

**COMMISSION OF INQUIRY INTO THE DECLINE OF SOCKEYE SALMON
IN THE FRASER RIVER**

In the matter of Her Excellency the Governor General in Council, on the recommendation of the Prime Minister, directing that Commission do issue under Part 1 of the *Inquiries Act* and under the Great Seal of Canada appointing the Honourable Bruce Cohen as Commissioner to conduct an inquiry into the decline of the sockeye salmon in the Fraser River

AFFIDAVIT #1 OF RANDALL PETERMAN

I, Randall Peterman, of the School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, MAKE OATH AND SAY THAT:

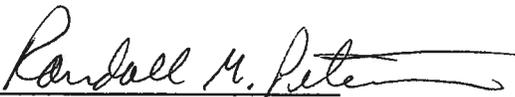
1. I am a Professor and Canada Research Chair in Fisheries Risk Assessment and Management, School of Resource & Environmental Management at Simon Fraser University, and as such, I have personal knowledge of the matters hereinafter deposed to except where stated to be based on information and belief, and where so stated I believe them to be true.
2. This affidavit is prepared in response to a request for information from commission counsel regarding habitat enhancement and restoration.
3. My curriculum vitae has been marked as Exhibit 749 in this Inquiry.
4. On April 27 2011, I was provided with a series of questions from commission counsel with respect to which I was asked to prepare written answers. A true copy of the questions with my answers set out is attached to my affidavit as **Exhibit "A"**.
5. I adopt the responses set out in Exhibit "A" as true statements as if contained within my affidavit.

6. Attached as the following exhibits to my affidavit are true copies of the journal articles I have referred to in Exhibit "A":
- a. **Exhibit "B"**: Ruggerone, G.T., R.M. Peterman, B. Dorner, K.W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 2:306-328 ("Ruggerone et al. 2010"),
 - b. **Exhibit "C"**: Pyper, B.J. and R.M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon, 1967-1997. *Can. J. Fish. Aquat. Sci.* 56:1716-1720 ("Pyper 1999"),
 - c. **Exhibit "D"**: Peterman, R.M. 1991. Density-dependent marine processes in North Pacific salmonids: Lessons for experimental design of large-scale manipulations of fish stocks. *ICES Marine Sci. Sympos.* 192:69-77 ("Peterman 1991"),
 - d. **Exhibit "E"**: Hilborn, R., Eggers, D. 2000. A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska. *Trans. Amer. Fish. Soc.* 129:333-350 ("Hilborn and Eggers 2000"),
 - e. **Exhibit "F"**: Hilborn, R. and Eggers, D. 2001. Comment: A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska: Response to Comment. *Trans. Amer. Fish. Soc.* 130: 720-724 ("Hilborn and Eggers 2001"),
 - f. **Exhibit "G"**: Wertheimer, A.C., Heard, W.R., Maselko, J.M. and Smoker, W.W. 2004. Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does size matter? *Rev. Fish Biol. Fish.* 14: 321-334 ("Wertheimer 2004"), and
 - g. **Exhibit "H"**: Wertheimer, A.C., Smoker, W.W., Joyce, T.L. and Heard, W.R. 2001. Comment: A Review of the Hatchery Programs for Pink

Salmon in Prince William Sound and Kodiak Island, Alaska. Trans. Amer. Fish. Soc. 130: 712-720 ("Wertheimer 2001").

7. Ruggeroni, G.T. 2010. Competition Between Fraser Sockeye Salmon and Pink Salmon. In: Appendix C2, part 2, pp. 87-90 of Peterman et al. (2010) report on the Pacific Salmon Commission's June 2010 workshop on the decline of Fraser River sockeye ("Ruggeroni 2010 June PSC"), referred to in Exhibit "A", is marked as Exhibit 573 in this Inquiry.

SWORN before me in the City of)
Vancouver, British Columbia, on)
May 2, 2011)
)
)
)
)
_____)
Commissioner for taking Affidavits
in the Province of British Columbia



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29 April 2011

Randall Peterman's answers to Affidavit questions related to the hearing at the Cohen Commission on "Habitat Enhancement and Restoration" on 2 May 2011

Witness: RANDALL M. PETERMAN, Professor and Canada Research Chair in Fisheries Risk Assessment and Management, School of Resource & Environmental Management, Simon Fraser University

Witness background

Background related to interactions between wild and enhanced fish

1. Ruggerone, G.T., R.M. Peterman, B. Dorner, K.W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 2:306-328.
2. Holt, C.A., M.B. Rutherford, and R.M. Peterman. 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. *Marine Policy* 32(4):607-617.
3. Pyper, B.J. and R.M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon, 1967-1997. *Can. J. Fish. Aquat. Sci.* 56:1716-1720.
4. de Young, B., R.M. Peterman, A.R. Dobell, E. Pinkerton, Y. Breton, A.T. Charles, M.J. Fogarty, G.R. Munro, C. Taggart. 1999. Canadian Marine Fisheries in a Changing and Uncertain World. *Canadian Special Publication of Fisheries and Aquatic Sciences* No. 129:1-199.
5. Peterman, R.M. 1991. Density-dependent marine processes in North Pacific salmonids: Lessons for experimental design of large-scale manipulations of fish stocks. *ICES Marine Sci. Sympos.* 192:69-77.
6. Guthrie, I.C. and R.M. Peterman. 1988. Economic evaluation of lake enrichment strategies for British Columbia sockeye salmon (*Oncorhynchus nerka*). *N. Amer. J. Fish. Management* 8:442-454.
7. Peterman, R.M. 1987. Review of the components of recruitment of Pacific salmon. In: M. Dadswell, R. Klauda, C. Moffitt, R. Saunders, R. Rulifson, and J.E. Cooper (eds.), *Common Strategies of Anadromous and Catadromous Fishes*, American Fisheries Society Sympos. 1:417-429.
8. Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 41(12):1825-1829.

This is Exhibit "A" referred to in the Affidavit of Randall Peterman sworn before me at Vancouver, BC this 2 day of May, 2011

Commissioner for taking Affidavits within
British Columbia

9. Peterman, R.M. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. *Can. J. Fish. Aquat. Sci.* 39(6):904-913.
10. Peterman, R.M. 1978. Testing for density dependent marine survival in Pacific salmonids. *J. Fisheries Research Board of Canada* 35:1434-1450.
11. Walters, C.J., R. Hilborn, R.M. Peterman, and M.J. Staley. 1978. Model for examining early ocean limitation of Pacific salmon production. *J. Fisheries Research Board of Canada* 35:1303-1315.

Interactions between wild fish and enhanced fish

2. Describe, in summary form, the potential for interactions between wild and hatchery (or other enhanced) salmon in the marine environment.

- a. Depending on the specific situation, overlap can occur between wild and enhanced salmon in space and time (on a local scale as well as on the scale of the North Pacific Ocean).
- b. On a local scale, there are some places where hatchery-produced salmon outnumber wild salmon, but I am not aware of detailed data for B.C. Also, conservation-oriented "supplementation" hatcheries exist that aim to rebuild extremely small wild populations.
- c. On the North Pacific scale, there is considerable potential for indirect interactions between wild and enhanced salmon. Ruggerone et al. 2010 provides an example of this potential, although the paper only considers hatchery fish and not fish produced by other enhancement methods such as spawning channels or lake fertilization.

- Across pink, chum, and sockeye salmon, 22% of adults in North Pacific are hatchery origin and plans exist to further increase annual hatchery releases, particularly in Russia and Alaska. Although relatively few sockeye are produced by hatcheries, wild sockeye appear to interact with pink salmon, as described below.

- Ruggerone et al. (2010) Fig. 1, p. 308: map.

- Ruggerone et al. (2010) Fig. 7, p. 318: Hatchery releases of pink and chum salmon have increased dramatically over the last 40 years, but note that there are very few hatchery-produced sockeye anywhere.

- Ruggerone et al. (2010) Fig. 2, p. 313: Total North Pacific adult abundances of wild pink and sockeye salmon are much higher in the 2000s than in the 1960s and 1970s, and hatcheries have added relatively small numbers on top of the wild fish *for those two species*. However, hatchery-origin *chum* salmon (mostly from Japan and Alaska) have outnumbered wild *chum* salmon in the North Pacific since the mid-1980s.

d. There are many documented examples of density-dependent interactions between wild and enhanced salmon (see e.g. Peterman 1991).

3. Possible mechanisms for interactions between wild and enhanced salmon

a. Competition for food can occur between wild and enhanced salmon because their diets overlap and to our knowledge, they generally pass through feeding areas at similar times and places unless the release of enhanced fish has been altered.

b. Predation-induced mortality on juvenile salmon can be influenced by large numbers of enhanced fish in two ways:

b1. Attraction of predators to high abundances of juvenile salmon driven by large hatchery releases, for example, will tend to **reduce** survival rate of co-migrating wild juvenile salmon, all else being equal.

b2. However, high total abundance of hatchery plus wild juveniles will tend to satiate predators (i.e. "swamping them with excess food"), thereby tending to **increase** survival rate of the wild juvenile salmon that co-migrate with the hatchery fish, which would tend to increase total abundance.

b3. The net effect of the two mechanisms listed immediately above depends on total juvenile salmon abundance. When it is very high, the "swamping" effect will dominate, thereby **increasing** survival rate of the group of wild salmon, as well as the hatchery salmon. When total salmon abundance is moderate or low, though, the attraction of more predators will dominate, possibly **reducing** survival rate of wild fish.

c. In places where adults of wild and enhanced salmon co-migrate through fishing areas, pressure is intense on managers to allow high harvest rates. However, wild stocks generally have lower productivity (adults per spawner) than enhanced fish, so high percentage harvest rates targeted on enhanced fish are known to eventually lead to overharvesting and depletion of abundance of wild co-migrating stocks that are subject to those same harvest rates.

d. After adults leave the ocean, large numbers of hatchery fish straying into spawning areas for wild fish can decrease biological diversity and fitness of the wild stocks.

4. Why are these interactions in the marine environment important for salmon users, managers, and others?

In general, increased numbers of wild and/or enhanced salmon can potentially lead to reduced body size at a given age of both wild and enhanced adult salmon. In some cases, survival rate (i.e., productivity from spawners to adults) can also decrease as a result of high abundances, although fewer examples of reduced survival rate are known than reduced body size.

In the overall picture for B.C. enhancement programs, such effects on body size and survival rate may be of relatively little consequence to fishable biomass, except in particular local situations, but again, I do not personally know the data on these programs. However, at the very least, the existence of ecological effects such as those

described below should be taken into account when planning and operating B.C. enhancement facilities.

a. **Body size at a given age of adult sockeye salmon** decreases as abundance of competitors increases. Here competitors refers to ALL sockeye salmon (wild plus enhanced). All of the following examples on body size are at the scale of the North Pacific Ocean.

a1. Pyper et al. (1999) Fig. 3, p. 1050, bottom panel for Fraser River sockeye, plus the other panels above it, show similar decreases in adult size-at-age over time, which means fewer dollars per fish for industry. Note that this paper merely describes changes in body size and not the reasons for these changes.

a2. Peterman (1991) Fig. 6, p. 75: Total dollars from the total biomass harvested may or may not increase substantially with increasing hatchery releases. Most certainly, though, above some level of juvenile abundance on the North Pacific scale, costs of producing them will exceed the benefits gained across the salmon-producing nations of the North Pacific Rim.

a3. Peterman (1991) Fig. 2, p. 71: Body length of Chilkco age 4 adults decrease with increasing total number of Chilkco sockeye and total number of sockeye competitors in the Gulf of Alaska. The within-stock and among-stock effects are about equally important.

a4. Peterman (1991) Fig. 2 above and Ruggerone et al. (2007) Fig. 7, p. 2787 show that large numbers of salmon from a given nation is associated with another nation's economic value of wild salmon through reduced body size of adults. The Ruggerone et al. 2007 Figure 7 shows that reduced wild Bristol Bay sockeye length at age is associated with increasing abundance of either wild Bristol Bay sockeye or East Kamchatka (Russian) pink salmon, which again means fewer dollars per fish for industry. However, as with any correlation analysis, such an association between two variables does not necessarily mean that there is a causal link. Instead, there may be other variable(s) that are also correlated and that are the actual causes of the observed response.

b. **Survival rate of sockeye salmon can decrease** as abundance of pink salmon competitors increases. However, there are only a few documented examples of this reduction in survival rate compared to examples of reduced growth rate (reflected by adult body size). Examples here come from both the local-scale and the scale of the North Pacific Ocean.

b1. Fraser River sockeye interaction with pink salmon: Ruggerone (2010 from the June PSC workshop) Figures 1 and 2 found reduced productivity (adults per spawner) for Fraser River sockeye in years when they were at sea with large numbers of pink salmon from the Fraser River, Southeast Alaska, and Prince William Sound in Alaska. Ruggerone suggested that competitive interactions were operating.

b2. Prince William Sound, Alaska: Hilborn and Eggers (2000, 2001) and Wertheimer et al. (2001, 2004) debated whether the pink salmon hatcheries in Prince William Sound (PWS), Alaska added to the wild pink salmon populations or largely replaced

the wild fish with hatchery fish. Their conclusions differ considerably, with Hilborn and Eggers arguing that wild populations decreased drastically due to increasing hatchery fish, whereas Wertheimer et al. argued that, although there was a loss of some wild fish, that amount was less than 5% of the huge increase in hatchery-derived fish.

b3. Ruggerone et al. (2003) Fig. 4, p. 215: Reduced Bristol Bay smolt-to-adult *survival rate* when they compete with large numbers of Asian pink salmon. Fewer surviving Bristol Bay sockeye means lower economic value of catches.

c. The concern about competing for limited resources may become considerably more acute if the North Pacific becomes less productive again.

5. Research priorities for wild-hatchery fish interactions in the marine environment

- a. Enhancement of salmon of any species should be planned as large-scale experiments and evaluations of such plans should take into account density-dependent processes in the benefit/cost analyses.
- b. Potential interactions between enhanced and wild fish are known and should be investigated further.
- c. Analyses of high-seas distributions and survival rates of salmon are seriously underfunded in Canada compared to the U.S., Russia, and Japan.

6. Relevant additional recommendations from Ruggerone et al. 2010 and Peterman 1991

- a. Coordinated programs should be organized by the North Pacific Anadromous Fish Commission or an analogous international treaty organization to address potential interactions on the high seas among salmon from different countries (Ruggerone et al. 2010, p. 321; Peterman 1991, p. 71).
- b. All hatchery-released juvenile salmon should be marked in some way so that the resulting adults can be estimated separately from wild fish (Ruggerone et al. 2010, p. 322).
- c. Managers should carefully examine assumptions behind program objectives (Peterman 1999, p. 69).
- d. Salmon management agencies around the North Pacific should develop plans for regulations and activities while considering the large numbers of enhanced fish and the high proportion of total adult abundance that is composed of hatchery fish (Ruggerone et al. 2010, p. 323).

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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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This is Exhibit B prepared to in the affidavit of R. Peterman sworn before me at Vancouver this 2 day of May 20 11
A Commissioner for taking Affidavits for British Columbia

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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

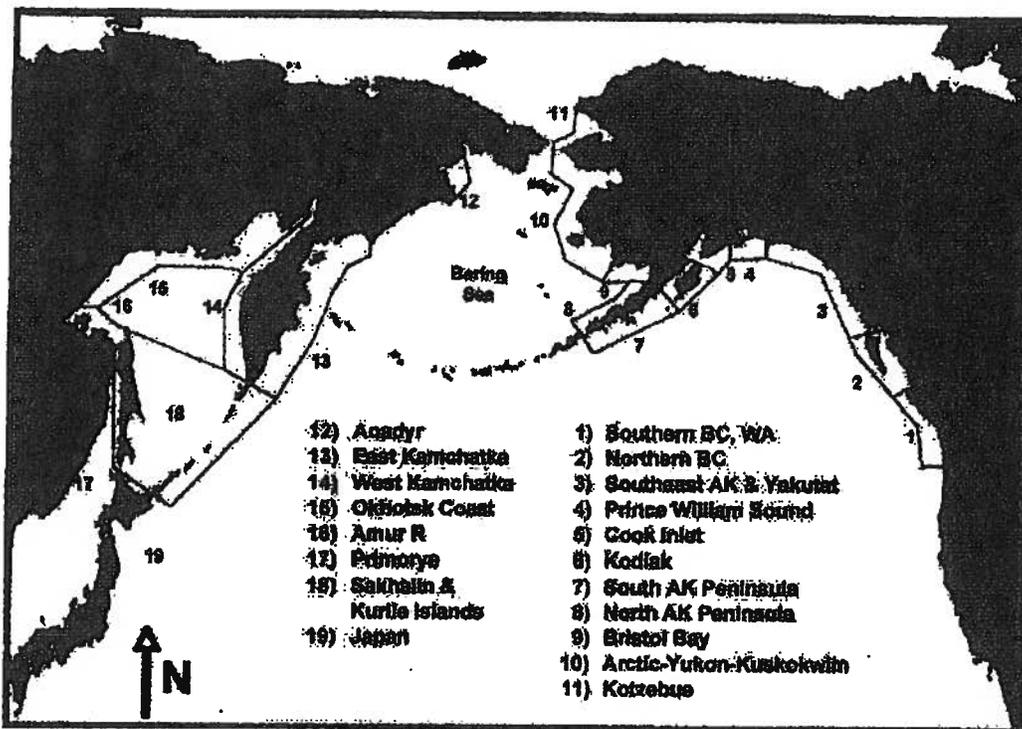


FIGURE 1.—Approximate geographic locations of regional stock groups included in this study. Area 1, southern British Columbia (BC) and Washington (WA), includes the Columbia River and all areas south of the central BC coast (~51°N). Area 2, northern BC, includes central and northern BC. Area 3, southeast 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

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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).

Area	Method			
	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 chin 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 $\log_e(\text{catch})$ 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 Heintz 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).

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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, Shioyama, 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%

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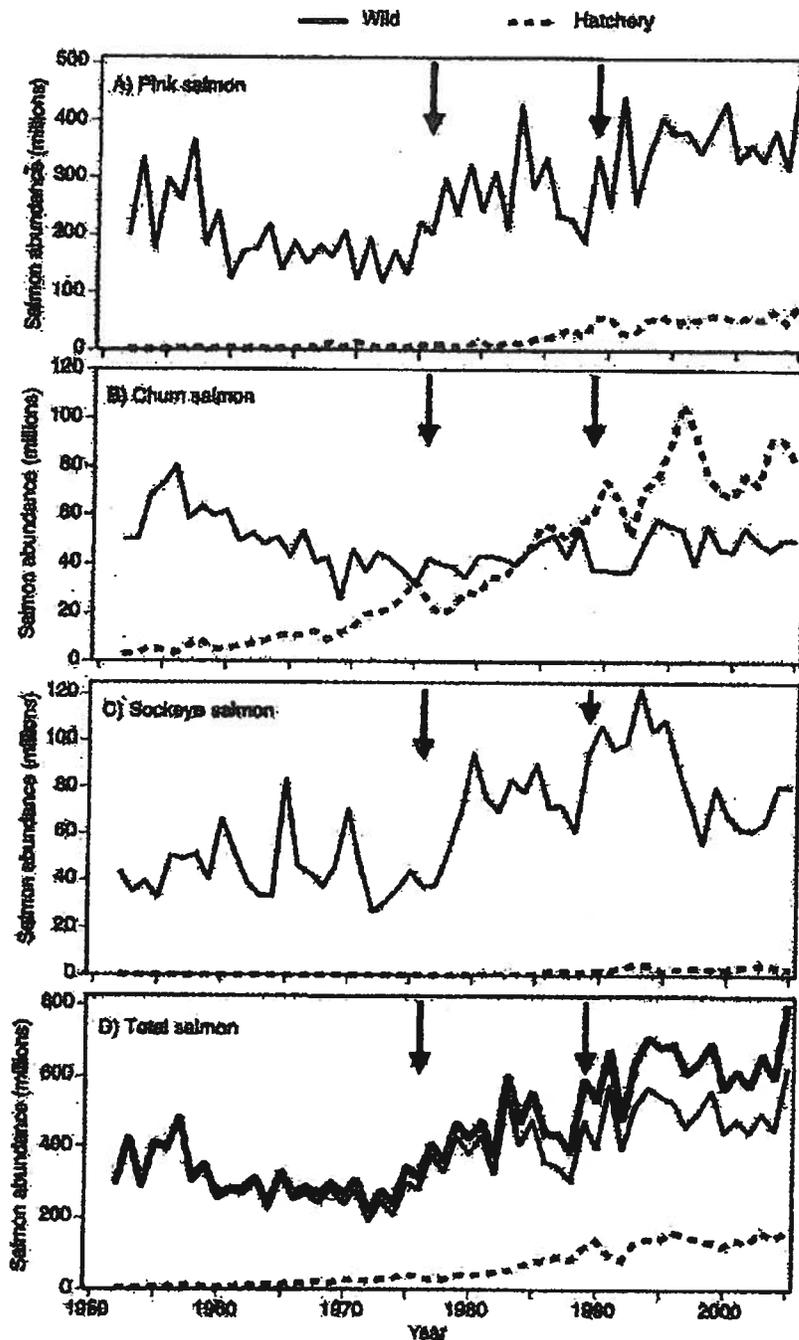


FIGURE 2.—Annual adult abundance (catch plus number of spawners) of wild (solid lines) and hatchery (dashed lines) (A) pink salmon, (B) chum salmon, and (C) sockeye salmon and (D) totals across species from 1952 to 2005. In panel D, the bold, solid-gray line is the total abundance of wild plus hatchery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

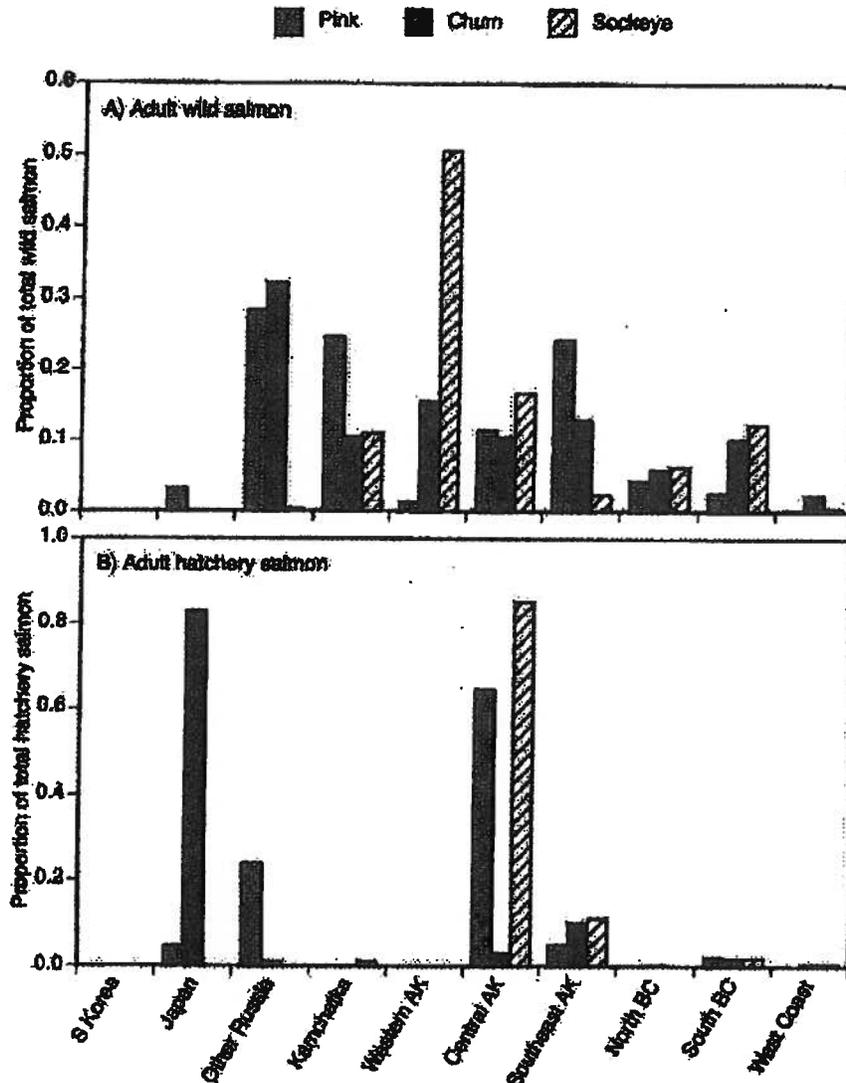


FIGURE 3.—Relative contribution of each region (Figure 1) to Pacific Rim production of adult (A) wild and (B) hatchery salmon during 1990–2005. For example, 51% of total wild sockeye salmon in the North Pacific returned to western Alaska (AK; panel A), and 83% of total hatchery-origin chum salmon returned 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

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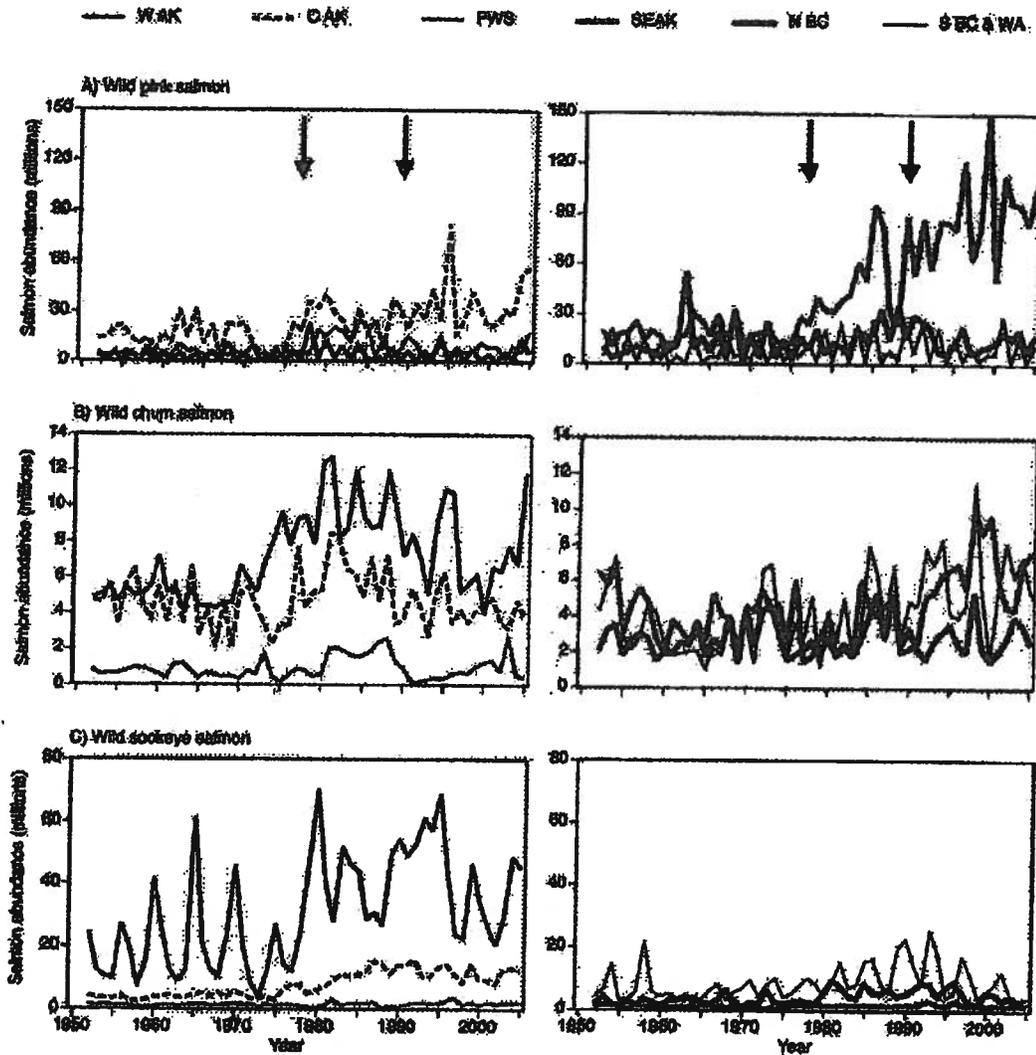


FIGURE 4.—Annual abundance (catch plus spawners) of wild (A) pink salmon, (B) chum salmon, and (C) sockeye salmon returning to regions of North America from 1952 to 2005. Central Alaska (C AK) data excludes Prince William Sound (PWS) values, which are shown separately to highlight PWS's unique patterns (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,

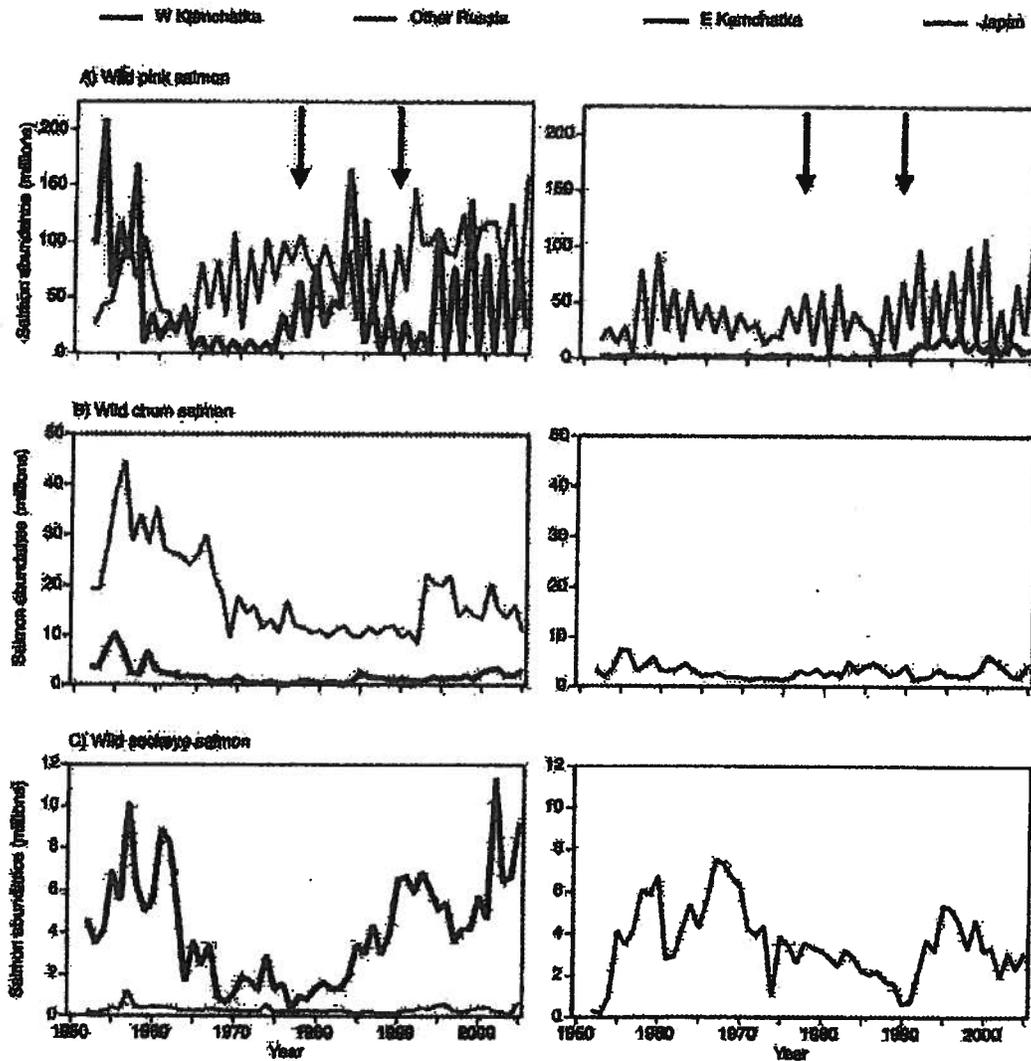


FIGURE 5.—Annual abundance (catch plus spawners) of wild (A) pink salmon, (B) chum salmon, and (C) sockeye salmon returning to regions of Asia from 1952 to 2005. Other Russia includes all areas of Russia except Kamchatka (see Figure 1). Arrows indicate the 1976–1977 and 1989 ocean regime shifts.

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),

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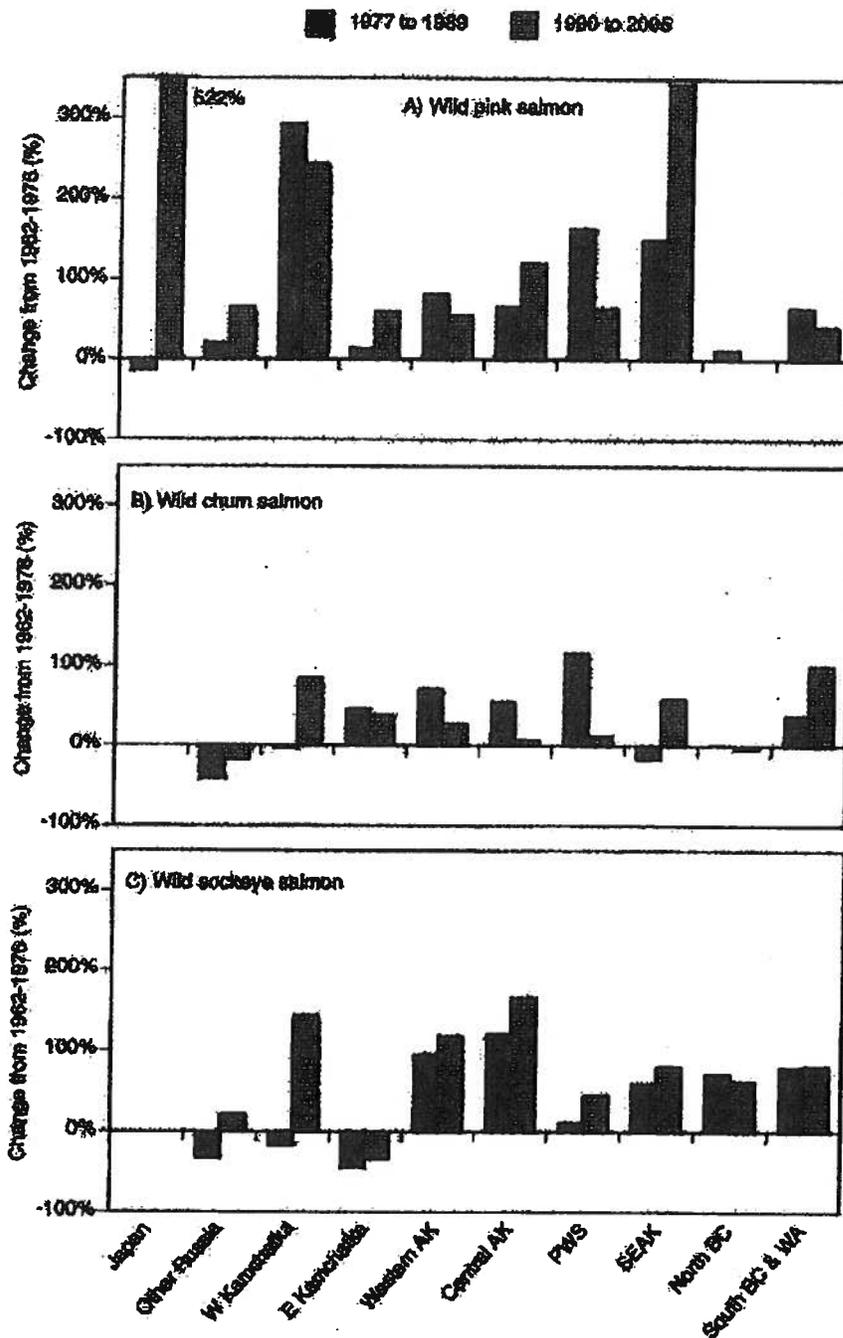


FIGURE 6.—Percentage change in abundances of wild (A) pink salmon, (B) chum salmon, and (C) sockeye salmon from 1962–1976 to 1977–1989 (black bars) and from 1962–1976 to 1990–2005 (gray bars), corresponding with the 1976–1977 and 1989 ocean regime shifts (Hare and Mantua 2000). For example, relative 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.

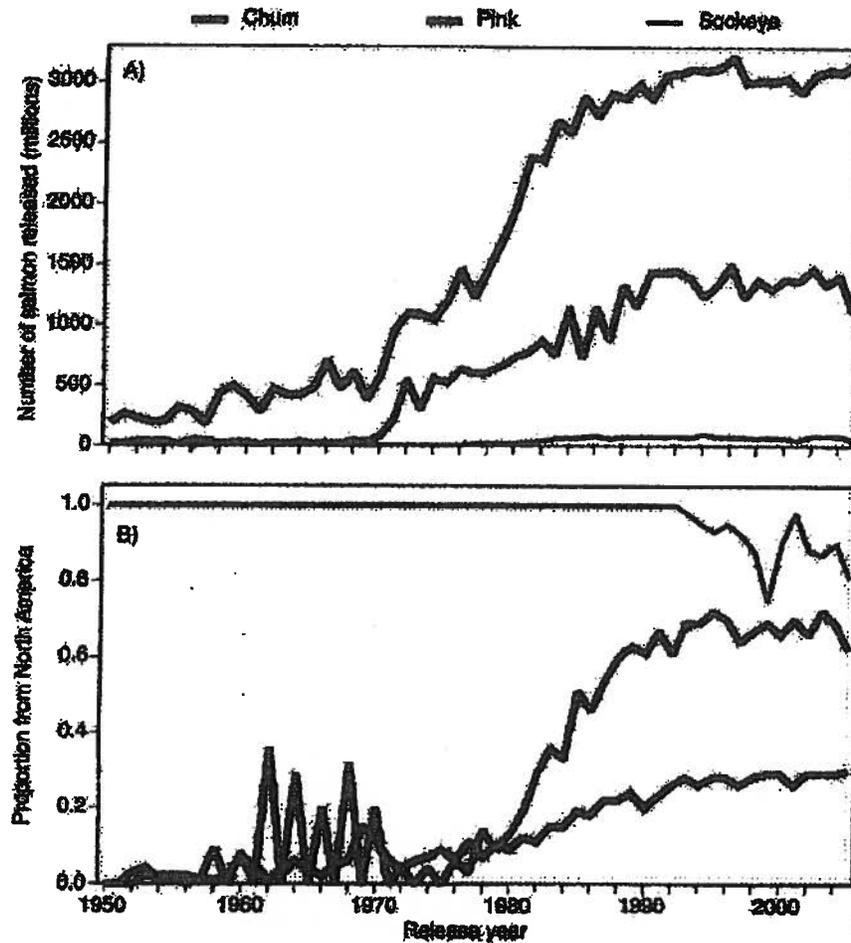


FIGURE 7.—(A) Annual releases of juvenile hatchery chum salmon, pink salmon, and sockeye salmon into the North Pacific Ocean and (B) the proportion of total hatchery releases originating from North American hatcheries, 1950–2005. Values exclude spawning-channel sockeye salmon. Values are updated from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

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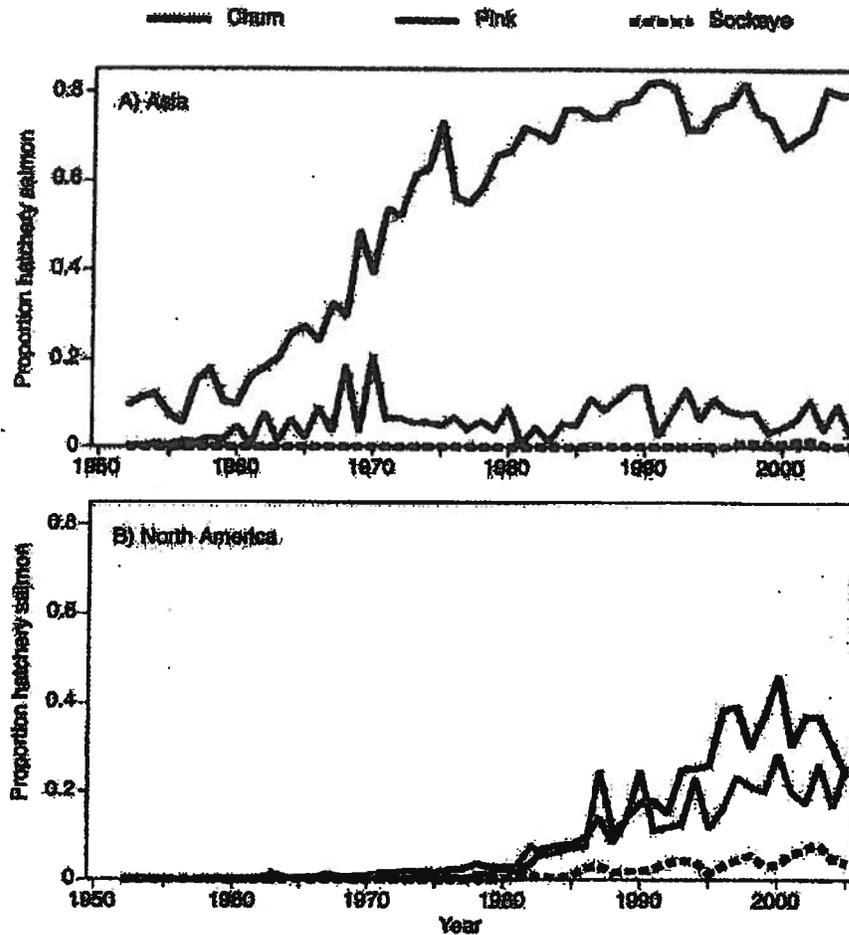


FIGURE 8.—Annual proportion of total adult chum salmon, pink salmon, and sockeye salmon represented by hatchery production in (A) Asia and (B) North America, 1952–2005.

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-

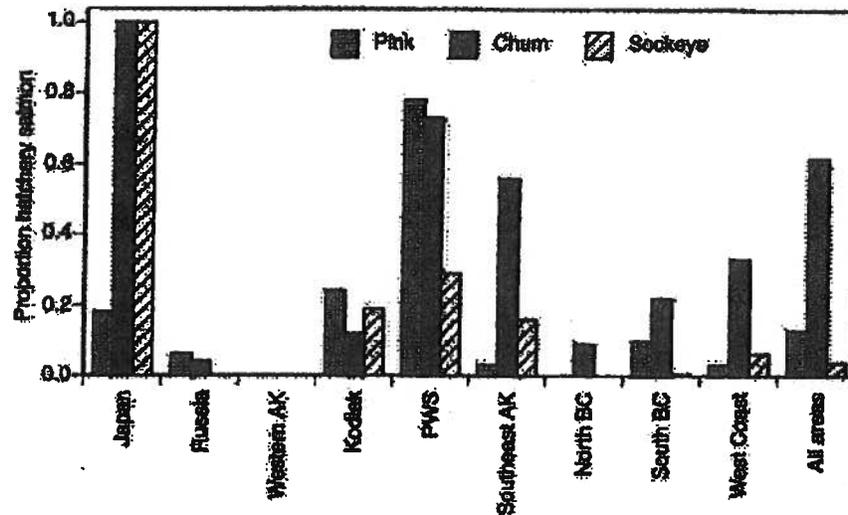


FIGURE 9.—Proportion of total adult chum salmon, pink salmon, and sockeye salmon represented by hatchery production in each region (Figure 1), 1990–2005. For example, 78% of pink salmon and 73% of chum salmon returning to Prince William Sound were of hatchery origin (West Coast = Washington and the Columbia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

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proximately 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 (British Columbia), 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. Sviridov, 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 character-

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istics 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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[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 abundances 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; Naiah 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; Pypor 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; Kasriyama 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

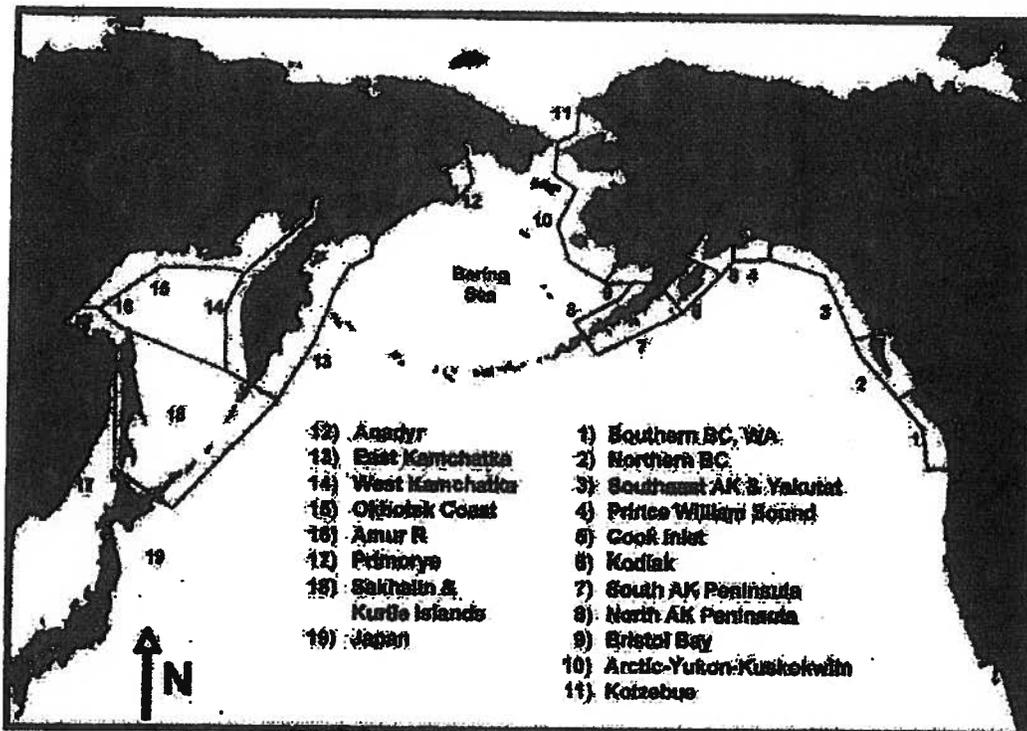


FIGURE 1.—Approximate geographic locations of regional stock groups included in this study. Area 1, southern British Columbia (BC) and Washington (WA), includes the Columbia River and all areas south of the central BC coast ($\sim 51^{\circ}\text{N}$). Area 2, northern BC, includes central and northern BC. Area 3, southeast Alaska (AK), includes the Yakutat coast. The central AK region extends from the Bering River ($\sim 60^{\circ}\text{N}$; near Prince William Sound, area 4) westward to Unimak Island ($\sim 166^{\circ}\text{W}$), 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

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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).

Area	Method			
	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 chin 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 Kuril 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 Kuril 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 $\log_2(\text{catch})$ 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 Heintz 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), Fyler et al. (2001, 2002), Mueter et al. (2002b), and Dörner 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., PFMCC 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).

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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%

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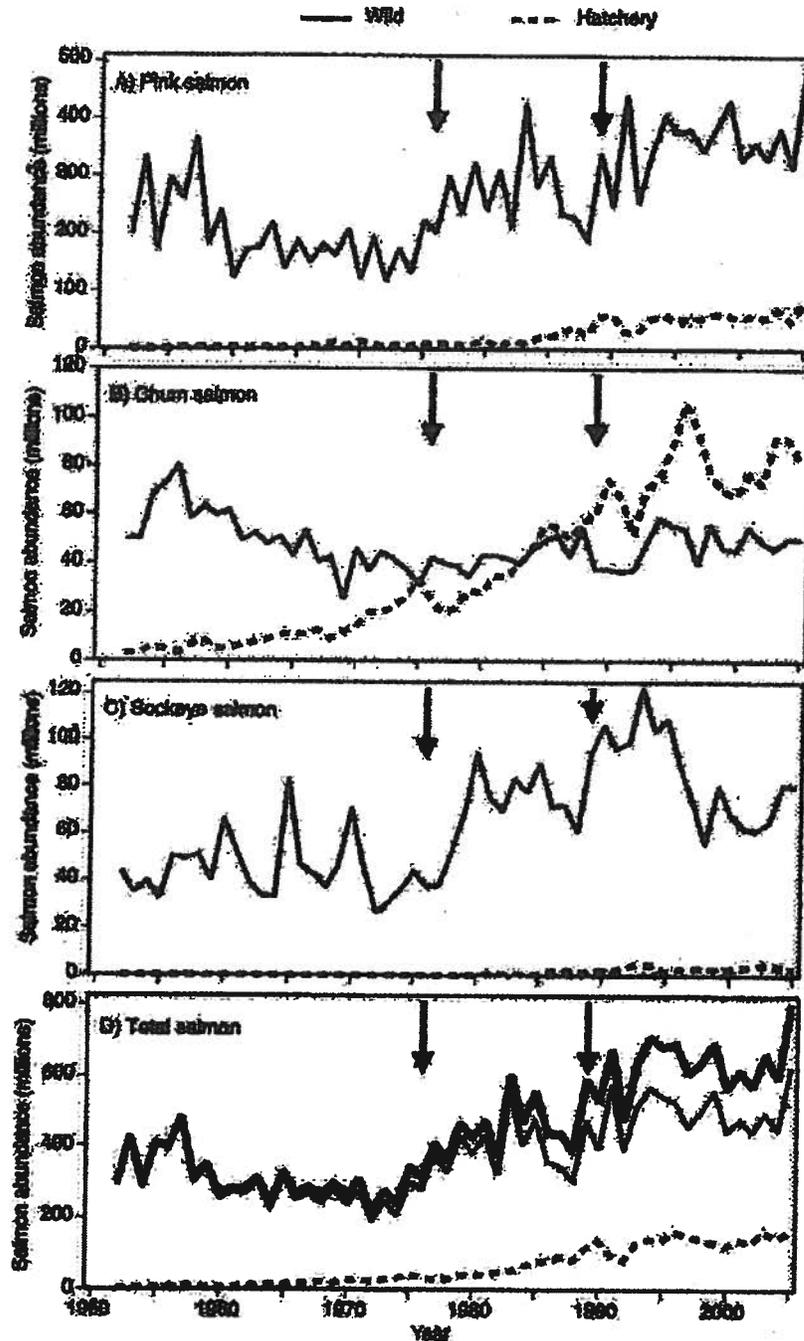


FIGURE 2.—Annual adult abundance (catch plus number of spawners) of wild (solid lines) and hatchery (dashed lines) (A) pink salmon, (B) chum salmon, and (C) sockeye salmon and (D) totals across species from 1952 to 2005. In panel D, the bold, solid-gray line is the total abundance of wild plus hatchery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

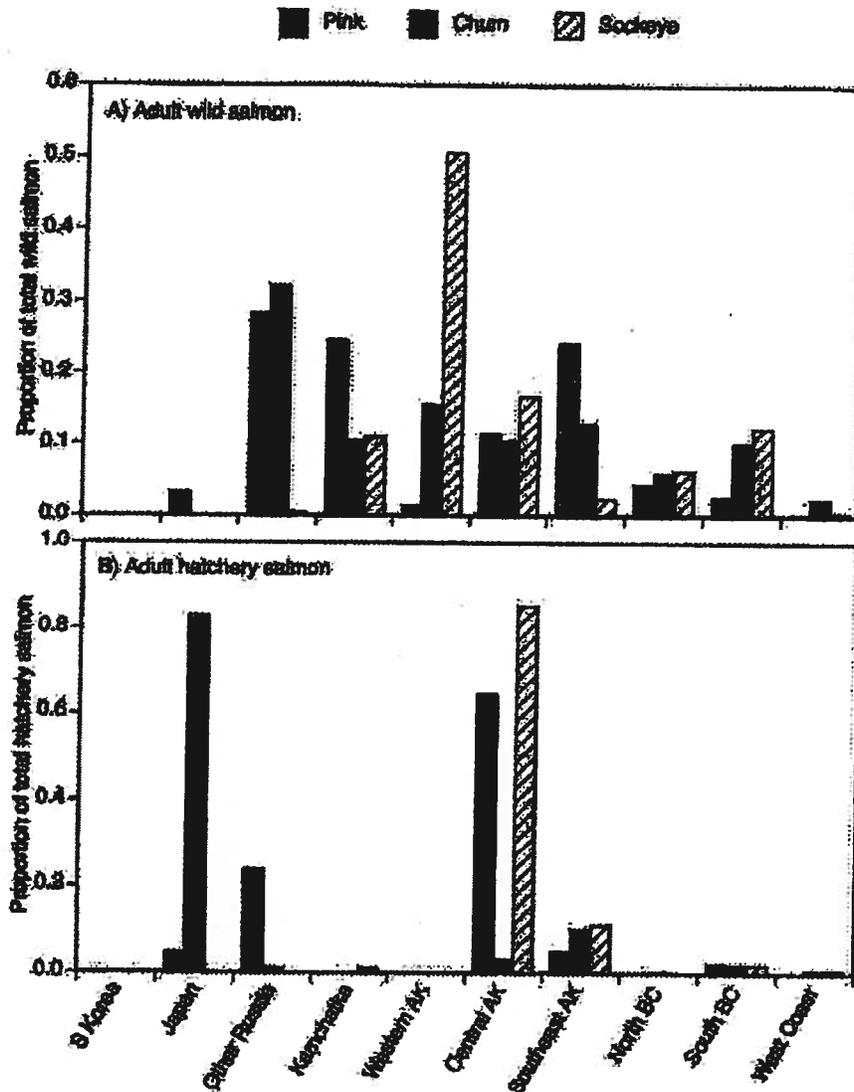


FIGURE 3.—Relative contribution of each region (Figure 1) to Pacific Rim production of adult (A) wild and (B) hatchery salmon during 1990–2005. For example, 51% of total wild sockeye salmon in the North Pacific returned to western Alaska (AK; panel A), and 83% of total hatchery-origin chum salmon returned 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

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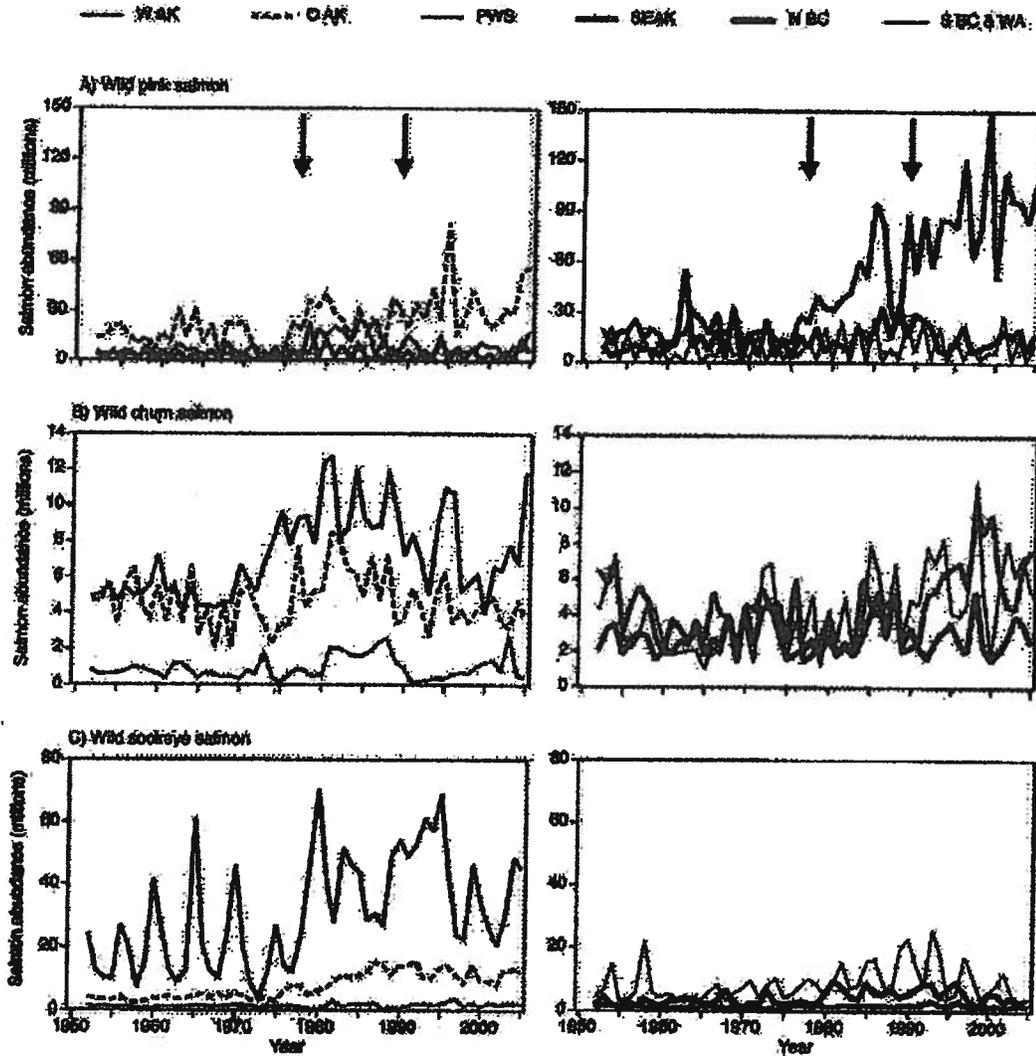


FIGURE 4.—Annual abundance (catch plus spawners) of wild (A) pink salmon, (B) chum salmon, and (C) sockeye salmon returning to regions of North America from 1952 to 2005. Central Alaska (C AK) data exclude Prince William Sound (PWS) values, which are shown separately to highlight PWS's unique patterns (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,

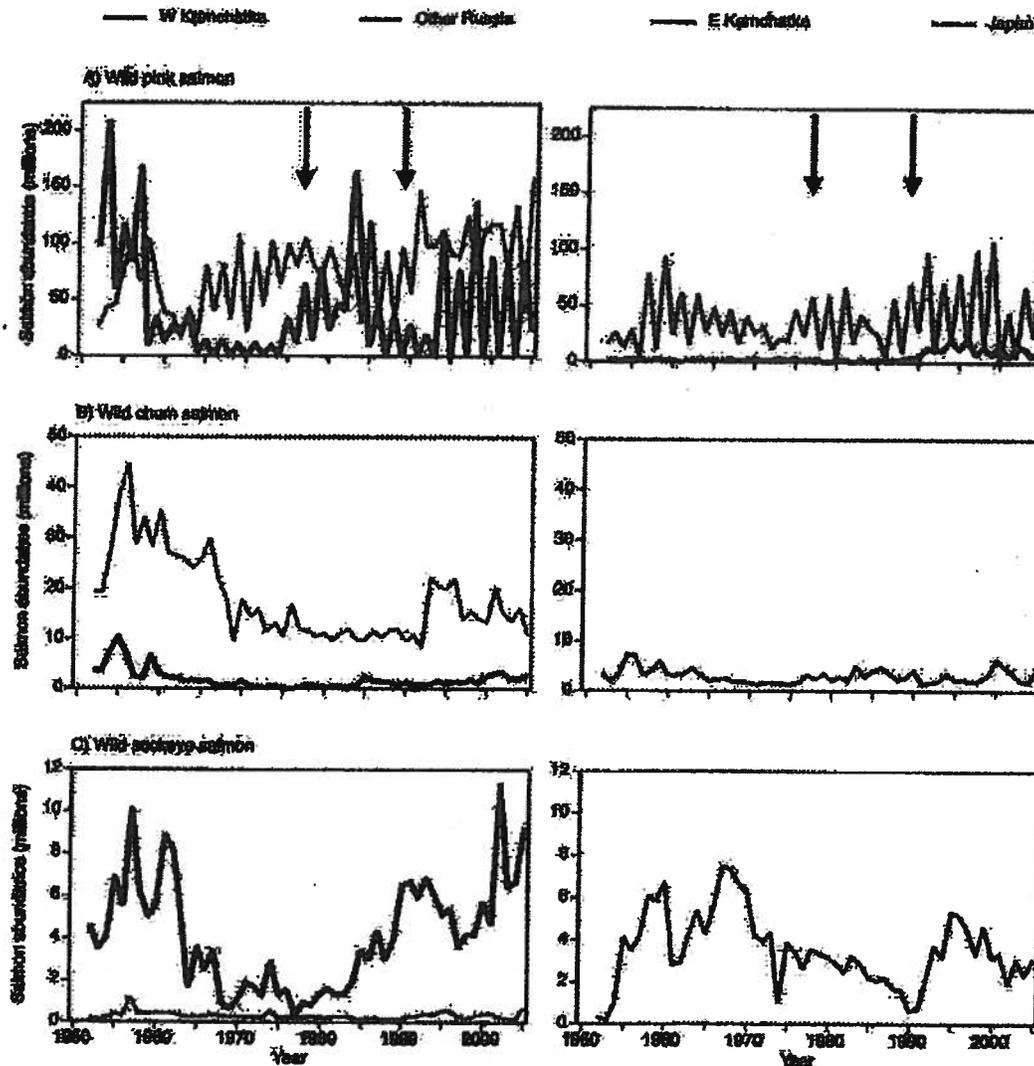


FIGURE 5.—Annual abundance (catch plus spawners) of wild (A) pink salmon, (B) chum salmon, and (C) sockeye salmon returning to regions of Asia from 1952 to 2005. Other Russia includes all areas of Russia except Kamchatka (see Figure 1). Arrows indicate the 1976–1977 and 1989 ocean regime shifts.

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),

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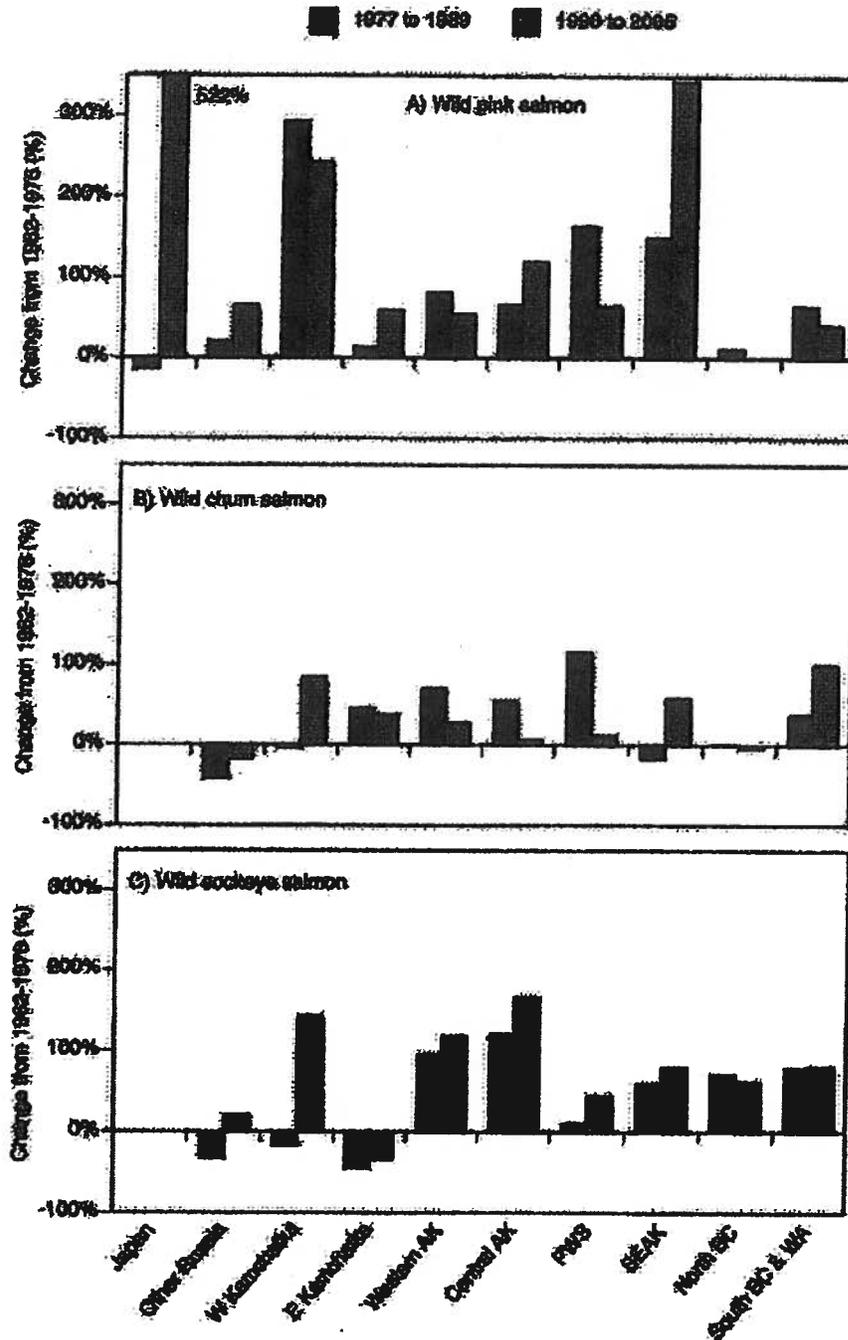


FIGURE 6.—Percentage change in abundances of wild (A) pink salmon, (B) chum salmon, and (C) sockeye salmon from 1962–1976 to 1977–1989 (black bars) and from 1962–1976 to 1990–2005 (gray bars), corresponding with the 1976–1977 and 1989 ocean regime shifts (Hare and Mantua 2000). For example, relative 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.

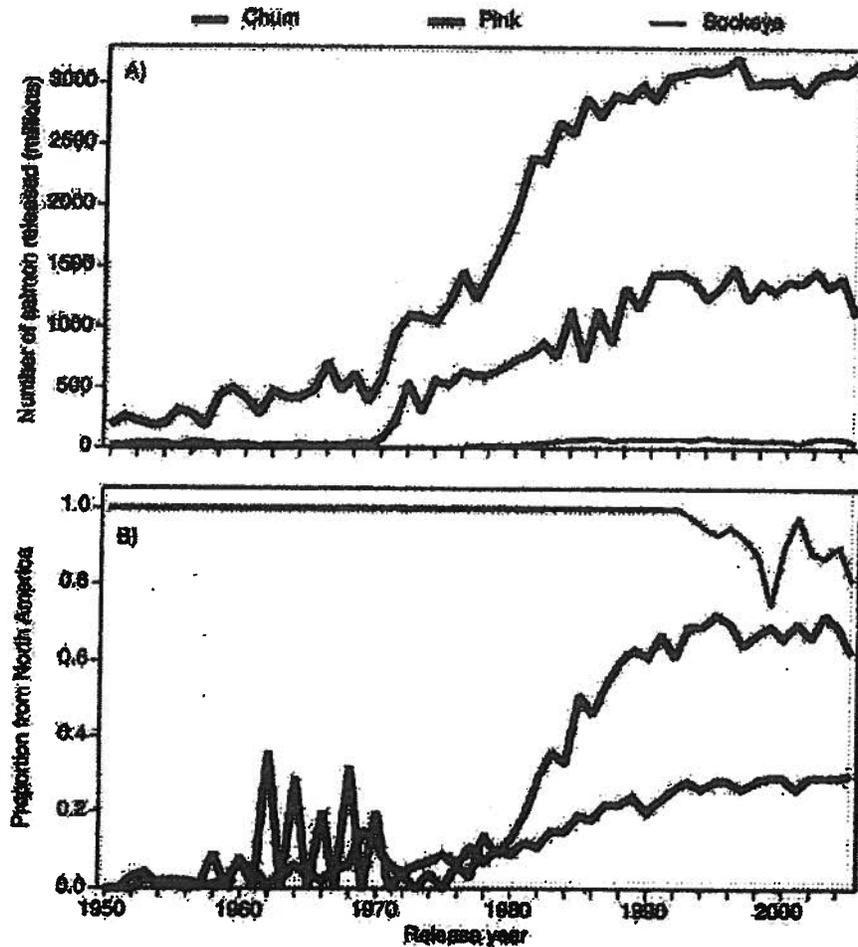


FIGURE 7.—(A) Annual releases of juvenile hatchery chum salmon, pink salmon, and sockeye salmon into the North Pacific Ocean and (B) the proportion of total hatchery releases originating from North American hatcheries, 1950–2005. Values exclude spawning-channel sockeye salmon. Values are updated from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

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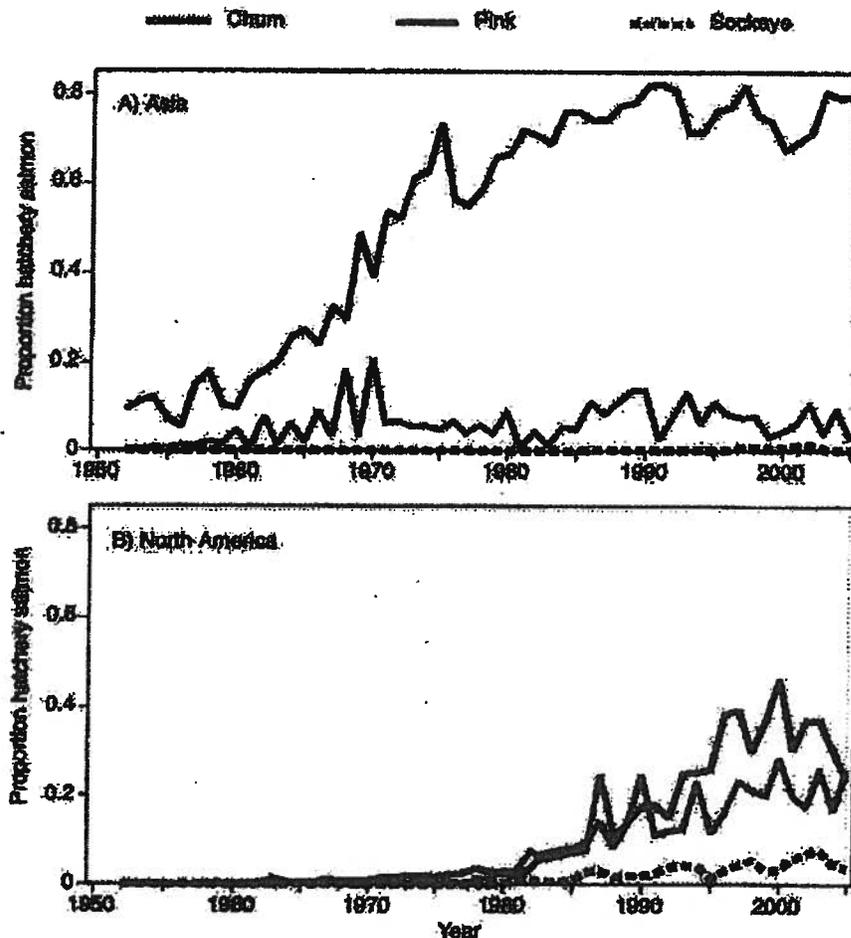


FIGURE 8.—Annual proportion of total adult chum salmon, pink salmon, and sockeye salmon represented by hatchery production in (A) Asia and (B) North America, 1952–2005.

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-

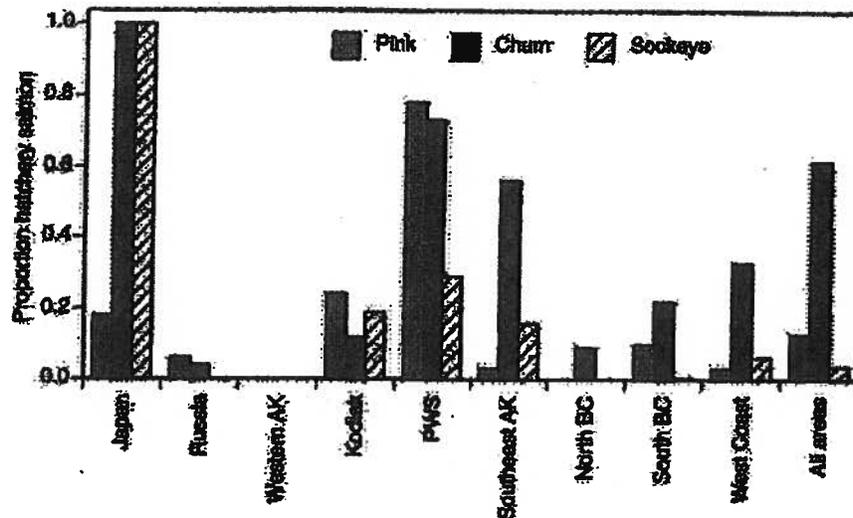


FIGURE 9.—Proportion of total adult chum salmon, pink salmon, and sockeye salmon represented by hatchery production in each region (Figure 1), 1990–2005. For example, 78% of pink salmon and 73% of chum salmon returning to Prince William Sound were of hatchery origin (West Coast = Washington and the Columbia 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 (Fyler 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; Myster 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; Karcv 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 ap-

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proximately 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 (British Columbia), 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. Sviridov, 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 character-

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istics 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., Pypker et al. 2001, 2002; Mueter et al. 2002b; Dorn 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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the affidavit of R. Peterman
sworn before me at Vancouver
this 2 day of May 2011

Patterns of covariation in length and age at maturity of British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*) stocks

Brian J. Pyper, Randall M. Peterman, Michael F. Lapointe, and Carl J. Walters

Abstract: We examined patterns of covariation in age-specific adult body length and in mean age at maturity among 31 sockeye salmon (*Oncorhynchus nerka*) stocks from western Alaska to southern British Columbia. Positive covariation in body length was prevalent across stocks of all regions (e.g., correlations (r) from 0.2 to 0.6), suggesting either that growth periods critical to final body length of sockeye salmon occur while ocean distributions of these stocks overlap or that large-scale environmental processes influence these stocks similarly while they do not overlap. We also found stronger covariation among body length of stocks within regions (r from 0.4 to 0.7), indicating that unique regional-scale processes were also important. Mean age at maturity also showed positive covariation both among and within regions, but correlations were weaker than those for length. We also examined patterns of covariation between length and mean age at maturity and between these variables and survival rate. Although length and mean age at maturity were negatively correlated, there was little evidence of covariation between these variables and survival rate, suggesting that environmental processes that influence marine survival rates of sockeye salmon are largely different from those affecting size and age at maturity.

Résumé : Nous avons examiné les profils de covariation de la longueur selon l'âge des adultes et de l'âge moyen à la maturité chez 31 stocks de saumon rouge (*Oncorhynchus nerka*) répartis de l'ouest de l'Alaska au sud de la Colombie-Britannique. On a observé une covariation positive de la longueur corporelle dans les stocks de toutes les régions ($r = 0,2$ à $0,6$), ce qui laisse penser que les périodes de croissance qui déterminent la longueur corporelle finale des saumons rouges ont lieu quand les distributions océaniques de ces stocks se chevauchent, ou que des processus environnementaux à grande échelle ont des effets similaires sur ces divers stocks en l'absence de chevauchement. Nous avons aussi observé une covariation plus forte des longueurs corporelles dans les stocks à l'intérieur des régions ($r = 0,4$ à $0,7$), ce qui indique que des processus régionaux particuliers étaient aussi importants. L'âge moyen à la maturité a aussi montré une covariation positive tant d'une région à l'autre qu'à l'intérieur des régions, mais les corrélations étaient plus faibles que pour la longueur. Nous avons aussi examiné les profils de covariation entre la longueur et l'âge moyen à la maturité, et entre ces variables et le taux de survie. Tandis que la longueur et l'âge moyen à la maturité étaient négativement corrélés, il ne semblait pas y avoir une covariation évidente entre ces variables et le taux de survie, ce qui laisse penser que les processus environnementaux qui influent sur les taux de survie du saumon rouge sont nettement différents de ceux qui déterminent la taille et l'âge à la maturité.

[Traduit par la Rédaction]

Introduction

Harvestable biomass for a given stock of sockeye salmon (*Oncorhynchus nerka*) is influenced by year-to-year variation in three recruitment processes: survival rate from eggs to adults, somatic growth rate (reflected by body size at maturity), and age at maturity. Although survival rates are typi-

cally the largest source of variation, variability in body size and age at maturity can also be important. For instance, interannual variability in size and age at maturity of sockeye salmon can affect the tonnage and economic value of catches, reproductive success of spawners (Healey 1987), and forecasts of available biomass (e.g., Fried and Yuen 1987). Furthermore, understanding more about what causes variation in size and age at maturity may be important for forecasting the effects of climate change on these variables (e.g., Hinch et al. 1995) or for evaluating and designing enhancement strategies (Peterman 1991).

Research has shown that variability in both size and age at maturity of sockeye salmon is affected by parental mechanisms (genetic and maternal effects) as well as environmental processes. For instance, Ricker (1972) and Wood and Foote (1996) documented genetic effects on growth rate and age at maturity, while Bilton (1970) and Bradford and Peterman (1987) demonstrated nongenetic maternal effects on age at maturity. Genetic effects also create the possibility that

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size-selective fishing might influence size and age at maturity over time; however, there is little evidence of such effects in sockeye salmon (Ricker 1982, 1995). In addition, environmental factors are also known to affect body size and age at maturity. For example, researchers have shown that adult body size of Bristol Bay (Alaska) and British Columbia sockeye salmon stocks is affected by ocean abundances of competing sockeye salmon stocks and oceanographic conditions such as sea surface temperature (Rogers 1980, 1984, 1987; Peterman 1984; Rogers and Ruggerone 1993; McKinnell 1995; Cox and Hinch 1997).

Although previous studies of size and age at maturity identified some important environmental sources of variation, they did not address two important questions. First, what are the spatial scales over which environmental processes affect size and age at maturity of sockeye salmon? Are they specific to stocks in a region or do they affect stocks throughout the northeastern Pacific Ocean? Second, to what extent do environmental processes simultaneously influence the three components of recruitment of sockeye salmon biomass: size at maturity, age at maturity, and survival rate?

Thus, our first objective was to identify spatial and temporal characteristics of environmental processes that drive variation over time in size and age at maturity of sockeye salmon. To do this, we used a comparative, multistock approach similar to that used in a companion paper (Peterman et al. 1998) on patterns of covariation in survival rates of sockeye salmon stocks. Here, we examine patterns of covariation in size and age at maturity for sockeye salmon stocks over a wide geographical area from western Alaska to southern British Columbia: Bristol Bay, Upper Cook Inlet, Copper River, central British Columbia (Skeena River and Nass River stocks), and Fraser River, B.C.

Our comparative analysis was based on "natural experiments" created by the different durations and extent of spatial overlap during ocean migrations of various cohorts of these stocks. Alternative hypotheses about ocean distributions of stocks and spatial scales of environmental processes lead to different predictions for patterns of covariation. For instance, one hypothesis is that size at maturity is primarily determined by unique, regional-scale environmental processes that influence growth when stocks of a given region (e.g., Bristol Bay stocks or Fraser River stocks) share distributions that are distinct from stocks of other regions. If this hypothesis is true, we expect to find positive covariation in body size among stocks within each region but not among stocks of different regions. Alternatively, if, during growth periods critical to final body size, stocks of different regions share ocean distributions or are jointly influenced by large-scale processes, then we expect to find positive covariation in body size both among regions and within regions. Analogous hypotheses and associated predictions apply to age at maturity.

Our second objective was to examine patterns of covariation between size and age at maturity and between each of these components of recruitment and the survival rates of Peterman et al. (1998). We examined across-component correlations because environmental processes such as favorable ocean conditions for growth may simultaneously affect more than one component of recruitment. The

extensive data set (up to 41 years, 31 stocks) available for sockeye salmon allowed a unique examination of such relationships.

Methods

Data

Juvenile sockeye salmon usually rear one or two winters in freshwater lakes and then migrate to the ocean where they spend two or three winters before returning to their natal streams to spawn. We use European age designations where, for example, 1.2 represents a sockeye salmon that spent one winter in a lake and two winters in the ocean before maturing. This corresponds to age 4_2 in the Gilbert-Rich notation, and 2.2 corresponds to 5_3 (see Burgner 1991 for age designations).

Length at a given age

We used 72 time series of length at age data as indices of somatic growth rate for 31 sockeye salmon stocks or stock complexes (i.e., sockeye salmon returning to a river or lake system, which could comprise various spawning populations). For Bristol Bay sockeye salmon, we used mean lengths (mideye to fork) of age 1.2, 1.3, 2.2, and 2.3 female spawners for eight stocks (Egegik, Igushik, Kvichak, Naknek, Nuyakuk, Togiak, Ugashik, and Wood River) over return years 1957–1997 (up to 1988 for Nuyakuk; B. Cross, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication). For the Upper Cook Inlet stock, we examined eight time series consisting of mean lengths (mideye to fork) of age 1.2, 1.3, 2.2, and 2.3 spawners (weighted average of both sexes) of the Kaslof and Kenai rivers over return years 1967–1997 (D. Waltemyer, Alaska Department of Fish and Game, Soldotna, Alaska, personal communication). Three time series were examined for the Copper River stock, consisting of mean lengths (mideye to fork) of age 1.2, 1.3, and 2.3 females harvested in Copper River District drift gillnet fisheries over return years 1968–1997 (J. Wilcock, Alaska Department of Fish and Game, Cordova, Alaska, personal communication). For the Skeena River stock, time series were calculated for age 1.2 and 1.3 female spawners over return years 1964–1997 by averaging (using standardized residuals) mean lengths (nose to fork) from four escapement sites (Fulton River, Pinkut Creek, and the two Fulton River spawning channels; D. Plotnikoff, Department of Fisheries and Ocean, Vancouver, B.C., personal communication). For Fraser River sockeye salmon, we examined 27 time series consisting of mean lengths (nose to hypural plate) of age 1.1 male spawners (jacks) of five stocks (Birkenhead, Cultus, Chilko River, Gates, and Weaver) over return years 1951–1997, mean lengths of age 1.2 female spawners of 20 stocks (Lower Adams, Birkenhead, Bowron, Chilko River, Cultus, Early Stuart, Fennel, Gates, Upper Horsefly, the Middle and Tachie River populations of the Late Stuart stock, Nadina, Pitt, Portage, Raft, Scotch, Seymour, Lower Shuswap, Stellako, and Weaver) over return years 1952–1997, and mean lengths of age 1.3 female spawners of two stocks (Birkenhead and Pitt) over return years 1953–1997 (J. Woodey, Pacific Salmon Commission, Vancouver, B.C., personal communication).

Mean age at maturity

We computed 32 time series of mean ocean age at maturity using recruitment data (catch plus escapement) described in Peterman et al. (1998). For each available brood year, we calculated mean ocean age separately for age 1.*x* recruits (i.e., all recruits that spent one winter in a lake) and age 2.*x* recruits. Sufficient data were available to calculate mean age of 1.*x* and 2.*x* recruits for nine Bristol Bay stocks (those noted previously plus the Branch stock) over brood years 1952–1991 (up to 1982 for Nuyakuk), the Upper Cook Inlet stock over brood years 1968–1991, the Copper

River stock over brood years 1961–1991, and the Nass River stock over brood years 1967–1991. Because Skeena River recruits were predominantly age 1.x, mean age was calculated only for recruits of this freshwater age group over brood years 1948–1992. In contrast with the more northern stocks examined, recruits of Fraser River stocks were predominantly age 1.2, with few 1.1, 1.3, or 2.x adults. Thus, we calculated mean age of 1.x recruits for only seven stocks (Birkenhead, Bowron, Chilko, Pitt, Raft, Stellako, and Weaver), which had at least 10% of age 1.x recruits other than age 1.2, over brood years 1948–1992.

Indices of survival rate

Indices of survival rate were developed by Peterman et al. (1998). These consisted of (i) residuals from the best-fit Ricker model (referred to here as spawner-to-recruit survival rates) for nine Bristol Bay stocks, the Cook Inlet, Copper, Nass, and Skeena stocks, and 16 Fraser River stocks, (ii) marine survival rates (i.e., smolt-to-adult survival rate) for four Bristol Bay stocks (Egegik, Kvichak, Ugashik, and Wood), the Skeena stock, and one Fraser River stock (Chilko), and (iii) "aggregated" spawner-to-recruit survival rates for Bristol Bay and Fraser River computed by averaging across their nine and 16 stocks, respectively (see Peterman et al. 1998 for details).

Statistical analysis

Autocorrelation and time trends

Positive autocorrelation and time trends were present in many of the time series of length, mean age, and survival rate. This indicates that low-frequency (i.e., slowly changing) variability is an important feature of these data. However, in standard inference tests of correlations, autocorrelation and time trends increase the chance that statistically significant but spurious correlations will occur (i.e., Type I error rates will be greater than the specified alpha). Thus, fisheries researchers often remove autocorrelation or time trends from data before computing and testing correlations (e.g., Thompson and Page 1989). Unfortunately, if low-frequency sources of variability are also sources of real covariation among data, then their removal can greatly reduce that covariation and the statistical power to detect it (Pyper and Peterman 1998). In other words, much of the "signal", or evidence of an environmental process experienced in common by different sockeye salmon stocks, might be lost.

We therefore used two approaches to examine correlations. First, we computed correlations using the original time series and based significance tests on the method recommended by Pyper and Peterman (1998), which adjusts degrees of freedom to account for autocorrelation. This test procedure is effective at maintaining Type I error rates near the specified alpha when autocorrelated data can be represented by simple, stationary time series models; however, it may not completely guard against spurious correlations caused by independent time trends. Thus, *P* values reported here may overstate significance levels in some cases. Our second approach was to first-difference the time series (subtract each data point from the next) and recompute correlations. First-differencing is often an effective method for removing positive autocorrelation and time trends from data (Thompson and Page 1989). Furthermore, when real covariation is largely due to low-frequency sources of variability, first-differencing is particularly effective at removing that covariation (Pyper and Peterman 1998). Thus, first-differencing allowed us to quantify the potential importance of low-frequency sources of covariation. For example, if correlations are systematically reduced after first-differencing, this provides evidence that slow-changing processes may be an important and shared source of variation in the data.

In addition, in some analyses described below, we compared correlations between data series at two or more time lags. How-

ever, if a real correlation exists at a given lag between two autocorrelated time series, large but spurious correlations are expected at adjacent time lags (Jenkins and Watts 1968). The test procedure described by Pyper and Peterman (1998) is not appropriate in this case. Again, a standard recommendation is to remove autocorrelation from data before computing correlations at multiple time lags (Jenkins and Watts 1968). To remove autocorrelation for these analyses, we used prewhitening (i.e., fitting an appropriate time series model to the data and using the residuals to compute correlations) rather than first-differencing because in some cases, first-differencing produced negative autocorrelation, which also creates problems when testing correlations at multiple lags.

Average correlations and combining groups of time series

To simplify presentation of results, we report average correlations for some groups of comparisons. These averages were calculated using the Fisher *z* transform of each correlation coefficient to normalize them (Zar 1984). In addition, for some analyses, we combined length or mean age data from stocks within regions into single time series, referred to as "aggregated" data series. These aggregated series were computed by first standardizing each stock-specific time series to have zero mean and unit variance and then averaging values across stocks within a region for a given year. Such aggregated data series will better depict the variability that is shared by a group of stocks (Thompson and Page 1989).

Patterns of covariation in length at age

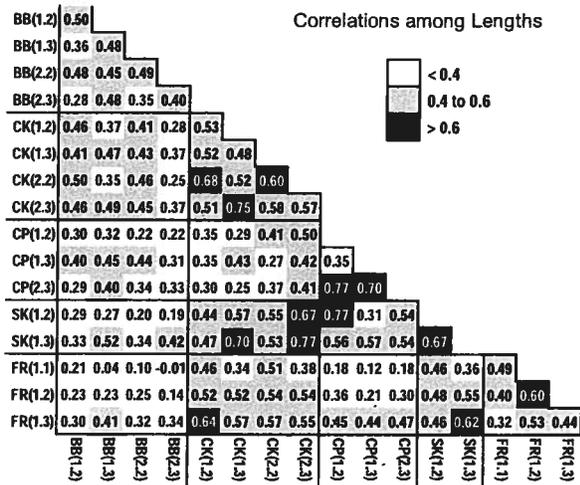
To test the previously stated hypotheses about environmental sources of variation in adult size, we examined patterns of covariation among length at age data both within and between regions. We calculated Pearson product-moment correlation coefficients for pairwise comparisons among the 72 time series of lengths, aligned to have the same return year (year in which they returned to their natal streams), giving a total of 2556 (i.e., $(N^2 - N)/2$) comparisons. Length series were aligned to have return years in common because recent research suggests that interannual variability in body size of recruits is largely determined by growth in their final year at sea (Rogers and Ruggerone 1993; McKinnell 1995).

We used principal components analysis (PCA) to further examine spatial and temporal covariation among lengths. Our purpose here was to reduce patterns of variability shared by each age class and region to a few defining time series (principal components (PC's)). For this analysis, we used region-specific aggregated lengths at age, computed across stocks in the Bristol Bay, Cook Inlet, and Fraser River regions, because these aggregated lengths should better depict the signal common to stocks in each region. Stock-specific lengths at age were used for the Copper and Skeena stocks to represent these two geographically distinct regions. We restricted this analysis to those years for which data were available for all length series and examined unrotated PC's with eigenvalues greater than 1 (Pielou 1977). To examine the importance of low-frequency sources of variability, we repeated the correlation analyses using first-differenced data.

Causes of patterns of covariation in length at age: conditions in early or late marine life?

Rogers and Ruggerone (1993) and McKinnell (1995) suggested the importance of late marine life in determining adult length. However, it is conceivable that interannual variability in adult length might also be heavily influenced by conditions during early marine life (e.g., first year at sea), when growth in length is proportionally the greatest (reviewed by Burgner 1991). The relative importance of early versus late marine life can be examined using lengths of fish with different ocean ages. For example, age x.2 and x.3 fish that enter the ocean in the same calendar year (referred to as ocean-entry year (OEY)) are at sea together during their first

Fig. 1. Summary of stock-specific, pairwise correlations among lengths of Bristol Bay (BB), Cook Inlet (CK), Copper River (CP), Skeena River (SK), and Fraser River (FR) stocks by age group (1.2, 1.3, etc.). For all comparisons involving Bristol Bay, Cook Inlet, and Fraser River stocks, cells in the matrix show average correlations. For example, the r of 0.29 for BB(1.2) versus SK(1.2) is the average of the eight sample correlations between the Skeena 1.2 length series and the 1.2 length series for the eight Bristol Bay stocks. Levels of shading, defined in the legend, reflect different ranges of correlations.



2 years but do not share their final year at sea. In comparison, the final year is shared by age groups that return in the same year (see life history time lines in Peterman 1985). Thus, to examine the importance of early versus late marine life (i.e., final year at sea), we compared correlations among lengths of fish with different ocean ages using data aligned by OEY with correlations between these lengths aligned by return year. We made these comparisons using aggregated length series for a given region to limit the influence of measurement error. Because lengths were autocorrelated and correlations were computed at two time lags (i.e., OEY and return year), we computed correlations using both prewhitened data and original data to help discern between real and spurious correlations.

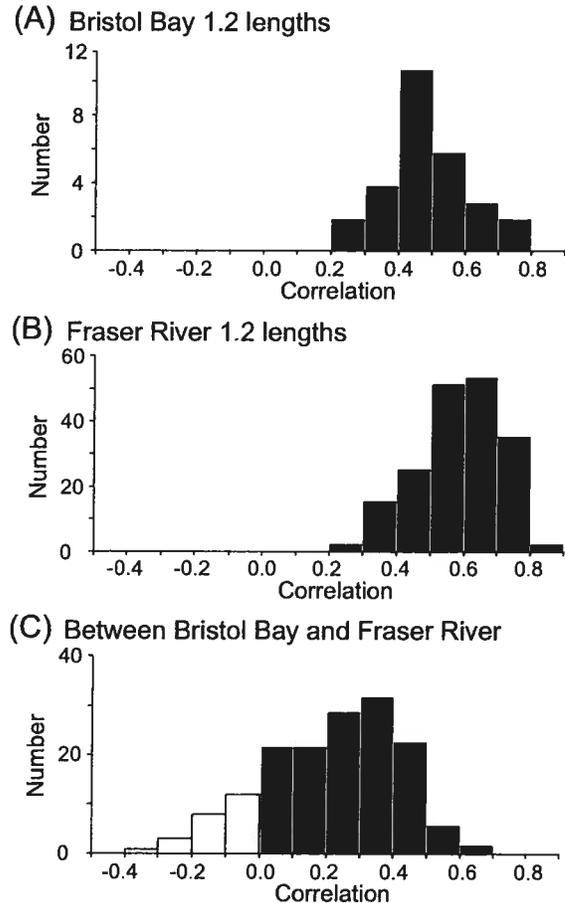
Patterns of covariation in mean age at maturity

To examine within-region and between-region patterns of covariation in mean age at maturity, we used analyses similar to those used for length. Correlations were calculated for pairwise comparisons among the 32 time series of mean age, aligned by OEY, giving 496 comparisons. Time series for age 1. x and 2. x fish were aligned by OEY because research suggests that environmental processes influence age at maturity of sockeye salmon during their early marine life (i.e., first 2 years in the ocean; Peterman 1985). Aggregated mean ages were computed for Bristol Bay and Fraser River stocks, respectively. We used these aggregates along with mean ages for the Cook, Copper, Nass, and Skeena stocks in a PCA. To examine the importance of low-frequency sources of variability, we repeated the correlation analyses using first-differenced data.

Patterns of covariation across the three components of sockeye salmon recruitment

To determine whether similar environmental processes influenced each of the three components of recruitment biomass of sockeye salmon, within-stock correlations were examined for the following comparisons: (i) length versus mean age, (ii) length ver-

Fig. 2. Histograms of correlations between lengths of age 1.2 sockeye salmon for comparisons (A) among Bristol Bay stocks (all 28 correlations positive; 23 significant at $P < 0.05$), (B) among Fraser River stocks (all 190 correlations positive; 161 significant), and (C) between Bristol Bay and Fraser River stocks (136 of 160 correlations positive; 25 significant positive correlations). Averages of these three sets of correlations are shown in Fig. 1. Open bars represent negative correlations; solid bars represent positive correlations.



sus survival rate, and (iii) mean age versus survival rate. Time series were aligned where covariation might be expected due to shared environmental influences (discussed in detail below). We repeated these comparisons using aggregated lengths, mean ages, and survival rates of the Bristol Bay, Cook Inlet, and Fraser River regions, where applicable.

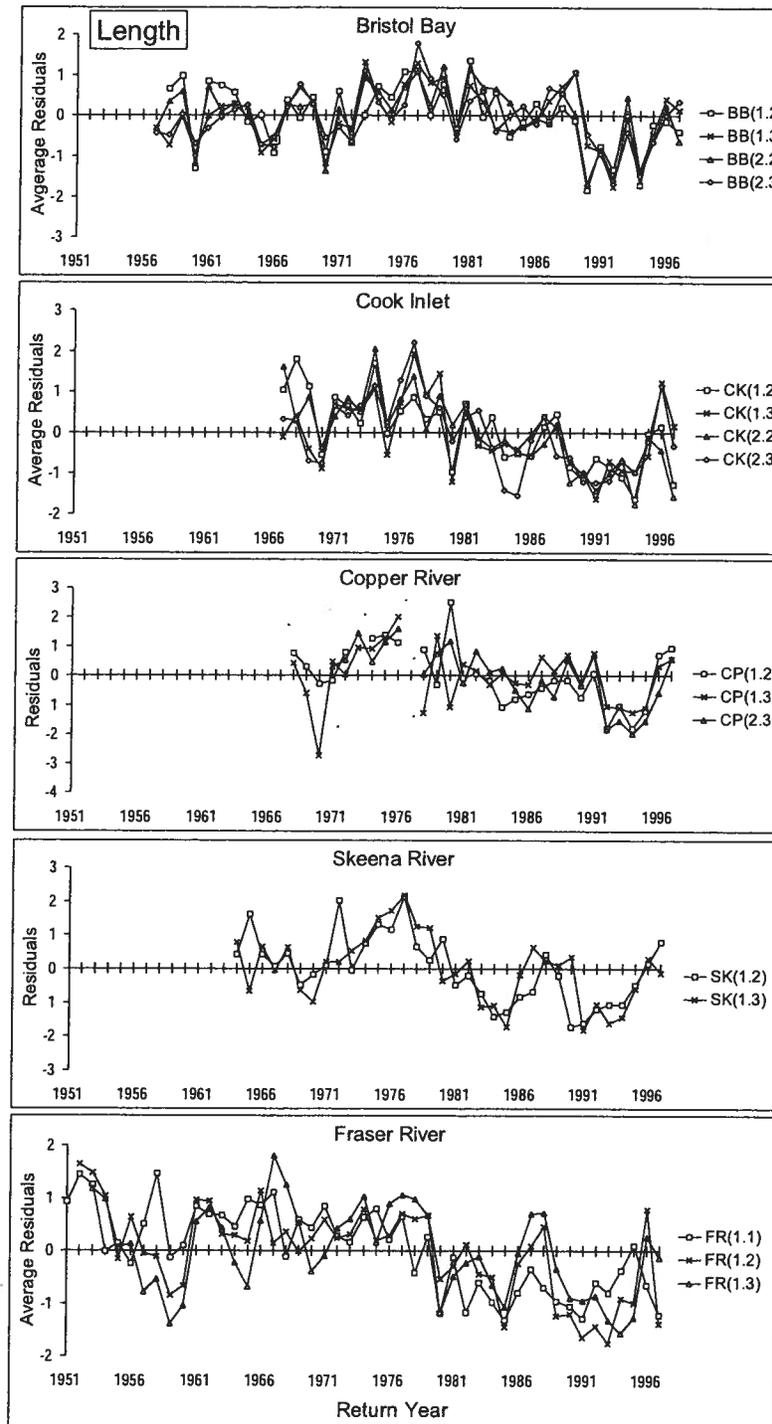
Results and discussion

Length at a given age

There was widespread positive covariation among the 72 body length time series, aligned by return year, both across stocks and across ages (Fig. 1). Of the 2556 correlations, 2335 were positive (43%, or 1006, of these were significant at $P < 0.05$) and only 221 were negative (with just three significant). The average of all correlations was 0.37.

These correlations provide strong evidence of positive covariation between regions as well as distinct patterns of

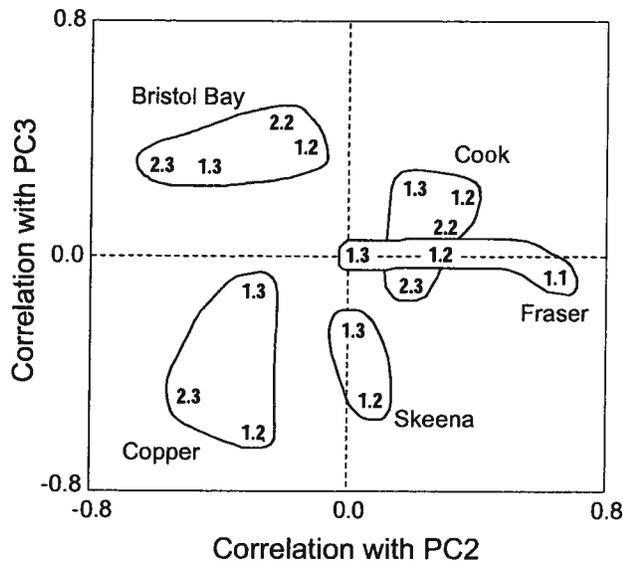
Fig. 3. Time series of region-specific lengths at age for various sockeye salmon stocks. Regional aggregated lengths (e.g., aggregated across the eight Bristol Bay 1.2 data series) are shown for Bristol Bay, Cook Inlet, and Fraser River stocks, whereas standardized lengths at age are given for the Copper River and Skeena River stocks.



covariation within regions. The first is indicated by the predominance of positive correlations among lengths of stocks from different regions (e.g., Cook Inlet versus Fraser River; Fig. 1). Evidence of additional within-region covariation is provided by the generally larger correlations among lengths

of stocks in the same region (e.g., larger correlations within Bristol Bay than between Bristol Bay and other regions; Fig. 1). This different strength of within-region and between-region covariation was most obvious among Bristol Bay and Fraser River sockeye salmon, for which we had data from

Fig. 4. Correlations (loadings) between the 16 length data series in Fig. 3 and the time series (scores) of the second and third principal components of the body length PCA. Regions or stocks are identified along with age designations (1.2, 2.3, etc.).



numerous stocks. For example, there was a tendency toward strong positive correlations among the eight Bristol Bay 1.2 length series (average $r = 0.50$; Fig. 2A) and among the 20 Fraser 1.2 data (average $r = 0.60$; Fig. 2B) but weaker, yet still predominantly positive, correlations between 1.2 lengths from these two geographically distinct regions (average $r = 0.23$; Fig. 2C). In general, the percent variation in length shared by stocks in the same region (27%; based on average $r = 0.52$ from Fig. 1) was about twice that shared by stocks from different regions (16%; based on average $r = 0.41$ from Fig. 1).

Combining length at age series within the Bristol Bay, Cook Inlet, and Fraser River regions, respectively, was very effective at increasing the signal shared among ages and regions (Fig. 3). Correlations among these regional aggregates were considerably greater than the average stock-specific correlations (Fig. 1) for all combinations of age class and region. For example, within Bristol Bay, correlations between aggregated lengths of age 1.2 and 2.2 fish and between aggregated lengths of age 1.3 and 2.3 fish were 0.87 and 0.93, respectively. By comparison, the average stock-specific correlation among lengths was only 0.48 in both cases (Fig. 1).

PCA of the 16 regional length series (Fig. 3) defined the temporal characteristics of variation shared among regions and also more clearly identified region-specific patterns. For return years 1971–1997 (i.e., years where data were available for all regions), the PCA yielded three PC's with eigenvalues greater than 1, accounting for 58.5, 11.0, and 9.6% of the total variance, respectively. The time series (scores) of the dominant component, PC1, had an obvious declining trend from 1971 to 1997 ($P < 0.001$; linear regression with autocorrelated error), which is also evident in the regional length data (Fig. 3). All 16 length series correlated strongly with PC1 (range 0.61–0.88), suggesting that much of the covariation among lengths of Alaska and British Co-

lumbia sockeye salmon resulted from a similar declining trend over this period. In addition, the PCA revealed distinct region-specific sources of variation in length at age over this period (Fig. 4).

Analyses using first-differenced data support the suggestion from the PCA that slowly changing, low-frequency patterns of variability, such as the declining time trends noted above, were important sources of covariation among lengths of stocks. After autocorrelation and time trends in the 72 stock-specific length series were removed by first-differencing, widespread positive covariation was still evident both within and between regions. However, correlations were consistently and often substantially lower than those computed using the original data. The average of the 2556 correlations was reduced from 0.37 to 0.23, the number of negative correlations increased from 211 to 578, and the number of significant ($P < 0.05$) positive correlations decreased from 1026 to 745. Thus, there is little evidence that the general patterns of covariation in lengths could be solely a spurious result of unrelated time trends; instead, to the extent that the observed covariation in length at age of sockeye salmon arises from shared processes, such processes appear to be largely characterized by low-frequency patterns of variability.

The correlation analysis and PCA thus support hypotheses that environmental processes similarly affect adult length of sockeye salmon stocks both among different regions and within regions. The distinct within-region patterns of covariation in length (Figs. 1, 2, and 4) may have a simple explanation. These patterns likely reflect differences in ocean distributions of fish from each region and subsequent differences in growth conditions that they experience. In particular, ocean distributions of maturing sockeye salmon from each region become increasingly distinct in their final few months at sea (French et al. 1976). At this time, sockeye salmon are feeding and growing at high rates (Ricker 1976), creating the potential for much interannual variation in final body size to be determined during this short period. Many of the distinct patterns of within- versus between-region covariation are consistent with differences in spatial distributions (Figs. 1 and 4). For example, covariation in length was weakest between Bristol Bay and Fraser River sockeye salmon (Fig. 1), which have spawning grounds that are separated by the greatest distance (about 2400 km).

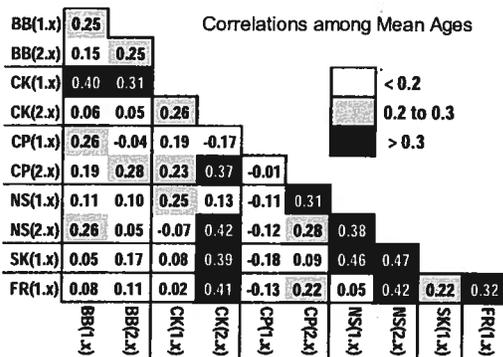
There are two plausible explanations whereby environmental processes could produce positive covariation in body size among stocks from different regions. Stocks may have similar geographical distributions when interannual variability in growth rate is most strongly determined, or stocks may have different distributions at such times but experience similar large-scale environmental conditions. There is some evidence for both possibilities. Regarding the first hypothesis, tagging studies (e.g., French et al. 1976) show that ocean distributions of sockeye salmon from Alaska and British Columbia overlap considerably in space and time in the Gulf of Alaska. Thus, the degree of covariation between lengths of stocks from different regions may reflect the extent to which stocks share similar distributions and hence growth conditions. Further support for this mechanism is provided by clear evidence of the effect on body size of competitive interactions among stocks from different regions (Peterman 1984; McKinnell 1995). Also, total ocean abundances of

Table 1. Correlations between aggregated lengths at age aligned by ocean-entry year or by return year.

Age groups compared	Ocean-entry year		Return year	
	Original data	Prewhitened data	Original data	Prewhitened data
Bristol Bay				
1.2 vs. 1.3	0.22	0.09	0.64	0.67
1.2 vs. 2.3	0.35	0.22	0.54	0.54
2.2 vs. 1.3	0.21	-0.06	0.80	0.85
2.2 vs. 2.3	0.36	0.09	0.69	0.72
Cook Inlet				
1.2 vs. 1.3	0.24	-0.06	0.65	0.70
1.2 vs. 2.3	0.29	-0.15	0.63	0.56
2.2 vs. 1.3	0.34	-0.07	0.62	0.57
2.2 vs. 2.3	0.50	-0.06	0.67	0.53
Fraser River				
1.1 vs. 1.2	0.66	0.19	0.67	0.34
1.1 vs. 1.3	0.47	0.09	0.44	0.36
1.2 vs. 1.3	0.61	0.00	0.77	0.71

Note: For each alignment, correlations were calculated using the original data as well as data prewhitened to remove autocorrelation.

Fig. 5. Summary of correlations among mean age at maturity of Bristol Bay (BB), Cook Inlet (CK), Copper River (CP), Nass River (NS), Skeena River (SK), and Fraser River (FR) stocks. Average correlations are shown for all comparisons involving Bristol Bay and Fraser River stocks. Levels of shading, defined in the legend, reflect different ranges of correlations.



sockeye salmon increased substantially after the mid-1970's (Rogers 1987; Bigler et al. 1996), so the declining trends in body size common to sockeye salmon from each region (Fig. 3) may be evidence of increased competition.

The second explanation for covariation across different regions is also plausible because physical and biological variables are known to vary coherently over large areas of the northeastern Pacific Ocean. For example, beginning in the mid-1970's, persistent and large-scale decreases in sea surface temperatures in the central North Pacific were recorded along with increases in coastal ocean temperatures (McLain 1984) and changes in other physical and biological variables (e.g., Venrick et al. 1987; Brodeur and Ware 1992; Graham 1994). Therefore, stocks from different regions may have been exposed to similar growth conditions despite having different distributions during periods critical to determining adult size.

However, it is also possible that between-region covariation in lengths, in particular the covariation arising

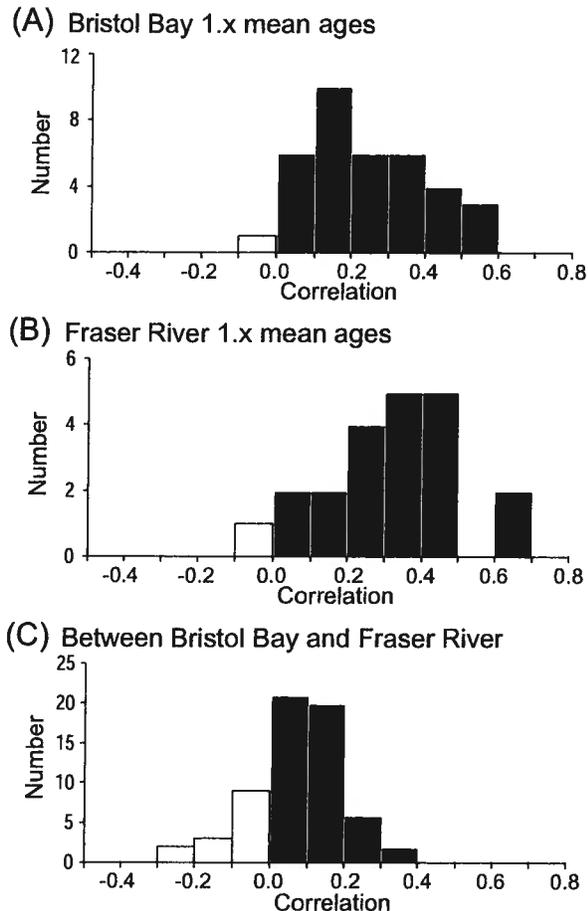
from similar declining trends, was due in part to coinciding but unrelated processes acting independently within different regions. For example, the persistent changes in ocean temperatures noted above were coincident with long-term increases in sockeye salmon abundance for the Bristol Bay, Cook Inlet, and Fraser River regions. It is currently unclear to what extent such variables may be important, region-specific determinants of adult body size.

In addition to distinct within- and between-region patterns of covariation in length, there is also some evidence of differences among age classes. For between-region comparisons involving Bristol Bay sockeye salmon, correlations were generally greater for older age classes (e.g., x.3) of Fraser stocks and the Skeena stock (Fig. 1). The result for the Skeena stock is consistent with tagging data reviewed by McKinnell (1995), which showed that age 1.2 Skeena sockeye salmon were distributed farther east in the Gulf of Alaska than age 1.3 fish. This could reduce similarity with Bristol Bay stocks in environmental conditions, including the degree of competition with other sockeye salmon in the Gulf of Alaska. Analogous age-specific distributional differences for Fraser River sockeye salmon may also account for the greater degree of covariation between lengths of older age classes of Fraser River fish and lengths of Bristol Bay stocks (Fig. 1).

Causes of patterns of covariation in length at age: conditions in early or late marine life?

In the above analyses, length series were aligned by return year under the assumption that interannual variability was primarily determined by growth conditions during the final year at sea (Rogers and Ruggerone 1993; McKinnell 1995). However, growth in length of sockeye salmon is proportionally greatest during their first year at sea. If early marine growth is an important determinant of final body length, there should be positive covariation in length among sockeye salmon that entered the ocean in the same year (i.e., had the same OEY and therefore experienced similar growth conditions during their early marine life) but that returned in different years (e.g., as x.2 and x.3 recruits).

Fig. 6. Histograms of correlations between mean ages of 1.x sockeye salmon for comparisons (A) among Bristol Bay stocks (35 of 36 correlations positive; 12 significant at $P < 0.05$), (B) among Fraser River stocks (20 of 21 correlations positive; six significant), and (C) between Bristol Bay and Fraser River stocks (49 of 63 correlations positive; none significant). Averages of these three sets of correlations are shown in Fig. 5. Open bars represent negative correlations; solid bars are positive correlations.



However, after possible confounding effects of autocorrelation were removed by prewhitening, there was little evidence of such covariation. Comparisons among aggregated lengths for the Bristol Bay, Cook Inlet, and Fraser River regions showed moderate positive correlations among the original (autocorrelated) lengths when aligned by OEY but weak or negative correlations among prewhitened lengths (Table 1). In contrast, when length series were aligned by return year, there were large positive correlations among original data for each region, and prewhitening made little difference to these comparisons (Table 1). These results suggest that the moderate positive correlations in the original data, when aligned by OEY, were due to a combination of autocorrelation and real covariation driven by processes operating primarily during the final year at sea rather than early ocean life. These findings are consistent with other analyses (Rogers and Ruggerone 1993; McKinnell 1995) and imply that interannual variability in growth conditions

during early marine life is not nearly as important a determinant of interannual variation in final sockeye salmon body length as is variability in conditions during late marine life.

Mean age at maturity

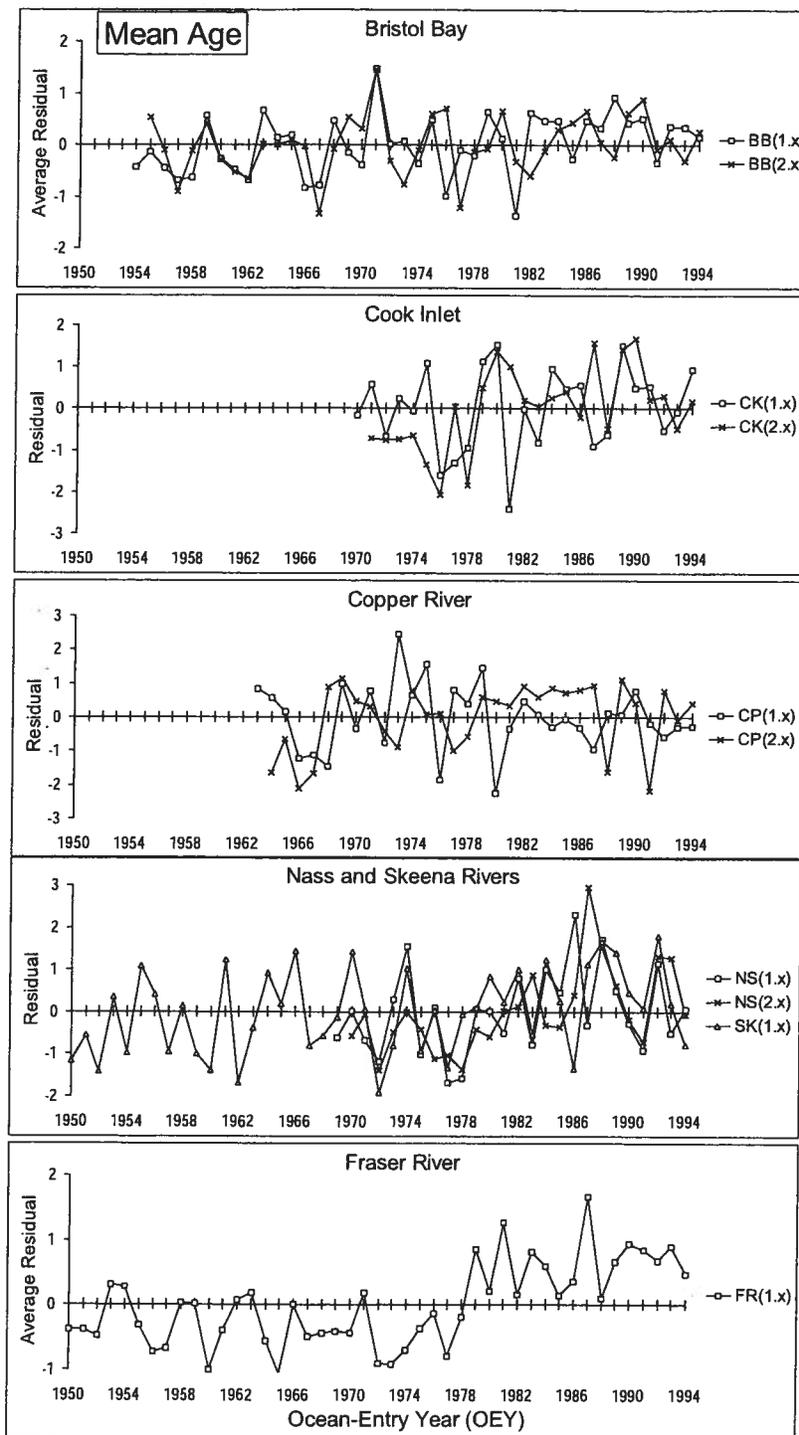
Correlations among the 32 time series of mean age at maturity, aligned by OEY, showed evidence of weak but predominantly positive covariation both within and between regions (Fig. 5). Although the average of the 496 correlations was only 0.17, 66 of 394 positive correlations were significant ($P < 0.05$), while none of 102 negative correlations was significant. Correlations among stocks of different regions were mostly positive, except those involving Copper River 1.x mean age (Fig. 5). Distinct within-region patterns of covariation were evident for comparisons among mean age series of the Bristol Bay and Fraser River regions, where we had data for several stocks. Mean ages tended to be positively correlated among stocks within those regions, with little evidence of positive covariation between the two regions (e.g., Fig. 6). In general, the proportion of variation shared among stocks, either within or between regions, was 10% or less.

Time trends were also an important source of covariation in mean age at maturity (Fig. 7). Aggregated Fraser 1.x mean age showed a clear shift towards older ages beginning with the 1979 OEY. There was also a tendency towards greater mean age for both aggregated Bristol Bay age groups, Cook Inlet 2.x, and Nass and Skeena age groups beginning in the early 1980's (Fig. 7). These shared trends were reflected by the PCA of the 10 regional mean age series (Fig. 7), which yielded four PC's with eigenvalues greater than 1, explaining 33.1, 18.3, 12.9, and 10.7% of the variance, respectively. Although the analysis did not yield a substantial simplification of the data, PC1 was moderately to strongly correlated (0.38–0.73) with all 10 mean age series except Copper River 1.x ($r = -0.29$). Moreover, the time series (scores) of PC1 had an increasing trend from OEY 1971 to 1994 ($P < 0.001$; linear regression with autocorrelated error), suggesting that much of the covariation among sockeye salmon stocks from Alaska and British Columbia was due to a shared trend toward greater mean age at maturity over this two-decade period.

Repeating the correlation analysis and PCA using first-differenced data confirmed the importance of low-frequency sources of covariation. For example, after first-differencing, the average correlation computed among the seven Fraser River mean age series was 0.13, compared with 0.32 for the original data. Furthermore, when the PCA was repeated using first-differenced data, there was no longer a clear dominant PC. Thus, after positive autocorrelation and time trends were removed from the data, there was little evidence of large-scale covariation in mean age at maturity across all regions. This supports the interpretation, as with length data, that long-term, slowly changing conditions account for a large portion of the shared variation in age at maturity of these stocks.

The tendency toward positive covariation between regions suggests that age at maturity of sockeye salmon from Alaska and British Columbia was in part influenced by similar environmental processes. However, such processes appear to account for only a small portion of the total variation (Fig. 5).

Fig. 7. Time series of region-specific mean age at maturity for various sockeye salmon stocks. Regional aggregated mean ages (e.g., aggregated across the nine Bristol Bay 1.x data series) are shown for Bristol Bay and Fraser River stocks, whereas standardized mean ages at maturity are given for the Cook Inlet, Copper River, Nass River, and Skeena River stocks.



As we discussed for length, covariation between regions may reflect either similarities in ocean distributions during periods critical to determining age at maturity or large-scale environmental conditions that influenced fish with different distributions in similar ways. Likewise, the general cross-

region increases in mean age during the 1980's may be related to coincident increases in ocean abundances of sockeye salmon, as suggested by Bigler et al. (1996), or to the mid-1970's shift in ocean conditions in the North Pacific.

Regional-scale environmental processes also had a nota-

Table 2. Correlations between length and mean age at maturity for comparisons within stocks and for comparisons between regional aggregates.

	Comparisons within stocks		Comparisons between aggregates	
	RY = OEY + 1	RY = OEY + 2	RY = OEY + 1	RY = OEY + 2
Length (1.1) vs. mean age (1.x)				
Fraser River	-0.29	-0.17	-0.73*	-0.66*
Length (1.2) vs. mean age (1.x)				
Bristol Bay	-0.21	-0.04	-0.39*	-0.23
Cook Inlet	-0.11	-0.01	-0.13	-0.01
Copper River	0.47	0.01		
Skeena River	-0.17	-0.36		
Fraser River	-0.28	-0.33	-0.58*	-0.61*
Length (1.3) vs. mean age (1.x)				
Bristol Bay	-0.02	-0.05	-0.16	-0.07
Cook Inlet	-0.27	0.03	-0.32	0.03
Copper River	0.07	0.45		
Skeena River	-0.34	-0.27		
Fraser River	-0.28	-0.22	-0.44*	-0.50*
Length (2.2) vs. mean age (2.x)				
Bristol Bay	-0.14	-0.13	-0.27	-0.10
Cook Inlet	-0.49	-0.53	-0.58	-0.56
Length (2.3) vs. mean age (2.x)				
Bristol Bay	-0.07	-0.01	-0.18	0.05
Cook Inlet	-0.58	-0.45	-0.61*	-0.47
Copper River	0.02	0.05		

Note: Two alternative lags for comparing lengths and mean age were examined: (i) return year (RY) of length data aligned to match the ocean-entry year (OEY + 1) of mean age data and (ii) RY = OEY + 2. Averages of within-stock correlations are shown for the Bristol Bay, Cook Inlet, and Fraser River regions.

*Significant correlations ($P < 0.05$) for comparisons between aggregates.

ble effect on interannual variation in age at maturity. The predominance of positive correlations within regions is consistent with Peterman's (1985) findings for Bristol Bay sockeye salmon stocks, which were based only on data through the 1980 return year. Although patterns of positive covariation in age at maturity found here were stronger within the Bristol Bay and Fraser regions than between them (e.g., Fig. 6), and generally greater among the neighboring (point of ocean entry 60 km apart) Nass and Skeena stocks (Fig. 5), correlations were generally weak. This suggests that most of the temporal variability in mean age was related to unique factors influencing individual stocks. Such factors likely include genetic (Ricker 1972) and other parental effects (Bilton 1970; Bradford and Peterman 1987), stock-specific environmental effects, as well as measurement error in data.

Covariation across the three components of sockeye salmon recruitment

The above patterns of covariation in size and age at maturity and those for survival rates of sockeye salmon stocks (Peterman et al. 1998) provide evidence of the spatial scales over which environmental processes affect these variables. In addition, by examining patterns of covariation across these components of recruitment, we can make further general inferences about the extent to which ocean conditions may simultaneously drive interannual variability in each component.

For comparisons between length and mean age, we might expect negative covariation if marine conditions favorable

for growth resulted in both greater length at maturity and younger mean age at maturity (e.g., Bilton et al. 1982; Wood and Foote 1996). As discussed above, interannual variation in adult length of sockeye salmon appears to be largely determined by conditions during the final year at sea. In contrast, environmentally induced variation in age at maturity likely occurs within the first 2 years of marine life, although the exact period is unclear (Peterman 1985). To address the main possibilities, we correlated length and mean age data at two lags. First, return year of length data was lagged to match the OEY + 1 year of mean age data (i.e., lengths of adults returning in the summer of 1980, for example, are aligned with the mean age data of smolts that enter the ocean in the spring of 1979, so that for their entire first year at sea, smolts are in the ocean along with returning adults). Second, return year was lagged to match OEY + 2 years (for their first 2 years at sea, smolts overlap with returning adults). To simplify the analysis, age 1.x lengths were correlated with age 1.x mean ages, and similarly for age 2.x indices.

For most regions, we found moderate negative correlations between length and mean age within stocks and between regional aggregates at both lags examined (Table 2). These results were not surprising because opposite time trends were observed in length and mean age series for many Alaska and British Columbia stocks (Figs. 3 and 7). Perhaps the best evidence of the coherence between size and age of adults was shown for Fraser River stocks, which exhibited abrupt shifts toward smaller length beginning in the 1980 return year (Fig. 3) and greater mean age in the 1979

OEY (Fig. 7). Correlations computed using prewhitened data did not help identify a critical lag. These correlations were generally negative at both lags and were much weaker than those among the original data series. Thus, while it was not possible to determine at which point during marine life the lengths and mean age share similar influences, it was clear that opposite time trends in these recruitment variables were the primary source of negative correlations.

Favorable ocean conditions for growth may also be associated with increased marine survival rates for sockeye salmon, with effects on survival rate likely to occur during the first year at sea. Thus, for comparisons among lengths and survival rates (marine, stock-recruit, and aggregate stock-recruit indices of survival rate), we aligned data series so that return year for lengths was the same as the OEY for survival rates. Results were similar when return year was aligned with the OEY + 1 year. For most regions, there was no evidence of either positive or negative covariation among lengths and survival rates. An exception was Bristol Bay stocks, for which within-stock correlations between length and stock-recruit survival rates (which had more years of data than marine survival rates) were positive in 28 of 32 cases (four length series for each of eight stocks). However, these correlations were generally weak (average $r = 0.18$; three positive correlations significant at $P < 0.05$). The four correlations among Bristol Bay aggregates of survival rate and length were also weak (average $r = 0.24$; none significant). The weak and inconsistent associations between length and survival rate suggest that different processes drive interannual variability in these components of recruitment. This conclusion is further supported by evidence that environmental processes influence these two variables at different spatial scales. Length shows much stronger between-region positive covariation (e.g., Fig. 2C) than survival rate (e.g., fig. 1C of Peterman et al. 1998); the latter only shows within-region positive covariation.

Finally, negative covariation between survival rate and mean age at maturity might be expected as a result of processes in early marine life, where conditions favoring growth might lead to higher survival rates and lower mean age. However, correlations among mean age and survival rate aligned by OEY of smolts were weak with no tendency toward negative or positive values. For example, the average of the 32 within-stock correlations (13 of which were negative) was 0.02. Similar correlations were found when OEY of mean age data was lagged either 1 or 2 years ahead of OEY for survival rates. Thus, there appears to be little association between environmental processes determining interannual variability in survival rates and those affecting mean age at maturity, although such relationships may be masked by measurement error or parental effects on mean age.

Conclusions

This paper on length and age at maturity and the Peterman et al. (1998) paper on survival rate report different patterns of covariation over space for each of these three variables. Adult length of sockeye salmon tends to be positively correlated among stocks across different regions and most strongly correlated among stocks within regions. Mean age at maturity shows similar but much weaker correlations than

for length data. In contrast, survival rates show positive covariation within regions but no covariation between regions (Peterman et al. 1998). These differences in patterns of covariation imply that to some extent, each of these components of recruitment is affected by environmental processes that operate at different spatial scales. Therefore, future models for forecasting annual salmon abundance (reflecting survival rates and changing age at maturity schedules) or body size should be based on appropriate measures of environmental conditions that reflect this information about spatial scales. For instance, instead of using sea surface temperatures averaged over the entire northeastern Pacific Ocean as an independent variable in a model to forecast variability in survival rates, a regional measure would be more appropriate. However, both large-scale and regional-scale measures of ocean conditions may be useful for forecasting changes in body length.

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Density-dependent marine processes in North Pacific salmonids: lessons for experimental design of large-scale manipulations of fish stocks

Randall M. Peterman

Peterman, R. M. 1991. Density-dependent marine processes in North Pacific salmonids: lessons for experimental design of large-scale manipulations of fish stocks. – ICES mar. Sci. Symp., 192: 69–77.

Density-dependent growth and survival processes occur within and among stocks and species of Pacific salmon (*Oncorhynchus* spp.) and other fishes. These processes, in addition to numerical responses of natural predators and fishermen, can generate lower benefits than expected from the increases in abundance that result from extensive mariculture. Benefit/cost analyses of proposed mariculture programmes should, therefore, take such processes into account. As well, such programmes should be designed as rigorous large-scale experiments so that managers can: (1) distinguish whether a change in stock abundance (or lack thereof) is due to mariculture or to changes in some natural processes such as ocean productivity, and (2) identify appropriate remedial actions, should they become necessary.

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Introduction

Pacific salmon (*Oncorhynchus* spp.) are economically important on the west coast of North America (1986 landed value in Canada and the United States of \$900 million Canadian currency). Since as early as the late 1800s, various agencies have attempted to increase the abundance of these populations of salmon by releasing artificially reared juveniles into the wild (Larkin, 1974). More concerted, large-scale efforts at enhancement have been made with varying degrees of success beginning in the 1960s and 1970s in Canada, the United States, and Japan. This paper reviews experience gained from enhancement of Pacific salmon, with the aim of improving extensive mariculture efforts on these and other species. Because of their anadromous life history, relatively precise estimates of abundance and biomass of Pacific salmon exist at several life stages, permitting a close examination of stock dynamics.

Enhancement efforts on Pacific salmon are examples of extensive mariculture; fish are manipulated by man through the egg or fry stage before being released into the wild. Numerous techniques are used in such programmes, including hatcheries, spawning channels, incubation boxes, fertilization of lakes, and others. These programmes are variously known as sea or ocean ranching, salmonid enhancement, or extensive mari-

culture. In keeping with the terms of reference for this volume, examples in this paper specifically exclude salmon farming, in which fish are captive throughout their lives.

Lessons

While the examples here are drawn from Pacific salmon, the lessons should apply to future extensive mariculture of other species, including non-anadromous fishes and invertebrates. Many extensive mariculture projects with Pacific salmon have apparently been quite successful, for example, Japanese chum salmon (*O. keta*) (Nasaka, 1988) and Alaskan pink (*O. gorbuscha*) and chum salmon (Royce, 1988). However, unexpected problems have arisen in numerous projects, either in the form of overt difficulties such as interactions with wild stocks, or in experimental designs that are inadequate to permit definitive attribution of apparent success or failure to specific causal mechanisms. Some of the lessons that we have learned from these experiences with Pacific salmon are reviewed here.

Lesson 1: Carefully examine assumptions behind programme objectives

A frequently stated goal in salmonid enhancement is to “Increase salmon catches to former levels”. In the case

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the affidavit of R Peterman
sworn before me at Vancouver
this 2 day of May 2011
A Commissioner for taking Affidavits
for British Columbia

of Canada's Salmonid Enhancement Program (SEP), a goal of doubling salmon stocks was stated in 1976; this goal was justified by assuming that previous catch levels (about twice the catches in the early 1970s) indicated sufficient productive capacity in the North Pacific to permit such an increase (MacLeod, 1977). However, this assumption is not necessarily valid for three reasons. First, ocean productivity may either improve or deteriorate, so past abundance may not be a good indicator of potential future abundance. For example, in the North Pacific, where adult Pacific salmon grow, the duration of zooplankton growing seasons has decreased significantly over a 23-year period (Peterman, 1984a and Fig. 1). Subsequent to that period, oceanographic conditions have reversed and survival rates of some salmon have increased (Eggers and Rogers, 1987). Second, changes in relative abundance of food species, competitors, and predators may alter the potential for increasing abundance of enhanced species. For example, the large increase in some North Sea demersal fish stocks, along with decreases in the pelagic stocks (Jones, 1983), shows that major shifts in fish communities can occur. If the oceanography or community structure shifts in a way that is unfavourable for those species being contemplated for extensive mariculture, then forecasted benefits of mariculture will not materialize. Conversely, if a favourable shift occurs, some portion of the resulting increased benefits will be wrongly attributed to mariculture, thereby biasing expectations for future mariculture operations. Finally, previous catches may not be a good indicator of future sustainable catches because of the commonly observed

"fishing-up" process. This process results in a large catch early in the development of a fishery relative to current or maximum sustainable catches, simply because of removal of the older-aged standing stock and not because of decreased stock productivity, overharvesting, or mismanagement (e.g. Ricker, 1973; Francis, 1986). While this concept is usually more applicable to longer-lived, non-anadromous marine species, a similar peak yield early in a fishery can occur in salmon through other mechanisms as well (Ricker, 1973). Thus, planners of extensive mariculture programmes may overestimate achievable goals by basing them on peak historical catches and ignoring "fishing-up" effects. Note, however, that analyses of historical data may identify the magnitude of fishing-up and the correction for it.

Lesson 2: Include density-dependent processes in benefit/cost evaluations of proposed extensive mariculture projects

Extensive evidence exists in the Pacific salmon literature for density-dependent interactions within and among populations and species (reviewed by Peterman, 1987). These processes can significantly reduce productivity of mariculture projects because such projects increase abundance in at least one life stage. These density-dependent processes thus can alter the way in which mariculture projects should be evaluated and managed. It is inappropriate, therefore, to calculate expected mariculture benefits by using constant, density-independent egg or juvenile survival rates when one or the other has been artificially increased. Yet such constant survival rates, called "biostandards", were used during planning of SEP's 1977-1984 projects in Canada (Shepherd, 1984). Such simple calculations may overestimate production from mariculture operations for the several reasons outlined below.

Within-population processes

First, within-population processes or mariculture practices may alter a stock's production in unexpected ways if changes occur in abundance, average body size, time of release into the wild, or other factors relevant to growth or survival. For example, the increased abundance of Babine Lake, British Columbia sockeye salmon (*O. nerka*) resulting from freshwater enhancement is associated with decreased survival rate of smolts (seaward migrating life stage) during their first 15 months of ocean life (Peterman, 1982; McDonald and Hume, 1984). As well, growth rate of salmon in the ocean is inversely related to within-stock abundance in several salmon stocks (Peterman, 1984b). Furthermore, in Fraser River, British Columbia pink salmon, a significant improvement in the correlation of the adult body weight vs. abundance relationship resulted from including an index of food supply in the analysis (Pet-

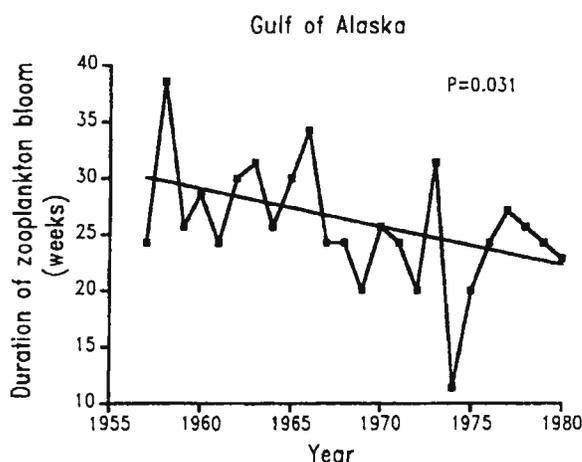


Figure 1. Zooplankton data from "Ocean Station P" in the Gulf of Alaska (50°N lat 145°W long.) (LeBrasseur, 1965; Fulton, 1983) showing a trend in the period in which total zooplankton wet weight was $>40 \text{ mg m}^{-3}$ in each year ($p = 0.031$). Similar trends exist for other threshold densities as well. The data series ended in 1980 when the weather ship at this location was taken out of service.

erman, 1987, $r^2 = 0.74$, $p < 0.001$). Density-dependent growth responses within populations also occur in immature marine fishes (reviewed by Ware, 1980). Therefore, unless density-dependent responses are explicitly incorporated into benefit/cost analyses, forecasts of future biomass yield from a manipulated stock may be too high. Furthermore, in coho salmon (*O. kisutch*), survival rate and total adult biomass result from a complex interaction between time and size at which juveniles are released into the wild (Bilton *et al.*, 1982). If the time and size are properly chosen, adult biomass can be increased over that of wild populations; if not, biomass may decrease.

Interactions among populations but within a species

Density-dependent growth also occurs in the ocean as a result of interaction among several populations of sockeye salmon in the Gulf of Alaska. For example, Rogers (1980, 1984) and Eggers *et al.* (1984) found that age-specific body sizes of adult sockeye from Bristol Bay, Alaska decreased with increased pooled abundance of the ten stocks from that bay. In addition, these very abundant Alaskan sockeye stocks overlap in space and time in the Gulf of Alaska with British Columbia sockeye populations, and mean weight of British Columbia adult sockeye is up to 22% less when abundance of sockeye salmon in the Gulf of Alaska is high (Peterman, 1984b and Fig. 2). These among-stock effects, probably due to competition for food, can contribute as much to the yearly variation in adult body weight as the density-dependent growth effect of within-stock abundance (Peterman, 1984b). Because abundance of sock-

eye salmon from one nation appears to affect the biomass yield of sockeye from another, coordinated international efforts would be prudent to avoid increasing the biomass of one population via mariculture at the expense of another. In non-salmonid species as well, such trade-offs among stocks can be minimized if it is possible to choose stocks for extensive mariculture that overlap relatively little in space and time with other stocks.

Further problems arise when stocks manipulated by mariculture are harvested together with wild stocks. Because enhanced stocks usually have higher egg-to-adult survival rates than wild stocks, enhanced stocks can withstand a higher sustainable harvest rate. But this higher rate may result in overharvesting of the less productive wild stocks, which may become depleted (e.g. Larkin, 1974; Oregon Department of Fish and Wildlife, 1982; Walters, 1988). Thus, priority for extensive mariculture should be put on those stocks that do not overlap with wild populations during periods of fishing.

Interactions among species

The response of predators to changes in abundance of Pacific salmon can be important because large proportions of juvenile salmon populations can be eaten by birds and fish as they enter salt water (Parker, 1968; Mace, 1983). In response to release of juvenile salmon from freshwater rearing sites, local abundances of predatory birds increased dramatically due to aggregation (Fig. 3; Mace, 1983; Matthews, 1983; Wood, 1985, 1987). Such numerical responses do not necessarily lead to fewer surviving juvenile salmon because of the

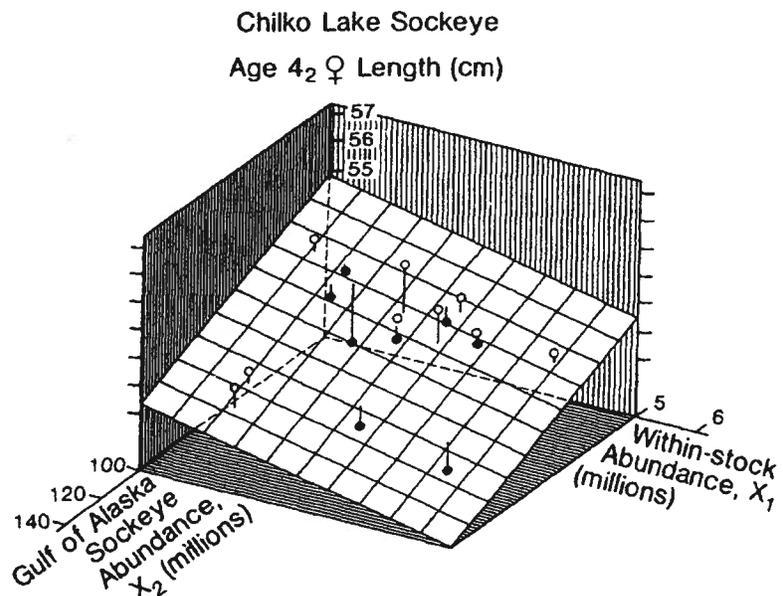


Figure 2. Body size of 4-year-old adult female Chilko Lake. British Columbia sockeye salmon is significantly inversely related to abundance of that stock, X_1 ($p = 0.046$) and to the pooled abundance of all sockeye salmon stocks resident in the Gulf of Alaska, X_2 ($p = 0.009$). Data are shown as positive residuals (open circles) or negative residuals (solid dots) from the multiple regression plane. Reprinted with the permission of Peterman (1984b).

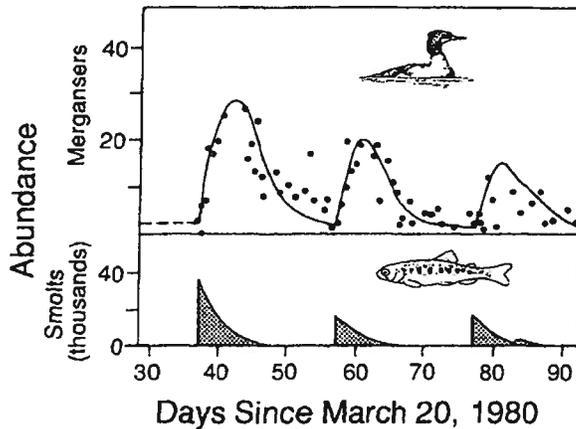


Figure 3. The number of predatory birds, common mergansers (*Mergus merganser*) increased when steelhead smolts (*Salmo gairdneri*) and chum salmon fry (*O. keta*; the small pulse at 84 days) were released from a hatchery on Rosewall Creek, Vancouver Island, British Columbia in 1980. For mergansers, dots that observed abundance and the curved line is from Wood's (1985) predictive model (redrawn from Wood (1985) with permission).

interaction between the numerical response and density-dependent consumption rate or functional response (Mace, 1983; Wood, 1987). Nevertheless, Mace (1983) found that losses to bird predation were reduced by 85% by releasing juvenile chinook salmon (*O. tshawytscha*) during high tide and low light level (making searching by predators less efficient) and by releasing large numbers of fish in a short period (quickly satiating predators). Similar release strategies might also be appropriate for fishes undergoing mariculture in the International Council for the Exploration of the Sea (ICES) region, where predation on juveniles is suspected to be important (Gunnerod *et al.*, 1988).

Increased abundance of fish may also attract more fishermen, as exemplified by the gillnet fishery for sockeye salmon in Barkley Sound, Vancouver Island, British Columbia. A 20-fold increase in sockeye abundance in that area, due in part to fertilization of a rearing lake for juvenile sockeye, led to a 15-fold increase in number of gillnet boats fishing there, in spite of a 50% reduction in number of gillnet boats in British Columbia over that period (Hyatt and Steer, 1987 and Fig. 4). The presence of such high-productivity enhanced stocks, combined with the aggregation response of fishermen, often increases pressure on management agencies to allow high fishing effort, in spite of its detrimental effect on less productive wild stocks (Walters and Riddell, 1986).

Synthesis

The variety of density-dependent growth and survival processes suggests that there is more than one life stage

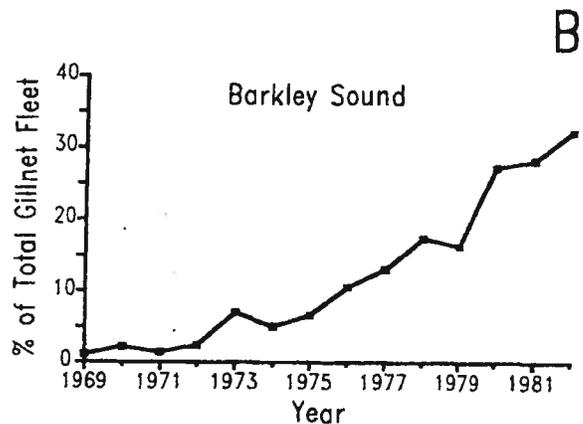
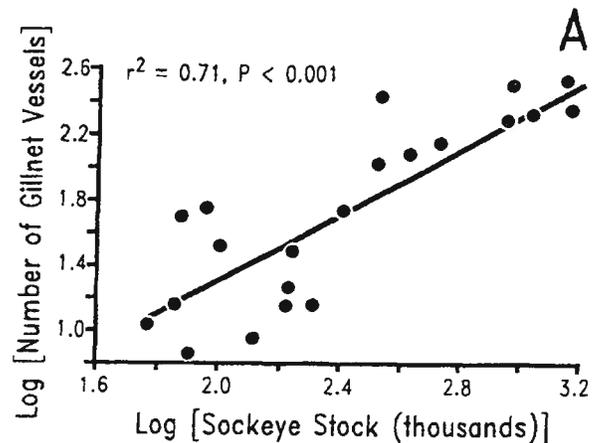


Figure 4. A. The index of boats fishing in Barkley Sound, BC, is significantly correlated with log abundance of the fishable stock, adult sockeye salmon, for 1961 to 1982 (redrawn from Hyatt and Steer (1987) with permission). B. The proportion of all British Columbia gillnet vessels fishing in Barkley Sound increased with time due to reallocation of vessels to that area (data on total British Columbia vessels from Anon. (1988) were not available before 1969; Barkley Sound gillnet data adapted from Hyatt and Steer (1987) by K. Hyatt, pers. comm.).

limiting the abundance and biomass of adult Pacific salmon populations. Thus, improved survival rate at the egg stage, for example, will only translate into increased biomass yield of adults if the compensatory growth or survival processes at later life stages do not offset the increased number of hatched eggs. Marine fishes may also have more than one limiting life stage. Thus, ongoing extensive mariculture programmes should not be evaluated by numbers released at an early life stage but rather by the resulting adult biomass, which integrates over all of the survival and growth stages. This evaluation will require a careful and extensive experimental design (see Lesson 4 below) to avoid confounding the response (change in adult biomass) to treatment (mari-

culture) with a response to naturally varying processes.

The above examples of density-dependent processes also imply that effective evaluations of proposed extensive mariculture programmes should include benefit/cost analyses that incorporate potential interactions at several levels of biological organization (e.g. Guthrie and Peterman, 1988). Evaluation frameworks should include density-dependent interactions within and among populations, and among species in the community, as quantified by analysis of historical data on the system in question. Failure to do so will most likely lead to an overestimate of expected benefits. Where current data are inadequate to do this, they can be gathered as part of causally-based research programmes while management proceeds; goals can then be continually updated (as in adaptive management – Walters, 1986).

Lesson 3: Keep extensive mariculture projects out of production mode until they have been thoroughly evaluated through experimentation

Pressure from management agencies to create high-profile successes may lead to some experimental mariculture projects being prematurely scaled up to production mode (i.e. applied to several populations) when initial trials appear successful. But because of limited budgets, less information is usually gathered during production than experimental phases. A good example is the Canadian Lake Enrichment Program (LEP), which is intended to increase abundance of sockeye salmon through nutrient enrichment of rearing lakes, which can lead to increased food for juvenile sockeye salmon. Initial trials with aerial fertilization of Great Central Lake in British Columbia in the early 1970s appeared very successful (LeBrasseur *et al.*, 1978), which prompted the Canada Department of Fisheries and Oceans (DFO) in 1977 to institute a large programme (up to 15 lakes per year) of lake fertilization (Hyatt and Stockner, 1985). However, about 10% of the nutrient additions resulted in large increases in the abundance of a competitor, three-spined stickleback (*Gasterosteus aculeatus*), instead of increases in juvenile sockeye salmon (Kim Hyatt, Head of Lake Enrichment Program, DFO, Nanaimo, BC, Canada, pers. comm.; Stockner and Hyatt, 1984). In other cases, nutrients were diverted to blue-green algae or diatoms rather than food for juvenile salmon, a problem that has been partially solved subsequently by changes in the composition of the fertilizer (Stockner and Hyatt, 1984). Unfortunately, the large number of lakes involved in the present lake enrichment programme, along with a limited budget, mean that DFO is able to gather sufficient information (i.e. adult as well as juvenile abundances) in only one quarter of these lakes to test quantitatively whether lake fertilization increases total adult biomass in particular lakes. While LEP appears to work in most of the cases in which complete adult

data exist, its current production mode precludes gathering the data required to further improve its performance by identifying the range of conditions in which it is successful, and the causes of failures (including the mechanisms discussed under Lessons 1 and 2). In retrospect, it may have been better to spend more time and money in the closely monitored, well-designed experimental stage before moving to the loosely monitored production mode. In addition, production modes should always be accompanied by thorough ongoing assessments of performance.

Lesson 4: Extensive mariculture projects should follow rigorous experimental design principles

In order to identify accurately situations in which various mariculture methods work best, both initial experiments and large-scale production projects should be rigorously planned to follow experimental design principles (Larkin, 1979). Ideally, they should have clearly testable hypotheses, treated as well as control stocks (both spatially and temporally replicated), and high statistical power (large enough sample size to have a high probability of detecting a treatment effect, if one occurs). Where appropriate, these experiments should include interspersions of treatments and controls in space and time (Hurlbert, 1984) and staggered starting times of treatments on different stocks in order to prevent confounding of interpretations of treatment effects with other independent, simultaneously occurring processes such as a shift in ocean productivity (Walters *et al.*, 1988). These and other design principles are reviewed by Toft and Shea (1983), Hurlbert (1984), Stewart-Oaten *et al.* (1986), Walters (1986), and Peterman (1990). While such principles are traditionally included in laboratory or small-scale field experiments, they are rarely used in large-scale management manipulations of fish populations. Yet it is just as important to learn what works and what does not (and why) in large-scale management projects as in laboratory experiments. Only through carefully designed experiments (accompanied by research into causal mechanisms of dynamics) will management agencies begin to accumulate the knowledge to make the best choices among the growing number of extensive mariculture opportunities. Finding adequate replicates among fish stocks is a major stumbling block to a rigorous application of experimental design principles. However, the best replicate stocks could be those that tend to covary in important characteristics such as parameters of density-dependent survival or growth rate (Walters, 1986).

An example shows how a lack of experimental design has led to uncertainty about the performance of hatchery-produced coho salmon in Oregon. Both hatchery and wild fish have shown significant decreases in marine survival rate, and adult abundance failed to increase since the mid-1960s in spite of a large increase in smolt abundance (Fig. 5A, B; Nickelson, 1986). However,

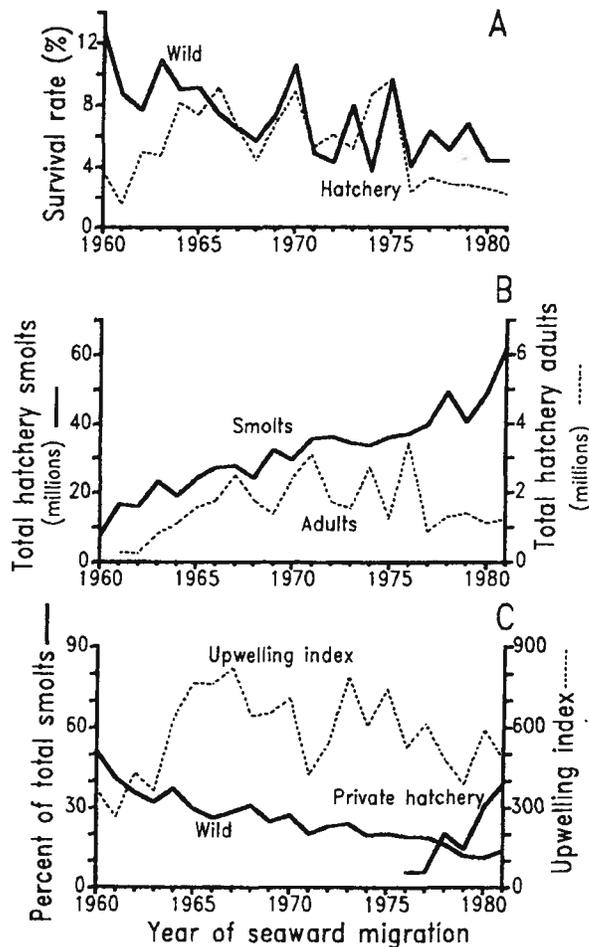


Figure 5. Data for coho salmon in the Oregon Production Index area, USA. A. Percent survival rate (mature adults per juvenile entering the ocean times 100) for hatchery and wild coho salmon. From 1964 to 1981 there was a significant decrease in the survival rate of wild ($r^2 = 0.23$, $p = 0.044$) and hatchery ($r^2 = 0.48$, $p < 0.002$) fish. B. Total hatchery smolt releases per year and the resulting adults (catch plus escapement). C. Upwelling index ($m^3 \times sec^{-1} \times 100 m^{-1}$) and percent of total smolts (wild + public hatchery + private hatchery) contributed each year by wild stocks and private hatcheries. Data from Nickelson (1986).

the cause of the decline in survival rate of hatchery fish is unclear because a number of factors changed simultaneously during this period: smolts were released in different months and at various mean sizes in different years, total smolt abundance (wild + hatchery) generally increased with time, upwelling changed, and wild stocks contributed a smaller portion of total smolts through time, while private hatcheries became significant producers in the last four years of the data set (Fig. 5B and C) (Nickelson, 1986; ODFW, 1982). Thus, the decline in marine survival rate of Oregon coho salmon could be due to degradation in genetic quality of hatch-

ery fish, density-dependent survival in the ocean, changes in oceanographic conditions, or a combination of these and other causes (Nickelson, 1986). Without a rigorously controlled experimental design, simultaneous, extensive monitoring of replicate non-hatchery stocks, and different starting years for replicate hatcheries, it is impossible to remove the confounding effects and distinguish among these alternatives, which would be necessary to choose remedial management actions. Marine survival rates of British Columbia hatchery coho and chinook salmon have also decreased significantly with time and their interpretation is similarly confounded by several simultaneously changing factors (Walters *et al.*, 1988).

Discussion

The experience with extensive mariculture of Pacific salmon in Canada and the United States shows that expectations are often too high. Interactions within and among populations of the same species, as well as among different species, necessitate carefully planned, rigorously designed mariculture and data gathering programmes in order to identify effective methods and situations for mariculture. Such programmes will be costly and may require long periods before complete evaluation is possible. However, this systematic approach is necessary to reduce the current uncertainty surrounding many extensive mariculture programmes. Such a rigorously designed approach is currently being developed for the large-scale (\$100 million/year) rehabilitation of Pacific salmon in the Columbia River basin in the northwestern United States (Lee and Lawrence, 1986; Northwest Power Planning Council, 1987).

In spite of careful experimentation, unexpected problems may still arise in any extensive mariculture project and agencies should, therefore, consider flexible, relatively inexpensive alternative modes of mariculture that can be shut down or modified as necessary. An example from Pacific salmon is lake fertilization; if it does not work on a particular stock, the operation can easily stop or move elsewhere. However, if a hatchery does not work well, it cannot be moved and the large initial capital cost often leads to the decision to keep the hatchery operating.

Recent interest in extensive mariculture has led some researchers to ask, "What is the maximum potential production capacity of a given region in tonnes of a given species per year" (e.g. Salo, 1988)? This question is inappropriate because, while density-dependent processes will cause biomass yield to be either an asymptotic or a dome-shaped function of juvenile abundance, costs will increase with juvenile abundance (Fig. 6). Therefore, the stock size that gives the *maximum* biomass yield is not necessarily the *optimal* stock size for maximizing net economic benefits. Instead, we should ask, "Given the known density-dependent and density-inde-

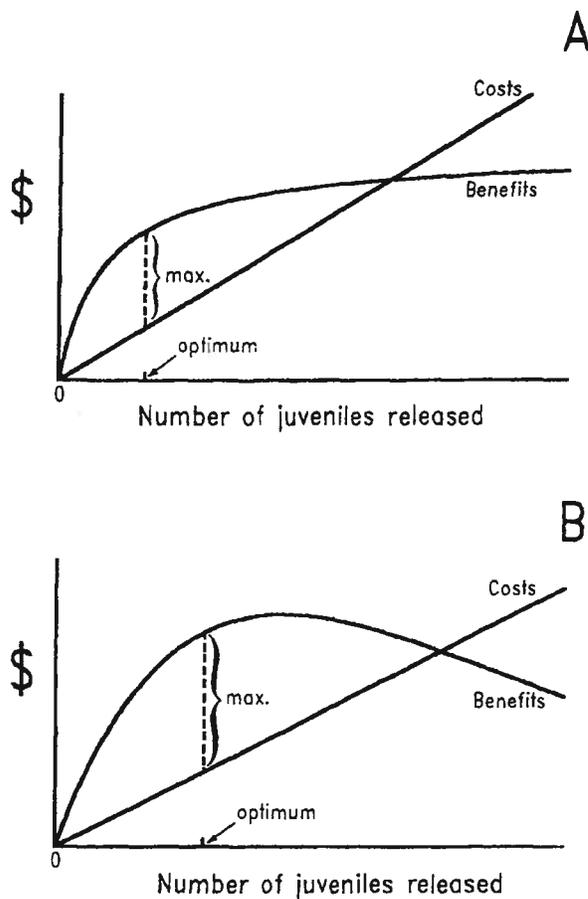


Figure 6. Two possible situations relating benefits (total dollar value of the biomass yield) to number of juveniles released from extensive mariculture facilities. A. Here benefits are asymptotically related to abundance of juveniles released. B. Here benefits are a dome-shaped function of juveniles released. Costs of producing juveniles will not necessarily be linearly related to the abundance of juveniles. However, in either situation, if the cost function crosses the benefit function, an optimum abundance of juveniles will occur where the difference between costs and benefits is greatest (max.). In the situation in A, this optimal juvenile abundance will never be the one that maximizes total biomass yield (dollar benefits), but in B the optimum may, but will not necessarily, occur where biomass yield is maximized.

pendent processes within and among populations, what is the optimal abundance of juveniles?" In other words, which abundance will produce the greatest difference between overall economic benefits and costs, if that is the stated management objective (see Fig. 6)? With this approach managers can explicitly take into account both economic considerations and trade-offs among populations and species that result from manipulation of a single population.

Extensive mariculture in Europe with cod (*Gadus morhua*), other fishes, and invertebrates may benefit

from applying the lessons outlined here. For instance, significant time trends in North Sea plankton data (Dickson *et al.*, 1988) and major shifts in species composition of North Sea fish communities (Jones, 1983) can influence the success of extensive mariculture projects and should be taken into account when setting production objectives. Second, density-dependent processes may cause localized, small-scale trials to lead to different results than large-scale projects because of interactions with wild or other enhanced populations in the latter case (through competition for food or enhancement of shared predator populations or fishing fleets). Thus, measures of success cannot always focus only on the manipulated population; in some instances it may be necessary to gather detailed data on other interacting populations to test rigorously the null hypothesis of no change in these other populations and to determine the overall benefits. If ICES nations begin to use mariculture on species that migrate across jurisdictional boundaries, they may also have to consider some of the issues that have emerged in Pacific salmon concerning competition among stocks from different nations for limited food resources in international waters (Larkin, 1980) and legal ownership rights (Hampson, 1988). ICES could be an ideal agency for coordinating mariculture efforts among nations to ensure that management objectives are met when such complexities arise. Finally, application of experimental design principles in both trial and production-scale projects will help avoid the confounded interpretation of results that has plagued fisheries management for decades and a clearer picture of successful techniques should emerge.

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This is Exhibit E "referred to in
the affidavit of R. Peterman
sworn before me at Vancouver
this 2 day of May, 2011
[Signature]
A Commissioner for taking Affidavits
for British Columbia

A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska

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Abstract.—Five hatcheries in Prince William Sound, Alaska, release more than 500 million juvenile pink salmon *Oncorhynchus gorbuscha* each year, constituting one of the largest salmon hatchery programs in the world. Before the program was initiated in 1974, pink salmon catches were very low, averaging 3 million fish per year between 1951 and 1979. Since 1980 the catch has averaged more than 20 million fish per year. However, catches in three other areas in Alaska with substantial fisheries for pink salmon (southeast Alaska, Kodiak Island, and the southern Alaska Peninsula) also increased equivalently during the same period, and the hatchery production did not become the dominant factor in Prince William Sound until the mid-1980s, long after the wild population had expanded. A hatchery program in the Kodiak area provides useful contrast to the Prince William Sound program because it is smaller and more isolated from the major wild-stock-producing areas of Kodiak Island. The evidence suggests that the hatchery program in Prince William Sound replaced rather than augmented wild production. Two likely causes of the replacement were a decline in wild escapement associated with harvesting hatchery stocks and biological impacts of the hatchery fish on wild fish. Published papers disagree on the impact of the 1989 Exxon Valdez oil spill, but none of the estimates would account for more than a 2% reduction in wild-stock abundance, and the decline in wild stocks began well before the oil spill. No evidence in the Kodiak area program suggests any impact on wild stocks. This analysis suggests that agencies considering the use of hatcheries for augmenting salmonids or other marine species should be aware of the high probability that wild stocks may be adversely affected unless the harvesting of the hatchery fish is isolated from the wild stocks and the hatchery and wild fish do not share habitat during their early ocean life.

In response to low salmon abundance in the 1960s and 1970s the state of Alaska began several hatchery programs, including the creation of the Fisheries Rehabilitation, Enhancement and Development division within the Alaska Department of Fish and Game (ADF&G). The state legislature also passed the Hatchery Act (1974) and the Fisheries Enhancement Loan Program, which provided for low-interest loans to regional aquaculture organizations (Hull 1993). Under this legislative framework the Prince William Sound (PWS) Aquaculture Corp. (PWSAC) was formed in December 1974 by a group of commercial fishermen based in Cordova, Alaska. It currently operates three pink salmon hatcheries in PWS, and the Valdez Fisheries Development Association (VFDA) operates a single hatchery (Solomon Gulch) in Valdez Arm (Figure 1A). Approximately 70% of the hatchery production in PWS comes from the

three PWSAC hatcheries, but we will use data from the entire hatchery program—that is, both PWSAC and VFDA. Some of the spirit and hope of the early days of salmonid aquaculture in Alaska are captured in Wilson and Buck (1978): "the future potential for significantly increased salmon harvests throughout the state is enormous. Alaska's approach to salmon aquaculture and fisheries enhancement bears watching in the next decade as this multifaceted program attempts to yield larger harvests and bring new stability to a historically cyclical resource."

The PWSAC is a private nonprofit corporation funded both by a 2% tax on landings of fishermen in PWS and by sales of fish captured in cost recovery fisheries. It now operates the largest hatchery program in North America, releasing more than 500 million fry of pink salmon *Oncorhynchus gorbuscha* each year and some juveniles of sockeye salmon *O. nerka*, chum salmon *O. keta*, coho salmon *O. kisutch*, and chinook salmon *O. tshawytscha*. Olsen (1994) and Pinkerton (1994) describe the biological and social history of PWSAC.

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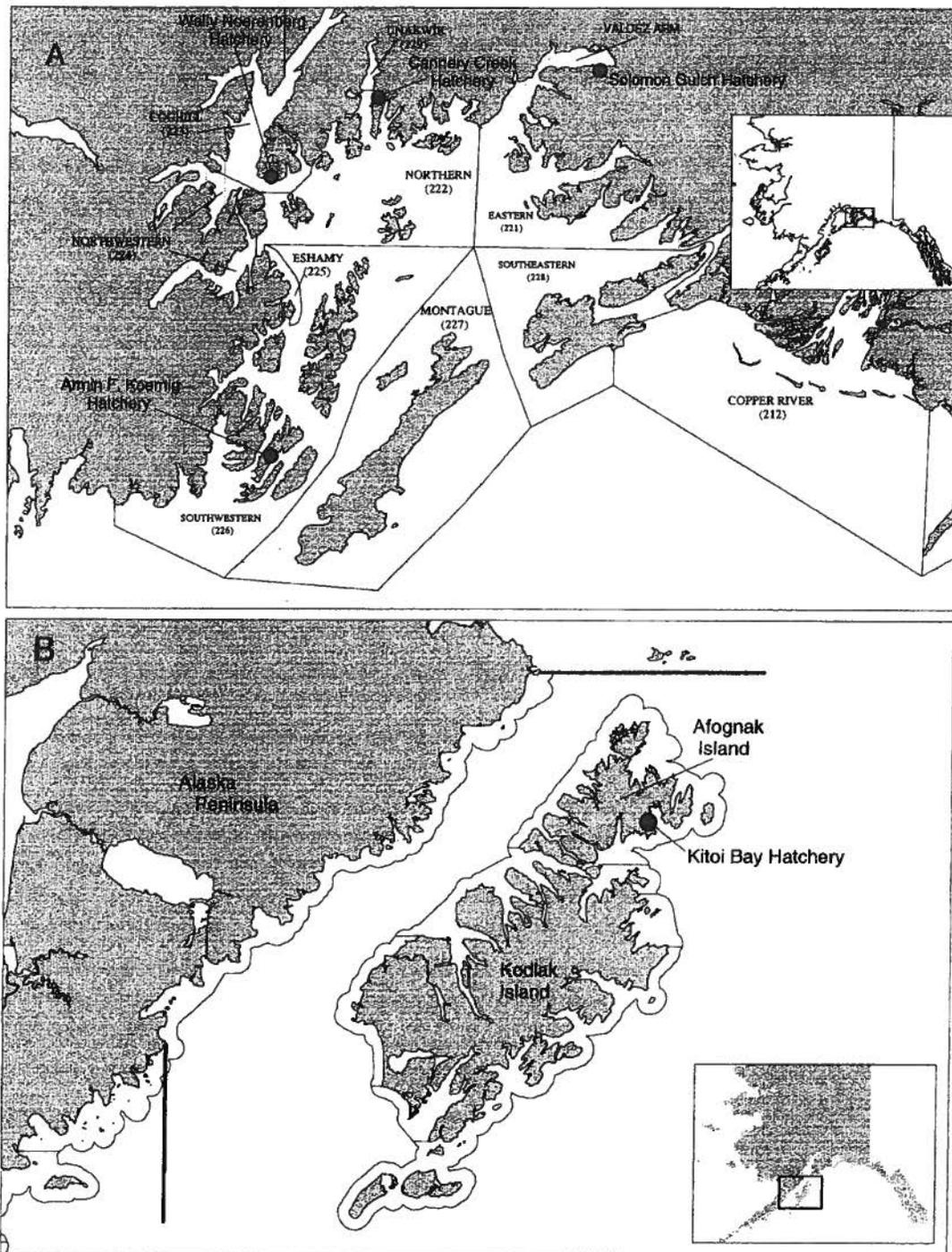


FIGURE 1.—Maps of (A) Prince William Sound (PWS) and (B) the Kodiak area, Alaska, showing locations of the hatcheries and, in PWS (A), the fishing districts (district numbers in parentheses).

The hatchery run of pink salmon to the Kodiak Island area is entirely supported by the Kitoi Bay Hatchery on Afognak Island (Figure 1B). The ADF&G rebuilt the facility, originally constructed in 1956, after its destruction in the 1964 earthquake. The facility was initially operated as a research facility, but emphasis switched to pink salmon production in 1976; it also produces sockeye salmon, chum salmon, and coho salmon. The ADF&G operated the facility before 1987 and Kodiak Regional Aquaculture Association (KRAA) assumed full operation of the hatchery in 1992. The KRAA is funded by a 2% tax on landings by fishermen in the Kodiak area as well as by earnings on a fund created from the proceeds of a one-time terminal area cost recovery fishery that occurred in 1989. This cost recovery fishery occurred because the *Exxon Valdez* oil spill in 1989 prevented harvest of returning salmon in the traditional fishing areas.

Concern about the biological success and economic viability of hatchery programs is increasing (Hilborn 1992; Meffe 1992; Hilborn and Winton 1993), and the PWS and Kodiak pink salmon programs appear to be excellent subjects for evaluating the biological success of large hatchery programs for four reasons. First, both programs are large and spatially quite discrete. Second, there are four regions of Alaska with significant wild pink salmon production, but only in PWS and the Kodiak area are there large-scale hatcheries. The other two areas provide the opportunity for natural controls that depict changes in wild stocks that occurred while the hatchery program came on line. The ADF&G has maintained a regular program of escapement monitoring throughout the PWS and Kodiak areas so that changes in escapement can be documented. Third, unlike the chinook salmon and coho salmon hatchery programs in Canada and the lower 48 United States, which have been ongoing for more than 100 years, the PWS and Kodiak pink salmon programs began in recent years, and there are reliable data on wild stocks before the program began. Finally, significant physical differences exist between the programs in PWS and the Kodiak area: the location of the Kodiak area hatchery is well isolated from the major wild spawning areas whereas the PWS hatcheries are not.

Previous papers have explored the implications of these hatchery programs. Eggers et al. (1991) compared the pink salmon production in PWS with that in the Kodiak area and with other wild Alaskan pink salmon stocks and noted that PWS production had increased at the same time as the other stocks.

They suggested that intense harvest of hatchery fish in PWS had been responsible for the decline of PWS wild stocks, replacing wild production with hatchery production. Tarbox and Bendock (1996) inferred that the hatchery program in PWS was a major contributor to declines in wild stocks. Smoker and Linley (1997) challenged the conclusions of Eggers et al. (1991) and of Tarbox and Bendock (1996) and considered alternatives to replacement of wild stocks by hatchery fish.

The purpose of this paper is to review the biological success of the PWS and Kodiak pink salmon hatchery programs. We now have considerably more years of data than were available to Eggers et al. (1991), and we have examined some additional areas of wild Alaskan pink salmon production. Further we also examined evidence for biological interaction between wild and hatchery fish in PWS and the Kodiak area and changes due to fishing. Finally we consider how our findings from the PWS and Kodiak areas can be applied to other hatchery programs for salmonids and marine species.

Methods

This analysis is strictly retrospective and is based on published data taken primarily from ADF&G reports on wild-stock catches and escapements as well as hatchery runs in southeast Alaska, Prince William Sound, Kodiak Island, and south Alaska Peninsula management areas.

For PWS, total catch numbers and delivery weights of pink salmon for the years 1965–1997 were taken from Morstad et al. (1998). The wild pink salmon peak aerial survey escapement index counts were not reflective of true escapement (Bue et al. 1998b). The escapements in Morstad et al. (1998) were estimated by dividing cumulative spawner-days, based on stream counts from aerial surveys, by the estimated stream residence time of 17.5 d (Helle et al. 1964). Multiyear studies of streams in the PWS aerial survey index program (Bue et al. 1998b) indicate that stream life is similar in streams within districts and between years. These estimates differed from the stream life used in the historical escapement calculations. Stream life estimated for Irish and Hawkins creeks (17.8 d) was used to adjust the index counts for the Eastern and Southeastern fishing districts (Figure 1A), and stream life estimates for the remaining streams were averaged (11.1 d) and applied to the remaining districts.

Runs of pink salmon to PWS hatcheries provide catches in common-property commercial fisheries,

cost recovery catches in hatchery terminal harvest areas, and broodstock. Numbers for catch of private nonprofit hatchery fish in mixed-stock commercial and cost recovery fisheries, as well as broodstock and unused fish, were taken from annual hatchery reports provided to ADF&G. Before 1987 the wild and hatchery fish contributions to the mixed-stock commercial fishery were estimated from the relative magnitude of returns to hatchery terminal areas and wild-stock escapement levels. Estimates of hatchery catches from 1987 to 1997 were based on a coded-wire-tagging program (Geiger and Sharr 1990; Peltz and Geiger 1990), and catches of wild stocks were approximated as the total common-property commercial harvest less the estimated hatchery contribution.

For the Kodiak area, total catch numbers of pink salmon for 1965–1996 were taken from Brennan et al. (1998), and those for 1997 were from ADF&G catch records (K. Brennan, ADF&G, personal communication). Catches of hatchery fish were assumed to be the entire commercial catch and cost recovery in the Izhut Bay, Duck Bay, and Kitoi Bay subdistricts. No significant populations of wild pink salmon exist near Kitoi Bay, and the hatchery there is not near traditional fishing areas for wild pink salmon. Catches of wild pink salmon do not occur in the hatchery terminal harvests, and catches of hatchery fish are negligible in fishing areas outside the terminal harvest area. Estimates of the commercial catch, cost recovery, and broodstock for the Kitoi Bay Hatchery, 1972–1997, were compiled from ADF&G catch records and from hatchery annual reports filed with ADF&G (Steve Honnold, Alaska Department of Fish and Game, personal communication). Wild-stock catch was estimated as total catch less hatchery catch.

Wild-stock escapement estimates were determined from cumulated weir counts and expanded peak counts of live fish derived from aerial or foot surveys (Brennan et al. 1998). Peak counts were expanded by a factor of 1.84 based on estimated stream life (Barrett et al. 1990). Escapements for streams not surveyed were interpolated from surveyed streams in the respective year, based on the historical average odd- and even-year escapement distribution among streams.

For the southern Alaska Peninsula area, total catch numbers of pink salmon were obtained from Campbell et al. (1998). Wild-stock escapement estimates were determined from peak counts of live fish derived from aerial or foot surveys (Campbell et al. 1998). Peak counts were expanded by a factor of 1.4 based on estimated stream life (B. A. John-

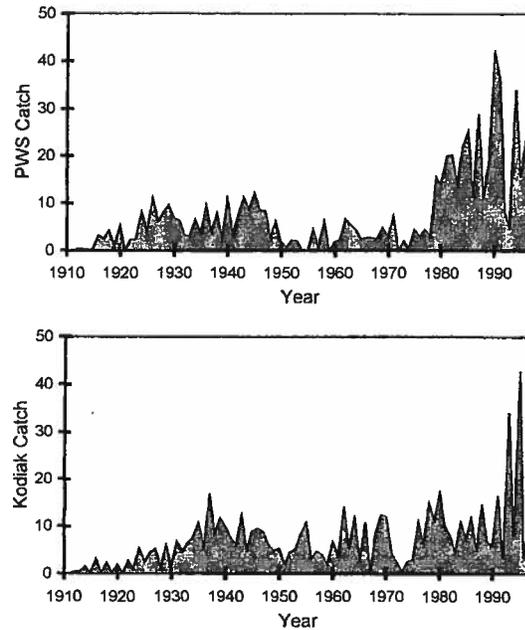


FIGURE 2.—The annual catch (in millions) of pink salmon in Prince William Sound (PWS; top panel) and the Kodiak Island area (bottom panel).

son and B. Barrett, ADF&G, unpublished manuscript).

For southeast Alaska, catches of pink salmon were obtained from ADF&G (1997). Estimates of wild-stock escapement were determined from peak counts of live fish derived from aerial surveys. The index counts were expanded for streams not surveyed in a particular year based on historical estimates of escapement distribution among streams. The index counts were standardized to account for differences in counting bias among individual observers (K. A. Hofmeister, ADF&G, unpublished, 1998). Standardized peak index counts were expanded by 2.5 to account for stream life (Dangel and Jones 1988).

Results

History of Pink Salmon Returns

The long-term history of pink salmon catches in PWS reveals four distinct periods. From 1896 to 1913, annual catch was less 1 million; 1916–1950 catches averaged 5.8 million fish per year; 1951–1979 catches dropped considerably to 3.3 million per year; and since 1980 catch has averaged 20.6 million fish per year (Figure 2). The dramatic rise since 1980 can be taken as evidence for success of the hatchery program. However, the three periods in PWS production since 1916 cor-

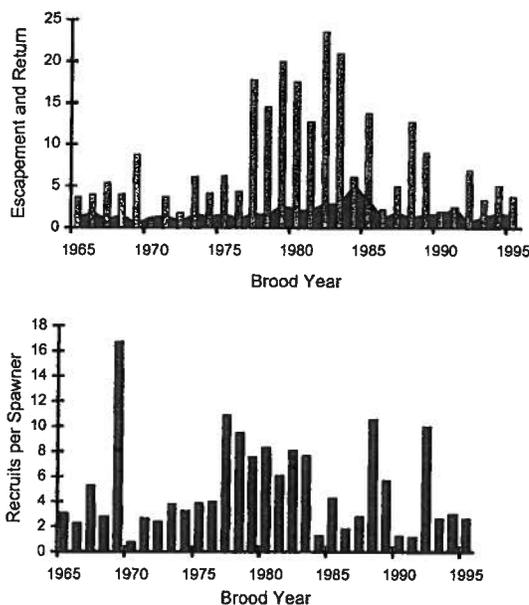


FIGURE 3.—Historical production of wild pink salmon in Prince William Sound, illustrated by (top) total return (vertical bars) and escapement (dark shaded area) of wild pink salmon (millions of fish) and (bottom) the index of wild recruits per spawner.

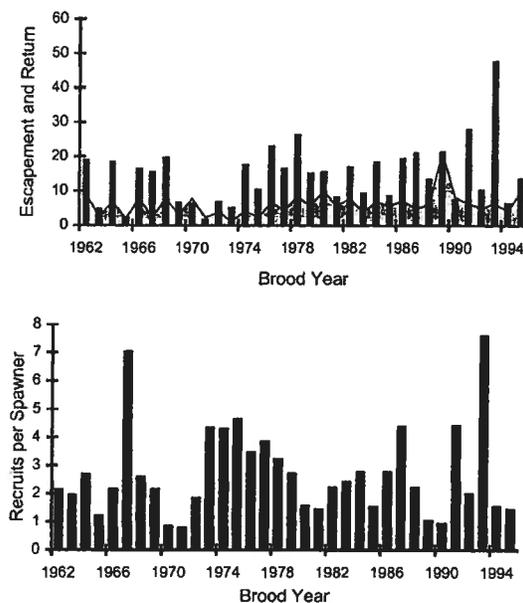


FIGURE 4.—Historical production of wild pink salmon in the Kodiak Island area, illustrated by (top) total return (vertical bars) and escapement (light shaded area) of wild pink salmon (millions of fish) and (bottom) the index of wild recruits per spawner.

respond to general patterns in abundance of pink salmon and sockeye salmon throughout Alaska, and these major changes are generally ascribed to changes in ocean conditions. These three periods are now commonly called “regimes” and fluctuation between regimes is the “interdecadal oscillation” (Francis and Hare 1994; Hare and Francis 1995; Mantua et al. 1997). Interpreting the impact of the hatchery program is closely connected with understanding and interpreting changes in other pink salmon populations in Alaska. Catch from the Kodiak Island area rose less dramatically after 1977 but, on average, was more than double the 1970s levels (Figure 2).

Figure 3 shows a major increase in total run to PWS in the late 1970s followed by an increase in escapement; then in the mid-1980s, wild-stock escapement and total runs declined. The index of wild recruits per spawner was elevated during 1977–1983 then experienced irregular but lower values from 1984 to 1993. In the Kodiak area both escapement and runs began to gradually increase in the mid-1970s (Figure 4).

History of Hatchery Production

The hatchery program in PWS began in the mid-1970s and by the early 1980s produced several

hundred million fry per year (Figure 5). The returns from hatchery production kept pace with the releases such that when pink salmon fry production increased to about 500 million in 1987, the subsequent adult returns were 15–35 million. Ocean survival apparently increased early in the program, but survival was poor in 1990 and 1991. In the 1990s, 20–40% of the total return was taken for cost recovery and broodstock.

In the Kodiak area, fry releases rose throughout the late 1970s and 1980s to about 150 million per year (Figure 6, top). The 1991 brood year produced a high of about 10 million fish and the 1987 brood was slightly lower, but only a few million fish were produced annually in other brood years. Although the Kodiak hatchery program is roughly one third the size of the PWS program in releases, survival is much lower, and only the 1991 hatchery brood year (1993 year of capture) produced a significant proportion of Kodiak pink salmon catch. As in PWS, hatchery ocean survival (Figure 6, middle) was more than 6% in the 1987 and 1991 brood years but only 1–2% in other years since 1980. In contrast, survival in PWS hatcheries was at least double the Kodiak average. Only in brood years 1985–1987 (harvest years 1987–1989) was there any cost recovery harvest

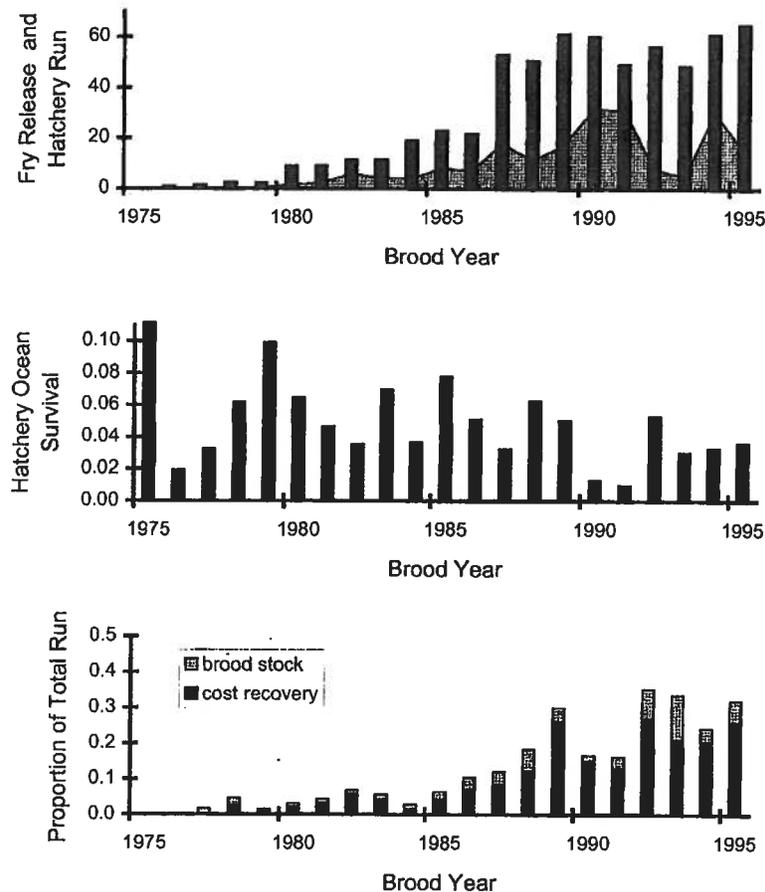


FIGURE 5.—Historical production of pink salmon from hatcheries in Prince William Sound, illustrated by (top) fry releases (vertical bars in tens of millions) and hatchery return of adults (shaded area in millions), (middle) ocean survival rate for hatchery fish, and (bottom) proportion of the total run of pink salmon that has gone to cost recovery fisheries and broodstock.

(Figure 6, bottom), and in 1989 almost all of the run was taken for cost recovery when the ocean salmon fisheries were closed because of the *Exxon Valdez* oil spill.

Pink Salmon Stock Changes Outside PWS

There are two other major pink salmon production areas in Alaska: southeast Alaska (the Alaska panhandle) and the southern Alaska Peninsula. Both of these areas also experienced a major increase in abundance since the 1977 regime shift. Some differences exist in the spawning habitat among areas, PWS having a high proportion of intertidal spawning. Pink salmon in all areas have similar marine life cycles, spending their ocean life in the Gulf of Alaska and northeast Pacific Ocean. Eggers et al. (1991) suggested that other populations of wild Alaskan pink salmon should reflect

what would have happened to PWS pink salmon in the absence of a hatchery program.

In southeast Alaska and the southern Alaska Peninsula, high production beginning in 1975–1976 followed low production in the 1960s and early 1970s (Figure 7). The catch in all four pink salmon regions has increased considerably since the mid-1970s. We normalized the data by dividing them by the average for 1976–1985, obtaining a 5-year running average to smooth the data, and then plotted all four pink salmon areas together in Figure 8. The 5-year running averages of total returns (hatchery and wild) to the four areas, divided by the 1976–1985 average for each area, show little clear discrimination among areas; returns increased in all areas with PWS having the lowest relative value in recent years. It is clear that PWS

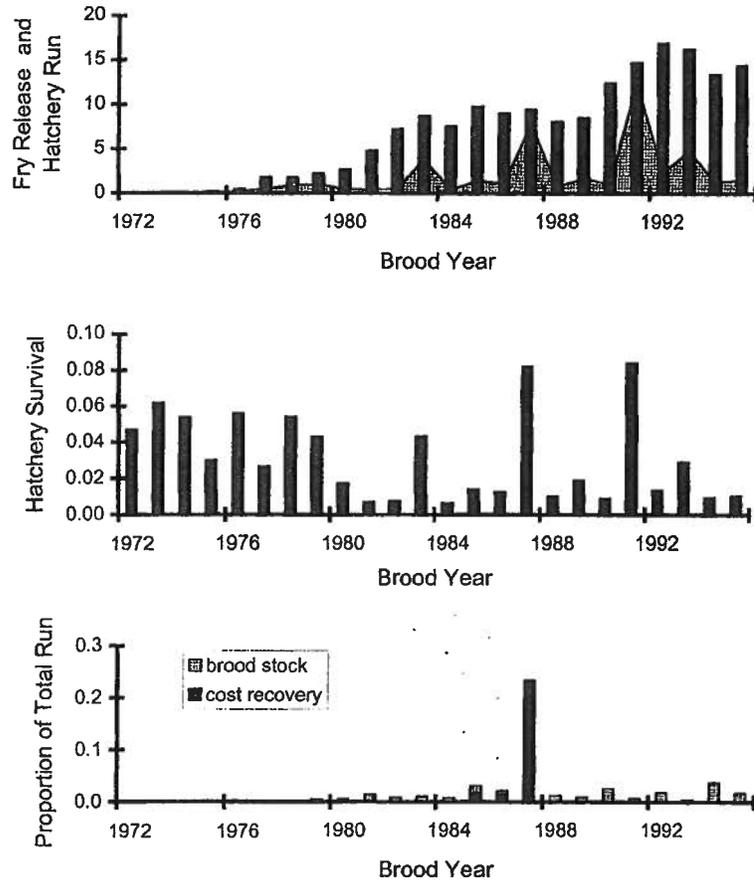


FIGURE 6.—Historical production of pink salmon from hatcheries in the Kodiak Island area, illustrated by (top) fry releases (vertical bars in tens of millions) and hatchery return of adults (shaded area in millions), (middle) ocean survival rate for hatchery fish, and (bottom) proportion of the total run of pink salmon that has gone to cost recovery fisheries and broodstock.

returns increased the most from the period before 1975, but this increase had taken place before 1984 when large-scale hatchery production began. For the 5-year running-average escapement, the general trend indicated increases in all areas except PWS, which has declined dramatically since the mid-1980s. For the 5-year running average of total return and wild return for PWS and Kodiak Island, almost no difference existed between total and wild pink salmon returns in the Kodiak area. In PWS, the wild return declined dramatically beginning in the mid-1980s while the total return stayed roughly constant, indicating that wild stocks were being replaced by hatchery stocks.

When the average return for 1986–1995 was compared with the return for 1965–1975 in each region, south Alaska Peninsula and Prince William Sound both increased roughly sixfold, southeast

Alaska increased 3.5-fold, and Kodiak increased about twofold (Table 1). However with the base period of 1976–1985 (after the improvement in ocean conditions and before large-scale hatchery production affected PWS), PWS, southeast Alaska, and south Alaska Peninsula all experienced very similar increases in returns—1.43, 1.55, and 1.37, respectively—while increases in Kodiak returns lagged behind at 1.13. From the pre-regime-shift base period (1965–1975), PWS and south Alaska Peninsula were highest, but this was accomplished by wild stocks in both PWS and south Alaska Peninsula.

Discussion

The purpose of the aquaculture program in Prince William Sound and Kodiak Island was to stabilize natural variability in the pink salmon runs

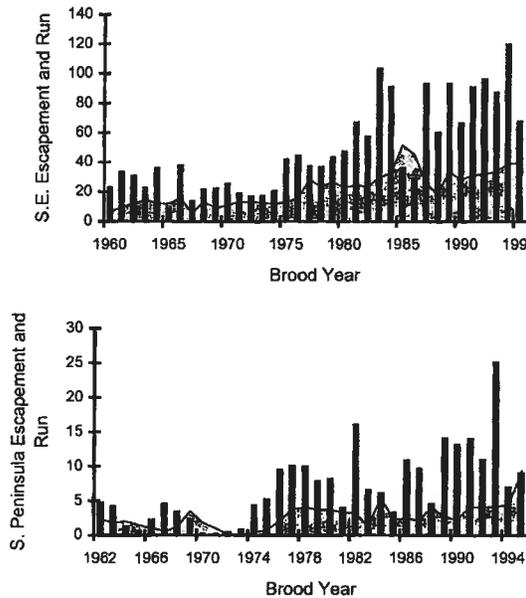


FIGURE 7.—Historical production of pink salmon in (top) southeast Alaska (S.E.) and (bottom) the southern Alaska Peninsula (S. Peninsula), illustrated by total catch (vertical bars) and escapement (shaded areas); all numbers are in millions.

to the area and to provide for a sustainable and economically viable fishery. The success of any enhancement program depends on meeting a series of biological criteria including (1) the successful production of fish that survive to be captured, (2) adequate survival, sustained for a long period, (3) hatchery production that can be harvested without affecting the production of the wild fish, and (4) production of enhanced fish that does not significantly reduce the survival and production of wild fish (so that there are true net benefits of the enhancement).

The data presented earlier show clearly that criterion 1 has been met: the PWS and Kodiak pink salmon programs produce fish that survive and contribute to the fishery. The survival rates achieved (particularly in PWS) are the envy of hatchery managers for chinook salmon and coho salmon up and down the coast, where a 5% survival rate is considered an incredible success, even for fish reared for a year in the hatchery, fed extensively, and therefore released at a very large size. It is more difficult to determine the long-term success of the fish culture; the middle panels of Figures 5 and 6 provide some indication that survival rates may be declining. However, fish survival rates fluctuate and it is impossible to know

whether the lower survivals in 1990 and 1991 broods portend things to come or are part of natural variation. Further, the estimates of survival rates before 1987 were not derived from coded wire tags (as are later survivals), so these periods may not be comparable.

The biological success of the programs is less obvious. If we accept the trends seen in southeast Alaska and southern Alaska Peninsula stocks as indicative of what would have happened in the absence of hatchery programs in PWS and Kodiak, then there appears to be little if any net production. As discussed earlier, pink salmon production in the other areas increased at the same time, and whereas pink salmon increased in PWS more than in two of the three control areas, the greater increase took place before the onset of large hatchery production.

This interpretation is supported by the increase in wild production in PWS that began in the early 1980s, only to have the wild production replaced by the hatchery production in the late 1980s and 1990s. This pattern of replacement in PWS can be interpreted as a classic example of the following concern stated by Brannon and Mathews (1988). "In the first place, rather than supplementing natural populations, hatchery production tended to replace natural production, with the result that naturally spawned fish no longer contributed effectively to the fishery. The net gain from hatchery propagation in this regard may have been very little." There is no evidence of replacement in the Kodiak area.

There are two independent items supporting the replacement theory for PWS. (1) The stocks in other areas without hatcheries increased at the same time, and (2) the wild stocks first increased in PWS, then as hatchery production increased, wild production declined.

These observations do not constitute "proof"; the other areas are not randomized controls, but rather "natural" controls with all of the possibilities of another covariate being responsible. Furthermore, the apparent replacement of wild fish by hatchery fish in the 1980s is based on an effective sample size of 1—that is, we only have one time series of data from hatchery and wild production in PWS.

Alternative Explanations for the Decline in PWS Wild Salmon

Why did the wild stocks decline after the 1985 brood year? There are four possible hypotheses, including harvesting, competition with wild fish,

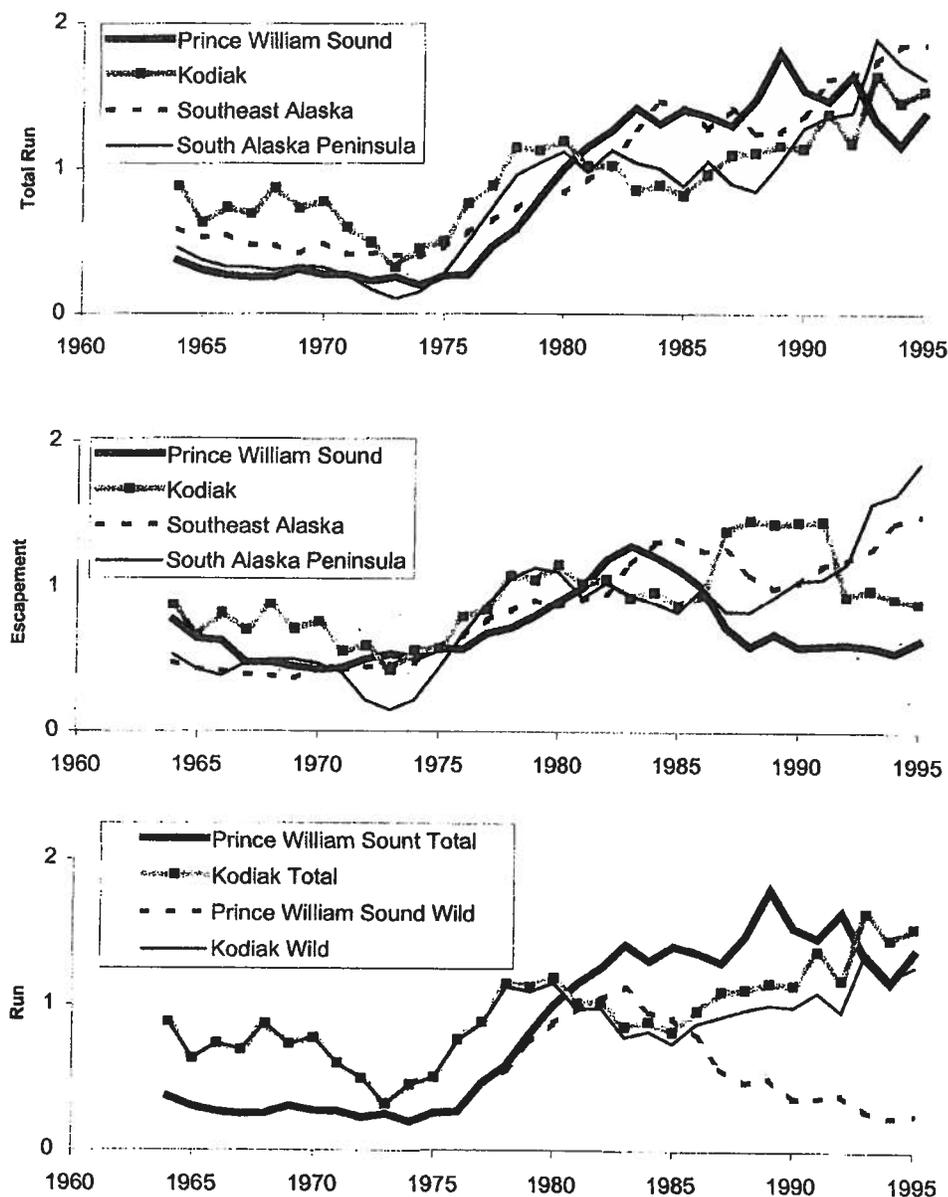


FIGURE 8.—Five-year running averages of run, escapement, and total run for the four pink salmon production areas in Alaska, scaled by the 1976–1985 average values for each area. (Top) Running average of total run (hatchery plus wild); (middle) running-average escapement; and (bottom) running averages of wild pink salmon run and total run including hatchery plus escapements (Prince William Sound and Kodiak areas only) divided by the average total run including hatchery for each area.

natural changes, and straying or genetic impacts of hatchery fish. We will deal with each of these in turn.

Impacts due to changes in escapement.—To examine the decline of the wild stocks in PWS we divided the data into two periods: (1) brood years

1977–1985, characterized by large returns after the rebuilding from the low runs of the 1960s and early 1970s, and (2) brood years 1986–1995, the recent period of low returns of wild fish.

The average wild return to PWS in the later period was 32% of the return in the first period,

TABLE 1.—Ratios of average run for 1986–1997 to averages for 1965–1975 and for 1976–1985, in four Alaskan pink salmon regions.

Base period	Region			
	Kodiak Island	Prince William Sound	Southeast Alaska	South Alaska Peninsula
1965–1975	1.90	5.74	3.54	5.93
1976–1985	1.13	1.43	1.55	1.37

whereas the escapement was 56% and the recruit per spawner was 57% of that during 1977–1985 (Table 2). Thus, we can conclude that part of the decline in wild stocks was due almost equally to a reduction in average escapement and a reduction in recruits per spawner. The escapement goal for PWS during both periods (brood years 1977–1995) was 1.8 million pink salmon; thus the average escapements in the 1977–1985 period were above the goal while the escapements from brood years 1986–1995 were slightly below the goal. Figure 9 shows the pattern, typical of net fisheries management, in which the actual wild-stock escapement during 1960–1985 and 1986–1995 in PWS increased with larger runs rather than the “ideal” of escapement holding constant regardless of run size. A strike by commercial fishing boat operators occurred in 1984, resulting in an escapement of 5.2 million fish, thus the data point for that year was not plotted. Two important conclusions can be drawn from Figure 9. First, the lower escapements in the later period appear to be due to the lower runs. Second, we see no difference in the escapement–return relationship between the two time periods. The analysis, at the PWS-wide scale, does not support a conclusion that the fishery was managed differently after large hatchery returns began.

It has been suggested that the presence of large hatchery runs led to higher exploitation and lower escapements. For instance, Geiger (1994) states “the entire 1992 wild run was needed for spawning escapement. Yet, for a variety of reasons related to the need to harvest the hatchery return, the har-

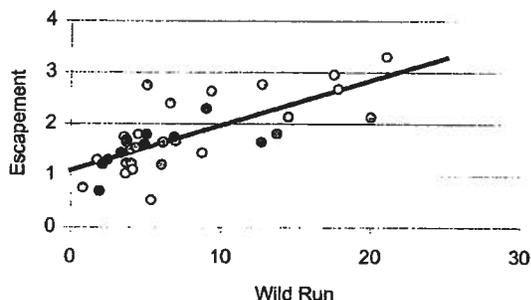


FIGURE 9.—Relationship between wild-stock escapement and total wild-stock return (both in millions of fish) in Prince William Sound for brood years 1960–1985 (gray dots; 1984 data excluded) and 1986–1995 (black dots).

vest rate on wild salmon was held to nearly the recent average.” The 1992 run is the lowest black dot in Figure 9 and may constitute a single instance of PWS-wide overharvest of wild stocks, but it is clearly not an indication of a systematic pattern of changed harvest policies in recent years.

However, when we look at the spatial pattern of escapements we see more evidence that the presence of hatchery fish led to a changed harvest pattern. The fishing districts in the north and west of PWS were heavily affected by the fishery for the hatchery stocks, whereas districts in eastern PWS were much less affected by these fisheries (Figure 10). The districts where the hatchery stocks passed have shown much stronger declines in escapement than the lightly affected districts.

The passage from Geiger (1994) above suggests that the economic pressure to exploit hatchery stocks in common-property fisheries was a major contributor to the reduced escapements in some parts of PWS, but overall we conclude that the reduced escapements after 1988 would have occurred regardless of the presence of large hatchery returns.

Impacts due to biological competition.—The lower escapement only explains part of the decline in wild stocks. There was also a reduction in the recruits per spawner in PWS to 57% of what it had

TABLE 2.—Data for Prince William Sound wild stocks, fry release, and common-property (CP) harvest rates for a period of high wild-stock runs (brood years 1977–1985) and low wild-stock runs (brood years 1986–1995).

Brood years	Average total wild return (millions)	Average brood year escapement (millions)	Average recruits per spawner	Average fry release (millions)	CP harvest rate
1977–1985	16.3	2.7	6.0	76	0.82
1986–1995	5.2	1.5	3.5	502	0.74

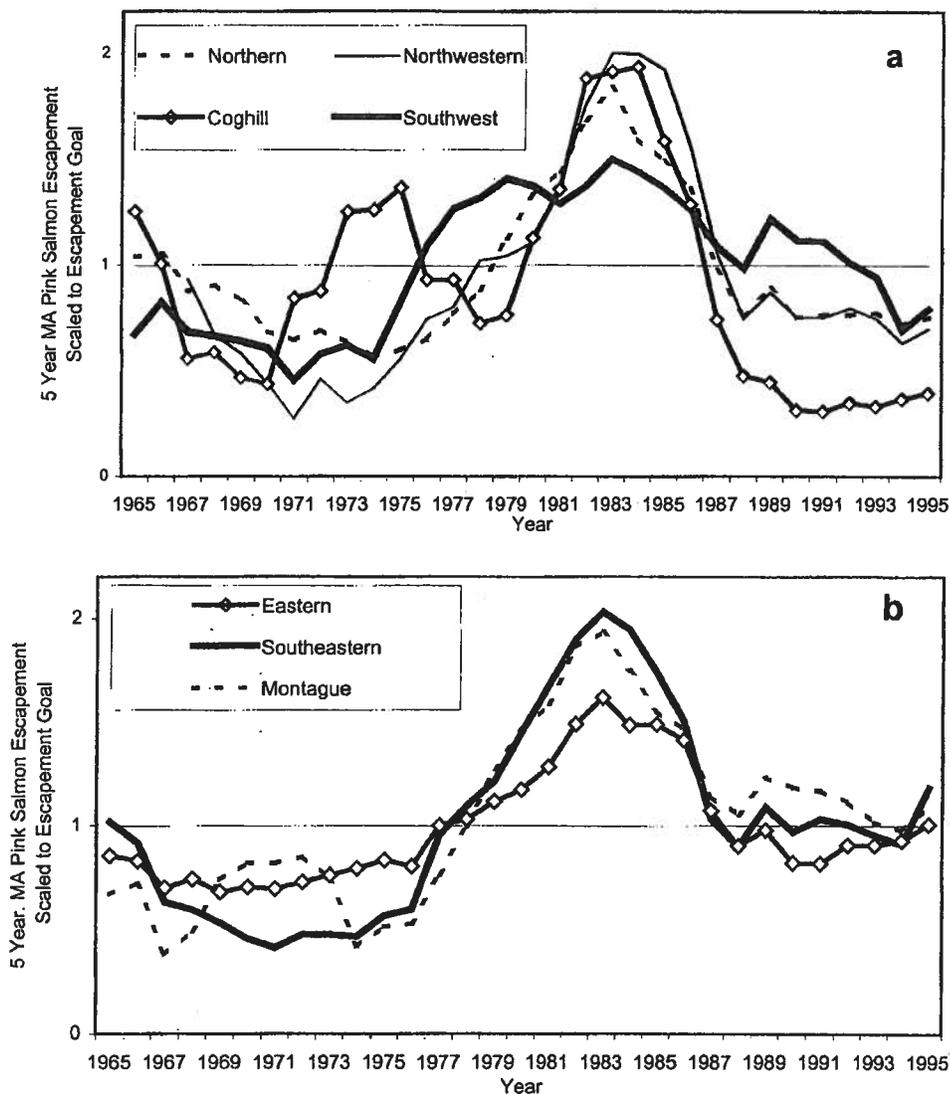


FIGURE 10.—Trends in escapement in different fishing districts within Prince William Sound (PWS). The 5-year moving average (MA) divided by the 1962–1997 average is plotted, which illustrates by contrast (a) four districts in the northwest and southwest of PWS that are strongly affected by hatchery production and (b) three fishing districts in the south and east that are less affected by the hatcheries.

TABLE 3.—Total return divided by escapement index for the four major regions producing pink salmon in Alaska.

Brood years	Region			
	Kodiak Island	Southeast Alaska	South Alaska Peninsula	Prince William Sound
1977–1985	2.32	1.98	2.37	6.03
1986–1995	2.39	2.46	3.03	3.47

been in the earlier period. The escapement numbers are more likely reliable as an index rather than as an unbiased count; therefore it is the change in the ratio of total return to escapement (Table 3), rather than the absolute level, that is of more interest.

In Kodiak Island, southeast Alaska, and the southern Alaska Peninsula, the return per spawner increased after 1985 while it decreased in PWS. A major difference between these regions is the

level of hatchery release in PWS and the close proximity of PWS hatcheries to the wild-stock production areas. In the Kodiak area, hatchery and wild stocks are physically separated, thus minimizing interaction and competition. Only PWS saw reduced recruits per spawner and only PWS had a large hatchery program during the more recent period.

Marine competition and freshwater genetic impacts by the hatchery stocks have both been hypothesized as mechanisms for hatchery impacts on survival of wild stocks. Sharp et al. (1994) documented high straying rates of coded-wire-tagged hatchery fish into wild streams in PWS, which suggests that this straying may lead to a decline in wild-stock productivity due to hybridization with hatchery strains. Using thermal marking of hatchery fish, T. Joyce and D. G. Evans (ADF&G, unpublished) confirmed very high rates of straying into streams near the hatcheries. Thus, if the hatchery stocks have poorer fitness when spawning in the wild, the intense straying by these fish is a plausible explanation for the decline in wild recruits per spawner.

In examining the impact of changes in both escapement and hatchery releases, we graphed the relationship between escapement and the natural logarithm of recruits per spawner in PWS (Figure 11, top). This is the traditional graph for fitting the Ricker curve to salmon data. The best-fit linear trend showed a decline in \log_e recruits per spawner as escapement increased, but the data were noisy.

We also graphed the relationship between wild recruits per spawner and the number of hatchery releases in the year the wild fish went to sea and presumably competed with the hatchery releases (Figure 11, bottom). Again we saw a downward trend, but the data were noisy with two outliers representing occurrences of high recruits per spawner in years of large hatchery releases. It happens that both of these outliers correspond to years of low escapement.

We fit a Ricker model treating smolt releases as an auxiliary variable (Hilborn and Walters 1992: equation 7.7.4), which we write as follows:

$$R_{y+2} = S_y \exp \left\{ \alpha \left[1 - \frac{S_y}{b} - c(H_{y+1} - \bar{H}) \right] \right\},$$

where R is the recruitment, S is the spawning stock, H is the number of smolts released from the hatchery system, \bar{H} is the average smolt release, $\exp(\alpha)$ is the recruits per spawner in the absence of density dependence, b is the value wherein recruits equals

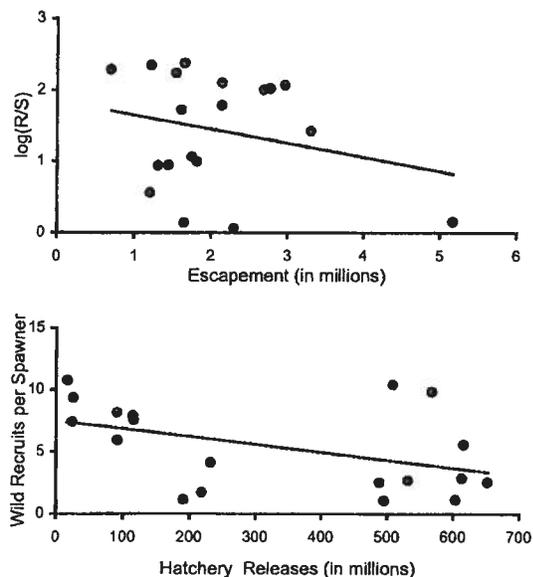


FIGURE 11.—(Top) Natural logarithm of recruits per spawner (R/S) for wild pink salmon in Prince William Sound plotted against escapement in the same brood year (for brood years 1977–1995). (Bottom) Wild recruits per spawner plotted against the hatchery release in the year the wild fish migrated to sea.

spawners, c is a parameter indicating the magnitude of the decrease in recruits due to smolt releases, and y is the calendar year.

Table 4 shows the results for five recruitment models. Our first model assumes that recruitment is constant with no effect of escapement or smolts. Next we fit the model above assuming no density dependence or hatchery effect; that is, b was set equal to a very large number and c was assumed to be 0. This second model assumes recruitment is proportional to escapement. The improvement in fit is highly significant ($P = 0.0087$), indicating that more spawners do produce more recruits (Figure 12, upper left). Values for P were calculated using a likelihood ratio test (Hilborn and Mangel 1997). Next we fit the normal Ricker model, which assumed $c = 0$ (Table 4, third model; Figure 12, upper right). The improvement in fit was indicated by $P = 0.16$ when compared with the proportional recruitment model. Then we fit a model with proportional recruitment and a hatchery effect; b was set equal to 10^{12} so there was no density dependence, and $P = 0.06$ (again compared with the proportional recruitment model; Table 4, fourth model; Figure 12, lower left). Finally we fit the full model with both density dependence and smolt effect. When compared with the proportional re-

TABLE 4.—Negative log likelihood and *P*-values for five models predicting pink salmon recruitment for the 1977–1995 brood years.

Model	df	Negative log likelihood	Model compared to	<i>P</i>
Constant recruitment	18	27.18		
Recruitment proportional to escapement	18	22.28	Constant recruitment	0.0018
Regular Ricker model	17	21.69	Proportional recruitment	0.28
Smolt impact only, no density dependence	17	20.31	Proportional recruitment	0.047
Both density dependence and smolt impact	16	17.18	Proportional recruitment	0.006

recruitment, $P = 0.006$ for this model (Figure 12, lower right). These statistics show that the best explanation for what happened to PWS wild pink salmon is a combination of changes in escapement and increasing hatchery releases. The *P*-level for the model with both effects is impressive, however hatchery releases were highly correlated with year, and the result could be due to any factor that changed with time in a similar fashion. Implications of these model fits are summarized in Figure 13: in the presence of larger smolt releases, expected recruitments are lower. The optimum escapement to maximize harvest of wild stock in the absence of smolt releases is 2.1 million.

We can now use this model to predict what

would have happened if no smolts had been released. Table 5 shows the wild escapement, wild recruits, and predicted recruits from the model just presented; “log residual” is the logarithm of observed recruitment divided by the predicted recruitment and is an estimate of the environmentally induced deviation in that year. Brood years 1990 and 1991 had very negative residuals whereas brood years 1989 and 1992 had very positive residuals. Scenario 1 (Table 5, column 6) shows what the run would have been using this model if the escapement had been 2.1 million each year and no smolts were released. Scenario 1 is unrealistic in that we have seen that managers do not control escapement to a fixed target. Scenario 2 (Table 5,

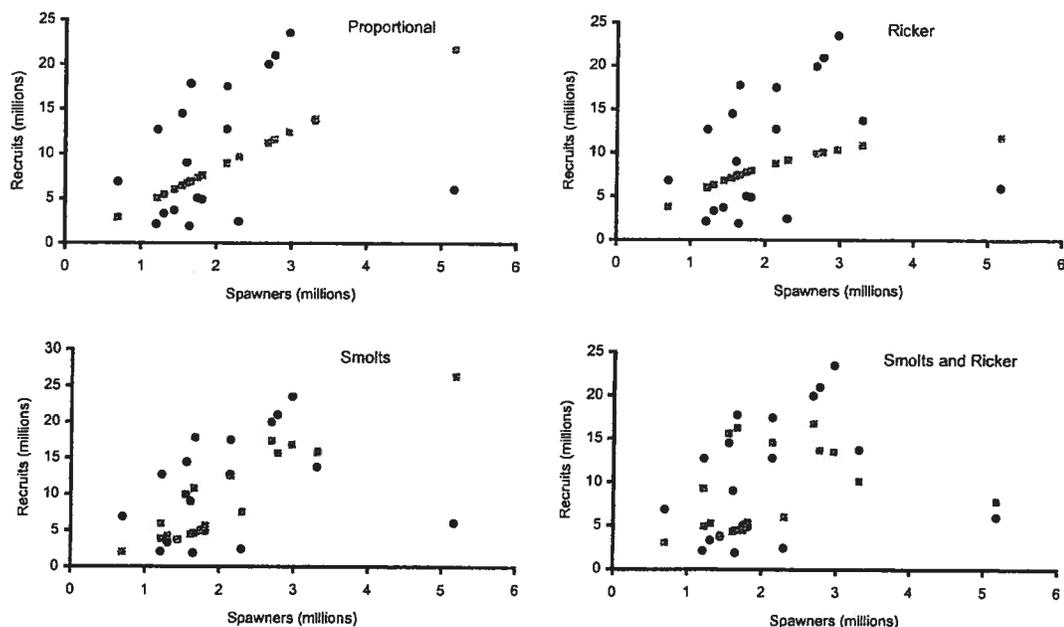


FIGURE 12.—Observed recruitment (circles) and predicted recruitment (squares) for four models (see Discussion, Table 4) of wild pink salmon recruitment in Prince William Sound from brood years 1977–1995.

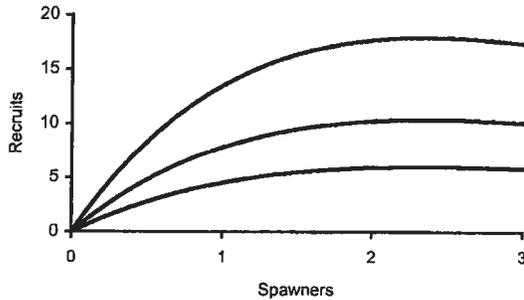


FIGURE 13.—Average expected wild-stock recruitment plotted against wild-stock escapement with releases of 0 (upper line), 250 million (middle line), and 500 million hatchery smolts (lower line).

column 7) shows what the run would have been using the actual escapements in the model and if no smolts were released. Scenario 2 is unrealistic also, because the anticipated higher wild returns without smolts would have led to higher realized escapements. The “predicted escapement” (Table 5, column 8) is what the escapement would have been if the solid line in Figure 9 had been used to predict the escapement based on the predicted total wild run under Scenario 3—what the total return

would have been if the simulated escapements had been used and no smolts were released (Table 5, last column). We believe this scenario is most realistic for the actual escapement.

With the averages for brood years 1986–1995, we would have expected 20.57, 17.52, and 19.05 million pink salmon returning under the three scenarios we just discussed. These expectations compare with an actual total return of 24.5 million during those years. Using our Scenario 3 we would thus estimate that the net increase due to hatchery production during this period was 5.5 million fish per year.

However, the other pink-salmon-producing areas all showed increased recruits per spawner in the later period, indicating better ocean conditions than during the earlier period. The average ratio of recruits per spawner in the later period to recruits per spawner in the former period for the other three areas is 1.18, indicating those areas saw an 18% average increase in recruits per spawner during brood years 1986–1995. The bottom row of Table 5 shows the predicted total returns allowing for an 18% increase in the later period. Thus our best estimate of the net production due to the

TABLE 5.—Predicted total returns in selected scenarios, all if no smolts were released. All numbers are millions.

Brood year	Wild escapement	Observed recruits	Predicted recruits	Log residual	Predicted run with:			Predicted run with simulated escapement (scenario 3)
					2.1 M escapement (scenario 1)	Actual escapement (scenario 2)	Simulated escapement using Figure 9	
1975								6.16
1976								4.32
1977	1.65	17.80	16.29	0.09	19.44	18.47	1.63	18.40
1978	1.54	14.48	15.64	-0.08	16.47	15.31	1.47	15.04
1979	2.68	19.99	16.85	0.17	21.10	21.08	2.70	21.06
1980	2.14	17.51	14.60	0.18	21.35	21.38	2.41	21.49
1981	2.13	12.74	14.57	-0.13	15.56	15.58	2.93	15.28
1982	2.96	23.54	13.55	0.55	30.91	30.29	2.97	30.26
1983	2.77	21.00	13.71	0.43	27.27	27.10	2.43	27.45
1984	5.17	6.05	7.88	-0.26	13.66	9.19	5.17	9.19
1985	3.30	13.74	10.13	0.30	24.13	22.82	3.49	22.28
1896	1.21	2.12	9.25	-1.47	4.08	3.42	1.89	4.01
1987	1.81	4.90	5.40	-0.10	16.14	15.72	3.04	15.70
1988	1.22	12.70	4.92	0.95	45.94	38.63	1.44	41.64
1989	1.61	9.00	4.36	0.73	36.78	34.66	2.46	37.01
1990	1.65	1.90	4.50	-0.86	7.51	7.13	4.73	5.56
1991	2.30	2.45	6.04	-0.90	7.21	7.26	4.33	5.80
1992	0.70	6.88	3.08	0.80	39.72	23.86	1.58	37.20
1993	1.31	3.34	5.31	-0.46	11.21	9.76	1.60	10.55
1994	1.75	5.04	4.48	0.12	20.00	19.32	4.34	16.03
1995	1.44	3.71	3.87	-0.04	17.07	15.48	2.01	16.97
1986–1995 average	1.50	5.20	5.12	-0.12	20.57	17.52	2.74	19.05
Average with 18% increase					24.27	20.68		22.48

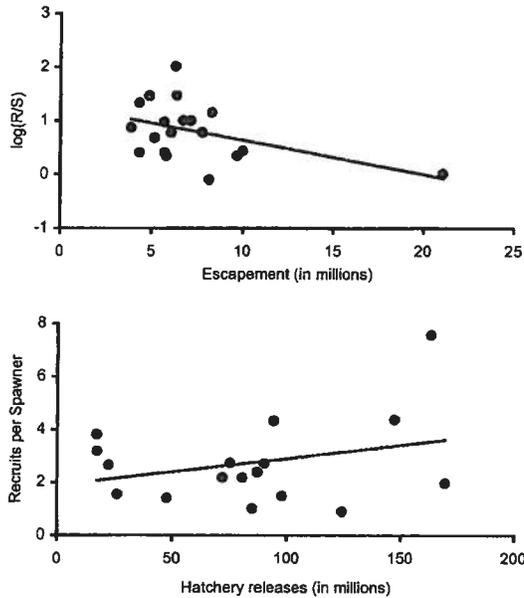


FIGURE 14.—(Top) Natural logarithm of recruits per spawner (R/S) for wild pink salmon in the Kodiak Island area plotted against escapement in the same brood year (for brood years 1977–1993). (Bottom) Wild recruits per spawner plotted against the hatchery release in the year the wild fish migrated to sea.

hatchery program (using Scenario 3) is 2 million pink salmon per year.

We repeated the same analysis for the Kodiak area, examining the relationship between $\log_e(R/S)$ and escapement and the relationship between recruits per spawner and hatchery releases (Figure 14). There was some evidence for density dependence, but only based on one year (1989) with a very high escapement, and no evidence that higher hatchery releases have led to fewer wild recruits per spawner.

We repeated the range of models for Kodiak that we had used for PWS. The proportional and smolt models (Figure 15, left top and bottom panels, respectively) did not provide an improvement in fit over the hypothesis that returns were constant, and only the Ricker model provided a significant improvement in fit, which was clearly due only to the one data point. We concluded there was no evidence that hatchery production affected wild production in the Kodiak area.

Decline in Wild Stocks in PWS was a Natural Change

This possibility cannot be eliminated. We know of no quantitative way to assess this probability because it depends on the degree to which the other areas serve as effective controls on ocean condi-

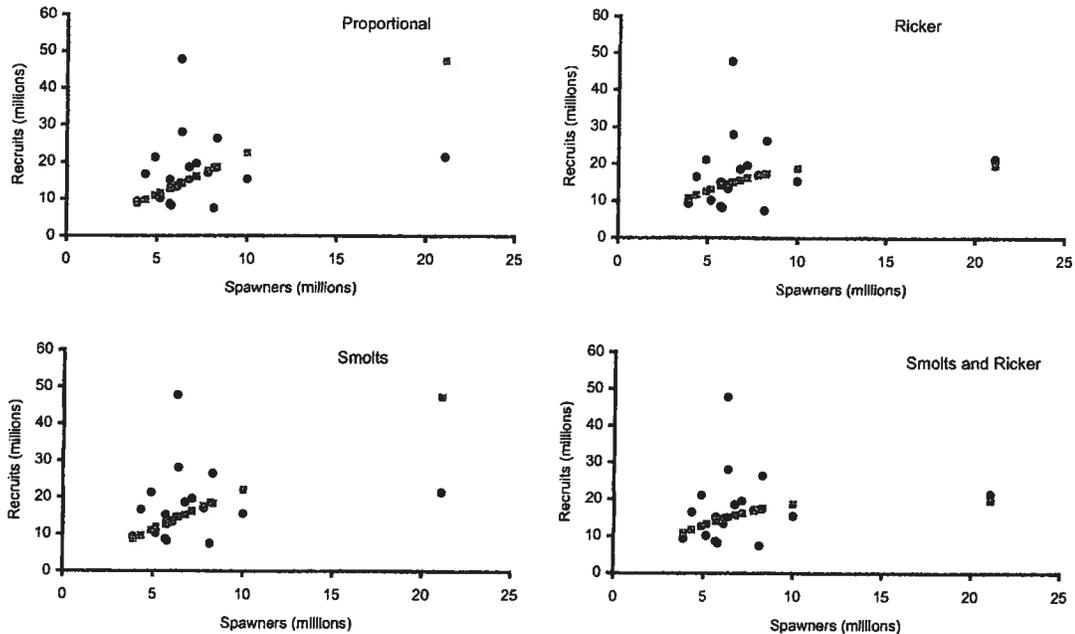


FIGURE 15.—Observed recruitment (circles) and predicted recruitment (squares) for four models of wild pink salmon recruitment in the Kodiak Island area for the 1977–1993 brood years.

tions and we accept that there is an unexplained factor that changed in the mid-1980s in PWS.

Earlier we discussed two plausible mechanisms for the hatchery impacts—genetic degradation due to straying and competition in the early life history. Smoker and Linley (1997) discussed these mechanisms and suggested they are unlikely given the short hatchery rearing period for pink salmon. Similarly, Smoker and Linley discounted the possibility of marine competition. Higher hatchery releases in PWS coincided with lower wild recruits per spawner, but it is possible that something in PWS changed starting in brood year 1986.

It is widely recognized that the *Exxon Valdez* oil spill in 1989 might have affected wild spawning pink salmon. There is disagreement regarding the amount of loss caused by the oil spill. Some investigators (Bue et al. 1996, 1998a; Geiger et al. 1996) estimated pink salmon damage ranged as high as 2% of the total wild return to PWS, whereas others (Brannon and Maki 1996) argued that even this loss was an artifact of the sampling regime and not a real effect. Thus none of the published work has suggested that the loss from the oil spill would even be detectable on a PWS-wide basis. The decline in wild recruits per spawner in PWS, illustrated in Figure 3, began well before the oil spill (beginning in the 1984 brood year); and brood years 1988 and 1989, most affected by the oil spill, had among the highest recruits per spawner in the period after 1986. Thus we found no evidence that the *Exxon Valdez* oil spill could account for the decline in recruits per spawner seen after 1986.

Smoker and Linley provided a defense of the PWS hatchery program, arguing that because escapements declined throughout PWS in the 1990s, it was a phenomenon unrelated to hatchery production. Their argument has a number of problems. First, the escapement clearly declined in the Southeastern District (Smoker and Linley 1997: Figure 1) from a high in the early 1980s, the same pattern as seen in PWS as a whole. We have shown that in areas where the wild stocks pass through the fisheries targeting on hatchery fish (Figure 10), escapement declined more than in areas less affected by the hatchery-oriented fisheries. Given our understanding of the relationship between escapement and total run (Figure 9), we conclude that the decline in escapement was due to the decline in the wild-stock run, which in turn was due to a decline in recruits per spawner, shown to be related to smolt releases.

Conclusions

The Prince William Sound and Kodiak Island pink salmon programs provide what may be the best opportunity to determine if mass production of juvenile fish can increase total fish production. The hatchery systems for chinook salmon, coho salmon, and steelhead *O. mykiss* throughout North America are so ubiquitous that it is difficult, if not impossible, to evaluate the impact of hatchery fish on wild production because there are few areas that can be considered to be controls. Further, escapement of chinook salmon and coho salmon are very difficult to monitor. In the PWS and Kodiak pink salmon fisheries we have the best possible situation: very large programs, which makes impacts more detectable, and areas of pink salmon production without large hatchery programs.

We suggest there was little if any increase in total abundance due to the hatchery program in PWS. Our best estimate is 2 million fish per year. The program was conceived in a period of low abundance of wild fish, but by the time large-scale hatchery production came on-line the wild production had increased. Hatchery production increased and wild production then declined. In contrast, abundance of wild stocks in the three other pink-salmon-producing areas of Alaska increased as much and stayed high while wild production in PWS declined. The Kodiak area appears to have experienced no impact of hatchery fish on wild production for three reasons. (1) The program there was smaller relative to the wild stocks; (2) the hatchery was physically isolated so there was little mixed-stock fishing on hatchery and wild fish, and there was little interaction by these fish during their early life history; and (3) the hatchery survival rates were much lower than in PWS, therefore the ratio of hatchery return to wild return was much lower.

This conclusion has wide consequences—because there are dozens, if not hundreds, of hatchery programs existing or planned—for many marine species around the world. Planners and operators of these programs rarely if ever consider negative impacts on wild production, and no marine hatchery program has any form of experimental design in place that could determine if the hatchery would replace wild production.

To our knowledge no one now argues that existing hatchery programs in the United States and Canada produce fish at a cost comparable with the value of the fish, but it is generally assumed by hatchery operators, politicians, and the public that

hatcheries augment total production. The lesson from PWS, however, is just the opposite: we should expect hatchery production to replace wild production rather than augment it whenever there is biological interaction and mixed-stock fishing. The PWS hatchery program for pink salmon provides by far the most dramatic evidence for this effect.

These conclusions apply to mass hatchery production where wild stocks are present. Obviously, if there are no wild stocks or if they are severely depleted at the onset of the hatchery program, the potential for the loss of wild-stock production is less. Also, these conclusions are not really relevant to various forms of supplementation hatcheries that use hatchery rearing as a short-term measure to rebuild wild production. There are many problems in evaluating supplementation hatcheries (Winton and Hilborn 1994), but we do not believe that the Prince William Sound or Kodiak Island hatchery programs are relevant models.

Acknowledgments

We thank Brian Bue, Brian Bigler, Claribel Coronado, Hal Geiger, Al Maki, Don Rogers, Jim Seeb, Bob Wilbur, John Winton, three anonymous reviewers, and numerous staff members of ADF&G for supplying data, discussion, and comments on the manuscript; R. Hilborn was supported in part by Exxon Corp.

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the affidavit of R. Peterman
sworn before me at Vancouver
this 2 day of May 2011
A Commissioner for taking Affidavits
for British Columbia

- from the coordination of capture and culture fisheries: the case of Prince William Sound pink salmon. *North American Journal of Fisheries Management* 14:262-277.
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COMMENTS

A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska: Response to Comment

Wertheimer et al. (2001) raise a number of issues regarding the analysis in our paper. There are two competing hypotheses that we test in our paper. The first hypothesis is that large hatchery programs such as the Prince William Sound (PWS) pink salmon hatcheries significantly increase the total production by augmenting wild production. The competing hypothesis is that in places where there are substantial wild stocks large hatchery programs primarily replace rather than augment wild production. We will refer to these hypotheses as augmentation and replacement.

PWS offers an excellent opportunity to test the augmentation and replacement hypotheses because there are before-and-after data and three other areas (Kodiak Island, Southeast Alaska, and the South Alaska Peninsula) with substantial wild production and no major hatchery programs. The data for these areas are given in Hilborn and Eggers (2000), but the major data for each area are Morstad et al. (1998) for Prince William Sound, Brennan et al. (2000) for Kodiak Island, ADFG (1997) for Southeast Alaska, and Campbell et al. (1998) for the South Alaska Peninsula. The major complicating factor in the data available is the regime shift in 1977 that caused production in all areas to rise.

If either hypothesis is correct, one should be able to see a strong signal; as the aphorism goes,

if you need statistics then there isn't a very big effect. Figure 1 shows the 5-year running average of total returns to the four systems. In this figure, area A is Prince William Sound, area B is Kodiak Island, area C is the South Alaska Peninsula, and area D is Southeast Alaska. We showed this graph to 18 individuals and asked them if it was obvious which of the four areas showed a major increase that was consistent with a large hatchery program adding to production; we then asked them to guess in which area and when the increase in production occurred. Only one respondent thought it was obvious and pointed to area A (which is PWS). Several others guessed area A having said it was not obvious. All who guessed area A pointed to the beginning of the increase (labeled "guess") as where they thought the hatchery program started increasing production. None identified the correct location in time. Because the augmentation hypothesis fails this simple test, it is not at all obvious where there was a large augmentation in natural production.

We then showed the same people Figure 2, which is the wild production, and asked each person if it was obvious where one of the areas saw a significant decline; the area designations are the same. All but one of those interviewed said it was obvious, and all pointed to area A (Prince William Sound) and correctly identified when hatchery pro-

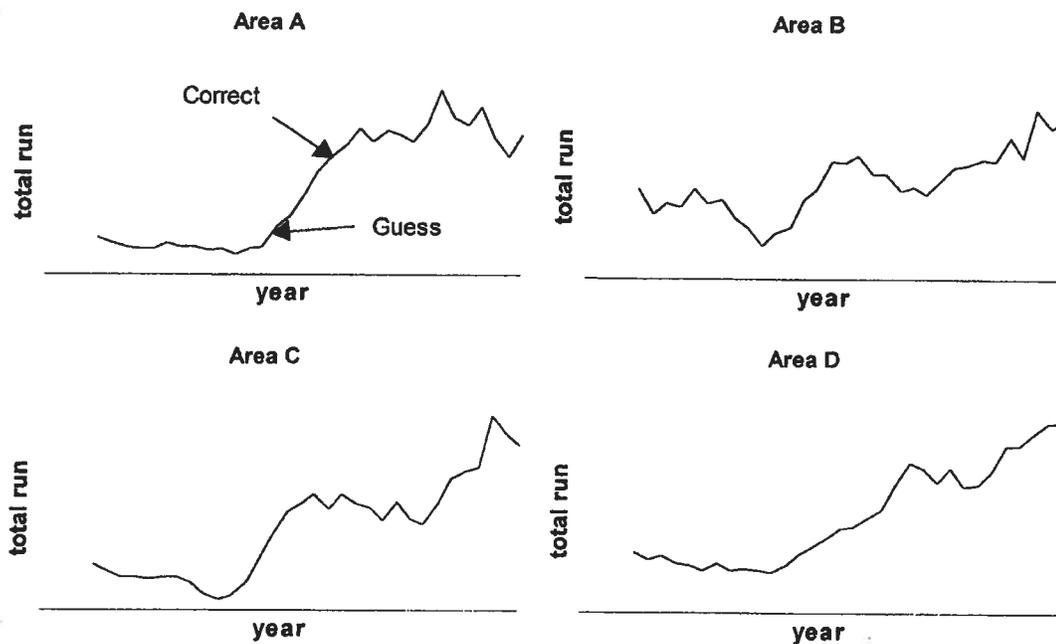


Figure 1.—Five-year running averages of total pink salmon returns in four Alaska areas. Area A = Prince William Sound, Area B = Kodiak Island, Area C = the South Alaska Peninsula, and Area D = Southeast Alaska.

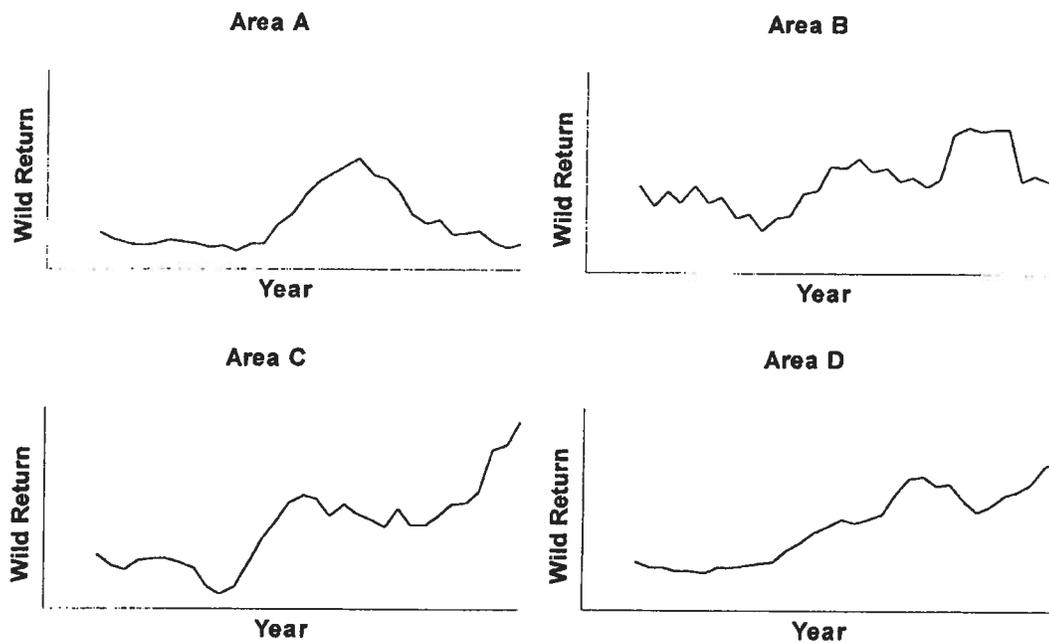


Figure 2.—Five-year running averages of wild stock returns in four Alaska areas.

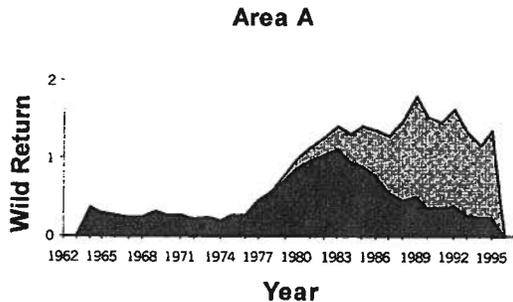


Figure 3.—Five-year running averages of total wild and hatchery returns to Prince William Sound. The more heavily shaded area represents wild returns, the lighter area hatchery returns.

duction became large. Because the replacement hypothesis passes the test, it is obvious where wild production declined.

Figure 3 shows the total return of pink salmon in PWS and the wild and hatchery components. This picture is the simplest, clearest way imaginable to show replacement rather than augmentation. The pattern is exactly what one would have predicted under the replacement hypothesis. However, because Wertheimer et al. raise a number of technical points, we will address them.

Proportionality

Wertheimer et al. argue that we have underestimated the increase in production due to hatcheries since the pink salmon in PWS have increased more from the previous peak production period in the 1930s and 1940s than the other three areas have. We do not dispute that the catch in PWS in the 1990s was proportionally higher (compared with that in the 1930s and 1940s) than in the other areas, but there are four fundamental flaws in their argument.

First, their argument requires that all areas were equally exploited in the the 1930s–1940s base period. During this period there were a number of constraints on harvest and processing that differed among areas. These included the length of the fishing season and the weekly closed periods. The base period of high PWS catches included substantial constraints imposed by World War II.

Second, their argument assumes that the productive potential for PWS did not change between the 1930s and the 1990s. In fact, pink salmon habitat was substantially altered by the 1964 earthquake. There were some direct negative impacts on the 1963 brood alevins in the streambed due to the exposure, shaking, and tsunamic effects. How-

ever, there were substantial new spawning areas created due to the general uplift of the PWS area (Noerenberg and Ossiander 1964). It is quite possible that the potential productivity of PWS is higher now relative to that of the other areas.

In addition, the pink salmon stocks during the base years assumed by Wertheimer et al. may have exhibited the effects of overfishing, and the catches observed were probably below the productive potential of the stock. During this time, the harvesting of salmon was constrained by market conditions, fishing seasons, and a mandatory weekly closed period that was 48 h in PWS and 36 h elsewhere. Fisheries were closed by regulation, generally before the runs were complete, and particularly so in PWS. Fishing was concentrated both by harvesting practices and by regulations on the early portions of the run. In Southeast Alaska, the pink salmon runs became progressively later and later in response to the selective fishing (Vaughan 1942, 1947; Alexandersdottir 1987). The increasing lateness of the run timing in Southeast Alaska was noticeable in the 1920s. In response to the declining early runs and intense lobbying by the Alaska canning industry cartel, fishing seasons were extended in Prince William Sound and in Southeast Alaska from the mid-1930s until the late 1940s (Cooley 1963). This action suggested a sequential overfishing, first on early portions of the run and then on later portions. The effects of this selective fishing on the early portions of the run were apparent in the observed timing at the Sashin Creek, Southeast Alaska, weir. The timing of the pink salmon run past the weir during the late-1940s was 2 to 3 weeks later than that observed in 1960s and 1970s (Heard 1978; Vallion et al. 1981). The number of eggs surviving to become migrating fry was inversely related to the entry timing of spawners (Skud 1958), suggesting a loss of population fitness due to selective fishing that would exacerbate the loss of production due to overfishing (Alexandersdottir 1987). By the 1950s the pink salmon runs in Prince William Sound, Southeast Alaska, and elsewhere were overfished and depleted. Although there are no direct observations on the effects of selective fishing on the early portion of the pink salmon run in PWS, the nature of the fisheries and management were comparable to those in Southeast Alaska. The effects of overfishing were very apparent in Prince William Sound with the extremely depleted pink salmon runs of the 1950s. The preseason run projections for PWS in 1952, 1954, and 1955 were so low that

the general fishing district was closed by regulation, effectively canceling the fishery.

Third, Wertheimer et al. ignore the fact that the high production of pink salmon in the 1990s that was built largely on hatchery fish was matched in the 1980s by wild production. The 1984 return of 23.5 million wild fish is larger than the average hatchery production of the 1990s. Wild returns in the early 1980s were growing rapidly while the hatchery program was in its infancy. There is every reason to believe that the production seen in the 1990s from hatcheries (with some wild contribution) could have been equaled by wild production alone because this level of production was nearly achieved in the mid-1980s.

Finally, while PWS total production declined in the 1990s, wild production in the other three areas has grown. This indicates that the wild runs of 20–24 million in 1983 and 1984 in PWS could have been even larger in the 1990s.

Pink Salmon Production Model

Wertheimer et al. argue that our quantitative model is not credible because of the high estimated value of recruits per spawner at very low densities. There are two flaws in their argument. First, the estimated spawning numbers in PWS are in fact an index, and the real number of spawners is certainly higher. Thus, the estimated recruits per spawner that Wertheimer et al. argue are not credible should be interpreted as relative recruits per spawner, not as absolute ones; thus, high values may indeed be credible.

Second, between 1977 and 1983 the PWS wild stock produced an average of 8.2 recruits per spawner with average spawning stock sizes of 2.1 million spawners, and this production was in the presence of growing but still small hatchery releases. While Wertheimer et al. focus on the technical details of our model, we are simply saying that if the high number of wild recruits per spawner had been maintained in PWS (as it has in the other pink salmon areas), then wild production alone in the 1990s would have been nearly equal to that attained in PWS by hatchery and wild fish during this period.

Escapement Declines

We find the arguments of Wertheimer et al. on this point almost totally irrelevant. When the wild stocks rebuilt in the late 1970s, escapements were well above the published escapement goal. The wild stocks produced extremely well at these escapements, and any analysis of spawner recruit

data would have indicated that higher escapement goals were appropriate. The only important question is what would have happened in the late 1980s and 1990s if wild stock returns had remained high. There are three hypotheses: (1) that escapement is largely a function of returns and escapements would have continued to be high; (2) that managers would have raised the escapement goals as large escapements consistently produced good returns; or (3) that managers would have ignored the data they had in hand and would have reduced escapement. We find it hard to believe that competent fisheries managers would have followed the third option.

Conclusions

The three technical issues that Wertheimer et al. raise are easily rebutted. There is no question that wild stock production had already increased prior to the large hatchery production and if that wild production had been maintained or even grown in the 1990s, as it did in the other three pink salmon areas, then PWS would now be producing strong wild runs without hatcheries. There is no question that the decline of wild production took place exactly at the time that hatchery production became significant. This pattern is exactly what would have been predicted by the replacement hypothesis. The PWS data, combined with the other three areas, provides strong evidence for the replacement hypothesis.

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This is Exhibit "G" referred to in
the affidavit of R. Peterman
sworn before me at Vancouver
this 2 day of May 20 11

Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does size matter?

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Key words: hatchery interactions, salmon ranching, stock enhancement

Abstract

Pink salmon (*Oncorhynchus gorbuscha*) returning to Prince William Sound (PWS), Alaska, have increased to historically high levels of abundance in recent years, but average body size at return has declined. We examined how body size at return of PWS pink salmon was related to 10 biophysical factors, including the scale of hatchery production. We also examined the effect of body size at return on productivity of wild pink salmon in PWS. For the 1975–1999 brood years, we found that an index of total abundance of pink salmon in the Gulf of Alaska and sea surface temperature during the year of return best explained the variation in pink salmon body size over time. Body size at return was significantly correlated with productivity of wild pink salmon. We used stepwise-regression to fit a generalized linear version of the Ricker spawner-recruit model to determine if body size would explain significant variation in wild-stock productivity in context with other environmental variation, including hatchery production. The results indicate that variability in wild-stock productivity is primarily driven by density-independent factors in the marine environment, but that body size of wild spawners also significantly affects productivity of wild PWS pink salmon. We conclude that the success of large-scale enhancement increasing the total run in PWS may have contributed to the decline in body size because of density-dependent growth in the Gulf of Alaska. We used a simulation model to estimate the impact of hatchery-induced changes in adult body size on wild-stock production in PWS. We estimated an annual wild-stock yield loss of 1.03 million pink

salmon, less than 5% of the annual hatchery return of 24.2 million adult pink salmon for brood years 1990–1999.

Introduction

Hatcheries have been used to create or maintain fisheries by mitigating for habitat degradation and circumventing factors identified as limiting production from a specific locale or region (Radonski and Loftus, 1995). Billions of Pacific salmon are now cultured and released into coastal ecosystems throughout the North Pacific (Mahnken et al., 1998). Some hatchery programs have been very successful in producing fish for harvest; for example, Japanese chum salmon (*Oncorhynchus keta*) hatcheries have produced annual returns of 40–87 million adults since 1990, exceeding historical production levels by more than an order of magnitude (Kaeriyama, 1989; Mayama and Ishida, 2003). As the scale of hatchery production has increased, however, concern for potential ecological effects on wild stocks has also increased (Hilborn, 1992; Meffe, 1992; Levin et al., 2001).

In Prince William Sound (PWS), Alaska, pink salmon (*O. gorbuscha*) have increased to historically high levels of abundance in recent decades (Wertheimer et al., 2001). Total pink salmon returns to PWS have averaged 31 million fish annually from 1990 to 2000 (Johnson et al., 2002).

Many of these fish have been produced from a system of four large hatcheries. The numbers of juveniles released by the hatcheries increased rapidly until the mid-1980s (Figure 1); 500–600 million juvenile pink salmon have been released annually since then (Johnson et al., 2002). Hatchery returns from these releases have averaged 25.3 million fish annually from 1990 to 2000 (Johnson et al., 2002), ostensibly providing large benefits to the region (Pinkerton, 1994; Smoker and Linley, 1997).

Concurrent with increasing hatchery production, however, the number of wild pink salmon returning to PWS has declined from record high levels for brood years 1977–1983 (Figure 1), and productivity (returns per spawner) of wild pink salmon has generally declined. The role of hatcheries in regard to the wild-stock decline is controversial. Hilborn and Eggers (2000) have attributed the decline in wild-stock abundance to interactions with hatchery production; they concluded that hatchery fish had largely replaced wild fish, and estimated a net annual benefit from hatcheries of only 2 million fish. Wertheimer et al. (2004), however, found that conditions in the marine environment, rather than number of hatchery

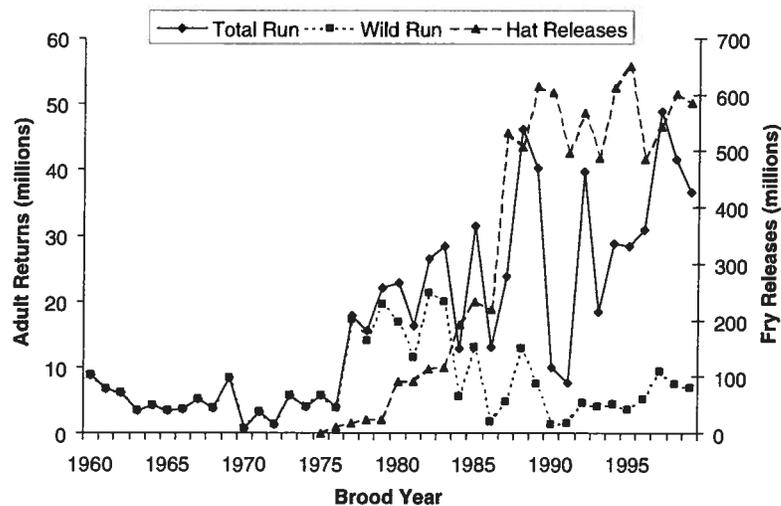


Figure 1. Total run, wild run, and hatchery releases of pink salmon in Prince William Sound, Alaska, 1960–2001.

juveniles released, best explained the variability in wild-stock productivity. They concluded that pink salmon productivity in PWS was driven primarily by density-independent marine conditions, and that the hatchery releases provided an annual net benefit of 20.6 million to 25.3 million pink salmon annually for the 1990–2000 returns.

None of the prior analyses investigating the interaction of large-scale enhancement and wild-stock productivity have considered the effect of body size at return. Abundance of Pacific salmon in the North Pacific Ocean has increased in recent decades, while body size of adult fish has generally decreased (Ishida et al., 1993; Bigler et al., 1996; Pyper and Peterman, 1999). Ricker (1995) noted that low adult growth rates and small body size of pink salmon have been associated with unusually high abundance in local regions. Bigler et al. (1996) found that the average body size of pink salmon in commercial fisheries throughout Alaska declined from 1970 to 1993, including PWS. Average body size of pink salmon in PWS has declined significantly since the inception of the hatchery program (Figure 2); average body size of adults at return from 1965 to 1975 was 1.86 kg, 26% larger than the 1.48 kg average for 1990–2000.

Our objectives in this paper are: (1) to use historical records of biophysical factors (including the scale of hatchery releases) to determine which of these factors significantly affect the body size at return of PWS pink salmon; (2) to examine the effect of body size of return on the productivity of PWS wild pink salmon in conjunction with the

scale of hatchery releases and other sources of environmental variation; and (3) to develop simulation models incorporating statistically significant factors to estimate the degree of impact of large-scale hatchery production on body size at return and wild-stock productivity.

Methods

Data sources

Productivity (returns per spawner) of wild pink salmon and body size at return of pink salmon in PWS, since the inception of the hatchery program (1975 brood) through the 1999 brood year, were evaluated in relation to parent body size and 10 measures or indexes of environmental conditions over time. The indexes reflect: (1) temperature experienced by pink salmon at different stages of their lives – a direct physiological determinant of growth and body size over the range of temperatures experienced by the salmon; (2) the abundance (density) of pink salmon – a putative depressor of growth, body size and survival; and (3) the aggregated effect of the biophysical environment on survival of pink salmon in the ocean, as indicated by the observed marine survival of hatchery releases. Variables used are listed in Table 1, and a short description of the parameters and the sources of the data are given below. Because pink salmon have an obligatory 2-year life cycle (Heard, 1991), returns (catch plus escapement) in a given year can be assigned entirely as the production from the brood

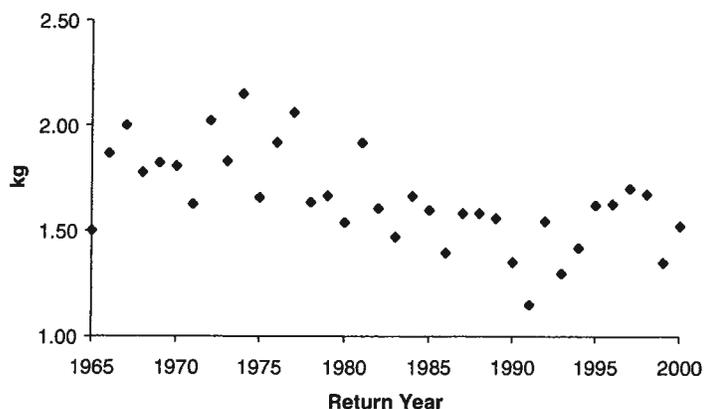


Figure 2. Average body size at return for pink salmon in Prince William Sound, Alaska, 1965–2000.

year 2 years prior to the return year. We identify the spawning or brood year as y , the year of entry into seawater of juvenile pink salmon as $y + 1$, and the year of return as $y + 2$.

Wild-stock spawners and returns by brood year

The numbers of wild-stock pink salmon harvested in PWS and spawning in PWS streams are estimated annually by the Alaska Department of Fish and Game (ADF&G). All commercial catches are reported to ADF&G; escapement estimates are based on weekly aerial surveys of 209 index streams. Data were available for the 1960–1999 brood years of pink salmon (Gray et al., 2002; Johnson et al., 2002).

Body size at return

Statistics on the average weight of pink salmon in the commercial fisheries in PWS are maintained by ADF&G (ADF&G, 2003). Average weight in the catch was used as the measure of adult body size (ParentSize, Table 1) of spawners for a given brood year y , and as the measure of body size at return of recruits in year $y + 2$ (Table 1, Table 3).

Table 1. Correlations of body size at return of pink salmon to Prince William Sound and productivity (returns per spawner) of wild pink salmon with 10 biophysical variables

Variable	Body size at return r	Productivity r
ParentSize	0.198	0.543**
SpringAir	0.032	0.318
GOASST-0	0.150	0.505**
GOASST-1	0.442**	0.144
PDO-0	-0.077	0.073
PDO-1	0.426**	-0.106
HatFry	-0.479*	-0.394
HatRun	-0.491**	0.034
GOARun	-0.589**	-0.100
MSI	0.013	0.602***

Time period encompassed 1977 through 2001 return years. Variables are described in Methods. The correlation coefficients, r , that were significantly different from zero are indicated by asterisks, where * indicates $0.05 < p < 0.1$, ** $0.01 < p < 0.05$, and *** $p < 0.01$. Critical values for the statistical significance of r for each correlation were adjusted to account for autocorrelation in the data series (Pyper and Peterman, 1998).

Spring air temperatures

Spring air temperatures (SpringAir, Table 1) in Cordova, Alaska, were used as an index of sea surface temperature (SST) conditions affecting initial marine rearing of juvenile pink salmon in PWS ($y + 1$). Air temperatures were used because a time series of SST observations for nearshore habitats in PWS extending prior to the 1990s was not available. Air temperatures in coastal areas have been shown to be related to the surface layer temperatures of nearby estuaries (Bruce et al., 1977), and have been used as a proxy for temperature regimes encountered by salmon (Adkison et al., 1996). Monthly average air temperatures for Cordova were retrieved from climate statistics summarized by the US National Weather Service, Alaska Region (www.wrcc.dri.edu/Summary/climsmak.html). Annual spring temperatures were computed as the average of the monthly averages for April, May, and June for a given year.

Gulf of Alaska summer SST

Summer sea surface temperatures in an area of the Gulf of Alaska (GOA) adjacent to PWS were used as an index of temperature conditions affecting PWS pink salmon: (1) in year $y + 1$ as juveniles after they migrated from PWS into the GOA (GOASST-0, Table 1); and (2) in year $y + 2$ as adults as they migrated from the GOA into PWS (GOASST-1, Table 1). Temperature records for the area lying between lat 58° N and lat 60° N, and long 146° E and long 149° E were extracted from the Comprehensive Ocean-Atmosphere Data Set (COADS; Mendelsohn and Roy, 1996) for 1976–1997 (affecting brood years 1975–1996) and from the Global Telecommunication System Data Base (www.pfeg.noaa.gov) for 1998–2000 (affecting brood years 1997–1999). Annual summer temperature was computed as the average of the temperatures recorded for July, August, and September in a given year.

Pacific Decadal Oscillation (PDO)

The PDO is an index of temperature changes in the north Pacific Ocean that has been related to basin-scale changes in the abundance and productivity of fishes in the north Pacific and GOA, including Pacific salmon (Mantua et al., 1997). Because the average PDO during winter is thought to be related to growth and survival conditions influencing sal-

mon populations in the subsequent spring and summer (Mantua et al., 1997), the annual PDO index was calculated as the average winter PDO. The average of the monthly averages for November of year y through March of the following year $y+1$ was used as a measure of basin-scale temperatures affecting juvenile pink salmon of brood year y in year $y+1$ (PDO-0, Table 1). The average of the monthly averages for November of year $y+1$ through March of the following year $y+2$ was used as a measure of basin-scale temperatures affecting juvenile pink salmon of brood year y in year $y+2$ (PDO-1, Table 1). Monthly PDO index values were extracted from data maintained by N. J. Mantua, University of Washington (<http://jisao.washington.edu/pdo/PDO.latest>).

Hatchery releases

The number of hatchery juveniles released into PWS in year $y+1$, where y is the brood year, was used as the measure of the impact of sea ranching (HatFry, Table 1). Hatchery fry could cause density-dependent interactions throughout the entire marine life history ($y+1$, $y+2$). Release numbers are from Johnson et al. (2002).

Hatchery returns

The number of hatchery fish returning in year $y+2$ (HatRun, Table 1) is an index of the density of hatchery fish in the marine environment during years $y+1$, $y+2$. Return numbers were from Johnson et al. (2002) and Gray et al. (2002).

GOA pink salmon abundance

The annual catch of pink salmon in fishing districts of Alaska adjacent to the GOA was used as an index of pink salmon abundance in the GOA (GOARun, Table 1) to examine potential density-dependent interactions (primarily in year $y+1$). Catch data were compiled from Byerly et al. (1999) and from ADF&G (2003).

Marine survival index

Average annual survival rates of hatchery juveniles released in PWS (Gray et al., 2002; Johnson et al., 2002) were used as an index of the marine survival conditions (MSI, Table 1) affecting wild-stock survival and productivity. The survival rate for a brood year y was computed by dividing the total hatchery return of pink salmon in year $y+2$ by the total number of hatchery pink salmon released as juveniles in year $y+1$.

Analytic approach

The association of wild-stock productivity and average body size at return to the biophysical factors in Table 1 was first examined by bivariate correlation. Wild-stock productivity was defined as $\text{Ln}(R_{y+2}/S_y)$, where R is the return, S is the spawning escapement, and y is the brood year. Time-series of data can be autocorrelated, which can affect the statistical evaluation of the correlation of two parameters. To account for autocorrelation, we adjusted the degrees of freedom for the hypothesis tests for significance of the correlation for each bivariate comparison using the methods recommended by Pyper and Peterman (1998).

We used a multiple linear regression model to determine which factors best explained the variability in body size at return:

$$\text{Size} = a + b_1X_1 + \dots + b_nX_n + \varepsilon_1 \quad (1)$$

where a is the intercept, b is the coefficient for variable X , and ε_1 is the residual error for the fit of Equation (1). The residuals of the final model were examined for significant autocorrelation or partial autocorrelation for time lags 1–6 years (Minitab, 2000).

We used the generalized linear version of the Ricker model (Quinn and Deriso, 1999) to determine which factors best explained the variability in wild-stock productivity:

$$\text{Ln}(R/S) = a + \beta S + \gamma_1X_1 + \dots + \gamma_nX_n + \varepsilon_2 \quad (2)$$

where a is the natural log of the Ricker productivity parameter α , β is the Ricker density-dependence parameter, γ is the coefficient for variable X , and ε_2 is the residual error for the fit of Equation (2).

We used forward–backward stepwise regression (Minitab, 2000) to identify significant variables in these models. A variable could enter a regression model at each step only if its coefficient was significantly different from zero at $p < 0.1$ (forward step); a variable already in the regression model would be dropped if its coefficient was not significantly different from zero at $p < 0.1$ after the addition of a new variable (backward step). The exception to this decision rule was that annual numbers of spawners, S , was kept in the regression model regardless of the p value for β , because it is

biologically appropriate for a spawner-and-recruit model. The Akaike Information Criterion (AIC) for multiple regression analysis (Gagne and Dayton, 2002), corrected for small sample size (Shono, 2000), and the coefficient of determination (R^2) were calculated at each step. The residuals of the final models were examined for significant autocorrelation or partial autocorrelation for time lags of one to six years (Minitab, 2000). The presence of significant autocorrelation in a regression model can affect the estimation of parameter coefficients and their statistical significance. No significant autocorrelation was detected for the residuals for either model, so no autocorrelative parameter was added to the models.

Simulation of hatchery effects

The models fit to Equations (1) and (2) were used to simulate the impact of hatchery production on body size at return and productivity of PWS wild-stock pink salmon. Hatchery releases or returns per se were not identified as significant parameters in either model. For Equation (1), however, GOARun and GOASST-1 were identified as significant. Because HatRun is a component of GOARun, we can simulate the annual effect on size at return in each year i in the absence of hatchery production by

$$\widehat{\text{Size}}_i = a + b_1(\text{GOARun}_i - \text{HatRun}_i) + b_2\text{GOASST-1} + \varepsilon_{1i} \quad (3)$$

where b_1 and b_2 are the coefficients estimated for GOARun and GOASST-1 by Equation (1), and ε_{1i} are the residuals from Equation (1). In turn, parent body size was identified as a significant parameter affecting wild-stock productivity. We can use the results from Equation (3) to simulate the annual effect of parent body size on the productivity of brood year y by

$$\widehat{\text{Ln}}(R_{y+2}/S_y) = a + \beta S_y + \gamma_1 \text{MSI}_y + \gamma_2 \text{ParentSize}_y + \varepsilon_{2y} \quad (4)$$

using the estimated average annual body size from Equation (3) for parent body size rather than the observed parent body size, and the parameter coefficients and residuals as estimated by Equation (2).

Confidence intervals for the point estimates from Equations (3) and (4) were generated by non-parametric bootstrapping of residuals from the regression models (Efron and Tibshirani, 1993). For body size at return, body size for each year for return years 1977–2001 were estimated by Equation (3), with ε_1 for each year of return selected randomly from the vector of residuals for all years from the model fit to Equation (1). This process was repeated 1000 times. Average values of body size for each of the 1000 permutations were computed, and the lowest and highest 50 values were truncated to identify the bootstrap 95% confidence interval. Similarly, bootstrap $\text{Ln}(R/S)$ values were estimated from Equation (4), using body size estimates from the bootstrap permutations of Equation (3), and adding ε_2 for each brood year selected randomly with replacement from the vector of residuals for all years from Equation (2). This process was also repeated 1000 times.

Results

Factors affecting body size

Five of the ten variables tested were significantly correlated with body size at return (Table 1). The two measures of temperature conditions affecting the adult ocean period, GOASST-1 and PDO-1, were positively associated with body size, while measures of temperature conditions affecting the juvenile marine period were not significantly correlated with body size. The three measures of pink salmon abundance, HatFry, HatRun, and GOARun, were negatively associated with body size at return. The correlation coefficient was greater for GOARun ($r = -0.589$), a basin-scale measure index of pink salmon density, than for HatFry or HatRun ($r = -0.479$ and -0.491 , respectively), which are more indicative of regional, PWS-scale pink salmon density (Table 1).

There was substantial cross-correlation among the variables identified as significantly associated with body size at return (Table 2). The three measures of pink salmon abundance that were significantly correlated and negatively correlated with adult body size were themselves significantly and positively correlated: larger hatchery releases (HatFry) were positively correlated with larger hatchery runs (HatRun), which were positively

Table 2. Cross-correlation matrix for variables with significant correlation ($p < 0.1$) with either body size at return or wild-stock productivity of Prince William Sound pink salmon (Table 1)

	GOASST-0	GOASST-1	PDO-1	HatFry	HatRun	GOARun	MSI
GOASST-0	–						
GOASST-1	.096	–					
PDO-1	.083	.277	–				
HatFry	–.210	–.190	–.477 **	–			
HatRun	–.001	–.230	–.436 **	.821 **	–		
GOARun	.093	–.260	–.459 **	.692 **	.689 **	–	
MSI	.120	–.128	.120	–.150	.282	.074	–
ParentSize	.279	.144	–.043	–.500 *	–.196	–.427 *	.126

The correlation coefficients, r , that were significantly different from zero are indicated by asterisks, where * indicates $0.05 < p < 0.1$, ** $0.01 < p < 0.05$, and *** $p < 0.01$. Critical values for the statistical significance of r for each correlation were adjusted to account for autocorrelation in the data series (Pyper and Peterman, 1998).

correlated with greater abundance of pink salmon in the Gulf of Alaska (GOARun). The PDO-1 was negatively and significantly correlated with these three measures of pink salmon abundance (Table 2). This inverse relationship of the PDO-1 to pink salmon abundance reflects the declining trend for the PDO over this time series ($r = -0.340$), a period during which hatchery releases and adult pink salmon abundance were generally increasing (Figure 1).

The stepwise regression fit for the linear model for body size at return (Equation (1)) identified two variables as explaining statistically significant variability in body size at return: GOARun and GOASST-1 (Table 3). The GOARun index was the first variable to enter the model and explained 31.9% of the variation in body size at return. The addition of GOASST-1 increased the R^2 to 38.5%. With these parameters in the model, no other variable of the 10 considered could be added at the $p = 0.1$ significance criterion. The AIC declined from Step 1 to Step 2, also indicating that the addition of the second parameter improved the model without decreasing information content.

Body size and productivity

Three of the 10 variables tested were significantly correlated with wild-stock productivity ($\ln(R/S)$), including ParentSize (Table 1). All of these variables were positively associated with wild-stock productivity: MSI ($r = 0.602$), the index of hatchery marine survivals; ParentSize ($r = 0.543$); and GOASST-0 ($r = 0.505$), an index of regional-

scale summer temperatures during juvenile ocean residency. The number of hatchery fry released, HatFry, was negatively associated with wild-stock productivity ($r = -0.394$), but the correlation coefficient was not significantly different from zero.

There was limited cross-correlation among the variables identified as significantly associated with wild-stock productivity. ParentSize was inversely and significantly correlated with HatFry and GOARun (Table 2), demonstrative of the same trends identified for body size at return. The correlation of MSI with HatFry was negative, but not significant ($r = -0.150$, $p > 0.5$), indicating that MSI was generally independent of the density of hatchery fry in PWS.

Table 3. Results of forward-backward stepwise regression fit of a multiple linear regression model for body size at return and associated biophysical variables for Prince William Sound pink salmon, brood years 1975–1999 (Equation (1), Methods)

Variable	Step 1	Step 2
Constant	4.07 (< 0.001)	1.82 (< 0.001)
GOARun	$-7.7 \times E^{-9}$ (0.002)	$-6.7 \times E^{-9}$ (0.006)
GOASST-1		0.18 (0.075)
R^2 (adjusted)	31.9	38.5
AIC_c	23.13	22.05

The regression coefficients, the associated probability, p , that a coefficient is significantly different from zero, adjusted R^2 (the coefficient of determination adjusted for degrees of freedom), and the Akaike Information Criterion corrected for small sample size (AIC_c) are shown for each step of the regression.

The stepwise regression fit of the generalized linear Ricker model (Equation (2)) identified four variables as explaining statistically significant variability in wild-stock $\ln(R/S)$: MSI, ParentSize, GOASST-0, and the index number of spawners (Table 4). Because the spawner index was arbitrarily kept in the model, this variable entered the model at the first step, although it was not statistically significant ($p = 0.261$) as the only predictive variable. When MSI entered the model at step 2, the adjusted R^2 increased from 1.4% to 43.5% (Table 4). ParentSize increased the R^2 to 64.0% and GOASST-0 to 69.2%. With these parameters in the model, no other variable of the ten considered could be added at the $P = 0.1$ significance criterion. The AIC declined for each step of the model, indicating that the addition of each parameter increased the amount of variability explained by the model without decreasing information content.

Impact of the hatchery program on body size and productivity

Estimates from Equation (3) of predicted body size at return in the absence of hatchery production are shown in Figure 3a. As hatchery runs increased, the predicted body size diverged positively from the observed body size. The predicted average body size at return from brood years 1990–1999 (return years 1992–2001) was 1.61 kg, 5% larger than the observed body size of 1.53 kg (Table 5). The bootstrap-predicted average for these years, 1.56 kg, was biased low relative to the determin-

istic point estimate. The bootstrap 95% confidence interval was 1.50–1.64 kg, which overlaps the observed body size; thus, the predicted hatchery effect on average body size was not significantly different from zero.

The effect of predicted body size changes in the absence of PWS hatchery fish on the productivity of wild fish over time is shown in Figure 3b. As the predicted body size effects become more pronounced, the predicted productivity from wild PWS pink salmon diverged positively from the observed. The predicted average $\ln(R/S)$ in the absence of hatchery fish from Equation (4) for brood years 1990–1999 was 1.26, 11% higher than the observed of 1.14 (Table 5). The bootstrap-predicted average of $\ln(R/S)$ was 1.39, biased high relative to the deterministic point estimate of 1.26. The bootstrap 95% confidence interval was 1.19–1.62 kg, and did not overlap the average observed productivity of 1.14; thus, the predicted body size effect on productivity was significantly different from zero. The exponents of the productivity values were calculated to estimate R/S , and applied to the average escapements for the 1990–1999 brood years to estimate average number of wild-stock returns at the different productivity levels (Table 5). The predicted average for Equation (4) were corrected for back-transformation bias by adding the variance divided by 2 before taking the exponent (Hilborn and Walters, 1992). The difference between the estimated wild-stock returns at observed and predicted productivities are estimates of yield loss from wild-stocks due to the hatchery production. We estimated a

Table 4. Results of forward-backward stepwise regression fit of the generalized linear version of the Ricker model for productivity ($\ln(R/S)$) to spawner/recruit data and associated biophysical variables for Prince William Sound wild-stock pink salmon, brood years 1975–1999

Variable	Step 1	Step 2	Step 3	Step 4
Constant	1.93 (<0.001)	0.97 (<0.014)	-1.74 (0.039)	-4.86 (<0.001)
Spawners	$-2.5 \times E^{-7}$ (0.261)	$-3.7 \times E^{-7}$ (0.034)	$-3.4 \times E^{-7}$ (0.017)	$-2.7 \times E^{-7}$ (0.057)
MSI		23.8 (<0.001)	21.6 (<0.001)	20.3 (<0.001)
Parent size			0.80 (0.001)	0.68 (0.004)
GOASST-0				0.29 (0.046)
R^2 (adjusted)	1.4	43.5	64.0	69.2
AIC _c	63.77	51.31	41.72	39.78

The regression coefficients, the associated probability, p , that a coefficient is significantly different from zero, adjusted R^2 (the coefficient of determination adjusted for degrees of freedom), and the Akaike Information Criterion corrected for small sample size (AIC_c) are shown for each step of the regression. Spawners were always included in the model; other variables could enter or remain in the model if $p < 0.1$.

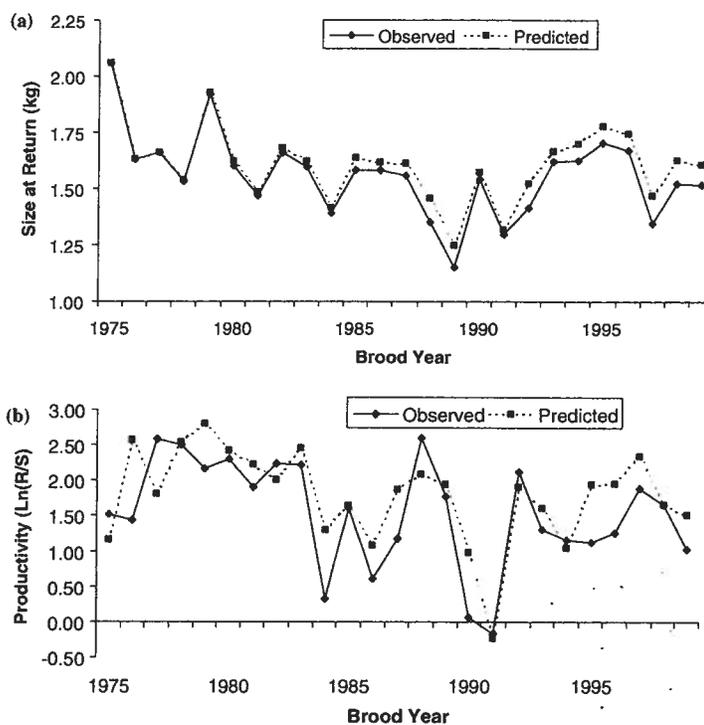


Figure 3. Observed and predicted body size at return (a) and wild-stock productivity (b) for 1975–1999 brood year pink salmon in Prince William Sound, Alaska. Predicted values are estimates from simulations of the effect of hatchery production of pink salmon.

wild-stock yield loss of 1.03 million fish, with a 95% confidence interval based on the bootstrap estimates of 0.21–2.70 million fish. The asymmet-

rical confidence interval is a result of the transformation from $\ln(R/S)$ to R/S for the bootstrap values.

Table 5. Observed and simulated averages for brood years 1990–1999 for body size at return and wild-stock productivity $\ln(R/S)$, where R is the recruits from spawners, S , of Prince William Sound pink salmon

	Observed	Simulations			
		Point estimates	Bootstrap average	Bootstrap 95% CI	
				Lower	Upper
Size at return (kg)	1.53	1.61	1.56	1.50	1.64
$\ln(R/S)$	1.14	1.26	1.39	1.19	1.62
R/S	3.14	3.86 ^a	4.03	3.28	5.04
Predicted average Wild-stock return (millions of fish)	4.45	5.48	5.72	4.66	7.15
Yield loss (millions of fish)	–	1.03	1.27	0.21	2.70

^aCorrected for back-transformation bias from log-transformed equation (Hilborn and Walters, 1992).

Point estimates and bootstrap predictions of body size and $\ln(R/S)$ in the absence of hatchery fish were derived from Equations (3) and (4) in the Methods. Yield loss is the difference between observed and simulated (absence of hatcheries) wild-stock productivity at average annual escapements of 1.42 million fish for the 1990–1999 brood years.

Discussion

The relationships between body size at return of PWS pink salmon with the index of abundance of pink salmon in the Gulf of Alaska and sea-surface temperature conditions during their last year at sea indicate that body size is significantly affected by the density of pink salmon in the Gulf of Alaska, and by environmental conditions during their adult growing season. These results are consistent with the paradigm that growth of salmon during their ocean life history is density-dependent and is affected by both regional and basin-scale abundance of conspecifics (Ishida et al., 1993; Ricker, 1995; Bigler et al., 1996; Pyper and Peterman, 1999).

Hatchery releases did not explain significant variation in body size at return when considered in the context of other biophysical factors such as the abundance of pink salmon in the Gulf of Alaska, although body size at return was significantly and inversely correlated with hatchery releases of pink salmon in a bivariate comparison. Hatchery releases were also significantly and positively correlated with the Gulf of Alaska abundance index. Because catches from PWS hatcheries comprised 24% of this index, we infer that hatchery production, by directly and substantially contributing to broad-scale pink salmon abundance, does affect body size at return.

We also found that parent body size explained a significant portion of the variation in wild-stock productivity of PWS pink salmon in the model relating productivity to biophysical factors. Both egg size and fecundity are positively correlated with body size in pink salmon (e.g., Foerster and Pritchard, 1941; Godfrey, 1959; Malecha, 2002). At a given escapement level, changes in fecundity directly affect the number of eggs transported into the spawning habitat (Forbes and Peterman, 1994). Smaller eggs result in smaller fry, which may have lower survival to adult (Bams, 1970; Parker, 1971). Because of these relationships, reductions in body size have been intuitively linked with reduced reproductive potential in salmon (Heard, 1991; Bigler et al., 1996; Cooney and Brodeur, 1998; Pyper and Peterman, 1999). Helle (1989) found that, for chum salmon in Olsen Creek in PWS, the larger the mean body size of spawners, the higher the survival to adulthood of their progeny. To our knowledge, our analysis is the

first time a direct association has been detected between body size and productivity of a pink salmon population.

While both egg size and fecundity are linked to body size, Malecha (2002) found that the relationship between an individual female's body size and egg size or fecundity was non-linear in a stock of pink salmon at the tails of the adult female size distribution. In the middle of the size distribution, egg size and fecundity changed linearly with body size, but within the lower end of the body size range, egg size was conserved and fecundity declined more rapidly with decreasing size. Because general decline in average body size will result in more fish returning in the size ranges at which egg size is conserved, the effects of decreasing egg size on productivity will diminish as fish become smaller, and the effect from reduced fecundity will increase. From a management perspective, the impact of reduced fecundity on potential egg deposition in a spawning stream could be mitigated by modifying annual escapement goals in response to inseason measures of body size at return.

We found that, while body size was a significant parameter affecting wild-stock productivity, density-independent conditions in the marine environment represented by the index of marine survival of hatchery fish and SST during the juvenile marine phase determined most of the variability in wild-stock productivity. The small and non-significant correlation of hatchery fry releases with hatchery survivals indicated that marine survival conditions were generally independent of the density of hatchery fry in PWS. The significant relationships of hatchery survivals with wild stock productivity indicated that hatchery and wild fish respond similarly to marine conditions. Coronado and Hilborn (1998a) also found that the marine survival trends were generally similar for hatchery and wild coho salmon (*O. kisutch*) within a geographic area, and Kovtun (2000) found a similar relationship for hatchery and wild chum salmon from the Tym River in Sakhalin, Russia. Boldt and Haldorson (2004) found that, while energy content of juvenile pink salmon in PWS varied by location, hatchery and wild juveniles were similar in energy content when captured at the same location.

Density-dependent marine growth and size at return and density-independent survival have also been observed for Japanese hatchery chum salmon (Kaeriyama, 1989; Mayama and Ishida, 2003). In

contrast to the evidence for density-dependent effects on adult size of salmon, evidence for density-dependent effects on survival is scarce (Brodeur et al., 2003; Ruggerone et al., 2003). However, Levin et al. (2001) concluded that density-dependent marine effects caused by large hatchery releases of 'spring/summer' Chinook salmon into the Columbia River basin reduced the marine survival of wild 'spring/summer' Chinook salmon stock in the Snake River, a tributary of the Columbia River; and Ruggerone et al. (2003) concluded that growth and survival of Bristol Bay sockeye salmon were reduced by density-dependent interactions with Asian pink salmon during their marine residency.

The association of productivity of PWS pink salmon with regional-scale rather than basin-scale temperatures (e.g., PDO) during the first year at sea is consistent with findings for pink, chum, and sockeye (*O. nerka*) salmon (Pyper et al., 2001; Mueter et al., 2002). Regional coherence in survival rates has also been observed for coho and Chinook (*O. tshawytscha*) salmon (Coronado and Hilborn, 1998a, b). Regional scale differences due to environmental variability, rather than the scale of hatchery production, is likely the primary reason for the differing trends in abundance and productivity of pink salmon that have been noted among different regions of Alaska (Hilborn and Eggers, 2000, 2001; Wertheimer et al., 2001, 2004).

Marine competition and freshwater genetic impacts have been proposed as possible mechanisms for hatchery impacts on the survival of wild pink salmon in PWS (Thomas and Mathisen, 1993; Hilborn and Eggers, 2000). The potential for ecological and genetic interactions of PWS pink salmon is well documented. Willette et al. (1999) found that growth of juvenile salmon in PWS was limited when juvenile densities were high. Reduced growth rates of juvenile pink salmon can directly affect survival (Parker, 1971; Mortensen et al., 2000; Willette et al., 2001). Also, Joyce and Evans (2002) have observed high rates of straying of hatchery adults into streams near the hatcheries in PWS, which could lead to negative genetic effects (Hindar et al., 1991; Busack and Currens, 1995).

Despite the potential for direct impacts on wild pink salmon, we did not find that the hatchery fry releases were significantly related to wild-stock productivity. In contrast, Hilborn and Eggers

(2000) found that hatchery fry releases were a significant parameter in their Ricker stock-recruit model. However, these authors did not consider other sources of environmental variation affecting PWS pink salmon, and thus fry releases were a proxy for other, more significant parameters such as the marine survival index and parent body size. In a previous analysis (Wertheimer et al., 2004), we also reported significant relationships between hatchery fry releases and wild-stock productivity for data for the 1975–1998 brood years, one of three time series of data we examined in that paper. However, we did not correct the significance test of the bivariate correlation for autocorrelation, and we did not consider the effect of parent body size in the spawner-recruit model for this time period. When parent body size was included in the stock-recruit model for this time period, hatchery fry releases no longer explained significant additional variation in productivity. We note that the bivariate correlations between fry releases and both wild-stock productivity and hatchery marine survival are negative (albeit not statistically significant), and thus we do not completely dismiss the possibility of density-dependent competition affecting survival. But we conclude that such impacts are small relative to the other parameters we have identified as significantly affecting wild-stock productivity.

Even though we found no direct effect of hatchery releases on wild-stock productivity, the impact of hatchery releases on body size at return represents an indirect effect because of the influence of parent body size on wild-stock productivity. This impact is contingent on the degree to which hatchery fish enhance, rather than replace, wild fish. Because our analyses indicate that productivity is largely driven by density-independent conditions in the marine environment, we attribute an incremental contribution to density-related body size changes in PWS pink salmon to the scale of hatchery production in PWS.

Based on these linkages between hatchery production, body size, and wild-stock productivity, we estimated that decreased adult body size due to hatchery production reduced yield of wild fish in PWS at 1.03 million fish annually, with a 95% confidence interval of 0.21 to 2.7 million, for brood years 1990–1999. This represents less than 5% of the average annual hatchery returns from these brood years of 24.2 million adult pink sal-

mon (Johnson et al., 2002). The resultant estimated net gain from hatchery production is 23.2 million fish, with a 95% confidence interval of 21.5 to 24.0 million.

The confidence intervals for our estimates accounted for process error in the underlying regression models. We did not, however, consider the effect of measurement errors in the data. The presence of substantial measurement error can obscure relationships among variables (Quinn and Deriso, 1999), but have not typically been considered when relating variation in size or productivity of salmon to environmental variation (e.g., Bigler et al., 1996; Pyper and Peterman, 1999; Pyper et al., 2001; Levin et al., 2001; Mueter et al., 2002; Ruggerone et al., 2003). Accounting for measurement error was outside the scope of this paper. Our objectives were to examine the relationship of indexes of size and wild stock productivity to a wide suite of environmental parameters or indexes, including the number of hatchery fry released, using modeling approaches similar to Hilborn & Eggers (2000) and Wertheimer et al. (2004); these authors also did not incorporate measurement error into their stock-recruit models.

Quantitative assessments of the impacts of sea ranching programs are essential to determine if programs are worth the economic and ecological costs (Blankenship and Leber, 1995; Laurec, 1999). The Alaska salmon hatchery program is designed to enhance the harvest of salmon while minimizing impacts to wild stocks; policies, statutes, and regulations have been established to protect and maintain the productive potential of wild stocks (McGee, in press). Our results confirm the conclusions of several previous analyses: the hatchery program in PWS has provided large benefits and net increases in catch to the region (Pinkerton, 1994; Smoker and Linley, 1997; Wertheimer et al., 2001, 2004). Wild stocks of pink salmon in PWS remain highly productive, in relation to their historical performance and relative to the productivity of stocks in other regions of Alaska (Wertheimer et al., 2001). However, our results also indicate that there has been some loss of productivity of the wild stock due to the hatchery program. Evaluation of the magnitudes and the mechanisms of such interactions, as well as the level of enhancement to the fisheries, are essential to provide constituent groups, managers, and policy makers the information they need to assess

the success of hatchery programs and to refine hatchery strategies and regulations to minimize impacts to wild stocks.

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This is Exhibit H "referred to in
the affidavit of R Peterman
sworn before me at Vancouver
this 2 day of May 2011
[Signature]
A Commissioner for taking Affidavits
for British Columbia

COMMENTS

Comment: A Review of the Hatchery Programs for Pink Salmon in Prince William Sound and Kodiak Island, Alaska

Recently, Hilborn and Eggers (2000) have asserted that hatcheries in Prince William Sound (PWS), Alaska, have caused a decline in the productivity of wild pink salmon *Oncorhynchus gorbuscha* in PWS and that hatchery fish to a large degree have replaced, not enhanced, pink salmon returns. Pink salmon catches in PWS are currently at historic highs, averaging 27 million fish per year over the past decade. Over 85% of the harvest is from a system of large hatcheries (Pinkerton 1994; McNair 2000). There is concern that hatchery production may have been deleterious to wild pink salmon in PWS, complicating management and the achievement of escapement goals and reducing productivity (e.g., Tarbox and Bendock 1996). Hilborn and Eggers estimate that more than 90% of the recent annual production would have been attained by wild stocks alone in the absence of hatchery production. We, however, find compelling evidence that hatchery fish have greatly increased the total pink salmon harvest in PWS and that Hilborn and Eggers's estimates of wild stock productivity in the hypothetical absence of hatchery fish are not credible. While countervailing trends in the abundance of wild and hatchery pink salmon in PWS superficially appear to support Hilborn and Eggers's arguments, careful consideration of the evidence indicates that the program has had substantial net benefits.

We address three central points of the Hilborn and Eggers paper: (1) that retrospective analysis indicates that the proportional increases in pink salmon production in PWS have been similar to those in regions of Alaska without major hatcheries, on the basis of which Hilborn and Eggers conclude there is no evidence from between-region comparisons that the large increases in the catch in PWS were due to hatcheries; (2) that, because wild stock productivity is correlated negatively with the magnitude of fry releases from hatcheries, wild stock fish would have produced more than 90% of the current record runs in PWS in the absence of hatcheries; and (3) that wild stock escapements (i.e., the number of reproducing wild salmon) have declined due to deleterious interactions with salmon released from hatcheries.

Proportionality Argument

Hilborn and Eggers retrospectively analyze the total returns from 1965 to 1997 of pink salmon from four regions of Alaska, Kodiak Island (KOD), PWS, southeast Alaska (SEAK), and the south Alaska Peninsula (SAP), to argue that increases in pink salmon production have been more or less proportional among regions. They summarize this analysis by dividing this period into approximately decadal periods: 1965-1975, 1976-1985, and 1986-1997 (Hilborn and Eggers 2000; Table 1). They selected these years because of the relationship between salmon catches and climatic conditions, which have been used to identify a "regime shift" in 1976-1977 from low productivity to high productivity for salmon in the Gulf of Alaska (Mantua et al. 1997; Downton and Miller 1998). The first period thus corresponds to low-production, "prehatchery" conditions, the second to high-production conditions when hatchery releases were increasing but were of lesser magnitude, and the third to high-production conditions when hatcheries in PWS were at full production.

Hilborn and Eggers argue that pink salmon have increased in PWS due to a climate regime shift in the Gulf of Alaska that has led to more favorable oceanic survival conditions. They submit that similar proportional increases have occurred among all four major pink salmon regions since the 1965-1975 period regardless of the extent of hatchery production. However, their comparisons actually indicate a wide range in proportional changes: 1.90 in KOD, 5.74 in PWS, 3.54 in SEAK, and 5.93 in SAP (Hilborn and Eggers; Table 1).

We took a longer view of the decadal fluctuations in pink salmon productivity to compare the several regions of Alaska. A previous high-production phase for Alaska salmon occurred in the 1930s and 1940s (Figure 1). Such fluctuations in historical catch data have been used as a proxy for total abundance (e.g., Beamish and Bouillon 1993; Downton and Miller 1998). We examined catch data from 1920 to 1999 (Byerley et al. 1999; ADFG 2000) for correlations of annual and 10-year moving average catches among regions and to compare the relative production among regions during periods of high productivity. We used mov-

TABLE 1.—Years and magnitudes of productive-regime maximums and interregime minimums of 10-year average catches of pink salmon for four regions of Alaska. Catch data are times 1,000. Data are from Byerly et al. (1999) and ADFG (2000).

Region	Early-regime maximum		Interregime minimum		Current-regime maximum	
	Years	Catch	Years	Catch	Years	Catch
Southeastern Alaska	1933–1942	36,856	1967–1976	8,615	1990–1999	50,520
Prince William Sound	1938–1947	7,884	1951–1960	1,831	1990–1999	27,386
Kodiak Island	1934–1943	9,717	1950–1959	5,043	1990–1999	15,941
South Alaska Peninsula	1934–1943	6,752	1966–1975	632	1990–1999	7,920

ing averages to examine long-term trends that may be masked by short-term (in this case, annual) variability, and accounted for autocorrelation in assessing statistical significance (Pyper and Peterman 1998). We selected a 10-year moving average because Hilborn and Eggers compare periods of approximately decadal duration.

We found that the historical variation of the harvest in PWS correlates significantly ($P < 0.01$) with that of other regions in both short and long term. Correlation coefficients were greater for the moving averages, indicating high correspondence for the long-term trend but with substantial interannual variation among regions. The percentages of variation explained (r^2) in the temporal variation in PWS catch data by the 10-year moving averages for the other regions were 55% for SEAK, 64% for KOD, and 63% for SAP. In contrast, r^2 values for the annual data were much lower: 32% for SEAK, 6% for KOD, and 21% for SAP.

This interannual variation results in differences in the timing of historical maximums and minimums (Table 1). Peak production in the high-production phase of the 1930s and 1940s occurred

several years later in PWS than in the other three regions; historical minimums before the current production phase occurred in the 1950s in PWS and Kodiak, and in the 1970s in SEAK and SAP (Table 1). Hilborn and Eggers use an arbitrary time period as a basis for their comparisons of different phases in the regional long-term trends. The similarity of recent increases in SAP and PWS in their comparisons (Hilborn and Eggers; Table 1) is an artifact of the time periods they select.

The decade of the 1990s records the maximum peak of both the current production phase and the entire time series (Table 1). To determine whether the different regions have comparable productivity in different regimes, the appropriate contrast is between the current peaks and the maximum production of the prior high-production regime. When we compared the high production of the 1990s to the maximum catches of the prior regime, we found that PWS production has increased substantially more than that of the other three regions (Figure 2). Although the other regions have increased 1.2–1.6 times, PWS has attained a level 3.5 times its maximum in the previous high-production phase. Contrary to Hilborn and Eggers' conclusions, the increase in total abundance in PWS is disproportionately larger than in the other regions, indicating substantial enhancement by the hatchery fish. Also contrary to their conclusions, much of this increase has occurred since the 1976–1985 returns, and a substantial (30%) part of the increase during the 1976–1985 period was already due to hatchery production (Figure 2).

We agree with Hilborn and Eggers that wild pink salmon production in PWS has changed disproportionately to that of other areas of Alaska. In the period 1976–1985, wild pink salmon catches were 1.3 times their prior historical (prior regime) maximums in PWS, compared with only 0.6 to 1.0 times in the other three regions (Figure 2). In the 1990s, catches of PWS wild stocks declined to 0.5 times their historical maximums, whereas catches in the other regions increased to 1.2–1.3 times their

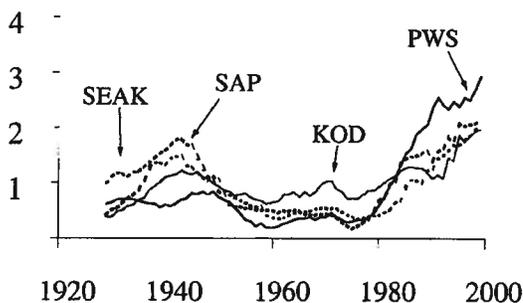


Figure 1.—Ten-year moving averages of pink salmon catches in four regions of Alaska for the years 1920–1999, scaled by the average annual catch in each region for the entire time series. Averages are plotted for the last year of the 10-year average; SEAK = Southeastern Alaska, KOD = Kodiak Island, SAP = South Alaska Peninsula, and PWS = Prince William Sound. Data are from Byerly et al. (1999) and ADFG (2000).

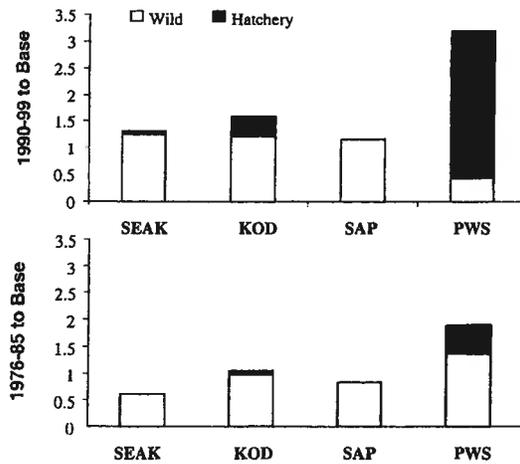


Figure 2.—Ratios of average annual pink salmon catches in four regions of Alaska for the time periods 1990–1999 (upper panel) and 1976–1985 (lower panel) to the maximum 10-year average catch in the “early” (pre-1950) productive regime. Data are from Byerly et al. (1999), ADFG (2000), and McNair (2000).

historical maximums. Two competing hypotheses could realistically explain these changes. Hilborn and Eggers hypothesize that large-scale hatchery production in PWS has caused the differential decline. This hypothesis does not explain the differentially greater increase of PWS wild stocks in the 1976–1985 period. The alternative hypothesis is that the changes in wild stock productivity reflect environmental variability and that the decrease in wild stock production would have occurred independently of the expansion of the hatchery program. In fact, average returns per spawner in PWS in 1976–1985 are by far the highest observed in any region, and even after declining in the later period are still the highest of any region (Figure 3).

If we accept Hilborn and Eggers’s argument that hatcheries have caused the reduction in wild stocks in PWS since the mid-1980s and assume that in the absence of hatcheries these stocks would currently be as productive (relative to the high-production phase of the 1930s and 1940s) as other regions of Alaska, we calculate that without hatchery production PWS wild stocks would have produced an average catch of 9.9 million in the 1990s. Actual catches in PWS in the 1990s have averaged 27.4 million, for a net gain of at least 17.5 million fish annually. If the changes in wild stock production in PWS have been due to ecosystem changes and are independent of the effects of salmon released from hatcheries, then the net gain from

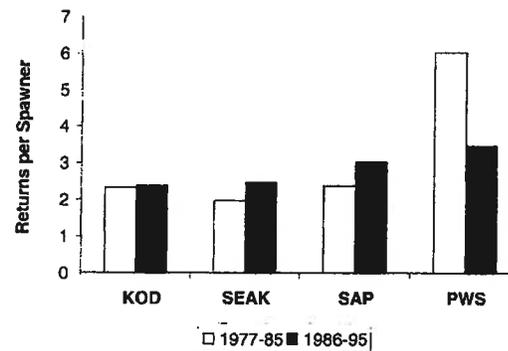


Figure 3.—Annual average index of returns per spawner for brood years of pink salmon in two time periods and four regions of Alaska. Annual averages were computed by pooling total returns and total index escapements. Data are from Hilborn and Eggers (2000), Table 3.

the pink salmon enhancement program is the actual catch of 23.7 million hatchery pink salmon.

Effects of Hatchery Releases on Wild Stock Productivity

Hilborn and Eggers use a Ricker model of pink salmon population dynamics to examine the historical effects of escapement (spawning stock size) and hatchery releases of fry on the production of wild pink salmon. This model establishes a statistical relationship of hatchery releases as an auxiliary variable affecting returns per spawner. Hilborn and Eggers use the model to simulate wild pink salmon production in PWS in the hypothetical absence of hatcheries. The effect of the auxiliary variable in the model is to decrease the productivity of wild spawners as hatchery releases increase.

The outcome of the simulation is not credible. The model produces simulated returns per spawner of wild pink salmon that are more than double the observed maximum for wild stocks in PWS (Hilborn and Eggers; Table 5). We compared the actual return per spawner data presented by Hilborn and Eggers with the return per spawners estimated by their model given observed escapements (Figure 4). Actual production in PWS for the 1977–1995 brood years did not exceed 11 returns per spawner and averaged 5.4 returns. For brood years 1977–1985, the maximum observed was 11 and the average was 7.0. This ratio is approximately concurrent with the period when catches of wild pink salmon in PWS had increased relative to their historical maximums to a level equal to that observed

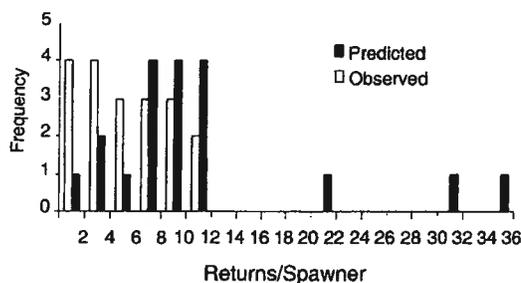


Figure 4.—Frequency distribution of returns per spawner of Prince William Sound pink salmon for the 1977–1995 brood years. Predicted returns are for the Hilborn and Eggers model assuming no hatchery releases and the observed escapement levels. Data are from Hilborn and Eggers (2000), Table 5.

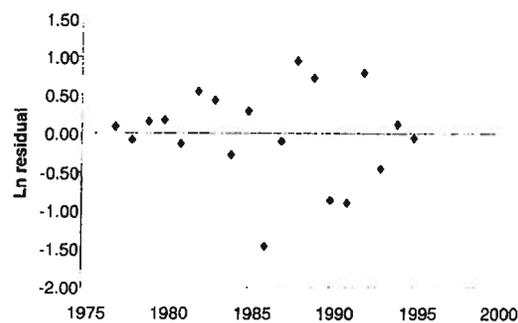


Figure 5.—Time series plots of residuals from Hilborn and Eggers's population dynamics model for Prince William Sound wild pink salmon. Data are from Hilborn and Eggers (2000), Table 5.

in any of the other regions to date (Figure 2). Data presented by Hilborn and Eggers (Figure 3, which was plotted from Hilborn and Eggers's Table 3) show that the productivity of 1977–1985 brood pink salmon in PWS was remarkably high, 2–3 times that observed in other regions of the state. Yet Hilborn and Eggers estimate that, absent hatcheries, there would have been 3 years of returns in excess of 20 returns per spawner, including 2 years in excess of 30 returns per spawner (Figure 4). The average simulated return per spawner in the absence of hatchery releases for the 1986–1995 brood years was 13.6 when Hilborn and Eggers used observed escapements in their simulation model. This level of productivity is far greater than the actual average historical returns per spawner observed in PWS and other pink-salmon-producing regions. Thus the wild pink salmon production estimated by Hilborn and Eggers in the absence of hatchery releases (17.5 million fish per year for 1986–1995 using observed escapements in their simulation) is unrealistically high.

Examination of the Ricker α parameter for the simulation model also indicated that the model is unrealistic. In a survey of Ricker α parameters, Myers et al. (1999) found that the average for 52 pink salmon populations was 3.4, with an SE of 0.07. A simple Ricker model for the observed PWS returns from the 1977–1995 brood years, with no hatchery auxiliary variable, estimates α at 6.3, which is indicative of a very productive pink salmon stock. In the Hilborn and Eggers simulation, the hatchery effect becomes a constant C , and α is increased by $C \cdot \alpha = \alpha'$, the "true" productivity parameter for the population in the absence of hatcheries. For Hilborn and Eggers's simulated results, α' is 20.6, a value far above one leading to

periodic cycles, chaotic dynamics, and even a high likelihood of extinction in a fluctuating environment (Ricker 1954; Fagen and Smoker 1989; Schaffer et al. 1986).

Bias in Hilborn and Eggers's simulation may result from the fact their model fits the data much better for the early "low hatchery release years" (1977–1985 brood years) than for the later "high hatchery release years" (1986–1995 brood years). The average absolute residual for the early period was 0.24; for the latter period it was almost three times as high at 0.64 (Figure 5). This trend indicates that some other factor may be having a large effect on the spawner–recruit relationship.

Another possible reason for bias in their estimate of stock productivity is their failure to consider the effects of measurement error, which can cause considerable positive bias in estimates of productivity (Hilborn and Walters 1992; Ludwig and Walters 1981). Measurement error in PWS escapement estimates is large both in observer counts and in estimates of stream life (Bue et al. 1998a). In addition, there is substantial measurement error in the allocation of catch between hatchery and wild production, especially prior to the representative tagging programs of hatchery fish that began in 1988. Allocations of catch in earlier years between production sources were essentially educated guesses.

Hilborn and Eggers further bias their simulation of PWS production in the absence of hatcheries by adding 18% to their simulated production. Their rationale for doing this is that it accounts for the increases in returns per spawner seen in other regions of Alaska over a period when returns per spawner declined in PWS (Hilborn and Eggers's Table 3; our Figure 3). We note that even during

the "depressed" recent years, pink salmon in PWS have had higher returns per spawner than other regions. But more troublesome is that this adjustment in returns per spawner is double counting: it is added to simulated production that already has increased returns per spawner to unprecedented levels. Observed returns per spawner in PWS averaged 7.0 for the 1977–1985 brood years. Using observed escapements, the Hilborn and Eggers simulation model estimates returns per spawner of 13.6 for the 1986–1995 brood years, an increase of 94% over the 1977–1985 average. To add an increment of 18% on top of this increase is clearly inappropriate.

Escapement Declines

We disagree with Hilborn and Eggers's assessment that declines in average escapements of wild stock in PWS have been caused by increased hatchery production. We assert that the "decline" they identify was primarily due to the improved capability of ADFG to enact its management policy and manage escapements within their defined target ranges. Average escapements have been lower for recent years than for the 1977–1985 brood years, but they have also been closer to management goals in recent years. However, Hilborn and Eggers explicitly reject the proposition that management policy and improvements in management resolution have influenced the decline in escapements. They argue that a statistical relationship of escapement to total run strength is evidence that run strength, not managed harvest, is the determinant of escapements.

The cumulative escapement goal over all PWS management districts is 1.4 million pink salmon. Hilborn and Eggers (page 342) used an escapement goal of 1.8 million pink salmon for PWS. This apparent discrepancy is due to their recalculation of the goal to account for the different assumptions they used for stream life and the resultant expansion of aerial survey counts (Doug Eggers, Alaska Department of Fish and Game, personal communication). We used the published ADFG goals and index escapements because these represent the actual management target and outcomes.

From 1979 to 1985 (near the beginning of the hatchery era), escapements over several years were extraordinarily high, consistently exceeding the escapement goal range (Figure 6). The reasons for the high escapements are complex, but in large part they were a consequence of restricted harvests owing to conservative management (due, in turn, to the inability of managers to separate the hatch-

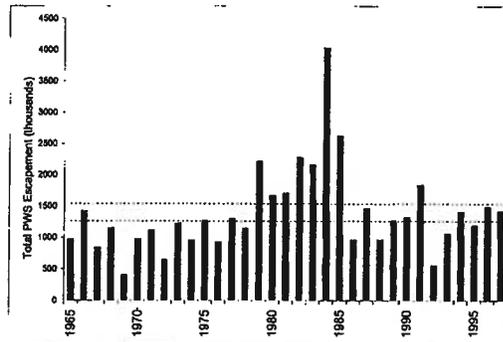


Figure 6.—Prince William Sound (PWS) pink salmon cumulative escapements for the 1965–1997 brood years. Escapement data are from Morstad et al. (1998). The cumulative escapement goal ranges established by ADFG (Fried 1994) are indicated by the two horizontal lines.

ery and wild components of the catch), strikes by fishermen over price disputes in three seasons, and limitations on harvests imposed by processing capability as total runs increased in PWS. To provide better management resolution of hatchery and wild catch composition, ADFG and hatchery operators began representative marking of hatchery salmon with coded-wire microtags (Peltz and Miller 1990), which allowed the fishing fleet to target hatchery fish more effectively through improvements in time-area management. In the 1990s, coded-wire tagging was supplanted by mass marking of hatchery pink salmon with otolith thermal marks, which further improved discrimination between hatchery and wild fish in the harvest.

When we examine cumulative escapements in PWS relative to escapement goals, we find clear evidence that management success in PWS has improved during the "hatchery" era. Management objectives in PWS are actually expressed as a 10% range around a point goal (Fried 1994). Before the regime-shift years defined by Hilborn and Eggers and before any hatchery enhancement in PWS, cumulative escapements rarely fell in the escapement range; during the 1963–1976 brood years (1965–1978 return years), 3 of 14 (21%) escapements were within the range, and the 11 other escapements were below the range (Figure 6). During the 1977–1985 brood years (1979–1987 return years), which constitute the "good" years in Hilborn and Eggers's assessment of escapements, only 1 of 9 (11%) escapements was within the management range; 7 were above the range, and 1 was below (Figure 6). During the 1986–1995 brood years

(1988–1997 return years), 5 of 10 (50%) escapements were within the management range, 1 was above the range, and 4 were below (Figure 6). An increasing ability to manage more precisely for escapement goals is also apparent from Figure 10 in Hilborn and Eggers (2000); in six of seven districts, the absolute deviations from the escapement goals have been less since 1986 than in previous periods, including the years of overescapement in the first half of the 1980s.

The impression given by Hilborn and Eggers is that consistently exceeding the PWS escapement goal in the early 1980s was good and that decline from these high escapements has been a negative impact of hatchery interactions. This argument contradicts the long-standing paradigm of pink salmon harvest management that overescapement of pink salmon triggers density-dependent reductions in returns per spawner. Hilborn and Eggers's analysis is actually an argument for higher escapement goals, not hatchery-induced escapement decline; certainly their production model indicates a higher maximum-sustained-yield escapement. Yet nowhere in their article do they advocate increasing escapement goals. Instead, they imply that the large investment and effort directed at meeting existing ADFG escapement goals through improving management resolution and the regulation of fishing effort have had no effect, and they conclude that escapement is simply an outcome of run size.

We are not surprised that Hilborn and Eggers find a significant relationship between run size and escapements. Harvest management is not perfect; it is difficult to balance the need to assess run strength and provide harvest opportunities for both hatchery and wild stocks with varying productivity with meeting district-specific escapement goals. Larger runs will tend to have larger escapements and smaller runs smaller escapements, resulting in a historical relationship between escapement and run strength. However, this statistical tendency should not be interpreted to mean that management efforts do not affect the realized escapements.

Alternate Explanations for PWS Wild Stock Declines

As Hilborn and Eggers note, the possibility exists that wild pink salmon stocks have declined in PWS from their high abundance in the early 1980s due to factors other than hatchery interactions. Climate change and oceanographic conditions may have caused differences in production cycles between regions; synchrony in the production history

is not perfect, and substantial interannual variation occurs (Table 1; Figure 1). In PWS, hatchery survivals have declined over the time periods examined by Hilborn and Eggers, averaging 5.8% for the 1976–1985 brood years and 3.7% for the 1986–1995 brood years (Morstad et al. 1998). If we assume that hatchery survival is an indicator of wild stock survival, this 36% reduction in survival can explain virtually all of the reduction in returns per spawner for the latter years. The change in marine survival could have been symptomatic of density-dependent interactions with increasing numbers of hatchery fish, as proposed by Hilborn and Eggers. However, the reduction could also be a density-independent response to declines in zooplankton production in PWS. Since 1986, indices of spring zooplankton abundance have declined by 45% on average relative to the early 1980s when hatchery marine survivals and wild stock returns per spawner were high (T. Cooney, University of Alaska–Fairbanks, and D. Reggianni, Prince William Sound Aquaculture Corporation, personal communications). Because the combined abundance of hatchery and wild salmon fry has only a minimal predatory impact on PWS zooplankton (Cooney 1993), large fluctuations in zooplankton abundance probably have strong density-independent impacts on pink salmon growth and marine survival.

Changes in predator populations may also have affected the survival of pink salmon in PWS. Willette et al. (1999) found that Pacific herring and walleye pollock were the primary predators on juvenile salmon and that their predation rates on salmon were a function of the availability of large copepods. Pacific herring populations in PWS have fluctuated dramatically, experiencing large increases in biomass in the late 1980s and early 1990s followed by a collapse in 1993 (Marty et al. 1998). Hydroacoustic surveys have also indicated large increases in walleye pollock biomass in PWS (Bechtol 1999).

Another event in PWS during the "hatchery" era that could have affected wild stock productivity was the *Exxon Valdez* oil spill in 1989. A similar "before and after" comparison to the one Hilborn and Eggers used to argue that hatcheries have disproportionately depressed returns per spawner in PWS relative to other regions (e.g., Figure 3) can be applied to demonstrate that the oil spill caused the decline. Returns per spawner for the 1977–1988 broods averaged 6.5. For the 1989–1995 broods spawning after the oil spill, returns per spawner averaged 3.7, a 43% decline that was

not observed in regions of Alaska not affected by the spill. Hilborn and Eggers point out that the maximum spill-induced losses estimated in the literature (Geiger et al. 1996) are too small to be detected on a PWS-wide basis. However, in the heavily-oiled Southwest District of PWS, Bue et al. (1998b) found elevated embryo mortality in oiled streams two generations after oiling. Heintz et al. (1999, 2000) showed that embryonic exposure to weathered oil not only results in elevated embryo mortality but also causes reduced growth and survival of individuals after incubation. Such indirect losses were a possibility that Geiger et al. (1996) specifically noted as a potentially large source of mortality not considered in their loss estimates. We agree that such effects might not be detectable in the aggregate production of pink salmon in PWS, but they would reduce returns per spawner on a site-specific basis and should be considered in comparisons of productivity among districts in PWS. We also note that simple time series comparisons can lead to simple, but not necessarily robust, conclusions.

How can we determine if declines in wild stock productivity in PWS are due to hatchery interactions or to some other ecosystem change? Both retrospective and empirical studies are needed. The retrospective population dynamics model of Hilborn and Eggers should be expanded to include a broad array of environmental variables. We are currently compiling historical data sets for such factors as temperature during different life history phases, spring zooplankton abundance, and predator populations in PWS to examine their effects relative to the magnitude of hatchery smolt releases on the productivity of the PWS wild stock.

The distribution of hatchery pink salmon in PWS provides an excellent opportunity for empirical research on the impacts of hatchery fish on wild stock productivity. The proportion of stray hatchery fish in streams in the Eastern and Southeastern districts of PWS is low, whereas in some streams in the western districts it is very high (Joyce and Evans 1999; Timothy L. Joyce, unpublished data). Similarly, the potential for interaction of wild and hatchery juveniles in nearshore marine habitats is much greater for wild populations in the western districts that are near hatcheries than for those in the Eastern and Southeastern districts. If straying and genetic introgression or competition in the marine environment have caused the decline in productivity, then very different responses in the different regions of PWS should be observable. A carefully designed study

comparing spawning success, fry production, and marine survival between several wild populations exposed to different levels of interactions with hatchery fish could quantitatively address the degree of impacts.

Conclusions

Although Hilborn and Eggers have raised important concerns in their paper, their conclusion that hatchery pink salmon production in PWS has been a replacement rather than an enhancement of wild production is not justified and does not provide good guidance to policy makers. If Hilborn and Eggers were correct and their "best estimate" of a 2-million-fish increase in total production annually due to hatcheries were credible, then Hilborn's (1992) call for termination of the PWS hatchery program should be seriously considered. However, Hilborn and Eggers have greatly overestimated the potential for production by naturally spawning pink salmon in PWS and as a result have greatly underestimated net hatchery production. We estimated the net annual gain in the catch of pink salmon from PWS hatcheries to be 17.5–23.7 million, a range dependent on whether changes in productivity of PWS wild stocks have been due to interactions with hatchery fish or to ecosystem changes independent of the effects of pink salmon released from hatcheries. Thus, the situation is more complex than is implied by Hilborn and Eggers's overstatement of potential wild stock production; the enhancement program provides large benefits, but these benefits may have come with some degree of impact on wild stocks. Policy makers and managers need good information on the interactions of hatchery and wild fish to define better the impacts on wild populations, so that they can develop management policies that minimize the impacts while gaining the substantial benefits.

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