

Replacement of Wild Coho Salmon by Hatchery-Reared Coho Salmon in the Strait of Georgia over the Past Three Decades

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Abstract.—The percentage of hatchery-reared coho salmon *Oncorhynchus kisutch* in the Strait of Georgia, British Columbia, increased from nearly 0% in the early 1970s to more than 70% by 2001. These estimates were derived from fin clip and coded wire tag data collected from commercial and sport fisheries, research surveys conducted in the summer and fall of 1997 to 2000, and examination of the microstructure of otoliths extracted from juvenile coho salmon collected during our marine surveys. The increasing trend may be related to the proportions of hatchery and wild smolts entering saltwater, fishing rates, and changes in the ecological processes regulating coho salmon production in the ocean. The consequence for management is that the abundance of wild spawning salmon (escapement) depends on hatchery as well as wild production. The consequence for policy makers is that future enhancement activities need to have clear policies for assessing the effects of hatchery fish on the population dynamics of wild fish as well as for producing hatchery fish.

Canada began a program of releasing coho salmon *Oncorhynchus kisutch* smolts produced in hatcheries into the Strait of Georgia, British Columbia, in 1971 (Cross et al. 1991). By 1988, over 50 facilities were releasing coho salmon fry and smolts. The management objectives of the hatchery program were to rebuild wild stocks and increase production. Hatcheries were considered to be effective because the egg-to-smolt survival in hatcheries was much greater than that in wild stocks and it was believed that the principal factor limiting the abundance of coho salmon available to a fishery was the number of smolts entering the ocean. It was generally recognized that hatchery production would not negatively affect wild stocks, but the negative effects were not clearly identified or monitored. Perry (1995) stated that if there were evidence of negative interactions between hatchery and wild salmon in the ocean or the percentage of hatchery coho salmon returning to the river exceeded 50% of wild production, management policy would require a reduction in hatchery production.

The protection of wild coho salmon is a rapidly developing priority for management agencies and thus it is important to be able to assess the impact of hatchery-reared salmon on the population dynamics of wild salmon. Assessments of the interactions between hatchery and wild stocks can be

made on a stock-by-stock basis, but it is difficult and expensive to monitor large numbers of stocks. However, an assessment of the overall changes in the percentages of hatchery and wild stocks can be readily made in the marine environment. The marking of large numbers of hatchery-reared coho salmon using either fin clips or coded wire tags (CWTs) prior to release into the Strait of Georgia from 1997 to 2000 facilitated our assessment of rearing type. Prior to 1997, tagging of coho salmon smolts had been limited to very small percentages (2–5%) of the total releases from the hatcheries. Historically, sampling fishery catches for these tagged fish provided a method of estimating the percentage of hatchery and wild fish. In recent years, estimates from research cruises were used because of the virtual elimination of commercial and recreational fishing from 1998 to 2000.

In our study, we include catch and exploitation rate data in addition to our research survey data to show that wild coho salmon have been replaced by hatchery-reared coho salmon. We suggest that this is relevant to other enhancement programs, even those for other species, as our results identify the need to have policies for the management of wild and hatchery stocks at the beginning of any enhancement program.

Methods

Coho salmon surveys and analyses.—Juvenile coho salmon were obtained in the Strait of Georgia using a modified midwater trawl (Beamish et al. 2000a). The net had an average opening of 14 m

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Received November 9, 2001; accepted August 13, 2002

(depth) \times 30 m (width) and was towed at an average speed of 5 knots (2.6 m/s) at the surface. Surveys were conducted in June–July and September from 1997 to 2000. Each survey followed a standardized track line utilizing a stratified randomized selection of fishing depths between the surface and 45 m below it at 15-m increments. Tows were conducted at different strata to ensure that a representative sample of the entire salmon population was obtained. Each trawl set was 30 min in duration. There was an average of 94 trawls (range, 69–135) in the eight surveys, of which an average of 56 trawls per survey captured juvenile coho salmon.

The numbers of coho salmon smolts (fish released from hatcheries after rearing for more than 1 year) and fry (fish released in their first year) that were released into the Strait of Georgia from Canadian hatcheries for the years 1997–2000 were obtained from the Mark Recovery Program (MRP; updated from Kuhn 1988). Fry survival in the natural environment is generally considered to be 10% (Sandercocock 1991). Therefore, we estimated the contribution of hatchery fry to the total smolt population in the following year as 10% of the fry released. For example, the 1996 release of 3.4 million coho salmon fry from hatcheries would contribute 0.34 million smolts to the 9.0 million hatchery coho salmon smolts entering the Strait of Georgia in 1997.

Large numbers of hatchery coho salmon are released into Puget Sound in the United States, and some of these fish enter the Strait of Georgia. Because of differences in clipping practices, however, it was possible to establish the contribution of Puget Sound coho salmon to the Strait of Georgia population for 1997 (from 1997 to 2000, coho salmon from U.S. hatcheries were marked by removing the adipose fin, whereas in 1997 Canada marked hatchery coho salmon by removing a pelvic fin rather than the adipose fin).

There are a variety of potential errors associated with using the tagging percentages of hatchery coho salmon to estimate the recapture percentages (Schnute et al. 1990; Cross et al. 1991). Schnute et al. (1990) identified a 22% discrepancy in the proportions tagged at release and recovered as adults. There is mortality associated with the tagging, handling, and clipping of various fins. Mortalities from clipping pelvic fins typically range from 6% to 25%, but can be as high as 50% (Pacific Salmon Commission 1995, 1997). Values ranging from 0% to 90% have also been reported (Pacific States Marine Fisheries Commission 1992). For

this study, we used 6% as an estimate of this mortality factor, which we believe to be conservative and which is the minimum mortality reported by the Pacific Salmon Commission (1995, 1997).

In addition to this mortality factor, there is a detection error (sometimes called an awareness factor). Not all of the fin is completely removed in all clipped fish, and partially clipped fish may or may not be recognized as clipped. To include both incomplete fin clipping and mark detection difficulties by observers, we again used a value of 6%. With these error estimates, the percentages of hatchery and wild coho salmon were calculated for all eight surveys (Table 1). Examples of the calculations are provided for the September 1997 and September 2000 surveys in Results.

A power analysis (Zar 1996) was employed to test the adequacy of our sample sizes in estimating the differences between the proportion of hatchery-marked and unmarked coho salmon. A power level of 0.8 was employed as suggested by Peterman (1990). The sample variance of the proportion of hatchery-marked coho salmon (expanded for tagging mortalities and detection errors) was used for the 55 sets in which coho salmon were caught in the September 1997 survey.

Otolith studies.—In 1997 and 1998, 100 random pairs of otoliths from ocean-age-0 coho salmon caught in the September surveys were prepared and examined for rearing type using the microstructure method of Zhang et al. (1995). The microstructure of hatchery-reared coho salmon had more uniform daily growth during the first marine year and a less prominent freshwater annulus than wild coho salmon. Whenever possible, the left otolith was used in the determination, but when the left otolith was crystalline or missing in the sample the right otolith was used. Normal otoliths contain aragonite crystals (Chesney et al. 1998), which are formed in greater density during periods of active growth and which transmit light poorly. Crystalline otoliths, on the other hand, contain high percentages of vaterite crystals, which transmit light better but make it difficult to detect daily growth increments. If both the otoliths were crystalline, the rearing type (hatchery or wild) was assigned using the proportions observed in those fish with a single crystalline otolith (Zhang et al. 1995).

Troll catches in 2001.—Coho salmon juveniles from the 2000 surveys (i.e., ones released in 2000) returned to the Strait of Georgia as ocean-age-1 fish in 2001. This was the first time ocean-age-1 coho salmon have been in the Strait of Georgia since 1994 (Beamish et al. 1999a). This was also

TABLE 1.—Data used to calculate the percentages of hatchery-reared coho salmon in the Strait of Georgia. Examples of the calculations for September 1997 and 2000 are included in the text.

Release year	1997	1998	1999	2000
Hatchery smolts released ($\times 10^6$)	9.0	9.7	9.9	10.0
Fry surviving from previous year ^a ($\times 10^6$)	0.3	0.3	0.4	0.6
Estimated total smolts ($\times 10^6$)	9.3	10.0	10.2	10.5
Percentage with fin removed	54.4	70.9	65.7	73.7
June–July surveys				
Number of trawls	69	95	98	84
Total catch	522	1,263	1,649	4,626
Fish with fin clips	159	470	660	2,143
Puget Sound fish	66	139	181	509
Canadian catch	456	1,124	1,468	4,117
Canadian hatchery percentage	71.8	66.1	76.6	79.1
September surveys				
Number of trawls	135	95	85	91
Total catch	2,403	1,517	2,022	1,321
Fish with fin clips	703	616	850	537
Puget Sound fish	264	167	222	145
Canadian catch	2,139	1,350	1,798	1,176
Canadian hatchery percentage	67.7	72.1	80.6	69.4

^a The survival of fry released in the previous year to the smolt stage was estimated to be 10% (Sandercock 1991).

the first opportunity to compare our estimates of the percentages of hatchery and wild ocean-age-0 coho salmon with those adults from the same brood year a year later. The comparison is important because the hatchery and wild percentages from 1973 to 1996 were for ocean-age-1 coho salmon in the Strait of Georgia, and the estimates from 1998 to 2001 were for ocean-age-0 fish. In 2001, ocean-age-1 coho salmon were captured from 30 June to 5 July using commercial troll gear. Lengths and weights were measured and the presence of fin clips noted. The number of hatchery-reared fish was determined by dividing the number of fish with missing adipose fins by the marking rate reported by the MRP database (updated from Kuhn 1988) for hatchery coho salmon released in 2000 (73.7%; Table 1).

Trends in hatchery percentages.—Estimates of the contribution of hatchery-reared coho salmon to the sport and commercial catches in the Strait of Georgia from 1975 to 1994 were made using the Canadian Department of Fisheries and Oceans commercial and sport catch database (Holmes and Whitfield 1991) and the procedures documented in Cross et al. (1991). We terminated the time series in 1994 because of the collapse of the sport fishery in the Strait of Georgia (Beamish et al. 1999a). The numbers of coho salmon released from Canadian hatcheries into the Strait of Georgia from 1997 to 2000 and their associated marking rates were determined from the MRP database (updated from Kuhn 1988).

Results

Power analysis demonstrated that the sample size and variance in the September 1997 survey were sufficient to detect a difference as small as 2% between the proportions of hatchery-marked and unmarked coho salmon. Using an arbitrary detection level of 5%, a total of 13 sets that captured coho salmon were required in any given survey to maintain a suitable level of power (0.8). As there was an average of 56 sets per survey that captured coho salmon, the survey design was sufficient to accurately and precisely detect hatchery-marked coho salmon. The catch distribution in all of our research surveys also showed that coho salmon were collected throughout the Strait of Georgia (Figure 1).

There was a steady increase in the percentage of hatchery-reared coho salmon from 1975 to 1987 (Figure 2A) that was consistent with the trend of increasing hatchery releases from 1972 to 1985–1986 (Figure 2B). The percentage of hatchery coho salmon peaked at approximately 50% in 1987 (catch year) and then decreased through the early 1990s (Figure 2A), dipping substantially (to nearly 20%) in 1991.

A total of 2,403 juvenile coho salmon were caught in the September 1997 survey, of which 703 had a missing pelvic fin and were thus Canadian hatchery releases (Table 1). There were also 40 coho salmon captured in the Strait of Georgia with missing adipose fins and no CWT or with

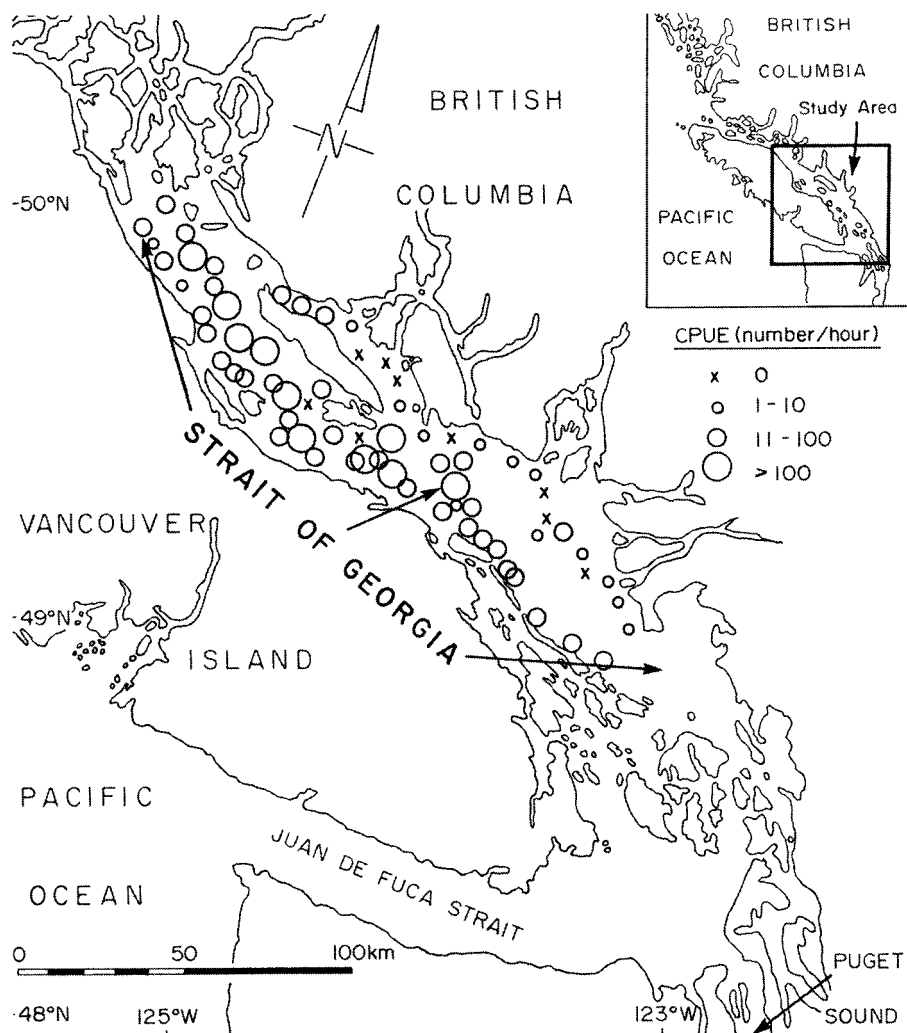


FIGURE 1.—Study area showing the distribution of catch per unit effort (CPUE; number per hour) of ocean-age-0 coho salmon in June–July and September surveys in the Strait of Georgia from 1997 to 2000. The inset map shows the western coast of Vancouver Island and British Columbia.

CWTs from Puget Sound hatcheries. With adjustments for tagging mortalities and detection errors, the estimated number of adipose-fin-clipped coho salmon from Puget Sound in our catch was 45. Sampling in Puget Sound during July 1997 had shown that 280 of 1,696 captured juvenile coho salmon (17%) had a clipped adipose fin (data not shown). Thus, the 45 adipose-fin-clipped coho salmon from the September 1997 survey were assumed to represent 17% of the total contribution of coho salmon from Puget Sound to the population in the Strait of Georgia. This meant that 264 of the 2,403 coho salmon (approximately 11%) caught in our September survey were from Puget

Sound. This percentage was used to calculate the U.S. contribution to the Strait of Georgia population for all subsequent surveys.

The remaining 2,139 coho salmon in the September 1997 survey were from Canadian stocks (Table 1). Correcting for tagging mortalities and detection errors, the 703 coho salmon with missing pelvic fins would increase to 787. Because 54.4% of all Canadian hatchery releases of coho salmon into the Strait of Georgia in 1997 had clipped pelvic fins (MRP database), we estimated that 1,447 of the coho salmon in the catch were from Canadian hatcheries and that 67.7% (1,447/2,139) of the coho salmon of Canadian origin in

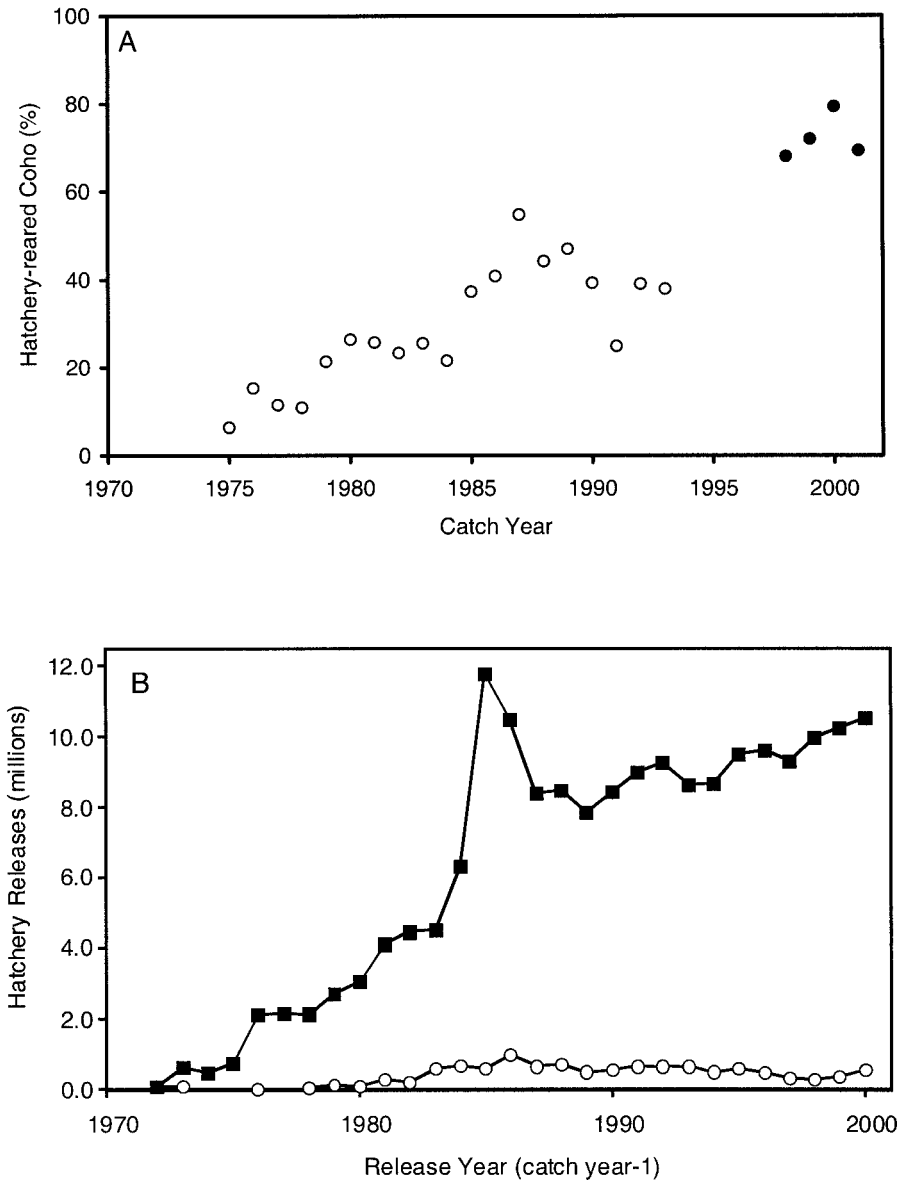


FIGURE 2.—Panel (A) shows the percentage of hatchery-reared coho salmon in the Strait of Georgia from 1975 to 1994 as determined from sport and commercial catches (open circles) and from 1997 to 2000 as determined from our research surveys (solid circles). Data from the research surveys are shown for the year after release so that they correspond to the catch estimates, which are for coho salmon 1 year older than those from our surveys. Panel (B) shows the releases of coho salmon smolts from hatcheries into the Strait of Georgia from 1972 to 2000 (solid squares), including the estimated contribution from fry, and the estimated smolt production from fry released in the previous year (open circles). The rate of increase in releases decreased after the exceptionally large releases in 1985 and 1986.

the Strait of Georgia were from Canadian hatcheries (Table 1).

Because Canadian and U.S. hatcheries released adipose-fin-clipped coho salmon from 1998 onwards, the calculations of hatchery percentages are

different for 1998–2000 than for 1997. We use the results of the September 2000 survey to illustrate the estimation of hatchery coho salmon percentages from 1998 to 2000 (Table 1). The total catch of coho salmon in the September 2000 survey was

TABLE 2.—Detection of hatchery and wild coho salmon by the otolith microstructure method. An explanation of the methods and results is included in the text.

Otolith category	1997	1998
Otolith pairs examined	100	100
Normal otolith pairs	62	56
Hatchery origin	39	33
Wild origin	23	23
Single-crystalline otoliths	17	23
Hatchery origin	15	20
Wild origin	2	3
Double-crystalline otoliths	21	21
Hatchery origin	18.5	18.3
Wild origin	2.5	2.7
Total hatchery	72.5	71.3
Total wild	27.5	28.7

1,321 (Table 1). Assuming that 11% were from Puget Sound (as previously discussed), 145 of these coho salmon would be of U.S. origin and the remaining 1,176 of Canadian origin. Adjusting the 537 adipose-fin-clipped fish (Table 1) for tagging mortality and detection errors produced an estimate of 601 marked salmon. In Canada, the adipose fins of 73.7% of the hatchery coho salmon smolts entering the Strait of Georgia were clipped in the year 2000 (MRP database). Therefore, the 601 marked fish in our sample represent a total of 816 Canadian hatchery fish, or 69.4% of the 1,176 Canadian coho salmon.

In 1997 and 1998, most of the otolith pairs had normal crystalline development, and microstructure analysis indicated that 39 and 33, respectively, came from coho salmon of hatchery origin (Table 2). Of the 17 pairs of otoliths in 1997 with a single crystalline otolith, 88% (15) were found to be of hatchery origin. Applying the same percentage to the 21 double pairs of crystalline otoliths, we determined that 18.5 were of hatchery origin. In 1998, 87% (20) of the 23 pairs with a single crystalline otolith were determined to be from coho salmon of hatchery origin, and thus 18.3 of the 21 double crystalline pairs were also of hatchery origin. Thus, the estimated total hatchery percentage for 1997 was 72.5%, and for 1998 it was 71.3% (Table 2).

From 29 June to 6 July 2001, 320 ocean-age-1 coho salmon were caught using troll gear in the Strait of Georgia, of which 151 were missing adipose fins. Assuming the same tagging mortality and detection error as previously noted, this represents 169 marked coho salmon. The hatcheries marked 73.7% of their releases for this brood year (MRP database), so these 169 adipose-fin-clipped coho salmon represent 229 hatchery fish or 71.6%

of the catch. This compares with a hatchery estimate of 69.4% for the same year-class in the Strait of Georgia in September 2000 (Table 1).

The percentages of hatchery coho salmon in the Strait of Georgia were estimated from 1975 to 2000 (Figure 2A). Although the estimates of hatchery percentages from our research surveys were made for the release year (i.e., the year of ocean entry), we show them for the return year in order to compare them with the recreational and commercial fisheries' estimates from 1975 to 1994. The trend shows increases of approximately 3.8% per year since the mid-1970s (Figure 2A). The trend could also be viewed as a series of staged increases associated with changes in hatchery releases or marine survival. The trends in hatchery releases (Figure 2B) changed in 1986, with an average increase of 0.47 million releases per year up to 1985 and 0.16 million releases per year after 1986 (including estimated contributions from fry releases).

Total coho salmon catches fluctuated between 450,000 and 1,500,000 fish from 1973 to 1994. After 1994, catches declined substantially as management actions reduced fishing opportunities (Figure 3A). The average coho salmon catch between 1973 and 1994 was approximately 750,000, with no indication of a trend (Figure 3A). The estimated exploitation rate (Figure 3B) ranged from 65.3% to 79.7% between 1976 and 1994. Exploitation rates between 1976 and 1994 appear to be relatively stable (Figure 3B).

Discussion

The percentage of hatchery coho salmon in the Strait of Georgia increased from 1973 to 2001. The increases appear roughly parallel to the trends in hatchery production up to the mid-1990s. In the late 1990s, the estimated percentage of hatchery fish increased substantially despite relatively stable hatchery releases. Our estimates show that from 1997 to 2000 the percentage of hatchery coho salmon in the aggregate coho salmon population was between approximately 68% and 81% (average, 72.5%) for Canadian releases. The high estimates of hatchery percentages in the late 1990s would have been even higher if the first generation of naturally spawning hatchery fish had been counted as hatchery fish and not wild fish.

The otolith microstructure method provided a similar range (71.3–72.5%) for the contribution of hatcheries to the coho salmon population in the Strait of Georgia. Zhang et al. (1995) ob-

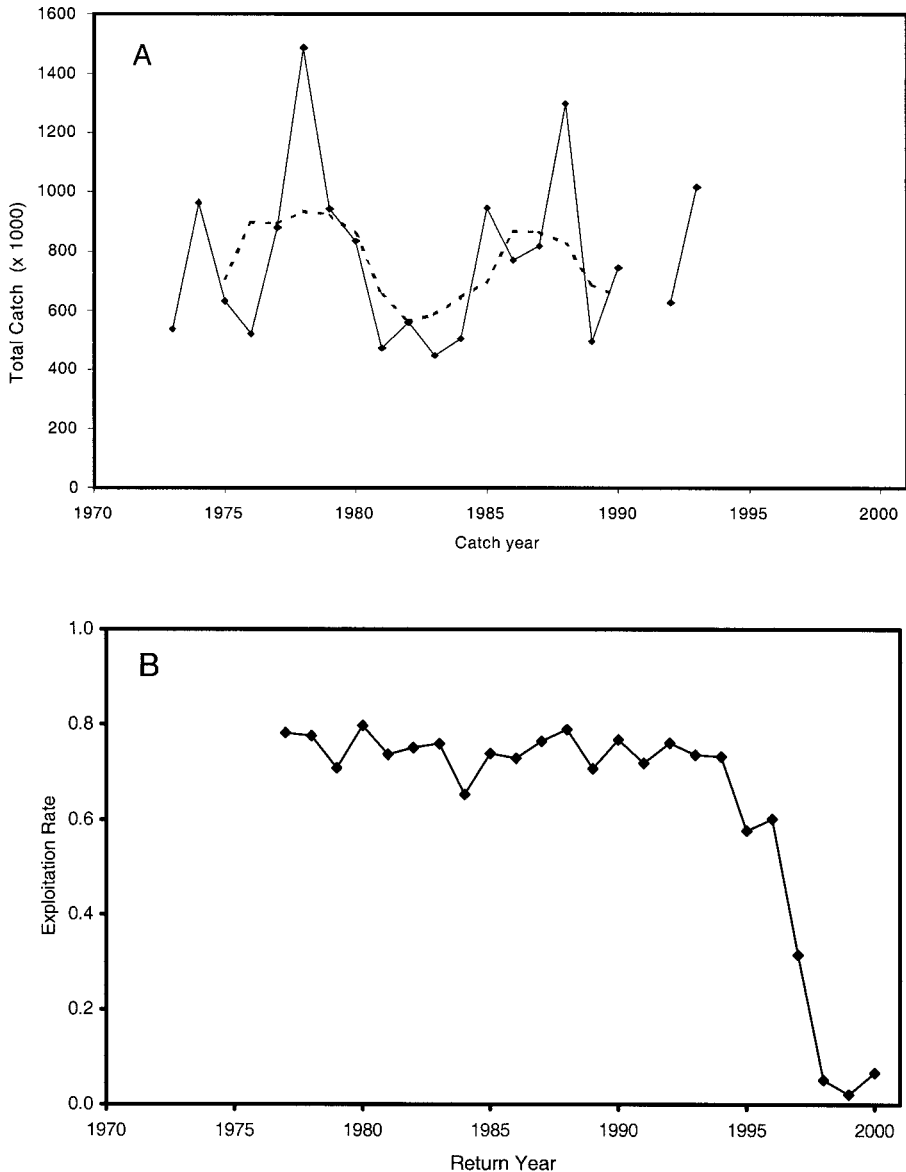


FIGURE 3.—Panel (A) shows the total catch of coho salmon produced from all Strait of Georgia stocks (solid line and diamonds), along with the 5-year moving average (dotted line). Panel (B) shows the exploitation rate for the fish in panel (A).

served that the accuracy of the otolith determinations for chinook salmon *O. tshawytscha* raised in hatcheries was approximately 91%. However, a pitfall with the otolith method of identifying rearing type is that it is difficult to validate the method for wild fish. Although large numbers of otolith pairs with crystalline structure complicated our identification of rearing type, we observed that crystalline otoliths are relatively common in hatchery-reared coho salmon and rela-

tively rare in wild coho salmon. Peck (1970) also found that crystalline otoliths were much more prevalent in hatchery coho salmon (55.9%) than in wild coho salmon (1.4%). The similarity in percentages of hatchery coho salmon in this study using two completely different methods is persuasive evidence that our calculated estimates of hatchery coho salmon are reliable.

A possible concern is the selective migration of either wild or hatchery coho salmon out of the

Strait of Georgia. In 1997, the percentage of hatchery fish in the September sample was slightly lower than the estimate in the June–July sample. For 1998 and 1999, the estimated hatchery percentages in September were slightly higher than those observed in the June–July surveys. For 2000, the September hatchery percentages were again slightly lower than the June–July values. The differences, however, were sufficiently small that there was a consistency of estimates within the two surveys across all years, indicating that there was no appreciable selective movement of rearing type out of the Strait of Georgia between the June–July and September surveys. The similarity in the estimates of ocean-age-0 coho salmon in September 2000 and those of the same brood year in 2001 as ocean-age-1 fish also indicated that all samples are representative of the population.

The commercial and recreational catch data are representative of total abundance through the early 1990s, as indicated by the relatively constant exploitation rates. There is no indication from these data of increases in abundance once hatchery releases stabilized in the mid-1980s to mid-1990s. Thus, there was a replacement of wild coho salmon by hatchery fish in both the catch and the population in the late 1980s and early 1990s in relation to the catch in the late 1970s and early 1980s.

There are other examples in which introductions of hatchery-reared salmonids have resulted in a reduction in the expected abundance of wild fish. In a study using hatchery coho salmon psmolts to rebuild wild populations in Oregon, Nickelson et al. (1986) found that the resultant densities of juveniles in stocked streams were actually lower than those in unstocked streams. Hatchery-reared pink salmon *O. gorbuscha* were first released into Prince William Sound, Alaska, in 1976 in an attempt to reduce the natural variability associated with the cyclic production typical of this species. As hatchery production increased in the mid-1980s, wild production decreased to pre-1977 levels even though the total returns remained high, suggesting that hatchery production replaced wild production (Cooney and Brodeur 1998; Hilborn and Eggers 2000). It was evident that the increasing trend in wild production was reversed as hatchery production increased (Cooney and Brodeur 1998), particularly as nearby regions without hatchery releases did not suffer decreases in wild production (Hilborn and Eggers 2000). In Glenariffe Stream, New Zealand, chinook salmon (from fall-run Sacra-

mento River, California, stock) were introduced into a population that had been supported by naturally spawning stocks since the mid-1920s. After the addition of hatchery fish in 1978, the total returns did not change but the proportion of wild chinook salmon declined to 34%, and hatchery fish have outnumbered naturally spawning fish every year since 1983 (Unwin and Glova 1997). Levin et al. (2001) reported that the survival of wild chinook salmon from the Snake River was reduced by density-related effects of hatchery-produced chinook salmon when ocean conditions were considered to be poor relative to an index of ocean productivity.

It is commonly accepted that hatchery coho salmon are larger than wild fish (Nickelson et al. 1986; Taylor 1986). However, it is difficult to compare the sizes of hatchery and wild coho salmon because there is considerable variation among stocks. There is a substantial body of literature indicating that during the juvenile stage larger individuals have a survival advantage over smaller ones due to enhanced resistance to starvation, decreased vulnerability to predators, and better tolerance of environmental extremes (Taylor 1986; Sogard 1997). Furthermore, higher smolt-to-adult survival rates for larger smolts in a given brood year have been observed in a number of salmon stocks (Foerster 1954; Ricker 1962; Parker 1971; Bilton et al. 1982; Henderson and Cass 1990). It remains difficult, however, to assess the extent to which this may affect the survival of wild and hatchery fish, as there also is evidence that hatchery fish may not be as successful as wild fish when they are in the ocean (Olla et al. 1998).

The increase in the percentage of hatchery fish in the late 1990s may be a consequence of the dramatic decline in marine survival to less than 2%. Marine survivals declined from an average of 11.2% in the period from the mid-1970s to the mid-1980s to an average of 4.6% in the period from 1990 to 1995 (Beamish et al. 2000b). However, exploitation rates were not reduced proportionally. We propose that this combination of reduced ocean productivity and high exploitation rates would reduce wild smolt production. Hatchery production would therefore represent an increasing proportion of total smolt production even though hatchery releases increased very little in the 1990s.

The decline in marine survival in the 1990s has been associated with a large-scale change in climate that occurred about 1989 (Beamish et al.

1999b, 2000b; Hare and Mantua 2000). The magnitude of the decline in survival is an indication that there was a change in the ocean ecosystem of coho salmon that reduced their productivity. A reduction in the capacity of the marine habitat to produce coho salmon is generally referred to as a reduced carrying capacity, although the term carrying capacity has some specific meanings that some feel restrict the use of the term. The increase in the percentage of hatchery coho salmon, therefore, occurred at a time of reduced marine survival, continued high exploitation rates, and a marine habitat that was less favorable for coho salmon.

A variety of mechanisms may be responsible for increases in the percentage of hatchery coho salmon, including the selective impacts of fishing on the less productive wild stocks (Ricker 1973). An increasing percentage would also reflect the increasing percentage of hatchery smolts that are added to the ocean. The possibility of the replacement of wild coho salmon by hatchery fish through competitive processes in the ocean may be important when marine survival declines, as reported by Levin et al. (2001). The percentage and abundance of wild coho salmon would decrease during periods of reduced ocean carrying capacity if there is an increasing percentage of hatchery coho salmon entering the ocean. Overall, we propose that at the beginning of the hatchery program it is the increasing number of hatchery coho salmon being released relative to the wild coho salmon production that is responsible for the increasing percentage of hatchery fish in the Strait of Georgia. A decline in wild smolt production probably occurred in the early 1990s as a result of declining marine survival and high exploitation rates. This decline was not matched by decreased hatchery releases. As a consequence, the percentage of hatchery coho salmon in the Strait of Georgia population increased in the mid-1990s even though there was only a relatively small increasing trend in hatchery releases compared with the 1970s and early 1980s. A number of climate and ocean indices, such as the Pacific Decadal Oscillation (Hare and Mantua 2000), shifted in 1998, indicating a new regime (Beamish et al. 2000; McFarlane et al. 2000). This regime shift may once again have altered the ocean's carrying capacity for coho salmon. If increased survival leads to increased escapements of wild coho salmon and hatchery releases remain stable, we would observe a decrease in the overall per-

centage of hatchery-reared coho salmon relative to wild production.

We propose that hatchery-reared coho salmon no longer be considered as additive to the wild production. Rather, hatchery fish should be considered as ones that interact with wild coho salmon through the natural competitive processes that select the individuals that will successfully occupy the available marine habitat. At the beginning of the hatchery program in the early 1970s, it was believed that the abundance of coho salmon could be rebuilt and wild stocks supplemented by adding more smolts to the ocean than would be produced naturally in rivers and streams. Thus, there was no policy that protected wild coho salmon. Levin et al. (2001) also noted the absence of a policy in the United States requiring an assessment of the impacts of artificially reared chinook salmon on wild ones. We now know that ocean and climate influences complicate the use of hatcheries as a management strategy. Much remains to be understood about the processes involved, but it is clear that strategies are needed for the management of both hatchery and wild coho salmon and that any enhancement program requires clear policies for both the wild and the enhanced stocks. Furthermore, these policies should include not only limits to the production of Pacific salmon in marine ecosystems but also provisions to vary production according to prevailing ocean conditions. Successful management of Pacific salmon in the future must recognize that the numbers of wild Pacific salmon that return to spawn (escapement) is a function of wild and hatchery production, of ocean carrying capacity, and of fishing rates.

Acknowledgments

We would like to thank Z. Zhang for determining the coho salmon rearing type using otolith samples. J. King was most helpful with the comments on the manuscript and discussions throughout the project. C. Cross, S. Lehmann, and M. Bradford all provided helpful comments on earlier versions of the manuscript. We would also like to extend our thanks to the crew of the *W. E. Ricker* for their assistance during the many sampling surveys.

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