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**The 6th Annual Alaska Salmon Workshop Ocean-
Climate Change & Variability In Fish Recruitment**

ADF&G Staff

March 1999

Alaska Department of Fish and Game

Divisions of Sport Fish and Commercial Fisheries



*The 6th Alaska Salmon Workshop
Ocean-Climate Change
&
Variability In Fish Recruitment*

MARCH 10 - 12, 1999

Alyeska Prince Hotel — Girdwood, Alaska

Organizing Committee

Hal Geiger

Bob Marshall

Bob Clark

Gordon Kruse

John Wilcock

Patti Nelson

Stan Carlson

Ben VanAlen

Russ Holder

Debbie Hart

Special Thanks

Kathy Wiest - Workshop Logo

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Hosted by the Alaska Department of Fish and Game
P.O. Box 25526, Juneau, Alaska 99802-5526

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**Alaska Department of Fish and Game's
6th Alaska Salmon Workshop
*Ocean-Climate Change and Variability in Fish Recruitment***

**March 10-12, 1999
Alyeska Prince Hotel, Girdwood, Alaska**

Agenda

Wednesday, March 10, 1999

Introduction

- 9:00 AM Welcome – Frank Rue, Commissioner
- 9:15 AM Introductory Remarks - Hal Geiger
- 9:45 AM *Dick Beamish* -The Regime Concept and Salmon

- 10:30 AM Break

- 10:45 AM *David Welch* - Ocean Climate Change and Population Status of British Columbia Salmon in the 1990s
- 11:30 AM *Fran Ulmer*, Lieutenant Governor - Keynote Address

- 12:00 PM *Lunch*

Physical and Biological Oceanography (John Wilcock, Chair)

- 1:00 PM *Alan Springer* - Higher trophic levels in the Gulf and Bering Sea *Sea Lions / Kitty Wakes*
- 1:30 PM *Nate Mantua* - El Nino, PDO, and Ocean Climate Change in the Eastern North Pacific
- 2:00 PM *Jim Schumacher* - Changes in the Physical Environment of the Eastern Bering Sea and some Potential Consequences for Biota
- 2:30 PM *Ted Cooney* - Oceanographic modification of decadal-scale pink salmon production variability in Prince William Sound, Alaska: some candidate mechanisms

- 3:00 PM *Break*

- 3:30 PM *Anne Hallowed* - Pacific Basin Climate Variability and Patterns of Eastern North Pacific Marine Fish
- 4:00 PM *Rick Brodeur* - Has the Carrying Capacity of the North Pacific Changed in Recent Decades?
- 4:30 PM *John Piatt* - Climate Change and Marine Food Webs in the Gulf of Alaska

Thursday, March 11, 1999

Ocean Phases of Salmon Life History (Patti Nelson, Chair)

- 9:00 AM *Kate Myers* - High Seas Salmon Research Issues and Results in the 1990s
9:30 AM *Jack Helle* - Coastal Ocean Salmon Research Issues in the 1990s
10:00 AM *Break*

Freshwater Phases of Salmon Life History (Patti Nelson, Chair)

- 10:30 AM *Jim Edmundson* - Integrating Limnological Data into Sockeye Salmon Production Models
11:00 AM *Bruce Finney* - A long-term perspective on the influence of lake production and climate change on Alaskan sockeye salmon abundance
11:30 AM *Mike Bradford* - Role of Freshwater Habitats in Population Regulation and Recruitment Variation in Coho Salmon
12:00 PM *Lunch*

Quantitative Models of the Recruitment Process (Stan Carlson, Chair)

- 1:30 PM *Terry Quinn* - Alaska salmon spawner-recruit analysis: New strategies for a new millennium
2:00 PM *Milo Adkison* - Implication of Climatic Fluctuations on Salmon Management
2:30 PM *Ed Farley* - Bristol Bay Sockeye Salmon Production: An exploratory analysis of the 1996-98 Decline in Sockeye Salmon Returns
3:00 PM *Break*
3:30 PM *Mark Willette* - Ecological Processes Affecting Mortality of Juvenile Pink Salmon in Prince William Sound
4:00 PM *Fritz Funk* - Linkages between climate and ocean processes and Pacific herring growth and recruitment

7:00 PM Poster Session / No Host Bar (Russ Holder, Chair)

Lake Becharof Ecosystem, Norma Jean Sands, ADF&G

Kodiak Island Sockeye Salmon Freshwater and Marine Survivals, and Size at Age Trends: Comparison of Wild and Enhanced Stocks. Steven G. Honnold, ADF&G

Does the growth record contained in the shells of geoduck clams reflect changes in marine production? Peter Hagen, Zeldia Swain, ADF&G and Ken Severin Department of Geology, University of Alaska, Fairbanks

Copper River Sockeye Salmon Forecast Methods. John A. Wilcock, ADF&G

A Modified Spaghetti Tag for use in Mark-Recapture Estimates of Chinook Salmon Abundance in Southeast Alaska. Ed Jones, ADF&G

The Effect of Warm Water on King Salmon Eggs taken from the Deshka River. Carmen Olito and Diane Starkey, ADF&G

Retrospective Analysis of Ocean Growth Zones on Yukon River Chum Salmon. Tim Sands and Bill Smoker, University of Alaska Fairbanks

Monitoring Freshwater Survival of Yukon River Chum Salmon. James E. Finn and E. Eric Knudsen, USGS, Alaska Biological Science Center

The Ilnik River Modified Floating Weir. Mark Witteveen, ADF&G

Kodiak Management Area Pink Salmon Forecast Modeling. Nick Sagalkin, ADF&G

Southeast Alaska Coastal Monitoring. Joseph A. Orsi, James M. Murphy, Donald G. Mortensen, and Bruce L. Wing, Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service

Can Remote Video and Time-Lapse Recording Technology Improve Salmon Escapement Monitoring in Alaska? Ted Otis, ADF&G

Rocket Science and Indexing Escapements of Pink Salmon in Southeast Alaska. Timothy P. Zadina, ADF&G

An exploration of forecast errors in selected major runs of Alaska pink and sockeye salmon. Mike Byerly, University of Alaska Fairbanks and Hal Geiger, ADF&G

Variability of Stikine sockeye run sizes. Kathleen Jensen, ADF&G

Friday, March 12, 1999

Fishery Management (Ben Van Alen, Chair)

- 9:00 AM *Ben Van Alen* - "Managing" Escapements in Southeast Alaska
- 9:30 AM *Dave Barto* - Assessing the Production of Chilkat Lake Sockeye Salmon Through the Paleolimnologic Sediment Record
- 10:00 AM *Alicia Perez* - Habitat Changes and Sockeye Salmon Production in the Chignik Lakes, Alaska Peninsula
- 10:30 AM *Break*
- 11:00 AM *Doug Molyneaux* - Recent Year Fluctuations in Kuskokwim River Coho Salmon Abundance
- 11:30 AM *Bev Cross* - Forecasting Bristol Bay Sockeye Salmon and What It Means to Management???
- 12:00 PM *Lunch*

Panel Discussion(s) (Debbie Hart, Chair)

- 1:30 PM Evaluating Freshwater Life Stages for Fishery Management. Bob Clark, Moderator *SF Anch*
- 2:00 PM Evaluating Saltwater Life Stages for Fishery Management. Bob Marshall, Moderator *CF Douglas Biometrician*
- 2:30 PM *Break*
- 3:00 PM Alternate Models of Recruitment. Hal Geiger, Moderator

Climate regimes and hatchery to wild ratios

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Department of Fisheries and Oceans, Pacific Biological Station
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In recent years it has been generally accepted that the abundance of salmon is regulated both in freshwater and in the ocean. It is also generally accepted that there are climate related shifts in the productivity of marine ecosystems that change quickly from one carrying capacity level to another. There is less acceptance that the carrying capacity for Pacific salmon changes as the climate-ocean regimes change. There is, however, some urgency in addressing the issue of carrying capacity. At a time when global warming threatens to warm freshwater habitats and alter the productivity of marine habitats, it is the evolved genetic variations in wild fish that represent the biological solutions to the expected extreme environmental variability. If the total return is regulated by growth based mortality in the first ocean winter according to the Beamish-Mahnken critical size-critical period hypothesis, it is possible that in less favourable conditions, wild fish will be replaced by hatchery fish. If this happens it will be more difficult to protect salmon from global warming impacts with the added possibility that the total returns will continue to diminish.

Ocean Climate Change and Population Status of British Columbia Salmon in the 1990s

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Rapid declines in the productivity of all species of British Columbia salmon occurred during the 1990s. Once lagged back to the year of ocean entry, adult returns of each species dropped beginning in 1990. The rates of decline in catch with time is almost identical to the rate of decline in indexed escapement to the rivers, indicating that the declines in catch are a reflection of overall population trends and are not the result of reduced harvest rates.

The patterns of change from 1990 to 1995 indicate that the reduced ocean survival of young salmon likely occurred in the coastal ocean off British Columbia during the first few months after ocean entry. After 1995, suddenly reduced marine survival of Alaskan salmon populations indicates that the region of poor ocean survival appears to have increased to include Alaskan coastal waters. This change off Alaska is likely to further reduce the ocean survival of British Columbian salmon, as well as populations to the south whose juveniles must swim through B.C. waters (i.e. Oregon and Washington state salmon stocks).

The cause of the precipitous declines in salmon abundance and productivity during the 1990s in British Columbia are only partially understood, but appear to be the result of oceanographic changes in the physical structure of the ocean. Biological productivity fuelling the food chain appears to be reduced over a vast region of the coastal ocean stretching from Vancouver Island north to the Aleutian Islands in the 1990s as a result of nutrient depletion in the surface waters. The observed oceanographic changes may also be partly attributable to the early stages of global warming. Further oceanographic changes in this region are likely, and may determine whether salmon survival improves or deteriorates further. However, the magnitude of these natural changes in survival are so large that, at least for some species, it may not be possible to reduce harvest rates sufficiently to compensate for the reduced ocean survival that is now apparently occurring.

There is an immediate need to recognize and react to these ocean changes much more rapidly than has occurred to date. This will require identifying what factors are reducing the marine survival of Pacific salmon, and understanding how these changes are linked to physical changes in the ocean and atmosphere. Our recent field research shows that juvenile salmon from the entire West Coast appear to travel through this region in their migration to the offshore North Pacific in a much more focussed migration than previously thought. As a result of the rapidity of the population declines, both escapement and total population size have dropped very rapidly in the most recent years from the record levels seen in the late 1980s. By 1996, escapement levels for British Columbia salmon have dropped from record highs in the late 1980s to the lowest (chum, coho, chinook) or near lowest (sockeye) levels seen since 1952.

The precipitous declines in population size and spawning escapements now occurring are the result of changes in ocean conditions, not overfishing. However, the only direct control that can be exercised over rates of population increase or decrease is to change harvest rates to ensure adequate spawning escapements. The reductions in escapement that occurred following 1990 are already large enough to substantially reduce future recruitment levels for all species of salmon. As ocean conditions appear to be deteriorating further for all species of Pacific salmon, the combined effect of reduced numbers of smolts entering the ocean and elevated ocean mortality on future productivity of British Columbia salmon is extremely serious.

El Nino, PDO and the ocean climate of the N/NE Pacific

Nathan Mantua
Research Scientist

Joint Institute for the Study of the Atmosphere and Oceans
University of Washington, Seattle, WA

A growing body of research has shown a close connection between fluctuations in north/northeast Pacific marine ecosystems and large scale features of Pacific climate. Large amplitude, year-to-year climate fluctuations, often associated with El Nino/La Nina, have dramatic impacts on the marine environment and ecology of the northeast Pacific. Typical El Nino-related environmental changes include a warming of the coastal upper ocean, raised sea levels, increased poleward coastal currents, and a deepening of the ocean surface layer. El Nino also typically brings mild winter and springtime temperatures to northwestern North America, with above average precipitation and subsequent spring/summer streamflow to much of coastal Alaska, but below average precipitation and streamflow to the Pacific Northwest. Off the west coast of the continental US, these frequent warming events often lead to a reduction in phytoplankton and zooplankton production, which in turn sets the stage for dramatic crashes in overall fishery productivity. For example, large die-offs have been observed among higher-level predators like sea-birds, marine mammals, and some salmon populations during the strong climate warming events of 1983 and 1997/98.

Perhaps even more important to northeastern Pacific marine ecology are the decade-to-decade environmental shifts associated with the Pacific Decadal Oscillation (PDO). The PDO has been described as an interdecadal El Nino-like pattern of climate variability. Warm phases of the PDO bring decadal-persistent El Nino-like environmental changes. Long-lived (20 to 30 year) climate fluctuations associated with the PDO have been linked to dramatic and persistent changes in the large marine ecosystems of the North Pacific Ocean. Since 1977 (the last switch from cold to warm PDO regimes) these changes include crashes in Alaska Murre (sea-birds) and Stellar Sea Lion populations, significant reductions in Halibut growth rates, sharp declines in Alaska King Crab and shrimp fisheries, altered salmon migration routes, and an era characterized by record salmon production in Alaska but very low salmon production in Washington, Oregon, and California.

In my talk I will first present an overview of the PDO and ENSO phenomena. I will also describe the physical climate connections that link these patterns of climate variability to ocean conditions in the north and northeast Pacific, with an emphasis on those processes that are thought to be critical for causing variations in the ocean ecology of Pacific salmon.

- 1) PDO is a "decadally" persistent El-Nino-like pattern of Pacific Basin climate variability
- 2) Pacific salmon production pattern appears to be esp. sensitive to PDO climate variations
 - * PDO influences on marine & stream environments working together!

Changes in the Physical Environment of the Eastern Bering Sea and Some Potential Consequences for Biota

By

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INTRODUCTION

Aspects of the physical environment of the Arctic are undergoing dramatic change (e.g., Weller et al., 1997). Air temperatures for Anchorage, Fairbanks, Nome, and Barrow for the period 1954-1994 considered together show a steep increase of nearly 2°C around 1977 and the warmer temperatures have persisted (Bowling, 1995). This is consistent with an overall long-term warming trend in the atmosphere over the arctic of 0.75°C per decade which occurred from 1961-1990 (Chapman and Walsh, 1993). Sea-ice extent shows a sharp decrease of more than 5% in the Bering Sea in approximately 1977; a lower areal coverage has persisted since then (Niebauer 1998). Sea-ice thickness and extent, sensitive indicators of climate change, appear to have decreased since 1976 (Wadhams 1995). Many of the local residents around the Bering Sea also have noted the changes in ice thickness and strength (Gibson and Schullinger, 1998). Precipitation in Alaska west of 141° (not including Southeast Alaska) has increased since 1970 (Groisman and Easterling, 1994). The extent of glaciers has decreased. Permafrost temperatures measured in boreholes in northern Alaska are 2-4°C warmer than they were 50-100 years ago (Lachenbruch and Marshall 1986). Discontinuous permafrost has warmed considerably and is thawing in some locations (Osterkamp 1994). The nature of these physical changes and their implications for biota of the Bering Sea are the focus of several ongoing research programs, including: the National Oceanic and Atmospheric Administration's Fisheries Oceanography Coordinated Investigations (FOCI: <http://www.pmel.noaa.gov/foci/home.html>) and The Coastal Ocean Program's Southeastern Bering Sea Carrying Capacity (SEBSECC: <http://www.pmel.noaa.gov/sebscc/index.html>). The Bering Sea Impacts Study (BESIS: <http://www.besis.uaf.edu/>) will focus on changes in the ecosystem and their attendant socio-economic ramifications.

Whether these changes, which are all related to warming, represent a natural long period cycle or a persistent trend due to the greenhouse effect (or a combination of both signals) is moot. Concentrations of carbon dioxide as measured in the atmosphere at Barrow show a trend of increase similar to that observed worldwide (Conway et al., 1994). This can be interpreted as supporting the belief that the greenhouse effect is a major source for the observed temperature changes in the atmosphere. All of the changes noted above are consistent with a warmer and wetter climate in the Arctic, as predicted by computer models which include the greenhouse effect (Weller et al., 1997; Folland et al., 1998). Others (e.g., Grotefendt et al., 1998) interpret warming of regions of the Arctic Ocean as being related to the inherent natural variability of the system with time scales of decades. The simple fact is that the climate of the arctic is warming.

Several groups of scientists have convened in the mid-1990's to hypothesize changes to the Bering Sea under a global warming scenario (US GLOBEC, 1996; Weller et al., 1997). Among the changes forecast for the eastern Bering Sea (Figure 1) were that wind mixing energy, the supply of nutrients and sea ice extent/thickness would decrease, while sea surface temperature would increase. The physical conditions observed during 1997 in the eastern Bering Sea fit these predicted changes well. During 1998, some abnormal conditions continued, although storminess increased in contrast to 1997, when winds were weaker than normal. The implication of these changes to biota is difficult to forecast, because of the complexity of the mechanisms which link them, and of the limited duration and spatial coverage of observations made in the Bering Sea.

RECENT ANOMALIES

A variety of anomalous conditions were observed in the Bering Sea during 1997 and 1998 (Schuamcher et al., 1998; Vance et al., 1998; Stabeno 1998; Napp and Hunt, submitted; Hunt et al., submitted), including: major coccolithophorid blooms (1997 and 1998), large die-off of shearwaters (1997), salmon returns far below predictions (1997 and 1998), the unusual presence of whales in the waters of the middle shelf (1997 and 1998), unusually warm sea surface temperatures (1997 and 1998), and a decrease in the onshore transport of slope water (1997). In order to determine how unusual conditions were, we now place some of them in context with conditions over the longest possible time period. For more complete examination of physical phenomenon, analyses and interpretation of results see Stabeno et al. (submitted).

Given the basin-wide scale of the atmospheric anomalies that dominate seasonal and longer-term variability, the conditions that occurred in 1997 and 1998 are related to the state of the entire North Pacific climate system. While no one index accounts for all of the natural variability, there is significant correlation between the atmospheric circulation over the North Pacific and the El Niño-Southern Oscillation (ENSO) which varies on 2-7 year time scales and the Pacific Decadal Oscillation (PDO) of North Pacific wintertime sea surface temperature (Mantua et al., 1997). The strength and position of the Aleutian Low is important to atmospheric conditions in the Bering Sea through its impact on surface winds (advection and mixing of the upper ocean and advection of ice) and heat flux (mixing and ice formation). A relationship exists between the seasonal mean Aleutian Low and both the ENSO (in terms of the NINO3 index of sea surface temperature across the equator) and PDO (Figure 2). The time series of both the ENSO and PDO indices show a marked change between 1976 and 1977; this is the well known "regime shift" (e.g., Trenberth, 1990). The Aleutian Low is generally stronger when the PDO and to a lesser extent the NINO3 are positive, and visa versa. The Aleutian Lows during 1996, 1997 and 1998 were slightly stronger than normal, while during 1995 it was weaker. As will be shown below, this contributed to substantial differences in sea ice timing and persistence.

Because there is a relative wealth of environmental observations at Site #2 (Figure 1), in particular the numerous time-series obtained from FOCI biophysical platforms (Stabeno et al., 1997), we use observations of sea ice at this location to create an index for the southeastern middle shelf. The time of arrival, persistence and departure of ice at this location (Figure 3) indicates that the most extensive ice years coincided with a strong negative PDO (Figure 2). Sea ice arrived at this location as early as January and remained as late as mid May. Between 1979-1981, ice was largely absent from the middle shelf near Site #2. Beginning in the early 1990s, ice once again became more common in this region, although not to the extent that was observed in the early 1970s. Neither the PDO nor ENSO account for all the fluctuations in sea ice over this region. While a statistically significant correlation (at the 0.01 level) exists between an index of sea ice extent and ENSO, the amount of variance accounted for is less than 7% (Niebauer, 1998). The manifestation of El Niño at high latitudes is not consistent. During two of the five El Niño events which occurred since 1972 (Figure 3), there was no ice at Site #2, and the presence of ice during other years was intermittent. These characteristics are not, however, uncommon to this time series; ice was also intermittent or absent in non El Niño years.

We divided the ice observations into three subsets according to generally agreed upon regime shifts and/or interdecadal variations (Stabeno et al., submitted: Figure 4): 1972-1976 (cold period), 1977-1988 (warm period), and 1989-1998 (weaker cold period) to characterize the temporal variability in the spatial pattern of sea ice. During the first period, ice covered the shelf out to and over the slope and remained around St. Paul Island for more than a month. During the later years, ice did not extend as far seaward and its residence time was typically 2 to 4 weeks less than during the cold period. The differences between the two latter regimes is more subtle, but still evident. Along 59°N, there were 2-4 weeks more ice during 1989-98, than during 1977-1988. Surprisingly, north of St. Lawrence Island and along the west coast of Alaska north of Nunivak Island, there were 1-2 more weeks of ice cover in the warm period than in the cooler third period. This resulted from either later arrival or more rapid retreat of sea ice over the northern Bering Sea shelf. Marked differences also exist in the ice distribution and extent along the Alaskan Peninsula. During the cold period, ice concentration extended seaward nearly to Unimak Pass, whereas in the other two periods contours of ice persistence were curved land ward into inner Bristol Bay. This pattern is likely related to variations of inflow and/or temperature of the Gulf of Alaska shelf water which flows through Unimak Pass onto the Bering Sea shelf. Either condition would move the thermodynamic limit of ice further into Bristol Bay.

Temperature records (Figure 5) collected from FOCI biophysical platforms reveal a large seasonal cycle which is typical for the southeastern middle shelf. In January, the water column is well mixed. This condition persists until buoyancy is introduced to the water column either through ice melt or solar heating. The very cold temperatures that occurred in 1995, 1997 and 1998 resulted from the arrival and melting of ice. During 1996, ice was present for only a short time in February when no mooring was in place. Generally, stratification develops during April. The water column exhibits a well defined two layer structure throughout the summer consisting of a 15-25 m wind mixed layer and a 35-40 m tidally mixed bottom layer. Deepening of the mixed layer by strong winds and heat loss begins as early as mid August, and by early November the water column is again well mixed.

During any given year marked variations are superimposed on the mean warming trend observed at Site 2. During 1995 ice persisted for more than a month, however, the water column was mixed to the bottom only for a short period in March because advection of warmer, more saline water in the lower layer created a strong density gradient between the upper and lower layers. This effectively insulated the lower layer, limiting warming of the cold pool to less than 0.3°C/month. The mixed layer was shallow (<20m), because of the weak winds that persisted in June and July. During 1996, sea ice arrived early in February and remained for only a short time. Since there was little buoyancy contribution from ice melt, the density gradient was weak and above average wind mixing resulted in a deeper surface layer than in 1995. Between April and August, the bottom temperature warmed by ~1°C/month. During 1997, ice was less persistent than in 1995, and weak winds and strong heating resulted in a shallow warm mixed layer. A storm during late May mixed the water column to 50 m, reducing the density gradient between the upper and lower layer. As in 1996, there was substantial warming (~1°C/month) of the cold pool. In contrast to 1995 and 1997, ice arrived early in February 1998, during a period weak winds. Thus, while the ice quickly cooled the upper layer, it did not affect temperatures of the bottom

layer. Only after the retreat of the ice in late February did wind energy become sufficient to mix the water column to the bottom. The combination of the warm bottom water with the cold surface water, produced above average water column temperatures. The water column then remained well mixed until late May. The weak of stratification permitted a steady warming of the bottom layer by $\sim 0.8^{\circ}$ C/month from June through August.

In addition to temperature and salinity, fluorescence and chlorophyll are measured at the FOCI biophysical platforms. A phytoplankton bloom occurred in March/April during 1995 and 1997, associated with the arrival and melting of sea ice. The bloom began even though the water column was not stratified. In 1996 and 1998, when ice was present early in the year (February) the earliest bloom occurred during May. It is likely that during 1996 and 1998, the ice was present too early in the year (insufficient sunlight) to initiate an ice associated bloom.

BIOTIC RESPONSES

Mechanisms, many of which are neither known nor understood, transfer climate changes via the ocean to biota (Figure 6). Identifying and understanding how these mechanisms function is central toward understanding ecosystem dynamics (Francis et al., 1998: Figure 1). Interannual variability in the atmosphere and in the ocean's response have significant implications for the biota of the North Pacific and Bering Sea (e.g., Mantua et al. 1997). Fluctuations in the physical environment can impact the ecosystem through both changes in the nutrient-phytoplankton-zooplankton sequence (i.e., bottom-up control), and/or by altering habitat resulting in changes in abundance and/or composition of higher trophic level animals (i.e., top-down control). For the eastern Bering Sea, top-down control may be responsible for year to year fluctuation of zoo- and phytoplankton biomass, while bottom-up control has been suggested as the mechanism for longer period (decadal) variations (Sugimoto and Tadokoro, 1997). A feature not present in more temperate ecosystems, sea ice and its interannual variation, has marked ramifications for both the physical and biological environment. Distributions of marine mammals (Tynan and DeMaster, 1997) and fish (Wyllie-Echeverria and Wooster, 1998) as well as survival of age-1 pollock (Ohtani and Azumaya, 1995) respond to the extent of sea ice itself and to that of the cold pool of bottom water which is directly related to ice cover. The substantial increase in jellyfish biomass over the eastern shelf of the Bering Sea may be linked to climate change through ice cover (Brodeur et al., submitted). The extent, timing and persistence of ice cover can dramatically alter time/space characteristics of primary production (Niebauer et al., 1995; Stabeno, et al., 1998), secondary production and hence food for larval fishes (Napp et al., submitted). Knowledge of mechanisms which link the intimately coupled atmospheric-ice-oceanic system to biota are crucial toward understanding the ecosystem of the Bering Sea.

The climate over the Bering Sea has warmed and many changes have occurred in sea ice and the ocean itself. It is clear that climatic factors have a profound impact on populations of marine biota in the Bering Sea (e.g., Napp and Hunt, submitted). Although the details of how this occurs typically is obscure, temperature, turbulence and transport are primary candidates for operative mechanisms. Recent results support the belief that interannual and decadal changes in the environment (using ocean temperature as an index or measure of the changing state of the physical environment) play a significant role in salmon production in Alaskan waters (Downton and Miller, 1998; Kruse, 1998; Welch et

al., 1998). Another study suggests the importance of turbulent mixing processes is the North Pacific Ocean to salmon production (Gargett, 1997). In the southeastern Bering Sea, the mechanism of advection of the planktonic stages of pollock (Wespestad et al., in press) and Tanner crabs (Rosenkranz et al., 1998) accounts for some of the observed fluctuations in year-class strength. In these studies the mechanism which links advection to yearclass strength is predation. The advection models use wind-drift of the planktonic stages either to or away from regions where strong predation pressure exists. In the case of marine mammals and seabirds, climate effects appear to be mediated through the food web, although in some cases the links may be direct (Springer, 1998). Such examples of research show that we are making progress towards linking climate changes and biological processes to form a more realistic and complete understanding of the ecosystem.

Many changes have occurred in the eastern Bering Sea for which our observations are not sufficient to develop a clear understanding. Coccolithophorid blooms existed in 1997 and 1998 under a different environmental conditions (Hunt et al., submitted). Why did this happen and what are the implications for the occurrence of blooms in to future? What are the implications of coccolithophores replacing the small flagellates that normally dominate in summer? It is likely that favoring another trophic level between primary producer and consumer (i.e., microzooplankton; Neĵstgarrđ et al., 1997) will affect ecosystem dynamics (Napp and Hunt, submitted). Attenuation and scattering of light by whole cells and detached liĥs alters submarine light fields (Voss et al., 1998), influencing competition among phytoplankton species and affecting the quality and quantity of light for subsurface visual predators (e.g. diving seabirds). Dense concentrations of coccolithophores also alter regional biogeochemical cycles making large positive contributions to calcite and dimethylsulfide production (e.g. Matraĭ and Keller, 1993; Brown and Podesta, 1997).

Other dramatic changes in the ecosystem have occurred which emphasize the importance of biological interactions. During the regime shift of the mid-1970's, the physical system of the Bering Sea experienced significant change. Atmospheric conditions which had favored strong winds from the north, extreme ice cover and an extensive cold pool became those which generated minimal ice cover and magnitude/extent of the cold pool. In addition, surface wind-drift (transport of planktonic material) also changed markedly (Wespestad et al., in press). The environmental conditions in winter and spring of 1977/78 established a set of crucial biophysical features which promoted the development of the extremely large 1978 yearclass of pollock. While the exact nature of this increase is unknown, the role of cannibalism resulting from the strong yearclass is being elucidated (Livingston and Methot, 1998). The abundance of a cannibalistic population began to increase sharply around 1983, when individual pollock in the 1978 yearclass became large enough to start eating juvenile pollock to a large extent and caused age-1 predation mortality to increase sharply (Figure 7). Livingston and Methot (1998) used a predation model to examine estimates of the absolute abundance of pollock yearclasses at the beginning of age-1 (i.e., the number that existed before cannibals ate them: Figure 8), and showed that there were several good yearclasses after 1978. These started out at age-1 in greater abundance than the 1978 yearclass, but, due to cannibalism, a lower yearclass abundance when seen as age-3 recruits into the fishery. The model results indicated the possibility of two different spawner-recruit relationships, one for average to cold years and one for warmer years.

This result would not have stood out as clearly if predation mortality was not understood and taken into account. Further, the results highlight the importance of studying the biotic interactions in order to pinpoint which life history stage of a given population is most influenced by abiotic factors. Although there have been above-average yearclasses since 1978, none have appeared quite so large when they recruit to the fishery because of this increase in predation mortality. We likely won't see a yearclass as large as the 1978 yearclass again until we get a combination of a relatively low adult population and winter/spring conditions favoring larval survival.

Smaller than average adult salmon (Kruse, 1998) and decreases in the numbers of seabirds breeding on the Pribilof Islands since the mid 1970s point to a recent change in the carrying capacity of the middle shelf region (Hunt and Byrd, in press). Food may be becoming a limiting resource for populations such as walleye pollock due to the increased abundance of some planktivorous marine mammals which are rebounding from decades of whaling (Tynan, 1998). Further pressure on food resources results from the marked increase in biomass of jellyfish (Scyphomedusae) (Brodeur *et al.*, submitted). As noted by Napp and Hunt (submitted), if food becomes limiting, then climate induced perturbations that affect production and availability of zooplankton may have an even greater effect on the structure of trophic webs than was observed in 1997.

These are only a few examples of changes in the ecosystem dynamics of the eastern Bering Sea. To make further advances in our understanding of how this ecosystem functions requires a greater monitoring effort of both physical and biological parameters. This will allow identification of the important fluctuations and elucidation of the mechanisms by which changes in physical phenomenon are transferred to biota. In addition, this would permit the development of more complete knowledge of the life histories of the central species in ecosystem and elucidate biological mechanisms such as predation.

ACKNOWLEDGEMENTS

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FIGURES

1. The eastern Bering Sea showing the location of the FOCI moored biophysical platforms.

2. Atmospheric indices for the North Pacific and Bering Sea: an index of ENSO (the NINO3 index), the PDO8 (after Mantua *et al.*, 1997) and the Aleutian Low (from Stabeno *et al.*, submitted)

3. The persistence of ice cover at the position of Site #2 is indicated by the dark bars. The shaded areas indicate periods when an El Niño was occurring on the equator (from Stabeno *et al.*, submitted).

4. Contours of the number of weeks that sea ice was present over the Bering Sea shelf. Show as the average ice coverage during: a) 1972 - 1976, b) 1977 - 1988, c) 1989 - 1998 and d) 1972- 1998 (from Stabeno *et al.*, submitted).

5. Time-series of water temperature and chlorophyll/florescence collected at Site #2. The coldest temperatures indicate the presence of ice (from Stabeno *et al.*, submitted).

6. Pathways that changes in climatic influence the biological environment (after Francis et al., 1998). We have added ice which couples atmospheric phenomenon to the ocean thereby effecting biota in a bottom-up mode. The presence of ice also directly influences distributions of marine mammals exerting an aspect of top-down control. Note that the presence of a coccolithophorid bloom also has direct influence on light penetration (primary production) and success of visual feeders.

7. (top panel) Predation mortality of age-1 walleye pollock from 1963 to 1995 estimated by the eastern Bering Sea pollock population model with predation by adult pollock, Pacific cod and northern fur seals. (bottom panel) Estimates of age-1 recruitment of pollock recruits versus pollock spawning biomass from the pollock population model with predators and the fitted Ricker stock recruitment curves. (from Livingston and Methot, 1998).

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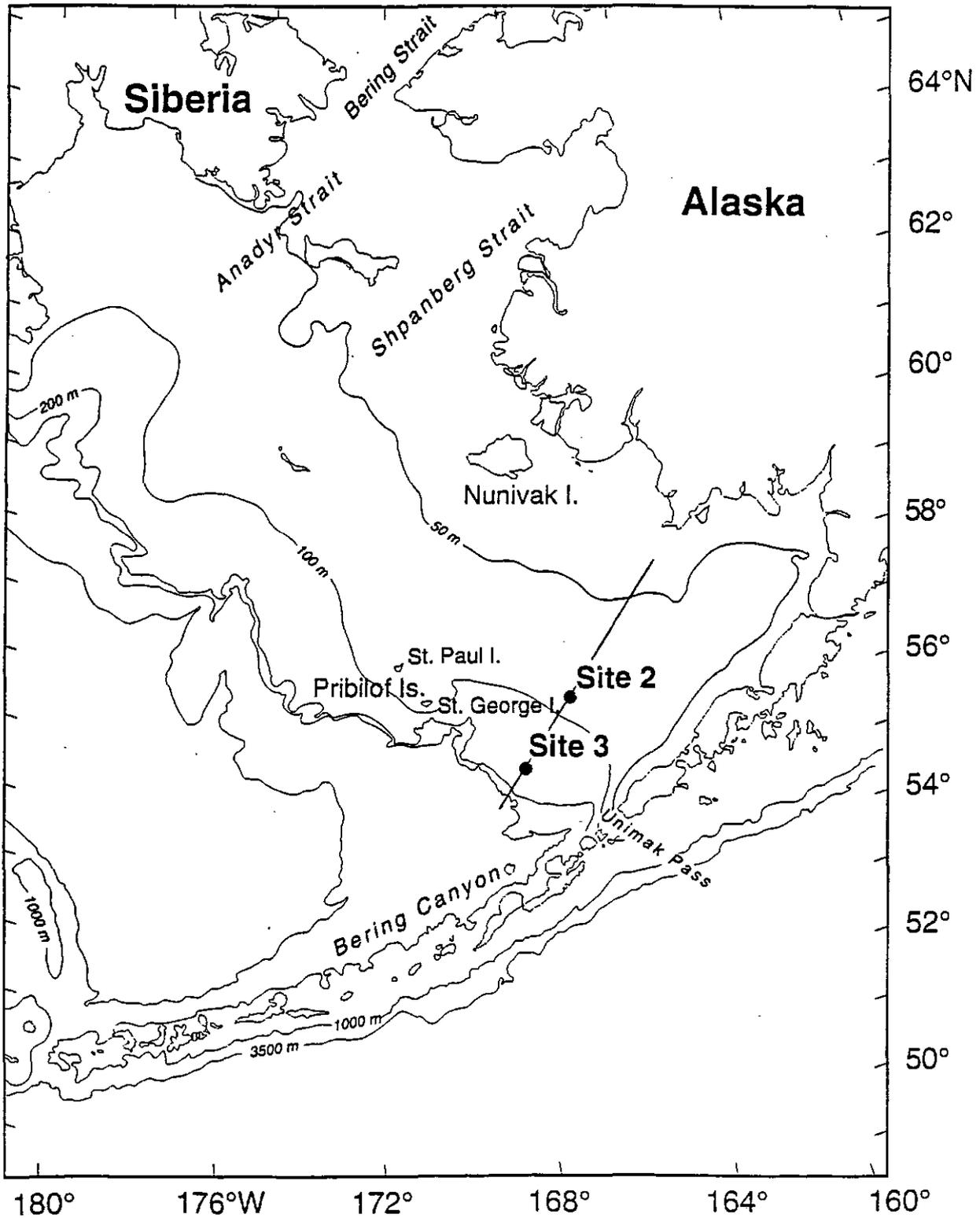
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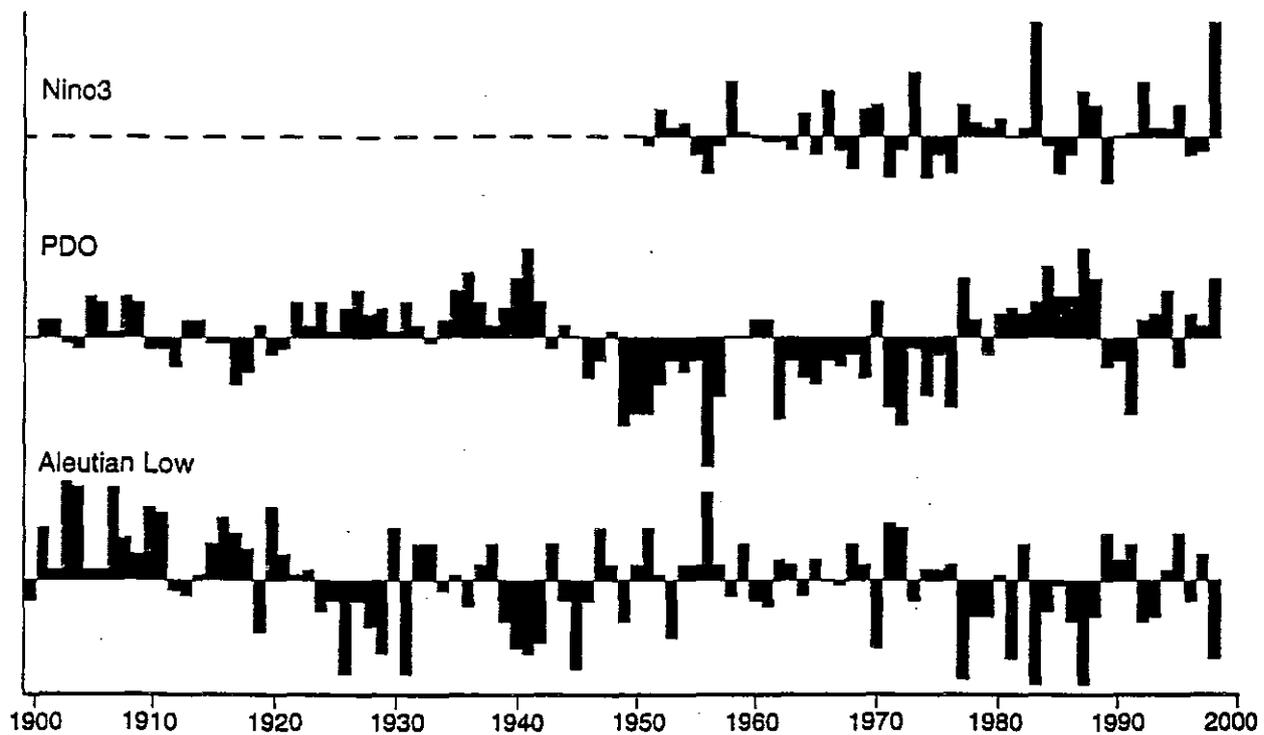
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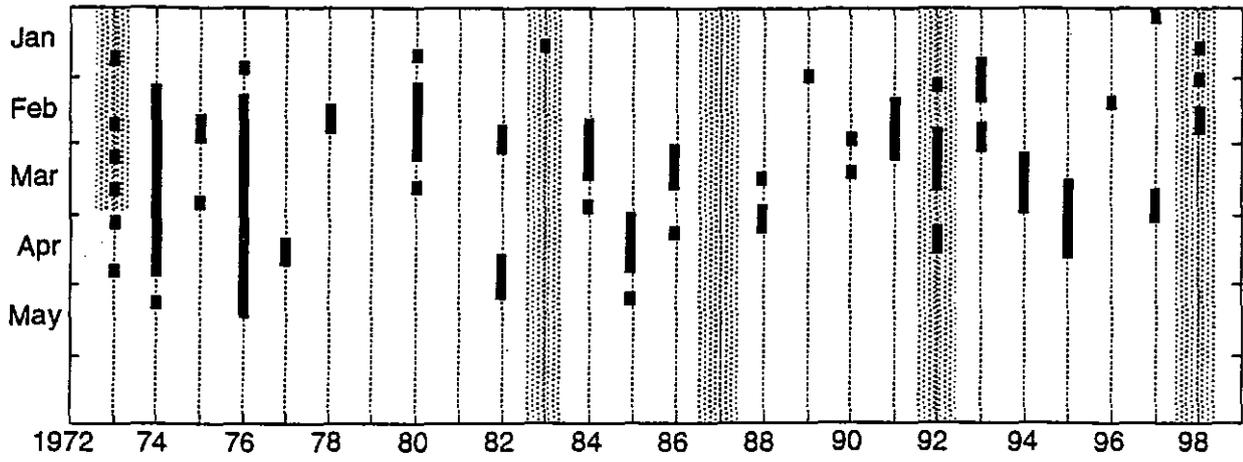
Eastern Bering Sea showing location of FOCI moored biophysical platforms (Site #2 & #3)



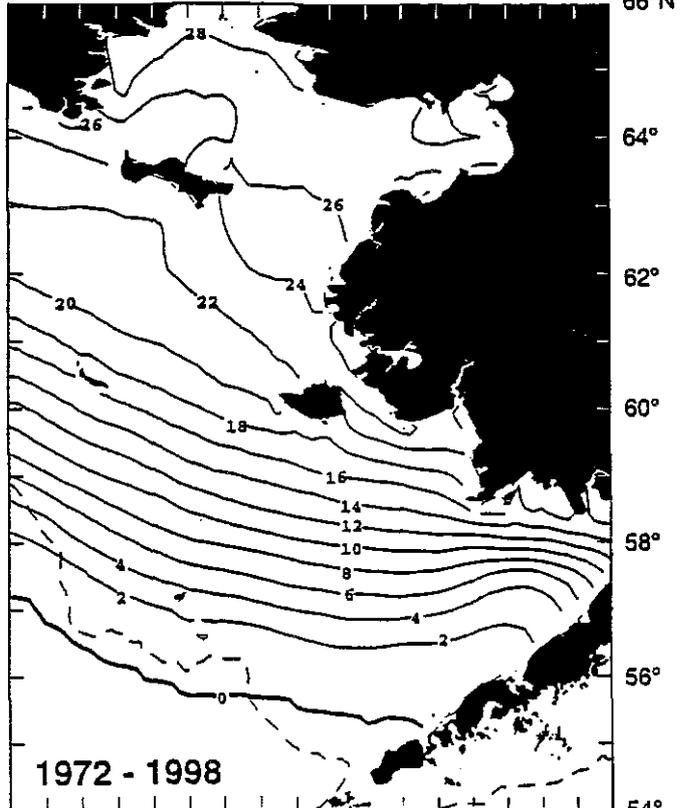
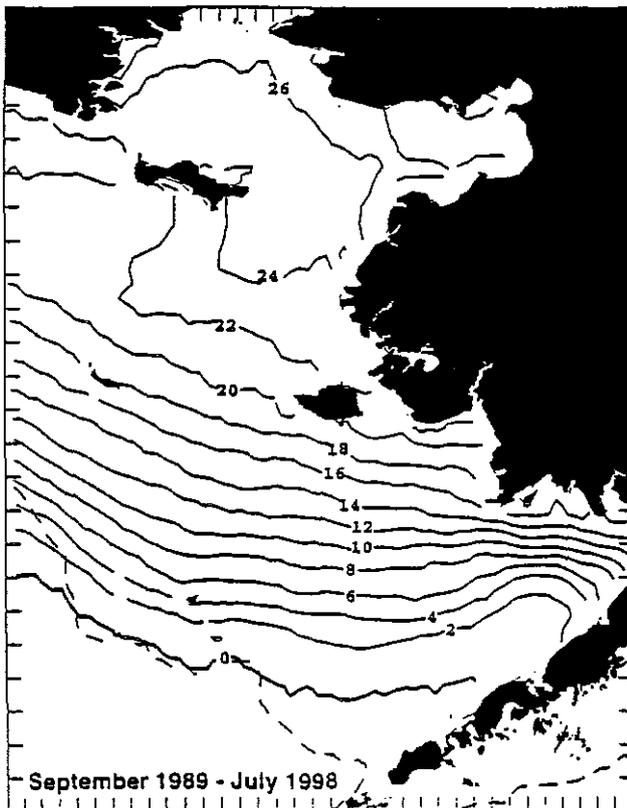
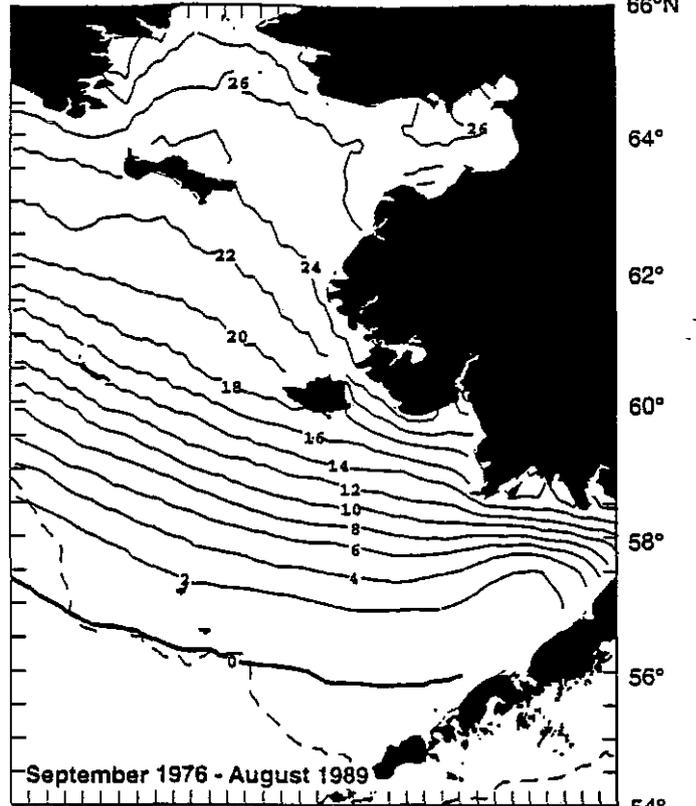
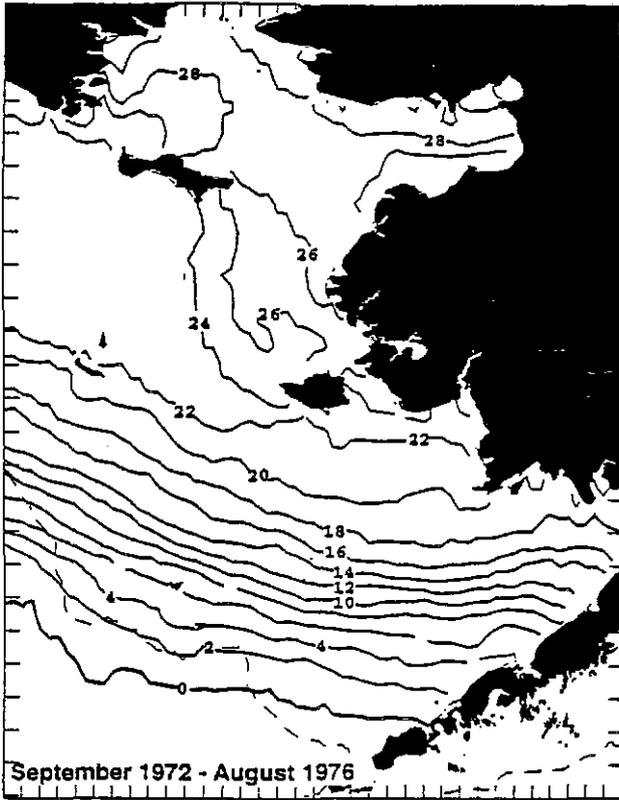
Atmospheric Indices



Persistence of Ice at Site #2



Ice Coverage



175°

171°

167°

163°

159°W

175°

171°

167°

163°

159°W

66°N

64°

62°

60°

58°

56°

54°

66°N

64°

62°

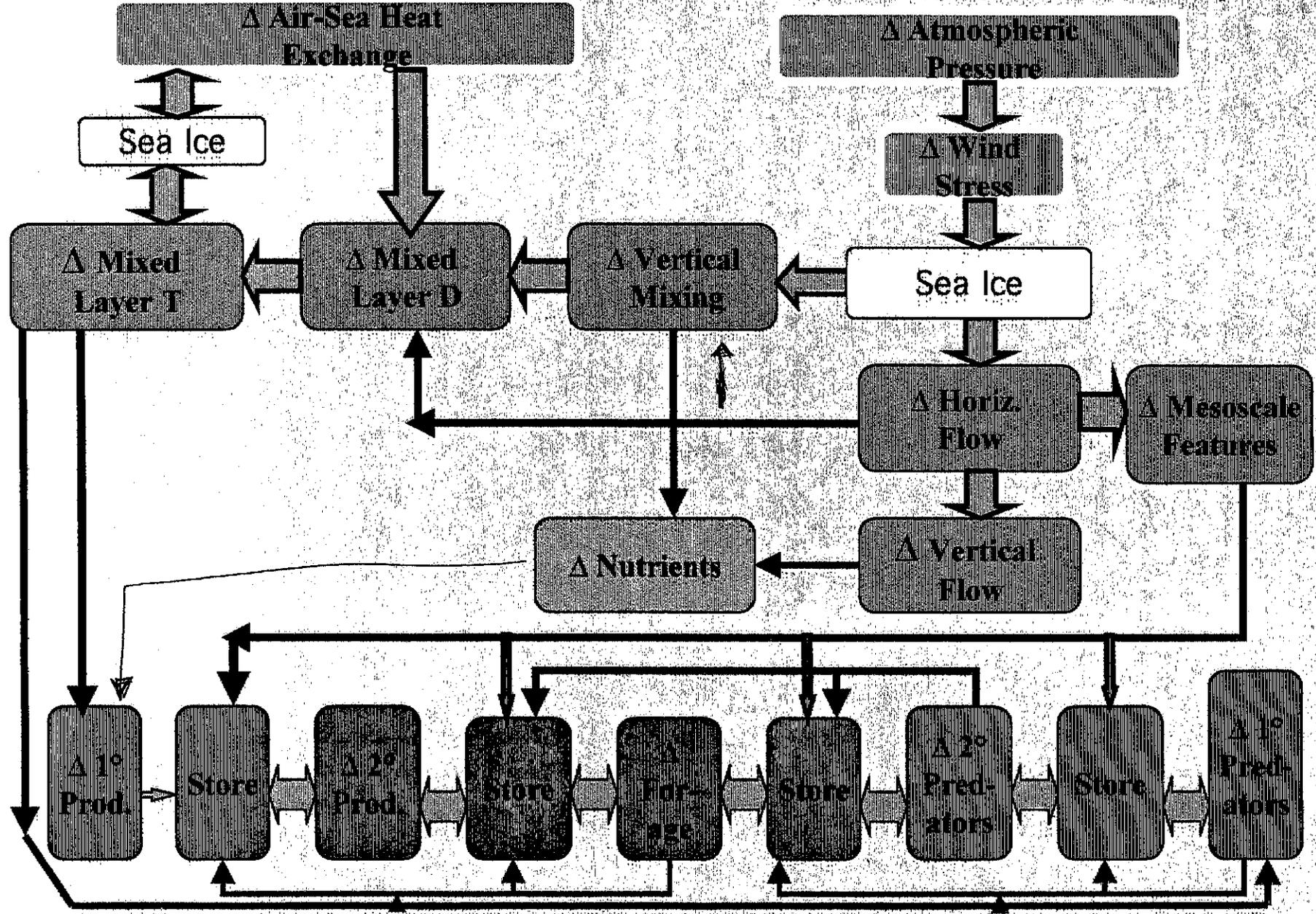
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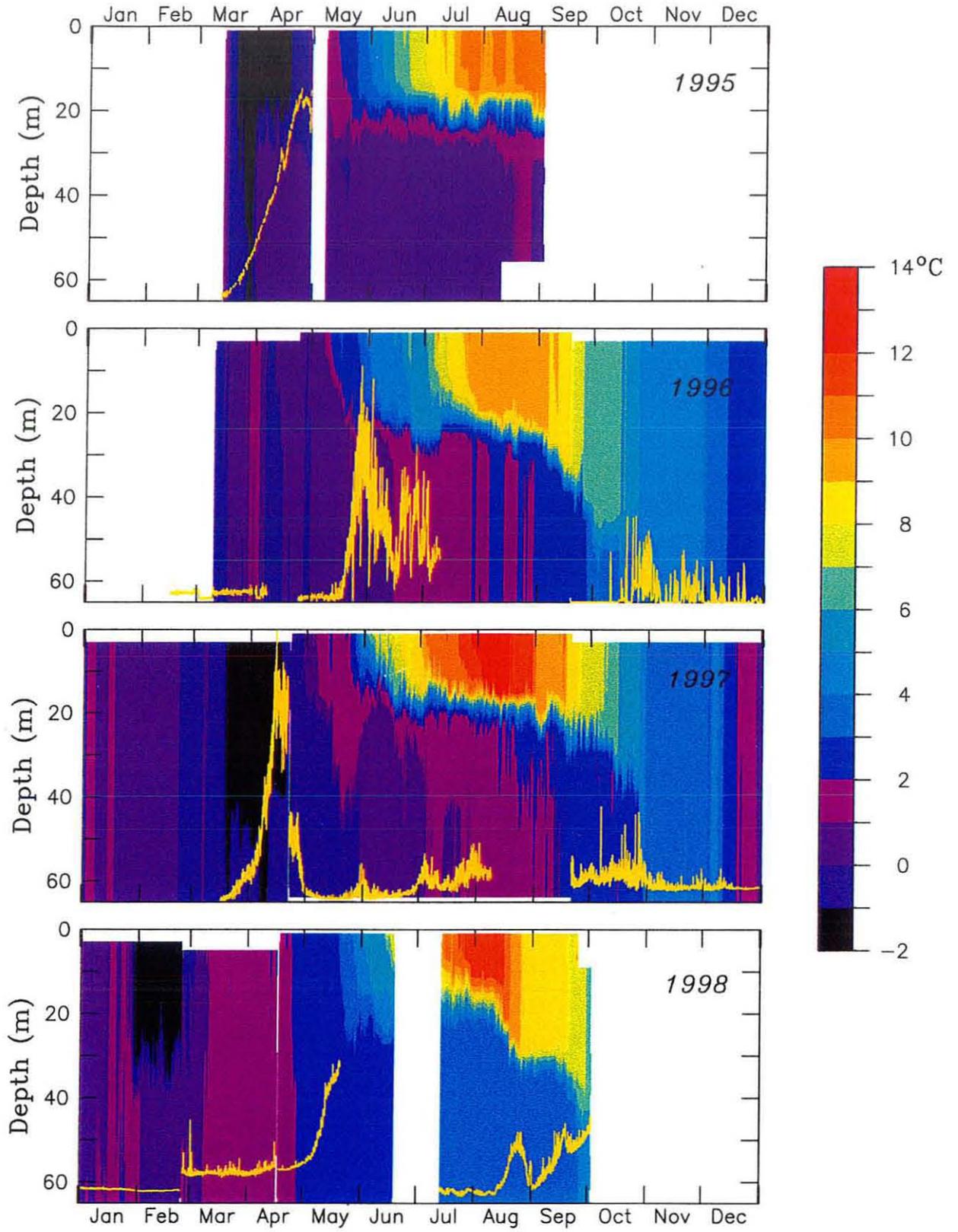
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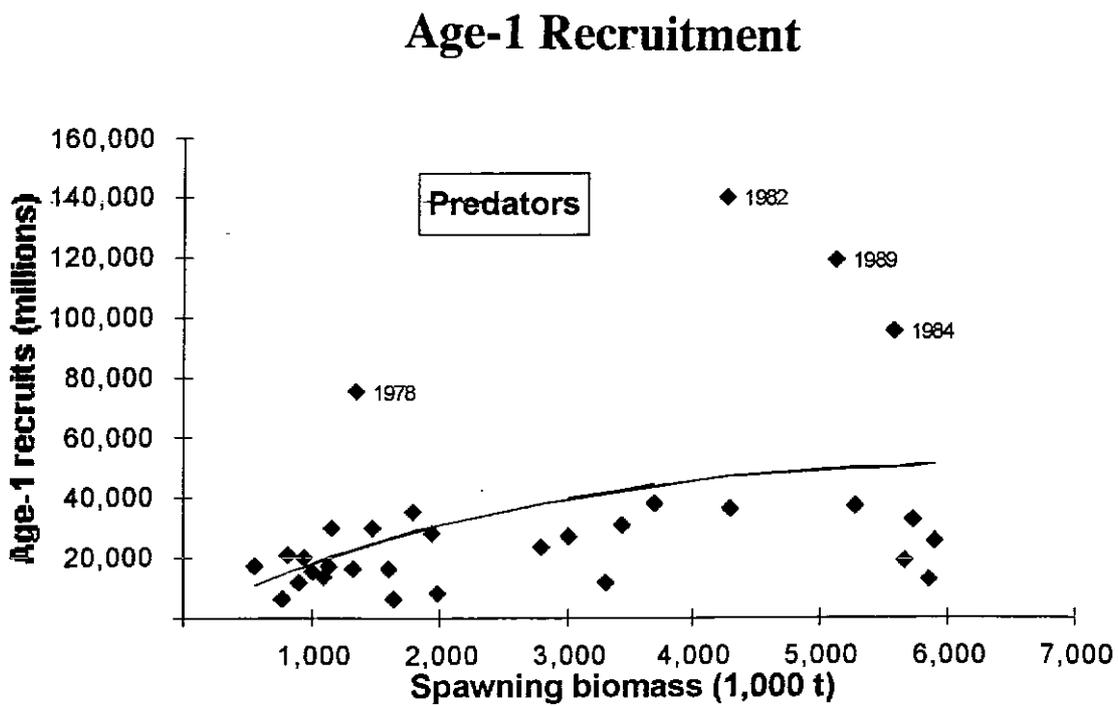
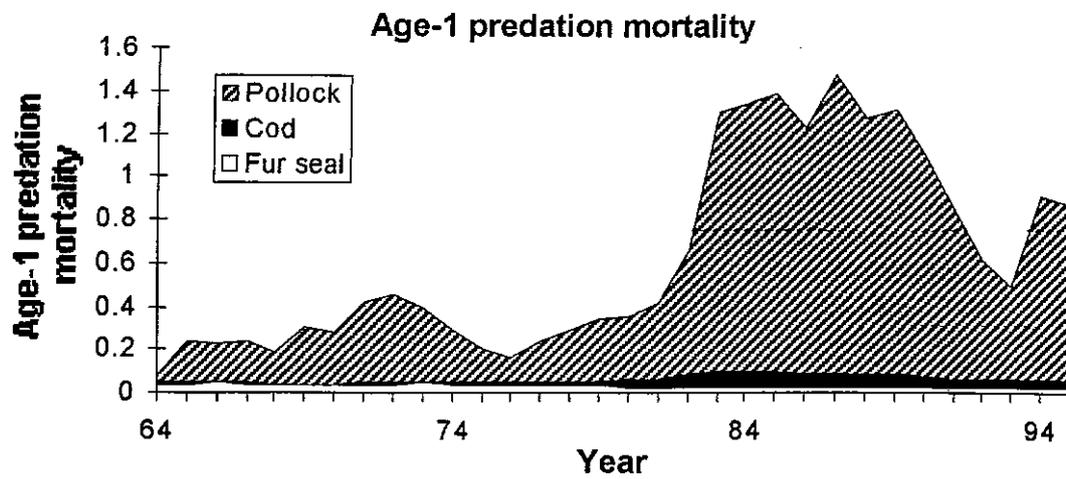
54°

Mechanistic Pathways from Changes in Climate to Marine Biota (after Francis et al., 1998)



Water Column Temperature & Index of chlorophyll at Site #2





Oceanographic modification of decadal-scale pink salmon production variability in Prince William Sound, Alaska: some candidate mechanisms

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An examination of wild pink salmon production records for Prince William Sound since the early 1960s portrays a dramatic response to a widely recognized Gulf-wide oceanic regime shift in 1978. Marine survivals were anomalously high for 7 consecutive years following the shift documenting a significant improvement in production conditions coincident with that event. Recent studies of pink salmon survival during early ocean residence in Prince William Sound point to specific mechanisms that may have been responsible for the historical pattern, and provide evidence for a more recent shift to what may be a lower level of regional carrying capacity. A unique correlative linkage between ocean-derived zooplankton and wind-forced surface circulation was operational during the decade of the 1980s, but absent before or after that time. This pattern, coupled with higher ocean source populations of large calanoid copepods in the 1980s, apparently resulted in about twice the average springtime stocks of macrozooplankton than presently observed. A general dependence of wild pink salmon production on levels of zooplankton encountered as juveniles is discussed in the oceanographic context of the Sound and its physical and biological relationships to the bordering shelf and open ocean.

Pacific - Basin Climate Variability and Patterns of Northeast Pacific Marine Fish Production

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Review of oceanographic and climate data from the North Pacific and Bering Sea reveals climate events that occur on two principal time scales: a) 2-7 years (i.e. El Nino Southern Oscillation and interannual variation), and b) inter-decadal (i.e. Pacific Decadal Oscillation, PDO). The timing of ENSO events and of related oceanic changes at higher latitudes is examined. The frequency of ENSO was high in the 1980s. Evidence of ENSO forcing on ocean conditions in the North Pacific (Ni±o North conditions) were more frequently observed along the West Coast than in the western GOA and eastern Bering Sea. Recruitment data for 23 groundfish and 5 non-salmonid pelagic species from three large geographic regions were examined for evidence of Pure Temporal Variability (PTV) caused by large scale forcing at one or more of the time scales noted in oceanographic and climate data. Most salmonids and some flatfish stocks exhibited high autocorrelation in recruitment coupled with a significant step in recruitment in 1977 suggesting a relationship between PDO forcing and recruitment success. Six of the dominant groundfish stocks (Atka mackerel, Pacific cod, Pacific hake and walleye pollock) exhibited low autocorrelation in recruitment. Pacific hake and GOA walleye pollock exhibited a significantly higher incidence of strong year classes in years associated with Ni±o North conditions. These findings suggest that PTV may play an important role in governing year class strength of some Northeast Pacific marine fish stocks. A conceptual ecological model is proposed to explain these patterns of fish production.

Has the Carrying Capacity of the North Pacific Changed in Recent Decades?

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To understand the interannual and interdecadal variations in marine fish production, researchers must identify factors related to growth and survival. These factors can include nutrient dynamics, food-web processes, physiological processes, all of which may be affected by both local and large-scale physical processes. As noted by a number of fisheries scientists from around the Pacific Rim, there appears to be evidence for food limitation for several salmon species in the North Pacific. This evidence comes in the form of density dependent growth and survival and is particularly striking in the inter-specific interactions among salmonids during high abundance periods.

In this paper, we review evidence for changing ocean conditions both in the coastal regions and also in the oceanic domain of these salmon. We give examples of modeling exercises attempting to estimate forage demand of salmonids and its relation to available food resources as well as the impact predators have on limiting salmon production. These include holistic ecosystem box models, spatially and temporally explicit bioenergetics models, and bottom-up trophodynamics models. These models reiterate the importance of the non-static environment in the production of salmon and other nonsalmonid nekton.

The overall food consumption by juvenile coho and chinook salmon along the continental shelf off Washington and Oregon was estimated for the summer months of 1981-84 using both a direct field and indirect bioenergetic modeling approach. Both models yielded similar estimates but the consumption estimated by the bioenergetic model was 14.8% and 3.2% higher for coho and chinook salmon, respectively. In a given year, overall consumption increased throughout the summer but there were substantial differences among the four years within the same month. A comparison of the consumption estimates for important prey taxa early in the summer with estimated available zooplankton suggested that sufficient food may have been available for salmon during 1981 but probably not during the El Niño of 1983.

Estimates of the forage demand placed on coastal and oceanic feeding areas by wild and ocean ranched pink salmon originating from Prince William Sound, Alaska, were derived

from a bioenergetic model. Annual food consumption for these stocks rose from less than 100,000 mt prior to 1976, to more than 300,000 mt after 1988 when hatchery production began dominating adult returns. Food demand was distributed nearly equally between survivors and non-survivors, and most of the food consumption occurred in the oceanic rather than coastal environments. The ratio between total annual consumption (coastal and ocean, surviving and non-surviving) and the biomass of fry entering each year from coastal nursery areas ranged from 640 to 2264, and averaged 1223 since 1962. On average, every metric ton of fry generates the need for about 1200 mt of food to support survivors and non-survivors in coastal and ocean feeding regimes every year. These model results suggest that recent levels of wild and hatchery production in the North Pacific Ocean have placed substantial forage demands on coastal and oceanic feeding domains.

The carrying capacity of Pacific salmon in the Alaskan Gyre, expressed in density dependent changes in population size or individual growth, may be dependent on between-scale feedback. Evidence collected across the 1976-77 regime shift suggests that two types of feedback may be important. Trophic feedback controls the change between bottom-up and top-down forcing of food webs and may play a role in determining the changing of carrying capacity across a regime shift. Growth feedback, the positive feedback between individual size and obtainable diet quality, may accelerate salmon growth and raise the returning biomass in a given year, especially in cases where micronekton such as squid are an important prey item. In the salmon rearing area typified by Ocean Station 'P', small squid are both a competitor for smaller salmon and food for larger salmon. This type of "intraguild competition/predation" creates dynamics that make carrying capacity impossible to model without including this interaction. Data, models, and analysis of the variation in available forage, competitive relations, salmon production, and biomass in the Alaskan Gyre show the importance of modeling these types of ecosystem interactions when measuring yearly salmon carrying capacity as it changes across multiple scales.

High Seas Salmon Research Issues and Results in the 1990s

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In the 1990s, concerns about the consequences of global warming and large-scale releases of hatchery salmon have stimulated new interest in research on factors affecting productivity and biological characteristics of salmon in the ocean. This paper focuses on these issues with respect to research on salmon distributed in international waters (high seas) of the North Pacific Ocean and Bering Sea.

In their first summer at sea, juvenile salmon (ocean age-0) are distributed in coastal and inside waters or estuaries, where growth and survival are maximized by high biological productivity and protective habitats. Although some races, stocks, and individuals never leave coastal areas, large aggregations of juvenile salmon of all species can be found in offshore, international waters by December.

Salmon migrate to the high seas to feed, grow, and mature. High seas catch data, generalized for all species, stocks, and age and maturity groups, show extensive, seasonal feeding migrations across broad fronts, to the south and east in winter and to the north and west in summer. Tagging and tracking studies demonstrate that movements of individual adult salmon returning from the high seas to coastal waters can be rapid and direct.

High seas tag data indicate that salmon distribution and migration patterns are stock-specific, but broadly overlap those of other stocks, resulting in extensive intermingling of Asian and North American salmon in international waters. Stock-specific migration patterns may result from natural selection of fish that migrate along efficient routes to the most productive feeding areas. Intra-stock variation in these patterns is related to biological and environmental factors, especially those affecting distribution and abundance of their prey.

High seas salmon put on most of their growth during summer months. Bioenergetic model simulations indicate that in summer high seas salmon are feeding at a rate close to their physiological maximum. At sea surface temperatures typical of those found in the Bering Sea and North Pacific Ocean in summer, any decrease in daily ration could cause significant decreases in growth over a time period as short as two months. When prey is abundant, conditions favorable to salmon growth may be bounded at high temperatures by metabolic rates and at low temperatures by consumption rates.

However, new data from thermal tags attached to salmon on the high seas and recovered in coastal fisheries in 1998 indicate that salmon behavior, presumably feeding activity, with respect to time and sea temperature is much more complex than previously thought (Fig. 1). For example, salmon spent less time in warmer (surface) waters during the day than at night, and variability in activity (smaller temperature range and less movement between temperatures) was lower at night than during the day. Mid-day peaks in sea temperature also indicate some surface feeding during the day.

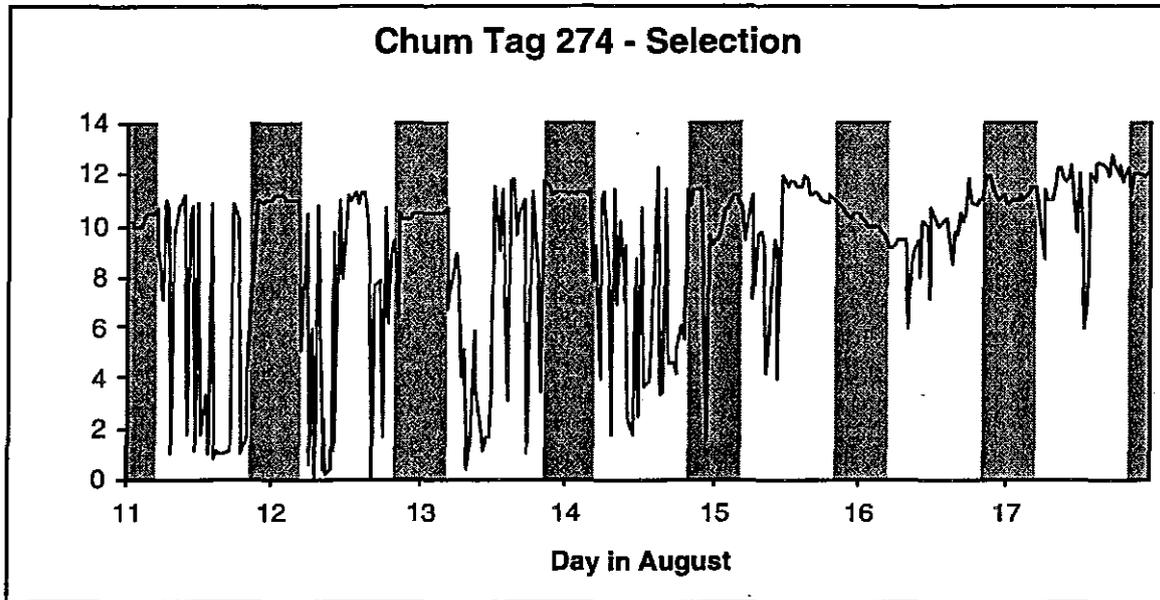


Fig. 1. Selection of data from an archival tag that records temperature and time. The tag was attached to a chum salmon tagged in the Bering Sea on 7 July 1998 and recovered in Hokkaido, Japan on 24 September (High Seas Salmon Program, School of Fisheries, University of Washington, unpublished data). Data points were collected every 30 minutes. Shaded bars represent approximate times of local night.

On the basis of relationships between sea surface temperature and salmon catch data, it has been hypothesized that a 1°-2° C rise in sea surface temperatures caused by global warming may drastically reduce the area of distribution of salmon on the high seas. However, the new thermal tag data indicate that high seas distribution of salmon may be more closely linked to their feeding behavior (prey distribution) than to sea surface temperatures.

One aspect of international cooperative high seas salmon research coordinated under the auspices of the North Pacific Anadromous Fish Commission has been to collect a new time-series of food habits data for assessment of feeding conditions and climate change effects in major salmon producing regions across the North Pacific and Bering Sea. A standardized, international salmon food-habits database is being developed for use in climate change-carrying capacity studies. For example, increased prey diversity and feeding on less nutritious prey are indices of unfavorable foraging conditions, which

result in decreased growth and maturation rates in salmon during years of low ocean productivity or high salmon abundance. Preliminary analyses of food habits databases with respect to 1997-98 El Nino conditions indicate poor feeding conditions in some high seas production areas. For example, prey consumption estimates for sockeye and pink salmon in the central Bering Sea in 1997 were approximately half of those estimated in previous years.

Global warming and increased hatchery production may affect high seas salmon most directly through effects on their forage base. However, salmon in offshore waters are highly migratory and opportunistic feeders, capable of adapting to changes in prey abundance and distribution. Because of their ability to feed at many different trophic levels, high seas salmon are very resilient, even to major changes in the ecosystem. Feeding selectivity and stock-specific migration patterns also impart a tremendous survival advantage to high seas salmon by reducing competition both within and between species. As a consequence, however, hatchery-wild competition is most likely to occur between salmon of the same species, stock, year class, and age group. During periods of low ocean productivity, aggregations of hatchery salmon on the high seas could swamp limited prey resources and attract salmon predators, reducing growth and survival of their wild cohorts.

A Long-Term Perspective On The Influence Of Lake Production And Climate Change On Alaskan Sockeye Salmon Abundance

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There is a tremendous range in relative productivity (annual salmon production per unit area or volume of a nursery lake) between different sockeye salmon systems. Within Alaska, productivity ranges from more than 50,000 adult sockeye per square km, to less than 100 adult sockeye per square km. A number of factors act to influence survival throughout the life history of sockeye, and recent changes in survival rate have been linked to variability in ocean conditions. However, freshwater conditions largely set the overall level of system productivity, and account for much of the range in productivity between systems. Therefore it is important to understand the factors limiting freshwater production of a system when assessing an escapement goal. In general, the two dominant controls on freshwater production are the quantity of suitable spawning habitat, and the abundance of food, generally zooplankton, available for juvenile sockeye. The amount of suitable spawning habitat may limit salmon production in some systems. Although difficult to quantify, knowledge as to how spawning success varies with escapement is important in predicting changes in production at different escapement levels. Lakes that maintain abundant stocks of zooplankton when spawning habitat is fully utilized are spawning-limited. The abundance of zooplankton can exert a strong control on the number of juvenile sockeye a non spawning-limited system produces. Zooplankton productivity in nursery lakes is influenced by a number of factors including lake morphometry, climatic setting, nutrient supply and water turbidity. Knowledge of the carrying capacity of a lake, that is the number of juvenile salmon the system is able to support, is critical in setting proper escapement goals and can be assessed by routine limnological surveys.

Freshwater conditions are not constant over time and may vary through both natural processes and human activity. Wise management must be aware of, and responsive to, any such changes. The amount of available spawning habitat may vary as a result of human activity in watersheds (i.e., logging, mining), and by climate change (i.e., changes in streamflow, storm/scour events). As in the ocean, changes in lake carrying capacity may result from climate change, through altering water temperatures and nutrient supply rates. Some glacial lakes may be particularly sensitive to increasing temperatures, which could lead to greater sediment input and hence increased lake water turbidity, and subsequently reduce light penetration, primary productivity and zooplankton abundance. Adult salmon carcasses are important contributors of nutrients (marine-derived nutrients) to some lakes, and thus influence carrying capacity. In such systems, a positive feedback

may exist in which increases in escapement lead to greater nutrient input, higher primary and zooplankton productivity, and subsequent increases in the abundance of juvenile and adult sockeye. If escapement goals are too low, long-term decreases in nutrient levels may occur which will lead to a reduction in carrying capacity, and system production at levels less than the maximum sustainable yield. The sensitivity of a system to marine-derived nutrients can be determined by constructing lake nutrient budgets, and by analysis of the stable isotopes of nitrogen ($\Delta^{15}\text{N}$) in lake biota. In addition, newly developed paleolimnological techniques allow reconstruction of records of escapement and carrying capacity, and a view of responses to climatic changes, and the impact of commercial fishing.

Integrating Limnological Data into Sockeye Salmon Production Models

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Considerable inter-annual and inter-lake variation exists in juvenile sockeye abundance, size, and age composition that cannot be explained solely by escapement or stocking levels. Hence, our perspective of sockeye salmon production assumes that freshwater limitations are equally as important as abiotic and biotic influences during the ocean rearing stage. The limnological approach used by the Alaska Department of Fish and Game (ADF&G) to understand sockeye production emphasizes factors such as lake morphometry, temperature, and nutrient inputs. We also recognize the role of primary (algal biomass) and secondary productivity (zooplankton), grazing, competition, and predation as interacting factors in lakes that regulate juvenile sockeye populations. Thus, to predict the carrying capacity of a lake to support juvenile sockeye and understand responses to variation in escapement requires the integration and analysis of limnological information with fisheries data.

Alaska sockeye nursery lakes span a broad geographic range, exhibit a variety of limnological characteristics, and are generally classified into clear, stained, and glacial types on the basis of water source (Table 1). Because of high loadings of colloidal (humic) materials which impart color and inorganic silt particles that produce turbidity, stained and glacial lakes exhibit shallower euphotic zone depths (EZD) and colder water temperatures compared to clear lakes ($P < 0.001$; ANOVA). Sockeye producing lakes in Alaska are also highly oligotrophic, with total phosphorus (TP) concentrations averaging $6 \mu\text{g L}^{-1}$ in clear lakes, $8 \mu\text{g L}^{-1}$ in stained lakes, and $13 \mu\text{g L}^{-1}$ in glacial lakes. However, the higher nutrient (TP) levels in stained and glacial lakes do not necessarily translate into greater algal biomass (chlorophyll) because much of the TP pool in these lake types is composed of unusable colloidal (30%) and inorganic particulate phosphorus (60%) compounds. At the secondary trophic level, crustacean zooplankton communities are also rather simple being composed of only a few species of cladocerans and copepods. This is particularly evident in glacial lakes where there is an absence of filter-feeding cladocerans. Reduced light penetration, colder temperatures, and lower chlorophyll concentration decreases seasonal zooplankton biomass levels in stained (mean 354 mg m^{-2}) and glacial lakes (mean 294 mg m^{-2}), compared to clear lakes (mean 512 mg m^{-2}). Given the diversity of lakes and fundamental differences in lacustrine productivity, associated in part with lake typology, it is not surprising that there is large variability in the size of sockeye smolt. For 35 Alaskan lakes, mean age-1 smolt population lengths ranged from 52 mm to 145 mm while mean weights ranged from about 1 g to nearly 30 g (Fig. 1). However, smolt (age-1) sizes tend to be larger in the clear lakes (mean 95 mm; 7.9 g) compared to both stained (mean 71 mm; 3.3 g) and glacial lakes (mean 69 mm; 2.6g).

Limnology studies by ADF&G have resulted in several empirical models using multiple lake data linking the physical environment, trophic status, and plankton biomass to sockeye smolt production (Table 2). Smolt biomass has been related to lake fertility, as indexed by the volume of water capable of photosynthesis or euphotic volume (EV). Specifically, smolt biomass (kg) is highly correlated with EV ($r^2=0.95$). However, EV represents an interaction term (area \times EZD) and the model is highly influenced by a few lakes with large surface areas. In large lakes, morphometry can be more important than the depth of light penetration in determining EV magnitude. Thus, EV does not predict smolt biomass very well in lakes with small surface areas ($<20 \text{ km}^2$). In contrast, EZD explains 49% of the variation in smolt biomass (kg km^{-2}). This model is diagnostically well behaved and is independent of lake size, making it preferable for predicting average numbers and biomass of smolt. When competition for food resources is limiting, smolt biomass (kg km^{-2}) is largely a function of zooplankton biomass ($r^2=0.83$). For 18 Alaskan lakes assumed to be at rearing capacity, average smolt biomass is approximately twice the mean dry weight of the seasonal (May–October) macrozooplankton biomass (mg m^{-2}). Although, juvenile sockeye growth and survival are closely tied to zooplankton biomass, it is the interaction(s) between food, competition and predation, and density-independent effects that underlies much of the variation observed in juvenile sockeye salmon growth. Considering 23 Alaskan lakes ($n=83$ lake-years), a multivariate regression with zooplankton biomass, fry density, and mean water temperature as model predictors accounts for 70% of the variation in mean age-1 sockeye smolt length and weight.

Our empirical models provide a means to predict the carrying capacity of lakes to support juvenile sockeye; however, to understand responses to variations in escapement requires the integration of limnological information with spawner-recruit data. Are there practical applications for such an approach? A brood-year interaction model has been used to quantify the spawner-recruit relationship for the Kenai River sockeye salmon. The hypothesized biological mechanism for adjacent brood-year interaction was based on empirical evidence that heavy grazing on a cohort of *Cyclops* from a large fry recruitment adversely affects growth and survival of a subsequent year-class of rearing fry through carryover (lag) effects on the forage base (zooplankton). The brood-year interaction model explained much ($R^2=0.65$) of the observed cyclical patterns in adult returns. The role of carcass derived nutrients in sustaining productivity and lake carrying capacity has also been used to consider escapement goals. Marine nitrogen trends in the sediment support the hypothesis that changes in nutrients, primary productivity, and zooplankton abundance and biomass are highly influenced by salmon carcasses, as seen by the correlation between historical sockeye escapement and sedimentary $\delta^{15}\text{N}$ profiles in Karluk Lake. The dependence of juvenile sockeye production on lake physical characteristics, forage availability, and density-dependent factors argues for including limnological data in stock-recruit modeling. Such an approach may lead to improvements in the ability to predict future fish stocks.

Table 1. Limnological characteristics for 87 Alaskan clear, stained, and glacial lakes.

Parameter	Clear (N=52)		Stained (N=21)		Glacial (N=14)	
	Mean	Range	Mean	Range	Mean	Range
Elevation (m)	101	6-640	120	3-778	221	9-575
Surface area (km ²)	4.2	0.3-39.4	5.6	0.2-38.2	49.6	2.0-294.5
Mean depth (m)	26.5	2.5-110	28.3	3.0-179.8	58.3	16.4-124.3
Maximum depth (m)	65.5	12-304	55.1	9-266	113.3	45-290
Secchi depth (m)	6.6	1.7-16.8	4.2	1.8-6.0	1.2	0.3-3.1
Euphotic zone depth (m)	17.3	3.2-45.6	6.8	3.3-11.4	5.6	1.2-5.6
Conductivity ($\mu\text{mhos cm}^{-1}$)	56	9-154	61	8-197	56	11-107
Turbidity (NTU)	0.9	0.2-5.8	0.9	0.4-1.8	15.9	0.5-48.6
Color (Pt units)	8	2-24	21	10-55	7	3-23
Total - P ($\mu\text{g L}^{-1}$)	6.4	1.3-21.3	8.4	2.7-20.3	13.3	4.1-32.8
Filterable reactive - P ($\mu\text{g L}^{-1}$)	2.3	0.9-7.5	2.5	1.0-4.6	2.9	1.6-5.9
Total - N ($\mu\text{g L}^{-1}$)	214	45-787	195	84-929	158	40-314
N:P ratio	89	13-151	54	17-135	51	8-235
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	1.3	0.1-9.9	1.2	0.2-5.8	0.5	0.1-2.0
Zooplankton biomass (mg m^{-2})	512	1-2,615	354	22-1,232	294	35-1,301

Table 2. Simple regression models for the dependence of sockeye smolt biomass (SB) on euphotic volume (EV), euphotic zone depth (EZD), and zooplankton biomass (ZB); and multivariate regression models for predicting age-1 sockeye smolt length (SL) and weight (SW) with ZB, total smolt per surface area (index of fry density, FDX) and mean water column temperature (TS).

Dependent variable	<i>n</i>	Independent variable	Coefficient	SE ¹	<i>P</i> -value	Partial- <i>r</i> ²	<i>r</i> ²	<i>R</i> ²
SB (kg km ⁻²)	16	y-intercept	-4.31	2.09	0.06			
		EV	0.147	0.009	<0.001	--	0.95	--
Ln SB (kg km ⁻²)	16	y-intercept	5.45	0.33	<0.001			
		EZD	0.095	0.026	0.002	--	0.49	--
SB (kg km ⁻²)	18	y-intercept	-68.9	100	0.5			
		ZB	2.07	0.15	<0.001	--	0.84	--
Log ₁₀ SL (mm)	83	y-intercept	1.722	0.069	<0.001	--		0.70
		ZB	0.121	0.018	<0.001	0.36		
		FDX	-0.062	0.011	<0.001	0.27		
		TS	0.024	0.005	<0.001	0.26		
Log ₁₀ SW (g)	84	y-intercept	0.122	0.216	0.575	--		0.70
		ZB	0.385	0.056	<0.001	0.37		
		FDX	-0.207	0.036	<0.001	0.28		
		TS	0.077	0.014	<0.001	0.26		

¹indicates 1 ± standard error

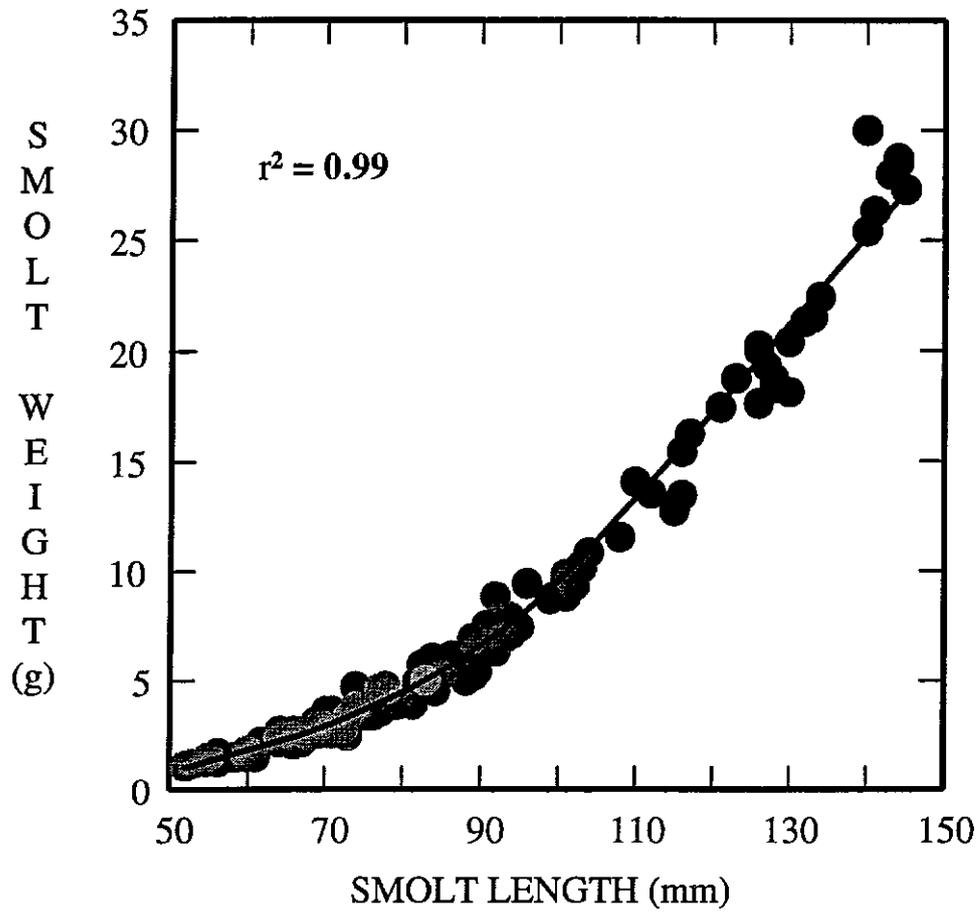


Fig. 1 The relationship between age-1 smolt length and weight for 35 Alaska lakes (130 lake years) representing clear (black), stained (dark gray) and glacial (light gray) lake types.

Role of Freshwater Habitats in Population Regulation and Recruitment Variation in Coho Salmon

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Historically, the freshwater environment was considered to be the major source of recruitment variation in Pacific salmon because field studies identified the effects of extreme river flows on survival. More recently though, as stock-recruit data has accumulated, there has been an increasing emphasis on the role of the ocean conditions on salmon abundance.

Here I review the role of the freshwater environment, with an emphasis on coho salmon. For coho, about half the life cycle is spent in streams, rivers and lakes, and most of the mortality (including all of the density-dependent mortality) occurs in freshwater. I propose that a basis for the precautionary management of coho salmon can be developed from our knowledge of processes in freshwater.

Coho smolt production is limited by the amount and quality of habitat in the natal streams and rivers, and various models have been devised to predict smolt production from habitat measures. Within an aggregate of coho streams (i.e. a management unit), the production of smolts from individual streams each stream appears vary independently of the other streams. There is no evidence for time trends in survival in freshwater, or large-scale climatic effects on smolt abundance. In contrast, neighboring populations often have similar marine survival rates, and there can be time trends in survival rates, resulting from large-scale oceanographic variation. As a result, freshwater and marine survival rates are not correlated.

Because freshwater production does not appear to be affected by large-scale climatic factors the way ocean survival rates sometimes are, guidelines for the harvest of coho salmon can be based on the freshwater production characteristics. I synthesized available data on coho smolt production, and developed a Limit Reference Point (LRP) harvest rate model. This model employs average freshwater production parameters and a forecast of the marine survival rate to estimate the limiting (maximum) harvest rate. Thus harvest rates are continually adjusted for changing ocean conditions. By basing management advice on freshwater production parameters, this method circumvents the problems that non-random (ie, trending) marine survival rates create for traditional stock-recruit analysis. However, it is not clear whether my parameterization of the model will be applicable to Alaskan coho because the data I used were from more southerly populations. Nonetheless, the method illustrates how an understanding of the dynamics of freshwater production can provide considerable guidance for the management of salmon populations in changing ocean conditions.

Alaska Salmon Spawner-Recruit Analysis: New Strategies for a New Millennium

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Analysis of spawner-recruit information in Alaska generally involves three steps: (1) parameter estimation based on the choice of a spawner-recruit model and a corresponding statistical framework, (2) development of a harvest strategy (commonly a fixed escapement policy) using estimated parameters from the spawner-recruit analysis, and (3) forecasting of future recruitment from parameter estimates and the harvest strategy (see Adkison's presentation). In this presentation, only the first step will be examined. This presentation will summarize current approaches for parameter estimation and suggest new strategies that stem from environmental influences on the recruitment process and measurement bias and variability in determining escapement and recruitment.

The typical spawner-recruit analysis conducted in Alaska and most other places involves either the Ricker or Beverton-Holt spawner-recruit models. If R is recruitment (*synonymous with returns*) and S is escapement (*synonymous with spawners*), then

$$R = \alpha S \exp(-\beta S) \text{ [Ricker]}$$

$$R = \alpha S / (1 + \beta S) \text{ [Beverton - Holt].}$$

Parameter α is called the productivity or density-independent parameter, and parameter β is called the density-dependent parameter. Parameter estimation is usually conducted with linear regression techniques by converting the above equations into linear ones, without necessarily considering what the appropriate error structure should be. If a Ricker spawner-recruit model is used, the dependent variable is $\ln(R/S)$ and the independent variable is S . If a Beverton-Holt model is used, then usually the dependent variable is $1/R$ and the independent variable is $1/S$. The three major assumptions underlying this analysis are that (1) the independent variable is measured without error, (2) the dependent variable has constant variance, and (3) the annual recruitment values are independent. In reality, we expect that (1) the independent variable, related to escapement, is measured with error, (2) the variance of the dependent variable, related to recruitment, varies from year to year and from dataset to dataset, and (3) environmental influences may introduce process error into the models that results in autocorrelation in recruitment.

Strategy 1. Process studies should be used to validate the assumptions contained in spawner-recruit models.

These models can be derived from assumptions made about biological processes affecting the salmon during early life history (Quinn and Deriso 1999). The Ricker model follows by assuming that mortality Z during this period is linearly related to escapement ($Z = a + bS$). The lack of a direct relationship of mortality to the population itself is what allows the Ricker

relationship to have a dome-shaped curve. The Beverton-Holt model results by assuming that mortality during early life history is linearly related to abundance N ($Z = a + bN$). In this situation, density dependence is postulated to occur during early life history. Field and lab studies would be helpful to understand what factors and mechanisms affect salmon during early life history (see Willette's presentation). This knowledge could then be used to help select the appropriate shape of spawner-recruit curves and to validate assumptions associated with their use.

Strategy 2. Environmental information should be routinely incorporated into spawner-recruit analyses. If it is assumed that an environmental variable X affects abundance independently of density-related factors during some time period of the early life history (say $dN/dt = cX$), then the resultant spawner-recruit relationship is multiplied by the factor $\exp(\gamma X)$. Hence the Ricker and Beverton-Holt models with environmental variables become

$$R = \alpha S \exp(-\beta S + \gamma X) \quad [\text{Ricker}]$$

$$R = [\alpha S / (1 + \beta S)] \exp(\gamma X) \quad [\text{Beverton - Holt}].$$

Incorporation of environmental effects may allow the underlying spawner-recruit curve to emerge from the analysis, but this does not always happen. An obvious consequence of this strategy is that environmental datasets must be routinely updated and maintained.

By an analogous argument, other independent factors that influence abundance during early life history should affect recruitment in a multiplicative manner, inducing lognormal variation in recruitment. If these factors are unmeasured, then they exhibit themselves as process errors in a spawner-recruit curve. Thus, the lognormal distribution should be considered the default distribution for recruitment, and recruitment data should be log-transformed prior to analysis. Under this default, nonlinear regression methods are generally more appropriate than linear regression techniques.

Strategy 3. A variety of models with spawner and environmental information should be considered. If density and environmental factors operate simultaneously, then the expected recruitment relationship is more complicated. For example, mortality in the Beverton-Holt model could be modified to be $Z = a - bN + cX$, equivalent to replacing the a parameter by $a + cX$. Then the resultant α and β parameters of the Beverton-Holt model both become functions of the environment [equation (3.6) in Quinn and Deriso 1999].

Alternatively, the environment could act on the population as a whole rather than as a per capita effect on mortality. In this case, the model would be $dN/dt = -ZN + cX$. For the Beverton-Holt model, the differential equation is the Riccati equation with a quite complicated solution. For the Ricker, the solution to a first-order nonhomogeneous equation is straightforward but also results in a more complicated model than the approach in Strategy 2.

Strategy 4. Autocorrelation in recruitment should be investigated with time series methods. If an environmental dataset is not available, then an environmental effect may manifest itself in a persistent sequence of positive or negative trends in the residuals from a spawner-recruit

analysis. If an environmental dataset is available, then the residuals analysis can be used to detect the influence of some other environmental variable(s). While analysis of residuals for autocorrelation has been the most common approach, the direct incorporation of autocorrelation into the spawner-recruit analysis should also be attempted. The error term ε_t in $\ln R$ at time t is modeled as $\varepsilon_t = \phi\varepsilon_{t-1} + \delta_t$, so that predicted recruitment at time t is modified by the error at time $t - 1$.

Alternatively, time series models should be investigated (see Farley's presentation). These models involve a series of analyses related to identification, estimation, and forecasting that have a wealth of theory and applications to support them.

Strategy 5. Spawner-recruit parameters could be considered as random variables.

If environmental effects are present, then the parameters in a spawner-recruit model may vary over time. If this effect cannot be detected with environmental data, then perhaps the parameters can be made time-varying. If a regime effect is present, then the parameters can be simply altered for the different regimes. If the change is more gradual, then an autoregressive or random walk process may be used. For example, a random walk process for the logarithm of the productivity parameter α may be written $\ln \alpha_t = \ln \alpha_{t-1} + e_t$.

Software for easily incorporating such processes into spawner-recruit analyses is available: AD Model Builder (Fournier).

Strategy 6. Managers' perceptions of environmental and other effects should be incorporated into spawner-recruit analysis using Bayesian methods.

The Bayesian paradigm has emerged as the dominant approach for incorporating uncertainty into analysis of fisheries data and management (Geiger). In this approach, perceptions of uncertainty are explicitly incorporated into the analysis through a prior distribution on parameters. A posterior distribution is developed from the prior and the likelihood of the data. The theory of decision analysis is then used to evaluate policies under different perceptions of the state of nature.

Strategy 7. Bias and imprecision in escapement measurement should be investigated and corrected.

Spawner-recruit analysis is inaccurate and possibly misleading if there are substantial errors in escapement. If those errors are directional (too high or too low), then estimated and optimal harvest rates are incorrect. In addition, it is possible to incorrectly determine the shape of the spawner-recruit curve. A field study to calibrate observers is one activity that can lead to improvements. A rigorous sampling plan that leads to unbiased escapements is another. One example of this being done is a study of escapement for SE pink salmon by ADF&G CF Division. A careful calibration study has led to revision of historical escapement data that indicates that historical escapements were higher than previously thought (Van Alen).

Strategy 8. Measurement / process error models should be investigated and used.

Both recruitment and escapement are measured with error. For salmon, the error u_t in recruitment is the identical to that in escapement, because recruitment is simply the sum of escapement and catch, the latter of which is measured with minor error at most. In addition, recruitment is subject to process error w_t due to environmental and other factors, whether

measured or not. A combined measurement / process error model (Ludwig and Walters) can be written

$$\ln R_{\text{obs},t+r} = \ln R_{\text{true}} + e_{t+r} = \ln R_{\text{det}} + w_{t+r} + u_{t+r}$$
$$\ln S_{\text{obs},t} = \ln S_{\text{true}} + u_t,$$

where recruitment occurs in year $t + r$ from escapement in year t , and “det” stands for deterministic. These models require knowledge of the variance of measurement error or the ratio of variances of measurement error to process error. Alternatively, the Kalman filter technique has been used to obtain reasonable parameter estimates (Pella).

Citation: Quinn, T.J., II, and R.B. Deriso. Quantitative Fish Dynamics. Oxford, New York. 542 pp.

Implications of Climatic Fluctuations on Salmon Management

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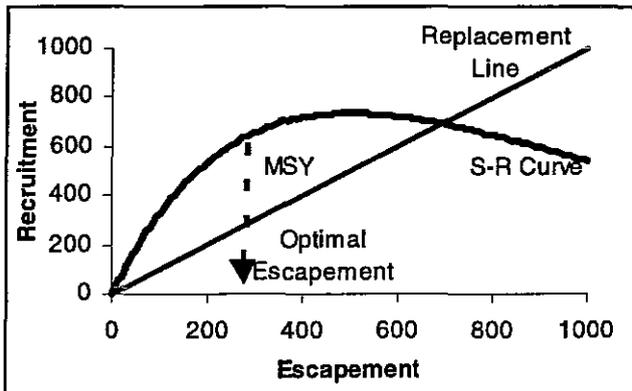
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Stock-recruitment curves and the optimal escapement. The relationship between spawning stock size and subsequent recruitment is usually described in terms of an average relationship, or stock-recruitment curve, and the degree of year-to-year variation about this average. Typical stock-recruitment curves have two parameters; the first describes the per capita potential productivity of the stock and the second the carrying capacity of the environment. An example is the Ricker equation:

$$R = aSe^{-\frac{S}{b}}$$

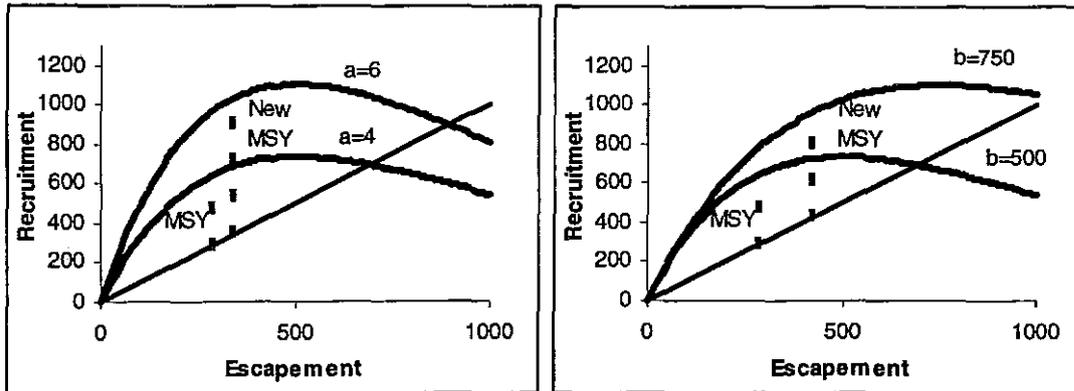
Here R is recruits, S is spawners, a is the per capita recruits/spawner at low stock abundance, and b specifies the degree of density-dependent reduction in productivity.

Escapement goals are often based on the stock-recruitment curve. The escapement that produces the maximum surplus yield (MSY) is that spawning stock size (S_{MSY}) where the expected recruitment minus the escapement to replace the spawning stock is maximal (Fig. 1).



How climate affects the optimal escapement. Climatic shifts could conceivably affect either productivity or carrying capacity, or more likely both. In a population limited by spawning habitat, climatic change might improve survival at some life stage and result in a higher overall egg-to-adult survival, thus increasing a . Climate change might also alter the characteristics of the habitat, making a larger area suitable for spawning and thus increasing b .

If climate increases the per capita productivity a , then the optimal escapement will generally increase (Fig. 2a). If climate increases the carrying capacity b (e.g., more suitable habitat), then escapement goals should increase proportionally to fully seed the space available (Fig. 2b).



In previous work with Randall Peterman (Adkison et al. 1996), we investigated the changes in parameters of the stock-recruitment curve for Bristol Bay sockeye salmon stocks associated with the 1976–1977 climate shift in the North Pacific (Hare and Francis 1995, Trenberth 1990). Productivity (a) increased in the majority of the Bristol Bay stocks, whereas the carrying capacity b showed no consistent pattern (Table 1).

Table 1. Ratio of parameter values of Ricker curve (here as $aSexp(-bS)$) after vs. before the late 1970's climate shift (from Adkison et al. 1996).

Stock	Togiak	Igushik	Wood	Nushagak	Kvichak	Branch	Naknek	Egegik	Ugashik
shift in a	1.73	2.02	2.38	3.64	3.06	4.67	0.75	2.61	6.21
shift in b	1.04	0.62	1.72	-1.65	-1.84	7.58	0.19	0.08	5.29

When we estimated how the shift affected the optimal escapement, we found that it had increased. We got this result whether we used a single, best-fitting curve, or whether we used Bayesian statistics to average across many possible curves, weighting each by how probable it was (Peterman and Adkison *in prep*).

How climate shifts affect management. As we've seen, climate changes can alter optimal escapement levels. Theoretically, managers should adjust goals in response to obtain maximum yields and stock safety. Unfortunately, it's difficult to respond quickly to a climate shift. Shift-induced changes are difficult to discriminate from the natural background variability about a stable stock-recruitment curve. The shape of the new curve may not be known for several years until sufficient data have been accumulated, and by then a new regime may be underway.

In addition to causing sub-optimal escapements, climate shifts can greatly reduce the reliability of forecasts. Following the mid-1970's shift, ADF&G forecasts for Bristol Bay sockeye returns averaged a significant downwards bias for several years. These sorts of errors have significant consequences. Harvesters and processors invest in gear and processing capacity based on their expectations of future harvests, and managers ability to

achieve escapement goals can also be affected by incorrect expectations (Bocking and Peterman 1988).

Climate can also disrupt management by differentially affecting stocks, altering the relative productivity of stocks in a mixed-stock fishery. The recent discrepancy between the strength of sockeye salmon returns to the Egegik and Naknek drainages and weak returns to the Kvichak has caused severe management headaches. A similar problem has occurred in the South Peninsula June fishery which targets strong Bristol Bay sockeye returns that unfortunately are mixed with recently weak runs of Western Alaska chum.

What can be done about all this? Many of the management headaches caused by the climate's effect on salmon stocks are due to uncertainty – how many fish are coming back this year, what the average return will be over the next ten years, what escapement levels will produce high and sustained harvests. Better forecasts of near- and long-term productivity would be very helpful and should be a research priority (Adkison and Peterman *in review*).

However, high variability and unpleasant surprises will likely be with us for some time to come. Management needs to be flexible and retain the ability to rapidly adapt to changed circumstances. Quite sensibly, modern salmon management uses test fisheries and in-season adjustment of fishing effort to achieve escapement goals despite large fluctuations in returns from year-to-year. The fishing industry itself needs to be flexible and make decisions that will allow them to weather the inevitable ups and downs. Management can help in this process by ensuring that its regulations aren't barriers to this flexibility.

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Bristol Bay Sockeye Salmon Production: An Exploratory Analysis of the 1996–1998 Decline in Sockeye Salmon Returns

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It has become increasingly apparent that variation in the marine environment contributes greatly to Pacific salmon (*Oncorhynchus* spp.) population variability (Francis and Hare 1994; Beamish and Bouillon 1995; Hare and Francis 1995; Mantua et al. 1997). Some of this variability is due to low frequency changes in salmon populations with periods of low or high abundance that may span decades (Hare and Francis 1995). Given the importance of decadal changes in salmon populations, many of the proposed Pacific salmon production models now include parameters related to causal mechanisms of large -scale physical changes in the environment of the North Pacific Ocean. However, the scale of inter-annual variation is also large – the abundance of returning adult salmon to a river system commonly varies by more than an order of magnitude between years – making it important for managers of these stocks to prepare annual pre-season forecasts of the allowable catch for each stock.

Sockeye salmon (*Oncorhynchus nerka*) returns (catch + escapement) to Bristol Bay, Alaska have fluctuated greatly over the last 43 years. Decreasing and increasing trends within the data series are punctuated with large year-to-year variations (Figure 1). During the early 1990s, Bristol Bay sockeye salmon returns reached record levels; since 1996, however, returns of sockeye salmon to Bristol Bay have fallen markedly, producing less than half of the expected return during 1997 and 1998.

In this paper, we examine inter-annual variability of sockeye salmon returns for three river systems in Bristol Bay (Egegik, Naknek, and Kvichak) by relating adult sockeye salmon returns to other sockeye salmon population data¹ (escapement, smolt outmigration, and sibling relationships) and environmental data² (Bering Sea surface temperatures (BSST), air temperatures (May – August) at Cold Bay, Alaska (CBMAT), Southern Oscillation Index (SOI), Aleutian Low Pressure Index (ALPI), and Pacific inter-Decadal Oscillation (PDO)). There were two objectives for this study: 1) identify environmental data possibly related to sockeye salmon return data; 2) determine if the addition of population and/or environmental data (identified in objective 1) to sockeye salmon return models could explain the rapid decline of sockeye salmon returns to Bristol Bay, Alaska during 1996 through 1998.

¹ Sockeye salmon population data were obtained from Beverly Cross, Alaska Department of Fish and Game, Anchorage, Alaska.

² See Farley and Quinn (1998) for details on environmental data.

We used time series analysis (Box and Jenkins 1976) to model sockeye salmon return data; time series models account for autocorrelation in the return data (Noakes et al. 1987) and have proved useful in forecasting salmon production (Quinn and Marshall 1989; Noakes et al. 1990; Marshall 1992; Farley 1996). Univariate models were created for the environmental data (1956 – 1995) and sockeye salmon return and return-per-spawner data (1956 to 1995) for age classes 1.2, 1.3, 2.2, and 2.3. Multivariate time series models included biological relationships between returns and escapement (Cushing and Ricker; see Noakes et al. 1987 for examples), sibling, and smolt. When relevant, environmental data were also included in multivariate models.

Since our intent was to determine the inter-annual relationships between the population and environmental data, we first analyzed cross-correlations between the white noise residuals from the univariate and multivariate time series models (many of these models contained significant autoregressive lag 1 components) and the white noise residuals from the environmental models. This form of “prewhitening” may be useful when the dominant source of covariation of interest is the inter-annual component, since it can remove the low-frequency variability that may obscure the detection of inter-annual covariation between time series (Pyper and Peterman 1998). Environmental variables were selected as possible explanatory variables in the multivariate time series models when significant relationships ($\alpha = 0.05$) occurred within hypothesized lagged relationships (Table 1) and when these significant relationships were consistent across age classes and river systems. If no significant relationships between sockeye salmon returns and environmental variables occurred, then the environmental variables were not included in multivariate models. Significant contemporaneous relationships (lag 0) were excluded from the environmental selection and modeling process, because of their inapplicability to forecast models.

Forecasts were made for 1996, 1997, and 1998 and model performance was evaluated by comparing the coefficient of variation r^2 , residual standard error (RSE), and Schwartz’s Bayesian Information Criterion (SBC) (Schwartz 1978, Adkison et al. 1996), a model selection criterion that penalizes highly parameterized models. Forecasts for 1996 were created for each of the time series models. The time series models were then re-estimated including the data for 1996, and forecasts were created for 1997. This process was repeated for 1998 forecasts. Since the forecasts are estimated using the logarithm of returns, a bias correction factor suggested by Beauchamp and Olson (1973) and Noakes et al. (1990) was used to produce unbiased forecast estimates. We included percent error (PE), mean percent error (MPE) and mean absolute percent error (MAPE) for 1996 through 1998 forecasts as alternative criteria of model performance.

In some instances, the time series models producing the best model statistics did not have the best forecast performance. Since our purpose was to determine which time series models produced the best forecasts for the years 1996 through 1998, we chose an arbitrary evaluation system that gave more points to models that produced the best forecast. For each statistic (RSE, r^2 , SBC), the best model was awarded 1 point, while the second best model was awarded 0.5 points. For the forecast statistics (MPE, MAPE), the best model was awarded 2 points, while the second best model was awarded 1 point. All other models received 0 points for those statistics. The best overall time series model was the model awarded the highest point total.

Results

Univariate and multivariate (Ricker and Cushing) models of sockeye salmon returns (and returns per spawner) for Egegik and Kvichak usually contained AR(1) noise models, suggesting that returns (and returns-per-spawner) of sockeye salmon in year t are related to returns in the prior year. For Naknek, most of the univariate and multivariate models of age class returns and return-per-spawner consisted of a constant, white noise, process. Most of the univariate environmental time series models were white noise processes, with the exception of PDO which contained a significant AR relationship with lag 1 and BSST which contained significant AR relationships with lags 1 and 2.

Cross correlations between residuals from the univariate and multivariate models of sockeye salmon return and environmental data produced mixed results. Cold Bay air temperature (CBMAT) was the only environmental variable that contained significant relationships across age classes that were within the hypothesized relationships. Most of the significant relationships with SOI, PDO, ALPI and BSST were either contemporaneous, not significant, or the significant relationships were not consistent between age classes or river systems. Therefore, CBMAT was the only environmental variable used in the multivariate time series models.

CBMAT parameter estimates were usually positive suggesting that warmer air temperatures from May through August in Cold Bay, Alaska were related to larger returns of sockeye salmon to Egegik, Naknek, and Kvichak Rivers. Significant cross-correlations between CBMAT and the return data generally occurred at lags 1 or 2 for age classes 1.2 and 2.2 and lags 1, 2, or 3 for age classes 1.3 and 2.3 implying that air temperatures at Cold Bay during May through August affect sockeye salmon survival during marine residence at the juvenile, immature, and adult life stages.

The best time series models were produced from a mixture of population and environmental data (Figure 2). For 2-ocean sockeye salmon returns, the best time series models included CBMAT and return-escapement relationships (Cushing and Ricker; Table 2; see Farley and Quinn (1998) for details on the other time series models). The best time series models for most of the 3-ocean sockeye salmon returns were sibling models (Table 2). The only exceptions were for age classes 2.2 and 2.3 in Kvichak where the multivariate smolt model and univariate model of returns produced the best overall model and forecast statistics, respectively.

Although the models presented above were judged best based on overall model and forecast statistics, their performance varied between years (Figure 3). The time series models for age classes 1.2 and 2.2 (2-ocean sockeye salmon) severely over-forecasted returns in 1996, particularly for Kvichak, implying that neither the environmental data used in this analysis or return-escapement relationships were good indicators of the decline in sockeye salmon returns for these age classes. The 1996 forecasts produced by the sibling models for age classes 1.3 and 2.3 (3-ocean sockeye salmon) tended to be more accurate, under-forecasting returns for these age classes in Egegik and Naknek and slightly over-forecasting returns for Kvichak. Forecast error of 2-ocean sockeye salmon models decreased in 1997 for Egegik and Kvichak, but increased for Naknek. For 3-ocean sockeye salmon returns, forecast error in 1997 remained the same in Egegik, slightly under-forecasting returns of 3-ocean sockeye salmon, but increased for Naknek and Kvichak over-forecasting returns of 3-ocean sockeye salmon to these rivers. Forecast performance improved for both 2-ocean and

3-ocean sockeye salmon during 1998 when compared with 1997 for each river system except Egegik, where forecast error for 2-ocean sockeye salmon increased.

Conclusions

1. There was a significant relationship between CBMAT and survival of sockeye salmon at the juvenile, immature, and adult life history stages. The significant relationship was consistent across the sockeye salmon age classes and river systems and was positive, suggesting that warmer May – August air temperatures at Cold Bay, Alaska were related to larger sockeye salmon returns. All other environmental variables contained either a significant contemporaneous lag (lag 0), or the significant relationships were not consistent across age classes or river systems.
2. Including CBMAT, escapement, or smolt data (Kvichak only) in forecast models produced the best model and forecast statistics for 2-ocean sockeye salmon returns; however, models that included these data produced large over-forecast error, particularly for Naknek and Kvichak sockeye salmon returns, implying that neither CBMAT, escapement, or smolt data were good predictors of declining sockeye salmon returns.
3. There is a strong relationship between returns of 3-ocean sockeye salmon and 2-ocean sockeye salmon returning the previous year. Including 2-ocean sockeye salmon data in sibling models produced the most accurate forecasts, implying that these data are good predictors of declining sockeye salmon returns.

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Table 1. Hypothesized lagged relationships (*) for Cold Bay May – August air temperatures (CBMAT), Bering Sea surface temperatures (BSST), southern oscillation index (SOI), Pacific inter-decadal oscillation (PDO), and Aleutian low pressure index (ALPI). Lags that are **bold** represent ocean residence, while non-**bold** lags represent freshwater residence.

Age Class	Lag	Environmental Variables				
		CBMAT	BSST	SOI	ALPI	PDO
1.2	1	*	*	*	*	*
	2	*	*	*	*	*
	3			*	*	*
	4			*	*	*
1.3	1	*	*	*	*	*
	2	*	*	*	*	*
	3	*	*	*	*	*
	4			*	*	*
	5			*	*	*
2.2	1	*	*	*	*	*
	2	*	*	*	*	*
	3			*	*	*
	4			*	*	*
	5			*	*	*
2.3	1	*	*	*	*	*
	2	*	*	*	*	*
	3	*	*	*	*	*
	4			*	*	*
	5			*	*	*
	6			*	*	*

Table 2. Time series models for Egegik, Naknek, and Kvichak logarithm of returns for age classes 1.2, 1.3, 2.2, and 2.3 (1956 – 1995) with parameter estimates and t-values (in parenthesis).

River System	Age Class	Model	
Egegik	1.2	Cushing	$\ln(R_t) = 0.88 \ln(E_{t-4}) + \frac{1}{(1-0.59B)} \text{Noise}$ (29.2) (4.5)
	1.3	Sibling	$\ln(R_{1.3(t)}) = 2.05 + 0.88 \ln(R_{1.2(t-1)}) + \text{Noise}$ (2.4) (12.7)
	2.2	CBMAT	$\ln(R_t) = 14.5 + 0.53(\text{CBMAT}_{t-2}) + \frac{1}{(1-0.63B)} \text{Noise}$ (47.3) (5.2) (4.9)
	2.3	Sibling	$\ln(R_{2.3(t)}) = 3.83 + 0.70(\ln R_{2.2(t-1)}) + \text{Noise}$ (3.0) (7.8)
Naknek	1.2	CBMAT	$\ln(R_t) = 12.9 + 0.24 \ln(\text{CBMAT}_{t-1}) + 0.41 \ln(\text{CBMAT}_{t-2}) + \frac{1}{(1-0.37B^2)} \text{Noise}$ (159.6) (2.4) (4.0) (2.2)
	1.3	Sibling	$\ln(R_{1.3(t)}) = 5.61 + 0.63 \ln(R_{1.2(t-1)}) + \frac{1}{(1-0.31B)} \text{Noise}$ (4.0) (5.7) (2.1)
	2.2	Ricker	$\ln\left(\frac{R_t}{E_{t-5}}\right) = 0.58 E^{-6}(E_{t-5}) + \text{Noise}$ (3.8)
	2.3	Sibling	$\ln(R_{2.3(t)}) = 9.3 + 0.31(\ln R_{2.2(t-1)}) + \text{Noise}$ (7.4) (3.2)
Kvichak	1.2	Cushing	$\ln(R_t) = 5.3 + 0.56 \ln(E_{t-4}) + \frac{1}{(1-0.48B^1)} \text{Noise}$ (1.9) (3.1) (3.2)
	1.3	Sibling	$\ln(R_{1.3(t)}) = 2.22 + 0.79 \ln(R_{1.2(t-1)}) + \text{Noise}$ (2.2) (11.1)
	2.2	Smolt	$\ln(R_t) = 0.87(\text{Smolt}_{t-2}) + \text{Noise}$ (78.7)
	2.3	Univariate	$\ln(R_t) = 13.7 + \frac{(1+0.56B)}{(1-0.15B^4-0.39B^5)} \text{Noise}$ (27.9) (-3.9) (2.8) (7.2)

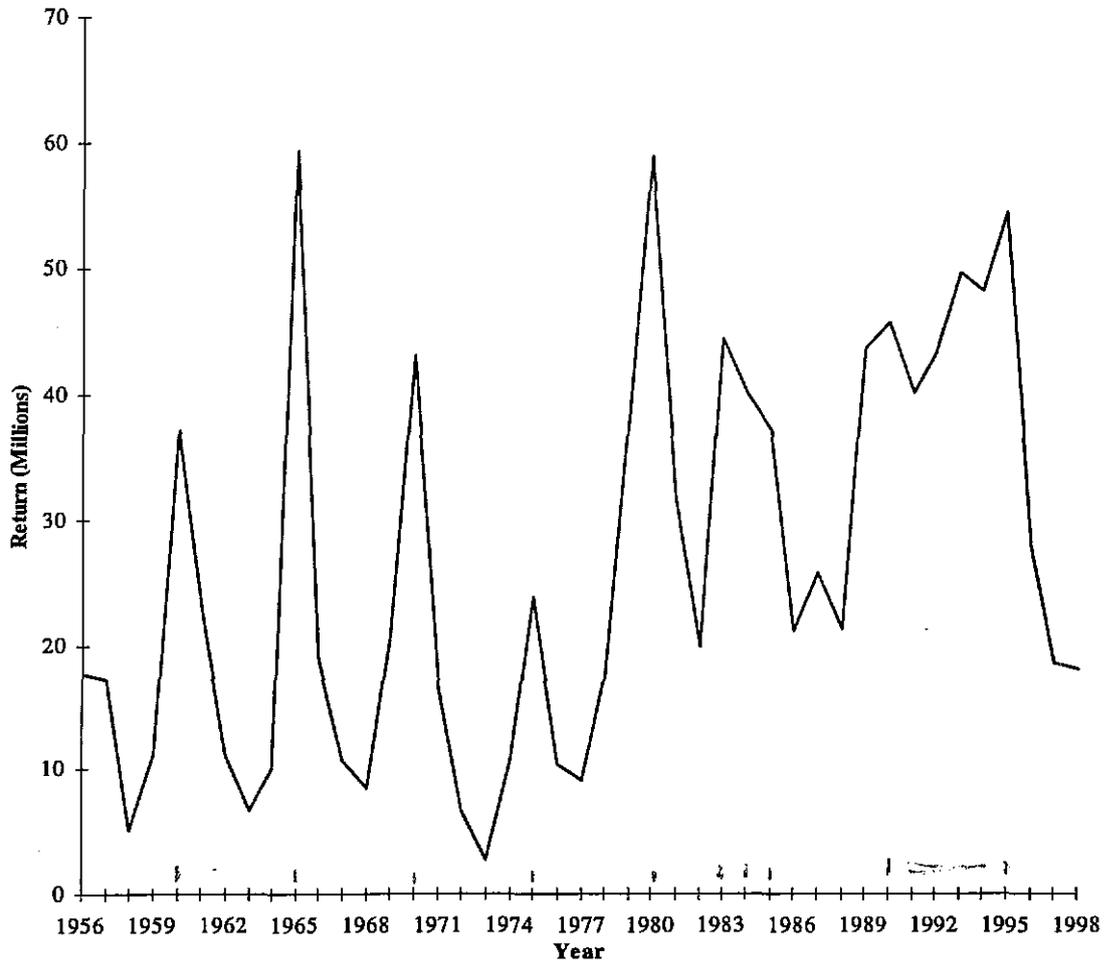


Figure 1. Returns of sockeye salmon to Bristol Bay, Alaska (1956 – 1998).

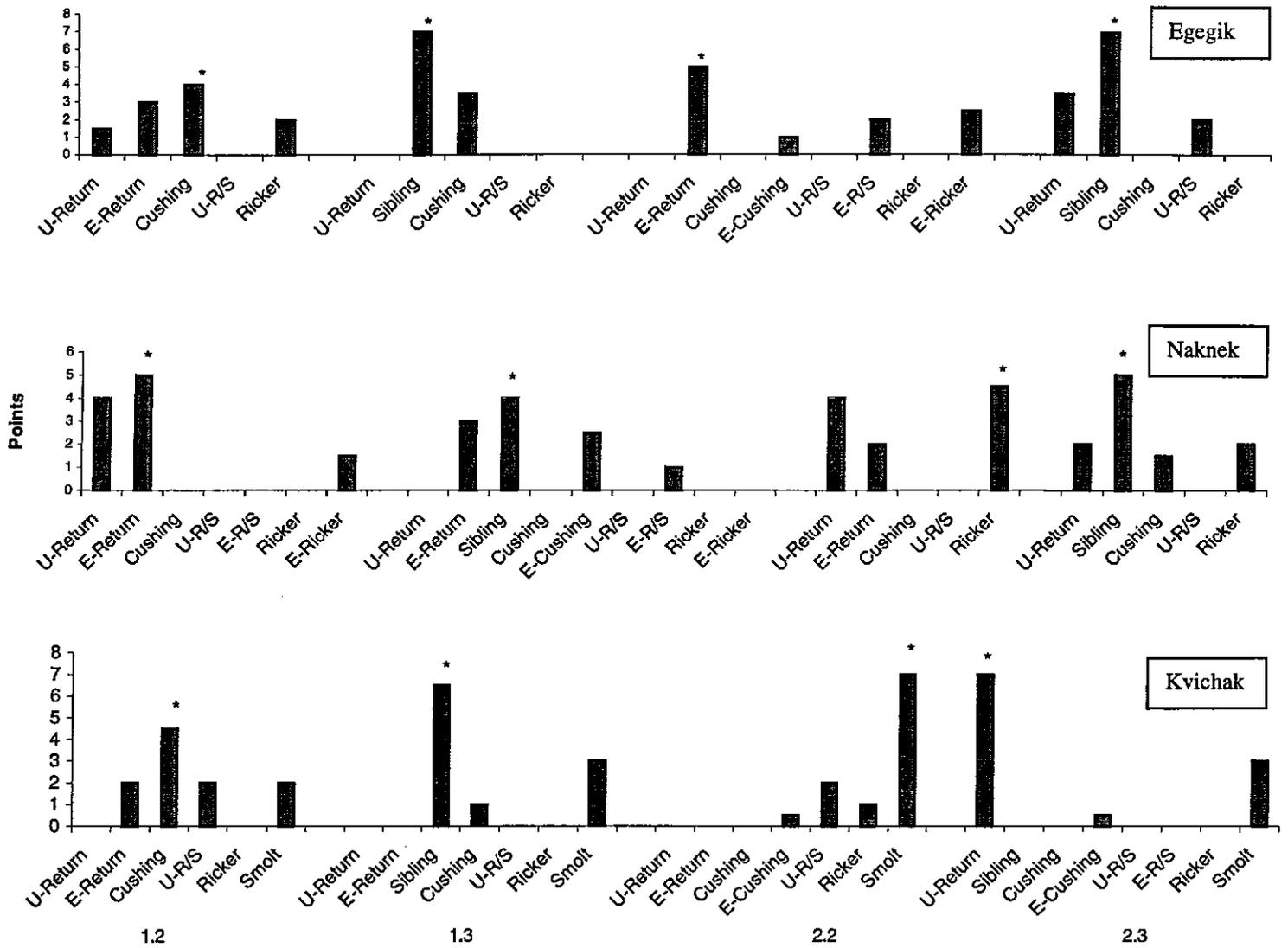


Figure 2. Number of points awarded to time series models for each age class and river system. The * indicates the model with the highest sum of points. (See Farley and Quinn 1998 for model descriptions and results).

U-Return: univariate model of age class returns
 U-R/S: univariate model of age class returns per spawner
 E-Return: multivariate model of returns including CBMAT
 E-R/S: multivariate model returns per spawner including CBMAT
 Ricker: Ricker model of age class returns
 Cushing: Cushing model of age class returns
 E-Ricker: Ricker model of returns including CBMAT
 E-Cushing: Cushing model of returns including CBMAT
 Smolt: multivariate smolt models

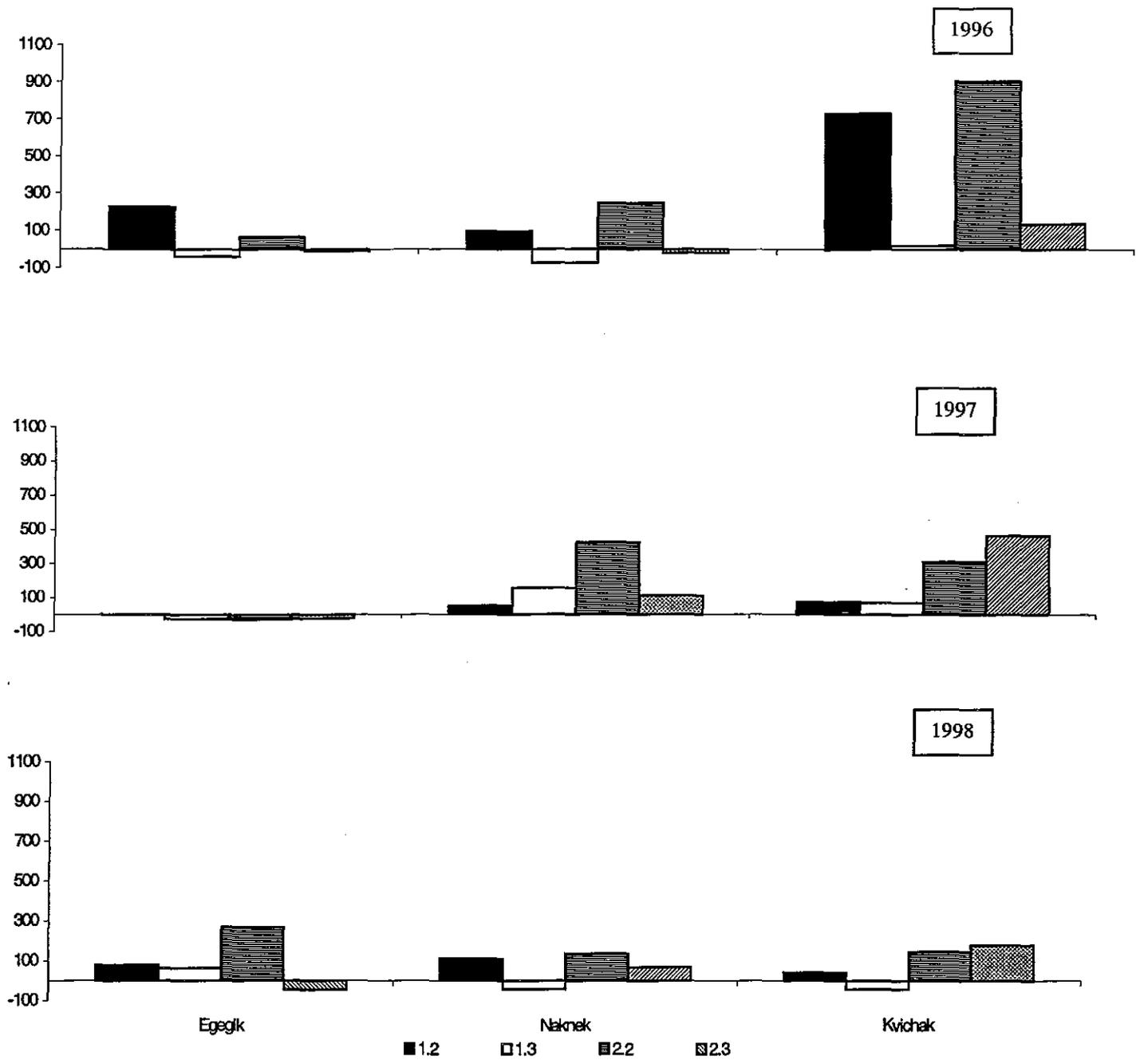


Figure 3. Percent error for time series forecasts in Egegik (1.2 [Cushing]; 1.3 [Sibling]; 2.2 [CBMAT]; 2.3 [Sibling]), Naknek (1.2 [CBMAT]; 1.3 [Sibling]; 2.2 [Ricker]; 2.3 [Sibling]), and Kvichak (1.2 [Cushing]; 1.3 [Sibling]; 2.2 [Smolt]; 2.3 [Univariate Return]).

Ecological Processes Influencing Mortality of Juvenile Pink Salmon in Prince William Sound, Alaska

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Approximately 726 million juvenile pink salmon (*Oncorhynchus gorbuscha*) enter Prince William Sound, Alaska from streams and hatcheries each year. We examined the ecological processes affecting mortality of these juveniles using field data collected during May–July, 1994–1997. Potential predators on juvenile salmon were sampled with variable-mesh gill nets inshore of the 20-m isobath and with small-mesh purse seines offshore of the 20-m isobath. A mid-water wing trawl equipped with a net sounder was used to sample fishes in pelagic habitats. Standard acoustic techniques for echo-integration, echo counting and dual beam processing of target strength were used to estimate the biomass of potential predators in pelagic habitats. The diet composition of potential predators was estimated from specimens collected in 1994 (n=5,886), 1995 (n=13,336), 1996 (n=6,008), and 1997 (n=4,634). The availability of alternative prey for these fish was estimated from zooplankton samples collected at each site. Coded-wire tagged (CWT) and otolith-marked juvenile salmon were sampled with small-mesh purse seines to estimate diet composition and growth.

Predation during the spring plankton bloom (May to mid-June) accounted for the mortality of 610 million juveniles (84%) and therefore appeared to be the primary mechanism causing mortality. Two planktivores, herring (*Clupea pallasii*) and walleye pollock (*Theragra chalcogramma*) probably consumed the greatest numbers of juvenile salmon. Several piscivores (*Gadus macrocephalus*, *Microgadus proximus*, and *Salvelinus malma*) probably consumed the second greatest numbers, and an assemblage of nearshore demersal fishes (Cottidae, Hexagrammidae, and *Sebastes spp.*) probably consumed the smallest numbers of salmon. Mortality of pink salmon (release to adult return) from Wally H. Noerenberg

Hatchery, adjacent to our study area was greatest in 1994 (-0.0091), decreasing in 1995 (-0.0074), 1996 (-0.0070), and 1997 (-0.0056). This decline in mortality corresponded to a decline in age 3+ pollock density in our study area.

Herring, immature pollock, and adult pollock diets were generally dominated by large calanoid copepods (mostly *Neocalanus*) during the bloom of these copepods in May, but both fish species switched to alternative prey in June (Willette et al. 1999). An analysis of the functional responses of herring and adult pollock feeding on large copepods was conducted to determine the copepod biomass at which these fish switched to alternative prey as well as their probable feeding modes. Functional responses of herring and adult pollock were best described by type III models with parameters consistent with particulate and filter feeding modes, respectively. Herring began to switch to alternative prey as the biomass of large calanoid copepods in the upper 20-m of the water column declined below 0.2 g m^{-3} . Adult pollock switched to alternative prey as copepod biomass in high-density layers declined below about 1.0 g m^{-3} . Analysis of covariance indicated that herring and pollock tended to switch from large copepods to nekton prey after the copepod bloom declined. Herring and pollock generally consumed juvenile salmon 3–6 cm in length, but they tended to select for the smaller juveniles within this length range.

Juvenile salmon dispersed offshore to feed and suffered greater predation losses when densities of large calanoid copepods in nearshore habitats declined. The geometric mean catch per net set of juvenile salmon in seines set offshore of the 20-m isobath was inversely correlated with the mean biomass of large copepods in nearshore habitats. The mean number of juvenile salmon in piscivore and demersal fish stomachs was positively correlated with mean catch per net set of juvenile salmon in seines offshore of the 20-m isobath and mean juvenile salmon length. Densities of large copepods were 0.5–3.0 times higher in offshore than nearshore habitats, and the proportion of large copepods in juvenile salmon diets was also higher in offshore habitats. Juvenile salmon preying on large calanoid copepods exhibited higher feeding rates, stomach fullness indices, and somatic energy content than those feeding on small copepods (primarily *Pseudocalanus*). Dispersion of juveniles offshore in response to declining large copepod densities was probably motivated by a need to sustain maximum growth rates and minimize later predation losses (Walters and Juanes 1993).

An analysis of covariance was conducted to test the null hypothesis that mortality of juvenile pink salmon was not related to the duration of the bloom of large calanoid copepods from ocean entry to the time the fish reach 6-cm in length (Willette et al. 1999). The analysis was structured to enable examination of the simultaneous effects of the zooplankton bloom on juvenile growth rate and predator switching behavior. Juvenile body weight at release, juvenile growth rate, number of juveniles released from each hatchery each day, and zooplankton bloom duration were included as independent variables in the model. Mortality of juvenile pink salmon from fry to adult was estimated for 147 CWT groups of pink salmon released from 4 hatcheries in PWS (1989–1995). Only CWT groups less than 0.35-g body weight at release were included in the analysis, due to small sample sizes for groups composed of larger fish. Growth of juvenile CWT salmon was estimated from an analysis of covariance function relating growth to juvenile release and environmental data. Mortality of

CWT pink salmon was significantly reduced when the zooplankton bloom was prolonged during the juvenile lifestage. This result was generally consistent with our analyses of predator stomach contents suggesting that predator switching behavior was the cause. However, mortality was also positively correlated with juvenile growth rate, juvenile body weight at release, and the number of juveniles released. The importance of these size-related parameters to mortality is consistent with planktivores as the dominant predator. Model predicted values exhibited some autocorrelation by date of juvenile release. Examination of temporal patterns in the independent variables indicated that changes in mortality by release date were probably caused by interactions among independent variables rather than the effect of any single variable. Temporal trends in the residuals were probably related to changes in predator abundance or size composition that were not accounted for in the analysis.

Our results indicate that the copepod *Neocalanus* plays a unique role in modifying predation losses of juvenile pink salmon. Reduced densities of this large copepod probably cause greater predation losses to planktivores as these fish switch to alternative prey. Dispersion of foraging juvenile salmon offshore in response to declining large copepod densities probably causes greater predation losses to piscivores and demersal fishes. The duration of the *Neocalanus* bloom in May is prolonged in years when frequent storms replenish nutrients to the surface layer. Thus, bottom-up processes affecting the spring *Neocalanus* bloom influence juvenile salmon foraging behavior, but also modify top-down processes by altering juvenile predation risk and the timing of a shift from planktivory toward piscivory among predators on juvenile salmon.

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Linkages Between Climate and Ocean Processes and Pacific Herring Growth and Recruitment

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In this presentation I will first look at three long-term time series that illustrate different observations of herring productivity (recruitment, biomass, and growth), then look at oceanic and climatic processes that may be driving changes in these observed time series. Gulf of Alaska herring show both a shorter term (3–5 year) and longer term (decadal or more) periodicity in these productivity time series, while in the Bering Sea the relevant time scales appear to be decadal or longer. Recent research by Erik Williams has helped to define the spatial scale of synchronicity in these productivity time series and the environmental forcing variables which may affect productivity. Temperatures during the first year of life strongly influence recruitment, but may be acting as an analytical proxy for a more direct phenomenon such as timing, duration, or strength of the spring bloom, which has not been directly observed. The recent dramatic oceanographic changes in the Bering Sea have raised concerns over the impacts on herring and subsequent ripple effects on higher levels of the food chain such as birds and marine mammals. How the recent oceanographic anomalies will affect herring recruitment in the Bering Sea remains to be seen, although recruitment forecasts for the largest herring spawning aggregation at Togiak have recently been revised downward. Herring weights at age declined by a biologically significant amount (15%–30%) during the 1990's, but increased in 1998, implying that recent conditions may not have a drastically unfavorable effect on herring.

Poster Session Abstracts:

- Lake Becharof Ecosystem, Norma Jean Sands, ADF&G
- Kodiak Island Sockeye Salmon Freshwater and Marine Survivals, and Size at Age Trends: Comparison of Wild and Enhanced Stocks. Steven G. Honnold, ADF&G
- Does the growth record contained in the shells of geoduck clams reflect changes in marine production? Peter Hagen, Zelda Swain, ADF&G and Ken Severin
Department of Geology, University of Alaska, Fairbanks
- Copper River Sockeye Salmon Forecast Methods. John A. Wilcock, ADF&G
- A Modified Spaghetti Tag for use in Mark-Recapture Estimates of Chinook Salmon Abundance in Southeast Alaska. Ed Jones, ADF&G
- The Effect of Warm Water on King Salmon Eggs taken from the Deshka River. Carmen Olito and Diane Starkey, ADF&G
- Retrospective Analysis of Ocean Growth Zones on Yukon River Chum Salmon. Tim Sands and Bill Smoker, University of Alaska Fairbanks
- Monitoring Freshwater Survival of Yukon River Chum Salmon. James E. Finn and E. Eric Knudsen, USGS, Alaska Biological Science Center
- The Ilnik River Modified Floating Weir. Mark Witteveen, ADF&G
- Kodiak Management Area Pink Salmon Forecast Modeling. Nick Sagalkin, ADF&G
- Southeast Alaska Coastal Monitoring. Joseph A. Orsi, James M. Murphy, Donald G. Mortensen, and Bruce L. Wing, Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service
- Can Remote Video and Time-Lapse Recording Technology Improve Salmon Escapement Monitoring in Alaska? Ted Otis, ADF&G
- Rocket Science and Indexing Escapements of Pink Salmon in Southeast Alaska. Timothy P. Zadina, ADF&G
- An exploration of forecast errors in selected major runs of Alaska pink and sockeye salmon. Mike Byerly, University of Alaska Fairbanks and Hal Geiger, ADF&G
- Variability of Stikine sockeye run sizes. Kathleen Jensen, ADF&G

Lake Becharof Ecosystem Model

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Lake Becharof is a nursery lake for sockeye and coho juvenile salmon that contribute to the Bristol Bay salmon fisheries. Sockeye runs have varied from around 2 thousand to 20 thousand fish in the past two decades in a pattern of increasing runs from 1977 to 1993 and decreasing runs since 1994. A similar pattern is noted for escapements, but the peak occurred in 1991. Smolt outmigration, measured since 1980, also varies annually, but the pattern has been more random, with no trend noted. Although correlation is weak between either returns and escapement or between returns and smolt migration, there is a stronger relationship between returns and smolt outmigrations. Understanding how to improve the survival of emergent fry to outmigrating smolts requires an understanding of the ecosystem. The current study develops an ecosystem model using ECOPATH to do so.

Besides salmon, Lake Becharof is the home of Dolly Varden, Arctic Char, and Northern Pike, which are predators on salmon juveniles. Other pelagic species, such as sticklebacks, are food competitors of the juvenile salmon. Young coho salmon prey heavily on sockeye juveniles. Zooplankton is an important component of the juvenile salmon diet. The zooplankton composition in Lake Becharof consists of mainly *Bosmina*, *Daphnia*, *Cyclops*, and *Diaptomus* species.

The ECOPATH model is a mass-balancing model. The model is run at several levels of observed escapement and smolt outmigration to see how other species' abundances would have to change to maintain mass balancing under fixed rates of production and consumption per biomass. Zooplankton does not appear to be limiting in Becharof Lake and Dolly Varden is probably the main predator, controlling levels of smolt production.

6th Alaska Salmon Workshop
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Kodiak Island Sockeye Salmon Freshwater and Marine Survivals, and Size at Age Trends: Comparison of Wild and Enhanced Stocks.

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Climate changes affect the production of salmon in both freshwater and marine environments. Commercial salmon harvest trends in Canada, the United States, Japan, and Russia indicate that common events may affect the production of salmon in the North Pacific Ocean (Beamish and Bouillon 1993).

Kodiak Island area sockeye salmon stocks have been rebuilding since the 1970's and harvests have increased accordingly. Karluk Lake is the largest sockeye salmon producer on Kodiak Island. The restoration of Karluk Lake sockeye salmon in the late 1970's and early 1980's was an important component of the island-wide rebuilding process. Frazer Lake also aided the rebuilding process, producing large runs of sockeye salmon in the late 1980's and 1990's. Frazer Lake production began with the introduction of sockeye fry and adults and the installation of a fish ladder in the 1950's and 1960's. This system now supports a self-sustaining sockeye salmon run with escapement needs provided by way of fish ladder passage. Spiridon Lake is the third largest lake (Karluk and Frazer are the largest) on Kodiak Island and, like Frazer Lake, was devoid of anadromous salmon prior to a sockeye salmon stocking project. This project was not intended to create a self-sustaining run due to extremely large barriers to escapement in the outlet creek. Annual stocking was started in the early 1990's to provide enhanced catches in traditional fisheries and mop up in a terminal fishery in Spiridon Bay. Together, these three systems produce ~ 2.5 million sockeye salmon, annually.

This poster describes and compares sockeye salmon freshwater and marine survivals and size at age trends for Karluk, Frazer, and Spiridon Lakes. These systems provide a unique opportunity to assess survival and size at age trends. Karluk Lake sockeye salmon production data have been reported in the literature since the early 1900's, which provides the opportunity to compare historical findings to more recent year production trends. Frazer Lake was one of the first barren lakes in Alaska in which juvenile and adults were introduced to develop a viable sockeye salmon run. Known numbers of juveniles and adults were stocked during the development phase of the project and resulting smolt migrations and adult returns were enumerated to assess freshwater and marine production. Recently, (1990's) Frazer Lake sockeye salmon runs have been large (~1 million fish) and a smolt assessment program has accompanied the annual run reconstruction. Thus, development phase production data can be compared to recent year self-sustaining phase production data for the Frazer Lake sockeye stock. Lastly, Spiridon Lake provides the most unique opportunity for assessment of a barren lake sockeye salmon stocking project. Fry stocked, smolt emigrations, and adult returns by age have been documented since the inception of the project in 1991. The freshwater scale patterns of Spiridon Lake smolt and adults are unique and easily identifiable and have provided reliable stock specific production estimates. Thus, freshwater and marine survival, as well as, size at age trends can be accurately determined.

Does the growth record contained in the shells of geoduck clams reflect changes in marine production?

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Geoducks (*Panope abrupta*) are the target of an emerging and valuable dive fishery in Southeast Alaska. To provide basic biological information for management of the resource, geoduck shells are collected after surveying new areas and from sampling commercial harvests. In addition to taking measurements from the shells, thin sections are cut from the shell hinges and age estimates are made by counting distinct dark and light bands as seen with transmitted light microscope. Validation that first five bands were formed annually was made by examining shells of known age geoducks obtained from a hatchery in Washington State. Validation of annuli in older geoducks was made indirectly by creating elemental maps of the thin sections with an electron microprobe. Counts of strontium and sulfur bands in the elemental maps were found to correspond with counts made through the microscope. Of 500 specimens obtained from several locations in Southeast Alaska during 1998, modal ages appear around 37 years and 54 years with a maximum age of 130 years. A common pattern seen in shells of all ages, is a compressed series of annuli spacings extending from early to late 1970's followed by a several years of more rapid growth through the mid 1980's. It is likely that other, more subtle patterns, may be revealed through careful measurements of annuli spacing and shell composition. Because geoducks are sedentary filter feeders, the growth history contained in their shells may reflect changes in primary and secondary production at specific locations and times. If so, this could provide a unique tool for investigating recruitment fluctuations in marine fish.

Copper River Sockeye Salmon Forecast Methods

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Methods used to forecast sockeye salmon runs to the Copper River since 1998 differed markedly from previous techniques, primarily in response to increasingly poor forecast performance. Forecasts prior to 1998 relied on the relationship between number of spawners and subsequent returns, using return per spawner (R/S) values for the 5 parent year escapements most similar in magnitude to that of the dominant age class (age 5) of the year for which the forecast was developed. This approach was used because it simplified calculations by approximating the results from linear regression, and because age composition data for some escapements and harvests were not yet available for the recent years. Most calculations and data archival were accomplished using various versions of Lotus 1-2-3 spreadsheet software.

Despite the simple methods employed, forecast performance for 1983-1992 exhibited a reasonable mean percent error of 5% below actual run. However, in the late 1990s, Copper River sockeye salmon runs exceeded all previously documented runs, although parent year escapements were generally only slightly above average. This period of unusually high survival produced R/S values well outside the range of historic values and forecasts under estimated actual runs by a mean percent error of 33%. High return-per-spawner values for the two most successful brood years on record (1991 and 1992) reflect this apparent increased productivity. These record large runs suggest that environmental conditions have been unusually favorable for Copper River stocks, although this pattern differed from observations for other sockeye salmon producing systems in the region.

Additionally, reliable estimates of survival and contributions from supplemental production for individual brood years have only recently become available through coded wire tag recoveries in harvest and escapements. Although historic estimates of Gulkana Hatchery production are thought to be inaccurate, improved contribution estimates for 1997 and 1998 indicated large contributions from supplemental production and provided smolt-to-adult survival estimates for two of three release sites. Smolt-to-adult survival estimates for one remote release site, Crosswind Lake, appear to have exceeded 30%.

The 1998 and 1999 Copper River sockeye salmon forecasts were calculated from linear regressions of brood year sibling returns or average return of age classes for natural runs, and from average smolt-to-adult survivals for marked releases or assumptions about fry-to-adult survival for unmarked releases from supplemental production. It was hoped that incorporation of information from later life stages than was used in prior forecasts (based on parent escapements and mean R/S) would improve prediction accuracy. Data archival and analysis was accomplished completely within Microsoft Excel97.

The forecast of the natural run of sockeye salmon to the Copper River was the sum of estimates for six age classes. Forecast for each age class was estimated from either linear regressions of sibling returns or average returns of the age class based on subjective examination of mean percent error from cross validation. Linear regression models using logarithm-transformed data were generally selected to predict runs for the most abundant age classes (ages 1.2, 1.3, and 2.2). The run of each of these three age classes was predicted from the relationship between returns of that age class and returns of the age class one year younger from the same brood year. For example, the model used to predict the run of age-2.2 sockeye salmon in 1999 used the

run of age-2.1 sockeye salmon in 1998 as the input parameter. Predicted runs of less abundant age classes (generally ages 1.1, 2.3, and 0.3) were calculated as the historic mean return of those age classes.

The 80% confidence bounds for the total forecast of natural production were estimated using either a cross validation technique for predictions based on regression models, or the confidence interval around the mean. The 80% confidence bounds for harvests of natural production were calculated using mean square error estimates for previous harvest projections. Calculation of 80% confidence bounds from cross validation was accomplished using simple procedures developed using Visual Basic for Applications (VBA) for Microsoft Excel97.

Supplemental production from Gulkana Hatchery remote releases to Crosswind and Summit Lakes was predicted using smolt-to-adult survival estimates based on coded-wire tag recoveries in harvests and enumerated adult escapements. Survival of juveniles released into Paxson Lake was assumed to lie between values estimated for Crosswind and Summit Lake. Average proportion of total Copper River sockeye salmon runs harvested in all fisheries 1996-1998 (70.5%) was used to project total harvest of Gulkana Hatchery stocks in 1999. The 80% confidence bounds for the forecast of supplemental production were calculated using mean square error estimates calculated for natural runs.

The 1998 actual run was 17% below the forecast run based largely on sibling regressions. This was a substantial improvement over 1996 (39% below) and 1997 (47% below), but still less than the average performance for previous years. In addition, the 1998 actual run appeared to signal a return to more typical production levels for the Copper River system, although it was still slightly above the average run. If realized, the forecast for the 1999 total run will still be 17% above the 1983-1998 average. Although the natural run is predicted to be slightly lower than the average for years prior to significant supplemental production, returns to the Gulkana Hatchery are anticipated to be nearly double those observed for recent years. If realized, this increase in supplemental production could seriously compromise management of Copper River sockeye salmon fisheries seeking to avoid excessive harvest rates on natural runs.

A Modified Spaghetti Tag for use in Mark-Recapture Estimates of Chinook Salmon Abundance in Southeast Alaska

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The abundances of chinook salmon *Oncorhynchus tshawytscha* that returned to spawn in the Taku, Stikine, and Unuk rivers of Southeast Alaska has been estimated in the past using mark-recapture experiments. Initially, hollow-core spaghetti tags sewn through the backs of fish just posterior the dorsal fin and secured with an overhand knot were used as primary tags. However, these tags proved unsuitable for estimating abundance and produced rates of tag loss as high as 38%. A primary tag had to be identified that could endure extended periods of time in the river environment and withstand the aggressive behaviors of spawning chinook salmon.

A new primary tag was developed by ADF&G and Floy Tag Co. that consisted of a solid-core spaghetti tag having a 2 1/4" section of laminated Floy tubing shrunk onto a 15" piece of 80-lb test monofilament fishing line. In addition, two secondary marks were used, one being a clip of the left axillary appendage and the other being a left upper operculum punch 1/4" in diameter. After the monofilament was sewn through the backs of the fish it was then secured with the use of a brass line crimp. The excess monofilament was then trimmed off. Each spaghetti tag was individually numbered and labeled with an ADF&G contact phone number.

Tag loss using the new primary tag has been relatively low ranging between 2% and 6% and the two secondary marks have proven to be fail safe indicators of tag loss. In addition, tag loss appears to be minimized when the time between sampling events is decreased and when experienced crews are used. In general, the use of the solid-core spaghetti tag has proven to be a reliable and durable tag when applied to chinook salmon immigrating into these large glacial rivers of Southeast Alaska.

Key words: abundance, chinook salmon, Taku, Stikine, and Unuk rivers, mark-recapture, hollow-core spaghetti tag, tag loss, solid-core spaghetti tag, operculum punch, axillary appendage.

The Effect of Warm Water on King Salmon Eggs taken from the Deshka River

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After many years of productivity, and after a series of sunny summers in the early 1990s, there was a dramatic drop in the king salmon harvested from the Deshka River in 1994. We felt that the warmer water present during the critical early incubation period may have increased the mortality of king salmon eggs and alevins. The warmer water may also have accelerated the development of king salmon eggs so that the fry emerged before food was available in spring. The water temperature in the Deshka River, which drains a large lowland area consisting of lakes, bogs, and beaver ponds, can climb to 20°C after a period of sunny weather. We tested our hypothesis at Ft. Richardson Hatchery by fertilizing and incubating king salmon eggs in eight incubators set at four initial temperatures (10°, 13°, 16°, and 19°C), and then reducing water temperatures in all incubators to match the Deshka's last 3-year average from late August through May.

In our preliminary results we found: 1) with increasing temperature there was a decline in the length of time that sperm were motile; 2) with increasing temperature there was a decline in fertilization rates from an average of 83% at 10°C to 70% at 19°C; 3) average survival from fertilization to pre-emergence was about 90% for the 10°C and 13°C test groups, and dropped to 37% for 16°C and 18% for 19°C test groups; and 4) some of the 19°C test groups emerged as early as January. Mortality did not occur when eggs were incubating in the warm water; rather, it occurred at later lifestages.

Monitoring Freshwater Survival of Yukon River Chum Salmon

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Compared to other, more southerly stocks of chum salmon, little is known about the ecology, behavior, and productive capacity of Yukon River chum salmon. While escapement indices, and in a few cases weir- or sonar-derived population estimates, are available for some of the most significant spawning populations, little is known about factors affecting production and survival during the freshwater portion (from egg deposition until smolt emigration) of the chum salmon life cycle.

We have established two intensive study sites, one summer-run and one fall-run, where we are quantifying spawning intensity, habitat, and survival. The overall goal of the study is to estimate the survival from spawner to smolt (fry emigrating from spawning areas). Nested within that are estimates of survival from spawner (potential egg deposition) to actual egg deposition, from egg deposition to pre-emergent fry, from pre-emergent fry to smolt emigration.

Spawner abundance is monitored at weirs, which define the upper and lower boundaries of the study areas. Unique color/numerically coded tags allow us to identify individual fish. Spawning locations (redds) are mapped using a digital theodolite and habitat variables measured (e.g., water depth, water velocity, inter-gravel water temperature, and substrate composition). Spawning distribution data are integrated with study site maps and used to define intragravel sample areas. A hydraulic redd pump is used to sample eggs and pre-emergent alevins through the fall and late winter. Funnel nets are used to collect out-migrating smolts. Mark-recapture techniques are used to evaluate smolt trap efficiency and expand trap catches to estimate total smolt production.

We have had several major successes but still have some difficult sampling challenges ahead. Our observations indicate that operation of weirs on the spawning grounds is possible without disruption of spawning behavior. Specific, detailed mapping of spawning locations will allow examination of inter-annual patterns of spawning and help to determine the degree of redd superimposition. The development of study site maps also sets the stage for spatial analysis of habitat selection and preference. Intragravel estimates at the within study site scale, appear to be possible, at least up to the eyed-egg stage. However, intragravel estimates of total production (i.e., in terms of numbers of individuals, either eyed eggs or alevins, per unit area) do not appear to be tenable due to high sampling variances. With further improvement of our smolt traps mark-recapture estimates of smolt production also appears to be realistic.

After 5 years of data are collected on some of these critical life stages, models relating spawner abundance and environmental drivers to critical life stages may reveal controlling factors and ultimately become useful in refining predictive management models.

The Ilnik River Modified Floating Weir

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The floating weir at the Ilnik River was developed to cope with the arduous conditions at the weir site. Conventional floating and tripod weir designs were not believed to be sufficient to consistently remain “fish tight” with the dynamic sand substrate, high water levels, and reverse tidal flow conditions that occur at the Ilnik River. A flexible weir panel made with riveted Polyvinyl Chloride (PVC) rubber strapping and PVC tubing was constructed to deal with the extreme conditions at the Ilnik. The weir was anchored to the substrate with a heavy chain that conformed to the ever-changing river bottom. The result was a weir that was able to change with the dynamic environment while remaining “fish tight” throughout the season. The Ilnik weir innovations can be applied to many other escapement enumeration projects with or without similar environmental conditions.

Kodiak Management Area Pink Salmon Forecast Modeling

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Pink salmon (*Oncorhynchus gorbuscha*) returns have accounted for as much as 80% of the total salmon returns to the Kodiak Management Area (KMA). Due to the importance of pink salmon to the KMA, formal forecasting began in 1966. Forecasts relied on a preemergent pink salmon survival index derived from annual overwinter egg to fry survival data collected in specific streams during March and April. A positive feature of the preemergent program was that in addition to the index of pink salmon fry survival, site-specific qualitative information was also obtained (e.g., scouring). These observations in conjunction with site-specific indices allowed the Alaska Department of Fish and Game (ADF&G) to forecast area wide estimates with qualitative assessment on a finer scale for each year. However, similar to many forecast models, the preemergent forecast model suffered from wide confidence intervals (approximately +/- 10 million) and periodic gross errors (e.g., 39% error in 1998).

In 1998 the Kodiak ADF&G preemergent program was discontinued due to budget shortfalls. Since the existing forecast model relied heavily upon an index developed from preemergent data, a new model was required to estimate pink salmon returns and harvest. The greatest difficulty was developing a new model with less program infrastructure, yet expectations (public and Departmental) to maintain similar forecasting resolution.

Recent published research has documented strong influences from physical variables (e.g., Aleutian pressure) on salmon returns. The strongest relationships appeared to be related to freshwater survival or early marine survival. Strong correlations (>0.6) of our The KMA preemergent fry index correlated strongly to pink salmon returns, indicating the importance of freshwater survival to Kodiak area pink salmon returns. While additional funding was not available to monitor or collect additional climatic variables, data collected by the National Weather Service or NOAA (e.g., NOMAD buoys) were available on the Internet.

The goal of this study was to develop a new forecast model to predict pink salmon returns to the KMA. Preliminary analysis of the relationship of historical climatic and pink salmon return data has been inconclusive; thus the 1999 pink salmon forecast was derived from a Ricker spawner recruitment analysis (treating odd and even years separately).

Southeast Alaska Coastal Monitoring

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In 1997, the Auke Bay Laboratory, National Marine Fisheries Service, initiated a coastal monitoring program in the northern region of southeastern Alaska. A primary goal of this program is to maintain and build a time series of biological and physical oceanographic indices related to the seasonal distribution and abundance of juvenile salmon along their principal seaward migration corridor in the region. In 1997 and 1998, juvenile salmon and oceanographic conditions were sampled along a series of transects progressing from inside waters to coastal waters 60 km offshore. Sampling was done approximately monthly from May to October. A key element of the program is to obtain stock-specific information from the recoveries of marked juvenile salmon. Stock-specific information on the growth, distribution, and abundance of juvenile salmon will be evaluated in the context of their ocean habitat. This information will provide insight into potential effects of climate change on growth, stock recruitment, and the utilization of marine habitat by juvenile salmon.

Can Remote Video and Time-Lapse Recording Technology Improve Salmon Escapement Monitoring in Alaska?

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Aerial survey has been used to monitor salmon escapement in clear streams throughout Alaska for over 35 years. This technique is often favored for small drainages which otherwise may go unassessed due to the high cost of more intensive monitoring methods (e.g., weir or sonar) relative to the stream's modest escapement. However, aerial survey has several drawbacks. Observer experience, water clarity, stream morphology and habitat type, timing of survey flights, and stream residency are just a few factors shown to influence the accuracy and precision of aerial survey estimates of salmon escapement. Video and time-lapse recording technology has proven effective for capturing images of adult salmonids in controlled field situations in the Pacific Northwest and Alaska. Herein, I report on our progress in developing an unmanned video system that will reliably record images of migrating adult salmon in small Alaskan streams. This system includes a camera mounted above the stream providing bank to bank coverage to facilitate total escapement enumeration. The camera and time-lapse videocassette recorder operate using 12 V batteries kept charged by solar and/or wind/hydro power generators, depending on site characteristics. Up to 9 days of fish passage can be recorded on a single 160-minute VHS tape when recording in time-lapse mode (1.5 sec/frame). The time required to review tapes varies with fish passage rate and behavior. With funding assistance from the *Exxon Valdez* Oil Spill Trustee Council (EVOS TC), in 1999 we plan to operate a weir concurrently with the video to evaluate the camera's performance under varying stream and escapement conditions. If the video system proves to be field durable and collects escapement data comparable to a weir, at less cost than aerial surveys, remote video and time-lapse recording systems may have wide application throughout Alaska and the Pacific Northwest.

Rocket Science and Indexing Escapements of Pink Salmon in Southeast Alaska

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Area management biologists (AMB's) in the Southeast region religiously fly around in SuperCub's counting pink salmon in streams. These surveys have proven invaluable for assessing the adequacy of the escapements and regulating openings to selectively harvest or protect fish returning to specific areas. A fair proportion of the 2,500+ pink producing streams are flown each season, many several times a season. Thanks to some careful record keeping we now have a 39-year database of mouth, intertidal, and stream counts of live and dead pink salmon from over 75,000 surveys of over 1,800 streams. Realizing that timely and reliable indices or estimates of escapement are essential for escapement-based management of this resource, Commercial Fisheries Division staff are seeking to make quantitative use of these qualitative counts. Our initial work has been to standardize methods used to index annual escapements.

A post-season index of escapements to each management district has been calculated for many years. These indices were calculated as the sum of "peak" aerial counts in all streams which happened to have been surveyed in a year plus the multiplication of the number of unsurveyed, but previously surveyed, streams times the average count in streams with counts of less than 10,000. Recent refinements have included: (1) stratification of the region's 2,500+ pink producing streams from 15 "management districts" into 49 "management stock groups" (Figures 1 and 2); (2) identification of the "key index streams" in each of these stock groups; (3) identification of the key observers (AMB's and their assistants who have more than 58,000 surveys on over 1,600 streams in 39 years); (4) calibration of each observers counting rate to that of the current area management biologist (Figure 3); and (5) application of an EM-algorithm to interpolate for missing counts. These measures to standardize indices reveal that our historical indices were biased high, particularly in the 1960's and 1970's when fewer streams were surveyed (Figure 4).

Future refinements are planned to: (1) make better use of all the survey counts made by key observers in each index stream each year (not just the "peak" live aerial count); (2) enhance inseason tracking of current versus historical escapements by stock group and stream; (3) calibrate counts to the actual number of fish present rather than to the counting rate of the current AMB (Figure 5); and, finally, (4) expand indices to estimates of total escapement.

An exploration of forecast errors in selected major runs of Alaska pink and sockeye salmon

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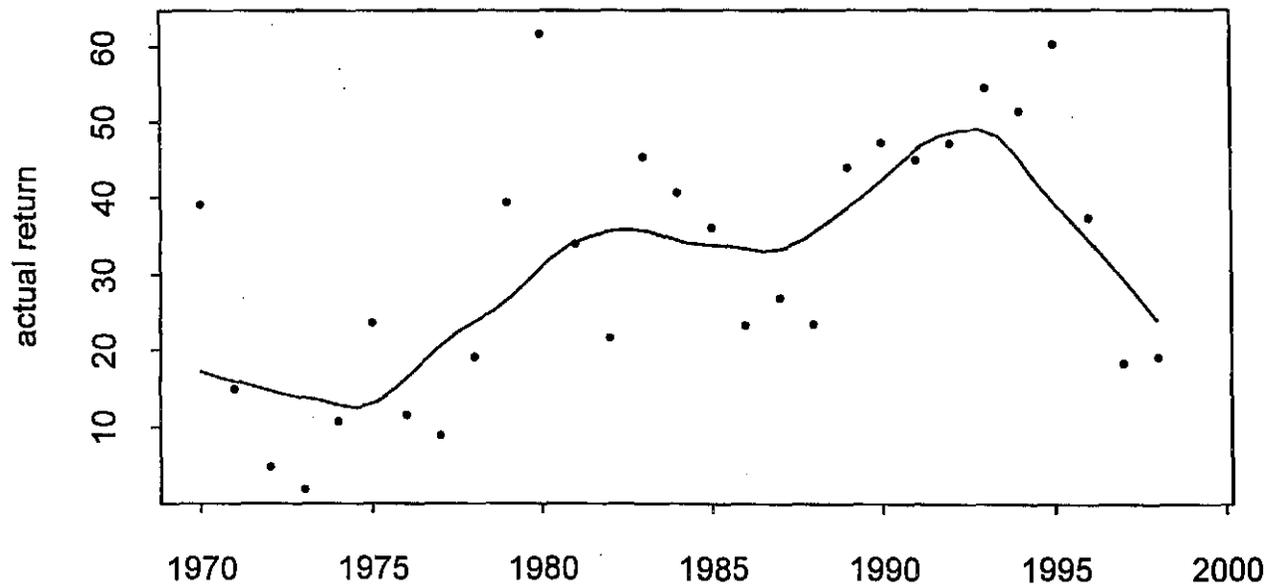
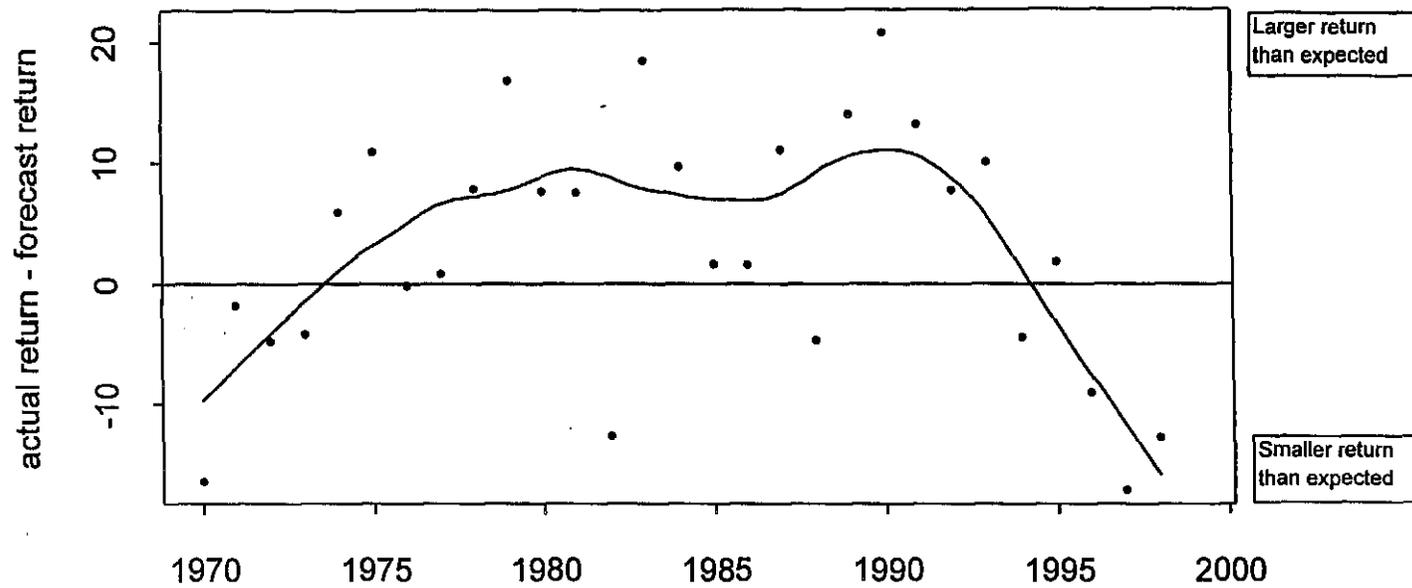
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Looking for obvious patterns, we have graphed forecast errors together with estimated run size, for four major pink and four major sockeye salmon producing systems in Alaska. Our hypothesis is that forecast errors reflect environmental or ocean-climate processes in addition to such things as changes in forecasting methods and hatchery enhancement. Even though large-scale hatchery contributions may mask structural changes in recruitment patterns, for pink and sockeye salmon these effects are largely restricted to Prince William Sound.

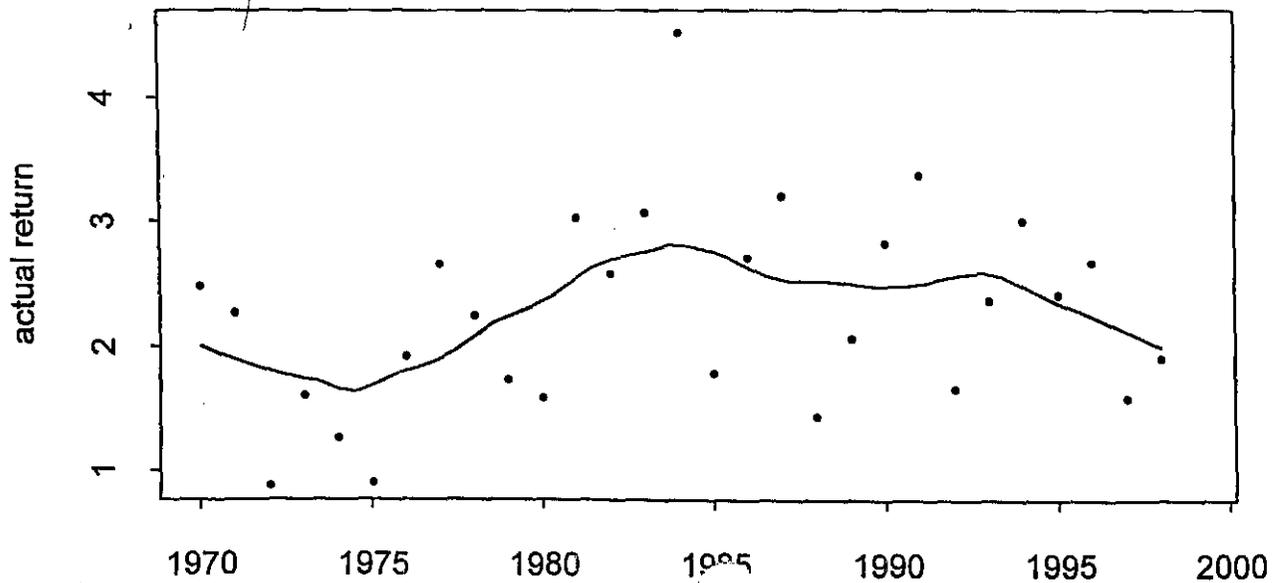
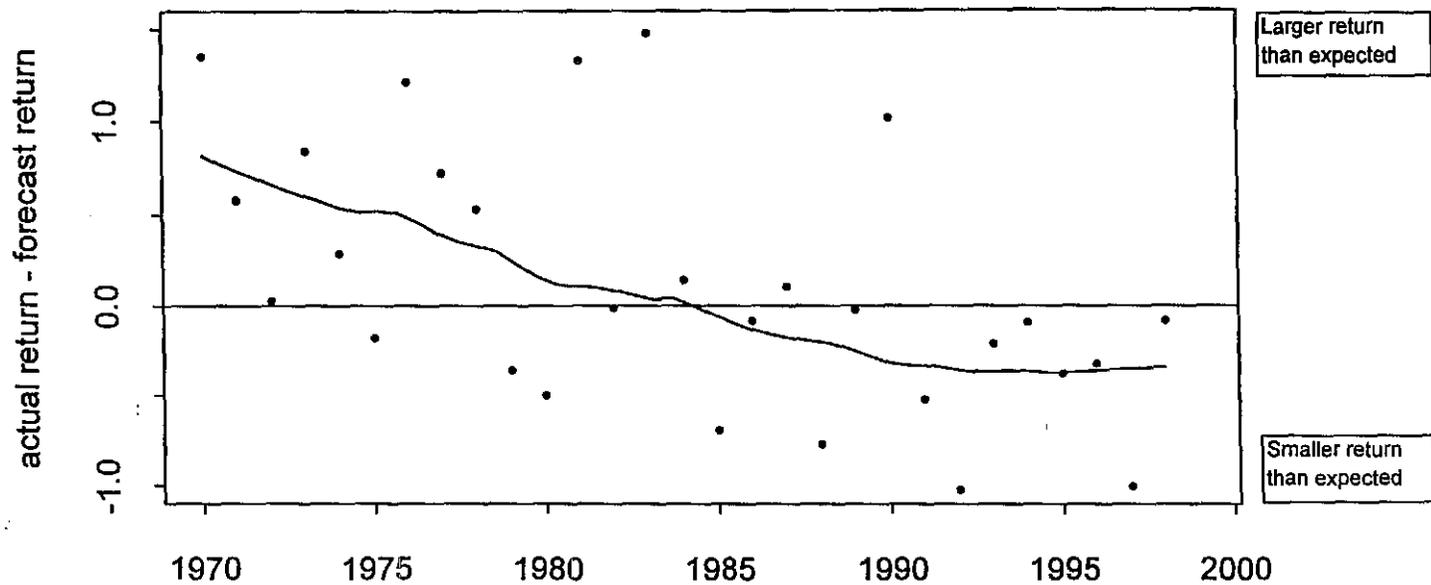
In Bristol Bay, sockeye salmon run sizes were consistently under-estimated from the middle 1970s to late 1980s. Upper Cook Inlet also experienced stronger sockeye returns than expected over a similar period. Forecast methods for Bristol Bay were changed in 1991, when an adjustment for a consistent under-forecast bias was added. Sockeye salmon in Bristol Bay and Upper Cook Inlet share a nearly linear trend from under- to over-forecasting during about 1990 to the present, however. Chignik sockeye forecasts share this increasing trend toward over-forecasting, but do so over a longer period. On the other hand, with the exception of 1998, Copper River shows an opposite trend. Copper River returns have increased steadily since the middle 1980s and forecasts have not kept up.

Statewide, pink salmon runs increased after the middle 1970s. Forecast errors started to increase in the mid-1980s. Increased variability in forecast, beginning in the early 1980s, may have been exacerbated by the introduction of microcomputers into fisheries management. These microcomputers may have encouraged the use of over-parameterized forecast models. Under-forecasts in pink salmon production was especially pronounced in Prince William Sound after 1985, coinciding with a period of increasing hatchery production.

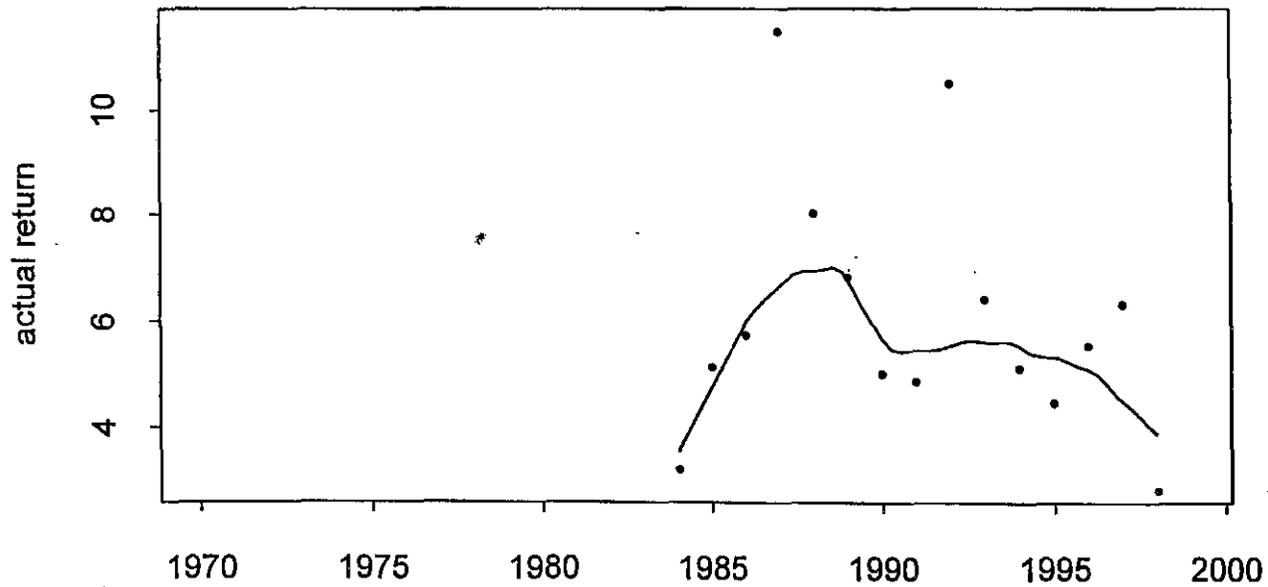
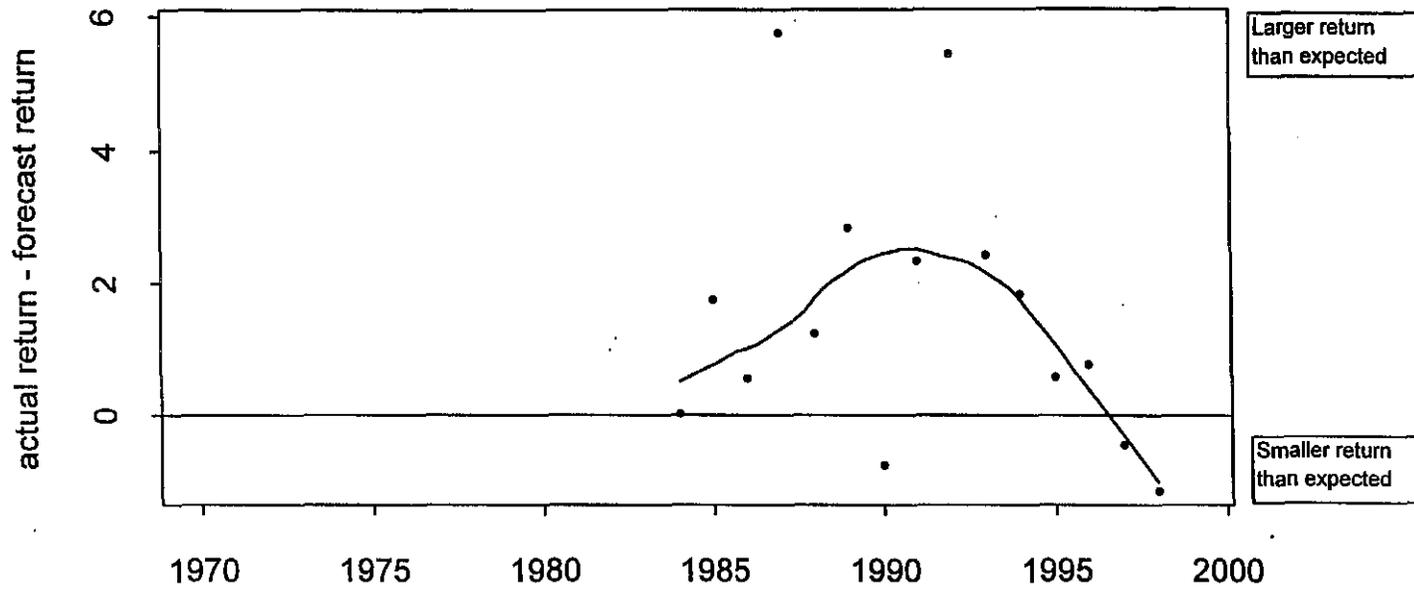
Sockeye Salmon Forecast Error - Bristol Bay



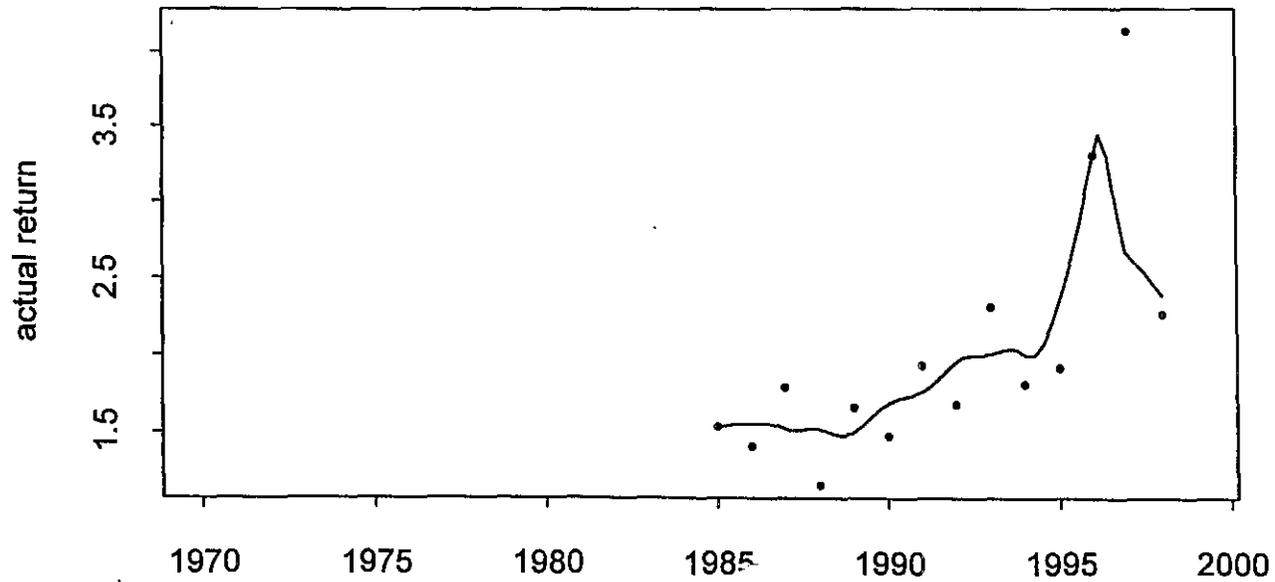
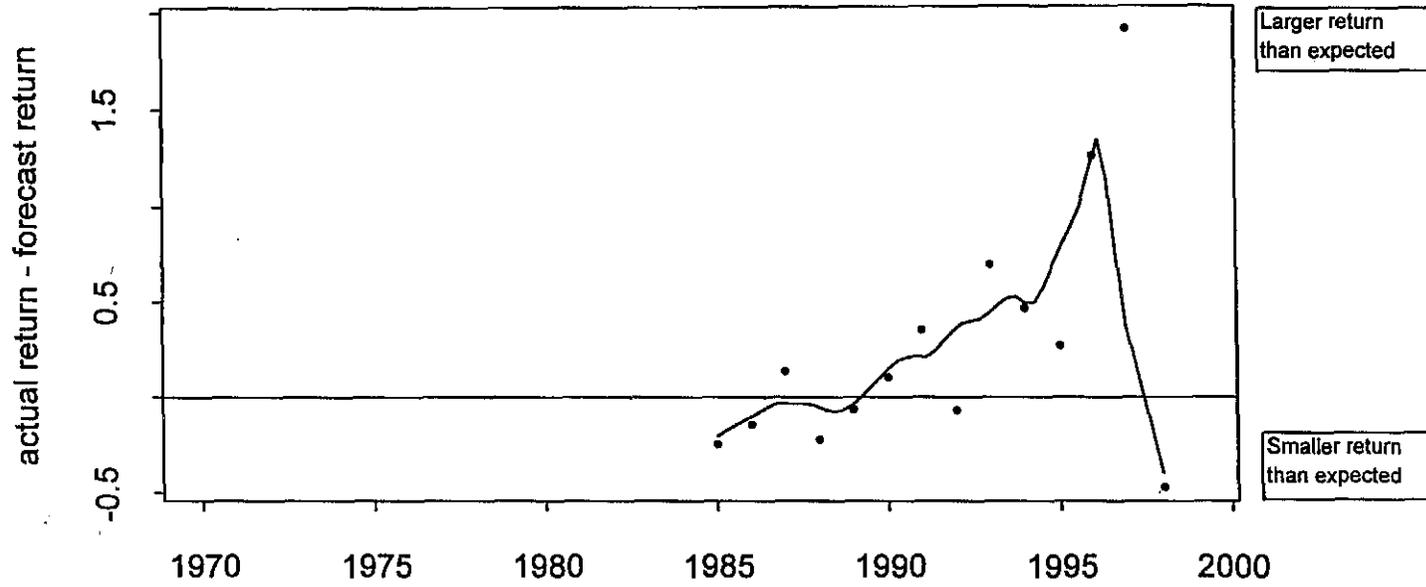
Sockeye Salmon Forecast Error - Chignik



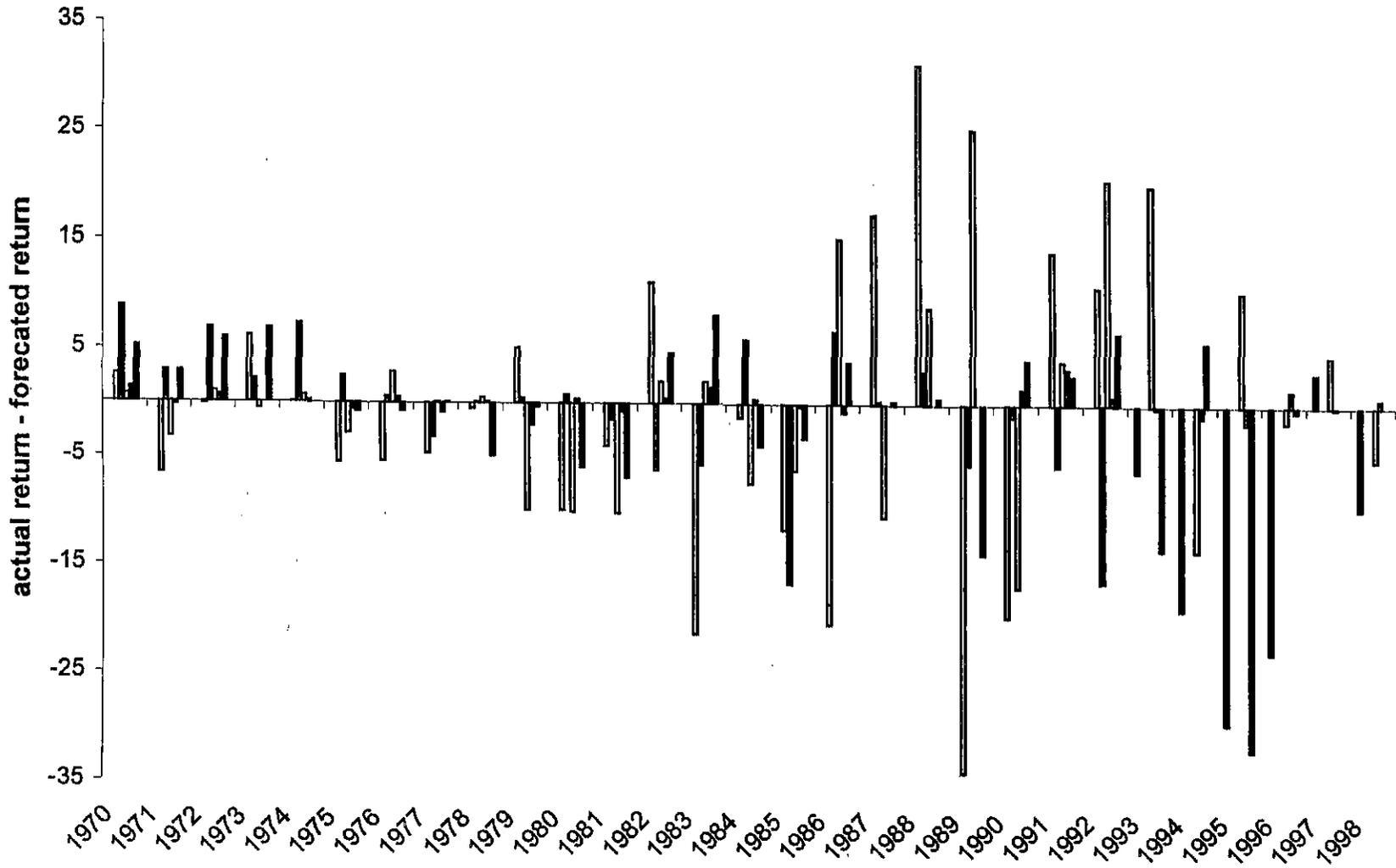
Sockeye Salmon Forecast Error - Upper Cook Inlet



Sockeye Salmon Forecast Error - Copper River



Forecast Error - Pink Salmon



■ Southeast

□ Southern Southeast

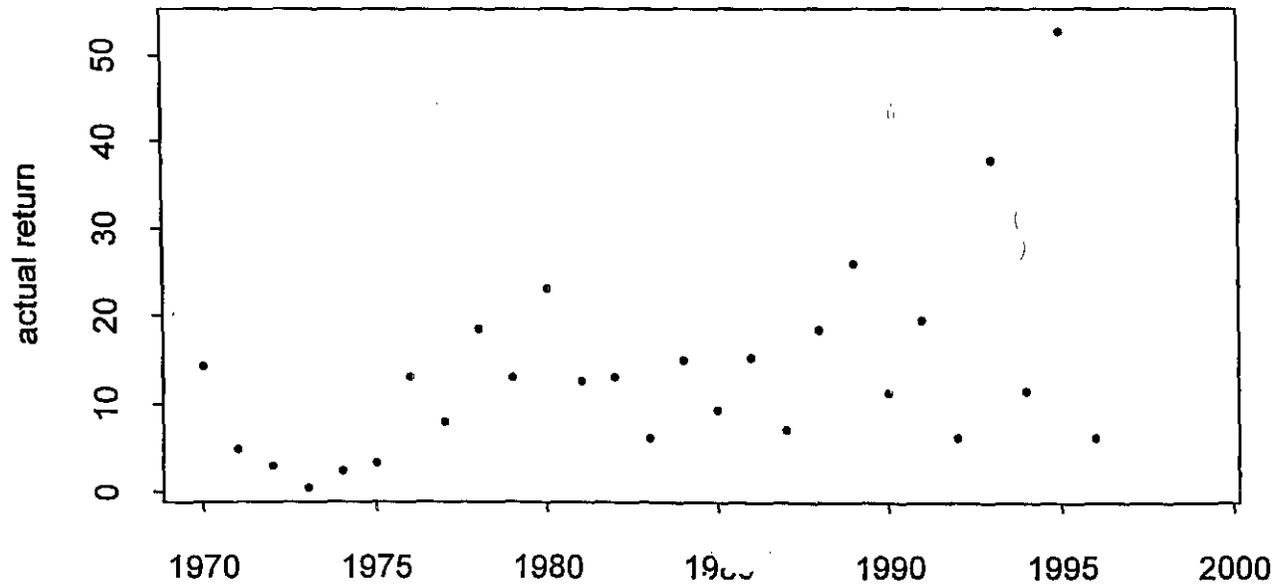
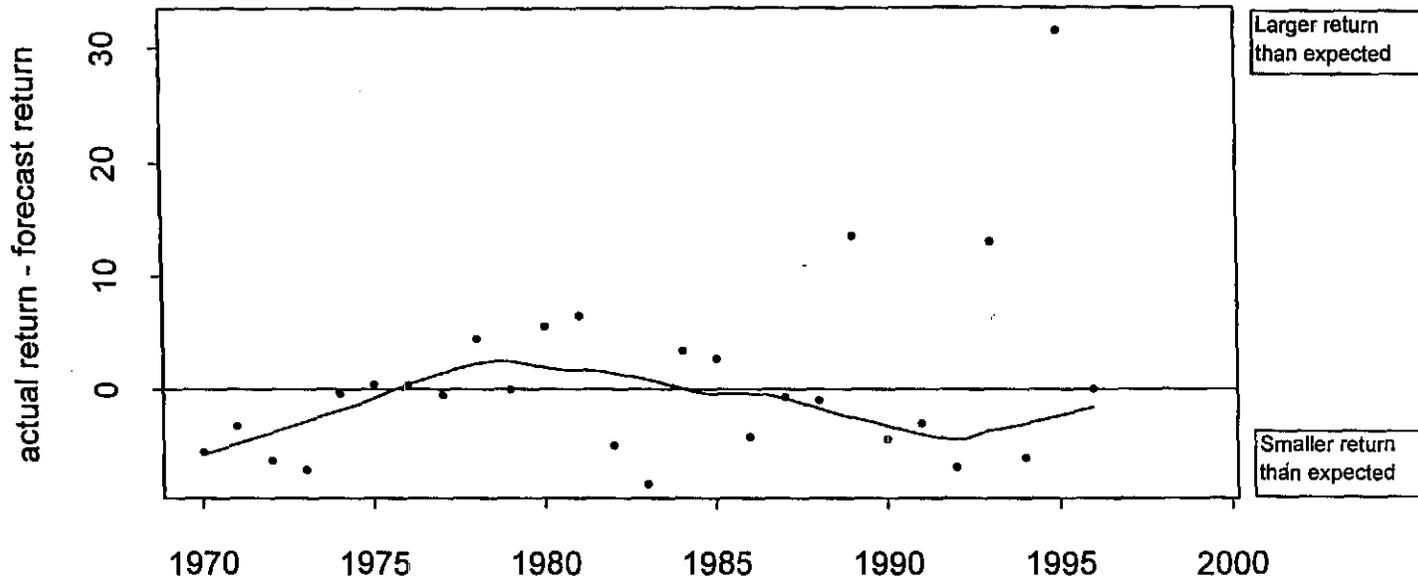
■ Northern Southeast

□ Prince William Sound

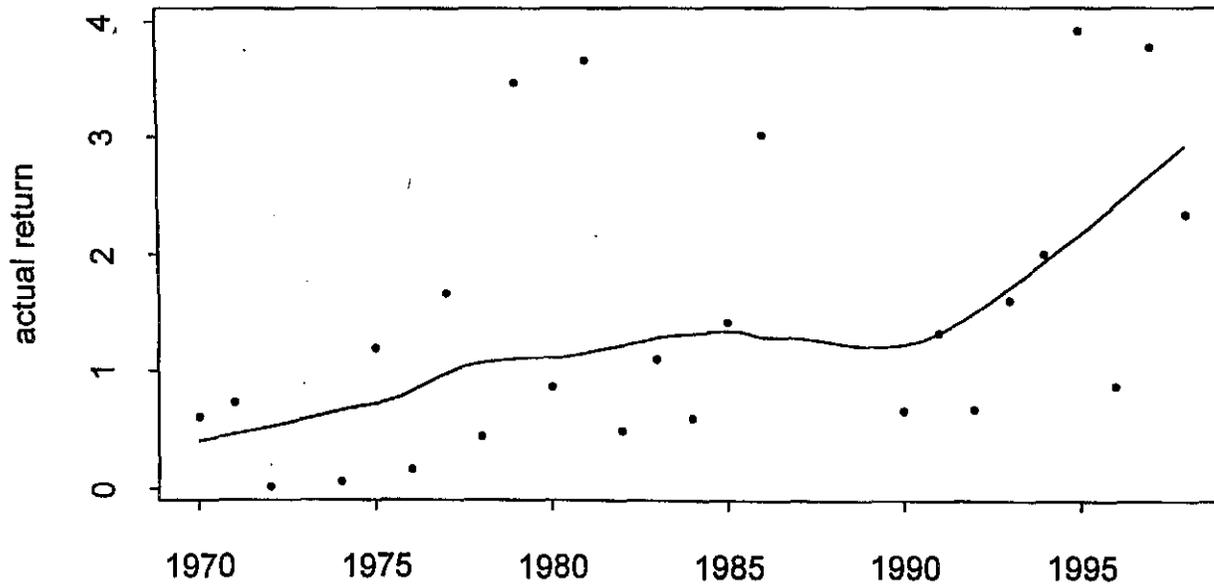
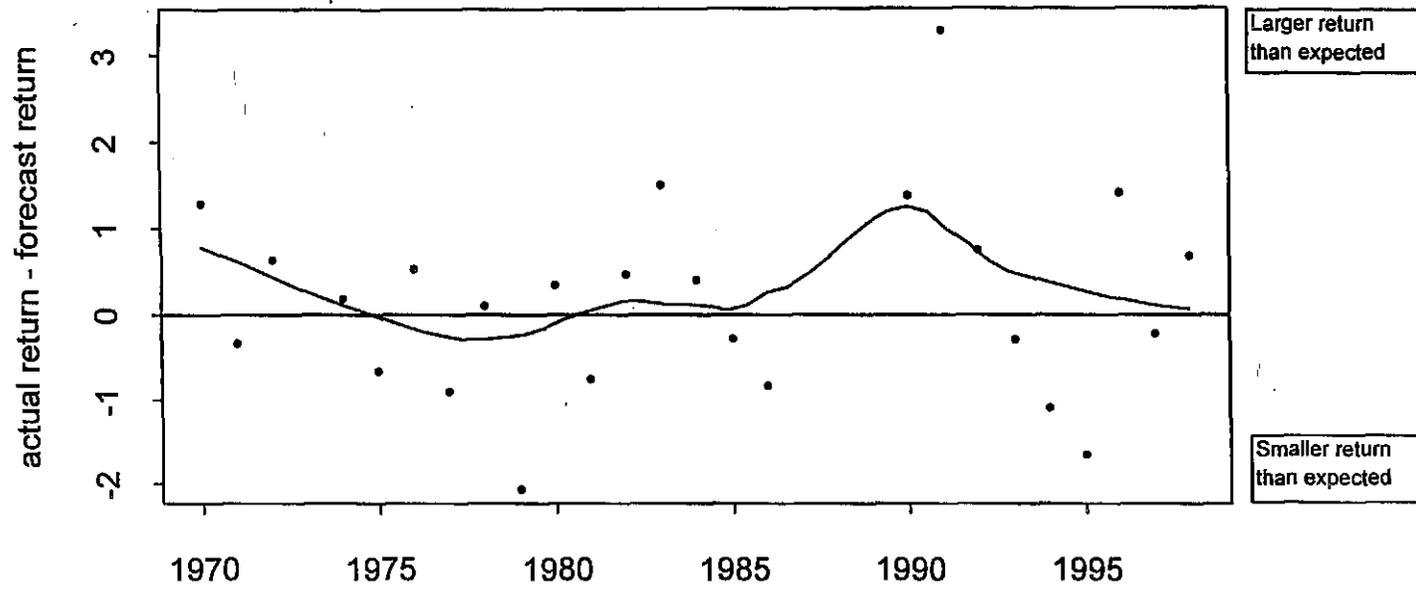
■ Lower Cook Inlet

■ Kodiak

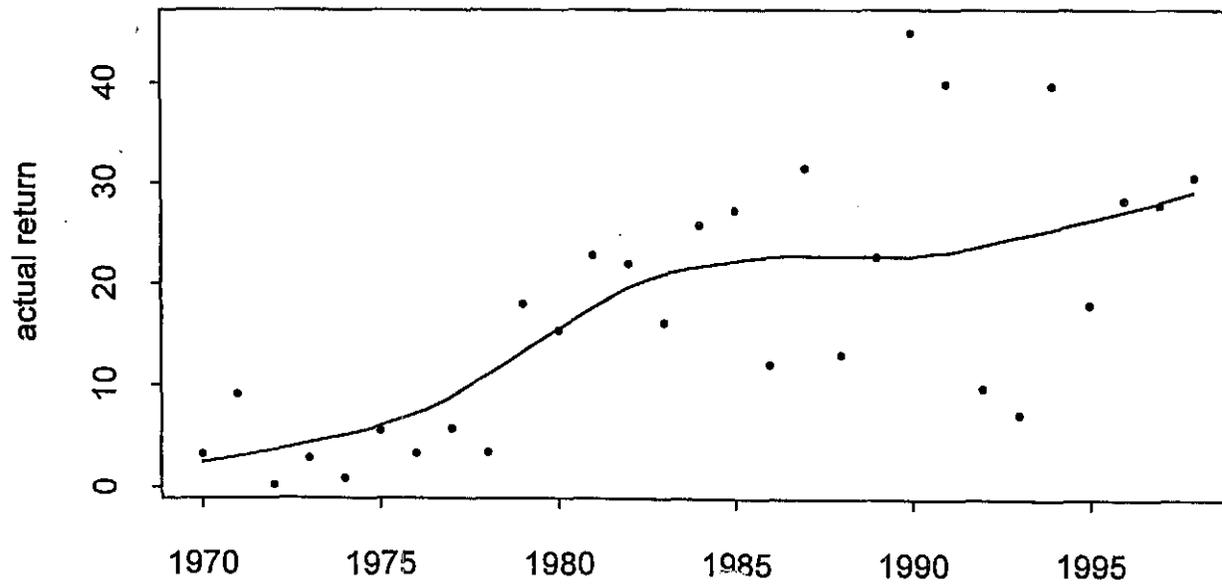
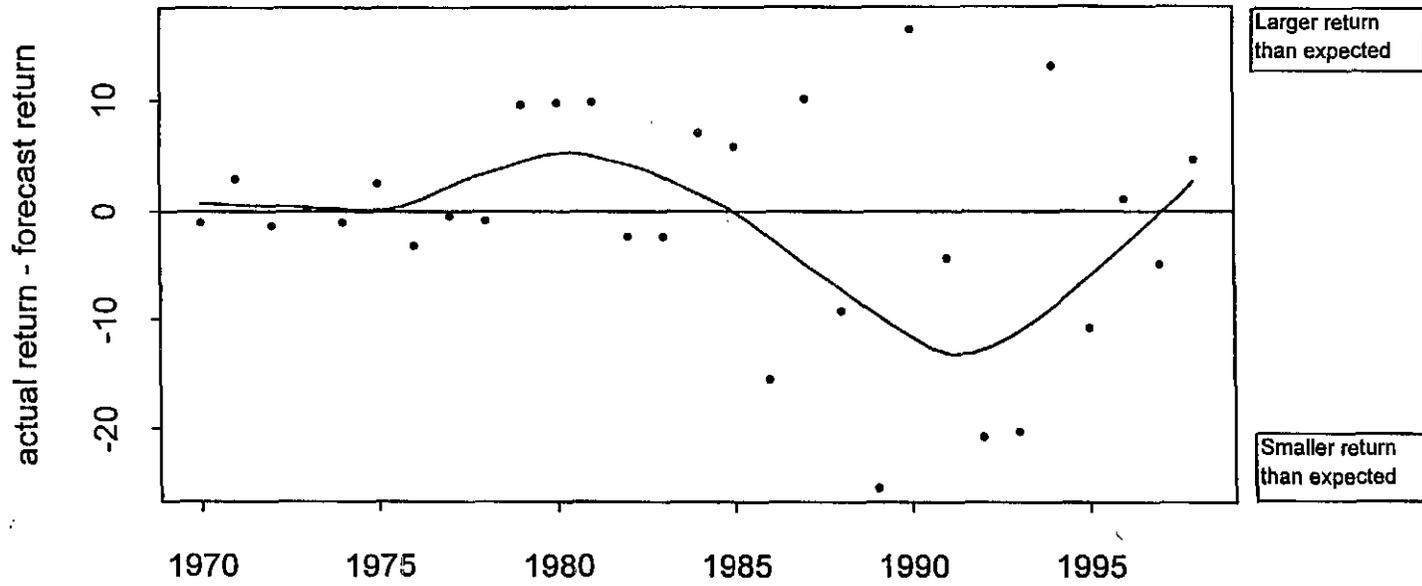
Pink Salmon Forecast Error - Kodiak



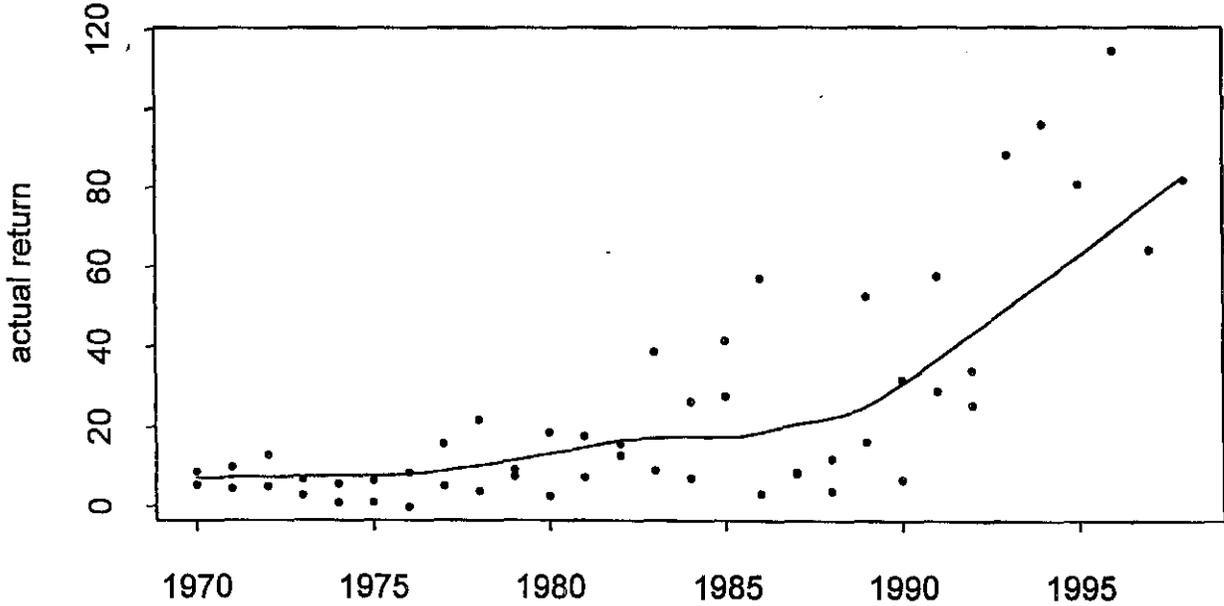
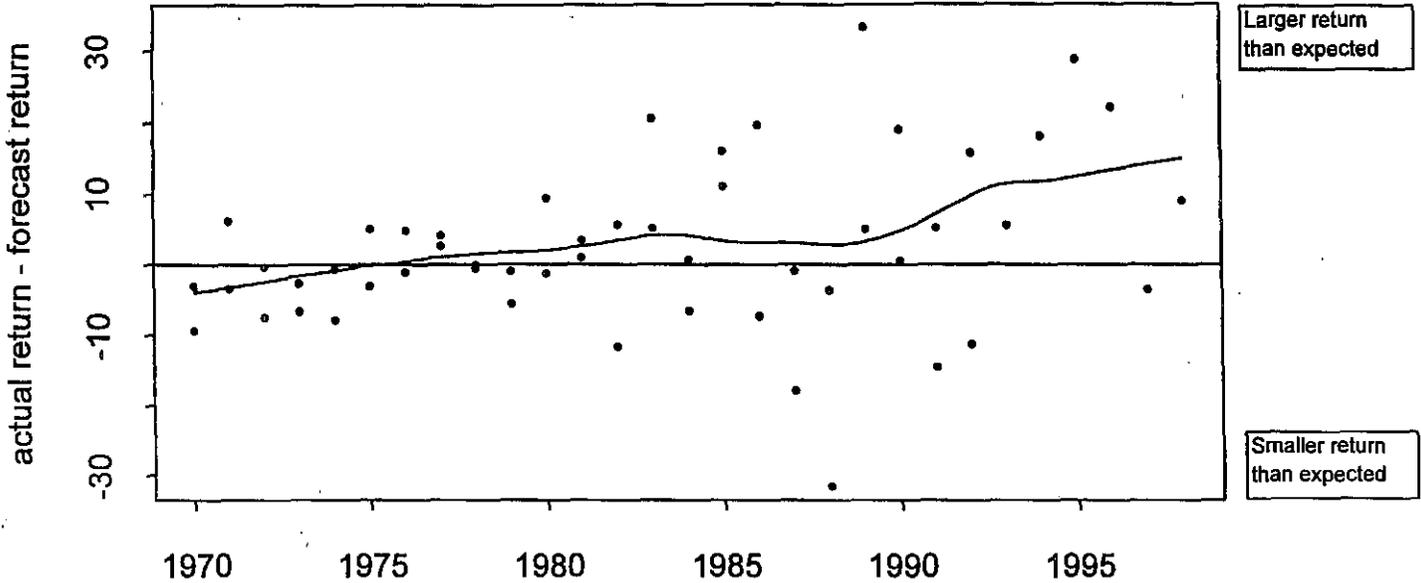
Pink Salmon Forecast Error - Lower Cook Inlet



Pink Salmon Forecast Error - Prince William Sound



Pink Salmon Forecast Error - Southeast



Variability of Stikine Sockeye Run Sizes

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The Stikine River is a large, glacial river that originates in British Columbia and flows through Southeast Alaska into the Pacific Ocean. Stikine sockeye salmon are harvested by U.S. and Canadian commercial and subsistence fishers. Cooperative research and management programs provide data used to manage fisheries under guidelines outlined in the Pacific Salmon Treaty. Two major Stikine sockeye groups are recognized, the Tahltan stock which spawns in Tahltan Lake and the Mainstem conglomerate which spawns throughout the mainstem river. The Stikine sockeye run size is highly variable and has ranged from 43,000 to 372,000 fish (1979-1998). Efforts to understand the processes underlying these fluctuations have met with underwhelming success. There is no obvious correlation between the numbers of Stikine spawners and returning adults with 50,000 spawners capable of producing 50,000 to over 250,000 returning adults. For the Tahltan stock, the return generally decreased when the spawners numbered more than 20,000 fish. Recruits per spawner peaked at 25 fish for escapements of 6,000 fish or less but declined to replacement level with more than 20,000 spawners. There is no strong correlation between the number of mainstem spawners and returning adults. There is a linear correlation between the number of smolts and the number of returning adults ($r^2 = .71$) for the Tahltan stock but no trend between the number of spawners and the number of smolts produced. Marine survival averaged 5% in the late 80's and 14% in the early 90's while average smolt outmigrations doubled from 600,000 to 1,200,000 during the same years. There are no smolt estimates for the mainstem conglomerate.

“Managing” for Escapements in Southeast Alaska

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Commercial harvests of salmon in Southeast Alaska (SEAK) in the 20th Century, and elsewhere in the state for that matter, generally follow a buildup to a high period early in the century, a low period mid-century, and a high period late in the century (Figure 1). This high-low-high harvest pattern has been associated with decadal scale shifts in climatic-oceanographic conditions (Beamish and Bouillon 1993; Francis and Hare 1994; Hare and Francis 1995; Mantua et al. 1997) and a general expectation that future harvests will return to an extended low abundance level. Salmon survivals are influenced by annual, cyclic, and decadal scale fluctuations in climate and ocean conditions but the influence that management for escapements and habitat quality have had on returns has been largely overlooked. This paper assesses the interrelationship of environmental and anthropogenic factors, which influenced the decline in harvests (production) in the mid-1900s and now drive the strong returns in the 1980s and 1990s. I also assess our understanding of the factors that limit coho, pink and sockeye production, our ability to manage for optimal escapements, and my expectations for the future production of SEAK salmon.

Our mission as salmon biologists is to simply determine what factors limit the production of salmon and act on those over which we have some control. Short of curbing greenhouse gas emissions and other pollutants, there's precious little we can do about climate-ocean processes and their affect on salmon survival. Thus, our focus is on protection of the freshwater/early marine habitat used by spawning, rearing, and migrating salmon and on managing for escapements that are naturally distributed and at levels believed to optimize salmon production and utilization. We're simply taking advantage of the surplus production potential inherent with salmon.

The production of wild salmon is dependent, first, on the quality and quantity of the spawning, rearing, and migration habitat and secondly, on the quality and quantity of the escapement (Baker et al. 1996; Gregory and Bisson 1997; Van Alen *in press*). Natural variability in climatic and oceanographic conditions have a universal influence on survivals but historic high levels of production are only possible if the habitat is intact and if there are sufficient numbers of eggs in the gravel to benefit from favorable survival conditions when they occur (Figure 2). Thus, in terms of salmon management, we must strive to maintain escapements at a high enough level that they are not an obvious constraint on salmon production. Assuming no rearing limitations in the ocean phase of salmon, our aim is simply to maximize the number of healthy juveniles that migrate out to sea.

The strategy for maximizing production varies by species and system but I'll make some general conclusions for coho, pink, and sockeye salmon in SEAK. For coho salmon, escapements in recent years, and perhaps all through history, have sufficiently seeded the available rearing habitat. Competition for space and food among coho juveniles limits the number produced from each system with little apparent over-compensatory mortality. Thus, production is primarily dependent on natural variability in survivals (Figure 3) and we simply manage for escapements of at least X. History has shown that widespread reductions in our traditional pattern of exploitation are only needed when runs are exceptionally small.

For pink salmon, 38-years of spawner-recruit data shows that recruits are positively correlated with spawners up to a point and then negatively correlated with spawners at the highest escapement levels (Figure 4). Superimposition of reds, limited carrying capacity in the early marine environment, and predator fields are the likely over-compensatory factors. Thus, we should manage for pink escapements to each stock group of at least X and probably not more than Y. This escapement goal range should be relatively broad to account for imprecision in spawner-recruit estimates, imprecision in management, abundance-based management of co-migrating species, and the desirability to continue to observe the recruitment response over a range of spawners. Limitations in gear and processing capacity have made it practically impossible to constrain escapements within the desired range in large run years. At present, these extreme escapements probably pose the greatest risk to maintaining harvestable returns. Since statehood (1959), local managers, without the aid, or encumbrance, of quantitatively-based escapement goals, run forecasts, and management models, have effectively managed passing- and local-stock seine and gillnet fisheries to achieve well distributed and abundant escapements of pink (and chum) salmon. Aerial surveys have proven invaluable for assessing the adequacy of escapements because pink and chum production is widely distributed among 2500+ streams in the region.

For sockeye salmon, we should also manage for escapements of at least X and probably not more than Y. However, Ricker stock-recruit curves should be used cautiously since the input of marine nutrients from carcasses helps maintain the productivity (return per spawner) of sockeye systems for future generations. Ideally, assessments of habitat capacity and historical production levels will also factor into assessments of escapement goals. Rebuilding escapements, and in-turn production, in a chronically under-escaped system is particularly difficult because the sockeye's freshwater rearing requirements make it most prone to over-compensatory mortality. For coastal sockeye systems in particular, we need to better understand the relationship among escapement, nutrient input from carcasses, and resulting production.

Intensive, competitive, and poorly regulated seine, trap, gillnet, and troll fisheries overharvested whole runs or temporal segments in pre-statehood years. Overfishing began with the first commercial salmon fisheries when barricades, traps, and nets were used in an unregulated effort to capture nearly all sockeye salmon returning to the many small island/coastal streams (Bean 1889). Moser (1899) pointed out that the pack was dominated by sockeye salmon until 1889 and that, only 10 years later, it was dominated

by pink salmon because “all the streams within 70 to 80 miles of the canneries have been scoured [of sockeye salmon] with all the gear that could be devised or used”. Sockeye and summer chum runs were the first to be overfished and have not rebuilt to historical levels. Pink, coho, and chinook stocks are now at historical high abundance levels.

Oceanwide, interdecadal shifts in environmental conditions help explain some of the variability in SEAK salmon production. The Pacific Decadal Oscillation Index (Mantua et al. 1997) and an Aleutian Low Pressure Index generally fit the high-low-high harvest pattern but deviations by species and stock were obvious. Increased returns of pink salmon in the 1980s and 1990s were correlated with increases in sea surface temperatures and winter air temperatures (Figure 5). However, escapements were also trending upward during these years. If favorable environmental conditions were primarily responsible for the increased returns in the 1980s and 1990s, then why was there a long period of declining returns of pink and other salmon species in the 1940s and early 1960s when these environmental parameters were also trending upward? I suspect that favorable environmental conditions in these years did not compensate for the cumulative effects of past overfishing.

I conclude that active management since Statehood to improve and maintain the distribution and abundance of escapements, and generally favorable climate-ocean conditions, are the principal factors contributing to the strong returns in recent years. Furthermore, if we maintain escapements at current levels, and continue protecting the habitat, then I expect salmon returns (harvests) to vary with natural fluctuations in the environment but average much higher than they were in the 1950s, 60s and early-70's. Southeast Alaska is near the middle of the natural range of pacific salmon; anomalous climate-ocean conditions are more likely to reduce survivals of stocks to the East and West.

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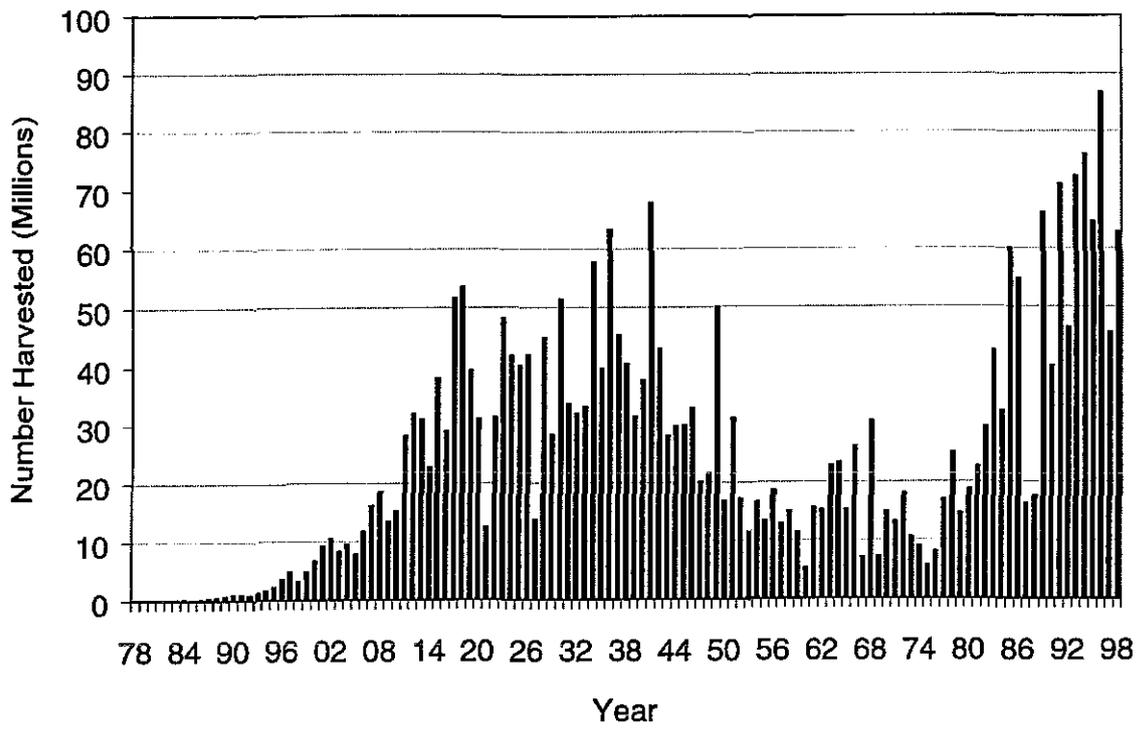


Figure 1. Annual commercial harvest of salmon in Southeast Alaska, 1878-1998.

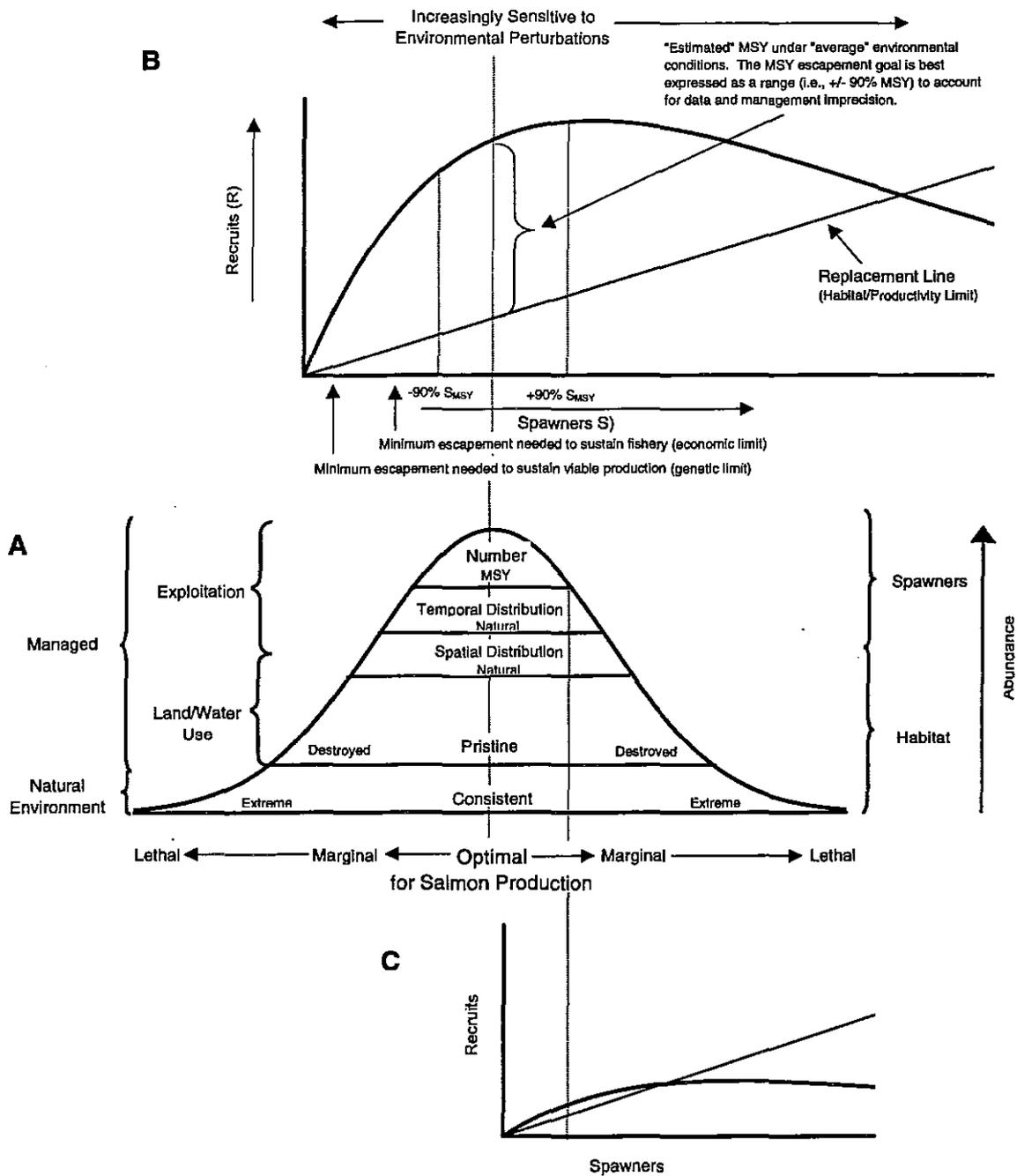


Figure 2. Hypothetical example of the influence that natural and managed perturbations of the environment and escapements have on the production and sustainability of salmon. Production (and sustainability and perhaps biodiversity) of salmon is optimized (maximized) at the center of the distribution (A) where the environment is consistent, the habitat is pristine, and escapements are naturally dispersed in space and time and at MSY levels (Ricker 1954, B). Conversely, salmon production, and sustainability, decreases if there are extreme environmental conditions, loss of salmon habitat, and poor quality and quantity of the escapement (C) due to overfishing or interbreeding with hatchery fish (Reisenbichler 1997).

Wild Coho Salmon Abundance and Marine Survival

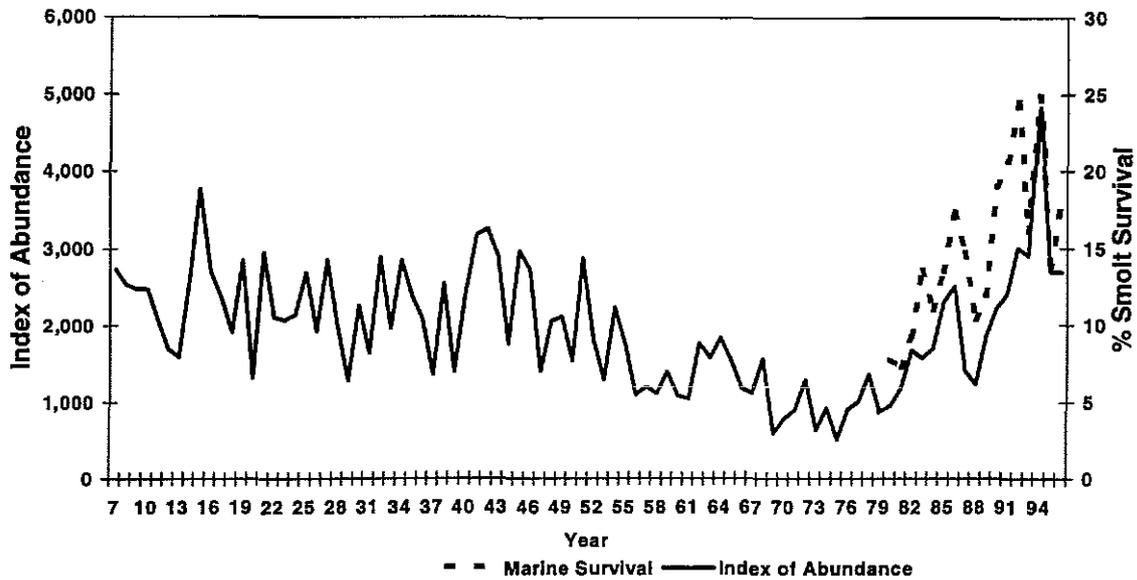


Figure 3. Abundance and marine survival of wild coho salmon in Southeast Alaska. (from L. Shaul, ADF&G, personnel communication)

Pink Salmon Return vs Brood Year Escapement Index for Southeast Alaska

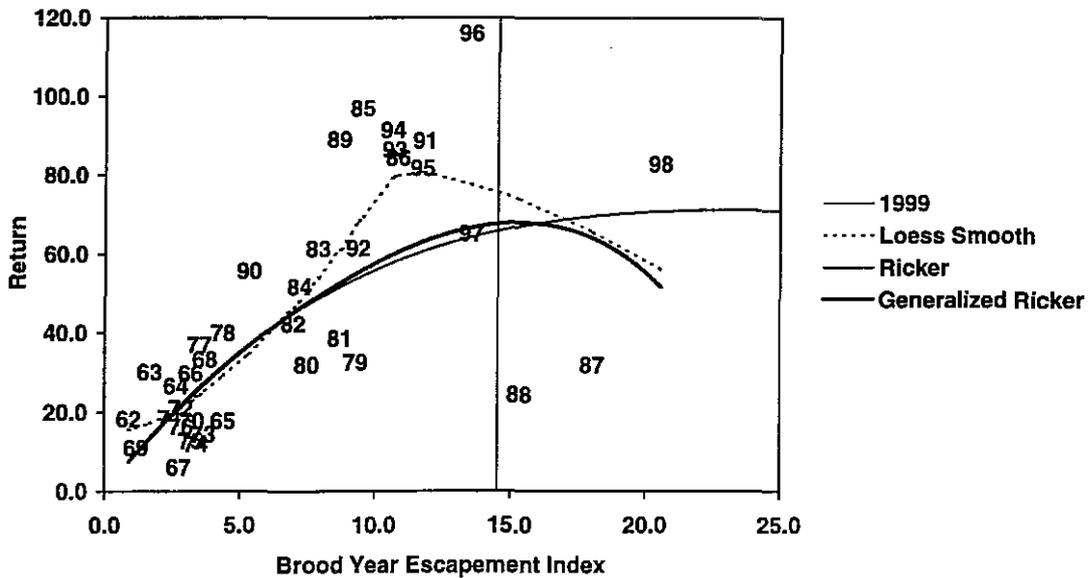


Figure 4. Return per spawner data for pink salmon in Southeast Alaska, plotted by return year, 1962-1998, with modeled prediction for 1999.

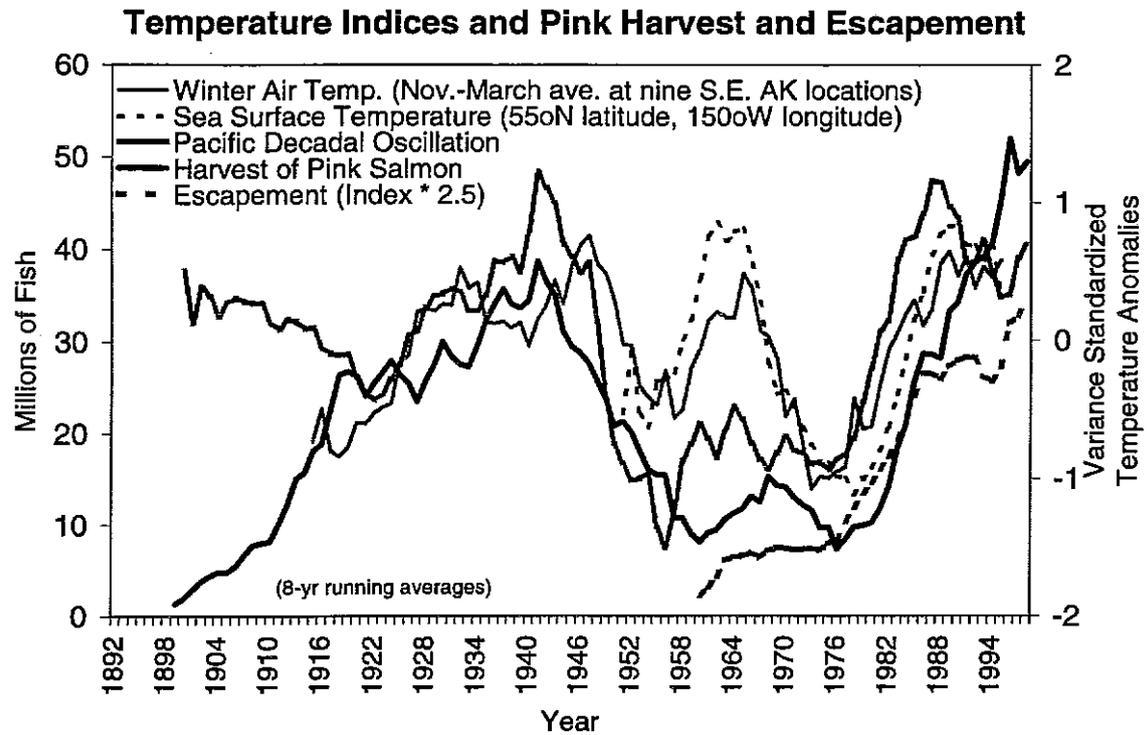


Figure 5. Winter air temperatures and sea surface temperatures and harvests and escapements of pink salmon in Southeast Alaska, 8-year moving averages, 1892-1998.

Assessing the production of Chilkat Lake Sockeye Salmon Through the Paleolimnologic Sediment Record

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The life cycle of the anadromous sockeye salmon is the only Pacific salmon that requires an extensive freshwater period in a lake environment. Marine derived nutrients (MDN) released from spawning adult salmon can be important nutrient sources to oligotrophic lakes and streams.

Recent studies suggest that changes in nutrient inputs to the lake are directly related to the magnitude of the annual spawning population (escapement), and can be quantified by sediment stable isotope analysis of nitrogen (^{15}N) and carbon (^{13}C). Nitrogen supplied by the adult salmon is enriched in marine ^{15}N relative to the other main source of nitrogen in freshwater salmon systems, atmospheric N_2 ($\delta^{15}\text{N}=0\%$). Since salmon populations fluctuate annually, the resulting MDN inputs and the resulting freshwater $\delta^{15}\text{N}$ will also fluctuate.

A mass balance analysis using recent limnological investigations and 29 years of annual escapement data, indicates that the input of sockeye salmon-derived phosphorous and nitrogen accounts for up to 84% and 59 % respectively of annual elemental inputs to Chikat Lake. Lake paleoproductivity over the last 1400 years has been estimated using organic carbon, biogenic silica and organic ^{13}C proxies in sediment cores. Organic carbon and biogenic silica results are inversely correlated with periods of high concentrations of sedimentary CaCO_3 . The source of these CaCO_3 inputs is believed to be the result of the intrusion of glacial melt-water from the Tsirku River.

Results of sedimentary $\delta^{15}\text{N}$ core analysis indicate a good correlation with existing escapement and climate data. The sedimentary $\delta^{15}\text{N}$ levels follow the paleoproductivity trends exhibited by the organic carbon and biogenic silica accumulation and are also inversely correlated to the periods of high concentrations of the sedimentary CaCO_3 . These $\delta^{15}\text{N}$ results also indicate a large decrease that coincides with an increase in glacial input to the lake and the recognized period of "Medieval Warming" from approximately 700 to 1200 A.D.

The frequency and duration of these glacial water intrusions are believed to be climate related. The resulting annual inputs of MDN are believed to influence the overall sockeye salmon production from this lake.

Habitat Changes And Sockeye Salmon Production In The Chignik Lakes, Alaska Peninsula

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ABSTRACT

The Chignik lakes (Black L. and Chignik L.) have historically been productive sockeye salmon lakes, supporting two genetically distinct runs. A series of natural degradation processes are taking place in the upper Black L. watershed, the rearing habitat for the fry from the early run. Black L. is a large and shallow lake (41.1 km², mean depth = 3 m), and is filling-up with sediment. This process is reducing sockeye fry habitat and is also creating conditions that can result in low dissolved oxygen (D.O) levels in the winter (under the ice). In addition, the major Black L. tributary (Alec River) has changed course and currently drains closer to the lake outlet. A sand spit has grown between the outlet of Black L. and the main basin, covering over two-thirds of the lake's width at that point. These changes in the watershed have prompted local research in order to mitigate or "recover" the Black L. rearing habitat.

It has been hypothesized that fry from Black L. leave this lake before freeze-up in the winter. The Black L. fry would, presumably, move into the lower Chignik L. Chignik L. is a large and deep lake (24.1 km², mean depth = 26 m) and is the rearing habitat for the late run fry. If the above hypothesis is true, Chignik L. would be supporting the recruits from the two sockeye runs for most of the year.

Because the degradation process in Black L. has been progressive over the years, I tested the hypothesis that scale measurements from sockeye salmon reared in the 1960's in the Black L. watershed would be different from those of fish reared during the 1990's, after the drainage changes. Scales were measured from sockeye that returned in 1964, 1965, 1967 and 1970 for the "sixties" group, and scales from 1995, 1996, 1997, and 1998 for the "nineties" group. The variables used were: number of circuli to the end of the first annulus, distance from the focus to the first, second, third, fourth and fifth circuli, distance from the focus to the end of the first annulus, and average circulus size. Two types of analyses were used to discern scale growth in the two time periods. The expectation was that scales from fish reared in the same environment in different years, would have some growth similarity that would prevail over inter-annual scale growth variations. Univariate ANOVA using years as blocks was used to contrast "sixties vs. nineties". A multivariate approach, Cluster Analysis, was used to find relatively homogeneous groups among years, without making any assumptions concerning groups or group structure. Clusters were formed on the basis of similarity or resemblance.

Results from the univariate ANOVA showed that for the early run, all variables explored were significantly different between the sixties and the nineties for age-classes 1.3 (major component of the run) and 2.3. In contrast, for the late run age-class 1.3, the number of circuli in the first annulus for the sockeye from the sixties and the nineties was not significantly different, and for age-2.3 (major component of the run) seven variables were not significantly different between time periods. The Cluster Analysis resulted in two clusters grouping the "sixties" years and the "nineties" years for the early run (age-1.3). The late run clusters included a mixture of years (age-classes 1.3 and 2.3). These results suggest that, despite the great variability that exists among individual scales and among years, changes in the Black L. watershed have been large enough to alter the use of the lake by the early run fry, as reflected by their scale growth. Changes in growth were not as strong in the scales from the late run, since they are still reared in the original Chignik L.

The current escapement goals in the Chignik system are the result of studies from the 1960's done by the Fisheries Research Institute (University of Washington). At that time, the erosion process in Black L. was at an earlier stage, and the lake supported the fry from the early run, presumably for most of the year. The escapement goals were based on studies of Black L. carrying capacity and on spawner-recruit relationships. The early run escapement goal was set at 400,000 spawners, and the late run goal was 250,000 spawners. These goals no longer correspond to the actual conditions of the lakes, with a large escapement to a degraded system, and a lower escapement to a healthy system that is rearing two runs of salmon. The escapement goals should be adjusted to the current nursery lakes condition.

Chignik L. can support the two salmon runs, as demonstrated by the permanence of the two runs during the last 5 years. However, the two adult sockeye runs alternate in dominance in different years, i.e., if the first run is strong, the late run will be weak, and vice versa. This kind of oscillation could indicate that the salmon runs are not in equilibrium with the rearing environment.

RECENT YEAR FLUCTUATIONS IN KUSKOKWIM RIVER COHO SALMON ABUNDANCE

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Headlines about the low Western Alaska salmon returns in 1997 and 1998 were dominated by reports about Bristol Bay sockeye, Kuskokwim River chums, and Yukon River chinook salmon. To the residents of the Kuskokwim River, the declines in returning coho salmon were just as profound and just as unexpected. Coho contribute about half the average annual commercial salmon harvest in the Kuskokwim River (Figure 1). Their average annual value to fishers is about \$2.2 million, which is more than all other species combined (Figure 2).

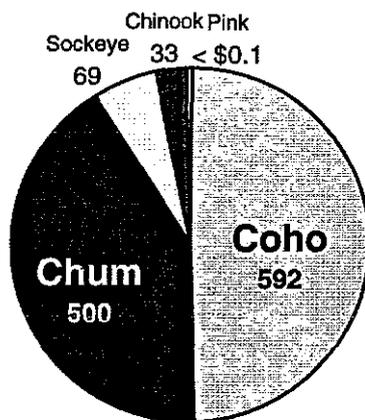


Fig. 1. Average annual number of salmon (X 1,000) harvested in the Kuskokwim River commercial fishery, 1988 to 1996.

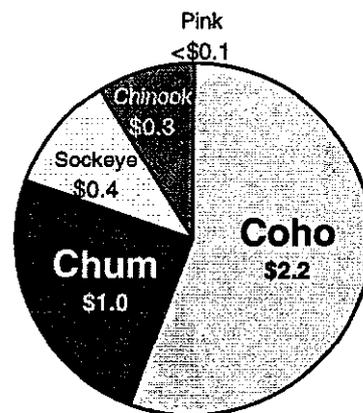


Fig. 2. Average annual value of salmon (in millions of dollars) harvested in the Kuskokwim River commercial fishery, 1988 to 1996.

Since the early 1970's the annual Kuskokwim River coho commercial harvest has generally been on the rise with a peak harvest in 1996 of 937,000 fish (Figure 3). The average annual commercial harvest between 1988 and 1996 was 592,000 coho. In 1997, the harvest dropped to 131,000 fish, 22 percent of average and the lowest catch since the mid-1970's. In 1998, the harvest increased moderately to 210,000 coho, still only 36 percent of average and most comparable to the harvest levels last seen in the 1970's. Coho escapement assessment is very limited, but the one tributary weir project operated since 1981 has demonstrated a similar pattern of abundance.

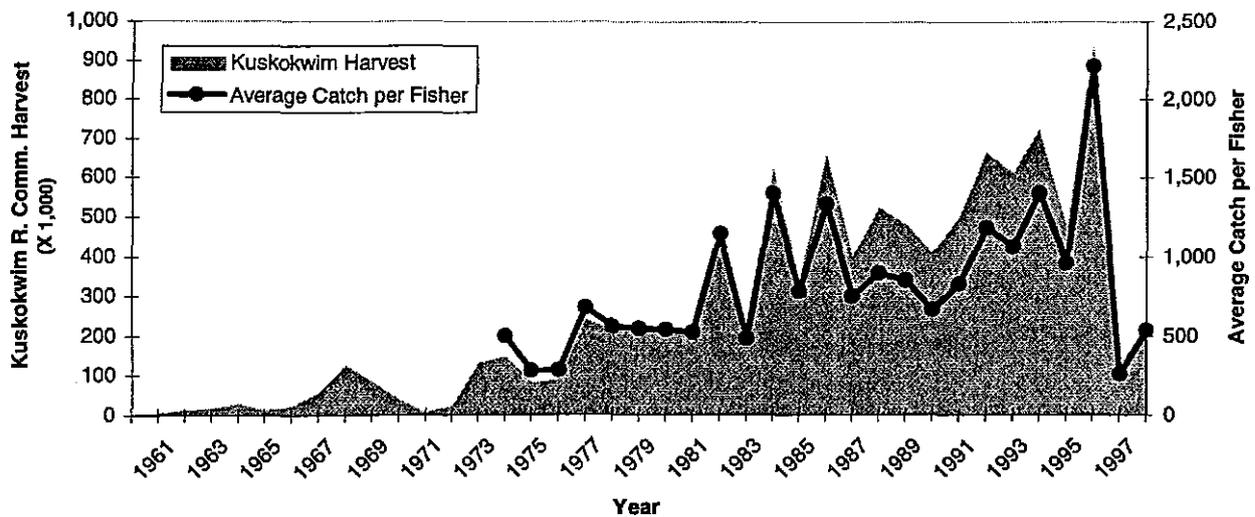


Fig. 3. Annual coho salmon harvest in the Kuskokwim River commercial fishery and the average annual catch per commercial fisher during August, 1960 to 1998.

The low coho harvests that occurred in the 1970's were due in part to the lower numbers of participating fishers and less effective fishing gear, however, these factors were compensated in part by much longer fishing periods which ranged from 6 to 72 hours compared to the 6 to 8 hour periods typical of the 1980's and 1990's. Relatively low salmon abundance was probably also a factor in the low harvest numbers from the 1970's. The catch per fisher in the 1970's was in the same range as observed in 1997 and 1998 (Figure 3).

The 1997 and 1998 coho salmon returns did not exhibit any obvious anomalies other than the low abundance. The age composition of the commercial catches was 90 percent or more age-4 fish, which is comparable to the 1984-1998 average of 88 percent. The average weight of 7.5 and 7.8 pounds per fish also differs little from the overall average weight of 7.2 pounds, and run timing was within the historic range. Anomalies did occur, however, in 1996, including the record high harvest of 937,000 coho, a record high average weight of 8.0 pounds per fish, and the earliest run timing ever documented.

Trends in Bristol Bay Sockeye Production and Forecast Performance

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Division of Commercial Fisheries

Bristol Bay, Alaska, supports the largest sockeye salmon fishery in the world, and one of the most variable. Sockeye salmon runs to Bristol Bay have varied from a low of 3 million in 1973 to a high of 66 million in 1980 (Figure 1). The most notable trend in production was the increase in total sockeye salmon runs beginning in 1979 compared to earlier years. Sockeye salmon runs to Bristol Bay averaged 18 million from 1961-1978 and increased to an average of 42 million from 1979-1996. Annual runs for the past two years, 1997-1998, dropped unexpectedly to 20 million sockeye salmon. Are the decreased run sizes observed in 1997 and 1998 indications of a short-term phenomenon similar to that in 1986-1988, or are they indications of a long-term shift towards lower production as observed from 1961-1978?

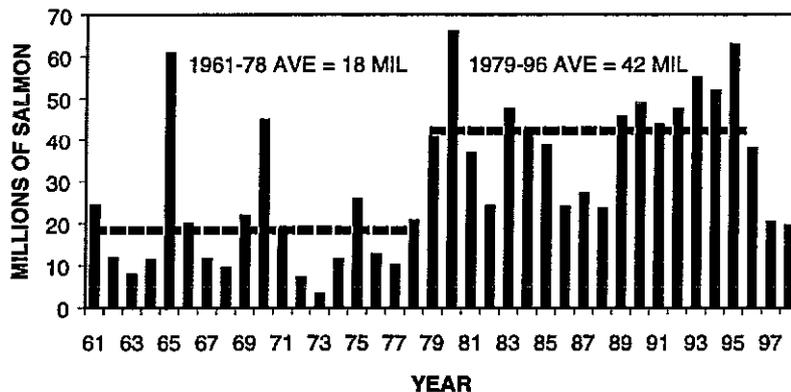


Figure 1. Total run of sockeye salmon to Bristol Bay, 1961-1998.

Return-per-spawner ratios for combined Bristol Bay rivers show similar trends as observed in the estimates of total run (Figure 2). Return-per-spawner ratios were generally lower for early brood years, 1956 through 1971, and higher for later brood years 1972-1988. However, return-per-spawner ratios have shown a steady decrease during the last four brood years, 1989-1992.

Estimates of marine survival for Kvichak and Egegik River smolt show the same trend observed in total Bristol Bay return-per-spawner ratios, a steady decrease for the past four brood years (Figure 3). Thus indications of decreased sockeye salmon production for Bristol Bay systems have been observed for the last four brood years.

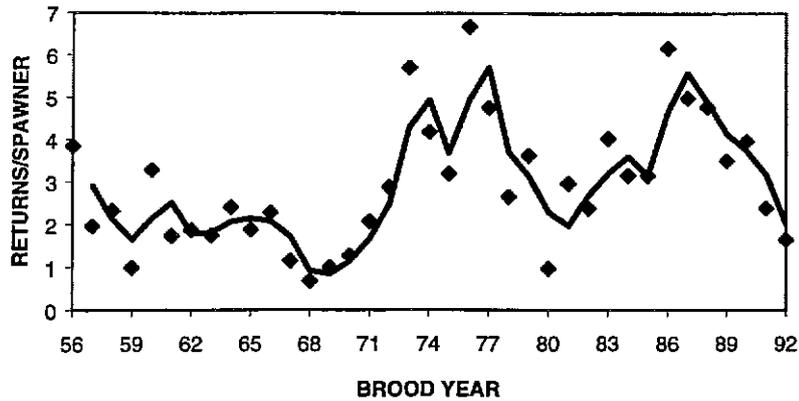


Figure 2. Return-per-spawner ratios for combined Bristol Bay sockeye salmon returns, 1956-1992. Line smoothed by 2-year average.

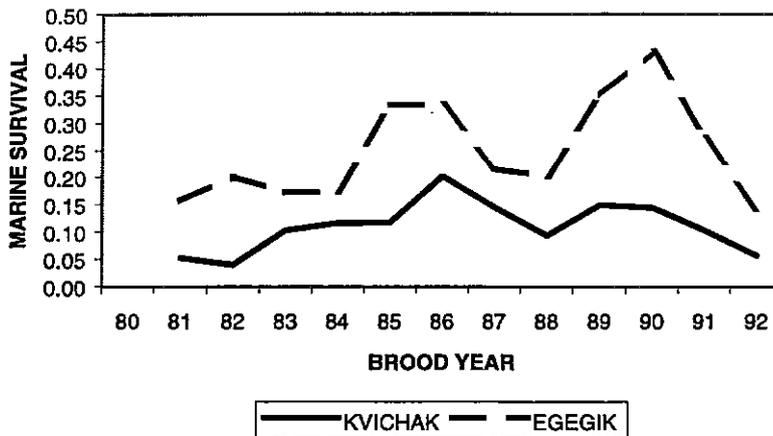


Figure 3. Estimates of marine survival for sockeye salmon returning to Kvichak and Egegik Rivers.

How well has the Alaska Department of Fish and Game done forecasting the variation in run sizes? General trends were predicted fairly well as shown by the comparison of observed sockeye salmon runs to forecasted total runs (Figure 4). Predictions increased as runs increased, and conversely as the runs declined so did the predictions. Large prediction errors occurred in some years, and the forecasts consistently underestimated runs during periods of increasing runs (1989-1993) and overestimated runs during periods of declining runs (1996-1998).

Although forecasts have generally followed the trends of the actual sockeye runs, the errors in numbers of fish have been substantial. The forecast was most often less than the observed run, 22 out of 35 years, and had an average error of -10.3 million sockeye salmon. Forecasts greater than the observed had an average error of 7.9 million sockeye

salmon (Figure 5). Forecast errors were highly correlated with time. From 1964-1973 the forecast was consistently greater than the run, and from 1974-1995 the forecast was generally less than the run.

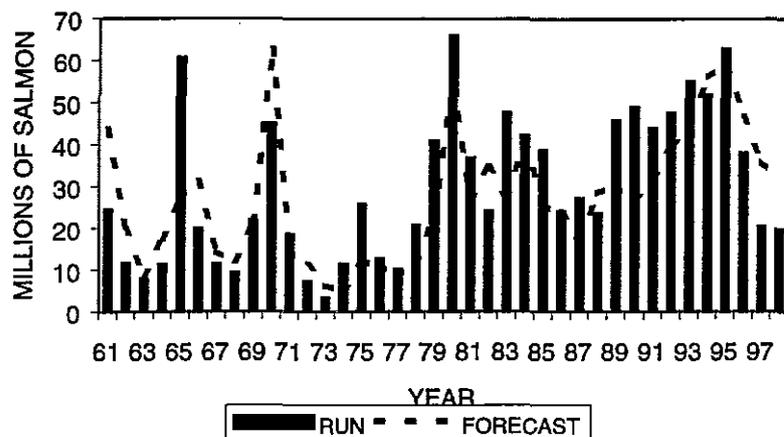


Figure 4. Observed compared to forecasted runs of sockeye salmon, Bristol Bay 1961-1998.

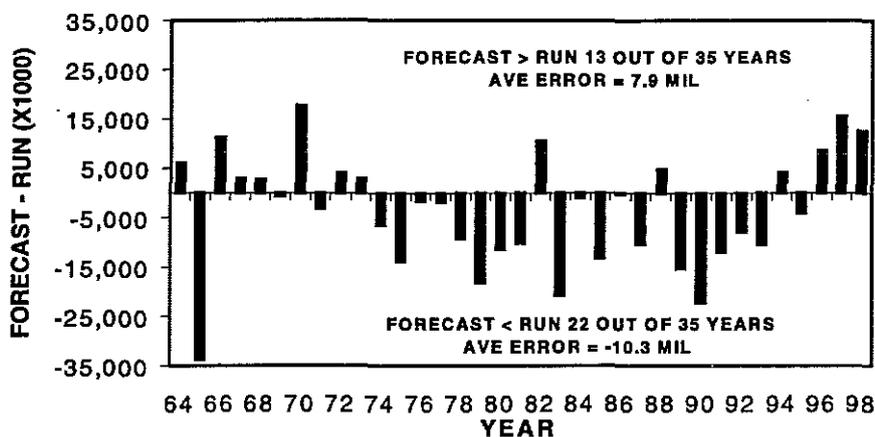


Figure 5. Errors in Bristol Bay sockeye salmon forecasts in numbers of fish, 1964-1998.

How does the forecast accuracy affect management? There is no doubt that if pre-season forecasts were accurate and reliable, then managers could obtain desired escapement goals more successfully. However, errors in obtaining escapement goals will always be somewhat correlated to run size because of industry limitations and market restrictions in harvesting and processing extreme volumes of fish. Also during large fish runs small

management errors in timing and duration of fishery openings equate to large numbers of fish escaping into the river and becoming unavailable to the fishery even if they are excess to spawning goals.

Management programs in Bristol Bay such as offshore test fishing, district test fishing, age composition analysis, river test fishing, counting towers were generally successful in meeting escapement objectives in spite of forecast errors. The relative deviations from the escapement goals were much less than the relative forecast errors (Figure 6). For years that combined escapements were greater than the combined Bristol Bay goal, excluding years of fishermen strikes, relative deviations averaged 25%. Similarly, during years that combined escapements were less than the goal, deviations from the goal averaged -24%.

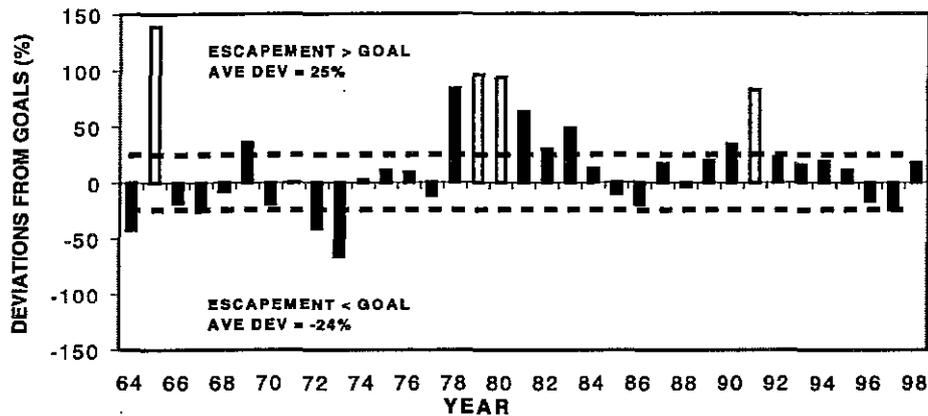


Figure 6. Deviations from combined sockeye salmon escapement goals, Bristol Bay, 1964-1998.

A comparison of forecast errors and escapement goal performance shows that on average escapement goals were met more closely than runs were forecasted (Figure 7). During years of under forecasts, excluding years of fishermen strikes, the average forecast error was -26%, while the average goal deviation was 19%. During years of over forecasts the average forecast error was 44% but the average deviation from the escapement goal was only -15%. It appears that information during the season allows managers to react to unexpected variations in run sizes especially when runs are smaller than forecasted.

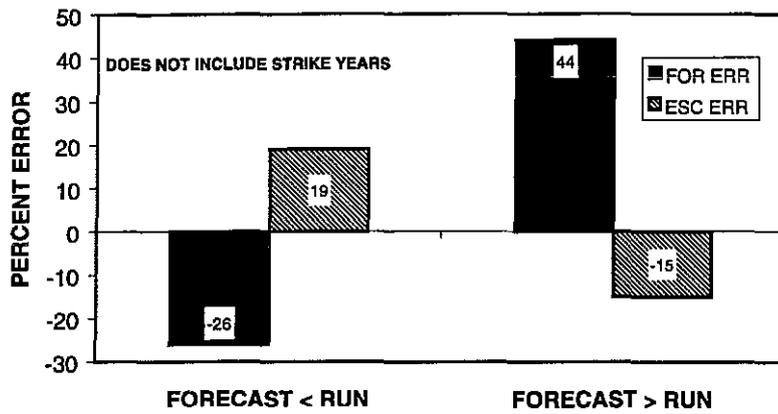


Figure 7. Forecast errors compared to deviations in escapement goals, Bristol Bay, 1964-1998.

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