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[Article]

Magnitude and Trends in Abundance of Hatchery and Wild Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean

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Abstract.—Abundance estimates of wild and hatchery Pacific salmon *Oncorhynchus* spp. are important for evaluation of stock status and density-dependent interactions at sea. We assembled available salmon catch and spawning abundance data for both Asia and North America and reconstructed total abundances of pink salmon *O. gorbuscha*, chum salmon *O. keta*, and sockeye salmon *O. nerka* during 1952–2005. Abundance trends were evaluated with respect to species, regional stock groups, and climatic regimes. Wild adult pink salmon were the most numerous salmon species (average = 268×10^6 fish/year, or 70% of the total abundance of the three species), followed by sockeye salmon (63×10^6 fish/year, or 17%) and chum salmon (48×10^6 fish/year, or 13%). After the 1976–1977 ocean regime shift, abundances of wild pink salmon and sockeye salmon increased by more than 65% on average, whereas abundance of wild chum salmon was lower in recent decades. Although wild salmon abundances in most regions of North America increased in the late 1970s, abundances in Asia typically did not increase until the 1990s. Annual releases of juvenile salmon from hatcheries increased rapidly during the 1970s and 1980s and reached approximately 4.5×10^9 juveniles/year during the 1990s and early 2000s. During 1990–2005, annual production of hatchery-origin adult salmon averaged 78×10^6 chum salmon, 54×10^6 pink salmon, and 3.2×10^6 sockeye salmon, or approximately 62, 13, and 4%, respectively, of the combined total wild and hatchery salmon abundance. The combined abundance of adult wild and hatchery salmon during 1990–2005 averaged 634×10^6 salmon/year (498×10^6 wild salmon/year), or approximately twice as many as during 1952–1975. The large and increasing abundances of hatchery salmon have important management implications in terms of density-dependent processes and conservation of wild salmon populations; management agencies should improve estimates of hatchery salmon abundance in harvests and on the spawning grounds.

Harvests of pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta* originating from regions along the North Pacific Rim exceeded their historical maxima in the 1990s (Fukuwaka et al. 2007; Radchenko et al. 2007). The portion of hatchery salmon in these large catches is not reported, but annual releases of juvenile pink salmon and chum salmon from hatcheries in both Asia and North America have increased substantially over time (Mahnken et al. 1998; Naish et al. 2007). The increased abundance of hatchery or other artificially enhanced salmon populations may have possible adverse effects on wild salmon populations (Peterman 1991; Cooney and Brodeur 1998; Heard 1998; Zaporozhets and Zaporozhets 2004). This concern arises in part from evidence that high salmon abundances in the ocean can reduce growth and survival among conspecific salmon (Rogers 1980; Peterman 1984a; McKinnell 1995; Kaeriyama 1998; Pyper and Peterman 1999; Helle et al. 2007) and among individuals of other salmon species (Peterman 1982; Ruggerone et al. 2003, 2005; Ruggerone and Nielsen 2004). Furthermore, salmon migrate across large areas in the ocean (Myers et al. 2007, 2009; Urawa et al. 2009), where both abundant and depleted stocks may intermingle.

In light of the evidence for density-dependent processes and the broad distributions of salmon stocks at sea, it is important for fishery scientists and

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managers to consider total salmon abundance and competitive interactions among wild and hatchery salmon in the North Pacific Ocean. Knowledge of such density-dependent processes may be essential for achieving harvest or spawning objectives and for maintaining productive wild salmon populations in the North Pacific Ocean (Peterman 1991). A key step in this evaluation is to document abundances of wild and hatchery salmon returning to each production area of the North Pacific.

Our purpose here is to estimate and describe trends in total abundance of adult wild and hatchery salmon in the North Pacific and adjacent seas using estimates of salmon harvest and total spawning abundance in each production area. Although previous estimates exist for wild and hatchery salmon catches and spawner abundances throughout the North Pacific (e.g., Rogers 1987, 2001; Beamish et al. 1997; Eggers 2009; Irvine et al. 2009; Kaeriyama et al. 2009), our objective was to estimate these quantities more completely by expanding spawner counts where appropriate and by separately enumerating hatchery salmon in all regions rather than just in some. We describe a comprehensive data set (1952–2005) on wild and hatchery salmon across the North Pacific, and we use these data to identify temporal and spatial trends in hatchery and wild components of total annual abundance (catch plus spawner abundance of pink salmon, chum salmon, and sockeye salmon *O. nerka* populations). Abundance trends of wild salmon were also compared with ocean regime shifts that occurred in 1976–1977 and 1989 (Hare and Mantua 2000). Pink salmon, sockeye salmon, and chum salmon constituted the dominant proportion (>93%) of total salmonid abundance returning from the ocean (NPAFC 2002), so other salmon species are not considered here. Such data form the basis for addressing questions about within- and between-species interactions among salmon populations in the North Pacific, including questions about how salmon from one nation affect salmon from another nation (Peterman 1984b; Ruggerone et al. 2003; Holt et al. 2008).

Methods

To estimate the total annual abundance of adult pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, we compiled all available annual data for the period 1952–2005 on catches, spawner abundances, harvest rates, and abundances of wild and hatchery-released adults of these species from South Korea, Japan, Russia, Alaska, British Columbia, and Washington (including the Columbia River). The resulting data series were aggregated into 135 major pink salmon, chum salmon, and sockeye salmon population groups (Mantua et al. 2009) within 19 regions (Figure 1). Data tables are available from Ruggerone et al. (2010). Such large aggregations had the benefit of greatly reducing problems of poor stock identification in catches that would, for example, incorrectly allocate fish from one population to another if the spatial extent of units was too small.

Our goal was to produce absolute total abundance estimates of wild and hatchery salmon for each region so that abundance could be compared across regions and time. The extent and quality of data collection programs varied among regions of the North Pacific, and for some areas the spawner abundance had to be estimated indirectly from harvest data, as described later. In general, the methods of data collection and verification were similar across regions.

Hatchery fish were not always segregated from wild fish in the reported data. When possible, we utilized government estimates of wild versus hatchery salmon abundance in the returning run, catch, and spawning population, but typically we had to estimate adult hatchery fish and remove them from total catch. We did not attempt to identify the proportion of river spawners represented by hatchery strays because few data were available. Therefore, hatchery estimates were low and wild salmon spawner estimates were high to the extent that hatchery salmon stray and spawn in streams.

Approaches to Estimating Wild Salmon Spawner Abundances

In many areas, estimates were available for total numbers of adult salmon in the catch and spawning populations. However, in most regions, data on spawner abundances of wild salmon did not extend back to the 1950s, were sometimes intermittent, or often only estimated part of the spawning population. We addressed these issues using a four-pronged approach.

Approach 1.—In British Columbia 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 filled in the missing values by interpolating values from the other stocks within the region (see English et al. 2006). First, the average contribution of each stock to total spawner abundance within the region was calculated by summing average spawner abundances across stocks and calculating the proportion that each stock contributed to this sum. We then summed spawner abundance for each year, skipping stocks with missing data. In the final step, we iteratively scaled the sum of spawner abundances to account for missing data. For each year

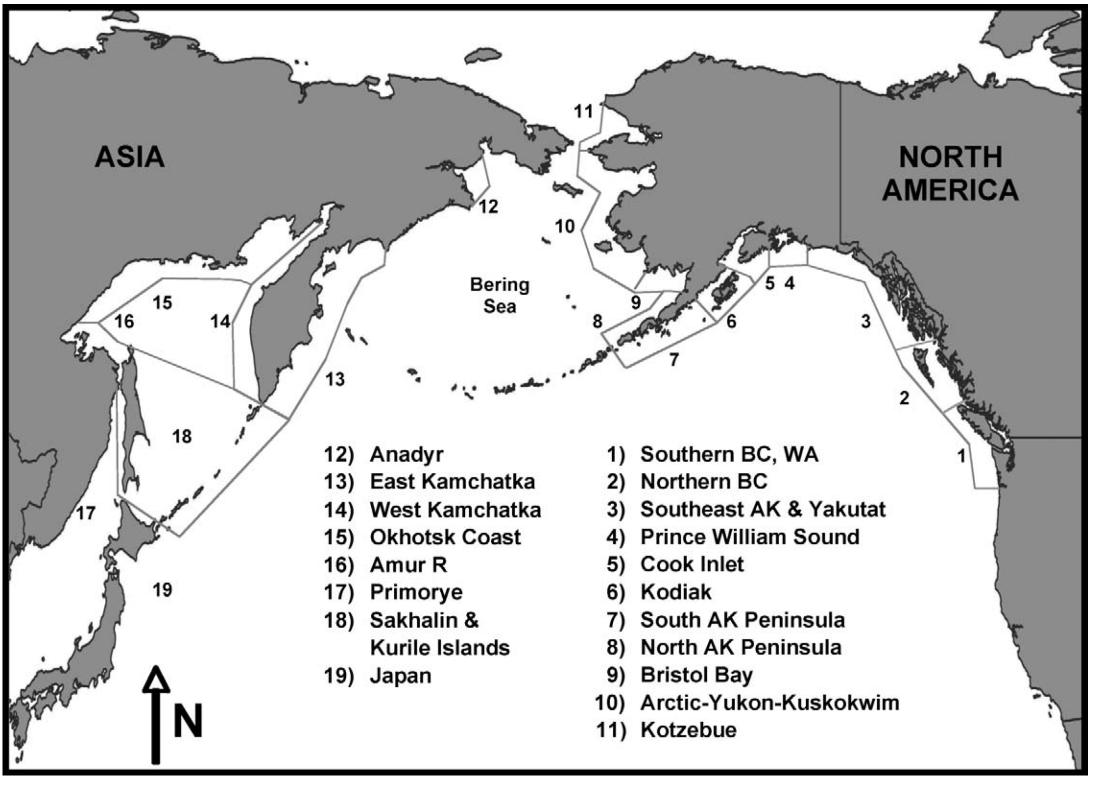

FIGURE 1.—Approximate geographic locations of regional stock groups included in this study. Area 1, southern British Columbia (BC) and Washington (WA), includes the Columbia River and all areas south of the central BC coast (~51°N). Area 2, northern BC, includes central and northern BC. Area 3, southeast Alaska (AK), includes the Yakutat coast. The central AK region extends from the Bering River (~60°N; near Prince William Sound, area 4) westward to Unimak Island (~166°W), thereby including areas 4–7. Western AK includes areas 8–11 and thus encompasses all North American drainages into the Bering Sea from Unimak Island to Kotzebue. Data for east and west Kamchatka (areas 13 and 14) are separated from data for the Russian mainland and islands (called "other Russia" here, which includes the Okhotsk coast, Amur River, Primorye, Sakhalin, Kurile Islands, and relatively small runs to the Anadyr River). Area 19, Japan, includes the islands of Hokkaido and Honshu and small hatchery production in South Korea (not shown).

in which data for a given stock were missing, we expanded the observed spawner abundance by the missing stock's average relative contribution to the total, thus accounting for the missing contribution of that stock. For example, if stock *X* contributed 5% of the region's spawning abundance on average, then spawning abundance estimates for years where data on stock *X* were missing would be expanded by 100%/95% to account for the missing contribution from stock *X* in those years. This infilling procedure was used for cases where data were available to cover at least 50% of expected spawning abundance as measured by the sum of average contributions from each stock. If the data represented less than 50% of expected spawning abundance, then spawning data for that year were considered unreliable and were treated as missing altogether.

Approach 2.—In some areas of British Columbia and Alaska, annual estimates of spawning abundance were consistently underestimated because coverage of spawning areas was incomplete. In these cases, we used information from area management reports (e.g., Bue et al. 2002, 2008; Geiger and McPherson 2004; Nelson et al. 2005, 2006; Baker et al. 2006; English et al. 2006; Dinnocenzo and Caldentey 2008) and managers (see Acknowledgments) to expand the index counts. These expansions were based on the proportion and relative size of total streams surveyed and the approximate proportion of total spawners counted in the surveyed streams.

Approach 3.—In most areas, including Asia, there were years in which spawning abundance could not be reliably estimated (Table 1); therefore, we estimated spawning abundance and total adult abundance from

TABLE 1.—Percentage of years (1952–2005) for which each method was the primary approach used to estimate total wild salmon abundance (catch plus spawners) in each area of the North Pacific Ocean (see Methods for additional description of each approach; BC = British Columbia; WA = Washington; SEAK = Southeast Alaska; AK = Alaska; WCVI = west coast of Vancouver Island; GS = Strait of Georgia).

	Method			
Area	Reported catch and spawners	Approaches 1 and 2: catch and expanded spawner index	Approach 3: based on catch and estimated harvest rate from regression	Approach 4: based on catch and assumed harvest rate
Wild chum salmon				
Southern BC and WA	0	48	52	0
Central Coast BC	0	48	52	0
Northern BC	0	48	52	0
SEAK and Yakutat	0	0	0	100
Prince William Sound	0	76	24	0
Cook Inlet	0	0	0	100
Kodiak	0	70	30	0
South AK Peninsula	0	81	19	0
North AK Peninsula	0	81	19	0
Bristol Bay	41	0	59	0
Arctic–Yukon–Kuskokwim	0	46	37	17
Kotzebue	81	0	19	0
Anadyr	26	0	74	0
East Kamchatka	26	0	74	0
West Kamchatka	26	0	74	0
Okhotsk	26	0	74	0
Amur River	26	0	74	0
Primorye	26	0	74	0
Sakhalin and Kurile Islands	26	0	74	0
Wild pink salmon				
Southern BC and WA	43	48	9	0
Central coast BC				
Northern BC	0	48	52	0
SEAK and Yakutat	0	83	17	0
Prince William Sound	83	0	17	0
Cook Inlet	0	0	0	100
Kodiak	0	70	30	0
South AK Peninsula	0	81	19	0
North AK Peninsula	0	81	19	0
Bristol Bay	0	0	0	100
Arctic–Yukon–Kuskokwim	0	0	0	100
Anadyr	26	0	74	0
East Kamchatka	87	0	13	0
West Kamchatka	87	0	13	0
Okhotsk	26	0	74	0
Amur River	26	0	74	0
Primorye	26	0	74	0
Sakhalin and Kurile Islands	26	0	74	0
Japan	0	0	0	100
Wild sockeye salmon				
WCVI, outer WA	0	48	52	0
GS, Puget Sound	100	0	0	0
Central coast BC	0	48	52	0
Northern BC	0	48	52	0
SEAK and Yakutat	44	0	56	0
Prince William Sound	52	0	48	0
Cook Inlet	54	0	46	0
Kodiak	56	0	44	0
South AK Peninsula	100	0	0	0
North AK Peninsula	81	0	19	0
Bristol Bay	93	0	7	0
Arctic–Yukon–Kuskokwim	0	0	0	100
Anadyr	26	0	74	0
East Kamchatka	26	0	74	0
West Kamchatka	26	0	74	0
Okhotsk	26	0	74	0

catch data and estimates of harvest rate. 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.

Approach 4.—In a few areas (Table 1), which typically included stocks with low abundances and low fishing effort, we used assumed harvest rates that were based on the fishing effort/harvest rates of 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 for wild chum salmon was 90% of the rate for pink salmon because many wild chum salmon were captured incidentally in fisheries for pink salmon (Geiger and McPherson 2004; 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 (Table 1). Reported total abundance (catch plus spawners) was available for only 24% and 30% of the stock-years in North America and Asia, respectively (Table 1). Reported catch plus expanded index spawner counts (approaches 1 and 2) were used in 32% of the stock-years in North America, but this method was not used in Asia. The regression method (approach 3) for estimating harvest rate was the primary method for 27% and 66% of the stock-years in North America and Asia, respectively, mainly during early years. An assumed harvest rate (approach 4) was used to estimate total abundance in 18% and 4% of the stock-years in North America and Asia, respectively, largely among relatively small stocks that were incidentally harvested.

Data were the most complete and reliable for sockeye salmon, followed by pink salmon and then chum salmon. For example, in North America, approximately 48% of total abundance estimates of sockeye salmon were provided by agency reports, whereas only 11% of pink salmon and 10% of chum salmon were reported. In Asia, approximately 70% of annual spawning abundance values were estimated from catch and harvest rates because spawning abundances were typically not available prior to 1992. The aforementioned procedures to estimate total spawning abundance were necessary for comparison of species and population abundances across the Pacific Rim.

North American Salmon Data

The largest portion of salmon population data on the West Coast of North America came from 120 populations of pink salmon, chum salmon, and sockeye salmon that were previously described by Peterman et al. (1998), Pyper et al. (2001, 2002), Mueter et al. (2002b), and Dorner et al. (2008), the latter of which includes the original data set through the early 2000s. The database was updated with catch and spawning abundance values from recent regional reports, run reconstructions (Starr and Hilborn 1988; English et al. 2006), and data that were not included in those specific populations.

In Alaska, the reported spawner counts for pink salmon and chum salmon were typically annual peak values rather than total estimates, and approach 2 (see above) was used to estimate total spawner abundance. Spawning abundance estimates were often not available for earlier years, and in these cases approach 3 was used to estimate total spawner abundance, which was then added to catch. Sockeye salmon abundances were typically reported as total abundances for major stocks within each region of Alaska. Estimates or approximations of adult hatchery salmon abundance in Alaska were reported annually and were subtracted from total salmon estimates when appropriate (e.g., White 2005).

In British Columbia, we supplemented the above data sets with recent run reconstructions of wild salmon (English et al. 2004, 2006; K. English, LGL Limited, Sidney, British Columbia, Canada, personal communication), which accounted for spawners in unmonitored streams as described previously. In these run reconstructions, sockeye salmon produced from spawning channels were included in wild salmon estimates, whereas chum salmon produced from channels were included with the hatchery salmon. Estimates of returning adult salmon from enhancement facilities in British Columbia were based on annual salmon releases and survival estimated from coded wire tag data or marked fish or from literature values (e.g., Heard 1991; Bradford 1995; Mahnken et al. 1998; Ryall et al. 1999; RMISD 2009). The mean of annual survival rates was applied when yearly survival values were not available (e.g., ~0.8–1.1% for chum salmon, 3.1% for pink salmon, and 0.2–5.0% for sockeye salmon fry and smolts). Recent estimates of salmon abundance from the coterminous United States (primarily Washington and the Columbia River basin) were provided by state biologists or were obtained from Pacific Fishery Management Council reports (e.g., PFMC 2007), but some earlier wild salmon spawning abundance estimates were based on approach 3.

Asian Salmon Data

For Russia, we relied upon catch and spawning abundance statistics for each district as provided in annual reports by Russia to the North Pacific Anadromous Fish Commission (NPAFC) beginning in 1992 (e.g., Pacific Research Fisheries Centre 2007a).

Spawning abundance estimates in Russia were often based on aerial counts or redd counts (e.g., Sinyakov 1998; Bocharov and Melnikov 2005), but estimates were not available prior to 1992; therefore, approach 3 and catch reported by the International North Pacific Fisheries Commission (e.g., INPFC 1979) were used for most earlier years. For Kamchatka pink salmon, we used recent run reconstruction estimates dating back to 1957 (Bugaev 2002). These statistics did not account for unreported harvests of salmon (Clarke 2007).

Russian statistics did not identify hatchery versus wild adult salmon; therefore, hatchery releases in Russia (W. J. McNeil, Oregon Aqua-Foods, August 4, 1976, personal communication; Morita et al. 2006; Sharov 2006; Pacific Research Fisheries Centre 2007b) and their assumed survival rates (see below) were used to estimate hatchery production of adult salmon, which was subtracted from total abundance to estimate wild salmon abundance. Russian hatchery releases prior to 1971 were not available except for the Sakhalin and Kurile Islands region, but they were likely small compared with releases in recent years (Zaporozhets and Zaporozhets 2004). Average survival rates of hatchery chum salmon (range of means = 0.21–0.64%) were available from Zaporozhets and Zaporozhets (2004) and N. Kran (Sevvostrybvod, Petropavlovsk-Kamchatsky, Russia, personal communication). Survival rates were lower in southern regions of Russia and during years prior to the 1990s, when hatchery fish quality was lower. Survival of hatchery pink salmon increased from approximately 1.38% in 1971–1983 to 5.08% in 1989–1997 owing to improved hatchery practices (Tarasyuk and Tarasyuk 2007; Kaev and Geraschenko 2008).

Abundances of Japanese hatchery salmon were largely available from NPAFC documents or other processed reports (e.g., CCAHSHP 1988; Hiroi 1998; Eggers et al. 2005; NASREC 2007). Most production of pink salmon in Japan was previously thought to originate from hatcheries (Hiroi 1998), but recent evidence (e.g., recovery of otolith-marked juvenile and adult pink salmon in rivers, hatcheries, and coastal areas; and body morphology) suggests that many pink salmon originated from natural spawners (Fujiwara 2006; Miyakoshi 2006; Hoshino et al. 2008). We used estimates of hatchery and wild pink salmon production provided by Morita et al. (2006). Recent evidence indicates that Japan also produces some wild chum salmon, but estimates were not available (Y. Ishida, Tohoku National Fisheries Research Institute, Fisheries Research Agency, Shiogama, Japan, personal communication). The relatively small production of hatchery chum salmon in South Korea was updated from Seong (1998) and is included with Japanese hatchery estimates unless noted otherwise (S. Kang, National Fisheries Research Development Institute, Yangyang-gun, Gangwon-do, Korea, personal communication). Small numbers of pink salmon return to North Korea, but quantities were unavailable (Kim et al. 2007).

High-Seas Harvests

Annual harvests of salmon in the Japanese high-seas fisheries (mothership fishery, land based fishery, and the more-recent fishery in the Russian Exclusive Economic Zone) were reported by Eggers et al. (2005) and updated by M. Fukuwaka (Hokkaido National Fisheries Research Institute, Fisheries Research Agency, Kushiro, Japan, personal communication). These harvests were relatively high during 1952–1979, averaging 40×10^6 pink salmon/year, 17×10^6 chum salmon/year, and 8×10^6 sockeye salmon/year. Proportions of mature and immature salmon were reported by Shepard et al. (1968), Fredin et al. (1977), Harris (1988), 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 wild fish based on the proportion of hatchery versus wild salmon returning to Asia in that year. The proportion of hatchery or wild fish returning to each region was used to allocate the high-seas catch to that region.

As with previous analyses of such data by Rogers (1987, 2001), Beamish et al. (1997) Eggers (2009), and Kaeriyama et al. (2009), we have had to make many assumptions. However, we believe that the general patterns and trends in abundances across time, regions, and species are likely robust to these assumptions. We urge readers to focus on these broad patterns rather than on particular year-to-year variations in regional estimates because the latter may be imprecise.

Results

Abundance of Wild Salmon Returning from the North Pacific Ocean

Pink salmon was the most numerous species among the wild adult salmon returning from the North Pacific

Ocean and Bering Sea during 1952–2005, averaging approximately 268×10^6 pink salmon/year, or 70% of the combined abundance of wild pink salmon, chum salmon, and sockeye salmon (Figure 2). Wild pink salmon abundance declined from the 1950s through the early 1970s; in the 29 years after the 1976–1977 ocean regime shift, wild pink salmon abundance increased by an average of 90% compared with the previous 15 years (Figure 2A). Sockeye salmon abundance averaged 63×10^6 fish/year (17% of the combined abundance of the three species) and increased by 82% after the 1976–1977 regime shift (Figure 2C). Wild chum salmon abundance averaged approximately 48×10^6 fish/year, or approximately 13% of the combined abundance (Figure 2B). However, in contrast to pink salmon and sockeye salmon, wild chum salmon abundance did not increase after the 1976–1977 ocean regime shift, and from 1980 to 2005 wild abundance was lower than that estimated for the 1950s (Figure 2B). Total abundance of the three species increased over the 54-year period and averaged 498×10^6 wild salmon/year during 1990–2005 (Figure 2D, thin solid line). Peak abundance occurred in 2005 due to the exceptional abundance of pink salmon in that year (495×10^6 pink salmon, or 79% of total abundance).

Distribution of Wild Salmon

During 1990–2005, wild pink salmon abundance was highest in Russia (53% of North Pacific total; primarily from Kamchatka, Sakhalin, and Kurile Islands), followed by southeast Alaska (24%) and central Alaska (12%; Figure 3A). Few pink salmon were present in western Alaska and the U.S. West Coast (coastal Washington and the Columbia River). Wild chum salmon abundance was highest in mainland Russia (32% of North Pacific total), followed by relatively equal percentages (10–16%) in Kamchatka, western Alaska, Southeast Alaska, central Alaska, and southern British Columbia (Figure 3A). No measurable populations of wild chum salmon occurred south of Russia or Oregon. Wild sockeye salmon abundance was greatest in western Alaska (e.g., Bristol Bay; 51% of North Pacific total), followed by central Alaska (17%) and southern British Columbia (12%; Figure 3A). Asia contributed relatively little to the total wild sockeye salmon population (11%), and all Asian wild sockeye salmon were produced in Russia (primarily Kamchatka).

Regional Wild Salmon Responses to Ocean Regime Shifts

Annual abundances of wild salmon in most regions of North America (Figure 4) tended to increase after the 1976–1977 ocean regime shift, whereas salmon abundances in Asia tended to increase in the 1990s (Figure 5), but there were exceptions (Figure 6). Shifts in abundance after the 1989 ocean regime shift were less consistent across regions. Immediately after the 1976–1977 ocean regime shift, wild pink salmon increased by 65% or more on average in all regions of North America except northern British Columbia, where the increase in abundance was more moderate (Figures 4A, 6A). Although pink salmon in Prince William Sound initially increased in the late 1970s, abundance declined in 1986 and remained low compared with abundances in adjacent regions (Figure 4A). Pink salmon abundance initially increased after the mid-1970s in western Kamchatka but not in other regions of Russia and Japan, where increases came later (Figures 5A, 6A). However, pink salmon in western Kamchatka declined precipitously in 1985 after the exceptional return and spawner abundance in 1983 (Bugaev 2002). Immediately thereafter, the pink salmon run switched from a dominant odd-year run to a dominant even-year run that was especially large beginning in 1994 (Figure 5A). For the overall period of 1977–2005, wild pink salmon in Southeast Alaska and western Kamchatka experienced relatively large increases (250% and 260%, respectively) compared with 1962–1976 (Figures 4A, 6A).

Pacific-wide abundances of wild chum salmon declined over time from the 1950s to the early 1970s and then remained relatively stable after the 1976–1977 ocean regime shift (Figure 2B). This pattern was largely a consequence of the 28% decline in chum salmon returning to mainland Russia (Figure 5B), which contributed the largest regional proportion of wild chum salmon in the North Pacific (see “other Russia” in Figure 3A). A relatively small run of wild chum salmon in western Kamchatka initially declined by approximately 5% after the mid-1970s ocean regime shift (Figure 6B) and then increased beginning in 1984. Eastern Kamchatka was the only region in Asia where wild chum salmon initially increased in abundance after the mid-1970s (a 45% increase). In North America, wild chum salmon abundance increased during 1977–1989 in all regions except Southeast Alaska (16% decline) and northern British Columbia (stable; Figures 4B, 6B). After the 1989 regime shift (1990–2005), wild chum salmon abundance declined relative to 1977–1989 in all regions of Alaska except for the southeast region (Figure 4B). The greatest decline occurred in Prince William Sound (48%). In contrast, wild chum salmon in mainland Russia increased several years after 1989, but abundance remained low relative to the abundance recorded in most years prior to 1977 (Figure 5B).

Wild sockeye salmon abundance increased by 60%

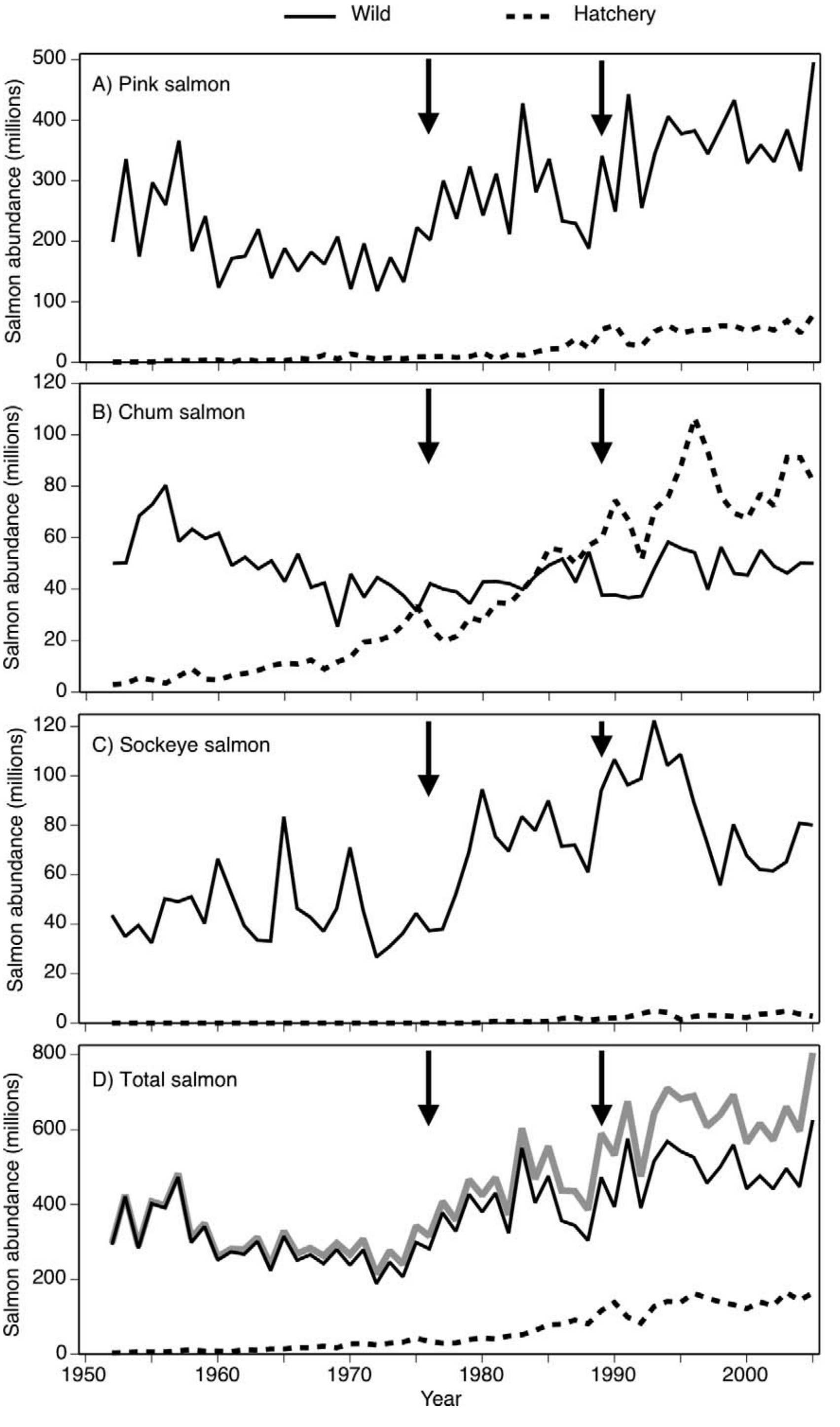

FIGURE 2.—Annual adult abundance (catch plus number of spawners) of wild (solid lines) and hatchery (dashed lines) **(A)** pink salmon, **(B)** chum salmon, and **(C)** sockeye salmon and **(D)** totals across species from 1952 to 2005. In panel D, the bold, solid-gray line is the total abundance of wild plus hatchery fish. Arrows indicate the 1976–1977 and 1989 ocean regime shifts. Note that the *y*-axis scales differ among panels.

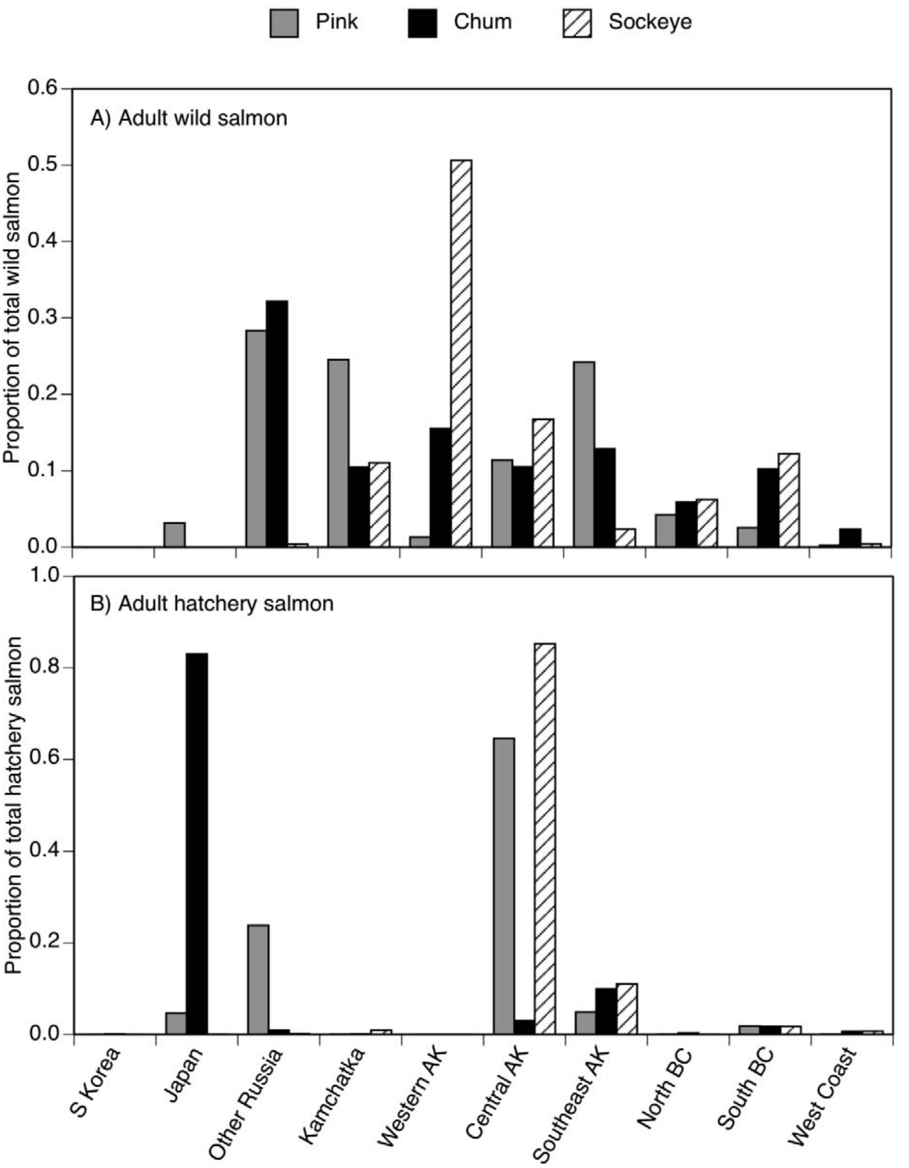

FIGURE 3.—Relative contribution of each region (Figure 1) to Pacific Rim production of adult **(A)** wild and **(B)** hatchery salmon during 1990–2005. For example, 51% of total wild sockeye salmon in the North Pacific returned to western Alaska (AK; panel A), and 83% of total hatchery-origin chum salmon returned to Japan (panel B). The West Coast region includes Washington plus the Columbia River basin; other Russia includes all areas of Russia except Kamchatka (see Figure 1; BC = British Columbia).

or more after the mid-1970s in all major sockeye salmon-producing regions in Alaska and British Columbia except Prince William Sound (Figures 4C, 6C). In contrast, sockeye salmon abundances in Russia (e.g., western Kamchatka) did not increase until the late 1980s or later (Figures 5C, 6C). Total sockeye salmon abundances were high in the early 1990s and then declined in the mid-1990s, largely in response to declining runs in western Alaska (Figures 2C, 4C). The cyclic patterns shown in western Alaska and southern British Columbia (Figure 4C) reflect large, cyclic runs returning to the Kvichak River watershed in Bristol Bay and to the Fraser River in British Columbia. The cyclic pattern in western Alaska was less pronounced

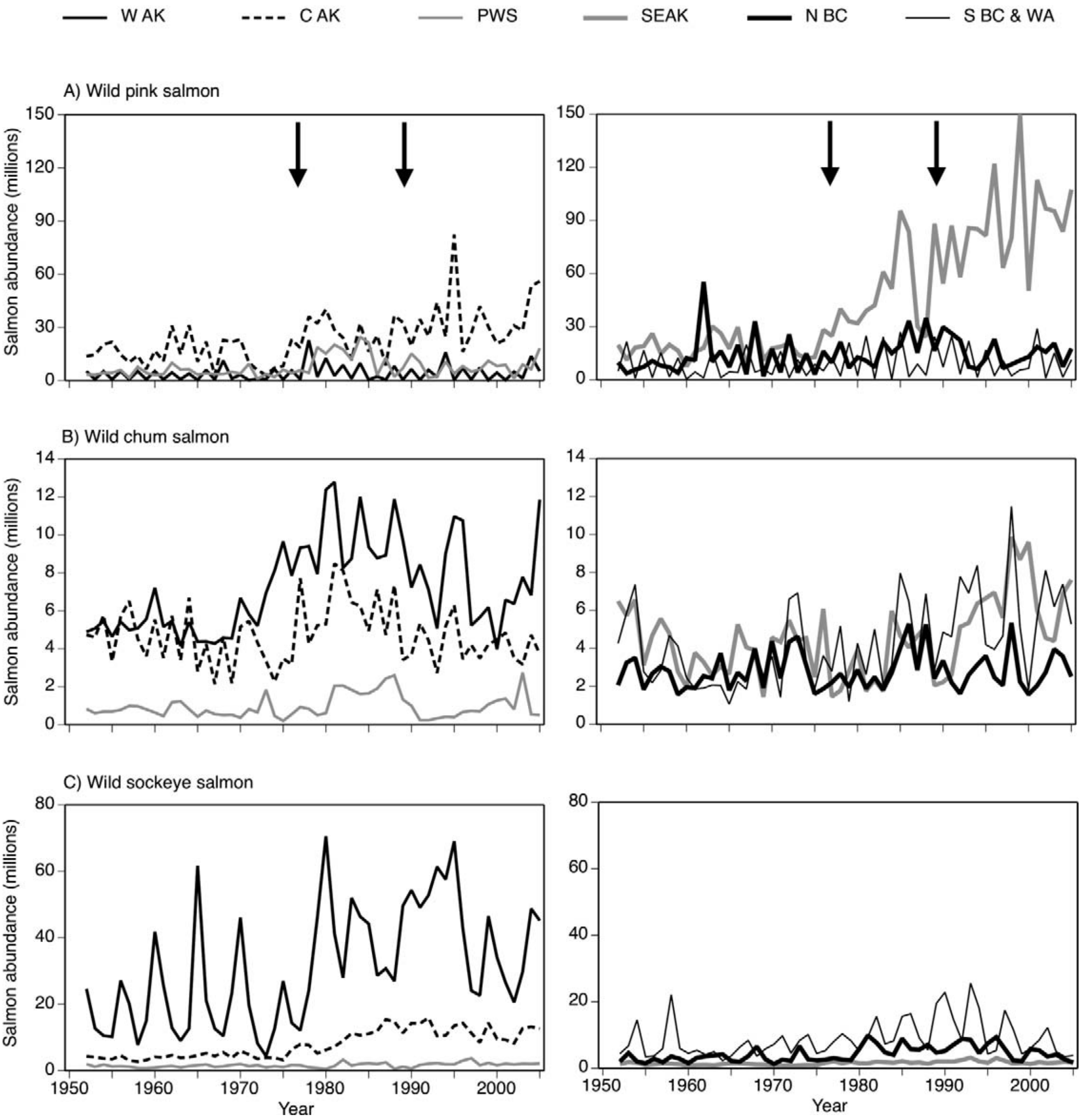

FIGURE 4.—Annual abundance (catch plus spawners) of wild **(A)** pink salmon, **(B)** chum salmon, and **(C)** sockeye salmon returning to regions of North America from 1952 to 2005. Central Alaska (C AK) data exclude Prince William Sound (PWS) values, which are shown separately to highlight PWS's unique patterns (W AK = western Alaska; SEAK = Southeast Alaska; N BC = northern British Columbia; S BC & WA = southern British Columbia and Washington). Arrows indicate the 1976–1977 and 1989 ocean regime shifts.

during the 1990s because the once-dominant Kvichak River run declined precipitously beginning with the 1991 brood year (Ruggerone and Link 2006).

Abundance of Hatchery Salmon Returning from the North Pacific Ocean

Prior to 1970, total annual releases of hatchery juvenile chum salmon, pink salmon, and sockeye salmon into the North Pacific Ocean increased from approximately 240×10^6 to 560×10^6 salmon, largely reflecting production of hatchery chum salmon (Figure 7A). During the 1970s and 1980s, releases of juvenile salmon from hatcheries increased sharply. By the 1990s, hatchery releases of the three salmon species had grown 10-fold to a total annual release of 4.5×10^9 juveniles. Hatchery salmon releases were relatively stable in the 1990s and early 2000s, when approximately 3.1×10^9 chum salmon, 1.4×10^9 pink salmon,

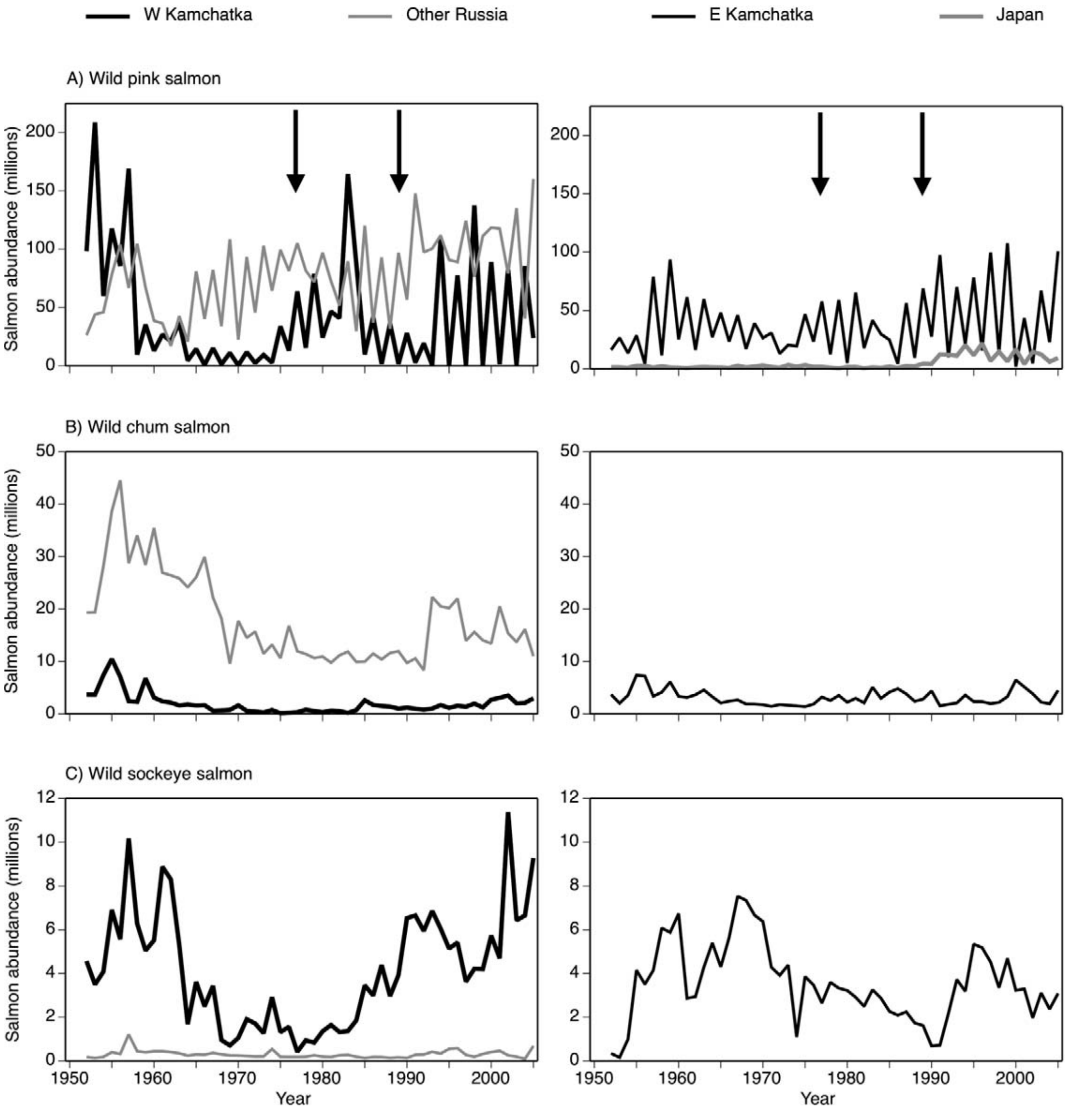

FIGURE 5.—Annual abundance (catch plus spawners) of wild **(A)** pink salmon, **(B)** chum salmon, and **(C)** sockeye salmon returning to regions of Asia from 1952 to 2005. Other Russia includes all areas of Russia except Kamchatka (see Figure 1). Arrows indicate the 1976–1977 and 1989 ocean regime shifts.

and 72×10^6 sockeye salmon were released per year. During 1990 to 2005, approximately 27% of total hatchery chum salmon, 67% of total hatchery pink salmon, and 92% of total hatchery sockeye salmon were released from North American hatcheries as opposed to Asia (Figure 7B).

Abundance of hatchery-origin adults increased steadily from the 1950s to the 1990s (Figure 2), largely attributable to the increasing releases of juvenile salmon (Figure 7A). Abundance of adult hatchery-origin chum salmon (all regions) exceeded that of wild chum salmon in the mid-1980s and thereafter (Figure 2B). During 1990–2005, production of hatchery-origin adults averaged 78×10^6 chum salmon/year, 54×10^6 pink salmon/year, and 3.2×10^6 sockeye salmon/year (excluding spawning-channel sockeye salmon).

Regions that contributed most to the overall production of hatchery-origin salmon during 1990–2005 were Japan (83% of total hatchery chum salmon production), central Alaska (65% of hatchery pink salmon and 85% of hatchery sockeye salmon),

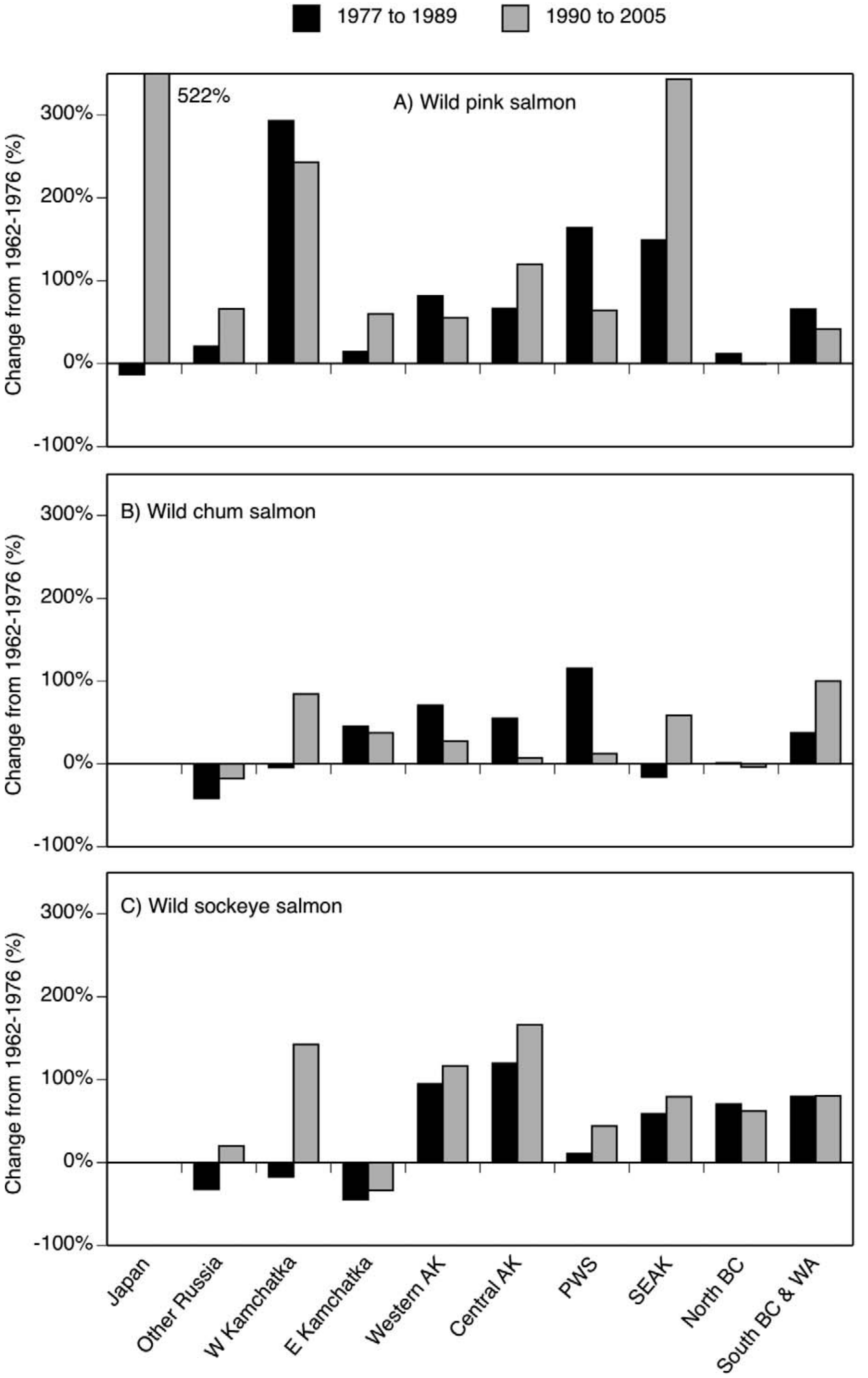

FIGURE 6.—Percentage change in abundances of wild **(A)** pink salmon, **(B)** chum salmon, and **(C)** sockeye salmon from 1962–1976 to 1977–1989 (black bars) and from 1962–1976 to 1990–2005 (gray bars), corresponding with the 1976–1977 and 1989 ocean regime shifts (Hare and Mantua 2000). For example, relative to 1962–1976, abundance of wild adult pink salmon in Southeast Alaska increased by 150% during 1977–1989 and by 340% during 1990–2005 (panel A). See Figure 4 for region code definitions.

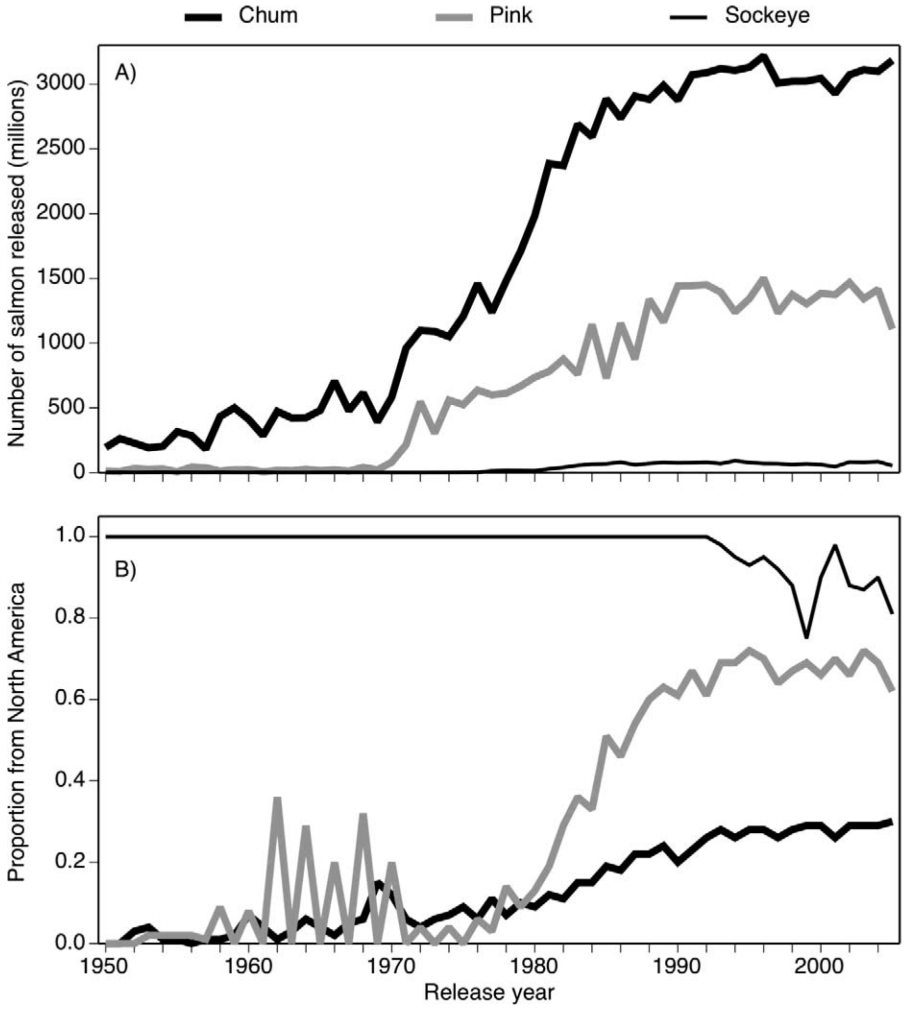

FIGURE 7.—**(A)** Annual releases of juvenile hatchery chum salmon, pink salmon, and sockeye salmon into the North Pacific Ocean and **(B)** the proportion of total hatchery releases originating from North American hatcheries, 1950–2005. Values exclude spawning-channel sockeye salmon. Values are updated from Mahnken et al. (1998).

Southeast Alaska (~10% of hatchery chum salmon and sockeye salmon), and southern Russia (24% of hatchery pink salmon, primarily from Sakhalin; Figure 3B). Contributions of hatchery pink salmon, chum salmon, and sockeye salmon to North Pacific hatchery production were less than 2% in western Alaska, British Columbia, Washington, and Kamchatka.

Total Salmon Abundance

Total (wild plus hatchery) abundance of pink salmon, chum salmon, and sockeye salmon decreased somewhat from 1952 to 1975, averaging (±SD) approximately $309 \times 10^6 \pm 64 \times 10^6$ adult salmon/year (Figure 2D). Total salmon abundance increased steadily after the mid-1970s and exceeded 700×10^6 fish in 1994 and 2005, reflecting the greater numbers of pink salmon. Total salmon abundance during 1990–2005 was relatively stable, averaging $634 \times 10^6 \pm 77 \times 10^6$ adults/year, or approximately twice as many adult salmon than during 1952–1975.

Contribution of Hatchery Salmon to Total Abundance

Hatchery-origin adult salmon represented approximately 62% of total chum salmon, 13% of pink salmon, and 4% of sockeye salmon in the North Pacific during 1990–2005. In Asia during this recent period, hatchery adults constituted on average 76%, 7%, and less than 1%, respectively, of the chum salmon, pink

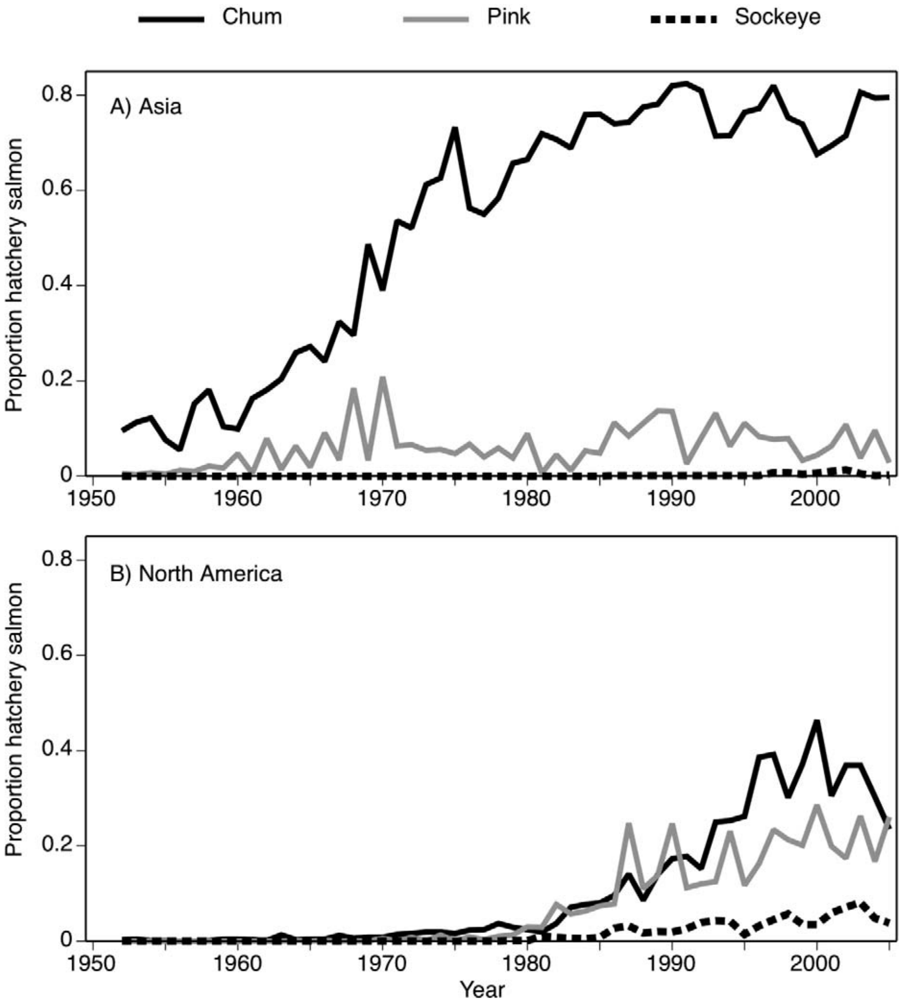

FIGURE 8.—Annual proportion of total adult chum salmon, pink salmon, and sockeye salmon represented by hatchery production in **(A)** Asia and **(B)** North America, 1952–2005.

salmon, and sockeye salmon total abundances (Figure 8A). In North America during 1990–2005, hatchery individuals represented 31, 20, and 4% of the chum salmon, pink salmon, and sockeye salmon total adult abundances on average (Figure 8B).

Regions where hatchery salmon contributed substantially to total adult abundance included Japan, Southeast Alaska, and central Alaska (i.e., Prince William Sound and Kodiak; Figure 9). In Japan, nearly 100% of chum salmon, 100% of sockeye salmon, and approximately 18% of pink salmon originated from hatcheries during 1990–2005. Less than 10% of total salmon production in Russia originated from hatcheries, but hatchery production has been increasing in recent years (e.g., Pacific Research Fisheries Centre 2007b). Hatchery salmon represented more than 70% of total pink salmon and total chum salmon in Prince William Sound and more than 55% of chum salmon in southeast Alaska. Hatcheries in southern British Columbia and the U.S. West Coast contributed approximately 25% to total chum salmon abundance in those regions. Hatchery sockeye salmon contributed relatively little to total abundance in North America except in Kodiak (19%) and Prince William Sound (29%). No hatchery pink salmon or sockeye salmon and few chum salmon were produced in western Alaska.

Discussion

Over the last 50 years, the combined abundance of adult pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean doubled from approximate-

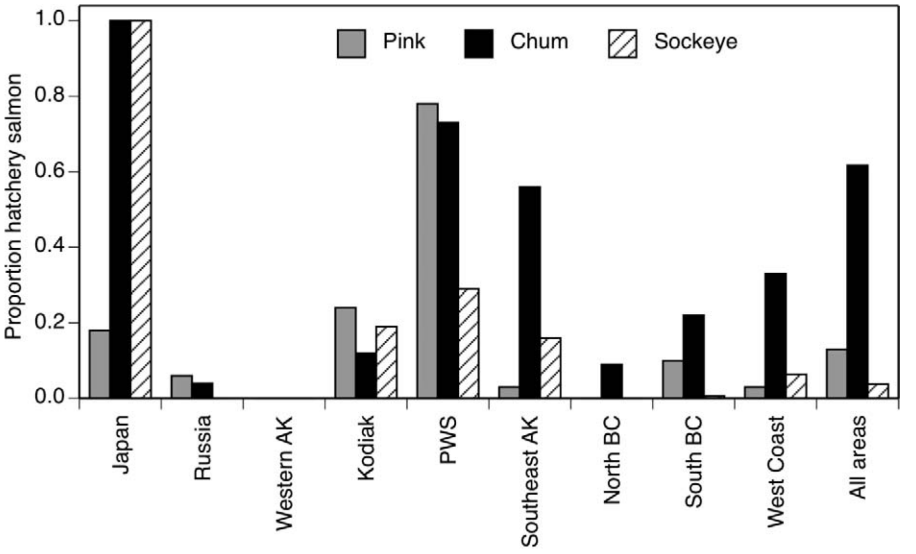

FIGURE 9.—Proportion of total adult chum salmon, pink salmon, and sockeye salmon represented by hatchery production in each region (Figure 1), 1990–2005. For example, 78% of pink salmon and 73% of chum salmon returning to Prince William Sound were of hatchery origin (West Coast = Washington and the Columbia River basin). See Figure 4 for region code definitions.

ly 309×10^6 to 634×10^6 fish. The largest contributors to this increase were wild pink salmon, wild sockeye salmon, and hatchery chum salmon stocks. During 1990–2005, hatchery fish (mostly from Japan and Alaska) made up a substantial portion of the overall abundance of North Pacific adult salmon (22%). In addition, the abundance of hatchery-origin adult chum salmon exceeded that of wild adult chum salmon in the North Pacific since the mid-1980s. We re-emphasize that these numbers take fishing into account because adult recruits are estimated by adding stock-specific catches to stock-specific spawner abundances.

The reason for the increase in abundance of wild pink salmon and sockeye salmon populations is not completely clear, but evidence leans toward increased survival rates (at least for some populations in northern areas; i.e., Alaska and Russia), increased spawning populations (Dorner et al. 2008), or both. For instance, sockeye salmon from Bristol Bay showed substantial increases in survival rate (measured as recruits per spawner) since the early to mid-1970s, even after correcting for within-stock density-dependent effects related to spawner abundance (Peterman et al. 1998, 2003). Pink salmon populations, even those in Alaska, did not show consistent increases or decreases in recruits per spawner (corrected for within-stock density-dependent effects), but spawners increased after the 1970s for most of those populations (Pyper et al. 2001).

Marine conditions affect productivity and abundance of pink salmon, chum salmon, and sockeye salmon. Productivity of these three species in North America was significantly associated with early summer sea surface temperatures at the time of juvenile entry into the ocean, with higher temperatures being associated with higher numbers of recruits per spawner in Alaska but fewer recruits per spawner in British Columbia and Washington (except for chum salmon in Washington; Mueter et al. 2002a). In Alaska after the mid-1970s, greater growth of sockeye salmon during early marine life contributed to their greater productivity and abundance (Ruggerone et al. 2007). Likewise, greater early marine growth of pink salmon in the Gulf of Alaska was associated with greater survival of stocks from central Alaska (Moss et al. 2005; Cross et al. 2008). In Russia, abundances of pink salmon and chum salmon similarly appear to be driven by ocean conditions, but degraded habitat and overharvest have also influenced trends of adult abundance in some regions (Radchenko 1998; Fukuwaka et al. 2007; Kaev et al. 2007; Radchenko et al. 2007).

Pink salmon is the most abundant species of wild salmon, representing approximately 70% of the total abundance of wild chum salmon, sockeye salmon, and pink salmon. Abundance of wild pink salmon has been relatively high since the mid-1990s, averaging 376×10^6 fish, or 76% of the total wild salmon abundance. Chum salmon and sockeye salmon represented approximately 10% and 14%, respectively, of total wild salmon abundance during this period. We hypothesize that warm temperatures and high abundance of plankton during the early 2000s (Overland and Stabeno 2004; Basyuk et al. 2007; Radchenko et al. 2007; Volkov et al. 2007) were especially beneficial to the survival of pink salmon, which enter the ocean at a smaller size and grow more rapidly than sockeye salmon or chum salmon (Ishida et al. 1998; Quinn 2005). The great abundance of pink salmon returning from the North Pacific Ocean is noteworthy because pink salmon can influence the growth, survival, and distribution of other salmon species (e.g., Ruggerone and Nielsen 2004) and because the long-range forecast is for an increasing ocean heat content that may favor pink salmon (Radchenko et al. 2007).

Unlike most sockeye salmon and pink salmon populations in the North Pacific, wild chum salmon did not increase in abundance after the mid-1970s regime shift. The lack of a response primarily reflects the declining abundance of wild chum salmon in mainland Russia, which supports the largest wild chum salmon runs in the North Pacific Ocean. Chum salmon in mainland Russia increased beginning in 1993, but abundances were still far below the levels recorded prior to 1970. Although overharvest and habitat degradation have been recognized as factors affecting the decline of Russian wild chum salmon stocks in the 1950s and 1960s, it is possible that competition with the approximately 2×10^9 chum salmon released annually from Japanese hatcheries and up to 360×10^6 chum salmon from Russian hatcheries has inhibited the recovery of Russian wild chum salmon stocks (Radchenko 1998; Kaeriyama et al. 2007). Japanese hatchery chum salmon are broadly distributed throughout much of the North Pacific Ocean and Bering Sea (Myers et al. 2007; Beacham et al. 2009; Urawa et al. 2009) and could potentially affect the growth of wild chum salmon populations originating from Russia, western Alaska, central Alaska, southeast Alaska, and British Columbia (Myers et al. 2004). In Alaska, wild chum salmon runs north of southeast Alaska declined during 1990–2005, especially those in Prince William Sound, where abundance of hatchery-origin chum salmon has grown rapidly since the late 1980s and now represents approximately 73% of total chum salmon abundance. This pattern raises the question of whether large-scale releases of chum salmon in Prince William Sound in addition to those in Japan and Russia have influenced growth and survival of wild chum salmon, as has been debated for pink salmon (Hilborn and Eggers 2000, 2001; Wertheimer et al. 2001, 2004a, 2004b).

Management Implications

Although the observed large increases in abundance of wild pink salmon and sockeye salmon during the last few decades may appear to contradict the intense conservation concerns about salmon in the North Pacific, these different viewpoints are both valid but at different spatial scales. Legitimate conservation concerns arise in spite of these general overall increases because for certain species, there are many individual populations and regions in which wild salmon abundance has decreased severely, such as chum salmon in Japan, South Korea, the Amur River (Russia and China), western Alaska, and the Columbia River; summer-run chum salmon in Hood Canal (Washington); and sockeye salmon in the Kvichak River (Bristol Bay), Rivers Inlet (British Columbia), the Fraser River (British Columbia), and the Snake River basin (Idaho); among many others. Salmon species and stocks have broad distributions in the ocean, and abundant stocks overlap and intermingle with those having low productivity (Myers et al. 2007, 2009). Potential density-dependent interactions arising from increased abundance of the more-productive stocks may potentially depress less-productive ones through reduced growth, reduced survival, or both (e.g., Peterman 1984a; Ruggerone et al. 2003), and increased fishing pressure on productive stocks may adversely affect less-productive stocks with overlapping distributions.

Important management implications of our wild and hatchery salmon abundance estimates emerge from the combination of four factors: (1) the growing public interest in maintaining abundant, productive, and biologically diverse wild salmon populations and sustainable salmon fisheries, (2) the large and increasing percentage contribution of hatchery fish to the total abundance of adult salmon in the North Pacific Ocean, (3) plans to maintain or increase hatchery production in the future regardless of ocean conditions, and (4) evidence of density-dependent interactions within and among species and within and among salmon from the same or even different geographic regions or nations. An important policy implication of this conjunction of factors is that salmon originating from different nations may compete for a limited "common pool" of food resources in international waters of the North Pacific. This is a potential "tragedy of the commons" situation, leading some to call for limitations or economic disincentives for hatchery releases (e.g., Peterman 1984b; deReynier 1998; Heard 1998; Holt et al. 2008). Coordinating leadership by the NPAFC or an analogous international treaty organization to address this issue would be beneficial (Holt et al. 2008). This concern about competing for limited resources may become considerably more acute if the North Pacific area occupied by salmon decreases due to climatic warming (Welch et al. 1998).

Hatchery production represents a large portion of total runs in some relatively pristine regions where wild salmon reproduction is not compromised by habitat degradation in freshwater (e.g., Prince William Sound, Kodiak, and southeast Alaska). If density-dependent feedback on growth, survival, or both is substantial and widespread among stocks that intermingle at sea, then questions arise about whether large hatchery production is appropriate or advantageous in such systems. In contrast with the dynamics of wild salmon populations, hatchery releases usually remain high irrespective of whether ocean productivity is high or low. An example of the difficulty in answering this challenge is the debate between Hilborn and Eggers (2000, 2001) and Wertheimer et al. (2001, 2004a) over the net benefit of hatchery pink salmon in Prince William Sound. Hatchery salmon may reduce variability in harvests but this benefit to fishermen may come with a cost to wild salmon productivity. Additionally, there can be substantial straying of hatchery fish into natural spawning areas, which can degrade the fitness and biological diversity of the wild populations (e.g., Levin et al. 2001; Ford 2002; Naish et al. 2007; Buhle et al. 2009).

Resource agencies often do not separately estimate and report hatchery and wild salmon in the catch, let alone the spawner counts. The presence of numerous hatchery salmon can reduce the accuracy of wild salmon abundance and productivity estimates, which are important for setting goals for harvest rates and spawning abundances. Furthermore, identification of hatchery salmon in mixed-stock fisheries is important for reducing the chance of overexploiting the wild stock. We therefore strongly recommend that all hatchery-released juvenile salmon be marked in some way so that the resulting adults can be estimated separately from wild fish (e.g., with clipped adipose fins or via thermal marking, as in Alaska).

Cautions Regarding Data Quality

The data presented here represent a more-complete accounting of wild and hatchery salmon abundances throughout the North Pacific than has been provided by previous estimates (e.g., Rogers 1987, 2001; Beamish et al. 1997; Eggers 2009; Irvine et al. 2009; Kaeriyama et al. 2009) because we expanded spawner counts where appropriate and accounted for hatchery salmon in all regions. Nevertheless, we caution readers that the quality of our salmon abundance data is variable among species and regions. Estimating stock-specific catch and spawning abundance of wild salmon is difficult, especially in large, remote watersheds, but it is much more difficult when hatchery and wild salmon are mixed in the catch and when hatchery fish stray to the spawning grounds. However, the key question is how would the caveats and assumptions below have led to incorrect conclusions about spatial and temporal differences in abundances? In most cases, we believe that errors in our assumptions would have produced more imprecision in year-to-year estimates rather than consistent bias in one direction or the other. Thus, the general patterns and approximate magnitude of hatchery versus wild salmon in the compiled data are likely valid.

Spawner abundance represents the least accurate component of total salmon abundance because only a portion of total spawners is typically enumerated. For example, in British Columbia, observed spawner counts were expanded by approximately $1.7x$ for pink salmon (where x is the field estimate of spawner abundance), $2.7x$ for sockeye salmon (often smaller populations), and $4x$ for chum salmon (e.g., English et al. 2006). In Alaska, similar expansion values were used for pink salmon and chum salmon, whereas most large stocks of sockeye salmon were close to complete counts. Price et al. (2008) noted that the quality of spawner counts in British Columbia has declined in recent years because fewer streams are now monitored; the decline in quality especially affects smaller streams in which populations may not be highly correlated with the monitored populations. In Russia, total spawning abundance has been reported by district since 1992, but information on expansion factors was not readily available (V. Svirdov, Pacific Scientific Research Fisheries Center, Vladivostok, Russia, personal communication) and it is not possible to evaluate the potential for error in spawner counts. However, as in British Columbia and Alaska, we suspect that the effort to enumerate spawning salmon in Russia has declined in response to declining budgets for salmon management.

The number of hatchery salmon on the spawning grounds is typically not reported because hatchery fish cannot be identified unless they are marked (which some hatcheries fail to do) and because spawning salmon, especially pink salmon and chum salmon, are typically enumerated using techniques (e.g., aerial flights) that prohibit identification of hatchery- versus wild-origin salmon. The degree to which hatchery salmon contributed to regional natural spawning populations in our data set reflects the ability of harvesters to remove most hatchery salmon in the region (e.g., terminal hatchery harvest area), the ratio of hatchery to wild salmon abundance, distance of the stream from the hatchery, species of salmon and associated degree of straying, and hatchery characteristics that attract homing hatchery salmon. As a result of these factors, our data set overestimates wild salmon abundance and underestimates hatchery salmon production in some regions such as Prince William Sound and southeast Alaska, where hatchery production of pink salmon and chum salmon is high. In these regions, the Alaska Department of Fish and Game (ADFG) has begun investigations to determine numbers of hatchery salmon on the spawning grounds (R. Brenner and S. Moffitt, ADFG, personal communication). The influence of hatchery strays on wild salmon counts was greater after about 1980, when hatchery production was relatively high.

Harvest rate estimation was a key approach for estimating total spawners, especially with regard to the early years of our data set, when fewer spawner counts were available. Years with low harvest rates could lead to greater error in total salmon abundance. However, in most regions, fisheries were fully developed by the 1950s and harvest rates were often greater than 50%, suggesting that harvest estimates, which are relatively accurate, typically accounted for most of total abundance. Again, even if our estimated harvest rates were imprecise (as opposed to consistently being biased either low or high), this would not change our overall conclusions about regional and temporal trends in abundance. Labor strikes may affect abundance estimates for some regions in some years, but their effect on the abundance trends shown here was likely small because abundances in recent decades were often based on estimated spawners and reported harvests and because the area influenced by the strike was often small.

Often, abundance of hatchery salmon in the harvest was not reported by the harvest management agency. We used hatchery abundances reported by the hatchery when possible, but we often estimated total abundance of hatchery salmon by using survival rate estimates and we removed these hatchery fish from the total abundance counts when appropriate. Species-specific survival rates were typically mean annual values for a region because most hatcheries do not estimate survival annually.

Regardless of these uncertainties in our data, we are confident that the spatial and temporal patterns and relative contributions of hatchery and wild fish that we have shown are robust. Some of these data have been used in a variety of earlier investigations (e.g., Pyper et al. 2001, 2002; Mueter et al. 2002b; Dorner et al. 2008), including a North Pacific-wide simulation study demonstrating that density dependence in the ocean was an important factor contributing to the observed trends in hatchery and wild salmon abundance (Mantua et al. 2009).

Recommendations

Four clear recommendations emerge from this synthesis of data. First, salmon management agencies and private salmon hatchery operators in the North Pacific should develop their plans for regulations and activities while considering the large numbers of hatchery fish and the high proportion of total adult abundance that is composed of hatchery fish, especially for pink salmon and chum salmon. Second, we recommend controlled manipulations of hatchery salmon releases at local and larger spatial scales as a means to experimentally evaluate density-dependent effects on wild salmon (see Peterman 1991). Such action is needed because stable releases of numerous hatchery salmon complicate efforts to further quantify density-dependent interactions involving salmon originating from local and distant regions as well as from different nations. A third recommendation is that all organizations and institutions involved in producing or harvesting salmon in the North Pacific should engage in serious discussions about how best to share the North Pacific food resources used by salmon, especially given that areas of suitable ocean habitat in this region are forecasted to decrease drastically due to future climatic conditions. Fourth, we recommend (1) the marking of all hatchery-released juvenile salmon to distinguish them from wild fish and (2) the rigorous sampling of hatchery and wild salmon in the harvest and on spawning grounds to evaluate the status of wild salmon and the net benefits of hatchery salmon. Abundances of hatchery and wild salmon should also be reported regularly by management agencies to identify trends and potential conditions of concern.

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