Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest

Claribel Coronado and Ray Hilborn

Abstract: Survival rates for coho salmon (*Oncorhynchus kisutch*) were estimated for all coded wire tag release groups in the Pacific Northwest between 1971 and 1990. The spatial and temporal patterns show considerable geographic variation, with most regions south of northern British Columbia showing declining survival since 1983, while northern areas have shown increasing survival during that period. The number of years of operation explained very little of the variation in survival, and many hatcheries showed major increases in survival after several years of operation. Survival of marked wild fish generally showed the same trend as hatchery fish. We conclude that the dominant factor affecting coho salmon survival since the 1970s is ocean conditions and that there are major geographic differences in the pattern of ocean conditions. The decline in survival seen in British Columbia and south over the last decade suggests that a major reduction in exploitation rates is necessary to maintain the populations.

Résumé : Le taux de survie a été estimé pour tous les groupes de saumons cohos (*Oncorhynchus kisutch*) marqués par fil codé et libérés dans le nord-ouest du Pacifique entre 1971 et 1990. Les allures spatiales et temporelles présentent une variation géographique considérable. On a noté, depuis 1983, un déclin du taux de survie dans la plupart des régions situées au sud de la partie nord de la Colombie-Britannique, mais une augmentation de ce taux dans les régions situées au nord. Le nombre d'années d'exploitation explique très peu de la variation du taux de survie et bon nombre de piscicultures présentaient d'importantes augmentations de la survie après plusieurs années de fonctionnement. La survie des poissons sauvages marqués présentait généralement une allure semblable à celle des poissons d'élevage. Nous concluons que le facteur qui a le plus influé sur la survie du saumon coho depuis les années 1970 est représenté par les conditions océaniques et que ces conditions présentent d'importantes différences en fonction du lieu géographique. Le déclin du taux de survie noté en Colombie-Britannique et dans les régions situées au sud au cours de la dernière décennie porte à croire que le maintien des populations exigera une importante réduction des taux d'exploitation.

[Traduit par la Rédaction]

Introduction

Coho salmon (*Oncorhynchus kisutch*) have been produced in hatcheries for over 100 years (Cobb 1931; WDF 1991). During the early years, rearing success was limited, but by 1965, there were 23 facilities in the United States and Canada releasing over 21 million fish annually. Concerns about population declines promoted an increase in hatchery production of salmonids, and by 1989, 420 hatcheries existed in the same region, releasing 147.8 million coho fry (Fig. 1). Hatchery production of coho has presently reached high proportions, and an estimated 40–50% of net-caught salmon in Puget Sound are hatchery reared (Laufle et al. 1986).

During the long history of hatchery production of salmonids, efforts have been made to improve rearing techniques, leading to an increase in the number of fish released. An initial focus on increasing the number of fish released has been questioned in the last two decades when it has become clear that an increase in the number of juveniles released does not necessarily mean an increase in number of adults recovered. Many factors have been proposed to explain variation in coho including changes in ocean conditions, predation at sea, density-dependent mortality, poor quality of hatchery smolts, and diseases (Pearcy 1988, 1992; Walters 1988). Correlations with ocean conditions have been intensively studied for the Oregon Production Index (OPI) area (Fig. 2). Upwelling and ocean temperatures have been correlated with smolt-to-adult survival of hatchery fish, while the correlations are weaker or nonsignificant for wild coho from the same area (Nickelson 1986).

In spite of some significant correlations, evidence supporting the changes in ocean conditions is still inconclusive and the causes of variation in smolt-to-adult survival are still speculative (Pearcy 1992). Upwelling may influence survival by affecting distribution at sea, food abundance, and predator distribution. In the present study, we compare coho survival over a broad geographic range to study geographical and temporal patterns in survival in the Pacific Northwest. Additionally, we explore the relationship between survival and the time that hatcheries have been in operation and test the hypothesis that declines in survival are caused by an increase in production from hatcheries located in less favorable locations.

Received September 23, 1997. Accepted May 8, 1998.
J14213

C. Coronado and R. Hilborn.[1] Fisheries Research Institute, University of Washington, Box 357980, Seattle, WA 98195, U.S.A.

[1]Author to whom all correspondence should be addressed.

Fig. 1. Number of facilities producing coho in the Pacific Northwest and millions of fish released by brood year.

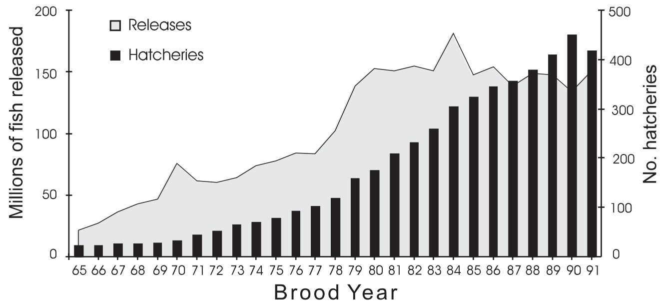
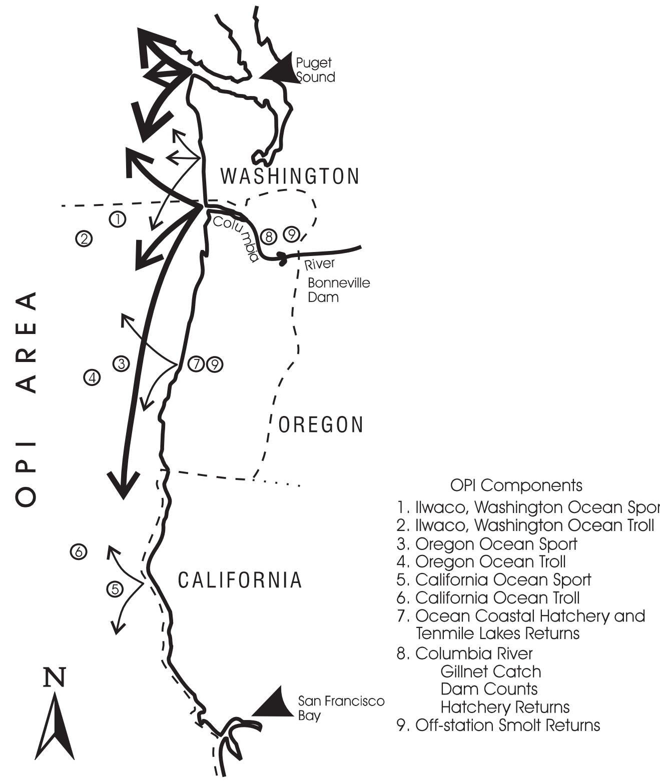


Fig. 2. OPI area and its components (after ODFW 1982).



Methods

Survival calculation was based on coded wire tag (CWT) recoveries (Jefferts et al. 1963) obtained from the CWT database of the Pacific States Marine Fisheries Commission (Gladstone, Oreg.). To avoid potential bias, only groups classified as nonexperimental were included in the analysis. The database contains information on observed number of tags recovered in a sample fishery and the estimated number of tagged fish, or expanded recoveries, that the recovery represents. Because most fisheries are sampled at different rates, our analyses were based on expanded recoveries. Throughout this study, hatchery refers to rearing facilities and age is calculated as recovery year minus brood year. CWT coho have been recovered at ages ranging from 1 to 7 years, but along this study's entire geographical distribution, 91% of fish return at age 3. Although most recoveries are made at age 3, the age distribution at recovery varies among the different regions. Because of this variation, standardization of the number of fish recovered was necessary to compare recoveries among regions. To standardize the recoveries, age 3 was chosen as the standardization age and a combination of forward and backward virtual population analysis (VPA) (Hilborn and Walters 1992, chap. 10) was used:

$$N_3^* = C_1 s_1 s_2 + C_2 s_2 + C_3 + \frac{C_4}{s_4} + \frac{C_5}{s_4 s_5} + \frac{C_6}{s_4 s_5 s_6} + \frac{C_7}{s_4 s_5 s_6 s_7}$$

where N_3^* is the number of fish that would be alive if they were not caught or escaped at an age different from age 3, C_t is the number of fish recovered (caught plus escaped) at age t, and s_t is the survival rate from age $t-1$ to age t (which can also be expressed as 1 minus mortality at age t). The mortality rate 0.5 (Argue et al. 1983) was used as a scaling factor and has no impact on the patterns presented and analyzed. Survival for each tag code was calculated as

$$\text{Survival} = \frac{N_3^*}{\text{No. released}}$$

Average survival was calculated as the arithmetic mean of survival for individual tag codes, grouped by hatchery location and (or) by brood year. The standard deviation of the mean was calculated as the ratio of standard deviation of the survival of individual tag groups and the number of tag groups. This statistic was included in the charts as error bars around the mean as a measure of variability of the average survival.

To compare the influence of geographic location of the hatcheries and rearing facilities, each state/province was divided into sectors and each sector into regions. The division into sectors corresponds approximately to the partitioning of management areas, while regions correspond approximately to production areas (Johnson and Thompson 1989). Geographical division by state/province, sector, and region is listed in Table 1. As an example, Washington State was divided into three sectors, Puget Sound, Washington coast, and Columbia River. The Columbia River sector was divided into two regions, lower Columbia River and upper Columbia River.

To test hypotheses regarding brood year, hatchery location, time of release, hatchery age, and weight at release, a generalized linear model (GLM) was fitted. Hatchery age represents the number of years that a hatchery has been operating. The GLM was log-linear with a scaled Poisson error distribution. Number of expanded recoveries was used as a predicted variable. Details of the model can be found in Green and Macdonald (1987), Cormack and Skalski (1992), and Pascual (1993). The independent variables brood year, hatchery location, and release month were categorical, while hatchery age and weight were used as covariables. The logarithm of the number of fish released was used as a weight, offset in GLM terminology, to account for differences in release numbers for the different tag codes. Changes in deviance were used as goodness-of-fit criteria (Green and Macdonald 1987). The deviance has a distribution that asymptotically approaches a chi-square, so it can be used as a guide for selection among alternative models. Model fitting emphasized the relative importance of the different sources rather than the search for the best model.

For the construction of the model, it was necessary to exclude the regions with the most incomplete history of tagged releases. The selection was made to include regions with at least one group of tagged releases in a minimum of 9 years during the period 1973–1990. Brood year 1973 was chosen as the lower bound of the range because it was then that the number of hatcheries releasing CWT coho started to increase. Brood year 1990 was chosen as the upper limit of the range because it was the last brood year for which complete recovery data were available. A total of 34 re-

Table 1. Geographical divisions by state/province, sector, and region.

State/ province	Sector	Region	Description
AK			Alaska
	AK.CC		Central Alaska
		COOK	Cook Inlet
		KODK	Kodiak Island
		PWS	Prince Williams Sound
	AK.SE		Southeast Alaska
		STEP	Stephens Passage
		C.OUT	Central Outside
		S.OUT	Southern Outside
		S.IN	Southern Inside
	ARTC		Arctic
		MYUK	Mid-Yukon
	AK.SEm		Southeast Alaska net pens
		STEPm	Stephens Passage net pens
		SOUTm	Southern Outside net pens
	AK.CCm		Alaska central coast net pens
		COOKm	Cook Inlet net pens
BC			British Columbia
	BC.NO		British Columbia north coast
		CCST	Central coast
		NASS	Nass River
		NCST	North coast
		QCI	Queen Charlotte Islands
		RIVR	River R
		SKNA	Skeena River
		TRAN	Transboundary
		YUKN	Upper Yukon
	BC.SO		South coast of British Columbia
		GSMN	Strait of Georgia mainland north
		GSMS	Strait of Georgia mainland south
		GSVI	Strait of Georgia Vancouver Island
		JNST	Johnston Strait
		LWFR	Lower Fraser River
		NWVI	Northwest Vancouver Island
		SWVI	Southwest Vancouver Island
		TOMF	Thompson River fork
		TOMM	Thompson River mainland
		UPFR	Upper Fraser
WA			Washington
	STWD		Statewide
		STWD	Statewide
	PGSD		Puget Sound
		NOOK	Nooksak–Samish
		SKGT	Skagit
		STILL	Stillaguamish–Snohomish
		HOOD	Hood Canal
		SPGT	South Puget Sound
		STJF	Juan de Fuca Strait
	W.CST		Coastal Washington
		NORC	Washington north coast
		SO.C	Washington south coast
		WILL	Willapa Bay
	W.CR		Columbia River, Washington
		LWC.W	Lower Columbia River, Washington
		UPC.W	Upper Columbia River, Washington
		SNK.W	Snake River, Washington
	PGSDm		Puget Sound net pens
		NOOKm	Nooksak–Samish net pens
		SKGTm	Skagit net pens
		STILLm	Stillaguamish–Snohomish net pens
		HOODm	Hood Canal net pens
		SPGTm	South Puget Sound net pens
		STJFm	Juan de Fuca Strait net pens
	W.CSTm		Coastal Washington net pens
		SO.Cm	Washington south coast net pens
		WILLm	Willapa Bay net pens
ID			Idaho
	SNKE		Snake River
		SALM	Salmon River
		CLWT	Clearwater River
OR			Oregon
	O.CST		Oregon coast
		O.NCS	Oregon north coast
		O.SCS	Oregon south coast
	O.CR		Columbia River, Oregon
		LWC.O	Lower Columbia River
		WILM	Willamette River
		UPC.O	Upper Columbia, Oregon
CA			California
	C.NCS		California north coast
		SMITH	Smith River
	C.CCS		California central coast
		GARC	Garcia River
		EEL	Eel River
		LTRV	Little River
		MAD	Mad River
		RUS	Russian River
	SCSJ		Sacramento, San Joaquin
		SCRM	Sacramento
		SJOAQ	San Joaquin
	C.SCS		California south coast
		SOUTH	South reach
	KLAM		Klamath
		KLAM	Klamath River
		TRNT	Trinity River

Fig. 3. Average survival of hatchery coho. Error bars indicate standard deviation of the mean.

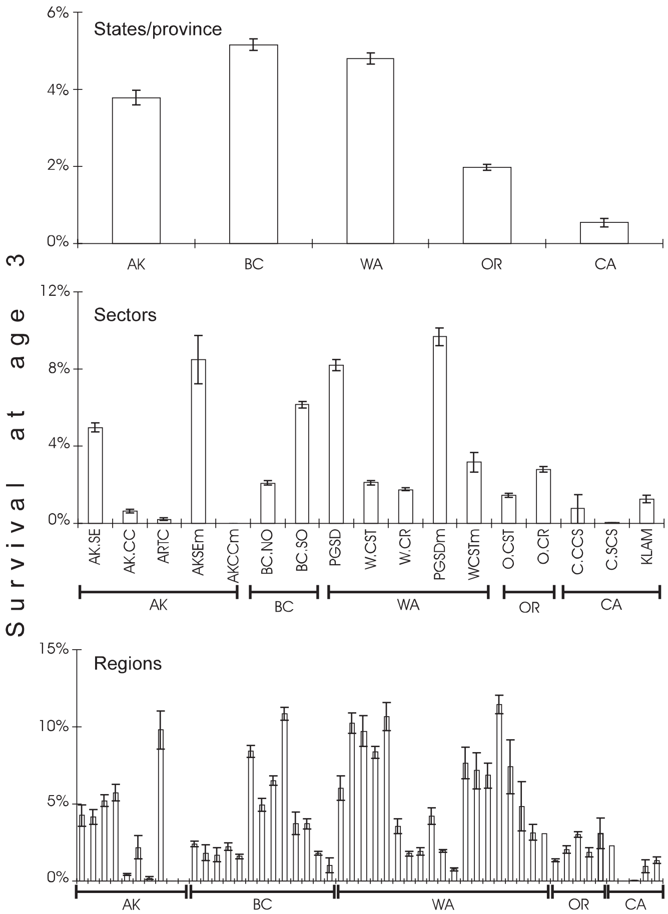
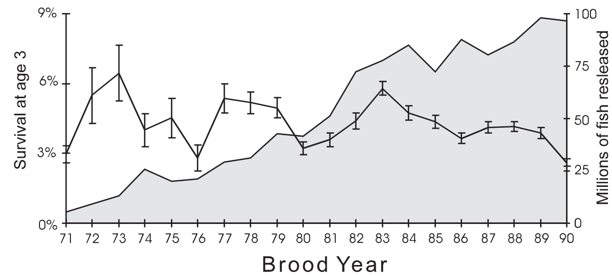


Fig. 4. Temporal trends in coho aggregated over the entire range. The line represents survival and error bars are standard deviation of the mean. The shaded area and right-hand axis represent millions of fish released by brood year.



gions, distributed among 12 sectors and four states and one province, complied with the selection criteria.

A cluster analysis compared survival trends in different hatcheries and tested the hypothesis that hatcheries from the same regions show similar survival trends. Average survival by brood year was tabulated, and because of the requirements for the cluster analysis, only hatcheries without missing data were included. The options ranged from a large number of brood years (longer trends, better data for clusters) but few hatcheries to a small number of brood years but more hatcheries. An intermediate option was selected to include as many hatcheries with as many brood years as possible. The cluster analysis was performed using the software package SPSS. The cosine coefficient measured similarity between hatcheries. Clusters were formed using the average distance between clusters (UPGMA) as the clustering algorithm.

Results

The average survival by state/province aggregated over time (Fig. 3) ranged between 6.21% in British Columbia and 0.92% in California with a mean survival of 4.27%. British Columbia, Washington, and Alaska exhibit the highest survival rates, all of them with averages over 3.7%.

The differences among areas are larger at the sector and region level. At the sector level, three areas, southeast Alaska (hatcheries and net pens), Puget Sound (hatcheries and net pens), and the south coast of British Columbia, all have mean survivals higher than 5%. At the region level, the differences are very strong. There are 21 regions with mean survivals higher than 4%, and eight of those show survivals above 8%. There are also many regions with mean survivals of 2% or below. Regions with poor survival are found across the entire geographic range but are more common in California, where only the Mad River facilities have a mean survival above 2%. Poor survivals are also common in central Alaska and on the north coast of British Columbia.

Trends

Temporal trends of survival aggregated over the entire study area (Fig. 4) show alternating increases and declines from 1971 to 1983. After 1983, the survivals declined, reaching an average below 3% in 1990, which is the last year included in the analysis. In sharp contrast, releases steadily increased since the beginning of the period, reaching the maximum in 1989 and 1990.

Production of hatchery coho in the different areas (Fig. 5) averaged 20 000 000 to 30 000 000 fish per year, with the exception of California which produced between 300 000 and 600 000 fish per year. When survival trends are examined at the state level, we see a basic pattern of declining survivals since the mid-1980s. Alaska is the only exception, showing two peaks in survival. The first one occurred in the 1980–1982 broods, with declines in the 1983–1985 broods and increasing survivals for the 1986–1989 broods. In British Columbia, the survival trend for coho is characterized by high survivals (around 12%) during the early 1970s when only a few groups were tagged and released. After brood year 1975 came a steady decline and subsequent stabilization at about 5%. Trends for Washington show periods of moderately high and moderately low survivals, with a tendency of stabilization around 5%. Survivals declined after brood year 1987. Oregon and California show low survivals when compared with the other states and province. In Oregon the maximum observed survival has been a little over 4%, while in California, it has been close to 2%. Survival trends in Oregon and California are not steady, alternating between years with high and low survivals during most of the period of study.

The two Alaskan sectors in which coho are produced and tagged are southeast and central Alaska (Fig. 6). In southeast Alaska, less than 3% of the coho produced are reared in net pens. When comparing trends from hatcheries and net pens, it is noticeable that even though the net pens showed considerably higher survival, the overall trends are very similar

Fig. 5. Survival trends for Coho. The line represents survival and error bars are standard deviation of the mean. The shaded area is number of fish released by brood year × 100 000.

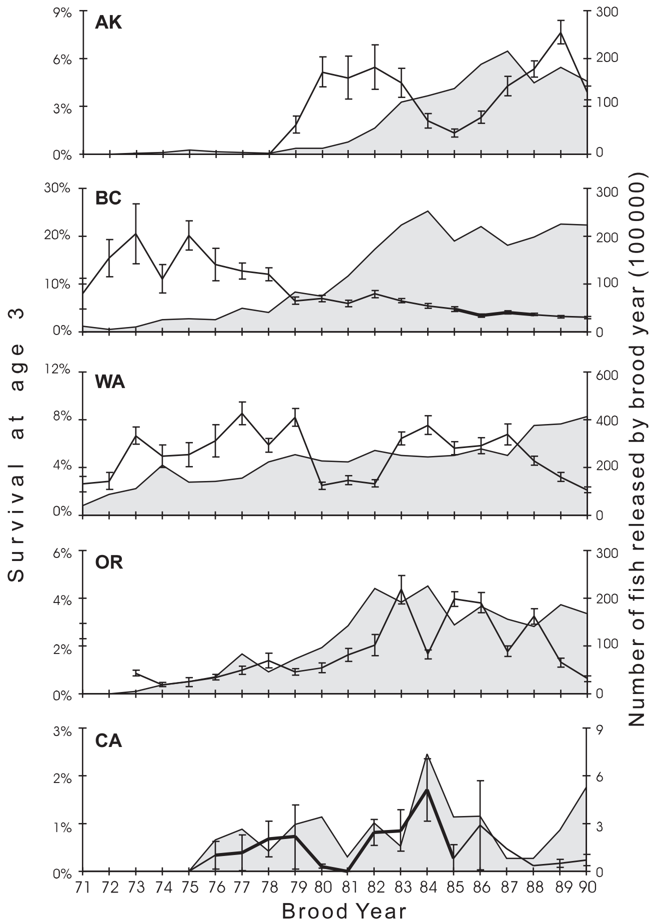
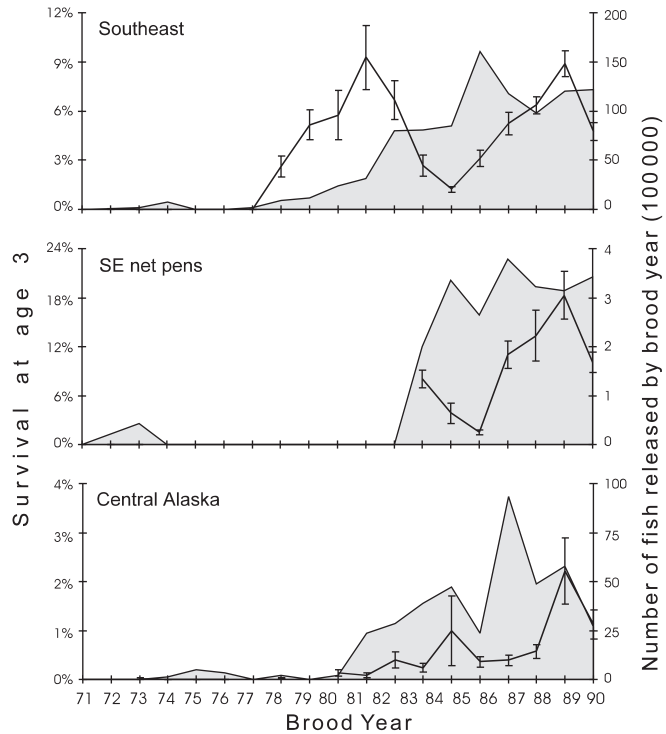


Fig. 6. Survival trends for coho in Alaska. The line represents survival and error bars sre standard deviation of the mean. The shaded area represents number of fish released by brood year × 100 000.



with a low in the mid-1980s followed by a rebound in the second half of the 1980s and a drastic drop in 1990. In central Alaska, survivals are considerably lower, but the overall survival trend shows a pattern very similar to the one observed in southeast Alaska.

In British Columbia (Fig. 7), coho salmon were produced only on the south coast during the 1970s. During that early period the annual production of coho was below 5 million fish per year, but the observed survivals were above 10%. In the 1980s, coho production on the south coast was increased, and by 1982 the annual production was above 15 million fish. Survivals, on the other hand, did not increase with production, showing a steady decline since 1975 and a tendency to stabilize at around 5%. During the early 1980s, along with increased production on the south coast, hatcheries on the north coast of British Columbia also began to rear and tag coho. The production level on the north coast was smaller, reaching a peak in 1989 when 35 million fish were reared. Survivals were below 4%.

In Washington (Fig. 8), the three sectors into which the state was divided have produced coho since 1965. Production increased in all three sectors during the 1970s and 1980s, but the increase is more noticeable in the Columbia River basin where by 1989, coho production was over 31 million fish per year. Puget Sound exhibits the highest survivals in the state with rates that often are double the rates from the other two sectors. Coho are produced in hatcheries and net pens, the latter showing a slightly higher survival rate. Since the mid-1980s, survivals in Puget Sound have been declining. The Washington coast shows alternating years of high and low survival with an average close to 2%. Net pens on the Washington coast released coho on a small scale during the early 1970s and then on a larger scale since 1987. These net-pen-reared tag groups show a slightly better survival. Coho production in the Columbia River basin in Washington shows survivals around 2% with a period of above-average survivals in the mid-1980s and a subsequent decline since 1988.

In Oregon (Fig. 9), coho are produced in the coastal area and in the Columbia River basin. In the Oregon coast sector, survivals showed an increase during the early 1980s, reaching a peak of 4% for the 1983 brood year. Since 1985, survivals have been steadily declining. On the Oregon side of the Columbia River basin, alternating years of high and low survivals are observed, a trend that is very similar to the one observed on the Washington side of the basin.

In California (Fig. 10), coho are produced on the south coast and in the Klamath River basin. California production of coho has been very small compared with production in the other states and province. During 1990, the production level sharply increased in the Klamath River basin. Survival rates from the south coast of California are minimal with an average close to 0.05%. In the Klamath area, survivals are higher, but still below average when compared with the other states and province.

Fig. 7. Survival trends for coho in British Columbia. The line represents average survival and error bars are standard deviation of the mean. The shaded area represents number of fish released by brood year × 100 000.

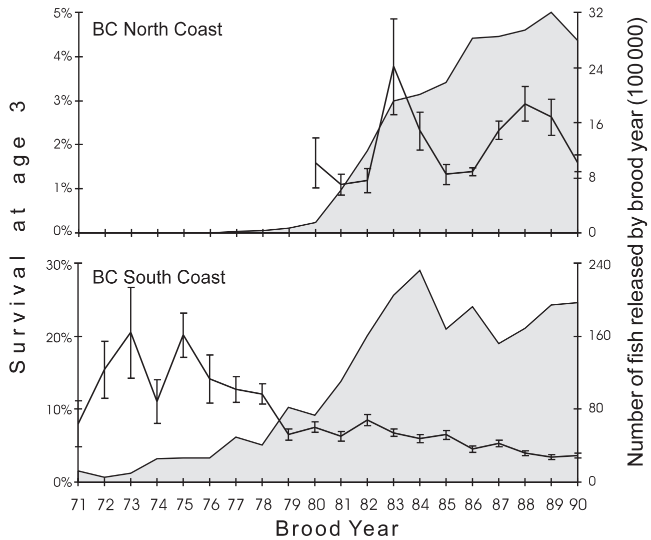


Fig. 8. Survival trends for coho in Washington. The line represents average survival and error bars are standard deviation of the mean. The shaded area represents number of fish released by brood year × 100 000.

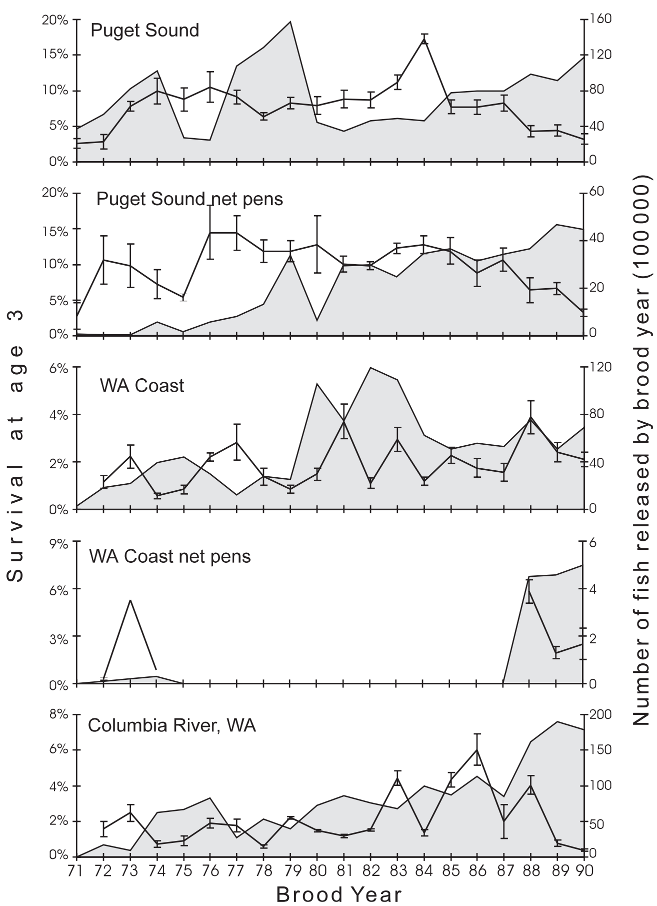


Fig. 9. Survival trends for coho in Oregon. The line represents average survival and error bars are standard deviation of the mean. The shaded area represents number of fish released by brood year × 100 000.

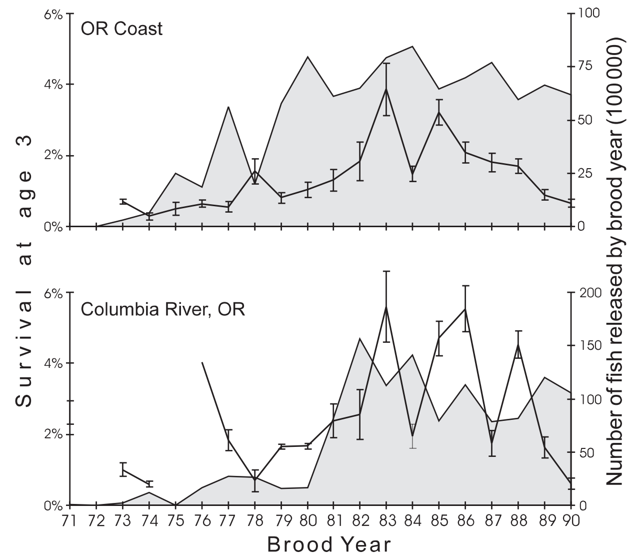
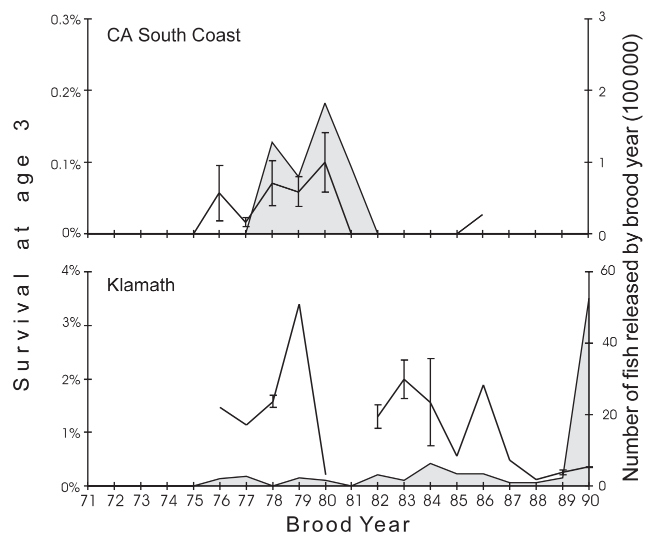


Fig. 10. Survival trends for coho in California. The line represents average survival and error bars are standard deviation of the mean. The shaded area represents number of fish released by brood year × 100 000.



GLM

A GLM was fitted by comparing nine alternative models. The data set tested consisted of over 3000 records, requiring large computing capabilities. The data set is overdispersed and shows high variability. In the first step, six alternative models, each of them containing one main factor, were tested (Table 2). From the six main factors studied, the three factors corresponding to geographical location (state/province, sector, and region) were the ones that explained the highest amount of variability. Since these three factors are nested, only one of them could be included at any time. The factor "region" was chosen because it explained a larger

Table 2. Summary of GLM analysis to study the relative importance of different factors affecting survival.

Model	Action	Dev.	df	Scaling factor	Scaled Δdev.	Δdf
Brood (b)		3 397 328	3655	929.50	175.00	16
State		3 285 669	3667	896.00	306.20	4
Sector		2 372 143	3660	648.10	1832.90	11
Region (rg)	*	1 912 891	3638	525.80	3132.60	33
Release month (rl)		3 308 226	3660	903.90	278.60	11
Weight (w)		3 516 643	3670	958.20	45.30	1
rg + b	*	1 774 990	3622	490.10	281.40	16
rg + rl		1 768 262	3627	487.50	296.68	11
rg + w		1 888 758	3637	519.30	46.47	1
rg + b + rl		1 627 785	3611	450.00	326.50	11
rg + b + w		1 746 963	3621	482.50	58.10	1
rg + b + rg·b	wk full					

amount of variability. In the second step, three alternative models were compared, each containing region plus another main factor. At this second level, both brood year and release month explained approximately the same amount of variability, while average weight at release had very little impact on the deviance. At the third level, alternative models with three main factors or with two main factors and an interaction term were tested. It was not possible to test the interaction because of lack of computer capability, but the model where the factors "region ," "brood year ," and "release month" were included was the most significant.

Cluster analysis

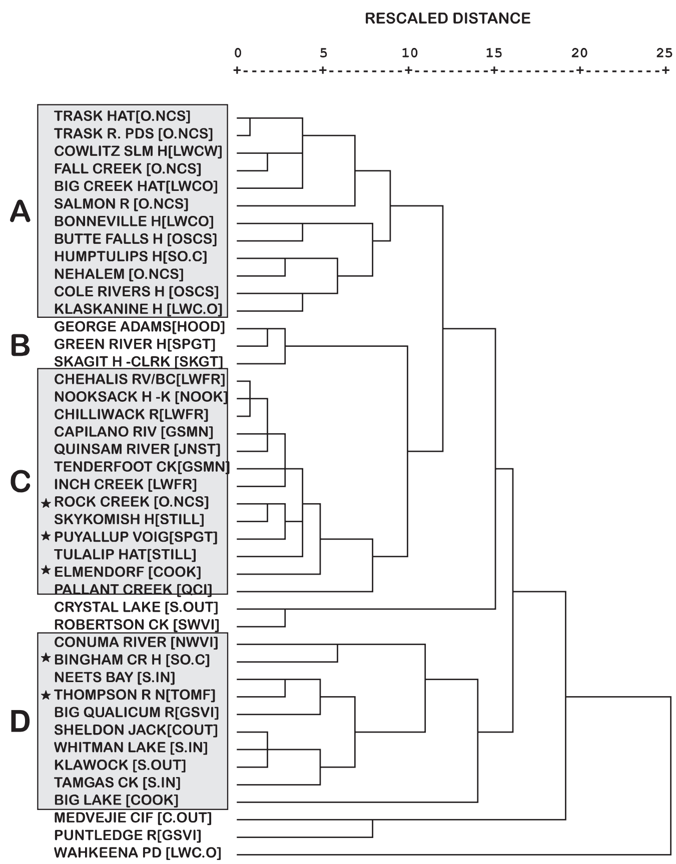
Using cluster analysis, 43 hatcheries were grouped in six clusters (Fig. 11). Hatcheries within clusters tended to be located in the same geographical area (Fig. 12), although some variability can be observed. Cluster A comprises 12 hatcheries, four of them located in the lower Columbia River and seven in coastal Oregon. Cluster B is formed by three hatcheries located in Puget Sound. Cluster C groups 13 hatcheries, six from the protected waters on the south coast of British Columbia and four from Puget Sound. Cluster D is formed by 10 hatcheries, five located in southeast Alaska and three on the south coast of British Columbia.

Discussion

The results show an increase in hatchery production coupled with a slight downward trend in survival when coho production is pooled over the entire geographic range. Grouping tag codes by location of the hatchery, an increase in survival during the mid- and late 1980s is evident in northern regions, central Alaska, southeast Alaska, and northern British Columbia. Conversely, declines in survivals are observed in all the other areas with the exception of coastal Washington where survivals appear to remain stable at around 2%.

The difference in survival trends between Alaska and the southern regions can be explained based on the concept of three major production domains identified in the northeast Pacific Ocean (Ware and McFarlane 1989). Alaskan stocks are located in the coastal downwelling domain, while southern stocks are in the coastal upwelling domain. Northern

Fig. 11. Clustering of coho hatcheries using release trends from brood years 1982–1990. Rescaled distance indicates the proportional distance among groups. A star indicates out of the group. See Fig. 12 and Table 1 for locations and abbreviations.



British Columbia stocks, on the other hand, are located in a transition zone, which could explain the differences between the north and south coasts of British Columbia.

Previous studies have reported population declines in coho. Cross et al. (1991) studied survivals from British Columbia hatcheries from 1975 to 1985 and found a decline in survival since 1975 but a significant recovery in 1985. A continued decline is evident with the inclusion of 5 more

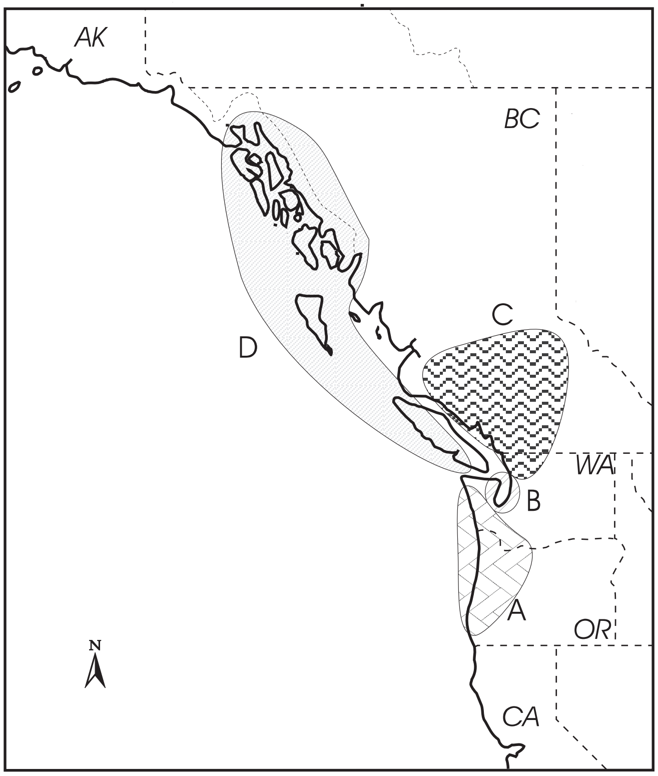


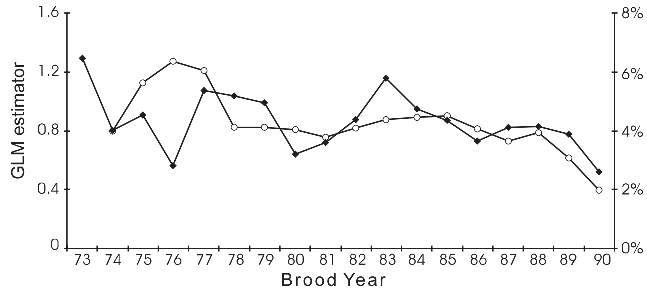
Fig. 12. General location of the groups resulting from the cluster analysis.

years of data (Fig. 7) and no signal of recovery has been observed.

Within the OPI (Fig. 2) the general perception (summarized by Pearcy 1992) is that an increase in coho production since the 1960s resulted in large fluctuations in adult returns between 1970 and 1975 and low returns from 1976 to 1986 with the exception of 1985 where high numbers of adult returns were observed. Recoveries of CWT, which started with brood year 1973, indicate that a decline in survival on the Oregon coast started after brood year 1983 (Fig. 9), while coastal Washington and the Columbia River continued to fluctuate (Figs. 8 and 9).

The cluster analysis detected higher similarities among hatcheries from the same region, indicating a geographic pattern in survival. From the dendrogram, all hatcheries in cluster A are influenced by the coastal upwelling regime, clusters B and C are in the transition zone, and half the hatcheries from cluster D are in the downwelling production regime. The most successful areas for the production of hatchery coho are evident in southeast Alaska, the south coast of British Columbia, and Puget Sound. All these areas tend to be located towards the center of the distribution range of coho whereas hatcheries that are located at either extreme of the distribution range tend to have poor survivals. Southeast Alaska, southern British Columbia, and Puget Sound are also areas where smolts first enter protected areas rather than directly entering the open ocean; these protected areas probably contribute to a higher survival rate (Nickelson and Lichatowich 1984). The higher survival for coho produced towards the central area of the geographical range was also reported by Pearcy (1992).

Fig. 13. Comparison of average survival and brood year effect from the GLM. ◆, mean survival; ○, estimate.



On a temporal scale, no period has better survivals overall, but some periods have good survivals for specific regions when the spatial scale is taken into consideration. For example, 1985–1989 were good brood years for Alaska, while the early 1970s were very good brood years for southern British Columbia. In terms of climatic changes, a regime shift has been identified in the mid-1970s (Graham 1994); some variability in salmon production has been explained based on this change in ocean conditions (Hare and Francis 1995). Unfortunately, CWT mark–recapture programs started only after 1971, which does not allow us to test for these long-scale variations.

Declines in survival could also be explained as a consequence of increased production from new hatcheries located in less favorable areas. Space in the preferred areas was limited, so new hatcheries were built in less favorable locations and fish reared there have lower survival. The opening of more hatcheries located in less favorable locations was thought to have increased the proportion of “low-survival fish” and to have driven survival trends downward. To explore the validity of this hypothesis, a GLM was fitted with region and brood year effects. The estimate of the brood year effect from that model was plotted and compared with the overall survival trends (Fig. 13). The very similar trends of both lines indicate that declines in survival trends are independent from the hatchery location, since that effect is already accounted for in the GLM.

Another common hypothesis relates declines in survival to the number of years that a hatchery has been operating, i.e., the older the hatchery the lower the survival (Walters 1988). Suggested causes have been disease buildup in the facilities and genetic deterioration of the stock. From the GLM analysis, it is evident that survival does not decline as a function of the number of years that the hatchery has been in operation. There are variables, such as hatchery location and brood year, that are orders of magnitude more significant for explaining the variation in survival (Table 3).

Similarities in survival trends between net pen groups, hatchery groups, and wild fish were noticeable. Net pen groups are reared mostly in marine water environments and are not held in tanks and ponds typical of hatchery-reared fish. Net pen reared fish usually have a higher survival rate, but survival trends are very similar to those of their counterpart hatchery fish. In regions where wild coho have been marked with CWT, both wild and hatchery fish show very similar survival trends (Figs. 14 and 15). Survival rates for wild fish are possibly underestimated because of the limited tag recovery programs for spawning grounds. Even with the

Table 3. Summary of the GLM analysis to test the “hatchery age” effect.

Model	Action	Dev.	df	Scaling factor	Scaled Δdev.	Δdf
Region (rg)	*	1 035 002	1971	525.12	2261	31
Brood (b)		1 974 154	1985	994.54	994.5	17
Release month (rl)		1 983 086	1995	994.03	240.8	7
Hatchery age (hg)		2 220 025	2001	1109.46	2.145	1
Weight (w)		2 221 996	2001	1110.44	0.3683	1
rg + b	*	904 347	1954	462.82	282.3	17
rg + rl		996 646	1964	507.46	75.58	7
rg + hg		1 025 034	1970	520.32	19.16	1
rg + w		1 034 243	1970	525.00	1.446	1
rg + b + rl		866 160	1947	444.87	85.84	7
rg + b + hg		875 094	1953	448.08	65.29	1
rg + b + w		902 230	1953	461.97	32.43	1
rg + b + rg·b	wk full					

Fig. 14. Survival trends of hatchery and wild coho in southeast Alaska and British Columbia. ◆, mean survival; ○, estimate.

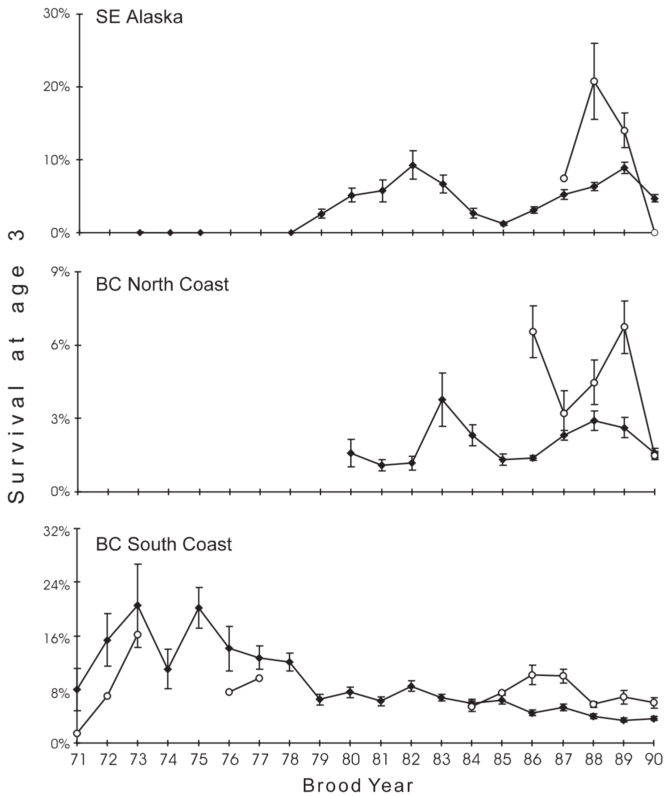
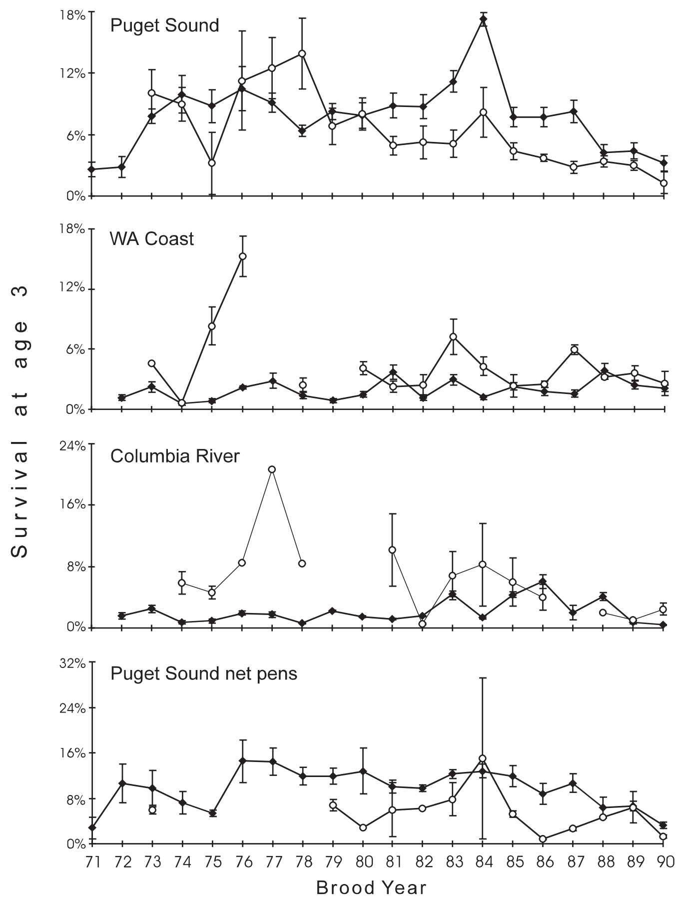


Fig. 15. Survival trends of hatchery and wild coho in Washington. ◆, mean survival; ○, estimate.



underestimation of wild survival rates, wild fish normally exhibit higher survival rates than hatchery fish. Observing the similarities in survival trends within regions between wild, net pen, and hatchery coho, it is likely that ocean conditions have a strong effect on the survival of coho.

In British Columbia (Fig. 7), there is a marked decline in survival when the number of fish released increases whereas this relationship is less clear in Washington, Oregon, and California and apparently nonexistent in Alaska. The negative relationship between survival and number of fish released supports the idea of density dependence, but the evidence is weak, and the effect is confounded by the major climate shift in the late 1970s. The density dependence hypothesis has been investigated by McCarl and Rettig (1983), Peterman and Routledge (1983), McGie (1984), Nickelson (1986), and Emlen et al. (1990), but there is still no consensus on whether or not it is responsible for the decline of coho populations. Making relationships more difficult to understand is the difference in survival of hatchery and wild coho. As pointed out by Nickelson (1986) and Emlen et al. (1990) and confirmed in this study, wild coho have better survival rates than hatchery coho. This difference, coupled with the change in stock composition from mainly wild fish to a majority of hatchery fish, makes it difficult to analyze the influence of other factors such as density dependence.

The similarities in survival trends of hatchery, net pen, and wild coho in the different areas strongly support the idea of the importance of ocean conditions on survival to adult. These changes in ocean conditions also make it more difficult to interpret the impact of human action. Pending possible return to more productive oceanographic conditions, rebuilding coho populations in the southern range is dependent on modifications of management in harvest and production. Declines in ocean survival lower the sustainable exploitation level; for example, in British Columbia the survival is now only one quarter of what it was in the early 1970s. This calls for a drastic reduction in or total cessation of exploitation. A reduced harvest needs to be matched by an increasing reliance on natural production and habitat restoration to maintain the existing genetic diversity required for long-term perpetuation of the species in its southern range.

Acknowledgments

We thank Ken Johnson and James Longwill from the Pacific States Marine Fisheries Commission for providing the raw data. Fred Utter made helpful comments to improve the presentation of this manuscript. We also thank Miguel Pascual, Tom Nickelson, and an anonymous reviewer for their helpful comments. Funding for this study was provided by U.W.H. Mason Keeler Endowment and Washington Sea Grant Program, University of Washington, pursuant to National Oceanic and Atmospheric Administration award No. NA36RG0071, project 61-9014. The views expressed herein are those of the authors and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration or any of its subagencies.

References

Argue, A.W., Hilborn, R., Peterman, R.M., Staley, M.J., and Walters, C.J. 1983. Strait of Georgia chinook and coho fishery. Can. Bull. Fish. Aquat. Sci. No. 211.

Cobb, J.N. 1931. Pacific salmon fisheries. U.S. Bur. Fish. Rep. U.S. Commer. Fish. 1930, Append. B. pp. 409–704.

Cormack, R.M., and Skalski, J.R. 1992. Analysis of coded wire tag returns from commercial catches. Can. J. Fish. Aquat. Sci. **49**: 1816–1825.

Cross, C.L., Lapi, L., and Perry, E.A. 1991. Production of chinook and coho salmon from British Columbia hatcheries, 1971 through 1989. Can. Tech. Rep. Fish. Aquat. Sci. No. 1816.

Emlen, J.M., Reisenbichler, R.R., McGie, A.M., and Nickelson, T.E. 1990. Density-dependence at sea for coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **47**: 1765–1772.

Graham, N.E. 1994. Decadal-scale climate variability in the 1970s and 1980s: observations and model results. Clim. Dyn. **10**: 135–159.

Green, P.E.J., and Macdonald, P.D.M. 1987. Analysis of mark–recapture data from hatchery raised salmon using log-linear models. Can. J. Fish. Aquat. Sci. **44**: 316–326.

Hare, S.R., and Francis, R.C. 1995. Climate change and northern fish populations. *In* Climate change and salmon production in the Northeast Pacific Ocean. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 357–372.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Jefferts, K.B., Bergman, P.K., and Fiscus, H.F. 1963. A coded wire tag identification system for macro-organisms. Nature (Lond.), **198**: 460–462.

Johnson, J.K., and Thompson, R.N. 1989. Status of chinook and coho salmon stock identification efforts for Pacific coastal production areas of the U.S. and Canada. Pacific Marine Fisheries Commission, Portland, Oreg.

Laufle, J.C., Pauley, G.B., and Shepard, M.F. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest) — coho salmon. U.S. Fish Wildl. Serv. Biol. Rep. No. 82 (11.48). U.S. Army Corps of Engineers, TR EL-82-4. 1800.

McCarl, B.A., and Rettig, R.B. 1983. Influence of hatchery smolt releases on adult salmon production and its variability. Can. J. Fish. Aquat. Sci. **40**: 1880–1886.

McGie, A.M. 1984. Commentary: evidence for density dependence among coho salmon stocks in the Oregon Production Index area. *In* The influence of ocean conditions on the production of salmonids in the North Pacific. *Edited by* W.G. Pearcy. Oregon State University Sea Grant Program, Corvallis, Oreg. pp. 37–49.

Nickelson, T.E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Can. J. Fish. Aquat. Sci. **43**: 527–535.

Nickelson, T.W., and Lichatowich, J.A. 1984. The influence of the marine environment on the interannual variation in coho salmon abundance: an overview. *In* The influence of ocean conditions on the production of salmonids in the North Pacific. *Edited by* W.G. Pearcy. Oregon State University Sea Grant Program, Corvallis, Oreg. pp. 24–36.

Oregon Department of Fish and and Wildlife (ODFW). 1982. Comprehensive plan for production and management of Oregon's anadromous salmon and trout. Part II — Coho salmon plan. Oregon Department of Fish and Wildlife, Fisheries Division, Portland, Oreg.

Pascual, M.A. 1993. The estimation of salmon population parameters from coded wire tag data. Ph.D. dissertation, University of Washington, Seattle, Wash.

Pearcy, W.G. 1988. Factors affecting survival of coho salmon off Oregon and Washington. *In* Salmon production, management, and allocation. *Edited by* W.J. McNeil. Oregon State University Press, Corvallis, Oreg. pp. 67–73.

Pearcy, W.G. 1992. Ocean ecology of north pacific salmonids. Washington Sea Grant Program, University of Washington, Seattle, Wash.

Peterman R.M., and Routledge, R.D. 1983. Experimental management of Oregon coho salmon (*Oncorhynchus kisutch*): designing for yield of information. Can. J. Fish. Aquat. Sci. **40**: 1212–1223.

Walters, C.J. 1988. Mixed-stock fisheries and the sustainability of enhancement production for chinook and coho salmon. *In* Salmon production, management, and allocation. *Edited by* W.J. McNeil. Oregon State University Press, Corvallis, Oreg. pp. 109–115.

Ware, D.M., and McFarlane, G.A. 1989. Fisheries production domains in the Northeast Pacific Ocean. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Edited by* R.J. Beamish and G.A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci. No. 108. pp. 359–379.

Washington Department of Fisheries (WDF). 1991. Historical production of coho salmon from Washington state hatcheries on the lower columbia River. Report submitted to ESA Administrative Record for coho salmon, April 1991. Washington Department of Fisheries, 115 General Administration Building, Olympia, WA 98504, U.S.A.