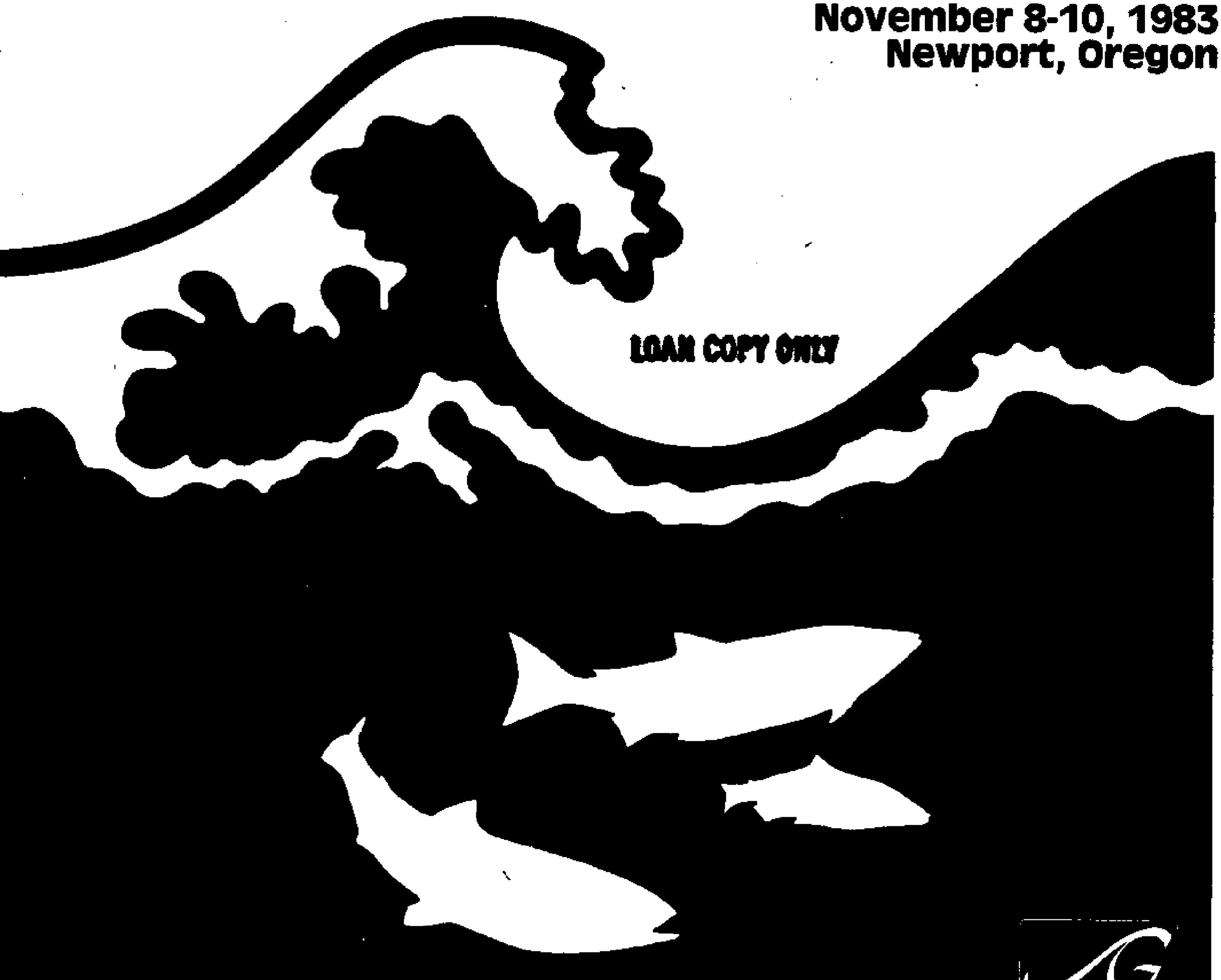
The Influence of Ocean Conditions on the Production of Salmonids in the North Pacific

A Workshop

November 8-10, 1983
Newport, Oregon



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Cooperative Institute for
Marine Resources Studies

Oregon State University
Sea Grant College Program
ORESU-W-83-001

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Contents

Preface

The timing of this workshop on the influence of ocean conditions on salmonid production could not have been more appropriate. Because of the devastating effects of the 1982-83 El Nino, ocean catches of coho and chinook salmon off Oregon and Washington were the worst in recent history. Runs of several salmon stocks in Alaska, on the other hand, were at or near record highs. Salmon biologists have never been more aware of the importance of the ocean environment on salmon production than today.

This workshop, held at Newport, Oregon, on November 8-10, 1983, had two major objectives: first, to review our knowledge of the effects of the ocean environment on the production of salmonid stocks of the North Pacific Ocean, emphasizing mechanisms linking interannual trends in survival, growth, and migrations with ocean variability; second, to identify important research needs in order to develop strategies for future investigations of salmonids in the ocean.

The first portion of the workshop, at the Mark O. Hatfield Marine Science Center of Oregon State University, was dedicated to review papers on salmonid biology and oceanography. Each review paper was followed by a commentary intended to provide a different viewpoint or approach. Following the reviews and commentaries, workshop participants were divided into working groups on hatcheries, inlets and estuaries, the coastal ocean, and the open ocean. Each working group was asked to identify problems and hypotheses that needed research in order to improve our understanding of the relationships between the ocean environment and salmonid stocks. The four working groups developed their reports independently. Therefore, the approaches of the groups are sometimes different, and important recommendations were sometimes repeated by several groups.

This publication on salmonid oceanography and biology is a companion to the one on nonsalmonid species, From Year to Year: Interannual Variability of the Environment and Fisheries of the Gulf of Alaska and Bering Sea (Warren S. Wooster, ed.), published by the University of Washington in 1983. Readers are referred to this publication for supplementary papers on oceanography of the subarctic Pacific.

William G. Pearcy

Attendees

William Aron, NWAFC; Jack Bailey, NMFS/ABL; Nicholas J. Bax, Compass; Richard Beamish, PBL; Don Bevan, UW; Margaret Birch, DFO; Dave Blackbourn, IPSFC; George Boehlert, OSU; Louis W. Botsford, UC Davis; Jim Bottom, ODFW; Richard Brodeur, OSU; Margaret Buck, DFO; Bob Buckman, ODFW; Robert Burgner, UW; Richard Carmichael, ODFW; Dudley Chelton, OSU; Alton W. Chung, OSU; Ted Cooney, UAK; David Damkaer, NWAFC; Earl Dawley, NWAFC; Walt Dickhoff, NWAFC; Bob Donnelly, UW; Nick Dudiak, ADFG; Wes Ebel, NWAFC; Doug Eggers, ADFG; T. Saunders English, UW; Joseph Fisher, OSU; R. B. Fridley, Weyerh; Art Gallagher, NWAFC; Bob Garrison, ODFW; Ron Gowan, Anad; Peter Hahn, WDG; Brent Hargreaves, PBS; Murray Hayes, NWAFC; W. R. Heard, NMFS/ABL; Paul Hubbell, CDFG; James Ingraham, NWAFC; Bob Jacobson, OSU; Herb Jaenicke, NMFS/ABL; David Johnson, Bodega ML; Steve Johnson, ODFW; Anne Kapuscinski, OSU; Marty Kjelson, USFW/CA; Kohei Kihara, Tokyo Fish; Charles Koski, NMFS; Jim Lannan, OSU; Colin Levings, West Van Lab; Dave Levy, Westwater; Jim Lichatowich, ODFW; John Loch, WDG; Carey McAllister, PBS; Marge McBride, Quinault; Alan McGie, ODFW; Douglas McLain, PEG; Bill McNeil, OAF; Conrad Mahnken, NWAFC; Cedric Mann, IOS; Chris Marlowe, NWIFC; Jim Martin, ODFW; Steve Mathews, UW; Charles Meacham, ADFG; Charles Miller, OSU; David R. Miller, NWAFC; Norm Moe, OAF; Bruce Mundy, OSU; Larry Mysak, UBC; Jay Nicholas, ODFW; Tom Nickelson, ODFW; T. Nishiyama, UAK; John A. Oh, Weyerh; Bori Olla, OSU; Kenneth S. Parker, IPHC; Steve Parker, UW; Cindy Paszkowski, OSU; Bill Pearcy, OSU; Robert Pedrick, NMFS/DC; Randall M. Peterman, SFU; Ellen K. Pikitch, OSU; Frank Ratti, OAF; Reg Reisenbichler, USFW/SEA; Don Rogers, UW; Tom Royer, UAK; Bob Schoning, NWAFC; Jim Schumacher, PMEL; Jon Shenker, OSU; Charles Simenstad, UW; Tim Slaney, Aquatic Res; George Snyder, NMFS/ABL; Mario Solazzi, ODFW; Nancy Swan, NWAFC; Sus Tabata, IOS; David H. Thomas, CDFG; John Thorpe, FFL; Dick Tubb, OSU; Bill Turnbull, PMEL; Jim Waldvogel, OSU; Steve Washburn, Weyerh; Norman J. Wilimovsky, UBC; John Williams, Corps Eng; Jim Winton, OSU; Robert C. Wissmar, UW; W. S. Wooster, UW; J. Wyland, NMFS/PDX

Acronyms

ADFG	Alaska Dept. of Fish and Game, Anchorage, AK
Anad	Anadromous, Inc., Corvallis, OR
Aquatic Res	Aquatic Resources Ltd., Vancouver, British Columbia
CDFG	California Dept. of Fish and Game
Compass	Compass Systems, Inc., Seattle, WA
Corps Eng	U.S. Corps of Engineers, Portland, OR
DFO	Dept. of Fisheries & Oceans, Vancouver, British Columbia
FFL	Freshwater Fisheries Laboratory, Pitlochry, Scotland
IOS	Institute of Ocean Sciences, Sidney, British Columbia
IPHC	International Pacific Halibut Commission, Seattle, WA
IPSFC	International Pacific Salmon Fisheries Commission, New Westminster, B.C.
NMFS/ABL	National Marine Fisheries Service, Auke Bay Lab, Auke Bay, AK
NMFS/DC	National Marine Fisheries Service, Washington, D.C.
NMFS/PDX	National Marine Fisheries Service, Portland, OR
NWIFC	Northwest Indian Fisheries Commission, Olympia, WA
NWAFC	Northwest & Alaska Fisheries Center, Seattle, WA
OAF	Oregon Aqua-Foods, Springfield, OR
ODFW	Oregon Dept. of Fish & Wildlife
OSU	Oregon State University
PEG	Pacific Environment Group, Monterey, CA
PBS	Pacific Biological Station, Nanaimo, British Columbia
PMEL	Pacific Marine Environmental Lab
Quinault	Quinault Tribe, Taholah, WA
SFU	Simon Fraser University, British Columbia
Tokyo Fish	Tokyo University of Fisheries
USFW/CA	U.S. Fish & Wildlife Service, Stockton, CA
USFW/SEA	U.S. Fish & Wildlife Service, Seattle, WA
UAK	Univ. of Alaska, Fairbanks, AK
UBC	Univ. of British Columbia
UC Davis	Univ. of California, Davis; Bodega Marine Laboratory
UW	Univ. of Washington, Seattle, WA
WDG	Washington Dept. of Game
Westwater	Westwater Research Center, Univ. of British Columbia
Weyerh	Weyerhaeuser Co., Tacoma, WA

Presentations

Factors Associated with Mortality of Coho Salmon (*Oncorhynchus kisutch*) from Saltwater Release Facilities in Oregon

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Abstract

Tagged groups of juvenile coho salmon released into Oregon estuaries were used to identify relationships between hatchery practices, juvenile release strategies, and marine survival. Size at release was strongly correlated with survival of underyearling and yearling smolts. Date at release was strongly correlated with survival of yearling smolts. Various hatchery practices, origin of parent stock, diet, and density of rearing were weakly correlated or unrelated to marine survival. Morphological measurements of smoltification were also weakly related or unrelated to marine survival. Type of release and length of salt water acclimation were significantly associated with marine survival.

Size at release into salt water was a good predictor of marine survival for underyearlings. The mechanisms relating size at release to survival remain to be explained. They are hypothesized to involve possible interactions among physiological processes (e.g., smoltification, growth, and swimming performance) and environmental factors such as predation and ability to acquire food.

Introduction

Oregon administrative rules for private salmon hatcheries require that juveniles be released in estuaries or into the ocean. This is done to minimize competition with other juvenile salmonids for space and food in streams.

Three companies have obtained permits from the Oregon Department of Fish and Wildlife to release coho into Coos, Siuslaw, and Yaquina bays. The program started in 1974 with the release of 88,000 juveniles into Yaquina Bay. Release numbers increased to 23,852,000 in 1981 (Table 1). Of the 59 million juvenile coho released through 1981, 3% went into Suislaw Bay, 38% into Coos Bay, and 59% into Yaquina Bay. This report reviews results of studies involving groups of tagged juveniles released into Coos and Yaquina bays.

Coded wire tags were applied on a significant scale beginning with the 1978 release year at Yaquina Bay and the 1980 release year at Coos Bay. Hundreds of groups of juvenile coho have been tagged and released, and recoveries of tags from fish recaptured in ocean fisheries and returning to release sites have been recorded. This report summarizes results from these extensive tagging studies in an attempt to identify factors which possibly affect marine survival.

Table 1. Numbers of coho juveniles released from private salmon ranches into three Oregon estuaries, 1974-1982. (From Cummings, 1983).

	Millions of Juveniles			
Year of Release	Coos Bay	Siuslaw Bay	Yaquina Bay	Total
1974			0.1	0.1
1975			0.1	0.1
1976	0.9		1.2	2.1
1977	1.0		1.4	2.4
1978	0.6	0.4	8.9	9.9
1979	1.1	0.7	3.9	5.7
1980	6.9	0.2	7.6	14.7
1981	11.9	0.2	11.9	24.0
	22.4	1.5	35.1	59.0

Size and time of release were two key variables selected for analysis because work by other researchers had indicated that manipulation of size and time did affect survival. Bilton (1978) estimated an optimum size (20-24 g) and time of release (June) in his study of coho in British Columbia. Hager and Noble (1976) reported that releasing larger coho smolts increased adult survival for coho released into Puget Sound. Johnson (1982) reviewed the size and time experiments conducted with coho salmon in Washington, Oregon, and British Columbia and concluded that in general the results were inconclusive as there was no coastwide optimum time and size of release. He did recommend however that Columbia River coho be released in May-June rather than March-April. A Washington Department of Fisheries study (1977) of time of release for coho into a Columbia River tributary found that June and July releases produced a better adult survival than April and May releases. A recent report by the Oregon Department of Fish and Wildlife (1982) indicated that releases in July produced the highest survival for coho in the Columbia River. However, the effect of time of release on adult survival for coho released from Oregon coastal hatcheries is somewhat inconsistent with these results. Johnson (1982) found no clear relationship between adult survival and time of release. Garrison (personal communication, Oregon Department of Fish and Wildlife) indicates that stream flow conditions prevent an evaluation of time of release for Oregon coastal hatcheries because many coastal streams have low flows and/or high temperatures in late spring and early summer which are hazards to smolt migration. Hager and Noble (1976) reported that increasing size of smolts at release increased adult survival for coho released into Puget Sound.

Laboratory experiments have suggested that the ability of a coho to adapt to salt water may be size or time dependent. Mahnken et al. (1981) postulated that there is a critical size that coho smolts must obtain prior to entering salt water in order to grow and survive. These authors hypothesized that once in salt water juveniles must maintain a certain minimum growth rate in order to avoid reversion to the parr stage. Size at seawater entry was chosen in our study as a variable to determine if there were any relationships between size and subsequent survival.

Wedemeyer et al. (1980) have shown that smoltification is initiated by increasing photoperiod once juvenile salmon reach a critical size. The size of coho juveniles has been shown to be positively correlated with gill Na+ K+ ATPase activities (Folmar and Dickhoff 1981), which indicates that larger fish are better able to osmoregulate. However, the relationship of smoltification and size at release to adult survival needs to be clarified.

General Methods

Salt water release facilities operated at Coos and Yaquina Bays by Oregon Aqua-Foods and Anadromous, Inc. have several features in common. They use pumps to circulate water from estuaries through concrete or asphalt-lined ponds. Pumping rates varied but were typically in the range of 300 to 600 l/sec. The ponds are located on land. Salt water re-enters the estuary after flowing from the ponds down a concrete fish ladder.

Juvenile salmon are transported by tank truck from freshwater facilities which are located inland from the estuaries and placed into the salt water ponds. This we call the time of entry into seawater. The fish are held captive and fed artificial diets in salt water release sites between date of transport from a freshwater hatchery to date of release into an estuary. This period typically varies between 10 and 30 days. Juvenile salmon are usually released during hours of darkness to avoid attracting birds and other predators to the point of release.

A single salt water release site has operated at Yaquina Bay. Two sites, which are 6 km apart, have operated at Coos Bay. Adults returning to Coos Bay have exhibited extensive straying between the two sites, probably because the two sites share a common water source. Data on release and return of the tagged fish are pooled for the two Coos Bay sites in the analyses presented in this report.

Numbers of juvenile coho in individual tagged groups have ranged from about 1,000 to 68,000. Juveniles were tagged prior to smoltification. They were transported to salt water after visual criteria of smoltification and size criteria had been satisfied. Some tagged groups were released as underyearlings and others as yearlings. Results are considered separately for underyearlings and yearlings.

Maturing coho caught by sport and commercial fishermen are routinely sampled by fishery agencies to recover coded wire tags. These recoveries are a fraction of the total number of tagged fish actually caught in the ocean fisheries. All coho returning to release sites are examined for coded wire tags where the recovery rate is nearly 100%.

Our objective in this analysis is to evaluate our rearing and release methods to determine which variables affect adult survival. The variables that we selected for analysis had to meet two criteria. One, we had to have measures of them. Two, they have been suggested by other researchers as having possible influences on adult survival.

The analysis consists of three parts. The first is a general overview of the data base using correlation analysis. This part of the analysis is aimed primarily at identifying variables which show a statistical relationship to survival. The second part is a regression analysis which uses measures of survival as dependent variables and size and time of release as independent variables. The third part is a review of the effect of various hatchery practices on survival.

Size at release, size at entry into seawater, date of release, and smoltification were factors that both companies had routinely measured over several years of release of coho juveniles. Survival was determined by three measures. The first was the simple proportion of each release that return to the release site (escapement). The second was the estimate of proportion of each release which was caught in the ocean fishery (catch). The third was the sum of the first two measures (catch plus escapement), which is an estimate of total survival. The ocean catch includes both sport and commercial catches.

Correlation Analysis

The three estimates of survival (escapement, catch, and catch plus escapement) were correlated with each other and with other variables (Tables 2 and 3). The data were treated separately for underyearling and yearling coho juveniles. Unfortunately the data set was too incomplete to allow for evaluation of interannual variation primarily for two reasons. In some years the number of tagged groups released and the range of the rearing variables (Table 4) were too small to allow for any meaningful evaluation. Second, the size range and maximum size at release has increased every year for both underyearlings and yearlings. Our purpose in the correlation analysis is to measure the intensity of the association between pairs of variables and to test whether it is greater than could be expected by chance alone (Sokal and Rohlf 1981). We do not have sufficient data to describe or imply causation but rather are more concerned with the degree of association among the variables involved.

Table 2. Matrix of correlation coefficients for tagged groups of underyearling coho salmon released into Coos and Yaquina Bays in 1978, 1979, 1980, and 1981.

	Size at Seawater Entry	Size at Release	Date at Release	Smolt Index	Ocean Catch	Escapement	Total Survival
Size at Release	r=.9659 n=40	---	---	---	---	---	---
Date at Release	r=.8482 n=40	r=.6015 n=105	---	---	---	---	---
Smolt Index	r=.1095 n=40	r=.1208 n=40	r=.0424 n=40	---	---	---	---
Ocean Catch	r=.8395 n=40	r=.6438 n=105	r=.4772 n=105	r=.2056 n=40	---	---	---
Escapement	r=.9257 n=40	r=.8979 n=105	r=.5455 n=105	r=.1169 n=40	r=.7692 n=105	---	---
Total Survival	r=.9111 n=40	r=.8344 n=105	r=.5474 n=105	r=.1513 n=40	r=.9256 n=105	r=.9538 n=105	---

Table 3. Matrix of correlation coefficients for tagged groups of yearling coho salmon released into Coos Bay in 1980 and 1981.

	Size at Seawater Entry	Size at Release	Date at Release	Smolt Index	Ocean Catch	Escape-ment	Total Survival
Size at Release	r=.6915 n=38	---	---	---	---	---	---
Date at Release	r=.5121 n=38	r=.3004 n=47	---	---	---	---	---
Smolt Index	r=.2812 n=38	r=.2653 n=38	r=.2401 n=38	---	---	---	---
Ocean Catch	r=.4447 n=38	r=.4596 n=47	r=.4973 n=47	r=.1883 n=38	---	---	---
Escape-ment	r=.2082 n=38	r=.3802 n=47	r=.6320 n=47	r=.2033 n=38	r=.7322 n=47	---	---
Total Survival	r=.3157 n=38	r=.4859 n=47	r=.5945 n=47	r=.3159 n=38	r=.8646 n=47	r=.9508 n=47	---

Table 4. Summary of coded wire tag groups released from salt water facilities in Coos Bay and Yaquina Bay, Oregon.

	ANADROMOUS (yearlings)		OAF (underyearlings)			
Brood Year	1978	1979	1977	1978	1979	1980
Release Yr.	1980	1981	1978	1979	1980	1981
Mean Size @ Release (g)	30.8	36.07	18.9	18.1	24.5	26.4
Range	22.8-41.8	25.8-51.8	15.5-22.5	15.8-25.8	17.6-37.8	16.4-69.0
Mean Date @ Rel. (Julian)	126.9	141.1	200.5	207.7	205.1	192.5
Range	90-157	83-189	164-250	185-262	158-248	147-251
Number of tag groups	9	38	16	7	39	43

Underyearlings

Size at seawater entry and at release were highly correlated with the three measures of survival. Seawater entry size, while showing a slightly higher positive correlation with survival than size at release, was only measured in one year, while size at release was measured for four years and reflects annual variation. Furthermore, size at release was highly correlated with size at seawater entry (r=0.97). Underyearling coho are held for short periods in salt water prior to release and do not show substantial growth prior to release. The two size measurements are not dissimilar enough to determine which most closely correlates with survival.

Smoltification, as measured by visual criteria, did not correlate well with other variables such as size at release. The release period for the analysis ranged from early May to mid-September. Correlation analysis assumes a linear relationship, and this may not be the case between size and smoltification, since the relationship is most likely to be time dependent. Smoltification also did not show any strong relationship to any of the measures of survival.

Ocean catch was positively correlated with adult survival (catch plus escapement). The implication of this is that one does not operate at the expense of the other. A negative correlation would have implied that rearing manipulations not only affect total survival but also determine the ratio of fish caught in the ocean to those which return to the release site. The positive correlation between ocean catch and escapement implies that as one increases so does the other.

Ocean catch does not correlate as well as escapement with size and date of release. Catch is estimated from tagged fish recovered in the fisheries and is subject to unknown error due to sampling procedures. The sampling scheme used to sample ocean catch of coho along the Oregon coast is a three way stratification procedure stratified by type of fishery, port of landing and time of landing (week). Within each strata the proportion of the total catch that was sampled ranged from zero to 100%, averaging more than 20%. Since recoveries of each coded wire tag code used in this analysis are usually less than a .01% of the total sample, the expected coefficient of variation would be high (Cochran 1977). Escapement, on the other hand, is enumerated directly and is not influenced by unknown sampling error.

Yearlings

For yearlings, survival (catch, escapement, and catch plus escapement) was more highly correlated with date of release, whereas with underyearlings the stronger correlation was with size. The increase in importance of date of release in comparison to underyearling coho is most likely due to the following circumstances. Yearling releases have a wider range of sizes over the release cycle, whereas the average size of underyearling coho tends to increase over time. Increasing size at release over time tends to confound the effect of each variable. Size at entry into seawater was poorly correlated with all measures of adult survival. Yearling coho released by Anadromous were held for short (10 days) to extended periods (54 days) prior to release, and there was considerable variation in the weight gained in salt water prior to release. The higher correlation between size at release and survival than with size at seawater entry and survival indicates that size at release is more important.

Visual assessment of smoltification did not correlate well with any measure of survival. Smoltification also did not correlate well with either size or date of release, which indicates that its potential reliability as a predictor of survival is doubtful.

The measures of marine survival were all positively correlated with each other. Total survival showed the highest correlation with size, a correlation only slightly greater than with ocean catch and size. Escapement showed the highest correlation with date at release. No particular significance is attached at this time to relative ranking of correlations of survival with size and date at release since no consistent pattern was observed.

Regression Analysis

Size and time of release were next regressed on the three measures of survival. The intent of the regressions was to develop predictive equations, not to describe functional relationships. This is an important point since what are considered the "dependent" variables may reflect other, unidentified variables which actually affect survival. Size at seawater entry was not used as a predictor since it was not measured over all years of release.

For underyearlings, the variable which best predicted survival was size at release. Date of release was also significant but did not appreciably improve the accuracy of the equation with size remaining in the multiple regression equation. Size at seawater entry was not used as a predictor since it was not measured over all years of releases. The fit of the equation with escapement as the dependent and size as the independent variable was quite good with an r^2 of 0.81 as would be expected from the simple correlates. The fit with ocean catch as the dependent variable was much worse, r^2=0.41, which most likely reflects the fact that ocean catch is not a direct measure but is an estimate.

The r^2 values obtained for yearling coho were not as good as those for underyearling coho. Date of release and size at release were both used in the predictive equation for yearlings, with a resulting r^2=0.44 based on escapement. The fit with ocean catch as the dependent variable was not as good (r^2=0.35) again, most likely because ocean catch is an estimated value rather than an actual value.

Hatchery Practices

A number of experimental groups of juvenile coho have been tagged and released to evaluate the effect of various hatchery practices on marine survival. Variables in these studies included origin of parental stock, diet, density of rearing, duration of salt water acclimation, and forced versus voluntary release.

Origin of Parental Stock

Several stocks of coho have been released. Some were local to the Oregon coast and some were introduced from Puget Sound. Males and females from four stocks were used in a breeding experiment which was designed to evaluate the effect of origin of stock on survival. Two parental stocks (Alsea and Siletz rivers) came from Oregon coastal hatcheries. A third parental stock (Green River) came from a Puget Sound hatchery. The fourth parental stock was a hybrid from Oregon Aqua-Foods which included genetic material from Oregon and Puget Sound hatcheries.

Ten combinations of matings involving males and/or females from four stocks were used in the matings (Figure 1). The number of tagged juveniles released ranged from 10,199 to 14,917 per combination. Hatchery rearing regimes were similar for all groups, which were released as underyearlings into Yaquina Bay on June 28, 1980.

Surviving adults returned in 1981. Tagged fish reported from the ocean fishery and recaptured at the release site were combined for analysis.

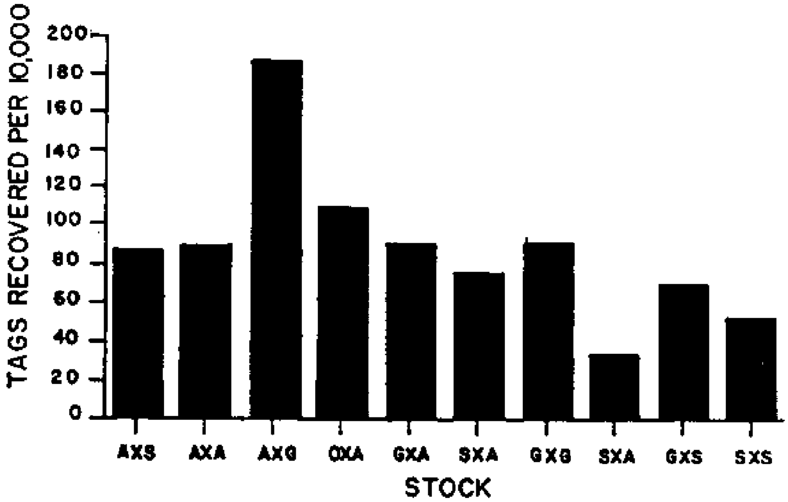

Figure 1. Marine survival (tags recovered per 10,000 fish released) from matings involving four stocks of coho released as underyearlings into Yaquina Bay. Males are listed first. The stocks are A= Alsea River; S= Siletz River; G= Green River; and O= Oregon Aqua-Foods mixed stock.

The numbers of total recoveries per 10,000 tagged juveniles are shown in Figure 1. A log likelihood test of the 10 proportions gave a G value (9 d.f.) = 56.70 which is highly significant at the .05 level. The null hypothesis was rejected; i.e., the proportion of total recoveries was not independent of test groups. The low return group was a hybrid Oregon stock (Siletz X Alsea). The high return group was a hybrid Oregon-Puget Sound stock (Alsea X Green). The remaining eight groups, including three Oregon coastal stocks, had intermediate return rates. If the Alsea X Green and Siletz X Alsea had been removed from the analysis the null hypothesis would not have been rejected. Thus, for eight of the ten stock combinations, there was no evidence that survival had been affected by origins of parents. There was no evidence that Oregon coastal stocks yielded better returns than non Oregon coastal or hybrid stocks.

Diet

A variety of artificial diet formulations is commonly fed to juvenile salmon. Although a number of studies have evaluated growth response to diet in fresh water, less is known about relationships between artificial diet and marine survival.

An experiment with underyearling coho salmon released in 1980 provides information on the effect of artificial diet on marine survival. Five test groups were fed different diets. Two of the diets (UW and OAF) were formulated especially for the experiment. The other three (OP-4, OP-2, and Abernathy) were purchased. Abernathy was a dry diet and the other four were moist diets. The test groups came from the same hybrid stock. The five groups were raised under similar conditions and released into Yaquina Bay on August 5, 1980, at an average body weight of 24.9 g. The number of tagged fish released per groups ranged from 7,547 to 10,285. Numbers of tags reported per 10,000 tagged juveniles are compared in Figure 2.

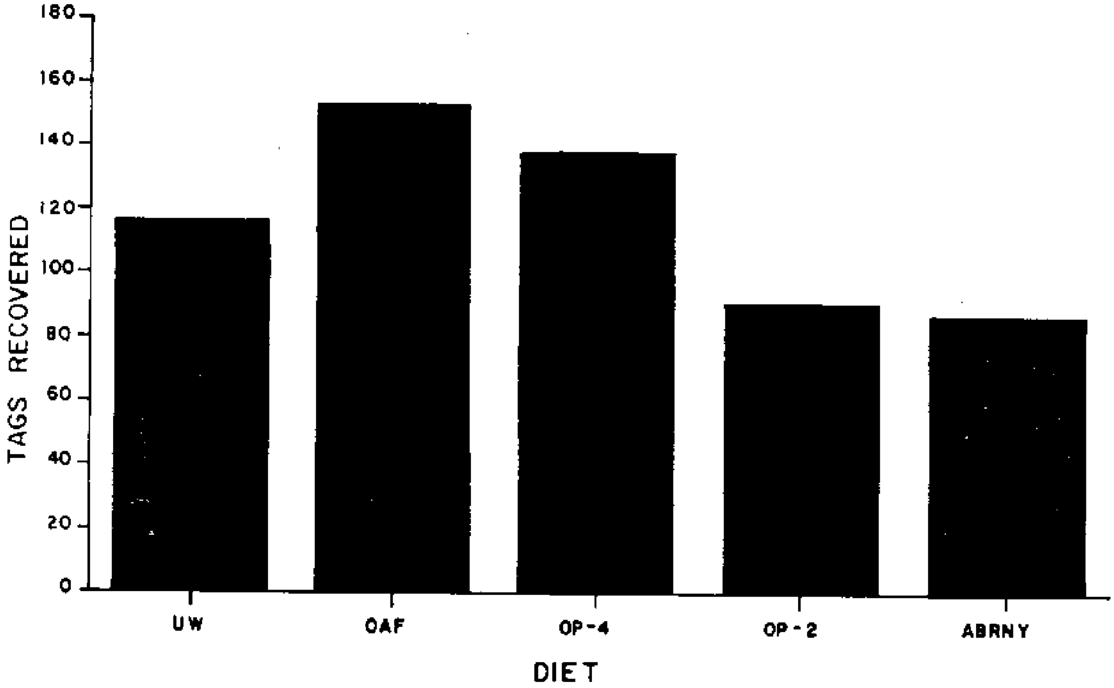

Figure 2. Marine survival (tags recovered per 10,000 releases) of groups of coho fed five experimental diets and released as underyearlings into Yaquina Bay, Oregon. UW= University of Washington experimental diet; OAF= Oregon Aqua-Foods experimental diet; OP-4 and OP-2= Oregon moist pellets; and ABRNY= Abernathy dry diet.

A log likelihood test of five samples gave a G value of 2.21 which was not significant. It appeared that marine survival was independent of the artificial diet fed in the hatchery.

Density

Density of juveniles at the Oregon Aqua-Foods hatchery approaches 25 kg of biomass per m^2 of raceway area at peak density. This density is two times or more the density commonly experienced at salmon hatcheries. Sandercock and Stone[1] (1979) reported a substantial increase in adult survival for coho reared at low densities in a British Columbia facility. Fagurland et al. (1981) reported poorer growth and retardation of smoltification with coho grown at higher densities in comparison with fish reared at low densities. The potential impact of high density rearing is of major concern due to facility restraints. Two releases with underyearling coho salmon provide information on the relationship of marine survival to density of rearing.

Experimental groups of tagged fish raised at different densities were released on June 21 (23 groups) and July 7, 1981 (34 groups). Tags reported from the ocean fisheries and from the release site were combined for the two release dates to estimate survival (Table 5). Observed peak densities ranged from 15 to 56 kg/m. Water supplies were oxygenated with liquid oxygen and nitrogen was removed to hold dissolved gases at approximately 100% saturation to maintain effluent levels at or above 6 mg/l. Results were similar for the two groups (Figure 3). Correlation coefficients were negative for both release dates, but the correlations were very weak. Neither value of r was significantly different from zero. Over the ranges evaluated the density of reared fish appeared to have little, if any, effect on marine survival. There were differences in size at release within each group, however the correlations between size at release and adult survival were weak (.06 for June 21 and .32 for July 7).

Table 5. Number released, peak biomass, size at release, and survival of coho groups used to evaluate rearing density.

	JULY 7, 1981 RELEASED					JUNE 21, 1981 RELEASED			
CWT #	# RELS.	DENSITY (kg/m^2)	SIZE (g)	SURVIVAL PER 1000	CWT #	# RELS.	DENSITY (kg/m^2)	SIZE (g)	SURVIVAL PER 1000
600352	2249	44.9	36.4	7.56	600355	2444	5.3	38.3	15.14
600361	1818	29	29.1	3.30	600425	1224	20.9	31.1	44.12
600362	3278	55.5	30.9	16.78	603215	2127	33.6	28.2	12.41
600417	1428	28.3	27.6	10.50	603217	2400	34.8	26.4	31.25
603210	1840	35.1	34.8	9.24	603218	2701	40.1	27.1	10.74
603213	2999	43.8	26.6	1.33	603433	1590	29.9	34.3	22.64
603246	2426	41.2	31	9.89	603435	1826	26.2	26.1	29.03
603249	1539	27.3	32.3	20.79	603437	2174	31.7	26.6	14.72
603431	1597	26.4	30.1	0.63	603442	1521	24	28.7	24.33
603434	1826	23.5	23.5	7.12	603446	1221	20.6	30.7	16.38
603438	1792	29.1	29.6	9.49	603447	2183	42.1	35.2	25.65
603439	1953	30.3	28.3	23.04	603449	1719	26.5	28.1	18.62
603440	1456	25.9	32.4	17.17	603450	1644	25.2	27.9	24.94
603441	2005	31.3	28.5	1.92	603451	1003	16.2	29.4	21.93
603443	1683	25.3	27.4	11.88	603455	1552	23.1	27.2	47.04
603444	2081	28.9	25.3	6.25	603463	1039	15.8	27.7	19.25
603445	2132	35.2	30.1	4.69	603515	2287	34.1	27.2	17.05
603453	1854	30.1	29.6	12.94	603515	1647	24.4	27	17.61
603454	1699	22.6	24.3	1.77	603518	1640	26.5	29.5	3.05
603456	1940	31.2	29.3	28.87	603520	2386	36	27.5	2.51
603457	2127	29.9	25.6	12.22	603534	2329	35.7	27.2	4.60
603458	1483	28.6	35.2	7.42	603549	2547	39.1	28	9.03

[1] Sandercock, F.K. and E.T. Stone, (mimeograph). The effect on rearing density on subsequent survival of capilano coho. Fish. and oc. salmonid enhancement. mog.2p.

Table 5. Number released, peak biomass, size at release, and survival of coho groups used to evaluate rearing density. (cont.)

JULY 7, 1981 RELEASED

CWT #	# RELS.	DENSITY (kg/m^2)	SIZE (g)	SURVIVAL PER 1000	CWT #	# RELS.	DENSITY (kg/m^2)	SIZE (g)	SURVIVAL PER 1000
603459	1966	29.3	27.2	5.60	603525	1812	28.6	28.8	1.10
603460	1753	33	34.7	21.90	603526	2221	36.9	30.3	0.45
603511	2349	29.9	23.2	2.13	603538	2672	39.8	27.2	13.47
603522	1910	28.8	27.5	3.14	603539	2980	35.1	21.5	1.01
603524	2067	35.6	31.4	2.90	603541	2604	45.5	31.9	8.83

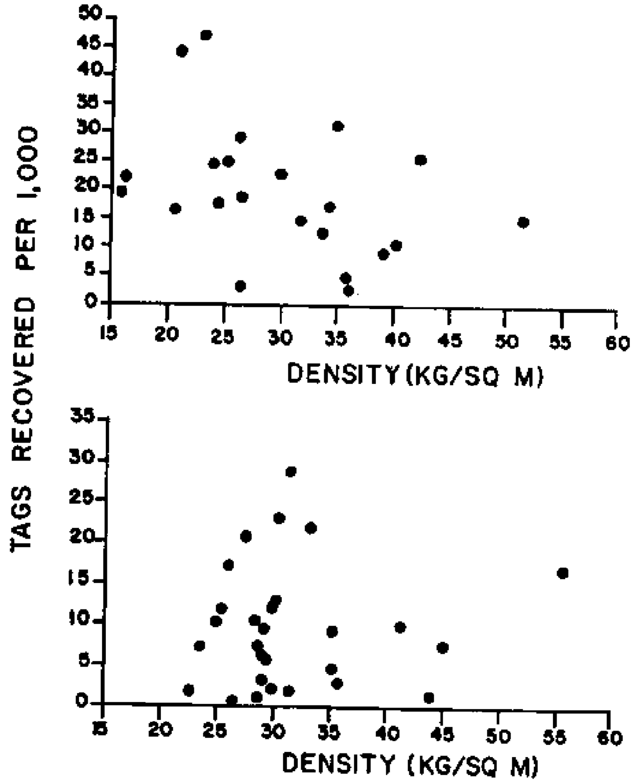

Figure 3. Marine survival (tags recovered per 1,000 fish released) of groups of coho reared at different densities and released as underyearlings into Yaquina Bay on June 21, 1981 (top) and July 7, 1981 (bottom).

Time of Salt water Retention

A 3 X 4 factorial experiment suggested by Mathews (1981)[1] was designed to evaluate the effects of date of release and salt water acclimation time. Fish were released on four occasions from April through July with three periods of salt water retention on each release. The effect of these manipulations was measured by escapement. Fish were self-released on the four release dates. Self-release means that the water level of a salt water raceway was lowered and the outlet screen removed. After two weeks, any remaining fish were crowded out of the raceway into the release channel.

Except for the April release, longer retention increased adult return (Table 6). The return from the ten-day retention group in April was better than the 24 and 54-day retention groups. The fish released in April were small (26-32 g) and the overall return from all groups was low, however. For the other three months, increased retention produced greater returns. July release produced the best returns followed in order by May, June, and April. The results were evaluated by analysis of variance. Time of release was significantly different at the 95% level and time of retention was significant at the 75% level. However, simply looking at retention time and time of release is misleading, as other factors, primarily size, also affect return. The analysis assumes that time of release and retention time are the only variables which affect return and that any variation is random. Other work has shown that size at release has a profound effect on survival.

Table 6. Adult escapement per 10,000 release of forced-released and self-released groups of coho salmon released as yearlings into Coos Bay.

	SELF-RELEASE						FORCED RELEASE	
Salt water Retention	10-24 days		23-47 days		54-68 days		30 days	
Month Released	Escapement	Wt.at Rel. (g)	Escapement	Wt.at Rel. (g)	Escapement	Wt.at Rel. (g)	Escapement	Wt.at Rel. (g)
April	17.9	25.8	12.4	26.4	13.5	27.7	31.9	32.1
May	73.9	33.1	123.5	36	136.3	41.2	158.2	36.6
June	73.4	37.7	95.0	35.8	103.0	41.4	184.1	38.0
July	37.0	36.4	101.7	41.8	203.1	35.1	281.3	41.0

1/ Mathews, S.B. 1982. Consulting report for Anadromous, Inc. Univ. of Wa., Seattle, Wa.

In order to release healthy fish in all months of the experiment, it was necessary to allow size to increase over time with the biggest increase in size occurring between April and May. For a given month there was also considerable variation in size between groups which also tends to confound the results. In spite of the size variation, the results show that later release produces better returns and that increased salt water retention prior to release usually produces better survival.

Forced Release Versus Self-Release

Other researchers have implied that volitional or self-released fish would return at a higher rate than fish "forced" out of a rearing facility, Brannon et al. (1982). To evaluate this, groups of coho salmon were force-released once a month over four months and compared to other groups which were self-released over the same time period.

Forced release means that on the day of release, fish were crowded out of the raceway into the release channel and forced down the ladder. Self release means that the water level in a raceway was lowered and the outlet screen removed. Fish were given two weeks to leave the raceway, and at the end of the two week period the remaining fish were crowded out of the raceway.

For all months forced-released fish returned at a higher rate than any group of self-released fish (Table 6). Comparing the forced-released groups with the most similar self-released groups (23-47 days), the forced releases returned at twice the rate of the self releases.

Discussion and Conclusions

Our evaluation of tagged groups of coho from the salt water release sites has helped to clarify some relationships that are potentially important to the success of salt water release facilities. Size and date of release are the best predictors of adult survival of the variables which have been examined to date. In the case of underyearlings size at release alone was quite successful in predicting survival. Considerable variation in survival was found for a given size at release, however.

The survival of yearling coho was best predicted by the combination of time of release and size at release. The overall accuracy in prediction of return of yearlings by these two variables was much poorer than size alone was for underyearlings. One possible source of the increased variability is the greater diversity in rearing histories of yearling coho. Some of the yearlings were reared at one freshwater site, others were reared at two or three different sites. Furthermore, the salt water retention time varied from 10 to 89 days for yearlings. In contrast, the underyearlings were all reared at one site, the salt water retention periods were less variable, and the release method was consistent.

Visual indices of smoltification were not strongly associated with marine survival. Saxton et al. (1983) reported that morphological measurements of smoltification are poor predictors of growth and survival of underyearling coho salmon placed in salt water pens. They found that size at entry to salt water was positively correlated and the best predictor of growth and survival in net pens. They also found that size was positively correlated with biochemical indicators of smoltification (viz, plasma sodium levels, Na+-K+ATPase activity, and thyroid hormones). However, there is a major difference between placing young coho in net pens and releasing them into the open ocean. The processes which determine adult survival are most likely to be completely different. Brannon et al. (1982) felt that too much emphasis had been placed on attempts to determine readiness to migrate by correlations between smolt indices and adult survival, apart from the fact that such correlates may be completely unrelated. They also felt that it was important that migratory readiness not be confused with the best release timing based on return survival. Although the ultimate objective should be to synchronize smoltification with optimum time of release, the two are separate issues.

We agree with their statement except that if a consistent correlation can be shown between adult survival and any measure of smoltification, either visual or biochemical, then it should be used. It is immaterial whether there is a cause and effect relationship, only that there be a relationship between the two, as a coho must smolt prior to becoming an adult. If any measure of that smoltification can be shown to correlate with adult return then that correlate allows some prediction of adult survival. Unfortunately no visual or biochemical measure or measures of smoltification have yet been shown to consistently correlate with marine survival.

Of the rearing factors examined only type of release and salt water holding time were found to have any impact on adult survival. Wagner (1968) found no difference in adult survival between self (volitional) and forced released steelhead from an Oregon coastal hatchery. Preliminary results from Cole River hatchery on the Rogue River also show no major difference in return rates for self and forced released steelhead from that facility (Mike Evenson, personal communication, Oregon Department of Fish and Wildlife). Each site determines the best release strategy. What is appropriate for a freshwater facility may not be optimum for a seawater site. The mechanism or mechanisms which explain why force-released fish from a seawater site survive better than self-released fish are unknown, but they may be related to predation in the estuary. Forcing fish out could swamp predators, whereas allowing fish to trickle out may allow a higher overall predation rate.

Increasing seawater retention was found to generally increase survival. Underyearlings may take as long as 21 days to physiologically adapt to seawater. Release in itself is a stress and fish released prior to completely recovering from the initial stress of seawater entry are more susceptible to predation.

Currently there are studies underway in Oregon and Washington to evaluate the effect of diet on the survival of salmonids to adulthood. Preliminary results of these diet trials have not shown the existence of a diet which increases marine survival (John Westgate, personal communication, Oregon Department of Fish and Wildlife). These results are consistent with ours. Diet formulations should meet certain nutritional requirements beyond which there is little advantage in exceeding.

Density was found to have no significant effect on adult survival. Several studies have evaluated the effect of density on salmonids held in a rearing facility (Wedemeyer 1976; Refstie and Kettelsen 1976; Fagurland 1981). Few studies however have evaluated the relationship of density and marine survival.

Sandercock and Stone1/ reported that coho reared at low densities returned almost twice as well as those reared at high density. This is contrary to our results but Sandercock and Stone did not provide supplemental oxygen to their high density groups. In our experiment supplemental oxygen was added to maintain an

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1/ Sandercock, F.K. and E.T. Stone. (mimeograph). The effect of rearing density on subsequent survival of Capilano coho. fish. and oc. salmonid enhancement. mog. 2p.

effluent level of 6 mg/l. Fagurland et al. (1979) indicated that size at release was more important than density in determining adult survival. In our experiment size did not vary enough to determine the effect of both size and density on return.

Other explanations for high marine survival of coho juveniles released at a large size may relate to swimming performance, which in turn may relate to predator avoidance and ability to capture prey. It is well known that swimming speed is positively related to size (Beamish 1978; Brett 1982). Thus, larger smolted juveniles possibly experience a lower mortality from predation and/or are better able to capture prey than smaller juveniles. Predator avoidance, if a significant factor, results from a combination of greater swimming speed of smolts and limitations of predators to catch and consume large prey.

Mechanisms controlling marine survival involve complex interactions among physiological processes (e.g., smoltification, swimming performance, growth, etc.) and predation. We need to better understand the processes which explain the roles of size and time of release and fish cultural practices as factors modifying marine survival of coho and other salmonid species. An understanding of these processes can provide a foundation to implement hatchery rearing and release strategies which will result in increased marine survival.

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Comments on the Mortality of Coho Salmon from Saltwater Release Facilities in Oregon

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Introduction

The authors and private sea ranching companies, Anadromous and Oregon Aqua Foods, are to be commended on their efforts to understand the complex factors affecting survival of their hatchery fish. The compilation of this extensive data set represents one of the most intensive tagging efforts ever mounted at either public or private Pacific salmon hatcheries.

It is not our intent to critize the techniques or statistics used to assess adult contribution from Oregon Aqua Foods and Anadromous hatchery releases. We recognize that there are inherent difficulties in estimating ocean catch and survival from coded wire tag recoveries. Instead we will comment on some of the underlying assumptions in these hatchery experiments, which were designed to evaluate potential increased production of adult fish. Specifically, we will address the following areas: (1) the adequacy of measures used to define the stage of smoltification, (2) the relatively poor contribution of underyearling fish when compared to releases of yearling smolts, (3) the rather considerable variability in survival observed in this and other studies in regard to size and time of release of juveniles, and (4) the need to expand these types of hatchery trials to partition the cause of density-dependent and size-dependent mortalities into ocean, estuary, and hatchery effects.

Smoltification Index

The authors state: "Significant changes in body coloration and shape accompany a metamorphosis from freshwater parr to a euryhaline smolt. Tagged groups were sampled to estimate the percentage of smolted and unsmolted juveniles in test populations--criteria for visual measurements are somewhat subjective. Nevertheless, changes in appearance are substantial between a juvenile that has smolted and one that has not." Classification of animals into parr and smolts was determined using five visual criteria. In our estimation, visual criteria are the least reliable indicators of smoltification since they show a poor correlation with numerous other smolt indices developed in recent years. In fact, the unreliable nature of visual criteria has led to the present interest of researchers in developing new smolt indices.

Recently, the adequacy of the classic terminology of "parr" and "smolt" has been brought into question when applied to the development of young Pacific salmon (Gorbman et al. 1982). A smolt is a larger and older fish in which deposition of guanine in the scales and skin give the fish a "silvery" color that obscures the "parr" marks. This definition generally implies that this is the form that migrates to sea. The basis for dissatisfaction with this terminology is that the process of guanine deposition is easily reversible and not necessarily correlated with size or with physiological or biochemical changes.

A similar argument can be developed against the use of blood osmolality as the single measure of smoltification. Even after arrival in seawater, coho salmon smolts may not retain their optimum "osmolality" and their normal progressive development; some may revert to blood osmolality values more characteristic of the parr. It would seem prudent to employ a wider variety of techniques for more meaningful descriptions of the physiological, morphological, and behavioral changes that take place in developing salmonids.

Recent measurable features of osmoregulatory and metabolic development and migratory readiness that have been shown to have merit when taken in combination with other measures are: blood plasma levels of thyroid and interrenal corticosteroid hormones; appearance of enzymatic activity (ATPase) in the gills; swimming efficiency and stamina; and migratory behavior. We agree with the authors and understand why *visual criteria* of smoltification are not good predictors of marine survival. Modern techniques must be applied to accurately evaluate the importance of smoltification in ocean survival.

Comparison of Underyearling and Yearling Returns

In the present study differences in the contribution of underyearling and yearling fish were observed. Such differences may have been due to different proportions of parr and smolt forms that may have been present in the two age groups. Evidence from this and other studies can be presented suggesting that while yearlings undergo a more normal parr-to-smolt transformation, underyearling fish exhibit a retarded and incomplete juvenile development.

The authors have presented correlation coefficients for size and date of release versus survival of *underyearlings* that reveal the following decrease in correlative strengths: size at transport > size at release > date of release. For *yearlings* the opposite was observed: date of release > size at release > size at transport. In our opinion this reversal in the correlative relationships between underyearling and yearling performance is most likely a consequence of good smoltification in yearlings and poor smoltification in underyearlings. For underyearlings which are poorly smolted, *size* or freshwater growth is the most important factor determining subsequent marine survival. For yearlings, a critical physical size has been attained and is therefore less important than *time* of release. Time of release of yearlings is probably important for ocean survival because of at least two interacting factors. A primary time-dependent factor is the animal's developmental state (smoltification), which determines its ability to adapt to the marine environment. The other major factor is the variable ocean productivity which defines the conditions to which the fish must adapt.

In coho salmon the parr-to-smolt transformation usually occurs during the second year after hatching. Development of coho salmon may be compared with that of masu salmon in this regard (Kubo 1974). Kubo hypothesized that during the first year of development masu salmon undergo a "phase differentiation" that selects certain individuals for the parr-to-smolt transformation during the second year. In studies of coho salmon, physiological measurements of either plasma thyroid hormone concentrations (Dickhoff et al. 1982) or gill Na^+-K^+ ATPase activities (Folmar and Dickhoff 1981) indicate a lesser degree of development during the first year than the second.

One procedure undertaken by the companies that may affect contribution is the period of seawater culture in ponds prior to release. For yearlings, but not for underyearlings, the period of saltwater culture between the time of transport and time of release has profound effects on survival. This may be due partly to protection from predation in the saltwater ponds while osmoregulatory capacity is developed during the critical period of seawater adaptation. Furthermore, a high degree of variability in seawater growth of yearling fish was observed. A significant relationship between size and escapement developed during this time. Several studies of coho salmon transferred to seawater net-pens have demonstrated that the timing of seawater entry is important for subsequent growth and survival (Clarke and Nagahama 1977; Bern 1978; Folmar et al. 1982). In the present study the relative importance of release date and size in yearlings may have been due to variation in the proportions of smolts in the populations at the time of seawater entry. The high degree of variability in seawater growth may have been due to parr reversion of incompletely smolted fish. Fish that entered seawater as smolts may have shown maximal growth during seawater residence, and these larger fish performed well after release (Figure 1). Thus, for yearlings, size at the time of seawater entry was not related to escapement but size became significantly related to escapement by the time the fish were released from the seawater ponds. For underyearlings, smoltification was retarded for the entire population so that parr reversion in seawater before release did not occur and could not influence the correlations with contribution.

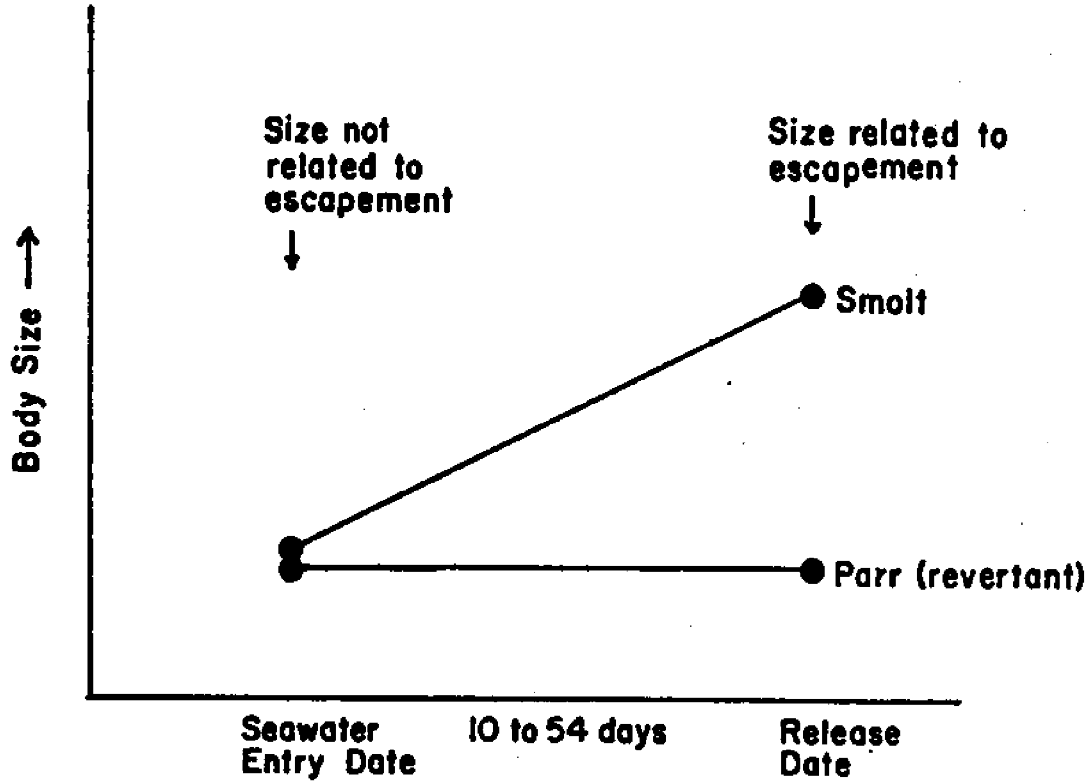

Figure 1. Possible growth pattern for yearling coho salmon resulting in a significant correlation between size and escapement with release date but not with seawater entry date.

Size and Time

The release experiments of Bilton et al. (1982) indicate strong size/time effects for returns of coho salmon in British Columbia. The adult returns varied 16-fold depending on either juvenile weight or time of release. These observations indicate the importance and potential in controlling size/time of releases at hatcheries, but the experiments do not indicate fully where or how these effects are induced in the system. Bilton viewed the juvenile release and adult returns as the boundary points in a "biological system whose central components as yet are imperfectly understood." They suspected that feeding and predation are the primary factors operating on juvenile survival, but they could have included physiological development and adaptation to seawater. Lack of information on status of smoltification in release groups complicates the interpretation of these size/time effects.

In similar experiments (Washington Department of Fisheries; Oregon Department of Fish and Wildlife) where size-groups were established by withholding food, the same criticism can be applied. In addition, there are unknown effects because of the retardation of growth through withholding food for the small size-groups.

The size/time effects on returns of coho salmon to Puget Sound or Columbia River hatcheries (Mahnken et al. 1982) show only a threefold spread in contribution. However, even this lesser range in noted effects suggests great value and potential in the control of size/time of juvenile salmonid release. Here, too, the concurrent smoltification state does not permit a separate analysis of that factor within the size/time variables.

For underyearling coho salmon, Gowan and McNeil observed that size at release had a major effect on returns. This might be expected because the independent time factor (not that which is merely expressed by older fish being larger) probably operates through the smoltification process. None of the underyearling juveniles would have begun the smolt cycle, so that only size effects are expected (and noted) in the survival of these groups. On the contrary, for yearlings, which are smolting, both size and time effects were observed, with time apparently being more influential.

Hatchery Trials

An experiment to separate the independent effects of release size, time, and smoltification state has yet to be performed. One such experiment is planned using an advanced photoperiod to accelerate smolting. In this way identical size-groups, all with maximum growth potential, can be released at the same times but with known large differences of smoltification. Returns should then reflect independent effects caused by all three variables: release size, time, and state of smoltification. From the analysis of returns, the influence of the separate variables can be partitioned. The independent, but probably critical, role of smoltification on ocean survival can then be evaluated. Direct studies in coastal areas, on the surviving juveniles, could then evaluate the separate effects of size and time at release, which probably operate through feeding and predation.

Many salmon biologists have held the opinion that the most important factors determining salmonid survival are of the freshwater environment. It has become clear that the marine environment is at least as important. However, it would be unwise to trade one narrow view for another by focusing solely on the ocean as the determining factor in salmonid production. The ultimate ocean survival of salmonids is the result of the interaction of marine conditions with the physiological state of the fish, which was predetermined by its freshwater experience. Therefore, it is necessary that research on the ocean survival of salmonids include the developmental history and smolt quality of evaluated populations.

The large-scale salmonid hatchery systems in the Columbia River Basin offer unique opportunities for research. Similar systems and controls over recruitment are not available for any other marine species. As information becomes available on the relationships between freshwater rearing conditions and specific ocean conditions that challenge fish adaptability, techniques may be developed to optimize the degree and timing of smolt development.

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The Influence of the Marine Environment on the Interannual Variation in Coho Salmon Abundance: an Overview

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Abstract

Coho populations of the major geographical areas bordering the Northeast Pacific have varied independently from each other in most years. Years of large-scale warm water intrusions appear to be the exception.

Oregon coho have exhibited the greatest annual variation in abundance compared with the other coho populations. Differences in abundance between regions may be attributed to differences in the freshwater and marine ecosystems, particularly differences in the marine ecosystem. The interannual variation in abundance of Oregon coho is correlated with the interannual variation in the relative strength of coastal upwelling during the previous spring and summer.

Introduction

The purpose of this paper is to review evidence that ocean factors influence coho salmon abundance. We apply three different approaches to this problem. The first is to review the nature and trends of variation in abundance of coho salmon stocks. The second is to review some differences in the freshwater and marine ecosystems that may help explain observed variation in coho salmon abundance. The third approach is to review an in-depth study of coho stocks in the Oregon Production Area.[1]

Different factors both in the freshwater and marine environments may influence the coho populations of different areas. Analysis of interannual variation in abundance of salmon can be useful in identifying factors that influence population abundance.

Interannual Variation in North American Coho Salmon Abundance

When researchers investigate factors influencing the abundance of coho salmon, the first question they should ask is: Do the populations in major geographic areas fluctuate together, thus suggesting the possibility of similar factors regulating abundance? To address this question we used commercial landings in the years 1920-82 for Oregon and California combined[2] (hereafter referred to as

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[1] *The area south of Leadbetter Point, Washington, as determined by the distribution of coho that originate in rivers from the Columbia River south.*

[2] *The majority of coho landed in California are Oregon stocks (Wright 1968).*

Oregon), Washington, British Columbia, and Alaska (Fredin 1980; unpublished data from Oregon Department of Fish and Wildlife [ODFW], Washington Department of Fisheries [WDF], Canada Department of Fisheries and Oceans, and Alaska Department of Fish and Game) as indexes of abundance. The disadvantages of using commercial landings as an index of abundance are (1) that harvest rates may vary through time and by region independently of fish abundance, in response to factors such as weather or market; (2) that the fish originating from a particular region are not caught only in that region; and conversely, (3) that the fisheries of each region catch fish originating from other regions. However, landings are the only long term data base available to compare abundance of coho salmon between regions. When examined over many years, landings should be an index of major trends in abundance.

Variation in Abundance by Region

The coefficient of variation in annual coho landings in Oregon during the last 60 years has been 70% greater than that for Washington, British Columbia, and Alaska (Figure 1). One reason for the greater variation for Oregon landings may be Oregon's location near the southern edge of coho distribution. The environment is likely to be sub-optimum more often near the edge of coho distribution than it is near the center of coho distribution, thus resulting in a more variable population.

Correlations in Abundance Between Regions

British Columbia and Washington have experienced significant increases in catches of coho since the 1920s, whereas such a long term trend is not apparent for Oregon and Alaska (Figure 2). During these same years, however, abundance of coho in Oregon was positively correlated with abundance of coho in Washington, ($r = 0.58$, $P_{r\ 0} < 0.01$) and negatively correlated with abundance of coho in Alaska ($r = -0.26$, $P_{r\ 0} < 0.05$). Abundance of coho in Washington was positively correlated with abundance of coho in British Columbia ($r = 0.46$, $P_{r=0} < 0.01$).

We hypothesized that these correlations were heavily influenced by increases in hatchery production of coho in Oregon, Washington, and British Columbia during the past 20 years. To test this hypothesis we examined the same correlations for the period prior to increased hatchery production (1920-1960) and for the period of increased hatchery production (1961-82). For the prehatchery period, the only significant correlation was a negative correlation ($r = -0.34$, $P_{r=0} < 0.05$) between abundance of coho in Oregon and British Columbia. For the period influenced by increased hatchery production, abundance of coho in Oregon and Washington was highly correlated ($r = 0.72$, $P_{r=0} < 0.01$). The increase in hatchery production apparently influenced the original correlations.

We examined the positive correlation between abundance of coho in Oregon and abundance of coho in Washington since 1961 more closely by separating Washington landings into Puget Sound landings and coastal landings (WDF unpublished data). We found a highly significant positive correlation between Oregon landings and coastal Washington landings ($r = 0.88$, $P_{r=0} < 0.01$), no correlation between Oregon landings and Puget Sound landings ($r = -0.05$, $P_{r=0} > 0.80$), and no correlation between coastal Washington landings and Puget Sound landings ($r = 0.07$, $P_{r=0} > 0.75$). These results are partially explained by the large contribution to the coastal Washington coho landings of fish originating from the Columbia River and Oregon coast (WDF 1981).

Although most correlations of coho abundance between regions are poor, in some years the populations in all regions fluctuate together. An excellent example of this is the low abundance of coho which occurred in all regions in 1960, likely the result of an intrusion of warm water into the Northeast Pacific in 1957-59. For the most part, however, Oregon coho stocks appear to have varied independently of other coho stocks.

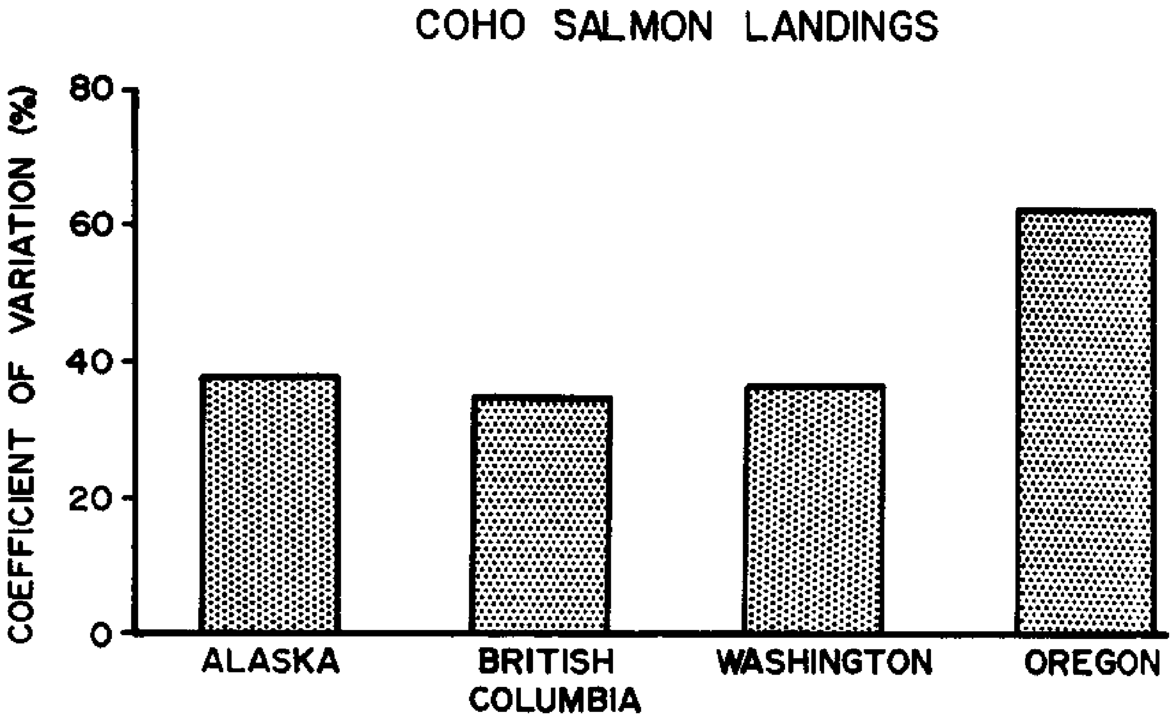

Fig. 1. Coefficient of variation in the number of commercially landed coho salmon by region for the years 1980-82.

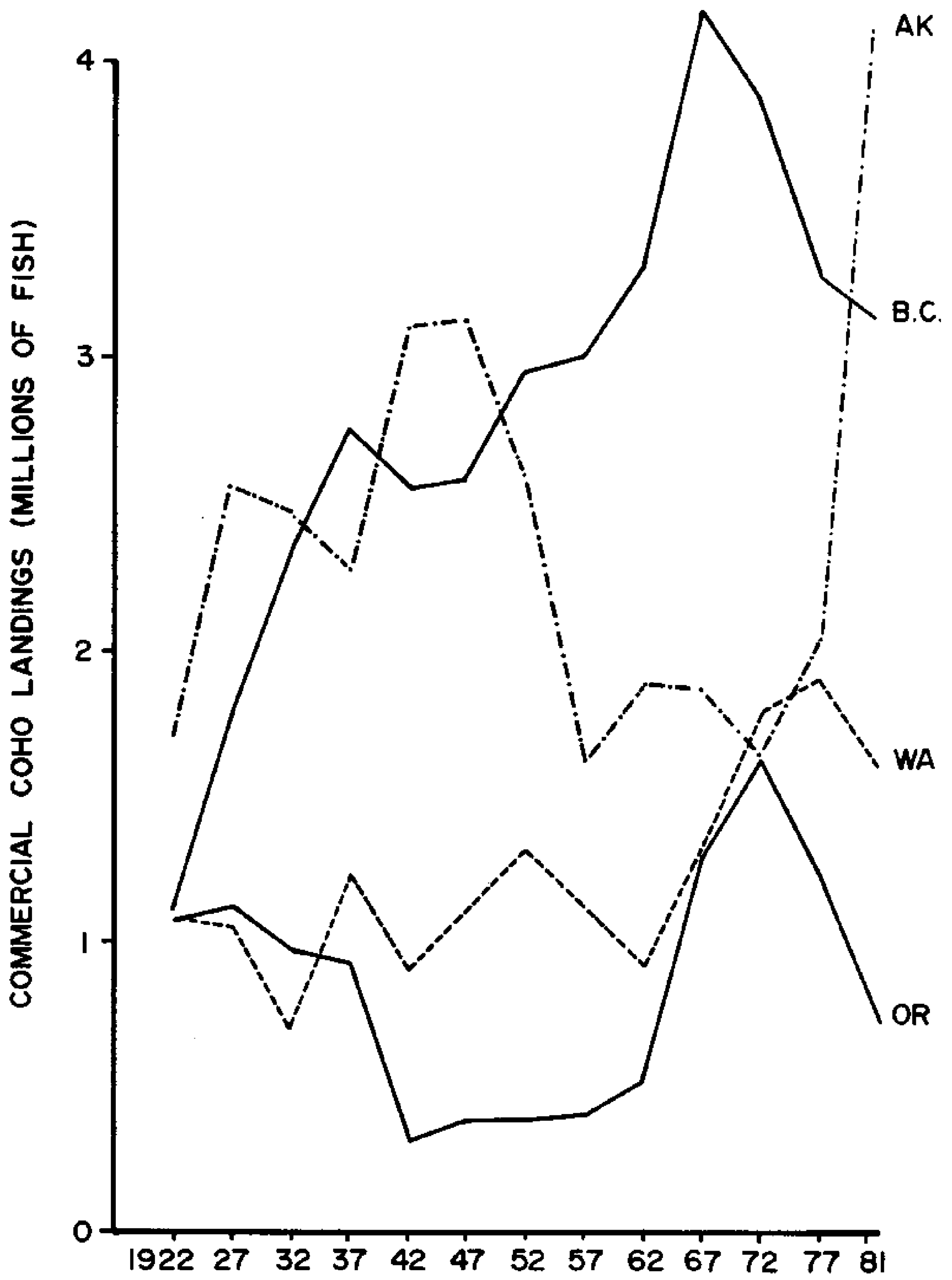

Fig. 2. Five-year average commercial landings of coho salmon plotted against the midyear of each period. The 1981 data point represents a three-year average of 1980-82.

Environmental Factors Influencing Variation in Coho Abundance

North-South Variation

Most coho populations along the west coast of North America tend to vary independently of one another because the freshwater and marine ecosystems vary considerably from northern California to Alaska. For example, lower water temperatures, shorter growing seasons, older coho smolts, and greater abundance of other salmonids characterize the freshwater ecosystems from south to north.

The marine ecosystem also changes from south to north. Two important aspects of the environment that change are coastal upwelling and shoreline development (the ratio of shoreline to straight coastline). The intensity of upwelling decreases from south to north between 39°N and 57°N (Bakun 1973), and shoreline development increases from south to north (Figure 3). The assemblages of coastal marine fishes also appear to change, shifting from predominantly pelagic spawners in the south to predominantly demersal spawners in the north (Figure 4).

Oregon has only moderate upwelling during spring and summer compared to northern California, and lacks the highly developed shorelines with large littoral production areas of Puget Sound and the Strait of Georgia. This situation may be important to coho production since two potential food sources, anchovies and herrings are more abundant south of Oregon, and north of Oregon, respectively (Table 1). Anchovies are a pelagic spawning fish more dependent on productivity in the open ocean, whereas herring are benthic spawners and are favored by highly developed shorelines. Herring eggs spawned in protective waters survive at twice the rate of eggs spawned on the open ocean coastline (Taylor 1964).

Table 1. Estimates of the relative standing stocks of herring and anchovy from California to Alaska (Blankenbeckler 1980; Barton and Wespestad 1980; Richardson 1981; Sprall 1981; letter dated Aug. 10, 1982 from R.J. Trumble, Washington Department of Fisheries, Olympia, WA; letter dated Aug. 23, 1982 from V. Haist, Pacific Biological Station, Nanaimo, B.C.; phone conversation on May 23, 1983 with A.D. Maccall, Southwest Fishery Center, La Jolla, CA.).

	Spawning Biomasses	
Area	Northern Anchovy 1,000	Pacific Herring 1,000
California	5,700 (1975) 2,367 (1976)	58 (1979-80)
Oregon	262-769 (1975) 144-1,005 (1976)	0.34 (1980)
Washington	Included in Oregon	9.3 (1980) [a]
British Columbia	Not reported	282 (1980)
Gulf of Alaska	Not reported	93 (1978-79)
Western Alaska	Not reported	260-640 (1979)

[a] *This estimate is only for the northern Puget Sound stocks. An estimate of the entire Puget Sound and coastal Washington stocks of herring would be much greater.*

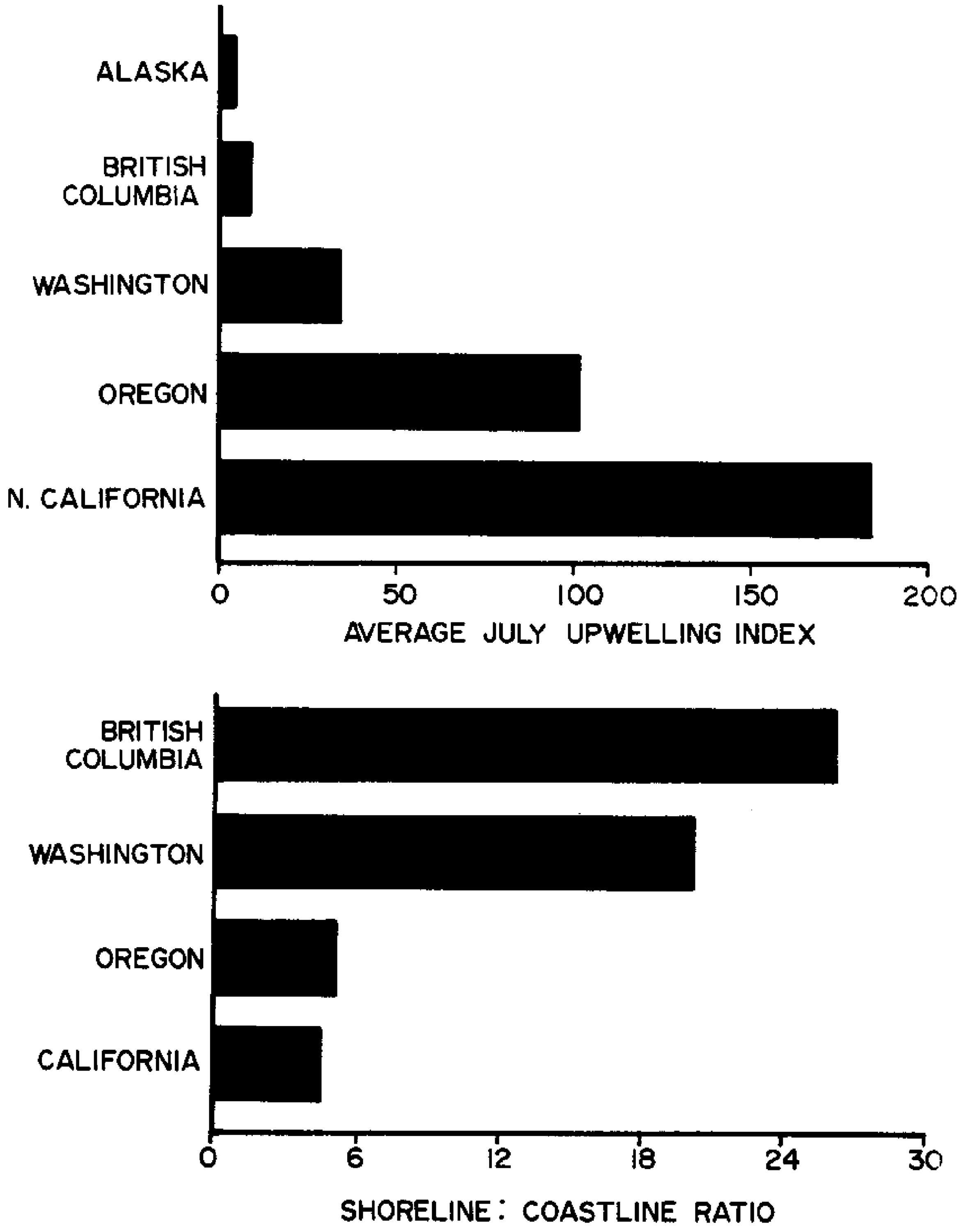

Fig. 3. The trends in upwelling intensity (Bakun 1973) and shoreline development on the west cosat of North America.

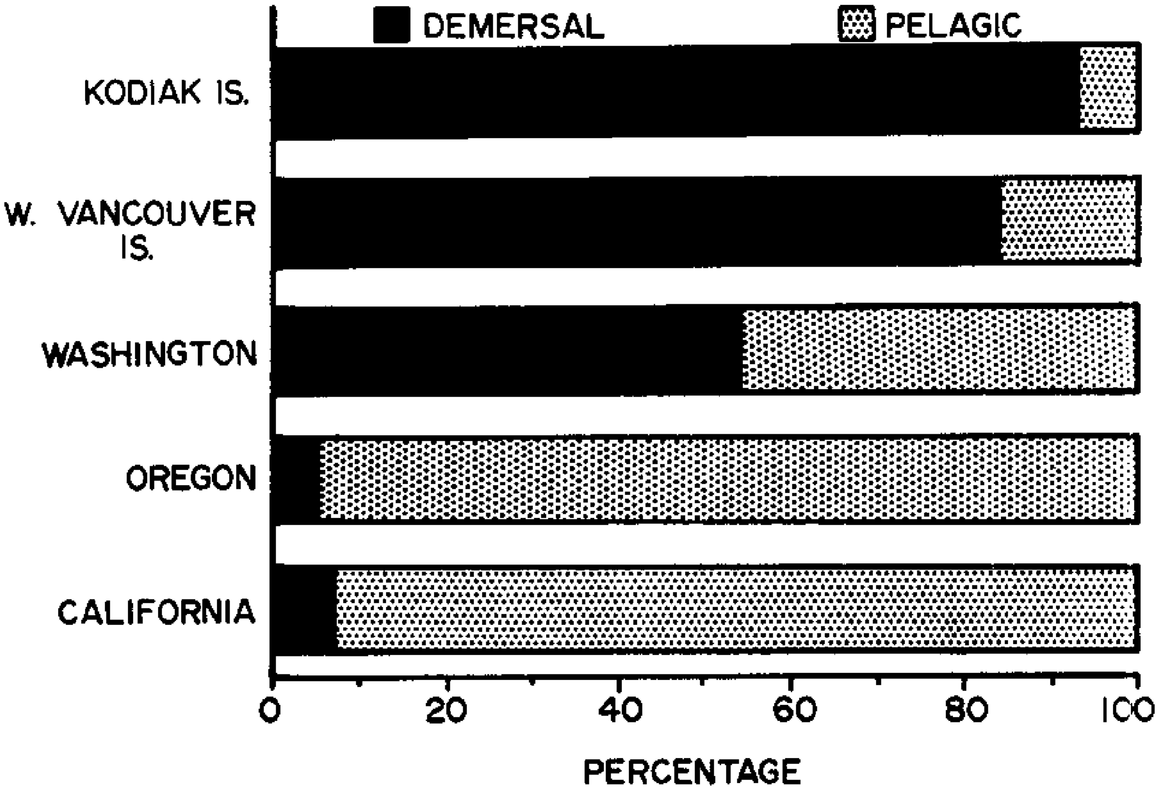

Fig. 4. The proportion (by relative abundance) of larval fish of species spawning pelagic and demersal eggs (data from Ahlstorm 1965; Waldron 1972; Richardson 1973; Kendall 1981; letter dated October 13, 1983 from Jean Dunn, Northwest and Alaska Fisheries Center, Seattle, Washington).

Differences we have identified between production systems off the Oregon and Washington coasts, (where coastal upwelling is important), and production systems in Puget Sound and the Strait of Georgia, (influenced by a highly irregular shoreline with large littoral areas), are not meant to imply cause and effect relationships with production of coho salmon in the two regions. We have not yet determined the specific factors or mechanisms are that cause differences in survival in the early ocean life history of juvenile salmon and, therefore, influence total production. However, we believe that the differences between the regions that we have described, may play an important role in survival of juvenile coho during the critical first months after ocean entry and should be investigated further.

The differences between the marine ecosystems of Oregon and Puget Sound are consistent with the lack of correlation between abundance of coho in the two areas. We would expect different factors to control the coho populations in these areas; this appears to be the case.

Abundance of coho salmon in Puget Sound is strongly correlated with streamflow during freshwater residence (Smoker 1955; Zillges 1977; Mathews and Olson 1980). In Oregon, however, correlations between abundance of coho and streamflow have been poor (McKernan et al. 1950; Scarnecchia 1981; Nickelson 1983), but correlations between abundance of coho and upwelling have been excellent (Gunsolus 1978; Nickelson 1983) (Figure 5). Conversely, attempts to develop correlations between abundance of Puget Sound coho and coastal upwelling have been unsuccessful (Tim Flint, Washington Department of Fisheries, personal communication, October 4, 1983).

Oregon Coho

Public hatchery production of coho in the Oregon Production Areas has increased from 7.5 million smolts in 1960 to 38 million smolts in 1981 (ODFW 1982). The development of private hatcheries has added as many as 24 million smolts in recent years (ODFW 1982). Adult abundance, as measured by the Oregon Production Index (OPI), initially followed the trend in smolt releases. However, since the late 1960s adult abundance has not increased with increased smolt releases (Figure 6), and since 1977 adult abundance has declined to pre-1960 levels (ODFW 1982; Nickelson 1983).

In a recent analysis of Oregon hatchery coho production, Nickelson (1983) concluded that the marine environment, particularly factors associated with coastal upwelling, is primarily responsible for the increase and subsequent decline in abundance of adults that has occurred since 1960. Two levels of production were identified: one characterized by strong upwelling (>625 units [$m^3 \cdot s^{-1} \cdot 100$ m] at 42°N, 125°W from March through September) and an average marine survival rate of 8.5% for hatchery coho; and one characterized by weak upwelling, (<625 units at 42°N, 125°W from March through September) and an average marine survival of 3.8% (Figure 7). Within each production level, the number of smolts released did not appear to influence survival rate. The decline in adult abundance since 1977 was attributed to a shift from a period of mostly strong upwelling to a period of weak upwelling.

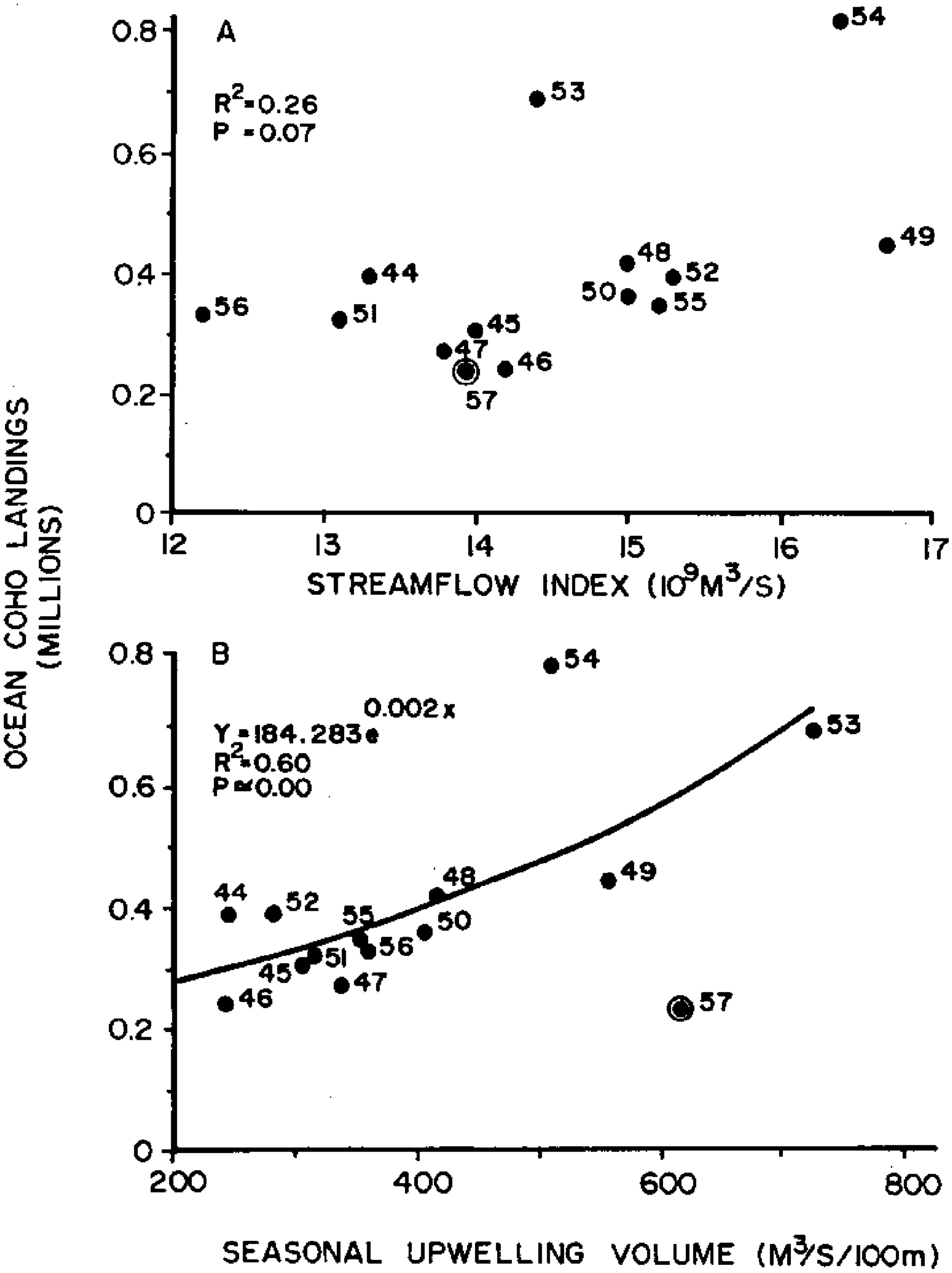

Fig. 5. The relationship with streamflow (A) and with upwelling volume (B). The unusually low abundance of the 1957 brood is also illustrated (after Nickelson 1983).

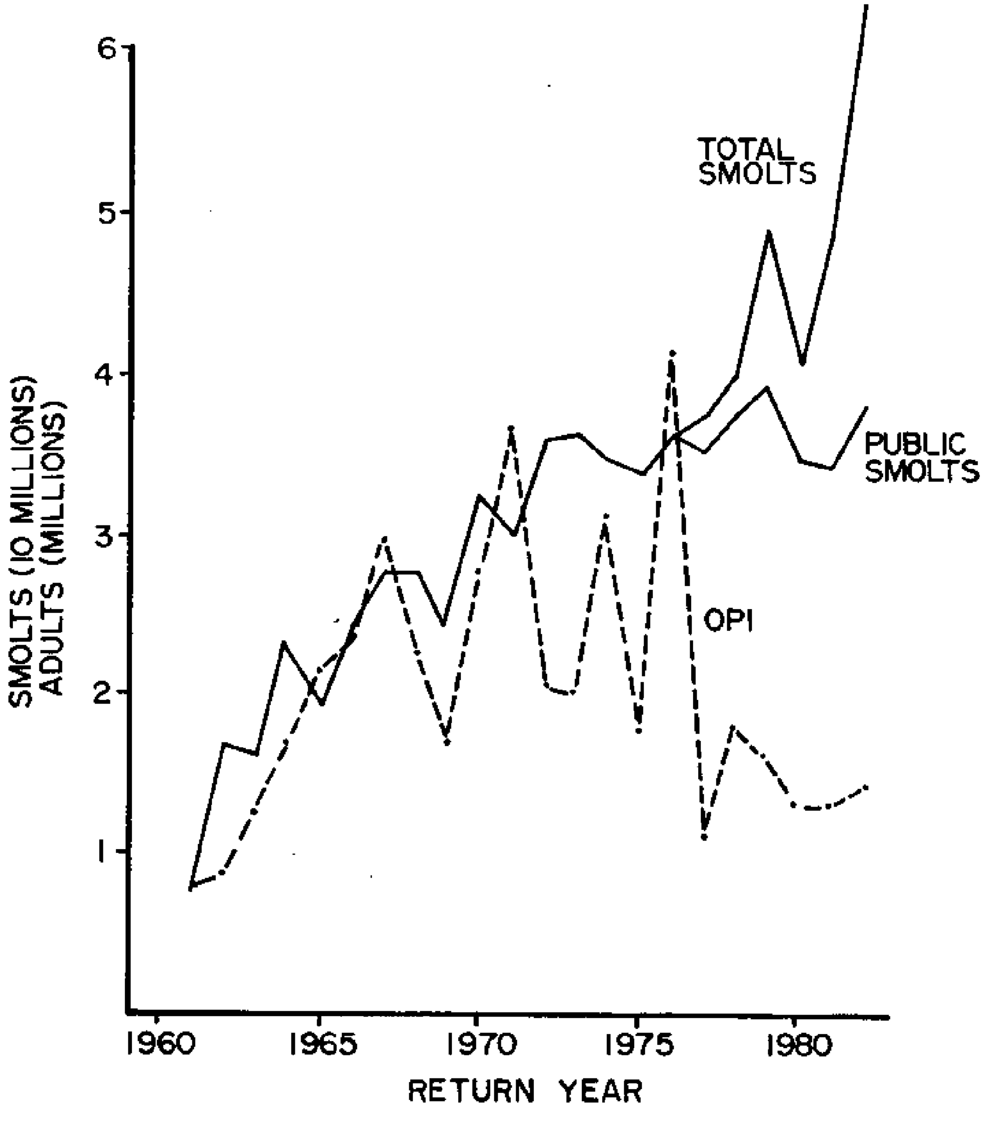

Fig. 6. Coho smolt releases and adult abundance (OPI) in the Oregon Production Area 1961-82. The differences between total smolts and public smolts are private hatchery smolts (after Nickelson 1983).

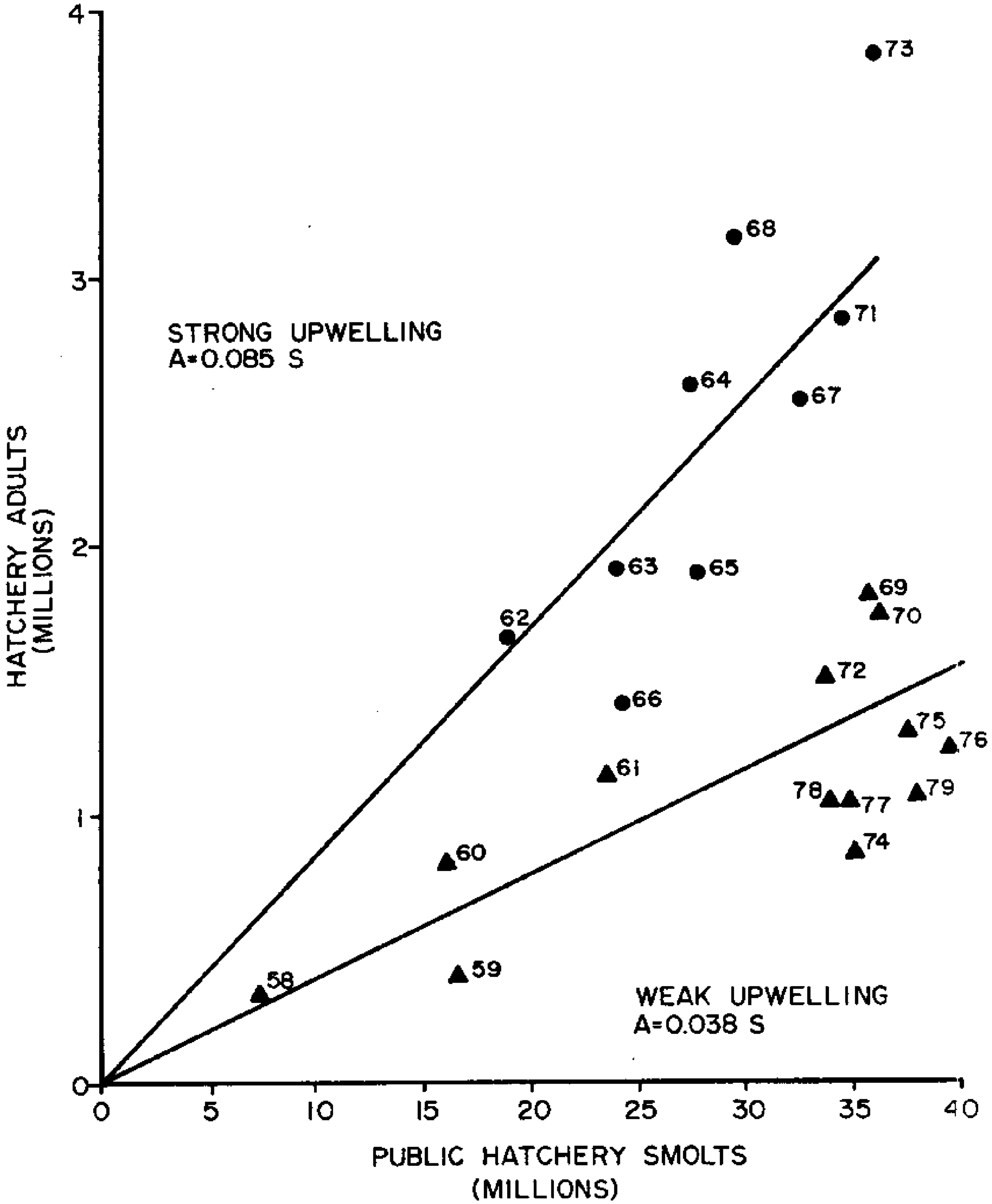

Fig. 7. The relationship between hatchery coho adults and hatchery smolts the previous year as described by separate models for brood years influenced by strong and weak upwelling (after Nickelson 1983).

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Commentary: Evidence for Density Dependence among Coho Salmon Stocks in the Oregon Production Index Area

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Introduction

Possible density dependence among salmon stocks in the eastern Pacific Ocean has come under increasing scrutiny in recent years (Clark and McCarl 1983; Gunsolus 1978; McCarl and Rettig 1983; McGie 1981; Nickelson 1983; Nickelson and Lichatowich, this workshop; Oregon Department of Fish and Wildlife 1982; Peterman 1978, 1982; Walters et al. 1978). These authors have often reported widely divergent interpretations of the role of density-dependent relationships between smolt and adult abundances in the marine environment. This is particularly true for coho salmon (*Oncorhynchus kisutch*) stocks found in the Oregon Production Index (OPI) area south of Leadbetter Point, Washington. Some scientists believe that existing data indicate density-dependent marine mortality is a factor governing stock size and further hatchery smolt releases are unwarranted. However, others feel that marine mortality of the stocks is primarily driven by density-independent factors and further smolt releases are justified.

Since 1960, public hatchery production of coho salmon smolts has risen from 7.5 million in 1960 to 38 million in 1981, while private hatcheries added about 24 million additional smolts since 1982 (ODFW 1982). Stock size indices of adults initially followed an upward trend but since 1965 have declined at an average annual rate of at least 7%/yr (ODFW 1982). Escapement indices of wild stocks in lower Columbia River and Oregon coastal streams followed similar trends. No directional trends in escapement were evident between 1950 and 1965 in coastal drainages and between 1949 and 1965 in Columbia River drainages. However, since 1965, the escapement of wild fish has declined 9.3%/yr in coastal rivers and 20.3%/yr in Columbia River tributaries (ODFW 1982). A central issue in managing coho stocks in the OPI area is whether these observed phenomena were simply due to vagaries in freshwater and ocean environments, changes in ocean troll and sport fisheries, or influences of increasingly larger hatchery smolt production.

The issue of density-dependent mortality in the marine environment is crucial since many state enhancement programs and private "sea-ranching" hatcheries operate under the assumption that fresh water rather than the ocean environment limits production of coho salmon. Under this assumption, fishery administrators and private hatchery managers logically expect a positive relationship between increased fish releases and adult production. However, if the assumption is false, millions of dollars will be wasted in various enhancement facilities, and dependent fisheries and wild stocks may be jeopardized.

Nickelson (1983) and Nickelson and Lichatowich (this workshop) analyzed the production of public hatchery coho in the OPI area and concluded that factors associated with coastal upwelling in the marine environment were primarily responsible for the early increase and subsequent decline of adults since 1960. Two levels of production were identified based upon Bakun (1973) upwelling indices as a surrogate indicator of ocean productivity. The first level was characterized by strong upwelling (> 625 units at 42° N 125° W from March through September) where survival rates were high compared with survival rates at low upwelling (< 625 units) for public hatchery stocks. Within each production level they concluded there was no evidence that smolt releases influenced survival rates.

These conclusions were reached by focusing on one component of the mixed stocks using the OPI area. Separating the stocks and treating public hatchery stocks alone implies that there is no interaction between other stocks in the area even though private hatcheries have released large quantities of smolts in recent years and wild stocks are also part of the biomass reared in the OPI area.

The purpose of this paper is to examine density dependence among coho salmon stocks in the OPI area from a broader perspective by including wild and private hatchery stocks in the analysis. Further evidence of density-dependent relationships between stock size and growth is included for Columbia River coho salmon. Optimum smolt production estimates are derived from stock-recruitment relationships between the combined smolts and adults.

Stock Size Estimates

The OPI is used by fisheries managers as a measure of the annual abundance of 3-year-old adult coho from Columbia River and Oregon coastal hatcheries and streams (catch plus escapement). The OPI is currently thought to measure about 90%-95% of the total wild and public hatchery stocks found south of Leadbetter Point, Washington (Pacific Fishery Management Council 1983, p. 6-III). The production of private hatchery fish and escapement of wild stocks in Oregon coastal rivers are the only major components absent in the index. The estimated escapements to Oregon coastal streams were taken from ODFW (1982) and escapements to Tenmile lakes from unpublished data compiled by ODFW. The coastal escapements were adjusted upwards based on recent field studies that indicated surveyors observed 75.5% of the adult coho spawners in index streams (T. Nickelson, ODFW, Corvallis, Oregon, personal communication). Total adult production was derived by adding the estimated escapements to Oregon coastal rivers and Tenmile lakes and adults originating from private hatcheries to OPI indices of abundance.

Smolt releases from government facilities in Washington, Oregon, and California were added to those liberated at private hatcheries in Oregon to obtain the total hatchery smolt production in the OPI area (ODFW 1982, p. II-C-8). The production of wild smolts from Oregon coastal rivers was estimated from stock-recruitment parameters for female spawners and smolt counts in Deer Creek, Alsea River (Moring and Lantz 1975) applied to the adjusted stock size required for maximum recruitment (186,000 females) and adjusted parental escapements in Oregon coastal rivers, assuming 50% were females. The production of smolts from Tenmile lakes coho was estimated by dividing jack and adult returns (brood year) by the estimated survival rates of the combined wild and public hatchery smolts in the OPI area for the same brood year. Estimated smolts from Tenmile lakes were minor (0.1 to 0.8 million) compared with those from coastal rivers and hatcheries.

Smolt production estimates from Oregon coastal wild stocks added to smolt releases from public and private hatcheries provided a reasonably complete picture of smolts present in the OPI area that can be compared with adult recruitment (catch plus escapement) in the area (Table 1). Some stocks are still excluded (primarily wild smolts and wild adult escapement in California, wild smolts from the Columbia River, and stocks contributing to the catch but escaping outside of the OPI area), but these are thought to be negligible.

Table 1. Data on upwelling indices and coho salmon smolt and adult production in the Oregon Production Index area.

Year of return (yr t)	Upwelling index (yr t - 1)	Smolts x 10^6 (yr t - 1)				Adult production x 10^6 (yr t)			
			Hatchery						
		Wild	Public	Pvt.	Total smolts	Wild escape.	OPI	Pvt. hatch.	Total
1961	371	7.8	7.5	—	15.3	0.4951	0.7762	—	1.2713
62	265	11.5	16.6	—	28.1	0.4112	0.8437	—	1.2549
63	430	8.9	16.1	—	25.0	0.2568	1.2255	—	1.4823
64	361	11.0	23.3	—	34.3	0.5972	1.7003	—	2.2975
65	636	11.2	19.0	—	30.2	0.4359	2.1229	—	2.5588
66	765	10.2	24.0	—	34.2	0.3829	2.2835	—	2.6664
67	764	9.8	27.4	—	37.2	0.2911	2.9377	—	3.2288
68	819	11.0	27.7	—	38.7	0.2792	2.2164	—	2.4956
69	644	10.9	24.3	—	35.2	0.1831	1.6782	—	1.8613
1970	652	10.7	32.5	—	43.2	0.3273	2.7941	—	3.1214
71	709	11.0	29.5	—	40.5	0.4285	3.6578	—	4.0863
72	424	9.0	35.7	—	44.7	0.1677	2.0365	—	2.2042
73	540	10.8	36.3	—	47.1	0.2090	1.9976	—	2.2066
74	791	10.9	34.5	—	45.4	0.1772	3.1285	—	3.3057
75	604	8.2	33.7	0.1	42.0	0.2115	1.7682	—	1.9797
76	744	9.1	36.1	0.1	45.3	0.2177	4.1135	—	4.3312
77	524	8.7	35.1	2.1	45.9	0.0873	1.1174	0.0143	1.2190
78	613	9.4	37.5	2.4	49.3	0.1017	1.7739	0.0202	1.8958
79	481	9.5	39.4	9.9	58.8	0.2306	1.5479	0.1107	1.8892
1980	385	5.4	34.7	5.8	45.9	0.1464	1.2538	0.0815	1.4817
81	593	6.1	34.1	14.8	55.0	0.1008	1.1658	0.2409	1.5075
82	481	9.8	38.0	23.9	71.7	0.1882	1.2968	0.2871	1.7721

Density-Dependent Marine Mortality

Peterman (1982) described two components of a test for density-dependent marine mortality. The first is a test for nonlinearity between adult recruitment and smolt production for which the null hypothesis of the slope (b) of the linear regression is $b = 1$. If the null hypothesis is rejected by a one-tailed t-test ($b < 1.0$), then increases in smolt abundance may not necessarily produce larger adult returns. Marine mortality rates will vary with smolt abundances. The second component is a test for a significant correlation in the log-log regression between adults and smolts where the null hypothesis is $r = 0$. Failure to reject this hypothesis indicates that survival is variable enough to obscure any simple relation between smolts and adults. Density dependence is indicated where both null hypotheses are rejected.

The test for density dependence was performed.for smolt abundances at low and high levels of upwelling (yr t - 1) and subsequent adult production (yr t). The predictive regression is used in the analysis rather than the functional regression (Ricker 1973) because error from smolt releases from public and private hatcheries is probably small and wild smolts comprise a relatively small proportion of the total smolt production. The predictive regression is the Morris (1959) test for density dependence.

Figure 1 illustrates the relationships between adult recruits and total smolts in low and high years of upwelling. The equation for years of low upwelling is $A = 0.710S^{0.234}$ and for high upwelling $A = 0.032S^{1.239}$, where adults (A) and smolts (S) are in millions of fish. Tests of the null hypothesis that $b = 1$ were rejected for years of low upwelling ($t = -5.072$; $P < 0.001$), but could not be rejected for years of high upwelling at $\alpha = 0.05$. The functional regression, which produces conservative estimates of density dependence (Peterman 1982), gave similar results for years of low upwelling

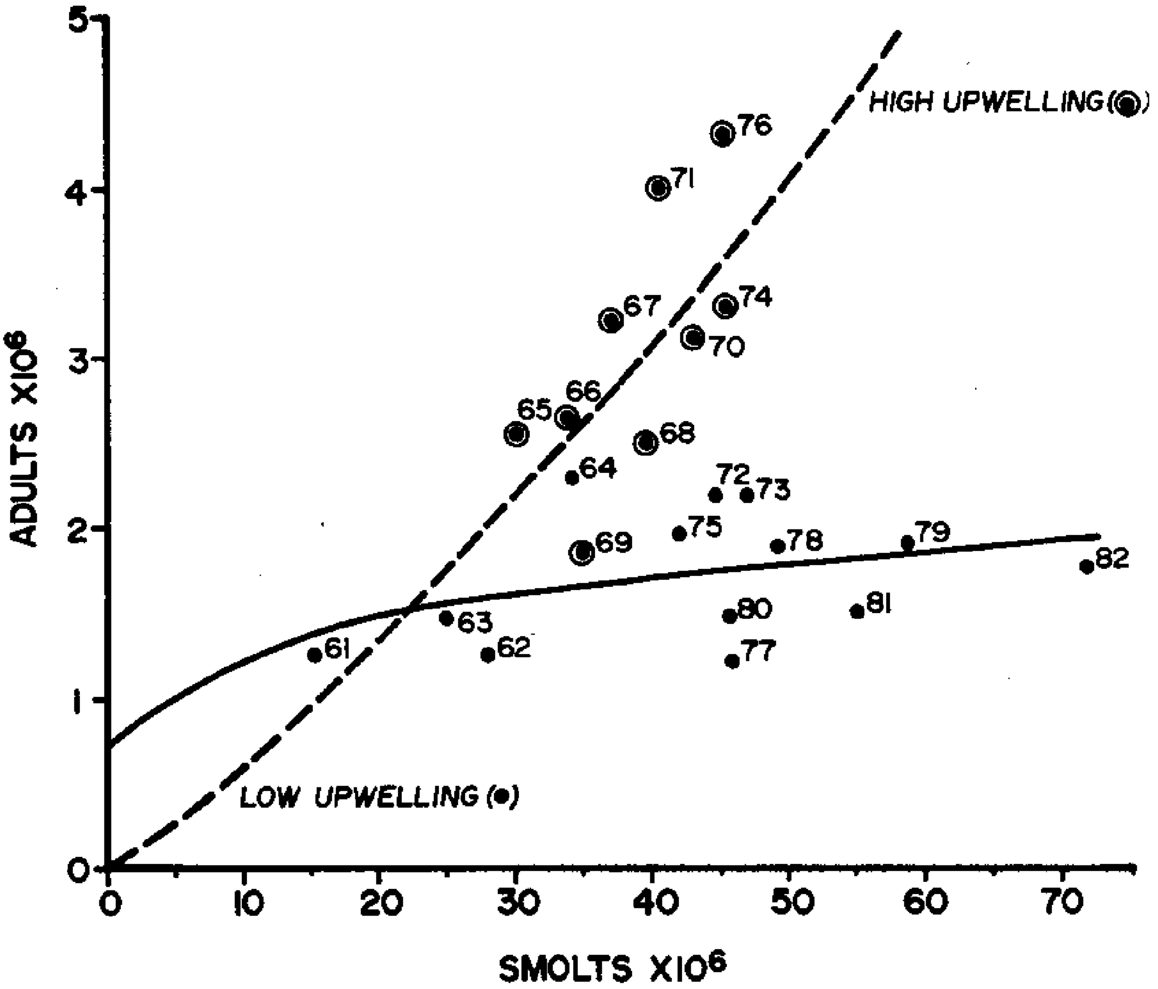

Fig. 1. Relationship between coho salmon adults (catch plus escapement) and smolts (hatchery plus wild) in the Oregon Production Index area by year of adult return. Data plotted for years of low upwelling (< 625 units) and high upwelling (> 625 units) in yr t - 1. Data fitted by predictive regressions.

($t = -2.960$; $P < 0.02$). The results of this test indicate that adult recruitment and survival rates were nonlinearily related to smolt abundance at low upwelling but not during years of high upwelling. However, the correlation of the regression between natural logarithms of adults and smolts during low upwelling lacked significance ($r = 0.423$; $P_{r=0} = 0.16$). This suggests that factors governing mortality were variable enough to obscure any simple relationship between adults and smolts. The results of these tests indicate that increases in smolt production do not result in significant increases in adult coho salmon production at low levels of upwelling.

Lack of precision in estimating the annual smolt production is a valid concern in analyzing density-dependent relationships, particularly from wild stocks. Observation errors may affect the calculated b of $\log_e A$ on $\log_e S$. Peterman (1982) addressed this issue for the Babine Lake sockeye salmon (*O. nerka*) stock where the regression between adult returns and smolt production were corrected for smolt measurement error. By using data presented in Peterman's study, I calculated that smolt variability in the OPI area would have to be 11.9 times that of the Babine Lake fence counts to conclude that coho do not show nonlinearity in marine mortality during low upwelling; i.e., $b = 1.0$. Unfortunately, there are no quantitative data available to estimate error terms in OPI-area coho.

Marine Mortality Rates

A rearrangement of the log-log regression of adult coho recruitment on smolt production illustrates the marine survival rate as a function of smolt production (Figure 2).

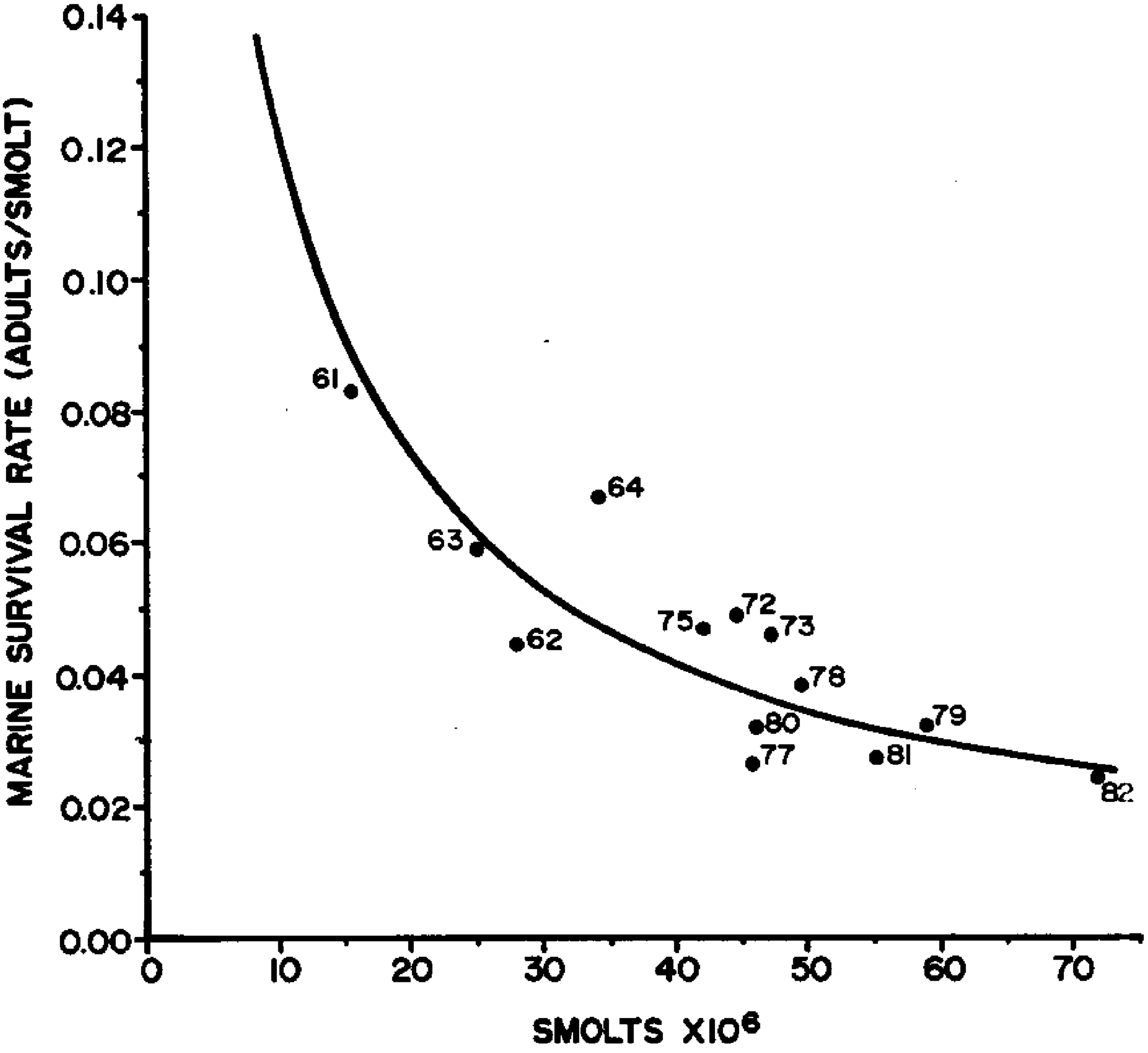

Fig. 2. Marine survival rate (adults/smolt) of coho salmon as a function of smolt abundance in years of low upwelling (yr t - 1) in the Oregon Production Index area by year of adult return. Curve drawn from regression coefficients for solid line in Fig. 1.

The survival curve is derived from regression coefficients computed for low upwelling in Figure 1. Since the regression coefficients were derived by regressing adults on smolts, the problem of interpreting statistics where the independent variable is contained in the dependent variable is avoided for the data plotted in Figure 2.

The curve in Figure 2 indicates that survival rates of adults have declined as smolt production increased at low levels of upwelling. Survival rates at high smolt densities are roughly one-fourth of those at low abundance.

Density-Dependent Marine Growth

Density-dependent relationships can affect growth as well as survival of salmon (Mathews 1980; Rogers 1980). The relationship between average weights of coho salmon taken in the terminal Columbia River gill-net fishery and stock size estimates from 1957-83 (catch plus escapement) in the OPI area is illustrated in Figure 3. Stock size estimates prior to 1961 were calculated by dividing the Oregon-California catch by 1 - 0.6, the assumed exploitation rate during the period (ODFW 1982).

There is some evidence of an inverse relationship between the average weight and number of adults in Figure 3, particularly in the early 1970s. Since 1976, average weights have been considerably below the 1957-75 average of 4.2 kg (9.2 lb). This might be a response to generally poor upwelling and high stock densities from expanded hatchery smolt releases. However, the decline is possibly influenced by the increased reliance on late Cowlitz River coho stock which tend to be smaller than other stocks (Paul Hirose, ODFW, Clackamas, Oregon, personal communication).

The relationship between average weights and stock size during El Niño in the eastern Pacific Ocean is particularly informative. During the severe 1957-59 El Niño (Radovich 1961; Tully et al. 1960) stock sizes were comparatively small (~ 0.3 to 1.0 million adults), yet growth was near average except in 1959 when oceanic conditions were especially poor (Figure 3). In 1983, the preseason prediction of adults in the OPI area was 1.66 million based on jack (age 2) returns in 1982 and catch estimates of private hatchery fish (PFMC 1983). The stock size was probably larger than 1.66 million since escapements to Oregon coastal streams and private hatcheries were excluded in the preseason projections. Therefore, the potential stock size was at least five times larger in 1983 than in the late 1950s as a result of expanded hatchery smolt production. When the severe El Niño struck in 1983 (Cane 1983), the average weight of adults in the Columbia River gill-net catch plummeted to 2.7 kg (5.9 lb). The small average size of adults was probably a density-dependent response to poor ocean conditions and relatively large stock size when El Niño intensified in 1983. The density-dependent feedback mechanism likely affected survival rates as well since the actual abundance of adults in the OPI amounted to only 42% of the preseason estimate, whereas, predicted and actual stock sizes were close in previous years (Figure 4).

Stock-Recruitment Relationships

The relationship of adult recruitment in year t to the combined effects of smolt production and upwelling indices in year t - 1 during the 22-year period (1961-82) was examined in a linear multiple regression. Constants derived from the multiple regression were used in a modified stock-recruitment model where smolt production and upwelling were treated as continuous variables:

$$R = a\,S\exp(b_1 S + b_2 U) \qquad (1)$$

where R = adult recruitment in the OPI area (millions)
S = total smolt production (millions)
U = upwelling indices
a, b_1, b_2 = regression coefficients

Data in Table 1 were fitted in the model by transforming the dependent variable to $\log_e R/S$ since the relationship between adult recruitment and smolt production was curvilinear. The transformed multiple regression, $\log_e R/S = -2.7097 - 0.0258S + 0.0015U$, is highly significant ($F_{2,19} = 20.99$; $P < 0.005$) at $\alpha = 0.05$. An analysis of

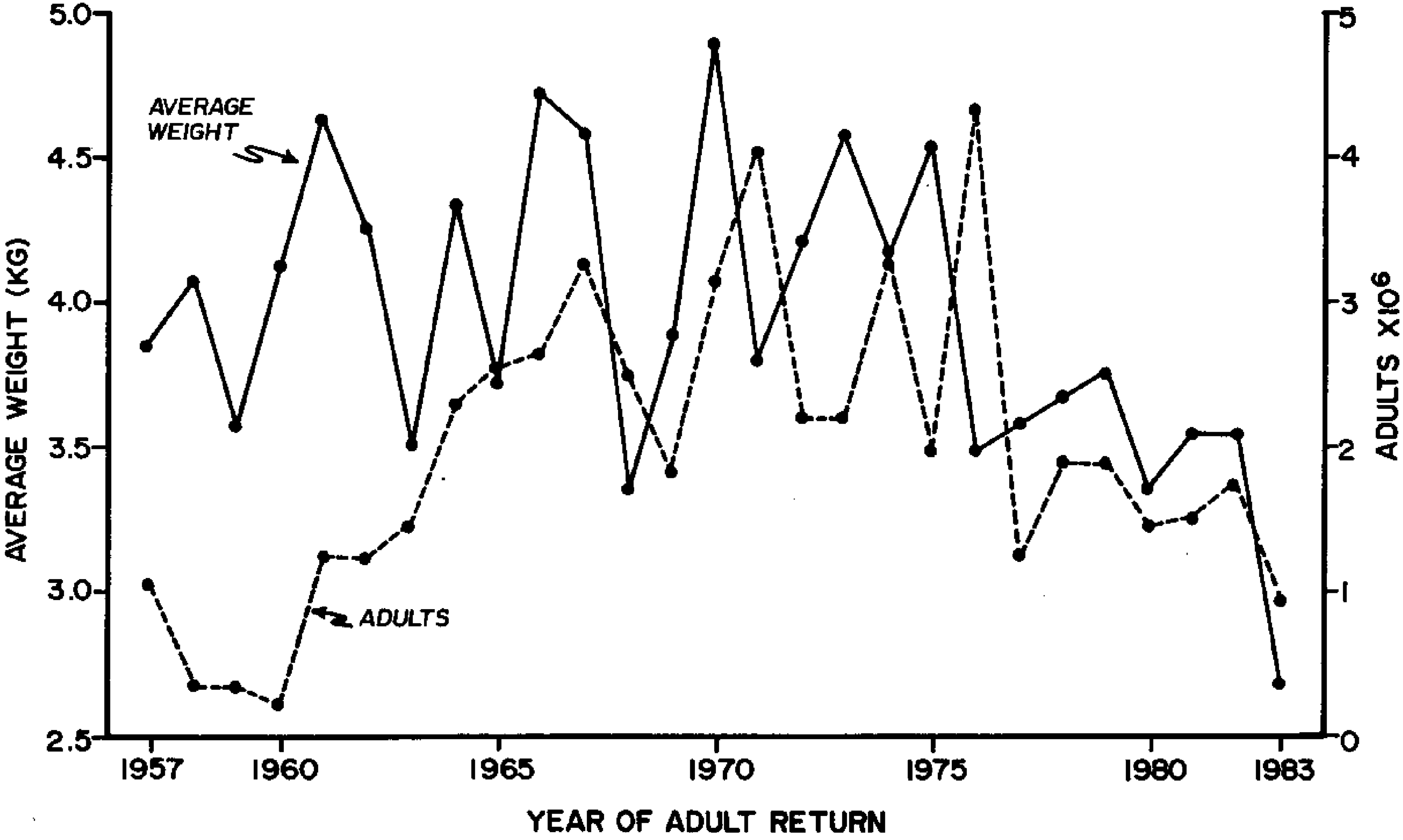

Fig. 3. Trends in the average weight of adult coho salmon taken in the Columbia River gill-net fishery and adult recruitment in the Oregon Production Index area, 1957-83.

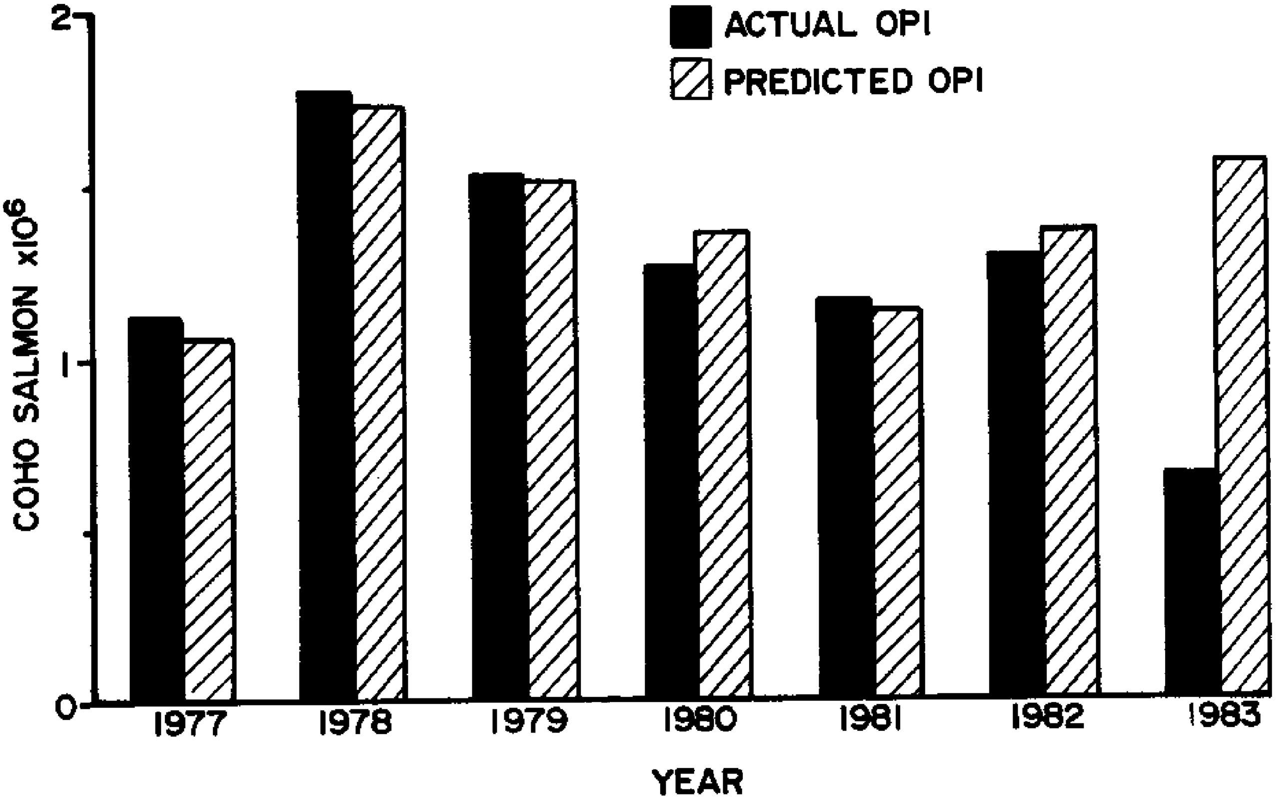

Fig. 4. Actual and predicted abundance of adult coho salmon in the Oregon Production Index, 1977-83.

partial regression coefficients in the multiple regression indicates that both variables are significant, although smolts have a larger influence ($F_{1,19} = 29.80$) than upwelling ($F_{1,19} = 17.53$).

The modified stock-recruitment model from the multiple regression is $R = 0.0666\ S \exp(-0.0258S + 0.0015U)$. Calculated recruitment curves at four levels of upwelling (200, 400, 600, and 800 units) are illustrated in Figure 5. According to this model, maximum recruitment in the OPI area corresponds to 39 million smolts. Predicted adult recruitment at this level of smolt production varied from 1.3 to 3.2 million from low to high extremes of upwelling or approximately ± 1.9 million fish.

The influence of upwelling and smolt abundance on the transformed dependent variable ($\log_e R/S$) was examined in a multiple regression during years of low upwelling. The resulting relationship of $\log_e R/S = -2.3015 - 0.0216S + 0.0001U$ was statistically significant at $\alpha = 0.05$ ($F_{2,10} = 12.67$; $P < 0.01$). However, an analysis of partial regression coefficients demonstrated that smolts were significant ($F_{1,10} = 18.80$; $P < 0.005$), while upwelling indices < 625 units had no influence ($F_{1,10} = 0.13$; $P > 0.25$). Conversely, at high levels of upwelling, the untransformed measurements of adult recruitment (R) were not statistically influenced by the independent variables ($F_{2,6} = 2.54$; $P > 0.10$), although smolts played a greater role than upwelling in the relationship. Transformed measurements of the dependent variable were employed to analyze the relationships at low upwelling because of the obvious curvilinear response illustrated in Figure 1, whereas, the response between adults and smolts was linear during years of high upwelling.

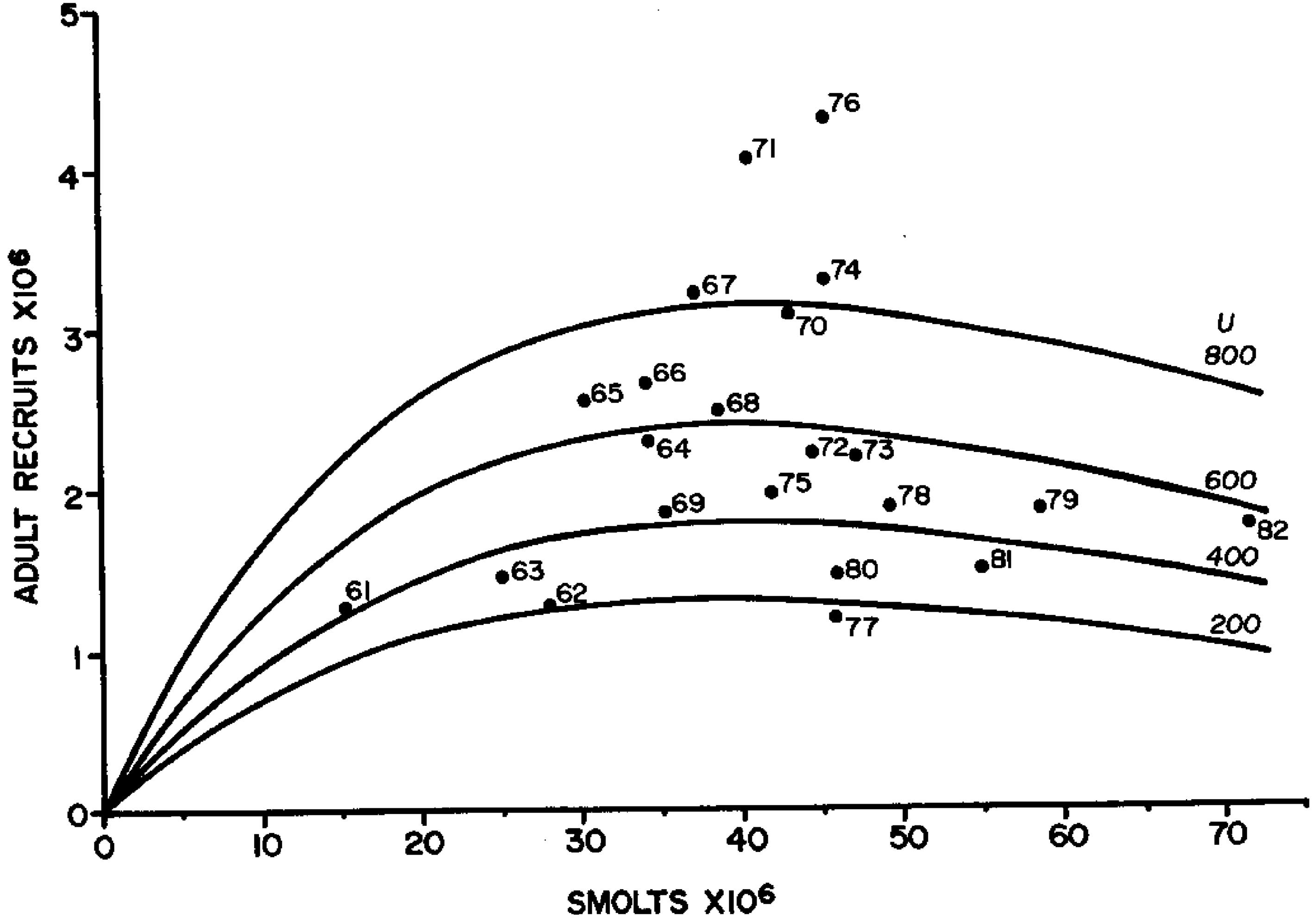

Fig. 5. Stock-recruitment curves of adult coho salmon in the Oregon Production Index area in yr t (1961-82) from hatchery and wild smolts and upwelling indices (200-800 units) in yr t - 1.

The results of this analysis suggest that upwelling has been a significant factor in governing adult recruitment only when treated as a continuous variable over the 22-year period. When upwelling is partitioned into low and high blocks, its importance diminishes and adult recruitment is primarily related to smolt densities. High upwelling has generally occurred when smolts were near or below optimal densities (39 million) predicted by the modified stock-recruitment model. Therefore, the lack of a significant influence of either smolts or upwelling on adult recruitment during years of high upwelling might be expected.

Since upwelling < 625 units apparently had no influence on adult recruitment, I fitted a stock-recruitment curve to adult recruitment resulting from smolts produced in the OPI area according to Ricker's (1975) model:

$$(2) \qquad R = \alpha S \exp(-\beta S)$$

The stock-recruitment relationship is significant ($r = -0.845$; $P < 0.01$). The stock-recruitment curve (Figure 6) is described by the relationship $R = 0.104 S \exp(-0.021 S)$. The estimated recruits are geometric mean (GM) values. Corresponding arithmetic mean (AM) values of recruits can be estimated by a factor of 1.02 applied to any given GM recruitment. Stock-recruitment parameters from the Ricker model indicate that optimum smolt production is 47.3 million combined wild and hatchery fish during low upwelling. At the optimum level of smolts, maximum adult recruitment ranges from 1.81 million (GM value) to 1.85 million (AM value).

An escapement goal of 200,000 wild adult coho salmon has been established for Oregon coastal streams (ODFW 1982). To achieve this goal, approximately 670,000 adults need to return to OPI-measured sites (PFMC 1984, p. V-32). At low upwelling, the harvestable surplus is about 1.14 million adults taken at an equilibrium exploitation rate of 63% by ocean fisheries. Somewhat higher exploitation rates would be permissible following years of high upwelling when survival of smolts would presumably improve.

Discussion

The results indicate that adult coho salmon stocks in the OPI area are not increased by releasing additional hatchery-reared smolts during years of low upwelling. The lack of a positive increase in production following increasingly larger hatchery smolt releases could be due to a nonlinear response between smolts and survival rates in the ocean, large variability in mortality processes that tend to mask any underlying relationship between adults and smolts, or a combination of these factors. Peterman (1982) demonstrated that most of the marine mortality of coho in the OPI area occurs in the summer of life prior to the return of age-2 jacks. However, as shown in Figure 4, a severe El Niño can result in a disproportionate increase in adult mortality rates that produces a significant predictive error when the normal linear relationship between jacks and subsequent brood year adults is disrupted.

The lack of a significant relationship between smolt releases and adult production has serious implications on future enhancement efforts for coho salmon stocks in the OPI area. Management efforts directed at increasing smolt releases to ameliorate declining adult returns become economically marginal and may be counterproductive if density-dependent mortality intensifies among smolts.

Current estimates indicate that wild stocks in Oregon coastal streams are capable of producing ~10 million smolts if optimum escapement levels are achieved. Stock-recruitment analysis suggests that the optimum smolt production at prevailing low levels of upwelling is about 47 million. Therefore, approximately 37 million hatchery

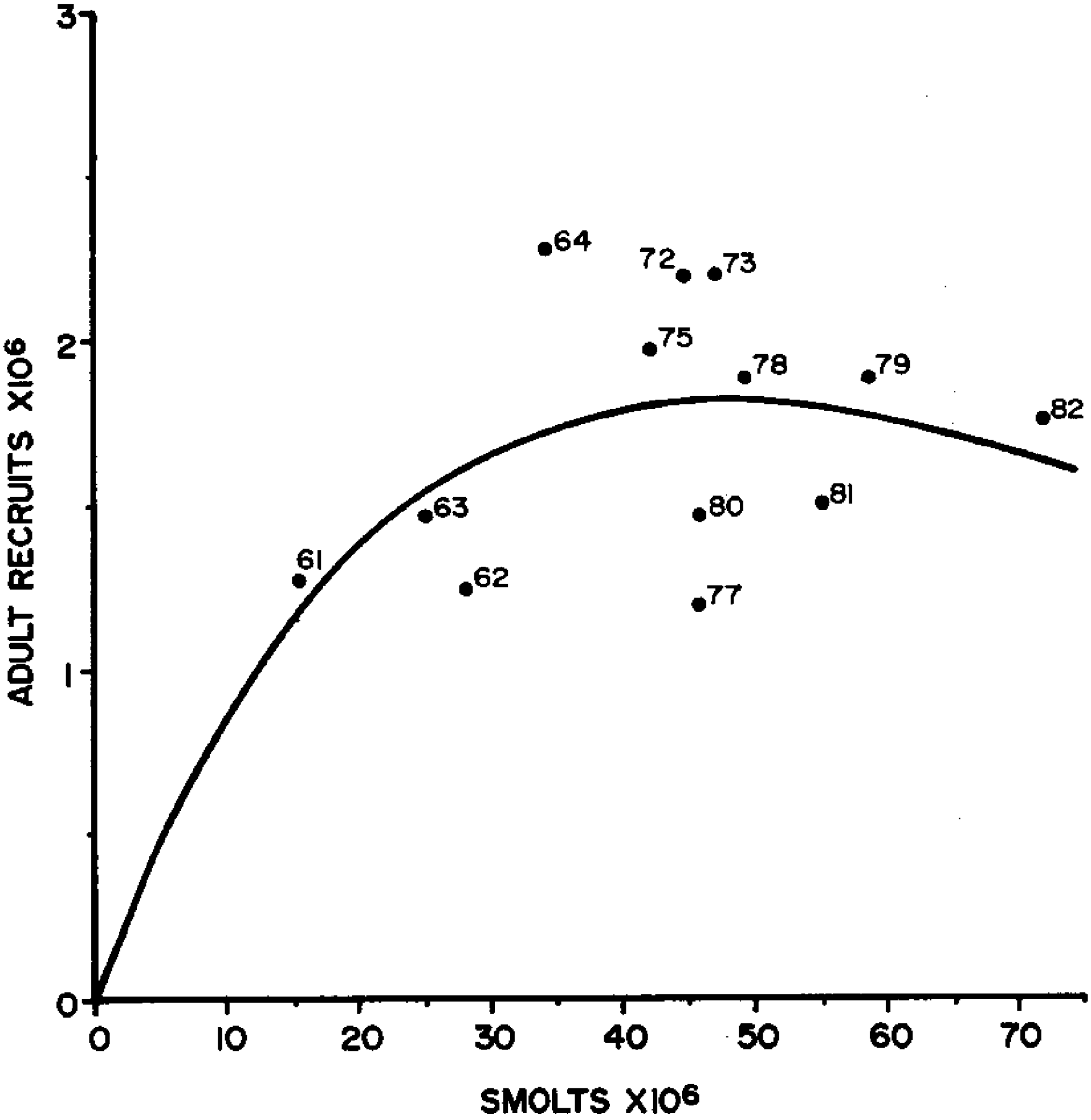

Fig. 6. Stock-recruitment relationship of adult coho salmon recruits (yr t) and smolts (hatchery plus wild) in the Oregon Production Index area during years of low upwelling (yr t - 1). Data plotted by year of adult return.

smolts may be sufficient to adequately stock the marine environment if wild smolt production levels are attained. Optimum smolt numbers may be larger during years of high upwelling since no upper limit has been fixed on the stock-recruitment relationship. However, managing smolt releases on the expectation of high upwelling is tempered by the low frequency of occurrence in the OPI area. Since 1946, high upwelling indices >625 units have occurred in only 26% of the years. Managing smolt releases for low upwelling may be a more realistic approach since upwelling intensities cannot be predicted in advance for efficient use of rearing facilities. Survival rates should improve when high upwelling occurs and potentially produce as many or more adults than the record high 4.33 million obtained in 1976 when an estimated 45.3 million smolts entered the ocean in 1975.

The apparent nonlinear or relation-masking mortality of smolts presents an interesting dilemma for managers of OPI-area coho salmon stocks. State and federal governmental hatcheries currently liberate ∿34-38 million smolts while private hatcheries liberate ∿24 million of their authorized 37.8 million juveniles in the OPI area. Either of these groups alone could potentially release the optimal number of smolts needed to achieve maximum adult recruitment in concert with productive wild stocks. Any attempted restrictions on smolt releases by either group will surely trigger considerable public and political debate over what is already a highly charged issue among fishermen, management agencies, and private hatchery interests.

The results of my analysis indicate it is unwise to assume there is a positive relationship between fish releases and adult production. There likely exists more than one limiting stage in the life history of coho salmon in the OPI area. Although massive enhancement efforts beginning in the early 1960s initially led to increased adult production, marine survival rates have declined in the interim as smolt releases continued to climb. The problem appears to be particularly acute when a severe El Niño occurs in the eastern Pacific Ocean which directly affects adults as well as smolts from the following brood.

Compensatory or variable mortality between smolts and adults has apparently occurred in the marine environment instead of fresh water alone. Managers planning future enhancement efforts should be cognizant of these potential limitations when calculating expected benefits. Unwarranted expectations for enhancement projects are not unique for coho salmon stocks. Peterman (1982) voiced similar concerns for facilities designed to enhance Babine Lake sockeye salmon. Classical management actions in the past were to increase the production of smolts to offset declining runs of adult salmon and satisfy the demands of fishermen. In view of the results, prudent management would seem to dictate alternate methods are necessary for enhancing coho stocks in the OPI area. However, it is more likely that current controversies regarding optimum coho salmon stock sizes will continue unabated until one or more large-scale experimental manipulations of juveniles are performed as suggested by Peterman and Routledge (1983) to formally test the hypothesis of linearity in smolt-to-adult relationships.

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Where Do All the Coho Go? The Biology of Juvenile Coho Salmon off the Coasts of Oregon and Washington

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Abstract

The first six months of ocean life are presumed to be the period when year class strength of coho salmon from Oregon is determined. To better understand this period of early ocean life, juvenile salmonids were sampled with purse seines off Oregon and Washington, 1979-1983. Juvenile salmonids occurred in most "blind" sets, with coho salmon comprising the majority of the salmonid catch. Juvenile coho salmon were most common within 37 km of the coast in 9-15°C water. Marked juvenile coho were usually found south of their river of ocean entry in May and north later in the summer in 1982. Fish from Columbia River and Oregon coastal hatcheries were caught in local coastal waters as late as August and September, suggesting that some juvenile coho have weak migrational tendencies. The strong correlation between upwelling and the production of coho the following year off Oregon suggests that survival of Oregon coho is determined by conditions in the California Current, not in far northern waters. Growth of juvenile coho salmon averaged 1-2 mm per day, similar to that found for fish from British Columbia waters. Mortality of juvenile coho salmon may be size dependent, with highest mortality rates soon after ocean entry.

Introduction

The highest mortality rates of salmonids in the ocean are thought to occur early in the marine life (Ricker 1976; Peterman 1978). Parker (1965, 1968) concluded that mortality rates of pink salmon from the Bella Coola River were high during their initial 40 days in coastal waters followed by a relatively long period of low mortality rates largely in oceanic waters. Hartt (1980) calls this initial period in the ocean the "critical first summer" for juvenile salmonids.

The first few months of ocean life of coho salmon from the Oregon region is believed to be the period when the success of the year class is established. Two observations support this assumption. First, the number of jacks returning after the first summer in the ocean is usually a good predictor of the catch and escapement during the next year (Gunsolus 1978; Pacific Fisheries Management Council 1983). Thus, year class success is determined by the time coho jacks return to spawn. Second, coastal upwelling off Oregon is strongly correlated with coho production (Gunsolus 1978; Scarnecchia 1981; Oregon Department of Fish and Wildlife 1982), suggesting that ocean conditions affect survival.

This study was initiated to improve our understanding of the distribution, abundance, movements, growth rates, and feeding habits of juvenile salmonids off Oregon and Washington. Although Hartt (1980) and Hartt and Dell (1978) sampled juvenile salmonids from the Straits of Juan de Fuca to Alaska, little research has been conducted in coastal waters off Oregon and Washington. Dawley et al. (1982) reported on limited purse seining in shallow nearshore waters near the mouth of the

Columbia River, and Miller et al. (1983) present results of their 1980 purse seining in coastal waters off southern Washington and northern Oregon. Our research off Oregon and Washington, extending from 1979 through 1983, is the basis for this report on the biology of juvenile salmon.

Methods

Four different purse seines were used to sample salmonids. All nets had 32-mm (stretch) mesh with a bunt of 32-mm or finer mesh. In 1979, 1980, and the first two cruises of 1981, a seine 457 m long and 800 meshes (about 30 m) deep was used. This seine had a 73-m 600-mesh panel attached to the vessel end of the seine. An additional 30-mesh deep panel of 127-mm mesh was hung along the bottom of the net. The bunt was made of 19-mm mesh. This net was fished from the 17-m drum seiner FLAMINGO in June 1979 and 1980 and from the 32-m KRISTIN GAIL rigged as a block seiner in May and June 1981.

During July and August 1981, a 457-m seine was used that was 1800 meshes deep with a 37-m bunt, 1200 meshes deep of 32-mm mesh. Panels of 3 and 30 meshes deep of 101-mm mesh were hung along the top and bottom, respectively of the net. This net was fished from the F/V SOUPFIN, a 21-m drum seiner. Fishing depth of 15 m was measured with a depth gauge attached to the bottom of the seine.

A British Columbia herring seine was used in 1982 and 1983 from the F/V PACIFIC WARWIND, a 28-m drum seiner. This seine was 495 m long. It was 2600 meshes (∿55 m) deep. A depth gauge attached to the bottom of the seine indicated fishing depths of 50-67 m. Roll-ups and net damage were a problem with this net in 1982. Therefore, strips of netting were removed to make the net 1800 meshes deep for the cruises in 1983.

The number of purse seine sets during the twelve cruises, 1979-1983, is listed in Table 1 along with the latitudinal range of sampling.

Table 1. Summary of number and latitudinal range of sampling, 1979-1983.

Year	Dates of Cruises	No. Sets[1]	Latitudinal Range of Sampling	
1979	June 18 - 29	56	Cape Disappointment to Cape Arago	46°20' - 43° 18'
1980	June 20 - 28	37	Cape Disappointment to Seal Rock	46°20' - 44°30'
1981	May 16 - 25	62	Leadbetter Pt. to Alsea River	46°35' - 44°25'
	June 9 - 18	67	Leadbetter Pt. to Cut Creek	46°35' - 43°11.3'
	July 9 - 19	67	Leadbetter Pt. to Alsea River	46°35' - 44°25'
	Aug. 8 - 19	67	Leadbetter Pt. to Cut Creek	46°35' - 44°11'
1982	May 19 - June 2	62	Waatch Pt. to Siuslaw River	48°21' - 44°00'
	June 7 - 22	56	Quinault River to Yachats	47°20' - 44°20'
	Sept. 4 - 14	42	Quinault River to Yachats	47°20' - 44°20'
1983	May 16 - 27	56	Waatch Pt. to Yachats	48°21' - 44°20'
	June 9 - 27	58	Waatch Pt. to Yachats	48°21' - 44°20'
	Sept. 15 - 24	54	Waatch Pt. to Coos Bay	48°20' - 43°27'

[1] to 25 nmi offshore

includes a few nonquantitative sets

The single cruises in 1979 and 1980 were exploratory. In subsequent years three or four cruises were made each year extending along the coasts of both Washington and Oregon. Purse seine sets were usually made along east-west transect lines from the 37-m (20-fathom) contour to 37 km offshore. The usual procedure was to continue sampling at 9.3 km (5 mi) intervals from the coastline until no salmonids were captured. Repeat sets were sometimes made when fish with missing adipose fins were common.

Generally, purse seine sets were "round hauls", where the seiner and the skiff made a circle with the net. Radar was sometimes used to determine the distance between the seiner and the skiff when a semicircle was made with the net (= diameter of the net circle). In addition to the "round" hauls, some "semicircular" sets were made in 1979, where the entire net formed a semicircle open in either a north or south direction. With these sets the seine was open for 15-45 minutes while the vessel and skiff towed the seine only fast enough to maintain a fixed net opening. The seine was fully pursed after about one-half its length was aboard (half-purse sets). All sets were "blind." We attempted to use sonar on the 1979, 1980, and 1982 cruises to locate concentrations of salmonids but were unsuccessful.

The purse seine catches were either dipnetted from the bunt of the seine while it was alongside the vessel, brailed aboard, or hauled aboard in the bunt, depending on the composition and size of the catch. Large catches (up to several tons) of the jellyfish *Chysaora* were common during some cruises and caused long delays in sorting the catch.

In 1979 and 1980, the juvenile salmon were usually preserved in formalin and sea water after their body cavity was slit to accelerate preservation of stomach contents. In 1981, 1982, and 1983, juvenile salmon were identified to species at sea, measured to the nearest millimeter (FL), individually wrapped in plastic bags along with a label identifying set number, species, and length, and frozen. When large numbers of juvenile salmonids were caught in a set, a sample was preserved; salmonids with marks or missing adipose fins were removed and preserved, and the remaining fish were released.

In the laboratory ashore, each salmonid was identified to species, measured, and examined for fluorescent marks under ultraviolet light (1981-82) and missing adipose fins or other marks (all years). Coded wire tags from the heads of salmonids with missing adipose fins were decoded by personnel from the Oregon Department of Fisheries and Wildlife, Clackamas Laboratory.

Juvenile or .0 (first year in the ocean) coho salmon were distinguished from .1 (second year in the ocean) coho by examination of size frequency histograms and scales. The division between .0 and .1 coho progressed from approximately 300 to 420 mm FL from May to August and September.

Results

Are Juvenile Salmonids Found Off Oregon and Washington?

The first cruise in June 1979 revealed that juvenile salmon were present off the coast of Oregon and could be readily captured in "blind sets" with a purse seine. In all cruises, 1979-1983, juvenile salmonids occurred in over 69% of the purse seine sets, except in June and September 1983 when frequency of occurrence was less than 50% (Table 2). Coho were the most common juvenile salmon. They were captured in most sets and averaged 68% of the numbers of juvenile salmonids caught. Juveniles of six other species of salmonids were also collected. Chinook were the next most common species, followed by chum salmon, cutthroat trout, steelhead trout, sockeye salmon, and pink salmon. During only one cruise, in September 1983, were juvenile chinook more numerous than juvenile coho.

Table 2. Percent composition of juvenile salmonids in purse seine catches, 1979-1983. All sets were within 50 km of shore. The frequency of occurrence of juvenile salmonids and the number of purse seine sets are given at the bottom of the table.

	1979	1980	1981				1982			1983		
	JUNE	JUNE	MAY	JUNE	JULY	AUG	MAY	JUNE	SEPT	MAY	JUNE	SEPT
COHO	57	73	80	82	71	78	66	72	65	54	77	47
CHINOOK	29	14	8.5	6.2	15	11	28	20	1.1	37	18	53
CHUM	9.4	1.3	4.9	5.0	5.9	7.4	0.1	4.8	26	3.2	1.1	0
SOCKEYE	0.4	0	0.1	0.5	0	0	0	1.8	0.2	3.2	0.4	0
PINK	0	0	0	0	0.2	0	0	0	8.0	0	0	0
STEELHEAD	1.8	2.7	4.0	4.2	0.4	0.2	4.2	0.2	0	0.9	0.8	0
CUTTHROAT	1.8	9.3	2.3	2.2	8.2	2.8	1.0	0.8	0	2.0	2.3	0
% F.O. JUV. SALMONIDS	70	71	78	69	85	77	76	75	79	69	48	47
NO. SETS	56	36	62	67	67	67	62	55	38	55	58	51

Miller et al. (1983) also found that juvenile (< 500 mm FL) coho salmon were the most common juvenile salmonid during their May 27-June 7, 1980 cruise off southern Washington and northern Oregon, but juvenile chinook predominated catches of their later cruises from July 4-15 and August 28-September 8, 1980.

Where Are Juvenile Coho Most Abundant?

The average catch per set of round hauls along inshore-offshore transects, usually as close inshore as the 37-m isobath and 9.3, 18.5, 28, and 37 km (5, 10, 15, and 20 n. mi.) offshore, shows that juvenile coho salmon were common in a broad zone of coastal waters within 37 km of the coast (Table 3). Catches were usually highest within 28 km of the coast and decreased to low numbers beyond 37 km. Within this coastal zone juvenile coho salmon inhabit waters over a wide range of sea surface temperatures (Table 4). Catches were made at temperatures from between 9° and 17.9°C. In 1982, and less obviously in 1981 and 1983, there was a trend for highest catches to occur in cooler waters (9°-14°C) in May and June and in warmer waters later in the summer. This was in part due to the absence of cool, upwelled water late in the summer. During September 1982 when warm water prevailed, juvenile coho were concentrated within 18.5 km of shore (Table 3). However, during May 1982, the month of the strongest coastal upwelling and lowest sea temperatures of all cruises, juvenile coho were also concentrated within 18.5 km of shore. Offshore dispersal of coho did not generally appear to be associated with strong upwelling, and conversely, coho catch rates were not always highest closest to shore when warm waters prevailed, such as those produced by the 1983 El Nino (Table 3).

Miller et al. (1983) also made highest catches within 25 km of the coast and often caught no juvenile coho salmon beyond 30 km of the coast. They associated low catches during their July cruise with warm water temperatures (average surface temperatures of 15.2°C).

North-South Distribution

Highest catch per set of juvenile coho within 50 km of the coast was usually between Willapa Bay and the Alsea River. Generally low catches were made south of the Alsea River to Cape Arago (Table 5).

Table 3. Average catch of juvenile coho per round haul for each cruise, 1979-1983. Parentheses indicate where less than three tows were made per interval.

		DISTANCE OFFSHORE				
	km	0-9.3	9.4-18.5	18.7-27.8	28-37.1	37.2
	n.mi.	0-5	5.1-10	10.1-15	15.1-20	>20
1979 June		6.7	6.5	4.8	5.8	(0)
1980 June		1.7	4.5	2.0	0	0.3
1981 May		5.6	24.0	10.7	5.5	1.1
June		9.0	4.9	9.6	7.2	0.8
July		1.5	6.0	11.6	4.6	0
August		2.9	5.2	11.1	3.3	0.5
1982 May		5.0	20.0	3.4	1.1	0
June		5.6	14.0	16.7	11.1	1.5
September		20.6	17.3	3.7	4.0	0
1983 May		5.3	6.4	1.1	1.2	(4.5)
June		1.1	6.0	2.1	7.4	(0.3)
September		3.7	4.4	4.2	1.5	(4.5)

Table 4. Average catch per set of juvenile coho salmon at various temperatures

	SEA SURFACE TEMPERATURE									
	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.0-13.9	14.0-14.9	15.0-15.9	16.0-16.9	17.0-17.9
1981										
MAY NO./SET			25.0	1.0	9.2	10.7	12.0			
JUNE NO./SET					0	6.2	3.9	11.8		
JULY NO./SET		0	1.0	2.8	10.3	2.75	4.7	4.8	10.8	1.0
AUG NO./SET				0	2.9	5.1	4.2	8.6	12.5	
1982										
MAY NO./SET		7.9	19.7	1.2	2.3					
JUNE NO./SET	0	2.2	2.2	21.3	23.7	4.6				
SEPT NO./SET					0	4.7	31.3	12.5	2.6	1.0
1983										
MAY NO./SET			0	3.2	3.3	2.6	8.2	0		
JUNE NO./SET					3.5	0.5	1.4	5.7	1.9	
SEPT NO./SET				0	2.8	1.3	7.5	1.7	0	

Table 5. Catch of juvenile coho per round haul set within different regions, to 50 km offshore, June 1979-June 1983.

	1979	1980	1981				1982			1983		
	JUNE	JUNE	MAY	JUNE	JULY	AUG	MAY	JUNE	SEPT	MAY	JUNE	SEPT
CAPE FLATTERY-GRAYS HARBOR							0.26	15.33	9.25	1.05	2.00	9.47
WILLAPA BAY-CAPE DISAPP.	9.25	0.63	1.79	15.91	1.63	4.09	0.63	18.29	12.45	2.00	11.86	0.20
COLUMBIA R.-NEHALEM	7.43	4.36	10.26	11.71	9.84	12.56	1.31	8.00	15.71	8.88	2.11	2.25
CAPE LOOKOUT-ALSEA RIVER	2.35	2.85	14.38	1.82	5.96	4.11	30.13	18.00	6.86	3.73	0.09	1.20
YACHATS-CAPE ARAGO	0.38			3.87		0.42	3.33	0.50	1.20	3.57	3.43	1.0
WILLAPA-ALSEA: AVE.	5.2	2.8	9.9	8.8	5.5	6.6	13.6	15.7	11.8	4.6	3.9	1.32

Highest catches were noted south of the Columbia River in May followed by peak catches north of the Columbia River in June of 1981, 1982, and 1983. Between Cape Flattery and Grays Harbor, catches also increased dramatically between May and June 1982. They were also higher off Cape Flattery than any other region of the coast in September of 1983.

Length-Frequency Distributions

Length-frequency distributions for all coho caught during the three cruises in 1982 are shown in Figure 1. During all cruises a distinct mode comprising .0 coho was present. In May this mode was between 151 and 160 mm. Highest catches were from Cape Lookout to the Siuslaw River. In June the modal peak was the same length, except off Cape Lookout to Yachats where it was about 180 mm. In September many .0 age fish were larger (250-400 mm), with the sizes progressively larger to the north. Age .1 coho were caught during all cruises. They comprised modes above 350 mm in May, 400 mm in June, and 500 mm in September. The difference in size between .0 and .1 coho averages about 350 mm, indicating an average growth rate for survivors between their first and second summer in the ocean of about 1 mm per day.

Are .0 Coho Highly Migratory?

Information on the movements of juvenile coho salmon can be derived from several sources: directional purse seine sets, recovery of marked individuals, and shifts in the catches along the coast.

The presence of large .0 coho off northern Washington in September 1982 (Figure 1, Table 5) is circumstantial evidence for movement of juvenile coho northward. This trend late in the summer for big catches of large juvenile coho at northern stations and small catches at southern stations also occurred during 1981 and 1983.

Paired directional purse seine sets, where the seine is set in a semicircle with the mouth held open to the north and followed or preceded by a set with the opening to the south at the same location, presumably provide data on the orientation or swimming direction of fish. Four such paired sets made in June 1979 showed that 98% of the juvenile coho (n=104) were caught in the sets open to the

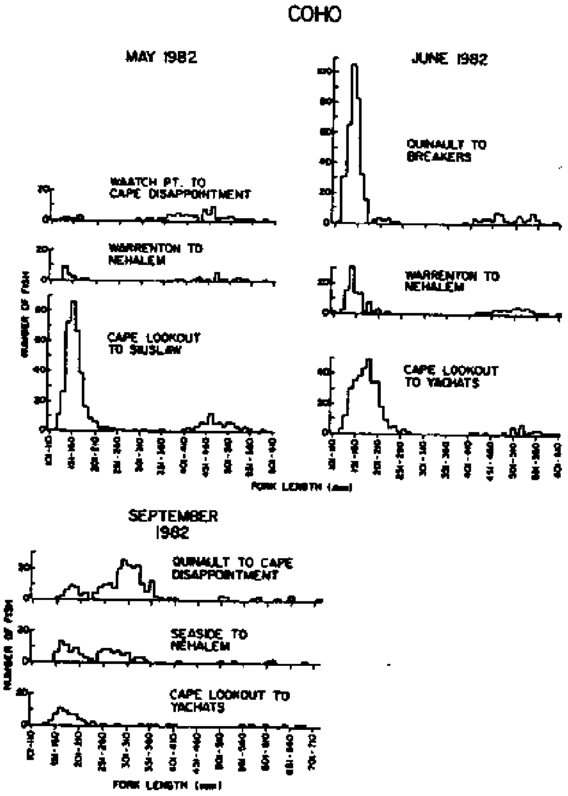

Figure 1. Length-frequency distributions of coho salmon collected on three cruises in 1982.

south, suggesting that fish were oriented to the north and less apt to swim out of the semicircle if the opening was facing the south.

Miller et al. (1983) made similar types of sets in 1980 and reported that 75% of the coho caught during their May-June cruise were taken in sets open to the south, but no relationship was found between direction of set and catches during cruises in July and August. Hartt and Dell (1978) found that 83% of the juvenile salmonids caught in 19 paired purse seine sets were caught in sets held open to the southeast and only 17% were caught in sets held open to the northwest or north along the coastal zone, Cape Flattery to Yukutat. From these differences and the recapture one year later of fish they tagged southeast of tagging locations, Hartt and Dell concluded that a strong northwest migration of juvenile salmon occurred in this region. They reported that about 37% of the coho salmon tagged as juveniles between Kodiak Island and 56°N were recovered the following year from the Columbia River and south.

Recoveries of marked fish off Oregon and Washington provide new data on movements of juvenile salmonids. The 1982 data shown in Figure 2 illustrate the distance that marked fish were captured north or south of their river of ocean entrance vs. days since release from hatcheries on (a) the Columbia River, (b) the coast of Oregon, (c) the coast of Washington, and (d) Oregon Aqua-Food (OAF) release site at Newport, Oregon. In May, highest numbers of marked .0 coho were recovered south of where they entered the ocean. Most of these fish were from the Columbia River hatcheries. Two fish from the Washington coast were recovered over 250 km south of where they entered the ocean less than 36 days earlier. Only one fish from the Oregon coast was found to the north of its ocean entry, 61 days after release.

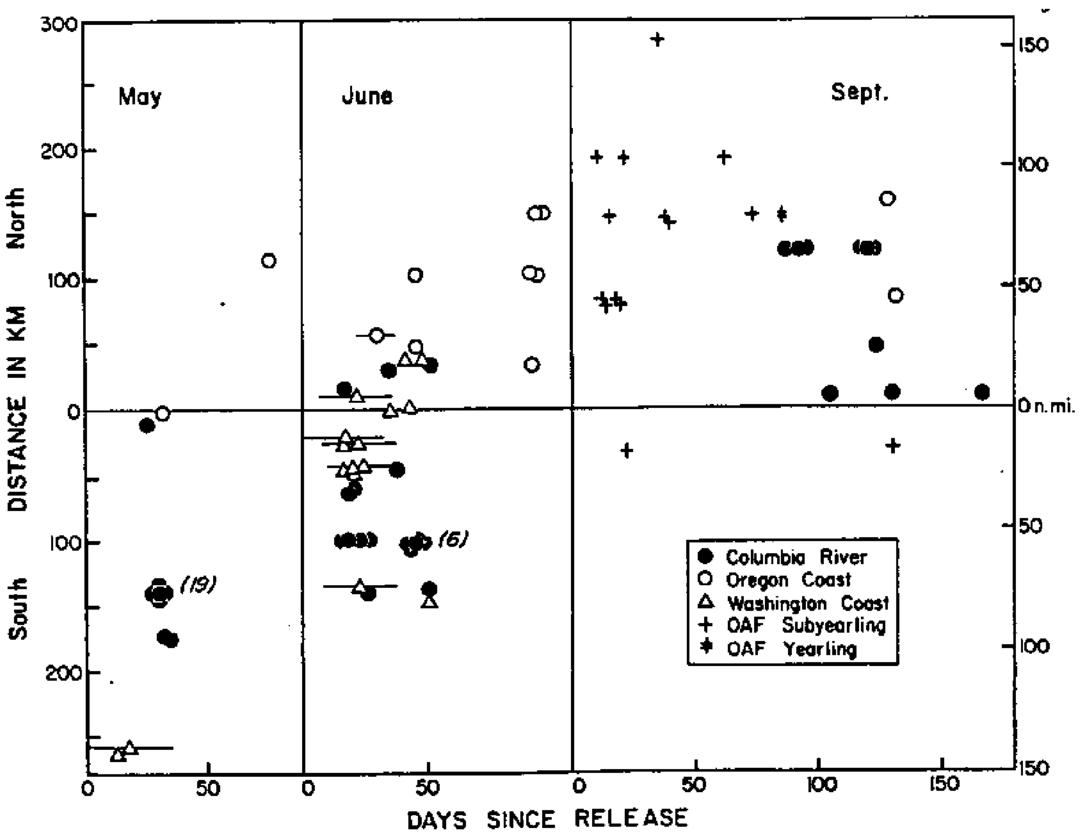

Figure 2. Distance north and south of the point of ocean entry vs. days since hatchery release for marked juvenile coho salmon captured in 1982.

During June, the distribution of marked fish was more uniform north and south of points of ocean entry. Most Columbia River and Washington coastal fish were again south of ocean entry locations, whereas all the Oregon coastal fish were captured north of where they entered the ocean.

During September, all but two of 28 .0 coho were caught to the north of their point of ocean entry. All of the fish captured within 87 days of release were from the Oregon Aqua-Foods release site. These fish showed a strong tendency to move to the north after release, some swimming over 100 km in three weeks or less. Nearly all the fish captured after 87 days since release were from the Columbia River, and all of these were captured north of the Columbia River. Two Oregon coastal fish were caught north of ocean entry. Marked fish from coastal Washington hatcheries were not captured in September.

These trends indicate southward movement of .0 coho in May, perhaps associated with transport to the south in the Columbia River plume or coastal currents. Northerly wind stress was high during May 1982, resulting in strong coastal upwelling (A. Bakun unpublished) and presumably intensified southward transport of near-surface waters. Definite movement of some fish to the north of their points of ocean entry occurred in June. Oregon coastal fish, which were found farthest to the north after 90 days from release, also were the largest .0 coho caught in June. In September, rapid northward movement of some OAF fish occurred. Some Columbia River fish averaging 316 mm were recovered a few kilometers north of the Columbia River.

In summary, evidence exists for southerly movement in May, northerly and southerly movement by June, and northerly movement by September of 1982. However, the occurrence of Columbia River and Oregon coastal stocks in all months, sometimes within the vicinity of their parent streams months after release, suggests that some individuals are relatively nonmigratory.

Growth Rates

Growth of .0 coho was estimated from the difference in size at ocean entry and size at capture of marked individuals. Size at ocean entry was estimated from the "ocean check" on the scales and a fish length-scale radius relationship. Figure 3 shows that most marked fish captured in 1982 had growth rates greater than 1.0 mm/day within 100 days of release. Since the days spent in the ocean are less than the days since release, these data underestimate ocean growth rate. These growth rates are similar or higher than the average growth rate of about 1 mm/day reported by Healey (1980) for coho salmon during their first six months in Georgia Strait.

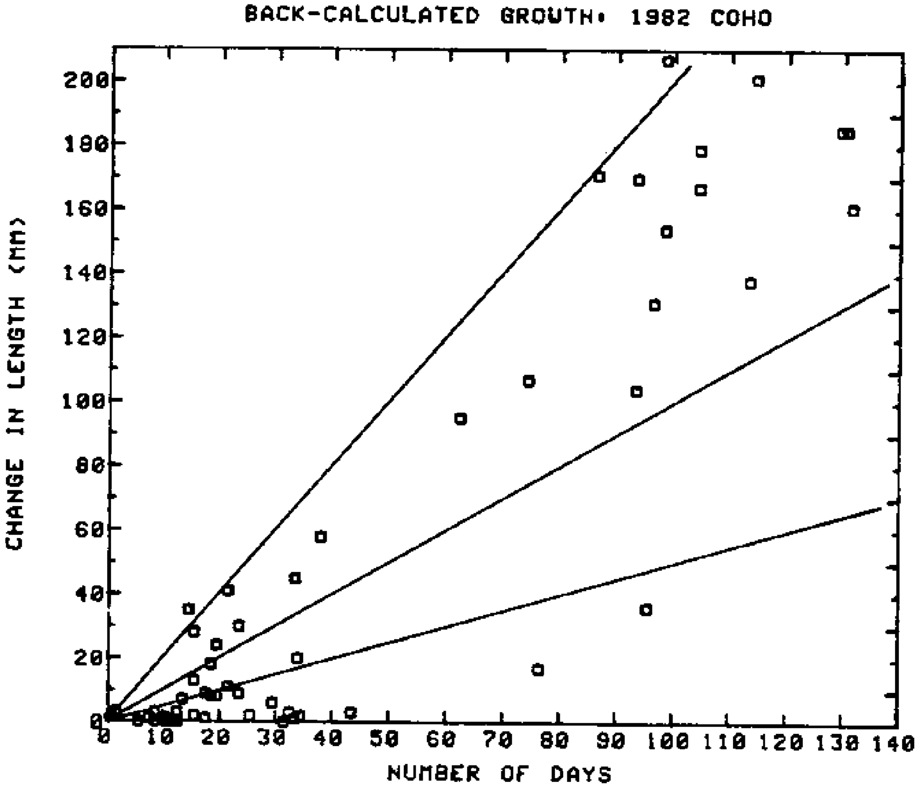

Figure 3. Growth rates of marked juvenile coho salmon captured in 1982.

Body condition (length weight) of marked Oregon Aqua-Food .0 coho captured at sea was lowest and most variable within 40 days of release and increased with days after release. Fatty acid composition of fish changed during residence in the ocean, indicating a switch to a diet of marine organisms (Gushee 1982). These data suggest that growth and condition of .0 coho surviving 30-40 days after release were generally favorable.

Discussion

Where do all the Oregon coho go during their first summer in the ocean? Do they migrate long distances or are they localized in coastal waters off Oregon and Washington? Tagging studies (Hartt and Dell 1978; Hartt 1980; Godfrey 1965) provide the best evidence for long migrations of Oregon and Washington coho stocks into waters off British Columbia and Alaska during their first ocean summer. Some marked fish in our sampling off Oregon and Washington showed a definite and rapid movement to the north, especially during the late summer. A northward movement was also indicated by catch per set and size frequency data. Directional purse seine sets, moreover, indicated a northward orientation of smolts during some cruises.

The linear regression between average catches of .0 coho off Oregon and Washington in June and jack returns in the Oregon production area during the same year has a positive slope but the intercept suggests that even if no juveniles were caught in June, the production of coho salmon the next year would be about a million fish, over half the total production in recent years. Therefore all juvenile coho were apparently not available to our June sampling, possibly because they migrated out of the local area.

The presence of fish from Oregon and Columbia River hatcheries during all cruises, even late in the summer several months after release is evidence that not all .0 coho migrate out of our sampling area. Juvenile coho salmon have also been reported in estuaries in Oregon during winter months. Moreover, the fact that coho production is correlated with coastal upwelling off Oregon suggests that local conditions, not those to the north off British Columbia and Alaska, affect the survival of juvenile coho salmon from the Oregon region. Thus even if fish from Oregon migrate far to the north, their year class strength appears to be determined while they inhabit local waters.

In summary, as Hartt and Dell (1968) and Hartt (1980) emphasized, evidence exists for both highly migratory and weakly migratory coho stocks. Reviewing all the evidence, this appears to be the situation off Oregon and Washington. However, Hartt did not tag salmonids south of Cape Flattery and our studies did not sample north of Cape Flattery; so the proportion of juvenile coho salmon that undertake long-distance movements is an open question. Moreover, Hartt's collections were from 1956 to 1970, a period before large-scale production of coho smolts by Oregon and Washington hatcheries and when oceanographic conditions may have been different.

The other side of the question "where do all the coho go?" pertains to survival and the mechanisms linking good production to strong upwelling. Many hypotheses have been proposed. Upwelling may affect food abundance and availability, hence growth and survival, with slow-growing or weak fish being subjected to high rates of predation. Upwelling may change ocean conditions (width of the "salmon water" habitat or water clarity) that in turn affect the degree of predation on smolts. Finally, upwelling may be related to water movements that influence migratory patterns and orientation.

Initially we thought that growth would be directly related to survival, i.e., that years of weak upwelling would produce slow growth. No significant differences were found, however, between strong and weak upwelling years in the distance between the ocean "check" and the first winter annulus on scales of coho collected on the same spawning stream the following year. Survivors apparently had similar juvenile growth in both weak and strong upwelling years (Fisher and Pearcy in prep.).

Growth rates and body condition of marked fish recovered during their first summer in the ocean do not reveal a large percentage of fish in poor condition that may experience high mortality. Slow growth within 30-40 days of release is difficult to detect from our measurements, however, because of the inherent uncertainties in making growth estimates. This early ocean period may, by default, be a period of high mortality, and future investigations should attempt to learn more about distribution, growth, and predation on juvenile coho during the period immediately after release.

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Coastal Ocean Warming in the Northeast Pacific, 1976-83

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Introduction

Anomalously warm coastal waters occurred in the northeast Pacific during the years 1976-83 with extremely warm conditions in 1982-83. Similar periods of unusually warm coastal water conditions have occurred many times is the past, including the following periods in recent decades: 1940-41, 1957-58, 1972-73, and 1976-77. The cause of the anomalous warming appears to be a combination of effects, including (1) a shift of the wind field over the northeast Pacific so that warm surface water is transported toward the coast, and (2) a northward propagating depression of the thermocline along the coast from "El Nino" conditions in the eastern tropical Pacific. Both processes depress the thermal structure along the coast and cause major physical and ecological changes. One effect is the occurrence of anomalously strong northward coastal currents in winter which transport tropical species northward along the coast. Radovich (1961) and Squire (1983) described occurrences of southern species such as barracuda, white sea bass, yellowfin tuna, and skipjack tuna off California during warm water periods.

A second effect of warm water conditions has been reduced biological productivity in the California Current. Zooplankton abundance in the California Current has long been known to be negatively correlated with water temperature (Reid 1962) and is seen in CalCOFI survey data (Figure 1). The cause of the reduction is thought to be a reduced supply of nutrients to the surface euphotic zone. Three major sources of nutrients to the California Current have been suggested: (1) southward advection of cold, nutrient-rich surface water from the north by the California Current (Chelton et al. 1982), (2) upwelling of cold, deep, nutrient-rich water along the coast in summer due to offshore transport of surface water under persistent northwesterly winds, and (3) transport of nutrients upward through the thermocline by wind mixing and other processes. Warming or thickening of the surface layer causes reductions in all three processes and causes reduced nutrient supply and reduced productivity. During 1976-83 and particularly during 1982-83, the reduced biological productivity off California resulted in poor growth and reproduction of many species.

In contrast to waters off California, warm years in the Gulf of Alaska and Bering Sea may result in increased biological productivity. In the California Current region nutrients are a limiting factor on biological productivity, and light is probably not limiting. In the Gulf of Alaska and Bering Sea, however, nutrients are abundant because of (1) entrainment and mixing of deep, nutrient-rich water into the lower salinity surface waters, (2) widespread upwelling in the central Gulf and (3) resuspension of nutrients from the bottom in the shallow eastern Bering Sea. In these subarctic waters, light and stability of the water column may be limiting factors (Parsons et al. 1966). Both factors are probably positively correlated with water temperature on an interannual basis. Also Frost (1983) noted that zooplankton volumes at Station "P" were inversely correlated with those in the California Current on an interannual basis.

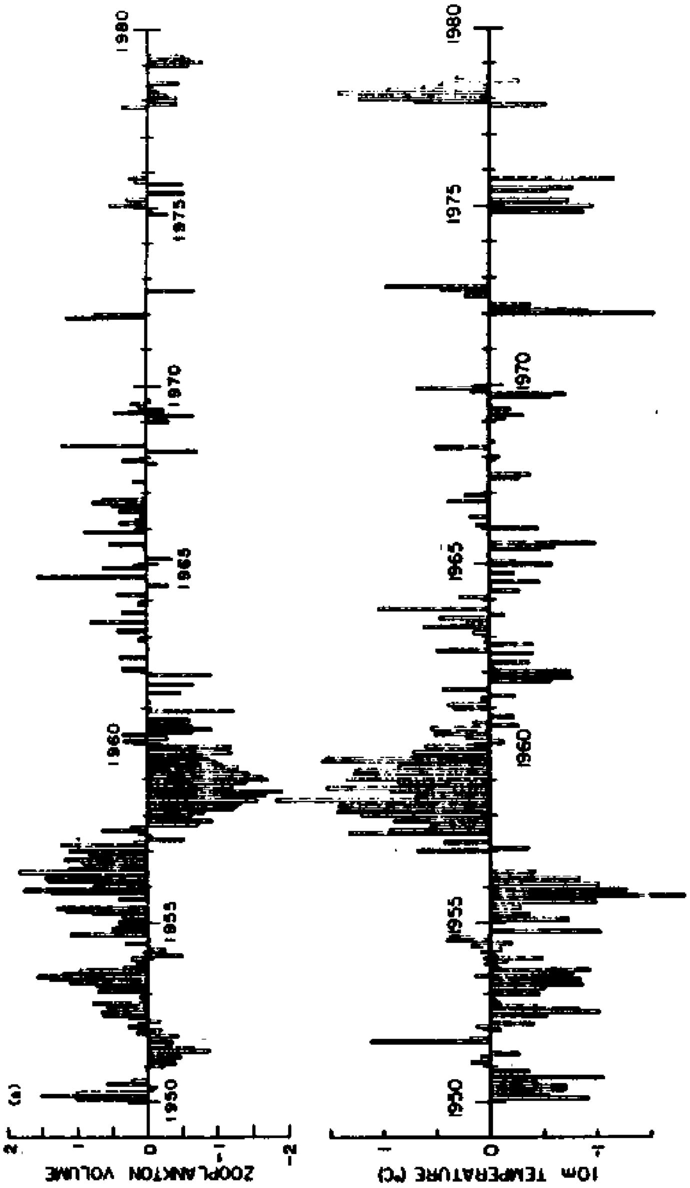

Figure 1. Zooplankton volume and 10 m temperature from CalCOFI survey data. Figure from Chelton et al. (1982).

The data shown in Figure 1 are mean zooplankton volumes collected on CalCOFI research vessel surveys in the California Current. These surveys had good temporal and spatial coverage in the 1950s and 1960s, but since 1970 the coverage has been reduced and the CalCOFI surveys are no longer as useful for monitoring long-term fluctuations of zooplankton. In the Gulf of Alaska and Bering Sea, the only extensive, long-term surveys that have been made are the observations at Station "P" and along Line "P" to and from the coast. Data collection at Station "P" is now being phased out after 20 years of intensive sampling. Because of the present inadequate time series sampling of productivity and plankton in the northeast Pacific, indirect information such as meteorological and physical oceanographic data series must be used for monitoring annual changes in the biological productivity of the region.

El Nino and Southern Oscillation

El Nino is an oceanographic phenomenon related to fluctuations of the global atmospheric circulation. The term, chosen because the phenomenon often occurs near Christmas, was originally used to describe anomalous ocean warming off South America. Over the last decade, effects of the phenomenon have been observed over a much larger area, and use of the term has been extended to describe related unusual events throughout the Pacific and even into the Indian Ocean.

Atmospheric circulation over the tropical Pacific is dominated by the meridional Hadley circulation of rising air over the equator and sinking air near 30°N and 30°S, causing oceanic high-pressure systems to occur at these latitudes. The oceanic highs are strongest in the summer and weakest in the winter of their respective hemispheres. Zonal circulation over the tropical Pacific is described as the Walker circulation of rising air, heavy rainfall, and low pressure over the warm western tropical Pacific (WTP) and sinking air, sparse rainfall, and high pressure over the cold, upwelled water of the eastern tropical Pacific (ETP). The trade winds result from these two components of the atmospheric circulation; the trades blow from the midlatitude oceanic highs toward the lower pressure at the equator and from the higher pressure over the ETP to the lower pressure over the WTP.

Interannual variations of the zonal strength of the trade winds are related to the difference of atmospheric pressure between the eastern and western tropical Pacific. The zonal pressure difference, called the Southern Oscillation Index, is often measured by the pressure at Easter Island minus that at Darwin, Australia (Quinn and Neal 1983a). The normal trade winds drive surface water westward in the north and south equatorial currents, piling up warm surface water in the western Pacific, depressing the thermocline, and raising sea levels there. Water flows away from the western Pacific in three directions: poleward into the North and South Pacific gyres and eastward in the equatorial countercurrent beneath the convergence zone between the northern and southern trade winds and in the equatorial undercurrent or Cromwell Current.

According to the hypothesis of Wyrtki (1975), El Nino occurs when a weakening of the trades (and zonal pressure difference) allows a stronger than normal counterflow of warm water toward the ETP, causing an intrusion of warm water against the South American coast, depressing the normally elevated density structure there and causing a rapid rise in sea level. Warming of the surface water destabilizes the atmosphere, and rainfall and occasional flooding occurs in Peru and Ecuador. The numerical model of McCreary (1976) suggests that the anomalous deepening of the density structure dissipates by spreading to the north and south along the coast and back westward along the Equator. The model predicts that waves of anomalous deepening of the density structure propagate poleward along the coast from the equator as low-frequency baroclinic waves. Such baroclinic waves would be observed as anomalous deepening of temperature and salinity surfaces adjacent to the coast and as anomalous rises of sea level at coastal tide gages. Poleward currents along the coast are created in geostrophic response to the anomalous deepening and change in slope of the density surfaces normal to the coast. The currents reverse to equatorward as the anomalous deepening dissipates. To some extent these processes occur each year, and anomalous warm years are merely an extreme condition of the normal annual cycle of events.

A time series of anomalies of the pressure difference between Easter Island and Darwin, Australia (Figure 2) shows the major El Nino events of recent decades. Note the strong pressure differences (and implied strong trade winds) during 1954-56 and 1970-71. Subsequent sharp declines in the pressure difference in the winters of 1956-57 and 1971-72 were followed by El Nino occurrences.

Effects off the West Coast

El Nino conditions are reflected in changes in the two major current systems off the west coast: (1) the California Current, flowing southward in a broad region off the coast and (2) the California countercurrent or undercurrent, flowing northward in a narrow region over the continental shelf and slope, inshore of the California Current. Under normal conditions, in summer when the oceanic high-pressure system is strong, northwesterly winds prevail along the coast and the surface flow is southward throughout the region. The southward surface flow overrides the inshore countercurrent and causes it to remain subsurface as an undercurrent at depths of 100 m or more. In winter the oceanic high-pressure system weakens and the northwesterly winds relax or even become southerly. The southward surface flow then relaxes and the countercurrent reaches the surface and is called the Davidson Current.

During an El Nino event, anomalous deepening of the density structure along the California coast causes poleward coastal currents which intensify the normal Davidson Current flow during winter. In addition to the remote forcing of coastal currents by baroclinic waves from the tropics, anomalous deepening of the density structure can also be caused by local onshore Ekman transport of surface water against the coast (McLain and Thomas 1983; Simpson 1983). Above normal sea levels and sea surface temperatures (SST's) are observed at coastal stations during winters of strong Davidson Current. Reversal of the coastal current to southerly flow may occur very rapidly in March or April in a "spring transition" (Huyer et al. 1979; Breaker et al. 1983).

Warming Trend since Summer 1976

A weak El Nino event began in spring 1976 when the Southern Oscillation Index fell below normal (Figure 2, Quinn and Neal 1983a). After the event, the S.O. Index did not return to positive values but has remained generally below normal since 1976. This index condition is an indication of El-Nino like conditions with a weak subtropical high-pressure system over the South Pacific Ocean and is associated with weak southeast trade winds over the equatorial region of the eastern and central tropical Pacific. A weakening of the southeast trade winds since 1976 has been observed in marine weather data from merchant ships (Gary Meyers, Scripps Institution of Oceanography, 1983, personal communication). The weak trade winds resulted in reduced upwelling and above normal SST's along the equator in the ETP. The weak trade winds piled up less than normal amounts of water in the western Pacific and as a result, thermocline depths in the WTP have been shallower than normal and thermocline depths in the ETP have been deeper than normal (Meyers, 1983, personal communication). Quinn and Neal (1983b) attributed the decline of anchoveta off Peru and northern Chile and increases in other species such as sardine, mackerel, and saury to these oceanographic changes.

Associated with the 1976 shift in the Southern Oscillation Index was a shift in the pattern of SST anomalies over the northeast Pacific. The pattern of SST anomaly over the northeast Pacific has two general types: (1) a pattern, here called "warm-cold" or "WC" pattern, with

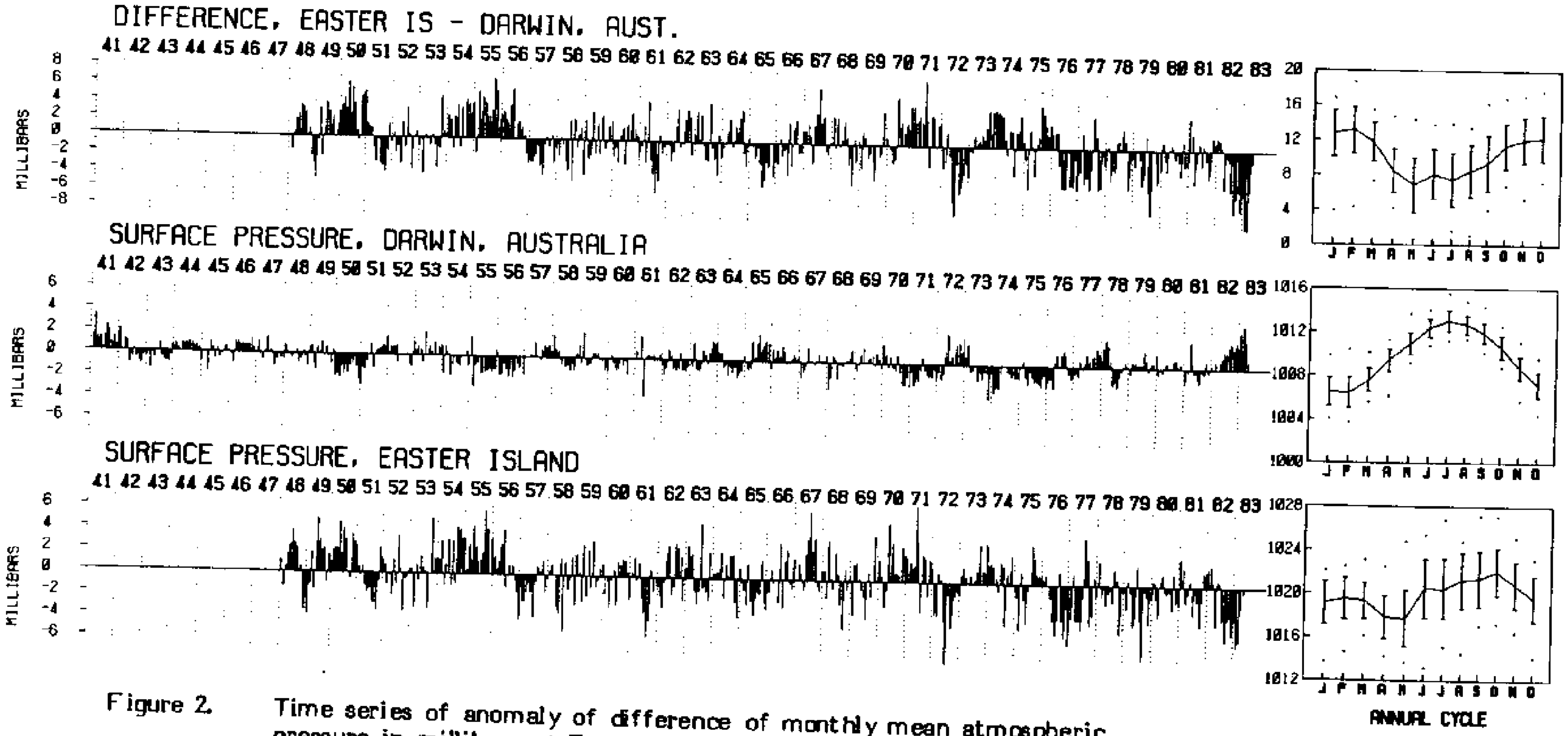

Figure 2. Time series of anomaly of difference of monthly mean atmospheric pressure in millibars at Easter Island and Darwin, Australia. Data from Dr. W. Quinn, Oregon State University, Corvallis, OR. 97331.

above normal SST's in a large area north of Hawaii and below normal SST's along the coast from the ETP to the Gulf of Alaska or even the Bering Sea (Figure 3A), and (2) a "cold-warm" or "CW" pattern with generally below normal SST's north of Hawaii and above normal SST's along the coast (Figure 3B). These patterns of SST anomaly correspond to the first eigenvector of SST fluctuation of Weare et al. (1976) and are summarized in Table 1. The SST anomaly pattern is best defined in the winter months; summer maps often show an intermediate or confused pattern. This is reasonable as the winter SST anomaly pattern may reflect a large scale oceanographic condition of the deep water which is obscured in summer months by the presence of the seasonal thermocline.

During periods when the anomaly of the Southern Oscillation Index has been positive, the SST anomaly pattern has often been of the "WC" type. With the fall of the S.O. Index in 1972, the "WC" SST anomaly pattern weakened to an intermediate "warm-cold-warm" pattern. The SST anomaly pattern reverted to "WC" type in the winters of 1973-74 and 1975-76 when the anomaly of the S.O. Index was positive. Then in summer 1976 when the S.O. Index fell, the SST anomaly pattern shifted to the "CW" type and has remained generally of that type since then. A similar large-scale shift in the SST anomaly pattern from "WC" to "CW" type may have also occurred in 1957-58 (Table 1).

Large-scale changes in the SST anomaly pattern over the North Pacific have been related by Namias, Davis, and others to large-scale shifts in the circulation of the upper atmosphere. Davis (1976) for example, showed that surface barometric pressure and SST anomalies are related by the mechanism of horizontal advection of the mean ocean temperature in the direction of the anomalous geostrophic wind. Other processes such as turbulence and Ekman pumping also are important in influencing SST anomaly patterns but are less important than the horizontal advection of ocean temperature by anomalous winds (Haney et al. 1983).

This implies that the switch from "WC" to "CW" SST anomaly pattern involved a shift in the atmospheric circulation over the North Pacific Ocean. Such an atmospheric shift can be seen in maps of upper air circulation as an eastward shift of a ridge of upper air circulation over the northeast Pacific and replacement of the ridge by a trough. This is consistent with the model of Horel and Wallace (1981), who found that during winters when SST's in the equatorial Pacific are above normal, there is a tendency for troughs of upper air circulation to occur over the central North Pacific and ridges to occur over western North America.

A general eastward shift of a ridge of upper air winds over the North Pacific in winters since 1976 is suggested by monthly mean maps of twice daily fields of height of the 500 mb pressure surface, computed by the Fleet Numerical Oceanography Center. During the winters in the early 1970s when the S.O. Index was positive, there was either a ridge of upper air circulation over the central North Pacific (causing northerly upper air winds over the coastal waters) or zonal flow (causing westerly winds over the coastal waters) (Figure 4A). In the winters since 1976-77, the ridge of upper air circulation that had been in the mid-Pacific often occurred over western North America, bringing southerly upper air winds to the coastal waters (Figure 4B). Downstream of the ridge over western North America, cold, arctic air blew southward over the eastern U. S., causing a series of three consecutive unusually severe winters (1976-77, 1977-78, and 1978-79) in the east.

The ridge over the mid-Pacific was well developed in several of the winters of the early 1970s and brought very cold, arctic air south over Alaska, causing a series of extremely cold winters over the Bering Sea and northern Gulf of Alaska (McLain and Favorite 1976). Warming occurred in the Bering Sea region from 1976-79 and above normal temperatures have persisted into at least 1982 (Niebauer 1983). Niebauer related the warming to a shift of atmospheric circulation and noted that 1976 was a pivotal year between two general modes of circulation of the "North Pacific Oscillation" which was described by Rogers (1981) as an opposition of winter

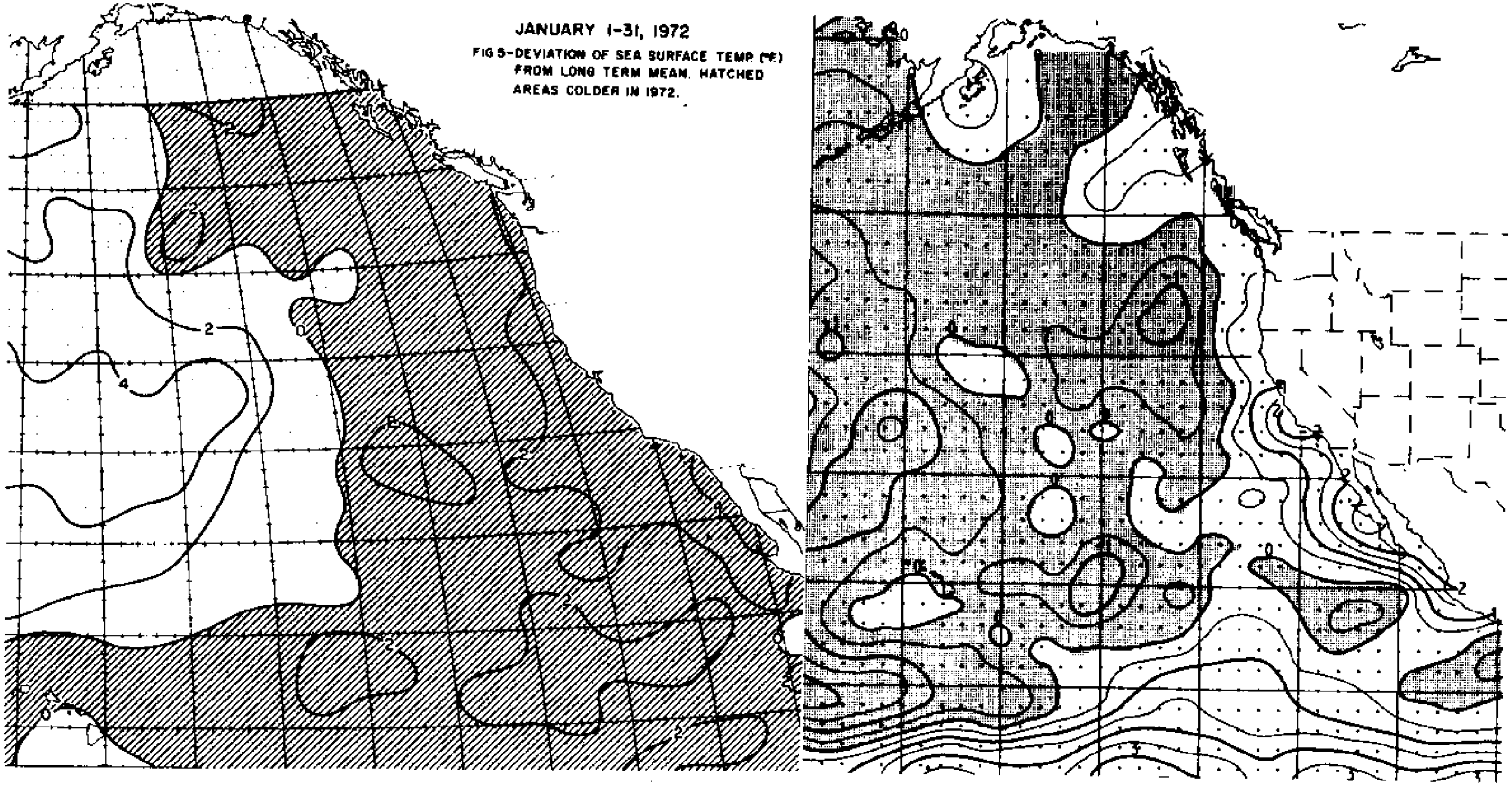

Figure 3. A) Pattern of SST anomaly in degrees Celcius over the northeast Pacific for January 1972. B) Same for January 1983. Figure A from Fishing Information, Southwest Fisheries Center, NMFS, NOAA, LaJolla, CA. 92037 and B) from Oceanographic Monthly Summary, National Meteological Center, NWS, NOAA, Washington, D.C. 20233.

Table 1. Pattern of SST anomaly over the northeast Pacific. "WC" refers to the "warm-cold" pattern (see text) while "CW" refers to the "cold-warm" pattern. Months with especially well defined SST anomaly patterns are underlined. Data from Eber (1971), McGary (1957-59), Fishing Information (1960-1980) and Oceanographic Monthly Summary (1981-83).

Year	J	F	M	A	M	J	J	A	S	O	N	D
1955		C						WC			WC	
1956								CW			WC	
1957	WC	WC	WC	?	WCW	WCW	WCW	WCW	CWC	CWC	?	CWC
1958	?	CW	CW	C	CW	CW	CW	CW	CW	W	?	CW
1959	CW	CW	CW	CWC	WC	?	?	?	WCW	CWC	CW	CW
1960	CW	CW	CW	CW	CW	CW	?	WC	WC	?	CW	CW
1961	CW	CW	CW	CW	WC	CW	?	?	WC	WC	WC	WC
1962	WC	WC	WC	CWC	CWC	CWC	WC	WC	WC	CW	W	W
1963	W	CW	?	WC	WC	WC	WCW	WC	WCW	WCW	WCW	WCW
1964	WCW	WC	WC		WC	WC	WC	WC	WC	WCW	WC	WC
1965	WC			WC	WC	CWC	WC	?	CWC	CW	WCW	WCW
1966	WC	WC	WC	WC	WC	WC	WC	CWC	CW	CW	WC	WCW
1967	WCW	WC	WC	WC	WC	WC	WC	WC	WCW	WCW	WCW	WC
1968	WC	CWC	CW	CWC	CWC						WC	WC
1969	WC	WC	WC	WC	WC	CW	CWC	WC	WC	CW	WCW	WCW
1970	WCW	CW	CW	CWC	?	?	?	?	WC	WC	WC	WC
1971	WC	WC	WC	WC	WC	WC	?	?	?	?	WC	WC
1972	WC	WC	WC	WC	WC	WC	?	CWC	?	CWC	CWC	CWC
1973	CWC	CWC	CWC	?	?	?	C	C	C	C	C	WC
1974	WC	WC	WC	C	C	C	?	?	CW	CWC	CWC	CW
1975	CWC	C	C	CWC	CWC	CWC	?	?	CWC	WC	WC	WC
1976	CWC	CWC	?	C	C	C	C	C	C	CW	CW	CW
1977	CW	CW	CW	C	C	C	C	CWC	C	C	C	C
1978	CW	CW	CW	CW	CW	WCW	CW	C	WCW	?	CWC	CWC
1979	CWC	CWC	C	?	CW	CWC	CWC	CW	CW	CW	CW	CW
1980	CW	CW	CW	CW	CW	C	WCW	CWC	CWC		?	CW
1981	CW	CW	CW	CW	CW	CW	?	?	?	WCW	CW	CW
1982	CW	CW	CW	WCW	WCW	C	C	C	C	C	WCW	CW
1983	CW	CW	CW	CW	CW	CW	CW					

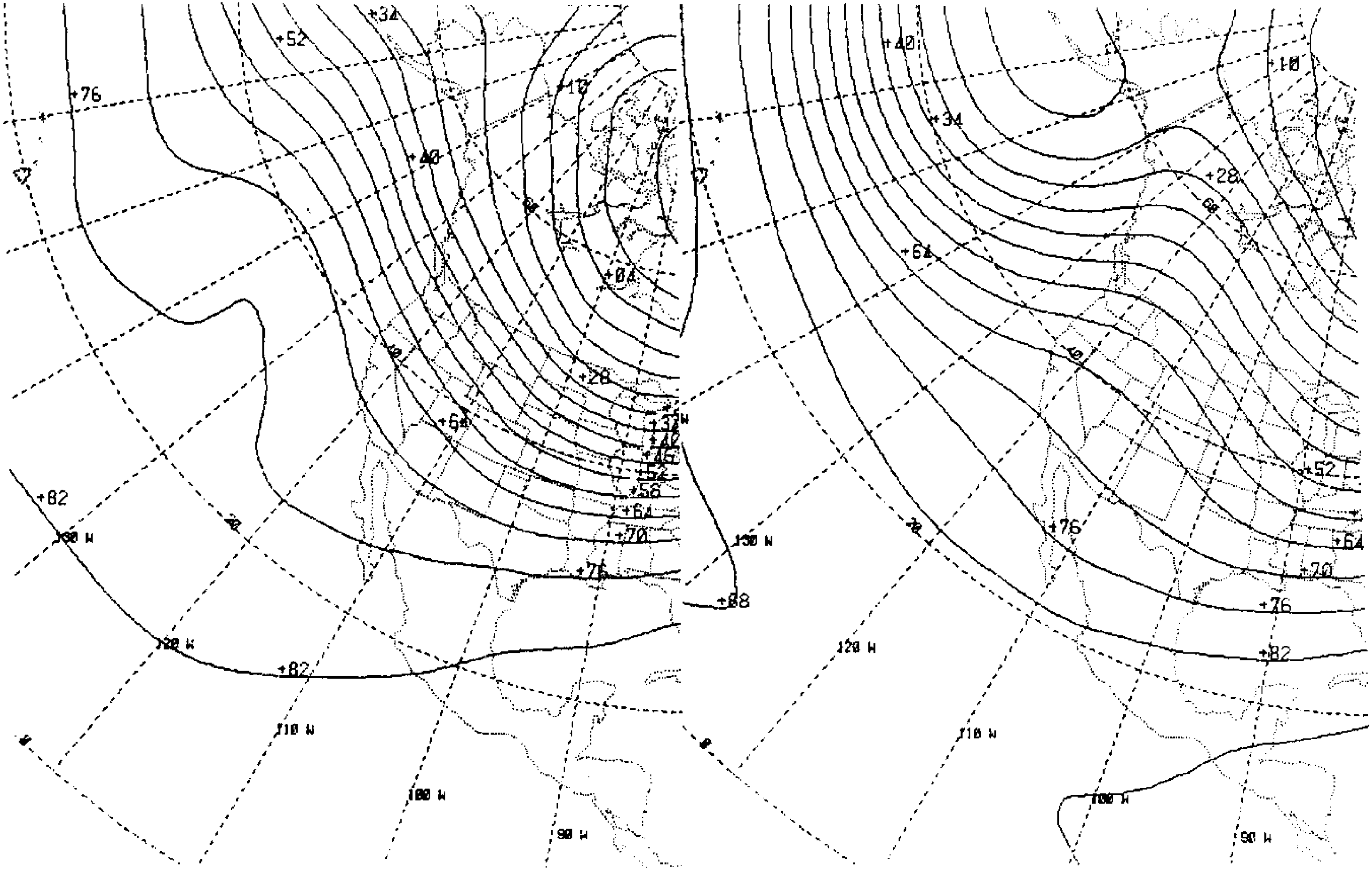

Figure 4. A) Monthly mean map of height of 500 mb height surface in hundreds of meters during January 1972. B) Same for January 1983. Computed from twice daily fields of 500 mb height analyzed by Fleet Numerical Oceanography Center, Monterey, CA. 93940.

mean temperature anomalies between the Bering Sea and western Canada. The oscillation is related to east-west shifts of the Aleutian low-pressure system from the western Aleutians to the Gulf of Alaska.

A similar eastward shift of a ridge of circulation also occurred in 1958-69 and brought southerly winds to the California coast. Huang (1972) showed that during the decade 1958-69 following the El Nino event of 1957-58, there was stronger flow from the west and weaker flow from the north into the California Current region than during the previous decade (1948-57). Johnson and McLain (1975) described the ridge pattern over western North America in the winter of 1957-58 and related cold weather in the eastern U.S.

Associated with the shift since 1976 of the winds off California to a more southerly direction, precipitation over California and the southwestern U.S. has been above normal during the winters of 1977-78, 1979-80, 1981-82, and 1982-83. Higher than normal precipitation might have been expected since 1976-77 rather than since 1977-78. A possible explanation for this delay may be that an intense high-pressure cell persisted over California during 1976 and 1977, blocking the southerly winds, preventing storms from reaching the state, and causing record drought. When the local high-pressure cell disappeared in 1978, greater than normal precipitation occurred and has reoccurred each winter since 1978. Markham and McLain (1977) found a correlation between historical SST anomalies in the Pacific and precipitation over California using data for 1931-72. They used the correlation for a prediction in 1977 but the correlation failed and its use as a predictor was abandoned. Perhaps the failure resulted from the presence of the high-pressure cell over California, a factor which was not common in the historical correlation.

Winter SST anomalies at stations along the west coast have been 1° to 2°C above normal since the winter of 1976-77, except 1978-79 (Figure 5). Summer SST's since 1976 were not above normal as the large-scale warming of the coastal waters was obscured in summer by formation of the seasonal thermocline. The warming trend appears greater at the northern region of the coast than off southern California--the trend is especially evident in SST values observed at British Columbia lighthouses (A. Dodimead, Pacific Biological Station, Nanaimo, B.C., 1983, personal communication). Breaker et al. (1983) also noted the warming trend in SST data for 1971-83 from Granite Canyon, near Big Sur, California.

The more southerly component of winds in winters since 1976-77 caused onshore Ekman transport of surface water against the coast, with the exception of the winters 1976-77 and 1978-79. El Nino conditions in the tropics in 1976-77 and 1982-83 caused northward propagating baroclinic waves of density depression during those winters. As a combined result of these processes and the general warming of the coastal waters, subsurface temperatures along the coast have been above normal and isotherms deeper than normal since 1976.

Although subsurface temperature data to verify this are sparse, an extract was made of subsurface temperature profiles from files of the Fleet Numerical Oceanography Center. These files include all available bottle cast, MBT, XBT, and STD profiles and real-time radio reports of subsurface temperature. Monthly means of the depth of the 14°C isotherm were computed for 1968-83 for 20 areas along the coast from Baja California to northern Chile (Figure 6). There were 40,528 temperature profiles used in the analysis and data from all years prior to 1968 were lumped into the single year 1967.

The long-term mean pattern of depth of the 14°C isotherm (Figure 7A) shows that the isotherm is deepest near the Equator and rises to depths shallower than 100 m at about 12°S and 24°N. The asymmetry about the Equator results from strong upwelling near the Equator (5-10°S) in the Southern Hemisphere but away from the Equator (20-40°N) in the Northern Hemisphere. This difference occurs because of the positions of the various high- and low-pressure systems and because of the orientation of the coastline relative to the winds associated with the pressure

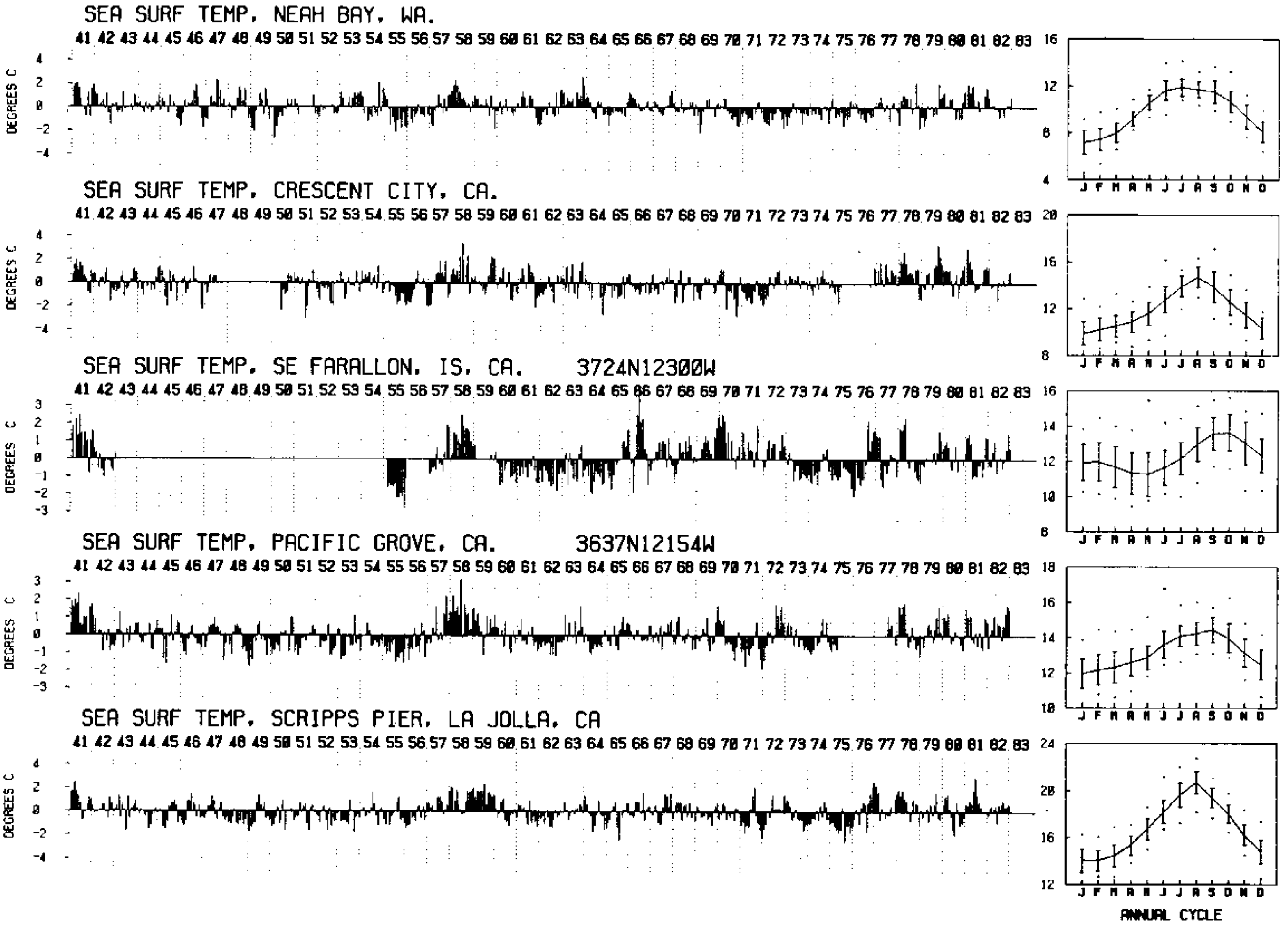

Figure 5. Time series of anomaly of monthly mean sea surface temperature in degrees Celcius at stations along the west coast. Data from Surface Water Temperatures at Shore Stations, Scripps Institution of Oceanography, Data Report Series, LaJolla, Ca. 92037.

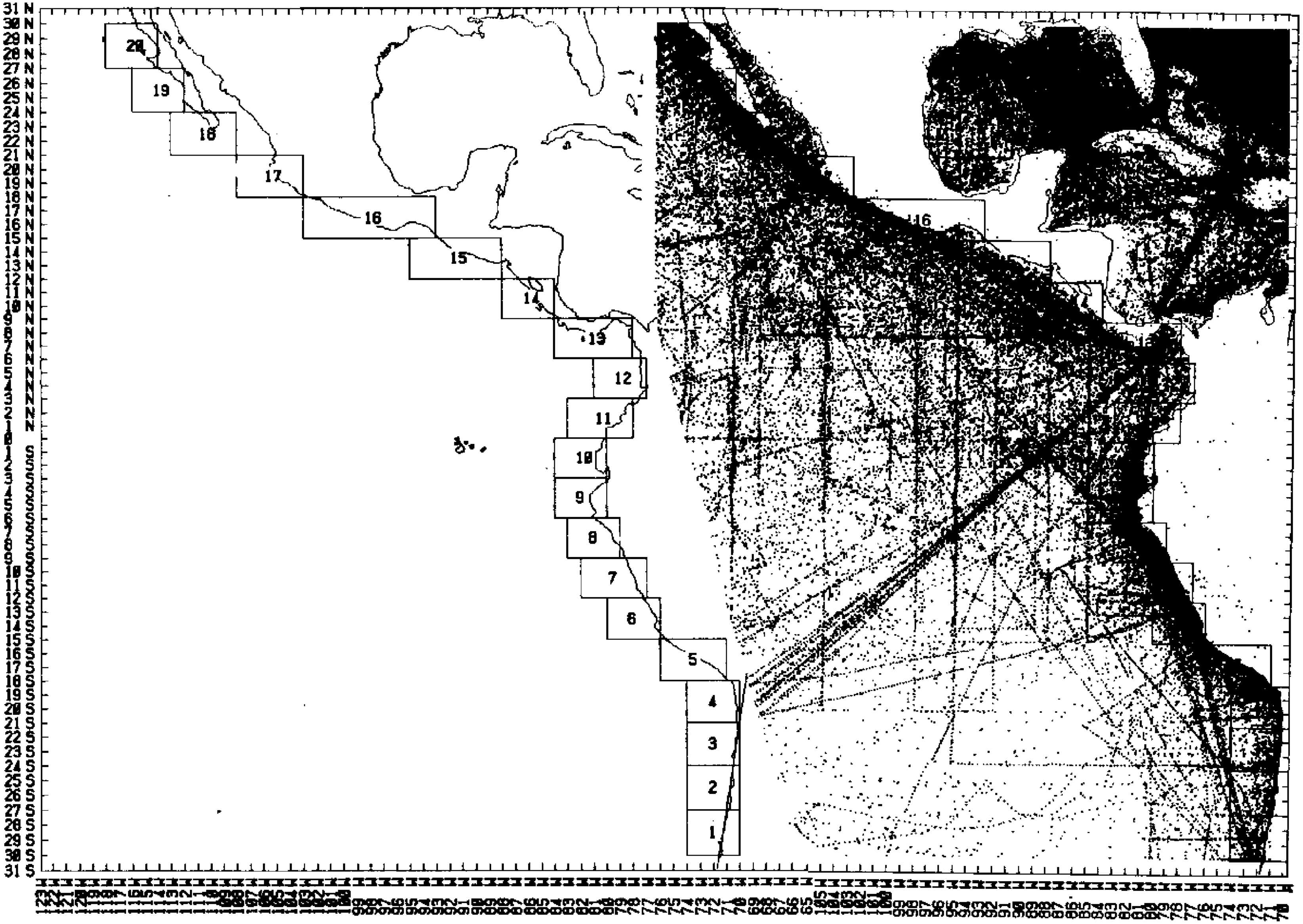

Figure 6. A) Location of 20 areas along west coast of North and South America from 30°S to 30°N where depth of 14°C isotherm was computed and averaged. B) Location of subsurface temperature profiles in Master Oceanographic Observations Data Set (MOODS), Fleet Numerical Oceanography Center, Monterey, CA, 93940.

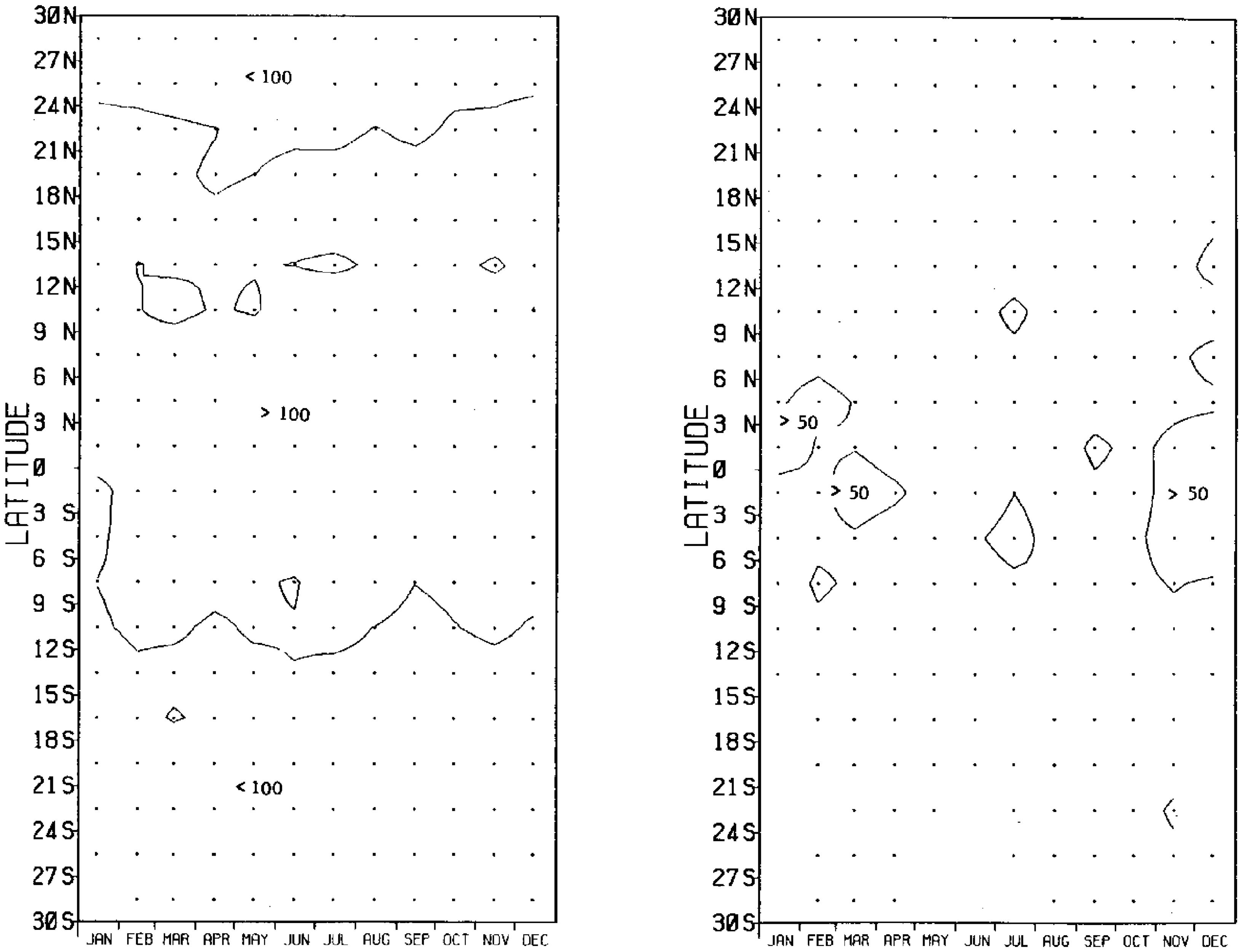

Figure 7. A) Annual mean pattern of depth of 14°C isotherm in meters by month and area along coast. Dots represent locations of one or more monthly mean values. Contour lines are 100 m isobath. B) Pattern of between-year standard deviation of the depth of the 14°C isotherm in meters. Dots represent locations of two or more monthly mean values. Contour lines are 50 m standard deviation.

systems. The interyear variability of the depth of the 14°C isotherm along the coast (Figure 7B) is greatest near the equator in January and December because of anomalous deepening of the density structure there as a result of El Nino phenomena.

A time-latitude contour plot of the individual monthly means (Figure 8) shows that the region along the coast where the 14°C isotherm is deeper than 100 m expanded from roughly 9°S-24°N to 18°S-27°N during the 1969 and 1972-73 El Ninos, returned to 9°S-21°N during 1971 and 1974-75, expanded to 18°S-24°N during spring 1976, and has remained expanded since then.

The monthly anomaly of depth of the 14°C isotherm is the difference of the individual monthly means and the long-term mean of the individual means. A time-latitude contour plot of the anomalies (Figure 9) is very noisy but does show large regions of coherent depth anomaly. Data coverage during the 1972-73 El Nino period is good and shows that positive depth anomalies began in May 1972 near the Equator, increased to values of over 150 m in November and December 1972, and then relaxed rapidly to zero values by April 1973 and negative values in June and July 1973. Wyrtki (1975) presented maps of the depth of the 15°C isotherm off Peru and Ecuador during 1972 which showed a similar progressive deepening of the isotherm during the year. Following onset of the anomalous deepening near the Equator, a band of anomalous deepening spread poleward, appearing to lag in time as it propagated, and reaching 30°N and 30°S after a lag of two to three months. Similar but less extensive and less well observed events occurred in 1968-69 and 1976-77. The lag in time during poleward spreading of anomalous deepenings may be evidence for the existence of baroclinic propagating coastal waves.

The warming after 1976 is also shown in Figure 9 with typical anomalies of 20 to 40 m after 1976. The anomalies increased to values of 50 to 100 m near the Equator in July to October 1976, August 1979 to May 1980, and March 1982 into early 1983. The anomalous deepening in 1979-80 has not been generally recognized as an El Nino event, but it was preceeded by a drop in the S.O. Index in summer 1979 (Figure 2).

Sea level data show a pattern similar to that of subsurface temperature data as would be expected, since sea level is related to the vertical integral of the temperature and density structure. Monthly mean sea level data from California tide gages (Figure 10) have been generally above normal each winter since 1976. Sea levels at Monterey were above normal during the 1972-73 El Nino, below normal during 1974 and 1975, above normal in 1976-80, near normal in 1981, and then far above normal during the 1982-83 El Nino.

The trend since 1976 is clearly shown in winter quarterly mean sea level data from San Francisco, California. (Figure 11). Huang (1972) showed that the shift in atmospheric transport to less northerly and more westerly transport in the decade 1958-69 (relative to the previous decade, 1948-57) caused an increase in winter quarterly mean sea level at San Diego. The winter quarter data after 1976 appear in San Francisco data as a continuation of Huang's trend. There has been a secular trend of increasing sea level at San Francisco for geological reasons but the data show previous periods of high sea levels in the 1880s and early 1900s.

The Davidson Current apparently has been stronger than normal each winter since 1976-77. McLain et al. (1979) and McLain and Ingraham (1980) reported unusual ocean conditions along the west coast during the winters 1977-78 and 1978-79 that were explained by an anomalously strong Davidson Current those winters.

Biological Effects of the Warming Trend

Biological productivity in the California Current region since 1976 apparently has been below normal because of reduced nutrification of the surface waters. Advection of nutrients from the north has been reduced because of the more frequent southerly winds in winter, and the

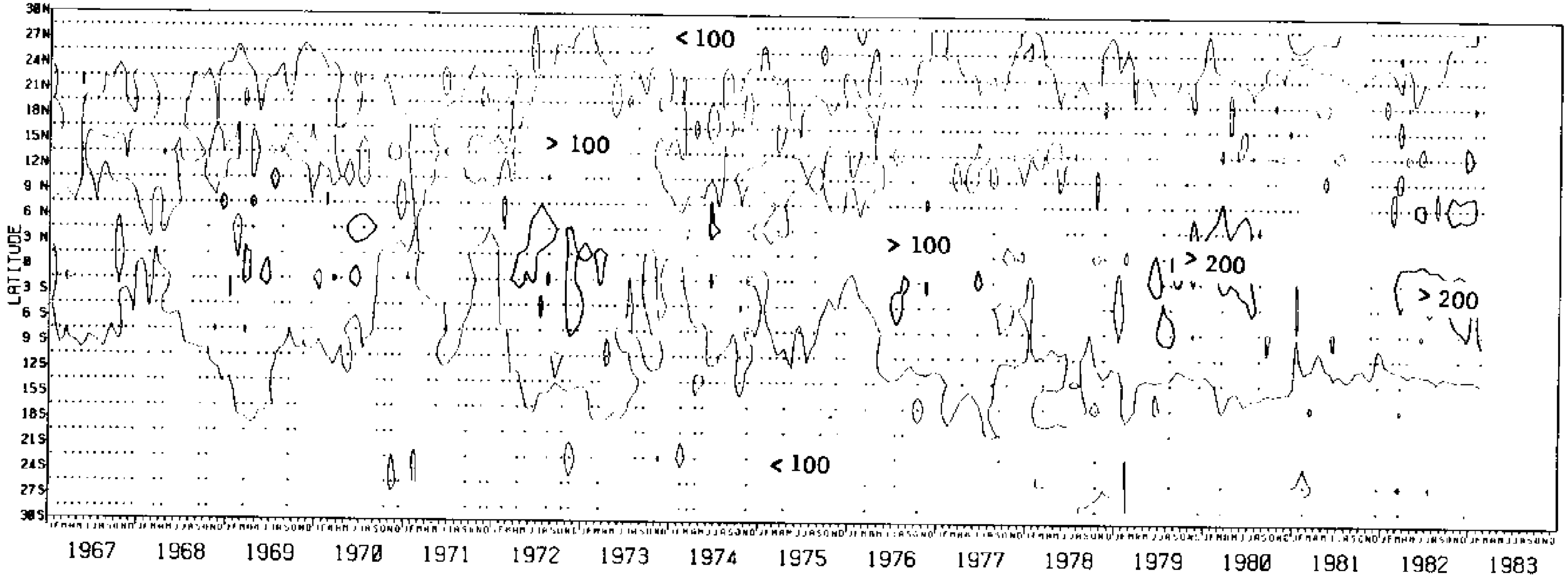

Figure 8. Time-latitude contour plot of monthly mean depth of 14°C isotherm in meters for 1968-83 and for 30°S to 30°N. All data for years prior to 1968 have been lumped into the single year 1967. Dots represent locations of one or more observations. Fine contour lines are 100 m isobath and heavy lines are 200 m isobath.

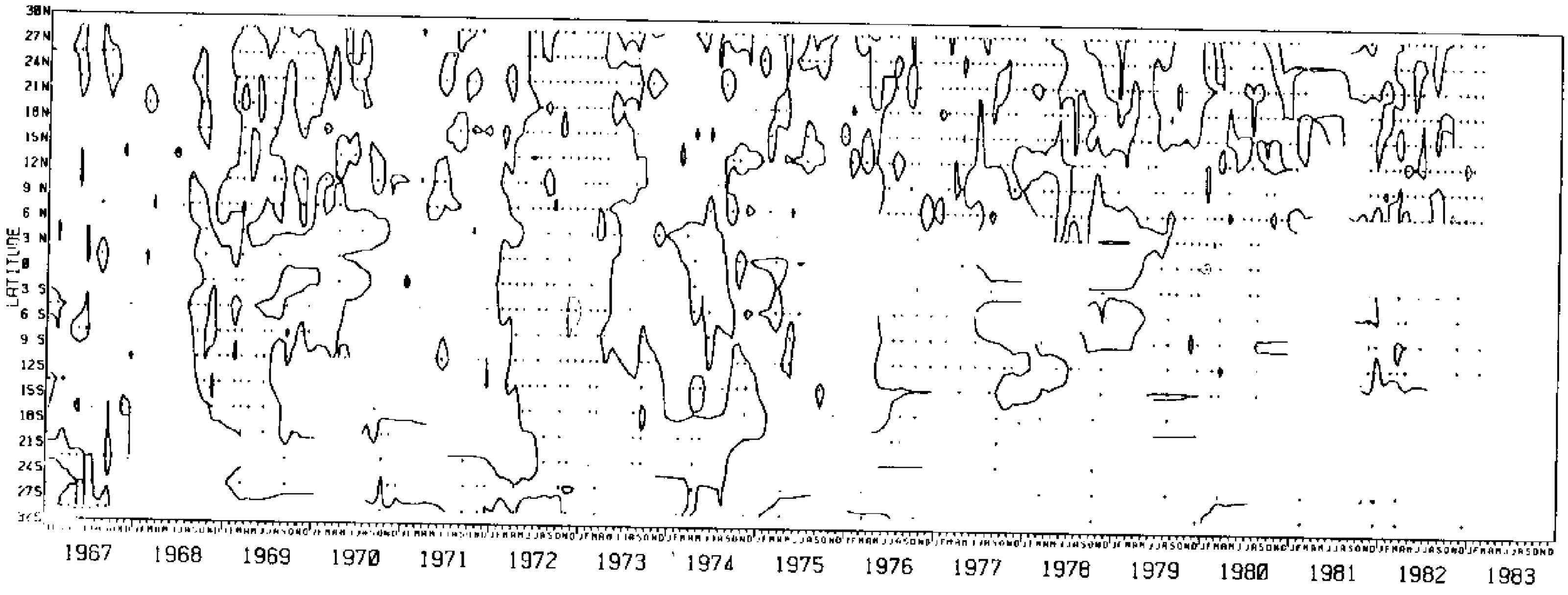

Figure 9. Time-latitude contour plot of anomaly of monthly mean depth of 14°C isotherm in meters for 1968-83 for 30^0S to 30^0N. Computed as difference of fields of Figure 8 and 7A. Plus signs show regions of positive depth anomaly and negative signs show regions of negative anomaly. Heavy contour line is zero anomaly and fine line is 100 m anomaly.

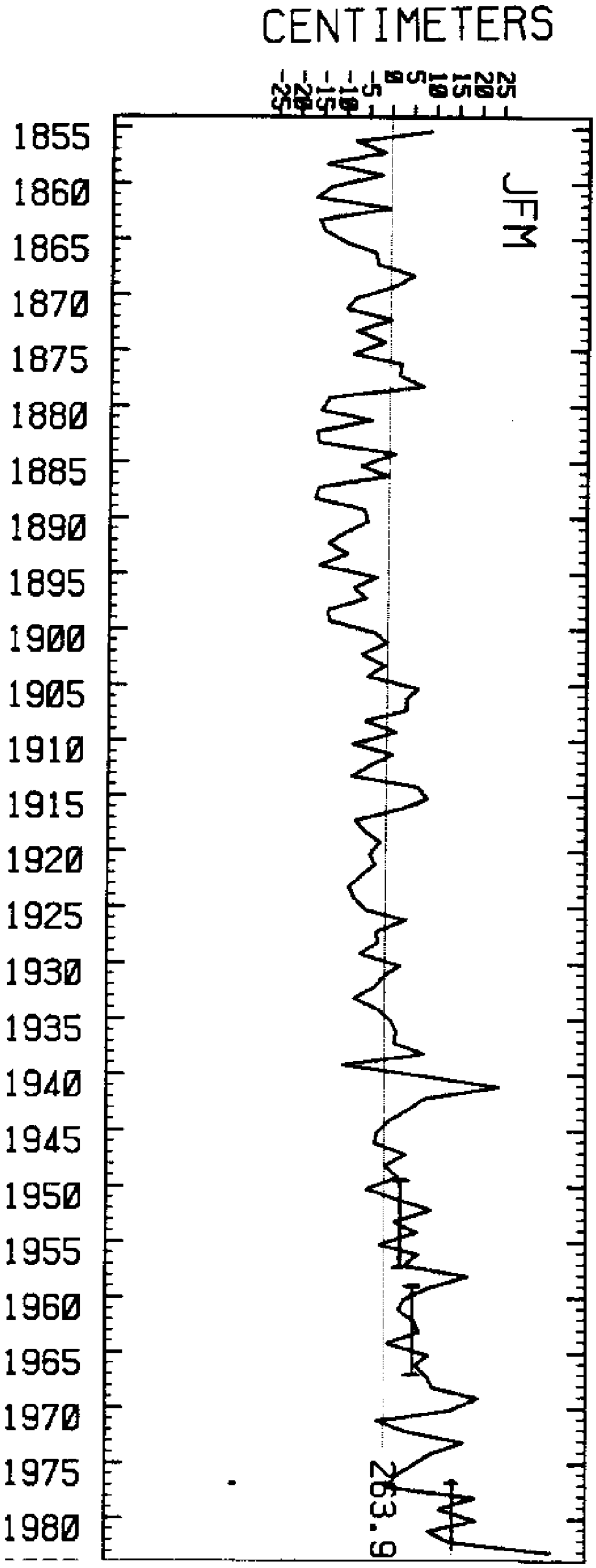

Figure 11. January-February-March mean sea level at San Francisco, CA. Data assembled from observations at Fort Point, Sausalito, and San Francisco, CA. Note long term, slow secular rise of sea level at San Francisco due to geological causes. Also shown are approximate mean values for decades 1948-57 and 1958-69 described by Huang (1972) and 1976-83.

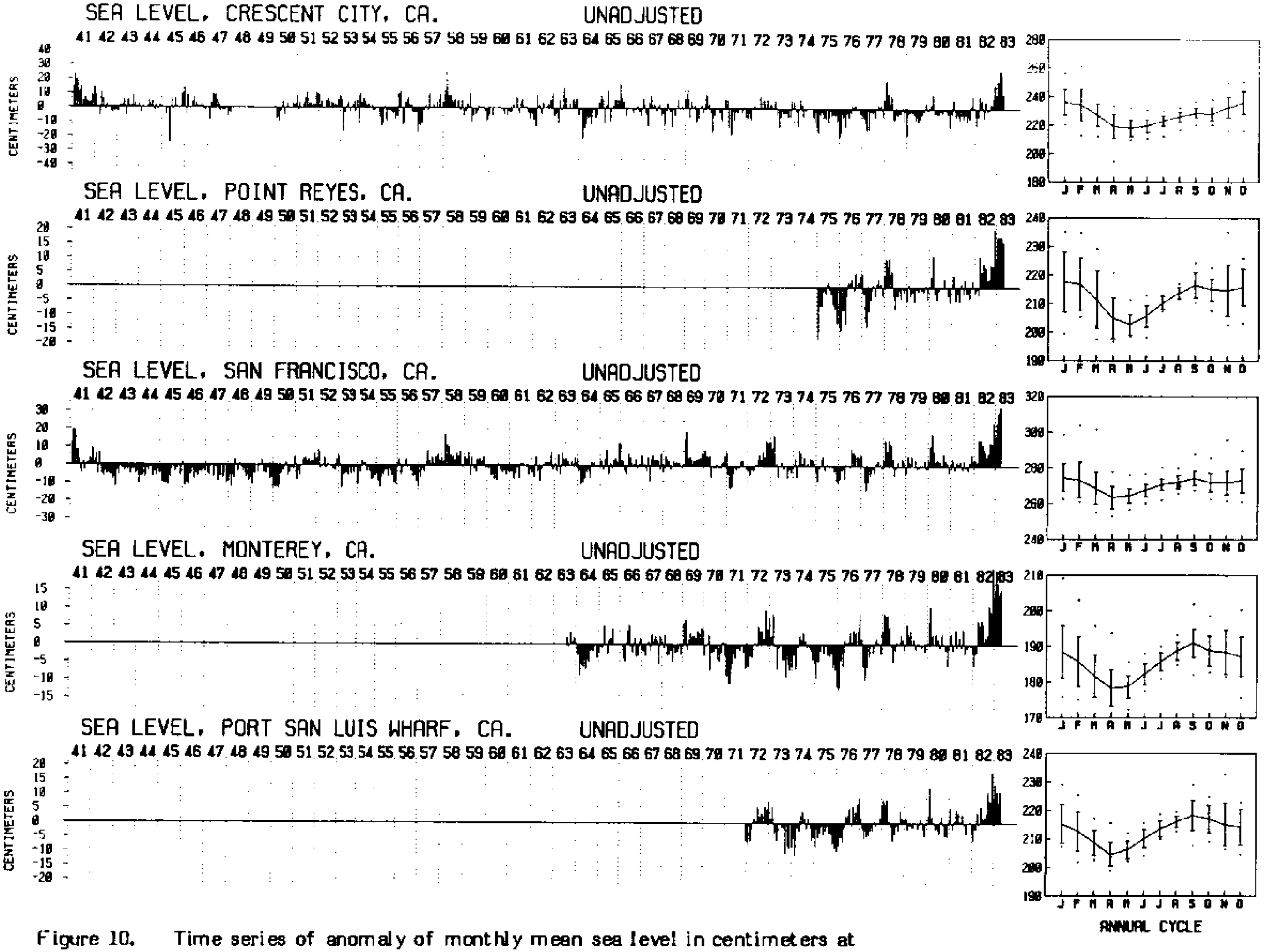

Figure 10. Time series of anomaly of monthly mean sea level in centimeters at California tide gages. Data from National Ocean Service, NOAA, Rockville, MD. 20852.

depressed density structure along the coast has reduced the effectiveness of the winds to cause upwelling of nutrients in summer. Such mechanisms probably also caused the reduced biological productivity in 1957-58 (Figure 1). Since 1976, kelp growth off San Diego, California, has been below normal, apparently because of lack of nutrients (Figure 12) (D.C. Barilotti, Kelco Co., San Diego, CA., 1983, personal communication). The marine survival of coho salmon from hatcheries in the Pacific Northwest declined during the mid-1970s to values one-half those of the previous decade (Nickelson and Lichotowichs 1983). Also residuals from a time series, statistical model of relations of populations of Dungeness crab to environmental parameters are larger in 1976-83 than in the previous record (R. Mendelssohn, NMFS PEG, 1983, personal communication).

The warming may have been related to declines of albacore catches along the west coast. Combined annual landings of albacore in California, Oregon, and Washington declined significantly during 1976-81 (Anon. 1983). Squire (1983) reported declines of recreationally caught albacore off southern California in 1958-59 and 1973-74 following warm water periods but did not suggest reasons for the declines.

An apparent northward shift of coastal ecosystems coincided with the warming trend. A strong and persistent shift in the migration route of maturing Fraser River sockeye salmon has occurred since 1978 (Figure 13) (D.J. Blackbourn, IPSFC, 1982, personal communication). The shift has occurred from the Strait of Juan de Fuca to Johnston Strait, from the southern entrance to the Fraser around Vancouver Island to the northern entrance. Halibut disappeared from Hecate Strait and Queen Charlotte Sound, B.C. (A. Dodimead, Pacific Biological Station, 1983, personal communication). Warming of the coastal waters may have caused the halibut to spawn north of their usual spawning grounds in Hecate Strait and Queen Charlotte Sound.

In the Gulf of Alaska and Bering Sea, the warming trend may have caused increased biological productivity and food supply for salmon. Bristol Bay sockeye salmon stocks declined to record low values in the early 1970s during a period of record cold winters (McLain and Favorite 1976). Possible reasons for the decline include (1) freeze-up of watersheds and consequent low stream flows and inadequate flushing of water past eggs in spawning gravels and (2) poor freshwater and marine growth rates and consequent high predation. Bristol Bay sockeye stocks rebounded dramatically in the late 1970s with the increased water temperatures and related mild winters (Rogers 1983) and probable increased biological productivity of the region.

1982-83 El Nino

In fall 1982 the Southern Oscillation Index dropped sharply and unexpectedly from a below normal value to a strongly negative value; i.e., low pressure developed in the ETP and high pressure in the WTP (Figure 2). Associated with the drop was a shift in the trade winds in the western and central tropical Pacific which began as early as July (Halpern et al. 1983). An eastward shift of the region of rising air occurred over the WTP and brought widespread drought to the WTP with famines in Indonesia and forest fires in Australia. Heavy rains occurred over tropical islands in the central tropical Pacific. Winds at islands near the equator in the central Pacific reversed from westerly to easterly for the first time on record.

Wyrtki's (1975) hypothesis is that a strong pulse of warm surface water apparently flowed eastward from the WTP as a more intense than normal equatorial countercurrent. Sea level began to rise in the ETP in July 1982 and by October was 22 cm above normal at the Galapagos Islands (Halpern et al. 1983). Depression of the density structure occurred over most of the ETP with the equatorial thermocline "nearly twice as thick and twice as deep" as that of a year earlier (Halpern et al. 1983). The 14°C isotherm was 80 to 100 m deeper than normal in the ETP (Figure 9) but was not well resolved in time and space from the available real-time reports. Although subsurface temperatures along the coast have been relatively widely observed in recent years, few of the observations are reported routinely in real-time. As more of the available data

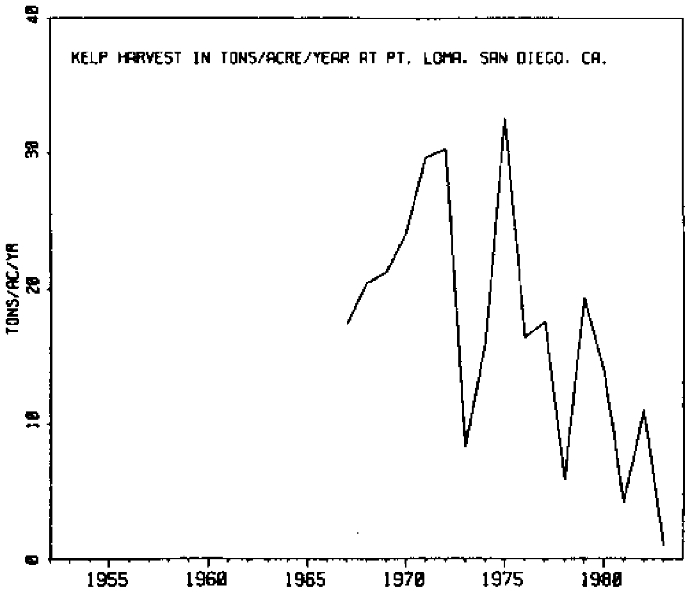

Figure 12. Average annual kelp harvest productivity in tons/acre/year off Point Loma, San Diego, CA. Data from D.C. Barilotti, Kelco Co., San Diego, CA. 92113. Note general decline of productivity after 1976 and collapse in 1982-83 due to reduced nutrient availability and to storm damage. The decline in 1973 was due to large waves in winter 1972-73 which destroyed many kelp plants.

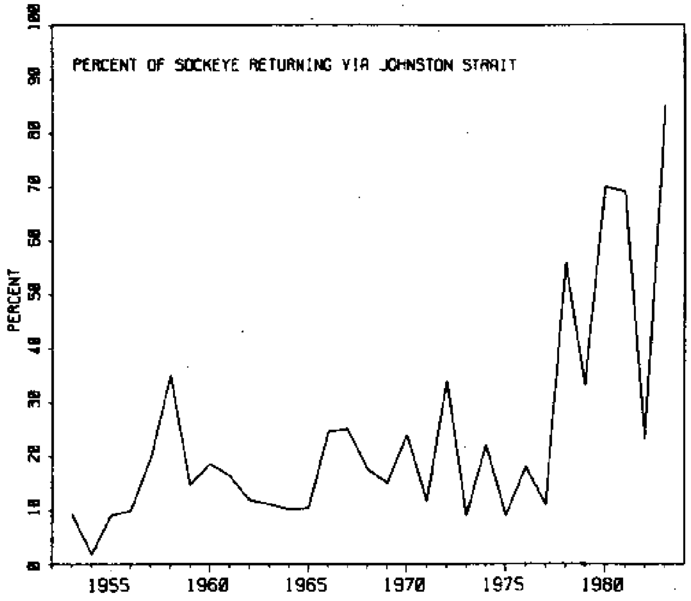

Figure 13. Percent of Fraser River sockeye salmon returning to the river around the north end of Vancouver Island (Johnston Strait) rather than around the south end of the Island (Strait of Juan de Fuca). Data from D.J. Blackbourn, International Pacific Salmon Fisheries Commission, New Westminster, B.C. V3L 4X9. Note peaks in warm water years 1958 and 1972 and general increase after 1977.

are assembled and processed, the spatial resolution of the fluctuations of subsurface temperature will improve. The surface water warmed in the ETP in response to the inflow of water from the west. SST anomalies were up to 6 °C above normal off Peru and Ecuador. Record rainfall and flooding in Peru and Ecuador resulted from destabilization of the atmosphere by the abnormally warm waters.

The anomalous deepening in the ETP propagated poleward along the coast (Figure 9) and caused strong poleward coastal currents. Southward movement of drifting buoys was observed off Peru and Chile in December, opposite to the local wind (Halpern et al. 1983). Off California, the Davidson Current was much stronger than normal during winter 1982-83. A large positive subsurface temperature anomaly was observed near the California coast on a CalCOFI survey in February 1983 and the resulting dynamic heights were the highest ever observed along the coast on a CalCOFI survey (Lynn 1983), implying a very strong northward flow. The flow was sufficiently strong to interfere with trawling off northern California (D.H. Thomas, CFG, 1983, personal communication). SST's were up to 4 °C above normal off California (Figure 5), continuing the period of above normal winter SST's since 1976. The Aleutian Low was larger and more intense than normal while the North Pacific High was weaker than normal (Simpson 1983). As a result, winds off California were strong from the west and south, causing record precipitation and strong onshore transport. The onshore transport was reinforced by a baroclinic wave from anomalous isotherm deepening in the ETP to depress the thermocline along the coast and cause record high sea levels. The 14°C isotherm was up to 70 m deeper than normal off central America and 10 to 50 m deeper than normal off Baja California (Figure 9). Sea levels off California were up to 20 cm above normal (Figure 10). Coastal erosion was severe as high waves and storm surges were superimposed on the higher than normal sea levels.

Eastward flow into the ETP ceased in January 1983 when the current reversed to westward with "exceptionally large speeds, up to 80 cm/sec" (Halpern et al. 1983), signalling the end of the anomalous density depression in the ETP. The relaxation of the anomalous deepening propagated north, reaching California in March or April and causing a dramatic reversal to strong southward flow over the shelf. The duration of the southward flow is unclear but a related offshore shift of a subsurface temperature anomaly was observed in May 1983 on a reoccupation of CalCOFI Line 90 off southern California (Lynn 1983). The southward flow was strong enough to again interfere with trawling operations off northern California (D.H. Thomas, CFG, 1983, personal communication).

Biological Effects of 1982-83 El Nino

Various anomalous biological observations were made in association with the anomalous coastal currents and related warming. From February to April 1983, barracuda were caught in Monterey Bay, California, bonito were caught north of San Francisco, and two tropical species had range extensions to the north (Popeye catalufa and Pacific burrfish) (R. Lea, CFG, 1983, personal communication). Catches of bocaccio and chilipepper rockfish on a port-to-port basis along the California coast suggest a northward shift in abundance during early 1983 (Henry 1983). Albacore tuna were caught close inshore off central California in response to the above normal surface temperatures. After the reversal of coastal currents in April, range extensions to the south occurred for quillback rockfish and Pacific tomcod (D.H. Thomas, CFG, 1983, personal communication).

Some fish that were transported northward in winter remained north of their usual range and were not carried back south by the reversed flow in summer. Shortbill spearfish were sighted in May in Monterey Bay and yellowfin tuna were being caught off southern California in summer 1983. Other fish were transported northward into the Gulf of Alaska and were carried further by the persistent northward and westward currents there. Bonito, for example, were caught off Kodiak Island in fall 1983.

The anomalous depressions of the thermocline in the equatorial and eastern Pacific caused reduced productivity of the surface waters. In the equatorial waters, catastrophic reproductive failures of many species of marine birds occurred at Christmas Island during fall 1982 (Schreiber and Schreiber 1983). Fur seals at the Galapagos Islands and at Punta San Juan, Peru, suffered high pup mortality during early 1983 (Limberger et al. 1983).

Along the coast of California, southerly winds in winter 1982-83 caused weakened advection of nutrients from the north. The upwelling-favorable northwesterly winds of summer 1983 were not effective in upwelling nutrient-rich waters but only stirred the anomalously thick surface waters. Little plankton growth has been observed (McGowan 1983). Clear, oceanic waters and related oceanic species persisted in inshore areas near Cape Mendocino, California, during summer 1983 (E. Hobson, NMFS Tiburon, 1983, personal communication).

Kelp growth off California was particularly low during the winter of 1982-83 as a result of the depressed thermocline and decreased nutrient availability. The availability of kelp at the surface where it is harvested commercially is the result of processes controlling frond growth, breakage, and sloughing. The temperature at the top of the thermocline off San Diego, California, is typically near 14°C, and thus the depth of the 14°C isotherm can be used as an index of the presence of nutrient-rich water. At Pt. Loma near San Diego during the winter of 1982-83, the 14°C isotherm was always deeper than the kelp bed depths, and temperatures in the beds were 15° to 16° C. During winter and spring 1983, kelp fronds took one to two weeks longer to grow to the surface and broke off one to two months earlier than in 1982. Besides the effects of the depressed thermocline and nutrients, large, long period waves occurred in eight episodes from January to March 1983 and caused extensive sloughing of the weakened fronds (D.C. Barilotti, Kelco Co., 1983, personal communication).

Many fish species had very poor growth in 1983 because of low biological productivity. The anchovy fishery in Mexico was greatly reduced and there was no anchovy fishery in California in 1983 partly because of economic reasons but also because of poor availability of fish. The few anchovy available to the fishery showed little or no growth (R.H. Parrish, NMFS PEG, 1983, personal communication). Squid abundance increased in Puget Sound (R. Mercer, NMFS NWAFC, 1983, personal communication) and decreased in Monterey Bay, southern California, and Baja California. Hartwick and Spratt (1979) related high sea level in winter with low squid adundance in Monterey Bay the following summer, and the relation held true in 1983. Many species of rockfish had very poor reproduction in 1983 (R.H. Parrish, NMFS PEG, 1983, personal communication). Coho salmon catches along the California and Oregon coasts were less than one half of normal and the fish were smaller than normal (Nickelson and Lichatowichs 1983).

Because of low food availability, reproductive failures of marine birds occurred in winter 1982-83 and spring 1983 at the Farallon Islands off San Francisco (Ainley 1983) and at Point Lobos, south of Monterey (A. Baldridge, Hopkins Marine Station, Pacific Grove, CA., 1983, personal communication). Brandt's cormorants, tufted puffins, and pigeon guillemots did not lay any eggs in spring 1983. Common murres, ashy storm petrels, and Cassin's auklets layed eggs late and in greatly reduced numbers. Western gulls were observed to have longer incubation shifts than normal and much more aggressive behavior than normal. The egg incubation shift by each parent is normally about one day but this spring, apparently because of low food availability, the other parent was gone for three to four days. The incubating parent left the nest after one or two days, leaving the eggs vulnerable to predators and exposure.

Summary

A well-developed ridge pattern of upper air circulation often occurred over the central North Pacific in winters in the early 1970s. Winds on the downstream limb of the ridge brought severely cold winters to Alaska and cool air to the U.S. west coast. SST's were above normal in mid-Pacific and below normal along the coast. Onshore transport of surface waters in winter was not common along the California coast.

A general eastward shift of the ridge occurred in 1976 to a position over western North America. Winds along the coast became more southerly on the upstream limb of the ridge. Onshore transport in winter occurred more frequently in California, piling water up against the coast and depressing the thermocline. The pattern of SST anomalies reversed to below normal in mid-Pacific and above normal along the coast. The eastward shift of the ridge occurred with warming in the ETP and persistent low values of the Southern Oscillation Index, consistent with the model of Horel and Wallace (1981). Weak El Nino conditions have persisted since 1976 with generally above normal SST's, sea levels, and rainfall in winter and anomalous depression of the thermal structure along the coast. Biological productivity in the California Current has been below normal since 1976, and a northward shift of some species occurred.

In winter 1982-83 the Southern Oscillation Index fell from below normal values to extremely low values, and a major El Nino event occurred in the ETP. A strong depression of the thermocline occurred in the ETP and propagated poleward along the coast. Off California, the propagating depression was reinforced by strong onshore transport and record high sea levels occurred. Strong Davidson Current flow resulted in geostrophic response to the anomalous deepening and southern species were transported northward along the coast as far as Alaska. Coastal currents reversed in spring 1983 and strong southward flows occurred in early summer 1983. Nutrient concentrations in the California Current were low all summer because of reduced advection from the north and because upwelling and mixing were not effective in elevating the anomalously deep, nutrient-rich water. Biological productivity off California was extremely low and was reflected in poor growth and reproduction of many species.

Salmon stocks in Alaskan waters responded oppositely to the warming of the coastal waters than those in the California Current. The cold winters in Alaska in the early 1970s saw disastrous declines in Bristol Bay sockeye salmon stocks, but the stocks rebounded dramatically with the warming in the late 1970s and early 1980s. In contrast, off California the warming caused low productivity in the California Current, which was reflected in declines in catches and returns of coho salmon to hatcheries. The extreme conditions of the winter of 1982-83 were reflected by below normal catches of coho off California and Oregon and by smaller than normal fish. These opposite effects of warming in Alaskan and California waters may reflect the inverse correlation of zooplankton concentrations in the two areas noted by Frost (1983).

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Commentary: Short-Term Climatic Variability in the Northeast Pacific Ocean

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Abstract

There are three important issues to be dealt with in the search for physical causes of year-to-year variability of salmon catches in the Northeast Pacific Ocean: (1) identification of data sets available for statistical analysis, (2) determination of the nature of variability from these data sets, and (3) statistical analysis of the data sets to reveal plausible causal connections. This paper addresses each of these issues. An inventory of atmospheric and physical oceanographic data available in the Northeast Pacific Ocean is given along with sources from which the data may be obtained. Examination of two of these data sets reveals interesting interannual variability of physical oceanographic conditions in the Northeast Pacific Ocean over the past few decades. Some speculations are made about possible consequences of the observed physical variability on salmon stocks in the Northeast Pacific Ocean. A review of statistical analysis techniques underscores limitations in drawing firm conclusions about cause and effect relationships from inherently low-frequency time series such as salmon catches.

Introduction

Significant interannual variations in the salmon stocks in the Northeast Pacific Ocean have been documented by Fredin (1980) and Rogers (this workshop). These year-to-year fluctuations undoubtedly result from a complex combination of physical and biological interactions. Modelling these interactions (either mathematically or statistically) is an extremely difficult task. The difficulty is compounded by the fact that measurements of the physical and biological variables required to adequately test hypotheses are, for the most part, nonexistent. Nonetheless, because of the economic importance of the salmon fisheries in the Northeast Pacific Ocean, there is a pressing need to identify the dominant factors influencing the salmon populations. Development of a capability to forecast salmon abundance with some degree of reliability is very important for fisheries management decisions.

This paper addresses two problems in identifying causes of variability in salmon abundance. The first is the general statistical problem of identifying cause and effect relationships from limited sample data records. Some significant advances have been made in recent years to improve the classical approach to determining the significance level of sample correlations. The fundamental problem is that salmon catches exhibit very low-frequency (interannual) fluctuations so that annual average sample values are not all statistically independent. The method for estimating the "effective number of independent samples" in a time series is reviewed in the next section.

The second problem is identification of the data sets available for statistical analysis of the casues of the variability of salmon catches in the Northeast Pacific Ocean. This paper limits attention to atmospheric and physical oceanographic data sets. An inventory of long time series of atmospheric and physical oceanographic measurements is given in a later section together with sources from which the various data sets can be obtained. This list is not all-comprehensive, and in some cases the data descriptions may not include as much detail as individual investigators may desire. However, the information presented is hopefully useful as a first step in obtaining data necessary to search for physical causes of variability of salmon catches.

Following the discussion of problems in identifying causes of variability of salmon catches, physical oceanographic variability in the northeast Pacific over short-term climatic time scales of months to decades will be examined from two separate data sets. A discussion of long-term biological variability is beyond the scope of this paper (and may be addressable to only a very limited degree because of a lack of available data). The physical oceanography likely to be of greatest importance to salmon survival is the variability of ocean circulation in the nearshore and open ocean regions. Ideally, we would like long time series (20-30 years) of direct current measurements throughout the Northeast Pacific Ocean. Unfortunately, no such data records exist. We are therefore forced to infer the water motion from historical records of such variables as sea surface temperature and coastal sea level. The low-frequency variability of open ocean sea surface temperature and nearshore sea level in the Northeast Pacific Ocean are examined in a later section. The intent of this paper is not so much to identify the causes of these variations as to establish the nature of the variability and suggest some possible scenarios by which the physical variations could affect salmon populations.

Statistical Significance of Sample Correlations

Identifying causality from statistical models is one of the fundamental problems of time series analysis. Computation of the sample correlation is simple. In fact, it is too simple since more than one investigator has been guilty of attempting numerous correlations chosen more or less at random, eventually settling on one that gives a particularly high value. It must be kept in mind that the 95% significance level implies that one out of twenty randomly selected correlations will appear statistically significant by chance alone. It is therefore essential that the analyst limit analysis to only a small number of statistical models chosen by a priori considerations. This is where dynamical modelling plays a key role. The dynamical models suggest the forcing variables that should be used in the statistical models.

Another important limitation in statistical modelling is that a high sample correlation value does not necessarily imply causality, even if the model was chosen by a priori considerations. Consider a pair of time series x(t) and y(t), where the independent variable t represents time. A high correlation between x(t) and y(t) may indeed reflect a cause and effect relationship between the two variables. Alternatively, the two variables may not be at all related but are both forced by a third variable z(t). Then the apparent strong relation between x(t) and y(t) actually reflects their independent relations to z(t). This difficulty in identifying causality is an ever present problem in time series analysis. As a consequence, conclusions drawn from sample correlations must always be interpreted with some degree of caution.

A problem that is often ignored (or handled incorrectly) is determination of the statistical significance level of a sample correlation in an a priori chosen model. This is one of the major challenges of statistical inference. The key to success in statistics is repeated realizations of the processes of interest. From a single or small number of co-occurring observations of processes x(t) and y(t), it is not possible to conclude with any confidence that the two processes are related. As the number of co-occurring observations increases, the confidence that the two processes are related also increases. It is clear then that, as the lengths of time series x(t) and y(t) increase, the ability of correlation analysis to detect a relationship (or the lack of one) improves.

The usual method of determining the significance of a sample correlation between time series x(t) and y(t) is to look up the 90%, 95%, or 99% significance levels from standard published tables. These significance levels are listed according to the number of degrees of freedom N in the sample correlation estimate. In practice, N is usually taken to be the number of sample observations in both times series x(t) and y(t). This method of determining significance of sample correlations is inappropriate for nearly all geophysical and biological applications. The problem is that taking N to be the number of sample observations effectively assumes that all of the observations are statistically independent (i.e., neighboring sample observations are uncorrelated through the data records). For interannual variations, this is clearly not the case.

Fortunately, a relatively simple formalism exists for estimating the "effective number of degrees of freedom" in a sample correlation. This formalism can be traced back to Bartlett (1946). More recent discussions of the problem can be found in Davis (1976) and Chelton (1983). For a pair of time series x(t) and y(t), each consisting of N sample observations, the effective number of degrees of freedom is approximately

$$N^* = \frac{N}{\sum\limits_{\tau=-\infty}^{\infty} \rho_{xx}(\tau)\ \rho_{yy}(\tau)}, \tag{1}$$

where $\rho_{xx}(\tau)$ and $\rho_{yy}(\tau)$ are the autocorrelations of time series x(t) and y(t) at lag τ. Thus, the effective number of independent samples depends on the autocorrelation time scales of the two variables. When either x(t) or y(t) are serially uncorrelated (i.e., $\rho_{xx}(\tau)$ or $\rho_{yy}(\tau)$ are zero at nonzero lag τ), N* is equal to N, the number of sample observations. This corresponds to the case where the sample observations are all independent. However, for time series dominated by low-frequency variability, $\rho_{xx}(\tau)$ and $\rho_{yy}(\tau)$ can be large out to long lags τ, in which case N* can be considerably smaller than N. In effect, the low frequency signals are oversampled in the relatively short data records.

The 90%, 95%, or 99% significance levels of a sample correlation can be estimated from standard tables using N*, rather than N, for the number of degrees of freedom. Alternatively, a more exact method (Chelton 1983) can be used. The square of a sample correlation value is related to a chi-square variable with 1 degree of freedom. Specifically, if the square of the sample correlation between x(t) and y(t) is denoted by S_{xy}, the so-called (1-α) critical value for the squared sample correlation is given by

$$\hat{S}^{crit}_{xy}(\alpha) = \frac{\chi_1(\alpha)}{N^*}, \tag{2}$$

where $\chi_1(\alpha)$ is the tabulated 100α percentage point of a chi-square distribution with 1 degree of freedom, defined to be the value of the chi-square variable χ_1 that satisfies $\mathrm{Prob}[\chi_1 > \chi_1(\alpha)] = \alpha$. Tables of the chi-square distribution can be found, for example, in Abramowitz and Stegun (1972). Values of the sample squared correlation S_{xy} exceeding $\hat{S}^{crit}_{xy}(\alpha)$ are statistically significant with 100(1-α)% confidence. Thus, for example, the 95% significance level can be determined by setting α = 0.05 in (2).

Estimation of the significance level of a sample correlation thus requires an estimate of the effective number of independent samples N* in the data records. In practice, this can be estimated using (1). While this is not difficult in principle, it can be tedious since the summation in the denominator must be carried out to long lags. A much simpler method of approximating N* when the data records are much longer than the autocorrelation time scales is to compute an estimate of the expected value of the squared correlation between x(t) and y(t) at long lags. (If the data records are not longer than the autocorrelation time scales, the analyst should wait for longer records to accumulate.) This long-lag squared correlation estimate may be obtained, for example, by averaging the squared values of the sample correlation at lags ranging from, say, 30% to 40% of the total record length. If this average squared sample correlation is denoted by A, then the effective number of degrees of freedom is given by

$$N^* = \frac{1}{A} \qquad (3)$$

This value of N* can be used in (2) to find the significance level of a squared sample correlation which leads to

$$\hat{S}_{xy}^{crit}(\alpha) = A\chi_1(\alpha). \qquad (4)$$

A more detailed discussion of this approach can be found in Chelton (1983).

An example which illustrates the reduction in the number of independent realizations caused by low frequency variability is shown in Figure 1. It is clear from this figure that coastal sea level off southern California is strongly correlated with sea surface temperature variability in the eastern tropical Pacific (an index of El Nino). The correlation between these two time series is 0.74. If it is assumed that all 348 monthly observations in the 29-year time series are independent, the 95% significance level for the sample correlation is 0.1 (computed from [2] by setting N* equal to 348 and taking the square root of S_{xy}^{crit}[.05]). However, computation of the average long-lag squared correlation gives a value of A equal to 0.04. Then, from (3), the effective number of independent samples N* in the 29-year record is only 25, which is considerably less than the total 348 samples. The corresponding 95% significance level for the sample correlation is 0.4.

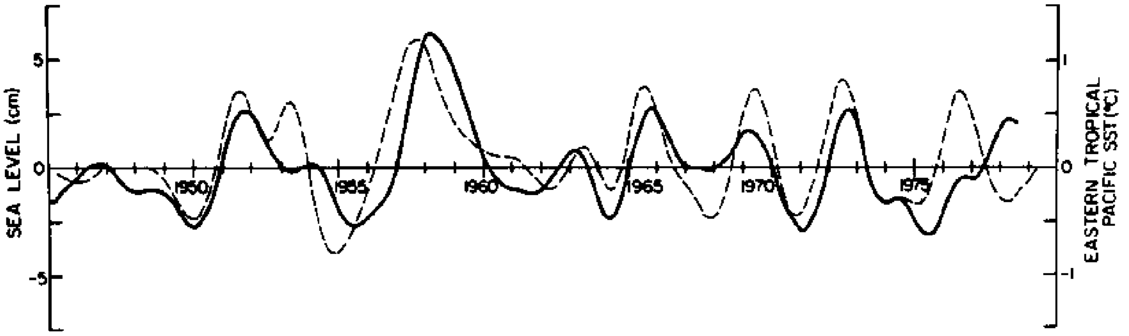

Figure 1. Low frequency (double 13-month running average) sea level off southern California (solid line) and sea surface temperature in the eastern tropical Pacific Ocean (dashed line). Sea level represents average value over San Francisco, Los Angeles, and San Diego. Sea surface temperature represents an average over the region from the equator to 10°S and from the coast of South America to 100°W.

Thus, inherent low frequency variability in sample time series significantly reduces the number of degrees of freedom in a sample correlation. The time scales of variability in Figure 1 are typical of those found in all physical oceanographic variables in the North Pacific Ocean. We can conclude that sample correlations must be very high to be statistically significant. Longer time series are often necessary to sufficiently increase the degrees of freedom in the sample correlations. This is not meant to sound overly pessimistic. Rather, it should be taken as indicative of the importance in continuing existing time series of biological and physical variability in the Northeast Pacific Ocean.

As a final caution, it should be noted that correlating a pair of time series assumes that the two time series are linearly related. The applicability of a simple linear relation is always questionable. This is particularly true for biological variables where the response is likely to be an extremely complex nonlinear function of the forcing variables.

Summary of Existing Physical Oceanographic Data in the Northeast Pacific Ocean

To help investigators identify and obtain atmospheric and physical oceanographic data relevant to salmon research, this section summarizes some of the data available in the North Pacific Ocean. The data sets can be categorized into four groups: (1) atmospheric data, (2) coastal ocean data, (3) open ocean surface data, and (4) nearshore and open ocean subsurface data. The available data sets are briefly described below and sources from which the data may be obtained are given. In many cases the data may be obtained from individual investigators who have used the data in their own research. However, in fairness to these investigators who are not generally funded to perform data copy services, the original sources of the data are given in the following list. The data sets are generally available from the indicated sources for a nominal fee which covers the cost of generating the printout or magnetic tape copy of the requested data.

This inventory includes only the data available in monthly average format (except for the hydrographic data in Category 4). This is probably the format most useful for studies of short-term climatic variability. More than one source is available for some of the variables of interest. The different sources generally use different analysis procedures so that the end products are never identical. Few attempts have been made to determine which products are the "best" in any sense. It is hoped that the different products differ only in detail, but even this has not been tested.

Atmospheric Data

a. "Namias" Pacific sea level atmospheric pressure. Monthly average sea level atmospheric pressure fields from 1947 through 1983 analyzed from ship observations by the Climate Research Group at Scripps Institution of Oceanography. Data are averaged into 5° squares between latitudes 20°N and 60°N and longitudes 130°E and 110°W. Source: Climate Research Group, Scripps Institution of Oceanography, La Jolla, California 92093, phone: (619)452-4555.

b. Fleet Numerical Oceanography Center (FNOC) atmospheric data. Monthly average fields of sea level atmospheric pressure, wind speed components, wind stress components and wind stress curl from 1946 to the present. The wind stress and wind stress curl fields were computed at 6-hour intervals from synoptic sea level atmospheric pressure fields and then averaged to form monthly mean values. These data were analyzed by FNOC from ship observations and model predictions on a 63-by-63 equally spaced grid overlaying a polar stereographic projection of the full Northern Hemisphere. The spatial resolution of the gridded data thus varies with latitude with a value of approximately 300 km at midlatitudes and 400 km at latitude 60°N. Source: Commander, Fleet Numerical Oceanography Center, Monterey, California 93940, phone: (408)646-2259.

c. National Meteorological Center (NMC) sea level atmospheric pressure. Monthly average sea level atmospheric pressure fields for the Northern Hemisphere from 1900 to the present on a 5° grid. Data earlier than 1946 were analyzed by NMC and post-1946 data were interpolated to the 5° grid from the FNOC 63-by-63 polar stereographic gridded sea level atmospheric pressure data described above. Source: Data Support Section, Scientific Computing Division, National Center for Atmospheric Research, P.O. Box 3000, Boulder, Colorado 80307, phone: (303)497-1215.

d. Upwelling Indices (also referred to as "Bakun" Upwelling Indices). Monthly average values of the offshore component of Ekman mass transport forced by the alongshore wind stress at the coast. Available from 1946 to the present at 15 selected grid locations along the west coast of North America between latitudes 20°N and 60°N. The wind stress used to determine the Ekman transport was computed at 6-hour intervals from synoptic sea level atmospheric pressure maps and then averaged to form monthly mean values. Source: Pacific Environmental Group, National Marine Fisheries Service, P.O. Box 831, Monterey, CA 93942, phone: (408)646-3311.

e. Coastal Station atmospheric data. An additional form of atmospheric data is the station measurements at specific locations along the west coast of North America. These data include sea level atmospheric pressure and wind vector components and are not generally used in research applications for three major reasons. First, they are not available from a single source or in a single format so that they are rather difficult and laborious to obtain and process. Second, the data records tend to be incomplete which makes analysis difficult. Third, the data are generally less reliable than gridded field data. This is particularly true of coastal wind data which are often dominated by local orographic effects and are therefore not representative of wind over the nearby ocean.

Coastal Ocean Data

a. Coastal tide gauge sea level. Monthly average sea level available for a large number of stations along the west coast of North America. The starting date differs for each time series, depending on when the tide gauge station was installed. Some records along the west coast of North America date back to the late 1800s. An attempt is made to update the data records each year. Source: Klaus Wyrtki, Department of Oceanography, University of Hawaii, 2525 Correa Road, Honolulu, Hawaii 96822, phone: (808)948-7037. Also available from Tides and Water Levels Division, National Ocean Service, Rockville, Maryland 20852, phone: (303) 443-8467.

b. Coastal sea surface temperature and salinity. Monthly average sea surface temperatures and salinities are available at several stations along the west coast of the continental United States and Alaska. Starting dates vary, with some records along the west coast of North America dating back to the early 1900s. Source: National Ocean Service, Rockville, Maryland, phone: (301)4438467.

Open Ocean Surface Data

a. "Namias" Pacific sea surface temperature. Monthly average sea surface temperature fields from 1947 through 1983 analyzed from ship observations by the Climate Research Group at Scripps Institution of Oceanography. Data are averaged into 5° squares between latitudes 20°N and 60°N and longitudes 130°E and 110°W. Source: same as "Namias" Pacific sea level atmospheric pressure described above.

b. Fleet Numerical Oceanography Center (FNOC) sea surface temperature. Monthly averages of sea surface temperature from 1962 to the present. These data were analyzed from ship observations by FNOC on a 63-by-63 equally spaced grid overlaying a polar stereographic projection of the full Northern Hemisphere. The spatial resolution of the gridded data thus varies from a value of approximately 300 km at midlatitudes to 400 km at latitude 60°N. Source: same as FNOC atmospheric data described above.

Nearshore and Open Ocean Subsurface Data

a. Master Oceanographic Observations Data Set (MOODS), Fleet Numerical Oceanography Center (FNOC). This data set contains individual subsurface profiles of temperature and (where available) salinity from Nansen bottle casts, mechanical bathythermographs, expendable bathythermographs, STD and CTD profilers from 1920 through 1980. Data were obtained by FNOC from the National Oceanographic Data Center (NODC) and other sources. The data are stored in a compact packed binary format and FNOC can supply a portable subroutine for reading the data. The MOODS file is presently being updated to include additional pre-1980 profile data and more recent observations through 1983. The spatial and temporal distribution of the subsurface data tends to be sparse over much of the ocean. Data density is greatest in the nearshore regions (within about 500 km of the coast). Source: same as FNOC atmospheric data described above.

Climatic Variability in the Northeast Pacific, 1945-1983

Open Ocean Variability

McLain (this workshop) has analyzed coastal sea surface temperature (SST) and sea level height (SLH) from 1941 through 1983 and suggested that there has been a large-scale warming in the Northeast Pacific Ocean since 1976. Coastal measurements are somewhat less than ideal in this respect since there are a large number of physical processes occurring over relatively short time scales that can influence nearshore SST. Examples include local wind-driven coastal upwelling, poleward-propagating coastally trapped waves, impingement of eddies onto the coast, and local heating and cooling from variations in solar insolation caused by coastal fog and stratus clouds. Because of all of these processes, nearshore SST is generally "noisier" than SST in regions farther offshore. In this section, the SST in the open ocean will be examined to eliminate the "noisiness" of nearshore SST.

The data set chosen for analysis here is the monthly average "Namias" North Pacific SST data. The grid pattern for this data set is shown in Figure 2. Prior to analysis, the long-term average was computed separately for each grid point for each calendar month. The resulting long-term average seasonal cycles were removed from the raw time series to produce time series of "anomalous" SST at each grid point. This procedure is customary in analysis of long time series and is an essential first step to statistical analysis of the time series. The reason this step is so important is that the presence of any strong, narrow frequency band signal, such as the seasonal cycle, reduces the effective number of independent samples in a time series. In the extreme case, a pure-tone sinusoid with annual period contains only 2 degrees of freedom, regardless of the record length. This problem is explained in greater detail and with examples in Chelton (1982).

For analysis here, the North Pacific Ocean was broken up into four quadrants, as shown in Figure 2. Within each quadrant, the anomaly time series at all grid points were averaged for each month. Because of occasional missing data values at some of the grid points, the spatial averages for each month were computed using the objective analysis method described in Chelton et al. (1982). The resulting average time series for each of the four quadrants were then smoothed with a 3-month running average to remove some of the high-frequency month-to-month noise. To isolate the

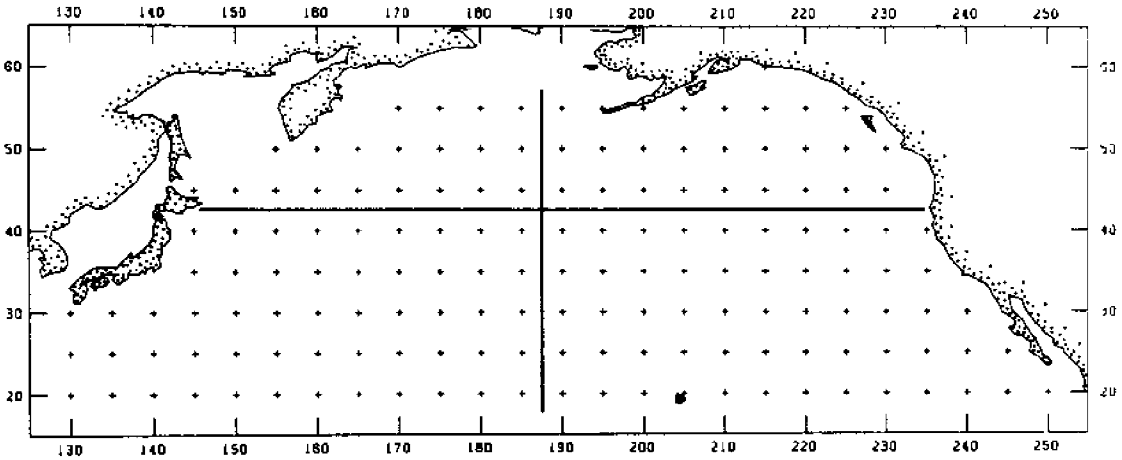

Figure 2. Grid pattern for the "Namias" monthly average sea surface temperature data set. The four quadrants of the North Pacific Ocean analyzed in this paper are defined by the solid lines.

longer term variability, the average time series were also smoothed with a 25-month running average. The resulting 3-month and 25-month running average time series are shown in Figure 3 for each of the four quadrants.

The post-1976 warming in the Northeast Pacific Ocean noted by McLain (this workshop) is very clearly evident in Figure 3. SST averaged over the Northeast Pacific steadily decreased by about 1.5°C from 1957 to 1976. Then, in late 1976, SST began to rise rather abruptly, ending the long-term cooling trend in the Northeast Pacific Ocean. Since 1980, SST in this region has remained relatively constant. It is interesting to note from Figure 3 that the post-1976 warming is not at all evident in the northwest and southwest quadrants of the North Pacific and is only slightly evident in the southeast quadrant.

Rogers (this workshop) noted similar variations in temperature in the Northeast Pacific Ocean from air and sea surface temperature station data at Kodiak and Bristol Bay, Alaska. He also pointed out that the catches of many stocks of salmon steadily declined from the 1950s until the mid to late 1970s when they began to increase. Adult salmon spend much of their life cycle in the open ocean. Rogers speculates that cool waters drive the salmon stocks farther south where they become concentrated and more vulnerable to predators. This explanation seems plausible and it is tempting to conclude that warm water may be beneficial to survival of some stocks of salmon. However, it is important to emphasize that this apparent statistical relation is based on a very small number of degrees of freedom (effectively only one realization) and therefore should be interpreted with a great deal of caution. Much longer records will be necessary to confirm (or deny) the hypothesized relation between water temperature and salmon survival.

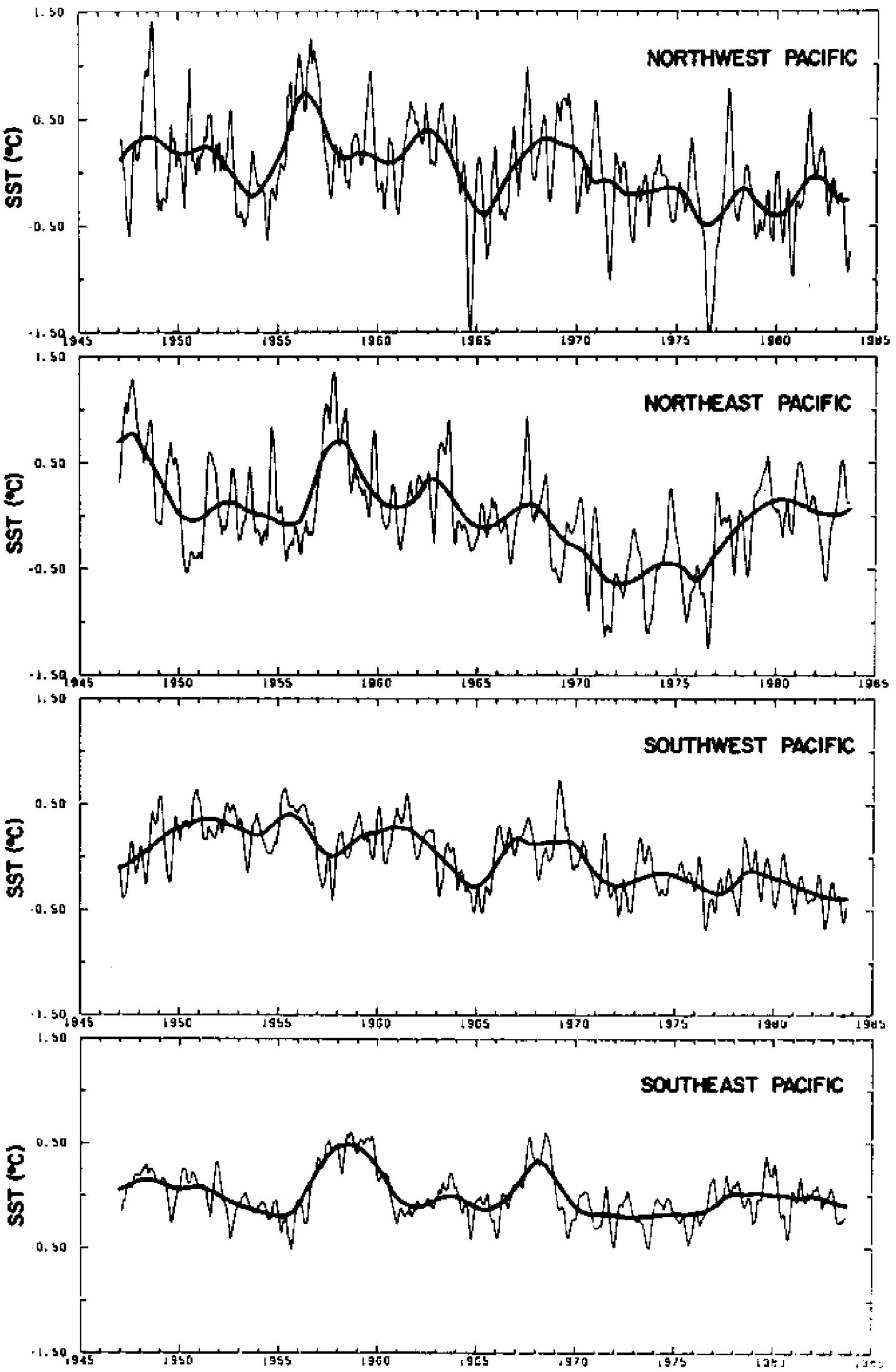

Figure 3. Time series of sea surface temperature averaged over the four quadrants of the North Pacific Ocean shown in Figure 2. Thin lines and heavy lines correspond, respectively, to 3-month and 25-month running averages. The running average values near the end points of the time series were computed using the objective analysis method described by Chelton and Davis (1982).

Coastal Ocean Variability

As noted previously, the post-1976 warming in the Northeast Pacific Ocean is also detectable in the coastal SST and SLH time series at the west coast stations discussed by McLain (this workshop). It is clear from McLain's figures that additional processes besides the open ocean pre-1976 cooling and post-1976 warming are influencing the coastal ocean variability. In particular, the extreme SLH anomaly in 1983 was the largest on record. While SST in the open ocean Northeast Pacific was high in 1983 (see Figure 3), the anomaly was not particularly unusual in the 32-year record. Large-scale, coherent, nearshore variability is discussed in this section because it suggests a physical process which may be important to salmon populations.

The SST and SLH time series in McLain (this workshop) show that the low-frequency (interannual) variations are very highly correlated at all stations examined. SLH is preferable to SST for examination of nearshore variability since it is more representative of dynamical processes in the nearshore environment. It also reflects the vertically integrated upper ocean heat content and is therefore less "noisy" than SST.

The spatial coherence of SLH has been discussed previously by Enfield and Allen (1980) and Chelton and Davis (1982). The dominant large-scale patterns of SLH variability can be extracted by empirical orthogonal function (EOF) analysis (equivalent to principal component analysis, see Davis 1976). The SLH variability along the west coast of North and Central America is examined here by computing the EOFs over the 20 stations shown in Figure 4. As before, the seasonal cycle of SLH was first computed and removed at each station to produce time series of anomalous SLH.

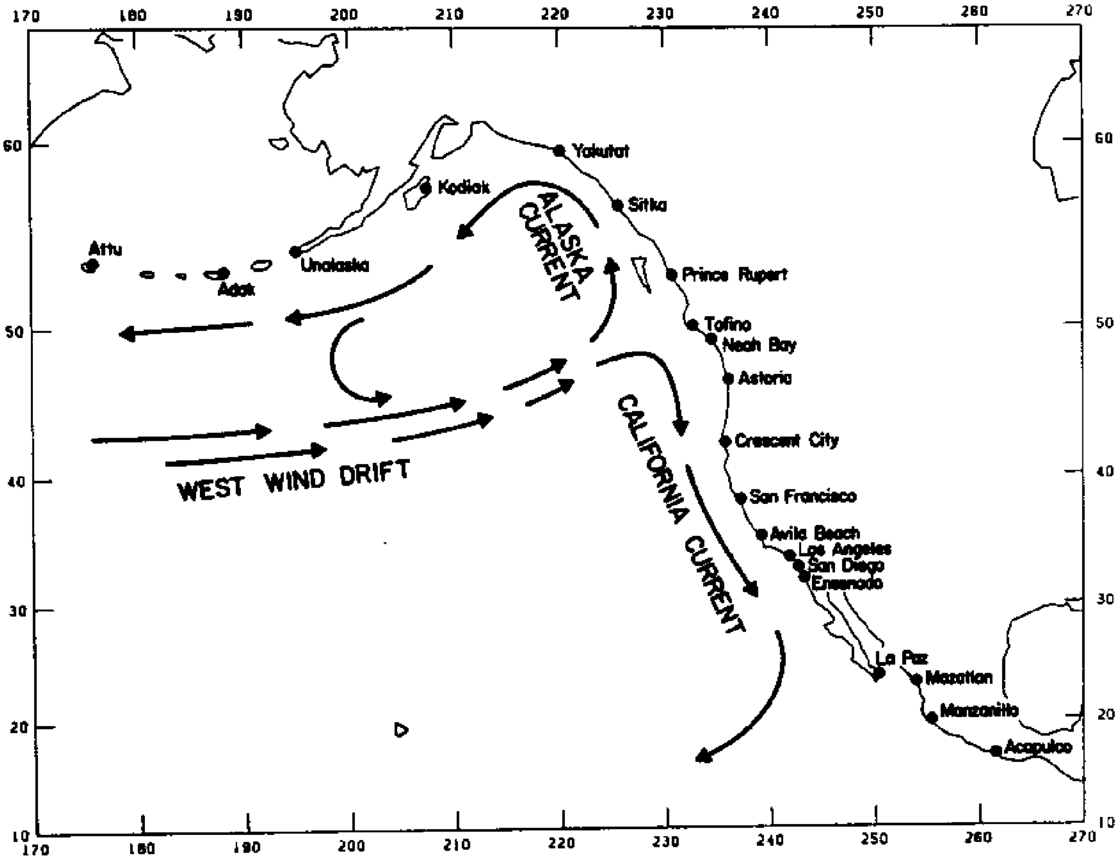

Figure 4. Locations of the 20 sea level stations analyzed in this paper. Also shown are the average current systems in the eastern North Pacific Ocean.

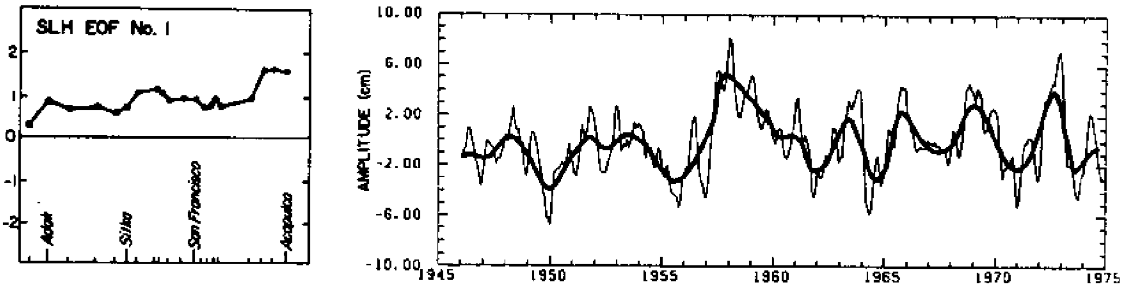

Figure 5. The most energetic spatial empirical orthogonal function of sea level (left panel) over the 20 stations shown in Figure 4 and the corresponding amplitude time series (right panel). Thin and heavy lines in the right panel correspond, respectively, to 3-month and 13-month running average amplitude time series.

The dominant spatial EOF (left panel) accounting for 40% of the anomaly variance summed over the 20 SLH stations is shown in Figure 5 together with the corresponding amplitude time series filtered with 3-month and 13-month running averages (right panel). The spatial pattern indicates that the dominant mode of variability consists of a general rise or fall in SLH over all 20 stations from Mexico to Alaska. When the amplitude time series was positive (as in 1958-59), SLH was generally high along the entire west coast of North and Central America. Correspondingly, when the amplitude time series was negative (as in 1955-56), SLH was generally low along the eastern boundary of the Pacific Ocean. Enfield and Allen (1980) and Chelton and Davis (1982) have shown that the low frequency aspects of this large scale variability are strongly related to El Niño occurrences in the eastern tropical Pacific Ocean (see also Figure 1 of this paper).

Coastal SLH is known to be a good indicator of nearshore geostrophic currents (see, for examples, Chelton et al. 1982; Huyer 1983). In the Northern Hemisphere, positive coastal SLH anomalies are indicative of anomalous poleward flow. For stations north of about 50°N (see Figure 4), high SLH means stronger than normal poleward flow of the Alaska Current. For the southern stations, high SLH means weaker than normal equatorward flow of the California Current (with the possibility of a reversal if the anomaly is strong enough). Correspondingly, negative SLH anomalies are indicative of weaker than normal poleward flow of the Alaska Current and stronger than normal equatorward flow of the California Current.

The universal rise or fall of SLH reflected in the dominant EOF has some interesting implications about the structure of eastern boundary current systems in the North Pacific Ocean. The Alaska and California Currents apparently fluctuate out of phase. That is, when one of the currents is stronger than normal the other is weaker than normal. One way this type of response could occur is shown schematically in Figure 6. We could imagine a quasi-permanent eastward transport of the West Wind Drift in the central North Pacific Ocean. This eastward transport bifurcates near the eastern boundary somewhere around 50°N to form the Alaska and California Currents (see Figure 4). If most of the eastward-flowing water in the West Wind Drift turns northward, the transport of the Alaska Current would increase while that of the California Current would decrease. On the other hand, if most of the transport turned southward, the flow of the Alaska Current would decrease and the flow of the California Current would increase. This type of behavior would produce the observed SLH response (other mechanisms could also produce the same response). These north-south shifts in the split of the West Wind Drift could be forced by wind stress curl over the interior Pacific Ocean or by instabilities in the eastern extension of the midlatitude jet in the North Pacific Ocean (the Kuroshio Current).

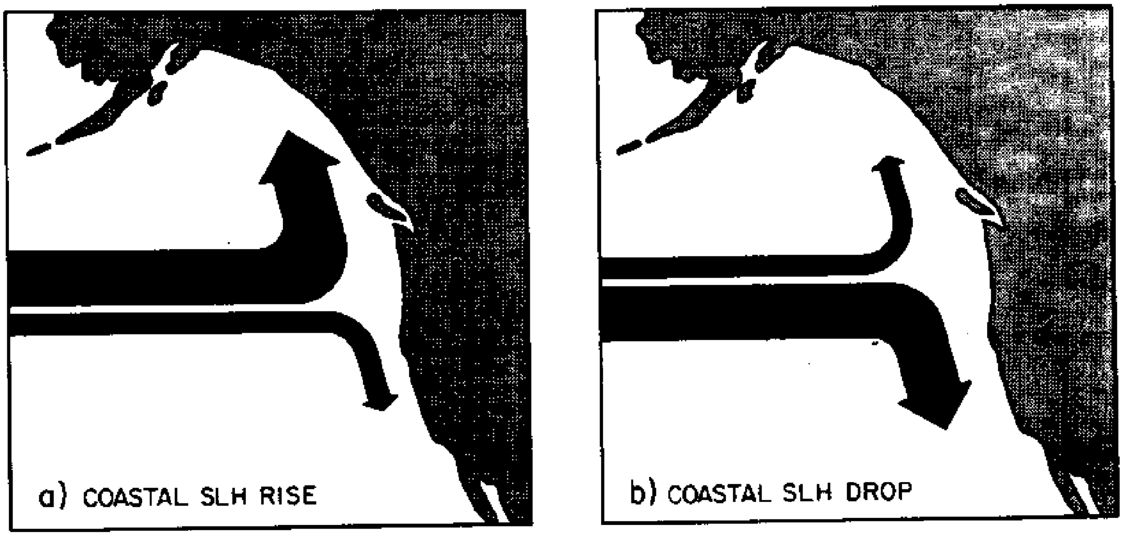

Figure 6. Schematic diagram of the hypothesized physical process which could account for the dominant behavior of sea level along the eastern boundary of the North Pacific Ocean. North-south shifts in the bifurcation of the West Wind Drift would lead to coherent changes in sea level along the entire west coast of North and Central America.

Unfortunately, there are not sufficient open ocean hydrographic data to determine whether this hypothesized physical process is indeed responsible for the observed coastal SLH variability. Dodimead and Hollister (1958) show large differences in the latitude of the bifurcation between the summers of 1956 and 1957, suggesting that interannual variations may be common. It is interesting to speculate how this type of process would influence salmon populations. Shifts in the bifurcation of the West Wind Drift could have a significant effect on the productivity and prey composition of waters inhabited by salmon, as well as on the distribution and migrations of salmon stocks at sea. The inverse relationship found between runs of sockeye salmon from Bristol Bay and the Fraser River in southern British Columbia (Peterman, this workshop) may be related to such interannual variations in major features of the circulation in the Northeast Pacific Ocean.

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Trends in Abundance of Northeastern Pacific Stocks of Salmon

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Abstract

Most of the large stocks of Pacific salmon had well-developed fisheries by the early 1900s. Catches increased to a peak in the late 1930s. Then there was a general decline in catches and probably abundances during the 1940s to early 1950s, and a low point was reached in the early 1970s. Since 1978 there have been historical record catches and abundances for most stocks in western and central Alaska and modest increases in southeastern Alaska. The main changes in salmon abundance were associated with major changes in temperatures, particularly during the winter months. The low point in the relative production of Bristol Bay sockeye salmon coincided with cold temperatures while the fish were at sea and the recent increase with warm temperatures while the fish were at sea. It is suggested that marine survival, especially during the final winter at sea, was affected by the large changes in temperature that altered the distribution of salmon and thus their vulnerability to predators.

Introduction

Most of the major stocks of Pacific salmon (*Oncorhynchus* sp.) were under extensive exploitation by commercial fisheries in the early 1900s. The annual harvests of salmon reached a peak in the 1930s and then a low point in the 1970s. Fredin (1980) reviewed trends in the catches of salmon from 1920 through 1977. Since then there have been some dramatic increases in the catches and abundances or runs (catch plus escapement) of all species in most of the fisheries in western and central Alaska.

This report describes the historical trends of Asian and Alaskan salmon stocks with emphasis on some Bristol Bay (western Alaska) stocks where annual abundances and some additional biological data are available. The main changes in abundance, particularly the recent increase, are then examined in relation to spawner abundances, growth, temperatures and high seas fishing. Finally, probable causes of the recent increase in salmon abundance are postulated.

Data Sources

Catch statistics through 1977 were obtained from Fredin (1980), and INPFC (1979), whereas those for recent years were from INPFC Documents and the Alaskan Department of Fish and Game (ADF&G) and are preliminary. Adult run and smolt statistics for Bristol Bay were obtained from informational leaflets and technical data reports by ADF&G. Mean lengths of Bristol Bay sockeye were calculated from raw data and summaries provided by ADF&G personnel.

The annual relative abundances of immature Bristol Bay sockeye salmon at sea were estimated from purse seine sampling south of Adak Island. The sampling was conducted by the Fisheries Research Institute, and the data are presented in Harris and Rogers (1979).

Air temperatures for Bristol Bay were calculated from monthly means for the Dillingham and King Salmon weather stations.[1] Sea surface temperatures by Marsden square were provided by Dr. D. R. McLain, and Kodiak Bay surface temperatures were recorded almost daily at Women's Bay and were available from U.S. Dept. Commerce, NOAA, National Ocean Survey.

Catch Trends

Annual salmon catches were examined for southeastern Alaska, central Alaska (northwestern coast of the Gulf of Alaska), western Alaska (Bering Sea coast), Japanese high seas fisheries (Figure 1), and Asia (Japan and U.S.S.R. coasts). The commercial catches of salmon probably reflect the major fluctuations in the abundance (run) of the major stocks within each region or district, e.g., the Bristol Bay sockeye salmon in western Alaska and the Kvichak stock in Bristol Bay. Annual fluctuations in the abundance of small stocks within a region or district would not be evident from catches, and catches of less abundant species within a region are usually not indicative of their fluctuations in abundance, e.g., coho salmon in western Alaska. In addition catches of chinook salmon in central Alaska (Cook Inlet) and southeastern Alaska have been kept low through management regulations in recent years, whereas catches of chinook salmon in western Alaska have increased since the 1950s because large fisheries were established on largely unexploited stocks (Yukon and Kuskokwim).

Catches of salmon in southeastern Alaska reached a peak in the 1930s and then declined in the 1940s (sockeye) and 1950s (Figure 2). Catches of the abundant pink salmon stocks increased somewhat in the 1960s, but then dropped to a historical low in the mid-1970s. The catches increased in 1978 and the catch in 1983 was comparable to the average annual catch during the 1930s. However, catches of the other species have remained relativley low in recent years.

Salmon catches in central Alaska reached a peak in the late 1930s to early 1940s and then declined in the early 1950s, except for chum catches (Figure 3). A low point was reached in the early 1970s, and then the catches increased to historical highs by the early 1980s. The catches of most species in most districts througout central Alaska have been high in the recent years. A major exception is the recent catches from the Karluk sockeye stock which in earlier years produced the bulk of the sockeye catch in the region. The Karluk stock continued at a low level of abundance through 1983. So the recent large catches of sockeye in the region came mostly from historically lesser abundant stocks (e.g., Chignik and Cook Inlet).

The catches of all species of salmon in western Alaska reached historical highs during the most recent six years (1978-83); however, only the sockeye stocks have been consistently exploited over the past 80 years (Figure 4). Fluctuations in the Bristol Bay stocks in western Alaska will be examined in more detail after the trends in Asian coastal and high seas catches are first examined.

Most of the Asian coastal catches were produced from stocks in the U.S.S.R. until the recent success of the Japanese chum salmon hatchery program. The Asian

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[1] Climatological Data, Alaska available from NOAA, EDS, National Climate Center.

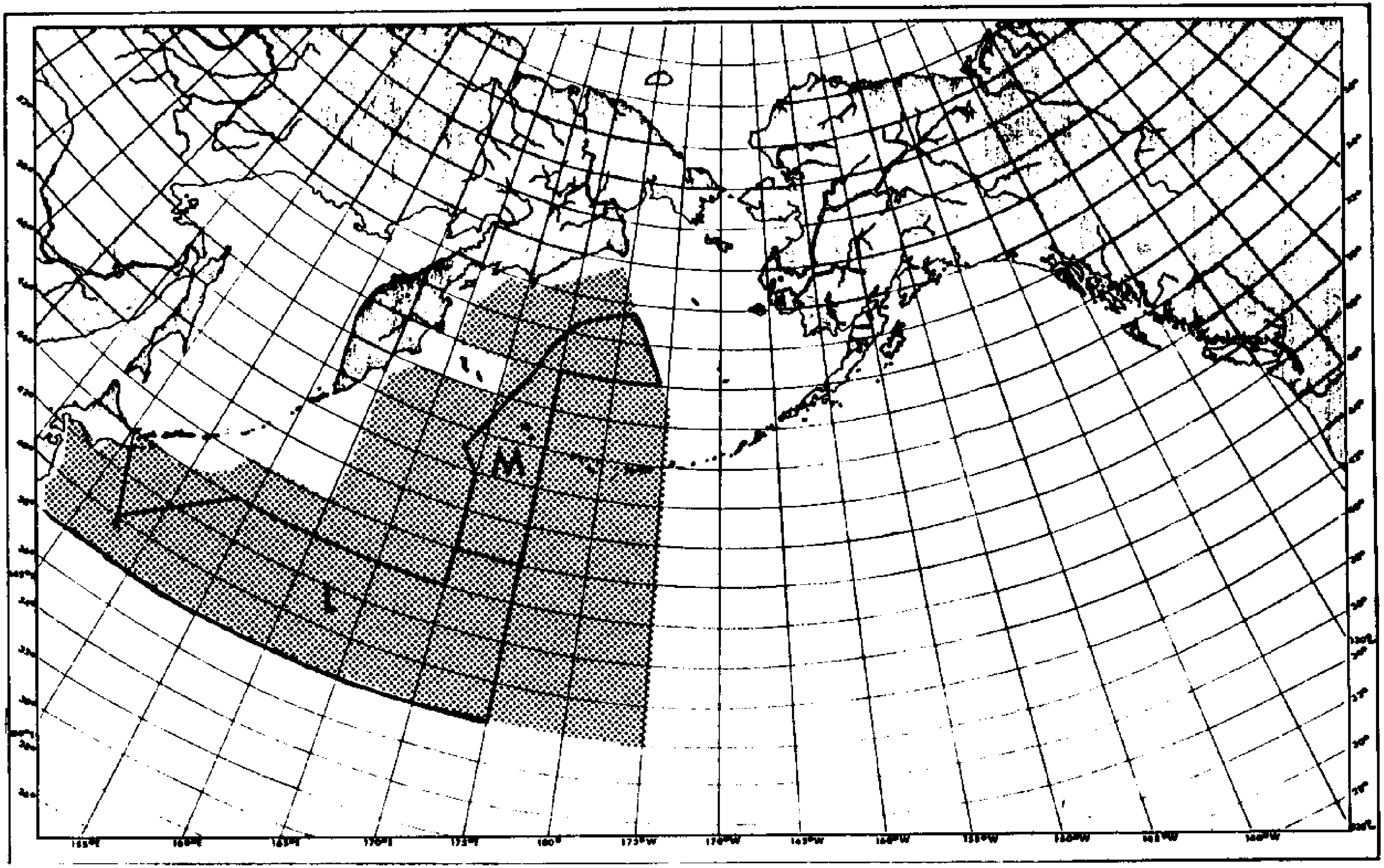

Figure 1. Fishing area for the Japanese mothership (M) and landbased (L) fleets since 1978 and the area fished in earlier years.

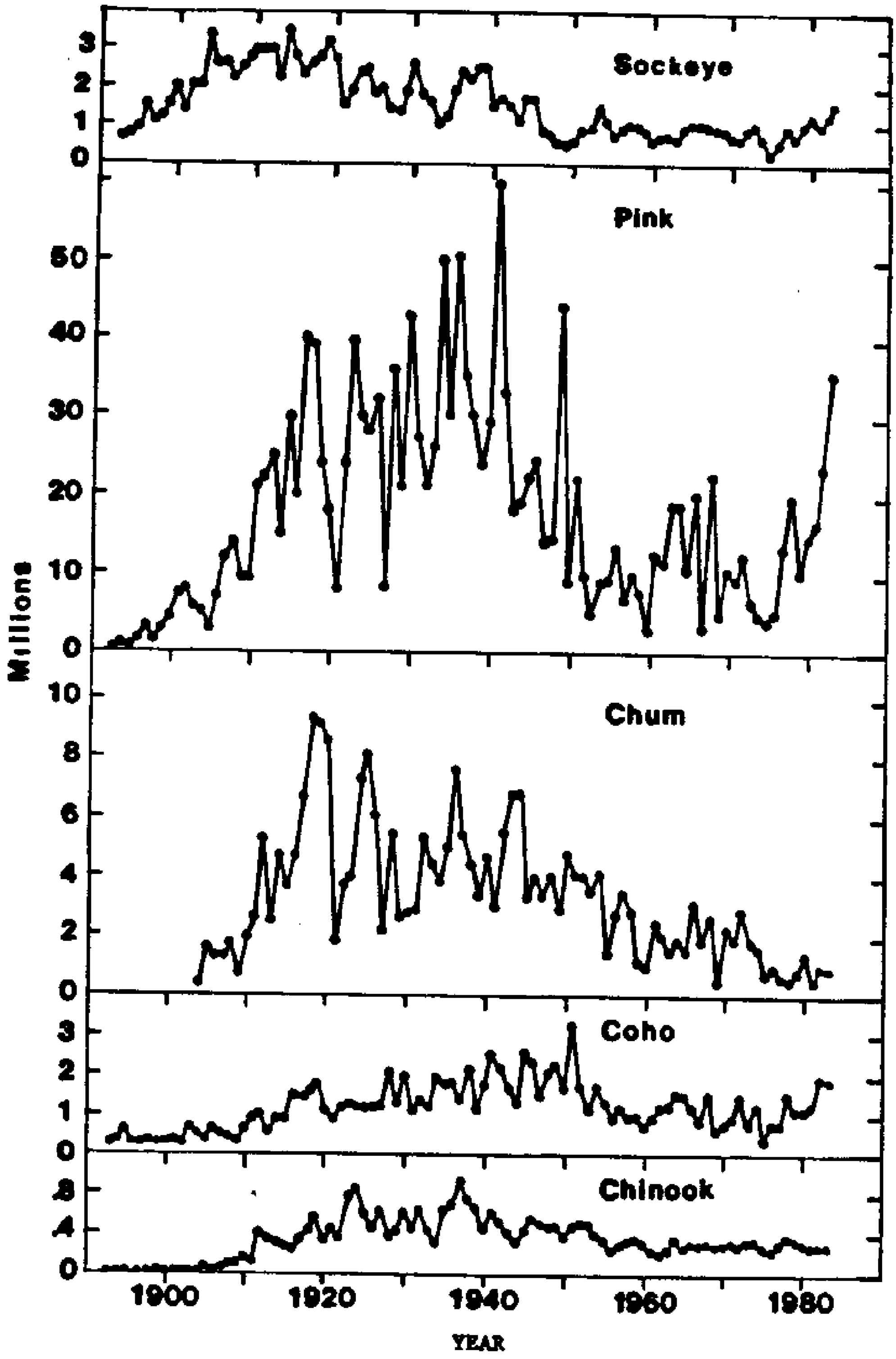

Figure 2. Annual commercial catches (numbers) of salmon in southeastern Alaska, 1893-1983.

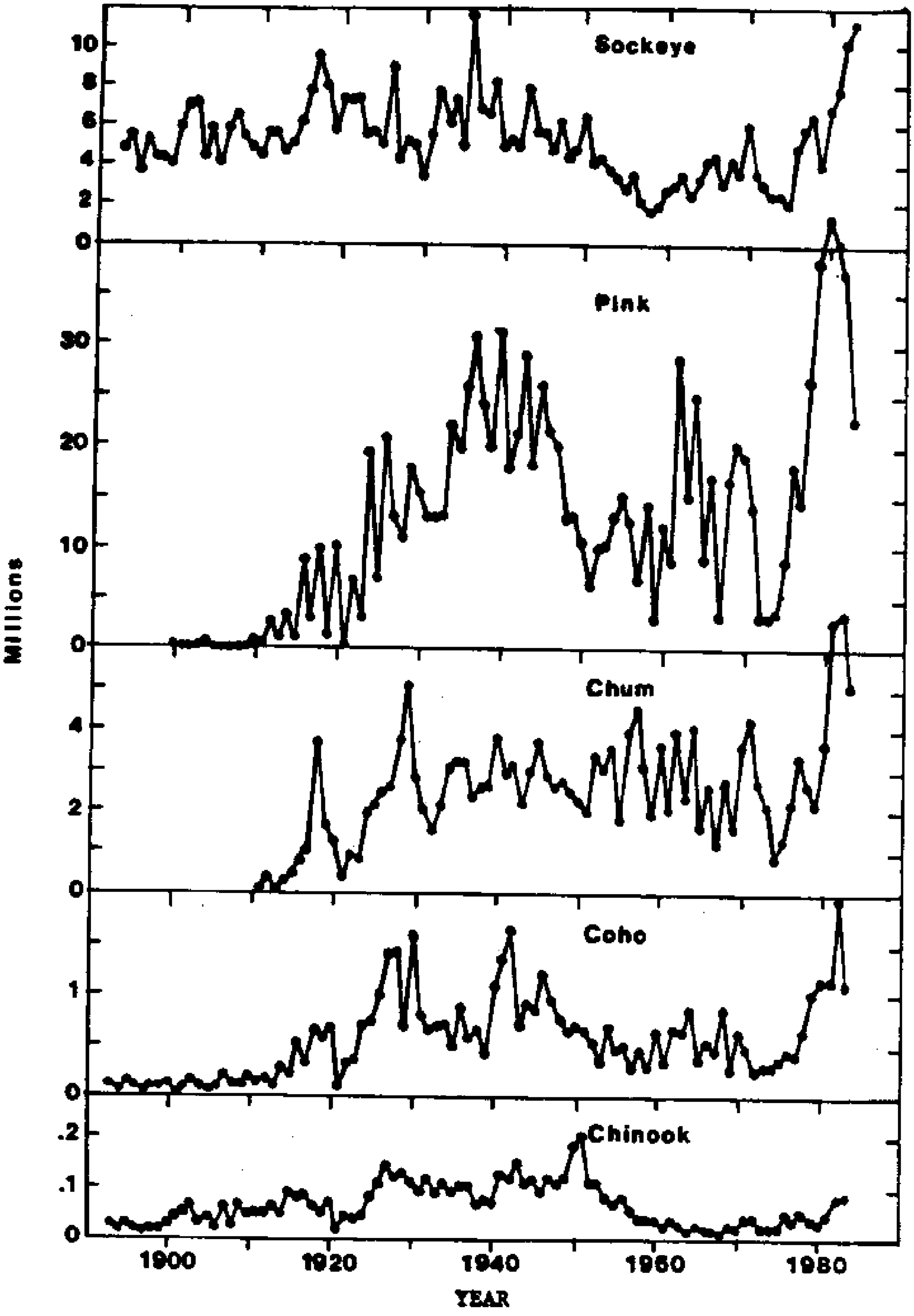

Figure 3. Annual commercial catches (numbers) of salmon in central Alaska, 1893-1983.

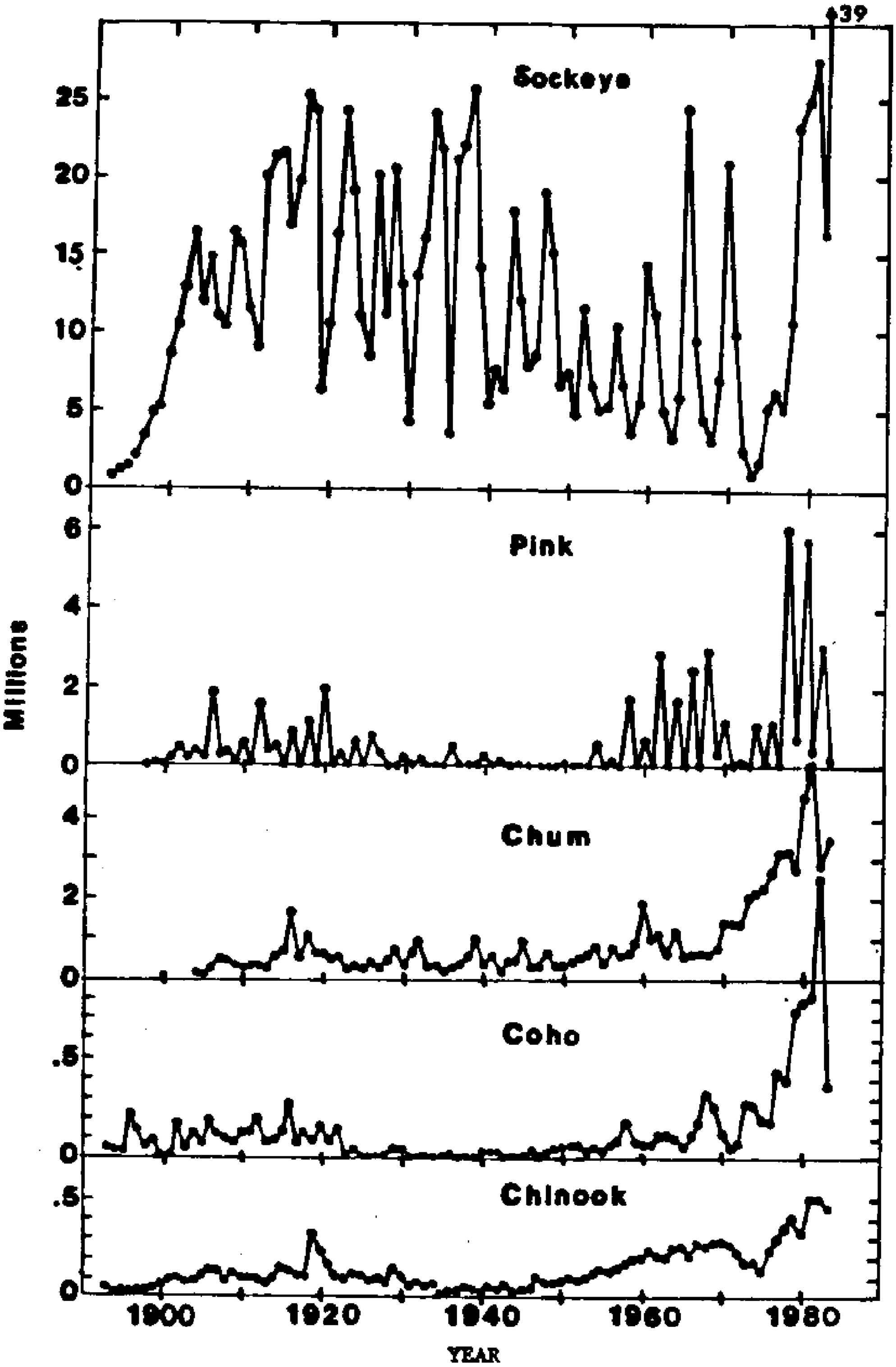

Figure 4. Annual commercial catches (numbers) of salmon in western Alaska, 1893-1983.

catches of salmon reached a peak in the 1930s, declined during the 1940s, and then increased in the 1950s from the catches of Asian and Alaskan salmon made by the Japanese high seas fleets (Figure 5). When the high seas fishing areas were reduced in 1978 there were only modest increases in the coastal catches in Asia except for chum salmon. The Japanese hatcheries produced about 60% of the total world catch of chums in 1981 and 1982 with catches of over 30 million in each year. Even with the large Alaskan catches in recent years, the total catches from central Alaska to Asia during the recent four to five years have not reached the level attained in the late 1930s and early 1940s (Figure 6).

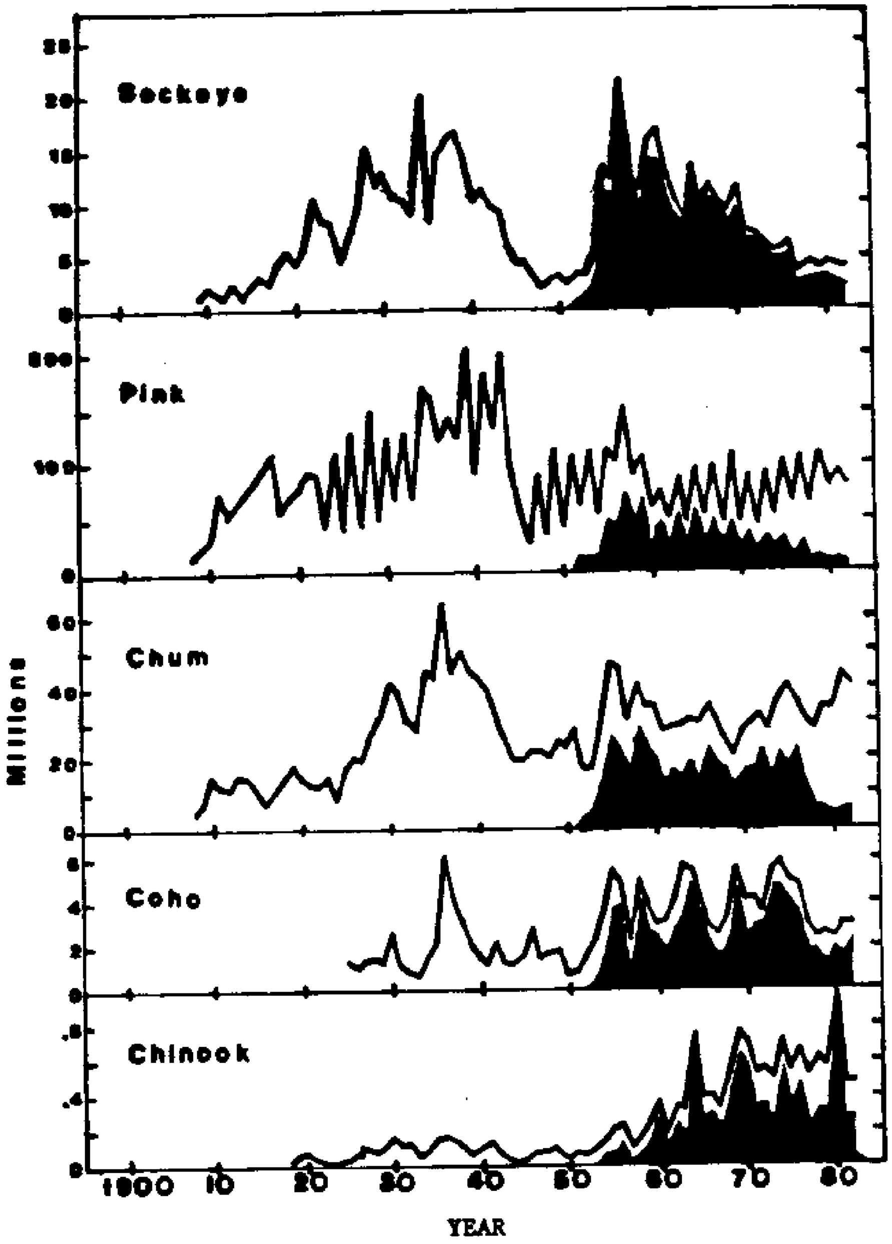

Figure 5. Annual commercial catches (numbers) of salmon by Japan and the U.S.S.R. High seas catches by Japanese mothership and landbased fleets are shaded.

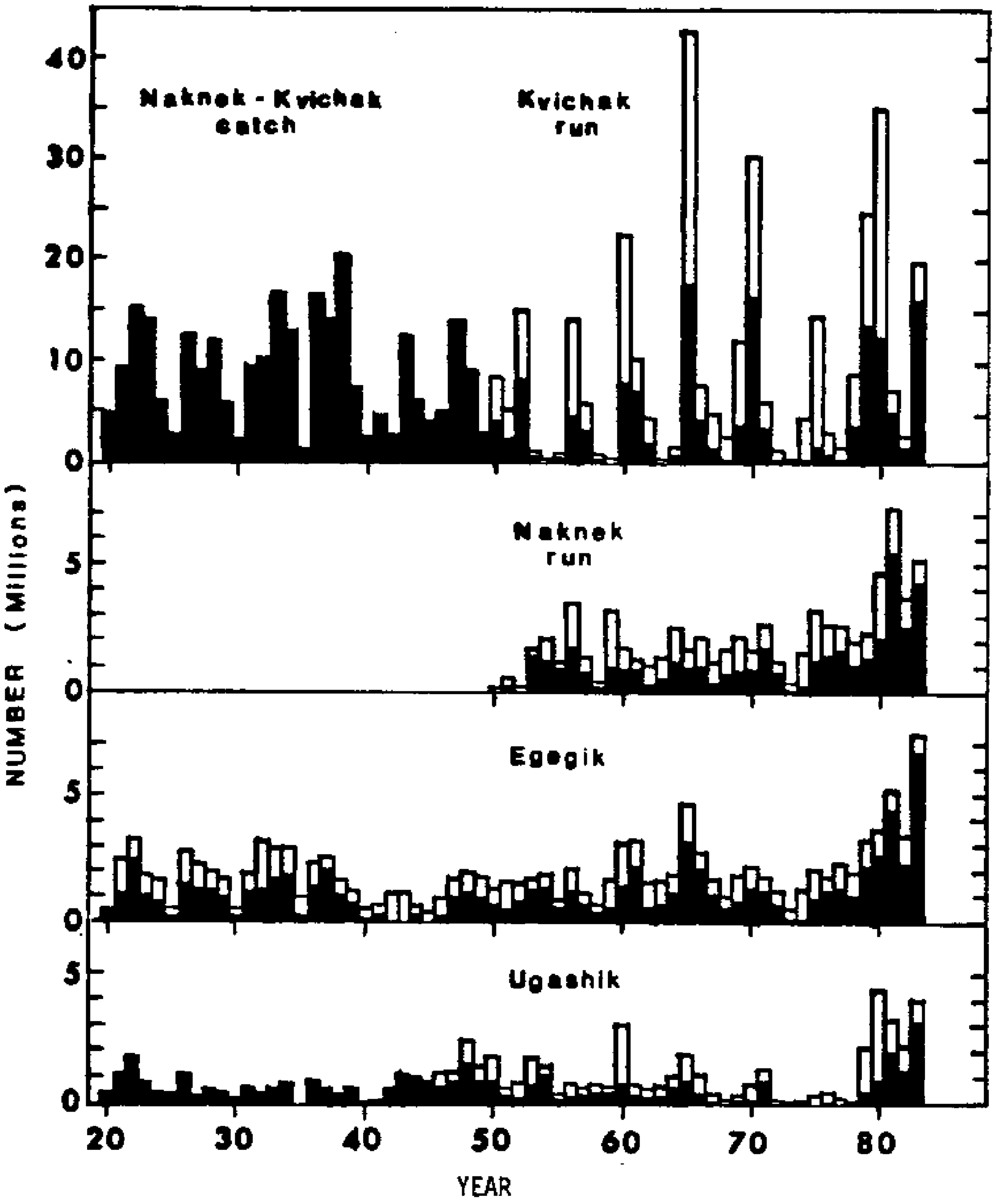

Figure 7. Annual catches (numbers) of sockeye salmon in the Naknek-Kvichak District (1920-1949), annual runs (catch + escapement) for the Kvichak and Naknek lake systems (1950-1983), and catches and runs for the Egegik and Ugashik lake systems since 1920.

Figure 14 shows the trend in relative production (return per spawner) for the 1952 to 1978 brood years of Bristol Bay sockeye salmon. The very poor runs in 1972 and 1973 were caused by failures of the 1967 and 1968 brood years. Temperatures became very cold while these fish were at sea, rather than when they were in fresh water. The 1973 and 1974 brood years were the first to exhibit exceptional production, and temperatures did not become exceptionally warm until after the fish had gone to sea.

Bristol Bay smolt migrations have been sampled since the 1950s. Unfortunately, since the methods of estimating abundance changed in the 1970s, it was not possible

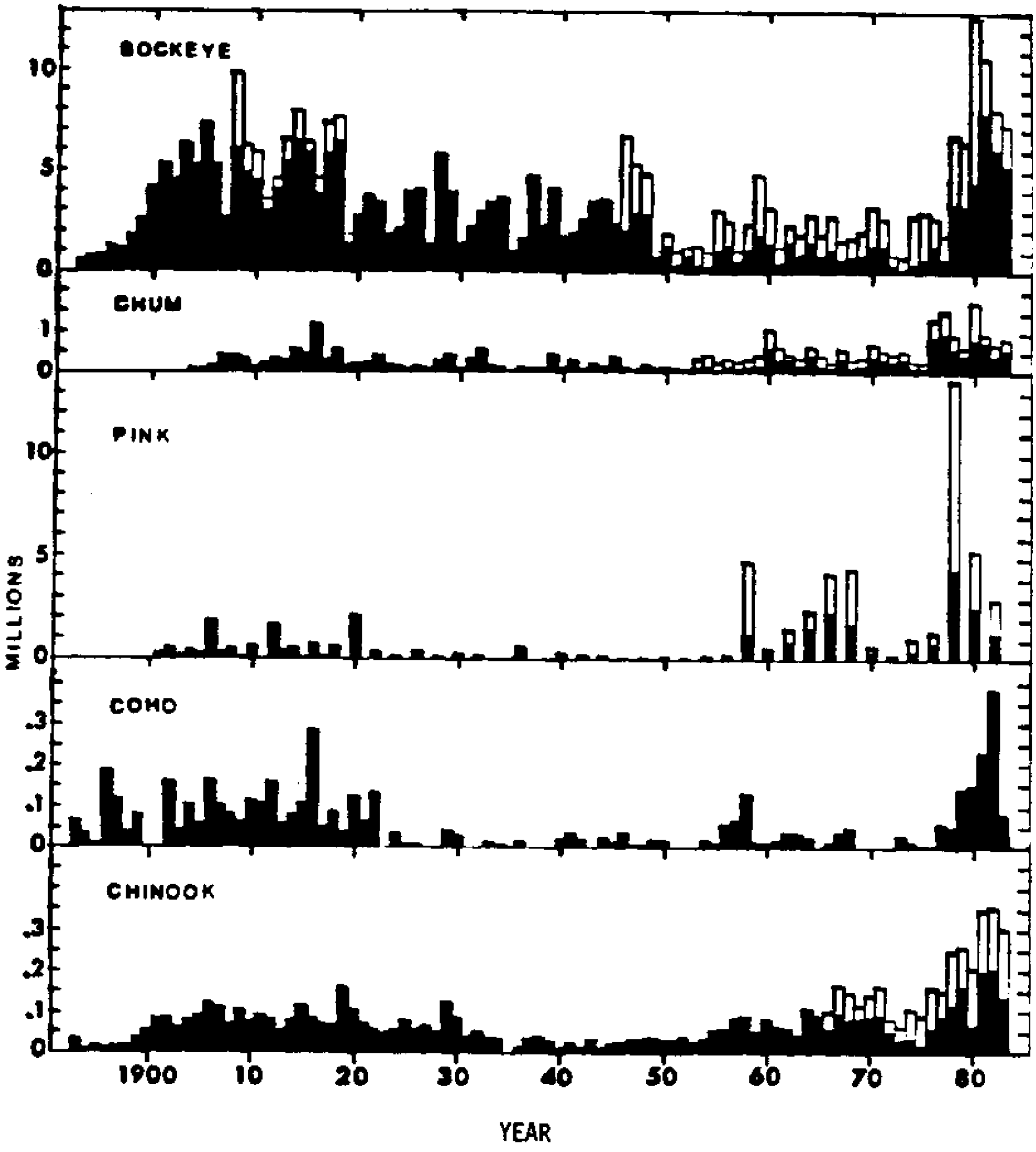

Figure 8. Annual salmon catches (solid) and escapements (open) of salmon in the Nushagak District of Bristol Bay, 1893-1983.

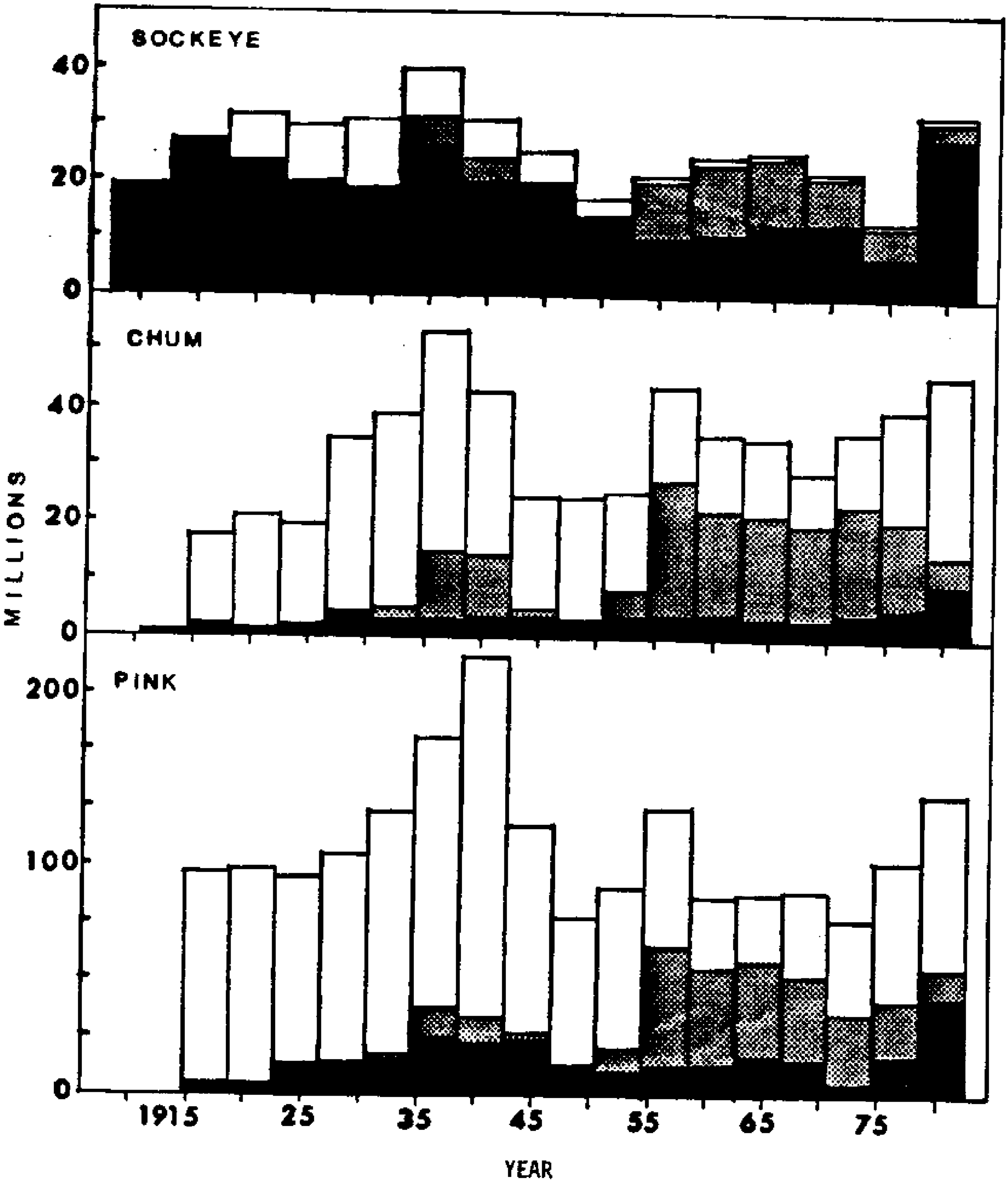

Figure 6. Five-year averages of sockeye salmon catches and four-year averages of chum and pink salmon catches from the North Pacific. Western and Central Alaska (black), high-seas (stippled) and Asian coastal (open).

Abundance Trends

The annual escapements of Bristol Bay sockeye and pink salmon have been estimated by tower enumeration for nearly all stocks since the 1950s, and aerial survey estimates were made for some earlier years in some districts. Aerial survey estimates were also made to estimate escapements of chum and chinook salmon in the Nushagak District.[2] The annual fluctuations in the runs and the historical trends differ among the Bristol Bay sockeye salmon stocks; however, all stocks had very low runs in 1972 and 1973. The fisheries were greatly restricted in 1974 and 1975 to build up the spawning stocks, and then there were some exceptionally large runs after 1977 (Figures 7 and 8). The even-year pink salmon run was unusually large in 1978, and the chinook salmon runs were consistently large from 1978 through 1983.

The large runs since 1978 may be attributed to good management (i.e., near-optimum escapements) and the reduction in high-seas fishing. However, the escapements that produced the recent large runs were not much different than escapements in earlier years, and the high seas mothership fishery that intercepted significant numbers of Bristol Bay sockeye salmon was restricted from fishing east of 180° longitude in the spring during 1974-1977. So the catches were reduced four years before the large increase in the runs (Figure 9). In addition the increase in abundance was a general phenomenon throughout western and central Alaska and included stocks that were not vulnerable to high seas fishing, e.g., central Alaskan pink salmon (Takagi et al. 1981).

The recent increase in the Bristol Bay sockeye runs was not uniform for the various stocks. In general, those stocks that had produced a high percentage of three-ocean aged fish tended to increase in abundance more than those that had produced a high percentage of two-ocean aged fish (Table 1). These differences may well be partially attributed to the reduction in high seas fishing because three-ocean fish were subjected to exploitation as immature fish as well as mature fish.

Temperature Trends and Effects on Salmon

The annual winter temperatures in Bristol Bay and at Kodiak are shown in Figure 10. Observations were missing for 1946-47, and data were sparse prior to 1919. Temperatures declined in the late 1940s, increased somewhat in the late 1950s and early 1960s, declined to a low point in the early 1970s, and then, beginning with the winter of 1976-77, were comparable to the temperature of the 1920s to early 1940s. This pattern generally corresponds to the main fluctuations in sockeye salmon catches in western Alaska and pink salmon catches in central Alaska (Figures 3 and 4). The spring through fall air temperatures are not as well correlated between Kodiak and Bristol Bay as the winter temperatures, and there has been less correspondence with the major changes in salmon abundance (Figure 11). The spring weather in Bristol Bay was very cold in 1971-72 and cold in 1975-77, and then very warm in 1978-81 (Figure 12). Spring temperatures affect the timing of ice breakup in the Bristol Bay lakes, the timing of smolt migrations, and the water temperatures during smolt migration.

The annual air temperatures for Bristol Bay since the 1950s were correlated with nearshore temperatures in the western Gulf of Alaska (Kodiak) and to some extent with offshore temperatures (Figure 13). The SST at Kodiak was much more elevated for the winter months after 1976-77 than for the summer months; e.g., the average SST for January during 1951-76 was 0.8 C (range - 1.7, 2.9), and during 1977-82 the average January SST was 4.5 C. In contrast the average SST for August was 11.8 C (range 9.8, 14.4) during 1951-76 and 13.1 during 1977-82.

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[2] Methods and annual estimates from Bristol Bay data reports by M. L. Nelson, ADF&G.

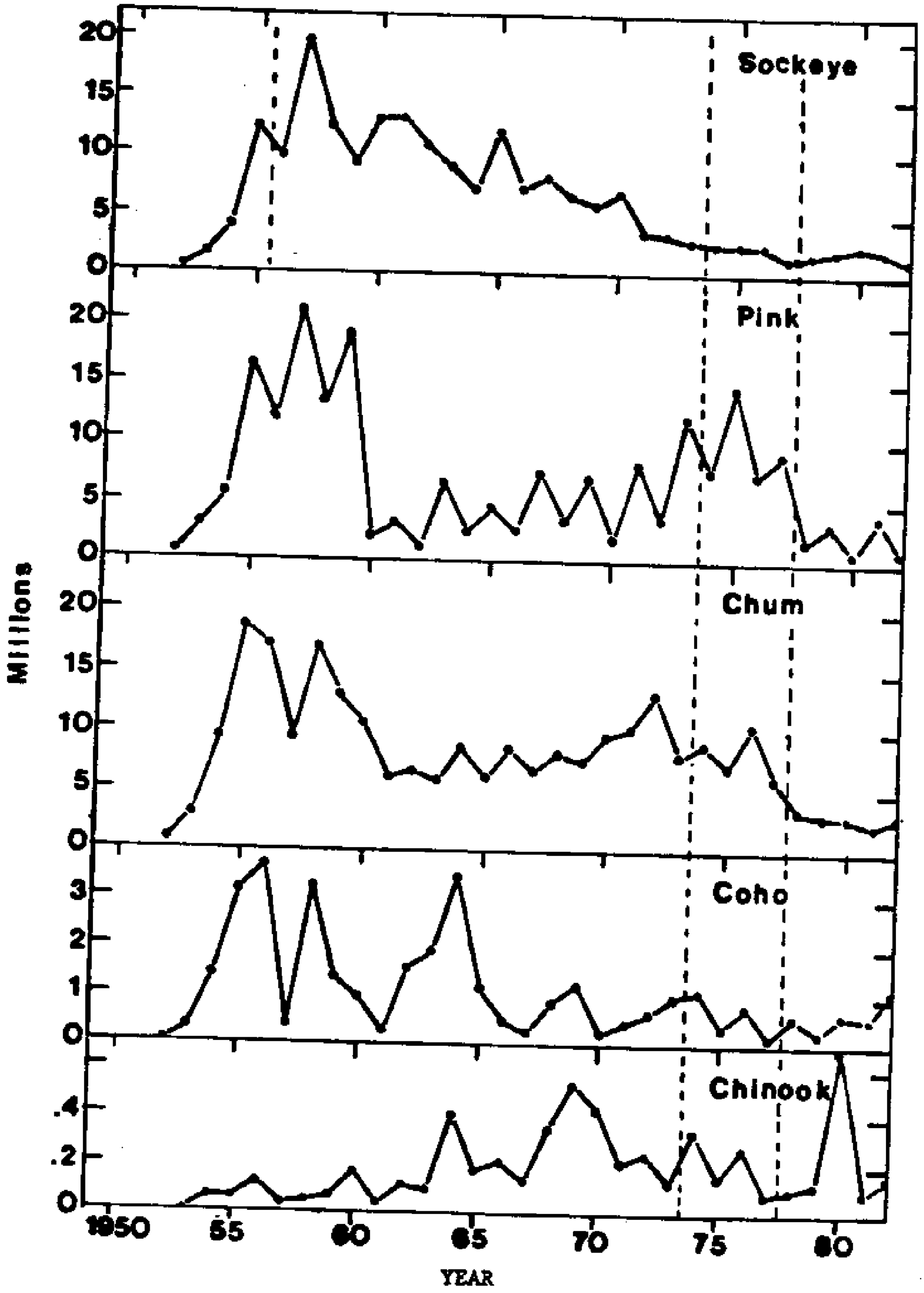

Figure 9. Annual catches of salmon (numbers) by the Japanese mothership fishery, 1952-1982.

Table 1. Average abundance of the main age groups in Bristol Bay sockeye salmon inshore runs for the years (1) 1956-77 and (2) 1978-83. Number of fish in millions.

Lake system	Years	Age				Total	Ratio 2/1
		1.2 4_2	2.2 5_3	1.3 5_2	2.3 6_3		
Kvichak	1	2.2	5.4	0.6	0.6	8.8	1.8
	2	6.2	8.3	1.2	0.4	16.1	
Branch	1	0.21	0.07	0.11	0.04	0.43	1.2
	2	0.25	0.08	0.16	0.04	0.53	
Naknek	1	0.30	0.58	0.48	0.50	1.86	2.3
	2	0.80	0.87	1.67	0.86	4.20	
Egegik[1]	1	0.18	0.96	0.24	0.45	1.91	2.2
	2	0.45	2.34	0.57	0.74	4.14	
Ugashik	1	0.25	0.24	0.17	0.07	0.73	3.6
	2	1.16	0.72	0.62	0.16	2.66	
Wood	1	0.76	0.16	0.47	0.05	1.44	2.8
	2	1.90	0.33	1.68	0.17	4.08	
Igushik	1	0.09	0.06	0.24	0.04	0.43	4.2
	2	0.39	0.13	1.18	0.12	1.82	
Nuyakuk	1	0.05	0.01	0.20	0.01	0.27	8.3
	2	0.29	0.03	1.82	0.09	2.23	
Togiak	1	0.09	0.02	0.15	0.02	0.28	2.9
	2	0.21	0.05	0.49	0.05	0.80	

[1] Totals include ages 3.2 (1 = 0.06, 2 = 0.03) and 3.3 (1 = 0.03, 2 = 0.01).

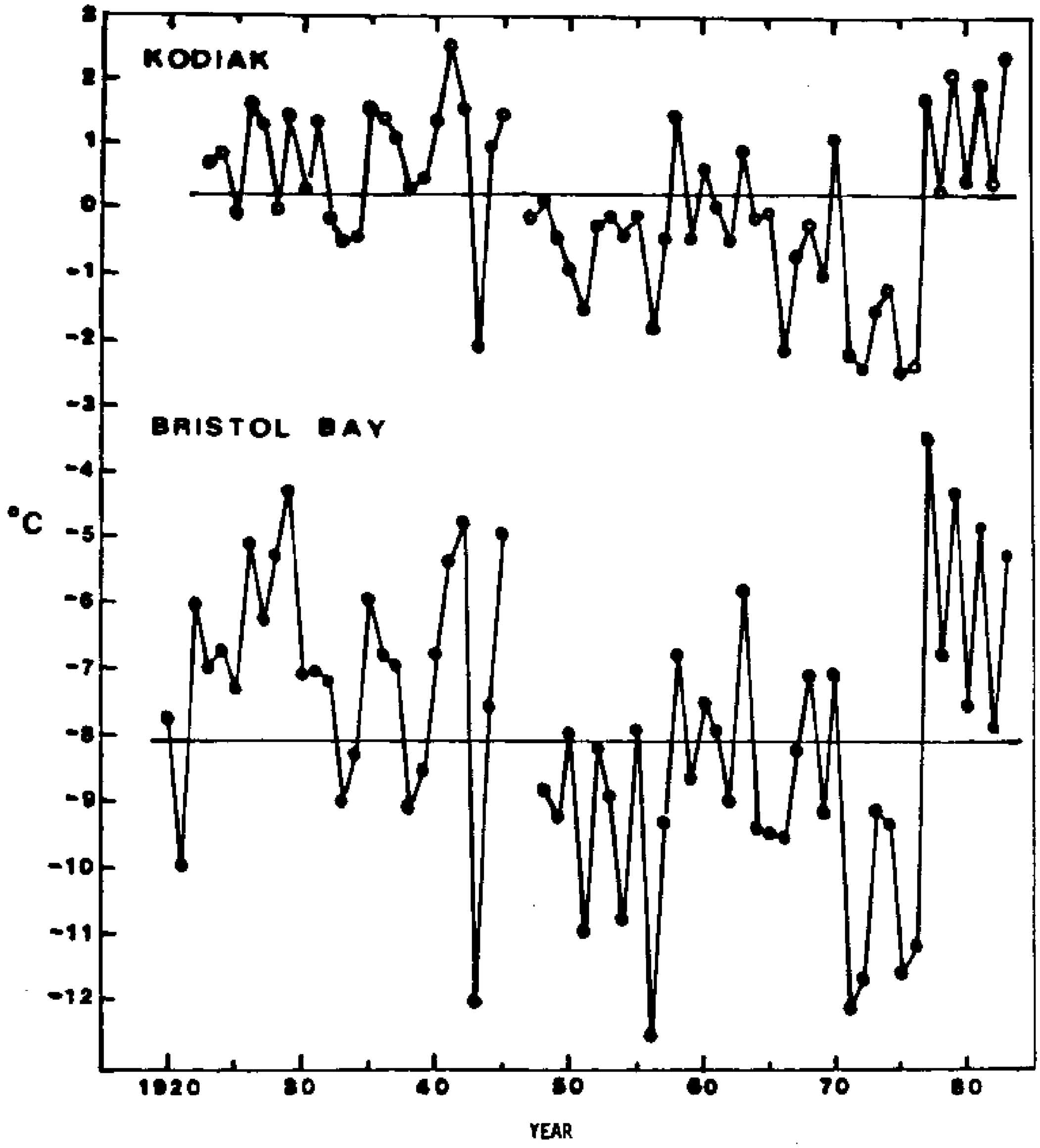

Figure 10. Average winter (Nov-Mar) air temperatures for Kodiak and Bristol Bay through the winter of 1982-83.

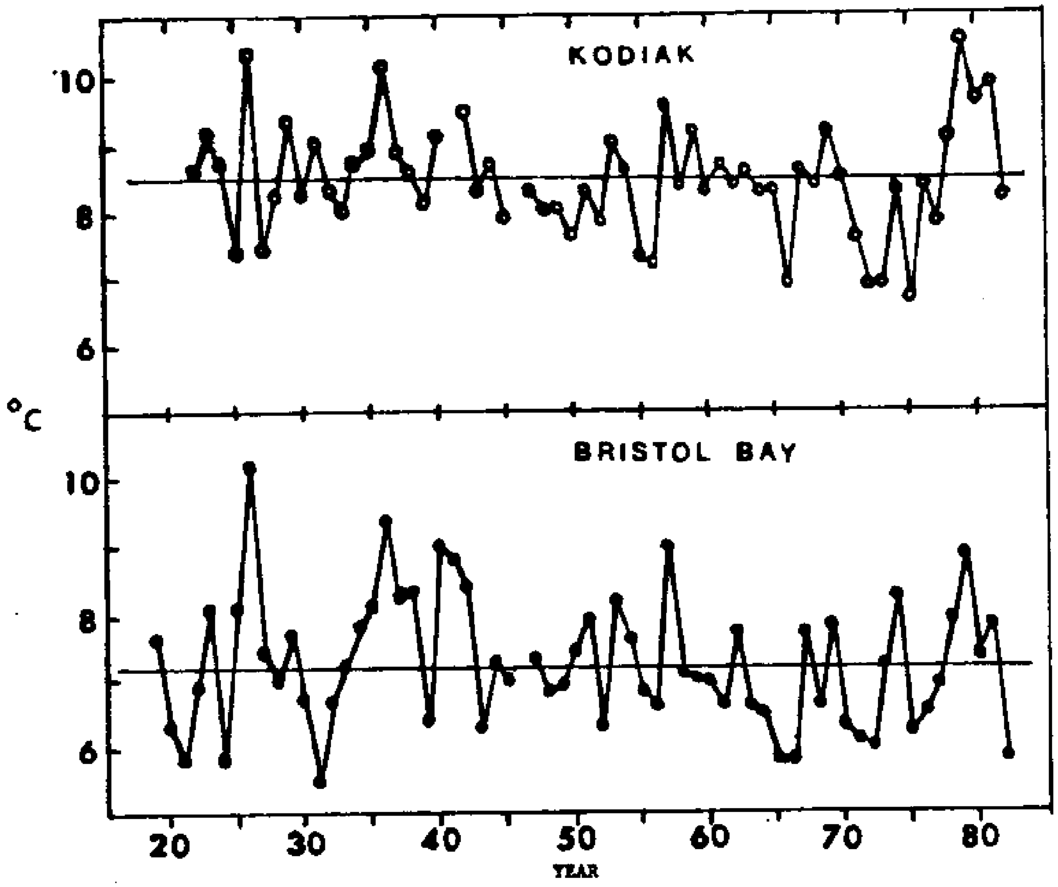

Figure 11. Annual April-October mean air temperatures for Kodiak and Bristol Bay through 1982.

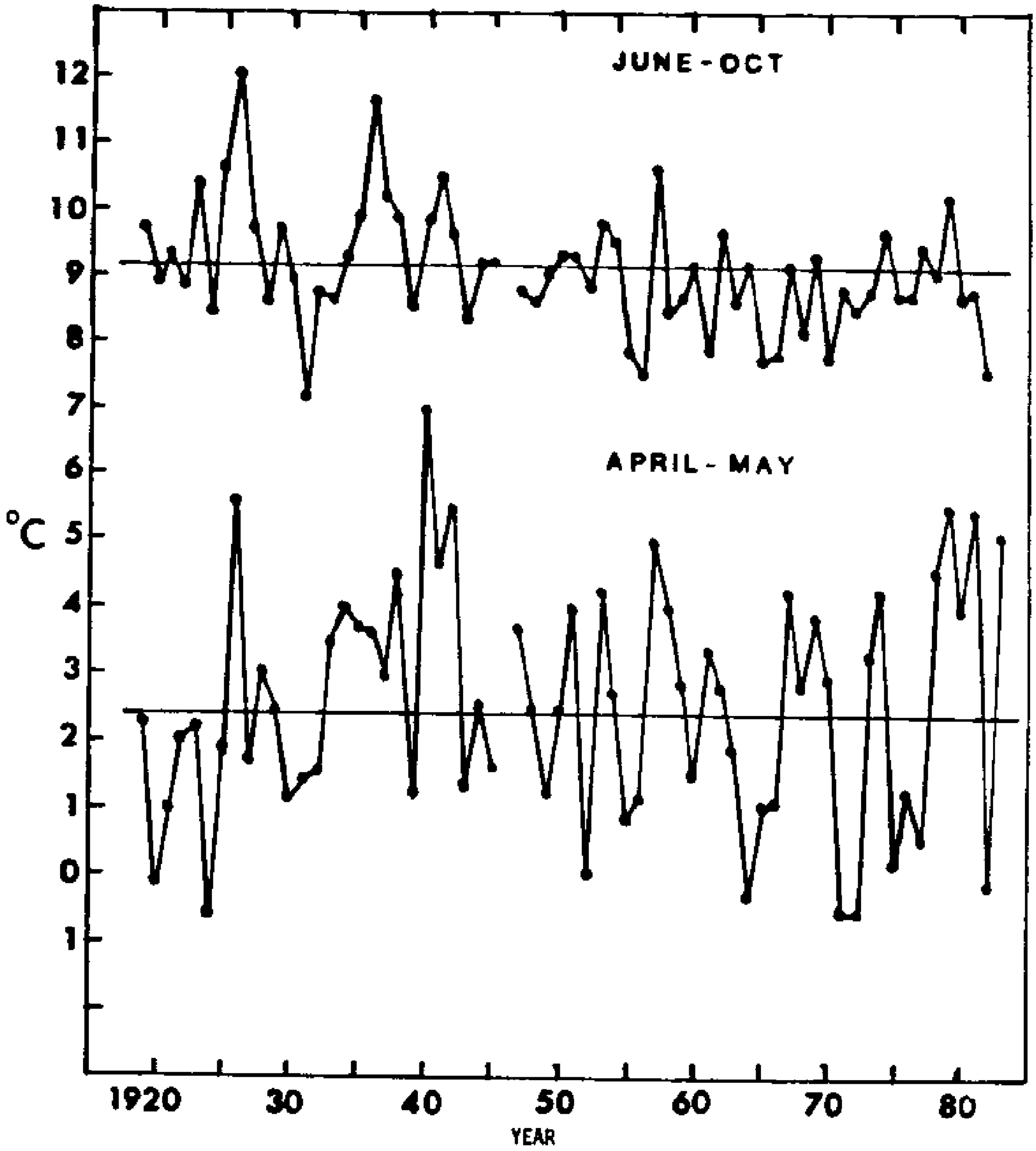

Figure 12. Annual mean air temperatures in Bristol Bay for spring (April-May) and summer-fall months, 1919, through April-May 1983.

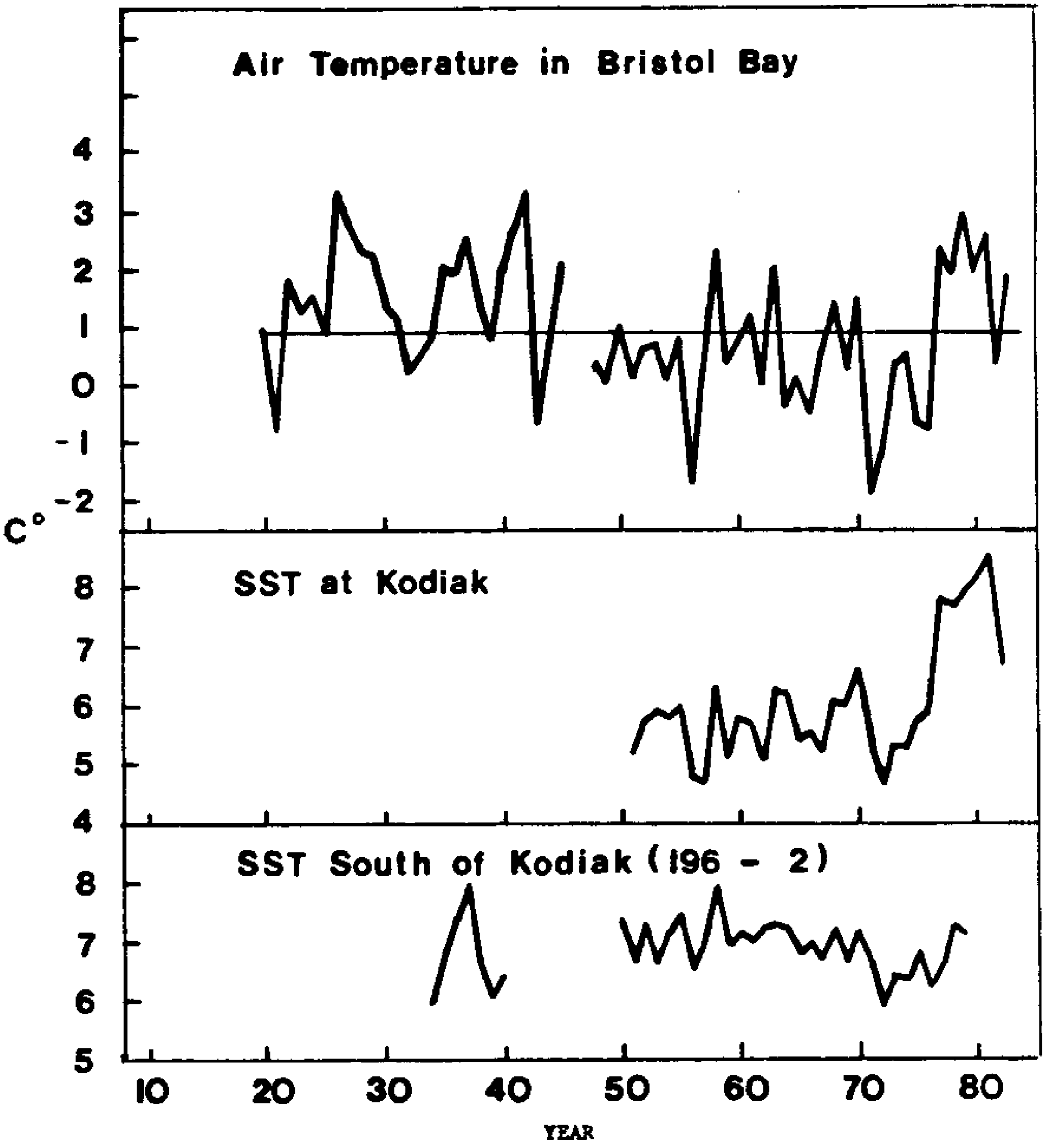

Figure 13. Annual (June-May) temperatures. Mean air temperature in Bristol Bay, 1919-20 to 1982-83; mean sea surface temperature at Kodiak (Womens Bay) 1951-52 to 1981-82; and mean sea surface temperature in Marsden Square 196 - 2 through 1977-78.

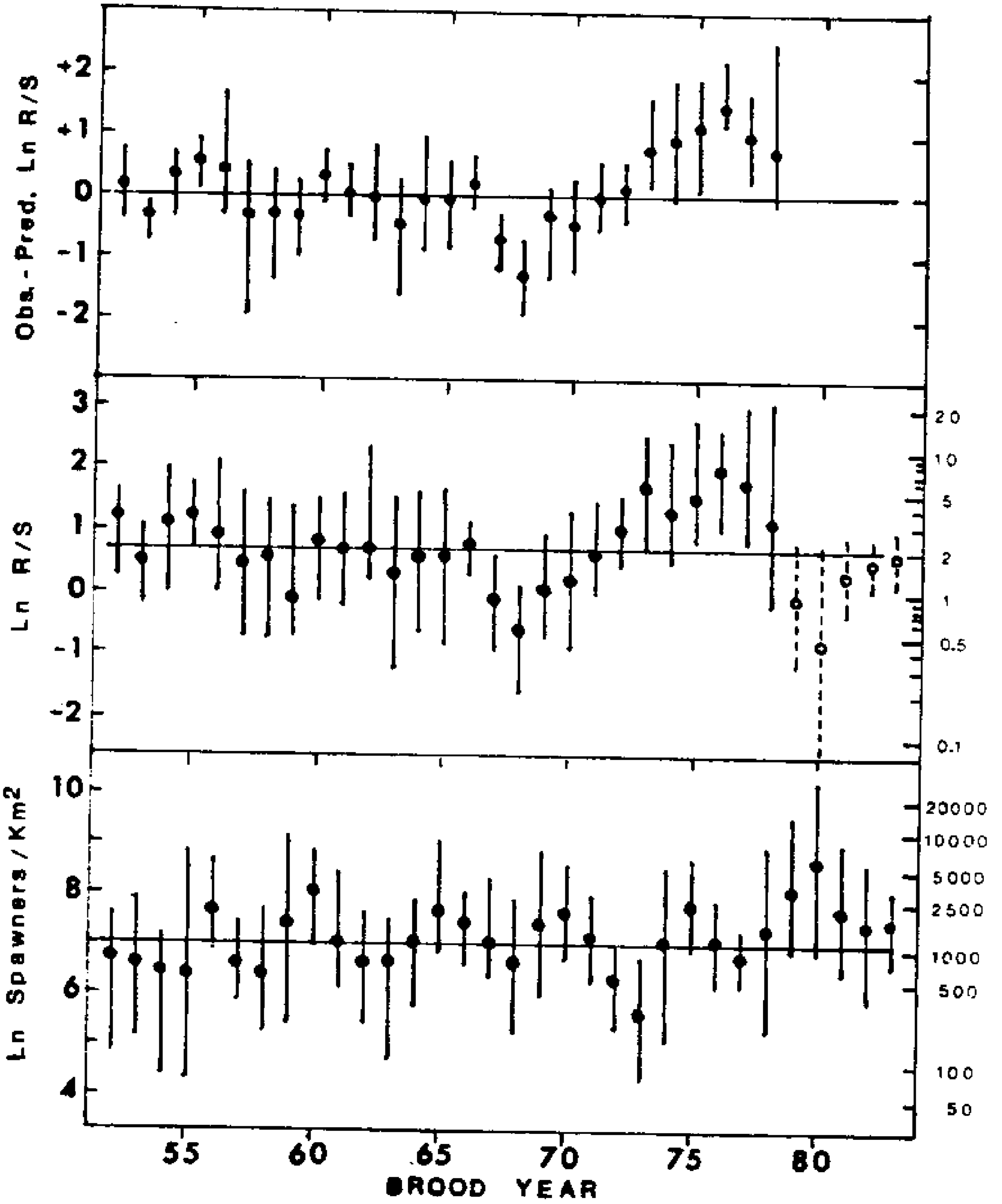

Figure 14. Means and ranges in spawner density (number per km^2 of lake area), adult return per spawner, and deviation from predicted return per spawner (from Ln R/S on S) for six sockeye salmon stocks (Kvichak, Naknek, Egegik, Ugashik, Wood and Igushik). The predicted R/S is given for the 1979-83 brood years. Data from the three other major stocks (Table 2) were not included because (1) statistics for Branch River were not as accurate as for the other systems, (2) the large recent returns to the Nuyakuk came from escapements that were generally larger than earlier escapements and (3) the Togiak stock is unique in that commercial fishing did not begin until the 1950s.

to determine whether freshwater or marine survival increased in recent years. The mean weights of smolts in the migrations did not change significantly (Table 2). So if there was an increase in marine survival, it was not associated with larger migrants.

The spring-summer temperatures affect the freshwater age composition of Bristol Bay smolts--warmer temperatures and higher percentages of age 1. fish in the returns (Table 3). However, there was no change in this relationship in the recent years.

The ocean age composition of the Bristol Bay returns is affected by the ocean age composition of the parent spawners (for the six stocks "r" ranged from .3, Kvichak, to .8 Wood and Igushik) and the freshwater age composition. The mean of the deviations in % age .2 was correlated with the mean % age 1. in Table 3 (r = -.55). However there were no significant changes in these relationships for the recent brood years. One might expect that with the warmer ocean temperatures a higher proportion of the fish would mature at age .2 if they had experienced better growth during their first year at sea. So far this is not evident; perhaps the genetic control of growth and maturity was not sufficiently altered by the temperature variation.

There has been a recent significant change in ocean growth, but it occurred during the last year and probably the spring before the mature fish returned. There were significant inverse correlations between the mean lengths of Bristol Bay adult sockeye and the number of fish in the runs through the early 1970s (Rogers 1980). The fish in the runs since 1977 were significantly larger relative to the abundances of the runs (Figures 15 and 16). However, it seems unlikely that this increased growth caused an increase in marine survival because it probably occurred late in their marine life. Purse seine sampling of immature sockeye salmon south of the Aleutians did not indicate a significant increase in the size of the fish in 1977-78 although the age .2 immatures were above average in length (Harris and Rogers 1979).[3]

The relative marine survival of Bristol Bay sockeye was estimated from the purse-seine catches of immature fish in July and the number of mature fish returning to Bristol Bay in the following year (for age .2 immatures to age .3 matures) or years (for age .1 immatures to age .2 and .3 matures). Variation in relative survival could be attributed to both variation in the availability of immature fish to the purse seine sampling and actual variation in marine survival.

The relative survival from age .1 immatures apparently increased after 1973 when high seas fishing was reduced (beginning in 1974), but did not increase significantly after 1976 when winter temperatures increased (Table 4). The relative survival from age .2 immatures was over a period of only one year and catches of age .2 immatures were less variable than catches of age .1 immatures. The relative survival of age .2 immatures for the fish sampled in 1962-1972 was inversely correlated with the SST during samping (Figure 17). This could mean that survival was higher when temperatures were colder or that the age .2 immatures were less available when temperatures were colder. The latter seems more likely. The relative survival of age .2 immatures increased slightly after 1973 and then increased significantly after 1976 when winter temperatures increased.

The complex and variable life histories of the Bristol Bay sockeye stocks seems to preclude simple relationships between relative production or survival and a single environmental parameter such as temperature. The Nushagak pink salmon stocks spawn primarily in two rivers, and their short life history provides an opportunity to examine environmental effects on production. The return per spawner ratios for escapements less than one million (the ascending limb of the spawner return

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[3] The sampling program was terminated after 1978. Japanese gill-net sampling has continued through 1983 but the sampling is selective to size of fish.

Table 2. Annual estimates of age composition and mean weights of sockeye salmon smolts in migrations from three Bristol Bay lake systems.

Year of migration	Kvichak % Age 1	Kvichak Mean weight (g) Age 1	Kvichak Mean weight (g) Age 2	Kvichak Mean weight (g) All	Naknek % Age 1	Naknek Mean weight (g) Age 1	Naknek Mean weight (g) Age 2	Naknek Mean weight (g) All	Wood % Age 1	Wood Mean weight (g) Age 1	Wood Mean weight (g) Age 2	Wood Mean weight (g) All
1955	7	6.0	10.8	10.5	--	--	--	--	98	4.7	8.4	4.8
56	39	6.3	13.0	10.4	--	--	--	--	78	4.2	6.9	4.8
57	72	7.3	14.4	9.3	58	13.1	13.1	13.1	81	3.5	6.1	4.0
58*	98	4.6	12.5	4.8	96	6.9	11.3	7.1	65	4.4	8.4	5.8
59	3	4.2	7.6	7.5	80	8.2	10.1	8.6	94	5.6	9.1	5.8
60	10	6.3	10.3	9.9	53	8.8	11.9	10.3	98	5.8	11.3	5.9
61	72	6.8	13.1	8.6	78	10.8	13.8	11.5	93	4.3	7.7	4.5
62	94	4.3	9.9	4.6	49	10.4	12.5	11.5	86	4.2	7.9	4.7
63*	3	4.8	7.5	7.4	41	8.1	12.8	10.9	84	5.1	9.3	5.8
64	22	5.2	9.8	8.8	31	7.7	11.0	10.0	99	4.8	8.5	4.8
65	4	6.8	11.3	11.1	60	8.4	13.0	10.2	92	5.6	9.9	5.9
66	92	7.4	12.6	7.8	34	10.6	14.2	13.0	94	4.3	7.5	4.5
67	93	5.9	14.2	6.5	43	13.1	14.7	14.0	60	4.5	6.2	5.2
68*	11	5.5	9.2	8.8	41	8.4	11.1	10.0	97	3.6	7.0	3.7
69	52	5.7	10.6	8.1	60	7.5	12.1	9.3	91	5.6	6.1	5.6
70	38	6.0	11.0	9.1	55	9.0	12.1	10.4	98	5.3	10.2	5.4
71	93	5.8	11.1	6.1	74	8.8	13.5	10.0	99	(5.2)[1]	(9.6)	(5.2)
72	1	4.2	10.0	9.9	6	9.1	11.9	11.7	99	(4.4)	(7.1)	(4.4)
73*	3	5.1	8.3	8.2	27	10.7	12.9	12.3	72	(5.3)	(8.5)	(5.6)
74	9	8.3	13.2	12.8	19	10.3	14.5	13.6	73	(5.6)	(9.1)	(6.2)
Mean	41	5.8	11.0	8.5	50	9.4	12.6	11.0	88	4.8	8.2	5.1
S.D.	38	1.1	2.0	2.0	23	1.8	1.3	1.8	12	0.7	1.4	0.7
1975	63	8.4	16.4	11.4	48	8.3	12.1	10.3	86	5.1	10.1	5.8
76	98	5.8	14.2	6.0	39	7.2	13.4	11.0	96	4.4	6.5	4.5
77*	38	5.5	10.1	8.3	11	7.2	11.9	11.4	83	3.4	9.3	4.4
78*	12	6.0	7.8	7.6	47	8.3	11.0	9.7	85	4.1	5.8	4.4
79	51	6.0	10.3	8.1	--	--	--	--	92	7.0	9.4	7.2
80	94	5.9	10.7	6.2	--	--	--	--	95	3.7	7.0	3.9
81*	89	5.4	10.2	5.9	--	--	--	--	66	5.5	8.4	6.5
Mean	64	6.1	11.4	7.6					86	4.7	8.1	5.2
S.D.	32	1.0	2.9	1.9					10	1.2	1.6	1.3

* Kvichak migrations that produced adult returns greater than 10 million.

[1] Estimated from mean weights of juveniles in the previous summer.

Table 3. Means of age compositions of adult sockeye salmon returns to the Kvichak, Naknek, Egegik, Ugashik, Wood, and Igushik lake systems.

Brood year	Ocean age of returns Mean % age .2	Ocean age of returns Mean deviation in % age .2[1]	Freshwater age of returns Mean % age 1.	Freshwater age of returns Mean deviation in % age 1.[2]	Mean temperature deviation[3]
1952	55	(- 3)	83	+ 32	+ 0.8
53	50	(- 3)	43	- 9	- 0.3
54	73	(+ 15)	25	- 27	- 1.5
55	62	(+ 4)	54	+ 5	- 0.6
56	53	- 5	89	+ 40	+ 1.5
57	53	+ 6	32	- 19	+ 0.1
58	65	+ 9	44	- 7	- 0.3
59	66	+ 1	46	- 2	0
60	62	0	44	- 3	- 0.3
61	37	- 2	57	+ 6	0
62	59	0	45	- 6	- 0.8
63	58	- 4	43	- 9	- 1.0
64	77	+ 10	38	- 13	- 1.3
65	64	+ 7	42	- 6	- 0.6
66	42	- 4	72	+ 22	+ 0.4
67	61	+ 5	57	+ 7	- 0.1
68	50	- 8	65	+ 14	+ 0.5
69	57	- 8	19	- 29	- 1.3
70	72	+ 8	29	- 18	- 1.6
71	56	+ 11	40	- 11	- 0.7
72	52	- 4	44	- 8	+ 0.4
73	28	- 12	57	+ 5	0
74	71	+ 5	38	- 11	- 1.1
75	58	+ 2	48	0	- 0.8
76	56	- 4	64	+ 13	+ 0.1
77	35	- 15	84	+ 32	+ 1.0
78					+ 1.3

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[1] Means of the deviations from predicted (from % .2 in parent escapement) for each lake system.

[2] Means of the deviations from predicted (from abundance of parent escapement) for each lake system.

[3] Means of the monthly air temperature deviations (from 60-year means) for April-October (year +1) and April-June (year +2). The linear correlation with the mean deviation in % age 1. is 0.85 (n = 26).

.96 (Nov.-May) and .98 for the 12 months (June-May) prior to return. The last relationship is shown in Figure 18.

Summary and Conclusions

The catches and probably the abundances of salmon in western and central Alaska declined in the mid-1940s to early 1950s, reached a low point in the early 1970s and

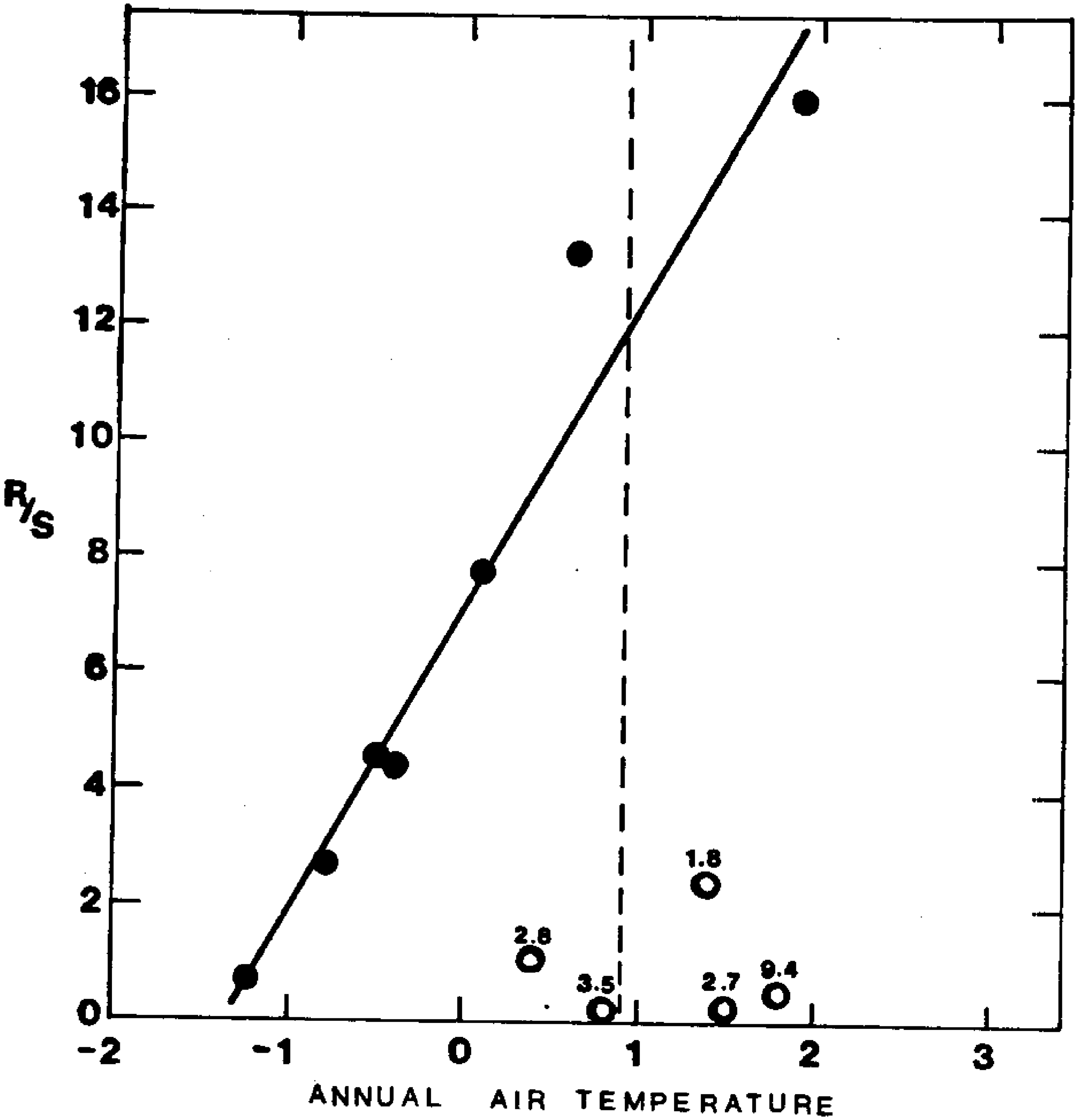

Figure 18. Relationship between return per spawner for Nushagak pink salmon and the annual air temperature during June-May prior to their return in July. Regression line fitted to observations where number of spawners was less than 1 million and dashed line indicates the long-term mean temperature.

then increased in the late 1970s. The other major salmon stocks along the North Pacific coast had similar fluctuations but did not increase to the same extent in the late 1970s. Large changes in temperature, particularly in the winter months while the fish were at sea, seem to correspond to the major changes in abundance. It is also in the winter months that salmon from western and central Alaska are most likely to share a common environment in the western Gulf of Alaska (Takagi et al. 1981; Bakkala 1971; Shepard et. al. 1968; French et. al. 1976).

Our knowledge of the oceanic distribution of salmon is based largely on observations made during the 1960s when there was relatively little annual variation in sea temperatures. During summer months salmon were concentrated over the continental shelf from the Gulf of Alaska to the western Aleutians and were relatively abundant in the Bering Sea, whereas during winter months they were distributed farther south away from coastal waters and were scarce in the Bering Sea. Their winter distribution may be affected by temperatures in that during very cold winters they are pushed farther south and are more concentrated, whereas during very warm winters they are distributed farther north and are less concentrated.

Predation is the most likely cause of mortality for salmon during their oceanic life. Major fluctuations in their distribution could very well cause fluctuations in their vulnerability to predators and hence in their marine survival. The most likely predators on salmon in the Gulf of Alaska during the winter would seem to be marine mammals, particularly the northern fur seal because it is relatively abundant and migrates through the Gulf of Alaska during the winter. If the distribution of salmon did not change significantly between very warm years and very cold years, their vulnerability to capture by marine mammals would still probably be greater at colder temperatures.

Further research is needed on the causes of mortality for salmon on the high seas (other than fishing) and the annual variation in SST in the North Pacific, particularly during the winter-spring months. An examination of the area encompassed by, e.g., the 4°C and 14°C, isotherms during the winters of the early 1970s with those during the winters of the late 1970s would be useful.

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Table 4. Geometric means of purse seine catches of immature sockeye salmon south of Adak and the returns (millions) of mature sockeye to Bristol Bay in the following year(s).

Year at Adak	Mean catch age .1	B.B. returns Age .2 (y+1)	B.B. returns Age .3 (y+2)	B.B. returns Total	R/C	Mean catch age .2	B.B. returns Age .3 (y+1)	R/C	July SST at Adak
62	7.1	3.9	2.3	6.2	0.9	3.5	2.9	0.8	8.0
63	17.4	8.4	4.2	12.6	0.7	2.9	2.3	0.8	7.7
64	47.8	48.9	13.1	62.0	1.3	4.1	4.2	1.0	7.0
65	8.0	4.4	3.4	7.8	1.0	10.0	13.1	1.3	6.9
66	14.5	6.9	2.8	9.7	0.7	4.4	3.4	0.8	8.4
67	13.0	5.0	2.2	7.2	0.6	4.2	2.8	0.7	7.7
68	27.4	16.2	3.7	19.9	0.7	4.1	2.2	0.5	7.8
69	60.7	35.6	9.4	45.0	0.7	5.7	3.7	0.6	8.7
70	18.4	6.4	2.7	9.1	0.5	8.1	9.4	1.2	7.1
71	5.7	3.7	2.0	4.7	0.8	2.6	2.7	1.0	6.7
72	3.3	0.4	2.0	2.4	0.7	2.6	2.0	0.8	7.0
73	7.6	8.8	5.0	13.8	1.8	2.1	2.0	1.0	7.4
74	14.7	19.0	4.2	23.2	1.6	4.1	5.0	1.2	7.9
75	8.1	7.2	5.0	12.2	1.5	3.5	4.2	1.2	7.4
76	12.2	4.5	7.8	12.3	1.0	2.4	5.0	2.1	8.3
77	21.4	11.3	7.6	18.9	0.9	4.7	7.8	1.7	9.2
78	17.3	32.4	15.7	48.1	2.8	3.1	7.6	2.5	7.5

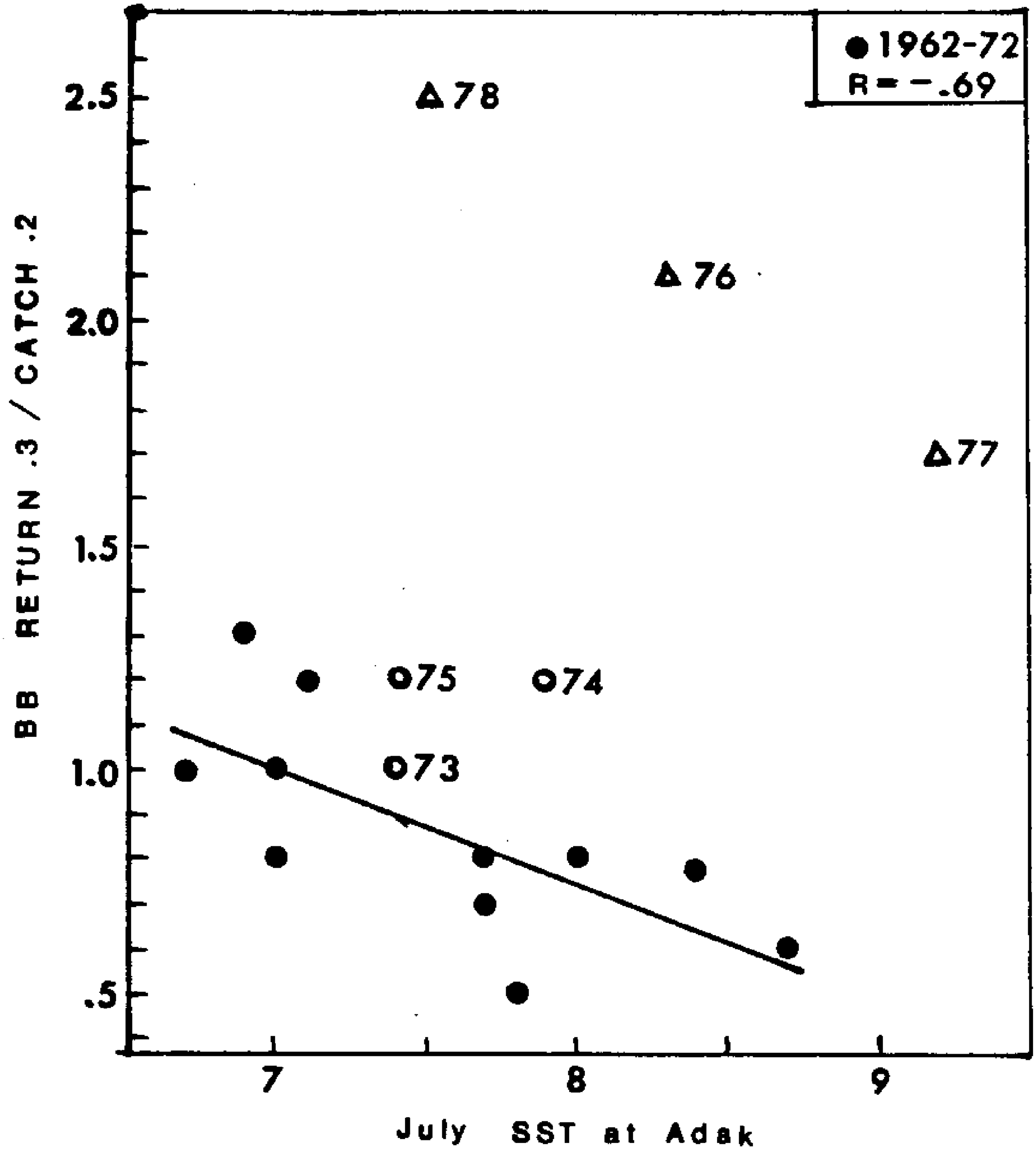

Figure 17. The relative survivals of Bristol Bay sockeye salmon (the run in millions of age .3 fish in year +1 divided by the mean catch at Adak of age .2 immature fish in the year shown) as a function of the SST during the sampling of immature fish: High seas fishing reduced for 1973-75 immatures, and warm winters and reduced fishing for the 1976-78 immatures.

relationship) were regressed on several combinations of air temperature. Although there were significant correlations with nearly all temperature combinations (e.g., winter and winter-spring in fresh water, summer, winter, and spring at sea), the highest correlations were those that included the winter months while the fish were at sea. The linear correlations between R/S and temperature were .88 (Nov.-Mar.),

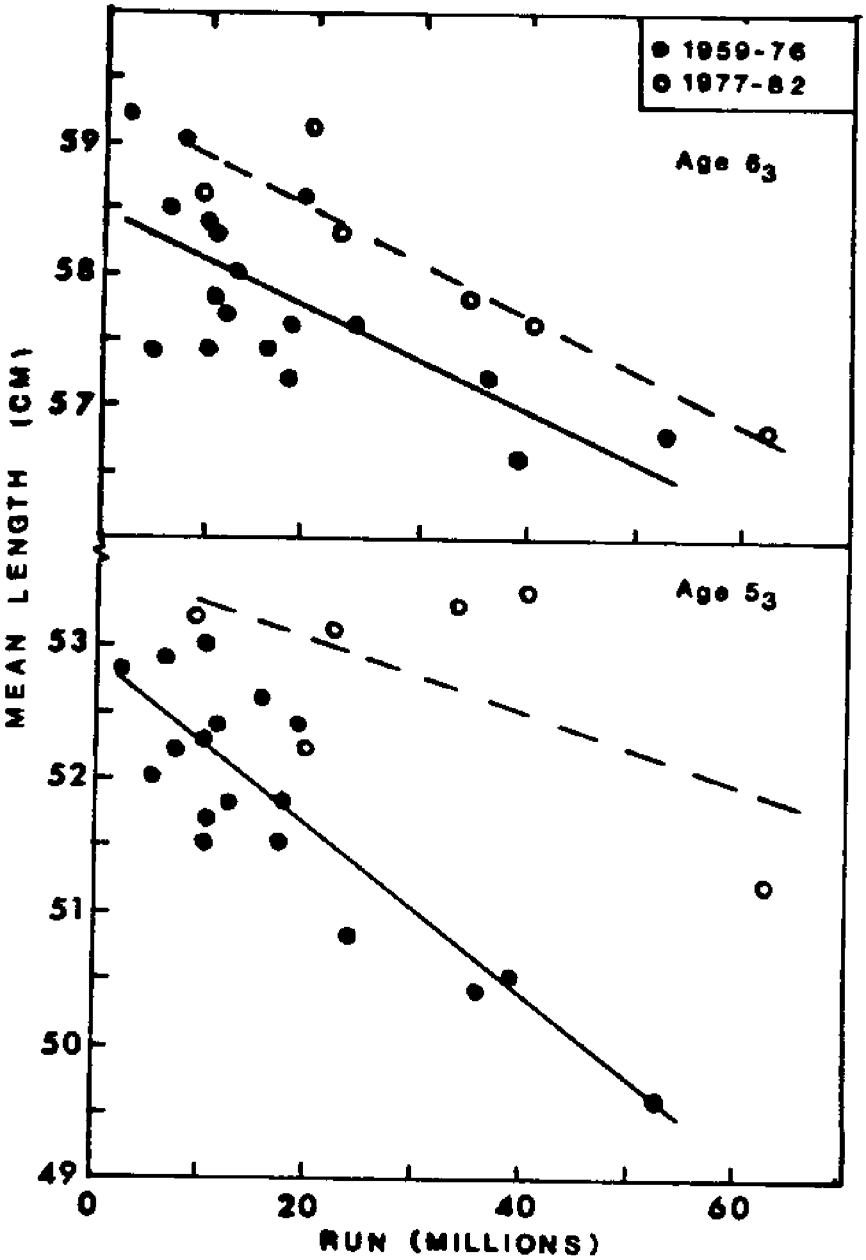

Figure 15. Linear regressions of the mean lengths of Bristol Bay sockeye salmon of ages 6_3(2.3) and 5_3(2.2) on the number in the run. Solid lines fitted to the 1959-76 data and dashed lines fitted to the 1977-82 data.

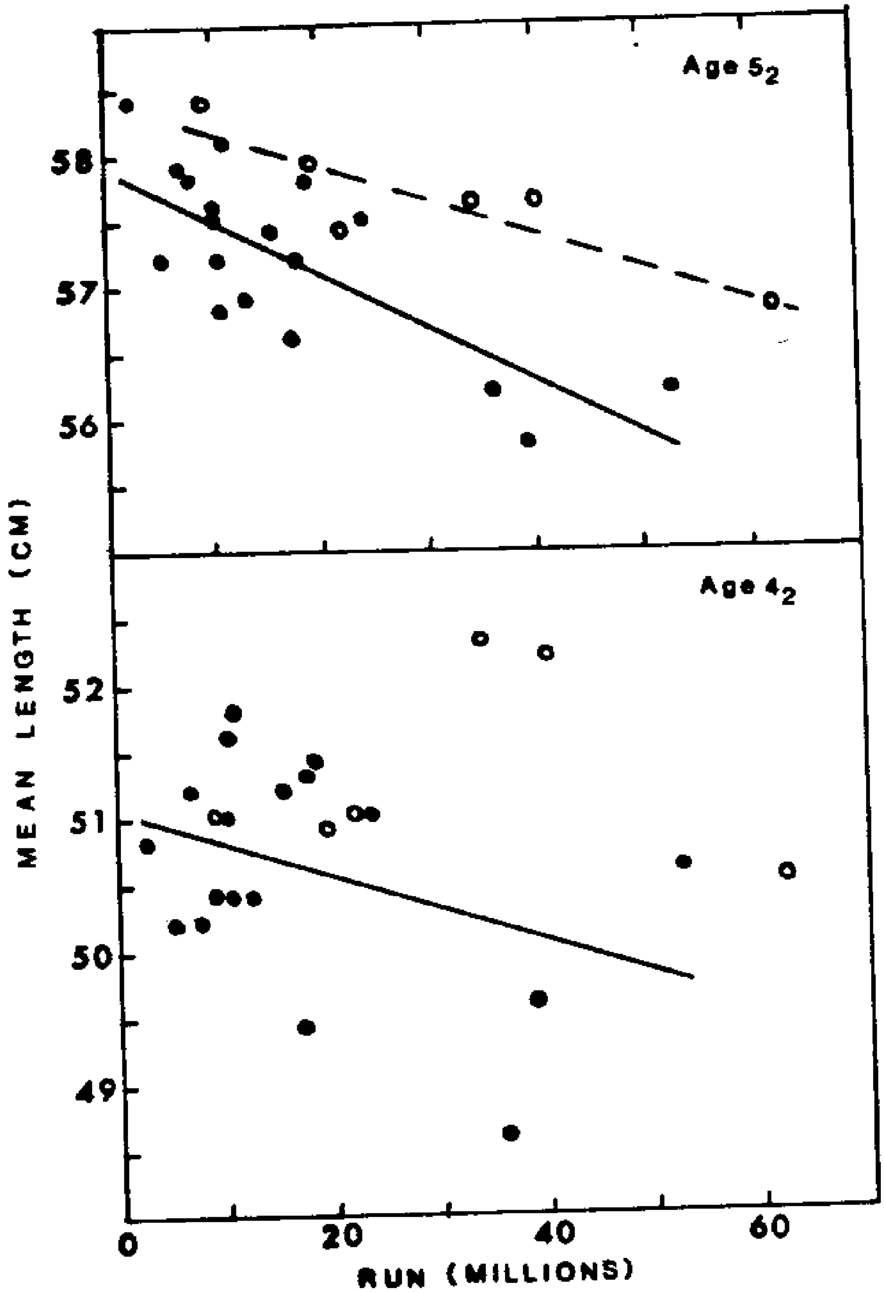

Figure 16. Linear regressions of the mean length of Bristol Bay sockeye salmon of ages 5_2(1.3) and 4_2(1.2) on the number in the run.

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Oceanographic Factors Influencing the Distribution, Migration, and Survival of Salmonids in the Northeast Pacific Ocean—a Review

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Abstract

Oceanographic factors influencing the distribution, migration, and survival of salmonids, particularly the Fraser River sockeye stock, are reviewed from the time of entrance into the estuary after completing their downstream migration to the time of return to the spawning river. Information is lacking as to the migratory routes of juvenile salmonids through coastal seaways, mortality, and the relation to oceanographic features during their first several months at sea. The limited data available suggest that juvenile sockeye are affected little by temperature and salinity in the Strait of Georgia. The variability of the Fraser River plume possibly influences the distribution of juvenile sockeye while in the Strait and its vicinity. Studies on pink and chum salmon suggest that coastal temperature and salinity during their juvenile stages may be important to survival but results are unclear. In the open ocean, surface temperature and salinity do not seem to affect the distribution of sockeye; however, subsurface features such as temperature fronts may be associated with their distribution. Long series of observations along Line P indicate that distinct features of surface salinity are present in the open ocean and they can persist for a year or more. Salmon may use these as cues to guide them toward the coast. Future studies to relate oceanography to sockeye biology (or other species of salmon) should seek cause-and-effect relationships that can be used as a reliable predictive tool for effective management of salmon fisheries.

Introduction

In recent years articles discussing the relationship between ocean environment and distribution, migration, and survival of marine fish have been published. They include an overall review by Lasker (1978), a discussion of the fish and oceanography along the California coast (Bakun and Parrish 1980), and an excellent paper on tuna of the Pacific Ocean by Sund et al. (1981). A comprehensive review on the relationship between salmonids and the oceanographic features of the North Pacific Ocean however, does not exist. Such a relationship is complicated by the fact that there are five species of salmon in the eastern Pacific, all with different life histories and supporting reproductive strategies. Further, salmon migrate through a number of distinctive ocean environments. First, there is the estuary where the fish arrive after completing their downstream migration; second, there are the coastal seaways they must move through in order to get to the ocean; third, there is the open ocean in which the fish spend one or more years, apparently moving in a counter-clockwise course between the northern and southern parts of the northeast Pacific (French et al. 1976). Finally, they return from the open ocean through coastal seaways and eventually to the river mouth. Each of these areas has its own annual and interannual variability of ocean conditions, and each is subject to different forcing functions. Even within the same species, different stocks are subject to different environmental conditions. All of these make it difficult to adequately review the general relationships between salmonids and oceanography.

I shall discuss mainly the oceanography of the northeast Pacific Ocean as it relates to only one species of salmon, the sockeye, during the period from when sockeye arrive at the estuary after completing their downstream migration to the time they return to the river mouth during their upstream migration to spawn. Of the many stocks of sockeye, those of the Fraser River will be considered. However, with some modifications, comments made with respect to the Fraser River sockeye may apply to other stocks and to other species such as pink and chum.

This paper is basically a review of the present state of knowledge of the relationships between oceanographic features and distribution, migration, and survival of salmonids. Discussions on salmon and particularly sockeye are included as background to provide oceanographers with some perspectives on the salmon biology.

Estuary and Inland Sea (Strait of Georgia)

After spending a year or more in nursery lakes, sockeye smolts migrate down-river and arrive at the estuary during late April through May (Foerster 1968). In the estuary, sea temperatures (of approximately 8°-12°C) in the spring are well within their tolerance limit (Brett 1952).

Salinity does not appear to be a problem to the juvenile sockeye. Barraclough and Phillips (1978) have observed that they (and chum) even swim away from the Fraser River plume to the clearer, more saline water of the Strait of Georgia. This was not the case for the pink, coho, and chinook which stayed with the plume for a longer period (Barraclough and Phillips 1978).

The circulation of the water in the vicinity of the Fraser River plume may have some bearing on the distribution of the juvenile sockeye. The plume is not well developed in April because of the relatively low discharge of the Fraser River. However, in May to June peak discharges occur and as a consequence the plume is well defined and developed and its effect can be seen as far north as Texada Island (Figure 1). If the smolts arrive at the Fraser River mouth (Sand Heads) in April they probably will not be affected by the movement of the plume as it is relatively weak (unless the freshet started earlier than usual). If, on the other hand, they arrive during freshet conditions, their eventual destination in the Strait may be affected. The Fraser River plume flows in a variety of ways, even in the absence of winds (Giovando and Tabata 1970). The plume, or when well developed, the jet, maintains its entrant direction (southwestward) until about the next low water, then it may

(1) persist northward toward the mainland shore west of Bowen Island,
(2) continue north and eastward toward Burrard Inlet, Howe Sound, and Lulu Island, or
(3) continue westward to the offing of the Canadian Gulf Islands, (i.e. Valdes, Galiano, and Mayne).

In mid-Strait the average plume speed has been found to exceed 3.6 km/hour (Giovando and Tabata 1970). Since the distance between the river mouth and Porlier Pass is only 23 km, water at the mouth can easily reach Porlier Pass in approximately 6 1/2 hours. If the flow is toward Active Pass (26 km from river mouth) it will take a little over 7 hours for it to reach this water passage. Some of the aerial photographs depicting the plume movement show evidence that the jet does indeed reach Porlier Pass within one falling tide (Tabata 1972). Thus, juveniles in the plume can cross the Strait in less than one-half day. If, on the other hand, they were to "ride" on the plume during its northward excursion they can be transported to the east side of the Strait, to the west of Howe Sound. The

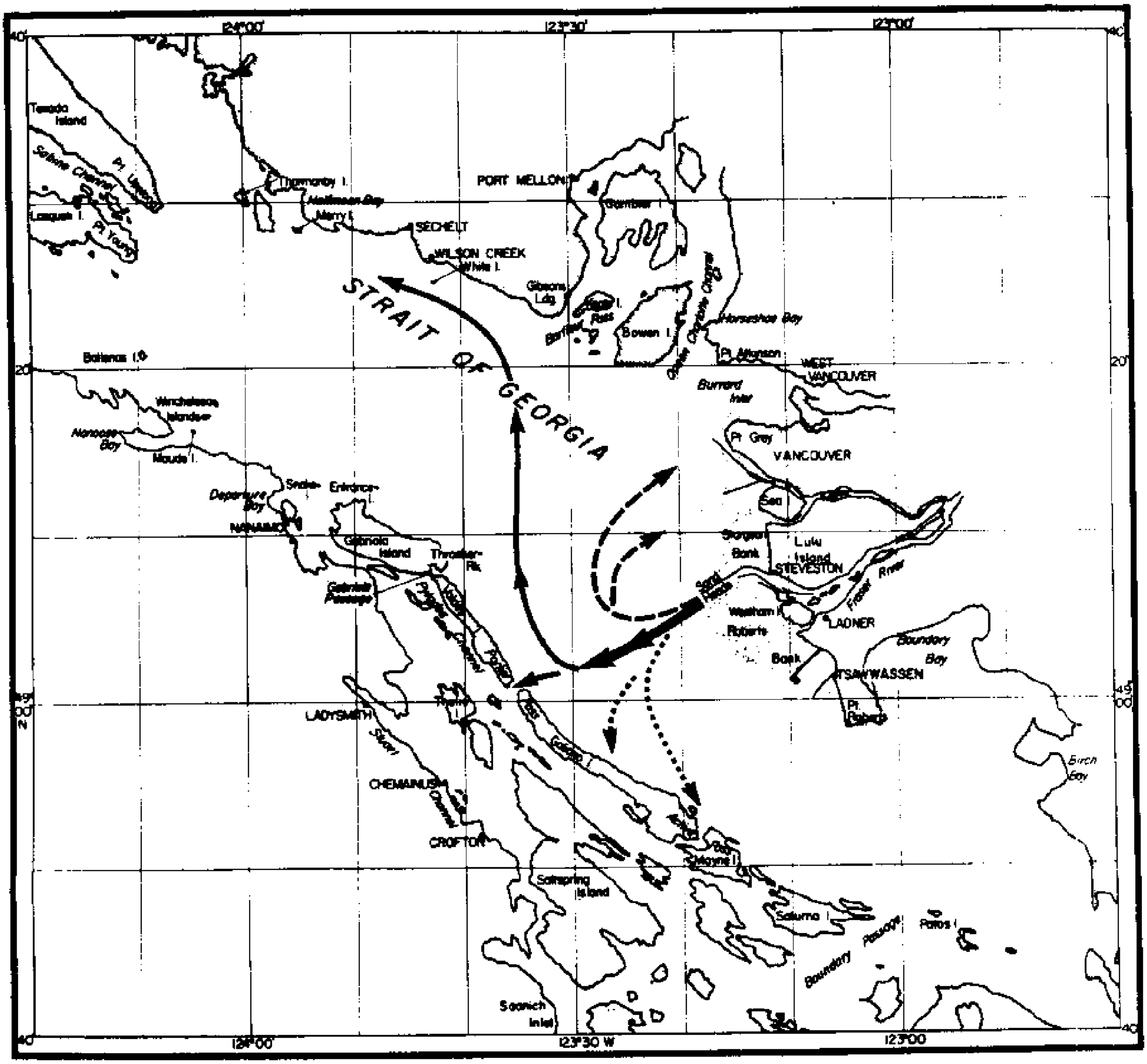


Figure 1. Chart of southern Strait of Georgia showing location of mouth of Fraser River and the various paths taken by the Fraser River plume.

fact that juveniles have been located in Howe Sound and west of it (Healey 1980) indicates that their migration could have been affected by the plume.

Since the upper layer containing the plume is only a few meters thick, it is easily affected by winds (Giovando and Tabata 1970). Consequently, strong southeasterly winds can carry these juvenile fish to the north. Alternately, with strong northwesterly winds they can be carried readily to the area of the southern Gulf Islands. The effects of surface currents in the Strait, which are influenced by the Fraser River discharge, tidal effects, and winds, are evident in the distribution of juveniles (Barraclough and Phillips 1978). There are other low-frequency currents that possess as much energy as that of the tidal currents, with characteristic periods of 10-30 days (Chang et al. 1976; Schott and Mysak 1980), but how these currents can affect the fish has not been examined.

The southward-moving juveniles then proceed seaward, spending some time along the shores of the Gulf Islands (Healey 1980; Groot et al. In Press). The northward-moving juveniles, on the other hand, are found along the mainland shores of the Strait (Groot et al. In Press) and juvenile pinks from the Fraser River are observed as far west as the Nanaimo estuary (Healey 1980).

To what extent oceanographic properties such as temperature, salinity, dissolved oxygen content, and turbidity play a role in influencing the distribution, migration, or survival of juvenile sockeye in the Strait is unknown. An earlier study made by Vernon (1958) showed that, at least for the Fraser River pink, there was an inverse relationship between sea surface temperature in the Strait during their seaward migration stage (April-August) and pink catches (total run or percentage survival) of the subsequent year. While this relationship held for the 1935-1957 data he used, it disappeared when later data (Blackbourn personal communication) were utilized. Studies made elsewhere indicate an opposite relationship. For example, for the central British Columbia pink, low sea temperature along the coast in June appears to be unfavorable to their survival (Wicket 1958). Helle (1980) examined the relationship between young chum and environmental factors in Alaska and concluded that sea temperatures in Prince William Sound and the northern part of Gulf of Alaska were directly related to the growth of chum salmon in Prince William Sound during their first summer at sea. Density (dominated by salinity here) apparently had no relationship to their growth. Although growth and survival are not necessarily associated, Helle's (1980) conclusion appears to be consistent with that of Wickett (1958).

In the Fraser River plume area the juvenile sockeye feed on a variety of food -- mainly insects, copepods, euphausiids and fish larvae; elsewhere in the Strait their diets include amphipods, crab larvae, and ctenophores as well (Healey 1980). Although it was possible to show that food resources limitation may be important at specific times, Healey (1980) found difficulty in demonstrating conclusively that food limitation affected their migration for the entire strait. The combination of oceanographic conditions and food availability appear to determine the growth of these juveniles. It has been shown, at least for pink, that during the first few months of sea life, their growth is rapid (LeBrasseur and Parker 1964). Juvenile chum and coho also grow rapidly while in the Nanaimo estuary (but more slowly in Nitinat estuary, west coast of southern Vancouver Island) (Healey 1982). Rapid growth is very important to juveniles because of the size selective mortality attributable to predation, not only from other fish but also from other species of salmon. For instance, Parker (1968) has estimated that pink salmon in the waters of central, coastal British Columbia suffer from heavy mortality in their early sea life. From a series of experiments conducted there, Parker (1971) found that juvenile coho can consume a large amount of pink and chum fry and concluded that the early sea mortality of pink and chum was due largely to predation by coho. He further showed that there was a strong selectivity on the part of the predator for smaller salmonid prey resulting from later entry into the estuary, from slower growing rate, or from being pink rather than chum. During the experiment juvenile coho grew at the rate of 0.7% in length per day. This compares with a rate of 1.8% per day for pink (Parker and LeBrasseur 1964). If the above rate for coho is applicable for the natural environment the individuals of the prey population would outgrow the predators and hence become unavailable to coho (Parker 1971). Thus for pink and chum, survival may well be dependent on their growth; similarly, rapid growth rate can be assumed to be important for sockeye. Ricker (1962) showed that the greater survival rate of Karluk and Dalnee sockeye stocks were attributable to their larger sizes when they entered the sea. However, no data have been presented to show direct evidence of the causes of mortality in the natural environment, except perhaps in the lower reaches of the river where coho have been observed to feed on fry (Parker 1971).

These interspecific interactions make it difficult to assess the possible role of oceanographic conditions to the survival of salmonids generally, since as a particular condition may favor one species, while concurrently, be harming the other. For example, the presence of turbid water may aid the prey (pink and chum) by making it difficult for the predator (coho) to consume them, thereby improving the survival rate of the prey, but this could decrease the survival rate of the predator.

The unavailability of reliable information on non-fishing ocean mortality appears to be one of the main problems to study the relationships between marine environmental factors and survival of salmon. This mortality may be due to fish disease, predation by mammals, fish and birds, environmental factors or any combination of these. Even before the sockeye leave the lake an average of 92% mortality has already occurred (Foerster 1968). About 90% of the fish which survived to leave the lake die before they return to the river mouth after completing their life stage in the ocean. Over 80% of the ocean mortality is believed to occur before juvenile sockeye from Fraser River leave the inshore seaways (Parker 1962). The reliability of the above percentage is open to question; further, there is little data to indicate where mortality is taking place for the Fraser River sockeye-- in the river during the downriver migration, at the estuary, in the open waters of the Strait of Georgia, along beaches of numerous islands in the Strait, or in inshore seaways. Information related to these questions is required before any useful relationship between the juveniles and oceanographic factors can be determined successfully.

Coastal Seaways (Juan de Fuca Strait, Johnstone Strait, and Queen Charlotte Strait)

Little is known about the distribution and movement of the juveniles through the coastal seaways -- Juan de Fuca Strait, Johnstone Strait, and Queen Charlotte Strait. At only three stations located at the western part of Juan de Fuca Strait (Hartt 1980) and at several stations in Johnstone Strait, Queen Charlotte Strait, and Queen Charlotte Sound (Manzer 1956) catches of juveniles have been made (for locations refer to Figure 2). According to these data, chum, pink, and coho occurred along the southern shores of Juan de Fuca Strait. On the other hand, juvenile sockeye tended to swim seaward along the northern side. The catches of these sockeye peaked prior to August (Hartt 1980) and therefore it can be assumed that they should be starting their ocean journey northwestward by August-September. In Johnstone Strait, Manzer (1956) reported many juvenile sockeye in late June through July but only moderate numbers by mid-August. There is no record indicating that the Fraser River juveniles were among those found, but it can be assumed that at least some of those captures had originated from the Fraser River system. Probably a good number of them were from the Nimpkish River situated adjacent to Johnstone Strait. In Queen Charlotte Strait, juvenile sockeye were caught from mid-August through September but were located over deep water around rocky islands offshore (Manzer 1956). Accordingly, September at this northern location also appears to be the time that juveniles start on their journey northwestward. Juvenile

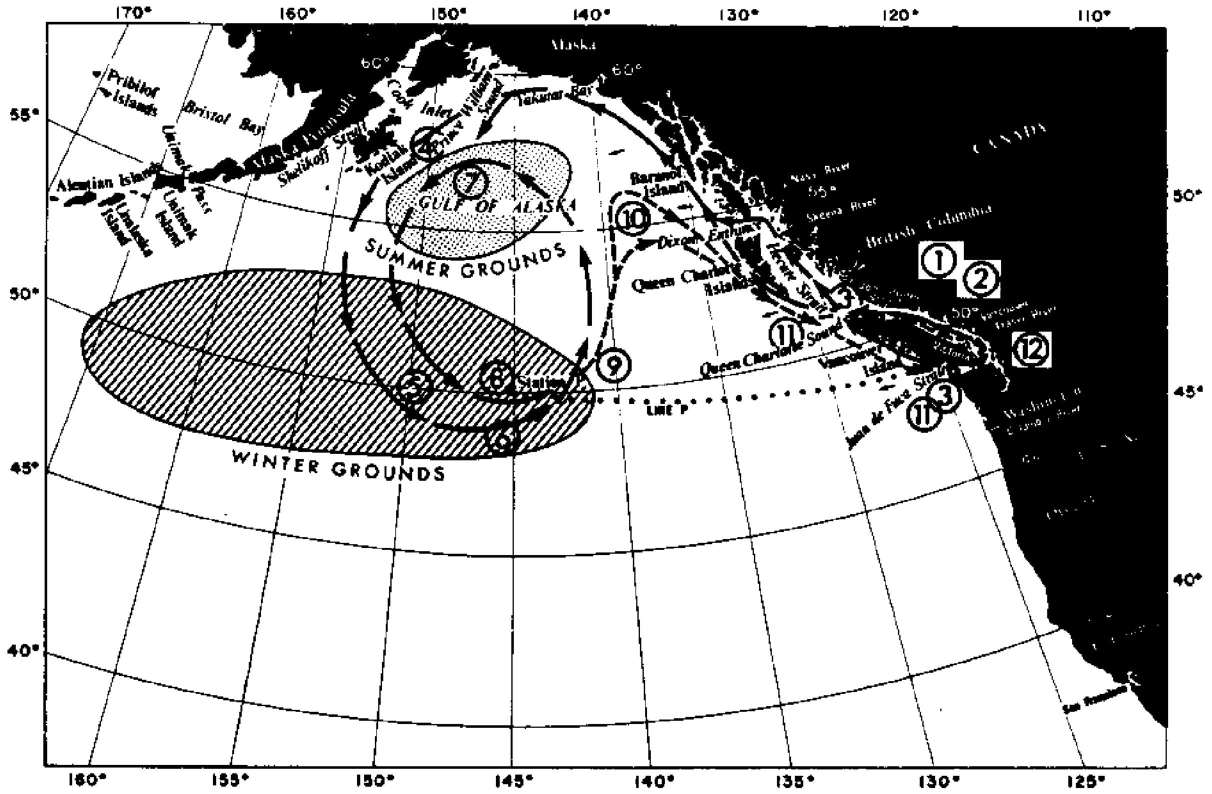


Figure 2. Probable migratory routes of the Fraser River sockeye. Other species of salmon may take this same route when migrating from the coastal areas to the open ocean. Relevant place names are indicated. Explanatory notes concerning the routes are attached.

1) Downstream migration: sockeye smolts arrive at estuary in late April-May.
2) Residence in Strait of Georgia: juveniles in Strait; southward-migrating fish in Gulf Islands area, north-ward migrating fish in eastern part of central Strait. By July most fish assumed to be out of Strait.
3) Juveniles at ocean proper, i.e., at approaches to Juan de Fuca Strait and in Queen Charlotte Sound in August-September, probably about a month later in the northern part.
4) Juveniles migrating northwestward along coast. Those in Queen Charlotte Sound probably travel along west coast of Queen Charlotte Islands and through Hecate Strait-Dixon Entrance. Probably arrive in the vicinity of Kodiak Island by November-December.
5) Immature fish migrate southward to the general vicinity of Station P along latitude 50°N. Arrive here by January-February.
6) Immature fish start migrating northward to summer feeding grounds in late spring (April-May).
7) Immature fish start migrating southward again by late summer (August).
8) Immature fish in winter grounds for the second time (January).
9) Both immature and maturing fish start moving northward again in early spring (March-April). Immature fish head for summer feeding grounds to north.
10) Maturing fish begin heading for spawning area in late spring-early summer (May-June).
11) Maturing fish at entrance to spawning streams and rivers in summer (July-August).

sockeye from the Skeena River have migrated out of the nearby estuaries by mid-July (Manzer 1956) and therefore they too can be expected to be at the western side of Dixon Entrance or in the Alaska panhandle seaways by September.

Oceanographic data are available for the coastal seaways, but they have not been used to compare with the distribution or migration of juvenile salmon. Areas such as Juan de Fuca Strait and, especially, Johnstone Strait, where juveniles pass through during their seaward migration, are characterized by swift currents, large turbulence and intense vertical mixing and are different to the other seaways such as the Strait of Georgia where conditions are relatively "quieter". How such an active environment affects the migration of juveniles is not known yet.

Coastal Region Over Continental Shelf

The assumed migratory route followed by Fraser River sockeye is illustrated schematically in Figure 2 (interpreted from information contained in Foerster 1968; French et al. 1976; Hartt 1980; and Groot et al. In Press). The sockeye (also pink and chum) move generally in a very narrow band less than 40 km wide (Hartt 1980). It is not known whether or not the juvenile sockeye from the Fraser River migrate along the west coast of the Queen Charlotte Islands or through Hecate Strait-Dixon Entrance, or both. In his study, Hartt (1980) observed that no juvenile salmon was caught along the west coast of the Islands and therefore suggested that they migrate through Hecate Strait rather than the outer coastal area. In November a large number of juvenile pink and chum salmon, and several sockeye were caught in Hecate Strait (LeBrasseur and Barner 1964), suggesting that Hecate Strait is used as part of the migratory route of juvenile sockeye. Hartt (1980) was able to determine from a number of paired seine sets opened in opposite directions along the coastal belt (from approaches to Juan de Fuca Strait to as far north as Yakutat Bay) that juvenile salmon moved persistently northwestward along this belt. He further noted that in the northern part of the Gulf of Alaska juveniles were distributed over a wider band, presumably because of a wider continental shelf in the area.

If the juveniles stay within the continental shelf then this has an important bearing on what oceanographic factors might be relevant to their distribution and migration; for example, here currents are likely to be different from those further offshore, and upwelling and tidal effects are likely to be greater over the shelf than in the deep ocean.

For the waters over the shelf off Vancouver Island, salinity plays a major role in determining the steric sea level, which in turn controls the baroclinic flow over the shelf. This is evident in its contribution to the annual variability of sea level. In the open ocean, however, temperature controls the annual variations and both temperature and salinity determine the interannual variability (Tabata and Thomas 1982).

In terms of the baroclinic currents, the flow over the shelf appears to be independent of that over the continental slope which in turn is different from that offshore (Tabata and Oliphant 1982). Figure 3 shows the monthly values of the baroclinic transport within 250 km of the coast of Vancouver Island. While a well-defined annual cycle of transport is present over the slope (Stations 3-4), its presence further offshore is not clear. At the shelf break (Stations 2-3), an annual cycle is again evident, but less so near shore (Stations 1-2). The reasons for the unclear annual cycle closest to the shore is probably due to the effects of a cyclonic eddy, present at the approaches to Juan de Fuca Strait (Tully 1942; Freeland and Denman 1982). Over the continental slope and shelf considerable interannual variability of transports occur as is shown in Figure 4.

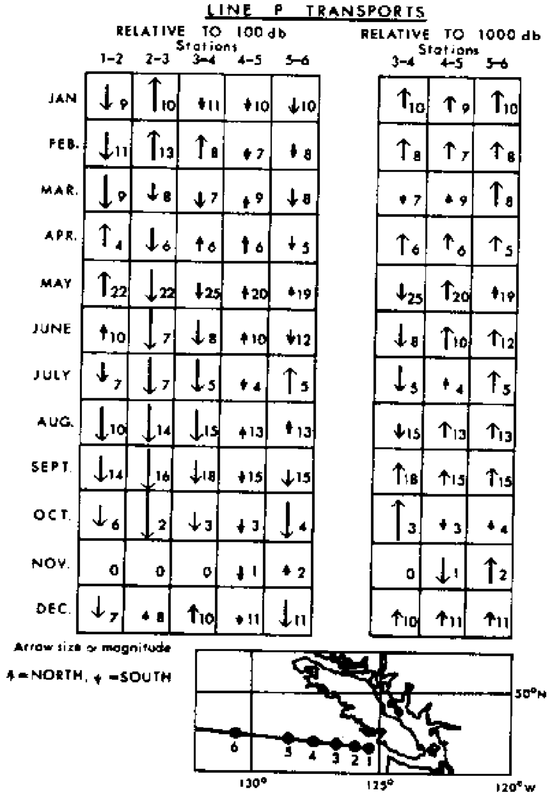


Figure 3. Monthly baroclinic transports (sverdrups = $10^6 m^3/s$) between Line P stations off Vancouver Island (Tabata and Oliphant 1982). Flow between Stations 3 and 4 represents slope currents, flow between Stations 2 and 3 represents part of slope and part of shelf currents, flow over Stations 1 and 2 represents flow over the continental shelf but appears to be affected considerably by the cyclonic eddy at the approaches to Juan de Fuca Strait. Numerals denote number of observations. Lower diagram indicates station positions.

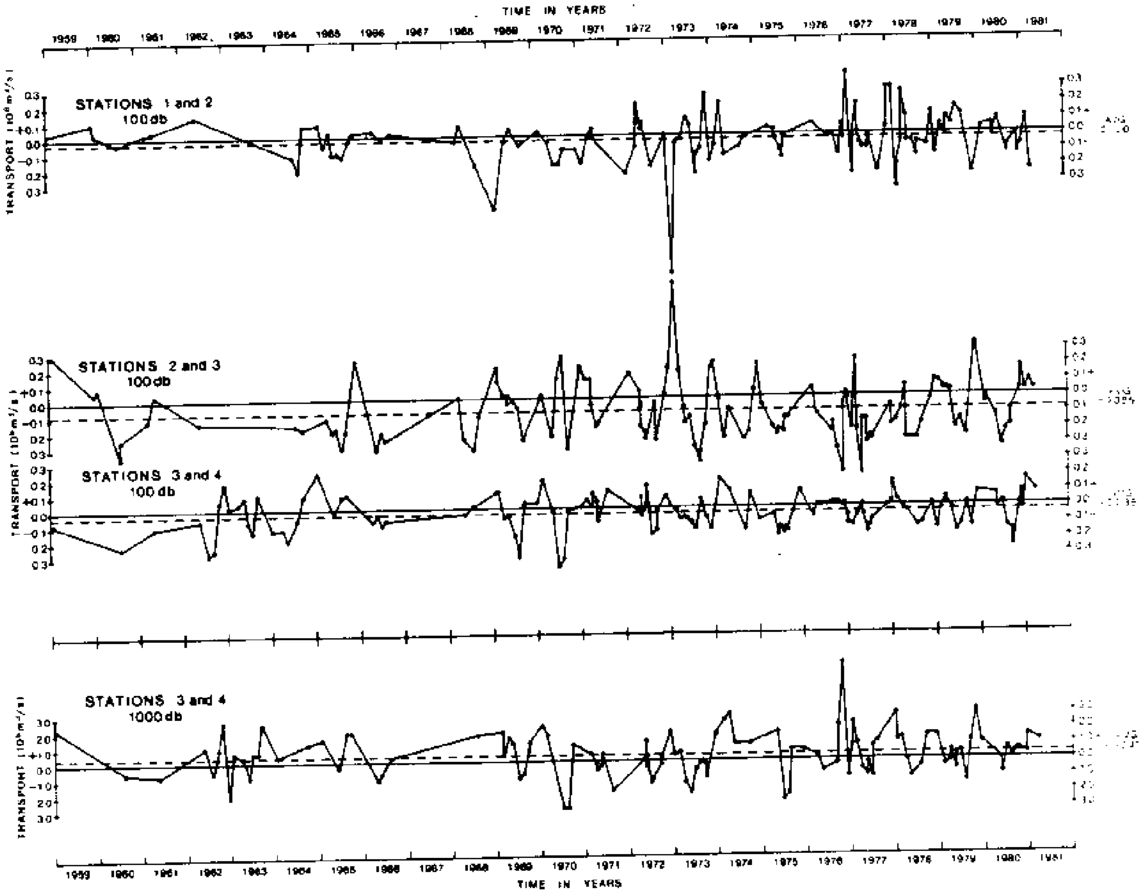


Figure 4. Interannual variability of baroclinic transports (sverdrups = $10^6 m^3/s$) over the continental slope (Stations 3 and 4 -- relative to 100 and 1000 db) and shelf (Stations 1 and 2; 2 and 3 -- relative to 100 db) (Tabata and Oliphant 1982).

In recent years a number of detailed current measurements were made from moored instruments over the continental shelf off Oregon, Washington, British Columbia and Alaska (e.g. Huyer et al. 1975; Hayes and Schumacher 1976; Lagerloef et al. 1981; Royer 1982; Freeland et al. 1984). They show that the coastal currents are different and not as simple as depicted in charts of general circulation. Even if areas over the continental shelf and slope are excluded, as the coast is approached, circulation becomes more complex due to the presence of eddies and meanders (Figure 5). These moored measurements have shown that a narrow, poleward-flowing, coastal current frequently appears independent of the current farther offshore. For example, Freeland et al. (In Press) observed a narrow, northwestward current that hugs the west coast of Vancouver Island with speeds reaching as high as 40 cm/s and persisting for most of the year. Similarly, Lagerloef et al. (1981) found a persistent northwestward-flowing current over the shelf off Yakutak, Alaska. Moreover, observations made by Royer (1982) over the shelf off Prince William Sound, Alaska, indicate a northwestward-flowing coastal current within 25 km of the coast with speeds in excess of 100 cm/s. In winter a similar, strong northwestward-flowing current or jet off the coast of Vancouver Island is apparent in infrared satellite imagery. Such a jet is interpreted from the sharp, tongue-like temperature distribution as shown in Figure 6.

In addition to these coastal currents meso-scale eddies of the open ocean off the coast (Figure 5) may influence the circulation near the coast. Such eddies may have surface current speeds well in excess of 100 cm/s (Tabata 1982) and that their outer perimeter may skirt the area over the continental shelf, thus modifying the current pattern there to a significant extent. For example, during the spring of 1975, a northward-flowing coastal current with a speed of about 50 cm/s existed over the shelf off Sitka, Alaska. Offshore of this an eddy with a diameter of 100 km created a southward-flowing current of about the same strength just west of the northward-flowing inshore current. A similar type of recurring eddy appears to occur off the Queen Charlotte Islands and may also influence coastal currents there in much the same way as does the eddy which occurs to the north. These anticyclonic eddies retard the northward-flowing coastal currents.

The effect of these currents on migrating juvenile salmon is not immediately apparent. Possibly they are rapidly carried to their destination (off Kodiak Island) or, if caught in the eddy, they might be dispersed offshore. The current distribution of the type observed in the spring of 1975 may have other implications. In areas of strong current shear (strong southward flow offshore and strong northward flow inshore) upwelling can bring nutrients from below and increase the primary productivity in the area. Zooplankton may be abundant in such an area, leading to concentrations of fish.

Other events complicate the circulation pattern over the shelf and slope. Mysak (1977) and Ikeda et al. (In Press) show that the presence of a wave-like pattern off the coast of Vancouver Island may be due to baroclinic instability resulting from appeciable vertical shear of the currents. Coastally-trapped baroclinic Kelvin waves can occur over the continental shelf, and in the northern hemisphere they propagate with the coast to the right. Mysak et al. (1982) have examined such waves with a phase speed of about 40 cm/s along the coast of British Columbia and have indicated that waves (having a period of about five years) are correlated with sockeye catches in British Columbia. Since the currents associated with the Kelvin waves have speeds comparable to the average swimming speeds (about 20 cm/s) of the sockeye juveniles during their northwestward migration in autumn, it is conceivable that the speed of the advecting water could be a factor. For example, fish can be transported to their destination earlier or later, depending on what stage of the phase of waves by which they are affected. The study further indicated that the 5-year peak the sea-surface temperature at Amphitrite Point, on the west coast of Vancouver Island, leads the weight anomaly of Fraser River

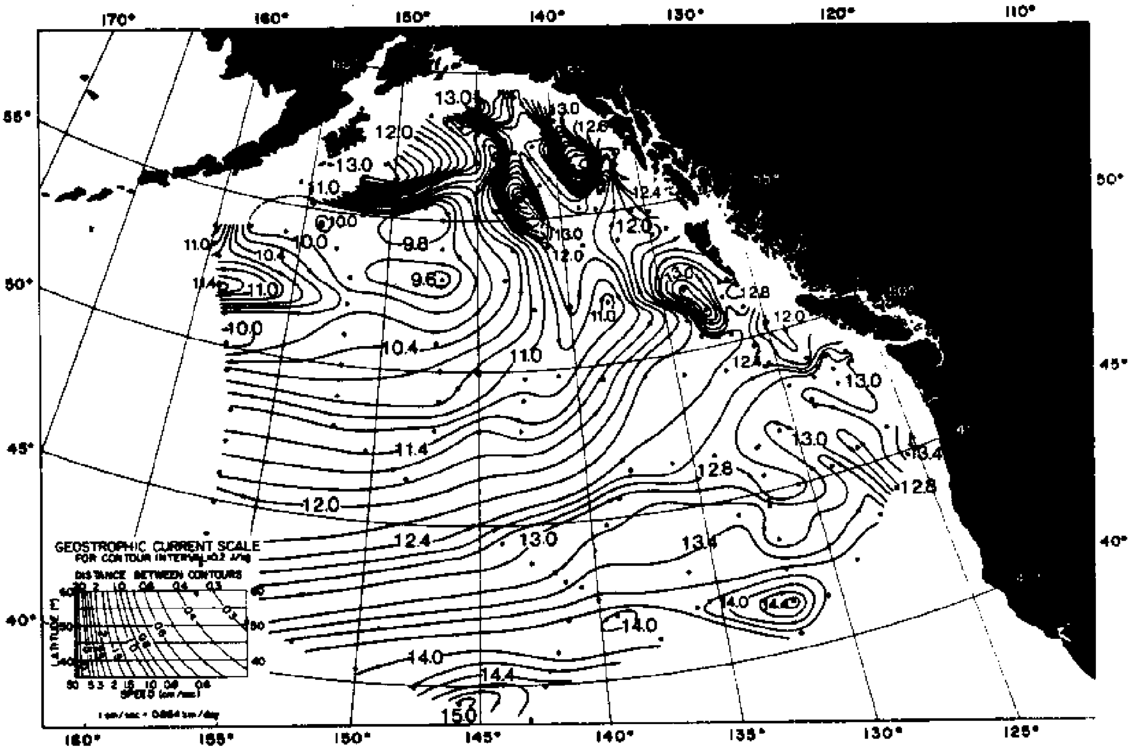


Figure 5. Chart of northeast Pacific Ocean showing pattern of surface baroclinic currents (relative to 1000 decibar level -- from May-July 1961 data). The distance between the contours is inversely proportional to the speed of the current.

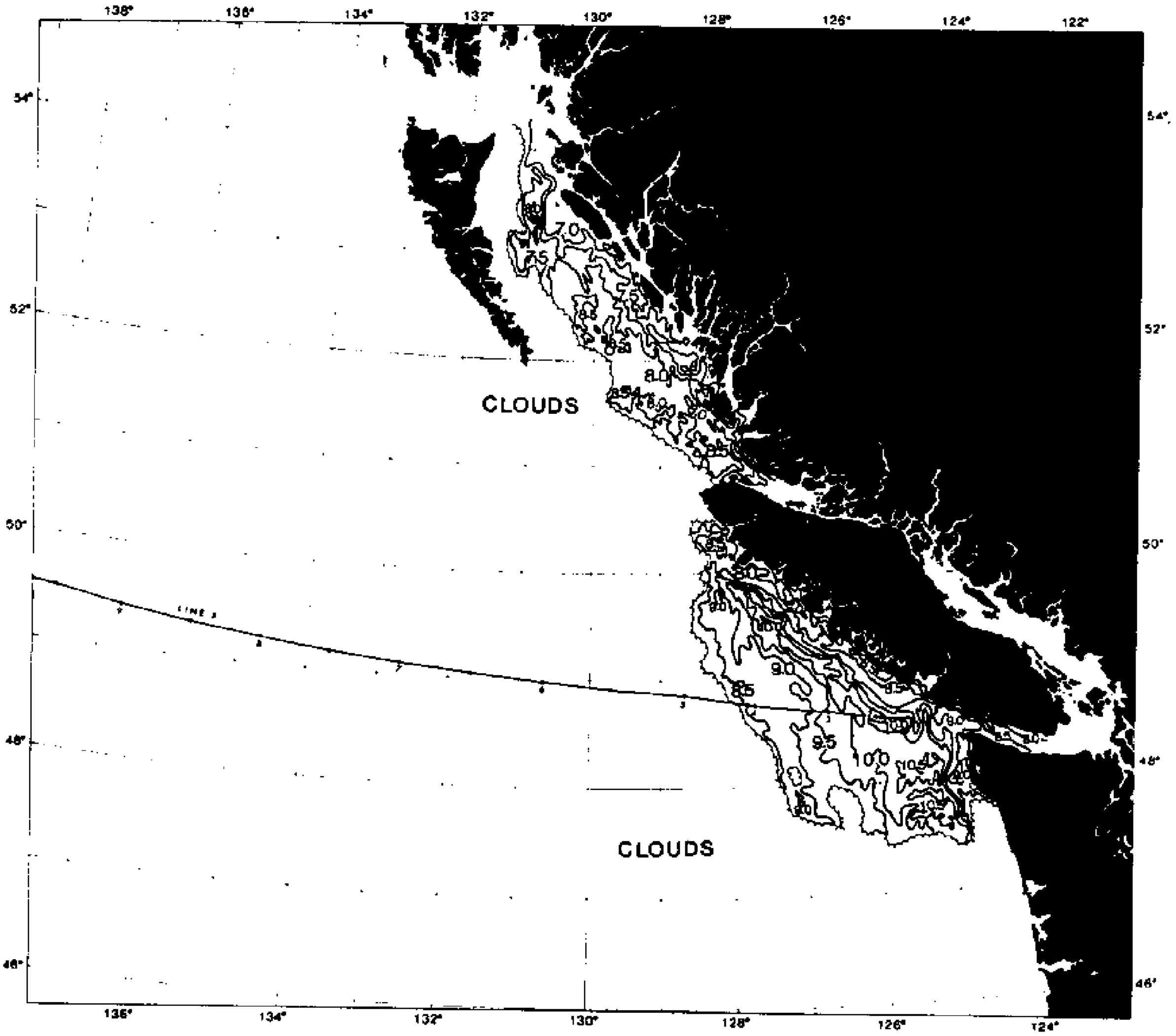


Figure 6. Sea surface temperature (^{0}C) derived from infrared satellite imagery from which it is possible to deduce the presence of a jet of warm, northward-flowing coastal water in winter (17 January 1980).

sockeye by three to four years. This could imply that these currents are affecting the juveniles, as the resulting adults return to the coast, generally, from two to three years later.

Except for the coastal currents and some eddies that possess surface speeds in excess of 100 cm/s, speeds of currents in the northeast Pacific are relatively small compared to the swimming speed of juvenile salmon. According to tag release and recovery data juvenile sockeye from the Fraser River can travel at a rate ranging from 16 to 31 cm/s (14 to 27 km/day) during their northwestward journey (Hartt 1980). Whether the large range of speed is due to the influence of currents, feeding habits of the juveniles, or other factors during their migration was not ascertained.

Coastal upwelling processes are important within this narrow band of water along the coast and result in enrichment of surface waters through import of nutrients from greater depths. However, north of latitude 48°N, upwelling of significance occurs off Vancouver Island and perhaps as far north as off the Queen Charlotte Islands (Bakun 1973) and is probably of minor importance off Alaska except during anomalous years. Previously it was shown that the large interannual variability of zooplankton abundance along the coast of California was attributed to wind-driven effects such as Ekman transport, upwelling, etc. (Bakun and Parrish 1980). In a more recent study Chelton et al. (1982) have indicated that this variability is the result of interannual changes of the strength of the California Current. Strengthening of the southward transport of the Current results in increases in zooplankton biomass; weakening of the current results in low biomass. The period of low biomass are usually associated with El Nino-Southern Oscillation event (ENSO). Chelton et al. (1982) also observed that there were occasionally strong oceanographic events off the coast of California which were unrelated to ENSO effects. The availability of some commercial species of fish and crustaceans has been related to zooplankton abundance off California (Bakun and Parrish 1980) but such relationship has not been examined seriously for salmon along the Pacific coast.

Hartt (1980) noted that some juvenile salmon caught along the coast during their autumn migration had scars on their bodies indicating encounters with predators such as lampreys, seals, sea lions, sharks, and other predaceous pelagic fishes. From this it can be assumed that considerable mortality due to predation might be occurring before the juveniles begin their life cycle in the open waters of the northeast Pacific.

Open Ocean

By late autumn many juvenile sockeye have reached the northwestern corner of the Gulf of Alaska ([4] in Figure 2) and head south to the winter grounds ([5] in Figure 2) by late autumn and winter. During spring and early summer they return to the same general location in the northwestern corner of the Gulf ([7] in Figure 2). The immature fish will then, for the second time, head southward by winter ([8] in Figure 2). At this stage some of the fish are maturing so both the immature and the maturing fish will migrate to summer feeding grounds once again, still others will make one or more additional cycles, while the maturing fish will start migrating to their home river in late spring ([10] in Figure 2).

Several authors have considered the relevance of oceanographic factors to the distribution and migration of sockeye in the open ocean. Oceanographic studies based on data collected during the period of salmon investigations (Uda 1963; Dodimead et al. 1963; Favorite et al. 1976) provide good reviews of the oceanography of the Subarctic Pacific. However, they do not, but themselves, deal specifically with the salmon distribution.

Manzer (1964) observed that sockeye caught in gillnets (capable of catching fish to depths of about 60 m) during late spring through summer in the northeast Pacific occurred within the upper 60 m of water in late spring and 40 m in summer. As can be seen from Figure 7 the salinity range in the upper zone (approximately 100 m) during this period is only about 0.1 °/oo. It is doubtful if the vertical range of salinity of this magnitude in the upper 100 m of water directly affects the vertical distribution of the fish. Note that the upper 30 m during the summer is a seasonal upper zone which gradually dissipates as mixing progresses from autumn through winter (Figure 7). The horizontal salinity range of the surface waters of the northeast Pacific frequented by both the immature and maturing sockeye is only about 0.5 °/oo in the open ocean. As shown from the May-July 1961 data (Figure 8), the salinity range is relatively small in most of the northeastern Pacific. Only when waters over the continental shelf are considered does the range become larger. With a range this small salinity probably has little direct effect on open-ocean distribution of salmon. However, over the continental shelf of the eastern Bering Sea the general absence of juveniles and older sockeye is believed to be due to the presence of low-salinity waters (French et al. 1976). Neither Favorite and Hanavan (1963) nor French et al. (1976) were able to find an obvious relationship between the sockeye distribution and surface salinity, as observed from experimental fishing and oceanographic data.

Annual variations of several degrees in temperature in the upper zone are common in the greater part of the North Pacific. At Station P in the northeast Pacific the average monthly surface temperature varies from a minimum of 5° in March to a maximum of 13° in August, as is shown in Figure 9. Such variations are also present in the wide area of the subarctic and subtropical regions as shown by examples in this figure. The thickness of the upper mixed layer and the depth of the associated thermocline vary from about 30 m in summer to more than 100 m in late winter. The thickness of the layer and the depth of the thermocline are similar to the corresponding layer and depth of the (seasonal) halocline (Figure 7) and therefore vary seasonally. Manzer (1964) noted that during late spring and summer sockeye were always distributed above the depth of the thermocline. The permanent halocline located below the depth of 100 m (Figure 7) is one of the characteristic features of the Subarctic Pacific (Dodimead et al. 1963). It prevents the upper mixed layer from extending beyond the depth of about 125 m. Consequently, it is possible to observe a temperature inversion at a depth of about 125 m with the temperature in the upper zone being less than at the halocline. Uda (1962) has referred to water having this feature as "dichothermal" structure and indicated that salmon are usually present where such a structure exists. The distribution of sockeye in spring-summer has been related to the presence of such temperature minima apparently caused by advection of cold water from the western Pacific and winter turnover (Favorite 1967). The southern boundary of this structure is denoted by a temperature front indicated by the vertical slope of the 4° or 5° isotherm in the central Pacific near latitude 45°N and is believed to denote the southern extent of the range of sockeye throughout the year (Favorite and Hanavan 1963; Favorite 1967). However, it is unclear why the temperature structure at depth of 125 m is important to fish concentrated near the surface.

A number of studies have indicated that sockeye inhabit areas of certain surface temperature ranges. They occur within a wide range between 0 and 16° but generally occupy a much narrower, preferred range, frequently within a few degrees (Table 1). Maturing sockeye may be associated with slightly lower temperatures than the immature sockeye during February-June (Manzer et al. 1965; French et al. 1976). The relationship between sockeye and temperature shown by French et al. (1976) is based on sockeye catch data from 1956-1971 whereas the temperature data are based on ships' reports collected over 100 years prior to 1961. Since the data sets are not from the same period their relationship can only be considered approximate. A more recent, quality-controlled monthly average temperatures based

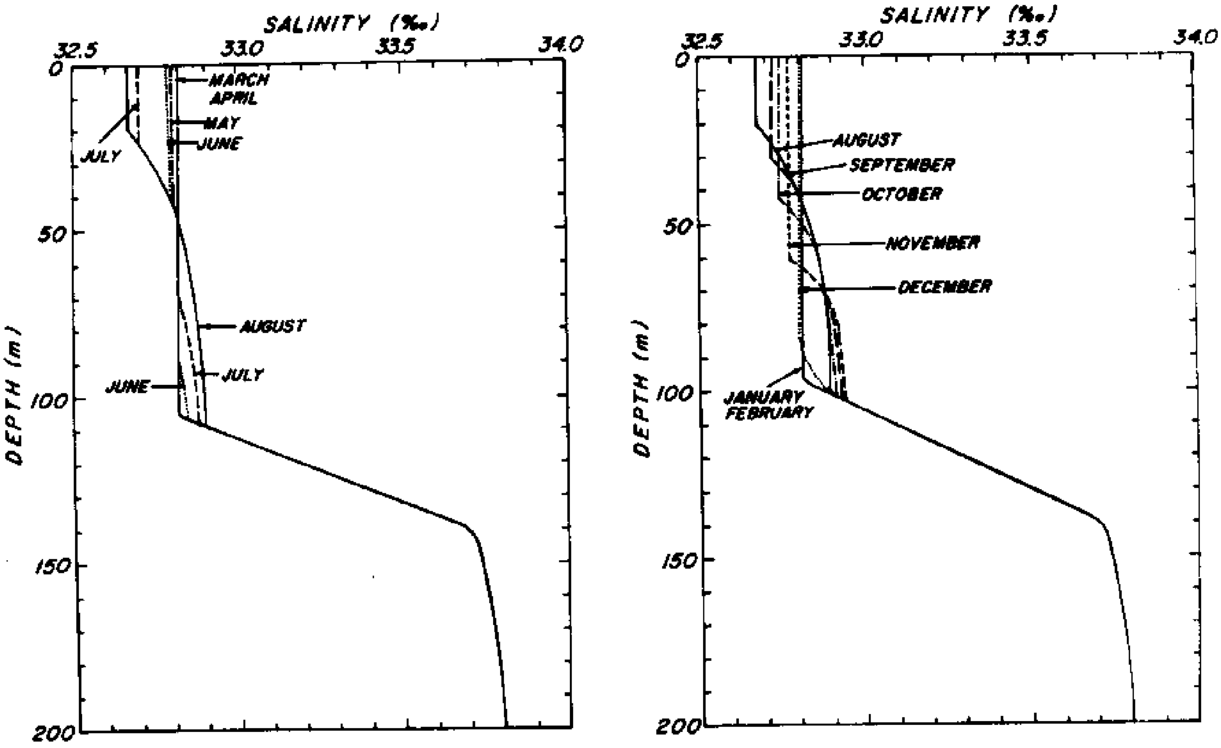


Figure 7. Mean monthly profiles of salinity (⁰/oo) at Station P (50⁰N, 145⁰W).

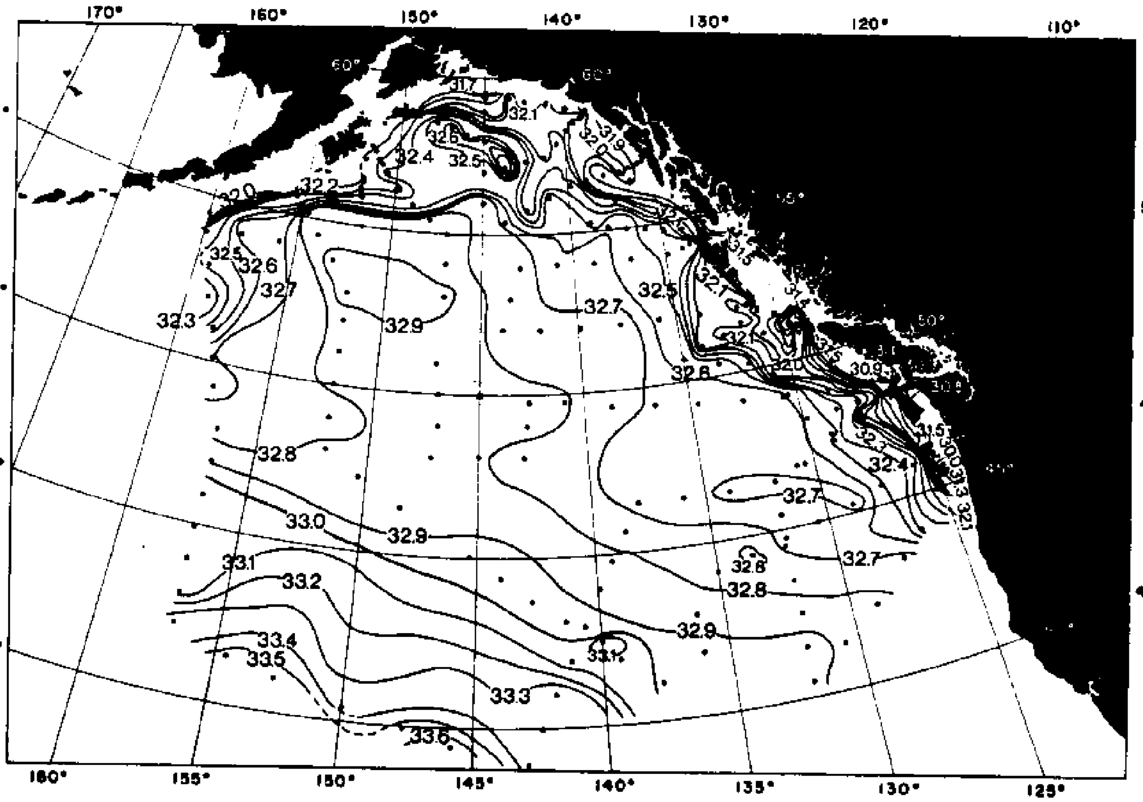


Figure 8. Sea surface salinity (^{0}/oo) of the northeast Pacific Ocean (May-July 1961) (observations from 10 m depth). Data from 10 m depth rather than from the surface are used as the latter contain too many errors (Tabata 1978).

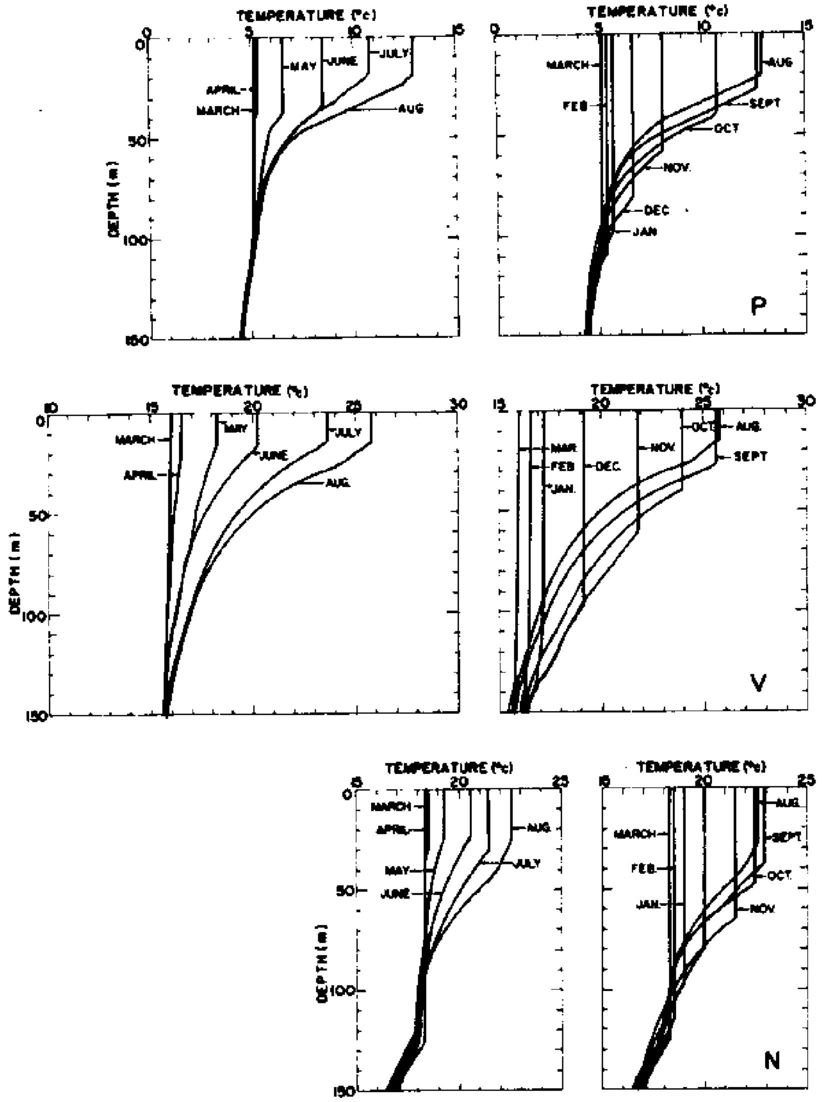
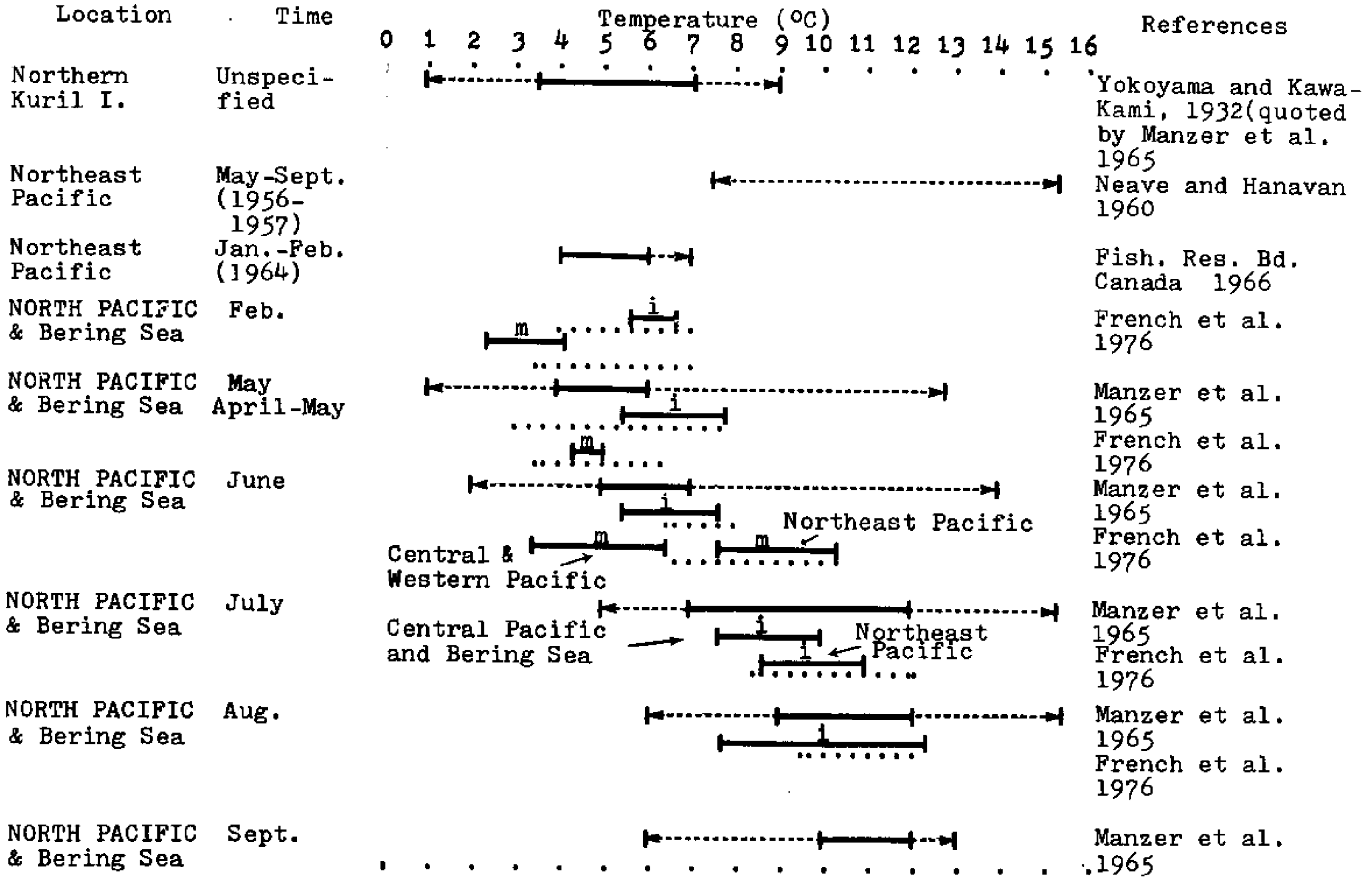


Figure 9. Monthly profiles of temperature (°C) at Stations P (50°N, 145°W), V (34°N, 164°E) and N (30°N, 140°W).



Location	Time	References
Northern Kuril I.	Unspecified	Yokoyama and Kawa-Kami, 1932(quoted by Manzer et al. 1965
Northeast Pacific	May-Sept. (1956-1957)	Neave and Hanavan 1960
Northeast Pacific	Jan.-Feb. (1964)	Fish. Res. Bd. Canada 1966
NORTH PACIFIC & Bering Sea	Feb.	French et al. 1976
NORTH PACIFIC & Bering Sea	May April-May	Manzer et al. 1965 French et al. 1976
NORTH PACIFIC & Bering Sea	June	Manzer et al. 1965 French et al. 1976
NORTH PACIFIC & Bering Sea	July	Manzer et al. 1965 French et al. 1976
NORTH PACIFIC & Bering Sea	Aug.	Manzer et al. 1965 French et al. 1976
NORTH PACIFIC & Bering Sea	Sept.	Manzer et al. 1965

Table 1. Relationship between distribution of sockeye salmon and sea surface temperatures (°C). Manzer et al. (1965) and French et al. (1976) utilized data taken during 1955-1960 and 1956-1971, respectively. Solid lines denote preferred ranges and dashed lines indicate tolerable ranges. Dotted lines represent relationship between sockeye distribution in the northeast Pacific and updated monthly averaged sea surface temperature climatology (Reynolds 1982) (i = immature fish; m = maturing fish).

on data taken prior to 1970 (Reynolds 1982) shows little difference in the temperature range between maturing and immature sockeye in the northeast Pacific (Table 1).

The north-south migration of immature sockeye is assumed to be due to the warming and cooling of water in the Subarctic Pacific; the northward migration being attributed to the warming of water and vice versa (Manzer et al. 1965; French et al. 1976). However, this assumption is difficult to substantiate as the following illustrations will show. If the climatological monthly sea temperatures for winter and summer shown in Figure 10 are compared to the winter and summer grounds of sockeye (Figure 2), during the winter and summer the sockeye are present where the temperature range is approximately 3.5-6.5° and 11.5-14.0°, respectively. If the fish inhabiting the winter grounds were to stay there instead of moving northward after winter, they would be in the waters where the temperatures range from 11.0 to 14.0° in summer. Similarly, if instead of moving southward after summer, the fish were to remain in the summer grounds, they would be in waters where temperatures range from 3.5° to 5.0° in winter. Thus sea surface temperatures do not appear to determine the seasonal, meridional migration of sockeye salmon.

Interannual variability of sea surface temperatures is appreciable in the northeast Pacific as shown by representative data from Station P (Figure 11). The magnitude of this variability is as large as the corresponding variabilities of well-mixed coastal waters (e.g. Pine Island off Queen Charlotte Sound). Some of the large anomalies of monthly temperature for Station P are in phase (e.g. 1957-1958) but others are out-of-phase (e.g. 1971). While this variability of sea temperatures by itself may not directly influence the year-to-year changes in the distribution or migration of sockeye, it may nevertheless reflect other changes in the ocean such as circulation or shifts of ocean boundaries that may be of importance to fish. However, insufficient data on sockeye catches in the open ocean are available to determine if there is any relationship between the interannual variability of ocean temperatures and the distribution of fish. On the other hand, there appears to be a correlation between winter-spring sea surface temperatures at a general location northeast of Station P (50-55°N, 140-145°W) and the timing of the return of the Fraser River sockeye to the coastal fishery (Blackbourn personal communication).

Each ocean province has its own unique water properties (salinity, temperature, dissolved oxygen content, nutrients, turbidity, etc.) and biological structure (Reid et al. 1978). The Subarctic Pacific, where the salmon occur, is essentially a divergent region where there appears to be a slow, continuous upward movement of deep water. It possesses a permanent halocline. It is relatively cold, rich in nutrients, with large annual changes of properties of water occurring above the halocline. The northeast Pacific in particular is, in a way, similar to an estuary as the supply of fresh water exceeds the losses by evaporation and freezing (Tully and Barber 1960). The Fraser sockeye are species that spend most of their ocean life in this unique region of Subarctic Pacific.

Whether the distribution and the migration of sockeye is related to specific water types or provinces within the Subarctic Pacific is not clear. On the one hand some evidence supports a relationship. For example, Royce et al. (1968) described the migration of Bristol Bay sockeye in relation to the Alaskan Stream and Subarctic Current. Similarly, French and McAlister (1970) suggested that during winter and early spring, maturing Bristol Bay sockeye are associated with the Alaskan Stream and the Alaska Gyre. Further, French et al. (1971) found that in May immature sockeye were mainly in the western Subarctic and in the transitional area between the Subarctic and Subtropic domain. On the other hand, there is another body of evidence that indicates such relationships are poorly defined. For instance, Bakkala (1971) points out that although there is some correlation between ocean currents and water types and the distribution of salmon, no clear relationship

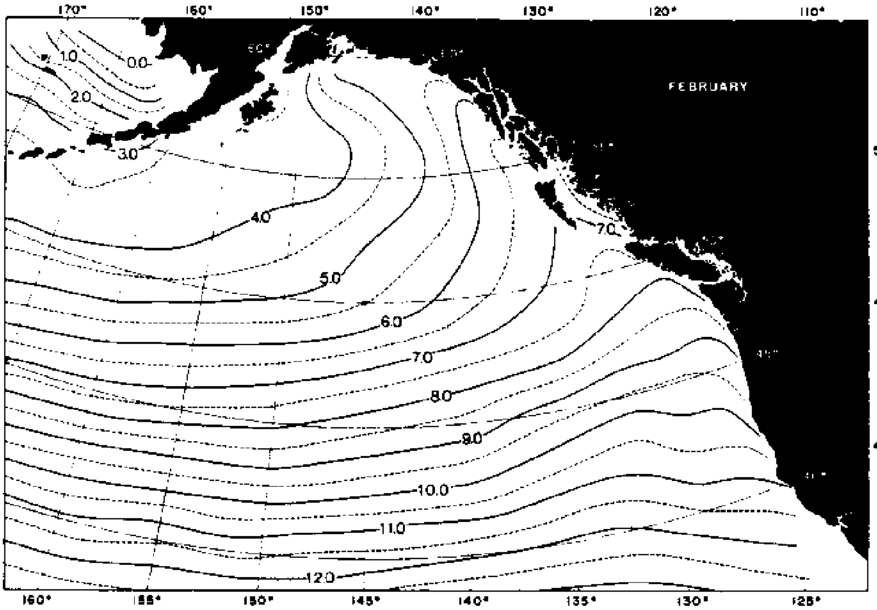


Figure 10a. Mean sea surface temperature (°C) of the northeast Pacific Ocean for February (based on data provided by Reynolds personal communication).

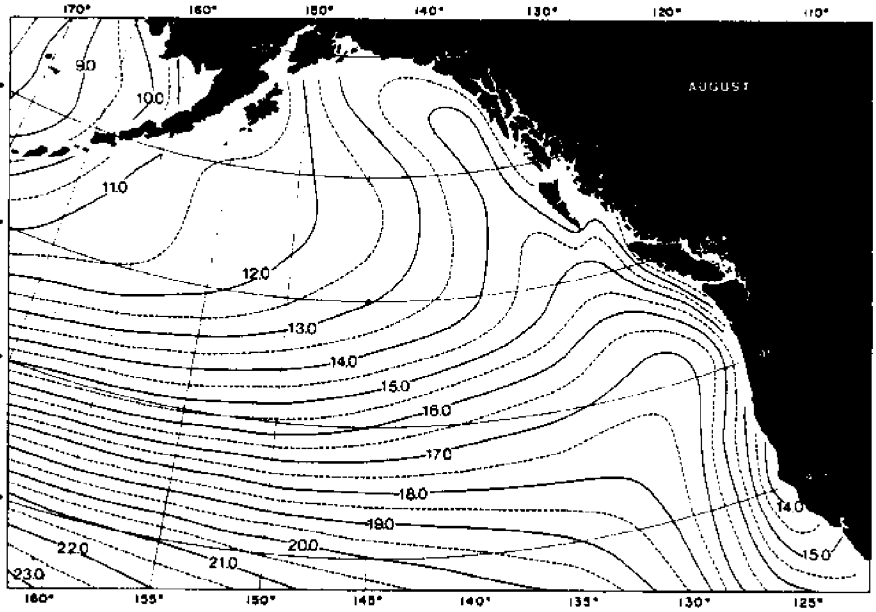


Figure 10b. Mean sea surface temperature (°C) of the northeast Pacific Ocean for August (based on data provided by Reynolds personal communication).

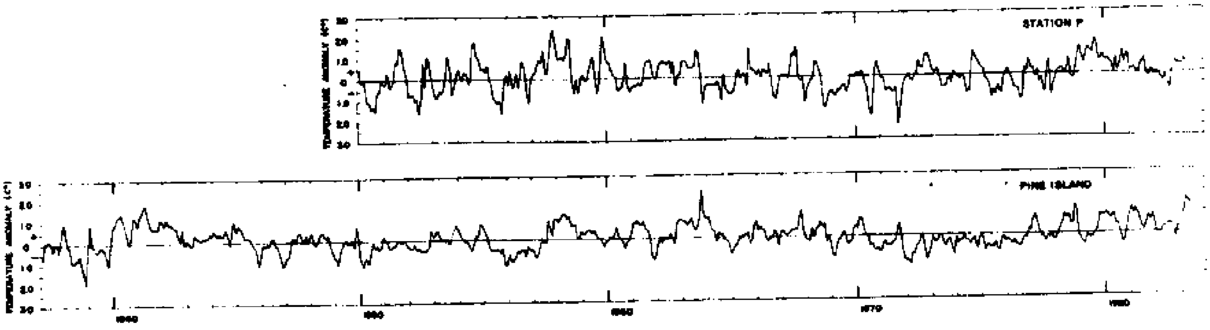


Figure 11. Anomalies of sea surface temperatures (^{o}C) at Station P and Pine Island.

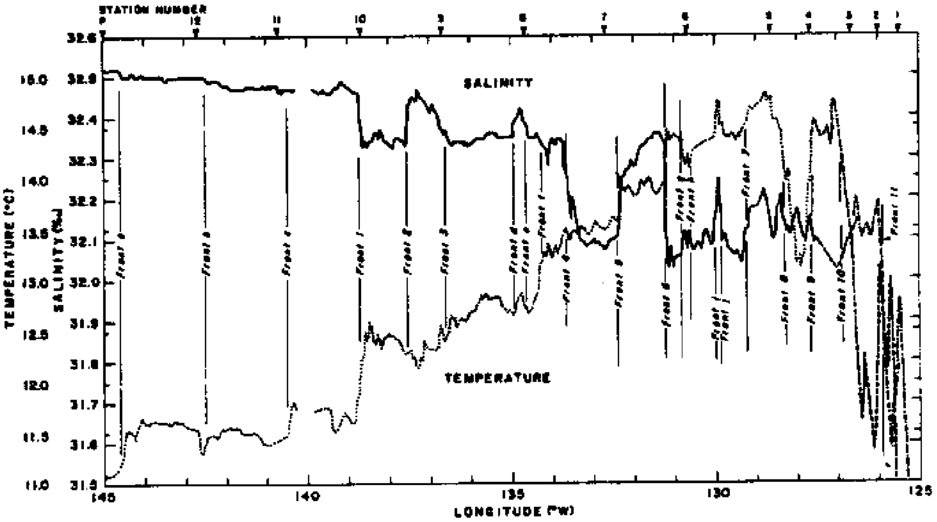


Figure 12. Sea surface temperatures (^{o}C) and salinities ($^{o}/oo$) along Line P (August 1975). A number of oceanic fronts featured by the relative maxima and minima can be seen (observations from 3-4 m depth).

was found with any single oceanographic feature. He further points out that immature fish were associated with two or three of the oceanographic features, such as areas and current systems, in any given season and area, but fish moved readily from one system (or water type) to another with no difficulty. In a more recent study French and Bakkala (1974) found no observable relationship between the migration of sockeye and certain oceanographic features; different oceanographic features did not affect the north-south movements nor their distribution. Clearly more systematic observations are needed to demonstrate relationships between oceanographic water masses and current systems and the distribution and migration of discrete stocks of sockeye.

The main food of sockeye in the northeast Pacific, as determined from examination of stomach contents of the captured fish, varied slightly with immature and maturing fish. At least for the summer, crustaceans seem to be the main food for immature sockeye and euphausiids, fishes and squids for the maturing sockeye (LeBrasseur 1966). French et al. (1976) compiled a list of food consumed by sockeye during spring-summer as observed by various investigators and concluded that euphausiids, fishes, crustaceans, squids, copepods, and amphipods were important, regardless of where the fish were found. However, the main food consumed differed among locations and among ages or sizes of fish. LeBrasseur (1966) noted that while the main food for both immature and maturing sockeye was similar, fishes were more important for the maturing sockeye while amphipods were the main food for immature sockeye. Further, he suggested that feeding was associated more with the availability of the food items rather than the preferences for specific organisms. Nevertheless, variability of food resources, both in time and space at any location may affect growth and/or residency at that location. Such varibility was found at Station P where at least a 10-fold difference in the standing stock of zooplankton occurs between the summer maximum and the winter minimum (Fulton 1978).

The maturing sockeye migrate northward ([9] in Figure 2) in early spring from the winter grounds and then head back ([10] in Figure 2) to the home river to spawn. Those not yet matured will complete another one or more cycles before they too will head to the spawning river.

Hypotheses and speculation concerning the "direction-finding" capability of salmon, especially their homing ability are numerous. Olfaction and celestial objects (Hasler 1971), electric potentials created by ocean currents (Royce et al. 1968) and earth's magnetic fields (Quinn 1980) have all been proposed as navigational cues.

Evidence is available to support the claim that olfactory imprinting of the salmon while in the native river is a guiding mechanism that leads them to a particular river (Hara et al. 1965). Hasler and Scholz (1978) have shown that experiments with coho provide conclusive evidence for olfactory imprinting. Hasler (1971) goes on to state that when salmon reach the coastal waters they can detect "odors" of the main rivers and select the correct one by the recognition of the odor imprinted as they left for the sea. In this respect, Brett and Groot (1963) have discovered that sockeye in fresh water can detect substance at a dilution of one part in 8×10^{10}. If they can detect such dilution in the open ocean it is possible that they might be able to select the "correct" coast before reaching the nearshore areas.

Favorite (1961) noted that the effects of coastal runoff on the surface salinity distribution could be traced over several hundred kilometers into the ocean. He suggested that the seaward extent of the diluted water may determine the location where homeward migrating salmon enter coastal waters. A similar type of surface distribution has been noted off the coast of Alaska (Ingraham 1979) which may be used as cues for homing salmon. In short, as with other animals, it appears that salmon utilize a variety of cues to migrate, switching from one set to another as circumstances warrant.

Detailed Observations of Sea Surface Temperature and Salinity

Sea surface temperatures (SST) and salinities (SSS) have been observed at discrete positions along a line between the southern coast of Vancouver Island and Station P (Line P) at approximately 6-week intervals since 1950 and 1957, respectively. These observations have shown that in the open ocean a number of identifying features such as relative maxima and minima of both SST and SSS are present. An example of SSS measured during August 1975 is shown in Figure 12. It is evident from this illustration that there are more than 10 oceanic fronts of various definition present in a distance of 1500 km. In terms of horizontal distribution some of the relative maxima and minima can be identified as part of a tongue of low-salinity water with sources along the coast, as shown in Figure 13. Another example from the November 1974 cruise, shown in Figure 14, also illustrates tongues of low-salinity water of coastal origin intercepting Line P. When the detailed measurements of SSS along Line P are plotted against time, it becomes evident that the relative maxima and minima can persist for a long time, at times longer than one year (Figure 15). These minima can be considered as presence of coastal surface water along Line P and they may be "sign posts" designating certain water masses originating at the coast. Some identifying features are present even at a location just east of Station P (Figure 15). These examples (Figure 12-15) clearly indicate that even as far as several hundred kilometers away from the coast there are features in the surface layers of the ocean that adult salmon could use to guide them to the coast.

During the sockeye's homeward migration, other oceanographic features may affect their migratory route. Until 1957 the bulk of the maturing Fraser River sockeye returned to the coastal waters off Vancouver Island and entered the Strait of Georgia via the Strait of Juan de Fuca. During the period 1953-1957 (when records were available), about 90% of the fish returned through the southern path and the remainder through the northern route, Queen Charlotte Strait-Johnstone Strait. In 1957 those choosing the northern route increased to 20%, and to 35% in 1958 (Royal and Tully 1961). The occurrence of this somewhat anomalous situation led Royal and Tully (1961) to examine the oceanographic data, and they concluded that the anomaly was the consequence of a warm water intrusion from the south that started in 1957 and continued to 1958. This period coincided with an anomalous global change in climate and is usually referred to as the 1957-1958 ENSO event. The diversion of the salmon and the lateness of the arrival of the fish to the river mouth was assumed to be due to the fish taking a circuitous migration path or the displacement of the fish to more distant feeding grounds to avoid the warm water intrusion. Another relatively large diversion (34%) occurred in 1972, which was another ENSO year. Although this event was not evident in coastal sea temperatures, the mean sea level observed in British Columbia showed that the ENSO effect was felt at least as far north as Vancouver Island. During the recent ENSO of 1982-1983 both the SST along the coast and the mean sea level heights were anomalously high, higher than during the previous large ENSO of 1957-1958 (Tabata In Press). The diversion of sockeye via the northern route was as large as 80-90% -- the largest percentage ever recorded (Blackbourn personal communication). Thus there is an apparent ENSO effect on sockeye migration. However, the northern diversion since 1977 has never been lower than 23% and were as large as 70% during 1980 and 1981 (Blackbourn personal communication) which were not ENSO years and is, therefore, unrelated to ENSO.

In order to examine the possible relationship between the coastal oceanographic factors and the diversion of the Fraser River sockeye, Wickett (1977, 1980 unpublished) used a multiple regression analysis taking two or three independent varia-

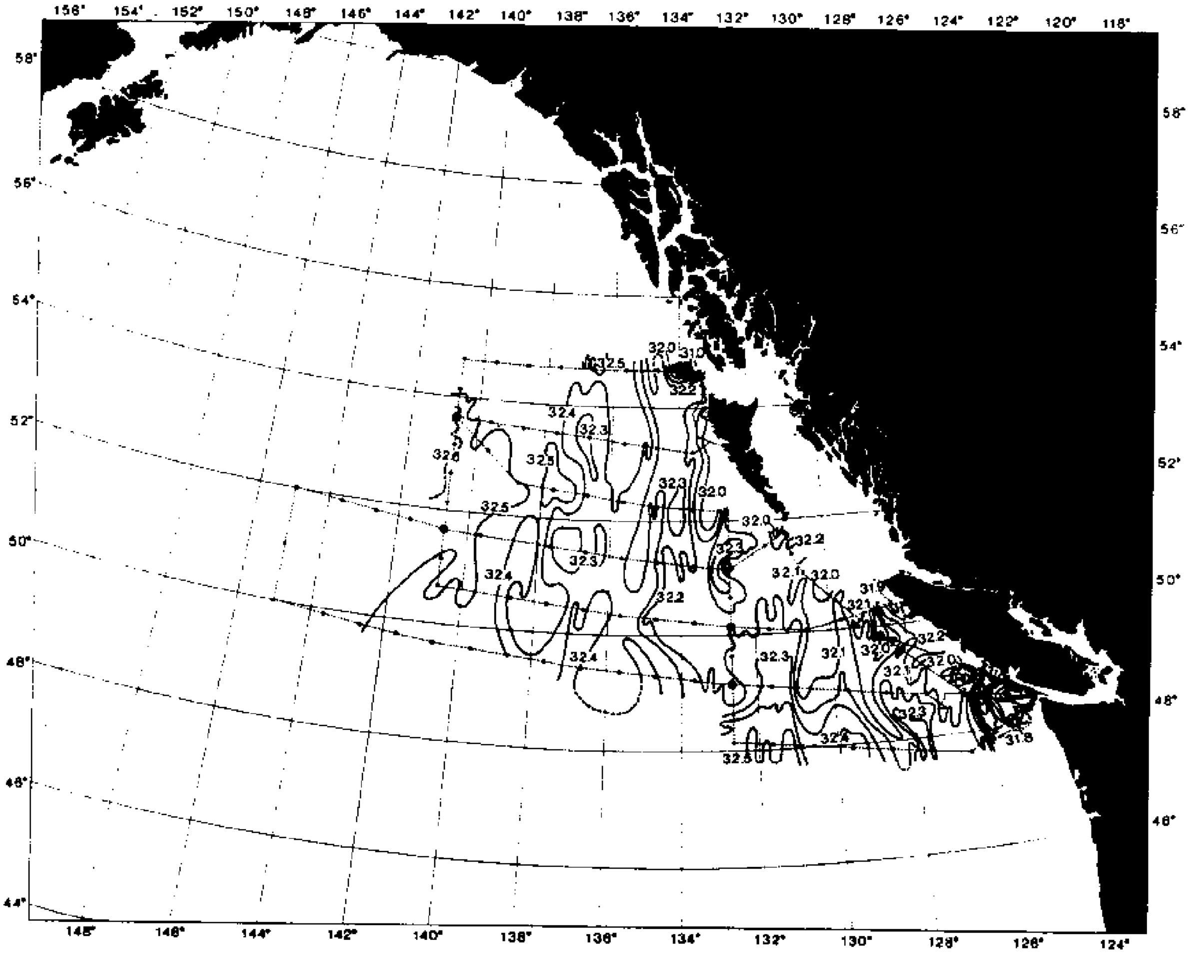


Figure 13. Horizontal distribution of sea surface salinities (°/oo) based on continuous salinity observations along the cruise tracks (August - September 1975) (observations from 3-4 m depth).

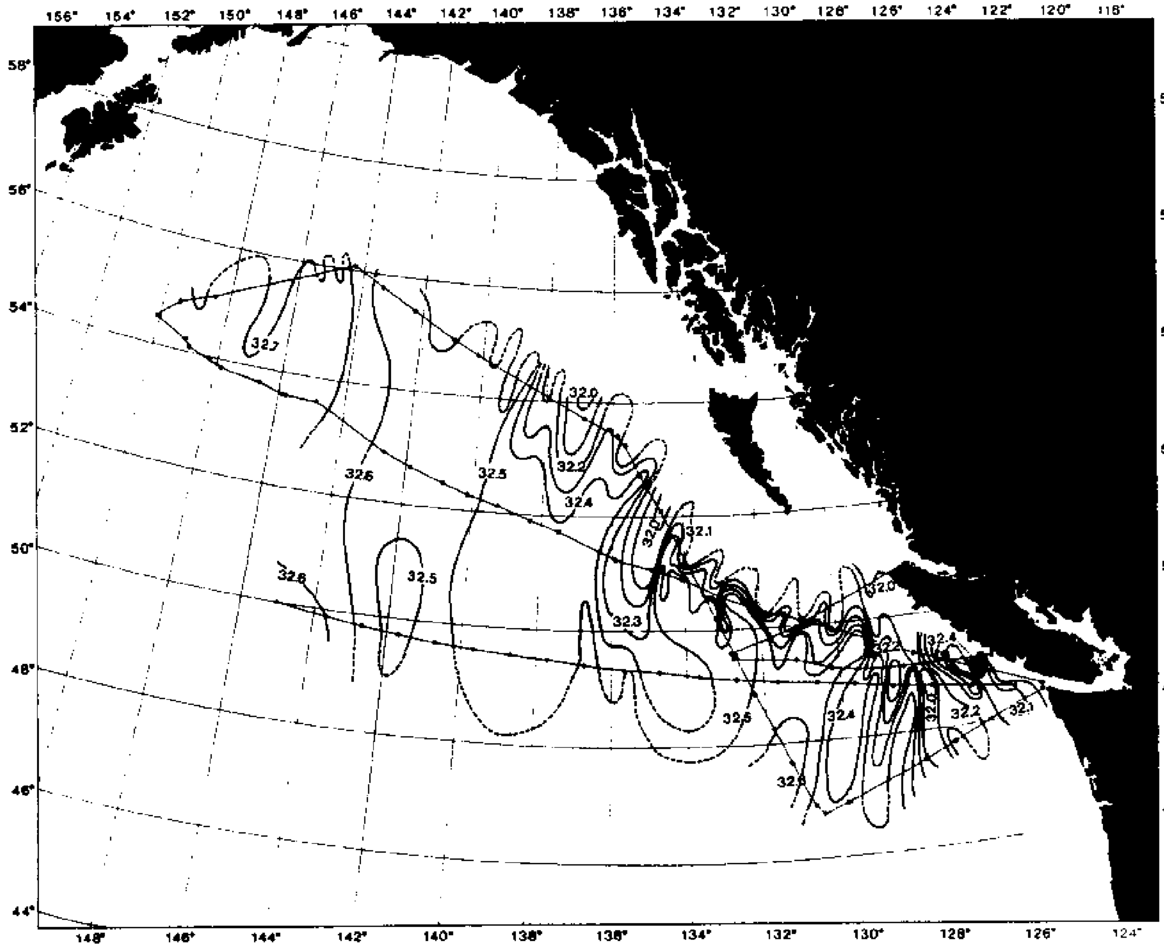


Figure 14. Horizontal distribution of sea surface salinities ($^0/oo$) based on continuous salinity observations along the cruise tracks (November 1974) (observations from 3-4 m depth).

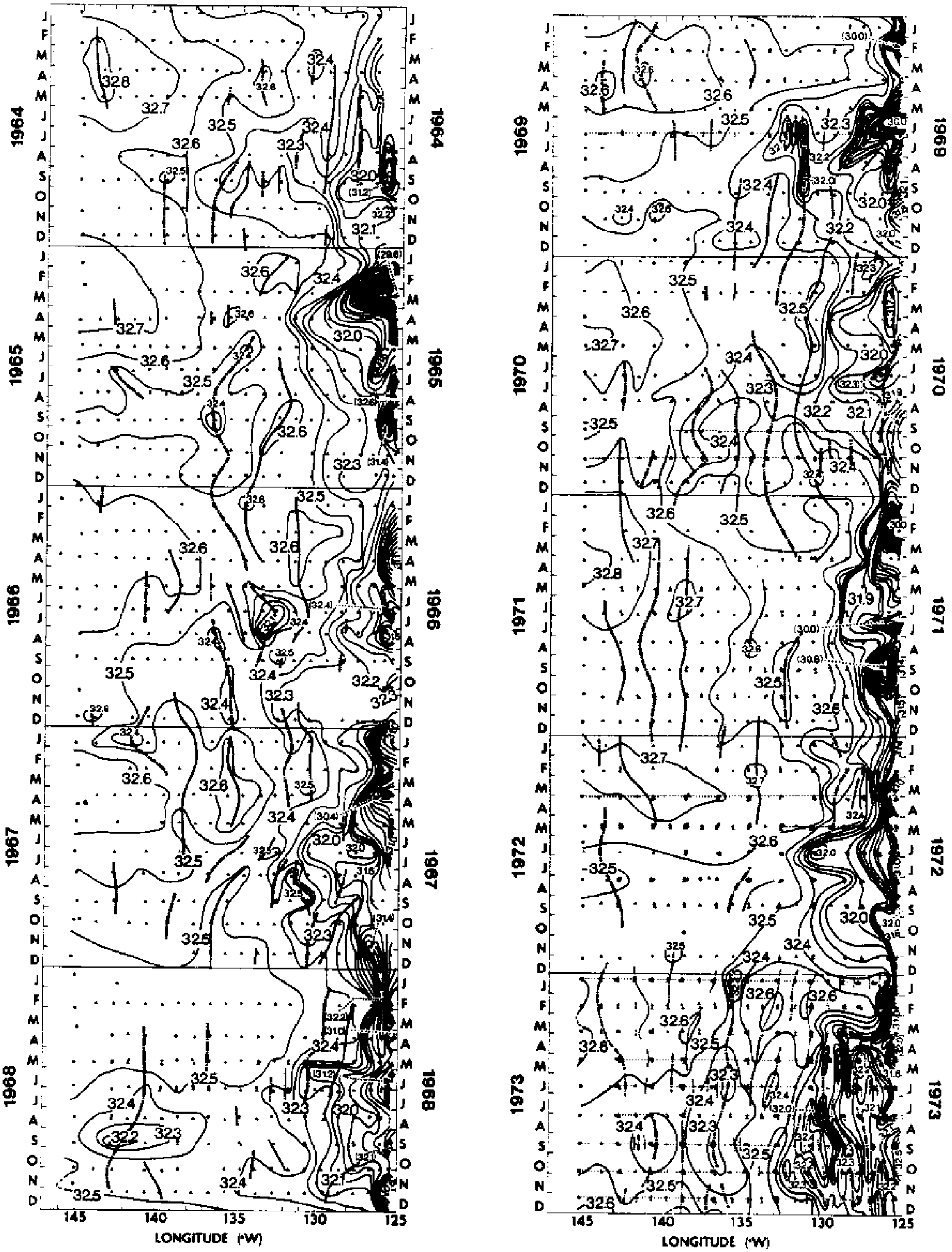


Figure 15a. Sea surface salinities (⁰/oo) along Line P plotted against time, 1964-1973. Note that some maxima and minima persist for more than one year (observations from 3-4 m depth).

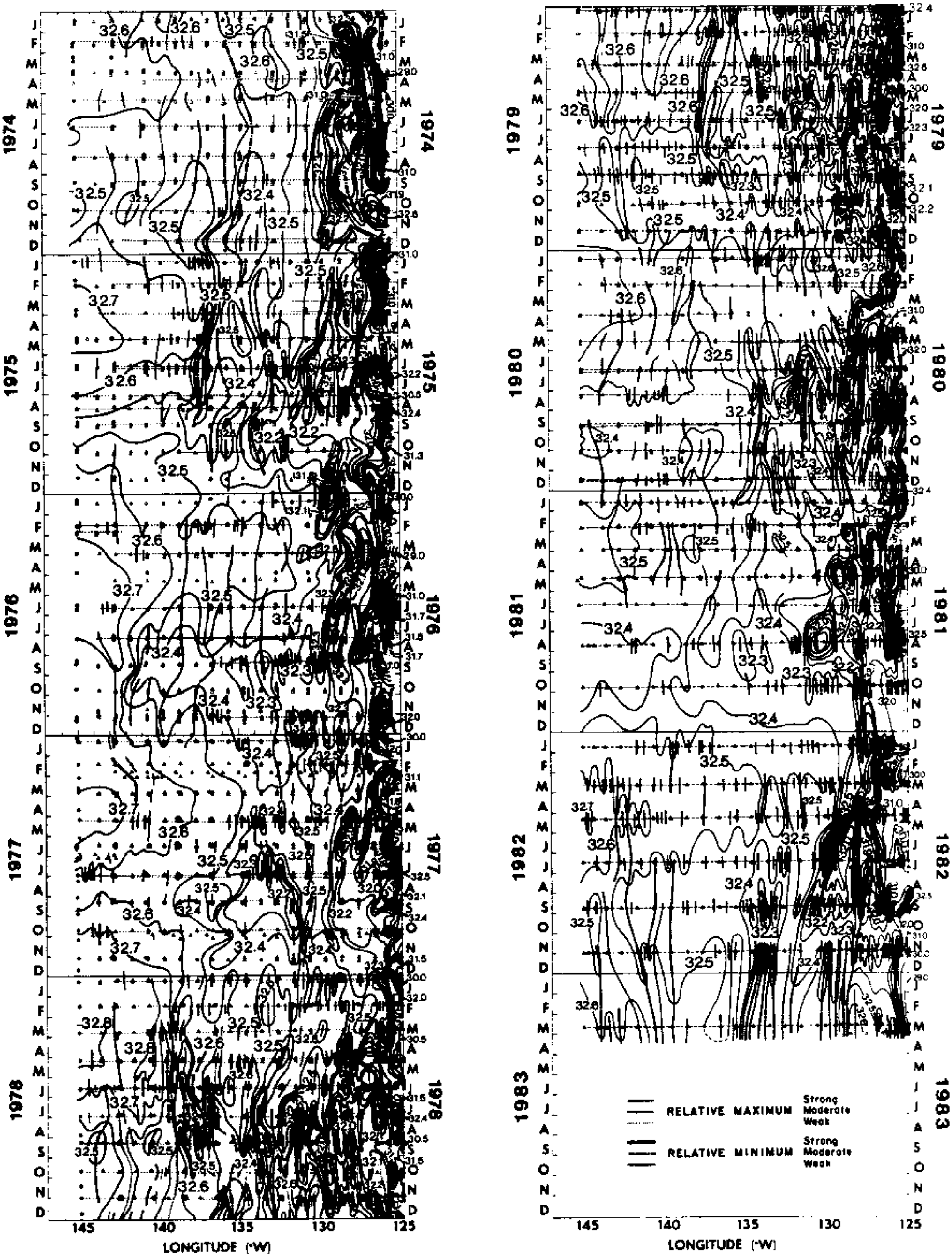


Figure 15b. Sea surface salinities (⁰/oo) along Line P plotted against time, 1974-1983. Note that some maxima and minima persist for more than one year (observations from 3-4 m depth).

bles at a time. By using the February to June mean sea level at Tofino (west coast of Vancouver Island) and April to June monthly mean Fraser River discharge he obtained a reasonably good relationship between the percentage diversion and the two physical variables (Wickett 1977). The addition of another variable, Ekman transport to the above relationship (Wickett 1980) did not materially improve the correlation. From these results, Wickett concluded that increasing the proportion of Fraser River water discharged into the ocean to the northwest of Vancouver Island increases the percentage of Fraser River sockeye migrating through the northern path. The more recent data on diversion do not appear to support this relationship (Blackbourn personal communication).

Conclusions

Despite the fact that the bulk of ocean mortality is believed to occur in the early ocean-life stage of the sockeye (or for any salmonids) almost no studies have been conducted on how oceanographic conditions affect the distribution, migration, and survival of juvenile sockeye. Joint oceanographic-biological studies are needed during the life stages of the sockeye from their entry into the estuary to their northern destination. More research is also needed on the effects of long-period phenomena such as Kelvin waves on sockeye migrations along the continental shelf, on the diversion of northward-moving and southward-moving juveniles in the Strait of Georgia, on reasons adults return via either the southern or northern routes around Vancouver Island, on the role of low-salinity surface waters of probable coastal origin in the open ocean as a guide to returning adults, and on the role of predators on ocean survival, and distribution of sockeye during their life cycle in the ocean.

Recent oceanographic studies indicate a narrow, poleward coastal currents off the coast of Vancouver Island and Alaska and well-defined eddies whose edges touch the continental shelf. These currents may be important to the migrating juveniles during their trek from the coastal areas off Juan de Fuca Strait and Queen Charlotte Strait to the region off Kodiak Island during the first several months of the sockeye's ocean life. The relevance of these currents depends on the proportion of juveniles that proceed through Juan de Fuca Strait, Queen Charlotte Strait, Hecate Strait or west coast of the Queen Charlotte Islands or head immediately westward into the open ocean upon leaving Juan de Fuca Strait and Queen Charlotte Strait.

Future studies to relate oceanography to sockeye (or other salmonids) biology should seek cause-and-effect relationships that can be used as a reliable, predictive tool for effective management of salmon fisheries.

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Variability of Marine Survival of Pacific Salmonids: a Review

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Abstract

Time series of total marine survival rate estimates for a number of North American salmonid stocks were reviewed. Only species with extended fresh-water rearing phases were considered. Variability in marine survival tends to be quite variable, and such variability is largely unexplainable from smolt data such as mean smolt size, age composition, or abundance. The causes of such variability in the marine environment are poorly understood. The best correlation so far found between marine survival and a marine environmental factor (strength of ocean-upwelling) is for coho salmon originating from the Oregon coast and Columbia River. However, the biological mechanism even for this case is not known.

Introduction

This paper reviews case histories of salmon runs for which the marine survival rate from smolt outmigration to adult return was well estimated (or indexed) for a series of consecutive years. The purposes were (1) to clarify the extent of variability in marine survival; (2) to review the state of knowledge about mechanisms for observed variability; (3) to discuss the extent to which such mechanisms are known to be related to broad changes in nearshore marine or oceanographic conditions; and (4) to point out any commonalities in marine survival trends among regions within a species or across species.

My choices of case histories for inclusion in this review may be arbitrary. I included North American stocks of those species with extended freshwater rearing phases: coho salmon (Oncorhynchus kisutch), sockeye salmon (O. nerka), chinook salmon (O. tschawytscha), and steelhead trout (Salmo gairdnerii). I discussed stocks for which (1) smolt out-migration had been estimated with relatively high precision, such as from direct count through a wier, known hatchery release numbers, marking, or acoustical means; and (2) the number of adults that resulted from known smolt numbers had been closely measured or indexed.

This review was intended to broadly elucidate whether marine survival of salmonids with extended freshwater rearing phases tends to be relatively constant or relatively variable. If constant, then freshwater factors may be more important than marine factors for explaining run-strength variability; if highly variable, this would amplify the need for further understanding or study of salmonids in their marine environment.

The term marine survival in the context of this review may be somewhat inappropriate, since for all case histories presented there is a freshwater transitional phase between times of smolt enumeration and entrance to the marine environment per se. Perhaps a better term is post-smolt survival rate, which is the fraction or percentage of smolts that survive to adulthood. I use the terms "marine survival rate" and "post-smolt survival rate" synonymously, implying that most of the mortality occurring between smolt enumeration and adult enumeration probably takes place in the marine environment, including both estuary and open sea.

Data from the following stocks are considered in this review:

Species		Stock	Years of smolt outmigration
Coho	1.	Oregon Production Index (OR, WA), hatchery	1960-1981
	2.	Big Qualicum River (BC), hatchery	1973-1980
	3.	Puget Sound (WA), hatchery	1959-1973
Sockeye	1.	Lake Washington (WA), nonhatchery	1969-1981
	2.	Chilko Lake (BC), nonhatchery	1951-1974
	3.	Babine River (BC), nonhatchery	1963-1979
	4.	Karluk Lake (BC), nonhatchery	1926, 1929-1933
	5.	Bristol Bay (AK), nonhatchery	1971-1981
Chinook	1.	Columbia River fall chinook (WA, OR), hatchery	1962-1965
Steelhead	1.	Snow Creek (WA), nonhatchery	1978-1980
	2.	Keogh River (BC), nonhatchery	1977-1980

Coho

1. Oregon Production Index (OPI)

The term OPI refers to hatchery and nonhatchery production from the Columbia River and Oregon coast. Over the past 25 years most of this production has been from public hatchery smolt releases (Mathews 1980). The ocean distribution of the catch is relatively well known from marking experiments. Consequently, estimates of post-smolt survival rates developed by the Oregon Department of Fish and Wildlife (1982) from catch and escapement data, public hatchery smolt release data, and judicious apportionment of total catch into public hatchery, private hatchery, and nonhatchery components (T. Nickelson, ODF&W, Corvallis, Oregon, personal communication) provide a good, long-term series for consideration of variability in marine survival of hatchery smolts released at mean sizes ranging from 15 to 30 g per individual release group (Washington, 1982). According to Table 1, post-smolt survival rate over a 22-year period has ranged from 2.4% to 10.7%, or about fivefold between low and high. The average has been 5.3%. In all of the most recent six years, survival has been less than average, which has prompted considerable effort to explain variability in survival. Of many factors considered by ODF&W (1982), including Oregon coastal ocean upwelling during spring and summer of smolt outmigration, overplanting the ocean (density dependent mortality), and declining trends in hatchery smolt quality, upwelling offers a relatively high degree of explanation (Gunsolus 1978; ODF&W 1982). There is a linear correlation (r) of .71 between post-smolt survival rate and the upwelling index developed by Gunsolus (Fig. 1). According to T. Nickelson (personal communication) there is an even higher correlation with an upwelling index that includes a broader range of spring and summer months than used by Gunsolus.

The ability to explain 51% (r^2 x 100) of the variability in survival over such a long time period with a single environmental measurement, is unique in the study of population fluctuations of salmonids. But the biological mechanism linking ocean upwelling to survival is not known. This linkage could be related to production of food for the salmon. If so, a negative correlation between survival and numbers of smolts released at a given upwelling intensity should be expected. The data of Table 1 were subjected to a multiple regression analysis, with upwelling and smolt

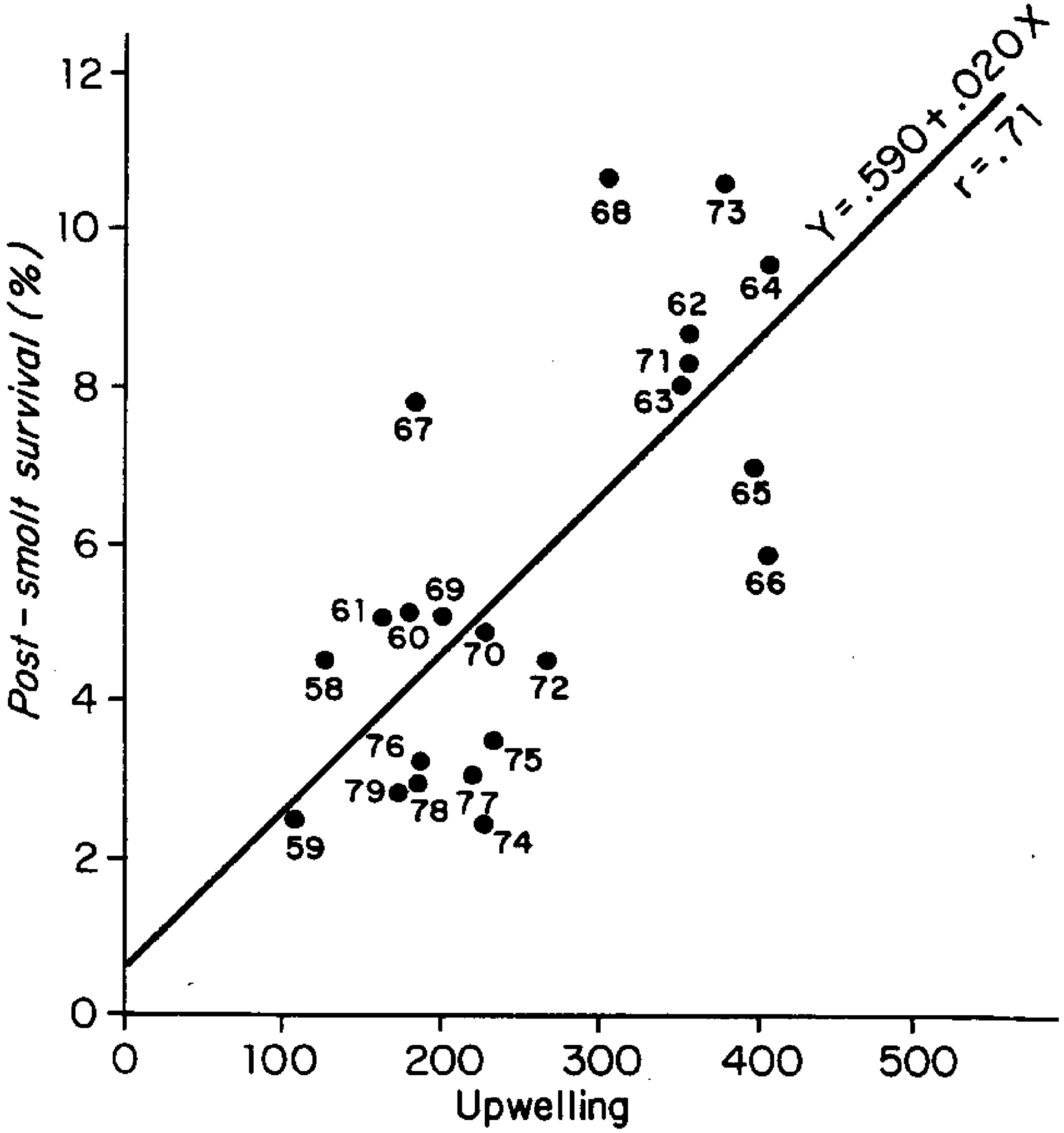

Fig. 1. Relationship between OPI upwelling index and post-smolt survival rate of public hatchery coho salmon. Brood years are indicated by the numbers.

numbers the independent variables and post-smolt survival rate the dependent variable. The partial correlation coefficient between survival and smolt numbers, given upwelling, was -.27, which only marginally implicates smolt numbers as a factor negatively affecting survival (t = -1.18 with 18 d.f.; $.10 \leq P \leq .15$).

Another mechanism suggested to explain the upwelling correlation involves predation by sea birds, specifically the common murre, Uria algae (D. Varoujean, University of Oregon, Charleston, Oregon, personal communication; and Varoujean and Matthews 1983). According to this hypothesis, out-migrating coho salmon smolts would become more widely dispersed as they enter the sea in cold water (high upwelling) years than warm water (low upwelling years). If the coho are more widely

Table 1. Post-smolt survival rate estimates of hatchery coho salmon in the Oregon Production Index region, 1958-79 brood years.

Brood year	Year of smolt outmigration yr_i	Public hatchery released smolts $year_i$ $(x\ 10^6)^1$	Post-smolt survival %	Upwelling index $year_i{}^1$
1958	1960	7.5	4.5	127.0
1959	1961	16.6	2.4	103.0
1960	1962	16.1	5.1	178.3
1961	1963	23.3	5.0	159.3
1962	1964	19.0	8.7	353.5
1963	1965	24.0	8.0	351.0
1964	1966	27.4	9.5	403.8
1965	1967	27.7	6.9	396.5
1966	1968	24.3	5.8	405.8
1967	1969	32.5	7.8	182.8
1968	1970	29.5	10.7	305.0
1969	1971	35.7	5.1	205.3
1970	1972	36.3	4.8	231.3
1971	1973	34.5	8.2	356.0
1972	1974	33.7	4.5	272.3
1973	1975	36.1	10.6	379.8
1974	1976	35.1	2.4	225.8
1975	1977	37.5	3.5	234.5
1976	1978	39.4	3.2	187.0
1977	1979	34.7	3.0	221.0
1978	1980	34.1	2.9	181.5
1979	1981	38.0	2.8	176.3
			$\bar{X} = 5.3$	

[1] Index developed by Gunsolus (1978):

$$\text{Cascade Head [April} + (\frac{\text{May+June}}{2})] + \text{Brookings [April} + (\frac{\text{May+June} + \frac{\text{July}}{2}}{2})]$$

Source: Oregon Department of Fish. Wildlife (1982), Appendix Table 3F-1, and Appendix Fig. 3G-6.

dispersed they may be relatively less attractive to murre predation than alternative schooling prey species such as anchovies.

2. Big Qualicum

This hatchery has released groups of wire-tagged coho smolts into Georgia Strait for a series of years beginning in 1973. Mark sampling in the catch and escapement has provided estimates of post-smolt survival for seven consecutive years (T. Perry, Canadian Department of Fisheries and Oceans, Vancouver, B.C., personal communication). Table 2 indicates that post-smolt survival has ranged from 15.5% to 41.6%, averaging 25.6%. Much of the variability in post-smolt survival may be due to variation in date of release. It is well known that date of release is one of the most important freshwater variables affecting survival (Mathews and Buckley, 1976; Bilton, 1980). For the Big Qualium data series there is a strong correlation between release date and survival rate (r = .76, Fig. 2). I statistically removed the variability due to this linear relationship by adding the deviation in each survival value from its predicted value on the regression line to the mean survival rate for all data points. The resulting adjusted post-smolt survival values ranged

Table 2. Post-smolt survival rate estimates of Big Qualicum (British Columbia) hatchery-reared coho salmon, 1971-1978 broods.

Brood year	Year of smolt outmigration	Dates of release	Size at release g (fish/lb)	No. marks released	Post-smolt survival rate % Catch	Escapement	Total
1971a	1973a	5/11/73	16.9(26.9)	32,156	17.5	8.4	25.9
1971b	1973b	5/25/73	18.4(24.7)	35,553	15.3	6.6	21.9
1971c	1973c	5/25/73	19.2(23.6)	13,652	15.4	9.0	24.4
1971d	1973d	6/01/73	17.1(26.6)	33,187	20.1	9.0	29.1
1972a	1974a	5/11/74	16.7(27.2)	30,076	10.9	9.1	20.0
1972b	1974b	5/23/74	21.2(21.4)	35,474	19.9	15.1	35.0
1972c	1974c	5/23/74	20.8(21.8)	11,494	14.6	11.7	26.3
1972d	1974d	6/06/74	19.1(23.8)	34,683	23.1	18.1	41.6
1973	1975	5/23/75	25.4(17.9)	57,425	21.3	6.9	28.2
1974	1976	5/14/76	26.5(17.1)	75,512	9.8	5.7	15.5
1975	1977	5/5-18/77	25.8(17.6)	90,520	11.4	9.1	20.5
1976	1978	5/1-20/78	18.2(24.9)	38,748	11.7	7.8	19.5
1977	1979	5/21/79	20.2(22.5)	50,224	17.3	7.0	24.3
1978	1980	5/20/80	18.1(25.1)	45,328	7.5*	-	-
							$\bar{X} = 25.6$

*Incomplete catch data; U.S. catches not included.

Source: Ted Perry and Carol Cross, Canadian Dept. of Fisheries and Oceans, Vancouver, B.C. (personal communication).

from 19.2% to 33.5%, which I would judge to indicate relative constancy of marine survival for this stock over this time period.

3. Puget Sound

For Puget Sound there has been no single hatchery or group of hatcheries for which marking or tagging has been done over a substantial series of years. Furthermore, it is difficult to estimate the annual hatchery component of the catch since nonhatchery coho are a major component of the catch in fisheries taking Puget Sound hatchery coho, in comparison to the OPI region where hatchery fish comprise about 80% of the catch (Mathews 1980). Therefore the total adult production, including both catch and escapement, from yearly smolt releases cannot be accurately estimated from fishery and escapement data alone.

A marking project involving all hatcheries for three consecutive brood years, 1964-1966 (Senn 1970a; Senn 1970b; Senn and Satterthwaite, 1971), provided good estimates of post-smolt survival, since all fisheries were sampled for their marks. A longer data series for considering variability in marine survival is provided by hatchery return rates to all 10 Puget Sound hatcheries for smolts released during the years 1959-1973. Hatchery return rate is the fraction or percentage of a smolt release that escapes the fisheries to return to the hatchery as spawners. During the 1959-1973 period, fishery management and hatchery rearing practices were relatively constant. Therefore, hatchery return rates may parallel total post-smolt survival rates sufficiently to allow reasonable inferences about variability in post-smolt survival from variability in hatchery return rates. This period was in the modern era of hatchery rearing in general terms of diet, size, and timing of release. Furthermore, the terminal area harvest rate was relatively constant over this time period; it was only after the 1974 Judge Boldt decision on Indian Fishery

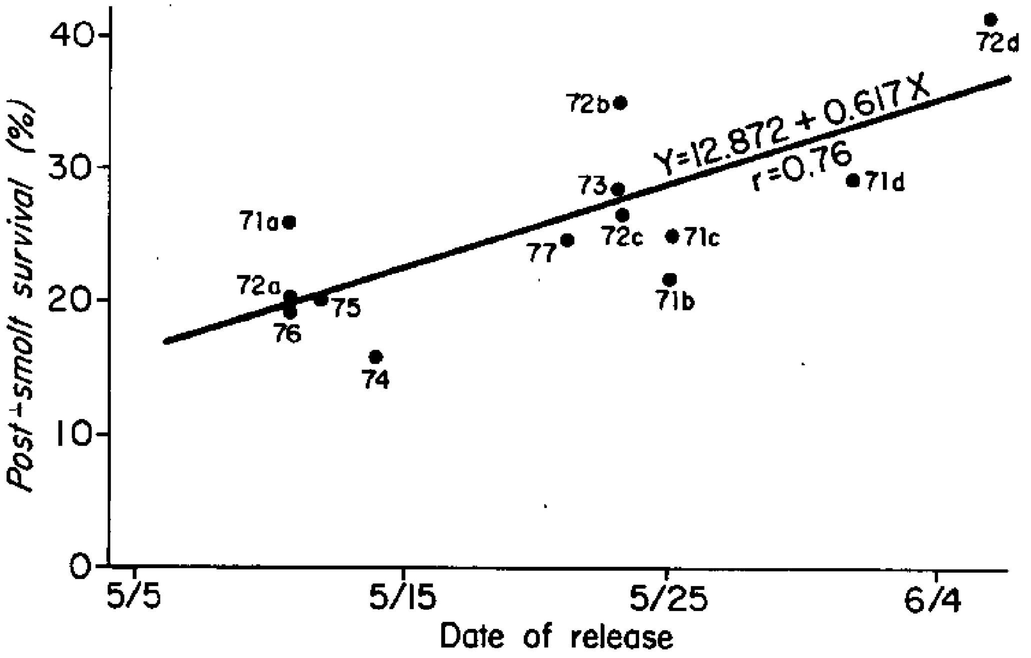

Fig. 2. Relationship between date of release and post-smolt smolt survival rate of Big Qualicum hatchery coho salmon. Brood years are indicated by the numbers.

rights that increases in terminal harvest rates sharply affected the ratio between total catch and hatchery return.

Table 3 lists the return rates by hatchery for the 1959-1973 Puget Sound yearling coho releases. The annual mean return rates over all hatcheries ranged from .81% to 2.97%, indicating almost a fourfold range in post-smolt survival, assuming that return rates were proportional to total survival rates as discussed above. I applied an analysis of variance to indicate whether or not return rates, and by inference total survival rates, varied significantly by year. Since there were apparent differences in survival among the hatcheries (e.g., Nooksack and Skagit tended to have low return rates whereas Issaquah, Green and Puyallup tended to have high rates), hatcheries were treated as blocks in a standard randomized block analysis of variance (see Zar 1974, pages 173-174). "Years" was a highly significant factor affecting return rate ($F_{10, 26} = 4.316$; $P<.001$). This indicates that years with low average survival tended to be that way for most hatcheries; in years of good average survival, there was a consistent pattern of good survival at most hatcheries. Since the fish migrate to sea soon after release and since the hatcheries are located on widely separate and distinctly different estuaries, it is my conclusion that the factor or factors producing parallel, significantly different responses in survival from year to year among the hatcheries occur at some point in life when the separate groups are mixed in the open marine environment, such as the Strait of Juan de Fuca or the Pacific Ocean. Ocean fishery mark recoveries indicate that the separate groups are distributed with a good degree of uniformity at sea.

Whatever may be affecting the survival of the several hatchery groups in common is not known. I treated several environmental factors as independent variables in a regression analysis attempting to explain the variability in average yearly return rate of fish released in year i to the 10 hatcheries:

Table 3. Return rates of smolts to Puget Sound hatcheries, expressed as percent of total plant returning to the hatchery site, 1957-1971 brood years.[1]

Brood year	Year of smolt outmigration	Hatchery										
		Nooksack	Samish	Skagit	Skykomish	Issaquah	Green	Puyallup	Minter	Geo Adams	Hoodsport	$\bar{X}_i$
1957	1959	0.22	1.98	1.42	1.05	1.31	0.63	0.19	0.44	(0.35)	0.05	(0.81)
1958	1960	0.32	2.60	0.36	2.49	0.91	2.83	0.17	0.72	(0.77)	0.41	(1.20)
1959	1961	0.63	3.17	0.24	1.76	1.32	4.83	0.26	1.77	(1.16)	0.16	(1.57)
1960	1962	0.56	1.02	0.45	1.32	0.44	2.07	0.08	1.35	0.92	0.36	0.86
1961	1963	0.41	2.44	0.47	2.11	2.25	4.08	1.37	0.68	1.29	0.64	1.57
1962	1964	0.43	0.75	0.30	1.29	1.31	3.99	2.83	2.53	1.28	1.31	1.60
1963	1965	1.06	0.99	0.84	3.84	3.15	5.20	4.28	2.82	2.53	3.91	2.86
1964	1966	0.30	1.40	0.85	1.58	2.39	2.50	2.38	1.88	1.18	1.52	1.60
1965	1967	0.17	2.97	0.61	1.42	1.40	4.52	2.56	1.15	1.02	0.88	1.67
1966	1968	0.34	2.48	0.95	1.68	2.09	2.37	2.54	1.89	1.04	0.51	1.60
1967	1969	0.28	3.65	1.81	2.40	2.92	3.53	3.10	6.66	2.40	(2.97)	(2.97)
1968	1970	0.39	2.31	1.94	1.11	1.99	1.79	2.53	1.22	0.95	2.08	1.63
1969	1971	0.25	1.37	0.98	1.25	1.84	0.80	1.14	1.50	2.25	(1.15)	(1.26)
1970	1972	0.16	1.72	1.30	1.63	1.90	0.73	0.34	1.17	0.26	5.80	1.50
1971	1973	1.03	1.63	2.25	3.81	2.47	3.31	2.07	2.47	0.49	2.90	2.24
	$\bar{X}_j$	0.44	2.03	0.98	1.92	1.85	2.88	1.72	1.88	(1.30)	(1.58)	(1.66)

Source: Olson (1978).

[1] Parentheses indicate missing values. Estimates were calculated according to Zar (1974, p. 174).

1) Ocean upwelling index for April, May, and June in year i at Neah Bay, WA (index developed by Gunsolus 1978)
2) Average annual sea surface temperature at Neah Bay in year i
3) May sea surface temperature at Neah Bay in year i
4) Quantity of yearling coho released in year i (lb)
5) Index of summertime streamflow in Puget Sound streams in year i-1 (index developed by Mathews and Olson 1980).

The following statistically significant simple linear correlations were found:

Independent Variable	r	r^2	P
Upwelling	.49	.23	P<.05
May temperature	-.48	.23	P<.05
Streamflow	.74	.54	P<.001

The direction of the upwelling effect is positive, as for coho in the OPI region. May temperature and upwelling were themselves significantly negatively correlated, so these two variables could be measures of a common biological mechanism affecting survival. A multiple regression analysis with both upwelling and May temperature as independent variables failed to explain a significantly greater fraction of the variability in hatchery return rate than either of the simple regression models with these two independent variables. In fact, no relationships were found in which a second independent variable was significant in a multiple regression model.

A streamflow correlation with nonhatchery coho is well known (Smoker 1955; Mathews and Olson 1980), but the reason why survival of hatchery coho should correlate with streamflow is not readily apparent. Mathews and Olson postulated a predation buffering mechanism: a high population of nonhatchery coho smolts following a summer of high stream flows could reduce the predation rate on the outmigrating hatchery population (which would tend to be relatively constant) through buffering. An alternative hypothesis is that annual fluctuations in summer streamflow may simply be a symptom of broader climatic or oceanographic variation which is affecting coho salmon survival in some obscure way.

The three-year marking study of the 1964, 1965, and 1966 broods provides precise estimates of post-smolt survival rates. Although the time frame is short, a review of these data is useful for the purpose of correlating differences in survival among years with differences in ocean distribution. Such correlation would be some evidence that variation in post-smolt survival is due to variation of some factor or factors in the ocean environment, rather than variation in smolt quality or some freshwater factor.

Table 4 summarizes relevant statistics for the 1964-1966 brood marking study. Fin marking was done at all 10 hatcheries, with three separate marks applied, one for northern Puget Sound hatcheries (Nooksack, Samish, Skagit), one for central Puget Sound hatcheries (Skykomish, Issaquah, Green, Puyallup, and Minter), and one for Hood Canal hatcheries (Hoodsport and George Adams).

Table 5 gives estimates of post-smolt survival rate by year and region of release. There was about a twofold difference within the range for just these three years. That the three regions exhibit parallel response in survival with the 1967 out-migrants surviving best for all regions is evidence of a factor probably in the marine environment commonly affecting survival of all fish.

Table 4. Median size and release dates for Puget Sound hatchery coho, 1964-66 broods. Also shown are total numbers marked and total numbers released.

	Year of smolt outmigration		
	1966	1967	1968
Central Sound			
Size at release (fish/lb)	22	18	17
Date of release	4/1	4/1	4/15
Total marks	418,562	396,779	430,987
Total released	4,319,525	4,094,723	4,443,166
Hood Canal			
Size at release (fish/lb)	24	17	20
Date of release	3/15	3/15	4/15
Total marks	104,616	161,137	193,668
Total released	1,451,146	1,662,923	1,996,574
Northern Sound			
Size at release (fish/lb)	23	22	18
Date of release	3/12	3/15	4/15
Total marks	483,435	232,954	291,165
Total released	1,924,780	2,400,774	3,001,702

Sources: Senn (1970); Senn (1970b); and Senn and Satterthwaite (1971).

Table 5. Post-smolt survival rate estimates[1] for 1964-66 brood coho released from Puget Sound hatcheries.

Brood year	Year of smolt outmigration	Central Sound	Hood Canal	Northern Sound
1964	1966	5.59%	3.53%	2.93%
1965	1967	11.07%	5.58%	4.55%
1966	1968	8.17%	3.19%	2.89%

[1] Excludes returns of two-year-old precocious males which, for Puget Sound hatcheries, average about 2% of the return each year.

Source: Senn (1970a); Senn (1970b); and Senn and Satterthwaite (1971).

The 1967 out-migrant group fared substantially better than the other two. However, the adults from the 1967 out-migration tended to be smaller than adults from the other two years (Table 6), which indicates that the higher survival for the 1967 group was not obviously due to a favorable abundance of food at sea.

Ocean catch distribution differed (according to X^2 contingency table analysis) significantly among the three years (Table 7). The 1967 outmigrants which were the best survivors of the three groups were apparently caught farther to the north than

Table 6. Mean weights of commercial net catches of marked coho for three consecutive brood years of hatchery evaluation (lbs).

Brood year	Year of smolt outmigration	Weights of adults: Central Sound	Hood Canal	Northern Sound
1964	1966	6.94	7.15	6.11
1965	1967	6.63	6.55	6.28
1966	1968	7.97	8.03	7.52

Sources: Senn (1970a); Senn (1970b); and Senn and Satterthwaite (1971).

Table 7. Ocean catch distribution of 1964-66 brood Puget Sound hatchery coho, in percent of ocean catch by region.

Brood year	Year of smolt outmigration	Region: AK	BC	WA	OR	CA
		Central Sound				
1964	1966	0	48	48	4	0
1965	1967	0	85	15	0	0
1966	1968	0	65	35	0	0
		Hood Canal				
1964	1966	0	54	41	4	0
1965	1967	0	82	18	0	0
1966	1968	0	66	34	0	0
		Northern Sound				
1964	1966	0	54	41	2	0
1965	1967	0	85	15	0	0
1966	1968	0	73	27	0	0

Sources: Senn (1970a); Senn (1970b); and Senn and Satterthwaite (1971).

the other two groups, a trend apparent for fish from all three regions of the Sound. Apparently coho from Puget Sound do respond differently to ocean conditions in different years, and such conditions may vary enough to cause substantial variation in survival.

Data sets on ocean upwelling, sea surface temperature, and sea surface salinity indicated relative year-to-year uniformity in these environmental conditions for the period covering the ocean life of these three marked broods (1966-1969). Thus, there are no ready explanations for the differences in distribution or survival of these three broods.

Sockeye

1. Lake Washington

Table 8 presents a series of acoustic estimates made from transect sampling of pre-smolt populations (Thorne and Ames 1983). This sampling was done one to three months prior to out-migration, which occurs for most of the sockeye rearing in Lake Washington at age I (one freshwater check). Most adults return after two years at sea (two saltwater checks). The acoustic estimates correlate well with annual tow net CPUE, and corrections for "noise" in such estimates caused by the presence of landlocked sockeye salmon (Kokanee) and other species have been made.

Table 8. Posts-smolt survival rate estimates for Lake Washington sockeye, 1967-79 brood years.

Brood year	Year of smolt outmigration	Hydroacoustic estimate of pre-smolt nos. (x 10^6)	Resulting adult run size (x 10^3)	Post-smolt survival %
1967	1969	7.5	559	7.4
1968	1970	3.2	299	9.3
1969	1971	3.7	476	12.9
1970	1972	2.0	150	7.5
1971	1973	1.7	144	8.5
1972	1974	3.6	180	5.0
1973	1975	3.0	593	19.8
1974	1976	0.8*	311	--
1975	1977	1.1	229	20.8
1976	1978	4.0	500	12.5
1977	1979	3.0	119	4.0
1978	1980	6.8	323	4.8
1979	1981	3.6	400**	11.1
				$\bar{X}$ = 10.3

*Known underestimate due to fish on bottom.
**1983 run estimate is preliminary.

Source: Thorne and Ames (1983).

Adult run size estimates are quite accurate. Most of the commercial and sport catch is taken in the lake. About 10% of the catch is preterminal in the Strait harvest since the Lake Washington run migrates through the Strait of Juan de Fuca, but it is separable from intermingling Fraser River stocks by timing and scale pattern analyses. Escapements are enumerated from a counting tower on the Cedar River.

Post-smolt survival rate estimates for 12 years ranged from 4.0% to 20.8%, or about fivefold 5 (Table 8). Richard Thorne (Fisheries Research Institute, University of Washington, Seattle, WA, personal communication) reported that smolts from Lake Washington do not vary significantly in mean size from year to year (such as negatively in response to rearing numbers in the Lake). J. Ames (Washington Department of Fisheries, Olympia, WA, personal communication) indicated he has found statistically significant correlations between post-smolt survival amd sea surface temperature and salinity from Neah Bay, Washington, during certain combinations of months thought to encompass out-migration. However, he does not report such correlations as being high enough for accurate predictability of runs. There is little indication of density dependence from Table 8; linear correlation between smolt numbers and survival was not significant ($r = -.379$; $.10<P<.25$). Although the causes for the variability in survival of Lake Washington smolts are obscure, it seems likely that such causes are in the marine phase. There is a very short passage from Lake Washington to Puget Sound, and the physical, chemical, and biological features of the freshwater environment have been very well monitored over the years in question with no known fluctuations that would significantly affect variability in survival shortly before or during passage from the Lake.

2. Karluk Lake

The sockeye populations in this system have been studies intensively (Barnaby 1944). For several years estimates of post-smolt survival were made by fin-marking the out-migrants and sampling the returning adults in the catch and escapement for marks. The estimates of survival are constant and remarkably high even though Barnaby did not adjust his survival estimates upwards to account for negative stresses from fin removals. Barnaby noted a consistent tendency for survival to increase with freshwater age of smolts, which was probably size related. In Table 9 I have reproduced Barnaby's survival rate estimates for age II and age III smolts, the two major freshwater-age groups. These two age groups averaged about 135 and 145 mm in length, respectively, for the years of study. The average survival rates for all smolts marked each year, which included small numbers of age I and age IV smolts, are also included in Table 9.

Table 9. Post-smolt survival rate estimates for Karluk Lake sockeye salmon.

Year of smolt outmigration	No. smolts marked	Post-smolt survival %	Post-smolt survival by freshwater age at outmigration	
			II	III
1926	46,791	20.8	20.0	23.7
1929	50,061	22.3	18.3	25.4
1930	55,000	20.7	16.5	27.3
1931	55,000	23.3	20.9	34.1
1932	59,000	18.4	19.7	16.9
1933	40,000	20.5	18.3	24.9
		$\bar{X} = 21.0$		

Source: Barnaby (1944)

Variability in survival rate was low for the six years of record; the range is 18.4% to 22.3%. Apparently because of this Barnaby makes no mention of possible factors influencing marine mortality. He simply comments on the "remarkable uniformity" of the survival rate estimates.

3. Chilko Lake

This may be the only Fraser River population with a long series of years of smolt enumeration and resulting adult returns estimates, including catch estimates in mixed stock fisheries derived from scale pattern and run timing analysis. Peterman (1978) summarizes these data for the 1949-1972 brood years in a graph. Reading from his graph, with perhaps some loss in accuracy, I computed estimates of post-smolt survival rate (Table 10). The indicated range in survival, 1% to 20%, is exceedingly high. Chilko Lake is relatively far upstream and substantial variation of in-river survival is more likely for such a system than for a system with a

Table 10. Post-smolt survival rate estimates for Chilko Lake (Fraser R.) sockeye, 1949-72 brood years.

Year of smolt outmigration	Smolt numbers x 10^6	Adult return x 10^6	Post-smolt survival %
1951	4	0.6	15.0
1952	2	0.2	10.0
1953	11	0.7	6.3
1954	25	1.8	7.2
1955	8	0.5	6.2
1956	3	0.6	20.0
1957	8	1.4	17.5
1958	23	2.4	10.4
1959	10	0.1	1.0
1960	7	0.3	4.3
1961	32	2.1	6.6
1962	33	0.9	2.7
1963	3	0.1	3.3
1964	8	1.0	12.5
1965	9	1.2	13.3
1966	23	1.8	7.8
1967	4	0.1	2.5
1968	17	0.8	4.7
1969	8	2.0	2.5
1970	31	2.4	7.7
1971	7	0.4	5.7
1972	4	0.6	15.0
1973	8	0.8	10.0
1974	20	2.0	10.0
			$\bar{X}$ = 8.4

Source: Peterman (1978).

shorter freshwater passage. Ward and Larkin (1964) accredited much of the variability in survival at that time to variations in mainstem Fraser River flow during out-migration. In a multiple regression analysis wherein survival was the dependent variable and discharge and smolt numbers the independent variable, they found a partial correlation between survival and discharge of .865 for an 11-year data series. I am not aware that anyone has attempted to correlate survival with Fraser River discharge for the entire 1949-1972 data series. I was unable to find in the literature any reference to possible marine environmental factors that might correlate with or explain variability in Chilko Lake survival rates.

4. Babine Lake

This system produces some 90% of the Skeena River sockeye run, and estimates of smolt out-migration from marking and re-capturing downstream have been made for many years. This excellent data series has been reviewed by Peterman (1978), Peterman (1982) and McDonald and Hume (1982) to assess the efficacy of investments by the Canadian government in spawning channels and related water flow controls designed to increase rearing fry populations in Babine Lake. Estimates of post-smolt survival rate have ranged from 0.9% to 10.3% over a 17-year time period (Table 11). The above authors concluded: (1) smolt populations increased substantially with spawning channels and other developments; (2) the average size of out-migrating smolts did not decrease with increased number of smolts; (3) overall there is some

Table 11. Post-smolt survival rate estimates for Babine Lake, 1961-77 brood years.

Year of smolt outmigration	Smolt abundance x 10^6	Adult return x 10^6	Post-smolt survival %
1963	12.53	1.12	9.6
1964	45.89	1.55	3.4
1965	23.67	2.43	10.3
1966	35.31	0.74	2.1
1967	16.57	1.20	7.2
1968	30.89	1.61	5.2
1969	46.19	2.27	4.9
1970	43.01	1.39	3.2
1971	52.51	2.90	5.5
1972	54.34	1.45	2.7
1973	88.75	2.16	2.4
1974	80.13	1.78	2.2
1975	34.05	1.95	5.7
1976	42.98	0.56	1.3
1977	61.64	3.47	5.6
1978	75.96	0.67	0.9
1979	108.22	5.96	9.2
			$\bar{X}$ = 4.8

Source: McDonald and Hume (In Press).

slight statistical evidence of density-dependent mortality indicated by a nonlinear response in size of adult run to increased smolt output; and (4) overriding a possible density-dependent mortality response is a strong odd-even pattern of survival, indicating interaction with pink salmon in the marine environment. Peterman (1978) suggests two possible biological mechanisms for a pink-sockeye interaction. One theory postulates buffering of a predation mortality force that may be operating on both species, and the other theory postulates predation by adult pinks on outmigrating sockeye smolts. (For further discussion see the 1978 Peterman article.) The above cited references apparently provide the only published analyses attempting to explain variability in survival for the Babine data series.

5. Bristol Bay - Kvichak and Wood Rivers

Estimates of outmigrating smolts have been made with sonar counters since 1971 for the Kvichak River (Bill 1983) and since 1975 for the Wood River (Bucher 1983). Such estimates have also been made for other Bristol Bay rivers but for periods of time too short for the present review. The sonar techniques are described by Randall (1977) and Krasnowski (1977). The outmigration is sampled in time and space by the counter, and the number of smolts is estimated by extrapolation. Adult returns are known with relatively good precision since the catches are mostly terminal. Total escapement estimates are available from sample counts at counting towers, and the freshwater and saltwater age composition, which is quite variable by river and year, is estimated from scale samples taken from both the catch and the escapement (see Krasnowski and Randall 1976 for descriptions of the fishery and the adult estimation procedures).

There are errors of unknown magnitude in the smolt estimates. Two sonar systems were used at the same time, one positioned 7 meters upstream from the other for a 6-day portion of the 1982 Naknek River smolt out-migration. Daily estimates of smolt numbers from the upstream counter were greater for all six days, averaging higher than the estimates from the downstream counter by a factor of 1.39. The differences were significant and not fully explainable (Huttenen 1983).

There are also errors in the adult return estimates of probably lesser relative magnitude than for the smolt estimates, arising from methods of apportioning the Japanese high seas catch to separate river systems, age sampling and determination difficulties, and mixing of portions of separate runs in the estuarial fishing areas.

On balance, however, estimates of post-smolt survival rates for the Kvichak and Wood Rivers are probably no worse than for the previous cases presented.

Post-smolt survival rate estimates for the Kvichak River are given in Table 12 by freshwater age of the smolts (I and II referring to one and two freshwater annuli), and for the total out-migration of both freshwater ages combined. Survival tended to be slightly higher for the larger age II smolts than age I smolts, and in total has tended to be quite variable, varying from 1.2% to 19.7% for the complete 10 years of record. Of the previous runs considered only the Chilko indicated such a high degree of variability. The data in Table 12 offer little evidence that size of out-migrating smolts or their survival correlates negatively with numbers of out-migrating smolts. To my knowledge no one has found any factor in the marine environment that explains the variability in post-smolt survival of Kvichak sockeye salmon. However D. Rogers (Fisheries Research Institute, University of Washington, personal communication) believes that there has been a significantly higher marine survival rate of most major Bristol Bay runs except the Kvichak, for the most recent four or five years compared with the late 1960s and early 1970s that may correlate with a general, recent warming condition of the ocean regions utilized by Bristol Bay sockeye (see Rogers and Eggers et al. in this symposium).

Table 12. Post-smolt survival rate estimates for Kvichak River sockeye salmon.

Year of smolt outmigration	Sonar estimate of smolt nos. (x 10^6)			Mean length of smolts		Post-smolt survival %[1]		
	Age I	Age II	Total	Age I	Age II	Age I	Age II	Total
1971	85.7	6.0	91.7	90	111	1	4	1.2
1972	0.6	67.0	67.6	80	106	9	7	7.0
1973	5.0	189.1	194.1	86	97	7	8	8.0
1974	4.0	33.8	37.8	96	111	10	7	7.3
1975	9.8	5.8	15.6	98	122	16	26	19.7
1976	99.9	2.9	102.8	88	121	8	28	8.6
1977	82.1	132.9	215.0	86	106	8	13	11.1
1978	31.3	238.5	269.8	88	97	19	12	12.8
1979	26.6	26.0	52.6	90	109	10	15	12.5
1980	162.6	10.1	172.7	88	110	2[2]	3[2]	2.1
1981	163.0	20.6	183.6	85	108	11[2]	6[2]	
					$\bar{x}_{71-80}$ =	9.0	12.3	9.0

[1] Survival estimates include estimates of total catch, including Japanese high seas catch, and escapement of all significant saltwater age components.

[2] Incomplete - includes only two-ocean-check returns in 1983.

Sources: Bill (1983); D. Eggers, Alaska Department of Fish and Game, Juneau, AK (personal communication).

Post-smolt survival rate estimates for the Wood River (Table 13) ranged from 5% to 10%, considerably less than for the Kvichak and also less than indicated for several other runs discussed previously. However, the data series for the Wood River covers only 6 complete years. This may be too short a series for a meaningful correlation analysis involving marine survival and marine environmental factors.

Table 13. Post-smolt survival rate estimates for Wood River sockeye salmon.

Year of smolt outmigration	Sonar estimate of smolt nos. (x 10^6)			Mean length of smolts (mm)		Post-smolt survival %[1]		
	Age I	Age II	Total	Age I	Age II	Age I	Age II	Total
1975	28.0	5.9	33.9	83	98	4.8	1.1	4.2
1976	101.4	4.8	106.2	84	95	4.4	2.1	6.2
1977	60.8	12.6	73.4	71	98	5.7	3.7	5.4
1978	46.6	8.4	55.0	79	90	9.7	12.5	10.1
1979	60.8	5.1	65.9	90	100	5.2	14.9	6.0
1980	46.3	2.0	48.3	78	95	5.0	4.1	5.0
1981	64.3	33.2	97.5	88	96	4.4[2]	3.4[2]	
					$\bar{X}_{75-80}$ =	5.8	6.4	6.2

[1] Survival estimates include estimates of total catch, including Japanese high seas catch, and escapement of all significant salt-water-age components.

[2] Incomplete - includes only two-ocean-check returns in 1983.

Sources: Bucher (1983); D. Eggers, Alaska Department of Fish & Game, Juneau, AK (personal communication).

Chinook

I could obtain only one short data series for chinook salmon, but this was for an extensive marking study of fall chinook from Columbia River hatcheries involving four brood years, 1961-1964. For each of these brood years approximately 10% of the out-migrants at most Columbia River hatcheries was marked by fin-clips (including in some instances removal of the tip of one of the maxillary bones). A common mark was applied each year for most hatcheries and in addition special marks were applied at certain hatcheries, notably Spring Creek and Kalama Falls. All significant fisheries from California to Alaska were extensively sampled for marks by trained observers during the year that adults from these four broods were being harvested. Spawning escapements were also sampled for marks. Wahle and Vreeland (1978), who summarized the results of this marking study, made adjustments for mortality due to marking and regeneration of fins in their final contribution and survival estimates. Table 14 indicates that general conditions of rearing and releasing were relatively constant for these four broods.

Table 14. Median fall chinook size and release dates for 13 Columbia River hatcheries included in the 1961-64 brood marking evaluation. Also shown are total numbers marked and total numbers released.

	Year of smolt outmigration			
	1962	1963	1964	1965
Brood year	1961	1962	1963	1964
Size at release (fish/lb)	194	190	181	144
Date of release	5/20	5/31	5/18	5/29
Total marks	5,446,439	5,249,079	5,986,464	4,638,237
Total released	53,659,498	52,490,790	60,105,060	46,756,421

Source: Wahle and Vreeland (1978).

Table 15 presents the post-smolt survival rate estimates, which include adult contributions to both catch and escapement. Survival was relatively good for three of the four years but quite poor for the 1962 brood. R. Wahle (National Marine Fishery Service, Portland, Oregon, personal communication) recalls that the 1962 brood had various rearing problems at the hatcheries related to disease and feeding. However, since survival of this brood was apparently poor across the board (Table 15) and since the relative range in variability of survival is well within that of other case histories previously discussed in this review, possibly the 1962 brood was negatively affected by a marine factor as well as perhaps some freshwater-rearing factor. I surveyed data series on sea surface temperature, sea surface salinity, and upwelling to determine whether or not the 1962 brood may have encountered any anomalous ocean conditions. One possible clue is indicated by Table 16, which shows average annual surface temperature at Neah Bay, Washington. This point is the approximate center of latitudinal distribution of Columbia River hatchery fall chinook. The highest ocean temperatures for a 23-year time period occurred in 1963, the first year at sea for the 1962 brood. Additional evidence that a warm ocean during early ocean life may negatively affect chinook survival is offered by preliminary reports that the 1983 production of adult fall chinooks from Columbia River hatcheries, which would be primarily three-year-olds and four-year-olds that outmigrated in 1981 and 1980, respectively, was close to a failure. Both 1980 and 1981 were warm-ocean years (Table 16).

Table 15. Post-smolt survival rate estimates for 1961-64 brood years of Columbia River hatchery-produced fall chinook salmon.

Year of smolt outmigration	Brood year	Spring Creek	Kalama Falls	All study hatcheries
1962	1961	1.1%	1.3%	0.8%
1963	1962	0.4%	0.5%	0.3%
1964	1963	1.5%	1.2%	1.1%
1965	1964	2.6%	1.1%	0.7%

Source: Wahle and Vreeland (1978).

The ocean catch distribution varied significantly by year ($p < .05$, X^2 contingency table analysis) for each of the three marked groups considered -- Spring Creek, Kalama Falls, and the group that had a mark common to all hatcheries (Table 17). However, the three groups did not vary consistently by year, nor was there anything outstanding about the ocean distribution of the low surviving 1962 brood.

To indicate where in the life cycle the additional mortality of the 1962 brood may have occurred, I summarized the catch by age for each of the four years. The age distribution of the catch was little different for the 1962 brood than for the other three (Table 18). Therefore it is likely that the additional mortality force on the 1962 brood occurred before age 2, the youngest age in the catch.

Steelhead

1. Snow Creek

The Washington Department of Game has trapped and enumerated all steelhead smolts out-migrating from this small stream since 1978 and has similarly enumerated all returning adults. T. Johnson (WDG, Pt. Townsend, Washington, personal communication) has provided the following survival estimates:

Year of smolt outmigration	Post-smolt survival %
1978	7.5
1979	13.0
1980	6.0

Table 16. Sea surface temperatures at Neah Bay, Washington. Also shown are Columbia River hatchery fall chinook post-smolt survival rate estimates, 1961-64 broods.

Year i	Annual mean temp. °C	Post-smolt survival of smolts outmigrating in year i
1959	9.8	--
1960	9.7	--
1961	9.8	--
1962	10.0	0.8%
1963	10.6	0.3%
1964	9.6	1.1%
1965	9.7	0.7%
1966	9.9	--
1967	9.9	--
1968	9.7	--
1969	9.6	--
1970	9.2	--
1971	9.3	--
1972	8.9	--
1973	9.4	--
1974	9.4	--
1975	9.3	--
1976	9.3	--
1977	9.7	--
1978	10.1	--
1979	9.9	--
1980	10.4	--
1981	10.6	--

Source: Temperature data furnished by Roger Mercer, NMFS, Seattle, WA (personal communication).

The smolts are of ages I, II and III. Ocean age also varies, with primarily 2 and 3 saltwater checks on scales of returning adults. According to T. Johnson the outmigrations in all three years were similar in terms of average size, timing, and age composition. The numbers of out-migrants varied within a relatively narrow range, 893-1,382 per year. Thus the range of 6% to 13% in survival is implicated as due to variability in marine survival. The data series is thus far too short for analysis of causes of such variability.

2. Keogh River

P. Slaney (B.C. Fish and Wildlife Branch, Victoria, B.C., Canada, personal communication) provided three years of smolt out-migration and adult return data. His returns include repeat spawners, which are about 1% of the adult run. Smolts are counted at a weir, and adult returns are estimated by marking and recapturing. Relevant data, including average size of smolts are presented below:

Year of smolt outmigration	Mean smolt size - gm	Post-smolt survival %
1977	40	8
1978	48	12
1979	50	15

Table 17. Ocean catch distribution of 1961-64 brood Columbia River hatchery fall chinook. (% of ocean catch by region.)

Brood year	Year of smolt out-migration	Region				
		AK	BC	WA	OR	CA
			Spring Creek			
1961	1962	0	32	60	6	1
1962	1963	0	30	67	3	0
1963	1964	0	44	52	4	0
1964	1965	0	32	59	9	0
			Kalama Falls			
1961	1962	3	65	31	1	0
1962	1963	1	68	28	2	0
1963	1964	2	47	48	3	0
1964	1965	0	69	26	3	1
			All study hatcheries			
1961	1962	Tr	48	48	4	0
1962	1963	Tr	53	41	1	1
1963	1964	Tr	45	49	6	0
1964	1965	Tr	34	55	11	0

Tr = trace

Source: Wahle and Vreeland (1958).

Table 18. Percentage of total ocean and river catch of marked Columbia River fall chinook by brood year and age, 1961-64 broods.

Brood year	Year of smolt outmigration	Age caught			
		2 yrs	3 yrs	4 yrs	5 yrs
1961	1962	3.27	60.23	33.57	2.93
1962	1963	4.27	63.82	29.89	2.01
1963	1964	6.76	60.64	29.45	3.14
1964	1965	6.59	58.74	32.29	2.38

Source: Wahle and Vreeland (1978).

According to P. Slaney, the outmigration consists of smolts of ages II, III, and IV. Age composition of the out-migrants varies considerably with year class recruitment. The mean size of smolts varies with age composition, being larger if there are more older fish. In the above data set, much of the variability in survival could be accounted for by size of smolts. If the trend in survival due to size of smolts were removed, which I did not do because the data series is so short, there would be relatively little remaining variation in survival. These data therefore indicate relative constancy of post-smolt survival.

Summary

Although this review may not be exhaustive, there are enough data series presented to allow some generalizations.

Perhaps only three of the series are indicative of relative constancy of post-smolt survival. Big Qualium coho, Karluk Lake sockeye, and Keogh River steelhead. The longest of these is only seven years. In all of the longer series and some of the shorter ones variability in post-smolt survival is relatively high and largely unexplained. In fact, there is only one case, OPI coho, for which a strong correlation has been found between survival and a marine factor for a long series of years; the other case histories offer only fragmentary clues at best, and even for OPI coho the mechanism affecting survival is not at all understood. Although such correlations are obviously useful in terms of predicting annual abundance, it is important to understand the biological mechanisms. For example, if the OPI upwelling correlation is related to food supply for the coho, this would suggest a whole range of management options including limitations on numbers and release locations of hatchery released smolts; if this correlation is due to predation, which may be density independent or even inversely density dependent, an entirely different set of release and control strategies might be prudent.

For Babine sockeye, the odd-even year pattern of survival has offered some insight into factors affecting marine survival, the suggestion being that there is some interaction involving pink salmon. Again, the causative mechanism is not understood.

It is not a new concept, of course, that there is a great deal of virtually unexplained variation in survivability of salmonids at sea. This paper only amplifies that we may be no closer to understanding such factors now than we were decades ago. Probably the mechanisms and causes affecting survival of a particular stock are themselves exceedingly variable. Consider this: a lowland lake in western Washington can be poisoned with rotenone and stocked with rainbow trout fry, producing a monoculture for rainbow trout. As long as this lake remains free of other fish species, one can expect a fairly constant, high rate of survival of fry planted in summer to be caught the next spring by anglers. It is well known, although there are no published studies that quantitatively document such effects, that the introduction of other fish species that may compete with or prey on the trout fry causes survival to vary downward. The ocean of course contains an exceedingly more complex mix of fish, bird, and mammal predators and competitors than the lowland lake model. The predator and competitor populations are themselves fluctuating from causes even more obscure than those regulating the much more studied salmon species. The salmonid food supply is also exceedingly variable in kind and quantity and mechanisms controlling populations of planktonic crustaceans and forage fish are also complex.

The variability in survival of salmon at sea therefore depends on complex interactions involving many fluctuating populations of predators, competitors, and forage species. Considering this, it is not suprising that variability in marine survival of salmonids is so poorly understood. Therefore, the likelihood seems low of correlating marine survival of any particular stock to single or simple environmental factors well enough or for long enough time periods to be useful in terms of predicting salmon abundance or guiding management decisions. Significant understanding of marine survival of salmon may only come about from a highly organized, focused, and ocean-oriented research program, of a scope and magnitude not yet seen.

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Comments on Marine Survival of Pacific Salmonids

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Mathews' review provides convincing evidence that post-smolt survival can have a substantial effect on adult year class strength in Pacific salmonids (with his proviso that the survivals he examined included part of the freshwater phase). A few comments on the search for underlying, causal mechanisms and the sampling theory underlying statements regarding significance will, I hope, complement his remarks.

The first comment regards the care that must be taken in establishing the statistical significance of correlations and regression coefficients in analyses involving oceanographic variables and marine survival. The most common oversight in these analyses is failure to account for intraseries correlation; samples in the time series are not necessarily independent, but may themselves be correlated. Because of this, when one computes the correlation between two time series or uses linear regression to estimate a model to describe one series in terms of the other, the standard confidence limits derived for independently chosen variables cannot be used. Differences between this and the correct procedure can be substantial. For example, a correlation of 0.7 between adjacent samples in one series will reduce the effective sample size by half.

There are basically two approaches to dealing with this problem. The first, called prewhitening, consists of removing the intraseries correlation by appropriate filtering. It is commonly used in time series, but has two drawbacks that make it less appealing in the application of concern here: (1) removal of all intraseries correlation reduces the chance of detecting a real effect of interest that involves dependence of one variable on another variable that contains intraseries correlation, and (2) removal of the intraseries correlation with the use of a fitted model may actually lead to underestimation of the significance of the resulting correlation coefficients (see Box and Pierce 1970; Durbin 1970).

The second approach is to account for the intraseries correlation by reducing the number of degrees of freedom from N, the number of samples, to an effective number of degrees of freedom which accounts for the lack of independence in the samples. This approach is based on the work of Bartlett who derived an expression for the variance of computed correlation coefficients (1946). A similar result for autocorrelations only was developed by Bayley and Hammersley (1946) and applied to fisheries by Sutcliffe et al. (1976). Box and Jenkins (1976, pp. 34 and 376) describe the application of Bartlett's results. Use of these results in fisheries involves two problems: (1) they are derived under the assumption of large N (rarely true in fisheries), and (2) the expression for the significance of each correlation is in terms of the true value of that correlation and all others at different lags. However, both of these problems can be overcome by using a finite number of properly chosen values of computed correlations. I have discussed this issue primarily in terms of correlation coefficients. A discussion of similar solutions to the same problem as it affects regression models can be found in Chelton (1983).

The second comment is to emphasize the fact that effects of environmental factors on salmonids may vary widely among species and locations. This lack of uniformity in response is apparent from Mathews' review, other papers in this volume, and the literature. Ocean temperature is a good example. Vernon (1958) found year class strength of pink salmon in the Fraser River to be negatively correlated with temperature encountered by the juveniles when entering the Georgia Straits. Van Hyning (1973) also found a negative relationship between sea water temperature during the first May and June of life and returns of chinook to the Columbia River for the years 1938-46. On the other hand, Botsford et al. (in preparation) found a significant positive correlation between sea surface temperature in the year Sacramento River chinook go to sea and eventual grilse, spawner, and catch returns. Ocean temperatures are also thought to influence migration routes and life history timing. Royal and Tully (1963) noted that during the warm water year 1958 Fraser River sockeye returned around the north end of Vancouver Island rather than through the Straits of San Juan de Fuca (also see Wickett 1975). Also, two extremely cold years while Bristol Bay sockeye were at sea resulted in two-to-four times as many fish remaining at sea for an extra year and returning as three year olds (Straty and Jaenicke 1980). This may be caused by southward displacement of these fish in the Gulf of Alaska. Changes in size distributions of chinook salmon returning to Columbia River hatcheries during the warmer water years 1957 and 1958 were attributed to an influence of oceanographic conditions on maturation rate (Junge and Phinney 1963). Higher ocean temperatures have a positive effect on growth rate of Bristol Bay sockeye (Straty and Jaenicke 1980), but sea surface temperature has a negative correlation with average weight in central California chinook (Botsford et al., in prep.). From these examples it is clear that we should not generalize a priori over species or locations with regard to the effect of a specific environmental factor, but rather must demonstrate a mechanism for each case individually. This is true not only because different salmon species at different locations may respond differently to their environment, but also because changes in the environmental factor may imply different oceanographic changes (e.g, currents, prey distribution) at different locations.

The third comment is that care must be taken in interpreting computed correlations and regressions because the environmental variables that we hypothesize are related to marine survival are often themselves not independent. It is well known that temperature and upwelling index are usually negatively correlated, and that interannual variations in temperature and sea level height are likely to be positively correlated (see Chelton this workshop). However, it is less obvious that the oceanographic variables that are correlated with survival may not affect marine survival at all, but rather smolt production in fresh water. For example, the positive relationship mentioned above between California central valley chinook and temperature during the spring of seaward migration (Botsford et al., in prep.) may be caused by a northward shift in marine prey that benefits the smolts, but may also be caused by an association between oceanographic conditions and precipitation. Stevens and Miller (1983) have demonstrated a positive relationship between winter flow rate in the Sacramento River and two indices of juvenile abundance in the following spring and fall. Also Kjelson et al. (1982) and Kjelson (personal communication) have shown a positive relationship between Sacramento River flows and both smolt survival through the San Francisco Bay Delta and abundance of juveniles in the estuary. A marine/terrestrial relationship such as this might also explain the coherence between deviations from average weight of Fraser River sockeye and temperature on the west coast of Vancouver Island three years earlier (Mysak et al. 1982). This lag implies oceanographic conditions are affecting the freshwater phase. Streamflow appears to be one variable that has a positive effect on many salmon stocks (Mathews and Olson 1980, Scarnecchia 1981, Ward and Larkin 1964, and others) and it is potentially related to oceanographic conditions.

My fourth comment is merely to reemphasize Mathews' closing statement. Identification of the oceanographic causes of fluctuations in Pacific salmonid populations *really will* take a concerted, cooperative research effort aimed at better measurement of both biological and physical parameters. However, economic studies indicate that the improvement in management brought about by the ability to forecast salmon abundance appears to be worth the cost (see, for example, Mathews 1971).

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Interaction among Sockeye Salmon in the Gulf of Alaska

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Abstract

Previous research documents that some salmon stocks (Oncorhynchus spp.) show density-dependent growth and mortality in their marine life stage. For sockeye salmon (O. nerka) in the Gulf of Alaska, density dependence in marine growth occurs with changes in the abundance of all sockeye stocks present in the Gulf of Alaska, as well as within-stock abundance. Most of the significant density-dependent effects of total ocean sockeye abundance occur within the first 16 months of ocean life of juveniles, and this influence on adult body size at a given age is at least as great as the effect of within-stock abundance. In one example stock, the weight of mature females is decreased by about 22% in periods of high Gulf of Alaska sockeye abundance. Time trends in duration of zooplankton blooms at Ocean Station P suggest that we cannot necessarily expect potential salmon production of the ocean to be the same as it was decades ago when salmon harvests were much larger than in 1960s and '70s. More research is needed on ocean migration routes and growth patterns of major individual stocks of salmon in the Gulf of Alaska and more coordination of research efforts among oceanographers and fisheries biologists is essential.

Introduction

Numerous cases have been documented in which salmon (Oncorhynchus spp.) exhibit density-dependent growth and/or survival in fresh water (e.g., Hunter 1959; Ward and Larkin 1964; Johnson 1965; Foerster 1968; Rogers 1973). In contrast, relatively few researchers have tested whether density dependent processes exist during the saltwater life phase of salmon. This is because of the logistical difficulties in gathering marine data and the paucity of long-term information.

The potential certainly exists for significant interaction among salmon stocks in the marine environment. First, Hartt (1980) found that salmon from Washington and British Columbia stocks migrate up the British Columbia coast in a narrow, 40-km wide band. A simulation model of migration of numerous stocks along this path (Walters et al. 1978) predicts that there are certain space-time locations in which high densities of salmon are found off the B.C. coast. Second, French et al. (1976) show from tag-recovery data that British Columbia and Alaskan (Bristol Bay) sockeye populations overlap considerably in space and time during their residence in the Gulf of Alaska. Third, well-studied terrestrial species show that density-dependent processes frequently exist at more than one life-stage, and there is no reason to believe that salmon are any exception to this pattern. Research on marine growth and survival of salmon has had relatively low priority in the past, but results from cases such as those discussed below suggest that more emphasis should be placed on research of this type.

Past and Current Research

Density-dependent Marine Growth

Several previous papers document the existence of density-dependent marine growth in salmon. Davidson and Vaughan (1941) first showed this for pink salmon (O. gorbuscha) in southeastern Alaska. Adult pinks were smaller in weight in years when pink abundances, summed across several nearby stocks, were high. Mathews (1980) found growth of Puget Sound coho salmon (O. kisutch) was slow early in their ocean life when their abundance, indexed by catches, was high. Rogers (1980) demonstrated that adult body size, by age, of Bristol Bay, Alaska sockeye salmon (O. nerka) decreased with increased abundance of total sockeye returns to Bristol Bay (catches plus escapement).

New Analyses

In my own work, I wished to test whether marine growth, survival, and other attributes of sockeye salmon were density dependent. I wanted an estimate of the abundance of all sockeye salmon resident in the Gulf of Alaska throughout the marine life phase, not just the abundance in the coastal environment in the year of maturation. These Gulf of Alaska sockeye abundances were reconstructed by using virtual population analysis on catch and escapement data, by age, for B.C. and Bristol Bay sockeye stocks (details will be published elsewhere, Peterman and Wong 1984). These stocks account for 80% of North American sockeye catches for 1952-1975. Because Bristol Bay sockeye stocks are much more abundant than B.C. sockeye stocks, reconstructed Gulf of Alaska sockeye abundances largely reflect variations in Bristol Bay stocks.

One interesting feature of the reconstructed ocean abundances of B.C. and Bristol Bay stocks is the tendency for the abundance of stocks from those two regions to be inversely related. The correlation coefficients are uniformly negative between B.C. and Bristol Bay ocean sockeye abundances, by age group, but only the sum of abundance of ages 3 and above shows a significant inverse correlation ($P < 0.04$, $r=-0.77$, $n=17$ years) after the autocorrelations of each time series are taken into account (see Peterman and Wong 1984). No complete explanation is possible yet for this inverse relation.

The ocean sockeye abundances reconstructed for individual stocks (X_1) and for the sum of all B.C. and Bristol Bay stocks (X_2) were used in multiple regression analyses to test whether various dependent (Y) variates show density dependence (details will be published elsewhere, Peterman 1984). Dependent variates were adult body size at a given age, smolt-to-adult growth rate, marine survival rate, residual in marine survival rate from the best-fit smolt-to-adult abundance relation, and weighted mean age at maturity for the brood class. The multiple regression equation was:

$$Y = a + b_1X_1 + b_2X_2 \qquad (1)$$

I focused on testing the null hypothesis that $b_2=0$, to determine whether there are significant effects of Gulf of Alaska sockeye abundances (X_2) in the presence of

Table 1. Sockeye salmon stocks used in multiple regression analyses.

British Columbia	Bristol Bay, Alaska
(all sub-2 life history types here)	(both sub-2 and sub-3 life history types)
Adams River	Branch River
Babine Lake	Egegik River
Chilko Lake	Igushik River
Cultus Lake	Kvichak River
Owikeno Lake	Naknek River
Stellako River	Nuyakuk River
	Snake River
	Togiak River
	Ugashik River
	Wood River

within-stock abundance effects on any of the above dependent variates. Estimates of the Gulf of Alaska sockeye abundances as well as within-stock numbers, by age, are available from the stock reconstruction data. These abundances were estimated for each of several segments of the total ocean life of sockeye: months 0-4, 5-16,17-28, etc. Each of these segments is referred to here as an ocean residence period, denoted respectively as OEY (ocean entry year), OEY+1 (ocean entry year + 1), etc. Most B.C. and Alaskan sockeye salmon are in salt water for about 28-40 months. Data for the dependent variates such as adult body size and marine survival rate exist for 6 British Columbia stocks and 10 Alaskan stocks, covering as many as 23 years for a given stock (Table 1). The Alaskan sockeye salmon stocks analyzed here are composed of sub-2 as well as sub-3 smolt life history types. "Sub-2" and "sub-3" refer to the year of life in which smolts go to sea. These designations are the subscripts in the Gilbert-Rich age notation; for example, an age 5_2 fish matured during its fifth year and went to sea during its second year. Unless specified otherwise, all ages in this paper refer to year of life since hatching of eggs.

It was not known a priori during which ocean residence period Gulf of Alaska sockeye abundances might be most important in affecting the dependent variates, nor which age category of those X_2 abundances would be most influential. Therefore, multiple regressions were repeated for each age category of X_1 and X_2 abundances and for each ocean residence period. The criteria for identifying the critical ocean residence period and most important age categories of abundances were those cases which gave the largest number of rejections (at the 0.05 level) of the null hypothesis, $b_2=0$. Because there were a large number of regressions performed, I avoided focusing on spurious sets of relations by using only those categories of ocean residence period and age in which there were more rejections of the null hypothesis than expected by chance alone. The binomial distribution provided this information by indicating the probability of obtaining "m" rejections in "n" trials.

Results are extremely complex, but to summarize briefly, most density-dependent effects of Gulf of Alaska sockeye abundances occur during the early ocean life phase

Table 2. Summary of results of multiple regression analyses showing for each group of sockeye stocks the ocean residence period and age category of ocean abundances in which most of the significant density-dependent effects occur. "Critical age" is the age during the "critical ocean residence period" of the fish which comprise the source of dependent variate data. For example, sub-2 stocks are late age 2, early age 3 during months 5 to 16 of ocean residence. "Significant age-abundance category" indicates the age categories of X_1 and X_2 ocean sockeye abundances which are most influential, i.e., which give rise to most of the significant density-dependent effects. Most significant cases arise for British Columbia stocks, for example, when age 2 plus 3 ocean sockeye abundances are used as independent variates <u>or</u> when age 5 abundances are used.

Stocks	Critical Age	Critical Ocean Residence Period	Significant Age–Abundance Category
British Columbia Sub–2s	2-3	OEY+1 (months 5-16)	2+3,5
Bristol Bay Sub–2s	2-3	OEY+1 (months 5-16)	3, "all"
Bristol Bay Sub–3s	3	OEY (months 0-4)	4+5, >2

(see Peterman 1984 for details). This is true for British Columbia as well as Bristol Bay stocks and for both sub-2 and sub-3 life history types (Table 2). While I did obtain results similar to those of Rogers (1980), who showed cases in which adult body size is inversely related to abundance in the last year of ocean life, I found considerably more significant cases of density dependence using abundances in early ocean life. Another finding here is that adult body size and marine growth decrease significantly when numerous conspecifics are present, but marine survival rates, survival rate residuals, and mean age at maturity are generally not significantly affected. Because sockeye abundance does not significantly affect marine survival rates, I conclude that these decreases in adult body size arise from competition for food and not indirectly from effects of size-selective predation or disease. The latter two mechanisms would have caused density-dependent changes in survival rate, which were not observed.

Results are generally consistent across stocks within the categories of the most influential age of conspecifics and the critical ocean residence period which are shown in Table 2. These categories of most influential age and most important period of ocean life are defined by the criteria discussed above, taking into account the large number of regressions done. For some stocks, such as the Chilko Lake case

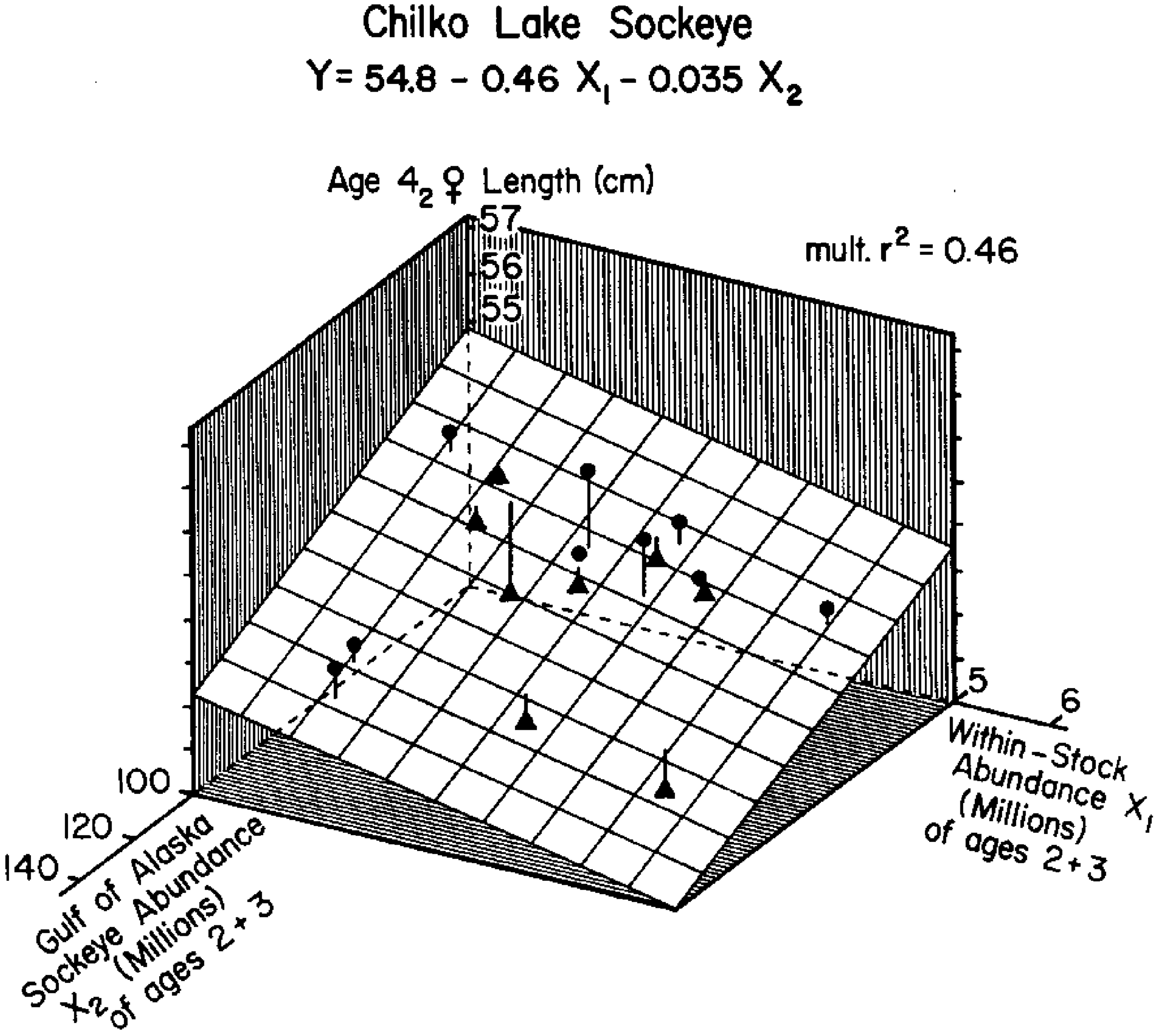

Fig. 1. Significant multiple regression plane fit through data for age 4_2 length of Chilko Lake sockeye females as a function of ocean abundances of Chilko sockeye (X_1) and B.C. plus Bristol Bay sockeye (X_2). The bottom back corner of the box is zero on both abundance axes. The 17 years of actual data points are shown in relation to the regression plane by solid circles (positive residuals) and solid triangles (negative residuals). See text for explanation.

shown in Figure 1, body size data were available by sex. In all but one case, when significant results are found for one sex, the other sex is also significant.

The representative example of results in Figure 1 illustrates the relation between the standard length of adult age 4_2 females and the two independent variates X_1 and X_2. X_1 is the within-stock (Chilko) ocean abundance in ages 2 and 3 measured in millions of fish and X_2 is the ocean abundance of ages 2 and 3 sockeye (also in millions) summed across all B.C. and Bristol Bay stocks. The equation for the regression plane is $Y=54.8 - 0.46X_1 - 0.035X_2$, and both of the slopes of the X_1 and X_2 variates are significantly different from zero ($P < 0.05$, $P < 0.01$, respectively). This Chilko Lake sockeye case (Figure 1) shows that even in the presence of within-stock (X_1) density-dependent effects on body size, the abundance of age 2 and 3 sockeye present in the Gulf of Alaska (X_2) has a significant influence on adult body size of given aged fish. The within-stock and combined stock abundances of ages 2+3 shown in Figure 1 are the abundances present during the period covering approximately 5 to 16 months after the Chilko Lake fish entered the ocean. Chilko Lake age 4_2 fish are in salt water about 28 months, but the influence of Gulf of Alaska sockeye abundance upon body size appears most strongly during that first segment of ocean life.

These effects on adult body size can be large as illustrated by the following example taken from two points on the Chilko Lake sockeye regression plane shown in Figure 1. At a low Chilko Lake sockeye abundance of 0.5 million and a low Gulf of Alaska sockeye abundance of 20 million fish, age 4_2 females will be 53.9 cm in length. At high abundances of 4.5 and 90 million for Chilko and Gulf of Alaska abundances, respectively, age 4_2 females will be only 49.6 cm long. Using a length-weight relation for Chilko Lake female sockeye, this 8% decrease in length translates into a 22% loss in average weight, which in turn significantly affects fecundity of spawners and weight of catch.

Table 3 shows detailed regression results for all sub-2 stock cases in which Gulf of Alaska sockeye abundance of young fish during the critical ocean residence period of months 5 to 16 of ocean life has a significant effect on adult body size or smolt-to-adult growth (see Peterman 1984 for results from all ages and critical periods). The abundance of young ages (2+3 for B.C. cases and age 3 alone for Bristol Bay) has a more consistent effect on dependent variates across stocks than older ages, and hence the former are focused upon here. With the exception of Wood River and Togiak River stocks in Alaska, all cases in Table 3 show a negative influence of larger Gulf of Alaska sockeye abundances on adult body size and growth. These two exceptions have one and two extreme outlier points, respectively, which may have affected regression results.

Because X_1 and X_2 abundances are in millions of fish, the associated regression slopes b_1 and b_2 in Table 3 show changes in body size per million fish. Note in Table 3 that the effect of Gulf of Alaska sockeye abundance, X_2, on a Y variate is usually less than one-tenth that of the within-stock abundance, X_1, per million fish. However, this comparison of the within- versus the across-stock effects on a per million fish basis is misleading because X_2 abundances vary over a much larger range (20-90 million fish in the Figure 1 example) than X_1 (0.5-4.5 million). When this "scale effect" is taken into account by the usual procedure of converting all data into standard deviation units, then in all cases in Table 3 the contribution of X_2 abundances to variation in the dependent variate is at least as great as the contribution of X_1 abundances (details will be published elsewhere). In the Chilko Lake example of Figure 1, the standardized slopes are $b_1=-0.43$ and $b_2=-0.60$. In other words, for every standard deviation unit (SDU) increase in the Gulf of Alaska

Table 3. Parameter estimates for equation (1) for all sub-2 stocks which have significant slopes (at $\alpha=0.05$) on Gulf of Alaska sockeye abundance, X_2, within the important lags and age categories, as defined in text. All examples are for cases with ocean sockeye abundances present in months 5-16 of the ocean life of the stocks shown. X age shows the age category for X_1 and X_2 abundances. Yrs = sample size. Parameter estimates are derived from analysis of raw data, in which some variates are in cm or mm. Probabilities are shown for the two hypothesis tests on the slopes.

Stock	Y variate	X Age	Yrs	Parameter estimates (raw values) a	 b_1	 b_2	$P_{b_1=0}$	$P_{b_2=0}$
Body size as affected by abundance of young ages -								
British Columbia								
Chilko	4_2 female standard length (cm)	2+3	17	54.83	-0.4593	-0.0347	0.046	0.009
Chilko	4_2 male standard length (cm)	2+3	17	57.29	-0.4606	-0.0371	0.042	0.005
Chilko	4_2 weight (lbs)	2+3	4	7.792	-0.6024	-0.0145	0.036	0.040
Stellako	4_2 female standard length (cm)	2+3	17	52.87	-0.2624	-0.0301	0.638	0.016
Stellako	4_2 male standard length (cm)	2+3	17	55.07	-0.3967	-0.0222	0.39	0.027
Owikeno	5_2 fork length gillnet samples (cm)	2+3	15	63.50	0.0576	-0.0364	0.82	0.036
Babine	5_2 fork length gillnet samples (cm)	2+3	15	64.90	0.1437	-0.0366	0.63	0.005
Babine	Inst. growth rate to 5_2 (gillnet)	2+3	12	2.198	-0.0199	-0.0011	0.22	0.025
Babine	Inst. growth rate to 5_2 female (test fishery)	2+3	8	1.981	-0.0178	-0.0010	0.009	0.008
Alaska								
Wood	3_2 fork length (mm)	3	7	402.53	-66.30	2.1647	0.046	0.035
Wood	5_2 fork length (mm)	3	15	571.25	- 2.04	-0.238	0.40	0.031
Egegik	5_2 fork length (mm)	3	17	586.3	3.076	-0.5738	0.21	0.025
Togiak	4_2 fork length (mm)	3	11	525.83	-28.72	0.2203	0.037	0.030

abundance of ages 2+3 sockeye, a 0.6 SDU decrease occurs in 4_2 female size, whereas one SDU increase in Chilko L. sockeye abundance only gives a 0.43 SDU decrease in female size.

My conclusion, therefore, is that it is important for fisheries managers and biologists to take into account the effect of Gulf of Alaska sockeye abundances on the growth of fish in individual stocks. If we ignore these effects, we will overestimate the potential biomass production of salmon from wild and enhanced stocks. Other management implications are covered in Peterman (1984).

Density-dependent Marine Survival

Decreases in marine survival with increases in abundance of individual salmon stocks have also been documented, most clearly for Babine Lake sockeye from northern British Columbia (Peterman 1982a). Unlike the case of Cultus Lake sockeye (Foerster 1954), this effect for Babine Lake fish is not attributable to a relation between smolt size and smolt abundance. Age structure analyses indicate that most of this density-dependent marine survival for Babine Lake sockeye occurs during the first 15 months of ocean life (Peterman 1982a, 1982b), a period almost identical to the most significant density-dependent marine growth period for several stocks, as discussed above.

Variability in Growth

Godfrey (1958), Killick and Clemens (1963), and Ricker (1982) show that growth of sockeye salmon is positively correlated among several British Columbia stocks. The greater the number of years of ocean growth shared simultaneously by these stocks, the stronger the positive correlation (Ricker 1982). Ricker concluded that at least 47% of variation in adult sockeye body size is caused by ocean conditions. While the studies of density dependence discussed above show that ocean abundance of sockeye salmon is a significant component of this variation, physical oceanographic variables such as temperature may also be important (Killick and Clemens 1963; Ricker 1982). These temperature effects could lead to a family of density-dependent growth relationships (Figure 2).

Species other than sockeye may also affect sockeye marine growth. Krogius (1960) shows that Asian sockeye body sizes are depressed from the long-term mean every other year when these fish are present with large numbers of pink salmon. Limited availability of detailed population data on other fish species in the Gulf of Alaska currently precludes extension of the above analyses to include more components of the fish community.

One final point is relevant to this discussion. Frequently the argument is made that because we used to catch approximately twice as much weight of salmon as we did in the mid-1970s (MacLeod 1977), we should be able to bring salmon production back up to that level through enhancement projects. One assumption implicit in this argument is that the biological oceanographic variables which affect potential salmon production have remained constant. To my knowledge the only long-term data set relevant to testing that assumption is the Ocean Station P zooplankton series taken at 50° N latitude, 145° W longitude (LeBrasseur 1965; Fulton 1978; J. Fulton, Pacific Biological Station, Nanaimo, B.C. personal communication). These zooplankton samples were analyzed by filtering the time series into various indicators such as the total

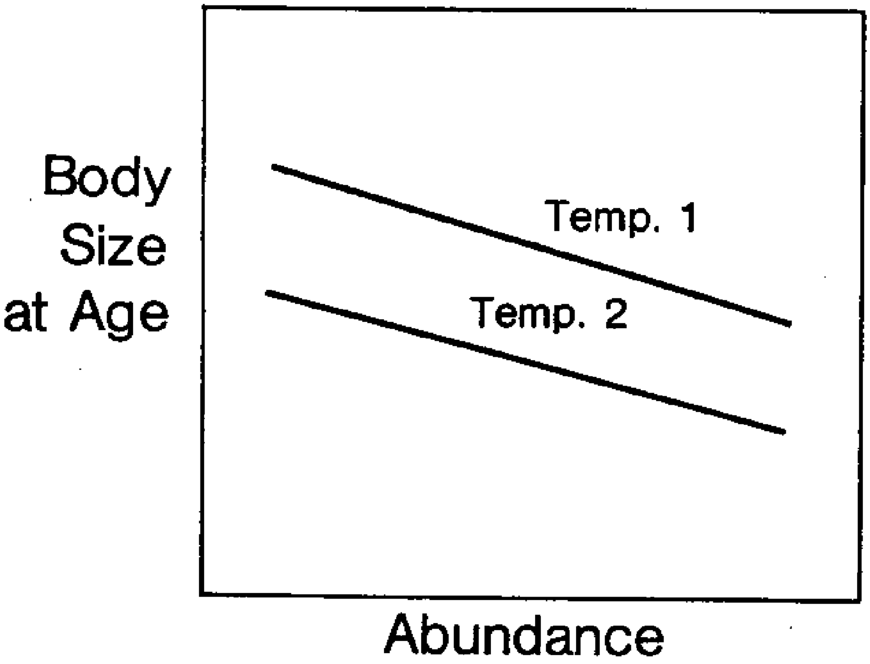

Fig. 2. Hypothesized effect of ocean temperature on the density-dependent relations between adult body size at a given age and ocean abundance of sockeye salmon.

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time each year that zooplankton density was above some arbitrary level. Figure 3 shows that over the 1957-1977 period there was a significant ($P < 0.02$) decrease in the duration of the zooplankton bloom. The regression line shows a drop from 215 days in 1957 to 148 days in 1977. Use of thresholds other than 40 mg/m^3 also results in similar significant time trends. Therefore, it may be incorrect to assume that the ocean capacity for producing salmon is constant. Because ocean capacity could be variable, more attention should be given to those processes which are affected by variable productivity: density-dependent growth and survival.

Future Research Needs

These results from studies of northeastern Pacific sockeye stocks suggest that it is worth examining other data to test whether density-dependent processes exist in the marine life phase of other salmon species as well. Several other extensions of past research are needed.

Given the large-scale salmonid enhancement plans in Alaska and Canada, we need to identify more precisely the ocean migration routes of major individual salmon stocks. We must identify which stocks occupy areas near the center of the space-time distribution of the largest abundance of mixed stocks in the Gulf of Alaska. Because

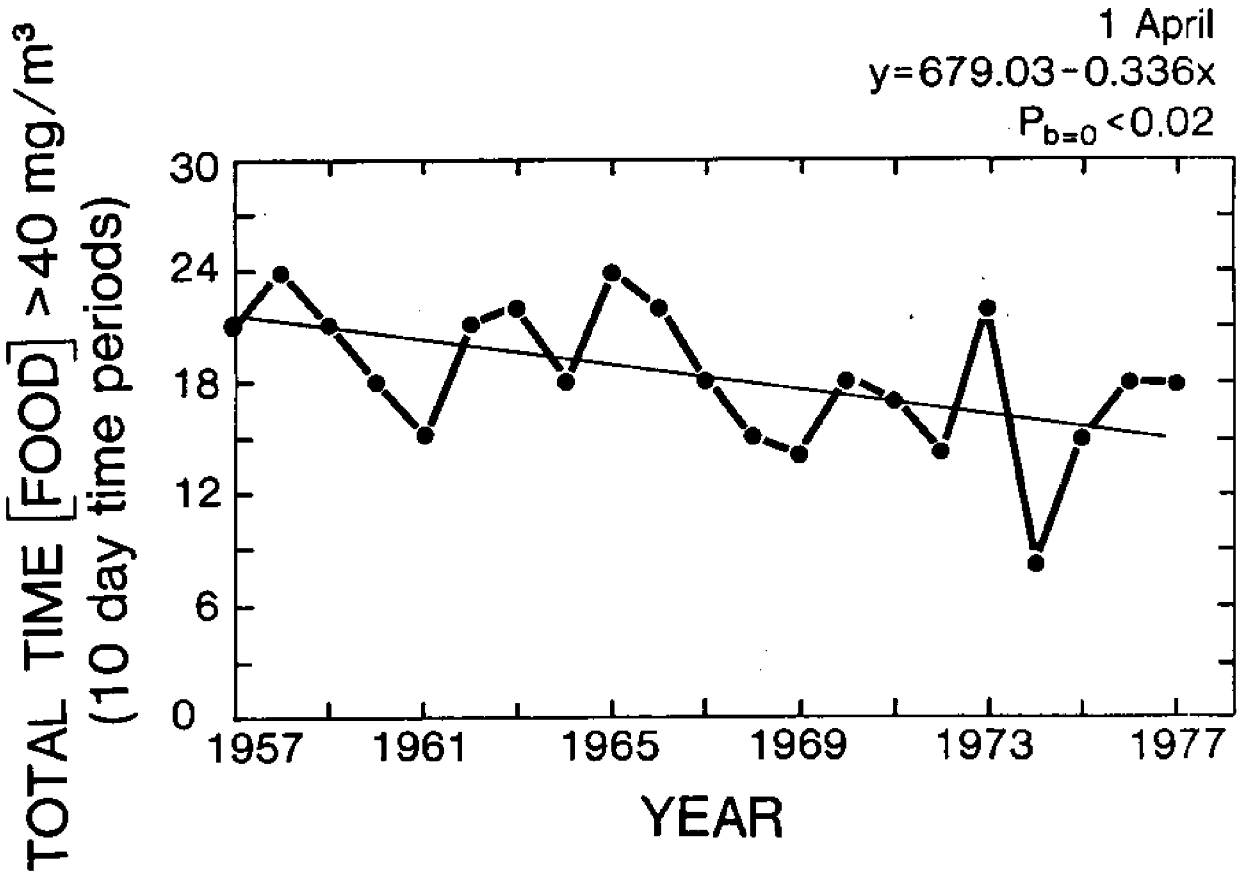

Fig. 3. Time series of duration of zooplankton bloom at Ocean station P, using 1 April as the start of each year. See text.

of density-dependent growth or survival, such stocks may show less potential for future enhancement than stocks near the margin of ocean salmon distributions. To get this detailed stock-specific information, we must reestablish a program such as that reported in French et al. (1976) and Hartt (1980) for tagging juveniles on the high seas and for intensively sampling them throughout their remaining life. We need to evaluate the "quality" of the ocean habitat occupied by the above stocks at the margins of salmon distribution to ensure these stocks are capable of responding to enhancement. Direct estimates of this capability could come from comparisons of growth and survival rates between these stocks and those near the center of the ocean distribution. Indirect estimates could come from samples of production at trophic levels below salmon (squid, euphasiids, zooplankton).

As part of these high seas tagging programs, we could validate methods of back-calculating sizes of fish from scales or other hard parts. No validation has been done for salmon back-calculations from adults back to the smolt or early ocean life stage. To do this validation, we need large numbers of field-measured sizes of young, individually tagged fish of known age (from scale sample) which are then recovered at some older age, measured and scale sampled. Juvenile sizes back-calculated from the latter scales can be compared with actual known juvenile sizes of those same individual fish, not just with mean size of the juvenile population as is normally done. Validation of the back-calculation method will permit additional independent analyses of periods of ocean growth during which most of the significant decreases in growth occur in years of high ocean sockeye abundance. We should also resume sampling programs for age distributions of salmon catches and escapements in British Columbia, which will permit extension of reconstructed estimates of Gulf of Alaska sockeye abundances beyond the early 1970s, when such programs stopped in B.C.

Finally, efforts should be made to closely coordinate high seas research among oceanographers and fisheries biologists. This symposium clearly illustrates the lack of communication which exists between these two groups of scientists. This is surprising, since at least some researchers in both disciplines have the same objective of understanding factors which ultimately affect fish population dynamics. Oceanographers and fisheries biologists each have their traditional spatial and temporal scales for making measurements of standard variables and for studying processes. The approaches have been so different that there is little overlap in the literature, certainly less than is desirable. This divergence of research methods is not unique to the marine environment, however; an exactly parallel situation exists in the different approaches of limnologists and freshwater fisheries biologists as outlined by Rigler (1982). More effort should therefore be made to focus research on tests of hypotheses dealing with the direct link between ocean conditions and fish growth, survival, and distribution.

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Population Dynamics of Bristol Bay Sockeye Salmon, 1956-1983

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Abstract

The recent phenomenal increases in abundance of Bristol Bay sockeye salmon are reviewed. These have been due to increased production, particularly, in river systems other than the historically dominant Kvichak River system. The increased production is coincident with favorable climatic conditions and drastic reduction in the interception of Bristol Bay sockeye salmon in high seas fisheries. The differential resurgence of stocks more vulnerable to high seas fishing suggests that the reduced high seas interception was a causative factor in the resurgence of Bristol Bay. However, Bristol Bay sockeye salmon have shown density dependent together with a high correlation between production and climatic indicators suggests that favorable climate was a causative factor. Two useful forecasting techniques based on the relationship among size, abundance, and climatic indicators are developed.

Introduction

The Bristol Bay fishery consists of five fishing districts and eleven river-lake systems (Figure 1). The Kvichak River system is the dominant river system in Bristol Bay, producing 315 of the 639 million adult salmon that have been produced in Bristol Bay since accurate monitoring of returns began in 1956. The Kvichak is a cyclic dominant system (Ward and Larkin 1964, Mathisen and Poe 1981), with peak year returns on a four year cycle 1956-1960 and on a five year cycle 1965-1980.

Bristol Bay produces a large component of the North American catch of sockeye salmon (Figure 2). For the years 1980-1983 the catch of western Alaska sockeye, almost all of which is from Bristol Bay, averaged 23.2 million, composing 55 percent of the total catch of North American sockeye for the same period. Returns to Bristol Bay have increased markedly since the very depressed fishery of 1972-1973 (Figure 3).

The recent resurgence of Bristol Bay sockeye has come from river systems other than the Kvichak (Figure 3). The return to the Kvichak in 1979 and 1983 was high relative to past cycle years, however, the other cycle year returns, since 1978, have been similar to earlier comparable cycle year returns. Except for years of peak cycle return to the Kvichak, the returns to Bristol Bay (particularly to the Nushagak and Ugashik Districts and to the Kvichak during off cycle years) have been depressed during the period 1949 through 1973 relative to earlier year returns (Rogers 1983). Air temperatures in Bristol Bay throughout the year were much lower than normal for this 25 year period. Rogers attributes the depressed state of the Bristol Bay fishery during this period to the cold climatic conditions.
higher (Figure 4).

Three notable changes have occurred in Bristol Bay since the early seventies. First, escapements to the non-Kvichak River systems have been higher (Figure 4). Second, climatical condition during the life history of sockeye salmon returning in 1978 and later have become significantly warmer (Rogers 1983). Third, the rate of interception of Bristol Bay sockeye salmon by the Japanese high seas fishery has been markedly reduced for returns in 1978 and later (Figure 5). The documented rate of interception of Bristol Bay sockeye during the period 1956-1977 averaged 11.2%, while the rate of interception during the period 1978-1983 averaged 1.4%. There was a reduction in the catches of sockeye in the Japanese Mothership driftnet fishery 1974-1977 by domestic action by the Japanese as a conservation measure in response to the poor Bristol Bay returns 1973-1974. (Burgner personal communication). In 1978, the mothership driftnet fishery as well as the landbased driftnet fishery were excluded from the area of the North Pacific where Bristol Bay sockeye were known to occur.

We will review the dynamics of the Bristol Bay sockeye salmon fishery from 1956 to the present, relative to the recent changes in climate, reduced high seas interception, and recent higher escapements to non-Kvichak River systems.

Methods

The analyses presented below are based on the Alaska Department of Fish and Game catch and escapement leaflet series (Yuen and Meacham 1983). The methods for estimating the magnitude and age composition of the Bristol Bay catch and escapement by river system were developed beginning in 1946 by researchers at the University of Washington (Mathiesen, Burgner, and Koo 1963). These methods were later adopted and modified by the State of Alaska. Accurate monitoring programs for all river systems were installed by 1956 and are being continued by the Alaska Department of Fish and Game. Briefly, catches were enumerated from fish delivery tickets. The age, length, and weight composition of the catch in the various fishing districts was estimated through catch sampling at selected processing plants in each of the respective districts. Escapements for the eight major river systems were enumerated by visually counting upstream migrating salmon from towers installed on both banks of the river near the outlet of the lowest lake in the respective river-lake system. Escapements to three minor river systems were estimated by aerial survey. The age and length composition of the escapements was estimated through daily beach seine sampling of the escapement of the major river systems near the system outlets.

Sockeye caught in the Naknek-Kvichak District and the Nushagak District were from mixed river system stocks, and were allocated to river system to determine the return (catch plus escapement) by river system. Each age class was apportioned independently, generally by applying the relative proportion of the escapement of an age class from the contributing river in question to the commercial catch of that age class.

In the following, the returns to the Kvichak were separated from the remainder of the Bristol Bay River systems, in order to separate cyclic effects unique to this system. Analyses were performed on returns to the Kvichak River system, Bristol Bay River systems other than the Kvichak, and the combined Bristol Bay River systems. Two methods of evaluating production were considered. The first relates the production or return from brood year escapement to the level of brood year escapement. Here the future returns from a given escapement were cumulated based on the age composition and level of returns in subsequent years. Returns from the escapements during the brood years 1956 to 1977 were considered in the analyses below. The latest brood year for which all significant age classes have returned was 1977. Projected returns to the Kvichak from the 1978 and 1979 brood years were estimated based on returns to date (1983) and the past average proportions of future returning age classes (Eggers, Meacham, and Yuen 1983).

The second method relates the returns in a given year to an estimate of the parent escapement responsible for that return. This "a priori escapement" was estimated by prorating the escapements four, five, and six years prior to the year of return by the long term average proportion of four-, five-, and six-year-old fish in the return. There was little difference in the the average proportion of four-, five-, and six-year-old fish in the return among the Kvichak (Table 1) River system, river systems other than the Kvichak (Table 2), or for the combined Bristol Bay River systems (Table 3). However, the standard deviation of the average proportion of four-, five-, and six-year-old fish for the Kvichak River system was roughly three times that for river systems other than the Kvichak. This high variability in age of the return to the Kvichak was due to cyclic variability in the age composition of the return as well as major variability in the age at seaward migration of the progeny from cycle year escapements. The variability in freshwater age composition resulted in changes in the periodicity of the Kvichak cycle. The Kvichak cycle changed from four to five year in returns from 1960. It now appears to be changing from five to four year in 1980. Returns in 1984 and 1985 will verify this change. Because of the variability in the age composition of the Kvichak return production based on the return from a priori escapements was not considered for the Kvichak. The returns from a priori escapements can be considered for the combined Bristol Bay River systems 1966-1983. During this period the Kvichak was on a five year cycle and age composition for the combined Bristol Bay River systems was comparatively stable. The age composition of the returns was remarkably stable for river systems other than Kvichak. Therefore, returns from a priori escapements can be considered for these systems for the return years 1962-1983.

Results

The major reason for considering returns from a priori escapement is that returns relative to this index of escapement have occurred during a specific period of time and can therefore be related to corresponding environmental management events. It is not possible to do so for returns from brood year escapements since the returns of the major age classes must be cumulated over a three year period of time. Factors that have influenced production have occurred over an extended period of time and cannot be readily reduced to a single variable or set of variables neccessary for application of statistical analytical methods.

The returns from a priori escapements 1966-1983 (Figure 6) showed the occurrence of three distinct periods characterized by a relatively constant ratio of return per a priori escapement. There was a period of intermediate return per a priori escapement (1966-1972, 1977), characterized by a full Japanese high seas fishery and normal temperatures; a period of very low return per a priori escapement (1973-1974), characterized by a full Japanese high seas fishery and very low temperatures; and a recent period of very high return per a priori escapement (1978-1979), characterized by a reduced Japanese high seas fishery and high to normal temperatures. The index of temperatures (Figure 5) that was used was the sum of the mean June air temperatures at Cold Bay during the two years prior to the year of return.

The relation between return and a priori escapement was also considered for Bristol Bay River systems other than the Kvichak (Figure 7). A temporal pattern of return per a priori escapement observed for the Bristol Bay River systems other than Kvichak was similiar to that observed for the combined Bristol Bay River systems. However, the difference in return per a priori escapement among the three periods (i.e., the early period of normal temperatures and high seas fishing, the period of low temperatures and high seas fishing, and the recent period of high temperatures and reduced high seas fishing), were not as great as that observed for the combined Bristol Bay River systems. The escapements to Bristol Bay River systems other than Kvichak during the recent period (1976-1983) were greater than those in earlier years. So the higher returns for the recent period are due in part to higher a priori escapements. Note that the temperatures corresponding to the 1978 return were the 1976 and 1977 mean June air temperatures at Cold Bay.

Return per a priori escapement was plotted against temperature both for the combined Bristol Bay River systems (Figure 8) and for Bristol Bay River systems other than the Kvichak (Figure 9). In both cases, return per a priori escapement increased with increasing temperature. Unfortunately, the period 1978-1983 was a period of the reduced Japanese high seas fishery as well as very high temperature. The temperatures 1978-1983 were generally higher than any temperatures observed for the earlier period, hence the effects of temperature were completely confounded with the effects of the reduced high seas fishery.

The major problem with considering returns relative to a priori escapements is that age composition does indeed vary so a priori escapement is only an approximation of the parent stock. This problem can be solved by considering returns from brood year escapement. Although it is difficult to consider environmental effects, returns from brood years including 1974 and later had significant reduction in high seas fishing mortality. For the Kvichak River system the returns per spawner for the 74, 75, 76, and 79 brood years reflected those of past cycle year escapements (Figure 10). The return per spawner for the 77 and 78 brood years reflected those of the past off cycle year broods. Therefore, in the Kvichak River system the production was only normal or slightly above normal for recent brood years not exposed to the past full high seas exploitation. For the Bristol Bay River systems other than the Kvichak the return per spawner for brood years 1974-1978 was substantially above the return per spawners observed for earlier brood years that were exposed to full high seas exploitation (Figure 11).

For Bristol Bay sockeye salmon populations the average length of returning adults was inversely related to the level of return (Rogers 1979). Rogers presented a detailed analysis of length and weight by major age class and sex relative to the level of return by fishing district. Rogers (1979) presented data only through 1973. Presented below is a brief expansion of that analysis through 1983. The analysis presented below considered length by ocean age ignoring differences due to freshwater age and sex. In addition, the Kvichak River was separated from the rest of Bristol Bay.

One would expect that even if the size at return for particular age classes were independent of level of return, the size of fish in the Bristol Bay return averaged over age classes would be inversely related to level of return. This was because in years of high return, the returns are predominantly bound for the Kvichak River. During cycle years, Kvichak fish tended to be mostly (approximately 90 percent) the smaller 2-ocean fish. The size at return was inversely related to level of return for specific age classes (Rogers 1979) as well as ocean age classes (Table 4). Size was also correlated among age classes (Table 5). These suggest that the depression of size by high returns was due to density dependent growth.

Rogers (1979) suggested that climatic conditions in the spring of return had the greatest effect, other than density of salmon in ocean, on the size of the returning fish. This was because air temperature in the spring of the return year (these are indexed by the April-May mean air temperature at King Salmon) of the return year described a significant portion of annual variation in weight that was not accounted for based strictly on size of return. The model relating weight to level of return and temperature used by Rogers (1979) worked better for three-ocean age classes than it did for two-ocean classes. The results presented here showed that the magnitude of the inverse correlation between size of fish at return was greater for three-ocean fish than it was for two-ocean fish (Table 4). This was consistent with Rogers' hypothesis that the density-dependent growth has occurred during the period of ocean residence.

Plots of the mean length of the inshore return for two-ocean, three-ocean, and ocean ages combined versus the total return showed that mean length in inversely related magnitude of the return but the effect of density dependent growth was much reduced in recent years (1978-1983) (Figure 12). These were also years of higher temperatures during the ocean residence. This suggests that effects of temperature have moderated the depression of growth by high density.

In the above, the magnitude of the return was related to the level of a priori escapement and temperature index. Since the independent variables are known well in advance of the inshore fishery, the above relations have been used to develop a forecasting model based on a priori escapement and the Cold Bay temperature index, (Eggers, Meacham, and Yuen 1983). The following model was used:

$$\mathrm{Ln}\ (R) = A + B_1\ \mathrm{Ln}\ (E) + B_2\ \mathrm{Ln}\ (T) \qquad 1.$$

Where, R = return in year i; E = a priori escapement; T = sum of the mean June air temperatures in year i-1 and i-2; and A, B_1, B_2 are constants fitted to past data by multiple linear regression. The model was fitted to years 1966-1983 (Figure 13) and yielded an R^2 of 0.834. Regression coefficients A, B_1, B_2 were -54.153, 0.754, and 12.286, respectively.

Since length is correlated with the size of the return, a model similar to equation 1 above is expected, incorporating length and temperature to also fit the historical data. The following model was used:

$$\mathrm{Ln}\ (R) = A + B_1\ \mathrm{Ln}\ (L) + B_2\ \mathrm{Ln}\ (T) \qquad 2.$$

Where L = mean length (age classes pooled) of the inshore return in year i. This model was also fitted to years 1966-1983 (Figure 14) and yielded an R^2 of 0.760. Regression coefficients A, B_1, and B_2 were 14.358, -10.3585, and 11.899, respectively. The mean length of the inshore return is not known until the catches and escapements have been enumerated, and all of the age, weight, and length samples processed. This occurs well after the inshore fishery. Equation 2 is unsuitable for forecasting the run strength. However, the average size of fish in the inshore return can be estimated from fish caught in the Port Moller test fishery (Eggers 1983). This test fishery occurs well in advance of the inshore fishery (7 -10 days), and estimates of mean length of the inshore return based on the Port Moller test fishery in conjunction with equation 2 can be used to develop inseason forecasts of run strength of the Bristol Bay return.

Discussion

In 1978, the Japanese high seas fishery was moved to the west in the area of the North Pacific Ocean where Bristol Bay sockeye salmon occur. This was accomplished through a renegotiated INPFC treaty in response to extending the fishery conservation zone to 200 miles off the coast. There is some conjecture as to when the rate of interception by the Japanese high seas fishery was fully reduced to present levels. There was some reduction prior to 1978 as the Japanese reduced their catches of sockeye (1974-1977) in the mothership fishery by domestic action in response to low inshore returns of sockeye to Bristol Bay 1972-1973. However, the landbased driftnet fishery still fished in their traditional area, during this period, catching substantial numbers of sockeye. The exact proportion of Western Alaska and Asian sockeye in the landbased fishery was unknown. However, based on the low inshore abundances of Asian sockeye relative to Western Alaska sockeye, a significant proportion of the landbased fishery catch of sockeye should have been Bristol Bay sockeye.

The landbased driftnet fishery was also moved further west in 1978. Thus, by 1978, the combined rate of interception of Bristol Bay sockeye was reduced to present levels. Some reduction in the high seas interception occured earlier, 1974-1977. There was a remarkable increase in the returns to Bristol Bay, coincident with the decrease in high seas interception of Bristol Bay salmon. This increase in returns also coincided with a change in climatical conditions in Bristol Bay as well as the North Pacific Ocean and the Bering Sea. Was the resurgence of the Bristol Bay fishery due to reduction of high seas fishing, improved climate, or a combination of both factors?

The analyses presented above have shown that the increased returns have resulted from increased production. The analyses included the documented Japanese high seas catch mothership catch. However, the Japanese fishery was a gill net fishery using vast amounts of gear soaked for extended periods in adverse weather and sea conditions. There was potential for occurrence of a large unreported dropout mortality. This unreported mortality would appear as increased production if the mortality ceased to occur. Likewise the catches of sockeye in the landbased fishery were also not considered, and the reduced catches of Bristol Bay sockeye would appear as increased production.

Although the returns to the Kvichak have been good during pre-peak, peak, and post-peak cycle years, the resurgence in Bristol Bay returns has come from river sytems other than the Kvichak. These tend to produce a higher proportion of three-ocean fish. The mean proportion three-ocean returns 1957-1983, non-Kvichak fish was 48.5 percent, where as the mean proportion for Kvichak fish during the same period was 24.3 percent. These were statistically different ($P < 0.001$). There has been no change in the proportion of three-ocean fish in the returns to the non-Kvichak River systems after 1978 relative to past years. However, Rogers (1983) has shown that increased returns to the river systems in the Nushagak District have come from the Igushik and Nuyakuk River systems, and from the large rivers of the Wood River system. These spawning populations were almost entirely three-ocean fish.

If reduction of high seas interception was responsible for the increased returns to Bristol Bay after 1978, returns of three-ocean fish should have increased more than returns of two-ocean fish. This is because of the greater vulnerability of three-ocean fish to high seas exploitation due to the extra year of residence in the ocean and greater size. The two-ocean returns, particularly to the Egegik, Naknek, and Ugashik systems, have shown increases in recent years similiar to those observed for three-ocean returns.

The index of climate used in the above analyses was the mean June air temperature at Cold Bay during the two years prior to return. This presumably reflects climatic conditions during the ocean phase of the sockeye life history. However, this variable also correlates with variables used by Rogers (1983) as indicative of climatic conditions during the freshwater phase of the sockeye life history after the late sixties. There were years of relatively high Cold Bay air temperatures during the late fifties and sixties (Figure 5). Production of sockeye during these years was lower than that observed for the recent period following the reduced Japanese high seas fishery. Rogers states that returns to the Nushagak District appeared to be building during the mid-fifties but the increase in Japanese high seas fishing effort coincident with the improved climate halted the rebuilding trend. If the Cold Bay temperature index is indicative of improved ocean carrying capacity, and admittedly this is not well documented, then the success of the Escapement Temperature model (Figure 13) suggests that increased production has occured in the oceanic phase of the sockeye life history.

Bristol Bay sockeye salmon also exhibit density-dependent growth during their oceanic phase. The magnitude of the depression of growth by density was less for sockeye returning 1978 and later. This suggests that oceanic carrying capacity has increased after 1978, presumably due to the more favorable climate. The level of returns was used as the indicator of density of salmon during the period of ocean residence. The Japanese high seas fishery targeted on sockeye during a fairly restricted period of time, May-July. Most of the immatures are caught during July. A large component of the mortality due to the Japanese fishery occurred following the period of oceanic growth. If unaccounted mortality due to dropout was the agent responsible for depression of Bristol Bay returns prior to 1978 then the actual densities of salmon in the ocean would be much higher than that indicated by the total return. Thus, the length density relationship in Figure 12 for the return years before 1978 should be shifted to the right to correct for the biased estimates of oceanic density given by the magnitude of total return. The shifted relationship would be closer to that observed for the more recent years.

In summary, it is not possible with the data at hand to determine whether the resurgence of the Bristol Bay sockeye salmon runs was due to reduced high seas interception or to favorable changes in climate. An interaction of these factors most likely contributed to the spectacular increase in returns.

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Table 1. Returns by age, Kvichak River including high seas catch. Total return includes all ages classes.

	Age at Maturity						
	4 Years		5 Years		6 Years		
Year	Number (Millions)	Percent	Number (Millions)	Percent	Number (Millions)	Percent	Total Return
1956	10.179	70.4	3.969	27.5	.305	2.1	14.454
1957	.069	0.7	8.645	87.1	1.210	12.2	9.924
1958	.092	7.8	.403	34.2	.677	57.5	1.178
1959	.256	25.7	.663	66.4	.063	6.3	.998
1960	23.509	96.9	.741	3.1	.0	.0	24.257
1961	.226	1.6	12.755	92.3	.796	5.8	13.823
1962	.070	1.5	3.437	71.2	1.316	27.3	4.824
1963	.194	30.5	.180	28.3	.261	41.0	.636
1964	1.407	79.3	.319	18.0	.026	1.5	1.775
1965	.317	0.7	46.326	99.3	.013	0.1	46.676
1966	.096	1.1	2.415	27.5	6.279	71.4	8.789
1967	.049	0.9	4.743	86.7	.666	12.2	5.472
1968	2.083	65.3	.675	21.2	.407	12.8	3.189
1969	9.787	76.3	2.662	20.8	.355	2.8	12.826
1970	.482	1.4	32.066	96.4	.681	2.0	33.247
1971	.329	4.7	5.254	75.7	1.346	19.4	6.940
1972	.271	16.7	1.007	62.0	.346	21.3	1.625
1973	.141	40.3	.131	37.4	.077	22.0	.350
1974	.083	1.8	4.459	94.9	.156	3.3	4.699
1975	.260	1.7	14.337	94.4	.593	3.9	15.192
1976	.273	7.4	2.192	59.7	1.222	33.3	3.672
1977	.587	26.2	1.351	60.3	.284	12.7	2.242
1978	6.538	80.8	1.244	15.4	.302	3.7	8.090
1979	5.821	23.5	18.364	74.2	.568	2.3	24.759
1980	5.107	14.4	29.461	83.3	.768	2.2	35.384
1981	1.840	26.2	4.627	65.8	.565	8.0	7.036
1982	1.729	56.1	1.042	33.8	.253	8.2	3.081
1983	17.709	88.3	2.268	11.3	.085	0.4	20.065
Mean		30.3		55.3		14.1	
Standard Deviation		32.4		30.9		17.8	

Table 2. Returns by age, Bristol Bay except Kvichak, including high seas catch. Total return includes all age classes.

	Age at Maturity 4 Years		5 Years		6 Years		
Year	Numbers (Millions)	Percent	Numbers (Millions)	Percent	Numbers (Millions)	Percent	Total Return
1956	2.673	23.2	6.405	55.6	2.382	20.7	11.525
1957	.605	7.5	3.653	45.5	3.598	44.8	8.033
1958	1.425	29.0	2.428	49.4	.851	17.3	4.917
1959	4.612	37.2	7.779	62.7	1.274	10.3	12.406
1960	8.608	54.7	4.865	30.9	2.161	13.7	15.732
1961	.428	4.2	8.415	83.1	2.802	27.7	10.121
1962	2.838	36.8	2.890	44.6	1.180	18.2	6.484
1963	1.989	27.7	3.268	45.5	1.863	26.0	7.177
1964	4.433	47.0	4.198	44.5	.727	7.7	9.429
1965	1.080	8.1	10.307	77.4	1.879	14.1	13.320
1966	1.280	12.1	4.753	44.8	4.490	42.3	10.605
1967	1.188	20.8	2.858	50.0	1.605	28.1	5.716
1968	1.299	23.0	3.659	64.9	0.909	16.1	5.642
1969	1.951	23.9	4.779	58.7	1.327	16.3	8.147
1970	3.225	32.1	6.020	59.9	0.766	7.6	10.046
1971	1.418	13.1	7.004	64.8	2.036	18.8	10.815
1972	.897	18.1	2.498	50.3	1.515	30.5	4.967
1973	.256	8.2	1.406	50.7	1.081	39.0	2.775
1974	2.043	30.4	3.952	58.8	0.699	10.4	6.718
1975	1.425	13.9	5.937	58.0	2.854	27.9	10.238
1976	1.443	16.5	6.263	71.4	0.924	10.5	8.771
1977	1.175	14.3	3.674	44.8	3.296	40.2	8.201
1978	4.465	36.9	5.284	43.6	2.206	18.2	12.113
1979	5.580	36.2	8.147	52.8	1.635	10.6	15.424
1980	7.186	26.1	18.715	68.0	1.573	5.7	27.533
1981	3.942	13.9	20.159	71.2	4.197	14.8	28.308
1982	2.474	8.7	13.450	47.5	3.497	12.4	19.487
1983	9.584	37.3	14.189	55.3	1.575	6.1	25.675
Mean		23.64		55.5		19.9	
Standard Deviation		12.9		11.8		11.4	

Table 3. Returns by age, total Bristol Bay, returns including high seas catch. Total return includes all age classes.

	4 Years		Age at Maturity 5 Years		6 Years		
Year	Numbers (Millions)	Percent	Numbers (Millions)	Percent	Numbers (Millions)	Percent	Total Return
1956	12.852	49.5	10.374	39.9	2.688	10.3	25.979
1957	.674	3.8	12.298	68.5	4.808	26.8	17.957
1958	1.517	24.9	2.831	46.4	1.528	25.1	6.095
1959	4.868	36.3	7.116	53.1	1.337	10.3	13.404
1960	32.117	80.3	5.606	14.0	2.161	5.4	39.989
1961	.654	2.7	21.170	88.4	1.988	8.3	23.944
1962	2.453	19.3	6.327	56.0	2.496	22.1	11.308
1963	2.183	27.9	3.448	44.1	2.124	27.2	7.813
1964	5.840	52.1	4.517	40.3	.753	6.7	11.204
1965	1.397	2.3	56.633	94.4	1.892	3.2	59.996
1966	1.376	7.1	7.168	37.0	10.769	55.5	19.394
1967	1.237	11.1	7.601	67.9	2.271	20.3	11.188
1968	3.382	38.3	4.066	46.0	1.316	14.9	8.831
1969	11.738	56.0	7.441	35.5	1.682	8.0	20.973
1970	3.707	8.6	38.086	88.0	1.447	3.3	43.293
1971	1.747	9.8	12.528	70.6	3.382	19.0	17.755
1972	1.168	17.7	3.505	53.3	1.861	28.3	6.592
1973	.397	12.7	1.537	49.2	1.158	37.1	3.125
1974	2.126	18.6	8.411	73.7	0.855	7.5	11.417
1975	1.685	6.6	20.274	79.7	3.447	13.6	25.430
1976	1.716	13.8	8.455	67.9	2.146	17.2	12.448
1977	1.762	16.9	5.025	48.1	3.580	34.3	10.443
1978	11.003	54.5	6.528	32.3	2.508	12.4	20.203
1979	11.401	28.4	26.511	66.0	2.203	5.5	40.183
1980	12.293	19.5	48.176	76.6	2.341	3.7	62.917
1981	5.782	16.4	24.786	70.1	4.762	13.5	35.344
1982	4.203	18.6	14.492	64.3	3.750	16.6	22.568
1983	27.293	59.7	16.457	26.7	1.660	2.7	45.240
Mean		25.5		57.1		16.4	
Standard Deviation		20.3		20.1		12.4	

Table 4. Correlation between length by various ocean age-river system groups and return by those river system groups.

Length by Ocean Age and Population	Kvichak Only	Bristol Bay Other Than Kvichak	Combined Bristol Bay
2-Ocean, Kvichak	-.36	-.04	-.28
2-Ocean, Non-Kvichak	-.43	-.10	-.36
2-Ocean, Combined	-.50	-.05	-.39
3-Ocean, Kvichak	-.46	-.36	-.49
3-Ocean, Non-Kvichak	-.65	-.41	-.64
3-Ocean, Combined	-.68	-.45	-.68
Ocean Age Combined, Kvichak	-.51	-.24	-.47
Ocean Age Combined, Non-Kvichak	-.49	-.18	-.43
Ocean Age Combined, Combined	-.63	-.19	-.54

Table 5. Correlation among various mean lengths by ocean age and river system groups. The correlation underlined are completely independent.

Length by Ocean Age and Population	Kvichak (K)	Non-Kvichak (NK)	River Systems Combined (C)	Kvichak (K)	Non-Kvichak (NK)	River Systems Combined (C)	Kvichak (K)	Non-Kvichak (NK)	River Systems Combined (C)
2-Oc, K	—	.57	.90	.59	.34	.40	.83	.53	.72
2-Oc, NK		—	.79	.38	.48	.52	.41	.51	.46
2-Oc, C			—	.56	.47	.52	.72	.52	.69
3-Oc, K				—	.60	.74	.56	.52	.57
3-Oc, NK					—	.97	.31	.56	.50
3-Oc, C						—	.36	.58	.54
Combined, K							—	.68	.88
Combined, N								—	.87
Combined, C									—

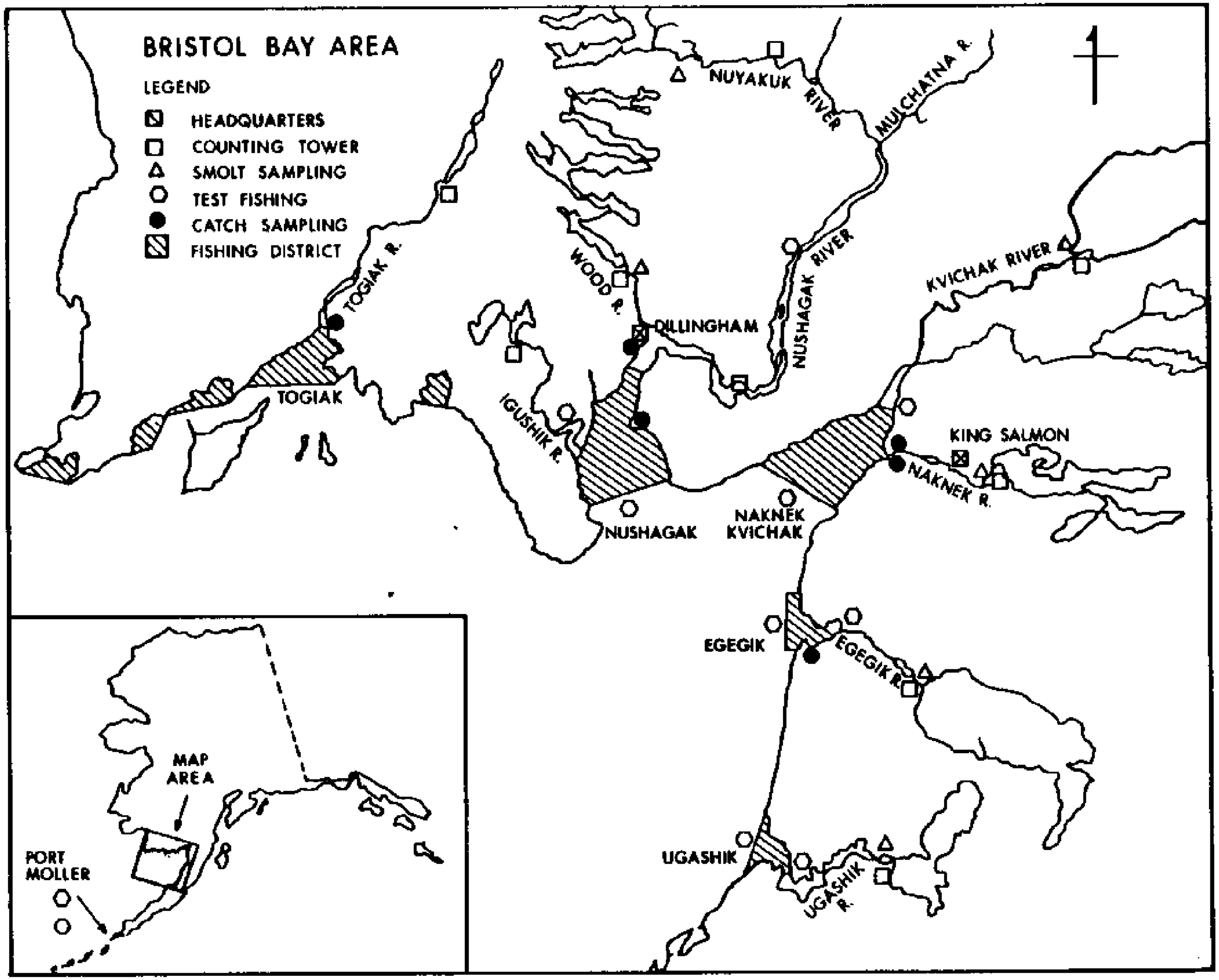

Figure 1. Bristol Bay sockeye salmon river systems, fishing districts, and sampling programs of the Bristol Bay management system.

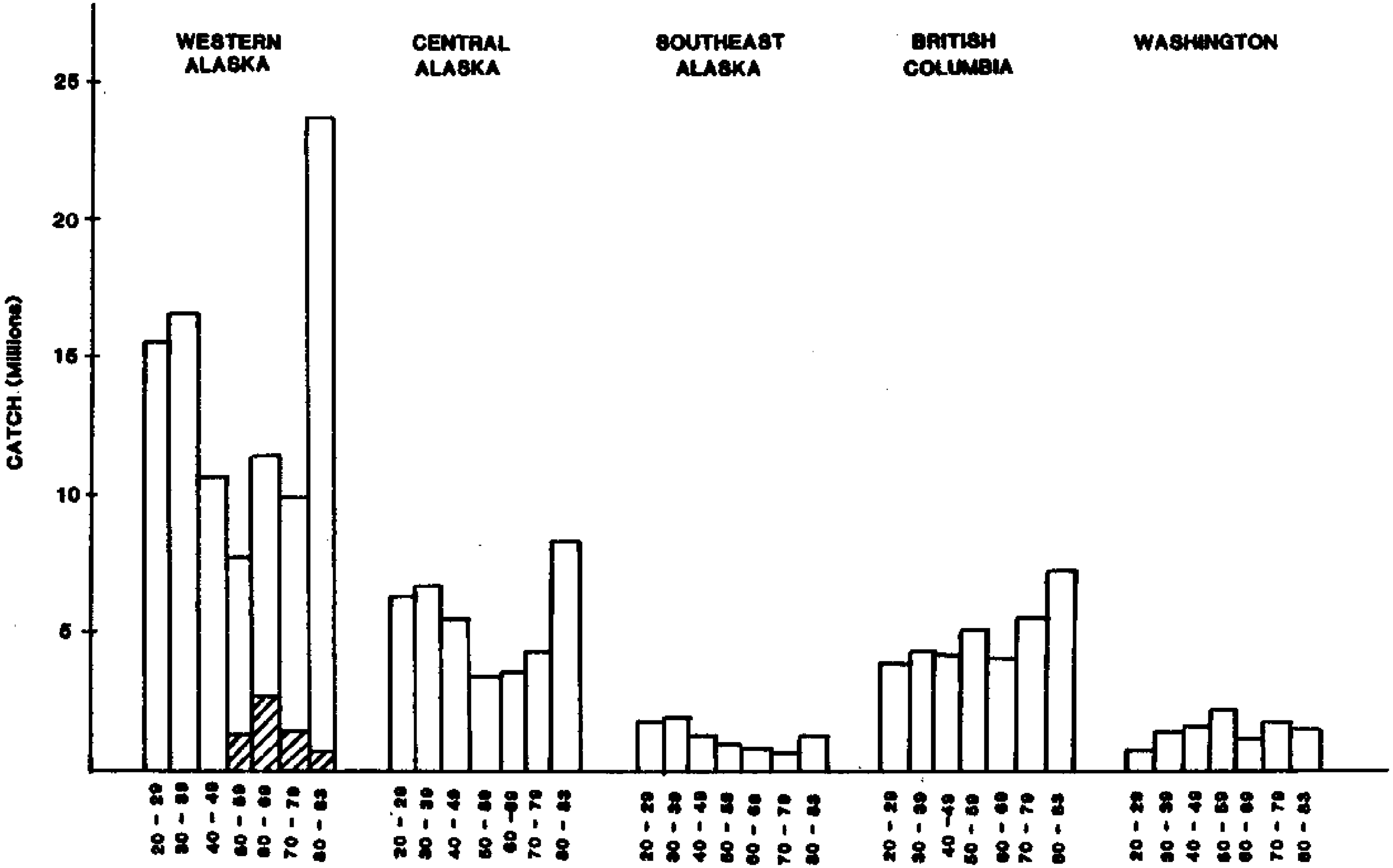

Figure 2. Catch of sockeye salmon averaged for 10 year periods 1920-1983, for western Alaska, central Alaska, southeast Alaska, British Columbia and Washington (after Fredin 1979). The hatched area is the estimated catch by Japanese high seas mothership fishery.

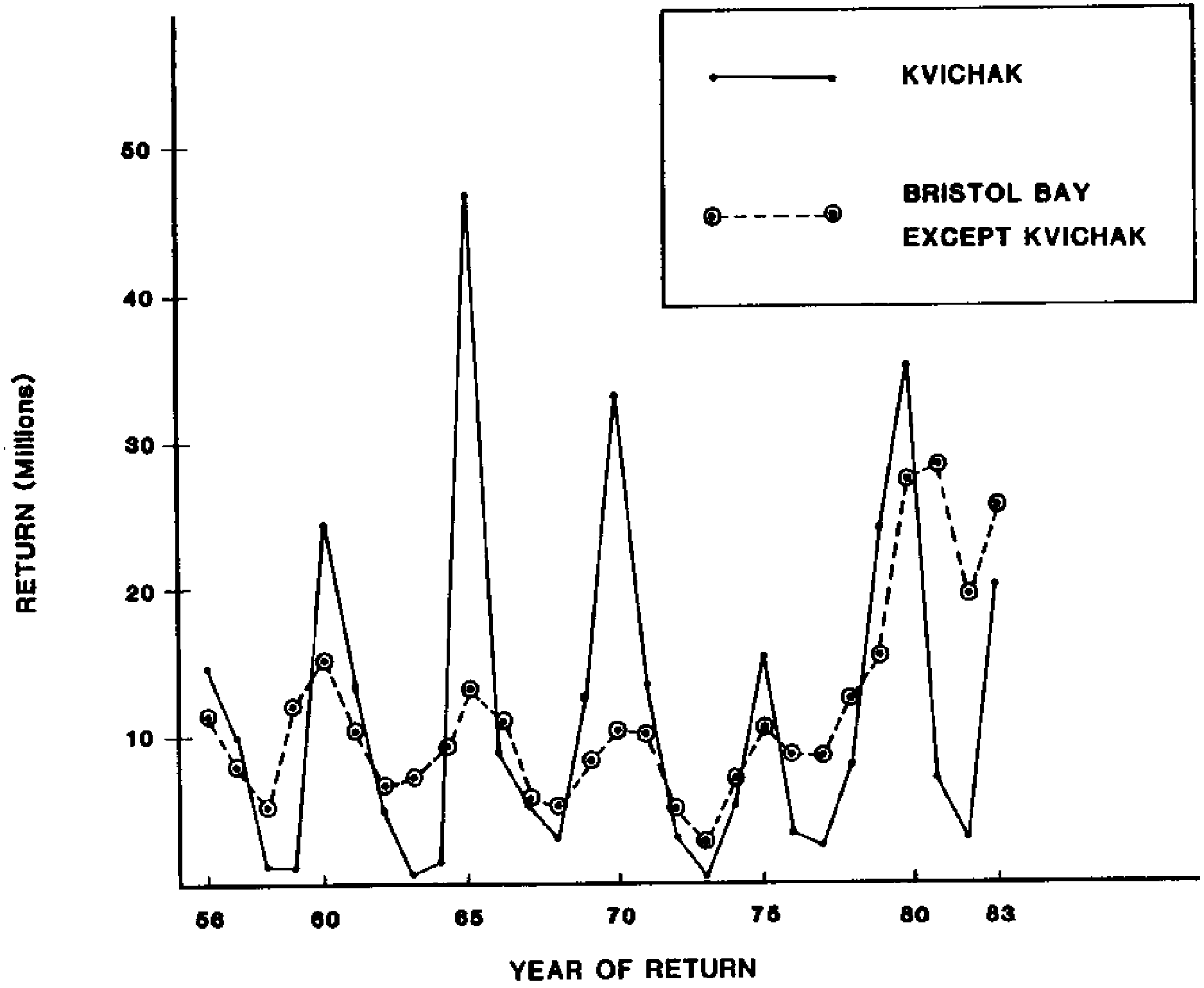

Figure 3. Total return of Bristol Bay sockeye salmon (including estimated catch by Japanese high seas mothership fishery) 1956-1983. Dashed line is river systems other than the Kvichak, solid line is the Kvichak River system.

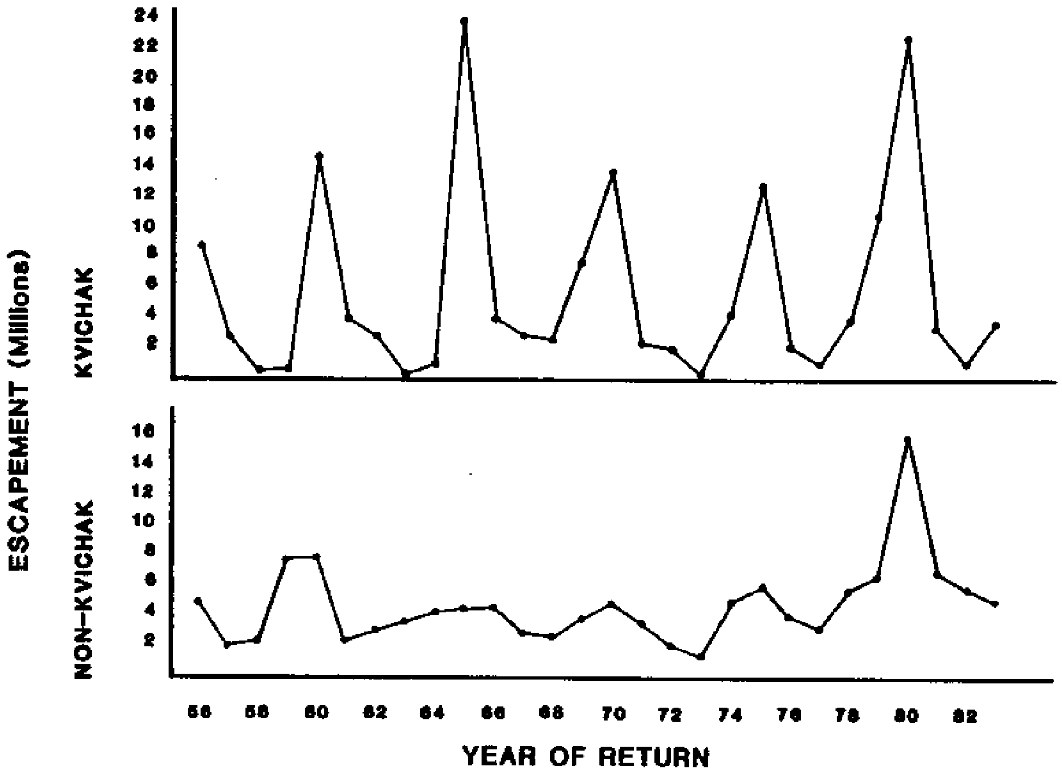

Figure 4. Escapement to Kvichak River system and river systems other than the Kvichak, 1956-1983.

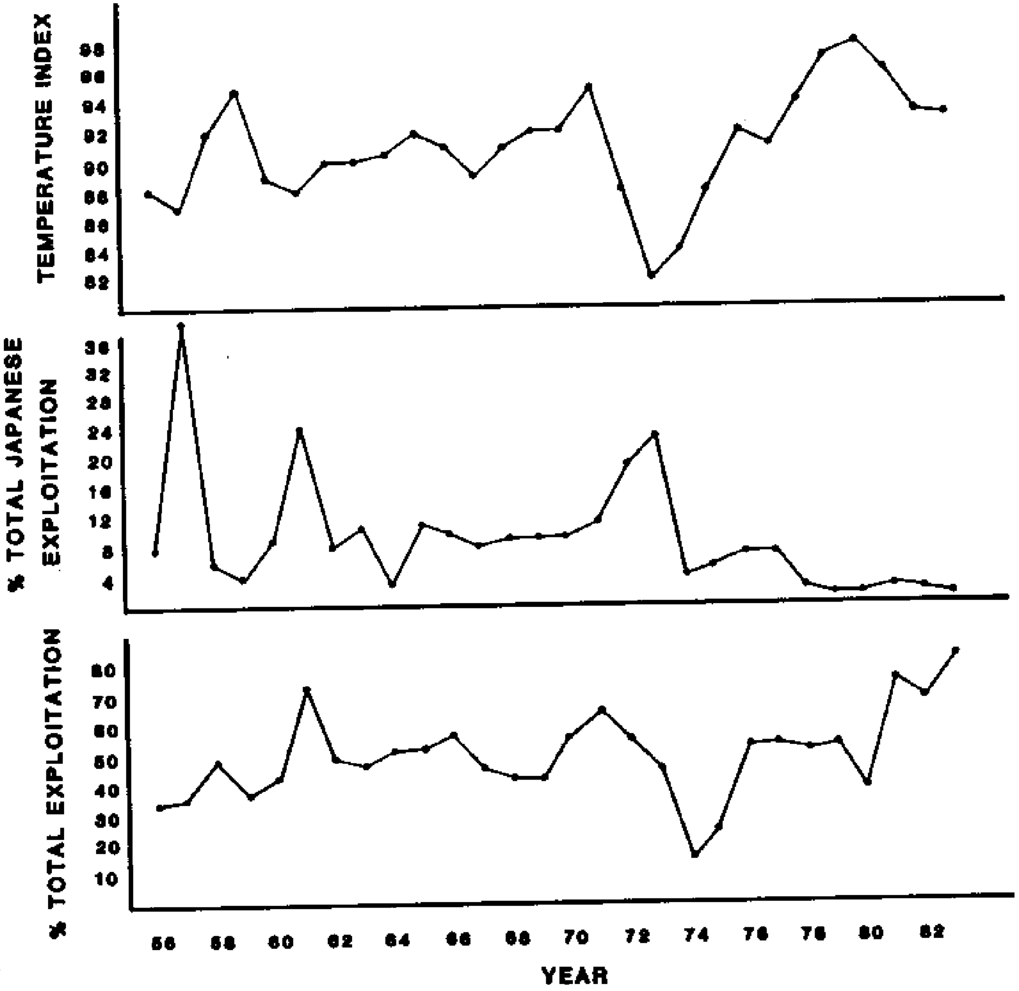

Figure 5. Temperature index (sum of mean June air temperature at Cold Bay, the two years prior to year of return, 1956-1983). Total rate of exploitation (percent of total return including high seas catch) by Japanese high seas mothership fishery, 1956-1983. Total rate of exploitation by inshore fishery and Japanese high seas mothership fishery, 1956-1983.

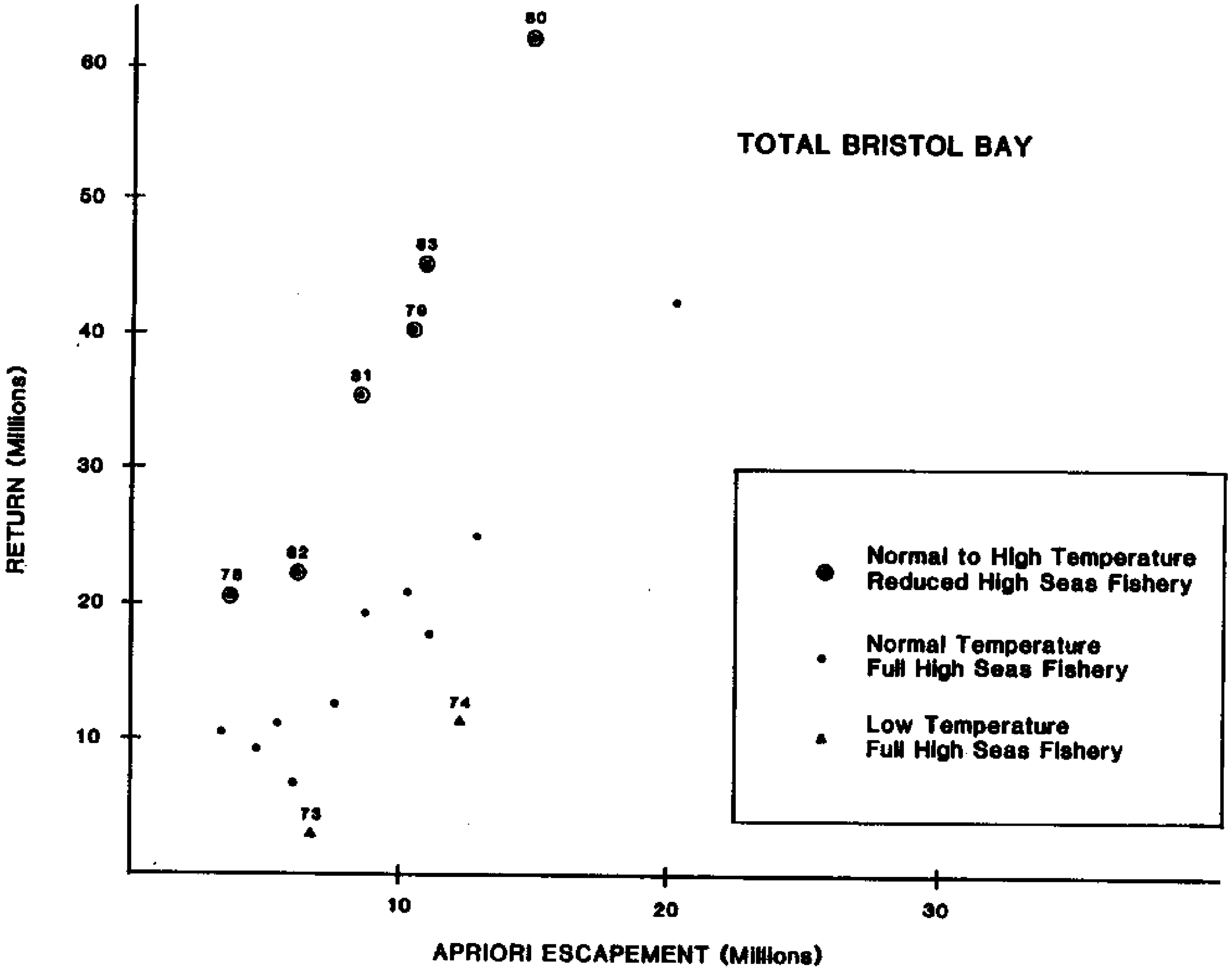

Figure 6. The relation of total return to Bristol Bay sockeye salmon to a priori escapement, 1966-1983.

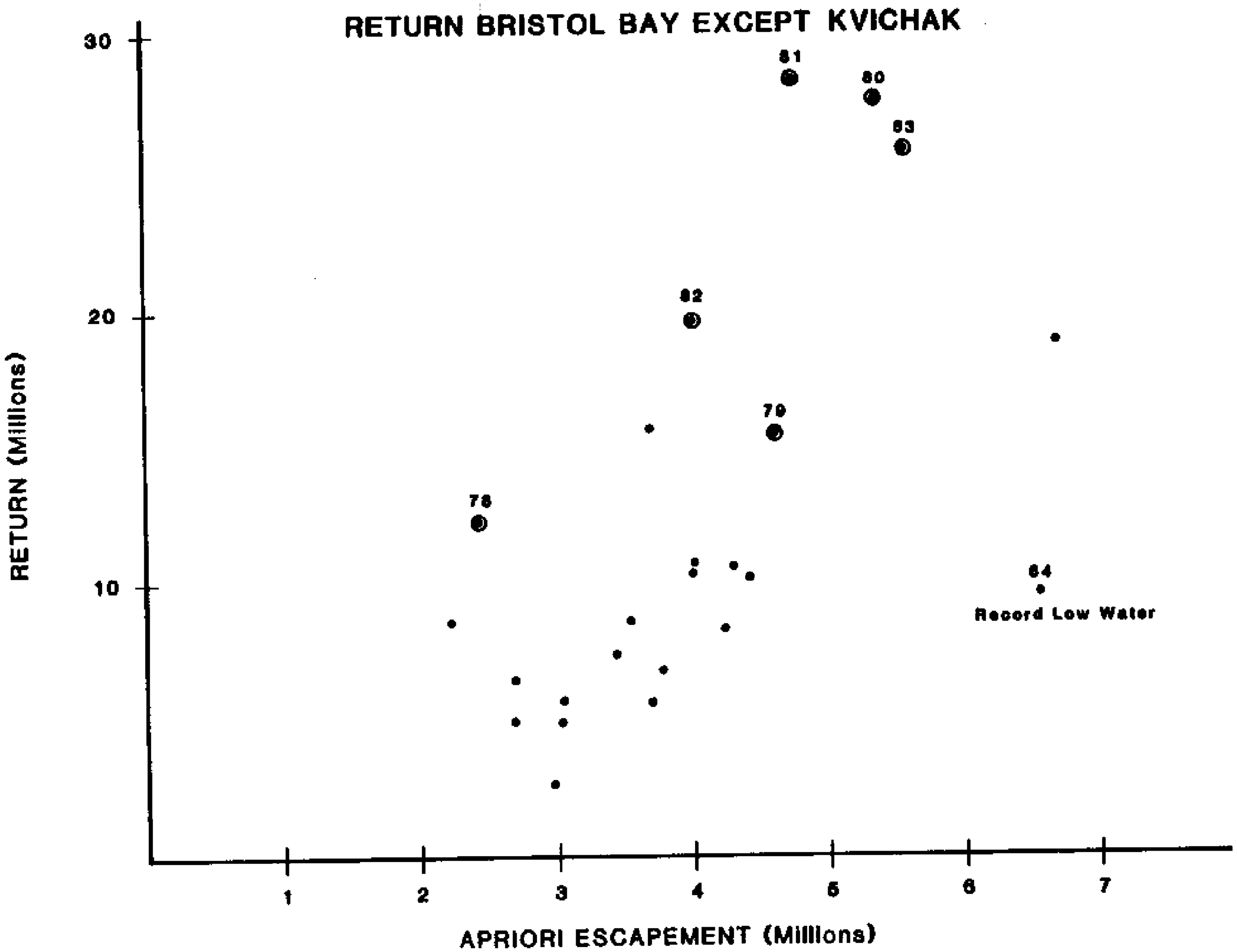

Figure 7. The relation of total return to Bristol Bay river systems except Kvichak to a priori escapement, 1962-1983.

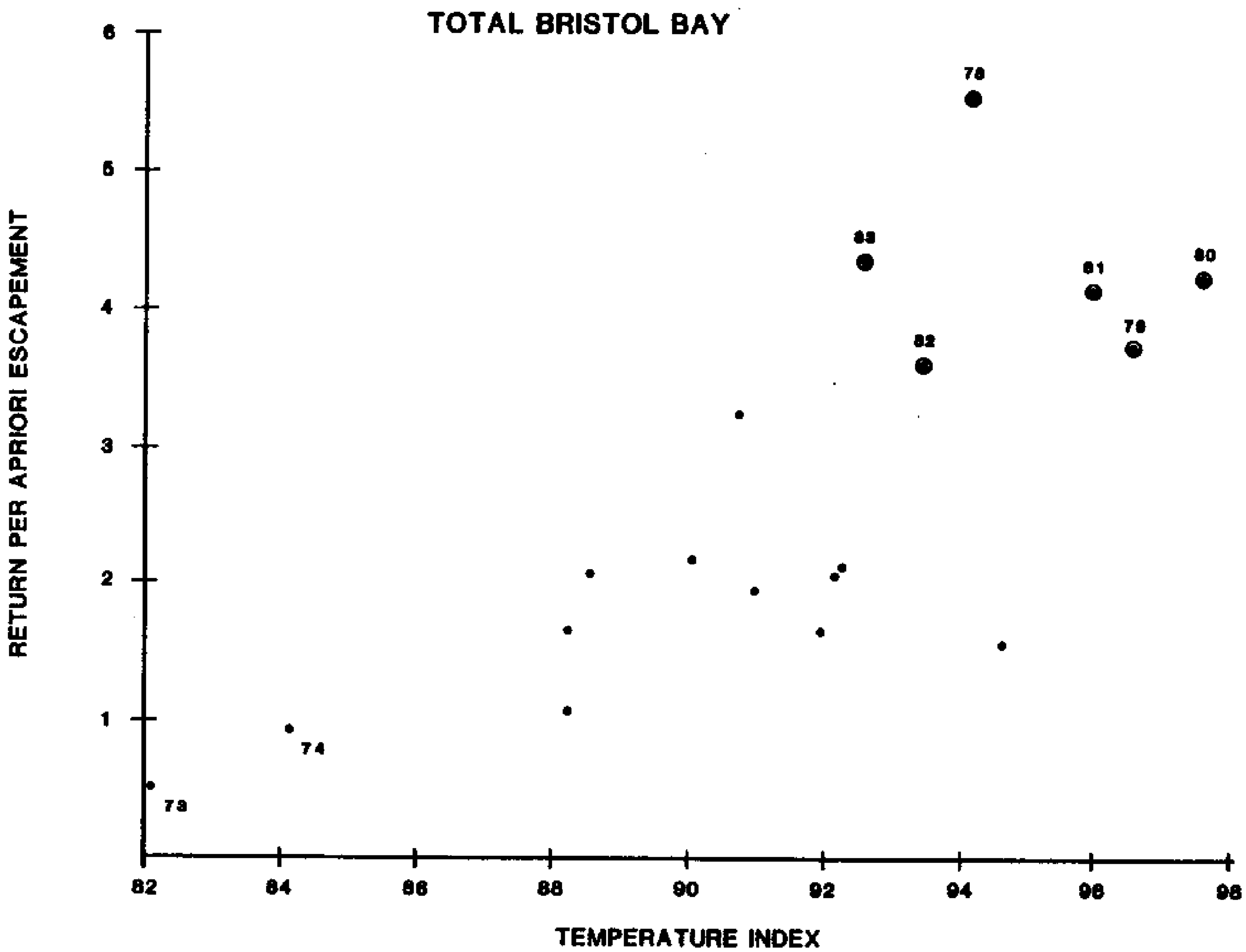

Figure 8. The relation of return per a priori escapement for the combined Bristol Bay river systems to the Cold Bay temperature index, 1966-1983.

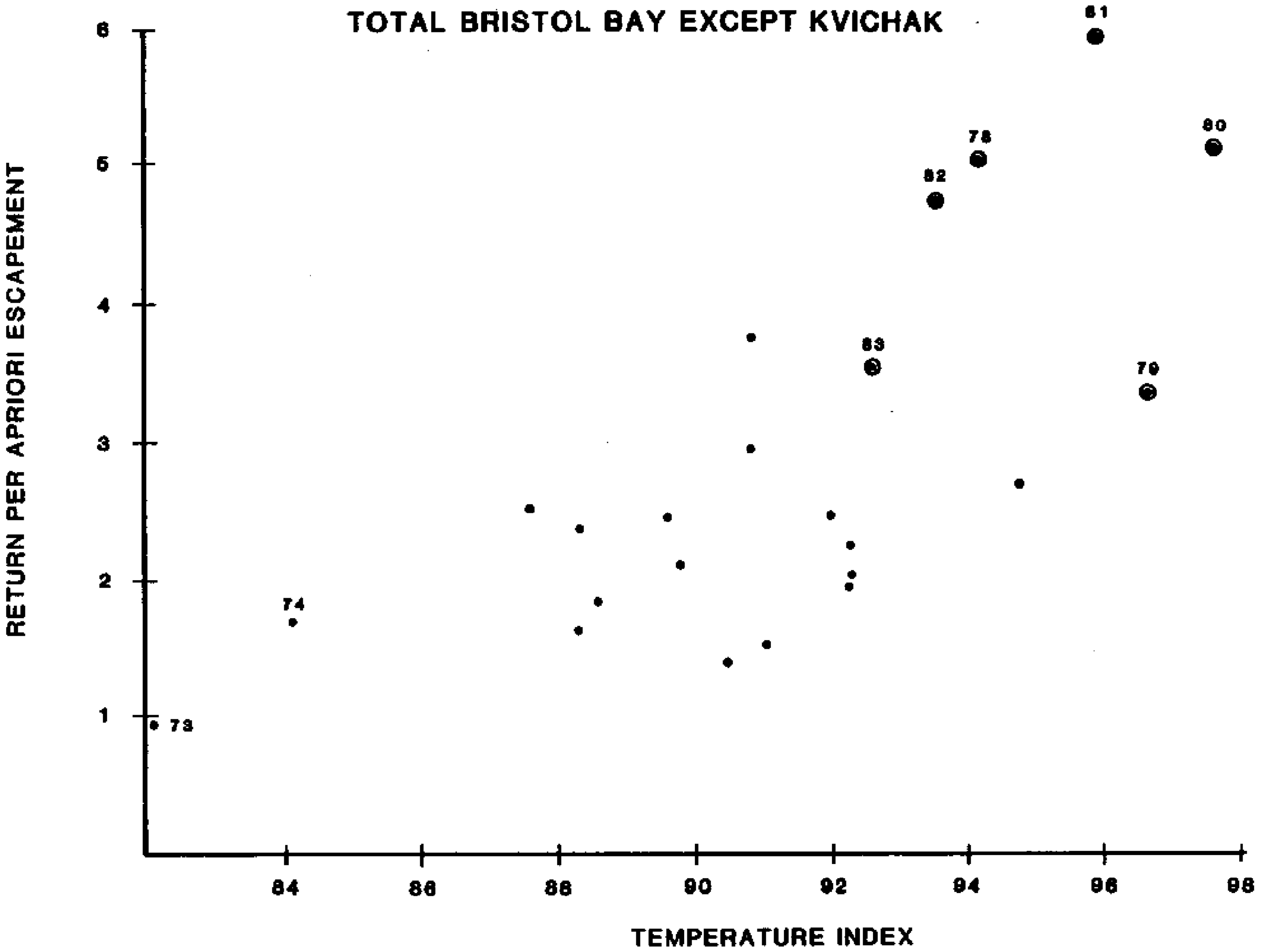

Figure 9. The relation of return per a priori escapement for the river systems other than the Kvichak to Cold Bay temperature index, 1962-1983.

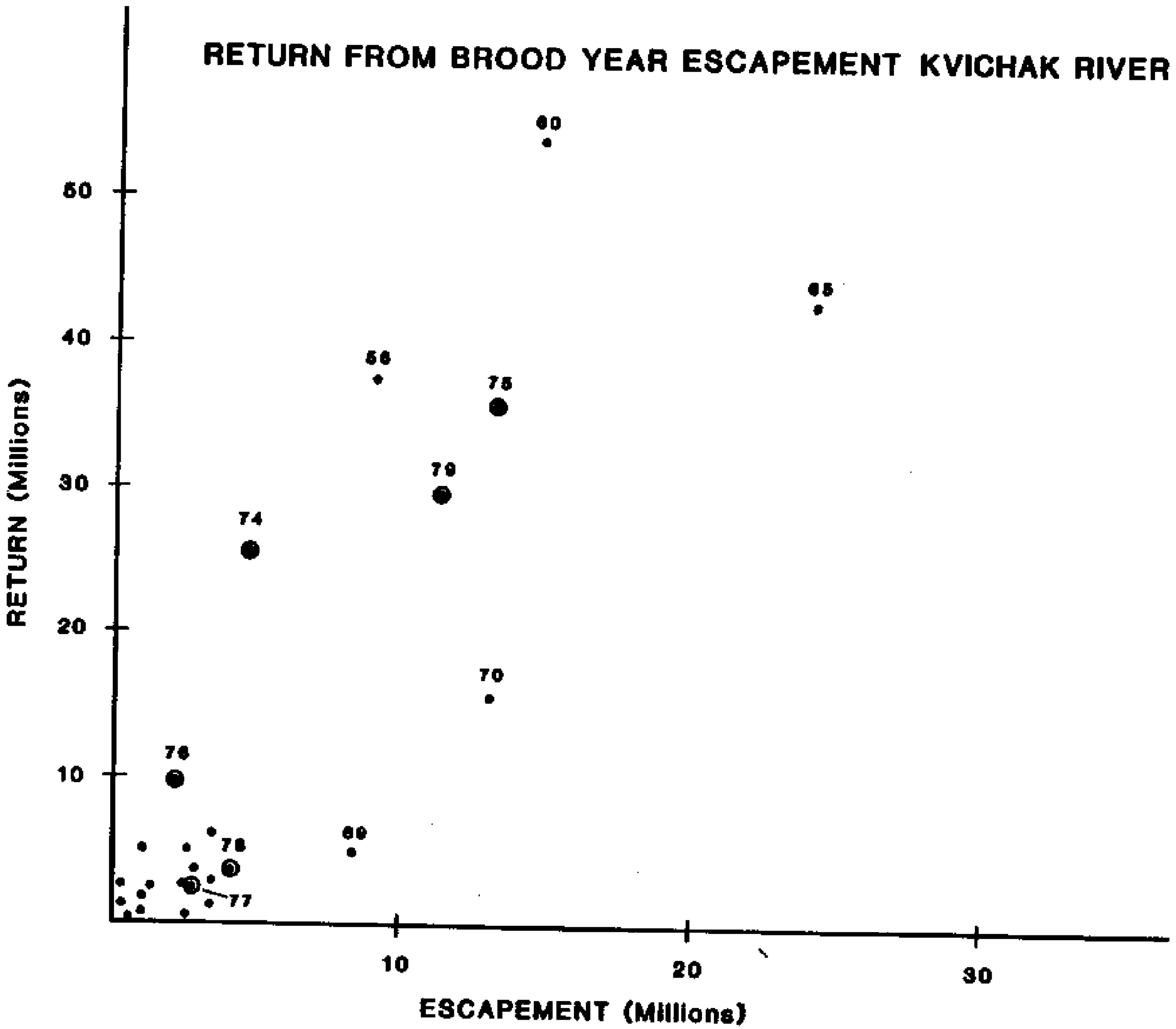

Figure 10. The relation of return from brood year escapement to brood year escapement, 1956-1979 brood years, for the Kvichak River system.

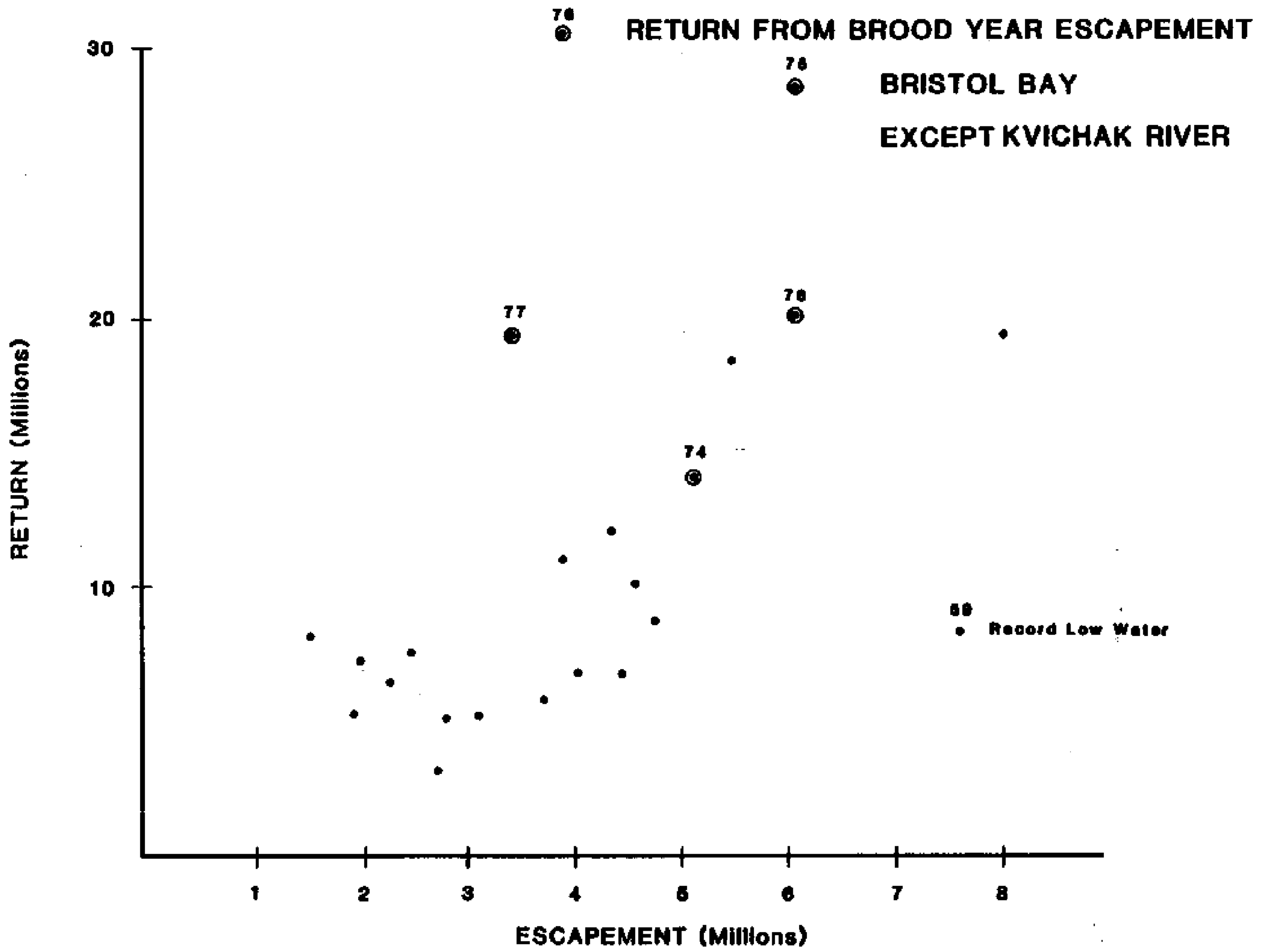

Figure 11. The relation of return from brood year escapement to brood year escapement, 1956-1977 brood years, for river systems other than the Kvichak. Both the October (1959) and the annual (1959) precipitation at King Salmon were the lowest observed in the monitoring period 1943-1983. Low water during the period of egg deposition and incubation for the 1969 brood year coupled with large escapements presumably contributed to the poor production observed for that brood year.

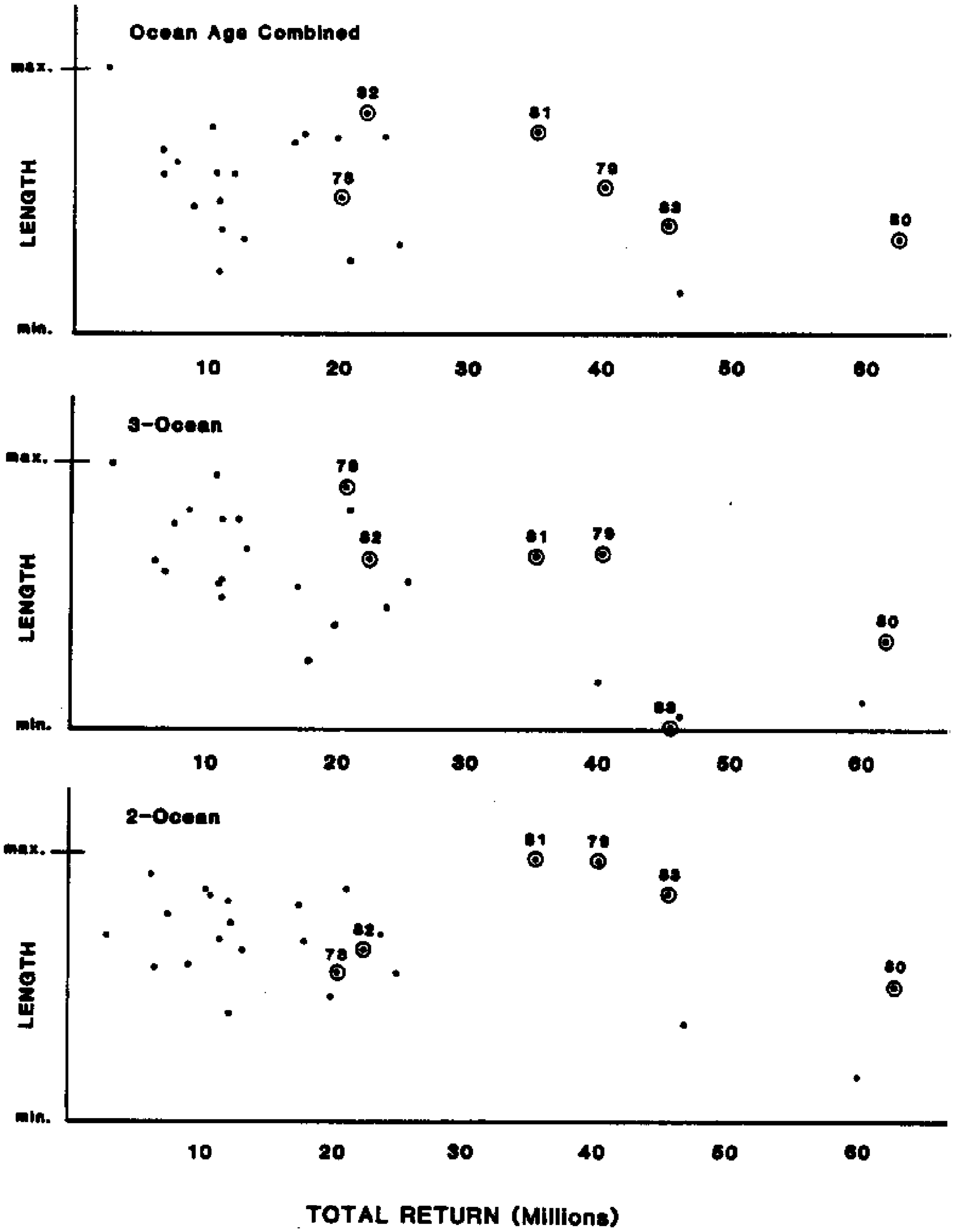

Figure 12. The relation of mean length of the inshore Bristol Bay return to the total return including high seas catch. In the computation of mean length, the mean lengths of the escapement and catch for the requisite river systems and age classes were averaged, weighted by their respective magnitudes.

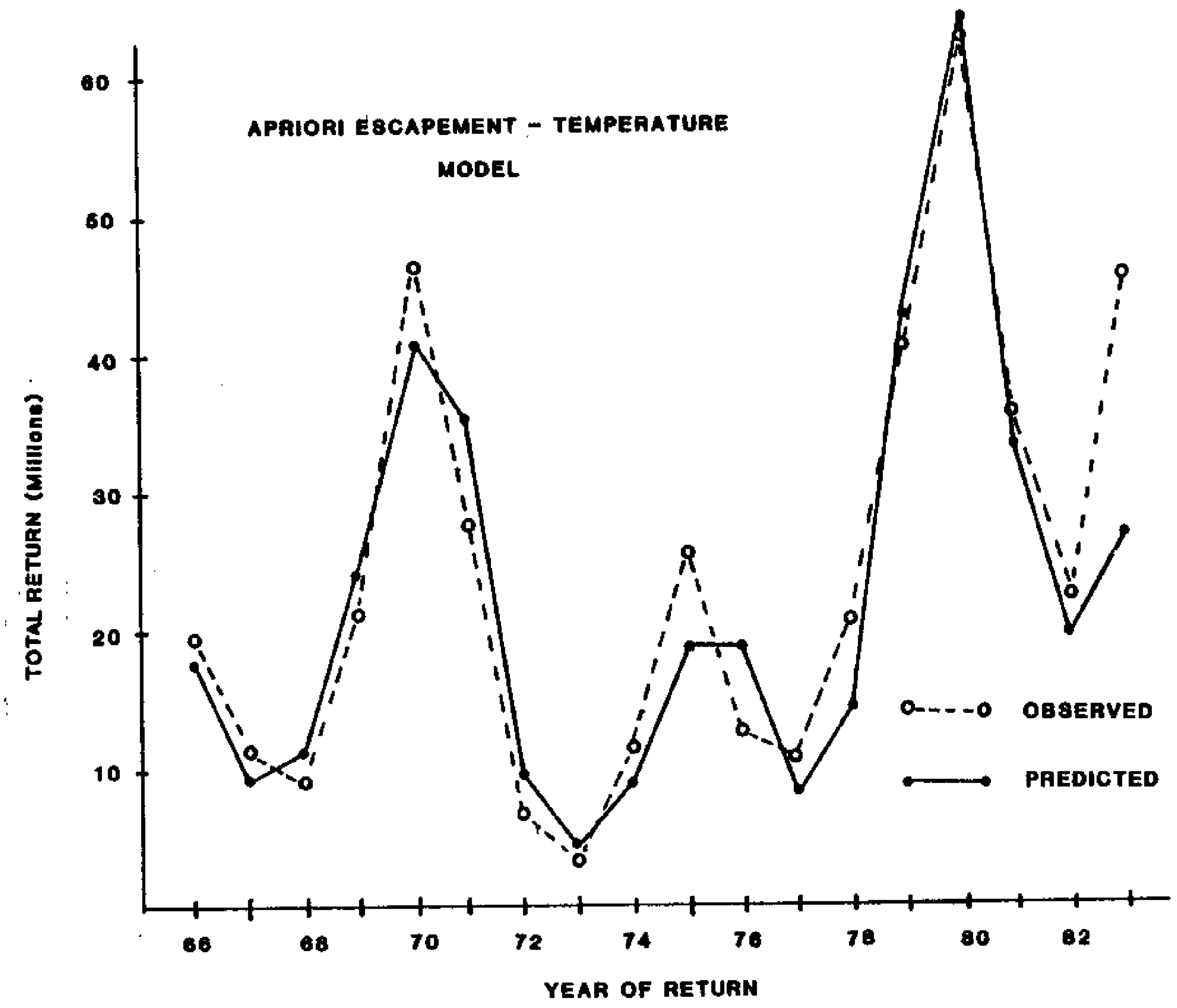

Figure 13. The observed total return (including high seas mothership catch) and that predicted by an a priori temperature -- escapement model, 1966-1983.

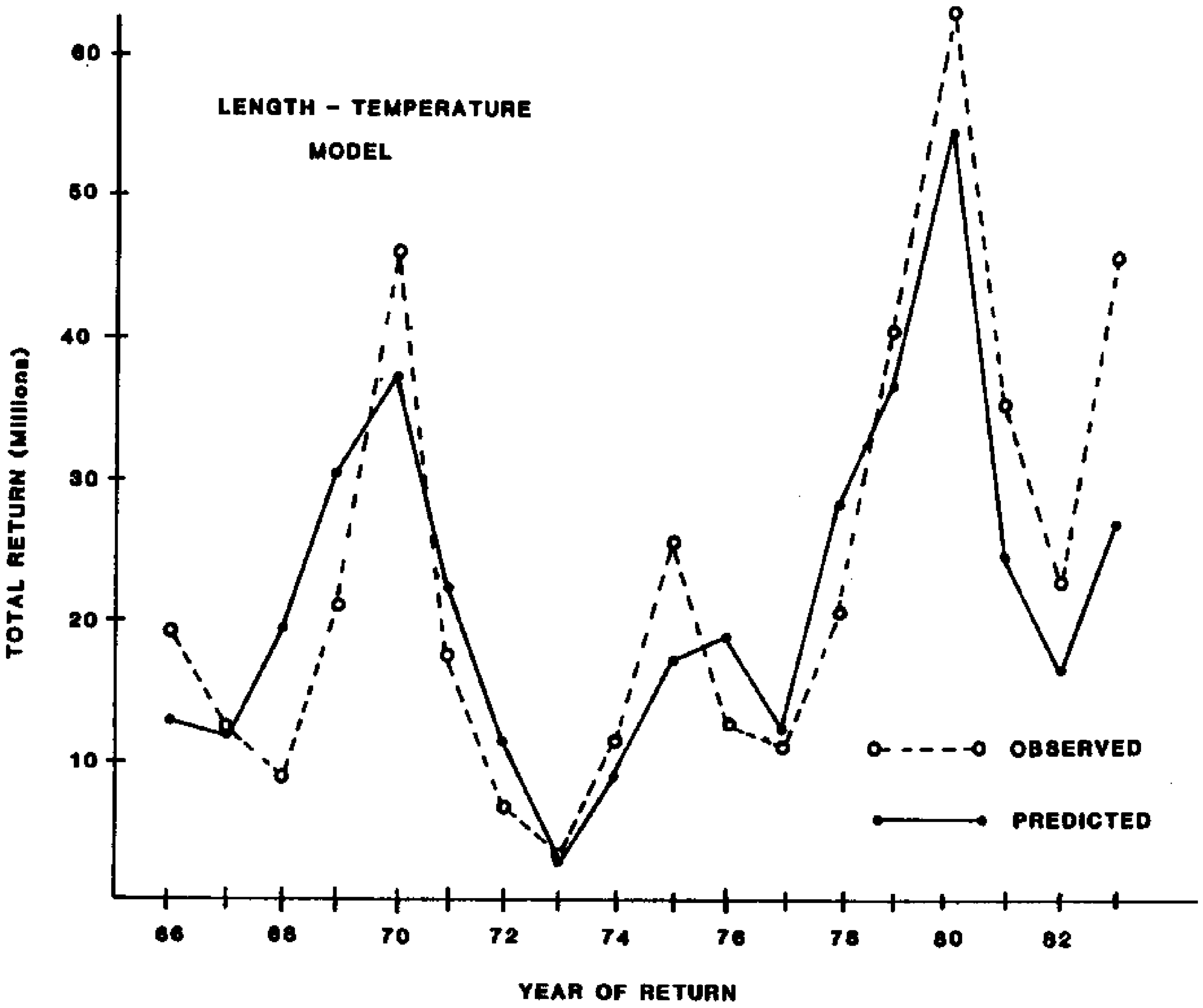

Figure 14. The observed total return (including high seas mothership catch) and that predicted by a length -- temperature model, 1966-1983.

Comments on the Presentation by Eggers, Meacham, and Huttunen

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The authors, Eggers, Meacham, and Huttunen, have evaluated existing catch and climatic data in an attempt to explain the resurgence of run magnitude of Bristol Bay sockeye in recent years to historic levels and beyond. They have concluded that the evaluation is confounded by the simultaneous decrease in interceptions of Bristol Bay sockeye by a Japanese mothership fishery and an improvement in ocean climatic conditions, both coinciding with the build-up in sockeye runs. They conclude further than an interaction of these factors most likely contributed to the spectacular increases in run magnitude.

The authors also note, as did Dr. Rogers (this workshop), that the increase in run magnitude in Bristol Bay has been primarily in the runs to the river systems other than the Kvichak. The Kvichak system has produced the large cycle run and a lower overall proportion of sockeye that spend three rather than two winters in the ocean. Since Bristol Bay sockeye spending the additional year in the ocean are also more vulnerable to high seas fishing, the reduction in Japanese high seas fishing might be expected to be reflected in a greater increase in survival of sockeye returning after three winters in the ocean. The authors point out that within river systems this has not been reflected by an increase in proportion of 3-ocean age sockeye and apparently discount to some degree the importance of the reduction in high seas fishing as a factor to explain the proportionately greater build-up of the runs in Bristol Bay systems other than the Kvichak.

I would like to make a few precautionary remarks about the analysis, and I believe the authors would concur. First, for the reader, I would note that in recent history, the years of highest catch (1981, 1983) have not coincided with the years of largest run (1965, 1980) because of considerable difference in exploitation rate. Runs were 35 million and 45 million in 1981 and 1983, and 60 million and 63 million in 1965 and 1980, respectively. Regardless, the returns per spawner, or the returns per a priori escapement as described by the authors, both show increases in recent years in river systems other than the Kvichak.

Second, the relevance of their temperature index is uncertain. The authors do not establish whether the Cold Bay air temperatures in June reflect ocean surface temperatures, and if so, for what period of time. Nor do they hypothesize in what way marine survival of sockeye might be affected. For sockeye returning after two winters at sea, June temperatures in the two years prior to the year of return would occur during smolt out-migration in the first and during age .1 migration and feeding somewhere in the North Pacific during the second year. For sockeye returning after three winters at sea, June temperatures in both of the prior two years would occur during their North Pacific migration as ocean age .1 and .2, but not as smolts. Thus, it is unclear to what extent and at what life stage ocean temperatures would affect survival.

Third, evaluation of the impact of the Japanese high seas salmon fishery offers some difficulties. (1) Although the renegotiated INPFC treaty did not take effect in

1978, the exploitation rate on Bristol Bay sockeye by the Japanese mothership salmon fishery had already dropped substantially in 1974 and remained low in the next three years. (2) We now know that the landbased driftnet fishery was also intercepting significant numbers of Bristol Bay sockeye prior to 1977, but estimates of the annual magnitudes of these catches are not available. The total sockeye catch of the landbased fishery exceeded that in the mothership fishery for five years prior to 1977, but dropped sharply in 1977 and has remained at about 30% of the 1972-1976 level as a result of changes in areas fished and gear reduction. (3) It has not been possible to assess accurately the high seas "dropout" mortality of Bristol Bay sockeye caused by these fisheries, but there is evidence that it was high and varied with ocean age of the fish.

By 1977, regulations imposed on the mothership and landbased driftnet fisheries had sharply decreased effort and total sockeye catch (Asian and North American). If in Figure 7 we include 1977 as a year of return affected by reduced high seas fishing (it falls closest to 1983 on the graph), it suggests that reduction in high seas fishing increased survival of Bristol Bay sockeye at a time when the return was not related to a high temperature index.

Dr. Rogers puts more emphasis on weather trends in the resurgence of western and central Alaskan salmon stocks because some stocks were affected very little by the Japanese fisheries. Certainly the resurgence in pink and chum stocks appears to be primarily related to climate because they are not believed to be intercepted to any significant degree. But the increase in coho catches may well be in large measure due to the decrease in Japanese fishing effort and catch, particularly between 175°E and 175°W south of the Aleutians, an area closed to high seas fishing since 1977. Total high seas coho catches since 1977 are about half the former level. Tagging and scale pattern analyses both indicate the presence of substantial numbers of Alaskan coho in the 175°E-175°W area, now closed to fishing.

The a priori escapement-temperature model being tested by the authors to forecast Bristol Bay runs gives a surprisingly good fit to actual return data. I suspect this is because (1) there is an underlying relationship between escapement and return that benefits from data smoothing, (2) the increases in run magnitude and warming trends have coincided in a block of years, and (3) June air temperatures have sufficiently represented the temperature trends. We still need to know more about the mechanisms that have resulted in such dramatic increases in survival of salmon in western and central Alaska in recent years.

Environmental Factors and the Abundance of Kodiak Archipelago Pink Salmon (*Oncorhynchus gorbuscha*)

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Abstract

Fluctuations in the survival and adult returns of Kodiak Archipelago pink salmon (Oncorhynchus gorbuscha) were statistically correlated with air temperatures, precipitation, fluctuations in the earth's magnetic field, sea-surface temperature, upwelling indices, and river runoff.

Forecast models were examined. The one with the highest correlation was

$$R = -70717.64 + 5.63(EM) + 1555.26(AVKBT);\ r = 0.930$$

where R is return, EM is an index of emergent fry density, and AVKBT is average Women's Bay sea surface temperature during the estuarine residence period of juvenile pink salmon (from March through September). This model is similar to the Alaska Department of Fish and Game's model, which does not use sea temperature and has an r of 0.708.

Introduction

Pink salmon (Oncorhynchus gorbuscha) is one of five species of Oncorhynchus native to the northwest coast of North America. Its life history on the Kodiak Archipelago begins with egg deposition between late August and October. The fry emerge the following March and April and move downstream into adjacent estuaries. The juveniles remain within the estuaries until August or September and then move offshore into oceanic waters. Ten to 11 months after entering oceanic waters they return to the estuaries as adults and enter their natal streams. Shortly thereafter, spawning commences. The total life span is two years.

The Kodiak Archipelago is a large island group physically isolated from the adjacent mainland by large bodies of water (Figure 1). Millions of pink salmon return each year to hundreds of streams. Data on escapement and catch have been collected for at least 29 years and emergent fry density for 18 years.

This is an investigation of fluctuations in abundance of Kodiak Archipelago adult pink salmon. Donnelly (1983) was unable to find convincing evidence of density dependent population control. Thus, environmental variables correlated with survival or abundance suggested by the available literature and pertinent data were analyzed and evaluated. Numerous authors have demonstrated that physical environmental factors are correlated with the survival or growth of marine fishes (e.g., Hyman and Tyler 1980; Sutcliffe 1972, Sutcliffe et al. 1977; Leim and Scott 1966). Helle (1979) correlated various environmental variables with growth and survival of chum salmon in Olsen Creek, Alaska. Temperature, precipitation, cloud cover, barometric pressure at sea level, and river discharge all showed significant

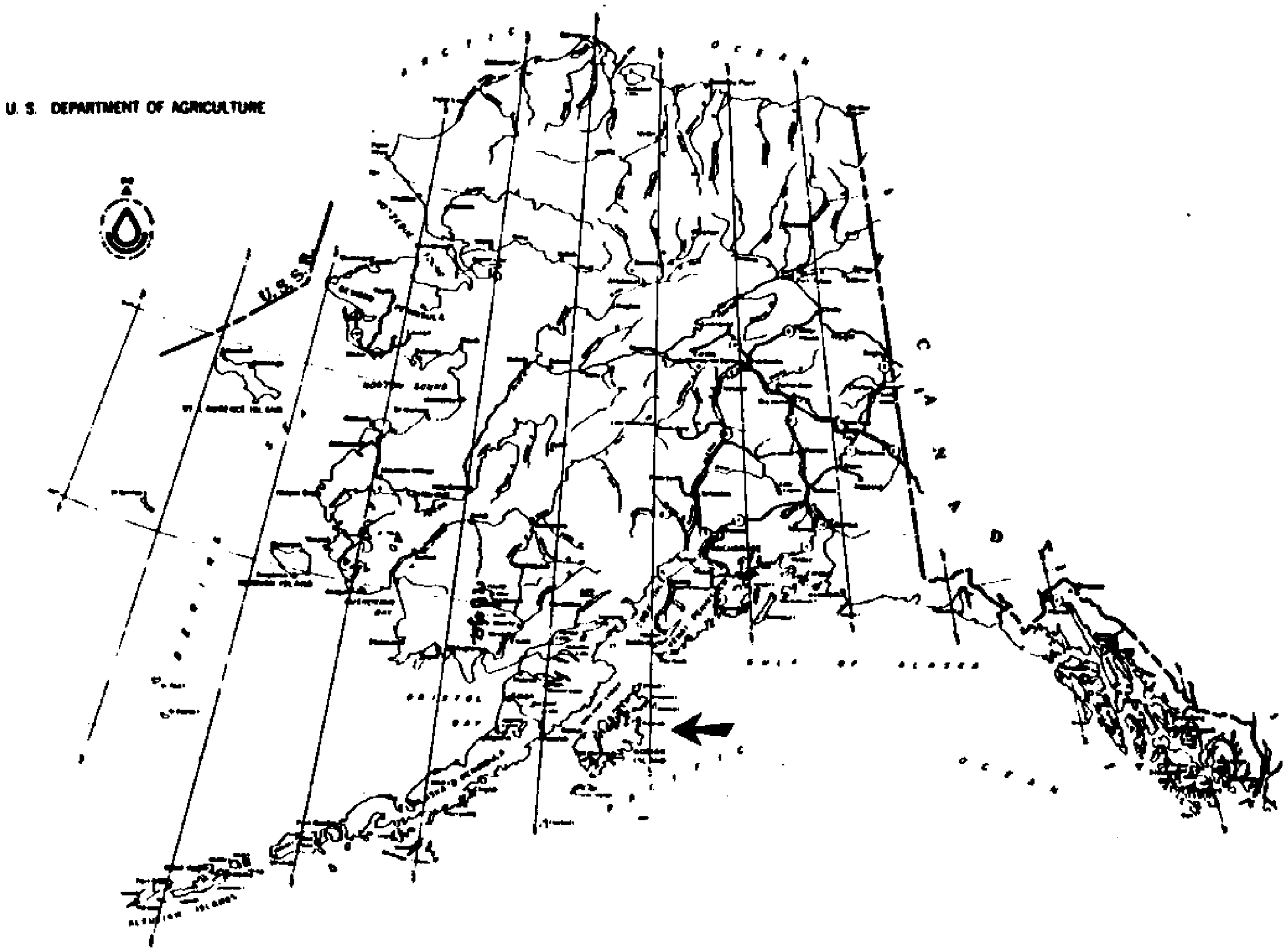

Fig. 1. State of Alaska showing the location of the Kodiak Archipelago (←).

correlations. Water temperature, stream flow, and precipitation all appear to be significant factors during the freshwater phase of Pacific salmon life history (Hunter 1959; Pritchard 1948; Vernon 1958; Wickett 1958; Koski 1975). Vernon (1958) and Wickett (1958, 1962) related estuarine water temperature and salinity to Pacific salmon survival. K-values (indices of magnetic disturbance) may be related to homing ability and therefore indirectly to survival (Quinn 1980).

The objective of this study was to investigate abiotic factors that are related to fluctuations in the abundance of Kodiak Archipelago pink salmon so that fluctuations can be predicted.

Materials and Methods

The biological data consist of statistics on total return and emergent fry densities (Table 1). The emergent fry data were obtained from the Alaska Department of Fish and Game (ADF&G) Kodiak office. The total return data are the sum of total catch, obtained from ADF&G, and escapement data. The escapement data are from Bevan et al. (1981, 1982). The escapement data was standardized by using weir counts and the peak aerial survey estimates from a specific set of streams (Table 2). To better reflect actual escapement, the peak escapements were multiplied by 2.5.

Table 1. Year of return (n), total return (year n), and emergent fry index (year_{n-1}) of Kodiak Archipelago pink salmon.

Year of return (n)	Total return year (n)	Emergent fry index year_{n-1}
1954	12,780	
1955	13,639	
1956	7,482	
1957	5,691	
1958	6,834	
1959	4,065	
1960	9,430	
1961	5,276	
1962	19,319	
1963	6,717	
1964	16,389	1,669
1965	4,014	
1966	13,159	1,728
1967	1,233	564
1968	11,701	1,546
1969	14,127	1,930
1970	14,307	2,866
1971	5,485	1,286
1972	3,176	1,646
1973	1,049	1,423
1974	4,402	856
1975	3,868	658
1976	13,614	2,034
1977	7,554	1,582
1978	19,349	2,451
1979	13,016	2,120
1980	22,163	2,346
1981	12,300	869
1982	12,648	1,300

Table 3 is a general list of the abiotic variables used in this study. All variable lists had missing observations except river runoff and K-values (average monthly measurements of fluctuations in the earth's magnetic field). K-values from Sitka (located in southeast Alaska) were used since Sitka was the closest recording station to Kodiak.[1] River discharge data from the United States Geological Survey (USGS) records (U.S. Geological Survey, Water Resources Division, water resources data for Alaska 1958-1980) were only recorded for the late spring, summer, and early fall months, probably due to winter freezing and the difficulty of maintaining a recording site during winter.

Marsden Square sea surface temperature data are collected by ships of opportunity passing through the specific area. The data are transmitted to the Fleet Weather Service at Monterey, California, where it is tabulated by Dr. Douglas McClain.

Table 2. Index streams, and stream number, from which peak escapement counts were used for Kodiak Archipelago pink salmon.

Stream name	Stream number	Stream name	Stream number
Even-numbered year spawning populations:			
Karluk River	255-101	Eagle Harbor Creek	259-424
Little River	254-101	Kiliuda Creek	258-207
Uyak River	254-202	Barling River	258-522
Brown's Lagoon	254-204	Kauignak Creek	258-542
Zachar River	254-301	Seven Rivers Creek	258-701
Uganik River	253-122	Humpy Creek	257-701
Terror River	253-331	Deadman River	257-502
Red River	256-201	Sulua Creek	257-603
Kizhuyak Creek	252-365	Horse Marine Creek	257-402
American River	259-231	Dog Salmon River	257-403
Kalsin River	259-243	Sturgeon River	256-401
Odd-numbered year spawning populations:			
Uyak River	254-202	Shearwater Creek	258-202
Zachar River	254-301	Kiliuda Creek	258-207
Uganik River	253-122	Barling River	258-522
Terror River	253-331	Kaiugnak Creek	258-542
Baumann's Creek	253-332	Seven Rivers	258-701
Kizhuyak Creek	252-365	Humpy Creek	257-701
Elbow Creek	252-371	Tom's Creek	257-601
American River	259-231	Sulua Creek	257-603
Olds River	259-242	Deadman River	257-502
Saltery Creek	259-415	Narrows Creek	257-401
Eagle Harbor Creek	259-424	Dog Salmon River	257-403

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[1] These data were obtained from the United States Dept. of Commerce, National Oceanic and Atmospheric Administration, Environmental Data and Information Service, National Geophysical and Solar-Terrestrial Data Center, Solar-Terrestrial Physics Division, 325 Broadway, Boulder, Colorado 80303.

Table 3. List of abiotic variables used in this study.

Variable	Years	Comments
Average air temp. Kodiak City	1932-1982	Some data missing
Precipitation at Kodiak City (monthly total)	1932-1982	Some data missing
.01-.49 inches of rainfall	1932-1982	Some data missing
Sea surface temperature, Women's Bay (Kodiak Bay)	1950-1982	Some data missing
K-values, Sitka	1950-1982	Complete
Marsden Square sea surface temperatures at 196/2	1946-1982	Some data missing
Upwelling at 54-134	1958-1982	Some data missing
Uganik River runoff	1958-1979	Complete

Kodiak Bay sea surface temperatures are recorded daily at Women's Bay by a National Oceanic and Atmospheric Administration observer.[2] The air temperature, precipitation, and rainfall category data are obtained from U.S. Weather Bureau records[3] for the city of Kodiak.

University of California at Los Angeles Biomedical Computer Programs, Series P (BMDP, Dixon and Brown 1979), computer programs were used to analyze the data. Missing observations were estimated using a predictor software package (Dixon and Brown 1979). Stepwise regression (Draper and Smith 1966) was employed to determine the important environmental variables. Abundance of returning adults (returns) and returning adults per emergent fry density (survival) were the dependent variables. Partial correlations between dependent and independent variables were inspected for the first four steps of each stepwise regression.

Results and Discussion

In general, air temperature and rainfall were expected to impact survival during the freshwater existence (McNeil 1966; Wickett 1962). It appeared from the analyses that air temperature in May, rainfall in November and December, and precipitation in December were influential on survival or total return (Tables 4 and 5). Precipitation in December was typically snow. The mean temperature for all Decembers was 33.8°F. The amount of snowpack may have determined how much insulation was present and therefore the prospects of the interstitial water remaining liquid in the gravel (Sheridan 1961).

After emergence the juveniles migrated almost immediately into the nearshore region of adjacent estuaries. Here sea temperatures were moderated while salinity had its greatest extremes. In addition, the freshwater outflow may cause inflow at the bottom of estuaries (Ingraham and Hastings 1974) resulting in rich, productive areas. Therefore, temperature and salinity were expected to be important to survival. Indeed, average Women's Bay temperatures correlated highly with survival fluctuations (Tables 4 and 5). Also, September Marsden Square sea-surface temperatures

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[2] Data available from the United States Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Survey, Rockville, MD 20852.

[3] These data, called Climatological Data, Alaska, are available from the National Oceanic and Atmospheric Administration, Environmental Data Service, National Climatic Center, Asheville, NC.

Table 4. The 15 exogenous variables that are related to density-independent population abundance of Kodiak Archipelago pink salmon (including abbreviations).

Variable
Air temperature at Kodiak City for May[1] (TMAY) of the first year of the life cycle.
Precipitation at Kodiak City for December (PDEC) of the first year of the life cycle.
Percentage of the month (in days) when rainfall was less than .5 inches per day for November (RINOV) and December (RIDEC) of the first year of the life cycle.
K-value, or index of disturbance of the earth's magnetic field for September (KVSEP2) and January (KVJAN2) of the second year of the life cycle.
Sea-surface temperature of Marsden square 196/2 for September (MSEP2) of the second year of the life cycle.
Sea-surface temperature of Kodiak Bay (Women's Bay) for May (KBMAY) and June (KBJUN) of the estuarine residence period; also the average of these temperatures from March through September (AVKBT) of the same period.
Upwelling index from 54°N latitude, 134°W longitude for April (U4APR2), May (U4MAY2), August (U4AUG2), and October (U4OCT2) of the second year of the life cycle.
Uganik River runoff for October (UGOCT2) of the second year of the life cycle.

[1] Each month was considered a separate variable in this study.

Table 5. Correlation values between the dependent variables (return/emergence and total return) and the independent variables listed in Table 4. Only the highest correlations are listed (see Table 4 for explanation of abbreviations).

Indepedent variable	Dependent variable	
	R/EM	R
TMAY	.504	
PDEC		.329
R1NOV		.636
R1DEC		.329
KVSEP2		.685
KVJAN2		-.372
MSEP2	.638	
KBMAY	.727	
KBJUN	.730	
AVKBT	.855	
U4APR2		.300
U4MAY2	.694	
U4AUG2	.736	
U4OCT2		.501
UGOCT2		.365

adjacent to Kodiak Island were correlated with survival. Good salinity data were not available for Kodiak Island; however, river discharge information was considered an indicator of salinity, in that increased flow was expected to reduce estuarine salinities and vice versa. Thus, the finding that Uganik River discharges in October were related to returns was not surprising. The October discharge was likely related to salinity conditions after the fish had left the estuaries but were still near land (Hartt et al., in press; Manzer and Shepard 1962). Another way that river discharge may have influenced survival was through the introduction of inorganic nutrients into estuaries which may affect production of food (Sutcliffe 1972, 1973). As the pink salmon grew and moved into the oceanic environment, freshwater influences were expected to cease. Indeed this appeared to be the case. April, May, August, and October upwelling at 54°N latitude, 134°W longitude (the closest reporting station to Kodiak Island) all correlated with survival or total return (Tables 4 and 5). Upwelling may directly impact the survival rate by changing the structure of water currents so that increased energy is needed to stay in a specific geographic region (Mathisen 1979). But the more likely explanation is that upwelling can enhance productivity, and thus increase the food supply.

K-values (specifically September and January) were also correlated to survival and total returns (Tables 4 and 5). Here again, the relationships were probably indirect. Quinn (1980) showed that salmon could detect and orient themselves in a magnetic field. Possibly pink salmon need to increase the number of orientations per unit of time, as magnetic variations increase, prolonging their migration and requiring additional energy during transit, resulting in decreased survival. This may explain the negative correlation (January) but not the positive one (September).

Abundance Fluctuation Forecast Models

Since several exogenous factors correlated with abundance fluctuations of Kodiak Archipelago pink salmon, the results suggested the possibility of forecasting total returns. Two forecast models were examined. One was an existing ADF&G forecast model; the other was similar but with average Kodiak Bay water temperature (AVKBT) added. The ADF&G model, $R = a + b(EM)$ was a linear regression of return (R) on emergent fry density (EM). The correlation of actual and predicted returns based on the ADF&G model was 0.708. The model with both emergent fry density and average Kodiak Bay water temperature had a correlation of actual and predicted returns of 0.930. Thus, the model with average Kodiak Bay water temperature described here is superior.

Conclusions

The results of this study confirm the findings and conjectures of many authors that abiotic factors are related to survival and abundance fluctuations. In contrast to Neave (1953), who postulated density-dependent mortality for British Columbia pink salmon, density dependence did not appear to be a major factor in controlling abundance fluctuations (Donnelly 1983). If, however, the effect of management was taken into account, it may be that the spawning population was not allowed to become large enough to demonstrate density-dependent mortality. Control of the abundance of Kodiak Archipelago pink salmon was therefore largely density independent at the levels of escapements found in the 29 year data set.

The increased forecast accuracy should improve management options. Specifically, preseason plans based on run size prediction may be formulated with greater assurance. Further collection of environmental data is indicated, and may provide significant insights into the factors that control abundance.

Summary

1) Several exogenous variables were statistically correlated with survival and total return. The following variables were important: air temperature in May, precipitation for December and rainfall for November and December, sea-surface temperature of Women's Bay between March and September, Uganik River runoff in October, Marsden square sea-surface temperature in September, K-values in September and January, and upwelling in April, May, August, and October.

2) Two forecast models were compared. One, $R = a + b_1(EM) + b_2(AVKBT)$, was considered the best. EM was the emergent fry index, AVKBT was the average sea-surface temperature of Women's Bay for the months of March through September of the juvenile life stage, and R was the return.

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Commentary: Observations on the Potential of Intraspecific Predation as a Possible Answer to the Odd/Even Year Phenomenon in Pink Salmon

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Introduction

The phenomenon of different sizes of runs of natural pink salmon (Oncorhynchus gorbuscha) in odd and even years has been well documented in the literature for many geographic locations. Ricker (1962) listed eight hypotheses to explain odd/even year cycles:

1. depensatory predation in freshwater;
2. depensatory predation in saltwater;
3. cannibalism by adults on young;
4. fouling of redds by large egg depositions;
5. depensatory fishing;
6. influence of density-independent fishing;
7. competition for food (adults vs. young);
8. separation of stocks at sea.

The actual reason for this cyclic strong/weak, alternate year run strength has not been determined. However, predation of the adults on the young has been offered by Barber (1979) and others as a possible reason for this disparity in run strength. Ricker (1962) also suggested possible cannibalism within pink salmon as one of the potential reasons for the odd/even year cycle.

The Alaska Department of Fish and Game's Fisheries Rehabilitation, Enhancement, and Development (FRED) Division was hoping to smooth out the peaks of the odd/even year cycle in the lower Cook Inlet area with production from the Tutka Lagoon Hatchery. However, a strong alternate year cycle has also been evident in hatchery production that closely parallels the trend observed in the natural runs.

This report presents data and observations that support the hypothesis of intraspecific predation of pink salmon. These data were collected during the evaluation programs for the FRED Division's Tutka Lagoon pink and chum hatchery located in the lower Cook Inlet area near Homer, Alaska.

Historic Natural Pink Salmon Runs

Figure 1 depicts the commercial salmon fishing districts of the lower Cook Inlet area. The majority of pink salmon are harvested in the Southern and Outer Districts.

Pink salmon run strength data for the Southern and Outer Districts are available from 1954 to present (Figure 2). In the mid-50s strong returns were in odd years which changed in the late 50s to strong even years. Strong even years persisted until 1970 and '71 when two severe winters back to back influenced the trend to strong odd years. Odd years have been by far the strong years since then.

Hatchery Pink Salmon Runs

The Tutka Lagoon Hatchery is located in the Tutka Bay subdistrict (241-16), a portion of the Southern District (Figure 1). Figure 3 presents natural pink return run strength data for the Tutka Bay area since 1962. The odd/even year progression was similar to the pattern exhibited in the Southern and Outer Districts. Extremely low run levels were also evident after the severe winter of 1970/71.

The Tutka Lagoon Hatchery, currently a 30 million egg facility, has made a significant contribution to the Tutka Bay pink salmon returns since 1978 (Figure 3). The excellent return of over a million pink salmon to the hatchery in 1981 contributed 29% to the entire harvest of lower Cook Inlet, a new record. The majority of the hatchery return originated from a short-term release of over 5 million pink fry that yielded over 16% ocean survival.

The 1982 return was the second lowest in the history of the hatchery at just less than 230,000 pink salmon. However, considering how low the natural return was, the hatchery did contribute over 32% of the lower Cook Inlet pink salmon harvest. In 1983 the pink salmon return to the hatchery was the second highest at 645,000 fish. Because of extremely low natural runs the hatchery contribution was 66% of the entire lower Cook Inlet pink salmon harvest.

The hatchery return survival rates also showed an odd/even year disparity with strong odd years, similar to the patterns displayed by the natural runs (Figure 4). We hoped for a potentially good return in 1982 which would have broken this odd/even year cycle, at least for hatchery fish. The conditions which would have beneficially influenced the early survival of pink salmon fry at release in 1981 appeared to be very good: the health of the fry was excellent; predation was minimal; plankton levels were high; and the temperature was ideal. However, the survival rate was the lowest in the history of the hatchery program (Figure 4).

Intraspecific Predation During Habitat Overlap

The extremely large number of adult pinks that returned in 1981 (over one million) could have adversely influenced the survival of the hatchery fry. As previously mentioned, Barber (1979), felt that the odd/even year phenomenon may be attributed to intraspecific predation when pink salmon adults return to temporarily inhabit fry nursery areas. Cannibalism may adversely affect survival rates of released hatchery fry in the Tutka Bay system.

Figure 5 depicts the typical Tutka Bay pink fry nursery areas used from May to August. About 10 million fry were released in 1981 (with minimal wild fry contribution), and the return in that same year was over one million adults, giving a "fry-to-adult" ratio within the Tutka Bay system of 10:1.

Over the years, biologists and commercial fishermen have observed that the fry and adults inhabit the same protected cove (nursery areas) during July and August (Figure 5). Many commercial seine sets collect not only large numbers of adults, but many pink and chum fry simultaneously. Manzer (1956) found many young-of-the-year pinks in coastal waters off British Columbia at the same time adults were passing through on their migration to spawning streams.

Unfortunately, it is difficult to examine large numbers of stomachs of commercially caught fish. Of 25 adult pink salmon examined during 1982, one bright female had a pink fry in its stomach; the remainder had unidentifiable food items.

In 1983 another brief, unfunded study was made of the stomach contents of pink salmon adults. Adult pink salmon were obtained directly from commercial purse seining operations in known pink salmon fry nursery areas. The adults were collected live from the seine prior to brailling into the fish hold. The fish were then transferred to a skiff for processing. Gastric lavage (washing) by pressure pump worked exceptionally well to evacuate the stomach contents without mutilating the fish. Stomachs of 114 adult pink salmon were flushed, and 30 stomachs contained obvious food items. Fish prey items were found in 24 stomachs or 21% of the entire sample group. The dominant prey by frequency of occurrence was Pacific sand lance (Ammodytes hexapterus) at 78%, followed by euphausids, decapods, and cottids.

Although no pink salmon fry were found in the 1983 study, it was significant that these fish were piscivorous when found in Tutka Bay. The fact that no pink fry were observed could be attributed to the abundance of sand lance and the opportunistic feeding of adult salmon.

In view of the piscivorous feeding habits of adult pink salmon, cannibalism in pink fry may be significant.

Summary and Recommendations

The odd/even year cycle is certainly a difficult and important problem to solve in obtaining maximum yield from hatchery production. We plan to study intraspecific predation in the future through analyses of adult stomachs and migration characteristics of fry and adults. Strategies to maximize marine survival rates by modifying hatchery production schedules for the alternate year cycle include:

1. Release of "off" or weak year fry at alternate sites to minimize habitat overlap of adults and fry;
2. Maximize growth of fry during short-term rearing programs to minimize predation;
3. Modify the time of release of reared fry. This option however, has site-specific constraints in the Tutka Bay system:
    a. If the fry are released early after a shorter rearing period, their survival would probably be adversely affected by other early season predators such as herring and Dolly Varden. In addition, these fry would probably still remain in their nursery areas during the entire summer period.
    b. If the fry are released after the peak of the adult return, they would be highly vulnerable to disease and potentially low dissolved oxygen within the pens. In addition, a scheduling conflict would occur in use of the lagoon float pens which currently serve as holding pens for both reared fry and adult brood-stock.
    C. Installation of barriers to adult pink salmon across the entrances to known fry nursery areas has not been considered, but are not feasible because of the extreme tidal ranges (6 m) and the distances involved (>500 m).

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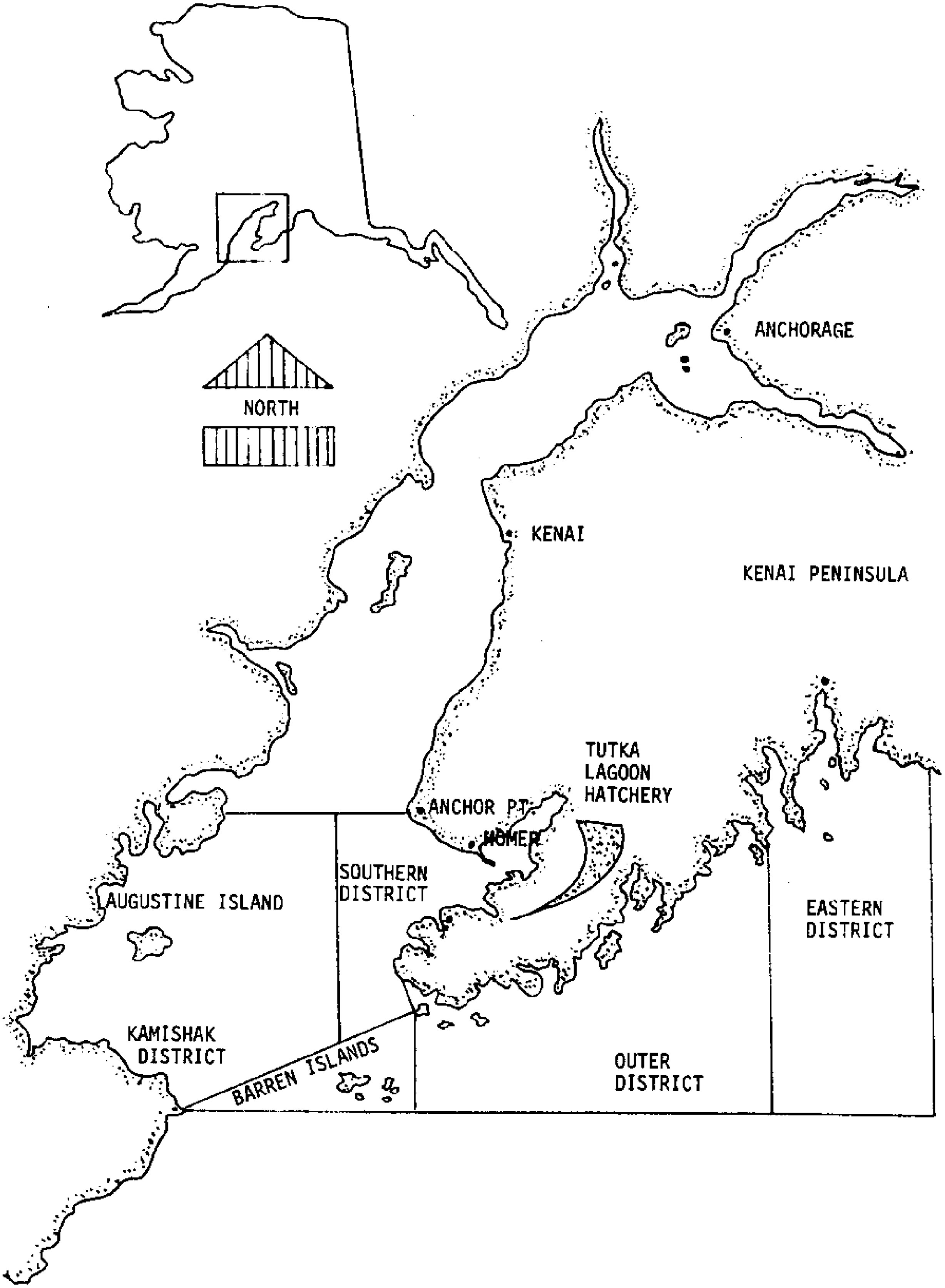

FIGURE 1. LOWER COOK INLET COMMERCIAL FISHING DISTRICTS.

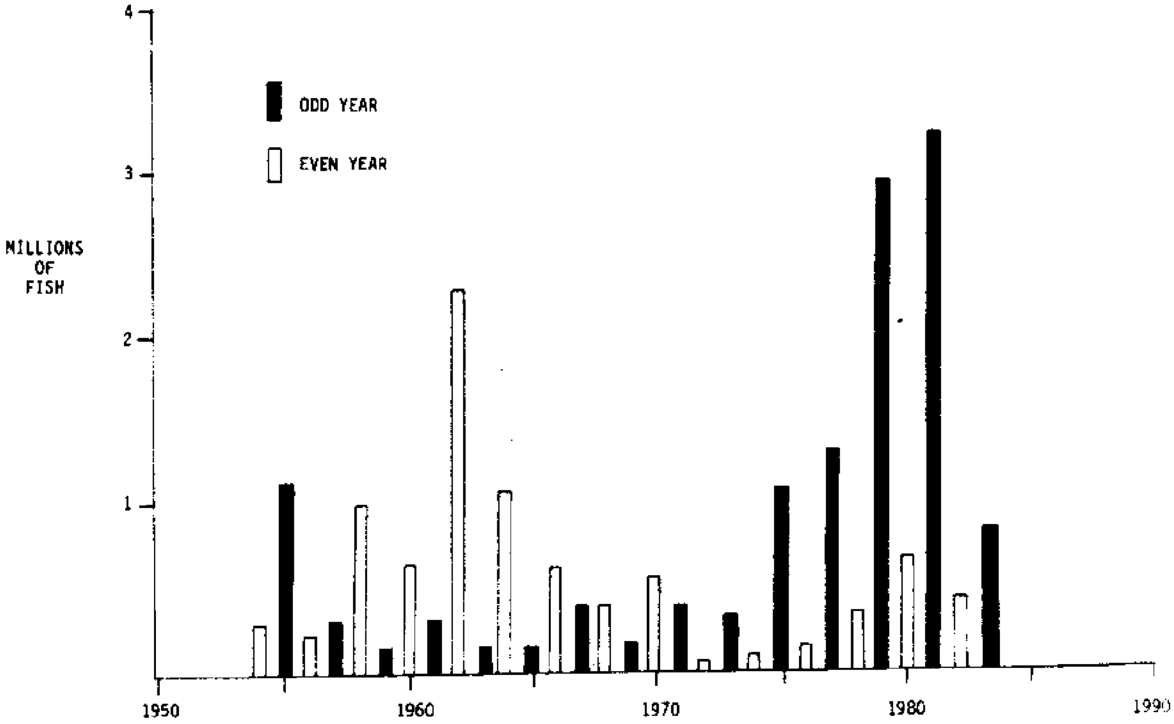

FIGURE 2. SOUTHERN AND OUTER DISTRICTS PINK SALMON CATCH 1954-1982.

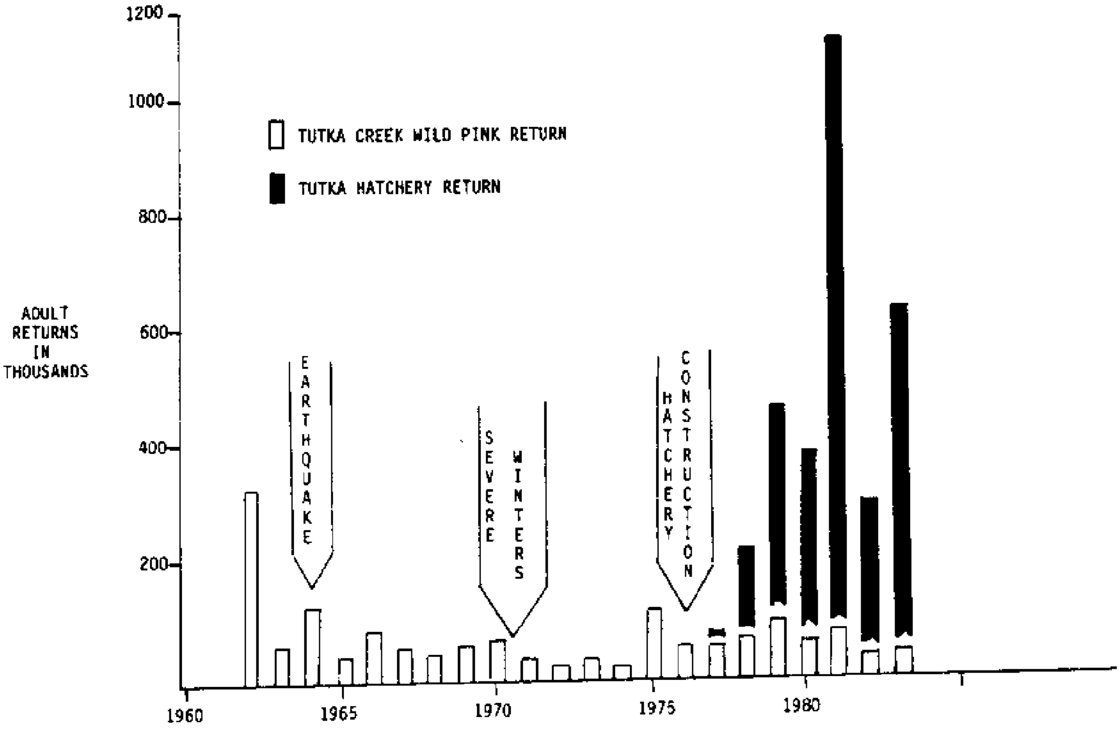

FIGURE 3. TUTKA CREEK WILD PINK SALMON RETURNS WITH RECENT YEARS' CONTRIBUTION.

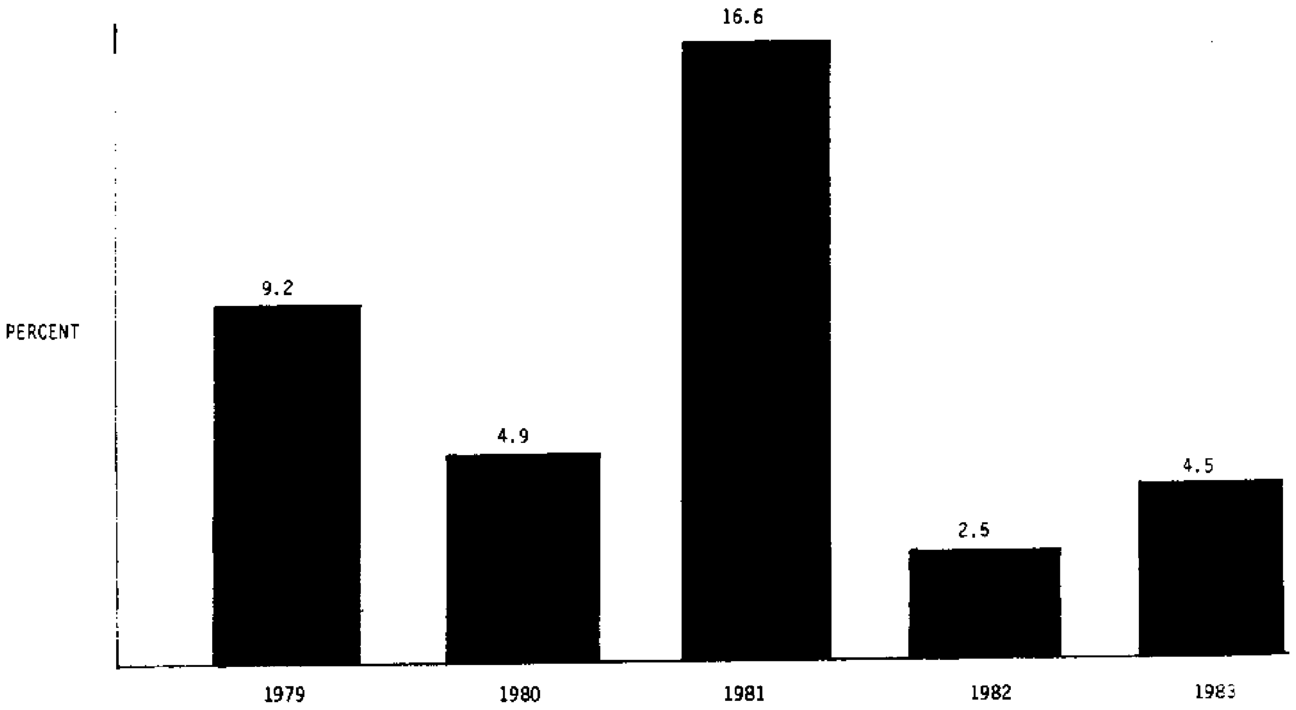

FIGURE 4. TUTKA LAGOON HATCHERY ADULT PINK SALMON RETURN SURVIVAL.

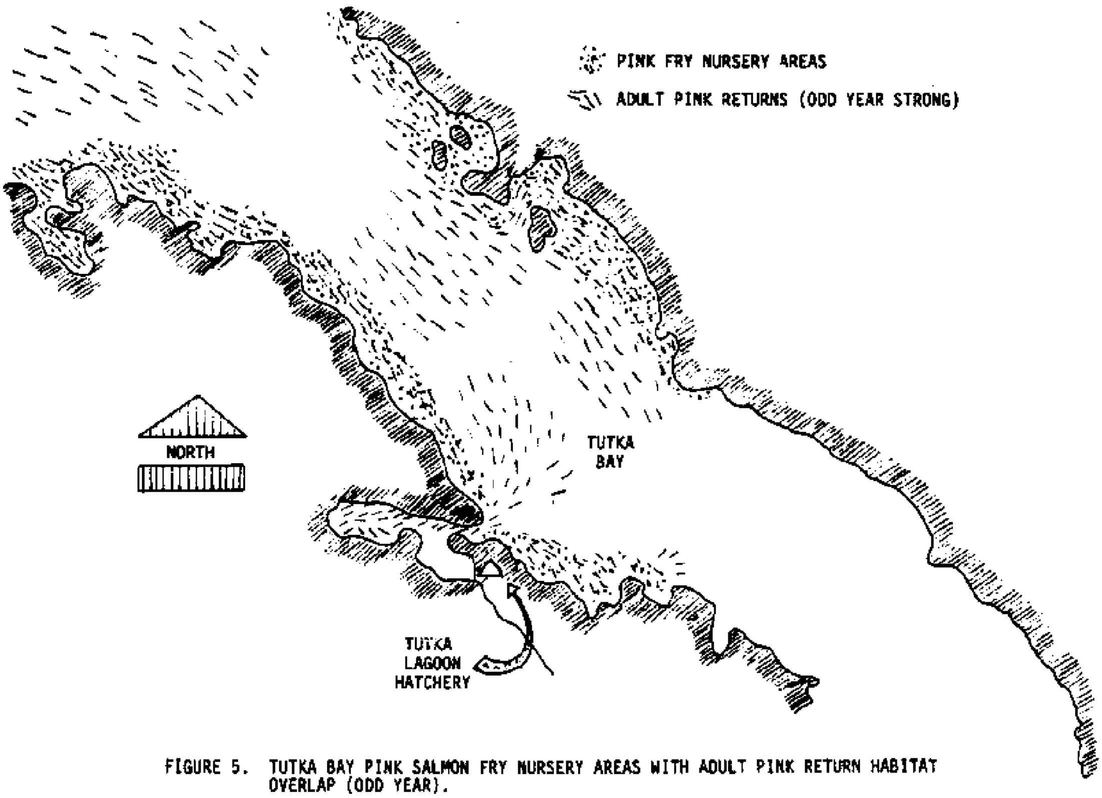

FIGURE 5. TUTKA BAY PINK SALMON FRY NURSERY AREAS WITH ADULT PINK RETURN HABITAT OVERLAP (ODD YEAR).

Annual and Interannual Variability of Temperature and Salinity in the Gulf of Alaska with Emphasis on the Coastal Waters

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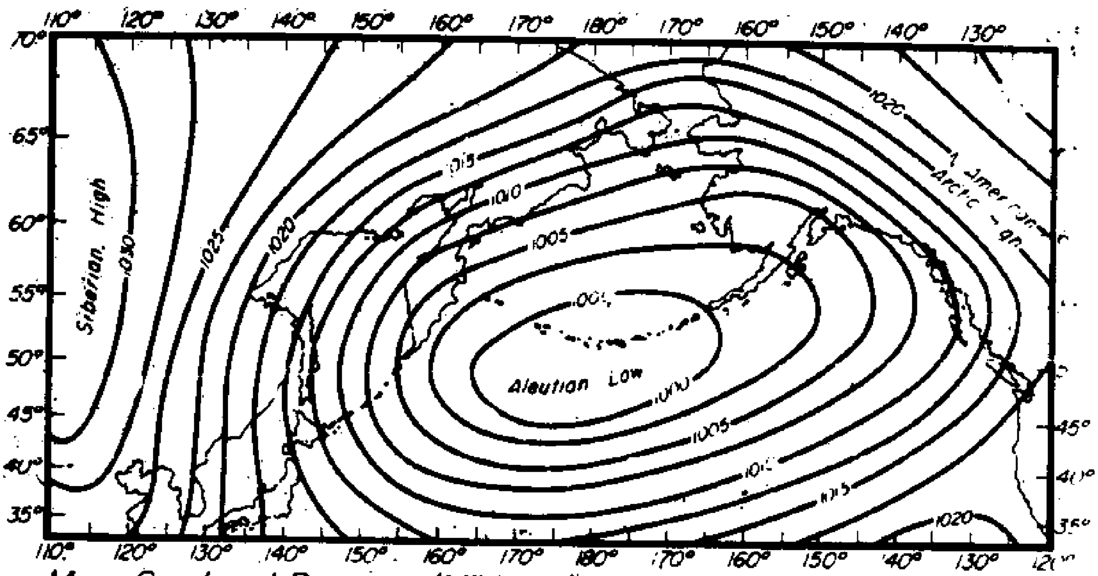
Abstract

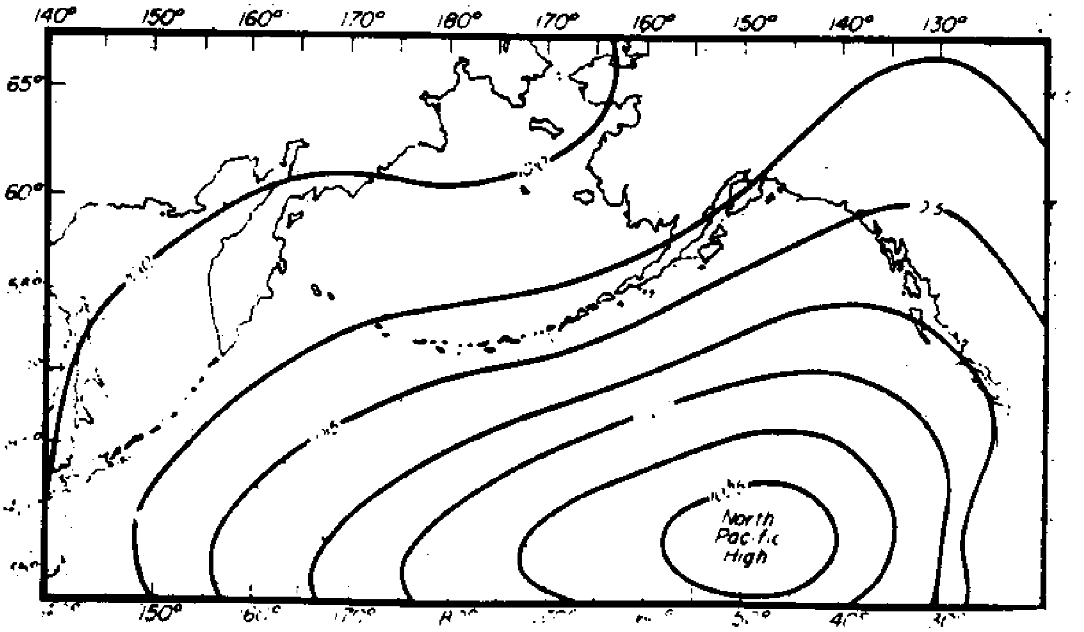
Using historical hydrographic data, we can describe the annual cycle of temperature and salinity for the northern Gulf of Alaska along with the departures from this annual cycle. These annual cycles have relatively large amplitude signals: on the order of 10°C and several °/₀₀ for the surface waters. The maximum surface temperature occurs in late summer, and the minimum surface salinity is found in fall concurrent with the maximum precipitation. Surprisingly, the maximum bottom salinity occurs at the same time as the minimum surface salinity though it appears that these bottom conditions are affected primarily by the wind stress. The interannual departures from this annual cycle are most evident in temperature with the maximum departures of about 2°C. There were significant warming events in 1976-1977 and 1983. The warming takes place throughout the water column and is believed to be due to advection rather than local warming. The first warming lasted for about eight months; the length of the latter one is unknown but has been verified to have spanned at least six months. The coastal circulation in the northern Gulf of Alaska is dominated by a freshwater driven coastal current, the Alaska Coastal Current, which begins along the British Columbia coast, flows first northward and then westward within 20 km of shore throughout the Gulf of Alaska and into the Bering Sea. The strength of this current is affected by local meteorological conditions such as precipitation, wind, and air temperature. About 20% of the coastal drainage is covered with glaciers, which can act as sources or reservoirs for the fresh water in the coastal current. Thus, the coastal circulation can be related to the growth or ablation of these glaciers.

Physical Setting

The Gulf of Alaska coastline forms a parabolic outline which opens to the south and west. Storms frequently become trapped by this coastline as they attempt to move northwestward. Usually, they either die out in place over the Gulf of Alaska or wander down the west coast of North America. It is very seldom that they move directly inland over the coastal mountain ranges that border the gulf. These mountains have heights in excess of 4 km. At these high latitudes, the tropopause is located at low elevations, which enhances the influence of the terrain on the local meteorology. Thus, migrating cyclones are trapped within the apex of the Gulf of Alaska where they cause alongshore (counter clockwise) winds and high rates of precipitation over the coastal margin. The circulation responds to the very large annual signal in wind and precipitation. This is very different than coastal circulation found elsewhere, which is usually controlled by wind stress alone. In summer, the region is dominated by the North Pacific High with weak winds possibly from the west (Figure 1), whereas in winter the Aleutian Low moves through the area frequently, bringing intense cyclonic pressure systems.



Mean Sea Level Pressure (Millibars), Winter



Mean Sea Level Pressure (Millibars), Summer

Figure 1. Atmospheric pressure over the Gulf of Alaska in winter (upper panel) and summer (lower panel) (from Royer 1975).

In the northern Gulf of Alaska, the continental shelf is quite broad, up to 200 km, and contains numerous deep troughs. The placement of shoals and islands possibly could be important for fisheries production. For example, Kodiak Island blocks the flow of water along the shelf (Lagerloef 1983), and intense vertical mixing occurs there. Kayak Island also obstructs the coastal flow, creating a mechanism by which the coastal current can mix with the Alaska Current. The Alaska Current flows in a cyclonic sense (counter clockwise) along the shelf break and is distinct from the nearshore Alaska Coastal Current, except near Kayak Island and west of Kodiak Island (Royer 1981). This coastal current is fairly narrow (< 25 km in the northern Gulf of Alaska), but is quite intense (speeds < 100 cm s^{-1}) (Schumacher and Reed 1980). It appears that the shoal areas on the shelf can mix the water column, bringing nutrient-rich water into the photic zone in areas such as the Kodiak Island shelf. This coastal current ultimately flows along the southern side of the Aleutian Island arc and into the Bering Sea through Unimak Pass (Schumacher et al. 1982).

The fresh water enters the Gulf of Alaska as a line source beginning along the British Columbia coast. While large rivers contribute some of this water, the vast majority is provided by small streams along the coast (Royer 1979). The average annual precipitation for the southeast and southcoast regions of the Gulf of Alaska is about 220 cm, with an extreme value being 844 cm. The impingement of the marine weather systems on the coastal mountain ranges is the cause for these high rates of precipitation. The annual rates of precipitation (Figure 2) increased from 1932 to 1940 and decreased slowly after that. The freshwater cycle is complicated by the glaciers which cover about 20% of the coastal drainage area. These glaciers can store or release water depending on the air temperature or the solar insolation.

The winds over the Gulf of Alaska are strongest when from the east and therefore cause a coastal downwelling (Figure 3) throughout much of the year (Bakun 1973; Livingstone and Royer 1980). There is some doubt as to whether there is a

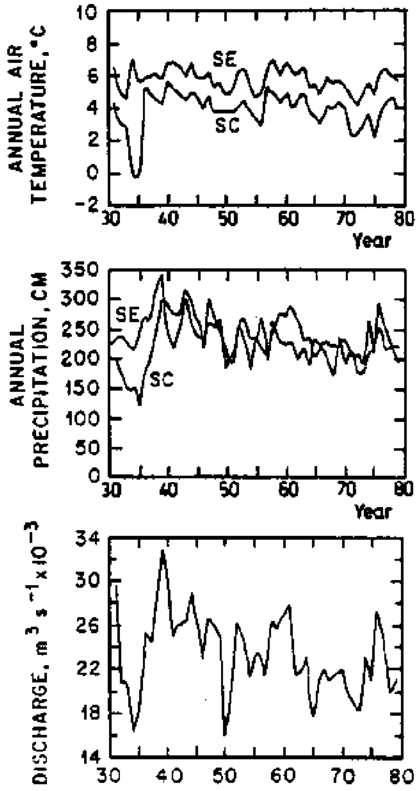


Figure 2. Annual mean air temperature (top) for southeast Alaska (SE) and southcoast Alaska (SC), precipitation (middle), and freshwater discharge (bottom) (from Royer 1982).

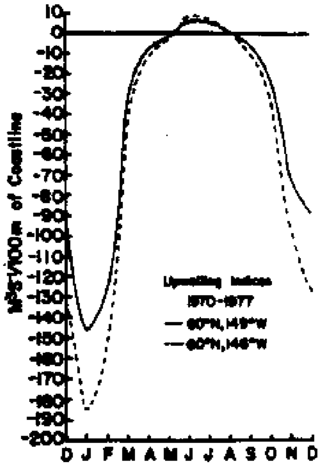


Figure 3. Annual downwelling cycle for 60°N, 149°W.

significant reversal to this wind system in summer to cause regional upwelling. Nevertheless, the decrease in the magnitude of the downwelling will result in changes in the water properties on the continental shelf and there is some evidence that local current reversals can occur, at least, in the Northeast Gulf of Alaska (Muench and Hachmeister 1982).

Seasonal Cycles of Temperature and Salinity

If we divide the year into four seasons (spring; March, April and May, summer; June, July and August, autumn; September, October, and November, and winter; December, January and February), we can observe the seasonal progression of salinity and temperature at the coast near Seward, Alaska (59°50.8' N, 149°28' W) (Figure 4) (Xiong and Royer 1983). In summer, there is a halocline in the upper 20 m and a more uniform layer beneath. Within the halocline the salinity increase is about 0.17‰/m. Beginning at the bottom of the halocline the salinity increases from 30.9 to 32.9‰ at a depth of 200 m and to 32.95‰ at the shelf bottom. The surface salinity is about 27.5‰. In winter, mixing causes the halocline in the upper 20 m to disappear. The salinity in this well-mixed layer is about 31‰. A well-developed thermocline exists simultaneously with the halocline in summer, but the bottom of the thermocline is much deeper (75 m) than the halocline (20 m). This indicates that there are different mechanisms causing the formation and decay of these two features. The average summer temperature is about 11°C. Below the thermocline, the temperature decreases gradually with depth to a minimum of 4.7°C at 150 m and then increases to about 4.9°C near the bottom at 264 m. In winter, there is a temperature inversion between 15 and 200 m. In spring this inversion begins much deeper at 75 m. Spring marks the extreme values in surface values with salinity being 31.4‰ and temperature being about 4°C. The seasonal progression in temperature (Figure 4a) shows, as one might expect, that the surface range is greatest, but also that the range of the bottom temperatures is greater than the mid-depths, such as 150 m. The seasonal salinity signal (Figure 4b) also demonstrates the large range of that parameter at the surface. This salinity range decreases with depth. With the exception of the surface salinity, the minimum salinity occurs in August in the upper 30 m, whereas the salinity at depths of 50 m and deeper is a minimum in November. An explanation for this is that the upper salinity is controlled by the freshwater runoff while the upwelling-downwelling wind systems influence the lower layers, causing a maximum salinity in autumn coincident with minimum downwelling. The month delay in the response of this system is a

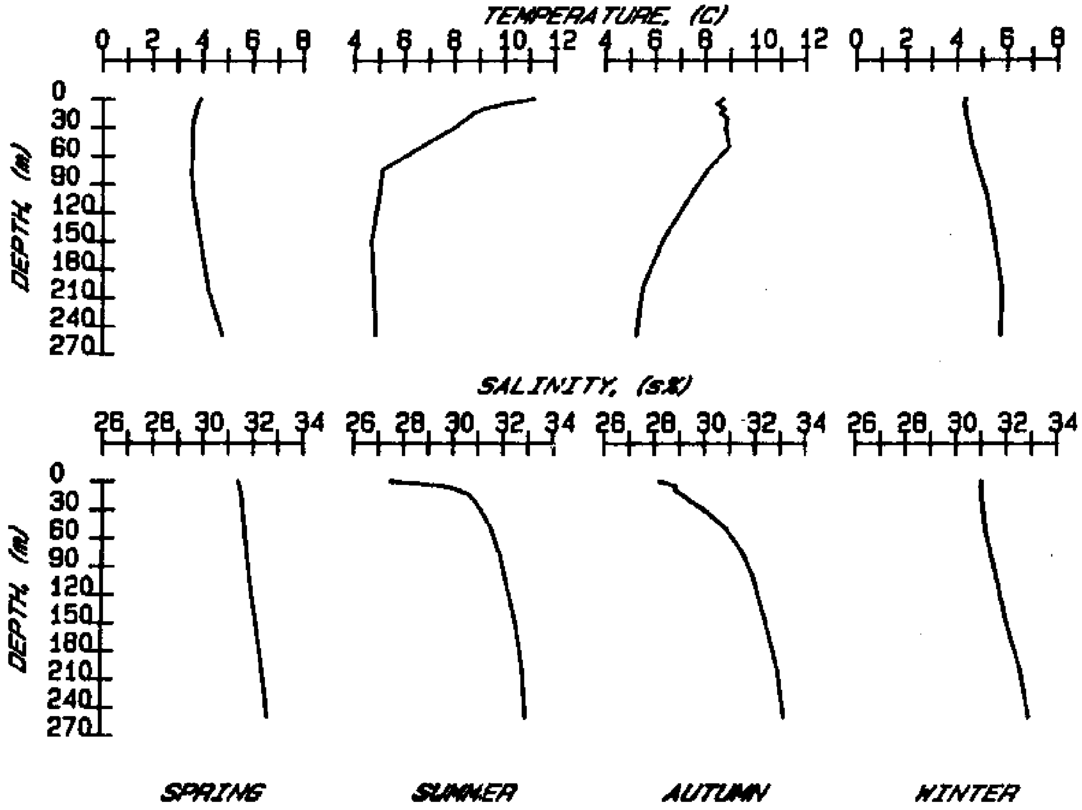


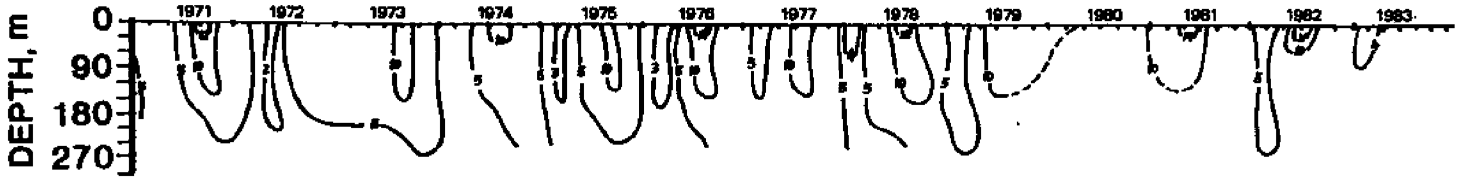
Figure 4. Seasonal temperature; (a) (upper panel) and salinity; (b) (lower panel) cycle at Seward (from Xiong and Royer 1983).

reasonable time for the transport of water across the shelf, for this higher salinity water has the deep Gulf of Alaska as its origin. Thus, the absence of a wind over this shelf can cause high salinity, warm, and possibly nutrient-rich water to be advected onto the continental shelf in the northern Gulf of Alaska. High production could be due to an inactive wind system, in contrast to other productive shelves where an active, upwelling wind system is necessary.

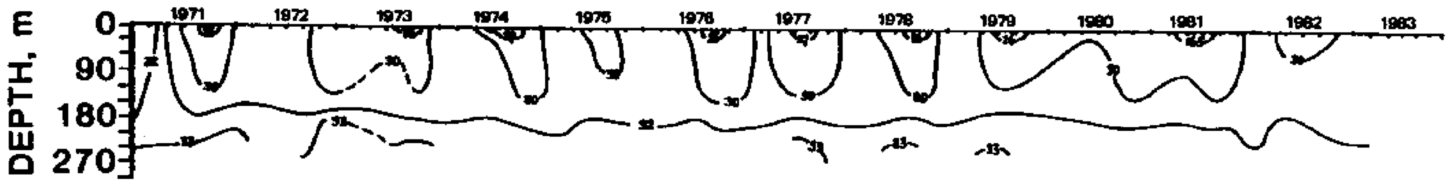
Interannual Variability of Temperature and Salinity

The annual and interannual variability of the temperature and salinity throughout the water column can be seen in Figure 5. Once again, the surface warming can be seen to propagate downward into the water column. The salinity cycle has a minimum at the surface in early autumn coincident with the bottom maximum, but the two are probably caused by different effects, as mentioned earlier. Caution should be used in any interpretation of these figures to determine interannual variability because the temporal spacing of the samples is not uniform. Remembering this limitation, a time-depth cross section of temperature and salinity anomalies (monthly means subtracted) at Seward (Figure 6) illustrates the interannual variability at this location. There have been two distinct periods of warming: 1976-77 and 1983-?. The pattern of the salinity accompanying these warming periods is not as vivid as the temperature, but the salinity appears to be slightly fresher than normal during the warming.

The time series of the anomalies of temperature and salinity for the depths of 0, 50, 150, and 200 m from 1971 to 1983 (Figures 7 and 8) further illustrate the

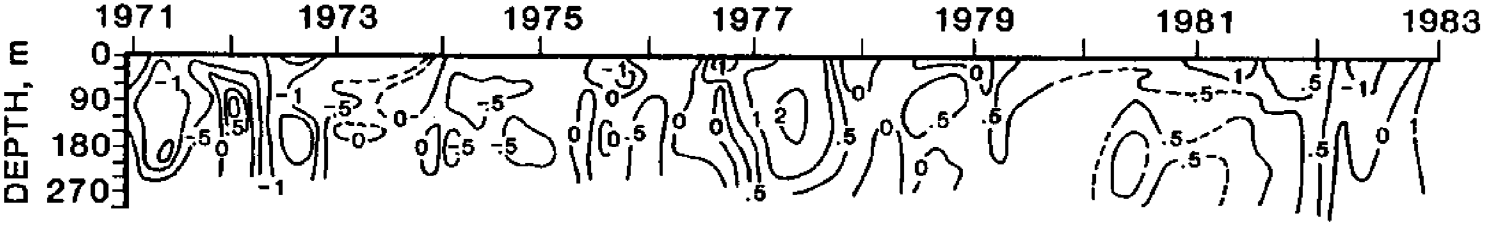


A. Time series of temperature at Seward.

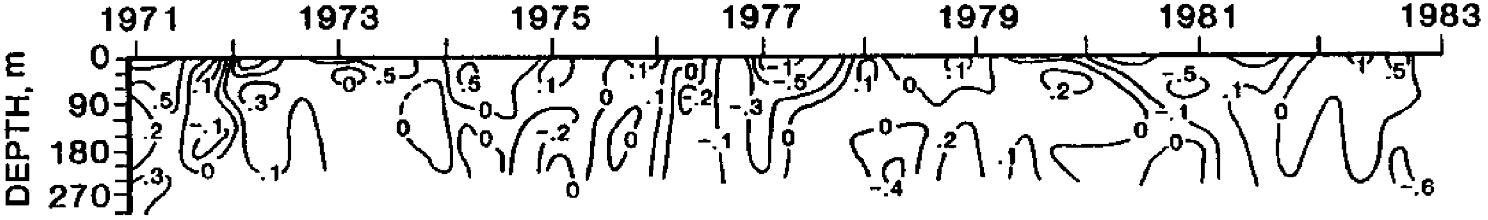


B. Time series of salinity at Seward.

Figure 5. Salinity and temperature cross-section for 1970-82 at Seward (from Xiong and Royer 1983).



A. Time series of anomalies of temperature at Seward.



B. Time series of anomalies of salinity at Seward.

Figure 6. Anomalies of temperature and salinity at Seward (from Xiong and Royer 1983).

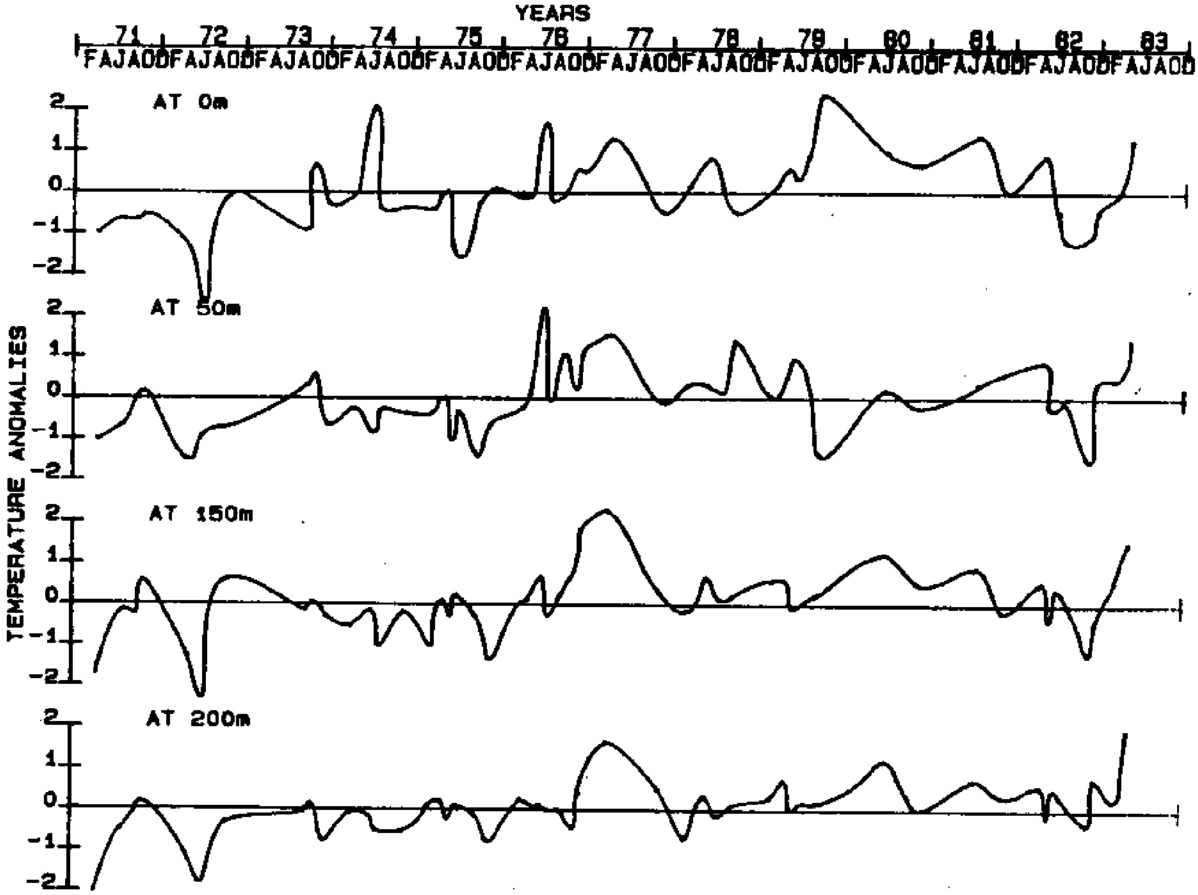


Figure 7. Time series of temperature anomalies at selected depths at Seward (from Xiong and Royer 1983).

lack of any relation between the temperature and salinity anomalies. Large fluctuations in surface salinity were limited to the early 1970s. Possible local or regional forcing functions for these anomalies are freshwater discharge, wind stress, and sea level elevation (dynamic height) (Figure 9). However, once again, there is no clear cause-effect relationship for these processes. There is a relationship between air temperature and freshwater discharge because the hydrology model, which is used to estimate the discharge, has a dependence on air temperature which converts rain to snow or ablates the glaciers.

In 1982-83 there was an apparent warming of the water column at the station at the mouth of Resurrection Bay (Figure 10). This warming event began after quite cold water was detected at this location in November 1982, nearly 2°C below normal throughout the water column. In December and February this cold feature began to dissipate, so that by April 1983 it had become a "warm" feature, with temperatures greater than one degree above normal. By June 1983, the average temperature for the 250 m water column was 1.48°C above normal with the maximum being 2.39°C at 50 m. The salinity did not demonstrate a significant departure from normal. In September, the mean temperature anomaly had decreased to 1.22°C above normal, with

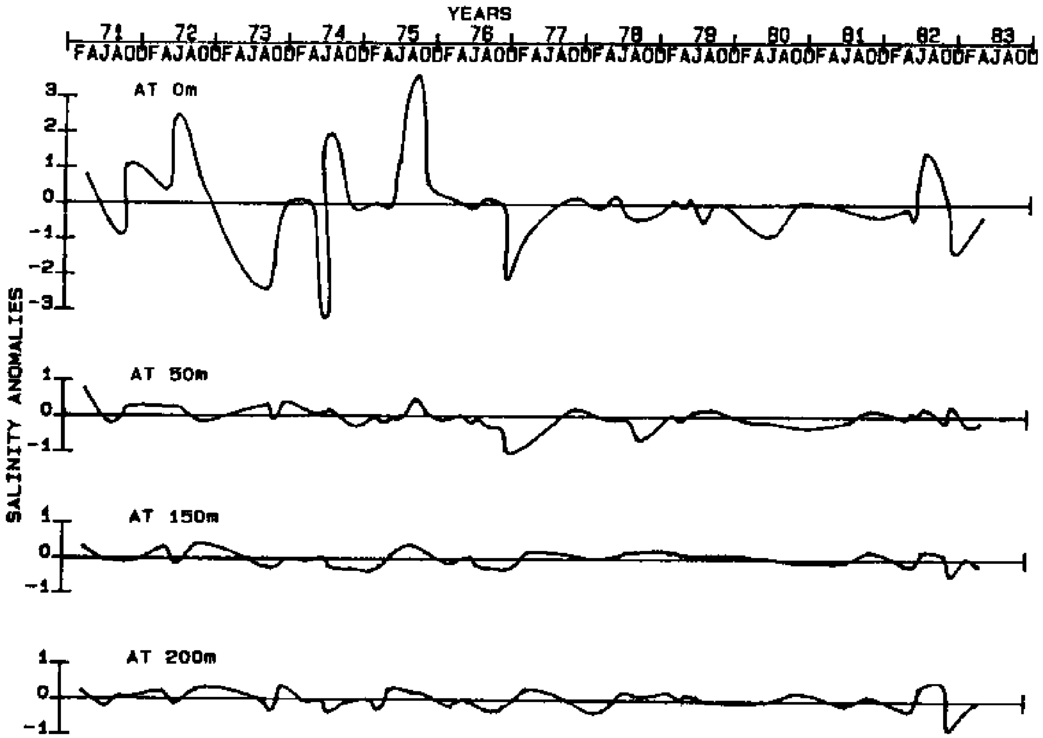


Figure 8. Time series of salinity anomalies at selected depths at Seward (from Xiong and Royer 1983).

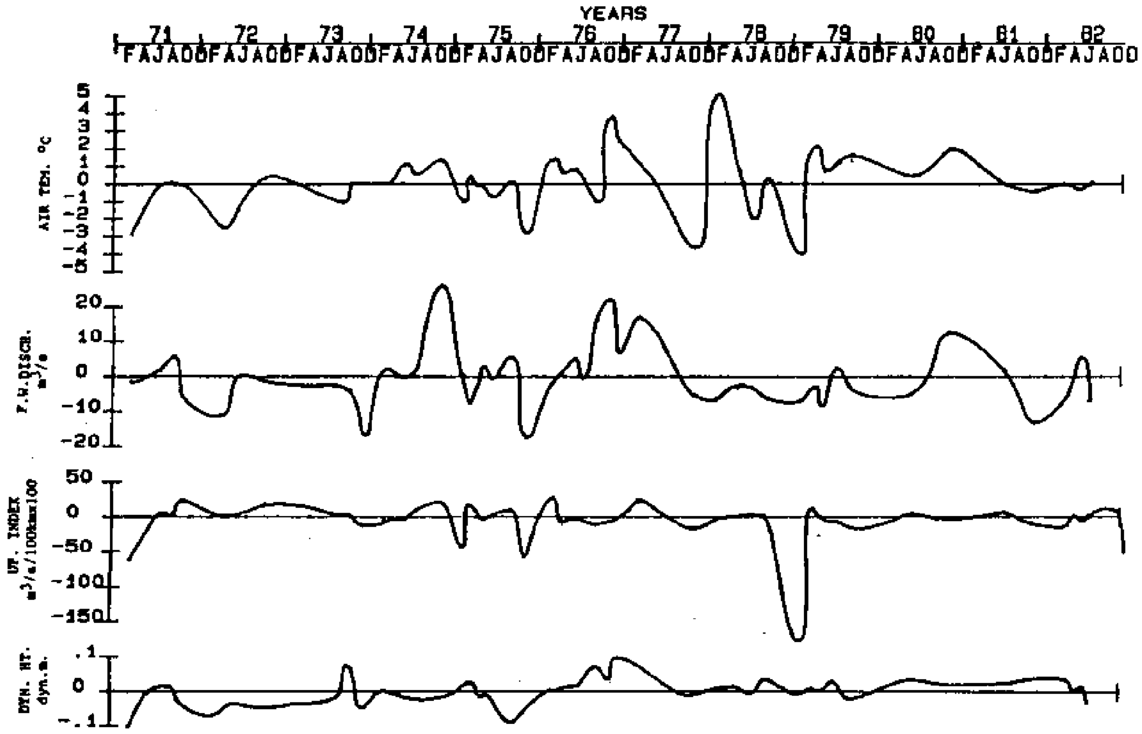


Figure 9. Time series of anomalies of air temperature freshwater discharge, upwelling index and dynamic height at Seward (From Xiong and Royer 1983).

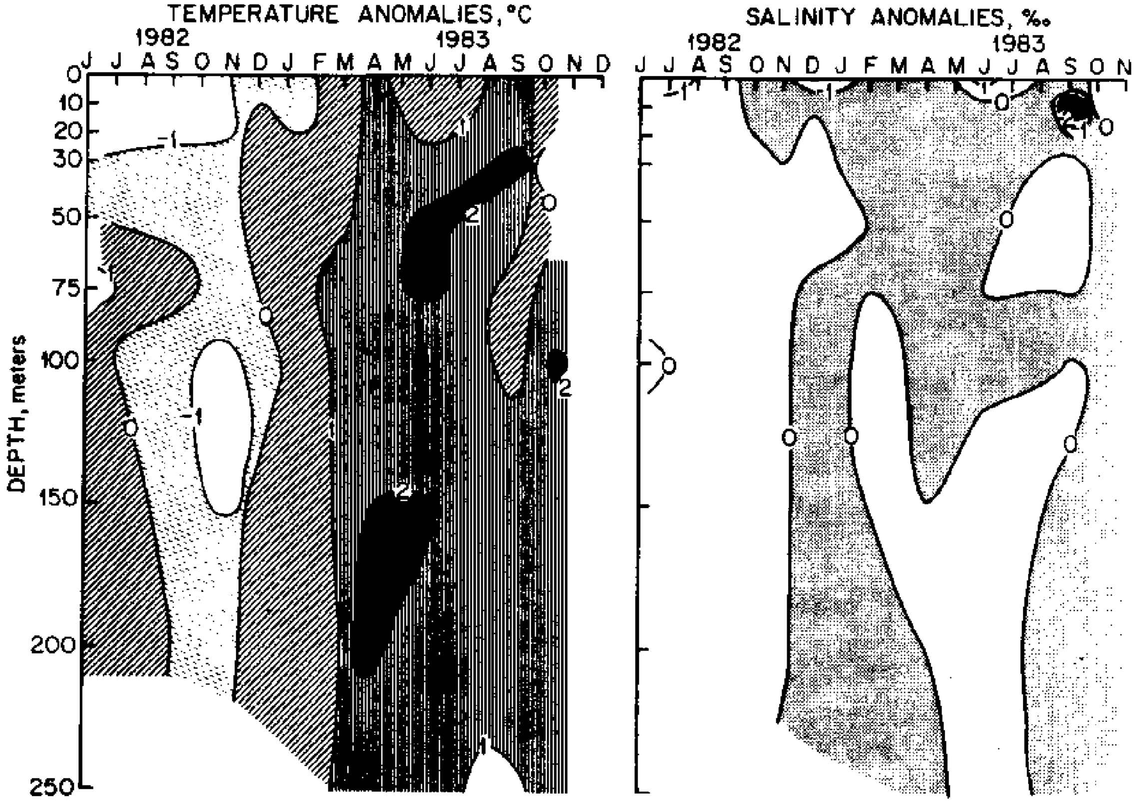


Figure 10. Temperature (left panel) and salinity anomalies near Seward from July 1982 through October 1983.

the maximum being 1.82°C at 50 m. (The average salinity departure at this time was 0.14°/oo, with both positive and negative salinity anomalies being present within the water column. In October 1983, the temperature anomaly at 50 m had diminished to 0.39°C above normal and the salinity decreased to 0.88°/oo below normal, twice the previous maximum negative anomaly. This 1983 warming event possibly could be larger than the 1976-77 event. The connection between these water temperature elevations and El Niño has yet to be determined, but the feature does correspond with the reported water temperature elevations along the British Columbia coast (Tabata 1983, personal communication) and possibly with the unusual conditions along the California coast in winter 1982-3 (Reid 1983, personal communication). In summary, this intense warming throughout the water column is caused by advection, with a significant change in salinity arriving later.

An important consideration when trying to establish the "average" conditions and their anomalies is whether the sampling period is "typical". Unfortunately, one seldom selects sampling times that are "average". So it appears with the data from the 1970s for this station near Seward. The large-scale meridional transport across the center of the Alaska Gyre 54°N (Figure 11) shows an anomalous northward component over the western half (173°-149°W) during the late 1970s (when compared with similar data from 1954-60 and 1974-82). This anomalous transport explains why drifting buoys released south of 45°N in 1976 entered the Gulf of Alaska instead of joining the California Current (Kirwan et al. 1978). In contrast, drifters released north of 45°N in the summer of 1981 had a tendency to move southward as they approached the west coast of North America. This southward movement might be the result of the decreased northward meridional transport over the western Gulf of

Alaska at this time (Figure 11). It should also be noted that the gyre in the Gulf of Alaska shifted very far westward in the summer of 1981. This shift was noted in hydrographic data obtained in August 1981 on R/V Alpha Helix. The only previously documented case of the gyre being as far westward as it was in 1981 was for the summer of 1958 (Dodimead et al. 1963), but the atmospheric conditions have very little similarity for the two periods.

Summary

The dominant circulation feature in the coastal area in the Gulf of Alaska is the freshwater-driven Alaska Coastal Current. Though this flow exists throughout the year, it reaches its maximum intensity in fall coincident with high rates of precipitation. The current is continuous from the British Columbia coast through the Aleutian Island passes, though it is sometimes interrupted by either coastal features or local winds. Though the salinity of this current is less than that of the adjacent water (26 versus 32°/₀₀) it is not fresh enough to be be considered a true freshwater current. The 1970-82 time series near Seward, Alaska, shows at least two periods with water temperatures well above normal. Those periods were 1976-77 and 1983.

The decade of the 1970s does not appear to be "typical" with regard to the wind stress over the Northeast Pacific. There was anomalously northward transport from about 1976 until 1980.

Observations of the Alaska Coastal Current at present are being made with an expanded effort. Current meters are now deployed near Seward, a meteorological station has been installed and hydrographic sections are being made on a routine basis from April 1983 through November 1984. It is expected that these data will help better delineate the seasonal response of the coastal current to the freshwater and wind forcing. This also represents an opportunity for other investigators to gather samples from this flow.

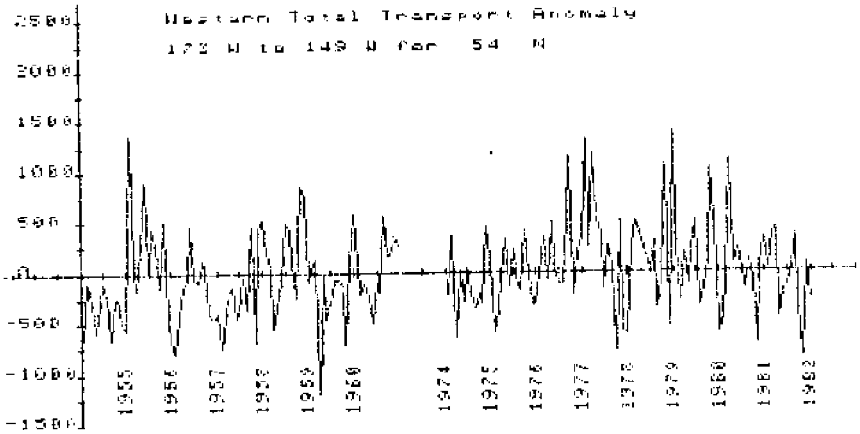


Figure 11. Meridional total transport along 54°N integrated from the 149 to 173°W with positive northward.

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Some Thoughts on the Alaska Coastal Current as a Feeding Habitat for Juvenile Salmon

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Abstract

The apparent use of the Alaska Coastal Current by millions of juvenile Pacific salmon each year raises a question about the trophic status of the coastal zone. Onshore flow of surface water during most months of the year is suggested as a mechanism that should theoretically enrich the coastal current with forage species relative to the adjacent shelf/ocean water. Estimates of the production of potential food in the current and that introduced by cross-shelf transport exceed the calculated salmon demand when competition and size/taxa are ignored. However, when both size selectivity and competition are considered, the ability of the current's production of forage species to feed the juveniles appears marginal in all seasons. Combining this *in situ* production with forage biomass introduced from the bordering ocean provides sufficient forage stocks in the spring and summer seasons although the estimated fall demand for food still exceeds the supply.

Oceanographic factors influencing the cross-shelf transport must affect the rate at which oceanically derived forage species are introduced into the outer margin of the Alaska Coastal Current from year to year.

Introduction

Royce et al. (1968) state that at least 750,000 juvenile salmon pass fixed locations daily in coastal Alaska from July to October each year. In seaward extent, the young fishes seem confined to a narrow band about 20 nm wide, corresponding to the approximate boundaries of the Alaska Coastal Current (Royer 1981). Juveniles entering this current from Washington and British Columbia waters allegedly travel 1000 nm to the north and west before turning south to ocean feeding areas off Yakutat (Takagi et al. 1981). Fishes from southeastern, south-central, and western Alaska join the coastal current as it flows 1500 nm further to the west. These juveniles presumably enter the open ocean somewhere south of the Fox Islands on the Aleutian chain (Figures 1, 2).

At a migration rate of about 10 nm d^{-1} (suggested for pink salmon by Royce et al. 1968) these fish spend between 50 and 150 days traveling from coastal/estuarine nursery areas to subsequent offshore oceanic feeding domains. This time in transit, combined with research on trophic ecology and rates of early salmon growth reported by Shelbourn (1980), Barber (1979), Phillips and Barraclough (1978), and Simenstad et al. (1980), suggest that the coastal current may be more than a convenient conduit to ocean feeding grounds--that in fact, it represents a critical early-feeding habitat.

Brett (1974) provides information on the size of pink salmon from the time they enter the coastal estuaries, at 0.2 g per individual until they return 12

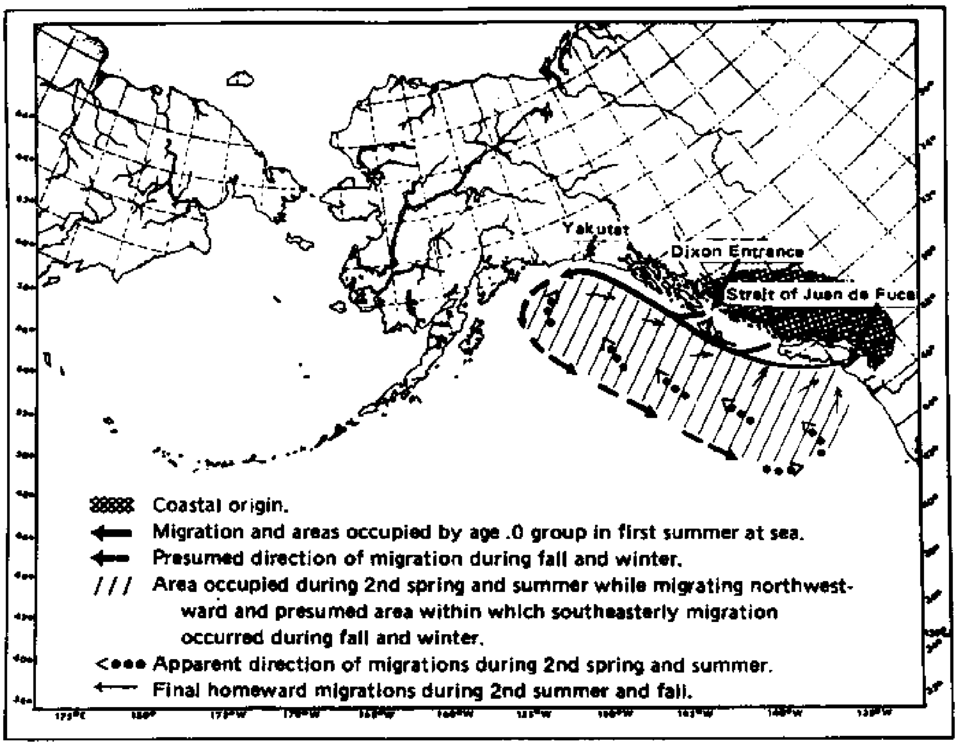

Figure 1. Diagram of the ocean migration of pink salmon originating in Washington State and British Columbia (from Takagi et al. 1981).

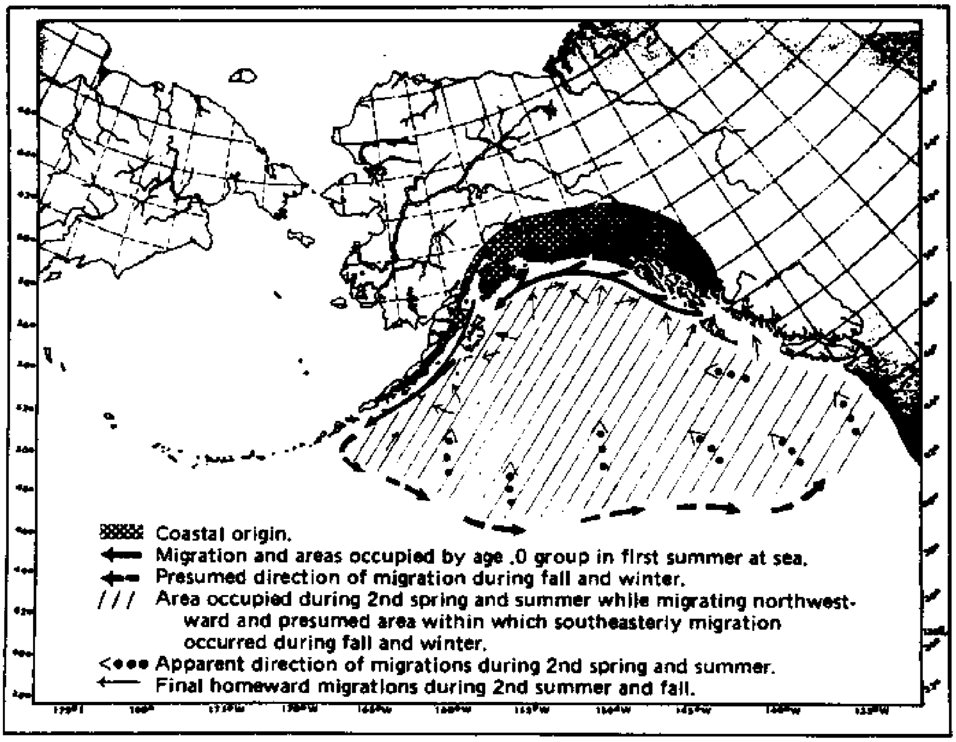

Figure 2. Diagram of the ocean migration of pink salmon originating in southeastern, central, and southwestern Alaska (from Takagi et al. 1981).

months later as spawning adults weighing approximately 1400 g. For the period June through November, the increase in weight, 0.2 to 200 g per individual, represents an average instantaneous growth of about 4.0% of their body weight per day. Much of this growth must occur in the Alaska Coastal Current. Following a short period of reduced winter production in the open ocean, the pinks enter a second growth stanza in February which ends six months later, reflecting a growth rate of only 1.1% of the body weight per day.

Since a significant portion of the early growth (pink and chum salmon) occurs in the coastal current (July to October), a question can be raised about the trophic significance of this habitat relative to alternative pathways the salmon could have adopted in their migrations to open ocean feeding areas. For many stocks, a straight-line distance to oceanic feeding grounds is several hundreds of nautical miles shorter than the route traveled via the coastal current.

The problem of early ocean growth and survival has been examined by Walters et al. (1978), using a computer simulation and information on the time of ocean entry, size-dependent mortality, ration and growth in relation to body size, and time-space distribution of zooplankton stocks and production along the British Columbia coast. These authors conclude that ocean limitation to early salmon growth is unlikely unless only a very small fraction of the zooplankton production is actually available to the young near-surface feeding fishes. Their study points to several areas of uncertainty associated with the modelling, not the least of which is the question of actual food availability.

Takagi et al. (1981), reviewed the literature describing the feeding preferences and requirements for .0 age pink salmon feeding in the coastal ocean habitat. Copepods, euphausiids, amphipods, larvaceans and barnacle cyprids are described as common major food items. A shift to larger size prey occurs as the fishes increase their size (Peterson et al. 1982); fish larvae (herring, smelt, and sandlance) and squid become important as the young pinks approach 150 mm total length. Apparently the juveniles feed only during the day, although Godin (1981) reports an increase in the feeding rate near, or at dusk, for pinks studied in a coastal estuary. This behavior might be an important adaptation later in life for using diel migrating prey that are consistently unavailable below the surface during the daylight hours (euphausiids, and some copepods, i.e., *Metridia* spp.).

The seasonal occurrence of *Neocalanus plumchrus* in the coastal/shelf surface waters (Fulton 1973) seemingly places stocks of this large oceanic copepod within the feeding domain of early entering juvenile salmon, April-July. A recent ichthyoplankton survey (Fulton et al. 1982) measured a combined copepod and euphausiid biomass exceeding 200 g m^{-2} in British Columbia coastal waters in April. These authors reported that 40-50 g m^{-2} were associated with *N. plumchrus* stage V copepodids (presumably in the upper 100 m), and that while this stock was only about half that measured previously for the Strait of Georgia (Harrison et al. 1983), it was approximately four times higher than that in the open ocean, 10 g m^{-2} (Fulton 1978).

These studies indicate that suitable forage stocks are present in the Canadian coastal zone from April into early summer. A similar availability (but less biomass) of oceanic zooplankton was reported by Cooney (1975) for the nearshore zone in the northern Gulf of Alaska between Yakutat and Seward. The general question of forage abundance and production later in the season, August-October, remains to be critically examined, particularly for northern Alaskan waters.

Kendall et al. (1980) reported the seasonality of zooplankton, including copepods, amphipods, euphausiids, barnacle nauplii and cyprids, larvaceans, and chaetognaths, in addition to larval fishes from collections taken over the shelf and from the open ocean near Kodiak Island (upper 200 m). Total zooplankton settled volumes were lowest near shore in the winter, spring, and fall (0.15, 0.11, and 0.12 ml m^{-3}, respectively) and highest in midsummer (0.44 ml m^{-3}). Unfortunately, this data set does not represent all months of the year; the critical months for salmon feeding (May, August, and September) were not sampled.

A Cross-Shelf Transport Mechanism

The evidence indicates that most, if not all, species of Pacific salmon have adopted a coastal current residence period early in their life history (Figure 3). Since considerable early growth (∼4% of the body weight per day for pink and chum salmon) occurs in the current, it seems reasonable to assume that this habitat preference evolved in the direction of food availability and perhaps predator avoidance. The fact that the young salmon travel further than the straight-line distance to ocean feeding areas further suggests an extended transit time in the coastal zone is beneficial both to growth and survival. I use this behavior to raise the following questions:

1. Do oceanographic factors associated with the coastal current flow enhance or otherwise enrich the nearshore feeding environment for juvenile salmon?
2. Do oceanographic factors associated with the coastal flow negatively effect the predation pressure on juvenile salmon populations?

Since the problem of ocean mortality of young salmon as a function of specific predator populations remains largely undescribed, I will not attempt to address this constraint to production. Rather, I will demonstrate that flow associated with the coastal current could supply oceanically derived zooplankton stocks to the outer edge of the coastal current. Suffice it to say, size-dependent mortality

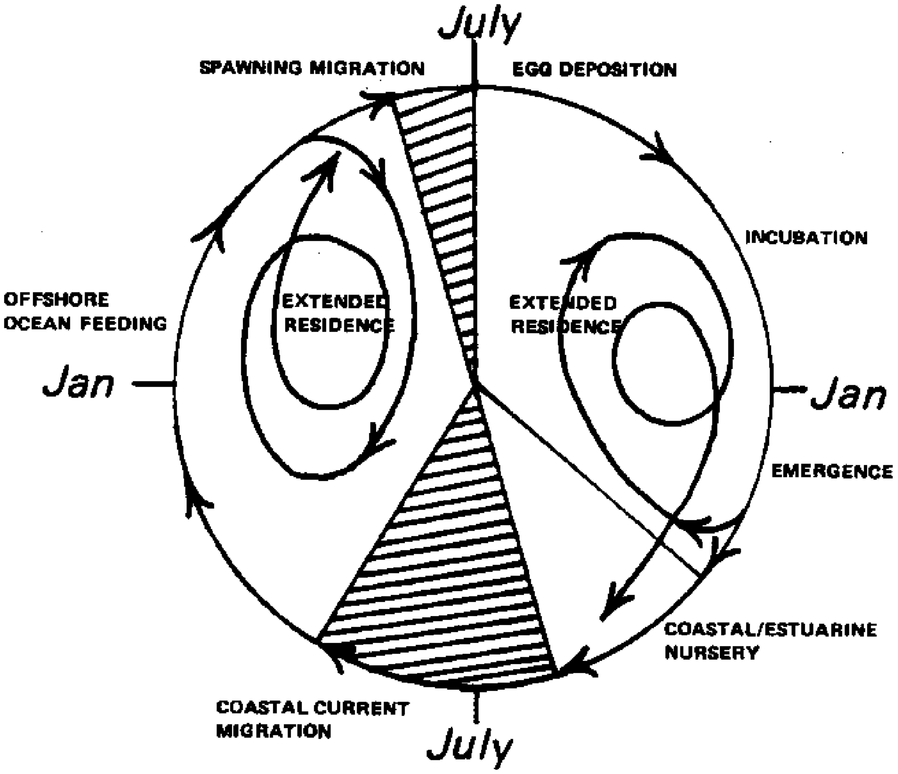

Figure 3. Chronological model depicting critical events and habitats related to the life history of Pacific salmon.

in juvenile salmon seems real (Parker 1965; Martin et al. 1981; Healey 1982; Bax 1983), and further, attempts to rear juveniles prior to release generally increase their probability of survival, but decrease their final size, perhaps by limiting the time the young fishes are free foraging in the coastal zone.

Some aspects of the physical structure of the coastal current and adjacent water seem pertinent to the question of possible food enrichment for salmon. During the months October to May, winds associated with the Aleutian low-pressure system drive an onshore Ekman transport most strongly developed in midwinter (Royer 1979). This flow (upper 50 m) converges near the coast and constrains the freshwater-driven coastal current to a narrow, high-speed jet (Figure 4).

Following a shift in wind direction responding to the changing locations of the North Pacific high- and low-pressure systems in the spring, the onshore Ekman flow relaxes, and conditions for weak coastal upwelling are established from June through August. At this time, a typical estuarine circulation pattern occurs with a thin freshened surface layer flowing seaward (upper 10-20 m) over a subsurface entrained flow (20-50 m) moving landward from the bordering ocean. Thus, in almost

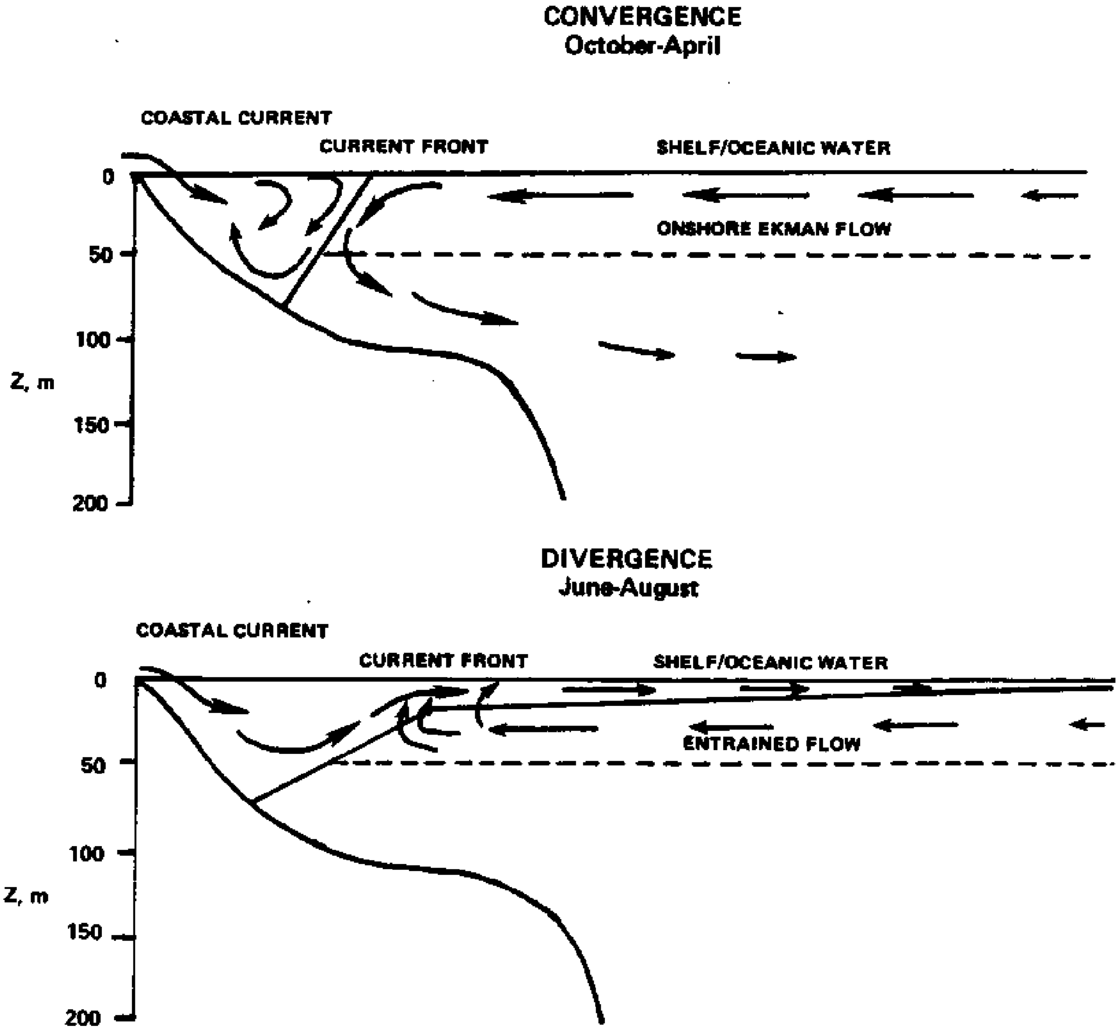

Figure 4. Generalized cross-shelf flow in the northern Gulf of Alaska for the convergence and divergence seasons.

all months of the year, the shelf and coastal waters of the northern Gulf of Alaska are influenced by oceanically derived surface or near-surface water.

I contend this transport represents a physical means capable of moving oceanic populations of near-surface zooplankton shoreward (Figure 5). If some portion of these populations become prey for juvenile salmon, the cross-shelf flow can be said to enrich the coastal waters.

The significance of oceanically derived forage stocks can only be evaluated when the difference between the production of prey species endemic to, or incorporated in the coastal current, and the influx of prey biomass introduced by the cross-shelf flow is known. If the former is high relative to the consumption demand by the salmon, the introduced prey may be of minor importance. I say may because it is highly probable that prey availability is a function of both production and patchiness. The lateral introduction of oceanic prey stocks conceivably produces a narrow band of high-density food, that because of its localization could be more important than an equal or greater production of coastal species spread evenly across the current.

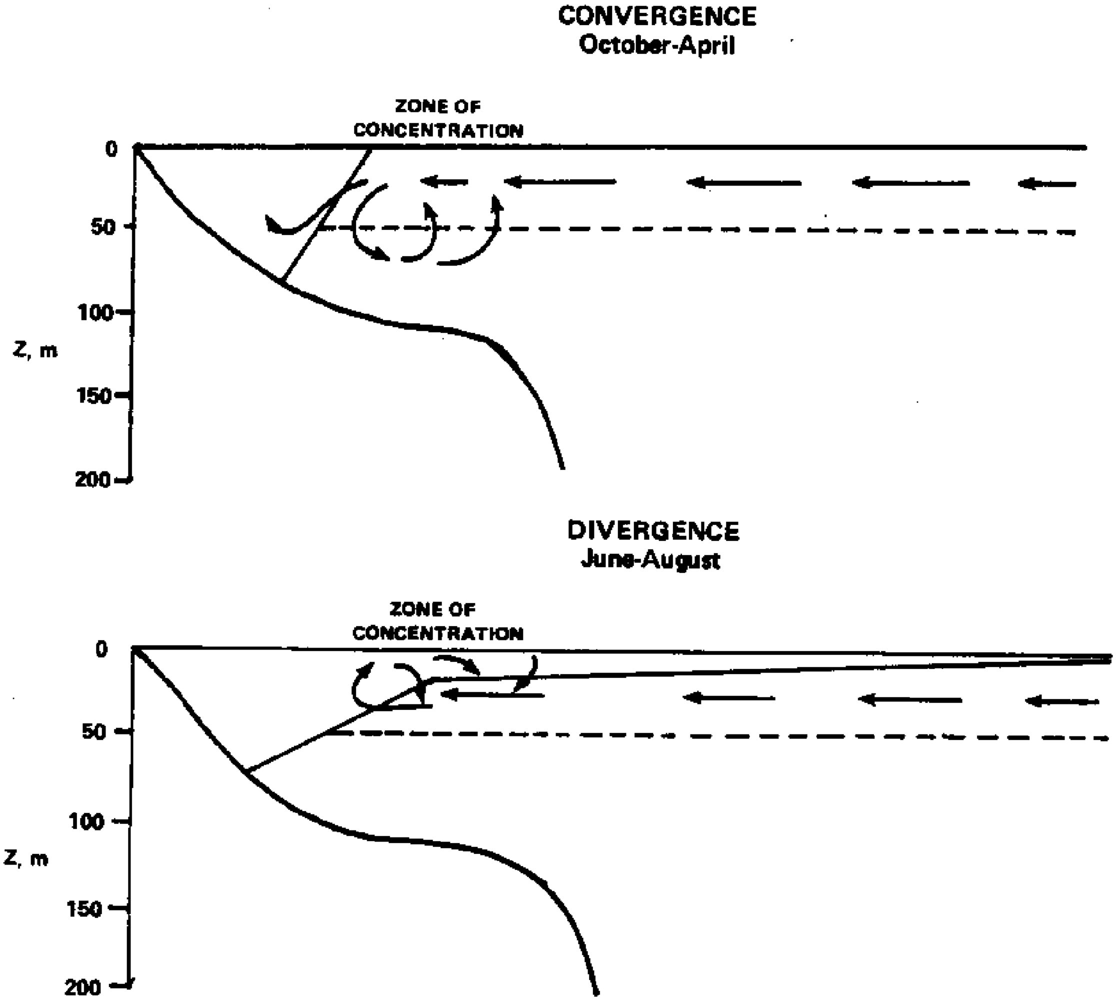

Figure 5. Hypothesized trajectories and zone of concentration for zooplankton populations under convergence and weak upwelling conditions.

To examine this possibility, the following hypothetical example is considered using existing zooplankton stock and production information and making some assumptions about prey utilization and how the oceanic forage species are introduced and retained by the cross- and along-shore flow. First, the standing stock of zooplankton is calculated for a strip of the coastal zone 20 km long (the estimated distance traveled by juvenile salmon each day) using the settled volume data of Kendall et al. (1980) converted to g m^{-2} for a 50 m water column in both the coastal current and adjacent shelf/oceanic water (Table 1). The resulting stocks exhibit similar seasonal patterns in each domain, with the greatest biomass occurring in the summer.

Secondly, it is further assumed that the species composition of zooplankton in the shelf water changes with the season, and that this change is reflected in daily production rates. Under convergence conditions, March/April, the surface populations in and adjacent to the coastal current should be dominated by the large interzonal copepods. If 5% of the body weight per day is used as a measure of the growth of these copepods (Vidal and Smith, unpublished), a production value for the 20 km strip of coastal current can be estimated (Table 1). By midsummer, the reproducing biomass will be dominated by smaller copepods whose turnover could be on the order of one month or less (Paffenhöfer and Harris 1976). Applying a 30-day turnover time permits the calculation of a summer daily production. In the fall, the production will still be associated with small copepods augmented by an increasing euphausiid biomass (Kendall et al. 1980). I will arbitrarily use a 30-day turnover for this production calculation also.

Assuming initially that all the biomass present in the water intercepting the outer edge of the coastal current is incorporated, the cross-shelf input is always in excess of the *in situ* current production (Table 1). This later calculation is based on the observation that satellite tracked surface buoys, drogued at 35 m, cross the shelf in a landward direction at 4-5 km d^{-1} during the weak upwelling season (Royer et al. 1979). Thus, the daily input is equal to the standing stock of forage species in a volume 4 x 20 km and 50 m deep (Figure 6).

Table 1. Standing stocks, production, and input of zooplankton in the coastal current and adjacent waters compared with the estimated salmon consumption ≈ 22.5 x 10^3 kg d^{-1}.

	Sources			
	Coastal Current		Bordering Shelf	
Season	Stock,[a] g m^{-2}	Production,[b] kg d^{-1}	Stock, g m^{-2}	Input,[c] kg d^{-1}
Spring (Mar-Apr)	5.5	110 x 10^3	5.5	440 x 10^3
Summer (Jun-July)	22.0	293 x 10^3	31.0	2480 x 10^3
Fall (Oct-Nov)	6.0	80 x 10^3	5.5	440 x 10^3

[a] Wet weight, upper 50 m

[b] 20 x 20 km area; upper 50 m

[c] 4 x 20 km area; upper 50 m, assuming all input is retained in the coastal current

The question of the significance of these two sources of forage biomass for juvenile salmon can be properly evaluated only if the consumption demand of the fishes per linear distance in the coastal current is known. A crude approximation of this value can be calculated as follows. Assume one million juveniles pass a given location daily. Suppose further, these fish move approximately 20 km per day (Royce et al. 1968). At 150 g each, the overall stock of salmon in this portion of the coastal current becomes 150 x 10^3 kg. If these fish ingest 15% of their body weight per day (Godin 1981), the total daily consumption becomes $\sim$ 23 x 10^3 kg. As estimated above, both the *in situ* production and lateral influx of forage species is greatly in excess of this demand in all seasons (Table 1).

However, it has been demonstrated that not all zooplanktonic taxa serve equally well as food (Takagi et al. 1981). It is also unlikely that the entire cross-shelf daily transport of biomass will be incorporated by the coastal current. In view of these further constraints on the availability of forage biomass, the large excesses represented in Table 1 must be considered very liberal estimates.

If, for instance, the fraction of the production or input available is actually a function of (1) prey size and taxa, (2) the fraction obtained through competition, and (3) for the lateral input, the percent retained by the current, these additional fractions must be included in the calculation of forage availability versus *in situ* production and input.

In terms of selectivity, I expect the spring near-surface zooplankton community to be dominated in biomass by the large interzonal copepods, *Neocalanus* spp. This being the case, I will assume that 75% of the *in situ* current production and cross-shelf input could serve as food for salmon (Table 2). In the summer and fall months, the small copepod-dominated coastal system (*Pseudocalanus* and *Metridia*, plus others) will reduce the fraction available as food, perhaps by about

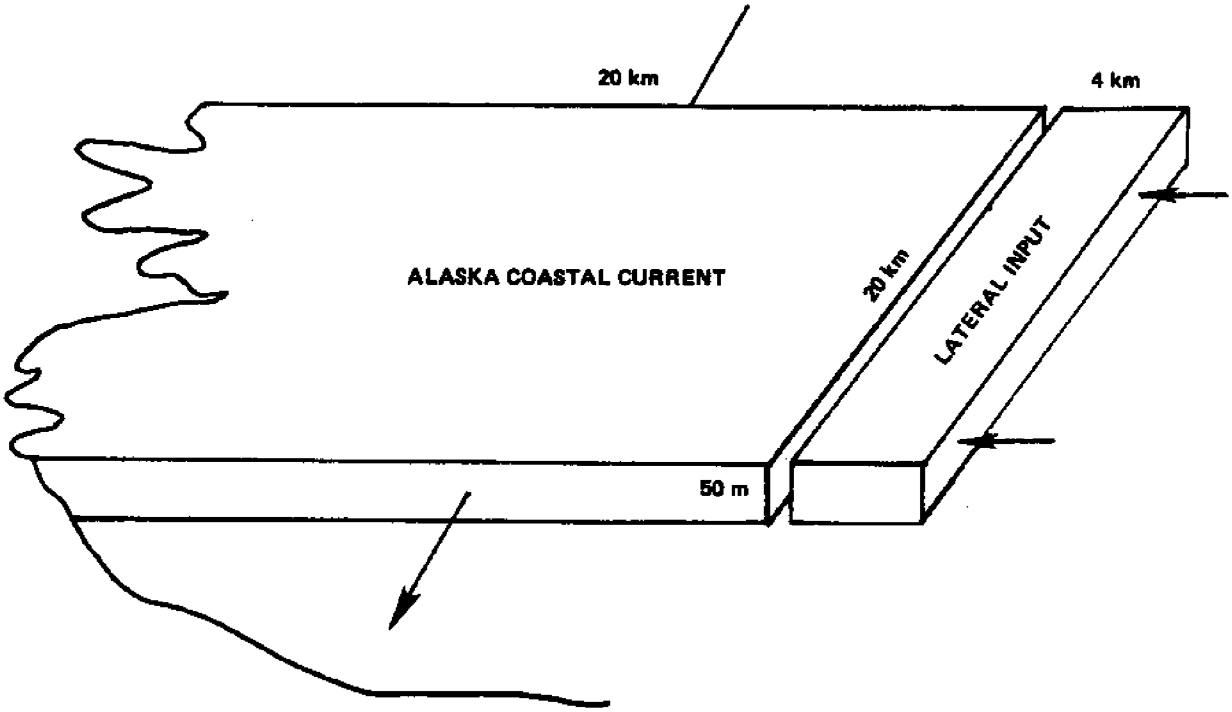

Figure 6. A diagramatic representation of the volumes used to calculate the estimated daily production of forage biomass in the coastal current and that introduced by lateral input (see Table 1).

Table 2. Estimates of the production and rate of input of forage biomass available to juvenile salmon through size/taxa selectivity and competition.

Season	Coastal Current Production kg d^{-1} Potential[a]	Selectivity[b]	Competition[c]
Spring	110×10^3	(.75) 83×10^3	(.20) 17×10^3
Summer	293×10^3	(.40) 117×10^3	(.10) 12×10^3
Fall	80×10^3	(.50) 40×10^3	(.10) 4×10^3

Season	Lateral Input, kg d^{-1} Potential[a]	Retained[d]	Selectivity	Competition
Spring	440×10^3	(.20) 88×10^3	(.75) 66×10^3	(.20) 13×10^3
Summer	2480×10^3	(.20) 496×10^3	(.50) 248×10^3	(.10) 25×10^3
Fall	440×10^3	(.20) 88×10^3	(.75) 66×10^3	(.10) 7×10^3

[a] From Table 1
[b] Fraction of the food of appropriate size and taxa
[c] Fraction shared through competition with other zooplankton feeders
[d] Fraction retained in the coastal current

50% of the spring value. The bordering shelf with developing euphausiid and amphipod biomass (*Parathemisto pacifica*) will exhibit a somewhat smaller decline in the fraction of the stock available as food in the summer.

In the fall, a return to convergence in the coastal zone will introduce juvenile euphausiids transported across the shelf to augment the small copepod community. Under these conditions I will assume the fraction of the introduced biomass or production available increases slightly at this time.

Kendall et al. (1980) report that pelagic larval fish are most abundant in the shelf and coastal waters near Kodiak during the summer months. I will assume that the competition for available food of the appropriate size and taxa is least in the spring when foraging salmon can obtain 20% (my guess) of the available food, and higher in the summer and fall when the young salmon share only 10% of the available food production.

The results of these serial calculations place the estimated daily consumption rate by juveniles ($\sim 23 \times 10^3$ kg d^{-1}) close to the combined food production through *in situ* growth and lateral input for the spring and summer seasons, 30×10^3 kg d^{-1} and 37×10^3 kg d^{-1} respectively. The combined fall value 11×10^3 kg d^{-1} is somewhat less than the consumption demand, although by this time (October-November) the peak of the migrating stocks has probably passed.

A final point involves the relative distribution of the rates of production and input as they might be reflected in the cross-shelf patchiness of food. If I assume that the lateral influx of stocks is confined to a strip 10 km wide along the frontal region (a generous estimate of the width of the front) and that the *in situ* production is uniformly spread across the current, the subsequent combined production and input in the outer 10 km is 2.5 times that of the adjacent 10 km strip landward in the spring, 3.0 times the adjacent production in the summer, and 4.5 times that of the rest of the current in the fall.

Thus, in all the seasons that juvenile salmon use the coastal current, a substantially higher proportion of the "production" of forage species could occur along the outer margin of the coastal current each day due to the cross-shelf supply mechanism described here.

Unanswered Questions

These admittedly simplistic pencil exercises are intended to point to missing information concerning the relationship between juvenile salmon and their food, relative to the Alaska Coastal Current. If it could be shown through field measurements that lateral flow associated with the coastal current is in fact responsible for enriching the nearshore zone in forage species, then oceanographic factors affecting this flow would presumably affect the year to year supply of food. Windy, calm, dry, or unusually wet conditions could influence the flow fields differently, and hence the food production and availability. In the spirit of predictability, these large-scale cause and effect relationships seem fruitful to pursue.

At present there is no information available describing the biological oceanography of the Alaska Coastal Current; the feature was unknown during most of the OCS studies in the northern and western Gulf of Alaska. The most recent work (Royer and Johnson, NSF-University of Alaska) on the physical oceanography has emphasized fine-scale hydrographic cross-shelf profiling and current measurements by season. A recently conducted continuous sonic survey across the shelf at Icy Cape, Alaska (Cooney, *Alpha Helix* Cruise HX 052), using a quantitative echo-integration technique at 200 kHz, encountered maximum estimated biomass in the outer edge of the coastal current (Figure 7). Daylight net tows (1-m net; 0.33 mm Nitex) in the upper 50 m contained insignificant numbers of small copepods and a few large pteropods. Midwater trawl samples (2-m Tucker trawl; 3.0 mm knotless nylon) taken at night contained large euphausiids and a few larval squids in the frontal zone of the current. Catches of these same large organisms were much reduced or absent in the current.

This latter observation may be important regarding the location of the outer edge of the coastal current relative to the shelf break. For many locations between British Columbia waters and northern southeast Alaska (Cape Spencer) the shelf is only about 20 nm wide, placing the outer portion of the coastal current quite near the shelf edge. It is here, because of sufficient depth that euphausiid populations occur in abundance. The availability of euphausiids as food, even restricted to short periods of time each day, might be extremely important, particularly late in the summer and during the early fall when the large interzonal copepods are absent from the shelf.

In summary, I suggest the following questions as relevant to determining the trophic importance of the coastal current habitat for juvenile salmon:

1. Do juvenile salmon demonstrate a strict preference for a coastal current habitat? Do they exit the current at specific locations.
2. What is the residence time of juveniles in the current? Do the juveniles swim with, against, or randomly in the current searching for food? What part of the water column is used by juveniles for feeding?
3. How are juvenile salmon distributed across the coastal current? Is there a relationship between location and size of fish.

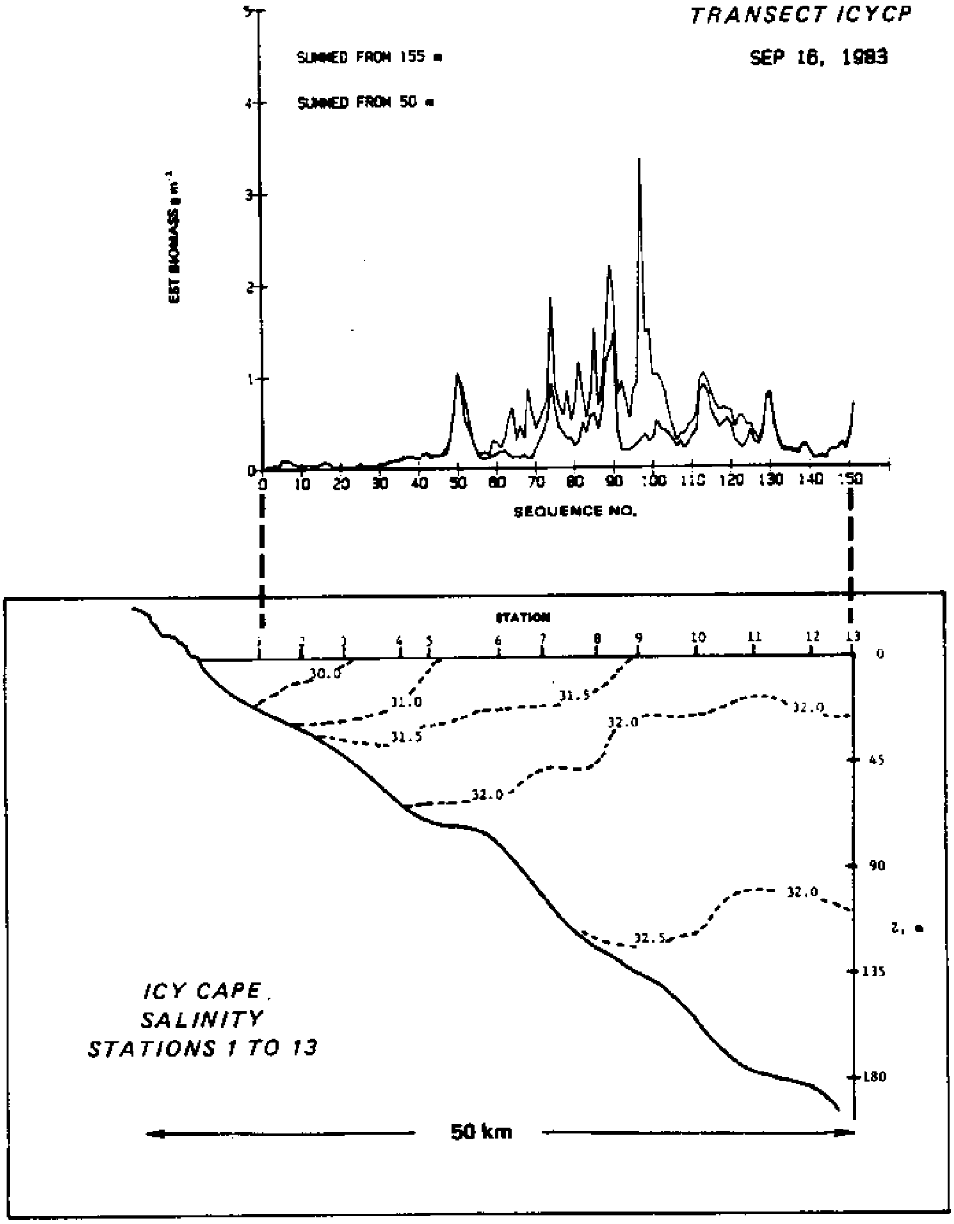

Figure 7. Cross-shelf salinity and acoustic estimates of biomass at Icy Cape, Alaska. (one acoustic sequence is 60 pings covering approximately 0.2 km of transect).

4. Which zooplankton populations serve as food for juveniles in the Alaska Coastal Current? How are these populations phased in their standing stock and production through the seasons, spring-fall?
5. What are reasonable production rates for salmon forage species occupying the coastal current? How do these rates change seasonally?
6. What fraction of forage species transported across the shelf actually enter the coastal current? How does the incorporation of food species change with oceanographic conditions in the coastal zone (i.e., convergence and divergence seasons)?

7. How important is the location of the outer edge of coastal current relative to the shelf edge for juveniles feeding in the current?
8. What are the major food species late in the season when surface shelf and ocean forage stocks are in low abundance?
9. Do high-density food stocks occur as a narrow band along the outer edge of the coastal current?

In my opinion, the coastal current habitat represents the next most tractable environment for salmon research. It is not surprising that many of the most recent studies have been carried out in the estuarine systems where both the salmon and prey are abundant and relatively easy to sample. If it can be shown that rapidly growing juveniles have a strict dependence on the coastal current system, its physical definition and biological characteristics are quite amenable to study. Compared with open ocean research, the coastal current environment seems particularly attractive.

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Comments on the Presentation by Cooney

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Attempts to increase the production of salmon through enhancement are proceeding in all major salmon-producing countries in the world. There is every indication that enhancement efforts will continue to expand in the future. For example, both British Columbia and Alaska have stated the intention of increasing present salmon production up to levels equivalent to historic levels (cf. Groot 1976, cited by Peterman 1978; Macleod 1977). This implies increases on the order of 2-4 times current production levels.

At this workshop we have seen ample evidence that there have been dramatic long-term trends in many characteristics of the oceans. There is also increasing evidence that such changes in the oceans can directly or indirectly affect the growth and/or survival of salmon and their food sources. This suggests that we should not automatically assume that the carrying capacity of the oceans for salmon is the same today as it has been in the past.

There is undoubtedly a finite limit to the amount of salmon that the oceans can support. If the production of salmon has already or will soon reach that limit any further enhancement would be futile. This provides a significant incentive for attempting to determine both the immediate and long-term carrying capacity of the oceans for salmon.

There is a wide variety of indirect evidence that can be cited when attempting to deduce whether the carrying capacity of the oceans is currently or has historically limited the production of salmon. However, in virtually every case where some data exist that appear to support the hypothesis of limited carrying capacity another source or type of information leads to the opposite conclusion. For example, it has been argued that salmon catches have historically been considerably higher than catches in recent years so that it is unlikely that current salmon production is limited by the food supply in the oceans. On the other hand there is convincing evidence of density-dependent growth and/or survival for at least some major salmon stocks (Peterman 1978; Peterman this workshop).

It could be argued that the various indirect indicators are actually proving of little value when attempting to assess the carrying capacity of the oceans for salmon. The obvious alternative is to devise some method of determining the carrying capacity directly. Not surprisingly however, this turns out to be an extremely difficult task due to our current ignorance about which factors actually control the carrying capacity of the oceans.

The amount of food available to salmon is one factor that may limit the amount of salmon the oceans can support. It is this aspect of the problem that Cooney has addressed for juvenile salmon off Alaska. Based on the calculations described in his paper, Cooney concludes that the addition of zooplankton to the coastal current by advection across the continental shelf may be an important source of food for juvenile salmon travelling in the coastal current. The data Cooney used in these calculations were derived from the literature and in a few cases from "best guess" estimates where no information is available.

In the interest of trying to assess the validity of Cooney's conclusions, I repeated his calculations using somewhat different data. Many of the values Cooney uses in the calculations are somewhat uncertain. Although Cooney states quite clearly how each parameter was chosen, he does not indicate how much the final results of the calculations would be affected had he chosen somewhat different values. Thus for each parameter used in the calculations I have attempted to extract from the literature two values that might reasonably be expected to represent the upper and lower limit for that particular value in the region of the Alaska coastal current. In some cases the range of values I identified are perhaps even more difficult to justify than the value chosen by Cooney for the same parameter. For example, the range of zooplankton biomass in the Alaskan coastal current I used is based on two sets of data--the first from samples collected at Station "P" during 1956-1964 (LeBrasseur 1965) and second from the Bering Sea and inner Bristol Bay during 1956-1970 (Motoda and Minoda 1974). I could not obtain a copy of the report Cooney used (Kendall et al. 1980) so the range of zooplankton biomass I used may not be the best available. For all parameters used in the calculations, however, the values chosen by Cooney fall within the range that I derived (Table 1).

By re-doing Cooney's calculations using the range of estimates for each parameter I obtained the following results: the total consumption of zooplankton by juvenile salmon in the coastal current would be 5,000-347,000 kg/day. The amount of food available to salmon in the coastal current would be 134,000-2,590,000 kg/day if the food available to salmon is not diminished by either competition or selectivity by the salmon feeding on the zooplankton. I was unable to derive alternative estimates for either salmon competition or selectivity from the literature. If I use the same values for these parameters that Cooney used (40-75% and 10-20%, respectively) the amount of food available to juvenile salmon in the coastal current would be 7,000-389,000 kg/day. All of these estimates are of the same magnitude as the estimated range of food required by the juvenile salmon. Given the uncertainty attached to each of the parameters used in the calculations, this suggests to me that the conservative conclusion is that there is probably sufficient food available for juvenile salmon within the coastal current and therefore no need to invoke advective transfer of zooplankton from further offshore. Although this differs from Cooney's conclusion, it still does not necessarily contradict the hypothesis that advection of zooplankton does in fact represent an important source of food for juvenile salmon in the Alaskan coastal current. It simply indicates the need for additional confirmation of the existence and importance of the advective transport of zooplankton.

A computer simulation examining early ocean limitation of salmon production in Georgia Strait also leads to the conclusion that ocean limitation of salmon production is unlikely unless only a small fraction of total zooplankton porduction is available to salmon (Walters et al. 1978). However, the authors also stated that the existing data were not sufficient to make firm predictions of ocean carrying capacity.

I suspect that this is perhaps the real purpose of Cooney's presentation--simply to emphasize how poorly we currently understand the factors controlling the carrying capacity of the oceans for salmon. Ted has again drawn our attention to the need for more effort directed at solving this problem. If this is not done, the carrying capacity of the oceans may ultimately be determined directly through rapidly diminishing returns from expanding salmon enhancement efforts. This will undoubtedly prove to be a very expensive method of obtaining the answer.

Table 1. Range and source of parameters used in calculations.

	Range of Parameter	Reference
Salmon:		
Total no.	0.5-7.7 x 10^6 day^{-1}	Hartt, 1980
Mean size	100-250 g	Hartt, 1980
Daily food	10-18% body wt. day^{-1}	Healey, 1980
Max. distance offshore	28-37 km	Hartt, 1980
Distance travelled each day	12-22 km	Royce et al., 1968
Selectivity	Unknown	
Competition	Unknown	
Zooplankton:		
Standing stock[a]	8-25 g m^{-2}	LeBrasseur, 1965 Motoda and Minoda, 1974
Production	3-14% body wt. day^{-1}	Fulton, 1973 Taguchi and Ishii, 1972
Depth[b]	10-75 m	Straty, 1974 Manzer, 1964

[a] Estimated standing stock from 0-50 m.

[b] Depth interval containing all zooplankton available to juvenile salmon.

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Variability of Estuarine Food Webs and Production May Limit Our Ability to Enhance Pacific Salmon (*Oncorhynchus* spp.)

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Abstract

The broad spectrum in physical and biological characteristics of estuaries along the rim of the northeastern Pacific Ocean coincides with equally diverse patterns of use by juvenile salmon. Although only a few data sets link abiotic and biotic conditions with juvenile salmon growth and survival, these studies and qualitative differences in estuarine residence times and food web relationships indicate that estuaries should not be assumed equivalent in terms of carrying capacity. Considerably more and perhaps dramatically different approaches to research will be required to quantify the functional relationships among juvenile salmon and important variables affecting estuarine contributions to net production of our Pacific salmon stocks. Any evolution of salmon management and culture strategies will be inhibited until we recognize the unique advantages and disadvantages of the region's divergent estuarine systems.

Introduction

Patterns of estuarine use among the five species of Pacific salmon (Oncorhynchus spp.) in the northeastern Pacific Ocean are extremely variable (see Healey 1980b, 1982b; Meyers and Horton 1982; and Simenstad et al. 1982 for reviews). However, intraspecific variation in the scope of estuarine use among different estuarine systems or over time series within estuaries is not well documented. Furthermore, the adaptive significance of different patterns of estuarine residence have seldom been considered in terms of the relationship between residence time and estuarine and marine survival.

Pacific Northwest estuaries are extremely diverse. A broad continuum of estuaries includes at least four general categories: (1) small coastal estuaries (i.e., Sixes River estuary) <10 km^2 in area which are often highly influenced by coastal marine conditions; (2) large coastal estuaries (i.e., Yaquina Bay and Grays Harbor) >25 km^2 which are more influenced by fresh water discharge but still have considerable intrusion by marine water low flow periods during the summer; (3) very large coastal (i.e., Columbia River estuary) and inland sea (i.e., Fraser River estuary) estuaries which are almost completely dominated by fresh water; and, (4) inland sea estuary-fjord systems (i.e., Nanaimo River estuary and Hood Canal). We would expect that within the limitations and capacities of the freshwater production systems, variability in both abiotic and biotic conditions among and within these estuaries should produce an equally variable spectrum of estuarine effects upon marine survival of salmonids. Unfortunately, changes in fresh water ecosystems, timing of entry of salmonids into estuaries, their estuarine residence, and marine production and survival have seldom been elucidated to estuarine factors.

This overview reviews our knowledge about juvenile salmonid use of estuarine habitats in the northeastern Pacific Ocean strictly in terms of the variability in production of juvenile salmon prey organisms and the diet composition of juvenile salmon in estuarine habitats. Other aspects of salmon use of estuaries (i.e., spawning) and related survival/mortality factors (i.e., predation) were not considered within the scope of this overview. Thus, our primary assumptions are that: (1) increased estuarine residence will enhance the scope for growth and survival of fish entering the nearshore oceanic environment; and, (2) the capacity of estuaries to enhance juvenile salmon production and survival varies among salmon species as well as the physical features and food web dynamics. Inherent in this argument are two aspects of variability: (1) system or among-estuary variability; and, (2) temporal or within-estuary variability. System variability is that associated with an estuary's intrinsic capacity to enhance salmonid production due to the estuary's unique physical and biological characteristics. As such, this source of variability can be considered deterministic. Temporal variability, on the other hand, relates to some climatic and other random (within the context of the salmons' life histories) events which affect an estuary°s capacity for production. This source of variability may be considered stochastic. We propose that system variability determines the upper limit to estuarine enhancement of total marine survival and that temporal variability determines the consequences of each salmon cohort's response within that prescribed "window" for survival. Estuarine use patterns of juvenile salmon, however, typically reflect integration of both sources of vari--ability, and they are difficult to separate. Although we will try to distinguish the effects of system variability in the following discussion, the results of temporal variability often complicate our interpretations.

Overview

Relationship Between Estuarine Use and Marine Growth and Survival

Much of the variation in estuarine use patterns originates from the genotypic variation in time and size of entry into the natal estuary. In general, smaller juvenile salmon such as pink (O. gorbuscha) and chum (O. keta) fry which immigrate directly from spawning redds to the estuary at 30 mm to 40 mm in size (FL) tend to maintain longer estuarine residence times than salmonid species which maintain some residence in freshwater. Extreme intraspecific variation is evident in the difference between chinook salmon (O. tshawytscha), which immigrate to estuaries as fry and may occupy estuarine habitats for six months to a year, and yearling smolts, which tend to migrate rapidly through the estuaries. Some underyearling chinook may, in fact, reside in estuaries and inland seas throughout their marine lives. Although some juvenile coho salmon may enter estuaries as fry, most migrate as yearling smolts and reside in the natal estuary for only a short period of time. Thus, chum and certain chinook stocks (e.g., those producing primarily fry as outmigrants, usually "fall" stocks) that have long residence times in estuaries would be the most vulnerable to estuarine variability. Salmonids that migrate rapidly to sea, such as pink, other chinook ("spring"), coho stocks which produce yearling (or older) smolts and sockeye salmon would be relatively less estuary-dependent.

Assuming that estuarine mortality is not proportional to estuarine residence time and that ocean mortality is size-dependent, increasing the size of the fish at ocean entry by increasing estuarine residence should produce higher ocean survival. However, we lack the data to test this idea. Quantitative documentation are inadequate for intra- and interannual variations in estuarine residence times, growth rates, and survival as they relate to subsequent marine survival rates.

Patterns of Estuarine Use

Despite these lacunae, the results of many studies indicate functional relationships between patterns of estuarine use and estuarine growth and survival. Some of the more pertinent examples include research conducted in the Sixes River estuary (Reimers 1973), Yaquina Bay (Meyers 1980; Meyers and Horton 1982), Columbia River estuary (Natl. Mar. Fish. Serv. 1981), Grays Harbor (Simenstad and Eggers 1981), Nanaimo River (Healey 1979, 1980a), Fraser River (Dunford 1975, Levy and Northcote 1982), Skagit River (Congleton and Smith 1977; Congleton 1978; Congleton et al. 1981), and Hood Canal (Simenstad and Salo 1982; Bax et al. 1980; Bax 1982, 1983). From these sources we can identify particular patterns of estuarine use which reflect direct effects of variability in estuarine carrying capacity upon salmon production.

Pink

Despite their numerical prominence in many rivers, the estuarine residence of juvenile pink salmon is not well documented, perhaps reflecting a comparatively rapid migration through estuaries.

Results of shallow sublittoral and neritic sampling of juvenile pink salmon in Hood Canal in 1978 suggested that fish immigrating into the fjord early in the outmigration period (February-March) outmigrated very rapidly (Bax et al. 1979). A very high proportion of these fry may have resulted from early hatchery releases of approximately $2\text{x}10^6$ fish. Sustained catches and increasing mean fish lengths later in the out-migration period implied longer residence times although a $0.5\text{x}10^6$ release of larger, reared pinks from the WDF Hoodsport hatchery complicates this interpretation.

Levy and Northcote (1982) indicated that juvenile pink salmon used marsh habitats of the Fraser River estuary less than chum or chinook salmon. Marked pinks were not recaptured in tidal channels after only two days into their experiments.

Chum

Grays Harbor is the only large coastal estuary (although see Healey 1982a for a description of chum out-migration in Nititat Lake) in which juvenile chum salmon outmigrations have been recently studied (Simenstad and Eggers 1981). Chum originating in the Chehalis River system emigrated into Grays Harbor somewhat earlier (January-March) than is the case for most other estuaries. Their progressive movement through shallow sublittoral habitats in the estuary was estimated to take two to four weeks. During this time their mean size appeared to increase approximately 3 cm, although this may be slightly overestimated because of the influx of hatchery-reared fish into the lower reaches in the estuary in the latter portion of the out-migration.

Congleton et al. (1981) estimated that juvenile chum salmon occupied their Skagit River salt marsh study area an average of between 1.7 and 4.0 days, and accumulated 4 to 5 mm FL growth during residence in the lower river and marsh. In the salt marsh habitats, dipteran adults and pupae (principally chirinomids) dominated the diet of the fish, supplemented by the amphipods *Anisogammarus confervicolus* and *Corophium salmonis*, the mysid *Neomysis mercedis*, and harpacticoid copepods (Congleton and Smith 1977; Congleton 1979). Feeding was most intensive during tidal inundation of the marsh flats, when the juvenile chum were presumed to prey upon chironomids attached to the marsh plants or substrate.

Healey (1979, 1982b) illustrated the potential importance of residence time of juvenile chum salmon in the Nanaimo River estuary. He interpreted his results to those of Sibert (1979), who related juvenile chum feeding to the availability and production of their preferred prey within the estuary. Healey and Sibert indicated that growth of chum fry in the estuary was greatest ($\sim$% body weight day^{-1}) during the middle part of the migration period, before a general decline in average stomach contents that occurred when the fry population reached maximum abundance in the estuary. Estuarine residence of juvenile chums in the Nanaimo River estuary was also shown to be closely tied to the population abundance of their preferred prey, e.g., the harpacticoid copepod Harpacticus uniremis, in that the principal emigration of the chums coincided closely with the decline in H. uniremis. Healey (1982b) later established that early marine mortality of Nanaimo River chum salmon was intense and size-selective over the size range 45-55 mm FL, the size range that juvenile chums typically emigrate out of the estuary and initiate neritic-feeding behavior.

Fisheries Research Institute's (FRI) studies in Hood Canal (Bax et al. 1979; Simenstad and Salo 1982; Bax 1982, 1983; C. Simenstad and R. Wissmar, Fish. Res. Inst., Univ. Wash., unpubl. data) provided an indication of the influence of physical and biological conditions in the fjord upon out-migrating juvenile chum salmon. Simenstad and Salo (1982) indicated that the migration rate of epibenthic-feeding fish <50 mm FL through Hood Canal may be inversely related to the relative availability of preferred epibenthic prey organisms. This argues that early out-migrants (i.e., those immigrating to the estuary in February-March) may have to travel more rapidly through Hood Canal to obtain an adequate daily ration than those which immigrate to the estuary when preferred food organisms were relatively more abundant (i.e. April-May). This implies that the total marine mortality rate is inversely related to the size of the juvenile chums when they leave Hood Canal. Koski's (1975) and Schroeder's (1977) unpublished data showing lower total marine survival rates for the earlier, short-residence out-migrant chums than for the later, lingering out-migrants may support this argument for limited prey resources during estuarine residence. Bax (1982), on the other hand, attributed seasonally variable out-migration rates of juvenile chum to passive movement in the surface water flow of Hood Canal, but in most cases he used data for larger (∿0 mm FL), more neritic-feeding fish. Thus, the residence time in Hood Canal of wild or unfed hatchery fish <50 mm FL may be determined principally by active behavioral mechanisms such as foraging success, while that of hatchery-reared fish or fish which have grown larger than 50 mm FL within the system appears to be influenced primarily by passive transport mechanisms.

Interestingly enough, the preferred prey of epibenthic-feeding juvenile chum salmon in Hood Canal and other parts of Puget Sound is also Harpacticus spp., the harpacticoid copepod prey taxa which Healey (1979) and Sibert (1979) found so consequential to juvenile chum salmon residence in the Nanaimo River estuary (C. Simenstad and J. Cordell, FRI, unpubl. data).

Interspecific competition with the highly variable occurrences and abundances of co-occurring juvenile salmonids may also influence the estuarine residence of juvenile chum salmon in Hood Canal. Gallagher (1979) and Washington Department of Fisheries (J. Ames, WDF, pers. comm.) data have indicated that total marine survival rates of Hood Canal chum salmon populations are statistically lower when juvenile chum and pink salmon co-occur (even-numbered years) as compared to when chum salmon out-migrate alone (odd years). Gallagher (1979) indicated that the depensatory interaction probably occurred within the estuarine environment, and Simenstad et al. (1980) have data showing extensive (∿5%) diet overlap between neritic-feeding chum and pink salmon of approximately the same size.

Among the three species of juvenile salmon using marsh habitats in the Fraser River estuary, Levy and Northcote (1982) determined the maximum residence time of marked juvenile chum was 11 days, intermediate between that of chinook and pink.

Coho

Apparently rapid movement through Yaquina Bay and the lack of increasing lengths indicated that wild juvenile coho do not reside within that estuary for any appreciable length of time (Meyers 1980; Meyers and Horton 1982). The residence time of hatchery (age-0) coho, however, was dependent upon the time of release, such that fish released early in the year (June) resided in the estuary for longer periods of time than fish released later (September-October). Most of the hatchery fish appeared to emigrate from the estuary within a month's residence time, but a smaller portion appeared to remain for up to three months. Meyers (1980) was able to fit a negative exponential model to the residence time decay pattern of the hatchery coho. Once the population had declined, the hatchery coho which remained in the estuary resumed a relatively high growth rate until they attained approximately 12 cm FL, at which time they either emigrated to the ocean or growth was suppressed.

Despite considerable variation in the time of release of hatchery coho into the Columbia River, peak immigration into the estuary of both hatchery and wild coho appears to occur consistently between May 6 and 16 (Durkin and Sims 1975). Residence time within the Columbia River estuary appears to be minimal, however. Dawley et al. (1981) and unpublished coded wire tag recovery data of the National Marine Fisheries Service (1981) indicate that residence time is generally a week or less as a result of average migration rates of 22-28 km d^{-1} (range 12-59). Dawley et al.'s (1981) data also implied some annual variation in the average migration rate; fish tended to move through the estuary more rapidly in 1978 and 1980 than in 1979.

Similarly, Simenstad and Eggers (1981) found rapid migration of coho smolts through Grays Harbor and little estuarine growth over the one to two months they occurred in the estuary.

Chinook

Reimers's (1973) detailed analyses of the scale patterns indicated that about 90% of the mature fall chinook returning to the Sixes River had reared about three months (June-August) in the estuary after rearing in fresh water for an equivalent period. Growth rates of the juvenile chinook in the estuary during this period appeared to be depressed at population levels greater than about 100,000 fish. Subsequent studies in the Sixes River and Elk River coastal estuaries in Oregon revealed that estuarine growth is a highly variable function of population abundance, temperature, prey composition and production, and rearing space. Growth to at least 12 cm FL before ocean entry was necessary, however, for acceptable marine survival (Reimers and Concannon 1977; Reimers et al. 1980; Reimers and Downey 1982).

One descriptive data set from ODFW (Herring and Nicholas in prep.) evaluates both inter-estuarine and annual variability in residence and growth of juvenile chinook (fry) in twelve estuaries along the Oregon coast. Sampling of juvenile chinook remaining in these estuaries at the end of the summer rearing period (September) provided indices of relative abundance (beach seine CPUE) and growth (mean length FL) between 1977 and 1982 which indicated low variations in growth within an estuary despite wide fluctuations in relative abundance. There was a definite relationship among estuarine rearing area (hectares of submerged habitat), relative abundance, and fish size, such that small fish in high abundance were found in small estuaries (<1000 hectares) whereas large fish in low abundance were found in large estuaries. However, the resulting density-dependent relationship between abundance and size in the estuary was highly variable from year to year. For instance, abundances were generally lower and fish larger in 1982 whereas abundances were higher and fish smaller in 1980 and 1981. Comparison of these data with information on the available spawning habitat and escapement in the estuaries' watersheds (A. McGie, ODFW, unpubl.) indicates that the estuary may be limiting the potential summer rearing production despite the potential freshwater production of chinook fry.

Dawley et al. (1981) reported that subyearling chinook migrated through the Columbia River estuary at an average rate of between 4 and 25 km d^{-1}. However, the pattern in annual variation did not correspond to that of the coho migration, since rates gradually increased from 1978 to 1980. As in other estuaries, the migration rates of co-occurring yearling chinook were always higher, averaging between 15 and 28 km d^{-1}.

The descriptive information on the out-migration of juvenile chinook (fry) from Grays Harbor (Simenstad and Eggers 1981) indicated residualization of a small proportion of the chinook entering the estuary. Although the lack of mark-recapture experiments precluded verification, the size demography of the subyearling chinook over their 27-week residence implied that rearing was occurring in the estuary and that the fish moved from shallow sublittoral habitats into neritic habitats as they grew larger. A more rapid emigration of larger juvenile chinook from the lower portion of the estuary in mid-summer was apparent, approximating the situation in the Sixes River estuary.

Congleton et al. (1981) estimated that subyearling chinook had mean residence times in salt marshes of the Skagit River estuary between 3.1 and 6.0 days, during which they grew between 6 to 7 mm FL. This potential growth differential and corresponding estimates of daily ration imply a growth rate of at least 6% of body weight per day.

Healey (1980a) determined that juvenile chinook occupied the Nanaimo River estuary approximately 25 days at densities of about 0.1 fish m^{-2}. Incorporating a disappearance rate of 11% to 12% d^{-1} of marked fish, Healey estimated the estuarine populations to range between 20,000 and 50,000 fish among the three study years (1975-1977). Although feeding conditions (weights of stomach contents) of juvenile chinook in the estuary appeared to be best during the year when the estuarine population was greatest, declines in stomach contents generally coincided with peak population densities. These data also indicated a progressive movement of juvenile chinook from in or near salt marsh habitats into deeper, more saline habitats during several weeks of the fishes' residence in the estuary.

Levy and Northcote (1982) also documented extended rearing (30 d maximum residence time of marked fry) and growth (to 70 mm FL) of juvenile chinook salmon in tidal channels of Fraser River estuary marshes.

Estuarine Production Supporting Juvenile Pacific Salmon

Although most of these studies of estuarine residency by juvenile salmon include description of their prey spectra and often specific aspects of their foraging behavior, few effectively relate prey resource production to fish residence time, growth, or other aspects of the estuary's "carrying capacity." Even in the detailed studies in the Nanaimo River estuary (Healey 1979, 1982b; Sibert 1979), annual variability in prey production or consumption rates by the juvenile salmon has seldom included more than two to three years. In addition, most research has been focused upon the selective foraging of juvenile chum and chinook (subyearling) salmon on epibenthic crustaceans (harpacticoid copepods, gammarid amphipods). Much less is known about the more more varied diets of neritic-feeding pink and chum >50-55mm FL, coho, and chinook >120 mm FL or yearling chinook, which are based more upon pelagic zooplankton. As a consequence, questions about estuarine carrying capacity for juvenile salmon has focused almost entirely upon the ecology of epibenthic-feeding salmon and their prey resources. As yet, there is little evidence of the production of such preferred prey affecting estuarine use by juvenile salmon. Predation by subyearling chinook salmon on *Corophium*, gammarid amphipods and chum and chinook on harpacticoid copepods provide two well-documented examples.

Subyearling Chinook Predation On *Corophium*

The relative importance of *Corophium* in the diet of subyearling chinook salmon and in the densities in three different coastal estuaries during approximately the same time span (1979-1981) are compared in Tables 1 and 2. Although densities of

Table 1. Relative importance of gammarid amphipods *Corophium* spp. in the diet of juvenile (subyearling) chinook salmon in Pacific Northwest estuaries.

Estuary	Sampling Design & Habitats	Sample Size, n	Fish Size (length, mmFL; weight, g wet)	Frequency of Occurrence (%)	Numerical Composition (%)	Gravimetric Composition (%)	% IRI*	Source
Sixes River	38-m beach seine; shores, beaches, and sandflats; 1980	562	53 - 122; ...	...	50 - 61	20 - 59	...	D. Bottom, ODFW, pers. comm.
Columbia River	200-m purse seine; channels	470	79.5 - 184.3; ...	4 - 67	5 - 60	1 - 60	...	Natl. Mar. Fish. Serv. 1981
Grays Harbor	37-m beach seine; shores of river and beaches and sandflats of estuary, Mar.-Oct. 1980	98	72.9 ± 18.1; 5.36 ± 4.45	26.5 - 40.8	0.54 - 0.96	1.48 - 2.97	1.05 - 1.16	Simenstad & Eggers 1981
Fraser River	channel nets; marsh tidal channels; 1979	280	45.1 - 45.4; ...	2.04 - 4.94	5.80 - 11.62	7.50 - 12.70	1.0 - 7.7	Levy & Northcote 1981

*IRI = Index of Relative Importance (see Pinkas et al. 1971)

Table 2. Density estimates (no. m^{-2}) of *Corophium* spp. in Pacific Northwest estuaries.

Estuary	Sampling Design and Habitat	Sample Size, n	Density (no. m^{-2})			Source
			mean	s.d.	range	
Sixes River	55.4 cm^2 cores; 9 replicates @ 3 sites, May 30-Sept. 10, 1979	216	12,351	10,789	2,125-33,671	Reimers et al. 1979
Columbia River	3.5 cm^2 cores; 5 replicates @ 3 salflat sites, monthly between Aug. 1980 and Sept. 1981	253	10,766	15,933	0-83,553	R. Holton, OSU (unpubl.)
Grays Harbor	4.1 cm^2 cores; 7 replicates @ four tidal elevations at 2 sites, biweekly March 12-May 28 & Aug. 1-Sept. 26, 1980	343	6,600-13,300	...	216-49,675	Albright & Armstrong 1982

Corophium are extremely variable both seasonally and within the estuaries, average densities were about the same order of magnitude in the Sixes River estuary, Columbia River estuary, and Grays Harbor. Despite this seemingly ubiquitous availability of Corophium, foraging on them by subyearling chinook differed greatly, from extensively in the Sixes River estuary to marginally in Grays Harbor; Corophium consumption in the Columbia River estuary changed dramatically over time but often accounted for over 50% of the diet in all aspects (National Marine Fisheries Service 1981). These differences could be related to any one of a number of system or temporal factors, including differing availability of alternative prey, physical constraints (i.e., light, turbidity) upon foraging success, or short-term availability of the amphipods.

The occurrence and distribution of Corophium can be affected by both physical and biological factors. Corophium salmonis sampled in Grays Harbor by Albright and Rammer (1976), Herrmann et al. (1981), and Albright and Armstrong (1982) showed wide variation in densities, both annually at the same site as well as spatially at the same time. Much of this variation could be attributed to the ephemeral occurrence of fine mud (primarily silt and clay) sediments. Albright and Armstrong (1982) also attributed a general trend of decreasing C. salmonis densities with decreasing tidal elevation across the littoral flat to predation pressure. Monthly sampling of Corophium at three littoral flat locations in the Columbia River estuary (R. Holton, OSU; unpubl. CREDDP data) also illustrated extremely different density patterns over time, which may be related to predictable trends such as river discharge and associated salinity intrusion as well as more stochastic events such as sediment erosion or deposition.

Reimers et al. (1979) interpreted trends in abundance and population dynamics of Corophium in the Sixes River estuary to be the result of seasonally variable changes such as salinity, the size and shape of the estuary, sediment composition, river discharge, and the direction and intensity of onshore winds. Of particular importance was the variable occurrence and magnitude of the sand sill at the mouth of the estuary, which they suggested promotes increased productivity as a result of nutrient enrichment, reduced flushing, and warmer temperatures. However, the sill can produce negative effects by depressing dissolved oxygen, which can produce Corophium mortalities under extreme situations (Reimers et al. 1979). Changes in the densities and dominance of C. salmonis and C. spinicorne in different parts of the estuary were also attributed to temperature and salinity stratification resulting from the sill. Thus, general productivity of the Sixes River estuary for Corophium, the principal prey resource of juvenile chinook over the summer, is ultimately dependent upon the occurrence of coastal upwelling and the extent of sill development.

Studies by Dan Bottom (ODF&W, contained in Reimers et al. 1979) have indicated that only a small fraction, <0.1-2.5%, of the Corophium estimated to exist in the sediment may actually be available to foraging salmon, amphipods walking on the substrate, partially visible in their tubes, or freely swimming. More important, his data fail to show any relationship between the number of Corophium available and Corophium density in the sediment. Furthermore, the availability of Corophium may also be affected by the "splayed" defensive posture of adult amphipods, which may limit the successful ingestion by small fish.

Juvenile Chum and Subyearling Chinook Salmon Predation On Harpacticoid Copepods

Epibenthic harpacticoid copepod assemblages have been assessed in several estuaries (Table 3) where predation on them by juvenile chum and subyearling chinook salmon is also highly variable. Harpacticoid densities in littoral flat and shallow sublittoral slope habitats of the Columbia River estuary have been estimated to average ∿8,370 m^{-2} and to range over 200,000 m^{-2} at peak abundances. Extensive food habit studies by the National Marine Fisheries Service (1981), however, failed to indicate any significant predation upon harpacticoids by juvenile salmonids occurring in that estuary during twelve months' sampling.

Juvenile chum salmon in Grays Harbor were found to prey almost exclusively (64% to 91% of total IRI until late April 1980) upon epibenthic harpacticoids during most of their residence in the estuary (Simenstad and Eggers 1981), while harpacticoids comprised less than 1% of the IRI in the prey spectrum of subyearling chinook in the same habitats.

Foraging upon epibenthic harpacticoids by juvenile chum and subyearling chinook is prevalent in inland estuaries of Puget Sound and the Strait of Georgia. During the peak of the 1975 out-migration through the Nanaimo River estuary, harpacticoids composed >80% of the chum fry diet (Healey 1979) and were important in the diet of subyearling chinook during March and early April. A variety of harpacticoid density estimates exist for the Nanaimo River estuary littoral flat: between 53.3 and 159.2 m^{-2} using an epibenthic sled (Sibert et al. 1977); 24,500 m^{-2} using an epibenthic sled (Sibert 1979); and, between 32 and 2,800 m^{-3} using an epibenthic pump (Sibert 1981).

Given that juvenile chum salmon forage on specific species and sizes of harpacticoid copepods, total harpacticoid densities do not reflect the prey resources actually supporting juvenile salmon production. For example, Sibert (1979) estimated an average density of only 630 m^{-2} for *Harpacticus uniremis*, the prevalent harpacticoid prominently preyed upon by juvenile chum in the Nanaimo River estuary; *Harpacticus* wasn't even listed in his later epibenthic pump samples (Sibert 1981). Simenstad et al.'s (1980) estimates of the density of harpacticoids in the preferred prey size range of juvenile chums in Hood Canal (i.e., >0.75 mm total length) ranged between 950 m^{-2} (late June) and 9,300 m^{-2} (late March) during the 1978 out-migration, but *Harpacticus uniremis* was never prominent in their epibenthic pump samples (C. Simenstad and J. Cordell, FRI, unpubl. data). Sampling of shallow sublittoral habitats of central Puget Sound has indicated that densities of harpacticoids important in the diet of juvenile chum in the region (*Harpacticus* spp., *Tisbe* spp.) average 400 to 750 m^{-2} (C. Simenstad, FRI, unpubl. data). Observations during some of our current experiments have further shown that *Harpacticus* is specifically associated with eelgrass (*Zostera marina*) beds and may swarm in the canopy formed by the eelgrass blades.

Discussion

Thus, although estuaries of this region are obviously diverse, at this point we have no data to directly compare their capacities to enhance the total marine survival of salmon. But obviously both the composition and standing stock of prey resources available to and used by juvenile salmon in estuaries vary considerably. As indicated by Herring and Nicholas (in prep.), system and temporal variation in salmon use and growth within different estuaries is highly variable, although the mechanisms determining the trends may be basically the same among estuaries with similar physical and biological characteristics. The basic problem is that, although the physical differences may be obvious, we do not understand the biological mechanisms responsible for producing variable survival during or subsequent to estuarine residence. Our examples of the potential variability in standing stock of epibenthic prey resources and relative prey availability is just one aspect of estuarine factors which may influence variability in juvenile salmon survival. Although the contrasts in potential prey availability and their representation in salmon diets are tenuous, they represent some of the only comparable information available. In comparison, the data on pelagic and neustonic prey used by juvenile salmon (i.e., calanoid copepods such as *Calanus* spp., hyperiid amphipods such as *Parathemisto*, and insects) are almost nonexistent. Similarly, the production and availability emergent insects (i.e., chironomids) fed upon by juvenile salmon in salt marsh habitats are poorly understood.

Factors affecting or contributing to secondary production in these systems could include the nutrient and organic matter concentrations of freshwater discharge, surface area of wetland and seagrass habitat, water column stability and transparency, temperature regimes, and extent of ocean water intrusion and mixing. In addition, other characteristics of estuaries probably influence the ability of juvenile salmon to effectively exploit their preferred prey, e.g., foraging efficiency and rate of encounter are affected by water transparency and metabolism and consumption rates are influenced by water temperatures. Therefore, estuarine use patterns by juvenile salmon are expected to be different among systems which have significantly different turbidity and temperature regimes.

The role of density-dependent estuarine mortality is generally an unknown factor which may negate the influence of variability in salmon prey resource production or availability. The estuarine mortality rate can be influenced by both physical (i.e., river discharge) and biological (i.e., predator population) characteristics which differ among systems as well as temporally. Unfortunately, we have yet to uncouple these factors from those related to prey availability. This is understandable, given how interrelated they can be. For instance, water turbidity is a highly variable characteristic among estuaries and seasonally. Turbidity can limit prey resource production through regulation of primary production (i.e., phytoplankton, benthic diatoms, macroalgae) and limit the juvenile salmons' foraging efficiency by reducing the effective visibility of preferred prey. Conversely, turbidity can also limit the efficiency of visually-feeding predators upon juvenile salmon.

In light of the many confounding factors influencing estuarine carrying capacity effects upon the growth and survival of juvenile salmon, we believe that more research efforts and funds should be directed toward elucidating important functional relationships among the fish and their prey and predators. Simple data sets such as mortality and migration rates in estuaries under variable system and temporal conditions are still required. The variability in sources of organic carbon to estuarine food webs that support juvenile salmon also needs to be examined. Even the ability, tendency, and metabolic cost of prey switching must be evaluated under controlled experimental conditions before the importance of variable prey resource production can be determined. We will be unable to assess the role of estuarine carrying capacity for juvenile salmon until we understand why specific taxa such as Harpacticus and Anisogammarus are selected as prey and the consequences of their absence or decreased abundance or availability. However, such a reductionist approach will be useless unless the results are used to develop hypotheses which can be experimentally (i.e., manipulation) tested in the estuarine environs, under the influence of natural variability. If properly designed, such experiments should be directly applicable to evaluation of proposed salmon enhancement programs and improvement of existing programs.

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Commentary: Progress in Attempts to Test the Null Hypothesis that Juvenile Salmonids Aren't Dependent on Estuaries

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Introduction

Simenstad and Wissmar's (S and W) paper has opened Pandora's box on current concepts, themes, and difficulties associated with research on juvenile salmon in estuaries. We should be grateful to S and W for drawing attention to many important problems and issues. For example, what evidence is there that mortality is minimal in estuaries compared to in alternative habitats? There isn't much, but inferences are strong for wild stocks of certain species. The problem is symptomatic of the difficulties of rejecting the null hypothesis that juvenile salmonids aren't dependent on estuaries. Unfortunately many subhypotheses need to be tested before we can relate estuary use to total mortality.

If a concerted and coordinated effort is to be launched in the northeast Pacific to evaluate the importance of estuaries to salmonid production, first of all a common vocabulary has to be established. A lexicon is needed similar to what is available for life history stages of the fish. Researchers from California to Alaska need to agree on usage. For example, S and W call all of Hood Canal an estuary whereas others might view it as a series of estuaries separated by segments of marine foreshore. The difference is not trivial if estuaries are going to be considered recognizable units that can be evaluated without effects of confounding habitat types. A river on the east coast of Vancouver Island (Big Qualicum) does not have an embayed estuary but opens onto Baynes Sound, a water body freshened by dozens of small creeks. Big Qualicum is often considered as an example of a highly productive (now almost all hatchery fish) chinook system that doesn't have an estuary but wild fish may have been using the brackish shorelines of Baynes Sound.

Another ubiquitous issue is the difference between hatchery and wild stocks. Where hatcheries have been operating for at least the return time of a particular species, there may have been interbreeding of naturally reared fish and fish that have been exposed to hatchery conditions. This might not be critical for species such as chum with "flexible" life histories. However, for chinook, whose three major life history types ("ocean-type" fry, 90 d fish, stream type) may be genetically distinct such interbreeding may be crucial.

Review

My review of the paper follows S and W's text fairly closely, focussing on certain passages which I hope are not lifted too far out of context.

"Increased estuarine residence will enhance the scope for growth and survival of fish entering the nearshore oceanic environment."

This assumption has not been adequately challenged by S and W and must be tested for each species and life history type within a species. There are important exceptions. In small, restricted estuaries (e.g., Big Qualicum, see above) simultaneous releases of hatchery coho smolts and hatchery chum fry can result in major mortality for the chums. If one of the species had totally bypassed the estuary, the predation would be avoided. Bird predation is also obviously minimized if hatchery fish (smolts or fry) leave an estuary rapidly (Mace 1983a). The situation for chinook wild stocks which are generally smaller at the same time may be very different, since they use shallower water where natural cover is usually available.

"System or temporal variability"

The physical characteristics of estuaries in fact are stochastic, and perturbations may become more frequent as man-made changes (logging, dams, urbanization) in watersheds proceed (e.g., Onuf et al. 1983). Whole portions of estuaries may be created or destroyed in a very short time frame. Some authors think estuaries are ephemeral; others don't. One thing is certain -- many estuaries are being filled in or disrupted. Certain types of habitat within an estuary (e.g.,sandflats) may be more ephemeral than others such as marshes.

"Capacity of estuaries to enhance juvenile salmon production and survival varies among salmon species as well as the physical features and food web dynamics"

There is no question about this, but the range of maximum densities, at least for wild stocks, may be set. For example, I collated beach seine data for a number of B.C. estuaries and found that most of the chum and chinook densities ranged between 0.1 and 0.9 fish m^{-2} (Table 1). The data are from widely different types of estuaries ranging in size from very large (>2000 ha: Fraser) to small (<20 ha: e.g., Cayeghle Creek, west coast of Vancouver Island). The total population sizes obviously will be greater in bigger estuaries, but there is an implication that secondary production supporting the fish might be similar.

It may be difficult to enhance juvenile salmon "throughput" when these densities are exceeded, even for short periods of time, without perturbating the preexisting natural system.

"Quantitative documentation are inadequate for intra- and interannual variations in estuarine residence times, growth rates, and survival as they relate to subsequent marine survival rates"

In addition to the effort and costs of mark-recapture experiments there is the matter of obtaining sufficient fish, especially for long term marks (e.g., CWT) on wild fish. If fish from fresh water are used, that is in the river above the estuary, sometimes enough can be caught using traps as did Healey (1980).

Presmolt fish are probably less susceptible to handling and marking stress (Strange and Kennedy 1982), and this is another advantage of working with small fish in fresh water. Argue et al. (1979) and Armstrong and Argue (1977) tried to collect sufficient wild chinook for a marking experiment at Cowichan Bay, east coast of Vancouver Island, but encountered difficulties because the fish were dispersed, not abundant and smolted up. Chinook in fresh or very brackish water may be more taggable but if wild stock fry are used, half-length CWTs may have to be used. This type of tag is routinely used on small hatchery chinook in the Sacramento system (Kjelson, et al. 1982).

Efforts are required to involve hatchery managers and production biologists in experimental manipulation of specially marked groups to test for habitat effects. With proper care and handling, there need not be major loss of production to the fishery, except for returning adults which might stray, presumably because of imprinting problems. Transport of fish need not result in mortalities. Chinook smolts have been transported from a hatchery at Red Bluff, California, on the headwaters of the Sacramento River, to San Francisco Bay (Kjelson et al. 1982) and show better survival (to ocean fisheries, at any rate) than those that must transit the lower reaches of the river (upper estuary). Presumably this is because the river is characterized by some substandard habitat or some feature leading to increased mortality (e.g., sculpin predation, Patten 1971). Chinook fry moved to San Francisco Bay (lower estuary) showed much lower survival rate than those planted in upper estuary and upper river habitats.

"Patterns of estuarine use"

S and W's review of literature requires expansion to cover certain species' specific and regional quirks. However, the major studies have been covered or at least referenced.

Pinks

Pink fry do not use estuaries extensively, and so presumably osmoregulation is not a problem as estimated by early physiological work (e.g., Hoar 1951). But feeding does occur in rivers and estuaries, and the first feeding after yolk-sac resorption may be critical. Use of shallow water along marine shorelines by pink fry was apparently first described by Gilhousen (1962). Use of shallow water along marine foreshores has been documented in B.C. (Healey 1980; Godin 1981) and Alaska (Jaenicke and Bailey 1983). The latter authors have ascribed importance to physical features associated with milling and migration habitats along beaches. Shoreline use may be significant in avoiding predation by large salmonids since larger fish are usually found in deeper water (e.g., Levings 1982).

Evidence from the northwest Pacific indicates considerable regional variation in pink growth in the coastal zone (Shershnev et al. 1982). Near Iturup Island the first scale circulus was initiated at about 70 mm whereas at Sakhalin Island the circuli were shown on fish as small as 44 mm. The authors suggest regional differences in food are responsible.

Estuaries in Alaska may be important spawning habitats for pink (Helle et al. 1964). This may be an example of obligatory use of estuaries for salmonid production, although further work is required to establish that estuarine spawning is a "first choice."

Chum

Chum fry may require exposure to brackish water for a short but finite period of time, possibly only a few hours. In situ observations in a Japanese estuary (Iwata et al. 1982) showed that chum fry were aggregated at the halocline and the authors suggested this behavior was required to complete smolting.

S and W's conclusion that migration rate of chums is inversely related to size in Hood Canal contradicts information from other salmonids. Smaller chums use shallow water and hence are more dependent on nearshore food than larger fish. They may also aggregate along shorelines to avoid predation by larger fish or to be in a more passive environment for feeding. Nearshore food is more diverse and is probably presented in a less pulsed manner through time than neritic crustaceans (e.g., calanoids). If emigration was a volitional response to food density I would expect the larger chums to migrate faster. In addition, is it realistic to assume that larger fish (>50 mm) are more susceptible to passive transport than smaller fish?

As with pink, protection from predation may be particularly important for this species. As mentioned above, coho are known predators on chums in estuaries. Chum predation in estuaries by staghorn sculpins (Leptocottus armatus) may be buffered by high abundances of a common gammarid amphipod (Eogammarus confervicolus) (Mace 1983b). Using intertidal experimental enclosures, Mace was able to show that decreases in amphipod abundance resulted in sculpins shifting to chum as prey. There may be more of these indirect benefits from maintenance of intact invertebrate communities.

Like pinks, chums also spawn in estuaries. In B.C. this is known from numerous localities including Carnation Creek on Vancouver Island (Scrivener and Brownlee 1982) and Kimsquit on the central coast of B.C. For these stocks of chum, estuaries may be essential.

Coho

It is generally acknowledged that coho smolts move to an offshore neritic habitat quite quickly and wild stock smolts presumably use estuaries only to a limited extent. Avian predation on hatchery coho smolts released into small estuaries can be severe, as mentioned above (Mace 1983a). As with most other species, larger individuals are found further offshore over deeper water (e.g. Levings and Kotyk 1983), presumably reducing predation on pink and/or chum fry inshore.

The coho issue in B.C. and possibly Alaska is survival of coho fry in estuaries. Coho are less abundant in surveys of B.C. estuaries compared to chinook and chum (Table 1). In some estuaries (e.g., Carnation Creek -- Tschaplinski 1982; Yakoun River -- Stockner and Levings 1982) there is some evidence of growth resulting from estuarine use. The prevailing thought is that these "surplus" fish are forced out of the streams (Mason 1975) and die at sea because of osmoregulatory problems. The evidence for mortality of these fish is weak and is primarily based on examination of adult scales from the commercial fishery. Pritchard (1936 cited in Hoar 1951) found that 22 (0.35%) out of 6312 adult coho examined had left fresh water as fry or underyearlings. Some scientists have suggested that fry might be salvaged and grown in ponds to augment production of stream-reared fish.

Chinook

I support the idea generated from the ODFW data set which indicated low fluctuations in estuarine growth despite wide fluctuations in relative abundance. A similar pattern has been observed at the Campbell River estuary when 1982 (high density) and 1983 (low density) growth data for wild chinook were compared (Levings, McAllister, and Chang, 1984). Year-to-year differences in growth may not be related to density in the system, and "stochastic" features such as temperature may override biological interactions, as recognized by S and W.

Density-dependent growth suggests competition for food. Few data are available concerning trophic relationships of hatchery and wild salmon in almost all habitats, so conclusions on this topic are very tenous.

The notion that small fish are found in small estuaries is not borne out by data from B.C. Chinook fry show constancy in size (April-May) when huge estuaries (e.g., Fraser) and relatively small ones (e.g., Campbell) are compared. The length (and growth) data for the 90-d and stream-type fish in estuaries, however, may be more variable. In addition, separating fry from the latter two types is difficult, especially late in the season when lengths begin to overlap. Available data suggests there is only one estuary in B.C., namely Squamish, where chinook fry appear to be totally absent (Levy and Levings 1978). Where unmarked hatchery fish are released, length separation becomes even more complicated.

Estuarine production supporting juvenile Pacific salmon

Is it possible to "effectively relate prey resource production to fish residence time, growth, or other aspects of the estuary's carrying capacity?"

It is probably naive to expect any reasonable correlation between the production of one species of prey and a fish unless the fish shows an extreme loyalty to one particular prey item or has only one available. This may be true for chinook at Sixes River where only Corophium is eaten and possibly for chums at Nanaimo and Hood Canal where only Harpacticus uniremus is used. At almost every other estuary there is considerable variation in diets when prey species composition is examined, indicating that fish are opportunistic. In many estuaries it is unrealistic to take a completely reductionist stance and laboriously compute the production of all the major species used as prey by juvenile salmonids.

However, there are important features of the prey that are independent of taxonomic classification, e.g., size, dependence on estuarine conditions or detrital foodwebs, and availability in a particular part of the water column. Biochemical features (e.g., vitamins) in certain prey species may be relevant to major life history changes such as smoltification. Each of these possibilities harbor sub hypotheses of a basic ecological nature, not necessarily related to fisheries science. The final answer on estuarine trophodynamics and salmon production may be a long time coming and may derive from another group of animals.

Research suggestions

Pave over an estuary

To test the null hypothesis that estuaries are unnecessary people have suggested destroying one to watch what happens. This of course has already more or less happened to many of our estuaries but unfortunately the critical data on changes in fish population dynamics have not been measured simultaneously. Often physical and vegetational changes are measurable (e.g., using charts and aerial photos), but corresponding data at higher trophic levels are not. Destroying an estuary is possibly feasible as an experiment at a small estuary used by chum. However, there are some other limitations to this approach. Unless flows were somehow directed to an underwater diffuser, the surface fresh water would still disperse and possibly the "transition zone" would be widened so fish would still have a "portion" of an estuary left, namely the brackish layer/salt wedge microhabitat. The significance of selected elements (e.g., brackish marshes) might be tested. CWT or similar marks would be needed to determine marine survival.

Open up or restore an estuary

This approach could be considered the converse of the above but is not as refined statistically or philosophically. There can be no null hypothesis unless flows are manipulated experimentally. This type of approach might be feasible at small estuaries where controlled dyke breaching (e.g., Englishman River in B.C., Tutty and Raymond 1980) is possible. At the Englishman, chum spawning and rearing habitat has been created, so production has been increased. At the Campbell River estuary, man-made islands are now producing fish food and being used by wild juvenile chum and chinook (Levings, McAllister and Chang, unpublished data).

Restoration or loss experiments require controls for both temporal and habitat effects. Extensive data series are obviously required to do proper experiments.

Model an estuary

A reductionist approach to the problem is the correct ecological strategy, which has the tremendous potential of predicting incremental change and effects of loss of production in various components. But no one has linked the loss of production in an ecological sense to the loss of production in a stock or population dynamics sense. J. Sibert and D. Moore developed the Nanaimo Estuary Management model which enables prediction of what happens to chum fry growth when carbon production from eel grass, POC from the river, and algae were changed, using

Harpacticus uniremus as an intermediary. Unfortunately the utility of the most important carbon source, namely the river, is not that well understood. Recent carbon isotope results show that POC from the river may not be as important as previously believed (Wissmar and Simenstad 1983).

Studies of prey production must be more highly focussed than they are at present. Unfortunately standing crop is usually measured in extensive surveys and very few projects study an area intensively enough to obtain production data. Scientists concerned with the pelagic environment have been able to focus on a few major species used by juvenile salmonids (see Harrison et al. 1983). In estuaries and nearshore environments the suite of potential prey species is much larger, and the production of important prey items can vary markedly over short, medium, and long scales of time and space. For example production by *Eogammarus conferivolus* was significantly different in habitats differing by <50 m at the Squamish estuary (Stanhope 1983).

Experimental transport of fish to test the signficance of particular habitats

This technique has been used at the Sacramento system in California (Kjelson et al. 1982; see above also). Chinook fry and smolts are transported by truck and released into river, estuarine, and coastal habitats, bypassing selected habitats. The groups are uniquely marked so that mortality rates associated with the different habitats can be determined.

A similar experiment was performed at the Campbell River estuary, B.C., in April 1983. Hatchery-reared chinook smolts (3-4 g) were moved by helicopter (with equalized flight times) to four habitat types (river, transition, estuary, marine). Released fish were tracked by beach seine for several weeks, and cage studies were conducted for about a month. SCUBA observations were made at the marine site (Deepwater Bay), considered the critical location (Figure 1).

Tests such as these provide information on the following major topics or pertinent to estuarine use by juvenile salmonids, namely, osmoregulation, predation, stress, and feeding. Releases to the marine site are to simulate a situation where an estuary has been totally removed and fish are moved directly to "fully oceanic" conditions. Obviously the effects of the four aforementioned factors are interactive, and inference will be required to interpret results. However, with careful selection of fish size and monitoring of conditions (e.g., food levels) well-designed experiments could unravel the important relationships and sources of mortality.

Preliminary results of the Campbell River experiments are given elsewhere (Levings et al. 1984). They are summarized below:

1) Osmoregulation -- fish were ready for sea as judged by seawater challenge but may have completed smoltification after release at Deepwater Bay.
2) Predation -- buffalo sculpins (*Enophyrs bison*) and Bonaparte gulls (*Larus philadelphia*) were observed preying on chinook at the marine site. The gulls were aggregated at the release site for a fortuitous herring spawn event. No predators were observed at the estuarine or transition marine sites.
3) Stress -- investigations of cortisol levels and kidney cell diameters showed that fish held in cages at the marine site showed the most evidence of long term stress and this was the only location were mortality was observed (total of 9% over the first 8 to 10 d only). SCUBA observations at the release location showed fish were disoriented upon release but did school up and aggregate along shorelines and structures.
4) Feeding -- some chinook started feeding at both marine and estuarine sites within a few minutes of release. However, those recovered at the estuary showed a lower proportion of empty stomachs, indicating more fish reinitiated feeding at the estuarine zone.

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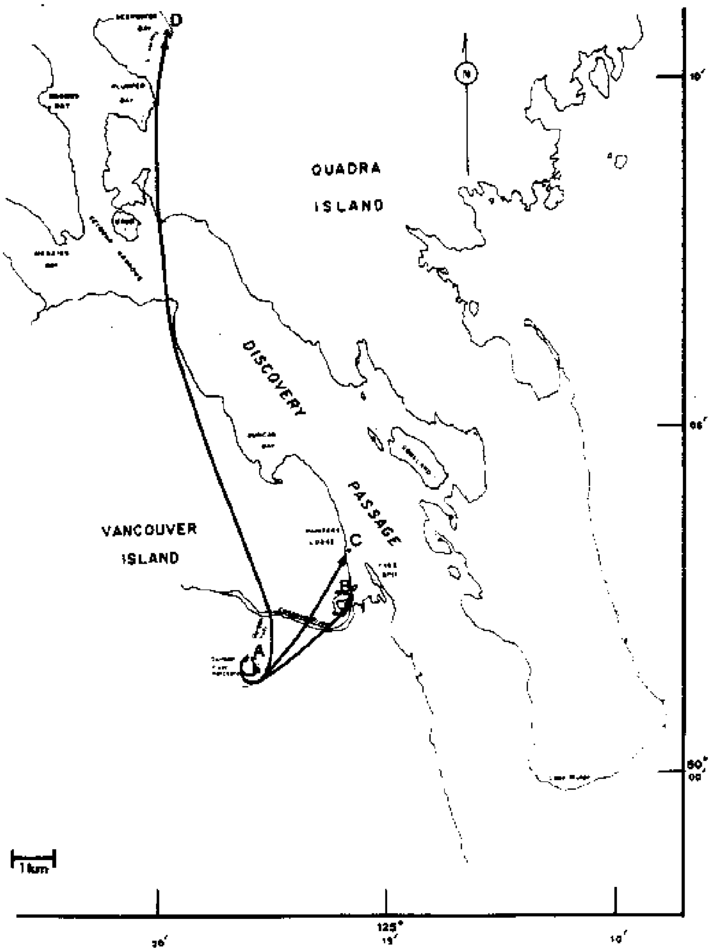

Figure 1. Locations where marked chinook were released into contracting habitats near the Campbell River estuary, B.C. A - river release (Quinsam R.); B - estuary zone release; C - transition zone release; D - marine zone release.

Table 1. Density ranges and number of estimates of densities for juvenile chum, chinook, and coho in 16 B.C. estuaries. Standardized beach seine data were assembled from papers, reports, and unpublished material, all reporting data obtained between1970 and 1982.

A. CHUM (n = 16)

DENSITY RANGE (m^{-2})	NUMBER OF ESTIMATES IN RANGE
0.01 to 0.09	1
0.1 to 0.9	12
1.0 to 1.9	3

B. CHINOOK (n = 16)

DENSITY RANGE (m^{-2})	NUMBER OF ESTIMATES IN RANGE
0.01 to 0.09	3
0.1 to 0.9	10
1.0 to 1.9	3
>2.0	

C. COHO (n = 7)

DENSITY RANGE (m^{-2})	NUMBER OF ESTIMATES IN RANGE
0.01 to 0.09	3
0.1 to 0.9	2
1.0 to 1.9	1
>2.0	1

Commentary: Variations in Estuary Utilization Among Juvenile Chinook Salmon Populations

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All species of anadromous salmon pass through the estuary of their natal river both early in life as juveniles and on their upstream spawning migration as adults. Chinook salmon show the longest periods of juvenile residency in estuaries, up to several months, and evidence from adult scale analysis of Sixes River (Oregon) chinook indicate that estuarine residents can be the dominant contributors to adult returns. Juvenile chinook residency in estuaries is widespread along the Pacific coast and has been observed in the Sacramento (Kjelson et al. 1982), Sixes (Reimers 1973), Skagit (Congleton et al. 1981), Fraser (Levy and Northcote 1982), and Nanaimo (Healey 1980) estuaries, suggesting that a significant component of the Pacific coast chinook production may be related to estuary use. But not all chinook are dependent upon an estuary, and some pass rapidly into the coastal environment following a variable period in fresh water. There is great diversity in life history patterns of chinook with latitute, within a river system, and even between neighbouring river systems. This paper reviews the variation in estuary use by juvenile chinook salmon along the North American Pacific coast.

Within a large chinook salmon river system like the Fraser River, three dominant juvenile types migrate downstream to the estuary at different times of the year:

(1) fry--those fish which migrate downstream very soon after gravel emergence.

(2) fingerlings--fish which rear in fresh water from about 60 to 150 days before migrating seaward (also called "90-day fry")

(3) smolts--juveniles which remain in fresh water for at least an entire winter and migrate to the coastal environment usually in their second spring.

Adult scale analysis can be an effective tool for distinguishing the latter type from the two former ones; while smolts possess an inner area of closely spaced circuli and a freshwater annulus, fry and fingerlings possess at least some widely spaced ocean circuli contained within the zone of first-year growth. Scale studies commonly identify the fish as either stream type or ocean type, depending on the presence or absence of a freshwater annulus. Under this designation, fry and fingerlings are classified as ocean type and smolts as stream type.

On the Pacific coast of North America, chinook salmon range between the Ventura River in California as far north as the Chukchi Sea adjacent to Alaska (Mason 1965). Chinook populations show differences in their juvenile migration characteristics along this latitudinal gradient. At the southern end of their range, chinooks in California migrate downstream as fry or smolts (Kjelson et al. 1982). In Alaska, juvenile trapping studies (Meehan and Siniff 1962) and the total predominance of stream type adult scales (Gilbert 1923) indicate that chinook invariably spend at least a year in fresh water prior to migrating to the ocean. In chinook rivers of Oregon, Washington, and British Columbia, all three migratory types (fry, fingerlings, and smolts) can be present.

Within a river system, chinook populations can show an impressive variability in juvenile life history characteristics. Reimers (1973) identified five different life history types for the Sixes River chinook based on their relative residency periods in fresh water, estuarine, and coastal environments. In the neighboring Rogue River, seven different life history types were identified through adult scale analysis (Schluchter and Lichatowich 1977). While it is possible to identify distinct juvenile life history types within a chinook population, many gradations of intermediate types probably exist which move between and use a variety of different habitats for the purposes of juvenile rearing.

Juvenile life history characteristics vary according to spawning bed location in some rivers. A large proportion of chinooks from upper Fraser River spawning locations are stream type (Tutty and Yole 1978). In downstream spawning areas of the Nanaimo River, the frequency of ocean type chinook is higher than in upstream spawning areas (Healey and Jordan 1982), reflecting the tendency for lower river chinook juveniles to emigrate from fresh water in their first year of life. Thus, there appears to be a gradient in chinook life history types, with more stream type chinook occupying headwaters, and ocean type chinooks increasing in frequency in lower river spawning grounds.

Review of published information on estuary use by juvenile chinook indicates that juveniles at the fry stage are the most frequently observed residents in estuaries:

River System	Period of Estuary Occurrence	Life History Stage	Initial Fork Length (mm)	Final Fork Length (mm)	Maximum Residency Time (days)	Reference
Sacramento	Jan.-June	fry	38	70	64	Kjelson et al. 1982
Sixes	April-Nov.	fry/ fingerlings	43	125	90	Reimers 1973
Skagit	April-July	fry	43	60	4	Congleton et al. 1981
Fraser	March-July	fry	41	70	30	Levy et al. 1982
Nanaimo	March-July	fry	40	70	57	Healey 1980

Individual chinook juveniles have been observed to reside in estuaries for between 4 and 90 days and show an increase in fork length of between 40% and 190%. Reimers (1973) has demonstrated the very important contribution of estuary juveniles to adult returns for the Sixes River chinook population. His results suggest that juvenile chinook which reside in estuaries may survive better than other life history types, although this may not be the case in all chinook river systems (Schluchter and Lichatowich 1977; Reimers and Concannon 1977).

Yearling chinook smolts pass rapidly through estuaries into the coastal environment (Reimers 1973; Healey 1980; Westwater Research Centre unpublished data). Headwater chinook stocks and northern chinook populations, both of which produce a high number of stream type juveniles, are probably less dependent on estuaries than are lower river stocks from southern latitude chinook rivers. Lower river chinook stocks between California and central British Columbia are probably the stocks most dependent upon estuaries. These stocks are of special concern, for not only are they particularly sensitive to estuary developments, but also, they are the stocks most likely to benefit from estuary habitat enhancement projects.

Chinook populations which use estuaries as juveniles may be especially important contributors to sport fishery catches. Preliminary results of coded-wire nose-tagging studies (Barnetson MS 1980) indicate that juvenile chinooks tagged in the Cowichan estuary are harvested (over 80%) by fisheries in Georgia Strait. In the Fraser River, the Harrison River stock has been identified as the lower river stock which probably makes the greatest use of the Fraser estuary as a juvenile rearing area (Levy and Northcote 1981). Preliminary nose tag returns (Fraser et al. 1982) suggest that large numbers of these fish become Georgia Strait residents. Because of the concentrated sport fishing effort in Georgia Strait (Anonymous 1982), the estuaries of Georgia Strait may have a particularly important role in providing chinook salmon which become available to a highly valuable sport fishery. Likewise, the estuaries of Puget Sound (Simenstad et al. 1982) may be important chinook producers for Washington State sport fishermen.

During the past century, most Pacific coast estuaries have undergone very drastic alterations (Figure 1) as they have been transformed into important agricultural, industrial, and urban areas. Many industries achieve significant economic advantages by locating in an estuary. Dykes and port structures can seriously impair productive fish habitats as well as fish access to rearing areas in many estuaries. However, some commonly perceived damaging activities, e.g., log storage, may have neutral effects on chinook fry in at least one well-flushed estuary (Levy et al. 1982).

Effective management of chinook-producing estuaries has been impeded because of the lack of critical information which evaluates the interaction between economic activities in estuaries and fish production. Beyond the need for evaluating industrial impacts, estuarine research on juvenile chinook salmon should be pursued to develop habitat enhancement techniques for those stocks which use estuaries as juvenile rearing areas. In this way, commonly occurring activities in estuaries, e.g., dredging and training wall construction, might be turned into habitat assets for chinook salmon instead of habitat liabilities.

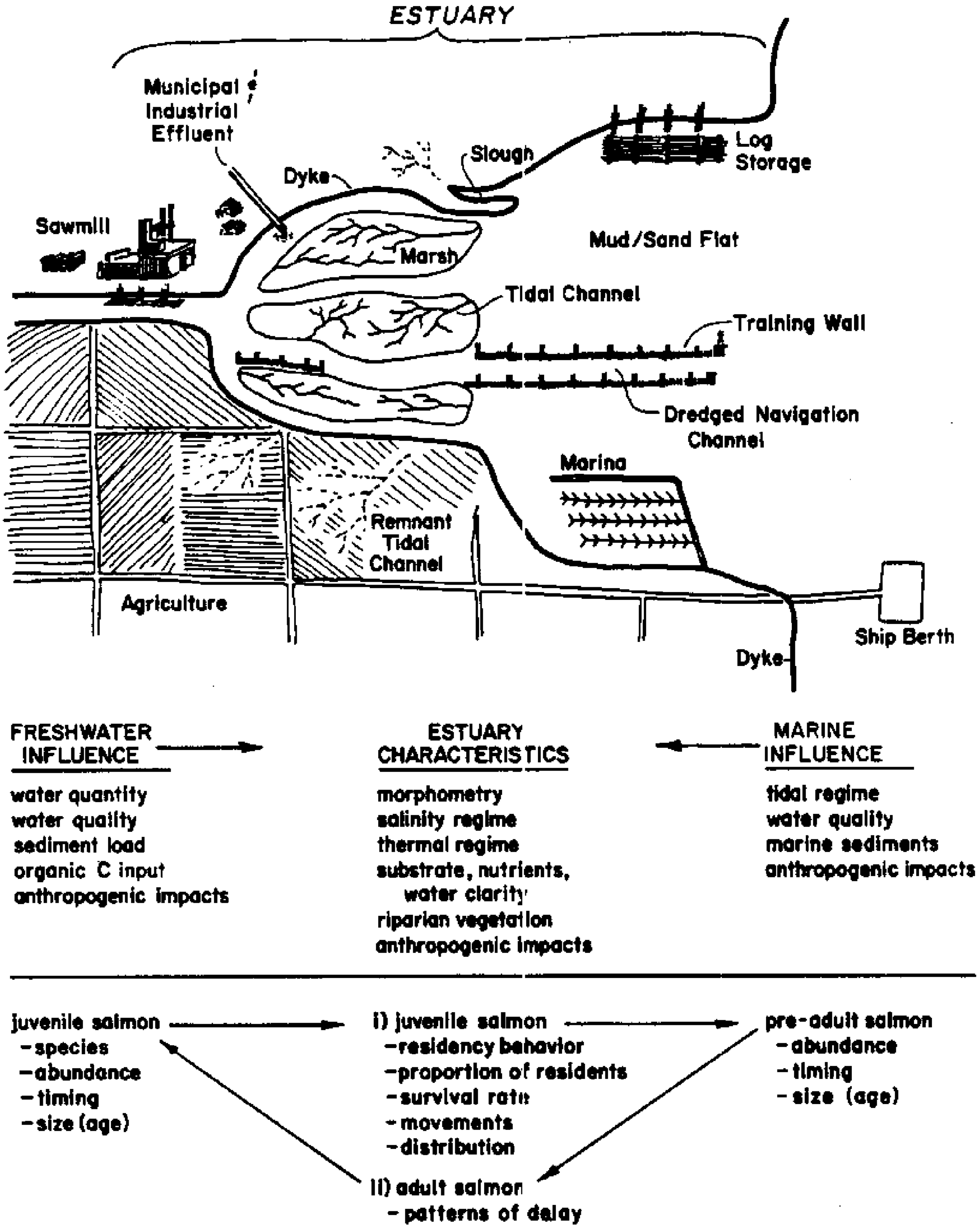

Figure 1. Environmental impacts commonly occurring in Pacific coast estuaries and major factors controlling salmon utilization of estuaries.

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An Overview

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For an Atlantic salmon biologist this workshop has been an intensive course in Pacific salmon biology with a useful leavening of Pacific oceanography. From such short acquaintance with the problems my comments must of necessity be general.

The papers and discussions have been of two types--analytical and innovative, with a heavy bias towards the former. I do not mean to imply any value judgement by such a distinction--analysis may be every bit as creative as innovation--but it seems that we are not yet at a stage when we can use much of the wealth of knowledge accumulated about the marine phase of salmon's life-histories. The papers have concentrated heavily on numbers and not on mechanisms, on the middle and later stages of life, and not a great deal on the beginning. The fish have been treated as passive elements and not as responsive actors. And finally, we have concentrated more on the potential rather than the actual.

To put the problems into a framework for discussion, the fundamental reason for all the work is that the salmon is a resource of high social importance. We are concerned with the production of fish flesh, through salmon's use of a highly productive environment. So the focus of study is the optimal yield from this resource, which can only be achieved if the fish survive, and survival will be promoted by rapid growth; or, as Horwood and Cushing (1978) put it, "an animal in the sea avoids death by growing." We are interested, then, in growth, in the performance of fish in the ocean, and hence in their physiology and behavior as well as in their numerical relationships in the face of a fluctuating environment.

As a freshwater salmon biologist with interests in developmental physiology, I am biased toward an ontogenetic approach to these problems. I start, therefore, at entry to the ocean and question the advisability of a static approach to smolt size at release: rates of development during the freshwater phase are better indicators of capacity and probably future performance, after the young fish have entered the ocean. Several biochemical and physiological indices (such as elevation of plasma thyroxine levels, increased gill Na-K-ATPase activity) have been suggested as guides to readiness for transfer of smolts to sea. But using these functional rather than morphological changes is exchanging one form of partial index for another. Until we find the integrator of these processes it would be preferable to allow the fishes themselves to tell us when they are ready to go to sea, by some behavioral bioassay, such as the salinity choice methods used by at least one commercial salmon rancher. However, none of these methods will be of much importance unless the smolts released are fully competent to fend for themselves in the wild. In this regard we should consider the nature of the hatchery environments in which the fish are reared. Compared with the physically and biologically complex world that the wild fish inhabit, the hatchery fish grows up like a deprived child: its world is plain and simple, and its sensory experiences severely limited in variety. In higher vertebrates such sensory deprivation commonly leads to behavioral abnormality in later life. In a word, are our fish neurotic? Are they still capable of adjusting to a bewilderingly complex world rapidly enough to learn how to use it successfully before they are eaten by something else? How long does it take to switch from pelletted food to a live prey diet? Such questions are now being asked experimentally here in Newport by Dr. Olla and are clearly critical in understanding problems of survival at entry to the ocean.

There has been discussion of food availability for the fish in estuaries and on movement to sea. What does the young salmon recognize as food, and what does it select? In experiments with young Atlantic salmon (Wankowski and Thorpe 1979), we found that this species was very precise in its choice of size of food item and that it grew successfully only when eating particles of this preferred size. That size was defined by the maximum width of the prey animal, and throughout the two-year period of freshwater growth, Atlantic salmon selected prey with a width equivalent to between 2.2% and 2.6% of their own body length. Since the jaw size, mouth gape, and gill-raker spacing maintained the same proportionate relationships to body size during the sea phase as they had done in fresh water, it seemed reasonable to predict that the optimal prey size would remain at 2.2% - 2.6% of fish body size in the ocean. On this basis we (Browne et al. 1983) examined the probable vulnerability of several fish species whose juveniles have been reported as present in the few Atlantic salmon stomach samples that have been obtained at sea. Species such as sprat (Sprattus sprattus) apparently grow fast enough to be a risk for a relatively brief period (Figure 1) whereas 0+ herring (Clupea harengus) are an almost ideal size as prey for salmon throughout their first 12 months at sea (Figure 2).

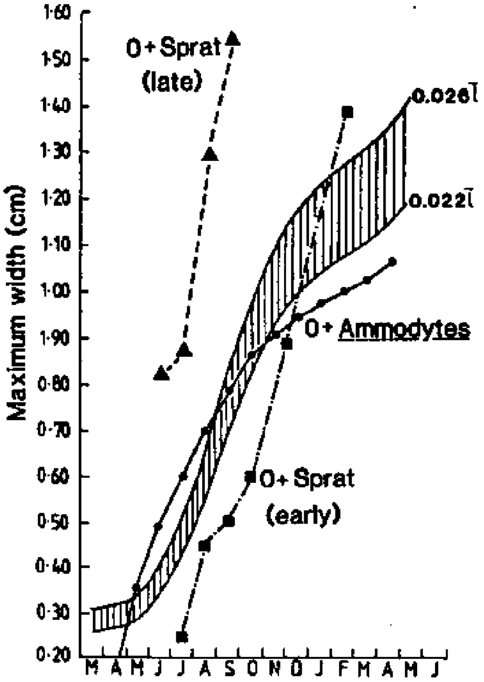

Fig. 1. Width growth of potential prey fishes of Atlantic salmon, in relation to predicted optimal food particle width to achieve observed salmon growth. I: sprat and Ammodytes. (From Browne et al. 1983)

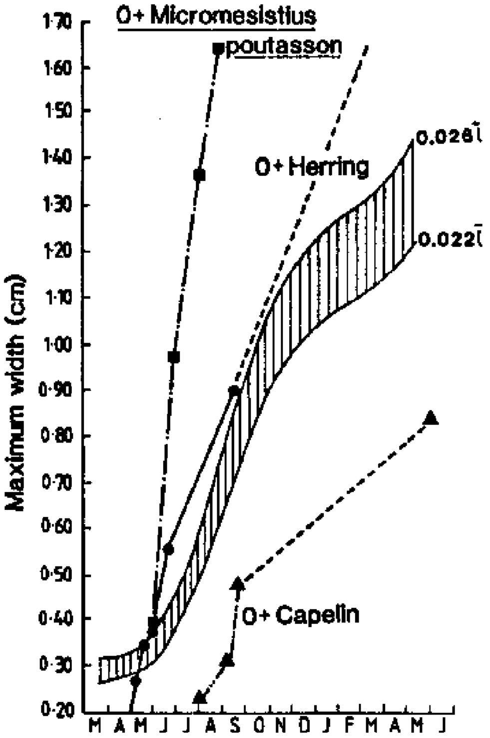

Fig. 2. As Figure 1. II: Herring, capelin and blue whiting (Micromesistius). (From Browne et al. 1983).

Such a coincidence is highly suggestive, and it would seem profitable to examine prey size preferences in Oncorhynchus spp. from a similar standpoint. Definition of such optimal prey sizes refines the subsequent questions that need to be asked about the seasonal composition and abundance of potential prey found in estuaries, inshore coastal, and offshore oceanic environments, in relation to their competence to support predicted numbers and size groups of salmon entering these areas. For example, it was mentioned that zooplankton cycles and oceanic abundance of sockeye were not correlated closely; if the fish at this stage were feeding on squid should we be surprised?

This approach may give functional and ecological meaning to empirical data on size and time of release of smolts and to the importance of supplementary feeding of pink and chum salmon fry, both from the point of view of their success as predators and their success in avoiding being eaten.

There has been much comment on the apparently critical period of the first 30 to 40 days at sea. Is this, too, a function of food availability? Our understanding of food availability as a concept would be improved by studies of prey particle size preference, as suggested above. The ideas of Walters et al. (1978) about the phasing of entry of young salmon of different stocks into the same coastal areas are worthy of careful testing. Their study emphasizes the importance of the timing of ocean entrance.

Not only at release, but after release, where are the young salmon at a particular time? How have they arrived there? Have they "ridden the current", as was suggested for small salmon in Alaska, or is there active navigation at this stage? The different oceanic distribution patterns of the later developmental stages of different species indicate differing dispersal mechanisms. Questions about survival need to take such mechanisms into account, and coastal circulation patterns must inevitably have a much greater impact on small fish than on the larger returning adult migrants. A more detailed understanding of these mechanisms, and the influence of oceanographic factors, is needed if the accuracy of predictions about harvests is to be improved.

For example, oceanic temperature changes are of topical importance at present. Two examples from Atlantic salmon can be added to the wealth of data presented at this workshop. Scarnecchia (In Press) found highly significant positive correlations between the mean sea temperatures at the time of smolt entry from several rivers in northern Iceland and the yield of adults returning from these smolt groups one year later. Concomitant data on primary productivity and zooplankton standing crops in cold springs suggested that poor yields of salmon a year later were probably related to reduced feeding opportunity as post smolts, reduced growth, and greater vulnerability to predation. Martin and Mitchell (unpublished) found that both the one-sea-winter proportion of a population returning to a single Scottish river and their mean size at return were negatively correlated with an oceanic temperature index from the subarctic Atlantic (Grimsey, Iceland). This temperature index was related to environmental changes likely to be experienced by the salmon at later developmental stages than those reported on by Scarnecchia. Colder sea temperatures at Grimsey suggested a southward penetration of the polar front, implying a shorter journey for salmon from their home river to the productive feeding grounds along this front. This would permit more rapid growth and, thus, both higher survival and a greater mean size at return the following year. Effects similar to these were noted at this workshop in relation to Bristol Bay Sockeye and Alaska pinks and relatively favorable oceanic conditions; and perhaps it is nearness to home which accounts for better survival of coho among Vancouver Island than among Oregon stocks?

Changes of location of salmon in the ocean, as a result of oceanographic changes, are likely to have other implications for the fish. It was reported that immature salmon were found in warmer waters than maturing fish, implying reduced temperature as a requirement for completion of the gonadal cycle. It was also suggested that changes in migration cues were related to time rather than place. At the Salmonid Reproduction Symposium in Seattle abundant evidence was presented for the directive role of photoperiod change in the initiation of critical phases of the maturation cycle. It would be physiologically imprudent for a species to migrate a long distance from oceanic feeding grounds to its spawning river in an inappropriate breeding condition. Hence, timing of the return migration should be precisely linked to the timing of the gonadal cycle. But if physical conditions are such that feeding fish are displaced substantially to the north or south of their characteristic area, the rate of day-length change that they experience will be modified and their gonadal timing altered (accelerated if too far north, decelerated if too far south). In this sense I suggest that time and place do not influence migration cues independently. A stock whose genetic programming is associated with life at a particular latitude at a specific time will show variation of physiological (growth and maturation) and behavioral responses (migration pattern and return timing) if oceanographic conditions result in early displacement from the "expected" localities in the ocean. This field of enquiry seems to be a high priority one now, from the point of view of both learning to manage wild oceanic stocks under highly variable environmental regimes and learning to identify the criteria necessary for selecting suitable stocks for ocean ranching and transplantations.

The unevenness of these first reactions to the papers in this workshop reflects the bias of my own interests. I am not competent to review the oceanographic papers acequately, but a very clear message comes through from all of them. Interpretation of variation in major oceanographic parameters depends on very long time-series of data. In some cases each year generates only a single data point. It is equally clear that the information on year-to-year and season-to-season variation is of vital importance in understanding the environmental impacts on salmonid populations at sea. Therefore, there exists a need for commitment by governments and administrators to long-term financing of research in oceanography and an equal need for biologists (myself more than most others) to take careful note of the oceanographers findings.

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Reports of the Working Groups

Coastal Working Group

Our working group agreed that our first priority is to obtain long-term data sets on both ocean conditions and fluctuations in survival of salmonid stocks. We must understand large-scale, long-period oceanographic fluctuations if we are to understand the effects of environmental variability on salmonid production.

We therefore recommend maintaining and improving our capabilities to monitor ocean conditions through shore stations, ships, buoys, and satellites. Except for shore stations supplying information on sea level, and in some instances temperature and salinity, our monitoring capabilities have decreased in recent years because of the phase-out of Ocean Station "P" and routine hydrographic cruises. This lack of good time series of ocean factors is a real limitation to studies on the relationships between fisheries fluctuations and the marine environment. The working group made the following specific recommendations:

1. development and installation of automated buoys and moored arrays to collect environmental information and possibly to transmit data via satellite links to shore stations;
2. better use of ships-of-opportunity to provide data on year-to-year variations in upper ocean conditions;
3. establishment of hydrographic transects strategically located along the west coast from Oregon to Alaska to provide consistent time series on oceanographic conditions; and
4. addition of automatic tide gauges at Port Moller in Bristol Bay and Unimak Pass to supplement existing time series on sea level.

Salmon Monitoring Program

Present trends should continue to improve precision of measurements of catch and escapement, and the age and size composition, of both of these components of all major stocks. Analyses should continue on the relationships among numbers and sizes of smolts released, distribution of ocean catches of marked salmon, and survival based on catch and escapement data. Although similar data on wild stocks are much more difficult and expensive to acquire, wild fish returns as indexed by counts on spawning streams, weirs, and passage past dams could be useful to develop basic data sets.

Scale samples from returning adults provide useful data on ages and life histories, and scales should be archived to provide a basis for future analysis of the historical data sets. In the future, scales should be sampled from smolts released from selected hatcheries and scale radius-fish length relationships should be determined by brood year. This will enable comparison of size frequency distributions of smolts back-calculated from adult scales with those known from smolt releases to estimate size selective mortality.

To monitor marine survival on a continuing basis, we should continue and improve programs of wire tagging and ocean sampling. Efforts are needed to better coordinate tagging studies among agencies and to more effectively communicate results. Additionally, we need wire tagging of outmigrants from selected nonhatchery stocks to demonstrate whether the marine survival rates of wild and hatchery stocks from a particular region have similar trends. Without measuring variation in survival of wild stocks we will not know whether negative trends in hatchery survival rates are reversible by improved fish culture or release strategies.

Research should be continued to determine the distribution and migration of immature salmon in the coastal zone through ocean sampling, recovery of marked fish, and tagging juveniles at sea. Sampling, such as conducted by Hartt and Pearcy, should be expanded to include the major portions of the ranges of selected species and should be sustained to provide data on interannual variability. New methods of distinguishing stocks sampled at sea are scale pattern analysis using digitized electronic data processing, and biochemical genetics.

Specific Studies

Because experiments to determine the mechanisms affecting survival, growth, and distribution of salmon in the ocean will be difficult and expensive, the coastal group recommended detailed studies on a limited number of carefully selected stocks. The selection process should be well thought out to ensure that the results can be generalized to an understanding of the mechanisms causing fluctuations in both hatchery and wild stocks over a wide area. Two stocks identified as candidates for intensive monitoring and research were the Oregon Production Index (OPI) coho and Bristol Bay sockeye. Both stocks have been monitored for many years. Ocean distributions of both are relatively well known, and correlations between marine survival and ocean conditions have been demonstrated--upwelling intensity for OPI coho and ocean temperatures for Bristol Bay sockeye.

Identifying Survival "Bottlenecks"

After a stock has been selected for intensive study and its general migration pattern is understood, we then need to estimate the variability and magnitude of marine mortality in order to estimate where and when run size or year-class strength is determined. The early ocean rearing period, involving the first 90 days in estuarine and coastal waters, is thought to be a "critical period" for several salmon stocks.

Several ideas were suggested to identify the period and area of heaviest mortality. Intensive marking and ocean recovery of key stocks may be helpful. A change-in-ratio estimation of standing stocks at the time of jack return has been used for coho salmon. Catch/effort data could be used as an index of change in abundance if the sampling effort was relatively intense and the migration pattern into and out of the sampling area was known. This method has been used in estuarine studies and perhaps could be applied to nearshore ocean areas. Another method is tagging at sea to allow sequential mark/recovery population estimates, but because of the low recapture rates this method is more practical in semi-enclosed estuaries than the open ocean.

Experiments are being conducted to release tagged fish at the same or different ages at different locations in estuaries or the ocean. The comparison of differential survival rates of these groups, based on adult catch and escapement, may help to identify the location and life stage of high mortality rates. Another approach is simply to assume the location and period of survival "bottlenecks" based on studies of other stocks and to begin in-depth studies.

Mechanisms and Hypotheses

Mortality usually occurs in two ways: starvation or predation. Thus, food abundance, availability and quality; abundances of predators and competitors; diseases; and environmental factors, such as currents, salinity, temperature, and primary and secondary productivity may all relate to survival. A thorough knowledge of food habits, competitors, and predators is needed for each life stage of the salmon stocks being studied. Environmental influences can then be hypothesized and possibly tested under actual or simulated conditions.

Hypotheses have been proposed to explain observed correlations between biological/physical factors and the survival rate. For example, the correlation between coastal upwelling and survival of OPI coho salmon may involve a growth mechanism (i.e., greater upwelling results in more production of food, allowing fast growth of juvenile coho, and therefore less predation on small, vulnerable sizes). Such a hypothesis could be tested by some combination of ocean sampling, experiments in large enclosures, and bioenergetic modeling.

The influence of numbers or densities of juvenile salmonids in the coastal ocean on their growth and survival is another problem that requires more research. Analyses of existing data on timing and numbers of smolts released vs. survival should be expanded, and specific experiments should be designed to test the hypothesis of density-dependence during early ocean life for selected stocks. In addition, the effects of massive hatchery releases on wild salmonids, as well as other coastal species, should be investigated.

Communications Should Continue

The working group agreed that scientists investigating salmon population dynamics in the ocean must develop more effective ways to share ideas, approaches, and results with colleagues in a more comprehensive and timely manner. This conference provided a good first step in sharing existing information and exploring coast-wide initiatives for cooperative research. Such efforts should be continued. Workshops similar to this one would be fruitful every one or two years.

Estuaries and Inlets Working Group

Estuaries and inlets, the marine environment initially encountered by juvenile salmon as they migrate seaward, have been implicated as important sources of variable ocean survival. The studies which have attempted to quantify mortality in estuaries and inlets by Parker and Bax suggest that mortality may be both extremely high and variable, particularly in the case of pink and chum fry. In addition to affecting the numbers and size of fish reaching the coast and open ocean, variable conditions in estuaries and inlets affect the fitness of the out-migrants to survive in the ocean.

Hypotheses on Mortality

In evaluating the influence of estuarine conditions on salmon production, the working group resolved that we must measure the rate of mortality. Mortality rates within the estuary, as well as offshore, must be directly linked to characteristics of juvenile salmon populations entering and exiting the estuary. Accordingly, five basic hypotheses are outlined, along with research needs for each.

H_1. Mortality in estuaries is size and density dependent. Initial research should focus on small enclosed estuaries and fjords where juvenile salmon of identifiable origins can be sampled sequentially. Marked groups of salmon should be sequentially sampled to determine the effects of size and density at the time of estuarine entry on subsequent survival. Data on number and size of the fish emigrating from the estuary are also obviously required. Otolith microstructure or scale characteristics may provide marks to separate stocks of salmonids from different freshwater systems or hatcheries. This may eliminate the excessive cost and effort involved with the customary mark-and-recapture.

Large estuaries and inlets are important nursery areas for salmonids. Although control and assessment of size and density of juvenile salmonids in these habitats is difficult, relationships between mortality rates and size or density may be revealed by natural variations in the size or density of juvenile salmonids entering and leaving the estuary or inlet. Discrete events in the estuarine out-migration (e.g., transition from shallow sublittoral to neritic habitats) could be the initial focus of research on mortality rates in these larger estuaries and inlets.

Many juvenile salmon occupying and migrating through large estuaries and inlets already are tagged with coded microwire tags (CWT's). Hatchery releases of different numbers and sizes of fish could be used to estimate differential mortality rates if accompanied by multiple marking of fish within the estuary and by appropriate sampling at the "outlets" of these systems.

H_2. Within-estuarine mortality is habitat-specific. Research to test this hypothesis requires stratification of estuaries into habitats and measurement of mortality rates within each habitat. Although we have indications of differential habitat utilization by juvenile salmon, the survival of salmon in different habitats within an estuary has not been estimated. Thus, it has been impossible to determine if high and variable mortality is associated with one critical habitat.

Experiments to evaluate patterns of habitat utilization by juvenile salmon could include: (1) cage, enclosure, or mesocosm experiments; (2) mark-and-recapture techniques for discrete subhabitats; (3) monitoring growth and prey consumption of CWT-tagged groups released into subhabitats; and (4) study of behavioral aspects (e.g., foraging, predator avoidance) of fish in different subhabitats. Initial experiments should be conducted in small estuaries where emigrants can be effectively sampled and the overall within-estuary mortality rate estimated.

H_3. Within-estuarine mortality is fitness-dependent. Three approaches were identified to measure the impact of fitness (e.g., size, condition, and physiological state) on within-estuarine mortality:

1. test the effect of smoltification fitness by releasing treatment groups in different physiological (smoltification) states and measuring mortality by systematic sampling at immigration to the estuary, and upon emigration from the estuary;
2. test other measures of fitness as single independent variables;
3. examine range of mortality rates for different fitness variables by conducting tests in different types of estuaries, and
4. test confounding effects of different fitness variables (e.g., smoltification on feeding readiness) by laboratory experiments as well as estuarine monitoring.

These fitness variables should be measured in different estuaries to better understand inter-estuarine differences in mortality mechanisms.

H_4. Timing and duration of estuarine residence affect within-estuarine mortality. Although we know the time and duration of out-migration of juvenile salmon from many estuaries, within-estuarine mortality rates very seldom have been related to estuarine residence.

Testing of this hypothesis depends upon two benchmarks: time of immigration to and time of emigration from the estuary or inlet. In many instances, we have had good information on the immigration of hatchery releases into estuaries. Data on emigration are less available. Sequential sampling of identifiable fish is needed within the estuary over the course of the out-migration period to determine emigration timing and rates (see H_1).

Intensive sampling of juvenile salmon immigrating to and emigrating from small enclosed estuaries is recommended to provide estimates of within-estuary mortality of identifiable groups of fish. Scale or otolith increment patterns may enable us to identify cohorts which entered the estuary and to measure the number of days since fish entered the estuary and somatic growth over that time. Again, intensive sampling of juvenile salmon leaving the estuary is needed to estimate the mortality rate of different groups of marked fish released at different times and at varying distances from the mouth of the estuary. Finally, we suggest comparison of mortality rates in different estuaries known to have highly variable run timing and estuarine residence times to determine the effects of these variables.

H_5. Size, density, condition, and time of emigration from estuaries influence coastal and oceanic mortality rates. This is a difficult hypothesis to test because of our inability to separate estuarine mortality from that occurring in ocean environments. Coordinated research programs to establish the functional relationships among the characteristics of the migrants at ocean entry and ultimate ocean mortality include:

1. comparison of scale patterns of returning adults with the patterns of groups of smolts which emigrated from the estuary (*vis a vis* Reimers);
2. comparison of mortality rates of marked fish released simultaneously into estuaries and into marine waters; and
3. comparison of total marine mortality rates of stocks exhibiting differing degrees of estuarine utilization, or of the same stock which has extreme interannual variability in the degree of estuarine utilization.

Discussion

Unanalyzed scales and scale impressions collected during many years, exist from some adult salmon stocks. These may provide valuable data on inter-estuarine and interannual variability of estuarine residence, growth and mortality. Similarly, the extensive CWT data for the Pacific Northwest and Alaska should be evaluated relative to estuarine migration rates, duration of residence, growth, and mortality.

Testing of these hypotheses will ultimately require structured experiments and systematic sampling designed to provide two basic types of data: (1) mortality rates within estuaries and inlets, and (2) the characteristics of the survivors emigrating to the ocean. This requires an "input-output" approach wherein densities and characteristics of identifiable fish are documented as they enter and as they exit estuaries. The resulting data describe quantitatively the "filter" character of each estuary under the different treatment conditions (e.g., timing, fish condition, etc.) and physical factors.

Obvious differences among estuaries were recognized. Physical, geomorphological, hydrological, and biological characteristics of estuaries along the North Pacific rim are almost as diverse as the number of estuaries, and these differences could affect attributes of out-migrating salmon, such as size, density, and fitness. Thus, there is a need to characterize estuaries relative to their "inherent mortality potential" so that hatchery release strategies can be developed to maximize survival.

Establishing residence times, growth rates, and corresponding estuarine and marine survival rates is a major task. Wherever possible, "habitat" scientists should therefore collaborate with "stock" scientists to study the same systems. Stock managers usually estimate survival rates from analyses of catches in a commercial fishery and enumerations of fish on the spawning grounds. Both groups of scientists should cooperate in the gathering of data on residence times and growth rates, data which are usually not routinely obtained. Similarly, studies of prey resources of juvenile salmon should involve invertebrate ecologists as well as fish behaviorists.

Although the working group focused on estimation of mortality, we acknowledge the need for understanding of the mechanisms of within-estuarine mortality. Mortality factors, whether predators, disease, or starvation, should increasingly be the focus of research as trends in estuarine mortality emerge. Equally important, estuarine hydrography, water mass characteristics, primary productivity, prey resources, and predator populations should be monitored. Concurrent gathering of these independent variables will be vital to elucidation of the actual mortality mechanisms. Eventually, decisions on salmon management and enhancement decisions may rely on a limited suite of critical factors monitored within the estuary.

Hatcheries Working Group

Our ability to maximize survival of hatchery fish depends upon our understanding of three broad questions:

1. Are hatchery juveniles ready to enter the sea?
2. Are the sea and intervening rivers and estuaries able to accommodate hatchery juveniles?
3. What can be done in hatcheries to better adapt juveniles for release?

Four priority research areas were identified by the working group on hatcheries. These are discussed in more detail below.

Adaptation To The Ocean

The key question is this: under given estuarine and ocean conditions, what can be done to better prepare hatchery salmonid juveniles to adapt to and to survive in the ocean? Several options were discussed. All require research to fully evaluate their potentials.

A. Modify smoltification of hatchery salmonids so that downstream migrations and ocean entries occur at the most favorable times for survival, considering food availability, predator abundance, river and ocean temperatures, and other influencing factors. Smoltification can be modified in several ways:

   1. Acceleration of adult maturation and spawning through adjustment of photoperiod and injection of gonadotropin-releasing hormone.
   2. Photoperiod control of smoltification. Smoltification in coho, spring chinook, and Atlantic salmon, and in steelhead trout has been accelerated or delayed by photoperiod adjustment, thereby providing a method of timing seaward migration and ocean entry to coincide with optimal environmental conditions. The potential of such control strategies should be determined.
   3. Temperature control of smoltification. Warm water can accelerate smoltification and can promote more rapid growth. Conversely, cold water can retard smoltification and can prolong the smolt stage once it has begun. Such flexibility might enable releases to more suitable river and ocean environments.
   4. Hormone control of smoltification. Feeding triiodothyronine (T_3) may accelerate smoltification. More rapid growth occurs when androgens are fed. These hormones, in addition to others that control growth and development of smolt physiology, may provide methods to regulate smoltification and the timing of seawater entry.

B. Enhance smoltification and sea water tolerance. Accumulating evidence suggests that juvenile salmon frequently do not develop maximum smolt physiology while under hatchery confinement and depend upon a migratory period to reach a fully smolted state. Thus, populations that are transferred directly to seawater or have only very short migratory runs may be severely stressed during initial seawater adaptation. The importance of downstream migration to survival of hatchery fish needs to be determined. Treatments that may enhance the ability of hatchery fish to adapt to a seawater environment include

1. Pre-exposure to seawater. Experiments have shown that chinook salmon in marginally smolted condition survive better in full strength seawater if pre-exposed for several hours to one-half strength seawater. Thus, pre-exposures to seawater under controlled conditions before release into the ocean may substantially increase survival.
2. Dietary effects. Certain dietary lipids, both in terms of quantity and quality, may affect seawater survival. Pilot experiments with added dietary salt have shown increased seawater and ocean survival. These effects need to be studied in detail.
3. Exercise. Preliminary results suggest that a period of exercise prior to release increases seawater survival.

C. Evaluating smolt quality. The fitness of juvenile salmon includes the ability of the fish to survive and grow in the marine environment. Several methods have been developed in the laboratory to determine the smoltification status of juveniles, but these methods should be tested on a long-term basis at hatcheries and in the field to determine their usefulness. Research on new methods to determine smolt fitness should continue. Existing and proposed methods can be divided into physiological and behavioral categories. Physiological measures include changes in gill Na^+-K^+ATPase activity, plasma thryoid hormone concentration, and blood sodium or osmolarity after seawater challenge. These methods should be employed at hatcheries with serial release programs, so that the performance or survival to adulthood of the various release groups can be related to the physiological measures. Furthermore, released fish should be sampled in rivers, in estuaries, and in the oceans so that changes in the physiology and the ability to migrate to the sea can be determined.

Behavioral measures of readiness of juvenile salmon for sea may include migratory disposition and seawater preference. The downstream migratory activity of smolts should be tested in volitional release programs. For example, preference for seawater may be tested in a two-compartment chamber containing both fresh and seawater. As with the physiological measures, the behavioral tests should be related to the downstream migration and survival and behavior of released fish.

Behavior

Hatcheries lack many of the sensory stimuli experienced by salmon smolts in nature. Presumably such deprivation may affect the behavioral development of fish and their subsequent success when released in the natural environment. Activities that may be affected include foraging, predator avoidance, orientational responses, and social interactions, all critical to the growth and survival of released smolts. To date, little effort has been expended investigating these problems. Controlled laboratory experiments offer a promising method to study behavioral patterns of smolts prior to release.

A. Foraging. The capabilities of smolts reared on artificial diets to recognize, locate, and capture natural prey items should be assessed and compared with the foraging success of wild populations of salmon.

B. Predation. Responses of hatchery and wild populations of smolts to predators should be studied to determine if hatchery-produced smolts are conditioned to behave in ways that increase their vulnerability to predation following release (e.g., broadcasting food at the surface). Additionally, it is important to determine what role learning plays in the ability of salmon smolts to identify and escape from predators. How do the performances of individuals raised in predator-free environments compare with those from natural populations?

C. Social Behavior. Little is known about the social behavior of salmon smolts in the ocean. For some species, agonistic patterns associated with freshwater dominance hierarchies and territoriality change to activities associated with aggregations and schools. The formation and maintenance of such groups may be important to food gathering and predator avoidance. Experiments comparing the behavior of hatchery and wild fish could determine if the hatchery environment modifies the social attributes of smolts.

Size and Date At Release

Considerable evidence indicates that marine survival is directly related to size at release. The functional relationship, however, between marine survival and size at release varies among species and probably among stocks. Is this relationship linear or curvilinear over a broad range of sizes at release? Are the observed relationships the result of physiological adaptation to seawater or of environmental interactions such as predator-prey relationships? Physiological and environmental processes probably interact. Research is needed to differentiate the relative importance of these processes affecting survival.

The relationship between marine survival and date at release is, from all indications, complex. Different species and different stocks seem to exhibit a wide variety of functional relationships. Interactions among date of release, migratory behavior, zooplankton production, and survival may be especially important for pink and chum salmon. Complex interactions with environmental variables need clarification. One serious confounding factor is the tendency for size of juveniles to be a time-controlled variable. It frequently is difficult, therefore, to differentiate the relative importance of size at release vs. date at release on marine survival.

Assessment of the effects of size and date of release of hatchery smolts on adult survival will require large numbers of observations replicated over a series of years. Coordination and standardization of studies on tagged groups of juveniles released from different hatcheries are recommended to improve our data base so these relationships can be understood.

Disease

Considerable progress has been made in recent years to improve the health of salmon in hatcheries and control the diseases of these fish in fresh water. Little has been achieved, however, to decrease the effects of disease in the ocean. We need to know

1. what diseases affect salmon in the ocean,
2. how these diseases affect ocean growth and mortality, and
3. how these diseases can be avoided or their impact can be lessened?

To answer these questions, research should be conducted to

1. isolate and identify the potential bacterial, viral protozoan pathogens of salmonid fishes in the ocean and test the pathogenicity of these agents for

salmonid stocks in seawater challenge studies, preferably at various temperatures.

2. transport groups of fish which have been infected with freshwater hatchery diseases to pathogen-free seawater and monitor their survival. This is especially important for those diseases which attack the kidney, such as bacterial kidney disease.
3. develop vaccines against important marine pathogens and examine other possible control methods for these disease agents.

Oceanic Working Group

Oceanic waters of the subarctic Pacific support the juvenile growth of the three most productive species of Pacific salmon: sockeye, pink, and chum. Ecological conditions in the least accessible part of the migratory circuit may be the source of much of the large variation in survivorship, individual size, and stock yields. However, that is by no means certain. First, virtually all information about stock variation concerns adults returning to their natal rivers. Attributing variation in these returns to estuarine, coastal, and oceanic phases can be done with very little certainty. Second, what data we have suggest most of the mortality is early, occurring in coastal and estuarine areas. Since larger variables tend to have greater variances, this hints that interannual changes in early, neritic survival may dominate the variation in adult returns. For these reasons, along with the great expense of research in the oceanic range of salmon, we were cautious in our recommendations for enhanced research. Nevertheless, with modest research programs, we can begin to assess the relative importance of estuarine, coastal, and high seas environments in determining the rate, and variability in rate, of growth and survival of salmon. Efforts in three major directions appear promising:

1. Renewed investigations of available time series. These include collections of fish scales, extant data on comparisons of interstock and interspecies yields and production, and environmental data.
2. An enlarged effort to characterize the interannual variations in habitat characteristics of the subarctic Pacific. Oceanic observations have recently been discontinued at Station "P" and regular hydrographic cruises have virtually ceased in the subarctic waters of the northeastern Pacific Ocean. These trends can be reversed by enhanced ship-of-opportunity efforts, exploitation of satellite technology, and ocean buoy deployment. In addition, we suspect that we could learn a great deal about the subarctic Pacific from Japanese oceanographers and fisheries biologists.
3. A program to quantify the contributions to total mortality occurring in estuarine, coastal, and oceanic habitats. In an adequate design, the importance of the oceanic sector can be approximated by the difference between total postsmolt mortality and estuarine and coastal mortality.

Some types of information that could be extremely valuable appear beyond the reasonable expectations of resources. In particular, direct detailed information about variations in oceanic dispersion and movements of salmon stocks could be acquired only at great expense. But even in these areas, creative research ideas with modest price tags are possible and should be pursued. For example, sonic tracking of single albacore at sea has produced great insight about daily movements and activities. Salmon could be similarly studied. High seas commercial fishing could be employed as a sampling tool in restricted areas and periods. Gill netting by Japanese vessels has produced interesting results on the distribution and migrations of North American salmonids.

Specific Recommendations

Growth

Several methods exist to increase our information on salmon growth in the ocean. One method that we deemed useful and very cost-effective was the detailed analysis of data from salmon scales. Scale data records of varying length and often of consistent quality exist in many agencies. Several collections of scales include more than 25 years of data.

Scale analysis would assist in the study of the ocean life of salmon in several ways:

1. to study the effects of oceanographic variables on growth and of purported interactions within and between stocks and species
2. to clarify the time and location of possible density-dependent growth within a stock
3. to improve our understanding of ocean distributions of specific stocks through use of discriminant functions which describe scale patterns
4. to improve stock separation techniques which are currently based mainly on freshwater characteristics
5. to enhance our ability to construct models of annual variables, such as final body size, return timing, and changes in migration routes, for purposes of research and management

A variety of existing scale data sets were discussed, and the working group agreed that because of suspected effects of growth interaction and oceanographic changes, initial work should focus on one or more of the following:

1. Bristol Bay and Fraser River sockeye
2. Fraser River and Puget Sound pink and chum stocks
3. Some hatchery and wild stocks (e.g., Oregon coho or central Alaska pinks)
4. Alaskan chinook salmon and other marine fish with comparable food

In each case, comparisons of the magnitude and variability in growth among stocks or species during ocean growth periods should span the same six to eight years, a minimum period required to encompass at least one major change in ocean climate.

Not only is the analysis of scale growth data extremely cost-effective, but our current knowledge can be greatly and speedily enhanced by the use of modern computer-aided, analytical technology. Large data banks of standard quality can be refined and increased in size, and long time series can be easily maintained. New scale data sets can be obtained during routine sampling programs, but it is crucial that the existing sets of long records not be lost or discontinued.

Oceanography

One of the difficulties in studying the influence of variability of the ocean environment on the behavior, distribution, and abundance of fish is that the state of the ocean environment is poorly known, particularly in the eastern subarctic Pacific. The present observation system is as follows. Sea level, surface temperature, and salinity are monitored at a few coastal stations. At sea, sea-surface temperatures and weather elements are routinely measured by ships of opportunity; satellite cloud observations are useful for weather forecasting, but sea surface temperature data in this cloudy region are of relatively limited value. The time series of subsurface observations at Station "P" has been abandoned and the section to "P" is seldom occupied. Some subsurface temperature data are available from ships of opportunity and experimental monitoring programs, but coverage is sparse and spasmodic.

Improved monitoring of ocean conditions is needed not only for fishery purposes but also for the study and prediction of weather and climate. Such monitoring is an appropriate responsibility for a government agency (NOAA in the United States), not for university laboratories. While expenditures on this function must be significantly increased, it is important to plan the monitoring system to be cost-effective. In part, this can be done by studying existing or recent programs (e.g., Station "P" and the CALCOFI data) to see how these might have been done less expensively by more limited sampling or simpler methods. In part, the design will depend on advances in technology, for example the operation of satellite altimeters, scatterometers, and microwave radiometers. Although questions exist on just what should be monitored, at what scales, and with what resolution and accuracy, the basic requirements would be to measure horizontal circulations, and temperature distributions in the surface layer (i.e., to 100 meters or to the upper thermocline). Monitoring salinity, dissolved oxygen, chlorophyll, particle size and concentration, and zooplankton standing stock in this layer are desirable, but it must be considered of lower priority. A monitoring system would be based, to the extent possible, on "smart" ships of opportunity (i.e., those that have been selected for the routes they follow and have been suitably instrumented to make comparable measurements) and on satellites, but would also use fixed and drifting buoys. Research vessels, especially those engaged in repetitive studies, could play an important role because they can be equipped to make better measurements of more variables.

An essential element in the operation of a monitoring system is long-term commitment from the agencies concerned. A ten-year time series is believed to be minimal for studying interannual variability. Obviously a commitment for continuing analyses of the observations must be made, and data and their analyses must be available to scientists and to management groups. These analyses could be linked with existing time series to reveal the recent history of conditions in the ocean environment.

Salmonid Survival

Accurate and precise preseason forecasts of salmon returns are important for both industry planning and within-season adjustments of fishing by management agencies. Good forecasts depend in part on prediction of survival rate during the estuarine, coastal, and high-seas phases of fish life. In most stocks, reliable estimates of abundance of seaward migrants are not available, so freshwater production estimates may also be needed. Few studies have documented the relative magnitude of the survival rates in these different phases of the salmon life cycle, and no study has continued long enough to identify where in the life history of salmon the mortality varies most from year-to-year. This distinction between magnitude and variability in survival is significant; for example, a relatively constant 80% mortality during the first 40 days of ocean life may be less important in determining the year-to-year variation in run size than the less severe but more variable mortality occurring during open-ocean life.

At a minimum, all current programs for estimating abundance of seaward migrants should be maintained, and new programs should be added wherever possible. These enumerations document a major source of variability in returns of these stocks caused by freshwater events. Unless there is a consistent relationship between fish size and mortality rate for particular species, it will be extremely difficult to separately estimate mortality rates in the estuarine, coastal, and high-seas environments. Intensive double-tagging experiments might be useful in estimating mortality rates during these different phases of saltwater life, but only if the assumptions of these methods can be met.

Coordination of Research

If the analyses suggested identify the segments of marine life most important for growth and survival of salmon, then more extensive and long term sampling programs can be developed for study of relevant physical and biological oceanographic variables in the most critical habitats.

To avoid duplication of efforts and to facilitate the increase in understanding of salmon marine life, a mechanism should be established to coordinate the collection, analysis, and exchange of the above types of information among research and management agencies. The Pacific Marine Fisheries Commission currently serves this type of coordinating role for salmon-tagging studies.

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