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Numbers and Biomass of Natural- and Hatchery-Origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925–2015

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Abstract
Numerical abundance and biomass values presented here for Pink Salmon *Oncorhynchus gorbuscha*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka* in the North Pacific Ocean span 90 years (1925–2015), representing the most comprehensive compilation of these data to date. In contrast to less populous species of salmon, these species are more abundant now than ever, averaging 665 × 10^6 adult salmon each year (1.32 × 10^6 metric tons) during 1990–2015. When immature salmon are included, recent biomass estimates approach 5 × 10^6 metric tons. Following an initial peak during 1934–1943, abundances were low until the 1977 regime shift benefited each species. 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%). 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. Although production of natural-origin salmon is currently high due to generally favorable ocean conditions in northern regions, 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 (Prince William Sound 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. Density-dependent effects are apparent, and carrying capacity may have been reached in recent decades, but interaction effects between hatchery- and natural-origin salmon are difficult to quantify, in part because these fish are rarely separated in catch and escapement statistics. The following management changes are recommended: (1) mark or tag hatchery salmon so that they can be identified after release, (2) estimate hatchery- and natural-origin salmon in catches and escapement, and (3) maintain these statistics in publicly accessible databases.

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Pacific salmon *Oncorhynchus* spp. are iconic species in North America and Asia that support subsistence, recreational, and commercial fisheries throughout the North Pacific Rim. Salmon are also recognized as keystone species in marine and freshwater habitats, and changes in their abundances may reflect changing climate patterns, competition effects, habitat conditions, and fishery management actions. Agencies routinely collect data on salmon harvests and spawning escapement, but most do not generate total adult salmon abundance estimates (i.e., catch plus spawner escapement) or determine the contribution of hatchery fish to these statistics. In addition, the potentially significant ecological role of immature salmon that may compete with older members of the same or other species is rarely considered because of a lack of recent estimates of their biomass. These data deficiencies can result in potentially misleading interpretations of mechanisms responsible for changing production trends of wild and other natural-origin salmon. In this paper, we refer to nonhatchery salmon as natural-origin salmon rather than wild because of various interpretations of what constitutes a wild salmon (e.g., DFO 2005). Hatchery salmon originate from hatcheries; all other salmon, including offspring of hatchery salmon that spawn in the wild, are natural-origin salmon.

In order to track salmon status, manage salmon in mixed-stock fisheries, and relate population trends to changing climate and environmental conditions, investigators have employed various approaches to assess numerical abundance and biomass trends for natural-origin and hatchery adult salmon (Eggers 2009; Ruggerone et al. 2010). Hatchery salmon production increased rapidly from the 1970s through the early 1990s, raising concerns about potential competitive interactions between hatchery- and natural-origin salmon in the ocean (Cooney and Brodeur 1998; Zaporozhets and Zaporozhets 2004; Holt et al. 2008), reduced fitness of natural-origin salmon caused by interbreeding with hatchery salmon that stray to natural spawning areas (Araki et al. 2008; Christie et al. 2014, 2016), and complications arising in mixed-stock fisheries (Naish et al. 2008). Increasing evidence indicates that high abundances of salmon in the ocean can alter the food web (e.g., zooplankton; Shiomoto et al. 1997; Zavolokin et al. 2014; Batten et al., in press), which can lead to competition for food among salmon, including those originating from adjacent continents (Ruggerone et al. 2003, 2012). This view is not universal, however. Shuntov et al. (2017) presented an alternative perspective held by some Russian scientists. Those authors found that salmon consume a small portion of the prey in the western North Pacific Ocean, and they suggested that the role of salmon in the ecosystem is rather moderate. Time series of salmon abundances may help researchers to critically evaluate these opposing viewpoints.

Here, we describe long-term (1925–2015) trends in natural- and hatchery-origin salmon abundance and biomass that include recent values affected by anomalously warm temperatures in the northeast Pacific Ocean (Bond et al. 2015), and we make these data available for other researchers to use (see Supplementary Tables S.1– S.24 available separately online). Our primary objectives are to (1) provide annual numerical and biomass estimates of the abundance (i.e., catch plus escapement) of natural- and hatchery-origin adult Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka* by region of the North Pacific Ocean, (2) expand adult biomass values to include the biomass of immature salmon in the ocean, and (3) present updated numbers of juvenile salmon released from hatcheries (NPAFC 2017a). Our abundance values build upon earlier time series reported by Ruggerone et al. (2010; numerical abundance) and Eggers (2009; biomass). We did not estimate abundances of Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Cherry Salmon *O. masou*, or steelhead *O. mykiss*, in part because (1) considerably more effort is needed to estimate natural-origin versus hatchery-origin components of these species and (2) these salmonids are much less abundant, representing approximately 1.25, 2.72, 0.15, and 0.02%, respectively, of the total reported catch by weight of Pacific salmon during 1992–2015 (NPAFC 2017b).

METHODS

Detailed methodology for estimating annual abundances of natural and hatchery adult Pink Salmon, Chum Salmon, and Sockeye Salmon (Tables S.1–S.8) in the North Pacific Ocean was previously described by Ruggerone et al. (2010) and was updated by Irvine and Ruggerone (2016). Here, we briefly summarize this methodology and highlight changes.

To estimate the total annual abundances of adult Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, we compiled annual data for 1952–2015 on catches (primarily commercial), spawner abundances, harvest rates, and abundances of natural- and hatchery-origin salmon from South Korea, Japan, Russia, Alaska, British Columbia, Washington State, and the Columbia River (Tables S.9–S.12). Small numbers of Chum Salmon occur along the Oregon coast (i.e., south of the Columbia River), but no directed fishery has occurred on these fish since 1962, and abundance estimates are incomplete (Johnson et al. 1997). In Asia, Chum Salmon have been reported in China (Chen et al. 2005), and Pink Salmon have been reported in North Korea (Heard 1991; Kim et al. 2007). Chum Salmon likely occur in North Korea and Pink Salmon likely occur in China since these species are found south and north of these locations. These presumably small populations are not well studied and are not considered further.

Data used to estimate abundances of salmon returning to Asia originated primarily from North Pacific Anadromous Fish Commission (NPAFC) documents and earlier International North Pacific Fisheries Commission documents (e.g., Hirabayashi et al. 2016; Hong et al. 2016; Klovach et al. 2016), whereas data for North American salmon originated primarily from agency and other regional reports that were the basis for North American salmon data supplied to the NPAFC. The resulting data series were aggregated into major Pink Salmon, Chum Salmon, and Sockeye Salmon population groups within 21 regions (Figure 1). These large aggregations had the benefit of greatly reducing problems of poor stock identification in catches that might, for example, incorrectly allocate fish from one population to another if the spatial extent of units was smaller.

Approaches to Estimating Total Salmon Spawning Abundances

Reported catch was assumed to be complete except in Russia, where poaching can be significant (Clarke et al. 2009). In contrast, spawning escapements were often indices of total abundance or were not reported. Therefore, the first task for most regions was to estimate total abundances of salmon escaping the fisheries and spawning naturally so that total abundances could be estimated and standardized for comparison across the North Pacific Ocean. Total spawning counts were typically only reported

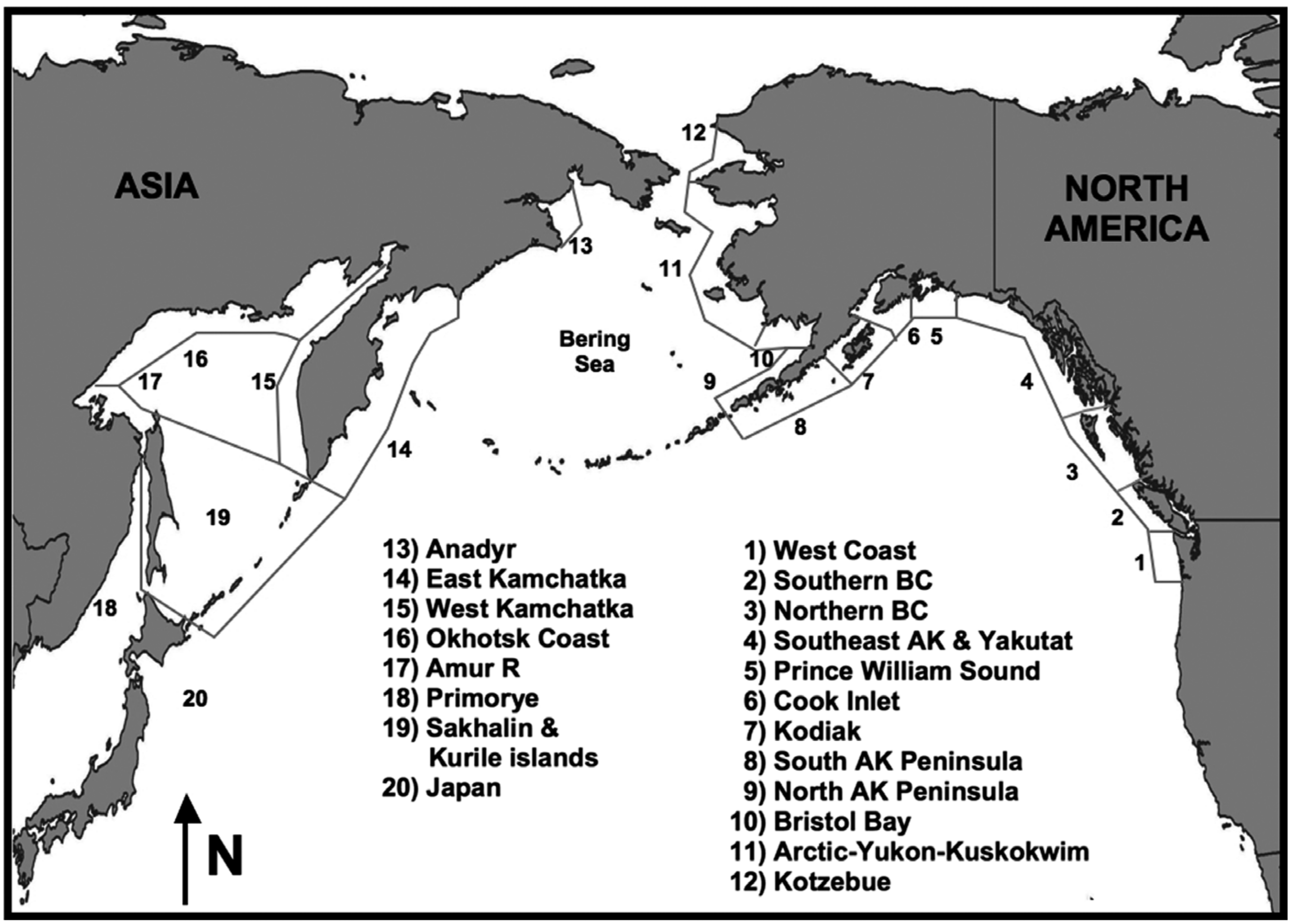

FIGURE 1. The approximate geographic locations of regional stock groups. Region 1, the West Coast of the United States, includes the Columbia River. Region 2 includes southern British Columbia (BC) south of the BC central coast (~51°N). Region 3, northern BC, includes central and northern BC. Region 4 encompasses Southeast Alaska (AK), including the Yakutat coast. The central Alaska region extends from the Bering River (~60°N), near Prince William Sound in region 5, westward to Unimak Island (~166°W), thereby including regions 5–8. Western Alaska includes regions 9–12 (that is, all North American drainages flowing into the Bering Sea from Unimak Island to Kotzebue). Data for east Kamchatka and west Kamchatka (regions 14 and 15) are separated from data for the Russian mainland and islands, which include the Okhotsk coast, Amur River, Primorye, Sakhalin and Kurile islands, and relatively small runs to the Anadyr River. Region 20, Japan, includes the islands of Hokkaido and Honshu. South Korea (region 21) is not shown.

for major Sockeye Salmon stocks in Alaska and British Columbia and for each species in each region of Russia (see Ruggerone et al. 2010; their Table 1). Methods for estimating spawning escapement in each country are summarized by the NPAFC (2017c). One or more of the four following approaches was used to estimate total abundance when total spawning escapement was not available.

Approach 1.— In much of British Columbia (BC) and Alaska, where spawning data were intermittently missing for some stocks within a region but were available for other stocks in the same region, we systematically filled in the missing values by interpolating values from the other stocks within the region. In southern BC, we revised previous abundance estimates of natural-origin salmon, including the 2015 estimates, using the methods described by Irvine and Ruggerone (2016).

Approach 2.— In northern BC and parts of Alaska, annual estimates of spawning abundance were consistently underestimated because coverage of spawning areas was incomplete. In Alaska, we used information from area management reports (e.g., Anderson et al. 2016; Gray et al. 2016; Jones et al. 2016; Haught et al. 2017; these and others available at www.adfg.alaska.gov/) and fishery managers to expand index counts. These expansions were based on the approximate proportion and relative size of total streams surveyed in the region and the proportion of total spawners counted within the surveyed streams. For BC north of Vancouver Island, return (and escapement) data were provided by Karl English (LGL Ltd., Sidney BC, personal communication); the procedures to generate these estimates were documented by English et al. (2013, 2016) and were reviewed by Price et al. (2017). Salmon abundances were estimated using procedures that ranged from simple summation of annual catch and escapement estimates to complex run reconstructions. Northern BC estimates for 2015, updated from Irvine and Ruggerone (2016), were generated for Chum Salmon and Sockeye Salmon based on high correlations between spawner escapements and total returns for the previous decade ($r^2 = 0.88$ and 0.92, respectively), whereas estimates for Pink Salmon were the mean of previous odd-year returns (2005–2013).

Approach 3.— In many areas, including Asia, spawning abundance could not be reliably estimated in some years; therefore, we approximated spawning abundance and total adult abundance values from catch data and harvest rate estimates. In most of these cases, we used a regression of harvest rate (proportion) on $\log_e$(catch) during years for which full data were available to estimate harvest rate as a function of catch (e.g., Rogers 1987). In tests with simulated data, this regression method provided better results than using a simple overall average of observed harvest rates (Ruggerone et al. 2010).

Approach 4.— In a few areas, which typically involved stocks with low abundances and low fishing effort, harvest rates were based on fishing effort and/or the harvest rates of other monitored species. For example, in Southeast Alaska, where only 82 of approximately 1,200 Chum Salmon streams were examined for peak period spawners, we assumed that the harvest rate on natural-origin Chum Salmon was 90% of the rate for Pink Salmon because natural-origin Chum Salmon were captured incidentally in fisheries targeting Pink Salmon (Eggers and Heinl 2008).

The degree of reliance on the four approaches used to address missing or questionable spawning abundance varied among regions, species, and years. Total abundance (catch plus escapement) estimates were available for only one-quarter and one-third of the stock-year combinations for North America and Asia, respectively. Catch plus expanded index spawner counts (approaches 1 and 2) were used in about one-third of the stock-years for North America, but this method was not used for Asia. The regression method (approach 3) for estimating harvest rate was the primary method for approximately one-quarter and two-thirds of the stock-years for North America and Asia, respectively, mainly during early years. An assumed harvest rate (approach 4) was used to estimate total abundance in about one-fifth of the stock-years for North America, primarily for relatively small stocks that were incidentally harvested, and was rarely used for Asia.

Data for Sockeye Salmon were the most complete and reliable, followed by Pink Salmon and then Chum Salmon. For example, in North America, approximately 50% of the final Sockeye Salmon abundance estimates were from agency reports, whereas only about 10% of reported Pink Salmon and Chum Salmon estimates were total counts. In Asia, approximately 60% of annual spawning abundance values were estimated from catch and harvest rates because spawning abundances were often not available for years prior to 1992.

Approaches to Estimating Hatchery- and Natural-Origin Salmon Abundances

Natural-origin salmon abundances in each region were typically estimated by subtracting estimates of hatchery salmon from total abundance estimates. Since hatchery-origin salmon that spawn naturally are rarely identified as such, their abundances are underestimated, and natural-origin abundances are overestimated. Salmon produced by spawning channels (e.g., in BC) were included with natural-origin salmon estimates. Estimates of hatchery salmon abundance are approximations, with the goal of capturing the magnitude of hatchery- versus natural-origin salmon production.

Abundances of hatchery salmon in Alaska were provided in annual agency reports (e.g., Stopha 2016), whereas values for the west coasts of Washington and Oregon were obtained from state biologists, agency Web sites, and Pacific Fishery Management Council reports (e.g., PFMC 2016;

WDFW 2017; A. Dufault, Washington Department of Fish and Wildlife, personal communication).

Estimates of adult hatchery salmon are rarely available in BC and Russia; therefore, we estimated adult hatchery salmon abundances by applying release-to-adult survival rates to releases of hatchery salmon (Ruggerone et al. 2010; NPAFC 2017a). References for salmon survival estimates in BC are listed by Irvine and Ruggerone (2016). For Russia, average survival rates of hatchery Chum Salmon (range of means = 0.24–0.64%; available from Zaporozhets and Zaporozhets 2004) were updated with annual values for the Sakhalin and Iturup islands (Kaev 2012). Survival of hatchery Pink Salmon from Sakhalin Island (average = 5.6%) and Iturup Island (average = 4.9%), which are primary hatchery regions in Russia, were updated with annual values provided by Kaev and Irvine (2016). In the Amur River, Russia, unusually high escapements of Chum Salmon were reported in 2007, 2009, and 2013. These estimates (20–100 million spawners) were based on very limited tag and recovery efforts (S. Zolotukhin, Pacific Research Fisheries Center, Khabarovsk, Russia, personal communication) and were therefore replaced by using approach 3.

Recent evidence suggests that many Pink Salmon in Japan originate from natural spawners rather than hatcheries, as previously thought (Miyakoshi 2006; Morita et al. 2006; Hoshino et al. 2008). We used estimates of hatchery- and natural-origin Pink Salmon production provided by Morita et al. (2006) and Ohnuki et al. (2015), recognizing high uncertainty in the estimates of natural-origin Pink Salmon. Recent evidence indicates that Japan produces some natural-origin Chum Salmon (Miyakoshi et al. 2012, 2013; Morita et al. 2013; Kitada 2014; Morita 2014) and that small numbers of natural-origin Sockeye Salmon are produced in the Bibi River, Japan (K. Morita, Hokkaido National Fisheries Research Institute, personal communication), but estimates are not available. Therefore, for Japan, we assumed that all Chum Salmon were of hatchery origin, and we did not estimate natural-origin Sockeye Salmon. Total abundance estimates in Japan assumed an 80% harvest rate on Pink Salmon and a 100% harvest rate on Chum Salmon, recognizing that in recent years, increasing numbers of Chum Salmon have been allowed to spawn naturally.

Chum Salmon production in South Korea is essentially all from hatcheries, although some adult salmon may escape capture in river weirs (Kang et al. 2016). Annual data are available from NPAFC reports (e.g., Hong et al. 2016).

High-Seas Harvests

Annual harvests of salmon in the Japanese high-seas fisheries (mothership, land based) and the more recent Japanese fishery in the Russian Exclusive Economic Zone (EEZ) are available from NPAFC (2017b). Significant high-seas catches prior to the establishment of the 370.4-km (200-nautical mile) EEZ off coastal states in 1977 (mean annual catch from 1952 to 1976 = 65×10^6 salmon, predominantly Pink Salmon and Chum Salmon) were much reduced after 1977 (1978–1991 mean = 21×10^6 salmon) and were essentially eliminated by 1992 prior to a United Nations global moratorium on all large-scale pelagic drift net fishing (NPAFC 2017b). Illegal high-seas fishing still occurs, and during 1993–2016, NPAFC countries detected 49 vessels conducting illegal drift net fishing operations for salmon, of which 21 vessels were apprehended (NPAFC 2017d). We did not attempt to quantify these illegal catches, as they appear to represent a small portion of the total abundance.

Proportions of mature and immature salmon harvested on the high seas were reported by Fredin et al. (1977), Myers et al. (1993), and Radchenko (1994). Catches of maturing and immature salmon were converted to adult-equivalent catch estimates based on monthly mortality schedules for each species (Ricker 1976; Bradford 1995). Continent of origin for the high-seas salmon catch was reported by Fredin et al. (1977), Harris (1988), and Myers et al. (1993). Some Sockeye Salmon—and to a much lesser extent Chum Salmon and Pink Salmon—harvested in the mothership fishery were from North American rivers. Sockeye Salmon and Chum Salmon originating from North America were allocated to western Alaska; harvests of North American Pink Salmon averaged less than 25,000 fish/year. The high-seas catch of Asian-bound salmon (after removing North American salmon from the total catch) was split into hatchery- and natural-origin fish based on the proportion of hatchery- versus natural-origin salmon returning to each region in Asia that year. Salmon harvested by Japan in the Russian EEZ were allocated to Russia. Allocation of adult-equivalent high-seas salmon catch to the country of origin led to markedly greater total salmon abundances in Russia and Japan than indicated by the terminal run size alone. Bycatch of salmon in nonsalmon fisheries was not included in our estimates of abundance (Radchenko 2017).

Salmon Biomass Estimates

Biomass of adult salmon returning from the North Pacific Ocean each year was estimated from abundance estimates and average weight of each species in each region (Tables S.13–S.16). We used NPAFC (2017b) catch data (numbers and biomass of fish) to calculate the average weight of salmon by species and region (Table S.24); natural- and hatchery-origin salmon weights were not independently estimated. Extreme outliers were compared with values in adjacent areas and years and with values provided in Bigler et al. (1996); when appropriate, these outliers were replaced with adjacent area values. To convert biomass of adult salmon to total biomass of salmon in the North Pacific Ocean (i.e., immature plus adult salmon; Tables S.17–S.20), we used annual species-specific ratios provided by Eggers (2009). Ratios varied relatively little from year to year compared with numbers of fish, so we used 2005 values for more recent years.

Abundance and Biomass Prior to 1952

We extended salmon abundance and biomass values (return and immature) for the North Pacific Ocean back to 1925 using values published by Eggers (2009). Since high-seas catches before 1952 were quite small, adult equivalent values were not calculated. Including these early annual values with more recent values produced a time series of total salmon abundance and biomass from 1925 to 2015 (Tables S.21–S.23).

RESULTS

Abundance and Biomass Trends

Total (natural- plus hatchery-origin) annual abundance of adult salmon was highly variable in the early part of the time series, peaking in the late 1930s at 530 × 10^6 fish (Figure 2A). Abundance declined near the end of World War II and remained near 310 × 10^6 fish until the mid-1970s, increasing to 543 × 10^6 fish after the 1977 ocean regime shift (1977–2004) and to 665 × 10^6 fish during 1990–2015. Total salmon abundance was higher during the most recent decade (2005–2015; 721 × 10^6 fish) than in any earlier period. During 1990–2015, numerical adult abundance was dominated by Pink Salmon (67% of the combined abundance of all three species), followed by Chum Salmon (20%) and Sockeye Salmon (13%).

Trends in adult salmon biomass reflected trends in numerical abundances and average salmon weights. Total annual adult biomass was relatively high during 1925–1943 (average = 1.0 × 10^6 metric tons), was low during 1958–1976 (average = 0.6 × 10^6 metric tons), and then steadily increased after the 1977 ocean regime shift until plateauing near 1.32 × 10^6 metric tons during 1990–2015 (Figure 2B). During 1990–2015, adult biomass was dominated by Pink Salmon (48% of the combined adult biomass of all three species), followed by Chum Salmon (35%) and Sockeye Salmon (17%).

Trends in adult plus immature salmon annual biomass in the ocean were strongly influenced by Chum Salmon, which are larger and spend more years at sea than Pink Salmon and Sockeye Salmon. Total adult plus immature salmon biomass was high during 1934–1943 (average = 3.6 × 10^6 metric tons), was low during 1960–1976 (average = 1.9 × 10^6 metric tons), and then steadily increased after the 1977 ocean regime shift until plateauing during 1990–2015 near 4.3 × 10^6 metric tons, with occasional annual values approaching 5 × 10^6 metric tons (Figure 2C). During 1990–2015, adult plus immature salmon biomass was dominated by Chum Salmon (60% of the combined biomass of all three species), followed by Pink Salmon (22%) and Sockeye Salmon (18%).

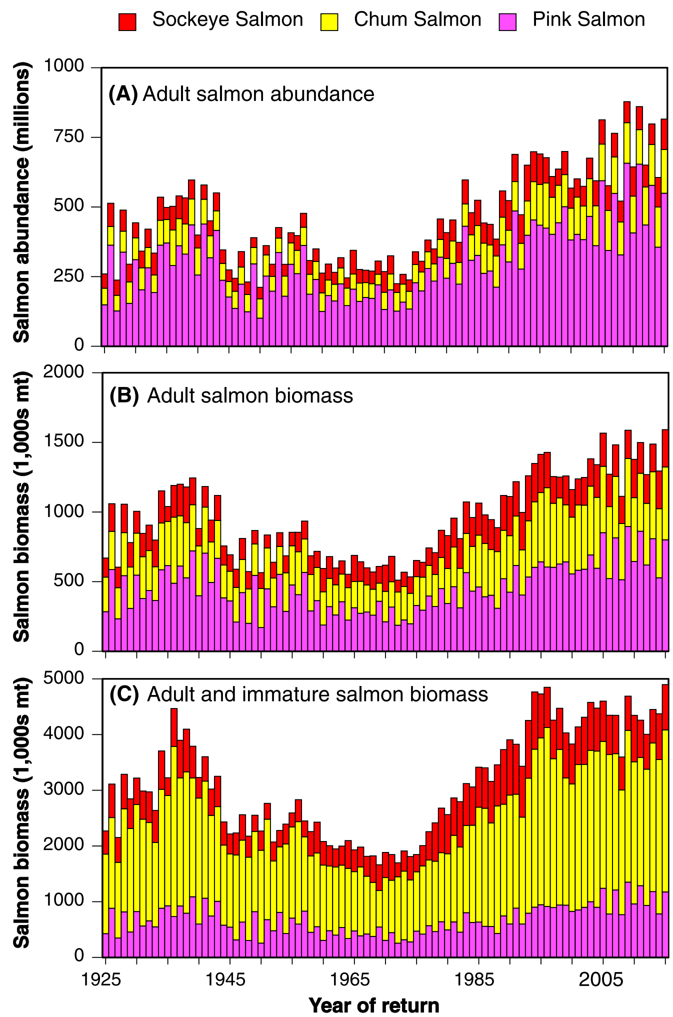

FIGURE 2. **(A)** Abundance (millions of fish), **(B)** adult biomass (thousands of metric tons), and **(C)** adult and immature biomass (thousands of metric tons) of Sockeye Salmon, Chum Salmon, and Pink Salmon in the North Pacific Ocean, 1925–2015. Values prior to 1952 are provided with permission by Eggers (2009).

Abundance and Distribution of Natural-Origin Salmon

Pink Salmon were the most numerous natural-origin species returning from the North Pacific Ocean and Bering Sea during 1925–2015, averaging approximately 280 × 10^6 fish each year, or approximately 69% of the combined abundances of natural-origin Pink Salmon, Chum Salmon, and Sockeye Salmon (Figure 3). Natural-origin Pink Salmon were especially numerous during 1990–2015, averaging 379 × 10^6 fish and up to 595 × 10^6 fish (81% of the combined abundance of the three species) in peak years, such as 2009 and 2011. Although even-year Pink Salmon tended to be more abundant than odd-year fish during 1925–1935, odd-year Pink Salmon were 27% more abundant than even-year Pink Salmon across all years, increasing to 37% higher abundance during 1990–2015. Approximately 61% of all natural-origin Pink Salmon originated from Asia in 1952–2015, remaining stable at 59% during 1990–2015. Natural-origin Pink Salmon were especially abundant along the Kamchatka Peninsula (27% of the total), other areas of Russia (29%), and Southeast Alaska (22%; Figure 4).

Sockeye Salmon abundance averaged 66×10^6 fish each year during 1925–2015 (16% of all species), increasing to 85×10^6 fish during 1990–2015 (16%; Figure 3). Approximately 86% of all natural-origin Sockeye Salmon originated from North America during 1952–2015, remaining stable at 85% during 1990–2015. Natural-origin Sockeye Salmon were most numerous in western Alaska, including Bristol Bay (49% of the total), central Alaska (17%), BC (17%), and the Kamchatka Peninsula (15%; Figure 4).

Annual abundance of natural-origin Chum Salmon averaged 58×10^6 fish across all years (14% of all species), declining to 53×10^6 fish during 1990–2015 (10%; Figure 3). In contrast to Pink Salmon and Sockeye Salmon, natural-origin Chum Salmon abundance did not increase immediately after the 1977 ocean regime shift. Approximately 51% of all natural-origin Chum Salmon originated from Asia during 1952–2015, remaining stable at 52% during 1990–2015. The large increase in total Chum Salmon beginning in 2009 primarily stems from the Amur River, Russia, where spawning escapement estimates are highly uncertain. Most natural-origin Chum Salmon originated from mainland Russia, including the Amur River (36%); the Kamchatka Peninsula (13%); and western Alaska (16%; Figure 4).

Abundance and Distribution of Hatchery Salmon

Annual releases of juvenile hatchery salmon into the North Pacific Ocean were relatively small during the early 1950s (average = $<2.5 \times 10^5$ per year; primarily Chum Salmon in Asia), increased rapidly from 1970 to 1990, and then stabilized to some degree through 2015 (Figure 5). During 1990–2015, approximately 4.4×10^9 hatchery salmon were released each year, consisting of 3.0×10^9 Chum Salmon, 1.36×10^9 Pink Salmon, and 79×10^6 Sockeye Salmon. Approximately 77% of juvenile Chum Salmon were produced in Asia, whereas 66% of Pink Salmon and 89% of Sockeye Salmon were produced in North America during 1990–2015. Production of juvenile hatchery salmon continues to increase in Russia (Sakhalin and Iturup islands; Klovach et al. 2016) and Alaska (e.g., Prince William Sound, Kodiak, and Cook Inlet; ADFG 2017), although at a slower rate than in the 1970s.

Abundance of hatchery-origin adult salmon increased steadily from the 1950s to the 1990s in response to increasing releases (Figure 3). During 1990–2015, annual production of hatchery-origin salmon averaged approximately 78×10^6 Chum Salmon, 61×10^6 Pink Salmon, and 3×10^6 Sockeye Salmon. Regions that contributed most to the overall production of hatchery-origin salmon were Japan (75% of total hatchery Chum Salmon production), central Alaska (64% of hatchery Pink Salmon; 84% of hatchery Sockeye Salmon), Southeast Alaska (11% of hatchery Chum Salmon; 11% of hatchery Sockeye Salmon), and southern Russia, primarily from the Sakhalin and Iturup islands (27% of hatchery Pink Salmon; 7% of hatchery Chum Salmon; Figure 4).

Contribution of Hatchery Salmon to Total Abundance and Biomass

During 1990–2015, a period of large and relatively stable salmon releases from hatcheries, the numerical contribution of hatchery salmon to total salmon abundance averaged approximately 60% for Chum Salmon, 15% for Pink Salmon, and 4% for Sockeye Salmon (Figure 6). Hatchery Chum Salmon were more abundant than natural-origin Chum Salmon from the mid-1980s through 2013. The decline in relative abundance of hatchery Chum Salmon in 2014 and 2015 (Figure 3) reflected the large return of natural-origin Chum Salmon to the Amur River, Russia, and the low survival of hatchery Chum Salmon from northern Honshu (Japan) due to losses caused by the tsunami in March 2011 (Watanabe et al. 2015). The contribution of hatchery salmon to total abundance averaged less than 2% in the 1950s and likely less than 1% in earlier years.

In Asia, hatchery production represented approximately 70%, 7%, and <1% of total abundances of Chum Salmon, Pink Salmon, and Sockeye Salmon, respectively, during 1990–2015. In North America, hatchery production contributed approximately 35, 22, and 4% to the total abundances of Chum Salmon, Pink Salmon, and Sockeye Salmon, respectively. Regions where hatchery production contributed substantially to total adult abundance included Japan, the Sakhalin and Iturup islands (Russia), South Korea, Prince William Sound, and Southeast Alaska (Figure 6). For example, in Prince William Sound, approximately 76% of Pink Salmon, 73% of Chum Salmon, and 36% of Sockeye Salmon originated from hatcheries. These percentages do not include the numerous hatchery Pink Salmon, Chum Salmon, and Sockeye Salmon that stray to streams within (Brenner et al. 2012) and outside of Prince William Sound (Hollowell et al. 2017). In Southeast Alaska, approximately 63% of Chum Salmon originated from hatcheries, excluding hatchery strays to the spawning grounds (Piston and Heinl 2012). Contributions of hatchery Chum Salmon to total abundance has continued to increase over time, reaching approximate

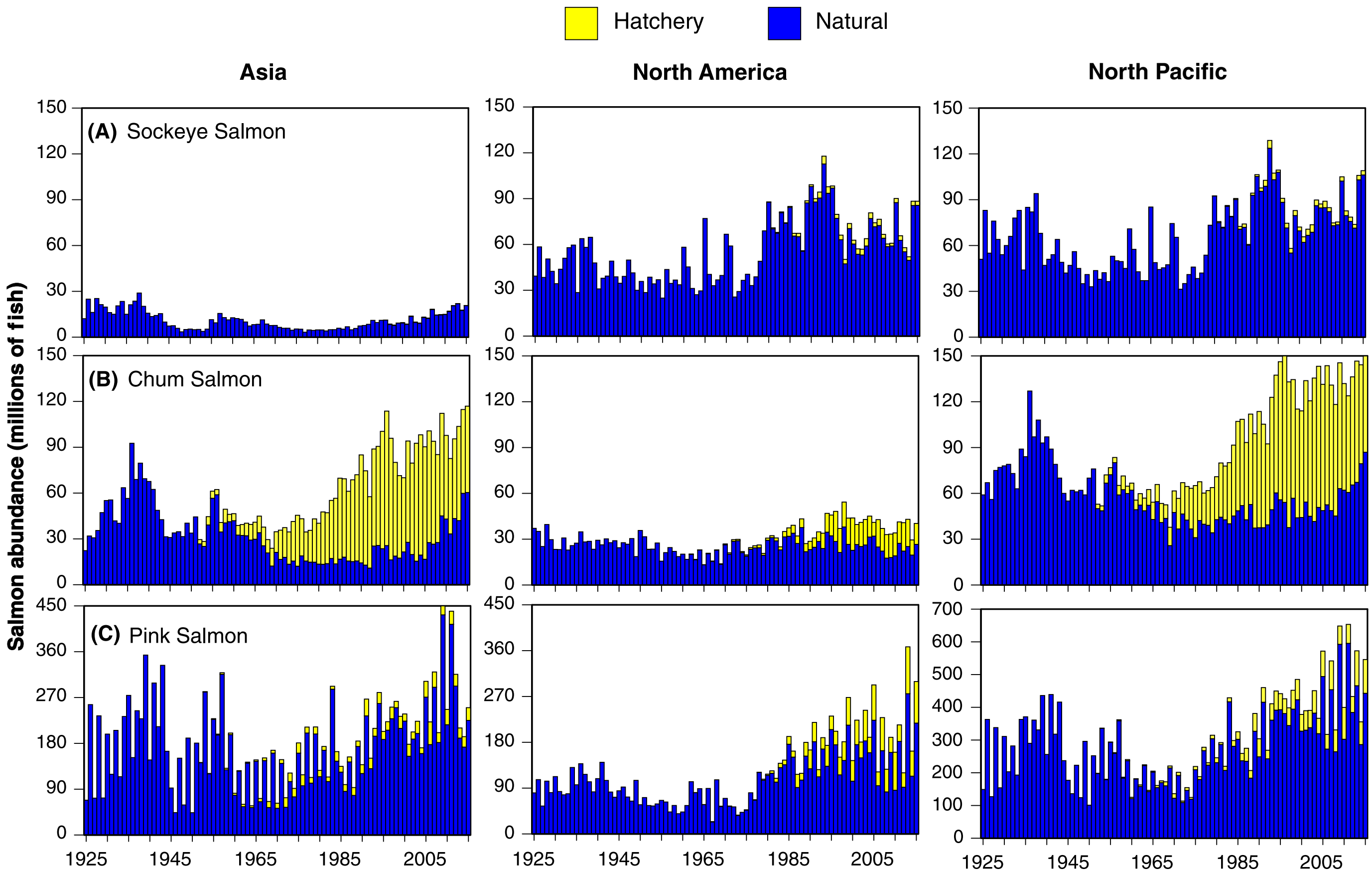

FIGURE 3. Annual abundances (catch plus number of spawners; millions of fish) of natural- and hatchery-origin **(A)** Sockeye Salmon, **(B)** Chum Salmon, and **(C)** Pink Salmon returning to Asia, North America, and the entire North Pacific Ocean, 1925–2015. Note that the *y*-axis scale is different for Pink Salmon.

values of 83% in Prince William Sound, 75% in Southeast Alaska, and 26% in the mainland and islands of Russia during 2005–2015. The only regions with little or no hatchery-origin salmon were western Alaska and the southern Alaska Peninsula (Figure 6).

Hatchery-origin salmon represented approximately 28% of the total adult biomass of all three species during 1990–2015 (Figures 2 and 3). The contribution of hatchery-origin salmon to the total biomass of adult plus immature salmon in the North Pacific Ocean was approximately 40%, reflecting the substantial contribution of hatchery Chum Salmon, which inhabit the ocean for more years than Pink Salmon and Sockeye Salmon.

Weight of Salmon

Average weight of Pink Salmon and Chum Salmon declined over the 90-year period, whereas Sockeye Salmon weight did not decline over time (Figure 7). For example, Pink Salmon and Chum Salmon weights declined 16% and 10%, respectively, from 1925–1950 to 1990–2015. Weight decline was greater for odd-year (22%) than for even-year (8%) Pink Salmon. Changing weights of Chum Salmon and Sockeye Salmon reflected changes in both growth at sea and age at maturation. During 1925–2015, the mean weight of Pink Salmon was inversely correlated with total Pink Salmon abundance (r = −0.46) and with the total abundance of all three species (r = −0.70). The mean weight of Chum Salmon was inversely correlated with total Chum Salmon abundance (r = −0.47) and with the total abundance of all three species (r = −0.46).

DISCUSSION

Salmon Abundance and Biomass Trends

The numerical abundance and biomass values presented here for Pink Salmon, Chum Salmon, and Sockeye Salmon span 90 years (1925–2015) and represent the most comprehensive compilation of data for natural- and hatchery-origin salmon to date. Recent abundance (numbers and biomass) estimates are the highest since the collection of relatively comprehensive statistics began in 1925. For

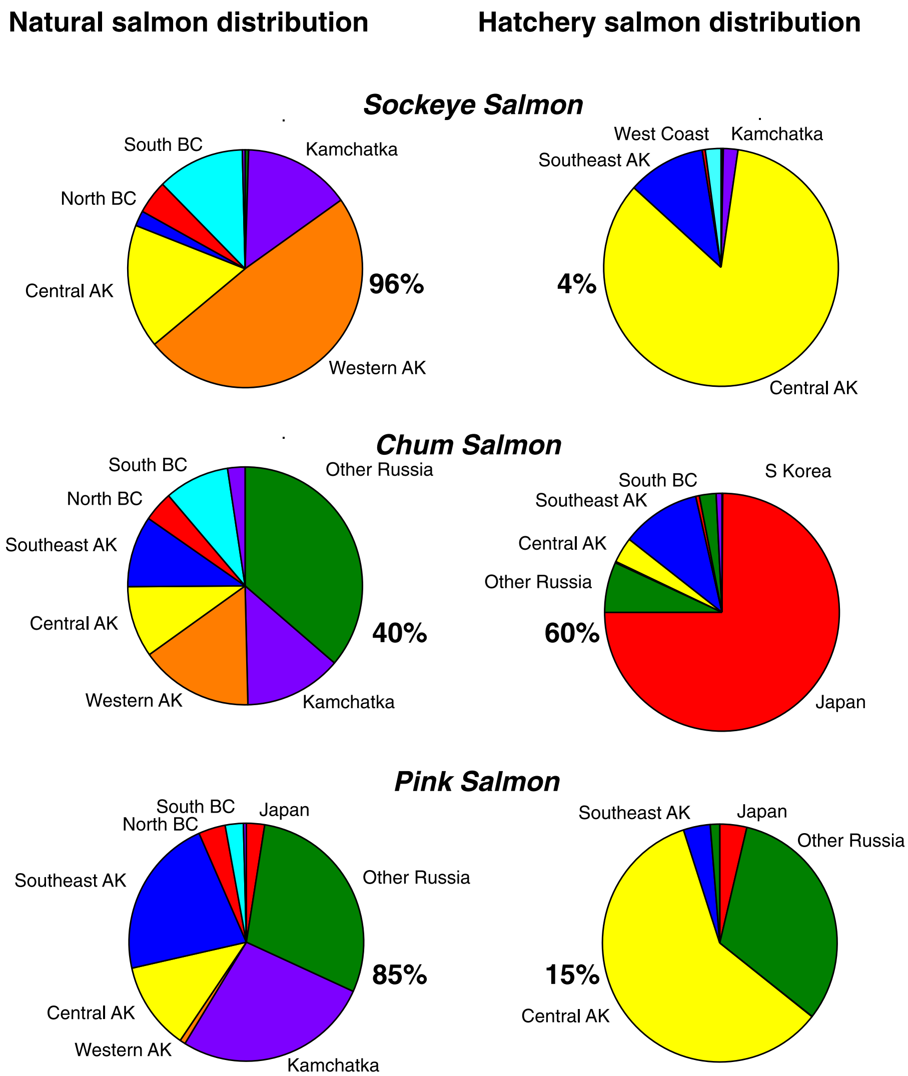

FIGURE 4. Relative regional contributions of adult natural-origin (left panel) and hatchery-origin (right panel) salmon to Pacific Rim production (see Figure 1) during 1990–2015 (BC = British Columbia; AK = Alaska). For example, 49% of total natural-origin Sockeye Salmon in the North Pacific Ocean returned to western Alaska (orange; upper-left pie segment), and 84% of total hatchery-origin Sockeye Salmon returned to central Alaska (yellow segment; upper-right pie). "Other Russia" includes all areas of Russia except Kamchatka (see Figure 1). Overall percentages of natural- and hatchery-origin salmon by species are shown adjacent to each pie.

example, combined numbers and biomass of adult Pink Salmon, Chum Salmon, and Sockeye Salmon were approximately 27% and 18% higher, respectively, during 1990–2015 than during the previous peak in 1934–1943. High abundance and biomass reflects increases in natural- and hatchery-origin Pink and Sockeye salmon and in hatchery-origin Chum Salmon. Mean sizes of returning Pink Salmon and Chum Salmon were negatively correlated with abundances of their own species ($r = -0.46$ and -0.47, respectively) as well as the aggregate abundance of all three species ($r = -0.70$ and -0.46, respectively), as one would expect in the case of density-dependent competition.

High overall abundances resulted from generally favorable ocean conditions and, in recent decades, releases of large numbers of hatchery salmon combined with improving hatchery technologies after 1990 (Irvine and Fukuwaka 2011). The first peak abundance in the 1930s stemmed primarily from abundant Chum Salmon and Pink Salmon in Asia (Klyashtorin and Smirnov 1995); thereafter, all three species were at relatively low abundances throughout the North Pacific Ocean until the 1970s. The 1977 regime shift benefited all three species in North America (especially in Alaska) and benefited hatchery Chum Salmon in Asia, whereas abundance changes with subsequent regime shifts were much less pronounced

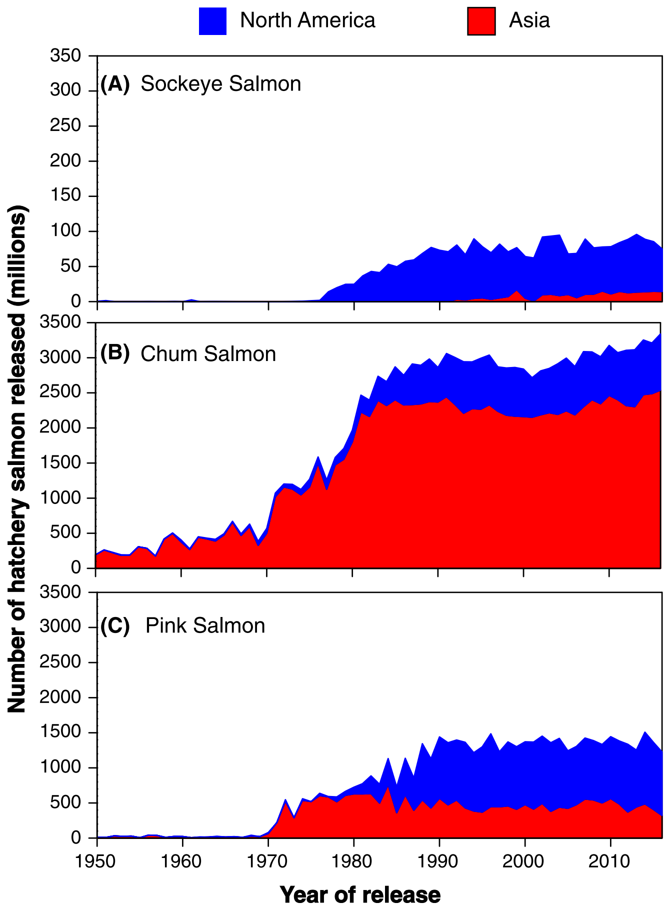

FIGURE 5. Annual releases of juvenile hatchery **(A)** Sockeye Salmon, **(B)** Chum Salmon, and **(C)** Pink Salmon into the North Pacific Ocean, 1950–2016 (1950–1951 from Mahnken et al. 1998; 1952–2016 from NPAFC 2017a).

(Hare and Mantua 2000; Ruggerone et al. 2010; Irvine and Fukuwaka 2011). Key oceanographic factors associated with high abundances of Pink Salmon, Chum Salmon, and Sockeye Salmon include warm sea surface temperature and the intensity of the Aleutian Low, which influences upwelling and an upward flux of micronutrients (Beamish and Bouillon 1993; Sugimoto and Tadokoro 1997; Stachura et al. 2014). Zooplankton abundance in the northeastern North Pacific Ocean increased after the mid-1970s (Brodeur and Ware 1992), contributing to greater early marine scale growth and survival of Sockeye Salmon in Alaska (Ruggerone et al. 2007). In southern regions of the eastern North Pacific Ocean, the North Pacific Gyre Oscillation (NPGO) and the north–south location of the North Pacific Current bifurcation influenced salmon productivity (Malick et al. 2016).

Since the 1977 ocean regime shift, oceanographic conditions have been most favorable for Pink Salmon, Chum Salmon, and Sockeye Salmon in northern regions, where many large salmon populations occur in relatively intact habitats (Mueter et al. 2002; Peterman and Dorner 2012). In contrast, many southern natural-origin populations along both continents have been more adversely influenced by habitat degradation, ocean conditions, interactions with hatchery salmon, and overharvest in mixed-stock fisheries (Radchenko et al. 2007; Lichatowich 2013; Barnas et al. 2015), resulting in abundance declines. In particular, we note that abundances of natural-origin Chinook Salmon, Coho Salmon, and steelhead in the eastern North Pacific Ocean, including Alaska (Irvine and Fukuwaka 2011; Atcheson et al. 2012; Lewis et al. 2015), and Cherry Salmon in Asia (Urawa 2016), have declined over time.

Interactions Between Hatchery- and Natural-Origin Salmon

Recent high marine abundances of both natural- and hatchery-origin salmon could be interpreted to indicate little or no adverse interaction between these groups. However, considerable evidence exists that salmon compete for food at sea, which can lead to reduced growth, delayed age at maturation, and reduced survival. For example, high abundances of Pink Salmon have been shown to alter the biomass of zooplankton, which in turn can affect phytoplankton biomass (Tadokoro et al. 1996; Shiomoto et al. 1997; Sugimoto and Tadokoro 1997; Azumaya and Ishida 2000; Batten et al., in press). These food web effects are also reflected in the diet, food consumption, growth, and survival of salmon (Pyper and Peterman 1999; Davis et al. 2005, 2009; Ward et al. 2017), and the reproductive success of seabirds (Toge et al. 2011; Springer and van Vliet 2014; Sydeman et al. 2017). In Alaska, declines in size at age and abundance of Chinook Salmon and Coho Salmon and a decrease in age at maturation in Chinook Salmon may be related to the alteration of the food web by highly abundant Pink Salmon and higher mortality during late marine life (Lewis et al. 2015; Ruggerone et al. 2016; Shaul and Geiger 2016). For example, length of age-1.4 Chinook Salmon from six Alaskan stocks was negatively correlated with Pink Salmon abundance in 1983–2012 (average $r = -0.55$, $P < 0.05$; G. Ruggerone, unpublished analysis). In southern BC, growth of Chum Salmon was reduced when marine abundances of competing salmon were high, particularly during years of reduced primary productivity, indicating an interaction between density-dependent competition and changing climate (Debertin et al. 2017).

Relatively few direct and systematic investigations of interactions between hatchery- and natural-origin salmon at sea exist, in part because consistent hatchery production provides little contrast to test hypotheses (Peterman 1991). Consequently, effects of hatchery salmon on natural-origin salmon in the ocean are largely inferred from studies where changing biological attributes (e.g., size, age, and

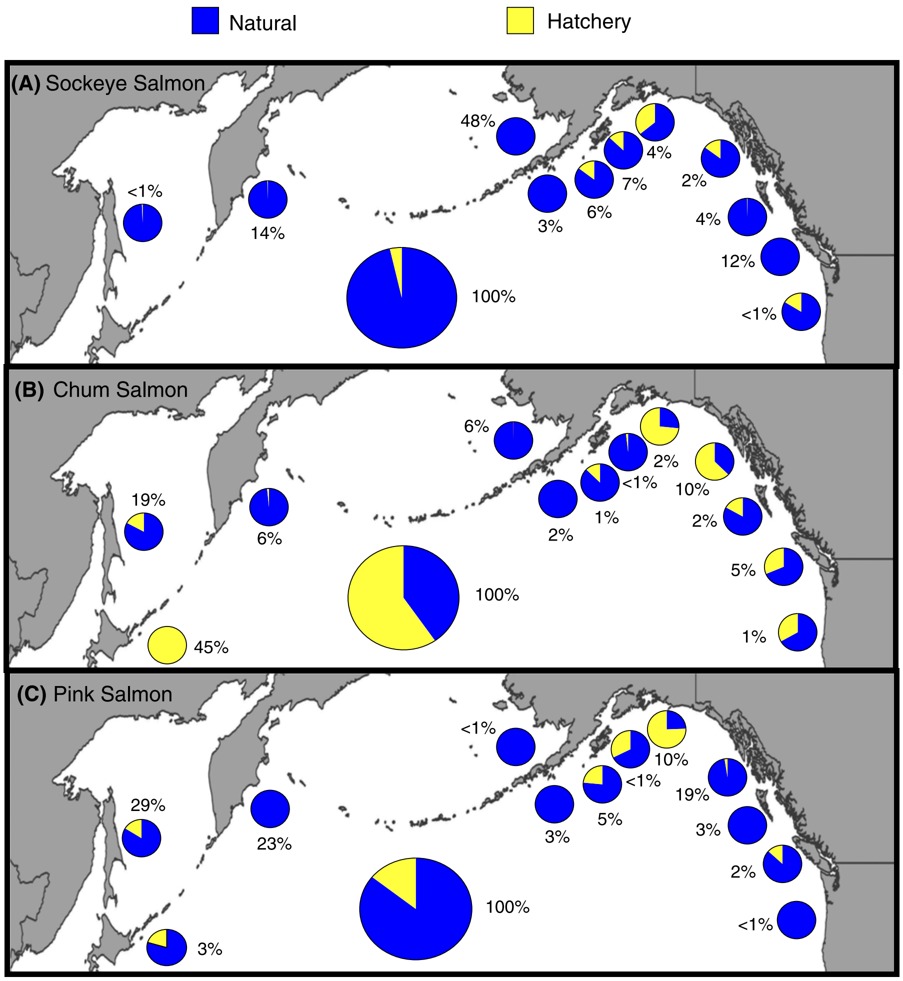

FIGURE 6. Color-coded proportions of natural- and hatchery-origin adult **(A)** Sockeye Salmon, **(B)** Chum Salmon, and **(C)** Pink Salmon for each region (small pies) of the North Pacific Ocean (see Figure 1) in 1990–2015 and for the entire North Pacific Ocean (large pies). Numeric values show the percentage of the total returns from the North Pacific Ocean for each species returning to each region. Value is not shown for South Korea, where 100% of Chum Salmon originate from hatcheries (<1% of total).

productivity) of natural-origin salmon are related to varying abundances of both natural- and hatchery-origin salmon (see above references) and our finding that the biomass of adult and immature hatchery salmon currently represents approximately 40% of total salmon biomass.

Nevertheless, some studies have specifically examined effects of hatchery salmon on growth, age, and survival of natural-origin salmon (Hilborn and Eggers 2001; Kaeriyama et al. 2012). For example, an empirical model based on several decades of data predicted an 18% decline in productivity of natural-origin BC Fraser River Sockeye Salmon (1.8 million fish each year) in response to an increase of 50 million adult hatchery Pink Salmon in North America (Ruggerone et al. 2016). When evaluating production trends of Pink Salmon in Prince William Sound, Amoroso et al. (2017) concluded that hatchery Pink Salmon adversely affected the survival of natural-origin Pink Salmon such that the net benefit of hatchery production to the local commercial catch was only 30% of the gross benefit. In other words, the net benefit of large-scale hatchery production in Prince William Sound to fishermen and private hatchery operators resulted in a significant adverse impact on natural-origin salmon production in this region.

Hatchery salmon are released into the ocean primarily so that returning adult salmon can support salmon harvests by local fishermen. However, hatchery salmon can migrate long distances at sea and intermingle with distant natural-origin stocks, leading to unintended consequences when those natural-origin stocks are less productive. Examples of this long-distance effect include the influence of Asian Chum Salmon (mostly hatchery origin) on Norton Sound Chum Salmon (Ruggerone et al. 2012) and the effect of Russian Pink Salmon on Bristol Bay and

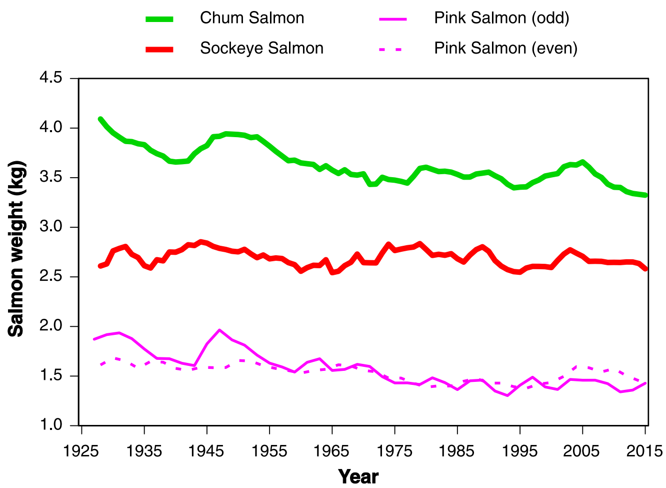

FIGURE 7. Average weight of Pink Salmon, Chum Salmon, and Sockeye Salmon captured in commercial fisheries, 1925–2015 (derived from NPAFC 2017b). Values are 4-year running averages for Sockeye Salmon and Chum Salmon and 2-year averages for Pink Salmon (even- and odd-year weights presented separately), corresponding to the typical life span of each species.

Fraser River Sockeye Salmon (Ruggerone et al. 2003; Ruggerone and Connors 2015). The effects of large-scale hatchery production on distant natural-origin salmon stocks are not typically considered by hatchery managers despite this issue being raised various times in the literature (e.g., Holt et al. 2008; Peterman et al. 2012; Malick et al. 2017).

It is noteworthy that total adult biomass—and especially adult plus immature biomass—has been relatively stable from 1993 through 2015 (Figure 2), suggesting that the carrying capacity of the ocean may have been reached during the post-1977 regime. This finding leads to the question: would natural-origin salmon rebound if hatchery production was significantly reduced? Additionally, if the ocean becomes less favorable for salmon, as it was from the 1940s through the 1960s, will natural-origin salmon abundances decline more than they would without hatchery salmon? Answering these questions is beyond the scope of our paper, but they are important areas for future research.

Management Implications

Governmental agencies rarely separate their catch and escapement data into hatchery- and natural-origin salmon, in part because hatchery-origin fish are difficult to identify. The lack of stock composition values in the catch and spawning escapement confounds interpretation of natural-origin salmon productivity and abundance, leading to less-certain management of the resource when hatchery production is moderate or high relative to natural-origin production. Large-scale hatchery production is often associated with significant straying of hatchery salmon and interbreeding with natural-origin salmon (Brenner et al. 2012; Piston and Heinl 2012). Studies indicate altered genetic composition (Jasper et al. 2013; Christie et al. 2016) and reduced reproductive success and fitness of natural salmon stocks that interbreed with hatchery strays (Christie et al. 2011, 2014; HSRG 2014). Ideally, hatchery salmon should be harvested at high rates in terminal areas that are distant from natural-origin salmon streams to minimize spawning of hatchery salmon in streams and to avoid overharvesting.

Research Implications

We describe two main categories of salmon abundance estimates and make these data sets available to other researchers: (1) return (catch plus escapement) estimates of hatchery- and natural-origin salmon (numerical and biomass) by species and region and (2) total biomass estimates of mature and immature salmon by species and region (hatchery and natural origin combined). Although total abundance, adult biomass, and adult and immature salmon biomass were highly correlated over the past 90 years (range of r = 0.92–0.98), the best choice of abundance category to use may vary depending on one's research objectives. For instance, if a researcher is investigating intraspecific competition, then biomass or numerical abundance estimates of that one species are likely appropriate. If one is investigating interspecific competition effects, then biomass of the competitor species may better reflect potential prey consumption than numbers of competitors. Additionally, including immature biomass may provide valuable additional information about a species' effects on the marine ecosystem, particularly for Chum Salmon, which are larger and spend more years at sea than Sockeye Salmon and Pink Salmon. For instance, Jeffrey et al. (2016) found that when the total biomass (mature and immature) of Chum Salmon, Pink Salmon, and Sockeye Salmon in the eastern North Pacific Ocean was high, the body size of BC Chum Salmon and Pink Salmon was reduced. When assessing potential competition effects, the strengths and weaknesses of the various abundance indices and the methods used to derive them should be considered (Debertin et al. 2017).

Although most researchers support the finding that density-dependent competition among salmon for prey in the ocean can lead to reduced growth and survival and delayed maturation, as mentioned earlier, there are exceptions (Shuntov et al. 2017). Shuntov et al. (2017) stated that salmon biomass in the North Pacific Ocean is no more than 4–5 million metric tons, which is similar to our estimates for recent years (Figure 2C). Those authors concluded that Pacific salmon consume only about 1–5% of prey consumed by all epipelagic nekton in the western Bering Sea and up to 15% near eastern Kamchatka, leading to rather moderate effects on the food web. We suggest that their viewpoint of inconsequential competition for prey is inconsistent with numerous observations of biennial responses of salmon and their prey to Pink Salmon in addition to negative correlations between Pink Salmon and the growth and survival of other salmon species (e.g., Bugaev et al. 2001; Ruggerone et al. 2003, 2016; Ruggerone and Connors 2015). In addition to these observations, we hypothesize that the clumped distribution of salmon (Hartt and Dell 1986; Jaenicke and Celewycz 1994; Peterson et al. 2010) and their prey, feeding selectivity, variable prey quality, and a requirement for salmon to maintain high foraging efficiency over their life span combine to make only a small portion of the epipelagic prey available to foraging salmon.

Cautions Regarding Data Quality

As with previous analyses of salmon abundance data by Rogers (1987, 2001), Beamish et al. (1997), Eggers (2009), and Kaeriyama et al. (2009), we had to make many assumptions. Many of our poorest quality estimates were associated with relatively small levels of abundance and low fishing effort (e.g., wild Pink Salmon in western Alaska). High uncertainty exists for estimates of natural-spawning Pink Salmon in Japan and relative abundances of natural- and hatchery-origin Pink Salmon and Chum Salmon in the Sakhalin and Iturup islands of Russia. Furthermore, we assumed that all Japanese Chum Salmon are of hatchery origin, and this is not true (Saito and Nagasawa 2009; Miyakoshi et al. 2012; Morita 2014).

Spawner abundance (escapement) represents the least accurate component of salmon abundance estimates because typically only a portion of total spawners is enumerated. The quality of natural-origin Sockeye Salmon abundance estimates is relatively high because agencies typically provide total counts (catch plus spawning escapement) and because hatchery production is low in most regions. In contrast, spawning escapement estimates for Pink Salmon and Chum Salmon need to be expanded for most regions. Additionally, the large production of hatchery salmon in some regions reduces the accuracy of natural-origin salmon catch and spawning statistics, especially when hatchery salmon are unmarked or are not adequately monitored.

Despite these caveats, we believe that the general patterns and trends in natural- and hatchery-origin salmon abundances across time, regions, and species are reasonably robust. We urge readers to focus on broad patterns rather than on particular year-to-year variations in estimates; the latter will be less precise.

Recommendations

To better understand interactions between hatchery- and natural-origin salmon and how they are influenced by major oceanographic and climate effects, we recommend that agencies (1) ensure that hatchery salmon can be identified after release, either by marking them (including otolith marks) or applying parentage-based tagging and genetic stock identification (e.g., Beacham et al. 2017); and (2) estimate and document abundance of natural- and hatchery-origin salmon in the catch and spawning escapement in publicly accessible databases.

Implementation of these recommendations is needed throughout much of the Pacific Rim, especially in regions where hatchery production is moderate to large or continuing to grow. Each country and their associated management agencies should be responsible for documenting natural-origin and hatchery salmon statistics and reporting data through an international organization, such as the NPAFC. These data are necessary to evaluate the abundance, productivity, and status of natural-origin Pacific salmon, an iconic group of species that support subsistence, cultural, recreational, and commercial fisheries in addition to freshwater and marine ecosystems throughout the North Pacific Ocean.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the supporting information tab for this article.