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Declines in chinook salmon catches in the Strait of Georgia in relation to shifts in the marine environment

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ABSTRACT

Chinook, *Oncorhynchus tshawytscha*, catches in the Strait of Georgia increased in the 1970s and reached maximum levels from 1976 to 1978. Catches then declined until they stabilized through regulation at levels approximately one-quarter of the 1976 to 1978 levels. The timing of the decline in catch was synchronous with an increase in the mean temperature of the Strait of Georgia, a decline in annual Fraser River flows, and an abrupt decrease in the marine survival of hatchery-reared chinook released into the Strait of Georgia. Surprisingly, the number of young chinook salmon (smolts) more than doubled over the period of declining catches compared with the number produced during the period of high catches. The increase in smolt abundance was a consequence of the production from hatcheries that was approximately equal to wild production.

We conclude that there was a change in the carrying capacity for chinook salmon in the Strait of Georgia in the late 1970s that contributed to the declines in abundance and that rebuilding stocks to the high abundance of the late 1970s is unlikely until the carrying capacity for chinook salmon changes either naturally or through manipulation. Although we did not separate density-dependent and density-independent effects on marine survival, the current total number of chinook smolts produced appears larger than required for the current marine carrying capacity.

Key words: chinook salmon, carrying capacity, climate change, Strait of Georgia

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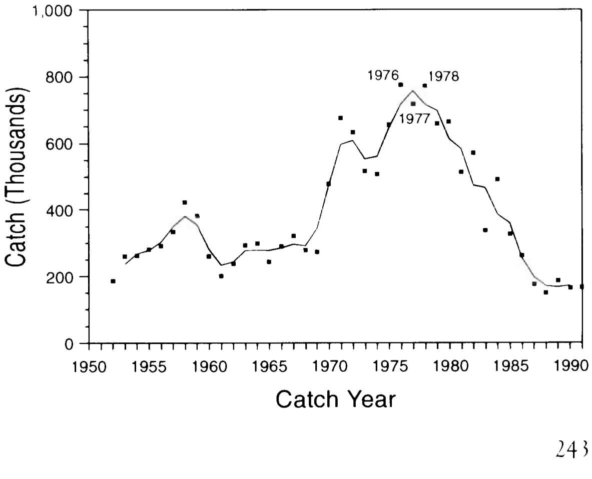
INTRODUCTION

When the abundance of a salmon stock declines, the management action that is frequently taken is to try to increase the number of spawners in order to rebuild the stock to previous higher levels of abundance. The rebuilding level may be a recent high level or it may be some historic high level, but the target for rebuilding is related to previous abundance or production and not to the current carrying capacity of the particular marine environment. If the productivity of the marine environment has not changed, except for random interannual fluctuations, then rebuilding to previous high levels should be possible. However, if there was a reduction in the carrying capacity of the marine environment at the time of the declining abundance, then it may not be possible to achieve historic high abundance even in the absence of fishing. In this paper we use the term carrying capacity to include all of the natural factors that interact to regulate the abundance of a species. In general, these factors could include both food and associated species.

Total catches of chinook salmon, *Oncorhynchus tshawytscha*, in the Strait of Georgia (commercial troll, seine and gill net, and sport) averaged 284 000 fish from 1952 (when the time series begins) to 1969 (Fig. 1). Beginning in 1970, catches increased rapidly to a maxi-

Figure 1. Total catch of chinook salmon in the Strait of Georgia sport and commercial fisheries, 1952–1991 (points). A three-year running average of total catch shows a change in trends in the late 1970s (line).



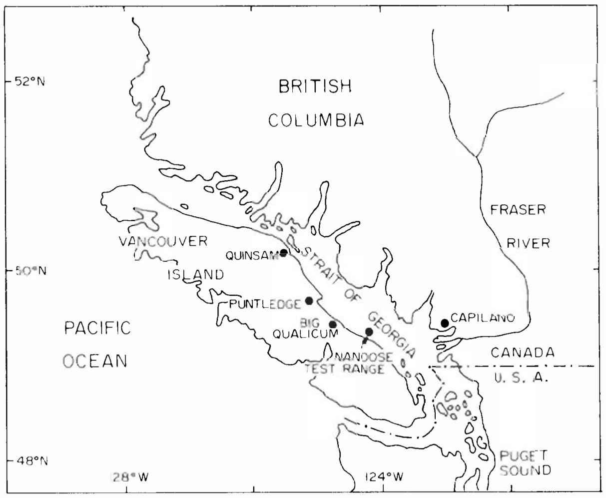
mum of 775 000 in 1976, averaging 755 000 from 1976 to 1978. In 1979 catches began declining steadily to 175 000 in 1987, when catch regulations that started in 1985 were broadened. From 1987 to 1991, catches averaged 168 000. In this report, we examine the catch trends beginning in the mid-to-late 1970s in relation to trends in the marine environment, to determine if factors other than fishing were associated with the decline.

METHODS

Information from hatcheries

The Canadian hatchery programme provides an accounting of hatchery releases of chinook salmon smolts and returns of these fish as adults. In particular, this information provides survival estimates for hatchery-reared chinook. Canadian hatchery releases of chinook salmon from major hatcheries into the Strait of Georgia began with the 1971 brood year (year of spawning). Estimates of smolt-to-adult survival rates are available since the 1973 brood year through the coded-wire tagging of juvenile chinook (Cross *et al.*, 1991). Coded-wire tags are inserted into the snout of the fish. The adipose fin of these fish is then removed as an external mark identifying these fish as tagged. Hatchery releases in the early-to-mid 1970s were dominated by the four main hatcheries in the Strait of Georgia (Big Qualicum, Puntledge, Capilano and Quinsam, Fig. 2).

Figure 2. Map of Strait of Georgia, Puget Sound and Fraser River showing location of major hatcheries in the Strait of Georgia and the water temperature monitoring location near Nanoose Bay.



Smolt output from most other smaller hatcheries and hatcheries in the Fraser River drainage began in the later 1970s and early 1980s. The releases of chinook salmon from all of these hatcheries remained below 8 million until the 1980s. By the late 1980s, releases of chinook salmon smolts were approximately 4 times as great as those in the late 1970s.

Hatchery releases of chinook salmon include fish released at the smolt and fry stage. Fry releases represent only about 4% of the total releases and to simplify the analysis in this report we use the term smolt to refer to the combined releases of 'smolt' and fry. Numbers of chinook smolts released by hatcheries in the Strait of Georgia, Fraser River and Puget Sound (Washington State) and the subsequent return of adults were obtained from the Department of Fisheries and Oceans' Salmon Stock Assessment Mark Recovery Program (MRP) database (Kuhn *et al.*, 1988). In most instances, a proportion of the chinook smolts released from the hatcheries have been permanently marked using coded-wire tags. Catches from commercial and sport fisheries, and escapements to hatcheries and some rivers are sampled for these tagged hatchery fish. Information on the number of hatchery fish released, with coded-wire tags, and the estimated number of coded-wire tagged fish recovered is used to estimate the survival of the hatchery fish.

Estimating smolt abundance

An estimate of the number of chinook smolts entering the Strait of Georgia in the mid 1970s was made using a cohort reconstruction (Starr and Hilborn, 1988). This technique uses spawning escapement and catch data by age-class, and assumptions concerning natural mortality rates and stock distributions, to reconstruct abundance at a previous point in time. The analysis was implemented in a Lotus 1-2-3 spreadsheet so that the effect of varying assumptions could be investigated. The number of chinook in June of their first year in the sea was estimated.

Commercial troll and recreational catches were averaged for 1975 to 1977 (Fig. 1). Age structure of the catches was reported in Argue *et al.* (1983). Net-caught chinook with the exception of the terminal gill net catches in the Fraser River were omitted from the analysis because the catches were small. Terminal net catches in the Fraser River are included in the terminal run data used for the Fraser chinook escapements.

Average escapements or terminal runs (terminal catch, native food catch, and spawning escapements) were determined for five major Canadian chinook stocks known to contribute to these fisheries. Age composition of the spawning population has in-

Table 1. Age composition (%) of spawning chinook salmon in Fraser River, Lower Georgia Strait (LGS) and Upper Georgia Strait (UGS).

		Age (years)			
Stock	Run	2	3	4	≥5
Fraser Late[1]	Terminal	0.1	24.5	67.5	7.9
Fraser Early, spring/summer[2]	Terminal	0.1	26.1	67.9	5.9
LGS, hatchery[3]	Spawners	15.8	42.2	40.3	1.7
LGS, natural[3]	Terminal	15.8	42.2	40.3	1.7
UGS, hatchery[4]	Spawners	0.5	4.1	34.7	60.7

[1] Data from Starr and Schubert (1990).

[2] Data from N. Schubert (pers. comm.). Fraser River chinook test fishery, 1980–1984.

[3] Age composition in escapement of coded-wire tagged chinook to Big Qualicum River 1974–1976. Hatchery stocks included are the Big Qualicum, Little Qualicum and Capilano. Natural stocks included are the Cowichan, Nanaimo and Squamish Rivers. The hatchery and wild stock have the same age structure since samples for ageing were not available from the natural population.

[4] Age composition in escapement of coded-wire tagged chinook to Quinsam River 1974–1976. Hatchery stocks included are the Puntledge, Quinsam and Campbell Rivers.

frequently been collected so several sources of age data were utilized (Table 1).

Escapements of Canadian chinook stocks are of varying quality and are seldom known with accuracy. To evaluate the sensitivity of the reconstruction to underestimation of escapement, two analyses were conducted. In scenario A, escapements were accepted as published and averaged for the years 1975–1979, with the exception of the 'Fraser Late' stock. In the 'Fraser Late' stock (i.e. Harrison River chinook) the visual estimates of spawners for these years were multiplied by 5.185 which is the average factor reported by Starr and Schubert (1990). In scenario B, escapements were increased to account for the likely under-reporting of spawners based on visual escapement surveys. The resulting escapements and/or terminal runs are listed in Table 2.

Table 2. Chinook spawning escapement and/or terminal run sizes to the Fraser River, Lower Georgia Strait (LGS) and Upper Georgia Strait (UGS). For explanation of scenarios, see text.

Stock	Scenario A	Scenario B
Fraser, late	99 000	80 372
Fraser, early	112 800	162 500
LGS hatchery	5 700	8 550
LGS natural	11 300	22 600
UGS hatchery	4 100	6 150

The proportion of each stock, by age, caught within the Strait of Georgia, was estimated using coded-wire tag recoveries, but the years of available recovery data varied. For the Lower Georgia Strait (LGS) and Upper Georgia Strait (UGS) stocks, recoveries of the 1974–1976 brood years were used. Tag groups for the 'Fraser Late' stock were not available for these years. The earliest tagging on this stock was for the 1981–1983 brood year releases from the Chilliwack and Chehalis hatcheries (using broodstock from the Harrison River). Recoveries for the 'Fraser Early' stock were provided by N. Schubert (unpubl. manuscript) based on the wild stock tagging conducted in upper Fraser stocks during the mid-to-late 1970s. The chinook populations included in these studies were the Chilko, Thompson, Shuswap, and Deadman Rivers. Inside recoveries were defined as recoveries from the Strait of Georgia sport and troll fisheries and any recoveries of immature chinook in nets (i.e. recoveries of age 2 or 3 chinook).

Because these stocks vary greatly in their abundance and are known to vary in their contributions to these inside fisheries, a weighted value across the stocks was calculated and used as an expected proportion of these stocks within the strait (Table 3). The weighting reflects a reasonable ratio of contributions by these stocks.

Reconstruction of US stocks from Puget Sound is extremely complicated due to their numerous terminal fisheries and stocks. We have addressed these stocks by removing a portion of the catch and then examining the sensitivity of the final smolt estimates to various assumptions about the contribution of Puget Sound

Table 3. Proportion of Strait of Georgia and Fraser River chinook stocks caught in the Strait of Georgia sport and troll fisheries.

Stock	Weighting	Age (years)			
		2	3	4	≥5
Fraser Late	0.4	0.686	0.5525	0.444	0.453
Fraser Early	0.2	0.391	0.391	0.141	0.059
LGS (both)	0.3	0.623	0.566	0.429	0.157
UGS hatchery	0.1	0.117	0.106	0.093	0.222
Weighted average		0.5511	0.4795	0.3436	0.2623

stocks. The catches were reduced by 15% in the troll fishery and 25% in the recreational. These values were used, for the period of interest, by the 'Informal Chinook and Coho Committee' to estimate interceptions of US chinook in these fisheries.

Due to changes in size-limit regulations, the total fishing mortality associated with the Strait of Georgia troll fishery must also account for incidental mortalities. These incidental mortalities were estimated using the size distribution of age 2 chinook in the Strait of Georgia, rates of encounters with age 2 chinook observed in the troll fishery, and a release mortality rate of 30%. Cohort analyses for Big Qualicum chinook (1974–1976 brood years) estimate that two incidental mortalities would be expected for every three chinook retained. Total fishing mortality of age 2 chinook was estimated as 1.67 times the age 2 catch.

Annual natural mortality rates assumed were: 0.1 for age 5, 0.2 for age 4, and 0.3 for age 3. These values have commonly been applied in several models of chinook population dynamics. Cohort reconstructions were performed back to age 2 recruitment to the fisheries (1 July was the assumed date of recruitment in these analyses). For the period before age 2 recruitment, the spreadsheet model allows various monthly rates of natural mortality to be applied.

$$(\text{Cohort size at age 2 recruitment}) * (1 / (1-x))^{t},$$

where x is the monthly natural mortality rate and t is the number of months to back-calculate the cohort size (t would equal 13 if calculating the number of smolts entering the strait by June of the previous year). The actual monthly mortality rate for chinook is unknown but can be estimated using the numbers of coded-wire tagged chinook released from hatcheries and the number which subsequently recruit to the fisheries. For the Big Qualicum hatchery-reared chinook from the 1974 and 1976 brood years, the survival from hatchery release to age 2 recruitment (1 July) ranged from 5.4% to 13.9% with an average survival of 10.5%. This is equivalent to a monthly mortality rate of 17.1% for June hatchery releases.

We used a second method to estimate the number of chinook smolts entering the Strait of Georgia that we termed the average survival method. This method does not attempt to reconstruct the abundance of each age group in the various fisheries. Instead we used total catches and escapements that were assumed to occur at an ocean age of 2 years or the brood year plus 3 years. We separated Canadian hatchery fish in the catch (Kuhn *et al.*, 1988) and we estimated the contribution of US hatcheries using their smolt production estimates and a per cent contribution based on our observed percentage of US coded-wire tagged smolts in our 1992 samples. We used hatchery survival estimates (Cross *et al.*, 1991) to represent the marine survival of wild smolts and we used these estimates to calculate the number of smolts entering the Strait of Georgia that would produce the observed catches and escapements. The estimates for the three years were then averaged.

Total smolt abundance in recent years was estimated using the known numbers of hatchery-produced smolts to estimate the abundance of wild smolts. The hatchery fish were equivalent to tagged fish in a mark-and-recapture study to estimate population size. To make this estimate we had to determine the percentage of hatchery and wild smolts in the Strait of Georgia. This determination was made by collecting chinook smolts in the lower Strait of Georgia at the time smolts entered salt water. Chinook smolts were collected using paired beam trawls that were fished continuously on each side of a chartered seine vessel or using the *W.E. Ricker*. For the seine vessel the nets were approximately 9 m wide and fished from the surface to 6–7.5 m deep. The cod-end mesh size was 2.5 cm with a liner of 1.5 cm mesh. Beam trawls fished from the *W.E. Ricker* had a slightly larger opening but the mesh sizes were the same except for the cod-end liner which had a 1.9 cm mesh. All chinook captured were identified using specialized keys, measured, checked for missing fins. Otoliths were removed and scales were obtained when possible. The sampling plan was designed to collect chinook from areas of known abundance, as well as to sample in the centre and both sides of the strait. We attempted to collect samples of 200–400 chinook in each cruise, but we considered it more important to sample throughout the strait than to obtain large catches from one area. The chinook smolts that were collected were identified as hatchery-reared or wild using the pattern of daily growth in the otoliths (Zhang *et al.*, 1995). All otoliths increase in size by producing a daily increment with two zones (Pannella, 1971). One zone contains more protein than the other and appears darker when viewed with a microscope using transmitted light (Campana and Neilson, 1985; Zhang, 1992). There are several factors that affect the width and appearance of each zone, including temperature, the amount of food and the schedule of feeding (Campana and Neilson, 1985; Zhang and Runham, 1992).

Changes in the ocean environment in the Strait of Georgia

Temperature Vertical temperature profiles were taken 8–20 times each month in the deep water at the Nanoose Bay Naval Underwater Weapons Test Range approximately mid-way between the north and south ends of the Strait of Georgia (Fig. 2). The temperature profiles were collected using several different continuous temperature and depth instruments. Data were checked for spikes and unrealistic parameter values and these data were deleted (Fissel *et al.*, 1991). In addition, the temperature data were compared to data collected once each month using reversing thermometers (Fissel *et al.*, 1991). The time series begins in 1970 and is the most complete series of vertical temperatures in the strait.

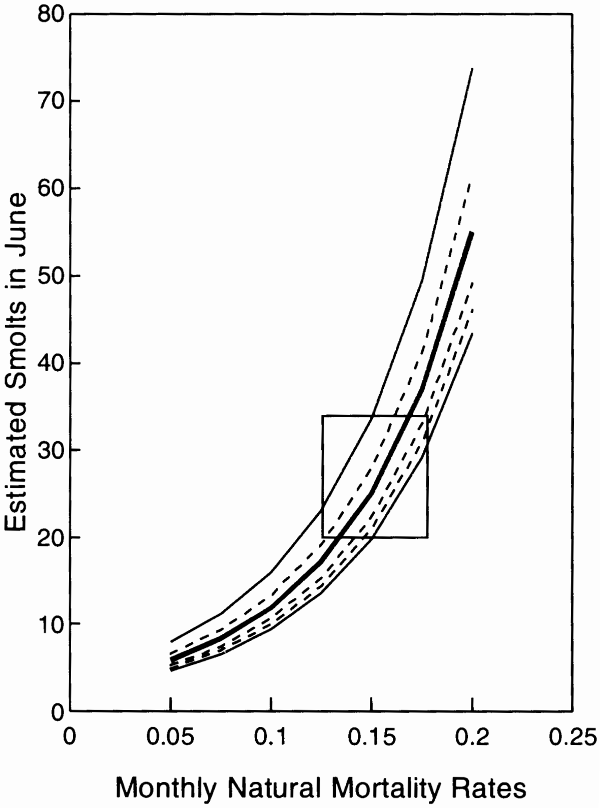
Fraser River flow Trends in flows of the Fraser River were examined using a cumulative sum analysis (Murdoch, 1979). This analysis is useful for the detection of changes in the trends as well as identifying the year the trends change.

RESULTS

Cohort reconstruction

The age 2 cohort of Canadian chinook at recruitment were estimated to be 2.02 million chinook smolts under scenario A and 2.10 million chinook smolts under scenario B. If one-third of the smolts were contributed from Puget Sound, and assuming a 15% monthly natural mortality rate, these age 2 cohort sizes would require average smolt population sizes of 22.3 to 23.2 million chinook in June of their smolt year (1974 to 1976). The range in smolt abundance was insensitive to the range in escapements used but is sensitive to the assumptions about Puget Sound stock contributions and monthly mortality rates (Fig. 3). Based on the range in coded-wire tag survival rates observed in the mid-1970 broods and a reasonable range of Puget Sound stock contributions, the probable range in smolt population size would be 22 to 35 million smolts. For the brood years contributing to the 1975–1977 catches, the average number of Canadian hatchery smolts released was only slightly over 1 million. The range in Canadian wild smolts would therefore be between 14 and 22 million.

Figure 3. Range of estimates of chinook smolt abundance (millions of fish) in the Strait of Georgia for the period 1975–1977. Curves represent various levels of smolt contributions from Puget Sound hatcheries (values 0.15 (bottom curve), 0.2, 0.25, 0.33, 0.4, 0.5). The bold curve represents the 0.33 Puget Sound value, and the box encompasses the approximate location of the most likely range of smolt estimates (22–35 million).



These values may seem low but given the fishing pressure being exerted in the 1970s and the reduced spawning population sizes, they may be reasonable.

Table 4. Estimates of chinook salmon production in the Strait of Georgia.

Brood year	Strait of Georgia Canadian catch			Escape ($\times 10^3$)	Wild return (total – hatchery) ($\times 10^6$)	Hatchery survival	Calculated releases from Puget Sound hatcheries in the Strait of Georgia ($\times 10^6$)	Total wild smolt ($\times 10^6$)	Total smolt release ($\times 10^6$)
	Commercial ($\times 10^6$)	Sport ($\times 10^6$)	Hatchery[1] ($\times 10^3$)						
1974	0.6	0.4	17.8	117.5	1.1	6.6	0.9	16.1	16.9
1975	0.7	0.3	21.6	98.2	1.1	2.4	2.7	46.0	48.7
1976	1.2	0.6	57.7	95.3	1.8	4.5	2.9	40.4	43.3

[1] Strait of Georgia and Fraser River production caught in Strait of Georgia fisheries (including Quinsam hatchery production).

Certainly 80+% of the production will have been reported in catch, making it unlikely that the age 2 recruitment could be significantly changed by simply increasing the error assumed in escapement estimates. A more serious concern, however, would be equating 'juveniles' between stock types. Downstream migration of chinook fry from the 'Fraser Late' stock and portions of the Cowichan and Campbell rivers production, could increase the numbers entering the strait but their early marine survival is unknown. The survival, however, would be less than the 15% used here for the larger chinook smolts. In the absence of any more detailed information, however, this reconstruction seems about as detailed as possible.

In the average survival method we used estimates of hatchery survival in the Strait of Georgia sport and commercial catch that ranged from 2.4% to 6.6% (Cross *et al.*, 1991; Table 4). The average total production for these brood years was 36.3 million chinook of which 34.2 million were wild. These estimates are very close to the higher range of estimates produced from the cohort analysis. These analyses indicate that the likely range of smolt production responsible for the high catches in the late 1970s was 22 to 36 million smolts.

Percentage of hatchery and wild fish in 1992

In 1992, 1043 chinook smolts were sampled from the southern Strait of Georgia from May to July using beam trawls and in 1993, 1756 chinook smolts were captured. The percentage of hatchery fish in the samples was 47% in 1992 and 49% in 1993. If the number of hatchery-reared smolts that are in the Strait of Georgia is approximately equal to one-half of all chinook smolts, then we can determine the total number of smolts that enter the strait once we determine the Canadian hatchery releases plus a percentage of the releases from Puget Sound hatcheries. We used 1992 to estimate the number of chinook salmon smolts from US hatcheries in the Strait of Georgia because our study started in this year. In 1992, 3 of 32 coded-wire tags from chinook smolts caught in our survey were from Puget Sound hatcheries. Puget Sound hatcheries released an estimated 61.5 million smolts in 1992, 6.8% of which were coded-wire tagged (MRP database, Kuhn *et al.*, 1988). Canadian hatcheries released approximately 34 million smolts, approximately 15% of which were tagged (Anon., 1993a, MRP database). Using these data, tagging percentages, and our recovery of 9% tagged US hatchery fish, we estimated that approximately 6.8 million Puget Sound hatchery-reared fish were present in the Strait of Georgia, raising the total number of hatchery fish to 40.8 million. Assuming a 50:50 ratio of hatchery to wild chinook smolts in the strait, approximately 81.6 million chinook smolts entered the strait in 1992.

Our estimate of the contribution of US-produced hatchery smolts to the Strait of Georgia is conservative and approximate. The catch of US-produced chinook in recent years is higher than 9% (Anon., 1993b), perhaps indicating that more US smolts enter the strait than estimated in our analyses. However, it is important to note that the chinook in the catch represent the less than 1% of the smolts that survive, and that these fish have been in the ocean for more than 1 year and not necessarily resident in the strait. If we use the catch data as an indication of the percentage of US hatchery smolts in the strait, our estimate of smolt abundance will be larger but would not affect the general conclusion.

Accuracy of the estimate of hatchery and wild smolts

The accuracy of our estimate of the percentage of hatchery and wild smolts in 1992 and 1993 can be

Figure 4. Percent contribution of chinook salmon from Canadian hatcheries to the Strait of Georgia sport (squares) with regression (solid line) and to the combined sport and commercial fisheries (crosses) with regression (dotted line).

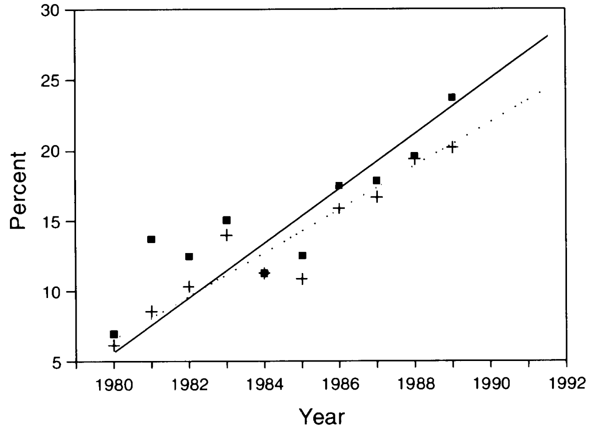


Table 5. Estimated proportion (%) of Washington State (US) adult chinook salmon in Strait of Georgia fisheries[1].

Year	Strait of Georgia troll	Strait of Georgia sport	Strait of Georgia seine	Strait of Georgia gill net
1980	15.5	25.9	19.0	19.0
1981	16.4	24.9	19.1	19.1
1982	13.2	25.4	17.7	17.7
1983	17.3	32.2	20.3	20.3
1984	17.9	30.8	18.1	18.1
1985	15.0	28.0	20.0	20.0
1986	15.3	35.3	26.6	26.6
1987	33.0	51.1	29.6	29.6
1988	35.1	52.6	25.3	25.3
1989	28.1	39.0	22.2	22.2
1990	15.4	30.5	15.1	15.1
1991	14.1	27.0	13.4	13.4

[1] Source: Anon. (1993b).

assessed using information on the percentage of hatchery and wild chinook in the catch. Data on the contribution of hatchery fish to the catch are not available for recent years, requiring that we estimate the percentages in recent years. Estimates of the percentage of Canadian hatchery-reared chinook in the Strait of Georgia catches are available up to 1989 for the sport and combined sport and commercial fisheries. In 1989 they were 24% and 20% respectively (Cross *et al.*, 1991). The percentages were increasing at about 2% a year throughout the 1980s. If the percentages continued to increase at the same rate, the estimated values for 1992 would be about 29% for the sport fishery and 25% for the combined sport and commercial fisheries (Fig. 4). Preliminary unpublished analyses of the combined percentage of Canadian hatchery-reared chinook in the sport and commercial fisheries after 1989 indicate that the percentage may be higher than 25%, but for this analysis we will use our forecasted estimate of approximately 25%.

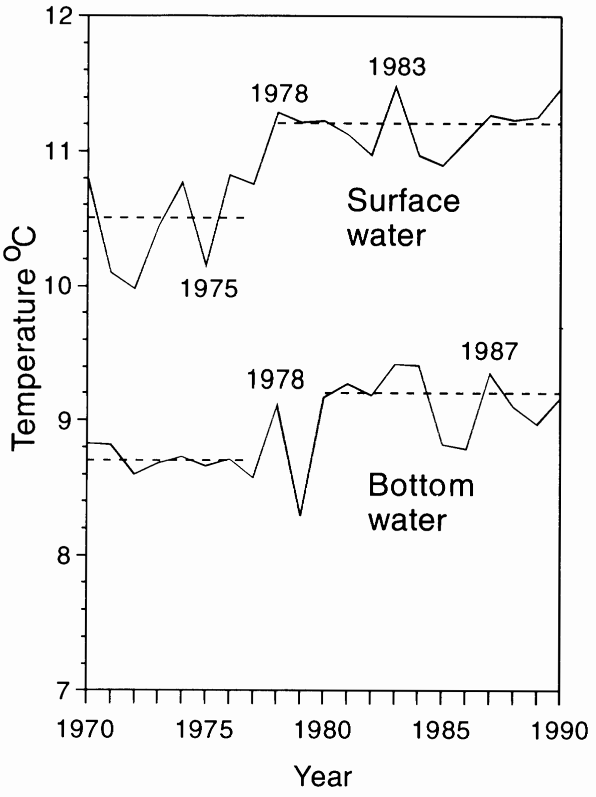
From 1986 to 1990, the average percentage of Washington State chinook in the Strait of Georgia sport, troll, seine and gill net fisheries was 42%, 25%, 24% and 24% respectively (Table 5; Anon., 1993b). An estimate of the percentage of Washington State chinook in the combined Strait of Georgia fisheries was calculated by applying the percentages from Table 5 to catch estimates from the four fisheries for the years 1986 to 1990 (Holmes and Whitfield, 1991; Collicutt and Shardlow, 1992). The weighted average percentage of Washington State chinook in the combined Strait of Georgia fisheries for this period was 35%. We assumed that all of the chinook produced in Puget Sound were reared in hatcheries. Thus in 1992, this 35% plus 25% from Canadian hatcheries or about 60% of the catch in the Strait of Georgia was from chinook produced in hatcheries. Our estimate of approximately 50% hatchery and wild smolts is similar to estimates of the percentage of hatchery and wild fish in the catch and thus appears to be a close approximation of the percentage of hatchery and wild smolts that enter the strait.

Changes in the ocean environment

Temperature The average yearly surface temperature from 1970 to 1977 was 10.5°C and from 1978 to 1991 it was 11.2°C. There was an abrupt increase in 1978 and average yearly surface temperatures have remained consistently higher than the pre-1978 levels. An intervention analysis (Noakes, 1986) indicated that the step shift in temperature in 1978 (Fig. 5) was significant (step intervention = 0.337, SE = 0.165, $P < 0.05$).

Average yearly bottom temperatures were taken at approximately 325 m (Fig. 5). From 1970 to 1977 the average annual bottom temperature was 8.7°C. There was an abrupt increase in 1978 as was observed for surface temperatures, but this was followed by an abrupt decrease in 1979. In 1980, bottom water warmed again and has remained warmer than the pre-1978 levels. The average annual monthly temperature from 1980 to the 1990s was 9.2°C. An intervention analysis identified 1980 as the year that a significant increase in temperature occurred (step intervention = 0.207, SE = 0.086, $P < 0.05$).

Figure 5. Average surface and bottom water temperatures in the Strait of Georgia showing the abrupt change in temperature in 1978. Data are average daily values summarized by year.



Fraser River flows The cumulative sum analysis indicated that from the early 1920s (when the time series begins) to the late 1940s the flows were below the long-term average (Fig. 6A,B). The pattern of flows changed in 1945 and from 1946 to 1956 flows were average. From 1957 to 1976 flows increased again. In 1977, the current period of reduced flows began and has continued to 1994.

Synchrony of environmental changes and changes in the biology of chinook and the dynamics of the chinook population

The survival of all Canadian hatchery-reared chinook salmon smolts from Strait of Georgia hatcheries averaged 4.82% from 1974 to 1977 but dropped dramatically for smolts that went to sea in 1978 (Fig. 7). The survival from 1978 to 1988 remained low and averaged 0.71% (i.e. approximately a sevenfold decrease in survival). We would expect a fourfold decrease in marine survival with a fourfold drop in catch if there was no major change in smolt production when the catches declined. Because smolt production doubled, as we estimated, the decline in survival should be eightfold or very close to the observed sevenfold decrease. That is, the current marine survival of hatchery fish is approximately what would be expected if there was a shift in carrying capacity and smolt abundance described. Although the decline in hatchery survival occurred synchronously with the decline in catch (Fig. 8), the increase in hatchery production occurred later and appears not to have had an impact on the trend in catch (Fig. 8). Again, this would be expected, if the carrying capacity were reduced after 1977.

Our estimates assume that the marine survival of hatchery and wild smolts are about equal. While this appears true for coho (Cross *et al.*, 1991), it is not known if it is true for Canadian hatchery-produced chinook. If we assume that marine survival of hatchery fish is the same or less, then we can assume that our estimates of wild smolt abundance are minimum estimates.

Possible explanations for the declines in chinook abundance

There are two potential explanations for the changes in production: (1) there was a change in the productive capacity of the environment, i.e. a reduction in the carrying capacity of the strait caused by an abrupt change in the oceanography of the strait, i.e. a regime shift, and (2) the productive capacity was stable but became fully utilized by an increased number of juvenile chinook, i.e. density-dependent survival of juveniles. The two factors may not be operating independently. To complicate the processes even more, there was a hatchery programme in Canada and the United States that started adding smolts to the ocean just before the physical regime changed. These alternatives may be compared in a schematic representation of production functions (Fig. 9). There are four possible comparisons from this schematic representation.

A. No regime shift and no density effect.
B. A regime shift and no density effects: under this hypothesis, the relationship between smolts released and production returning would be linear, and any decrease in productivity would be evident as a lower slope in the relationship over time. We show two slopes, but in theory there could be a series of declining slopes.
C. No regime shift but a density effect: this hypothesis would suggest that only one productivity function would describe the time series of data. As the number of released smolts increased, the carrying capacity was reached and the return rate per smolt decreased.

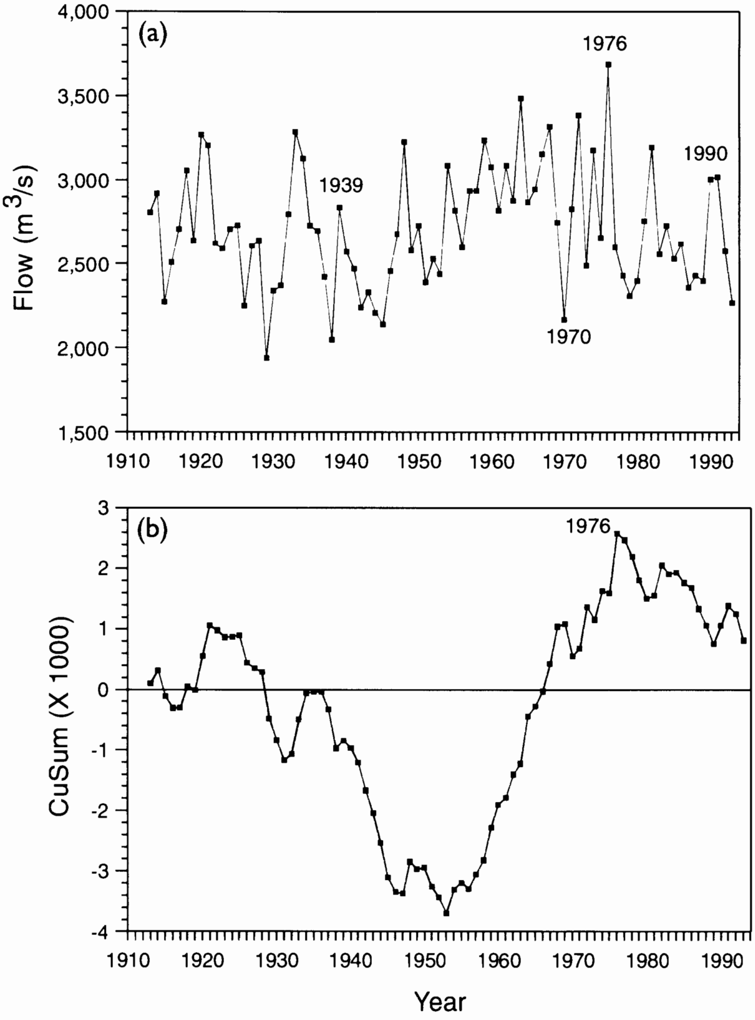


Figure 6. (A) Average annual daily discharge rate of the Fraser River at Hope. The highest discharge in the time series occurred in 1976. (B) Cumulative sum (CuSum) analysis of the average annual daily discharge of the Fraser River at Hope showing that there was a period of above-average flows from 1953 to 1976 (positive slope of the CuSum plot) and that after 1976, the trend is below average (negative slope). The CuSum analysis indicates that 1977 was the year the trend changed.

D. A regime shift with density dependence: this hypothesis would suggest that the productivity function shifted when the physical regime shifted (i.e. two production functions better define the relations over time).

We can get some indication of the validity of these four hypotheses by looking at hatchery data, but we must note that these data describe a developing hatchery programme as well as the physical and ecological processes that affect the survival of hatchery smolts. We compared total returns with the releases for all hatcheries releasing chinook smolts into the strait using Ricker and Beverton–Holt curves (Fig. 10). As with almost all fishery productivity data the variability was sufficiently large that one fit was not better statistically than the other, although the Beverton–Holt curve appears more reasonable. Both relationships indicate that a maximum return was achieved at release levels substantially lower than at present. The Ricker relationship indicates that a release from Canadian hatcheries of about 16 million smolts for all hatcheries produced the maximum production. The current release from Canadian hatcheries of approximately 34 million chinook salmon exceeds the number that would be required to produce a maximum return. We adjusted the data to account for the shift in age composition that occurred in the 1980s as a result of management actions. Catches were con-

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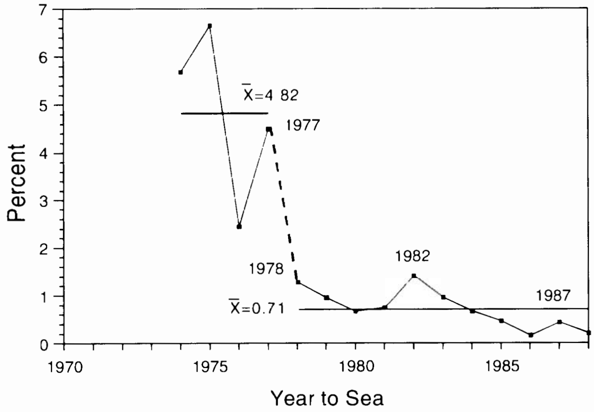
Figure 7. Survival of chinook salmon from Strait of Georgia and Fraser River hatcheries. There was a dramatic decline in average survival between the period 1974–1977 and the period 1978–1988.



verted to 'adult equivalents' using mortality rates for ages 2–3, 3–4, 4–5 of 30%, 20% and 10% respectively. Both the Ricker curve and the Beverton–Holt curve were fitted to the adjusted data (Fig. 11). Again, the adjusted data clearly indicate that the current number of smolts released far exceeds the numbers required to provide maximum returns.

We can reject explanation A as it is clearly inconsistent with the data in Figs. 10 and 11. If the flattening of the curves is real, and if survival in recent years is declining as smolt releases increase, then there is a density-dependent effect and explanation B could also be rejected.

We interpret the synchronous reduction in marine survival of hatchery fish (Fig. 7) with the physical environmental changes to indicate that the hypothesis of no regime shift and increasing density-dependent effects (Fig. 9C) is also unlikely. The flattening of the production curves (Fig. 11) occurred much earlier than the maximum hatchery releases (Fig. 8), also supporting the view that the change in production was not gradual. However, the trend in the data in Figs. 10 and 11 appear to be similar to the trend in Fig. 9(C), i.e. there is no apparent regime shift in the hatchery survival data. A possible explanation is that the hatchery production data should be represented by two productivity regimes: 1974 to 1976 and 1977 to the present. If the physical process had not shifted in the late 1970s, it is possible that returns would have continued to increase. If the regime change had occurred later in the 1980s, there could have been a drop in returns, clearly showing the impact of the physical or density-independent physical change. We did not fit a straight line to the 1974 to 1976 data because the data are confounded by the developing hatchery programme.

As explanations A–C are rejected, explanation D (Fig. 9) is left as the probable explanation for the decline in chinook abundance. We say probable because the physical or density-independent effects may still be occurring, making it difficult to separate the physical variability from the ecological interactions. Although the processes responsible for the decline in survival are unclear, it does appear that there was a combination of density-independent and density-dependent effects, with the density-dependent effects becoming more important as the number of hatchery smolts increased.

The relevance of explanation D for the management of chinook is that the carrying capacity of the environment should not be considered to be stable over decadal scales. Therefore, issues such as rebuilding chinook production to historic levels, or maintaining a stable catch at past levels, would be inconsistent with this explanation. The current smolt abundance would not be limiting adult production, and rebuilding stocks to the levels of the mid 1970s would not be possible at this time unless there is some manipulation of the factors that regulate carrying capacity.

DISCUSSION

The evidence that the decline of chinook abundance is a result of a shift in the physical oceanographic regime in the Strait of Georgia is strong, but circumstantial. It is common in fisheries management science not to have proof for some critical assumptions – for example, most stock assessments assume that there is a long-term equilibrium in the ocean production system over the time series of data, i.e. the opposite hypothesis to the one that we are proposing. Large-scale experiments that involve the manipulation of smolt releases could be undertaken to test our hypothesis. However, until these experiments are carried out, the potential for periodic changes in the marine production capacity should be accounted for in the management of chinook production in the Strait of Georgia.

A number of assumptions and approximations are evident in our study. For example, the estimated total number of smolts could be affected by movement of fish out of the strait, but young chinook salmon are supposed to be resident in local areas throughout the summer months (Healey, 1991). Also, our estimate of the percentage of hatchery and wild smolts using catch data was only slightly less than the percentages determined using otoliths to identify rearing types. If the percentages in the catch data represent the actual number of

Figure 8. Strait of Georgia commercial and sport chinook catch and releases and per cent survival of chinook from hatcheries releasing into the Strait of Georgia and Fraser River. Note that as hatchery releases have increased, hatchery survival (%) has decreased.

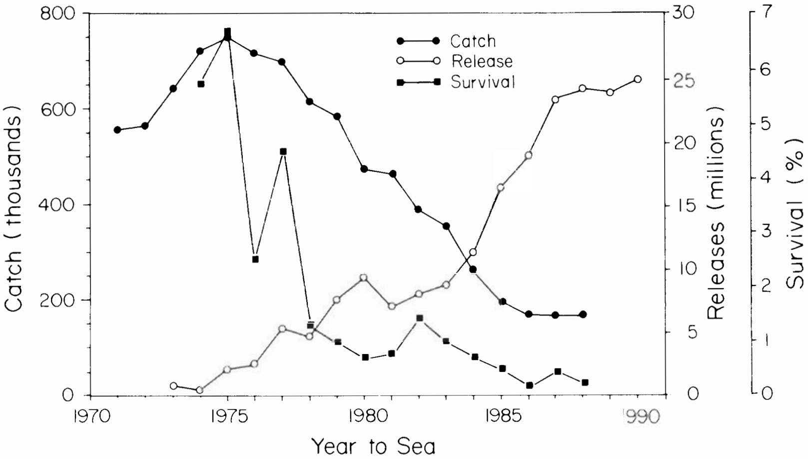
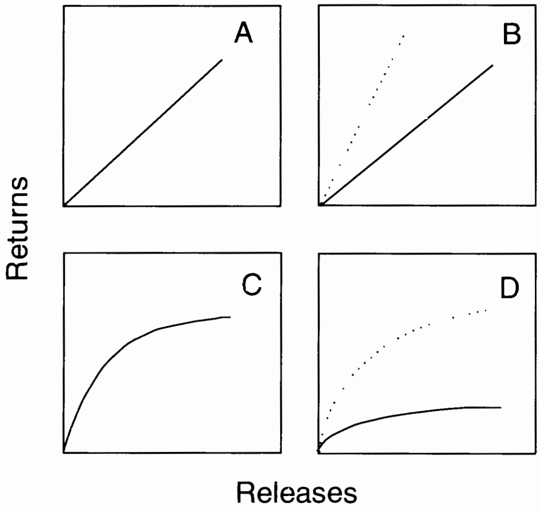


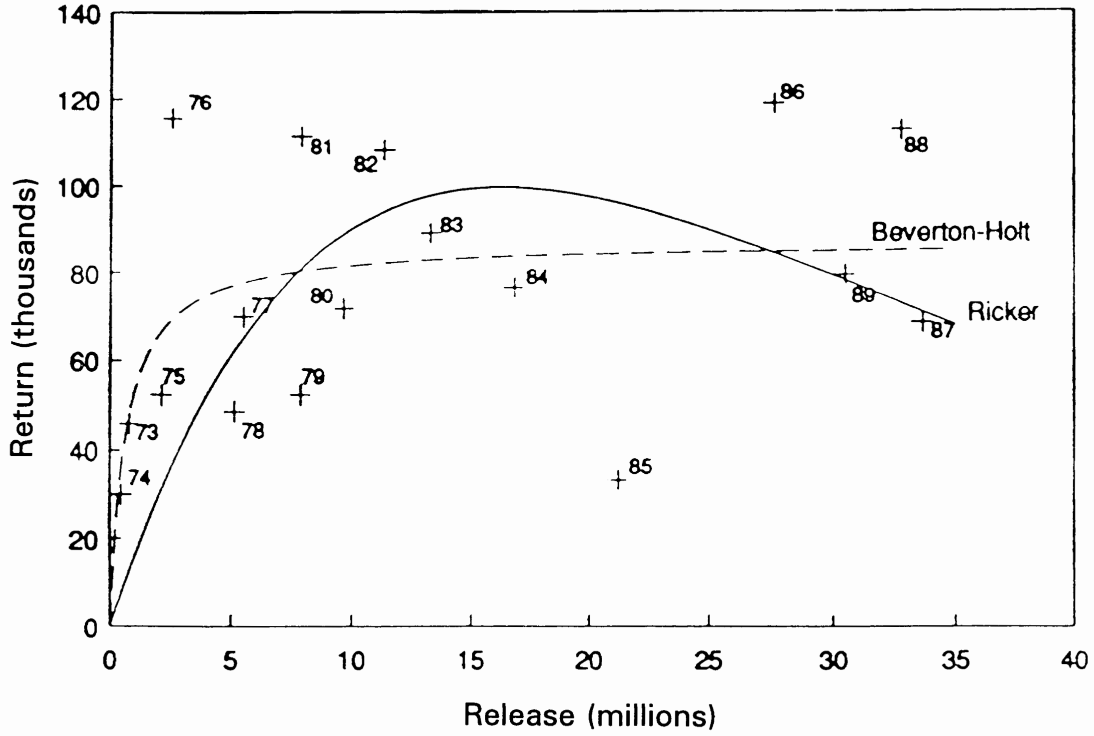
Figure 9. Schematic representation of possible alternatives for the declines in chinook abundance. (A) No regime shift and no density effect. (B) A regime shift (dotted line to solid line) but no density effect. (C) No regime shift (dotted line to solid line) but a density effect. (D) A regime shift and a density effect.



smolts that entered the strait, then total smolt production in 1992 would still be double the total production we estimated in the mid 1970s. If the marine survival of hatchery smolts is lower than wild smolt survival, then total smolt production could be similar to our estimate even if we have overestimated the percentage of hatchery smolts entering the strait. The main consideration is that the increases in smolt abundance are so large, that the level of error associated with our assumptions should not affect our main conclusion that there has been a large increase in smolt abundance during the period of declines in catches. The estimate of smolt production in 1992 of approximately 81.6 million chinook is more than double the production in the late 1970s. The number of hatchery smolts in the Strait of Georgia in 1992, therefore, greatly exceeded the estimates of the combined wild and hatchery production in the 1970s. Surprisingly, the wild smolt production estimates in 1992 appear to be greater than the wild production in the late 1970s. Escapements in recent years have not been declining, suggesting that the increased wild smolt abundance may be related to the increased escapements and to the increase in the individual size of chinook reported by Ricker (1995).

The hatchery survival data indicate that the decline in survival was as abrupt as the increase in temperature. Earlier, we defined carrying capacity as all of the factors that interact to regulate the abundance of a species, and in this study, chinook salmon. The two principal predators on chinook smolts are spiny dogfish, *Squalus acanthias*, and river lamprey, *Lampetra ayersi* (Beamish *et al.*, 1992; Beamish and Neville, 1995a). While both of these resident predators can cause high levels of early marine mortality of chinook salmon, their main sources of prey are other animals. Although we do not understand the mechanisms that were responsible for the rather abrupt changes in the survival of hatchery (and wild) chinook smolts, we suspect that they were associated with changes that increased the marine mortality caused by these predators. We did not determine how

Figure 10. Unadjusted returns of adult chinook salmon compared with releases for brood years 1971-1989 from hatcheries on the Fraser River and hatcheries releasing juvenile salmon directly into the Strait of Georgia. Years represent the year of entry into salt water. For explanation of fitted curves see text.



the biological processes that led to increased marine mortality were altered in the Strait of Georgia, but because marine organisms are very sensitive to temperature changes (Regier *et al.*, 1990), it is highly probable that some biological processes in the strait were affected by the temperature shifts.

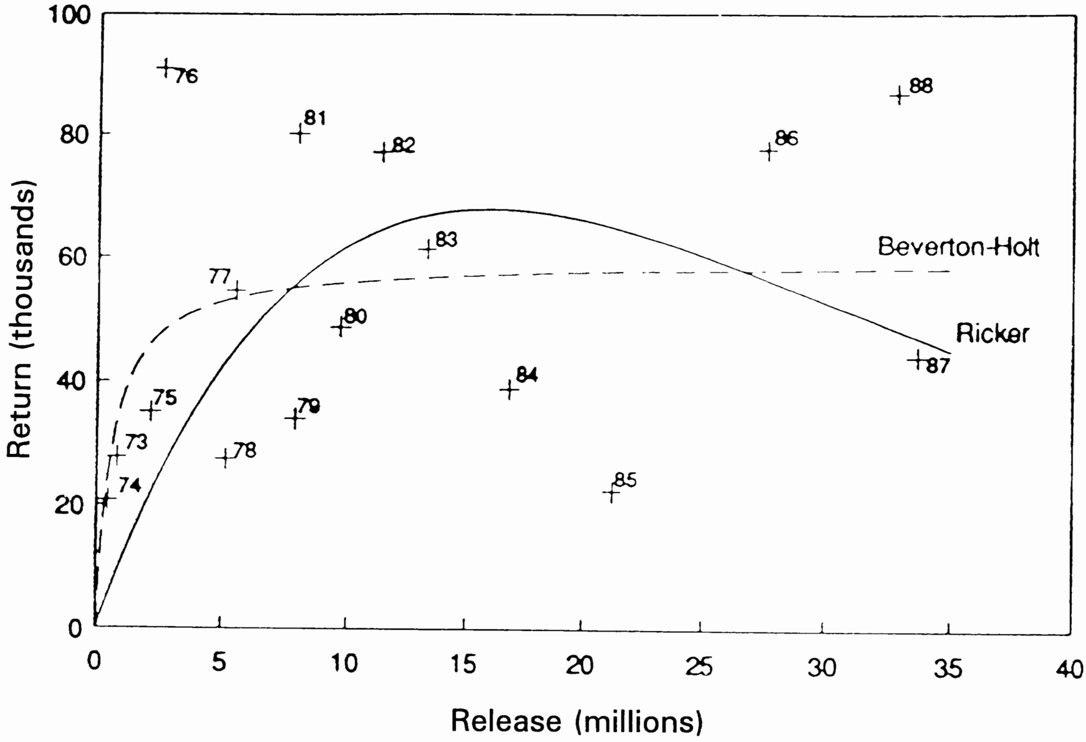
It is clear that the increased hatchery production in Canada and in the US has not increased returns. It is possible that in the early 1970s the addition of hatchery smolts increased returns, but after the regime shift, it appears that the marine environment was not capable of producing the anticipated level of return. Matching enhancement targets with possible marine production, therefore, is important for effective and efficient management of chinook stocks around the Strait of Georgia.

Relationship of physical changes with other basin-scale climate changes

Moore (1991) identified a relationship between mean annual Fraser River flow and maximum annual snow accumulation. Because the decline in the average snow depth in the Fraser River drainage from 1977 to 1988 relative to the 1956 to 1976 period (22%) was similar to the declines in flows (28%) for the same period, Moore (1991) proposed that the climate change beginning in 1977 caused the decrease in snow levels and the declining trend in flows. The change in flow patterns in 1977 has also been shown to be synchronous with a shift in the climate over the Pacific (Ebbesmeyer *et al.*, 1991; Miller *et al.*, 1994).

An increase in the production of Pacific salmon and other non-salmon species occurred at approximately the same time that the catch of chinook started to decline (Beamish and Bouillon, 1995; Hare and Francis, 1995) and when catches of coho started to decline off Oregon (Pearcy, 1992). The climate shift in the winter of 1976–1977 (McLain, 1984; Nitta and Yamada, 1989; Trenberth, 1990; Ebbesmeyer *et al.*, 1991; Graham, 1994) resulted in a drop in sea surface temperature in the central Pacific and an increase in sea surface temperature in coastal areas off Canada and the United States (McLain, 1984; Venrick *et al.*, 1987). The changes have been shown to be linked to changes in the sea surface temperatures in the tropical Pacific (Graham, 1994). The climate change in the tropical Pacific in the 1976–1977 winter was considered by Graham (1994) to

Figure 11. Adjusted returns of adult chinook salmon compared with releases for brood years 1971–1988 from hatcheries on the Fraser River and hatcheries releasing juvenile salmon directly into the Strait of Georgia. Years represent the year of entry into salt water. Note change in vertical scale compared with Fig. 10.



be a shift in the background state of the climate. This change in the background state of climate is linked to changes in mid-ocean processes, coastal processes and the pattern and volumes of river flows. It is interesting that after almost 20 years we have no clear explanation for the step-like shift in climate that occurred (Miller *et al.*, 1994) and we are just beginning to appreciate the impact on fisheries. The physical changes observed in the Strait of Georgia, therefore, were linked to other changes in the North Pacific, which in turn are closely associated with climate/ocean events in the tropical Pacific (Graham, 1994; Miller *et al.*, 1994). Thus it appears that the 1976–1977 climate event had both positive and negative effects on Pacific salmon produced in Canada (Beamish and Neville, 1995b).

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