

## Changing the Balance: Interactions between Hatchery and Wild Pacific Coho Salmon in the Presence of Regime Shifts

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**Abstract:** Nearly 5 billion salmon are released from enhancement projects on an annual basis into the Pacific Ocean by Canada, Japan, Russia, and the United States. Although these large-scale enhancement programs contribute substantially to salmon fisheries in the North Pacific, there is growing evidence to suggest that these hatchery fish may negatively affect wild salmon stocks both from a genetic and ecological perspective. There is also some evidence that hatchery fish have replaced wild fish particularly chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) stocks. The percentage of hatchery fish in the waters off southern British Columbia, marine survival and climate trends, and hatchery policies and practices are used to examine potential interactions between hatchery and wild stocks. Shifts to lower productivity regimes such as occurred in 1989/90 may amplify the negative interactions. Decisive management action such as significantly reducing harvest pressure and protecting freshwater habitat may reduce these effects, but longer-term solutions are likely only if enhancement activities are viewed in a broader ecological context.

### INTRODUCTION

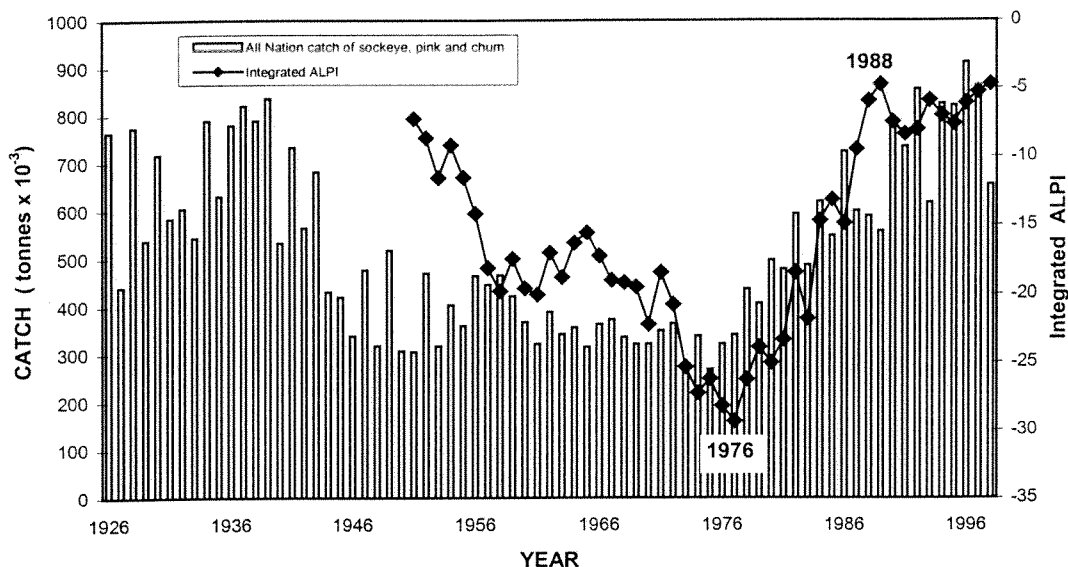
Salmon production in the north Pacific has fluctuated widely this century and there is some evidence to suggest such fluctuations have occurred naturally for hundreds and perhaps thousands of years (Finney et al. 1998; Beamish et al. 1999). An increase in production started in 1977 and coincided with significant shifts in climate and the ecosystem of the north Pacific (Ebbesmeyer et al. 1991; Beamish and Bouillon 1993). By the mid-1980s, total Pacific salmon catch exceeded 900,000 t annually. Salmon catches in Canada began to decline sharply around 1990, again coincidentally with a significant shift in the climate/ocean environment of the north Pacific (Beamish et al. 2000). Declines in salmon catch occurred for coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon despite large additions of hatchery-reared fry and smolts. These declines have resulted in managers in both Canada and the United States adopting restrictive harvest strategies and other conservation measures to protect wild salmon stocks.

In addressing these complex salmon management issues, it is important to take into consideration the significant salmon enhancement activities around the Pacific, because the introduction of these hatchery

fish constitutes a major human intervention in our ecosystem. Each year, nearly five billion juvenile salmon from hatcheries, spawning channels, and lake enrichment programs are released into the north Pacific by Canada, United States, Japan, and Russia (Mahnken et al. 1998). These fish, henceforth referred to as “hatchery fish”, contribute substantially to fisheries in each country (Beamish et al. 1997) but scientific evidence is accumulating that suggests these large-scale enhancement activities also have significant adverse effects on both wild salmon production as well as the entire ecosystem (Meffe 1992; Thomas and Mathisen 1993; NRC 1996; Grant 1997; Brannon et al. 1998; Waples 1999).

When salmon enhancement programs were being initiated, there was a common belief that the productive capacity of the Pacific Ocean was vastly underutilized with respect to wild salmon production (Perry 1995). In part, this belief stemmed from the relatively large catches of wild salmon in the early part of this century compared to the much smaller catches during the 1950s and 1960s (Fig. 1). In a review of the Canadian initiative in 1980, the long-term objective of the program was to double salmon production from previous levels to 86,000 t annually. There was, at that time, no evidence to suggest to the program

Fig. 1. All nation catch of sockeye, pink, and chum salmon (bars) and the Integrated Aleutian Low Pressure Index (Beamish et al. 1999).



managers that the capacity of the ecosystem was incapable of sustaining this level of production. Salmon enhancement was seen as a means to compensate for declining freshwater production (lost through overfishing, urbanization or the construction of control structures/dams on rivers) or to take advantage of unproductive (or barren) freshwater systems (Beamish et al. 1997; Bradford and Irvine 2000).

Salmon enhancement has been practiced intensively in British Columbia since the early 1970s (SEP—Program Coordination and Assessment Division. 1998). In each of the last 20 years, nearly 500 million hatchery or enhanced salmon have been produced and released in British Columbia coastal waters (Table 1). Sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon production from hatcheries, artificial spawning channels or lake enrichment (fertilization) programs represents about 85 percent of the total production. Chinook and coho salmon are of particular significance to the sport fishery and on average 42.5 million chinook and 17.6 million coho fry and smolts are released from hatcheries and other enhancement projects annually (Table 1). The United States also releases significant numbers of hatchery salmon each year (Beamish et al. 1997; Didier 1998; Mahnken et al. 1998). Alaskan salmon enhancement began in the mid-1970s and is primarily focused on the production of sockeye, pink, and chum salmon with recent combined annual releases for these three species in the neighborhood of 1.25 billion fish (Beamish et al. 1997; Mahnken et al. 1998). Salmon enhancement in Washington State began in 1895 and by the early 1950s more than 100 million chinook and coho salmon were being produced and released each year (Beamish et al. 1997).

In contrast to the situation in British Columbia and Alaska, the bulk of the Washington, Oregon, Idaho, and California enhancement efforts are focused on the production of chinook and coho salmon. In the 1990s, approximately 250 million hatchery chinook and 68 million hatchery coho, or roughly five times the Canadian production for these two species combined, were released annually by Washington, Oregon, Idaho, and California (Table 2).

By the mid-1980s concerns and questions were being raised about the dramatic drop in survival for hatchery coho and chinook salmon in British Columbia. Marine survival for coho salmon decreased from about 20% in the mid-1970s to less than 2% by the 1990s. During the same period, marine survival for chinook salmon decreased from about 7% to less than 1%. Similar concerns had been raised in the United States (Washington State) in the early-1970s about its hatchery programs and, in retrospect, this was an ominous foreshadowing of the problems in British Columbia. To address this issue, several studies were initiated to determine the optimal size and time of release of hatchery salmon to maximize survival (Bilton et al. 1982). Despite these efforts, the marine survival for hatchery chinook and coho salmon continued to decline.

In this paper, we examine trends in the marine survival of coho stocks at the southern end of their freshwater distribution as well as the relative abundance of wild and hatchery coho in the Strait of Georgia. The implications of various past and current hatchery practices are discussed from a genetic, ecological, and fisheries perspective. Finally, the plausible effects of regime shifts are examined.

**Table 1.** Releases of juvenile salmon from Salmon Enhancement Program facilities in British Columbia (SEP—Program Coordination and Assessment Division, 1998).

Brood Year	Chinook	Chum	Coho	Pink	Sockeye *	Total
1977	13,620,370	54,031,652	5,058,281	31,029,220	201,309,000	305,048,523
1978	14,253,404	54,524,319	4,857,722	1,268,250	141,574,350	216,478,045
1979	16,379,080	82,652,695	8,756,923	36,254,543	220,701,122	364,744,363
1980	19,850,845	106,217,696	7,719,900	38,852,965	199,054,901	371,696,307
1981	17,428,192	129,893,114	12,277,121	92,109,022	211,604,372	463,311,821
1982	24,854,529	166,389,988	17,760,471	10,928,339	218,317,433	438,250,760
1983	29,374,066	178,391,768	22,625,999	106,863,812	144,301,195	481,556,840
1984	34,864,768	167,775,075	25,259,448	16,512,153	254,991,214	499,402,658
1985	42,761,623	158,534,388	19,141,208	80,406,993	175,808,962	476,653,174
1986	53,840,001	198,818,282	22,594,254	55,936,910	200,924,044	532,113,491
1987	63,693,726	199,054,154	17,819,451	61,138,919	158,654,299	500,360,549
1988	64,528,141	228,053,816	22,030,433	106,523,161	231,737,734	652,873,285
1989	63,628,249	203,541,458	23,276,342	70,654,343	223,568,392	584,668,784
1990	66,461,805	218,150,978	22,413,456	77,412,349	258,861,158	643,299,746
1991	59,540,198	200,152,670	22,147,770	62,785,065	277,228,098	621,853,801
1992	58,038,721	228,417,050	18,718,352	45,940,900	276,430,119	627,545,142
1993	51,094,315	216,634,268	19,220,749	65,091,522	192,659,518	544,700,372
1994	54,176,102	215,923,666	23,264,803	67,425,282	160,575,488	521,365,341
1995	45,370,507	155,671,013	20,343,257	60,366,993	120,842,893	402,594,663
1996	57,483,942	140,238,676	17,087,290	14,779,572	252,059,228	481,648,708
Average	42,562,129	165,153,336	17,618,662	55,114,016	206,060,176	486,508,319

\* includes lake enrichment projects

**Table 2.** Estimated enhanced salmon releases from Washington, Oregon, California, and Idaho, 1993–1997.

Year	Chinook	Coho	Chum	Pink	Sockeye	Total
1993	210,387,445	68,586,446	59,773,153	0	3,492,161	342,239,205
1994	258,621,084	72,053,589	59,997,531	3,482,400	8,628,644	402,783,248
1995	287,691,217	71,591,160	59,141,900	100,000	16,397,960	434,922,237
1996	259,185,757	72,288,540	58,651,021	4,591,440	5,792,978	400,509,736
1997	232,847,517	55,067,267	42,048,963	0	14,470,295	344,434,042
Average	249,746,604	67,917,400	55,922,514	1,634,768	9,756,408	384,977,694

## METHODS

Marine survival estimates for coho were determined using hatchery released coho that were tagged with a coded wire inserted in the nose (Beamish et al. 2000). The survival rate estimate was made by expanding the number of coded wire tags (CWT) recovered by the appropriate tagging percentage for each hatchery and calculating the percentage of total hatchery fish that survived. For the Strait of Georgia, the brood year survival was calculated using the number of hatchery fish released directly or indirectly into the Strait of Georgia and dividing the release

estimate into the estimate of the number that were caught in fisheries and returned to spawn. For Puget Sound, marine survival was calculated from CWT data stored at the Pacific States Marine Fisheries Commission regional mark information system (Pinix 1998). The Oregon Production Index (OPI) measures the survival of coho that enter the Pacific Ocean from California, Oregon, and southern Washington, north to Willapa Bay. The survival index is determined by summing the Washington, Oregon, and California smolt releases and dividing this number into the estimated adult and jack returns. Releases from private hatcheries or enhancement facilities are

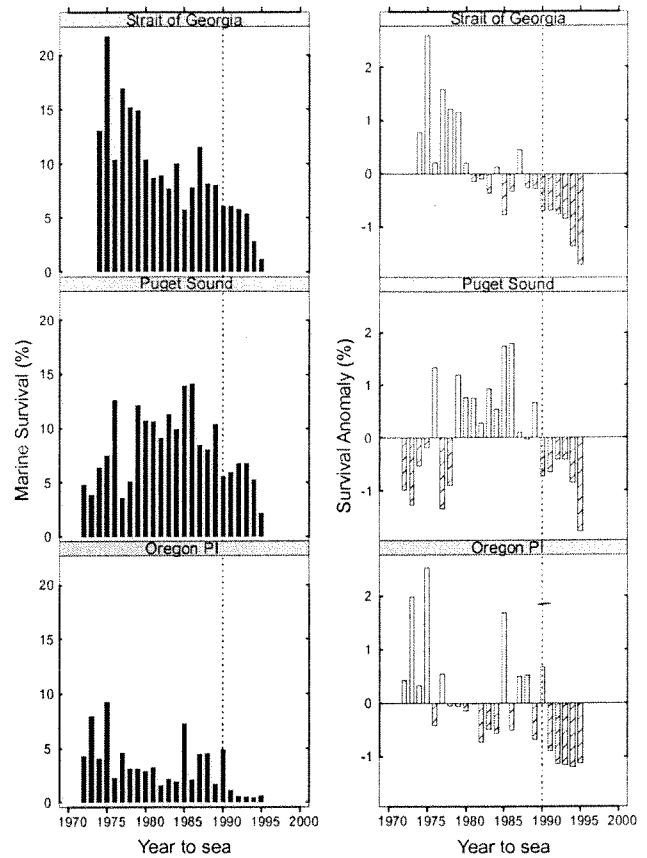
not part of the index. Data from 1972–1995 are from Pacific Fisheries Management Council (PFMC 1997). In addition to examining the estimated survival rates, all survival estimates were subtracted by the mean of the time series and divided by the standard deviation to produce standardized anomalies.

Estimates of the percentage of hatchery and wild coho salmon were obtained from samples of juvenile salmon collected using trawl gear (Beamish and Folkes 1998; Sweeting et al. in review). The trawl net was a modified rope trawl with an average opening of 14 m (depth) by 30 m (width) and was towed at an average speed of 5 kt (2.6 m/s). The gear was trawled throughout the surface waters of the Strait of Georgia from the Canadian Coast Guard vessel *W.E. Ricker*. Surveys were conducted in May and September in both 1997 and 1998 (Sweeting et al. in review). Similar but larger rope trawls that have an opening of about 50 m X 50 m have been used to study the abundance and distribution of Asian stocks of Pacific salmon (Shuntov et al. 1988, 1993). All juvenile coho salmon were examined visually for clipped fins as well as with a coded wire tag detector to determine if a CWT had been inserted into the head. The heads of all fish with a CWT were frozen and the tag was removed and decoded at a later date. In addition, one hundred coho were randomly selected and the otoliths were examined for rearing type using the microstructure of the otolith (Zhang et al. 1995). Whenever possible, the left otolith was used in the determination, but if the left otolith was crystalline or if it was missing in the sample, the right otolith was used.

**RESULTS**

Average survival rates for coho salmon stocks associated with the OPI (3.2% survival) were approximately one third the rates observed for Strait of Georgia (9.4% survival) and Puget Sound (8.1% survival) stocks. In all three areas, marine survival rates after ocean year 1990 decreased substantially (Fig. 2). Compared to average survival rates prior to 1990, the observed reductions in survival were on the order of 60% for Strait of Georgia (from 11.2% to 4.6%) and OPI (from 3.9% to 1.3%) coho stocks, and 40% for Puget Sound (from 9.0% to 5.4%) coho stocks (Fig. 2). Lower than average marine survival was estimated for Puget Sound stocks in the early and mid-1970s while survival rates for Strait of Georgia and OPI coho stocks were either above average or average for the period prior to 1990. An intervention analysis (Hipel and McLeod 1994) of the standardized anomaly series (Fig. 2) identified a significant shift in 1990 in the Strait of Georgia and Puget Sound survival trends and in 1991 in the OPI (Table 3). These changes in marine survival coincided with significant shifts in the Aleutian Low Pressure Index and

**Fig. 2.** Marine survival rates and survival rate anomalies for hatchery coho released into the Strait of Georgia, Puget Sound, and stocks contributing to the Oregon Production Index (OPI) (Beamish et al. 2000). The dashed line in each of the six panels identifies ocean year 1990.



**Table 3.** Step intervention parameters,  $\omega_0$ , and estimated (standard errors) for the coho marine survival data.

Series	Year	$\omega_0$ (se)
Strait of Georgia	1990	-4.61 (2.22)
Oregon Production Index	1991	-3.23 (1.00)
Puget Sound	1990	-0.73 (0.22)

other ocean-climate indices around 1990 (Beamish et al. 1999).

In 1997, 2,925 ocean age 0 coho were caught in the Strait of Georgia trawl surveys. An additional 2,760 ocean age 0 coho were caught in similar surveys in 1998. Based on fin clips and CWTs, approximately 75% of the juvenile coho caught in the Strait of Georgia in the 1997 survey were of hatchery origin. A similar estimate (70%) was obtained from the 1998 survey (Sweeting et al. in review). On average, hatchery coho were larger than wild coho in the

May survey with mean lengths of 136 mm and 125 mm, respectively. The size difference had largely disappeared by the September survey with mean lengths for hatchery and wild coho of 268 mm and 263 mm, respectively (Sweeting et al. in review). Percentages of hatchery fish estimated using the otolith microstructure were similar: 72.5% in 1997 and 71.5% in 1998. A high percentage (> 85%) of fish with one crystalline otolith were determined to be of hatchery origin.

## DISCUSSION

A comparison of survival for hatchery and wild coho salmon is difficult primarily because of the lack of good data for wild stocks. Spatial and temporal differences in marine survival have been noted but the general trends in marine survival for both wild and hatchery coho salmon from the same geographic region appear to be similar (Coronado and Hilborn 1998). It is generally accepted that survival in the early freshwater stages of development is substantially better for hatchery reared salmon. There is also some evidence (Nickelson et al. 1986; Solazzi et al. 1990; Reisenbichler 1996) to suggest that hatchery fry out-planted in streams have better survival rates than wild fry due to a size advantage for the hatchery fish. This may be important since in some cases fry releases have been significant with more than 10,000 fish/km of stream out-planted in years when the streams were likely to be already fully seeded by progeny from wild spawners (Pitre and Cross 1992). It is plausible that both short and long term ecological and genetic consequences resulted from these activities although no quantitative studies have been conducted. There are also potential disease concerns because fish health checks are typically not conducted when the fry are out-planted into watersheds associated with the hatchery. Although the same pathogens are likely present in both the hatchery and the watersheds, the pathogens could be inadvertently amplified in the hatchery and spread to the wild fish (Noakes et al. 2000). Solazzi et al. (1990) also noted that the hatchery coho generally returned to spawn earlier than the wild coho but the resultant offspring from the adult hatchery coho had poorer survival. It is quite likely that differences in spawning time are designed to buffer the effects of environmental variation and that the percentage of early and late spawning wild coho shifts over time to adapt. These shifts could be in response to changes in either spawning or rearing habitat or food availability in fresh or saltwater. If wild coho were replaced by hatchery coho as a result of hatchery fry being out-planted, it is plausible that the stocks' ability to adapt to adverse environmental conditions has been seriously impaired. Solazzi et al. (1990) also found that for the 30 streams in Oregon

considered in their study, the number of adult coho caught in fisheries or returning to spawn was not substantially influenced by the level of enhancement.

The information for British Columbia is much more limited with only three wild indicator streams actively monitored for Strait of Georgia coho stocks and no experiments on the same or similar scale to Solazzi et al. (1990). Although reasonably good estimates of the number of juvenile coho (and other salmonids) released from hatcheries are available, the same is not necessarily true for indicator stocks where wild juveniles are tagged and released. In some years, a high percentage (more than 60%) of the adults returning to the wild indicator streams do not have coded wire tags (Simpson et al. 1999). These untagged fish are either stray hatchery fish from nearby hatcheries or represent the returns from wild juveniles that were missed during the tagging and monitoring programs conducted each year. The low straying rates for both coho and chinook salmon (Sandercock 1991; Labelle 1992; Candy and Beacham 2000) suggest that these fish are more likely returns of wild juvenile salmon that were not tagged. The exclusion of the unmarked adult fish as well as potential problems stemming from not tagging an unknown portion of the wild juvenile coho may result in a biased estimate of the marine survival for the wild fish (Noakes et al. 2000). The marine survival of the tagged fish may not be representative of the entire population given differences observed in other systems (Solazzi et al. 1990).

It is possible, however, to examine the relative abundance of hatchery and wild coho. Surveys of juvenile salmon in the Strait of Georgia and BC coastal waters indicated that between 70% and 80% of the juvenile coho salmon are now of hatchery origin (Beamish et al. 1998; Sweeting et al. in review). Also, some hatchery managers have suggested that up to 50% of the salmon spawning in rivers with hatcheries are first generation hatchery fish. These are in addition to the hatchery fish that may stray into streams without hatcheries to spawn with wild salmon (Simpson et al. 1999). Depending on one's point of view, these fish and their offspring could be viewed as 'wild' fish although there are serious genetic issues to consider (Hindar et al. 1991).

Estimates of the percentage of hatchery coho in the Strait of Georgia have been made over time (Cross et al. 1991; Sweeting et al. in review). The percentage of hatchery fish has increased from about 25% in the early 1980s to nearly 50% in 1990 and to approximately 75% in 1998 (Table 4). These estimates suggest a gradual replacement of wild fish with hatchery fish over time. If the annual rate of replacement (either through differences in marine survival between hatchery and wild salmon or differential harvest rates) was approximately 5% per year, then a

**Table 4.** Approximate percentage of hatchery origin Strait of Georgia coho salmon. Estimates from Cross et al. (1991) and Sweeting et al. (in review).

Period	Percentage
1980–1984	24
1985–1988	39
1989	45
1997–1998	75–80

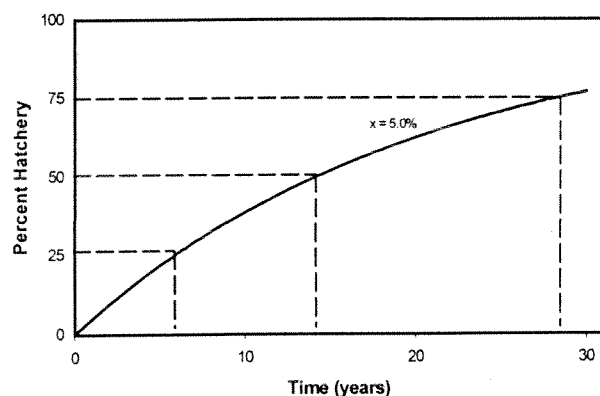
simple calculation shows the proportion of hatchery fish would be approximately 25%, 50%, and 75% after 5, 13, and 28 years of enhancement, respectively (Fig. 3). This rate is only slightly higher than the rate of increasing hatchery percentage reported in Sweeting et al. (in review). It appears that the rate of replacement may have changed over time and was perhaps slightly less than 5% from the mid-1970s to the late-1980s and slightly more than 5% in the 1990s (Table 4 and Fig. 3). This could be due to changes in ecosystem productivity or some sort of positive feedback mechanism whereby the shift to hatchery fish accelerates as the proportion of hatchery fish increases. It is important to note that the increase in the percentage of hatchery coho has occurred at the same time the total abundance has declined.

Beamish and Mahnken (1998, 1999) proposed that coho salmon abundance is controlled according to a critical size and critical period hypothesis. They propose that early marine survival occurs in two major stages. In the first stage, marine mortality is primarily predator based occurring shortly after entry into salt water. The size of the coho smolts as well as their density and the abundance of predators are all contributing factors at this stage. The second stage of significant marine mortality occurs in the fall and winter although slower growing salmon may also die during the summer months. Juvenile salmon not reaching a critical size by the fall equinox are unable

to survive until the next season. Both density dependent and density independent factors are important to the phase of growth related mortality. The negligible difference in the size of hatchery and wild fish in the fall (as observed during the September surveys) tends to support this size selective hypothesis although a faster growth rate of wild fish would also be an explanation. Since hatchery fish are larger than wild fish when they first enter the ocean (as observed during the May surveys), this may result in an advantage for hatchery fish during the size related, predation based mortality stage, ensuring that a greater percentage of hatchery fish than wild fish reach a critical size by the fall. This could, in part, explain the observed shift in the percentage of hatchery coho over time (Table 4). According to this view, the overall abundance of both wild and hatchery coho are governed through the critical size and critical period theory limited both by the overall carrying capacity of the ocean and through competitive interactions with other salmonids or other species such as herring (*Clupea harengus*) and hake (*Merluccius productus*).

Another likely factor contributing to the relative shift from wild to hatchery fish is non-selective mixed stock fisheries. In mixed stock fisheries, the catch is composed of salmon from a variety of wild and hatchery stocks and the various stocks are frequently subjected to differential harvest rates. This is particularly true when fewer wild salmon are mixed with a large number of co-migrating hatchery salmon. Because of the non-selective nature of these fisheries, significant portions of less abundant stocks can be intercepted during an intensive fishery opening where the capacity of the fishing fleet is excessive. The problem is compounded when stocks are in decline, such as after the regime shifts in 1990. The actual harvest rate (calculated only after the fishing season ends) can be much higher than the pre-season target harvest rate if salmon abundance is declining, thus increasing the probability of smaller runs of salmon being fished to near extinction levels. If the form of the production function for the stocks under consideration is known or can be assumed, it is possible to estimate an appropriate harvest rate for the mixed stock fishery. For instance, assuming a Ricker type production function Paulik et al. (1967) developed a method to determine an appropriate harvest rate. Differences in productivity may be a function of both density-independent and density-dependent factors as well as the current state of the stock. In reality, the complex interactions present in the ecosystem are likely to result in these factors being significantly confounded and difficult to separate. This is an important concept to consider in developing strategies to manage mixed stock fisheries and is often overlooked when stocks are considered in isolation during the assessment and management process.

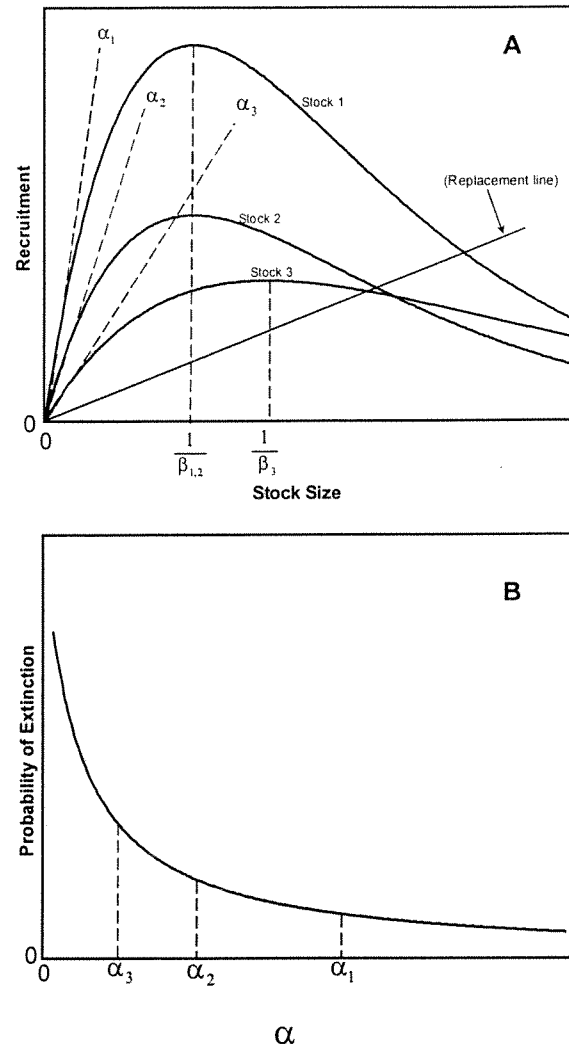
**Fig. 3.** Estimated percentage of hatchery fish over time (years since enhancement began) assuming average annual replacement rates (i.e. hatchery fish replacing wild fish) of 5.0%. The percentage of hatchery fish would be approximately 25%, 50%, and 75% after 5, 13, and 28 years, respectively.



If a Ricker stock recruitment function is considered appropriate, the density-independent factor,  $\alpha$ , will be the determining factor at low levels of abundance with more productive stocks ( $\alpha_1 > \alpha_2 > \alpha_3$ ) being able to withstand a higher harvest rate (Fig. 4A). Routeledge and Irvine (1999) showed that if the harvest rate is too high for too long (perhaps only a few generations), the lower productivity stocks will eventually become extinct and that the probability of extinction is a function of  $\alpha$  (Fig. 4B). Climate shifts are likely to result in changes to the density independent component of the recruitment function ( $\alpha$ ) and perhaps to the density dependent component ( $\beta$ ) through various complex ecological interactions. A shift to a less productive regime (such as occurred in 1990) will tend to reduce  $\alpha$ , further compounding both the overall and relative declines of hatchery and wild coho. Also, hatchery stocks tend to have higher values of  $\alpha$  (relatively few adults are required to produce a large number of juveniles) than wild stocks and are thus less likely to become extinct than wild stocks. A shift in climate may also increase the relative difference in  $\alpha$  between hatchery and wild stocks and may, in part, explain the shift towards a higher percentage of hatchery fish in the combined population.

Enhancement activities have changed over the past century but it is clear that some practices have negatively affected wild stocks (Meffe 1992; NRC 1996; Brannon et al. 1998; Waples 1999; Noakes et al. 2000). The practices have tended to reduce genetic diversity in some cases (Withler 1988; Withler and Beacham 1994). In other instances, transfers within and between watersheds were done with little or no evaluation of the genetic consequences (Foerster 1946, 1968; Ricker 1987; Williams 1987; Roos 1991; Withler et al. 2000). While some limited degree of straying is generally believed to be beneficial in increasing local genetic diversity, the consequences of these larger scale and uncontrolled interventions are not known although they are commonly thought to be negative. The ecological consequences of enhancement have been equally significant through both biological and fisheries interactions. Climate shifts to lower productivity regimes and the inability to detect and react to these changes quickly have compounded the problem. The net result has been an overall decrease in coho abundance and an increase in the percentage of hatchery fish that seems to be accelerated by changes in environmental factors. It is clear a better understanding of the mechanisms controlling abundance and links to climate change is necessary.

**Fig. 4. A.** Ricker stock recruitment curves for three hypothetical stocks. Each stock is defined by a unique density-independent parameter,  $\alpha$ . Stocks 1 and 2 have the same density-dependent parameter,  $\beta$ . **B.** Probability of stock extinction as a function of the Ricker  $\alpha$  parameter. The replacement line represents the point where the stock (escapement) is just adequate to maintain the population at a fixed level of production.



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## REFERENCES

SEP—Program Coordination and Assessment Division. 1998. An assessment of Canadian enhanced salmon production, 1977–1997. (NPAFC Doc. No. 332) 18p. Dept. of Fisheries and Oceans, Habitat and Enhancement Branch, Vancouver, B.C. V6B 5G3.

- Beamish, R.J., and D.R. Bouillon. 1993. Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* 50: 1002–1016.
- Beamish, R.J., and M. Folkes. 1998. Recent changes in the marine distribution of juvenile chum salmon off Canada. *N. Pac. Anadr. Fish Comm. Bull. No. 1*: 443–453.
- Beamish, R.J., and C. Mahnken. 1998. Natural regulation of the abundance of coho and other species of Pacific salmon according to the critical size and critical period hypothesis. (NPAFC Doc. 319) 29p. Dept. of Fisheries and Oceans, Canada.
- Beamish, R.J., and C. Mahnken. 1999. Taking the next step in fisheries management. *Ecosystem Approaches for Fisheries Management, Alaska Sea Grant College Program, AK-SG-99-01*.
- Beamish, R.J., C. Mahnken, and C.M. Neville. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. *ICES. J. Mar. Sci.* 54: 1200–1225.
- Beamish, R.J., R. Sweeting, and Z. Zhang. 1998. Estimating the percentage of hatchery-reared coho salmon in the Strait of Georgia in 1997. *Pacific Stock Assessment Review Committee Working Paper S98-8*.
- Beamish, R.J., D.J. Noakes, G.A. McFarlane, L. Klyashtorin, V.V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56: 516–526.
- Beamish, R.J., D.J. Noakes, G.A. McFarlane, W. Pinnex, R. Sweeting, and J. King. 2000. Trends in coho marine survival in relation to the regime concept. *Fish. Oceanogr.* 9: 114–119.
- Bilton, H.T., D.F. Alderdice, and J.T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Can. J. Fish. Aquat. Sci.* 39: 426–447.
- Bradford, M.J., and J.R. Irvine. 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia coho. *Can. J. Fish. Aquat. Sci.* 57: 13–16.
- Brannon, E., J. Lichatowich, K. Currens, B. Riddell, D. Goodman, R. Williams, and C. McConnaha. 1998. Review of salmonid artificial production in the Columbia River basin. *Northwest Power Planning Council, Doc. No. 98-33*.
- Candy, J., and T.D. Beacham. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fish. Res.* 47: 41–56.
- Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* 55: 2067–2077.
- Cross, C.L., L. Lapi, and E.A. Perry. 1991. Production of chinook and coho salmon from British Columbia hatcheries, 1971 through 1989. *Can. Tech. Rep. Fish. Aquat. Sci. No. 1816*.
- Didier, A.J. Jr. 1998. Estimates of salmon harvests and hatchery releases in Washington, Oregon, California, and Idaho, 1993–1997. (NPAFC Doc. 359) 14p. Pacific States Marine Fisheries Commission, Oregon, USA.
- Ebbesmeyer, C.C., D.R. Cayan, D.R. McLain, F.H. Nichols, D.H. Peterson, and K.T. Redmond. 1991. 1976 step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1984. *In Proc. Seventh Annual Pacific Climate (PACCLIM) Workshop, April 1990. Edited by J.L. Betancourt and V.L. Tharp. Calif. Dept. Water Resource Interagency Ecol. Study Program Tech. Rep. 26*: 115–126.
- Finney, B. 1998. Long-term variability in Alaskan sockeye salmon abundance determined by analysis of sediment cores. *N. Pac. Anadr. Fish Comm. Bull. No. 1*: 388–395.
- Foerster, R.E. 1946. Restocking depleted sockeye salmon areas by transfer of eggs. *J. Fish. Res. Board Can.* 6: 483–490.
- Foerster, R.E. 1968. The Sockeye Salmon; *Oncorhynchus nerka*. *Fish. Res. Board Can. Bull.* 162.
- Grant, W.S. 1997 (Editor). Genetic effects of straying of non-native hatchery fish into natural populations: Proceedings of the Workshop. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NMFSC No. 30.
- Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. *Can. J. Fish. Aquat. Sci.* 48: 945–957.
- Hipel, K.W., and A.I. McLeod. 1994. Time series modeling of water resources and environmental systems. Elsevier, Amsterdam.
- Labelle, M. 1992. Straying patterns of coho salmon (*Oncorhynchus kisutch*) stocks from southeast Vancouver Island, British Columbia. *Can. J. Fish. Aquat. Sci.* 49: 1843–1855.
- Mahnken, C., G. Ruggerone, W. Waknitz, and T. Flagg. 1998. A historical perspective on salmon production from Pacific rim hatcheries. *N. Pac. Anadr. Fish Comm. Bull. No. 1*: 38–53.
- Meffe, G.K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific Coast of North America. *Conservation Biol.* 6: 350–354.
- Nickelson, T.E., M.F. Solazzi, and S.J. Johnson. 1986. Use of hatchery coho salmon presmolts to rebuild wild populations in Oregon coastal

- streams. *Can. J. Fish. Aquat. Sci.* 43: 2443–2449.
- National Research Council (USA) (NRC). 1996. Upstream: salmon and society in the Pacific Northwest. National Research Council Committee on Protection and Management of Pacific Northwest Anadromous Salmonids. National Academy Press, Washington, D.C.
- Noakes, D.J., R.J. Beamish, and M.L. Kent. 2000. On the decline of Pacific salmon and speculative links to salmon farming in British Columbia. *Aquaculture* 183 (3–4): 363–386.
- Pacific Fisheries Management Council (PFMC). 1997. Preseason Report 1. Stock Abundance Analysis for 1997. Ocean Salmon Fisheries.
- Paulik, G.J., A.S. Hourston, and P.A. Larkin. 1967. Exploitation of multiple stocks by a common fishery. *J. Fish. Res. Bd. Can.* 24: 2527–2537.
- Perry, E.A. 1995. Salmon stock restoration and enhancement: strategies and experiences in British Columbia. In *American Fisheries Society Symposium 15: Uses and effects of cultured fishes in aquatic ecosystems*. Edited by H.L. Schramm and R.G. Piper. pp. 152–160.
- Pinnix, W. 1998. Coho and climate: a Puget Sound perspective. M.Sc. Thesis. University of Washington, School of Fisheries, Seattle, WA.
- Pitre, K.R., and C. Cross. 1992. Impacts of coho enhancement on three Thompson River tributaries. In *Proceedings of the Coho Workshop*. Edited by L. Berg and P.W. Delaney. Nanaimo BC, May 26–28, 1992. pp. 140–150.
- Reisenbichler, R.R. 1996. Genetic factors contributing to declines of anadromous salmonids in the Pacific Northwest. In *Pacific salmon and their ecosystems, status and future options*. Edited by D.J. Stouder, P.A. Bisson and R.J. Naiman. Chapman and Hall. pp. 223–224.
- Ricker, W.E. 1987. Effects of the fishery and of obstacles to migration on the abundance of Fraser River sockeye salmon (*Oncorhynchus nerka*). *Can. Tech. Rep. Fish. Aqua. Sci.* No. 1522.
- Roos, J.F. 1991. Restoring Fraser River Salmon. Pacific Salmon Commission.
- Routledge, R.D., and J.R. Irvine. 1999. Chance fluctuations and the survival of small salmon stocks. *Can. J. Fish. Aquat. Sci.* 56: 1512–1519.
- Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In *Pacific Salmon Life Histories*. Edited by C. Groot and L. Margolis. University of British Columbia Press, Vancouver. pp. 397–445.
- Shuntov, V.P., A.F. Volkov, and A.Y. Efimkin. 1988. Composition and present state of pelagic fish communities in the western Bering Sea. *Biologiya morya* 2: 3–41 (in Russian).
- Shuntov, V.P., A.F. Volkov, O.S. Temnykh, and E.P. Dulepova. 1993. Pollock in the ecosystems of the far eastern seas. *TINRO Sci. Rep. Vladivostok* No. 2-53.
- Simpson, K., R. Semple, S. Baillie, B. Adkins, and S. Lehmann. 1999. Status of coho salmon stocks adjacent to the Strait of Georgia including the lower Fraser River. Pacific Scientific Advice Review Committee Working Paper S99-199.
- Solazzi, M.F., T.E. Nickelson, and S.L. Johnson. 1990. An evaluation of the use of coho salmon presmolts to supplement wild production in Oregon coastal streams. *Fish. Res. Rep. No. 10*, Oregon Dept. Fish and Wildlife, Portland, Oregon.
- Sweeting, R.M., R.J. Beamish, J.R. King, and D.J. Noakes. In review. Recent percentages of hatchery-reared coho in the Strait of Georgia are substantially higher than wild coho.
- Thomas, G.T., and O.A. Mathisen. 1993. Biological interactions of natural and enhanced stocks of salmon in Alaska. *Fish. Res.* 18: 1–17.
- Waples, R.S. 1999. Dispelling some myths about hatcheries. *Fisheries* 24: 12–21.
- Williams, I.V. 1987. Attempts to re-establish sockeye salmon (*Oncorhynchus nerka*) populations in the upper Adams River, British Columbia, 1949–84. In *Sockeye salmon (Oncorhynchus nerka) population biology and future management*. Edited by H.D. Smith, L. Margolis, and C.C. Wood. *Can. Sp. Pub. Fish. Aquat. Sci.* 96: 235–242.
- Withler, R.E. 1988. Genetic consequences of fertilizing chinook salmon (*Oncorhynchus tshawytscha*) eggs with pooled milt. *Aquaculture* 68: 15–25.
- Withler, R.E., and T.D. Beacham. 1994. Genetic consequences of the simultaneous or sequential addition of semen from multiple males during hatchery spawning of chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture* 126: 11–23.
- Withler, R.E., K.D. Le, J. Nelson, K.M. Miller, and T.D. Beacham. In press. High levels of intra- and inter-population genetic variation in exploited populations of Fraser River sockeye salmon, *Oncorhynchus nerka*.
- Zhang, Z., R.J. Beamish, and B.E. Riddell. 1995. Differences in otolith microstructure between hatchery-reared and wild chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 52: 344–352.

