that body-size of pink, chum, and sockeye salmon from Alaska to Oregon generally declined in after the 1977 regime shift as salmon abundance increased, until 1994. After 1994, body size of these species generally increased, during a period when biomass and abundance was at sustained high levels. They attributed the initial decline to density-dependent competition, and the lack of relationship of abundance to size in the latter period as an outcome of favorable ocean conditions. They concluded that the carrying capacity of the North Pacific Ocean for producing Pacific salmon is not a constant value and varies with changing environmental and biological factors.

In their study on size of British Columbia salmon, Jeffrey et al. (2017) examined the relationship of size trends to estimates of salmon biomass in the North Pacific Ocean. They found that the biomass of North American pink salmon entering the Gulf of Alaska was the most important biomass variable in explaining size variation in BC pink salmon. The direction of the effect was negative, suggesting intraspecific competition was affecting size. For chum salmon, combined biomass of North American pink, sockeye, and chum salmon was the most important biomass variable explaining size variation. The direction of the effect was negative, suggesting some degree of competition among these congeners. Biomass of North American chum salmon was the most important biomass variable explaining size variation in sockeye salmon. Adding Asian chum salmon to this (or combined measures of biomass) did not improve the fit. The direction of the effect was positive, indicating that when chums are abundant, growth conditions for sockeye are positive.

These associations (and lack of associations) between ocean abundance and size at return of Alaska and British Columbia salmon indicate that while competition can affect size and growth, density-independent ocean conditions drive the variability in abundance and can override the impacts of density-dependent competition. We reiterate the findings of Radchenko et al. (2018) that generally, no significant correlations occur among pink salmon growth rate, stock abundance, or zooplankton standing crop.

Reduced survival and productivity of wild stocks in Alaska have been attributed to competitive interactions with Asian pink salmon (Bristol Bay sockeye salmon; Ruggerone et al. 2003) and hatchery pink salmon (PWS pink salmon; Hilborn and Eggers 2001). Alternate analyses and recent trends have refuted these conclusions. In Bristol Bay sockeye salmon, Ruggerone et al. (2003) estimated reduced survivals of even-year sockeye salmon smolts from Bristol Bay at 23-45% less than odd-year smolts for the 1977 to 1997 smolt years. Even-year smolts enter the ocean when odd-year pink salmon are on average more abundant. They concluded that competitive interactions with Russian pink salmon reduced growth of even-year smolts, and resulted in substantially lower average smolt survival. However, the abundance of Russian pink salmon was highly variable over the time period for both odd and even year lines. When pink salmon abundance was considered in a time series analysis of the survival data, rather than using odd/even year average survival, there was no discernable effect of pink salmon abundance on survival (Wertheimer and Farley 2012). Subsequent to the 1997 smolt year, both Asian pink salmon and Bristol Bay sockeye salmon increased in abundance, and a marine survival index for Bristol Bay sockeye salmon smolts was positively associated with abundance (Farley et al. 2018.) Thus increasing biomass of Asian pink salmon has not constrained the continued high productivity of Bristol Bay sockeye salmon.

In PWS, Hilborn and Eggers (2000) concluded that hatchery production provided no net benefit in terms of pink salmon harvest, but was simply replacing wild production through density-dependent interactions. However, Wertheimer et al. (2004a, 2004b) showed that a density-independent index of marine survival explained much of the variability in wild pink salmon productivity, and that there was a large net benefit from enhancement to the PWS pink salmon harvest, albeit with some reduction in wild stock production attributed to the effects of size at return on fecundity. Amorosa et al. (2017) also showed large net gains from hatchery production, albeit lower than would be expected from the authors own argument for proportionate increases in wild pink salmon production following the 1977 regime shift. They minimize the contribution of hatchery fish in PWS by focusing on changes in the common property fishery, dismissing the annual cost-recovery harvest of an average of eight million pink salmon in their evaluation of benefits. The cost-recovery harvest is important to the fisheries economy of PWS, and an important benefit of the enhancement program (Pinkerton 1994). The recent analysis of productivity of PWS pink salmon for the re-certification of sustainability of PWS pink salmon showed continued sustained production of wild stocks during the hatchery era (Figure 9; Gaudet et al. 2017). The historical record returns of wild pink salmon in 2013 and then again in 2015 are particularly demonstrative that wild stocks in PWS retain their high production capacity after 40 years of hatchery enhancement.

Our discussion thus far has focused primarily on the abundance trends of pink, chum, and sockeye salmon, which combined make up most of the biomass of salmon in the North Pacific Ocean. Besides interactions among these species, there is concern that their high overall abundance is negatively impacting coho and Chinook salmon (Ruggerone et al. 2018).

The commercial harvest of coho salmon averaged 1.5 million fish from 1970-1977, then increased rapidly following the 1977 regime shift, peaking at over 9 million in 1994. From 1995 until 2017 the harvest has ranged from 3 to over 6 million fish annually, averaging 4.5 million, with no apparent trend during this period (Figure 10). Approximately 22% of the commercial harvest during the latter period has been produced from Alaska hatcheries. Recreational harvest has increased in recent years, and averaged 1.2 million fish from 2007-2017 (M. Stopha, ADF&G, personal communication).

Mallick et al. (2008) examined marine survival of 14 stocks of coho salmon in Southeast Alaska. They found evidence of effects on marine survival at local, regional, and basin scales. There was high covariation in survival regionally, and no trend was noted over the recent time period. Abundance of juvenile hatchery releases in the year coho smolts went to sea was identified as affecting marine survival, but the effect could be positive or negative, depending on stock. This result exemplifies the complex competitor/predator interactions that have been posited for coho and pink salmon. Negative impacts of large hatchery releases could indicate competition for prey resources or aggregation of prey (Beamish et al. 2018). Positive influences could be a result of "predator sheltering," where the abundant hatchery juveniles act as a buffer on predation on the less abundant, larger coho smolts (Holtby et al. 1990; Briscoe 2004; LaCroix 2009). Abundant hatchery fry and juveniles could also provide an important forage base for coho salmon. Coho salmon juveniles are a major predator of juvenile pink salmon in nearshore marine areas (Parker 1971, Hargreaves and LeBrasseur 1985) and as adults when returning to coastal areas as the juvenile pink salmon emigrate towards the ocean (Sturdevant et al. 2012).

Shaul and Geiger (2017) showed a negative trend in marine survival in recent years for Berners River coho salmon which they related to ocean biomass of North American pink salmon. They attribute the negative impact to predation of pink salmon on squids that are the major prey for coho salmon in offshore areas. They propose that pink salmon are keystone predators of squid, exerting top-down control and thus directing the energy flow in the system. In contrast, Aydin (2000) concluded that the squid, with its high biomass and productivity, was controlling energy flow to salmon. Aydin (2000) found that squid abundance, while highly variable, had increased greatly (as did salmon) after the 1977/1978 regime shift. That squid abundance increased commensurate with salmon abundance indicates the species were responding similarly to the increased productivity in the North Pacific (Brodeur and Ware 1992). Aydin (2000) also found differences in odd and even year distributions of squid in the North Pacific, which could contribute to the odd/even differences in coho salmon size observed by Shaul and Geiger (2017).

If pink salmon impacts on squid were driving marine survival for coho salmon, we would also expect decreasing trends in abundance and marine survival for coho salmon over the 1995-2015 time period of high pink salmon abundance. Instead, catch has been stable, and marine survival declines, at least in southeast Alaska, are a recent phenomenon. Commercial harvest data for coho salmon and pink salmon show very strong correlation annually (LaCroix et al. 2009). If density-dependent interactions were primary, we would expect negative correlation. The correlation is actually strongly positive; from 1960 – 2017, it had an r value of 0.82 ($P < 0.001$; Figure 10). Because returning adult coho and pink salmon have roughly the same period of time in the marine environment, this indicates that shared ocean conditions are driving their year-class strength.

Size trends in coho salmon have varied regionally, with very different relationships to ocean salmon biomass. Shaul and Geiger (2017) found that size at harvest of coho salmon in southeast Alaska increased from 1970 until 1984, then declined from 1985 to 2015. They associated the decline with an index of the biomass of North American pink salmon. Their model did not indicate direct competition, but rather lagged effects at 2- and 4- years affecting the population dynamics of the squid (*Berryteuthis anonychu*s). The lag response model requires that the squid have an obligate two-year life-history cycle as proposed by Jorgensen (2011). This is contradicted by other literature, which characterizes *B. anonychus* as an annual species with high productivity (Katugin et al. 2005, Drobney et al. 2008). Aydin (2000) cites studies showing that *B. anonychus* is highly productive, and spawns twice a year.

Regardless of mechanism, coho salmon size has declined in Southeast Alaska. In contrast, coho salmon body size has increased in British Columbia in recent years. Jeffrey et al. (2017) showed coho body weight declined from the 1950s, and did not reach its minimum until around 1985. Since then it has increased and is now at the highest level in the data series. The combined biomass of North American pink, sockeye, and chum salmon was the most important biomass variable explaining size variation in coho salmon, and had a positive effect on size. The authors speculate that the positive relationship may be driven by environmental conditions, which when favorable allow for greater total biomass of salmon species and higher growth (thus larger size) in coho salmon. Shaul and Geiger (2017) and Jeffrey et al. (2017) both use basin-scale measures of environmental conditions in their models exploring factors affecting coho salmon size. The contrasting results for Southeast Alaska and British Columbia are indicative of the variability in response of different populations to these conditions. This may be caused by different migration patterns in the ocean environment, or different local and regional responses of availability of salmon forage to basin-scale environmental factors.

The recent disastrous returns of Chinook salmon in Alaska has precipitated considerable focus on the least abundant but (on a fish by fish basis) most highly valued salmon species (ADF&G 2013). Chinook salmon have a highly varied and diverse life history, generally more complex than other Pacific salmon exemplified by numerous variations in run and spawn timing, freshwater biology, ocean distribution and behavior patterns, diet, slower ocean growth, and older age at maturity (Healey 1991). In the eastern North Pacific most juvenile Chinook salmon from Oregon to Southeast Alaska remained within 100-200km of their natal rivers until their second year at sea, regardless of their freshwater history (sub-yearling or yearling) and spring, summer, or fall adult run timing (Trudel et al. 2009). Healey (1983) reported that most fall type Chinook salmon tend to remain continental shelf and slope oriented during much of their ocean life history whereas many spring type fish spend much of their ocean life in more offshore waters. In recent years, based on coded-wire tag recoveries, it was found that many Alaska spring-type Chinook salmon also utilize slope and continental shelf waters as immature adults. Coded -wire tagged Chinook salmon from Southeast Alaska (SEAK) and Cook Inlet frequently are recovered in Bering Sea Aleutian Island and Gulf of Alaska trawl fisheries for Walleye Pollock (Meyers et al. 2001; Celewycz et al. 2006).

Marine habitats of Chinook salmon related to depth distribution and migration patterns are diverse and often distinct from most other Pacific salmon. Juvenile Chinook salmon distribute deeper than coho and other juvenile salmon in their first summer and fall at sea (Orsi and Wertheimer 1995; Beamish 2011). Immature Chinook salmon are associated with colder temperatures and deeper depths than other salmon species (Walker et al. 2007; Walker and Myers 2009; Riddell et al. 2018). Diel vertical migrations have been documented in a number of data storage telemetry studies, with movement to greater depths during daylight hours (Radchenko and Glebov 1998; Murphy and Heard 2001; Walker et al. 2007). One Chinook salmon tagged in the Bering sea typically was between the surface and 100 m depth, but occasionally moved to depths in excess of 350 m (Walker and Meyers 2009).

Marine diets of Chinook salmon are distinctly different than diets of pink, chum, and sockeye salmon and more similar to coho salmon (Brodeur et al. 2007; Riddell et al. 2018). Juvenile (first-ocean year) Chinook salmon in coastal waters initially have highly varied diets composed of fish, zooplankton, and insects, then become predominately piscivorous in costal habitats (Brodeur et al. 2007). Fish made up from 65% to 99% of stomach contents by weight for juvenile (ocean- age 0) Chinook salmon sampled within the inside and outer coastal waters of SEAK (Landingham et al. 1998: Weitkamp and Sturdevant 2008). Fish were also the primary prey for immature (mostly ocean-age 1) fish in SEAK (Cook and Sturdevant 2013), coastal British Columbia (Herz et al. 2017), and northern and southern Bering Sea (Farley et al. 2009). Primary prey species included capelin, sand lance, lanternfish, and Pacific herring. In more offshore habitats, Chinook salmon consume primarily fish and squid, although euphasids can make up a substantial portion of their diet (Davis 2003; Shuntov et al. 2010; Karpenko et al. 2013). Herring and sandlance dominate the diets of older immature and maturing Chinook salmon (ocean-ages 2+) in coastal waters (Reid 1961; ATA 2016), with sandlance the dominant prey in outside waters of southeast Alaska and herring the dominate prey in inside waters (ATA 2016).

Run sizes increased across AK after the 1977 regime shift, and were variable but consistently above average until a precipitous decline starting in 2006 (Figure 11). This decline was consistent with reduced marine survival of southeast Alaska stocks after the 2000 and 2001 brood years (ADF&G 2013; Ohlberger et al. 2016; CTC 2018). Thus the decline began well after the current period of high biomass of salmon in the ocean started (Figure 1), and well after hatchery releases into the North Pacific peaked and stabilized at 5 billion per year in 1988 (Figure 7).

Size at maturity and age at maturation has declined over the last three decades for Alaska Chinook salmon stocks from southern Southeast Alaska to the Yukon River (Lewis et al. 2017). The size declines are coincident with high abundances and biomass of the Big Three (pink, chum, and sockeye salmon). Could competitive interactions with the Big Three be driving the decline? There are several lines of evidence that indicate this is not the case.

First, the differences in marine ecology we noted in the preceding paragraphs suggest that Chinook salmon, by their propensity to utilize deeper depth strata and distribute more broadly on shelf and slope areas during marine residency, are segregated to a large degree from other salmon in their use of ocean habitats with correspondingly different temperatures, prey fields, and predator complexes. These differences are exemplified by the growth differences of Chinook salmon and coho salmon in their first winter at sea. Although approximately the same size in the fall, by the following year coho salmon of the same ocean cohort are over three times larger than Chinook salmon (Riddell et al. 2018).

Second, while Lewis et al. (2017) found predominately declining size for older (ocean age 3 and 4) Chinook salmon, size of ocean age 2 fish has generally not changed over the time period (Figure 12). If competition was driving the size decline, competition should be most intense for the younger age Chinook salmon, which have a more extensive overlap in size and type of prey with other salmon. Also, lower ocean growth in Pacific salmon is typically associated with shifts in age distribution towards older ages (Hard et al. 2008), but instead average age at maturity has declined. Thus there has not been an apparent decline in growth of 1-ocean and 2-ocean age Chinook salmon during the “high abundance” period.

Third, British Columbia Chinook salmon have been increasing in average size over this time period (Jeffrey et al. 2017). These authors found a positive relationship between biomass of North American salmon and British Columbia Chinook salmon average size, indicating that size was a function of the same favorable ocean conditions sustaining the record overall biomass.

Size declines of Chinook salmon are not new in Alaska waters; Ricker (1981) found a significant decrease in size of Chinook salmon harvested in the SEAK troll fisheries from 1960 to 1974, and identified selective fishing for older, larger fish as a factor in the decline. Research by Hard et al. (2009) and others indicate selective harvesting of large older age groups of Chinook salmon can introduce reductions in fitness and cause genetic drift in growth, size, and age of maturity due to the heritability of these characteristics. However, fishing alone does not explain the decline across the geographic range of Alaska Chinook salmon, because the degree to which populations are exposed to directed selective fishing varies considerably across the range. It also does not explain the sudden decline in marine survival, as fishing pressure and exploitation rates in the ocean have not increased (CTC 2018b).

Another large predator besides humans also target larger, older Chinook salmon. Resident killer whales have been found to preferentially feed on larger Chinook salmon (Olesiuk et al. 1990; Hanson et al. 2010). In northern British Columbia and southern Alaska waters killer whales have increased at annual rates of 2.9% and 3.5%, respectively (Hilborn et al. 2012; Matkin et al.2014), more than doubling their abundance since the 1970s. Intense predation on larger fish, coupled with lower marine survival, could contribute to the changes at size at age and age at maturity of Alaska Chinook salmon.

There is substantial evidence that much of the variation in Chinook salmon marine survival is due to conditions in the first summer and winter at sea (e.g., Greene et al. 2005: Duffy and Beuchamp 2011; Sharma et al. 2013; Murphy et al. 2017). Local conditions encountered by juvenile Chinook salmon during early marine residency thus play an important role in determining year-class strength. However, the concordant trends in survival across such a broad geographic range indicate that large-scale processes are affecting stocks across regions. Increasing populations of pinnipeds could also be affecting early marine survival. Chasco et al. (2017) estimated predation on juvenile Chinook salmon by pinnipeds in Puget Sound had increased an order of magnitude from 1970 to 2015, and was now, expressed as adult equivalences, more than six times greater than the combined commercial and recreational catches in Puget Sound.

For Pacific salmon species that spend multiple years at sea, annual marine survival generally increases with size and age (Ricker 1976). For cohort reconstruction of Pacific northwest and SEAK Chinook salmon, natural mortality is assumed not to vary interannually and to decrease with ocean age, from 40% for ocean-age 1, 30% for ocean-age 2, 20% for ocean-age 3, and 10% for ocean-age 5 or older (Sharma et al. 2013; CTC 2018b). These assumptions are simplistic and undoubtedly not always correct, but there is little information to better inform the assumptions. Changes in the North Pacific ecosystem, such as increased killer whale populations, could introduce more mortality at older ages, and further depress realized survival during periods of poorer environmental conditions for Chinook salmon.

VI. **Conclusions**

In spite of concerns over exceeding the carrying capacity of the ocean, Alaska salmon have been at unprecedented levels of abundance over the past 25 years. Conditions influencing survival in the ocean, rather than density-dependent interactions, seem to be driving both the high abundance at the basin-scale and the high variability in salmon populations at local and regional scales. The Alaska salmon harvest over the past 25 years has been characterized by sustained high production from wild stocks and large contributions of hatchery fish. Enhancement has made large net contributions to supplement wild stock harvest in some areas of the state. Density-dependent interactions have been observed at different life history stages of salmon and in nearshore and oceanic habitats during this period, but have not constrained the recovery of Alaska salmon from its nadir in the 1970's, or it sustained high abundance. Rather, density independent responses to climatic factors affecting ocean conditions appear to have largely driven the high and variable productivity of Alaska salmon.

Recent climatic and oceanographic events such as the marine heat waves of 2004/2005 and 2014/2015 in the Gulf of Alaska are demonstrative of the intrinsic variability of ocean conditions affecting salmon at local and regional scales. Will density-dependent interactions become increasingly important if and when ocean conditions become less favorable to salmon? Would then large releases of hatchery fish put wild stocks in more jeopardy? Or will hatchery fish provide a buffer to sustain fisheries when wild stock productivity is low in response to varying environmental conditions? The enhancement program in PWS offers empirical support for the latter concept. Even during the recent period of generally high productivity, wild pink salmon production in PWS has fluctuated dramatically (Figure 9). In 2009, wild stock harvests were below one million fish, while over 17 million hatchery fish were harvested. By focusing harvest on hatchery fish, managers met escapement goals (Gaudet et al. 2017). Subsequently, both hatchery and wild pink salmon set new historical highs for harvest and production in 2013 and 2015. Large releases and returns of hatchery pink salmon in years of both low and high wild stock abundance did not limit the production potential of the wild stocks.

Authors

Alex Wertheimer retired after 35 years working for the National Marine Fisheries Service Fisheries as a Fisheries Research Biologist in Alaska. He has carried out research and published extensively on salmon in Alaska on issues including salmon enhancement technology and strategies, hatchery and wild salmon interactions, bycatch mortality of Pacific salmon, the impact of the Exxon Valdez oil spill on salmon in Prince William Sound, and the nearshore and pelagic marine ecology of Pacific salmon. He was a member of the science team that wrote the Alaska Genetic Policy, the National Oceanic and Atmospheric Administration (NOAA) Biological Review Team assessing status of Chinook salmon in the Pacific northwest, and the Chinook Technical Committee of the Pacific Salmon Commission. He was awarded the Wally Nuremberg Award for Fisheries Excellence by the American Fisheries Society Alaska Chapter. Upon retirement in 2009 after 35 years of Federal service, he received the NOAA Distinguished Career Award. Since retirement, he has continued to consult on scientific studies and reviews, including forecasting of Pacific salmon, quantification of by-catch mortality, and the Pacific Salmon Recovery Plan. He currently serves on the Pacific Salmon Commission’s Standing Committee on Scientific Cooperation and on the Science Panel overseeing the Alaska Hatchery Research Program. He is the President of the Board of Directors of the Southeast Alaska Land Trust, and is a member of the Board of Directors for DIPAC, Inc., a major non-association private non-profit hatchery based in Juneau. He was supported in his work on this paper by the Northern Southeast Alaska Aquaculture Association.

William (Bill) Heard retired in 2012 after 52 years of Federal Service as Fishery Research Biologist. Much of his career was with NOAA Fisheries Alaska Fisheries Science Center’s Auke Bay Laboratories, but he also worked for the U.S Fish and Wildlife Service Bureau of Commercial Fisheries and Bureau of Sport Fisheries and Wildlife. He did extensive research and published frequently on Alaska salmon and other fishes. Bill authored or co-authored peer reviewed publications on all five species of North American Pacific salmon. For over 35 years he supervised research at Little Port Marine Research Station focused on enhancement technology and ecology of pink, coho and Chinook salmon. He actively participated on many technical committees and focused groups involved with Alaska, National, and International salmon issues, including Governor Jay Hammond’s Fisheries Council concerned with policies and development of salmon hatcheries in Alaska, North Pacific Fishery Management Council Plan Development Team for Fishery Management Plan (FMP) on salmon fisheries, Pacific Salmon Commission (PSC) Northern Boundary Technical Committee, North Pacific Anadromous Fish Commissions (NPAFC) Committee on Scientific Research and Statistics (CSRS) and U.S.-Japan Natural Resources (UJNR) Aquaculture Panel involved with salmon hatcheries in Japan. Participating in NPAFC, PSC, and UJNR afforded opportunity for travel to most North Pacific rim countries with populations of salmon including Russia and Republic of Korea . Bill received fre awards for research excellence in fisheries from ADF&G, Alaska Chapter American Fisheries Society, U.S. Department of Commerce Bronze Medal Award, NOAA Fisheries Employee of the Year and NOAA Fisheries Distinguished Career Award. He was an Affiliate Associate Professor, University of Alaska Fairbanks, School of Fisheries and Ocean Sciences.

Figures

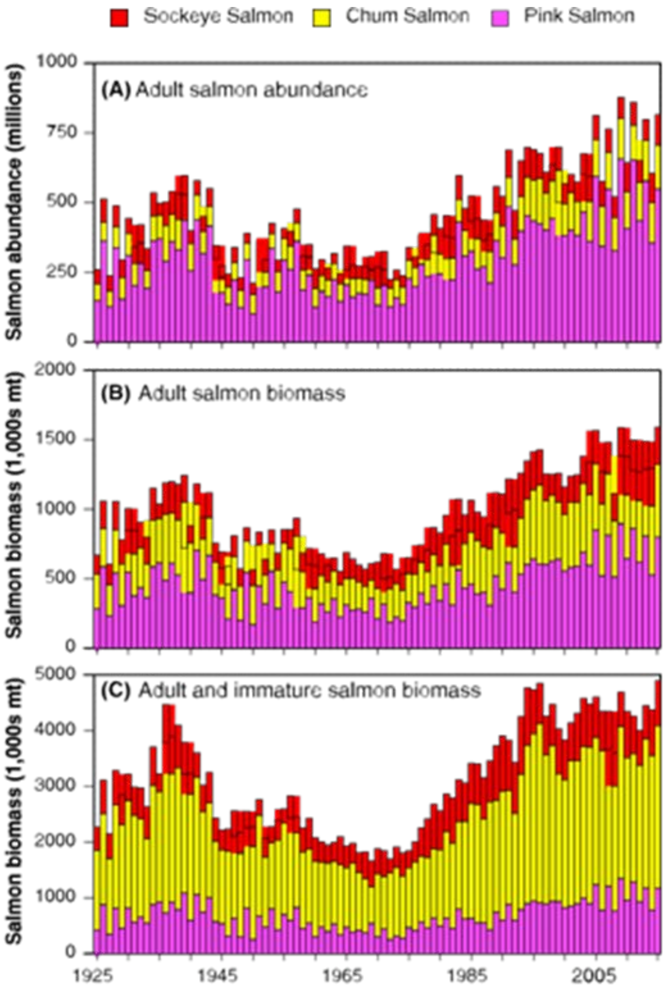

Figure 1. (A) Abundance (millions of fish), (B) adult biomass (thousands of metric tons), and (C) adult and immature biomass (thousands of metric tons) of Sockeye Salmon, Chum Salmon, and Pink Salmon in the North Pacific Ocean, 1925–2015. From Ruggerone and Irvine (2018).

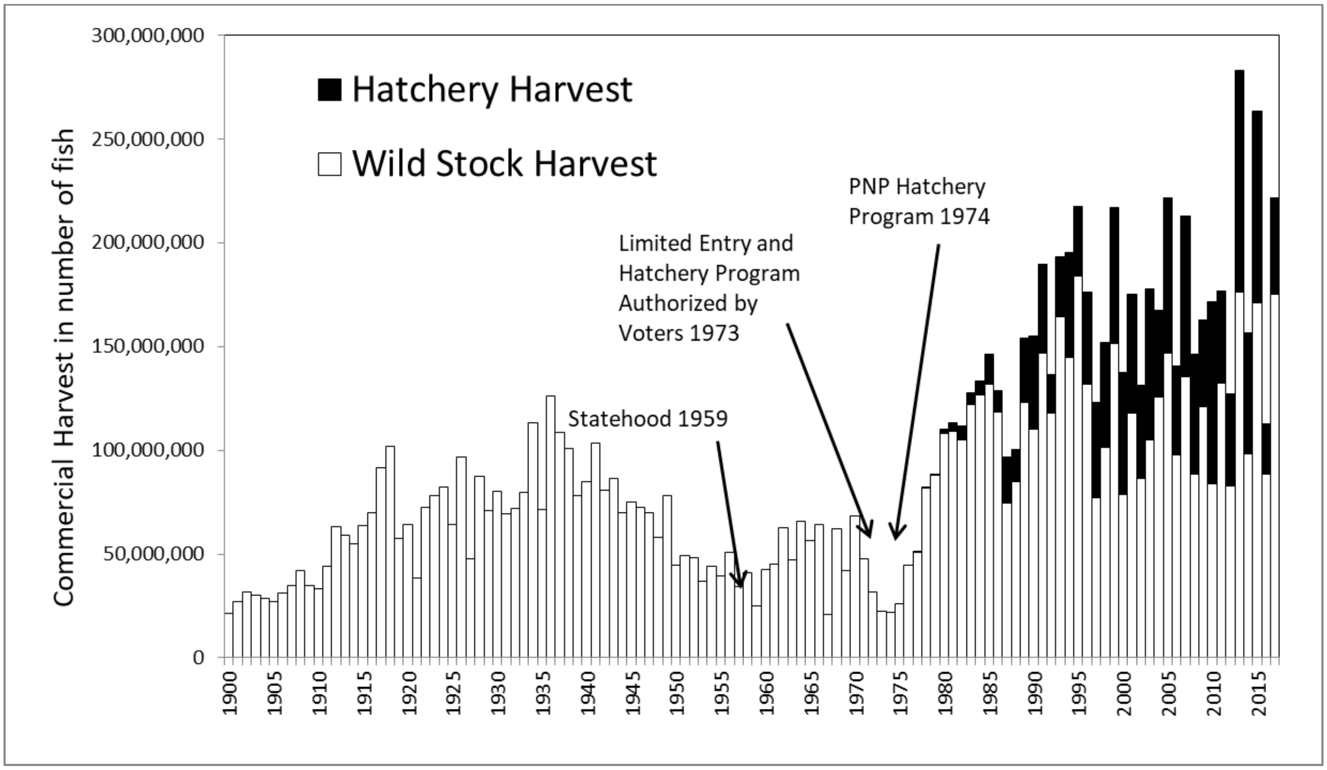

Figure 2. Commercial salmon harvest in Alaska, 1900-2017. From Stopha (2018).

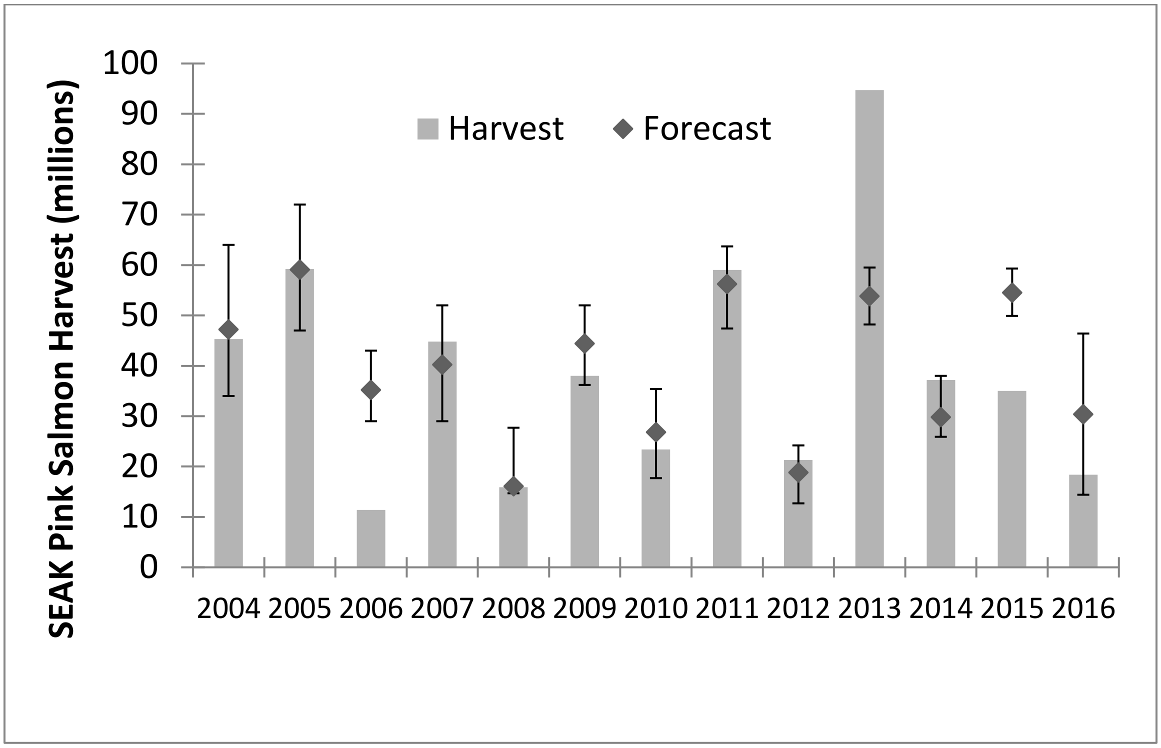

Figure 3.—Southeast Coastal Monitoring (SECM) project pink salmon harvest forecasts for Southeast Alaska (SEAK; symbols), associated 80% confidence intervals (lines), and actual SEAK pink salmon harvests (grey bars), 2004-2016.

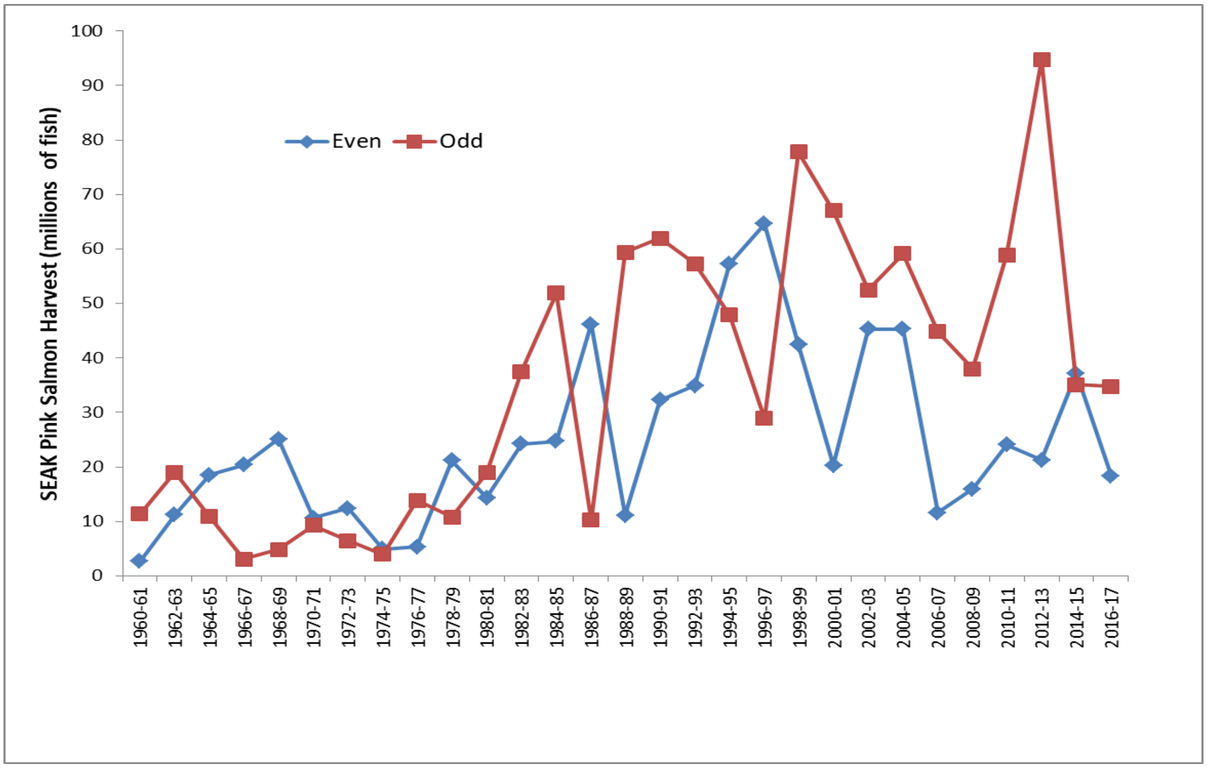

Figure 4. Even- and odd-year harvests of Southeast Alaska pink salmon, 1960-2017. Data are from Alaska Department of Fish and Game catch statistics.

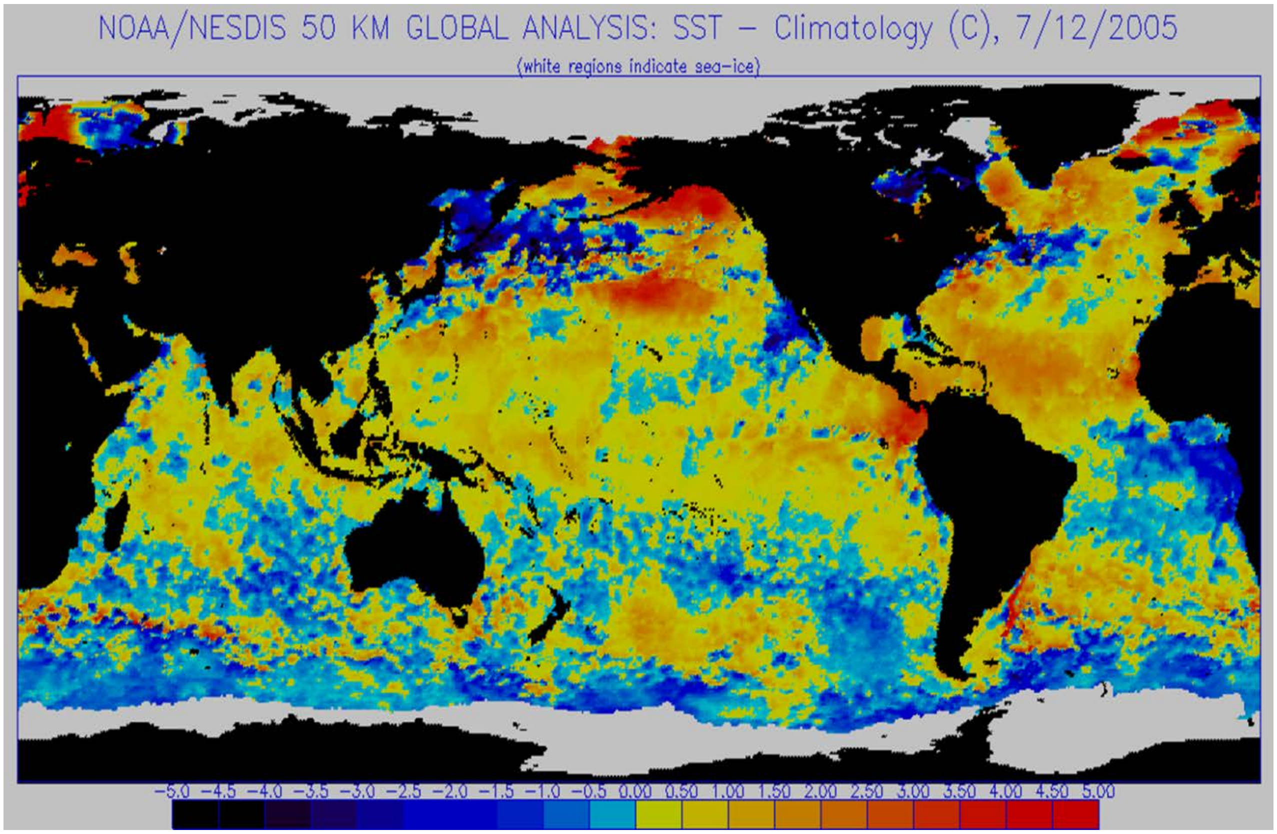

Figure 5. Sea surface temperature anomalies, July 12, 2005. NOAA Satellite and Information Service, National Environmental Satellite, Data, and Information Service (NESDIS) http://www.osdpd.noaa.gov/PSB/EPS/EPS.html

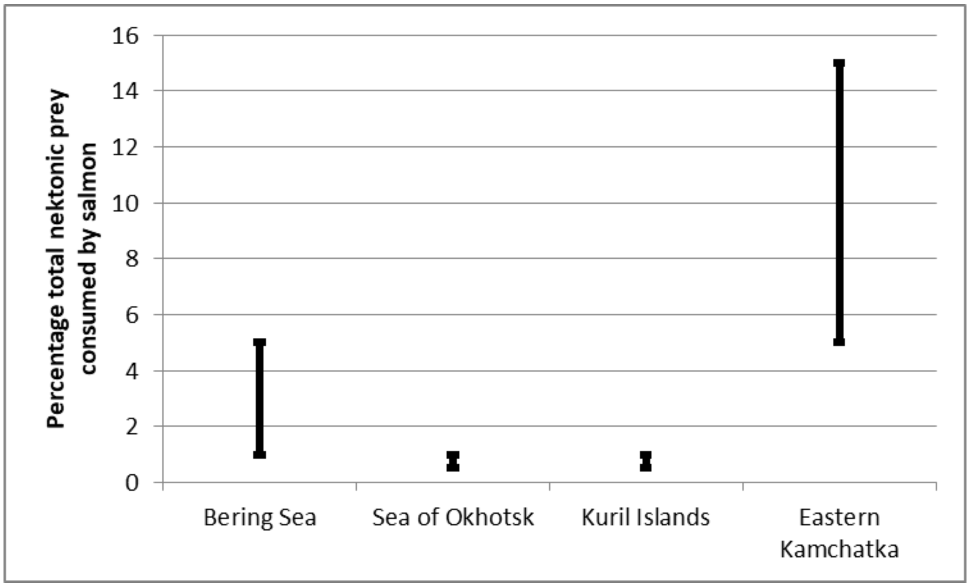

Figure 6. Percentage total nektonic prey consumed by salmon in the western North Pacific Ocean. Estimates are from Shuntov et al. (2017).

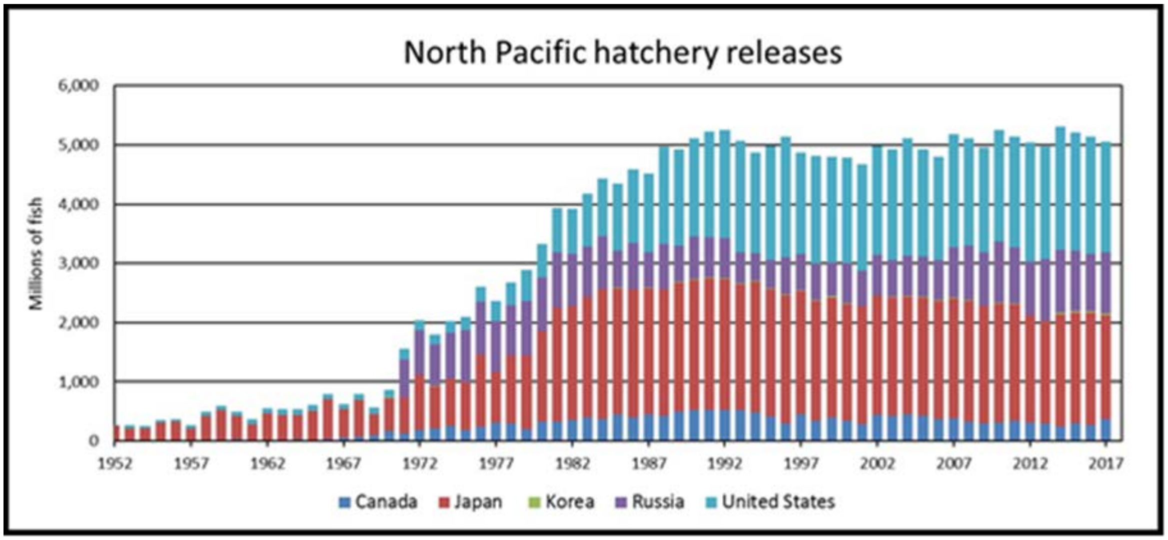

Figure 7. Hatchery releases of salmon into the North Pacific Ocean, 1952-2017. Source: North Pacific Anadromous Fish Commission.

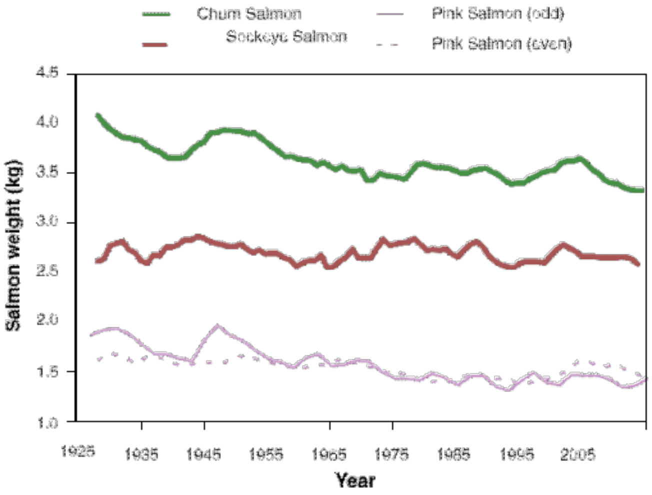

Figure 8. Average weight of pink salmon, chum salmon, and sockeye salmon captured in commercial fisheries, 1925-2015. From Ruggerone and Irvine (2018).

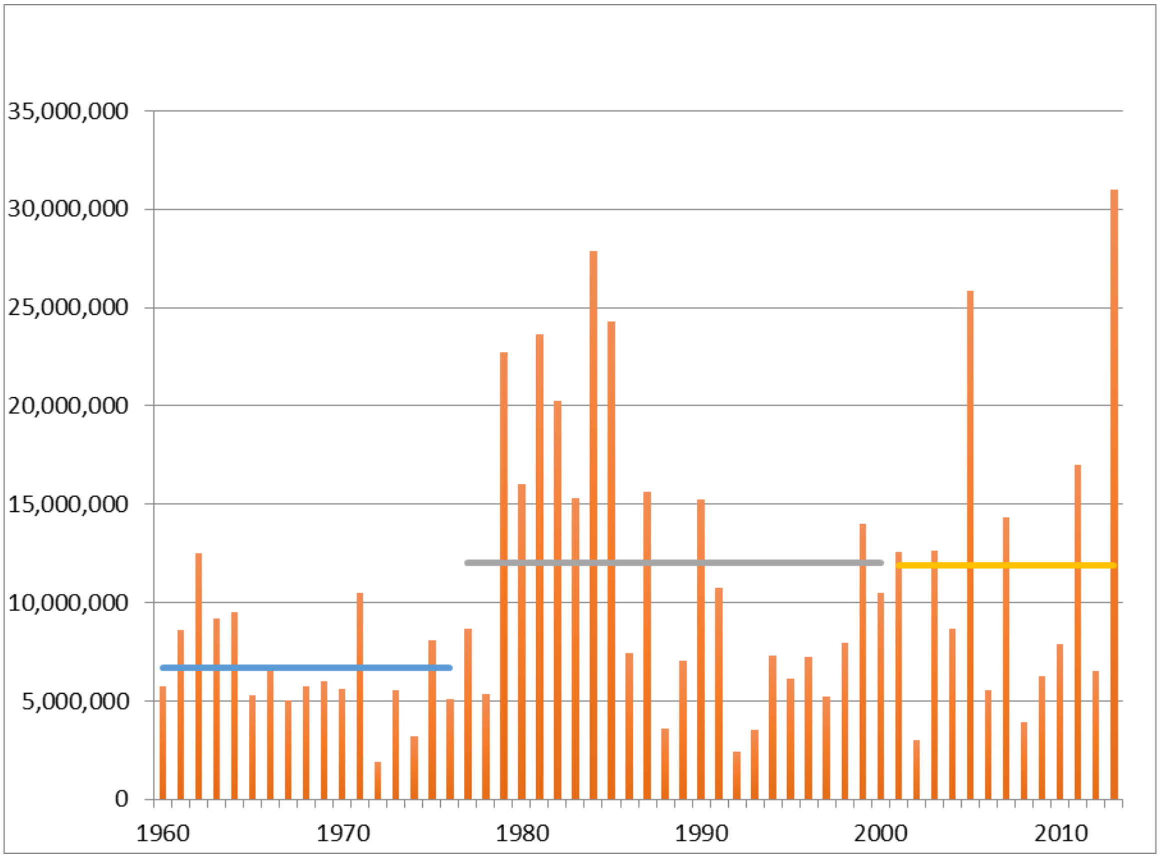

Figure 9. PWS Wild Pink Salmon Production for 1960-2013. Lines indicate average production for pre-hatchery years (1960–1976) and two hatchery time periods: 1977–2000 and 2001–2013. From Gaudet et al. (2017).

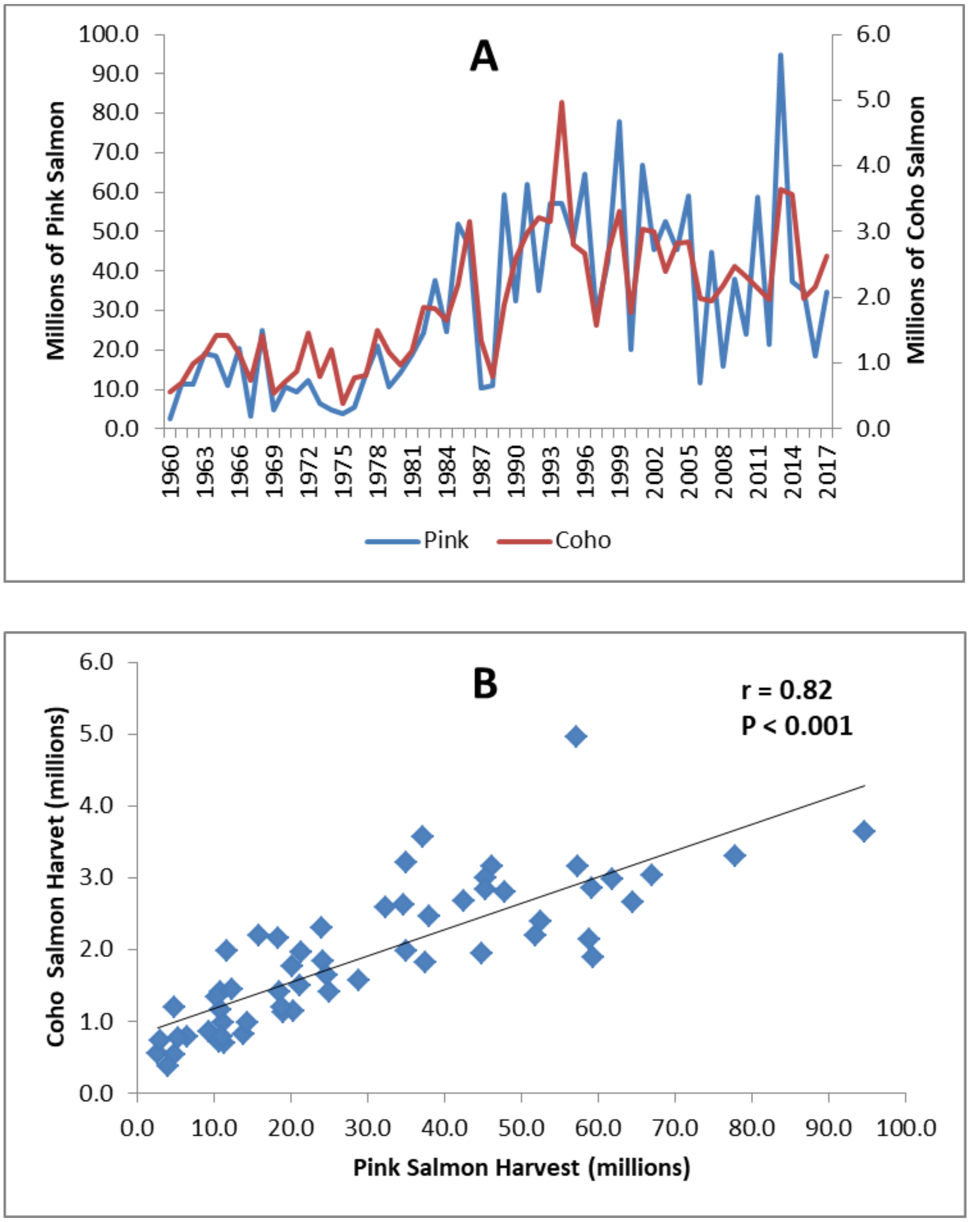

Figure 10. Commercial harvest of Southeast Alaska pink and coho salmon, 1960-2017 (A), and their correlation (B). Data are from Alaska Department of Fish and Game catch statistics.

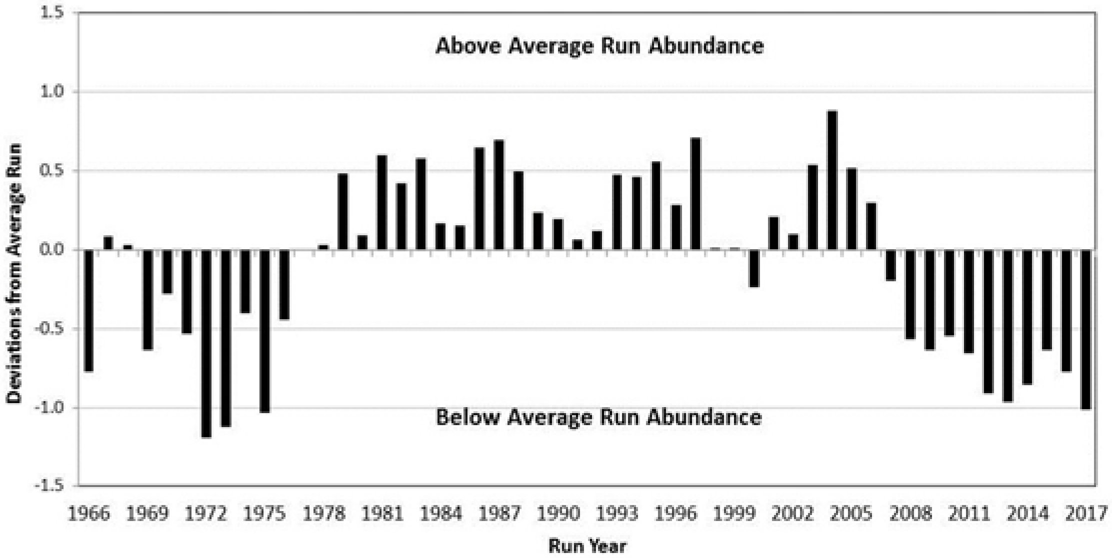

Figure 11–Average of standardized deviations from average run abundance for 21 stocks of Chinook salmon in Alaska (the Unalakleet, Nushagak, Goodnews and Kuskokwim in western Alaska; the Chena and Salcha on the Yukon River; the Canadian Yukon, the Chignik and Nelson on the Alaska Peninsula; the Karluk and Ayakulik on Kodiak Island; the Deshka, Anchor and late run Kenai in Cook Inlet, the Copper in the northeastern Gulf of Alaska, and the Situk, Alsek, Chilkat, Taku, Stikine, and Unuk in Southeastern Alaska). From CTC (2018a).

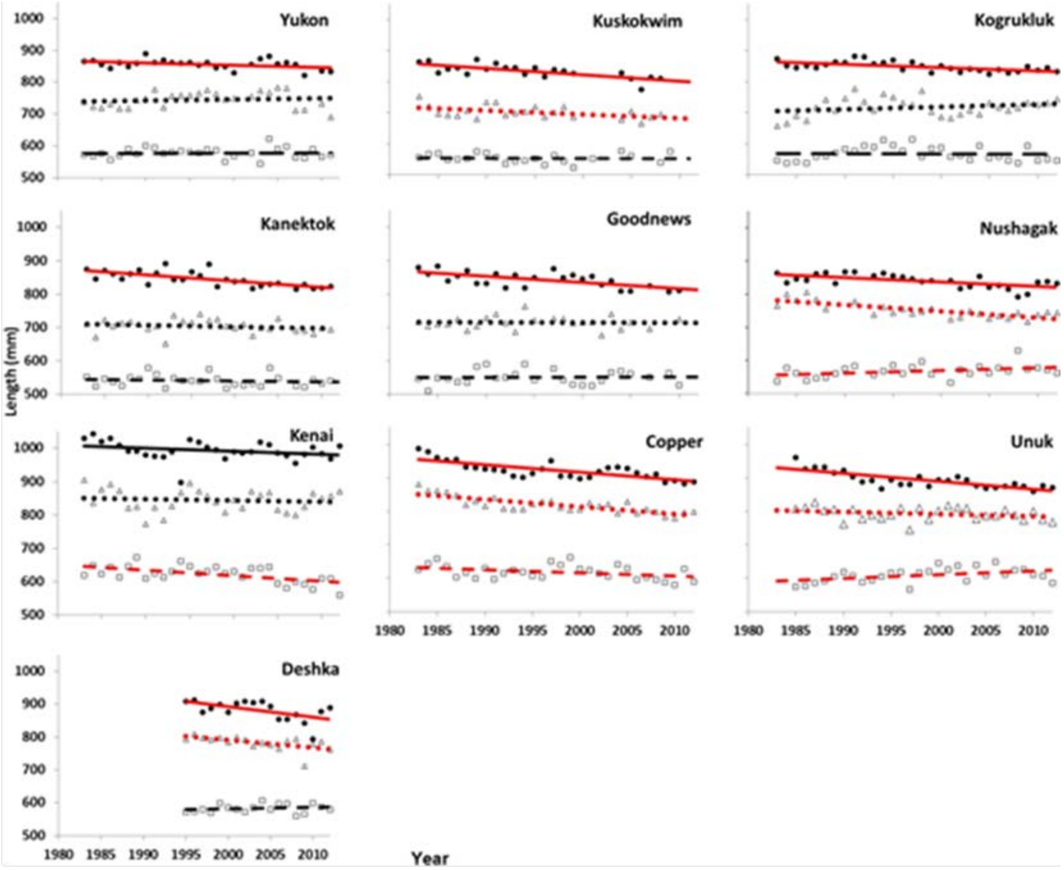

Fig 12. Linear regression of mean annual length (mm) Chinook salmon by stock, age class, and year. Closed circles and solid line = 4-ocean; triangles and dotted line = 3-ocean, open square and dashed line = 2-ocean. Red lines indicate slopes significantly different from zero ($P < 0.05$). From Lewis et al. (2017).

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