

Survival, Maturation, Ocean Distribution and Recruitment of Pacific
Northwest Chinook Salmon (*Oncorhynchus tshawytscha*) in Relation to
Environmental Factors, and Implications for Management

Rishi Sharma

A dissertation submitted
in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy

University of Washington

2009

Program Authorized to Offer Degree:
Quantitative Ecology and Resource Management

University of Washington
Graduate School

This is to certify that I have examined this copy of a doctoral dissertation by

Rishi Sharma

and have found that it is complete and satisfactory in all respects,
and that any and all revisions required by the final
examining committee have been made.

Chair of the Supervisory Committee:

Robert C. Francis

Reading Committee:

Robert C. Francis

Ray W. Hilborn

Thomas P. Quinn

Date: _____

In presenting this dissertation in partial fulfillment of the requirements for the doctoral degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of the dissertation is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for copying or reproduction of this dissertation may be referred to ProQuest Information and Learning, 300 North Zeeb Road, Ann Arbor, MI 48106-1346, 1-800-521-0600, to whom the author has granted "the right to reproduce and sell (a) copies of the manuscript in microform and/or (b) printed copies of the manuscript made from microform."

Signature_____

Date_____

University of Washington

Abstract

Survival, Maturation, Ocean Distribution and Recruitment of Pacific Northwest Chinook Salmon (*Oncorhynchus tshawytscha*) in Relation to Environmental Factors, and Implications for Management.

Rishi Sharma

Chair of the Supervisory Committee:
Robert C. Francis
Quantitative Ecology and Resource Management

This dissertation discusses three facets of Pacific Northwest (PNW) Chinook salmon, *Oncorhynchus tshawytscha*, ecology that are relevant to current management models used for this species: 1) life history and migration pathways, 2) the impacts of spatial and temporal variability on PNW Chinook survival and maturation as determined using coded wire tags, and 3) the relationship between recruitment variability and environmental variation, explored via development of a new age-structured model.

Chinook salmon are commonly categorized as ocean-type (migrating to the ocean in their first year of life) or stream-type (migrating after a full year in freshwater). To test the hypothesis that stream-type and ocean-type Chinook have different migration pathways, I used a pair-wise design based on coded wire tagging data to compare the marine distributions of stream- and ocean-type Chinook salmon from a suite of rivers producing both forms. In cases where there is minimal gene-flow between both types of Chinook, the hypothesis is true, but in other cases it is not.

For the second element of the study, I examined PNW Chinook survival and maturation as estimated using coded wire tag data and related them to environmental conditions. PNW Chinook variability in survival and maturation is summarized for twenty three different PNW stocks and analyzed using multivariate data analysis techniques. Results indicate that survival is grouped into eight distinct regional clusters. Age at maturation did not exhibit regional patterns. Environmental data indicate that

PNW salmon survival is only weakly correlated with ocean conditions and co-vary at distances of 500 kms, while age at maturation appears to have no linkage to ocean conditions.

Finally, in order to demonstrate how direct measures of environmental conditions can be integrated into Chinook salmon stock assessments I developed a catch-at-age model of Chinook salmon life history which fits estimated parameters to observed data on ocean catches, terminal catches, and terminal escapement by age. The model quantifies uncertainty so that managers can use precautionary approaches to managing these stocks that would help protect the resource in the long run, and is tested for one of the stocks used in management.

TABLE OF CONTENTS

LIST OF TABLES	iii
LIST OF FIGURES	v
CHAPTER 1: AN INTRODUCTION TO PACIFIC NORTHWEST CHINOOK SALMON (<i>ONCORHYNCHUS TSHAWYTSCHA</i>) SURVIVAL, RECRUITMENT, MATURATION, AND DISTRIBUTION OVER TIME: WHY IS IT IMPORTANT TO TAKE THE PHYSICAL ENVIRONMENT INTO CONSIDERATION WHEN MANAGING CHINOOK SALMON STOCKS?	1
1.1 INTRODUCTION	2
1.2 CHINOOK SALMON LIFE HISTORY	3
1.3 CHINOOK SALMON FISHERIES AND ECOSYSTEMS	5
1.4 RECENT TRENDS IN PNW CHINOOK ABUNDANCE	8
1.5 OCEAN ENVIRONMENT AND PNW SALMON	9
1.6 PNW SALMON MANAGEMENT	17
1.7 UNDERSTANDING VARIATION IN PNW SALMON DISTRIBUTION, SURVIVAL, MATURATION AND RECRUITMENT: THE FOCUS OF THIS DISSERTATION	22
1.8 DISSERTATION OUTLINE	23
CHAPTER 2: LINKAGE BETWEEN LIFE HISTORY AND ECOLOGY IN FRESHWATER AND MARINE ENVIRONMENTS: DO STREAM-TYPE AND OCEAN-TYPE CHINOOK SALMON DIFFER IN MARINE DISTRIBUTION?	42
2.1 INTRODUCTION	43
2.2 MATERIALS AND METHODS	48
2.3 RESULTS	53
2.4 DISCUSSION	60
APPENDIX 2.1: RESIDUAL DIAGNOSTICS OF THE LOG-LINEAR MODEL FIT BY AREA	78
APPENDIX 2.2: RESIDUAL DIAGNOSTICS OF THE POISSON RESPONSE MODEL FIT BY AREA	86
CHAPTER 3: RELATING SPATIAL AND TEMPORAL SCALES OF CLIMATE AND OCEAN CYCLES ON PACIFIC NORTHWEST CHINOOK SURVIVAL AND MATURATION	94
3.1 INTRODUCTION	95
3.2 MATERIALS AND METHODS	100
3.2.1 Coded Wire Tag Data	100
3.2.2 Ocean Environmental Data	101
3.2.3 Spatial Cluster Analysis Used on Survival and Maturation Data (Correlation Analysis) on a Large Spatial Scale	102
3.2.4 Relationships Between Physical Ocean Conditions and Chinook Survival	103
3.2.5 Building Time and Space Lag-Based Models for Understanding Survival and Maturation Dynamics	104
3.3 RESULTS	106
3.3.1 Chinook Salmon Survival in Relation to the Environment in the Pacific Northwest	106
3.3.2 The Effect of Environment on Chinook Maturation in the Pacific Northwest	108
3.3.3 Localized Effects on Survival	112
3.3.4 Building Lagged Models of Survival by Region	114
3.4 DISCUSSION	115
3.4.1 Survival and Scale	115
3.4.2 Maturation and Scale	116
3.4.3 Large-scale Environmental Conditions in the PNW	117
3.5 OVERALL CONCLUSIONS	118

CHAPTER 4: DEVELOPING STATISTICAL CATCH-AT-AGE MODELS FOR CHINOOK SALMON: AN ALTERNATIVE MODELING TOOL FOR CHINOOK SALMON STOCK ASSESSMENT	155
4.1 INTRODUCTION	156
4.2 MATERIALS AND METHODS	158
4.2.1 Data Sources	158
4.2.2 Estimations of Variance	160
4.2.3 Effort Data	161
4.2.4 Model Formulation	162
4.2.5 Model Selection.....	168
4.2.6 Model Diagnostics	168
4.2.7 Parameter Uncertainty	169
4.2.8 Simulation Model	169
4.3 RESULTS	170
4.3.1 Model Selection.....	170
4.3.2 Simulation Model Results.....	171
4.3.3 Uncertainty in Derived Parameters	172
4.3.4 Model Convergence Monte Carlo Markov Chain Diagnostics (Appendix 4.2)	174
4.4 DISCUSSION	174
4.4.1 Understanding Recruitment Variation in an Environmental Context	175
4.4.2 Forecasting Model with Hindcasting Test (2005).....	179
4.4.3 Comparisons with the Current Pacific Salmon Commission (PSC) Chinook Model	181
4.5 CONCLUSION.....	182
APPENDIX 4.1: SIMULATION MODEL RESULTS	213
APPENDIX 4.2: MONTE CARLO MARKOV CHAIN CONVERGENCE DIAGNOSTICS	222
APPENDIX 4.3: CHINOOK SALMON TERMINAL FORECAST MODEL.....	231
APPENDIX 4.4: AGE STRUCTURED FITS FOR OCEAN FISHERIES AND ESCAPEMENT	233
CHAPTER 5: WHERE WE ARE AND WHERE WE SHOULD GO WITH RESPECT TO CHINOOK SALMON STOCK ASSESSMENT	235
5.1 INTRODUCTION	236
5.2 THE CURRENT STATUS OF PNW CHINOOK EXPLOITATION RATES	238
5.3 WHY DO WE TEND TO OVER HARVEST CHINOOK SALMON?.....	242
5.4 BUILDING A RISK-AVERSE FRAMEWORK FOR HARVEST INCORPORATING ECOSYSTEM INDICATORS	244
5.4.1 CRITERIA USED IN THE PRECAUTIONARY FRAMEWORK	245
5.4.1.1 Survival Rates	245
5.4.1.2 Escapements Trends.....	245
5.4.1.3 Pre-Terminal Exploitation Rates	246
5.4.1.4 Ecosystem Indicators	247
5.5 DEVELOPING A DECISION MATRIX THAT WOULD GOVERN FISHING LEVELS AS A FUNCTION OF THE FOUR CRITERIA	247
5.6 INCORPORATING UNCERTAINTY IN THE FORECASTS: THE BACKUP APPROACH	248
5.7 OVERALL CONCLUSIONS.....	249
APPENDIX 5.1: EXPLOITATION RATES ON INDICATOR STOCKS USED BY THE CHINOOK TECHNICAL COMMITTEE	264
APPENDIX 5.2: SUPPLEMENTING SPAWNER-RECRUIT DATA WITH WATERSHED SIZE TO IMPROVE ESTIMATION OF S_{MSY} : A BAYESIAN HIERARCHICAL MODELING APPROACH.	268
BIBLIOGRAPHY	292

LIST OF TABLES

Table 1.1: Natural and hatchery stock aggregates displayed in Figure 1.3.....	28
Table 1.2: Indicator stocks, location, run type, and age of smolt at release, based on Chinook Technical Committee's Tag codes that were used in the analysis.....	29
Table 2.1: Comparison of various life history and behavioral traits between North American ocean-type and stream-type Chinook salmon (based on Taylor 1990a, 1990b; Healey 1991, Roni and Quinn 1995).....	67
Table 2.2: Locations where both stream-type and ocean-type stocks exist, and CWT data used to analyze the spatial distributions	68
Table 2.3: ANOVAs showing results of equation 2 (log-linear model) applied to each of the particular areas	69
Table 2.4: ANODEV showing results of equation 3 (Poisson Response models) applied to each of the particular areas	70
Table 3.1: Exploitation rate indicator stocks, location, run type, and age of smolt at release.....	121
Table 3.2: Correlations over time for survival data anomalies and ocean data anomalies for the Pacific Northwest	123
Table 3.3: Correlation of stock survival with environmental station (>10.4l) showing a positive (blue) or negative (yellow) relationship	124
Table 3.4: ANOVAs using equation (3.4) and log-transformed equation (3.6) indicating significance of ocean variable SST in months indicated in Figures 3.17 and 3.18 Each SST effect is different although for simplicity it is referred to as SST in the Table.....	125
Table 3.5: ANOVAs using equation (3.7), equation (3.8) and equation (3.9) demonstrating significance of ENSO in predicting PDO, then the PDO in predicting conditions of the Columbia, Washington and Oregon coasts, and the then relating the PCA off the Columbia to the Oregon coast station at 44°N 124°W	127
Table 4.1: Notation used for the modeling approach used.....	185
Table 4.2: Harvest data in numbers of fish used in the assessment	186
Table 4.3: Effort data used for the model. Ocean data is an index based on equation 4, and terminal data is obtained using boat days (number) as a measure for the commercial in-river fishery	187
Table 4.4: Priors used on recruitment deviates and maturation to enable model convergence. These were primarily based on tag data for maturation, and recruitment variation for Chinook.	188
Table 4. 5: Model selection procedures using negative log-likelihoods and AIC criteria. The models were sequentially developed from one to six with varying levels of complexity. The first model estimates maturation by year and age, age recruitment over time, and has one estimate of catchability and selectivity over all years by gear type (fishery). The second has a decadal structure on maturation, and everything else is the same as model 1. The third has a decadal structure for maturation, as well as catchability. The fourth has decadal structures for maturation, catchability and selectivity by fishery. The fifth has constant recruitment, but catchability changes by year, and selectivity and maturation changes by decade. The sixth model has recruitment vary by year, and catchability, selectivity and maturation changes by decade. The seventh model has the same structures as the previous model but has decadal structures with maturation that worked by ocean changes in productivity, and catchability and selectivity changes by different fishing regimes.....	189
Table 4.6: Data on Upriver Bright age-2 recruitment, spawning stock size and environmental covariates	190
Table 4.7: ANOVA on the linear model fit using Equation 22, and flow and SST as covariates	191

Table 4.8: Incorporating environmental signals and corrections into forecasts based on weighting factors, and standard deviations of environmental conditions	192
Table 4.9: Percentiles of terminal forecasts based on distributions on Figure 14.	193
Table 4.10: MSE calculations on the PSC Model (TC-Chinook 08-01 <i>in prep</i>) and SCAA model.....	194
Table 4.11: SCAA comparisons with current model	195
Table 5.1: Quartiles on optimal harvest rates for Chinook	253
Table 5.2: Current brood year harvest rates	254
Table 5.3 (taken from Peterson et al. 2006): Ocean and ecosystem conditions in the Northern California Current. Colored dots indicate whether the index was positive (green), neutral (yellow), or negative in the year salmon entered the ocean. The last two columns forecast adult returns based on ocean conditions in 2005. The year 2000 is included as an example of conditions during a "good" year, in contrast to the "poor" conditions observed in recent years, 2004-2006.	255
Table 5.4: Decision matrix for determining fishing levels.....	256

LIST OF FIGURES

Figure 1.1: The Pacific Northwest region from Northern California to Southeast Alaska including Oregon, Washington, and British Columbia. The main drainages displayed are the Klamath, Columbia (including the Willamette and Snake), the Fraser and the Stikine Rivers.	32
Figure 1.2: Chinook Salmon Life History (courtesy I. Ortiz, SAFS, University of Washington, Seattle, WA 98195)	33
Figure 1.3: Estimated Chinook salmon ocean abundance trends based on the Chinook technical Committee CTC Ocean management model (CTC 2008) for Southeast Alaska, Northern BC and West Coast of Vancouver Island.....	34
Figure 1.4: Location of various fisheries of significance to Pacific Northwest Chinook northern migrating stocks	35
Figure 1.5: Ocean currents and regions of upwelling in the Northeast Pacific (courtesy Jodie Little, University Of Washington)	36
Figure 1.6: Coastal Upwelling dynamics (Courtesy Pacific fisheries Environmental Laboratory (http://www.pfeg.noaa.gov)	37
Figure 1.8: Schematic used to estimate Age 2 recruitment, catchability, vulnerability and maturation using statistical catch at age techniques for a simple 2 area model (ocean and terminal).....	39
Figure 1.9: Runs size distributions by age	40
Figure 1.10: Total terminal run prediction with uncertainty	41
Figure 2.1: Areas where stream-type and ocean-type Chinook occur in close proximity as well as the regions that were used in the analysis.	72
Figure 2.2: Histograms indicating proportion of recoveries by ocean or stream type Chinook recoveries in the Highseas, southeast Alaska (AK), Northern BC (NCBC), West coast of Vancouver island (WCVIGST), Washington and Oregon (WAOR) and terminal areas aggregated by region.....	73
Figure 2. 3: Recovery patterns and migration pathways of lower Columbia River Chinook salmon (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area.....	74
Figure 2.4: Recovery patterns and migration pathways of upper Columbia River and Snake River Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area	75
Figure 2.5: Recovery patterns and migration pathways of Fraser River Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area	76
Figure 2.6: Recovery patterns and migration pathways of northern BC and Oregon coast Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area.....	77
Figure 3.1: Chinook Populations tracked with coded wire tags. Some locations (such as Puget Sound or Columbia) have multiple tag codes.....	130
Figure 3.2: Survival rescaled to survival anomalies by area. Red indicates lesser than average survival and a blue denotes higher than average survival for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1. White areas denote missing data	131
Figure 3.3: Cluster Analysis exploring survival anomalies by region. Refer to Table 3.1 for stock and region acronyms. Each circle denotes a broad scale region where survival anomalies seem to correspond to numerous stocks.	132
Figure 3.4: Absolute survival for clustered regions shown in Figure 3.3.	133
Figure 3.5: CWT survival data and ocean upwelling data clusters by time period. Arrows indicate similarities across ocean conditions and Chinook survival.	134

Figure 3.6: Spring upwelling (green) and fish survival (red) across the Pacific Northwest between 1981 and 2004 using the PC loadings.....	135
Figure 3.7: Significant relationship between the third principal component loadings on survival and ocean conditions	136
Figure 3.8: Maturation for age 2 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.....	137
Figure 3.9: Maturation for age 3 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.....	138
Figure 3.10: Maturation for age 4 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.....	139
Figure 3.11: Regional based cluster analysis on maturation rates by ocean age. Stocks are identified by the three-letter acronym shown in Table 3.1.....	140
Figure 3.12: Yearly clusters based on maturation rates by ocean age. Arrows indicate similarity across ages.....	141
Figure 3.13: Lag 1 effects on maturation anomalies using PCA (displaying only the 1 st PC).....	142
Figure 3.14: Lag 1 effects on maturation anomalies using PCA (displaying the first three PCs). The upwelling data (green) and maturation by age (red) is shown for each age separately	143
Figure 3.15: Same-year effects on maturation anomalies using PCA (displaying only the first PC)	144
Figure 3.16: Same-year effects on maturation anomalies using PCA (displaying the first three PCs). The upwelling data (green) and maturation by age (red) is shown for each age separately.....	145
Figure 3.17: Relationship between survival and SST for Klamath, Salmon River (Oregon Coastal Chinook), Spring Creek Tules (Columbia) and the Columbia Upriver Brights. The SST was obtained from COADS database for locations near the coastal shelf and were the most highly correlated with survival during the first few months after smolts emigrate into the ocean. Stations reported are 40°N 124°W, 44°N 124°W, 46°N 124°W and 48°N 124°W. Linear fits (solid) and non-linear fits (dashed line) are shown for each set of data.	146
Figure 3.18: Relationship between survival and SST for Puget Sound, West Coast of Vancouver Island (WCVI), Georgia Straits and South East Alaska (SEAK). The SST was obtained from BC lighthouse database for nearest locations that could be used as surrogates for these systems. Linear fits (solid) and non-linear fits (dashed line) are shown for each set of data	147
Figure 3.19: Rescaled likelihood profiles of the Beta parameter as a function of a one-degree change in SST at each of the locations specified in Figures 3.17 and 3.18. A 1°C increase in SST (solid line) indicates the absolute amount of decrease in overall survival might be expected for the stock, whereas a 1°C decrease in SST (dashed line) indicates the absolute increase in survival that might be expected for a particular stock. These figures assume a linear fit	148
Figure 3.20: Lag time effects from different scales affecting survival at the local scale for the Columbia and Oregon coast Chinook stocks. The top left panel relates ENSO conditions the previous year to PDO conditions in the current year, the top right panel relates June PDO conditions in the NE Pacific to conditions off the Washington and Oregon coast in the vicinity of the Columbia, and the bottom	

two panels relate conditions off the Columbia to sea surface temperatures that are related to survival of Columbia Bright and Oregon coastal Chinook.....	149
Figure 3.21: The effect of a positive or negative ENSO on Oregon Coastal Chinook survival.....	150
Figure 3.22: Correlation analysis displaying correlation between stocks and regions as a function of distance	151
Figure 3.23: Four distinct patterns of environmental conditions that may have consequential impacts on PNW Chinook survival during the spring transition period (April through July). The upper and lower left hand panel shows warmer than average conditions indicating poor upwelling in 1983 and 1992 impacting survival coast-wide (Figures 3.2 and 3.4). The right hand panels indicate cooler than average conditions in 1985 and 1999 that had a positive effect on survival coast-wide (Figure 3.4).	152
Figure 3.24: Conditions in 2005 to 2008 during spring transition	153
Figure 4.1: Ocean fisheries and geographical areas encountering Upriver Bright Chinook Stocks	197
Figure 4.2: Schematic used to estimate age 2 recruitment, catchability, vulnerability, and maturation using statistical catch-at-age techniques for a simple two-area model (ocean and terminal)	198
Figure 4.3: The simulation and estimation process	99
Figure 4.4: Age 2 recruitment, observed versus estimated catches for each fishery and escapement	200
Figure 4.5: Simulated and estimated age 2 recruitment over time	201
Figure 4.8: Simple ERs over time for terminal fisheries.....	204
Figure 4.9: Maturation uncertainty	205
Figure 4.11: Catchability uncertainty.....	207
Figure 4.12: GLM and GAM fits to observed variation in data using SST and flow as covariates	208
Figure 4.13: Deviations from the spawner-recruit fit (> 1 indicates greater than S-R model projection and <1 indicates lesser than S-R model projection)	209
Figure 4.14: Likelihood profiles as a function of flow and SST (independently)	210
Figure 4.15: Age specific forecast distributions with the observed values in 2004 (the red line indicates observed values and the green line indicates current forecasting techniques)	211
Figure 4.16: Comparisons of this approach with existing model for terminal fisheries by age	212
Figure 5.1: Optimal harvest rate based on the watershed area SMSY relationship (using hierarchical models)	258
Figure 5.2: Simple Exploitation Rates (SER) on ESA-listed and depressed stocks in the US and Canada.....	259
Figure 5.3: Survival rate patterns for four exploitation rate indicator stocks.....	260
Figure 5.4: Escapement trends for WCVI and Oregon Coastal Chinook (TC-Chinook (08)-1)	261
Figure 5.5: Total mortality pre-terminal exploitation rates for WCVI and Oregon Coastal fall Chinook indicator stocks (Data from Appendix E, TCChinook (08)-1)	262
Figure 5.6: Total allowable catches in a mixed-stock ocean fishery based on overall aggregate abundance of all stocks encountered in the fishery. Best case, intermediate case, and worst case catch levels are depicted	263

Acknowledgements

The author wishes to express sincere appreciation to the Quantitative Ecology and Resource Management program, and the members of the exam committee. Of particular importance are Bob Francis, Ray Hilborn, Tom Quinn, and Nate Mantua. None of this would have been possible without their experience and guidance. In addition the author wishes to thank his wife, Richa, daughter Uma and mother Lakshmi Sharma in always encouraging and having belief in me.

Dedication

To my father, Jitendra Nath Sharma and my mother Lakshmi Sharma.

**CHAPTER 1: AN INTRODUCTION TO PACIFIC NORTHWEST
CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)
SURVIVAL, RECRUITMENT, MATURATION, AND
DISTRIBUTION OVER TIME: WHY IS IT IMPORTANT TO
TAKE THE PHYSICAL ENVIRONMENT INTO
CONSIDERATION WHEN MANAGING CHINOOK SALMON
STOCKS?**

1.1 INTRODUCTION

Salmon are an icon on the West Coast of North America. They have been a source of sustenance, culture, and identity for the people of this region for thousands of years. When Lewis and Clark first made their journey west along the Snake and Columbia Rivers, they were amazed at the prosperity and organization of the cultures along these rivers (Taylor 1999). Their prosperity and existence can, without a doubt, be attributed to the salmon (Taylor 1999, Lichatowich 1999). In fact, to this day, their culture is defined by the fish. The sanctity of the first caught spring Chinook salmon in many of these cultures, marked by the ceremonies in the longhouses, signifies how important this first salmon was as it signified the beginning of a new cycle, and whether the coming year would be prosperous or otherwise (Hunn 1990). The native emphasis on the cyclical extends to salmon, as abundant years are balanced by years of scarcity. Cyclicity is present in most environmental processes, and is the focus of this dissertation. To quantify the cyclical aspects of the salmon life cycle and relate them to environmental processes that are also cyclical, I intend to present a topic that is well understood in the philosophical sense, but is difficult to quantify and present in an objective manner.

Salmon (*Oncorhynchus* spp.) are a genus of fishes within the family Salmonidae. There are three distinctive aspects of the biology of these fish: anadromy, homing, and semelparity (Quinn 2005). Anadromy is the phenomenon in which fish transition from a freshwater site where they were spawned to a saltwater environment for feeding and growth and back again to freshwater for spawning, and they must adjust their physiology accordingly; homing refers to the fact that the surviving fish

come back almost without exception to the identical place (or within a few hundred meters) where they were spawned; and semelparity refers to the fact that these fish reproduce during only one season and then inevitably die. There are five species of fish that fit into the Salmonidae category that are collectively known as Pacific salmon: pink (*O. gorbuscha*), coho (*O. kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and Chinook (*O. tshawytscha*). Two closely related species, rainbow/steelhead trout (*O. mykiss*), and cutthroat trout (*O. clarki*) tend to be both iteroparous (spawn multiple times) and includes some strains that could be anadromous or freshwater depending on the most viable life history strategy. My dissertation will focus on the Chinook salmon.

1.2 CHINOOK SALMON LIFE HISTORY

Chinook range throughout the North Pacific. The region of focus for this dissertation is the Pacific Northwest (PNW): While the term "Northwest" is used loosely, here it is defined as the area shown in Figure 1.1 between northern California, i.e. the Klamath River, and parts of southeast Alaska, including, Oregon, Washington, Idaho, and British Columbia. It should be noted that the species ranges farther to the north and south and is also found in parts of Asia (Quinn 2005).

Chinook have a complex life history which can be categorized into six sequential stages for the “ocean type” life history and seven for the “stream type” life history (Figure 1.2). “Ocean-type” Chinook salmon are found towards the southern end of their range, and are found especially in low elevations. Juveniles of this variant typically migrate to sea as fry shortly after emergence from the gravel or as sub-yearlings after a few months in fresh water. This pattern is also associated with

relatively early emergence and rapid growth in the river (reviewed by Taylor 1990a; Healey 1991). Chinook salmon that spend a full year in fresh water before migrating to sea at a larger size are termed “stream-type” fish. Populations north of about 56° N latitude (i.e., the Skeena and Nass rivers, British Columbia) are virtually all stream-type (Taylor 1990a); the Situk River in south central Alaska (59° 30' N) is an exception, producing primarily ocean-type juveniles (Johnson et al. 1992). The life stages are shown below:

- 1) Adult spawner
- 2) Fertilized eggs in gravel
- 3) Juveniles, called alevins, with a yolk sac
- 4) Juveniles called fry
- 5) Summer parr that spend a year or more in the freshwater environment (stream-type only)
- 6) Smolts, the life history stage in which the fish undergo physiological changes in order to migrate to the ocean
- 7) Ocean adults.

As Figure 1.2 and the list of stages denote, the fish enter rivers to spawn at different times of the year, primarily spring (April-June), summer (June-August), and fall (late August-November). These fish, termed adult spawners, can spend from a few weeks to six months in this environment before they spawn. Once they spawn the eggs are deposited in the gravel where they eventually develop into “alevins” and spend a portion of their life below gravel. They emerge using their egg sacs to develop into

“fry.” They remain in this stage (“summer parr” if it is a “stream-type” Chinook) for several months to a year before they undergo a physiological process, changing into a “smolt” as they move from freshwater into an ocean environment. There they experience rapid growth, spending 1-6 years (more typically 2-4) in this environment before they mature and return to their natal rivers to spawn.

This dissertation will focus on the latter half of the life cycle, quantifying variation in survival from the smolt to the ocean adult stage, and examining maturation by age and ocean migration pathways. This dissertation will also build a mathematical model of this part of the Chinook life cycle, incorporating environmental data that will shed light on why PNW populations vary in recruitment and overall abundance over time. I present data and techniques to analyze different areas and systems. I term each unique life history type within a particular area or system a “stock.” Although I analyze coded-wire tag codes that represent natural stocks, there are some runs (e.g. Spring Creek in the Columbia River system) that are primarily a hatchery stock.

1.3 CHINOOK SALMON FISHERIES AND ECOSYSTEMS

Chinook salmon have provided a livelihood and a means of existence for sophisticated Native American cultures in the Pacific Northwest region for millennia. These cultures have thrived for thousands of years amid the cycles of abundance that are inherent in most natural systems. However, in the span of a few hundred years many of these salmon populations have become severely depressed or extinct. How and why did this happen?

To answer this question, the patterns of Chinook salmon population abundance must be placed in the context of the ecosystem. As Buddha once stated, “All things appear and disappear because of the concurrence of causes and conditions. Nothing ever exists entirely alone; everything is in relation to everything else” (Titmus 2001). This quote aptly describes the case of PNW Chinook salmon. These fish exist in both freshwater and oceanic environments, and to understand their dynamics one has to place them in a context of change within these environments.

The terms “fishery” and “ecosystem” are used extensively from here on. A “fishery” refers to the activities of humans, acting separately or collectively, to harvest Chinook salmon from the freshwater or marine environment. The term fishery is typically associated with a geographical region (e.g., west coast of Vancouver Island) and a type of fishing method (e.g., trolling, purse seining, gillnetting, or recreational angling). These fisheries could act independently of one another, or in consort with one another, depending on the spatial and temporal aspects of where they are prosecuted. The “ecosystem” refers to the system in which these fish exist, i.e. both the natural and anthropogenic environment that is affected by processes such as climate forcing and human induced management actions (as well as food web structure, species composition, and inter and intra-specific competition).

Two hundred years ago the cities of Portland, Seattle, and San Francisco did not exist. Human populations have grown exponentially in the PNW region, and with that growth came freshwater habitat degradation, river modifications (e.g., irrigation side channel diversions for agriculture, hydropower-generating dams), and unsustainable

harvest and concomitant hatchery augmentation (Taylor 2001, NRC 1996). McEvoy (1996) and Taylor (2001) provide a perspective on how fisheries changed both temporally and spatially with the arrival of early European settlers, and the impact of the new fishing gear that they employed. Prior to the arrival of the early settlers in California and the Oregon Territories, much of the fishing was for subsistence with some effort going towards trade based fisheries. However, as more people earned a livelihood from these natural resources, the salmon populations declined, and many were over-fished by the early 1900s. The ability to preserve salmon in cans was a key development because it uncoupled fishing from consumption (Taylor 2001). McEvoy (1996) describes the Sacramento fishery between 1879 and 1883, which amounted to over 10 million pounds (500,000 to one million in numbers) of Chinook salmon landed per annum. This incredible biomass far exceeds the current harvest (1-2 million pounds) in the entire Columbia River, Oregon, Washington, and northern California region in recent years (PFMC 2008). As the industry collapsed in northern California, people moved north and successively depleted each fishery, starting with the Columbia, followed by Puget Sound, and eventually heading for Alaska. While the initial reason for Chinook salmon population decline was overfishing, the collapse of these runs cannot be entirely attributed to fishing. Habitat modification to dewater rivers (e.g. in the Klamath River) for agriculture and hydropower generation (in most of the Columbia) also contributed to their decline along with fishing at high harvest rates (Taylor 2001). In parts of California and southern Oregon, mining played a destructive role as well (Taylor 2001).

Other stages of the Chinook salmon life cycle occur in the open ocean. If juveniles overcome the obstacles to their survival in the rivers and reach the ocean, they face an ocean environment that can vary substantially from year to year and from decade to decade (Quinn 2005, Ware 1995). One such variable is food supply. In the early marine life stages, the salmon consume euphausiids and other zooplankton (Koslow et al. 2002, Logerwell et al. 2003), while adult marine stages feed on juvenile fish such as herring (Willette 2001). The Chinook also need to avoid predators like hake (Willette 2001), lamprey (Beamish and Neville 1995), and spiny dogfish (Beamish et al. 1992), and marine mammals, some of which, like killer whales, seem to prey on them out of proportion to their abundance (Ford et al. 1998).

Ocean conditions have fluctuated dramatically in the last few decades (Ware 1995, Mantua et al. 1997, Francis and Hare 1994, Hare et al. 1999), influencing both salmon food and predator abundance. These inter-annual and inter-decadal fluctuations have been tied to salmon survival on both long (Francis and Sibley 1991, Mantua et al. 1997, Hare et al. 1999) and short time scales (Logerwell et al. 2003, Lawson et al. 2004). These fluctuations in ocean conditions could explain annual and decadal fluctuations in PNW Chinook salmon populations, and might need to be taken into account in an adaptive management context (Holling 2001, Lee 1993).

1.4 RECENT TRENDS IN PNW CHINOOK ABUNDANCE

In the past several decades, Chinook salmon abundance trends have cycled with an approximately eight-year periodicity from high to low abundances, with a high in 1986-1987, a low in 1994-1995, and another high in 2003 (Figure 1.3).

Figure 1.3 illustrates the estimated combined ocean abundance of 30 natural and hatchery Chinook stocks (Table 1.1) that are encountered in three ocean troll fisheries: Southeast Alaska, Northern British Columbia (NBC) and West Coast of Vancouver Island (WCVI). Currently the Pacific Salmon Commission (PSC) assesses catches for 25 regional fisheries including troll, net, and sport gear in the regions extending from the Oregon coast through southeast Alaska (Figure 1.4). These 25 regional fisheries are divided into finer strata to address regional management concerns. For example Washington Troll (Figure 1.4) has four ocean areas on the coast, three in the Strait of Juan de Fuca, and eight areas in Puget Sound.

Abundance of these 30 Chinook stocks has varied dramatically over the 1979-2007 time period as well (Figure 1.3). The terminal abundance has varied; large runs were seen in most areas in the mid 1980s, lower abundances through most of the 1990s and higher abundances were again observed in 2001 through 2005.

1.5 OCEAN ENVIRONMENT AND PNW SALMON

Chinook salmon in the Pacific Northwest have complex life cycles. From southern Oregon to southeast Alaska these stocks exhibit a range of life history trajectories. They are either sub-yearling freshwater fish (six months old at the time of migration to the ocean) or yearling freshwater fish (greater than one year old at the time of ocean migration). After the freshwater phase of their life history, these salmon spend 50%-90% of their entire life in ocean environments (Healey 1991).

Chinook salmon exhibit a complex combination of life history and migration patterns (Healey 1991, Quinn 2005) and little is known about the way they behave in

response to ocean conditions (Pearcy 1992, Quinn 2005). This problem has been discussed for many decades. For example, the work of Percy (1992) and Francis and Hare (1994) showed that many of the major changes in salmonid abundance could be related to changes in ocean conditions. It is therefore important to understand the fluctuations of the physical, biological, and ecosystem indicators in the northeast Pacific, the system in which these fish spend a large portion of their lives.

Most of the stocks studied in this dissertation leave a freshwater environment to enter an ocean that is in some state of flux. As Peterson et al. (2006) describe, large scale ocean-atmospheric processes like the El Nino Southern Oscillation (ENSO, Wolter and Timlin 1998) and the Pacific Decadal Oscillation (PDO, Mantua et al. 1997) affect basin-scale winds and currents that drive the oceanic systems in the PNW. I attempt to link some of these broad-scale dynamics to local processes. In the next few paragraphs, I will describe some aspects of these broad-scale ocean-atmospheric processes and relate them to biological and ecosystem indicators that might be important for salmon survival.

To understand the context in which PNW Chinook carry out their life cycles, the northeast Pacific ecosystem needs to be described and understood. The northeast Pacific can be broadly classified into three distinct regions (Figure 1.5), the coastal upwelling domain, the coastal downwelling domain, and the central sub-Arctic domain (Ware and McFarlane 1989). The coastal upwelling domain covers roughly Baja California to the Northern tip of the west coast of Vancouver island. In between the northern tip of Vancouver island and the Queen Charlotte Islands is a zone known as

the transition region (Francis et al. 2008, Field et al. 2006). The downwelling region corresponds to the area from Queen Charlotte Sound in Northern BC along the coast of southeast Alaska to Prince William Sound and then on to the Aleutian Islands. The central sub-Arctic domain is bounded by the sub-Arctic current to the south, the Alaska current to the east, and the Alaska stream to the north (Figure 1.5). A key characteristic of this system is the Alaska Gyre which, due to positive wind stress, rotates in a counter-clockwise direction, creating upwelling at the core of the gyre (Ware and McFarlane 1989). The geographic focus of most of the work on PNW Chinook presented in this dissertation is the coastal upwelling region (Figure 1.7), and downwelling at the very extreme areas like southeast Alaska. Most of the work done in this dissertation is in the region dominated by the California current system (CCS) (Hickey 1978).

The CCS has two (Agostini et al. 2006), three (Peterson et al. 2006), or four (Hickey 1978, 1998) major currents which provide a dynamic mixture of subarctic and subtropical waters in the California current ecosystem. As shown in Figure 1.5, the California current (CC – subarctic, cool, fresh) is a broad (~500 km) slow equatorward flow that extends southward from the trans-Pacific flow of the West Wind Drift. The poleward California Undercurrent (CU – subtropical, warm, saline) is a seasonal (March – September) narrow (10-40 km) sub-surface current, trapped along the continental slope and strongest at depths of 100-300 m. In the winter (October – February) this countercurrent comes to the surface and is referred to as the Davidson Current (DC). Depending on the time of year (spring or fall) the current has annual

transitions from northward to southward occurring roughly between March and April (spring transition) or September and October (fall transition). The northern region of this current is between the northern tip of Vancouver Island and Cape Mendicino (Cape Blanco to Cape Mendicino is the boundary between the northern and the southern California current). The timing and shifts in current strength that occur during the spring and fall transition also create seasonal shifts in pressure fields and dominant wind flows (southwest after the fall transition and northwest after the spring transition). If we account for this, the seasonal variation in the Northern California current accounts for a north-south push and pull between cool, nutrient rich sub-arctic water and warm nutrient poor subtropical water (Francis et al. 2008, Field et al. 2006).

Next, it is important to understand how basin-scale and local-scale effects might affect the overall dynamics of PNW Chinook. Pacific Northwest coastal waters are influenced by atmospheric conditions not only in the northeast Pacific Ocean (as indexed by the PDO, Mantua et al. 1997), but also in equatorial waters, especially during El Niño events (Peterson et al. 2006). These El Niño events result in the transport of warm equatorial waters northward along the coasts of Central America, Mexico, and California and into the coastal waters off Oregon and Washington. The strength of these ENSO events affects weather in the Pacific Northwest, often resulting in stronger winter storms and transport of warm, offshore waters into the coastal zone. The transport of warm waters toward the coast, either from the south or from offshore, also results in the presence of different mixes of zooplankton and fish species. The effects of these events are quite variable off the coasts of Oregon, Washington, and

British Columbia (the primary focus areas in my dissertation, Figure 1.5), and I relate basin scale effects from the tropical Pacific (ENSO) to the North Pacific (PDO), and finally to local biological indicators that are important to salmon survival.

The PDO is a basin-scale index that correlates well with changes across much of the North Pacific (Figure 1.5). It is a climate index based upon spatial patterns of variation in sea surface temperature of the North Pacific (North of 20° N) from 1900 to the present (Mantua et al. 1997). Although this index is derived from sea surface temperature, it is also correlated with other PNW climate and ecological records like sea-level pressure, winter land-surface temperatures, precipitation, and stream-flow (Peterson et al. 2006). Hare et al. (1999) also demonstrate that the PDO has been correlated with salmon landings in Alaska, Washington, Oregon, and California.

As Francis et al. (2008) state, the northern California current (in the region of British Columbia, Washington, and Oregon, Figure 1.5) is largely a coastal upwelling and surface transport driven system that affects biological production. Peterson et al. 2006 also indicate that upwelling in the region dominated by the northern California Current occurs primarily from April to September coinciding with the spring and fall transitions. A combination of upwelling itself along with the advection of subarctic water (and its associated plankton communities) feeds the inshore arm of the NCC, creating conditions favorable for the development of a huge biomass of subarctic zooplankton. This in turn is a key factor that could affect the survival of juvenile Chinook that feed on copepods. The subarctic copepod community tends to be dominated by large, abundant, fatty species that greatly enhance survival of Chinook in

this region. In contrast, the subtropical copepod community, which enters the coastal NCC from the south and offshore, is dominated by small, less abundant, low lipid species which tend to reduce juvenile Chinook survival (Francis et al. 2008, Peterson et al. 2006). Peterson et al. (2006) also show that the occurrence of these plankton communities in the northern California Current tend to vary with the dominant North Pacific climate signals, e.g., the PDO and ENSO. Thus, during “cold” PDO regimes, a larger amount of cold subarctic water enters the northern California Current from the coastal Gulf of Alaska as opposed to the (offshore) West Wind Drift. During “warm” PDO regimes, smaller amounts of subarctic water enter the CCE from the coastal Gulf of Alaska and more transition or subtropical water enters from the offshore West Wind Drift or from the south.

Peterson et al. (2006) also note that basin-scale phenomena can impact other locally important systems and factors, including the source waters that feed into the northern California Current, zooplankton and forage fish community types, and abundance of salmon predators such as hake and sea birds. However, SST changes could also occur in response to local features such as coastal jets or eddies in the California Current (Hickey 1978), demonstrating that it is important to understand the atmospheric and physical characteristics of the system in which the stock of salmon being studied occurs. Therefore, the times when salmon are in specific places will determine which factors are most important to their overall persistence and survival. Implicitly, there has to be a biological mechanism by which basin scale indices like the PDO affect fish growth and survival. For example, shifts in zooplankton community

composition and density, appearance of a southerly-distributed predatory fish species, or metabolic demand of juvenile Chinook salmon changes in elevated water temperatures. This mechanism is captured by local scale signals such as upwelling indices and sea surface temperatures at local stations.

As stated above, the environment in which juvenile Chinook salmon spend a large proportion of their lives is very dynamic in space and time. Patterns of macronutrient distributions on the continental shelf are dominated by seasonal and event-scale patterns in upwelling processes (Francis et al. 2008, Peterson et al. 2006, Landry et al. 1989, Hickey 1989). Upwelling is caused by northerly winds that dominate from April to September along the PNW coast. These winds transport offshore surface water southward (yellow arrow in Figure 1.6), with a component transported away from the coastline (to the right of the wind, light blue arrow, Figure 1.6). This offshore, southward transport of surface waters is balanced by onshore northward transport of deeper, cool, high-salinity, nutrient-rich water (blue arrow, Figure 1.6). Wind-driven upwelling of nutrients from deeper layers fuels coastal productivity, resulting in both a strong seasonal cycle and several-day fluctuations in productivity that follow changes in wind direction. In order to quantify the magnitude of an upwelling event, Bakun (1973) developed an index known as the Coastal Upwelling Index (CUI), which estimates intensity of offshore transport of surface waters due to geostrophic wind fields.

During an upwelling event, phytoplankton responds to the infusion of nutrients near the coast and this "bloom" is moved offshore, continuing to grow while depleting

the nutrient supply. The deep source waters for upwelling are as important for the overall bloom as the wind stress (Peterson et al. 2006). If the deep waters are warm and nutrient-poor (Peterson et al. 2006) then resulting low levels of plankton production can impact all higher trophic levels, including salmon. Variation in the California Current system can also affect zooplankton populations directly. For example, in years when waters originating in the southern part of the California current (Baja and Southern California) are transported north off the coasts of Oregon and Washington, warm-water copepod species such as *Nyctiphanes simplex* are found in those northern waters. As Peterson and Schwing (2003) indicate, cold water copepods rich in lipid content are observed off the coastal waters of Oregon and Washington in colder and wetter regimes, while warm water copepods poor in lipid content are found there in warmer periods. The cold-water copepod species composition positively affects overall survival of salmon in the northeast Pacific as they are higher in caloric density than the warm water copepods (Peterson and Schwing 2003).

Another key process is the timing of wind shifts. In autumn, when winds reverse, and come out of the south (contrary to Figure 1.6) in winter, there is a strong onshore flow. Corresponding with this reversal, the undercurrent in the California current system brings up deeper water of the coast of Oregon and Washington from southern California and Baja. In spring when the direction of the winds change, and the upwelling process begins, the Californian Current species composition changes as a function of the transport of colder subarctic water into the California current, and brings some of the boreal copepod structure from northern waters to areas off the coast

of Washington and Oregon. The timing and the strength of this current is important to the population dynamics of PNW Chinook salmon as noted in previous sections.

Logerwell et al. (2003) and Lawson et al. (2004) demonstrate how these local-scale factors such as the timing of the wind-shifts, local upwelling, and sea surface temperature, are important in key life-cycle stages for Oregon coastal coho salmon (Logerwell et al. 2003). Logerwell et al. (2003) show that the timing of three mutually independent processes are important for coastal coho survival: the winter pre-conditioning of the northern California current upwelling zone, the timing of spring transition, and the intensity of the upwelling winds themselves.

It is important to therefore note the interconnection between signals and processes in both time and space in the north Pacific. Large scale forcing from the tropical Pacific has an effect on the basin-scale observations in the northeast Pacific as a whole, resulting in changes in both the physical and biological aspects of the coastal upwelling region of the northeast Pacific.

1.6 PNW SALMON MANAGEMENT

As Quinn (2003) says about stock assessment science in his paper referencing Hilborn (1992), stock assessment is a “special priesthood gather[ing] for their annual rites that affect lives of millions.” The ritualistic nature of the salmon (coho and Chinook) stock assessment process is so rigid that it is unlikely that it can be replaced by something that might work more effectively. Morishima and Henry (2000) point out that the requirements of the Endangered Species Act (ESA) place an increasing

demand on management and suggest that a regime change needs to occur in which management moves from point estimate models to models that incorporate risk.

Why hasn't such a change come about? To answer this question we need to understand how the management system has evolved over time. Prior to 1850, salmon fisheries had always been terminal area fisheries (in which adults were harvested on their upriver migration before spawning; Taylor 2001, Morishima and Henry 2000). For thousands of years, the indigenous people of North America had sustained and lived off this resource. As discussed earlier, with non-native settlers moving from the East Coast to California, fisheries expanded along the coast starting in Northern California, and then moved north to areas like the Columbia, Puget Sound, and Alaska. As the people migrated north to Oregon, Washington, and Alaska, a few remained in their original settlements and continued to fish; these fisheries grew in both temporal and spatial distribution from the sustainable fisheries that the Native Americans had developed over time (Taylor 2001). Technological innovations also developed over time, and some fisheries moved out into the ocean (Morishima and Henry 2000). This evolution placed higher exploitation pressure on the resource, diminishing it further. This depletion was primarily due to the fact that historically only the adult components of these salmon runs were targeted by fisheries in terminal areas. It is easier to manage a resource in a terminal area because it is easier to monitor the strength of the run there than in the ocean. When the fisheries moved from terminal areas into the ocean, the immature component of the stock was targeted as well, complicating management and leading to over-exploitation of some stocks. Finally, in the 1970s, when the decision in

US vs. Washington termed the Boldt decision (Morishima and Henry 2000) affirmed the treaty tribes' rights to the salmon fisheries and established fifty percent of the allowable harvest as their fair share, tribal members were assured access to the resource in their usual and accustomed areas (Morishima and Henry 2000). Coinciding with these events hatchery production was also ramped up in the late 1970s and 1980s to sustain ocean and terminal fisheries. This exploitation of hatchery fish to maximum potential coinciding with a decline in marine survival led to the over exploitation of natural stocks. In the 1990s, numerous salmon stocks in the Pacific Northwest were listed as endangered or threatened under the Endangered Species Act (ESA), and some management actions were revised in an attempt to recover and protect these species (NMFS 1997). This has led to reduction in most fishery catches coastwide, but for some stocks has had a very minor effect.

As a society starts exploiting a natural resource, law and management are required to interface and govern the use of the resource. In the case of salmon, eventually local involvement (state and tribal agencies) became important in managing terminal areas, and then in managing ocean waters. Off the coast of California, Oregon and Washington, and in waters within the 200 mile Exclusive Economic Zone (EEZ), ocean regulation is carried out by the Pacific Fisheries Management Council (PFMC), established in 1976 after the Magnuson Stevens Act. The Canadian Department of Fisheries and Oceans (CDFO) manages ocean fisheries off the BC coast. The North Pacific Fishery Management Council (NPFC) manages all the ocean fisheries of the EEZ off the coast of Alaska including southeast Alaska. Finally, as salmon are a highly

migratory species and cross international boundaries, management agreements become necessary for intercept fisheries in both the US and Canada. For this purpose, the US and Canada negotiated the Pacific Salmon Treaty (PST) in 1985. While the sockeye convention had been in place since 1937, it only covered fisheries on sockeye and pinks entering the Fraser River (Smith 1994). Other salmon species had not been discussed in a joint management context until the early 1980s, when tag data from various jurisdictions indicated that both Chinook and coho were highly migratory and crossed borders between the US and Canada. In addition Canada desired reductions in US harvest of Fraser River sockeye and pink salmon. For these reasons the Fraser sockeye agreement was replaced in 1985 by the more comprehensive PST covering intercept fisheries on all salmon stocks, including Chinook. In 1999, coho and chum were also included, as part of the US-Canada international treaty (PSC 2000).

As this history illustrates, salmon management today is extremely complicated. In almost all of these management frameworks, a system of pre-season planning is required. However, the system often suffers from inaccurate forecasts which tend to be used by all management jurisdictions. These forecasts are eventually fed into pre-season planning models like the PSC Chinook Model (TC-Chinook 2008) or the PFMC Model (PFMC 2008). Once these forecasts are made, there is a rigid process by which this information is incorporated into the regulatory process. First harvest limits are agreed upon by the US and Canada through the PSC process, then in federal jurisdictions, matched by consistent regulations for state waters off Washington,

Oregon, and California, and finally in terminal areas where various court decisions have established forums to allocate harvest between Native Americans and the states.

While the pre-season modeling tools can be problematic, they do provide a baseline which everyone in multi-lateral jurisdictional areas can utilize for planning and management purposes. The inputs into the pre-season planning models are terminal and ocean run forecasts for different areas and stocks. These simplistic forecasts are based on either sibling-regressions or average recruits per spawner based on and predicted using the spawning abundance at the previous year and age multiplied by the average recruits per spawner. While this system is simplistic, it can perform well under stable or near constant equilibrium conditions in which ecosystem factors remain relatively constant (Mantua and Francis 2004). The ecosystem does not remain constant, however, and so there are inherent biases in these forecasts which then creep into the pre-season planning models, leading to over or under-allocation of harvest. While the latter is not a concern for the resource, the former is. Therefore, improvements need to be made to this process. As Mantua and Francis (2004) point out, more measures of uncertainty and risk need to be considered, and the system needs to be moved from pre-season modeling approaches to in-season modeling techniques such as those used in the Columbia River and for sockeye salmon in Bristol Bay, Alaska (Hilborn et al. 2002).

Amending salmon management frameworks is complicated and/or constrained by their relationship with court rulings (e.g., US vs. Oregon, US vs. Washington), federal laws (Magnuson Stevens Act, ESA) and international treaties (PST)

(Morishima and Henry 2000). It is difficult to modify the existing management system because there are legal requirements to use a certain forecasting system under US vs. Oregon, US vs. Washington, the Columbia River Compact (a Congressionally chartered management forum for OR and WA), and the Pacific Salmon Treaty. The challenge is that science (and forecasting) can often evolve and improve more quickly than it can be adapted and utilized in policy and decision making forums. However, if enough members of scientific technical teams are able to utilize better information, and are able to demonstrate that it will improve their ability to provide more accurate predictions, the policy makers may be convinced to change an otherwise inflexible system, provided the techniques are sound and result in a more consistently accurate forecast.

1.7 UNDERSTANDING VARIATION IN PNW SALMON DISTRIBUTION, SURVIVAL, MATURATION AND RECRUITMENT: THE FOCUS OF THIS DISSERTATION

There are four objectives of this dissertation. They are the following:

- 1) I will test for regional and life history based differences in ocean migrations.
- 2) I will test for spatial and temporal variation in survival and maturation for PNW Chinook and relate this to variation in environmental forcing.
- 3) I will estimate variability in recruitment through a new age-structured modeling approach, and relate that to environmental forcing, and
- 4) I will combine items from the first three pieces to design a management system that incorporates uncertainty.

To accomplish the first objective, I test Healey's (1983) hypothesis with empirical data and demonstrate regional and life-history based differences in migration pathways in the Pacific Northwest. The second objective of this project will improve understanding of the relationship between external environmental variables as indicated by upwelling and sea-surface temperatures during the spring transition and ocean survival, and maturation of PNW Chinook (estimated through coded wire tags). The third objective is to demonstrate how direct measures of environmental conditions can be integrated into Chinook salmon stock assessment through a complicated age-structured model. Finally, I will incorporate the results from items 1-3 in designing a management system that incorporates uncertainty and is precautionary in nature.

The overall goal is to synthesize assessment and climate data for the PNW region and determine if there are any spatial and temporal signals that might be important factors to consider for overall population dynamics of the Chinook in this region. Based on these results, a better understanding of the relationships between variability in environmental indices and variability in Chinook salmon abundance in the PNW will be generated. This knowledge could be used directly or indirectly to increase pre-season or in-season management precision.

1.8 DISSERTATION OUTLINE

The next few pages will provide a general background and outline of the approach used in each of the subsequent chapters of the dissertation.

Chapter 2 tests the hypothesis that stream-type and ocean-type Chinook salmon differ in ocean distribution, implying the use of different migration pathways by the two types. The basic approach used here is to conduct a paired analysis of tag data

from a series of rivers that produce both ocean- and stream-type Chinook salmon. If life history based difference do not occur in salmon migrations the data would reflect similar recovery patterns by life history type that would be consistent across all rivers. The hypothesis is that stream-type Chinook salmon would tend to migrate to offshore waters to rear, and that fewer stream-type fish would be recovered in coastal fisheries, and they would be primarily recovered near the mouth of the natal river and in the river itself.

Chapter 3 focuses on the effects of phenomena occurring over large and regional (local) scales as represented by upwelling and sea surface temperature at stations along the coastal areas of the northeast Pacific, on PNW Chinook salmon survival and maturation. Research in recent years has indicated that ocean and freshwater conditions affect survival for coho (Lawson et al. 2004, Logerwell et al. 2003, Ryding and Skalski 1999a, Coronado and Hilborn 1998). While studies on Chinook have demonstrated correlations between survival and ocean (near shore/estuarine) conditions (Magnusson 2002, Ryding and Skalski 1999b, Greene and Beechie 2004), few studies have been performed for the entire PNW. In addition, the relationships among broad scale signals like the PDO or ENSO, local signals like localized upwelling and sea surface temperatures, and survival are well understood (Peterson et al. 2006), but have not been demonstrated in a comprehensive coastwide manner.

In order to demonstrate fluctuating spatial and temporal patterns of Chinook survival and maturation, I analyzed indicator tag code data (TCChinook 08-1, Table

1.2, Figure 1.7) and estimated survival and maturation for numerous stocks managed by the PSC. In order to relate this to the environmental data sea surface temperature and upwelling was analyzed during the summer months after spring transition to relate to survival. For maturation, yearlong conditions of upwelling were evaluated and related to the maturation data obtained for a subset of stocks shown in Table 1.2.

Chapter 4 presents a modified catch at age model for Chinook populations to estimate temporal and spatial recruitment variability. This approach is preferable to the approach currently being used by the Pacific Salmon Commission because it can incorporate environmental variation and tie physical indicators of ocean conditions to recruitment variation, it is a statistically robust technique which could improve management precision on a fishery and age specific basis, and it provides estimates of variance on estimated parameters like abundance and exploitation rates.

My approach develops a catch at age model using the life history of Chinook salmon, a time series of coded wire tag (CWT) data (Johnson 1990, Lapi et al. 1990), and terminal run data to estimate recruitment and fishing mortality by area and age (Figure 1.8). The method uses a forward projection algorithm that is based on estimation of certain key parameters, namely recruitment to age 2 ocean fish; maturation of age 2, 3 and 4; catchability by ocean and terminal fishery; and vulnerability by gear type in each fishery. It uses an optimization function that minimizes the difference between model projections and observed ocean catches of the stock by age and fishery of concern (Deriso et al. 1985) and modelled and observed escapement. This is done by maximizing the likelihood functions between observed

and predicted catches in the various fisheries and escapements (Deriso et al. 1985).

One of the parameters estimated in this model is age-2 recruitment. The estimates of age-2 recruitment are used along with independent covariates to understand how recruitment varies as a function of both the freshwater (as indicated by flow anomalies during the smolt outmigration phase) and the ocean environment (as indicated by sea surface temperatures off the near-shore coastal shelf closest to the river mouth), or both.

Once a retrospective analysis has been completed, the next step is to use the approach in a predictive model. I incorporate these results directly into the model using properties of Markov chain processes to forecast future scenarios in the short term based on age (Figure 1.9) or terminal runs across all ages (Figure 1.10). This will help move from management based on point estimates to management based on estimates of uncertainty and risk (Mantua and Francis 2004, Pielke 2003, Morishima and Henry 2000).

Chapter 5 will put this into perspective from a management point of view. I will retrospectively evaluate how we have managed these stocks for the last few decades, and propose an alternative management framework that will be built on evaluating uncertainty through an ecosystem context as well as a stock based context.

List of Tables

Table 1.1: Natural and hatchery stock aggregates displayed in Figure 1.3.

Table 1.2: Indicator stocks, location, run type, and age of smolt at release, based on Chinook Technical Committee's Tag codes that were used in the analysis.

Table 1.1: Natural and hatchery stock aggregates displayed in Figure 1.3.

Number	Stocks encountered in 3 ocean fisheries
1	Alaska South SE
2	Northern/Central B.C.
3	Fraser River Early
4	Fraser River Late
5	West Coast Vancouver Island Hatchery
6	West Coast Vancouver Island Natural
7	Upper Strait of Georgia
8	Lower Strait of Georgia Natural
9	Lower Strait of Georgia Hatchery
10	Nooksack River Fall
11	Puget Sound Fingerling
12	Puget Sound Natural Fingerling
13	Puget Sound Yearling
14	Nooksack River Spring
15	Skagit River Wild
16	Stillaguamish River Wild
17	Snohomish River Wild
18	Washington Coastal Hatchery
19	Columbia River Upriver Brights
20	Spring Creek Hatchery
21	Lower Bonneville Hatchery
22	Fall Cowlitz River Hatchery
23	Lewis River Wild
24	Willamette River
25	Spring Cowlitz Hatchery
26	Columbia River Summers
27	Oregon Coastal
28	Washington Coastal Wild
29	Snake River Wild Fall
30	Mid Columbia River Brights

Table 1.2: Indicator stocks, location, run type, and age of smolt at release, based on Chinook Technical Committee's Tag codes that were used in the analysis.

Origin	Stock Name	Location	Stock Acronym	Run Type	Smolt Age
S.E. Alaska	Alaska Spring	Southeast Alaska	AKS	Spring	Age 1
British Columbia	Kitsumkalum	North/Central BC	KLM	Summer	Age 1
	Robertson Creek	WCVI	RBT	Fall	Age 0
	Quinsam	Georgia Strait	QNSAM	Fall	Age 0
	Puntledge	Georgia Strait	PUNTL	Summer	Age 0
	Big Qualicum	Georgia Strait	BQR	Fall	Age 0
	Chilliwack (Harrison Stock)	Lower Fraser River	CHILLIWAC/CHI	Fall	Age 0
Puget Sound	Stillaguamish Fall Fingerling	Central Puget Sound	STL	Summer/Fall	Age 0
	George Adams Fall Fingerling	Hood Canal	GAD	Summer/Fall	Age 0
	South Puget Sound Fall Fingerling	South Puget Sound	SPSF	Summer/Fall	Age 0
	Nisqually Fall Fingerling	South Puget Sound	NIS	Summer/Fall	Age 0
	White River Spring Yearling	South Puget Sound	WSY	Spring	Age 1
Washington Coast	Queets Fall Fingerling	North Wash. Coast	QTS	Fall	Age 0
Columbia River	Cowlitz Tule	Columbia Rvr. (Lower WA)	CWF	Fall Tule	Age 0
	Spring Creek Tule	Columbia Rvr. (Mid)	SPR	Fall Tule	Age 0
	Columbia Lower River Hatchery	Columbia River (Lower OR)	LRH(Big Creek Hatchery)	Fall Tule	Age 0
	Upriver Bright	Upper Columbia Rvr. (Hanford)	URB	Fall Bright	Age 0
	Lewis River Wild	Lower Columbia Rvr.	LRW	Fall Bright	Age 0

	Lyons Ferry ¹	Snake River	LYF	Fall Bright	Age 0
	Willamette Spring	Willamette	WSH	Spring	Age 1
	Summers	Columbia Rvr. (Upper WA)- Wells Dam	SUM	Summer	Age 1
Oregon Coast	Salmon River	North Oregon Coast	SRH (ORC)	Fall	Age 0
Southern Oregon/CA	Klamath River	Southern OR coast/ Northern CA coast	KLAM	Fall	Age 1

¹ Lyons Ferry and Summer Chinook have an incomplete shorter time series and are excluded from the Cluster Analysis

List of Figures

Figure 1.1: The Pacific Northwest region from Northern California to Southeast Alaska including Oregon, Washington, and British Columbia. The main drainages displayed are the Klamath, Columbia (including the Willamette and Snake), the Fraser and the Stikine Rivers.

Figure 1.2: Chinook Salmon Life History (courtesy I. Ortiz, SAFS, University of Washington, Seattle, WA 98195)

Figure 1.3: Estimated Chinook salmon ocean abundance trends based on the Chinook technical Committee CTC Ocean management model (CTC 2008) for Southeast Alaska, Northern BC and West Coast of Vancouver Island.

Figure 1.4: Location of various fisheries of significance to Pacific Northwest Chinook northern migrating stocks.

Figure 1.5: Ocean currents and regions of upwelling in the Northeast Pacific (courtesy Jodie Little, University Of Washington).

Figure 1.6: Coastal Upwelling dynamics (Courtesy Pacific fisheries Environmental Laboratory (<http://www.pfeg.noaa.gov>)).

Figure 1.7: PNW Chinook CWT stocks analyzed for survival and maturation trends over the last few decades. The figure covers the broad regions covered in the analysis.

Figure 1.8: Schematic used to estimate Age 2 recruitment, catchability, vulnerability and maturation using statistical catch at age techniques for a simple 2 area model (ocean and terminal)

Figure 1.9: Runs size distributions by age

Figure 1.10: Total terminal run prediction with uncertainty



Figure 1.1: The Pacific Northwest region from Northern California to Southeast Alaska including Oregon, Washington, and British Columbia. The main drainages displayed are the Klamath, Columbia (including the Willamette and Snake), the Fraser and the Stikine Rivers.

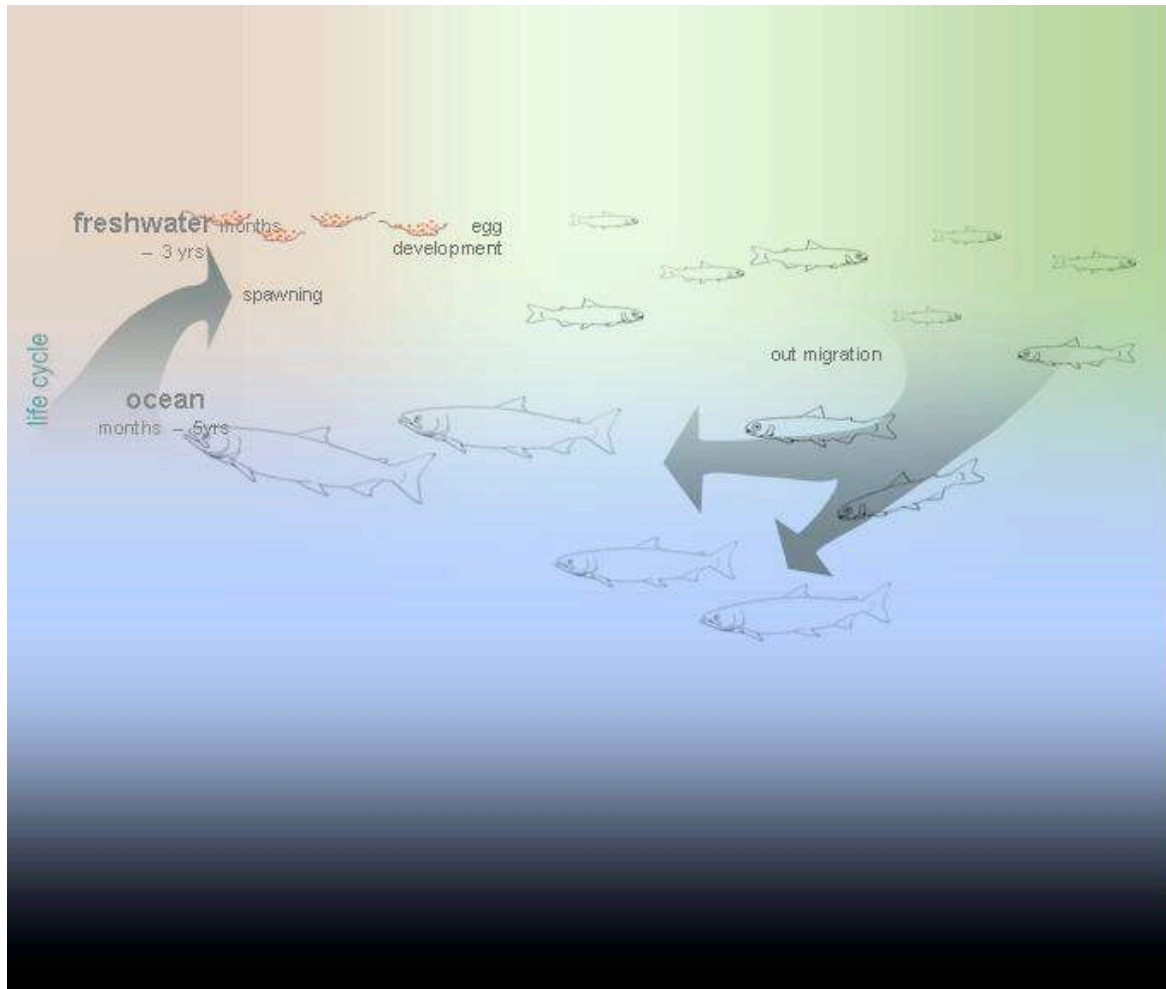


Figure 1.2: Chinook Salmon Life History (courtesy I. Ortiz, SAFS, University of Washington, Seattle, WA 98195) ∞

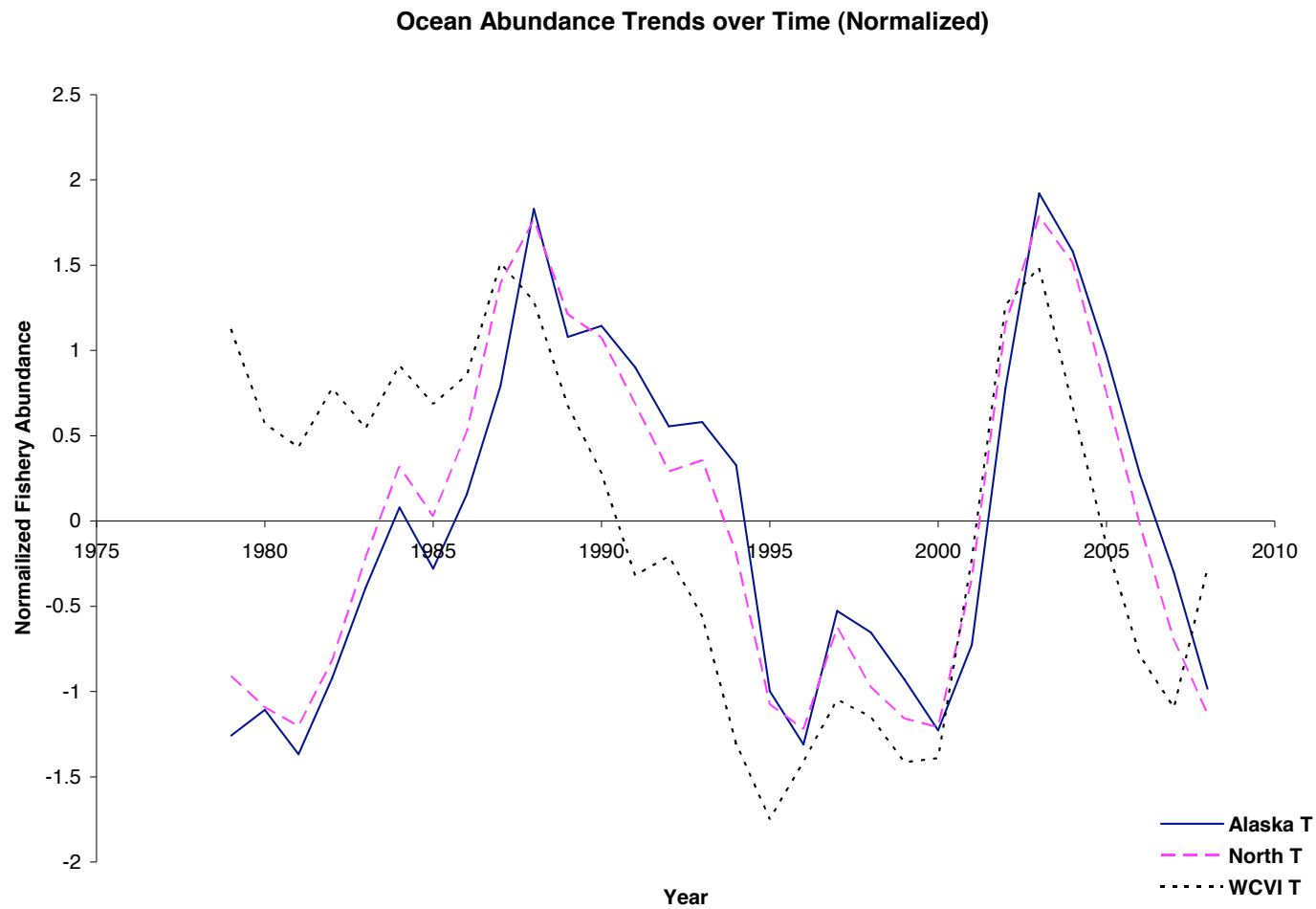


Figure 1.3: Estimated Chinook salmon ocean abundance trends based on the Chinook technical Committee CTC Ocean management model (CTC 2008) for Southeast Alaska, Northern BC and West Coast of Vancouver Island.



Figure 1.4: Location of various fisheries of significance to Pacific Northwest Chinook northern migrating stocks

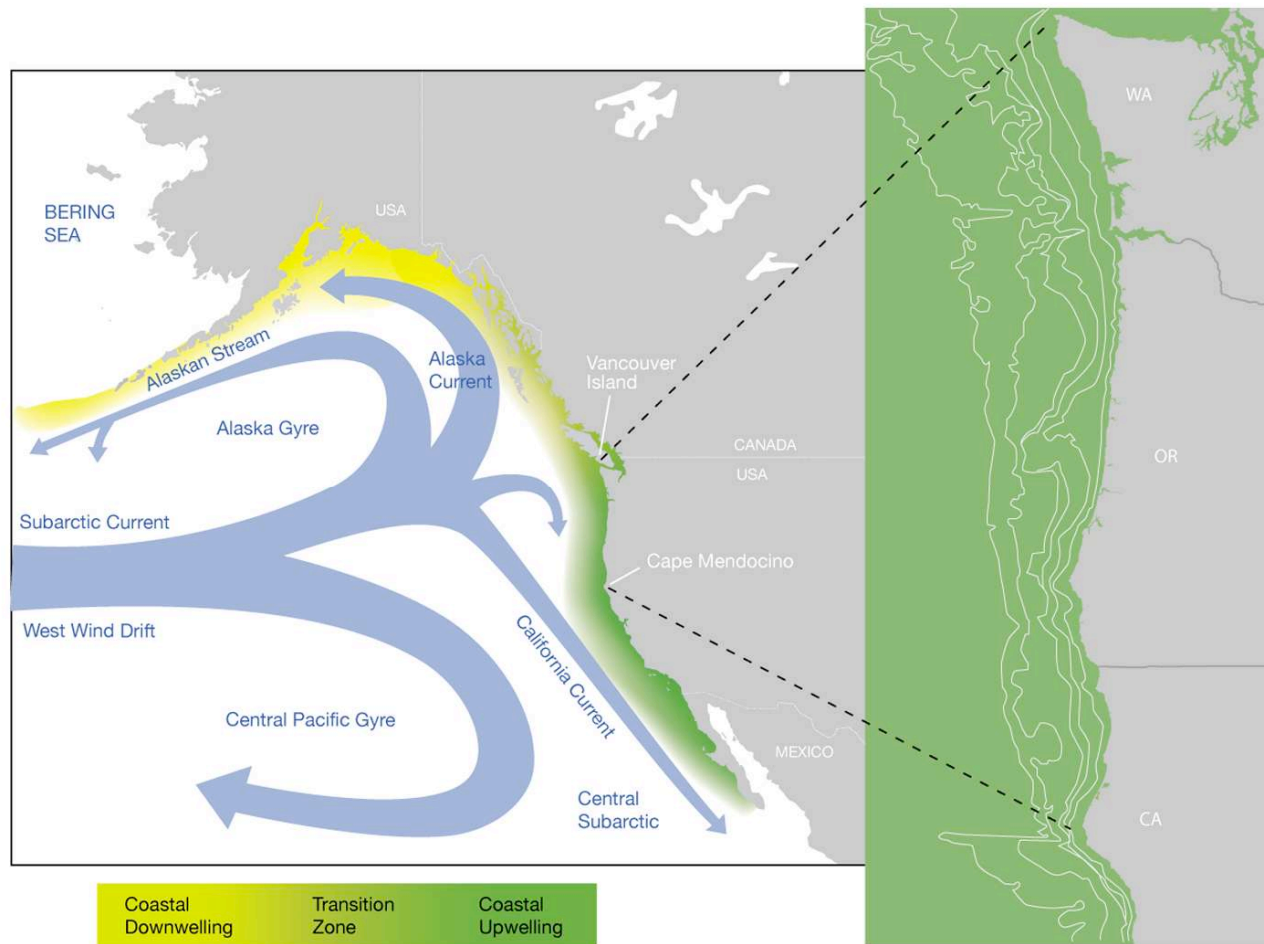


Figure 1.5: Ocean currents and regions of upwelling in the Northeast Pacific (courtesy Jodie Little, University Of Washington)

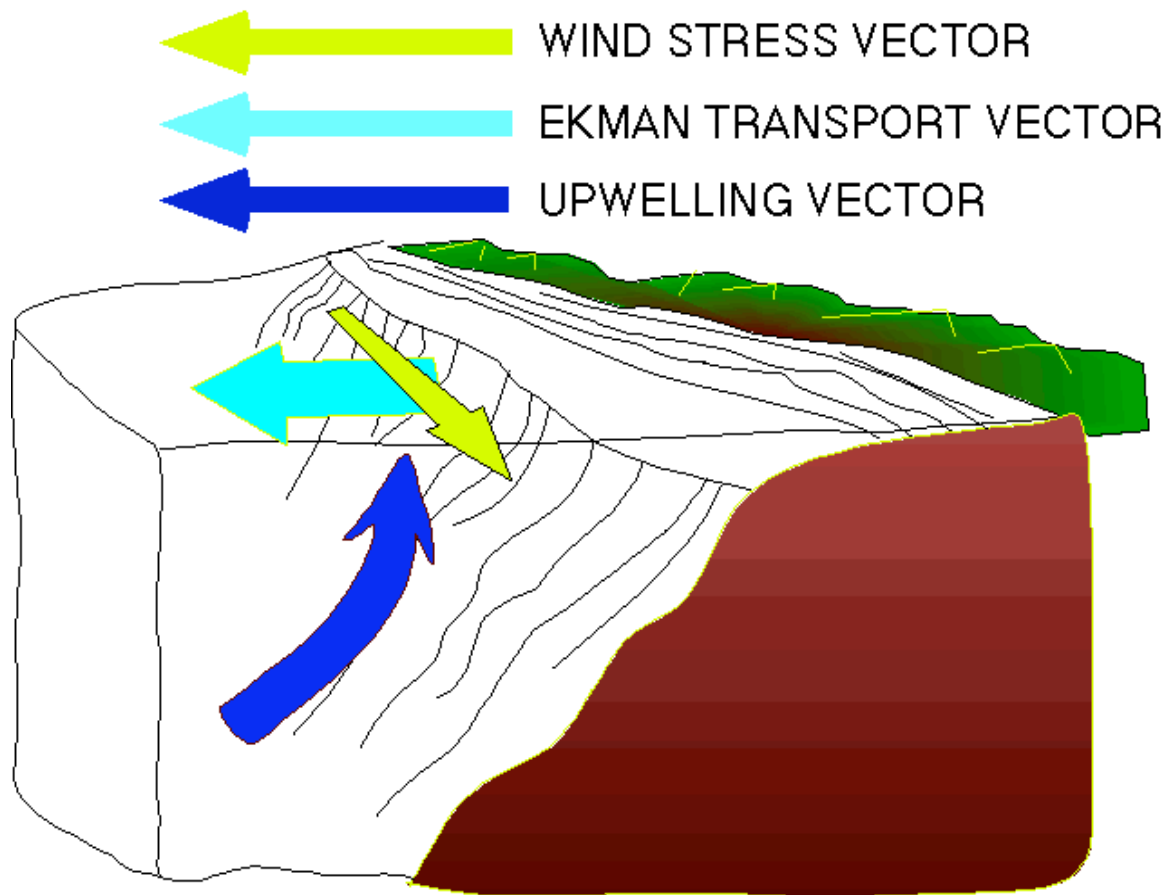


Figure 1.6: Coastal Upwelling dynamics (Courtesy Pacific fisheries Environmental Laboratory (<http://www.pfeg.noaa.gov>))

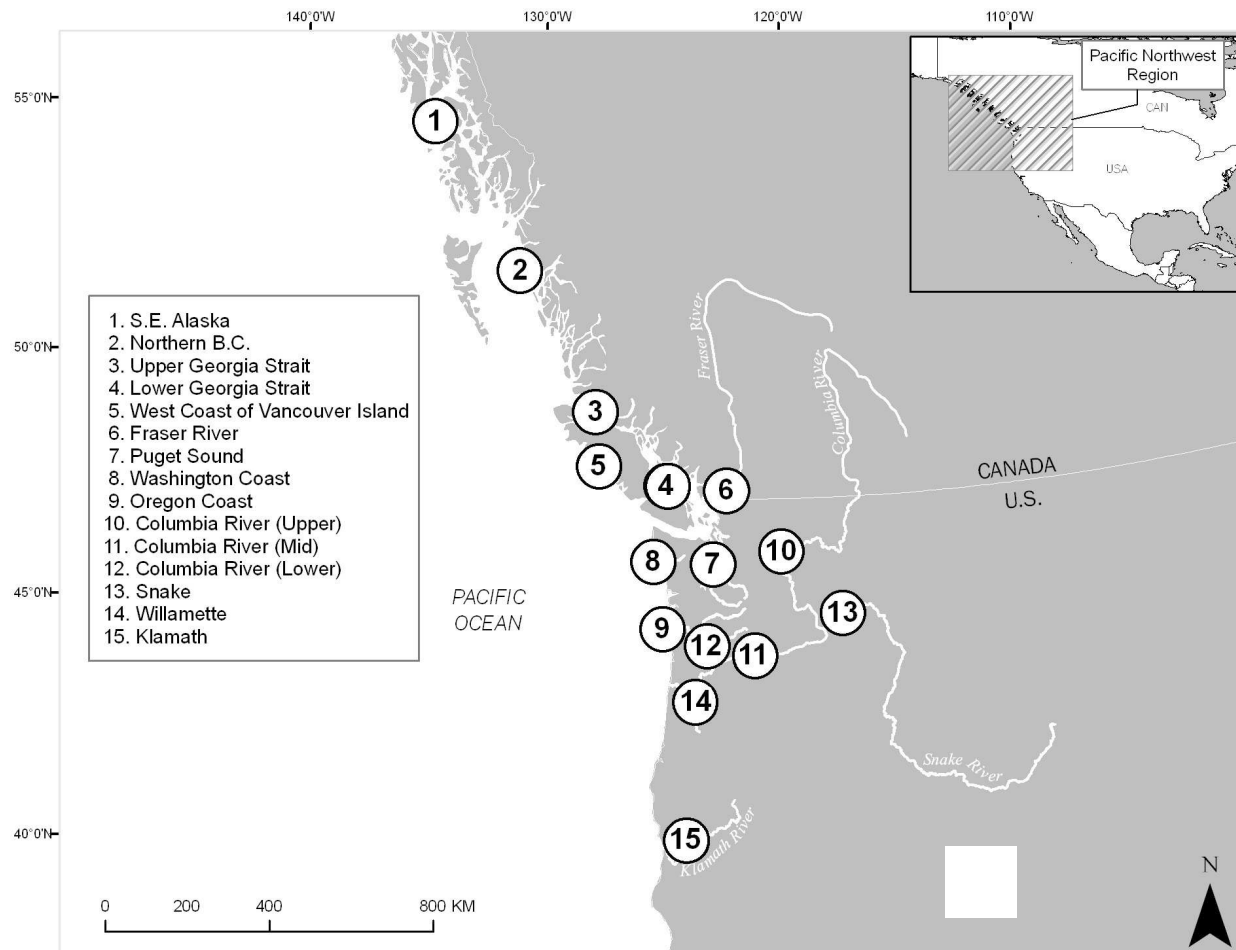


Figure 1.7:PNW Chinook CWT stocks analyzed for survival and maturation trends over the last few decades. The figure covers the broad regions covered in the analysis.

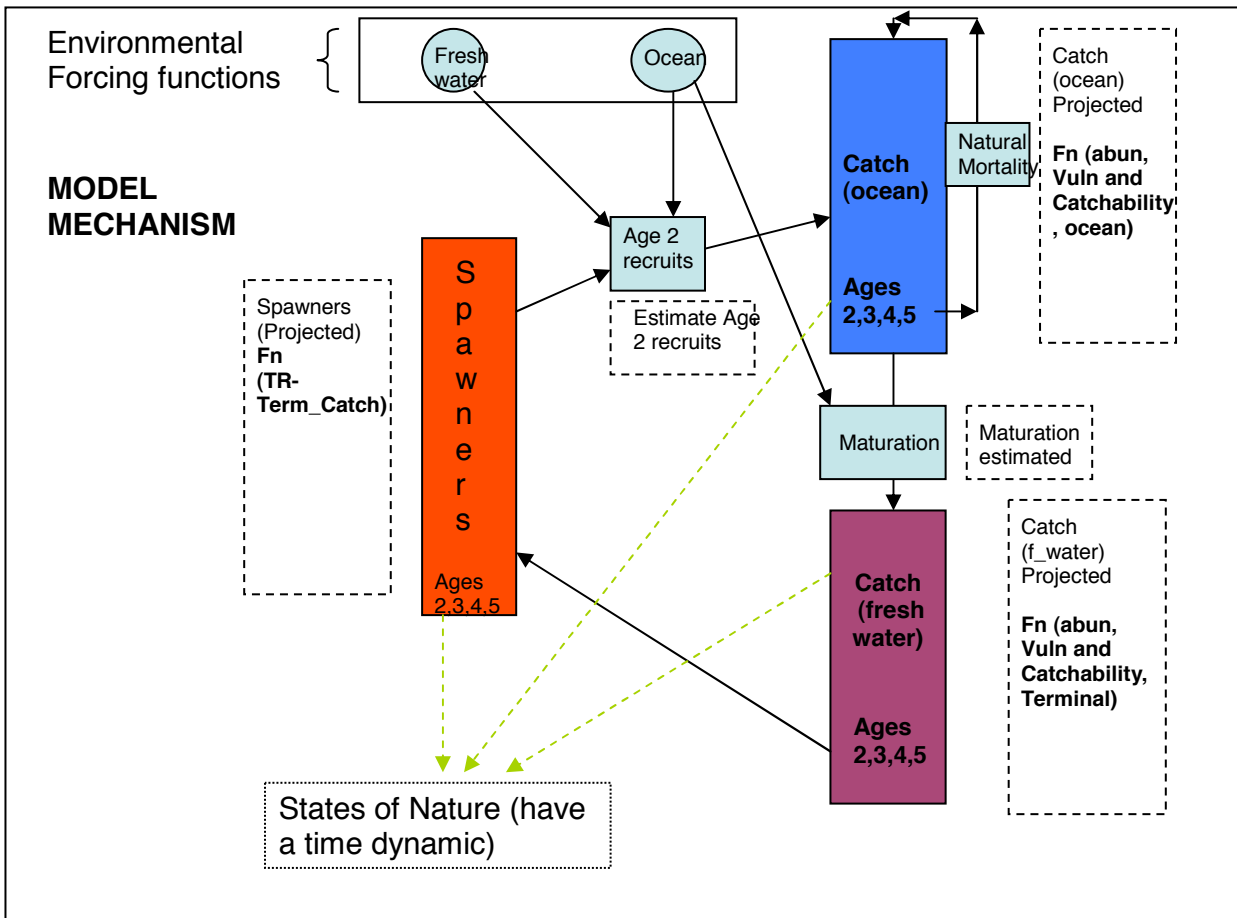


Figure 1.8: Schematic used to estimate Age 2 recruitment, catchability, vulnerability and maturation using statistical catch at age techniques for a simple 2 area model (ocean and terminal).

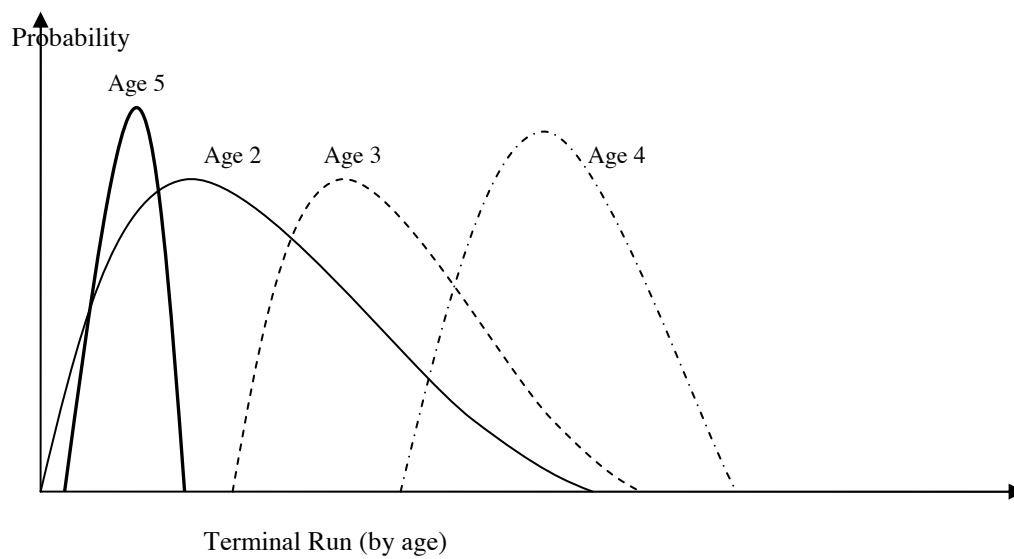


Figure 1.9: Runs size distributions by age

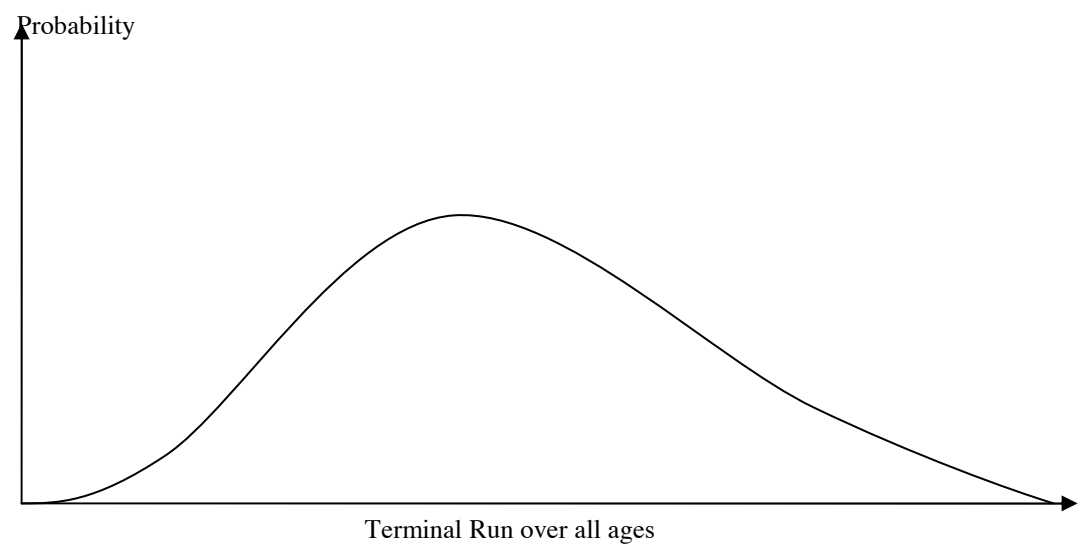


Figure 1.10: Total terminal run prediction with uncertainty

**CHAPTER 2: LINKAGE BETWEEN LIFE HISTORY AND
ECOLOGY IN FRESHWATER AND MARINE ENVIRONMENTS:
DO STREAM-TYPE AND OCEAN-TYPE CHINOOK SALMON
DIFFER IN MARINE DISTRIBUTION?**

2.1 INTRODUCTION

The ocean phase of the life history of anadromous fishes is critical, as the great majority of their total growth is achieved at sea after having left less productive freshwater environments (Gross 1987; McDowall 1988). There are complex linkages between the life history patterns in these two environments, including the size, age, and timing of seaward migration, the duration of marine residence, and the size and timing of return migration (Quinn et al. 2009). There is considerable variation in size and age at seaward migration, within and among species, parameters which determine the suite of prey, competitors, and predators the salmon encounter in the ocean (Quinn et al. 2009). Upon entering marine waters, juveniles can occupy a wide range of estuarine, nearshore, shelf, and open ocean habitats. The families of anadromous fishes vary greatly in the habitats that they occupy, and even within the genus of Pacific salmon and trout (*Oncorhynchus*, the best studied group) there can be considerable variation in marine migration patterns. Cutthroat trout, *O. clarki*, seem to restrict their foraging largely to estuarine and nearshore waters in the vicinity of their home river. Steelhead, *O. mykiss*, have similar freshwater ecology to cutthroat trout but exhibit very different marine migrations, migrating directly to offshore waters and staying there until they mature (Quinn and Myers 2004, Myers et. al. 1996). Sockeye, *O. nerka*, chum, *O. keta*, pink salmon, *O. gorbuscha*, coho, *O. kisutch* migrate along the continental shelf as juveniles during their first summer and fall at sea before moving to offshore waters to feed, followed by migration in coastal waters at maturity.

Perhaps the most complex combination of life history and migration patterns is exhibited by Chinook salmon, *O. tshawytscha*. Towards the southern end of their

range, and especially in low elevations, juveniles typically migrate to sea as fry shortly after emergence from the gravel or as sub-yearlings after a few months in fresh water. These have been termed “ocean-type” Chinook salmon, and this pattern is associated with relatively early emergence and rapid growth in the river (reviewed by Taylor 1990a; Healey 1991). In higher elevations within the southern part of the range, and in all cases in the northern part of the range, Chinook salmon spend a full year in fresh water before migrating to sea at a larger size, as “stream-type” fish. Populations north of about 56° N latitude (i.e., the Skeena and Nass rivers, British Columbia) are virtually all stream-type (Taylor 1990a); the Situk River in south central Alaska (59° 30' N) is an exception, producing primarily ocean-type juveniles (Johnson et al. 1992). Healey (1991) argued that stream-type and ocean-type Chinook salmon represent distinct “races,” characterized by profound differences in many aspects of their behavior and ecology (Table 2.1), whereas Brannon et al. (2004) emphasized the importance of environmental conditions (especially temperature) in determining the life history and behavior of the two types. Evidence pertaining to this controversy is mixed. The forms differ in behavior and morphology as juveniles (Taylor 1990b), in the physiology of the smolt transformation (Clarke et al. 1992, 1994), and in the tendency to produce mature parr (Taylor 1989). Genetic analysis by Waples et al. (2004) indicates that in most cases the two types¹ diverged independently in many different rivers (i.e., are polyphyletic), and ocean-type fish transplanted to New Zealand quickly displayed both stream-type and ocean-type life histories (Quinn et al. 2001). However, the interior

¹ I use the term “type” rather than “race” when referring to these life history variants for consistency with the common and long-standing use of “stream-type” and “ocean-type” but this does not imply a judgment regarding the evolutionary status of these salmon.

Columbia River basin populations seem to represent a distinct lineage from coastal populations (Waples et al. 2004).

One important covariate of the juvenile life history is the timing of adult return from the ocean to fresh water. Stream-type populations, especially those in the southern part of their range, often return in spring, whereas ocean-type populations typically return in fall. Both types spawn in fall, so the duration of holding in fresh water differs greatly between forms. This pattern of “premature migration,” well-known in Chinook salmon (e.g., Healey 1991; Myers et al. 1998; Waples et al. 2004) and other salmonid species (Quinn and Myers 2004), presumably occurs in response to upstream thermal or hydrological barriers to migration that occur shortly before spawning. However, Healey (1983) pointed out an even more intriguing aspect of the migration of these two forms: ocean-type Chinook salmon seem to be distributed primarily along the continental shelf during their marine residence while stream-type Chinook salmon are more common off the shelf and on the open ocean. “Stream-type Chinook salmon migrate far offshore whereas ocean-type Chinook salmon remain in coastal waters throughout their ocean life” (Healey and Groot 1987: p. 298). Myers et al. (1998: p. 31) concluded that “The causal basis for this difference in migration pattern is unknown.”

The ocean migration patterns of these two types of Chinook salmon represent not only a critical linkage between the behavior of salmon in freshwater and marine environments, but also a profoundly important factor to consider in their conservation and management. Salmon fishing on the open ocean is negligible since the elimination

of the high seas fisheries in international waters (first eliminated in 1953 with the High Seas Agreement for foreign vessels, then eliminated in 1957 through the Surf Line Agreement for North American vessels). Thus chum, pink, and sockeye salmon are almost exclusively taken as maturing fish on their homeward migration in coastal waters. In contrast, Chinook salmon are vulnerable for several years (i.e., the period they spend at sea: Roni and Quinn (1995)) if they remain in coastal waters, as many do. The tendency to migrate into offshore waters to feed would greatly reduce their vulnerability to fisheries as they operate on the coastal shelf.

Many Evolutionarily Significant Units (ESU) of Chinook salmon have been designated as Threatened under the United States Endangered Species Act (Snake River, Puget Sound, lower Columbia River, upper Willamette River, California Central Valley, and California coast) and two ESUs are listed as Endangered: the Sacramento River winter-run and upper Columbia River spring-run (Good et al. 2005). Improved understanding of Chinook migration and exploitation patterns would greatly assist conservation efforts, as many of these population complexes are still exploited in commercial and recreational fisheries. Conservation and management of Chinook salmon are governed by a complex combination of regulations set by individual states, Native American tribes with treaty rights, inter-tribal commissions, and the governments of the United States and Canada (PSC 2000).

Despite the time, effort, and money that have been spent studying Chinook salmon, surprisingly few studies have used analytical methods to demonstrate differences in Chinook migration pathways. The few studies that have shown

differences in recovery patterns (e.g. Healey 1991, Aro 1972, Kondo et al. 1965, Hartt and Dell 1986, Hartt 1966) failed to account for the geographical origins of the populations. In addition, the data in these studies were not sufficient for proper statistical analysis and did not consider critical variables such as age at maturation and interannual variation (Kondo et al. 1965, Aro 1973, Major et. al. 1978).

Analysis of the migration patterns of stream- and ocean-type Chinook salmon is complicated by variations in behavior within each of the two types. Some ocean-type Chinook salmon from Oregon, for example, tend to be caught south of their river of origin whereas others are caught to the north (Nicholas and Hankin 1989), and the spatial distribution of Chinook salmon from inland waters (e.g., Puget Sound and the Strait of Georgia) may differ from that of fish from the outer coast (Healey and Groot 1987). In addition, ocean-type populations tend to spend more years at sea, presumably because they entered at a smaller size, than stream-type populations (Roni and Quinn 1995), and this needs to be considered in any analysis of catch patterns. Perhaps more fundamentally, the two life history types are segregated to a large extent by latitude, which greatly affects the marine environments that they experience as smolts. Southern populations (e.g., California, Oregon, and Washington) find suitable conditions for rearing (in terms of temperature and food) in the coastal waters strongly influenced by upwelling (Pearcy 1992), while the waters directly offshore in Washington, Oregon, and northern California are too warm and unproductive for salmon. In contrast, populations in the north (e.g., Gulf of Alaska) can migrate offshore and find cool, productive waters for rearing in addition to the suitable waters along the coast. Thus it

is not clear whether the differences in distribution between the types reported by Healey (1983) resulted from the juvenile life history or the region where the smolts entered the ocean.

The purpose of this study is to test the hypothesis that stream-type and ocean-type Chinook salmon differ in marine distributions. I conducted a paired analysis of data from a series of rivers where both types of Chinook salmon are produced and tagged. There is very limited fishing on the high seas but tagged salmon might be recovered in three general regions: 1) far northern (distant from natal areas) waters along the coast, 2) coastal waters in the immediate vicinity of the home river, and 3) the home river (either in the river or at the natal site itself). If the ocean distributions of salmon from a given river are similar for both types, no difference in relative recoveries among these three regions would be expected, although there might be variation in distributions of salmon from different rivers. The predicted alternative, based on the hypothesis that stream-type Chinook salmon tend to migrate to offshore waters to rear (i.e., where they would not get caught), is that fewer stream-type fish would be recovered in distant coastal fisheries; instead they would be primarily recovered near the mouth of the natal river and in the river itself. A second hypothesis is also tested with these data, namely that there are differences in marine distribution between life history types which vary among regions.

2.2 MATERIALS AND METHODS

Coded wire tags (CWT) have been used extensively to understand harvest and migration patterns of salmon since 1972 (Lapi et. al. 1990). I used coded wire tag

(CWT) data from hatcheries that had both stream- and ocean-type releases in Washington, Oregon, Idaho, and British Columbia (Figure 2.1; Table 2.2). Although not perfect, as hatchery Chinook differ from natural Chinook populations in terms of survival and maturation, they still provide valuable information on harvest and migration patterns coastwide. The implicit assumption made in this analysis is that hatchery fish are representative of natural Chinook populations in describing migration patterns in the ocean. Recovery data were categorized by the different fishery areas along the West Coast (Figure 2.1).

The recovery rate (I) per fingerling or yearling released was estimated using equation 2.1.

$$I_{f,g,t} = \frac{\sum_{i=t+2}^{i=t+6} R_{i,f,g}}{S_{g,t}} \quad (2.1)$$

where R is the number of recoveries of the particular group (g, either stream or ocean type) at age (i), fishery (f), and at time (t), and S is the number of smolts released for that same group in year (t). I first compute this rate for different ocean fishing areas (f) (e.g. regions such as high seas, southeast Alaska, northern and central British Columbia, west coast of Vancouver Island (including the Strait of Georgia), Washington/Oregon coast, and freshwater, Figure 2.1). Then I use these results in a Generalized Linear Model (GLM) form of Analysis of Variance which tests for statistical significance of different design variables that might affect the recovery rate by area. The design variables tested were “stock-type (G),” fishery (F) and year (T) for differences between recovery rates.

I test both a log-linear model (eq. 2.2) as well as log-transformed Poisson model (eq. 2.3) as suggested by Green and McDonald (1987).

$$\ln \left(\frac{\sum_{i=t+2}^{i=t+6} R_{i,f,g}}{S_{g,t}} \right) = \ln(I_{f,g,t}) = \left(\alpha + \sum_{t=1}^n \beta_t T_t + \sum_{f=1}^6 \gamma_f F_f \right) + \theta G_g + \sum_{f=1}^6 \omega_{f,g} (G_g : F_f) + \varepsilon \quad (2.2)$$

where $\sum R_{i,f,g}$ is the observed recovery of either stream-type or ocean-type Chinook (over all ages), T is the year effect design variable (between 10 and 25 years for any given stock), F is the fishery area design variable (six in our case: high seas, Alaska, northern British Columbia, the west coast of Vancouver Island, the coast of Washington and Oregon (combined), and terminal areas (i.e., river mouth and in-river locations, note that all stock recoveries are summed separately by terminal areas, thus Columbia River stocks only sum up terminal Columbia recoveries, and northern BC stocks only sum up northern BC terminal recoveries)), S is the number of outmigrating smolts (hatchery releases) from either the stream- or ocean-type Chinook salmon of the corresponding brood year, G is the group (stream- or ocean-type Chinook) effect variable, and $\omega_{f,g}$ is the parameter which describes the interaction between fishery, F and stock type, g . The first parameter (α) is the intercept, the second set of parameters, β_t , are year effects, which will change the overall intercept by year (if significant), and the third set of parameters (γ_f) are fishery effects by area. To test if recoveries are

different by stock type (G), a design variable is included for the stock type (stream- or ocean-type which will be zero for an ocean-type and 1 for a stream-type Chinook), and a parameter θ . Note that this term will also change the intercept term in the model. Finally, the model includes a stock-fishery interaction design variable which will change the intercept by fishery and stock type if significant. This type of analysis is very similar to a contingency table analysis which is a function of stock type, year and fishery, and possible interactions (Zar 1995).

Under the null hypothesis $\beta_t = \gamma_f = \theta = \omega_{f,g} = 0$. Under the alternative hypothesis β_t and/or γ_f and/or θ and/or $\omega_{f,g} \neq 0$. The most important terms to test for are θ and ω_f , to test whether there is any group effect (i.e., difference in recoveries between ocean- and stream-type groups) by area.

I also tested a Poisson Response log-transformed Model (Cormack and Skalski 1992) to explain the large number of zeros seen in some strata (i.e. fishery recovery strata). Ocean recovery data is very sparse for some regions and locations. Hence, the model normally used to test these low number of recoveries uses a Poisson error structure.

$$\mu_t = \exp \left(\left(\alpha + \sum_{t=1}^n \beta_t T_t + \sum_{f=1}^6 \gamma_f F_f \right) + (\phi S_t(G_g)) + \theta G_g + \sum_{f=1}^6 \omega_f G_g : F_f + \varepsilon \right) \quad (2.3)$$

where μ_t is the exponent of the linear predictor of the sum of recoveries in a strata

(i.e. $\mu_t = \sum_{i=t+2}^{t+6} R_{i,g,f}$). Note taking logarithms on both sides of equation 2.3 makes it a

linear model (eq. 2.4).

$$LP = \left(\alpha + \sum_{t=1}^n \beta_t T_t + \sum_{f=1}^6 \gamma_f F_f \right) + \kappa S_t + (\phi S_t (G_g)) + \theta G_g + \sum_{f=1}^6 \omega_f G_g : F_f + \varepsilon \quad (2.4)$$

where LP is the Linear Predictor, S is the releases, T is the year effect, G is a stock effect, and F is the fishery (area) effect. This model is slightly different from the first model as it takes into account a continuous variable (releases, S which is a covariate) to determine if there are any interactions by stock type (G). Such interactions would change the slope of the model based on “stock-type.” Other terms affect the outcome of the model as described in equation 2.3. That is, the model includes a term for the stock type (stream- or ocean-type, set as 0 for ocean-type and 1 for stream-type fish) which would change the intercept term in the model (the effect of a design/categorical variable changes the overall intercept of the model), and a stock-fishery interaction term which would change the intercept by fishery if significant. Thus, we now have 3 design (categorical) variables namely, stock-type (G), fishery (F), year (T), and a continuous variable (covariate) releases (S).

This type of analysis is very similar to an analysis of covariance (ANCOVA) which is a function of stock type, year, and fishery, and possible interactions (Zar 1995). Under the null hypothesis: $H_0: \beta_t = \gamma_f = \theta = \kappa = \phi = \omega_f = 0$. Under H_A : $\beta_t \neq 0$ and/or $\gamma_f \neq 0$ and/or $\theta \neq 0$, and/or $\phi \neq 0$, and/or $\omega_f \neq 0$. In order to analyze an under-dispersed

dataset, the F-test was used (Dr. Loveday Conquest, School of Fisheries and Aquatic Sciences, University of Washington, Seattle 98195, USA).

2.3 RESULTS

Oregon Coast: Results indicated that ocean- and stream-type Chinook follow similar migration pathways (Figure 2.2 a). Both groups were recovered in all areas sampled. However, ocean-type Chinook were recovered at lower rates than stream-type Chinook salmon in areas close to the natal region, implying either a deeper ocean migration (Quinn 2005) or an off-shore migration for ocean-type Chinook salmon near Washington and Oregon. This pattern also implies that, for Oregon coast Chinook, stream-type fish are prevalent in larger numbers on the coastal shelf than ocean-type fish, in contrast to the prediction. When testing for differences using the two models (Table 2.3 and Table 2.4) all design (categorical) variables, namely year, area and stock type (group), were significant, as were group-area interactions, implying that these fish have different recovery rates in these fisheries. Regardless, the two types of Chinook salmon were recovered in similar areas of the ocean, and exhibited similar migrations across the shelf (evident from Figure 2.2(a)). These results support the hypothesized migration patterns (Figure 2.6), and are contrary to Healey's hypothesis indicating a similar pattern of recovery for both ocean and stream-type Chinook salmon.

Lower Columbia (Oregon side): Both ocean- and stream-type Chinook were recovered from the lower Columbia River (primarily the Willamette and lower Columbia tributaries like Big Creek) in all ocean areas. However, ocean-type Chinook do not migrate as far north as stream-type Chinook (Figure 2.2 b) from the lower Columbia River on the Oregon side. Stream-type Chinook were recovered in small

numbers in all areas, but primarily in terminal fisheries. Tables 2.3 and Table 2.4 indicated that all design (categorical) variables were significant, though stock type-area interactions were marginally significant in the log-linear model ($p=0.06$). The obvious differences in distribution patterns (Figure 2.2(b)) between stock types support Healey's hypothesis (1983), although some stream-type fish were recovered on the coastal shelf (Figure 2.2 (b)). Hypothesized migration patterns for ocean- and stream-type Chinook (Figure 2.3) indicated that stream-type fish exhibit a more northern migration route than that utilized by ocean-type Chinook salmon.

Lower Columbia River (Washington side): Both ocean- and stream-type Chinook were recovered from the lower Columbia River (primarily the Cowlitz, Kalama, and Lewis River and tributaries) in all ocean areas at similar rates (Figure 2.2(c)). Stream-type and ocean-type Chinook were recovered at different rates in northern areas (Alaska and northern British Columbia). Both groups were recovered at equal rates in all other ocean areas (Figure 2.2 (c)). All design (categorical) variables were significant for this region (Table 2.3 and Table 2.4) including area-stock type interactions. Migration pathways of the two types of Chinook salmon thus overlap for fish from this region of the Columbia River (Figure 2.3) contradicting Healey's hypothesis again.

Upper Columbia River: Chinook salmon from the upper Columbia River showed different ocean and freshwater recovery patterns (Figure 2.2(d)). The results from this region indicate an off-shelf migration for stream-type Chinook versus coastal shelf migrations for ocean-type Chinook salmon, supporting the hypothesis that Healey presented (1983). All design (categorical) variables were significant although stock

type was only marginally significant ($p=0.06$) in the log-linear model (Table 2.3). The stock-area interaction was highly significant (Table 2.3), implying differences in stock recovery patterns by area. It is evident from the histogram (Figure 2.2(d)) that almost all recoveries of stream-type Chinook salmon were in terminal areas, whereas ocean-type fish were recovered in all ocean areas from Alaska to the Columbia River.

Accordingly, stream-type Chinook salmon ocean migrations are shown in Figure 2.4 as occurring off the shelf, whereas ocean-type fish are shown in the figure to follow the shelf.

Snake River: Snake River fish showed similar recovery and migration patterns as those from the upper Columbia River. Few stream-type fish were recovered in ocean areas (Figure 2.2 (e)). All design (categorical) variables were significant ($p<0.05$) and the stock type-area interaction was significant as well (Table 2.3 and Table 2.4). These fish also conformed to Healey's hypothesis (1983) in which stream-type fish migrate back to the natal river by following an offshore path whereas ocean-type Chinook follow a migration pathway along the coastal shelf (Figure 2.4).

Lower Fraser River: Fraser River fish appeared to follow Healey's (1983) hypothesis. Lower Fraser River stream-type Chinook salmon (Figure 2.2 (f)) appeared to follow an open ocean migration pathway, being recovered off the west coast of Vancouver Island and in the Strait of Juan de Fuca on their return migration. Ocean-type fish, on the other hand, followed a coastal shelf migration that splits between Georgia Straits and the west coast of Vancouver Island on their return migration (Figure 2.5). All design (categorical) variables were significant in the log-linear model (Table 2.3) although all

were not significant in the log-transformed Poisson model (Table 2.4). However, area (categorical), stock type (categorical), and stock-area interaction were significant (Table 2.4).

Upper Fraser River: These populations also showed distributions that were consistent with Healey's (1983) hypothesis; stream-type fish displayed an offshore migration pathway whereas ocean-type fish were closer to the coastal shelf. The histograms (Figure 2.2(g)) indicate that most recoveries (75%) were in terminal areas for stream-type, with some ocean recoveries off Vancouver Island and Washington. All design (categorical) variables are significant in the log-linear model (Table 2.3) and stock type-areas interactions (Table 2.4) are significant in the Poisson model. Migration pathways (Figure 2.5) indicate that stream-type Chinook migrate along the coastal shelf for some portion of their adult life. The ocean-type Chinook have a clear shelf migration pattern with a large number encountered in southeast Alaska, northern British Columbia and the west coast of Vancouver Island.

Northern British Columbia: The migration pathways of northern British Columbia Chinook salmon overlapped significantly in southeast Alaska and northern BC for both types of Chinook salmon (Figure 2.2 (h)). While the stock type and stock type-area interactions were non-significant terms in the log-linear model (Table 2.3), the stock type was marginally significant ($p=0.06$) and stock type-area interactions are significant in the Poisson response model (Table 2.4). It is evident that these fish exhibited different recovery rates in these areas by stock type. Their migration pathways overlapped to a large extent (Figure 2.6), with a migration along the shelf by

ocean-type Chinook and a shelf, then open-ocean then back to shelf pathway by the stream-type Chinook.

Aggregated Results from the Pacific Northwest

When aggregated over space and time, distinct patterns in the data emerged (Figures 2.2). As suggested by Healey (1991), there was a clear distinction between recovery patterns of stream- and ocean-type Chinook salmon from the upper Columbia and Snake rivers (Figure 2.2(d) and 2.2(e)), and to some extent the lower and upper Fraser River (Figure 2.2 (f) and 2.2 (g)) by stock type. The data from the upper Columbia and Snake rivers support the hypothesis that stream-type fish have an offshore distribution and so were more often recovered in terminal areas, whereas ocean-type fish are more often caught on the continental shelf. However, the distributions of Fraser River tag recoveries exhibited more overlap (Figure 2.2 (f) and 2.2(g)), and some coastal shelf migrations of the stream-type Chinook salmon in these systems cannot be ruled out especially for the mature adults returning to the river. Specifically, 25% of the recoveries from upper Fraser River stream-type fish were from fisheries operating on the coastal shelf. These results contrast with those of the upper and lower Columbia River populations. In contrast to the upper Fraser populations, 15% of the lower Fraser River stream-type fish recoveries were from the coastal shelf versus 85% in terminal areas (Figure 2.4).

The data are summarized for the eight regions shown in Figure 2.2 and discussed above (the Oregon coast, the lower Columbia River in Oregon, the lower Columbia River in Washington, the upper Columbia River, the Snake River, the lower

Fraser River, the upper Fraser River, and northern British Columbia). Both stream- and ocean-type Chinook salmon from the lower Columbia River were found in all recovery areas, indicating that the ocean distributions of the types did not differ. The patterns shown by the lower Columbia River fish were similar to those observed for the Oregon coast and northern British Columbia fish. However, the ocean distribution of the two types differed for the upper Columbia and Snake rivers, and the upper and lower regions of the Fraser River (to a certain extent). In the upper Columbia and Snake River systems, ocean recoveries were negligible (stream-type fish were only recovered beyond the continental shelf), whereas ocean-type Chinook salmon were found in all areas along the shelf. For the lower and upper Fraser River, 15% and 25%, respectively, of stream-type recoveries were observed in ocean areas, with most recoveries occurring on the west coast of Vancouver Island and Georgia Straits for the lower Fraser, and the west coast of Vancouver Island and northern BC for the upper Fraser stream-type Chinook.

Summaries of the outputs from equation 2.2 and equation 2.4 are shown in Tables 2.3 and 2.4. In each of the regions, stock was a significant variable, indicating that the proportion of recoveries by stock type differed among regions, although they still occurred in the regions (and in some cases to a large extent, as is evident in Figure 2.2).

In some cases (e.g., Oregon coast and Cowlitz River; Table 2.3 and Table 2.4) the area-stock interaction was not significant, indicating that the main effect of the stock type (stream- or ocean-type) was significant with respect to the number of

recoveries by area, but this effect was not different from the average effect by area (i.e. the ratio of the recovery patterns across areas by stream- or ocean-type remains the same across most regions). Thus, the insignificance of the stock-area interaction means only that the ratio between the two stock types was found to be constant over all regions where these stocks are recovered.

Examination of the residual diagnostics of the fit for each of the regions and stock types revealed no apparent trend or bias for either the log-linear model (Appendix 2.1) or the log-transformed Poisson response model (Appendix 2.2), although most of the diagnostics (quartile plots) suggested a concentration of data towards the center of the distribution and less at the tails (i.e. platykurtic). This result was expected, as the data were largely zeros with few recoveries in some years and fisheries, and numerous in other years and fisheries. In addition, the log-response model displayed some clear residual patterns in different clusters. These patterns did not appear when a Poisson response model was used. The latter method was probably the most appropriate way to analyze the data because there were so many zeros (Cormack and Skalski 1992). Regardless of the model chosen, in all cases the log-linear model indicated a significant stock and stock-area interaction effect, implying that there was a difference in recoveries by life-history type that varied by region. In the case of the Poisson response model, the stock effect was almost always significant, and the stock-area interaction effect was always significant ($p < 0.05$), implying that recovery patterns differed by life history type in all areas analyzed. The stock effects were not significant in the upper Fraser River, northern BC, and the upper Columbia

River populations in the Poisson response model. However, in all three cases the stock-area interaction was highly significant, indicating a difference in distribution patterns (Figure 2.2). The only other case that showed no difference in area-stock recovery patterns once the main effect (i.e., life history type) was included in the model was the lower Columbia River (Cowlitz River) where the distributions of the two life history types overlapped considerably (Figure 2.2).

When a simple test of proportions (Zar 1995) was used on recoveries by year using release size as the denominator, proportions of recoveries by area were almost always significantly different by area across stock types. I do not to present these results as they are essentially the same results as those displayed in Tables 2.3 and 2.4 using generalized Linear Models (GLM).

2.4 DISCUSSION

This study tested the following hypotheses: i) juvenile life history type affects marine distribution (inferred from recovery data) regardless of where the fish entered the ocean (the alternative is that the two life history types have the same distribution in each region), and ii) there is a difference in marine distribution between life history types which varies among regions of origin. The results clearly supported both hypotheses. In some cases (notably the Cowlitz River) ocean- and stream-type Chinook salmon were recovered at similar rates in all ocean areas, but in populations from the interior (the upper Columbia, Snake, and upper Fraser rivers) there was a marked difference in marine distributions between life history types. In some cases there was a large difference in recovery pattern that mirrors differences in life history, whereas in other cases the differences were small (though statistically significant) where both

stream-type and ocean-type Chinook were recovered in all areas, but at different rates. The genetic basis for salmon migration patterns at sea indicated here is consistent with work on Atlantic salmon, *Salmo salar*, in the Baltic Sea (Kallio-Nyberg and Koljonen 1999; Kallio-Nyberg et al. 1999, 2000) and with previous but less extensive work on Chinook salmon (Pascual and Quinn 1994).

Given the large number of releases and replicates (about 200,000 tagged fish of each life history type on average over 10 years) it was not surprising that differences were detected once the recoveries were aggregated by area. However, it is particularly important to note that substantial numbers of stream-type fish were recovered in some of the same geographical areas where ocean-type fish were recovered. This result was not consistent with Healey's (1983) hypothesis that ocean-type fish have a more coastal distribution whereas stream-type fish are farther off-shore, and that the two types will have correspondingly different ocean migration pathways at maturation.

The data from the continental interior (upper Fraser, upper Columbia, and Snake rivers (Figures 2.4 and 2.5)) supported Healey's (1983) hypothesis. Healey's analysis had to rely on sparse data because standardized surveys using coded wire tags were only implemented coast-wide in the late 1970s and early 1980s (Lapi et al. 1990, Johnson 1990). Prior studies of ocean migration (Aro 1972, Aro 1973) tagged fish in the ocean and had limited knowledge of stock origin. In contrast, this approach (pair-wise analysis of stocks with both stream and ocean types from different regions) was both more powerful and had the benefit of many more recoveries.

In contrast to the results with interior populations, both stream- and ocean-type Chinook salmon from the lower Columbia River (Cowlitz River), lower Fraser River, Oregon coast, and northern BC were recovered in similar areas (Figures 2.3 – 2.6). Interestingly, ocean-type Chinook salmon from the lower Fraser River (Figure 2.5) were evenly distributed between the Strait of Georgia and the west coast of Vancouver Island, but the ocean-type populations from the upper Fraser River, and stream-type Chinook salmon from both the lower and upper Fraser River, were rarely recovered from the Strait of Georgia. These latter populations appear to follow a shelf migration, followed by a wide ocean turn into the North Pacific, and then exhibit a coastal shelf distribution pattern west of Vancouver Island on their return passage. In years of anomalous ocean conditions (e.g., El Niño in 1992) some of these fish were recovered off the northern coast of British Columbia, suggesting a shift in distribution in response to ocean conditions.

These patterns of population-specific recoveries and, by implication, ocean distributions, have considerable implications for management. For example, some stream-type Chinook populations on the middle and upper Fraser River are of conservation concern because they are less productive than lower Fraser stream-type and ocean-type Chinook on the Fraser (Parken et al. 2008). Based on Figure 2.2 (g), 25% or more of the upper Fraser River population may be intercepted by ocean fisheries (fisheries operating west of Vancouver Island and northern BC caught 80% of these fish at sea, accounting for a 20% overall harvest impact on this stock). Fisheries agencies have been regulating in-river fisheries in the Fraser during the season by

determining upper river population abundance from a test fishery in the lower river.

While past assumptions of negligible ocean catch of stream-type populations have caused management to focus on in-river fisheries, these results demonstrate that ocean catch is significant as well. However, there has been very little ocean fishery management for these depleted stream-type Chinook salmon populations (Parken et. al. 2008).

Why were the ocean migration patterns of the two juvenile life history types very different in pairs of populations from upriver regions but less distinct in the pairs from lower rivers or coastal areas? I hypothesize that the degree of overlap in spawning may play a role by regulating interbreeding between forms. The lower river and coastal pairs of populations (Cowlitz River, lower Columbia River, Oregon coast, lower Fraser River and northern BC) partially overlap in their ocean distributions and their spawning times also overlap (Narum et al. 2004, Waples et al. 2004). This overlap would allow some genetic exchange between the two life history types. In contrast, populations farther upstream seem to be more specialized in terms of their breeding location, timing, and life-history patterns. In the Snake, upper Columbia and upper Fraser rivers there is little or no overlap between the two types in their ocean recovery distributions (Figure 2.4 and Figure 2.5), and little overlap in spawning timing that would allow gene flow between the two types.

Brannon et al. (2004) hypothesized that the evolution of stream-type and ocean-type Chinook salmon in different parts of the Columbia River was mainly influenced by temperature. Stream-type juveniles emerge in cooler, more growth-limited

environments in the upper parts of the river system and cannot grow large enough to overcome size-selective marine mortality in their first year of life, whereas ocean-type juveniles emerge earlier and grow more quickly in the lower elevations. Ocean-type fish in the upper reaches of the river both spawn and rear in different areas than their stream-type counterparts, and move into larger expanses of water (like Hanford reach on the upper Columbia River mainstem) where they feed voraciously in May and June before reaching a threshold size for migrating out to the ocean.

Stream-type Chinook salmon migrate to sea as juveniles at a larger body size than their ocean-type conspecifics, they move more quickly through the estuary (Dawley et al. 1986; Ledgerwood et al 1991), and seem to travel farther north initially. Some stream-type Chinook salmon from the Snake and upper Columbia Rivers have been detected with acoustic tags near the Aleutian Islands, Alaska within a period of months after entering the ocean (Dr. David Welch, Kintama Research, Nanaimo, BC, personal communication). These differences in marine migration and distribution patterns may be the key to understanding complex variation within and among years in survival of stream- and ocean-type populations, including some of these ESA-listed and depressed stocks in the upper Columbia and the Fraser rivers.

Chinook salmon have complex life history trajectories and have evolved to colonize and persist in numerous areas throughout northern California, Oregon, Washington, British Columbia and Alaska, as well as Russia. Due to the broad array of geographical regions and habitat types utilized by these fish, growth rates and timing/size of seaward migration vary greatly, with a mix of environmental and genetic

regulation (Quinn 2005). In some cases these juvenile differences are linked to differences in marine distributions but in other cases they are not. Populations that are genetically more similar are also more similar in migration patterns. This hypothesis is consistent with studies (Narum et al. 2004, Waples et al. 2004) indicating considerable gene flow between the two life-history types in the lower Columbia, but minimal gene flow between populations in the upper Columbia and upper Fraser rivers. As is evident in most ecology there is no standard that is followed in all types of the species; life-history behavior is quite complex in Chinook salmon, and thus Healey's (1983) hypothesis is not uniformly correct in all areas, but is partially true for highly specialized populations as seen in the upper Columbia, Fraser, and Snake rivers.

Acknowledgements

I thank David Graves (CRITFC) for his help in mapping some of the recovery data in Figures 2.3, 2.4, 2.5 and 2.6, and NOAA for funding this research.

List of Tables

Table 2.1: Comparison of various life history and behavioral traits between North American ocean-type and stream-type Chinook salmon (based on Taylor 1990a, 1990b; Healey 1991).

Table 2.2: Locations where both stream-type and ocean-type stocks exist, and CWT data used to analyze the spatial distributions.

Table 2.3: ANOVAs showing results of equation 2 (log-linear model) applied to each of the particular areas.

Table 2.4: ANODEV showing results of equation 3 (Poisson Response models) applied to each of the particular areas

Table 2.1: Comparison of various life history and behavioral traits between North American ocean-type and stream-type Chinook salmon (based on Taylor 1990a, 1990b; Healey 1991, Roni and Quinn 1995).

Stream-type	Ocean-type
Dominant form in the northern part of the range in fresh water, and in the interior and at high elevation in the southern part of the ranges	Dominant form in the southern part of the range in fresh water, especially in lower elevation, coastal rivers
Juveniles reside in streams for about a year, including a winter, then migrate directly to the ocean in spring	Juveniles reside in streams for less than a year, migrating to sea shortly after emergence or after a few months in streams, with a broad distribution of migration timing from spring to early fall.
Larger in size as smolts (70-140 mm long) but smaller for their age	Smaller in size as smolts (50-100 mm long) but larger for their age
Migrate rapidly through estuaries, primarily in the open water	Longer period of estuarine residence (as individuals and as populations), primarily in nearshore habitats
Typically 2-4 years at sea, about 1 year less than ocean-type from the region	Typically 2-4 years at sea, about 1 year more than stream-type from the region.
Enter the rivers in spring and summer months and reside in river to spawn in the early fall.	Enter rivers in late summer or early fall and spawn in late fall.

Table 2.2: Locations where both stream-type and ocean-type stocks exist, and CWT data used to analyze the spatial distributions

Region/Location	Hatchery Name	River	Brood Years	Ocean or Stream
Lower Columbia River, Washington Side	Cowlitz Fall	Cowlitz	1979-2000	Ocean
	Cowlitz Spring	Cowlitz	1979-2000	Stream
Lower Columbia River, Oregon side	Willamette	Willamette	1975-2000	Ocean
	LRH Tules	Big Creek	1976-2000	Stream
Upper Columbia River	Summers (Wells)	Upper Columbia	1975-2000	Ocean
	Leavenworth Spring	Upper Columbia/ Icicle/Yakima	1977-2000	Stream
Oregon Coast (North)	Cedar Creek	Nestucca River	77-81,91-00	Stream
	Salmon River	Salmon (Siletz).	1977-2000	Ocean
Snake River (Idaho)	Lyons Ferry Fall	Snake	84-90, 92, 94,98, 2000	Ocean
	Dworshak Hatchery	Clearwater	1977-2000	Stream
Northern Coastal British Columbia	Kitimat	Kitimat/Hersch Cr	1980-2000	Ocean
	Terrace Hatchery	Kitsumakalum R.	1979-2000	Stream
Upper Fraser River	Shuswap River ²	Shuswap River	1984-2000	Ocean
	Penny Creek ²	Dome Creek/James Creek	1984-2000	Stream
Lower Fraser River	Spius Creek ²	Nicola R/ Bonaparte/ Deadman/Coldwater	1984-2000	Stream
	Chilliwack Hatchery	Harrison R/Chilliwack	1981-2000	Ocean

² Recovery data on escapement for broodyears between 1997 and 2000 were applied to escapement data for all preceding years due to missing data prior to 1999 (Chuck Parken, Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC).

Table 2.3: ANOVAs showing results of equation 2 (log-linear model) applied to each of the particular areas

Lower Columbia (WA Side)

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			299	5322.8	
t (Year)	28	776.2	271	4546.6	4.4 <0.0001
f (Fishery/Area)	5	2715	266	1831.6	87.0 <0.0002
G (Stock type)	1	140.9	265	1690.7	22.6 <0.0003
G:f (Stock:Area)	5	67	260	1623.7	2.1 0.06

Lower Columbia (OR Side)

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			311	6075.2	
t (Year)	26	760.6	285	5314.6	6.0 1.31E-15
f (Fishery/Area)	5	2134.3	280	3180.3	87.8 < 2.2e-16
G (Stock type)	1	726.6	279	2453.6	149.5 < 2.2e-16
G:f (Stock:Area)	5	1121.9	274	1331.8	46.2 < 2.2e-16

Upper Columbia

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			269	8389.8	
t (Year)	25	1054.6	244	7335.2	8.4 < 2.2e-16
f (Fishery/Area)	5	2548.6	239	4786.7	101.3 < 2.2e-16
G (Stock type)	1	2297	238	2489.7	456.3 < 2.2e-16
G:f (Stock:Area)	5	1316.8	233	1172.9	52.3 < 2.2e-16

Snake

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			179	55	
t (Year)	18	587.9	161	49	6.8 2.71E-16
f (Fishery/Area)	5	1928.5	156	2993.3	80.4 < 2.2e-16
G (Stock type)	1	1713.3	155	1280	356.9 < 2.2e-16
G:f (Stock:Area)	5	560	150	720	23.3 < 2.2e-16

Lower Fraser

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			227	4566.9	
t (Year)	20	245.4	207	4321.5	1.6 0.04829
f (Fishery/Area)	5	2274.6	202	2046.9	60.5 < 2.2e-16
G (Stock type)	1	358.5	201	1688.4	47.7 6.81E-11
G:f (Stock:Area)	5	215	196	1473.5	5.7 5.98E-05

Upper Fraser

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			191	3389.4	
t (Year)	16	151	175	3238.4	1.2 0.3092
f (Fishery/Area)	5	910.9	170	2327.5	22.3 < 2.2e-16
G (Stock type)	1	312.2	169	2015.3	38.2 4.84E-09
G:f (Stock:Area)	5	675.9	164	1339.5	16.6 3.26E-13

North Central BC

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			251	7531.5	
t (Year)	21	140.9	230	7390.6	1.2 0.26559
f (Fishery/Area)	5	6084.5	225	1306.1	215.0 < 2e-16
G (Stock type)	1	4.4	224	1301.7	0.8 0.37726
G:f (Stock:Area)	5	62.3	219	1239.4	2.2 0.05527

Oregon Coast

	Df	Deviance	Resid. Df	Resid. Dev F	Pr(>F)
NULL			227	3238.4	
t (Year)	24	316.6	203	2921.8	2.1 0.004138
f (Fishery/Area)	5	1342.8	198	1579	41.7 < 2.2e-16
G (Stock type)	1	210.9	197	1368.1	32.8 3.94E-08
G:f (Stock:Area)	5	132.7	192	1235.4	4.1 0.001395

Table 2.4: ANODEV showing results of equation 3 (Poisson Response models) applied to each of the particular areas

Lower Columbia (WA Side)

Variable	Df	Deviance	Resid Df	Resid Dev	F	p>F
NULL	299	729919				
S (Releases)	1	73328	298	656591	33.3	<0.0001
t(Year)	28	339081	270	317511	10.3	<0.001
f (Fishery/Area)	5	254047	265	63463	212.2	<0.0001
G (Stock Type)	1	38590	264	24873	409.6	<0.0001
S:G (Releases:Stock)	1	1217	263	23656	13.5	<0.001
f:G (Area:Stock)	5	723	258	22933	1.6	0.31

Lower Columbia (OR Side)

Variable	Df	Deviance	Resid. Df	Resid. Dev	F	p>F
NULL	311	1023544				
S (Releases)	1	335597	310	687947	151.2	<0.0001
t(Year)	26	121990	284	565956	2.4	0.006
f (Fishery/Area)	5	425863	279	140093	169.6	<0.0001
G (Stock Type)	1	35912	278	104181	95.8	<0.0001
S:G (Releases:Stock)	1	2440	277	101741	6.6	0.02
f:G (Area:Stock)	5	43894	272	57847	41.3	<0.0001

Upper Columbia

Variable	Df	Deviance	Resid. Df	Resid. Dev	F	p>F
NULL	269	171002				
S (Releases)	1	74530	268	96472	207.0	<0.0001
t(Year)	25	29939	243	66532	4.4	<0.0001
f (Fishery/Area)	5	42826	238	23706	86.0	<0.0001
G (Stock Type)	1	463	237	23243	4.7	0.06
S:G (Releases:Stock)	1	2.70E-01	236	23243	0.003	1.92
f:G (Area:Stock)	5	15661	231	7581	95.4	<0.0001

Snake

Variable	Df	Deviance	Resid. Df	Resid. Dev	F	p>F
NULL	179	48028				
S (Releases)	1	20	178	48008	0.1	1.5
t(Year)	18	10826	160	37182	2.6	0.002
f (Fishery/Area)	5	28910	155	8272	108.3	<0.0001
G (Stock Type)	1	1808	154	6464	43.1	<0.0001
S:G (Releases:Stock)	1	3	153	6461	0.071	1.58
f:G (Area:Stock)	5	3464	148	2998	34.2	<0.0001

Lower Fraser

Variable	Df	Deviance	Resid Df	Resid Dev	F	p>F
NULL	227	251959				
S (Releases)	1	1481	226	250478	1.3	0.51
t(Year)	20	23708	206	226770	1.1	0.7
f (Fishery/Area)	5	175738	201	51031	138.4	<0.0001
G (Stock Type)	1	10755	200	40276	53.4	<0.0001
S:G (Releases:Stock)	1	650	199	39626	3.3	0.14
f:G (Area:Stock)	5	10500	194	29127	14.0	<0.0001

Upper Fraser

Variable	Df	Deviance	Resid Df	Resid Dev	F	p>F
NULL	191	17008.8				
S (Releases)	1	1512.7	190	15496.1	18.5	<0.0001
t(Year)	16	1046	174	14450.1	0.8	0.999
f (Fishery/Area)	5	7772.7	169	6677.4	39.3	<0.0001
G (Stock Type)	1	7.9	168	6669.5	0.2	0.999
S:G (Releases:Stock)	1	101.1	167	6568.4	2.6	0.21
f:G (Area:Stock)	5	3507.7	162	3060.8	37.1	<0.0001

Northern BC

Variable	Df	Deviance	Resid Df	Resid Dev	F	p>F
NULL	251	45415				
S (Releases)	1	760	250	44655	4.3	0.07
t(Year)	21	5737	229	38918	1.6	0.08
f (Fishery/Area)	5	28806	224	10113	127.6	<0.0001
G (Stock Type)	1	216	223	9897	4.9	0.06
S:G (Releases:Stock)	1	121	222	9776	2.7	0.2
f:G (Area:Stock)	5	4541	217	5235	37.6	<0.0001

Oregon Coast

Variable	Df	Deviance	Resid Df	Resid Dev	F	p>F
NULL	227	182548				
S (Releases)	1	58132	226	124416	105.6	<0.0001
t(Year)	24	21053	202	103363	1.7	0.05
f (Fishery/Area)	5	92620	197	10743	339.7	<0.0001
G (Stock Type)	1	1528	196	9215	32.5	<0.0001
S:G (Releases:Stock)	1	0.2226	195	9215	0.005	0.99
f:G (Area:Stock)	5	2250	190	6965	12.3	<0.0001

List of Figures

Figure 2.1: Areas used in the analysis where stream-type and ocean-type Chinook occur in close proximity

Figure 2.2: Histograms indicating proportion of recoveries by ocean or stream type Chinook recoveries in the highseas, southeast Alaska (AK), Northern BC (NCBC), West coast of Vancouver island (WCVIGST), Washington and Oregon (WAOR) and terminal areas aggregated by region.

Figure 2.3: Recovery patterns and migration pathways of lower Columbia River Chinook salmon (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

Figure 2.4: Recovery patterns and migration pathways of upper Columbia River and Snake River Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

Figure 2.5: Recovery patterns and migration pathways of Fraser River Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

Figure 2.6: Recovery patterns and migration pathways of northern BC and Oregon coast Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

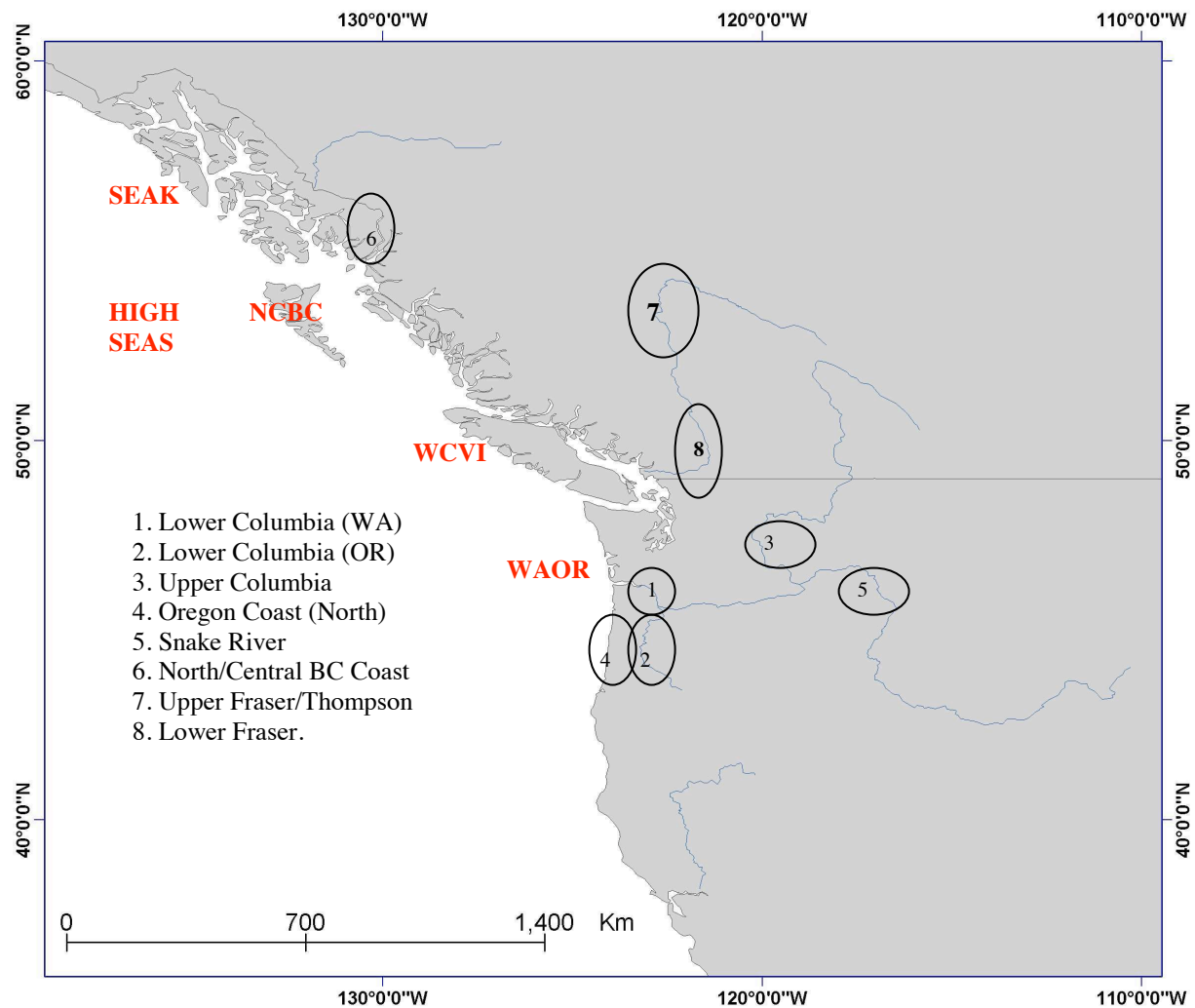


Figure 2.1: Areas where stream-type and ocean-type Chinook occur in close proximity as well as the regions that were used in the analysis.

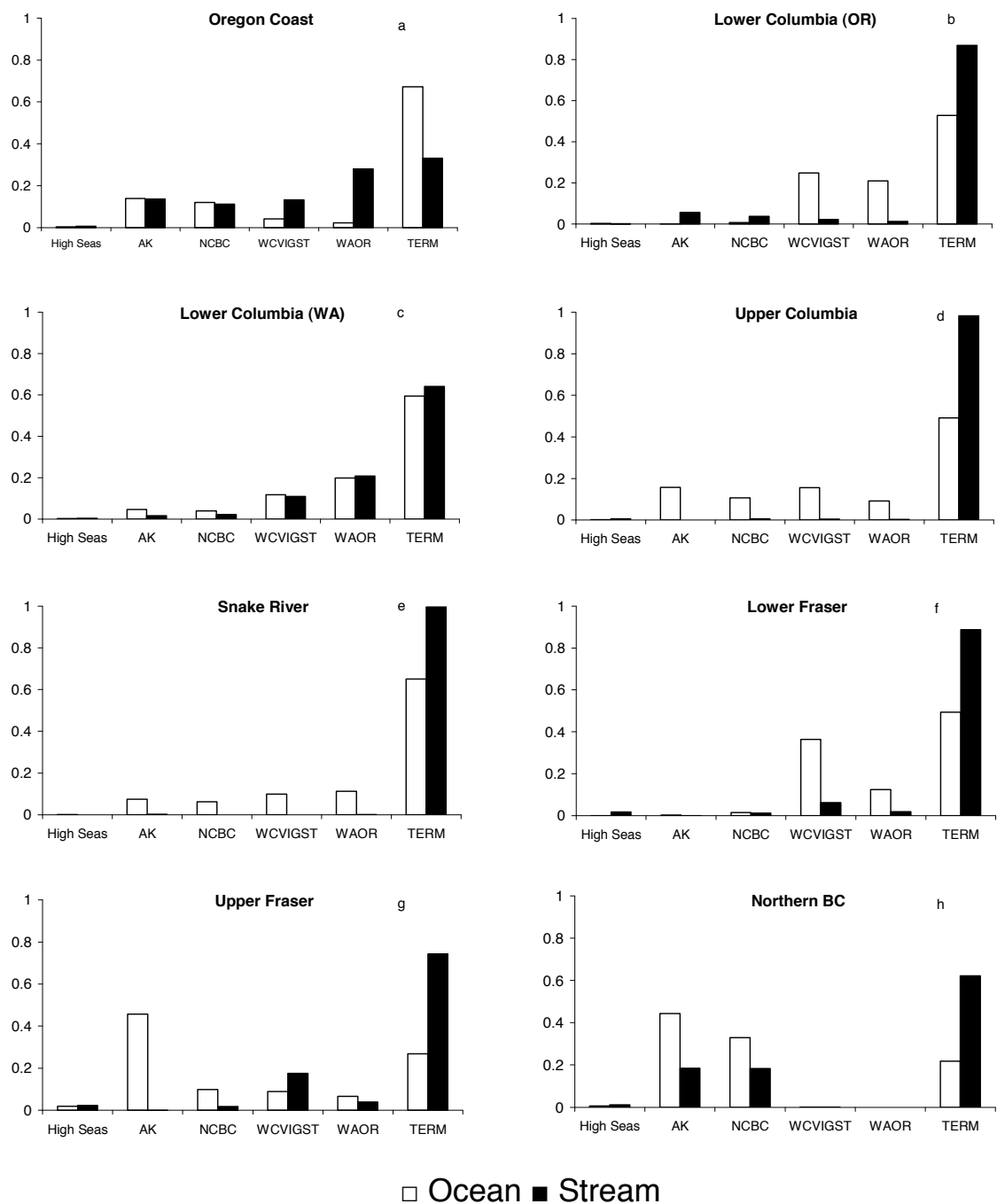


Figure 2.2: Histograms indicating proportion of recoveries by ocean or stream type Chinook recoveries in the Highseas, southeast Alaska (AK), Northern BC (NCBC), West coast of Vancouver island (WCVIGST), Washington and Oregon (WAOR) and terminal areas aggregated by region.

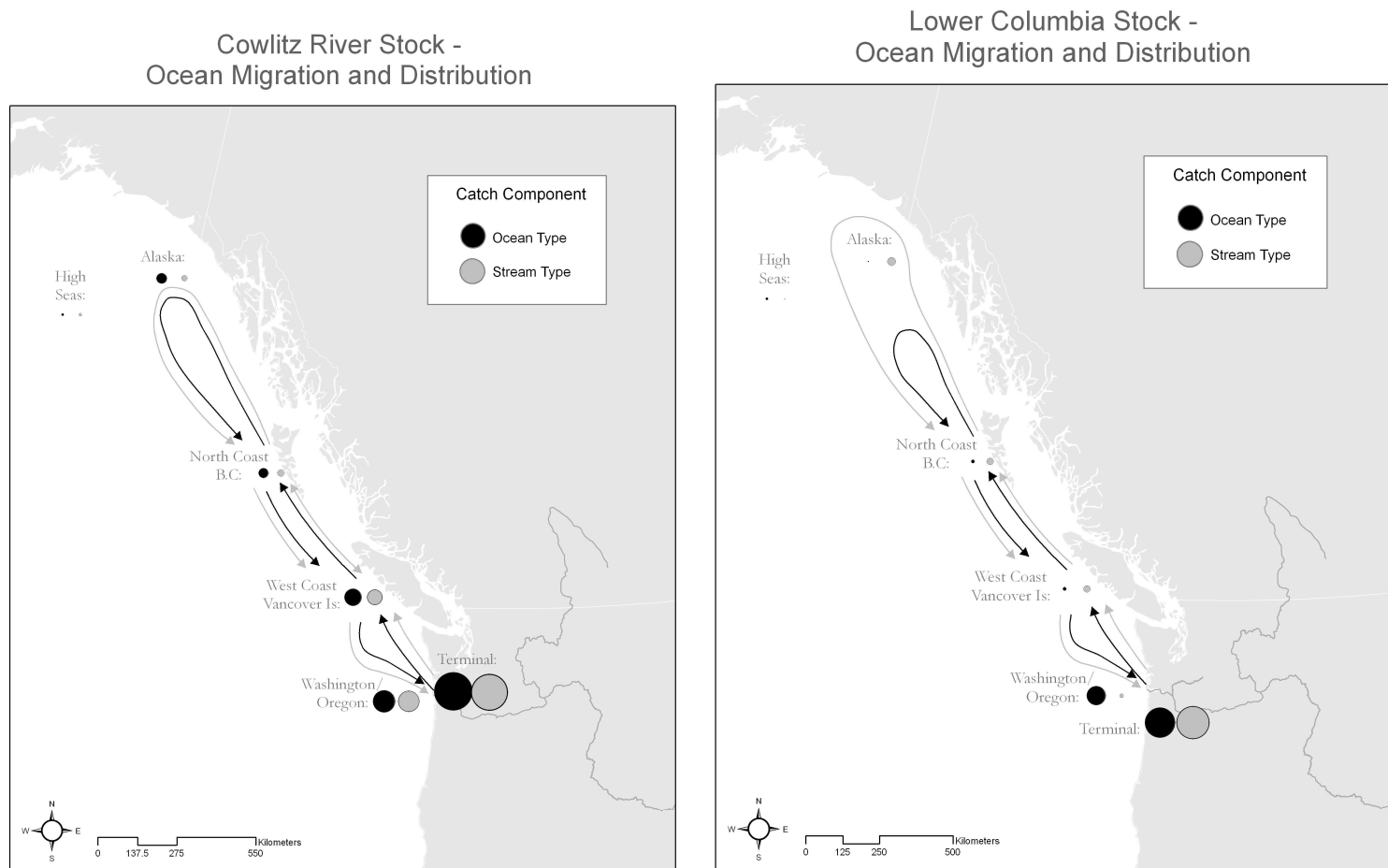


Figure 2. 3: Recovery patterns and migration pathways of lower Columbia River Chinook salmon (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

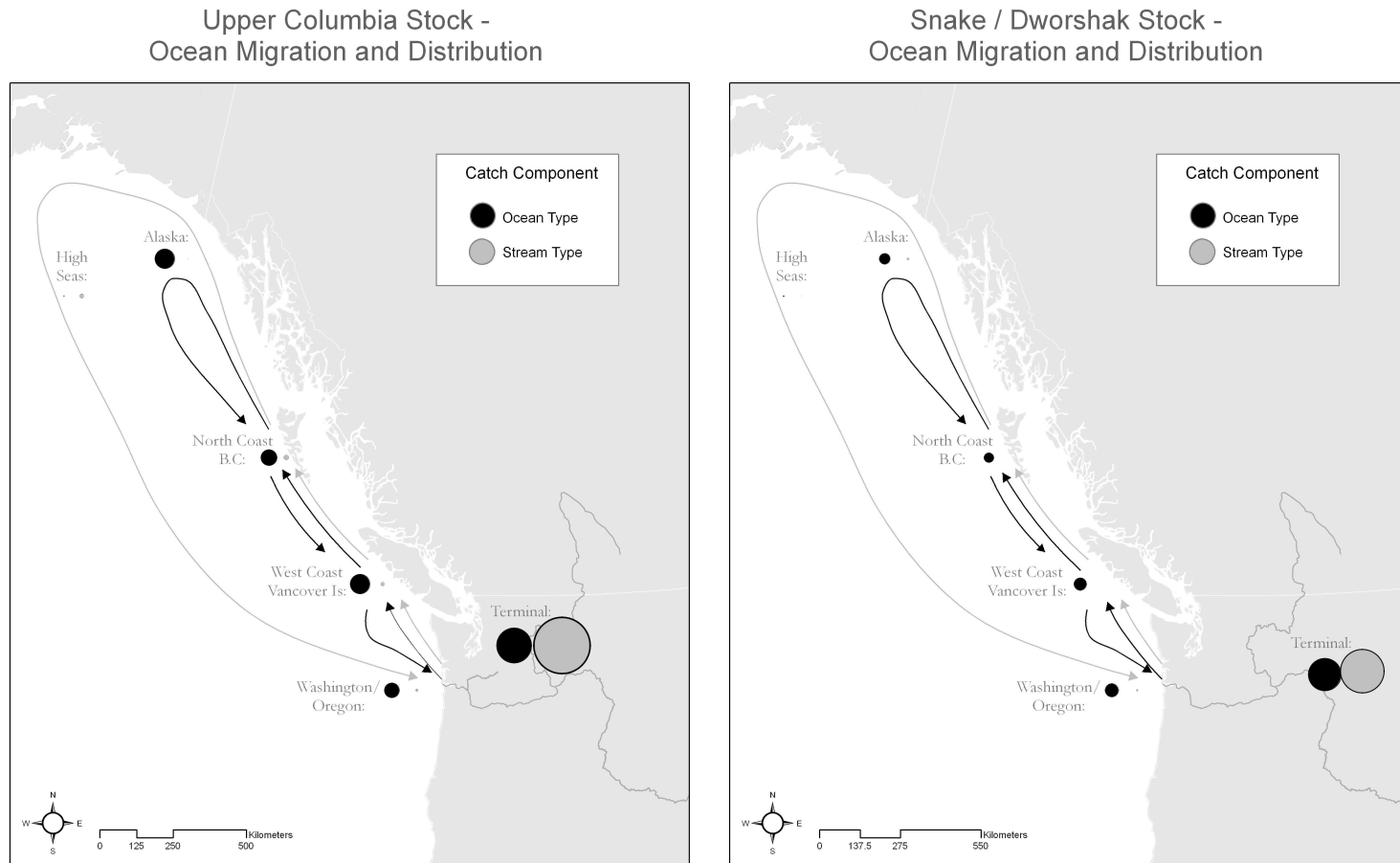


Figure 2.4: Recovery patterns and migration pathways of upper Columbia River and Snake River Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

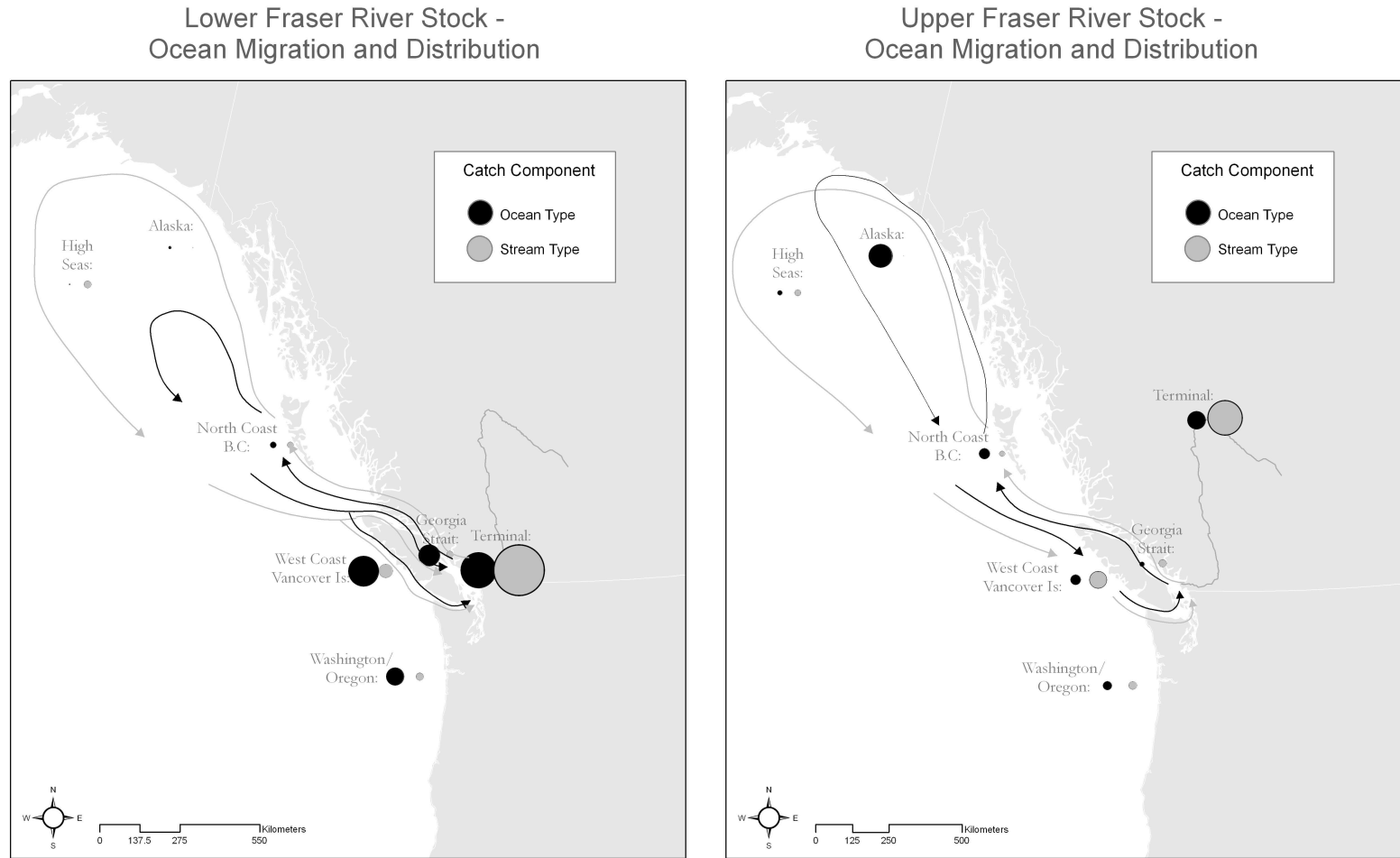


Figure 2.5: Recovery patterns and migration pathways of Fraser River Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

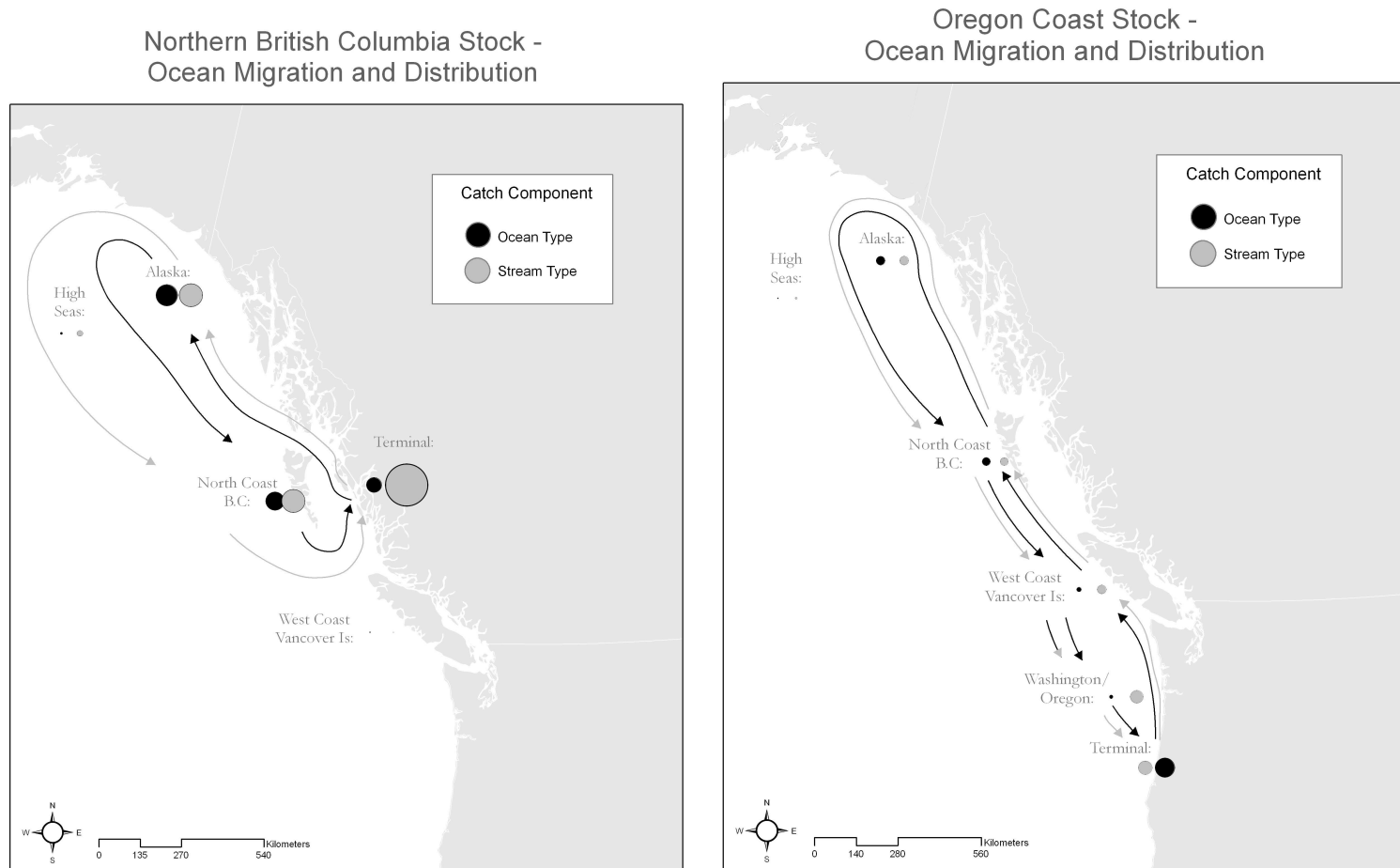


Figure 2.6: Recovery patterns and migration pathways of northern BC and Oregon coast Chinook (arrows showing upstream and downstream migration). Magnitude of the circle indicates proportion of overall recoveries in a particular area

APPENDIX 2.1: RESIDUAL DIAGNOSTICS OF THE LOG-LINEAR MODEL FIT BY AREA

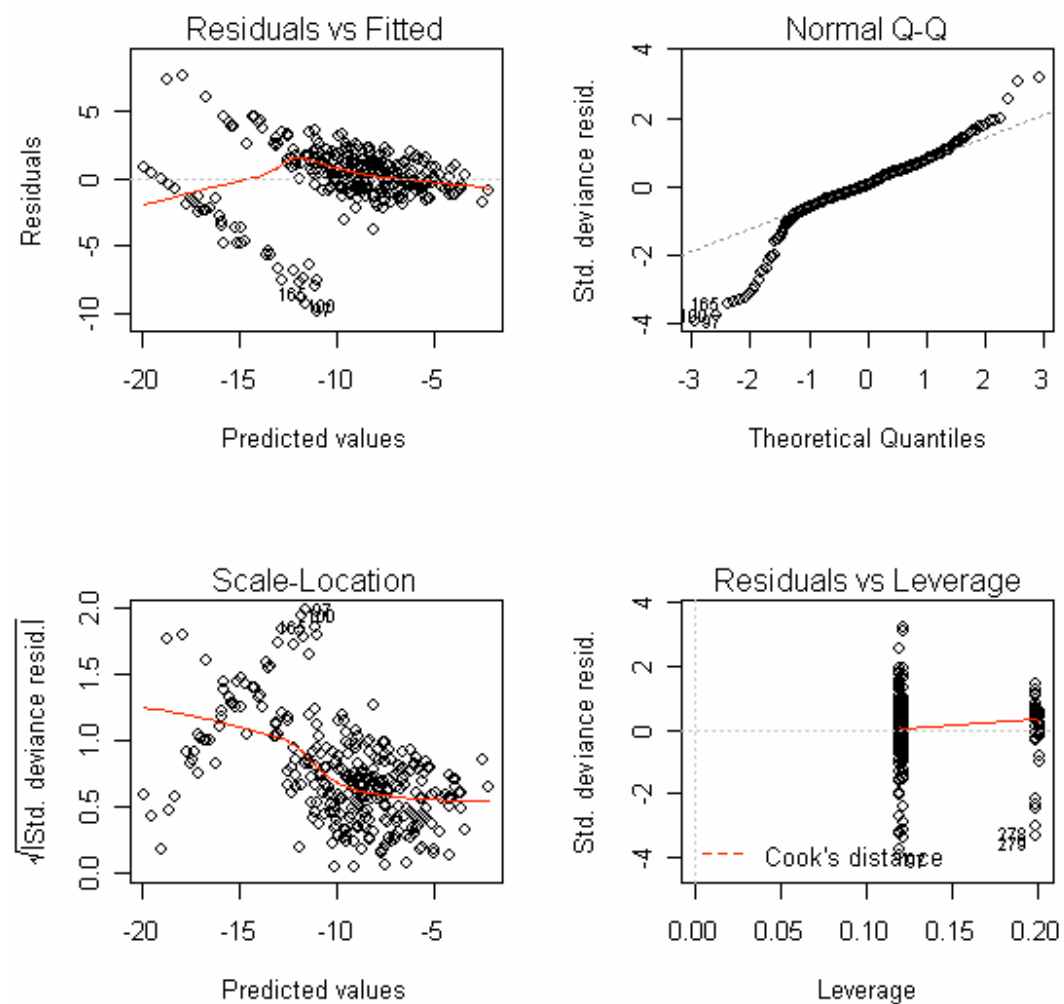


Figure 2.1A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the Lower Columbia (WA Side).

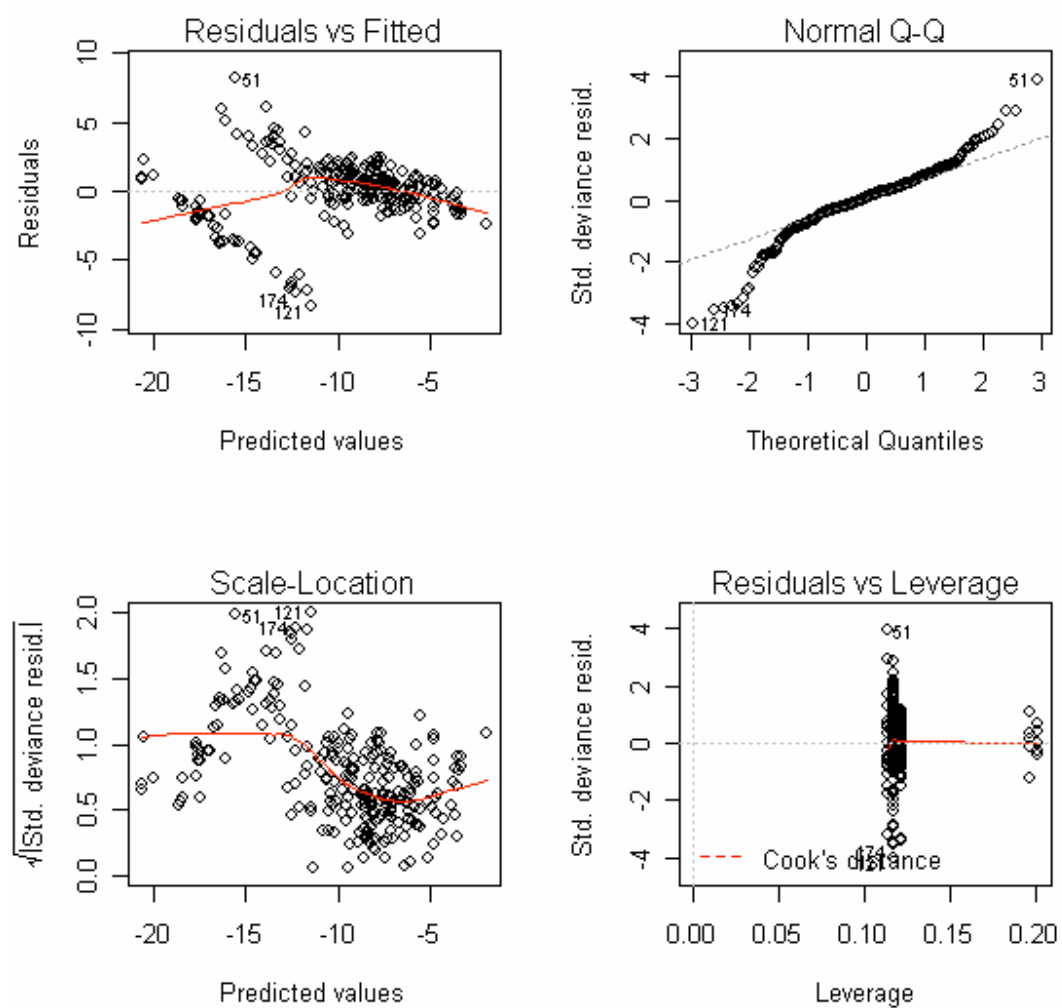


Figure 2.2A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the Lower Columbia (OR Side).

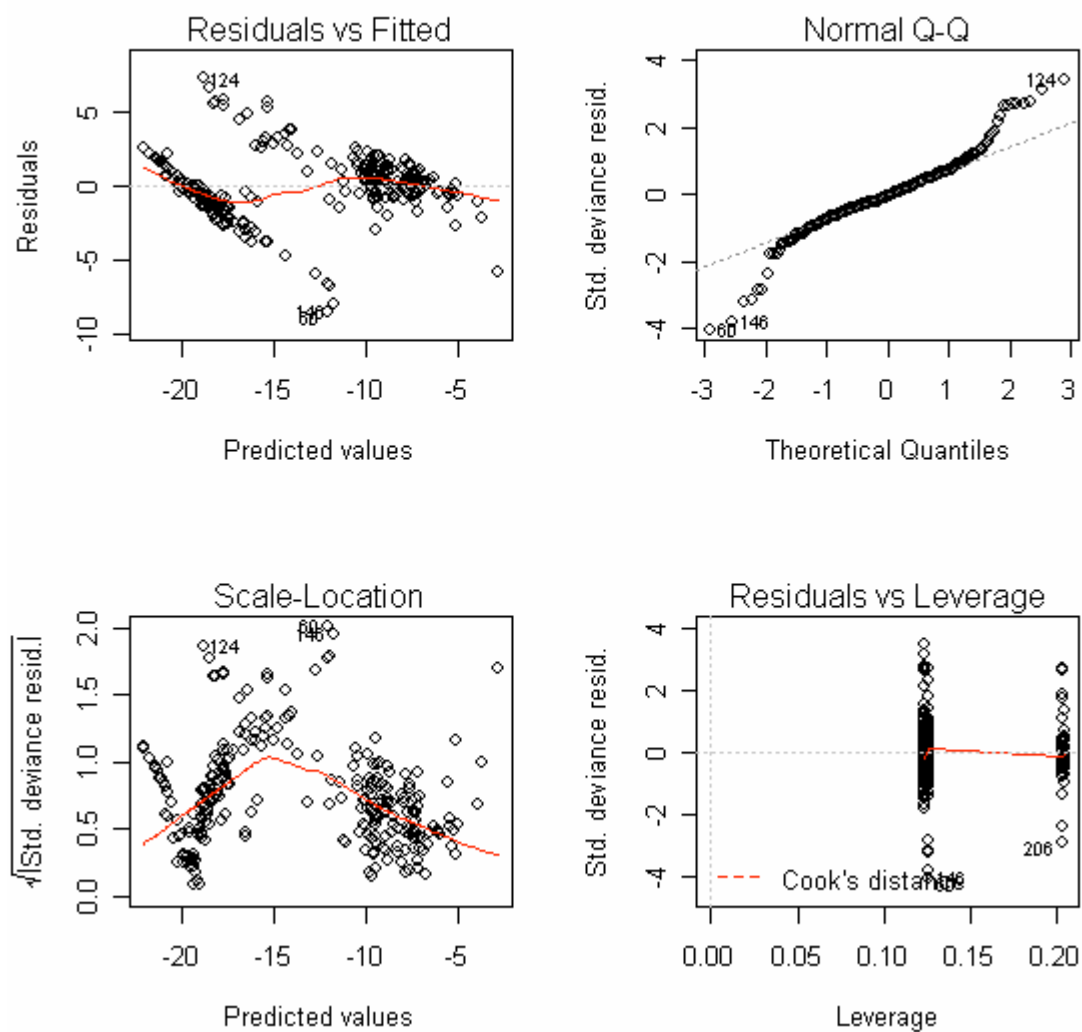


Figure 2.3A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the Upper Columbia.

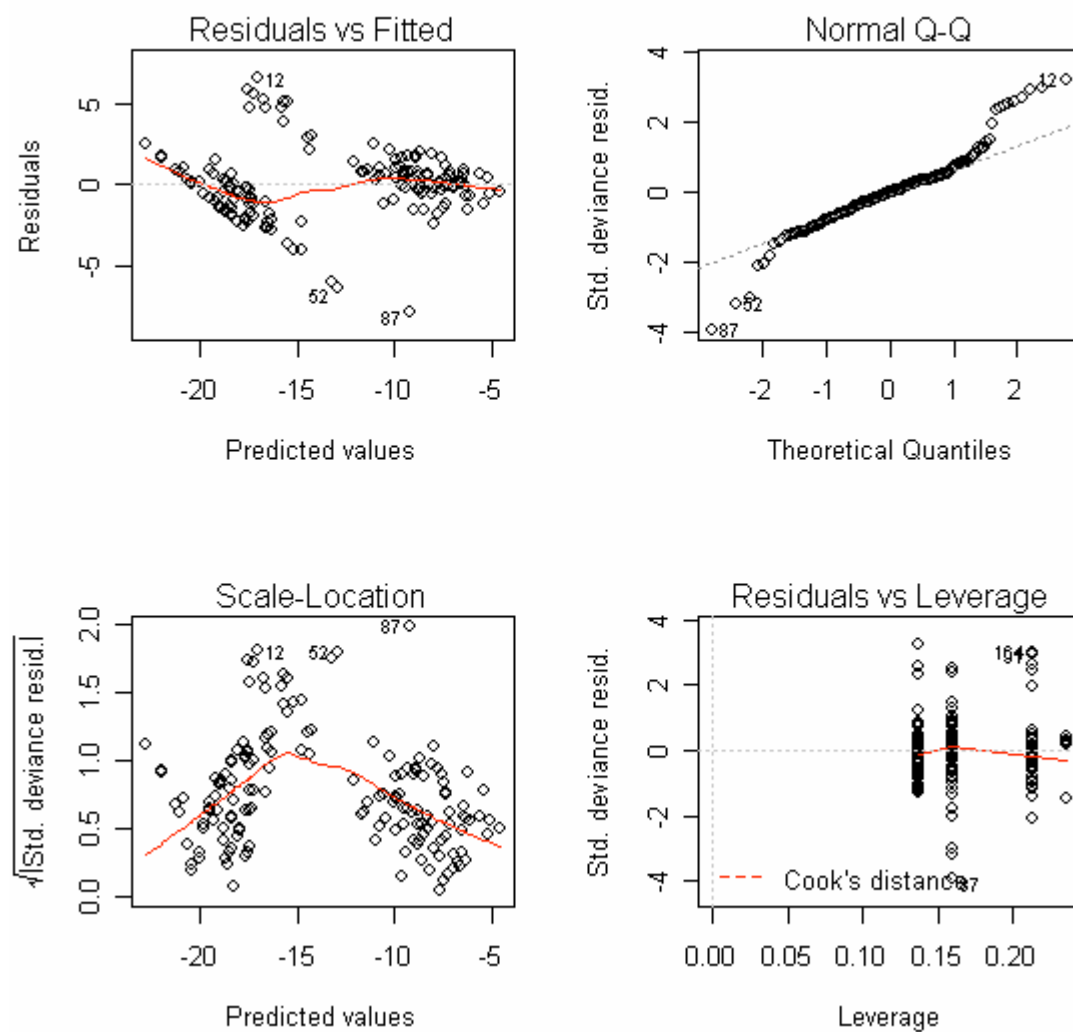


Figure 2.4A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the Snake River.

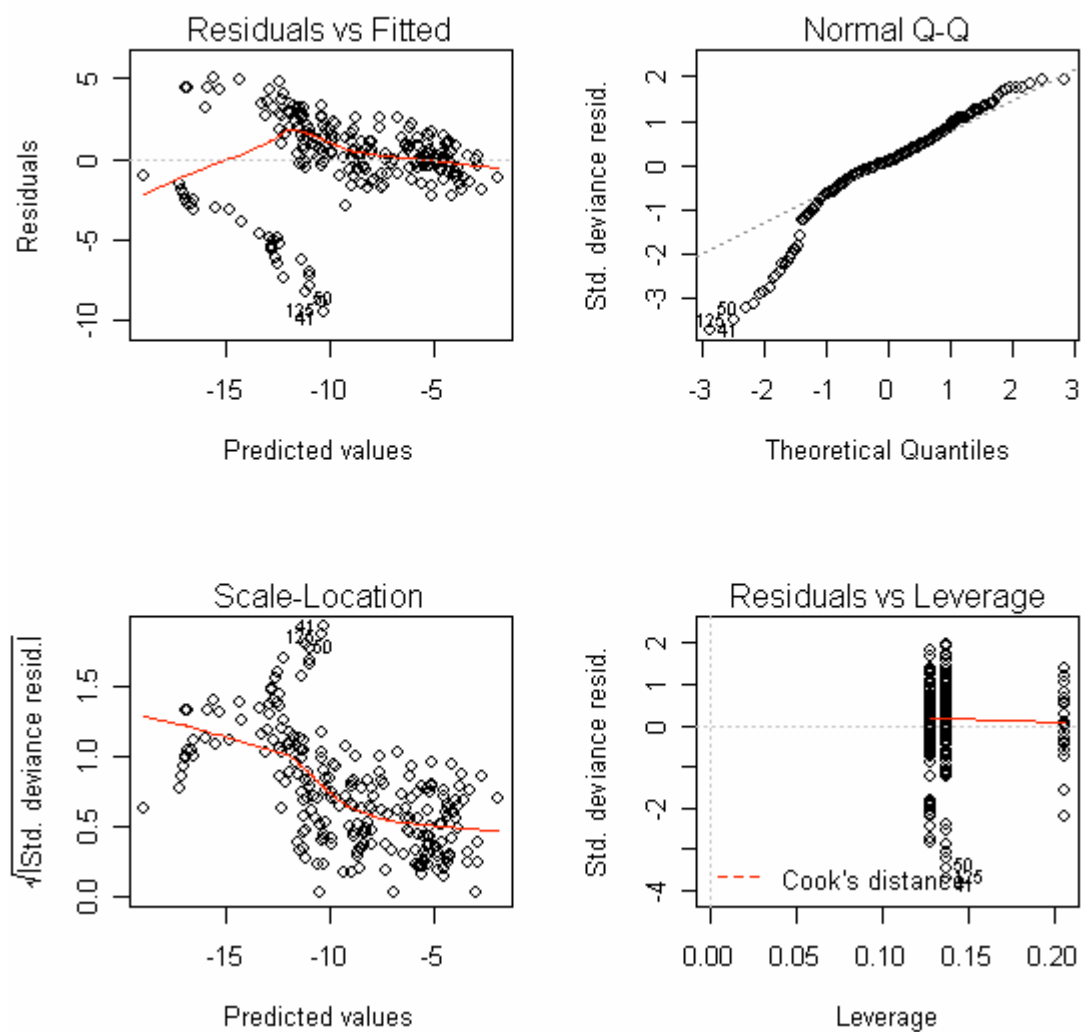


Figure 2.5A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the lower Fraser.

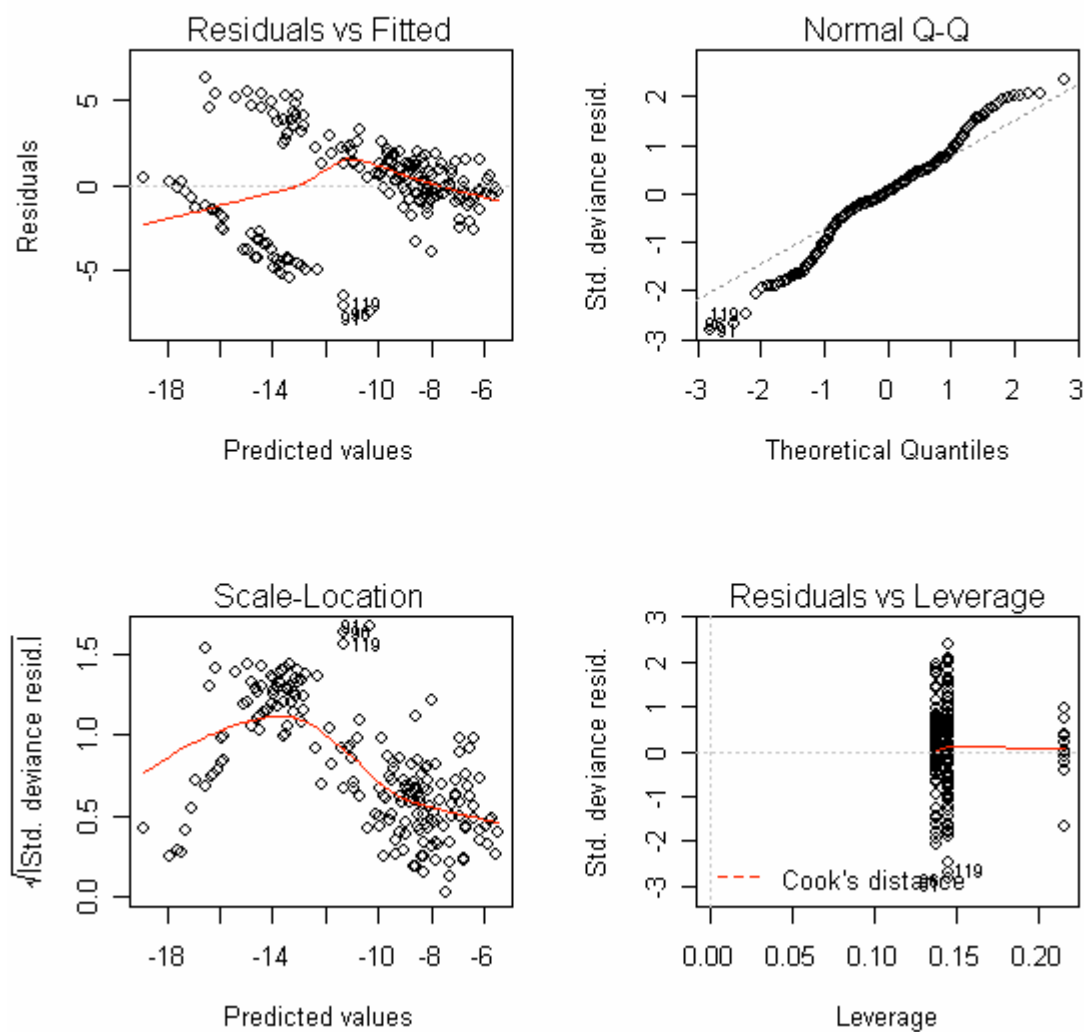


Figure 2.6A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the upper Fraser.

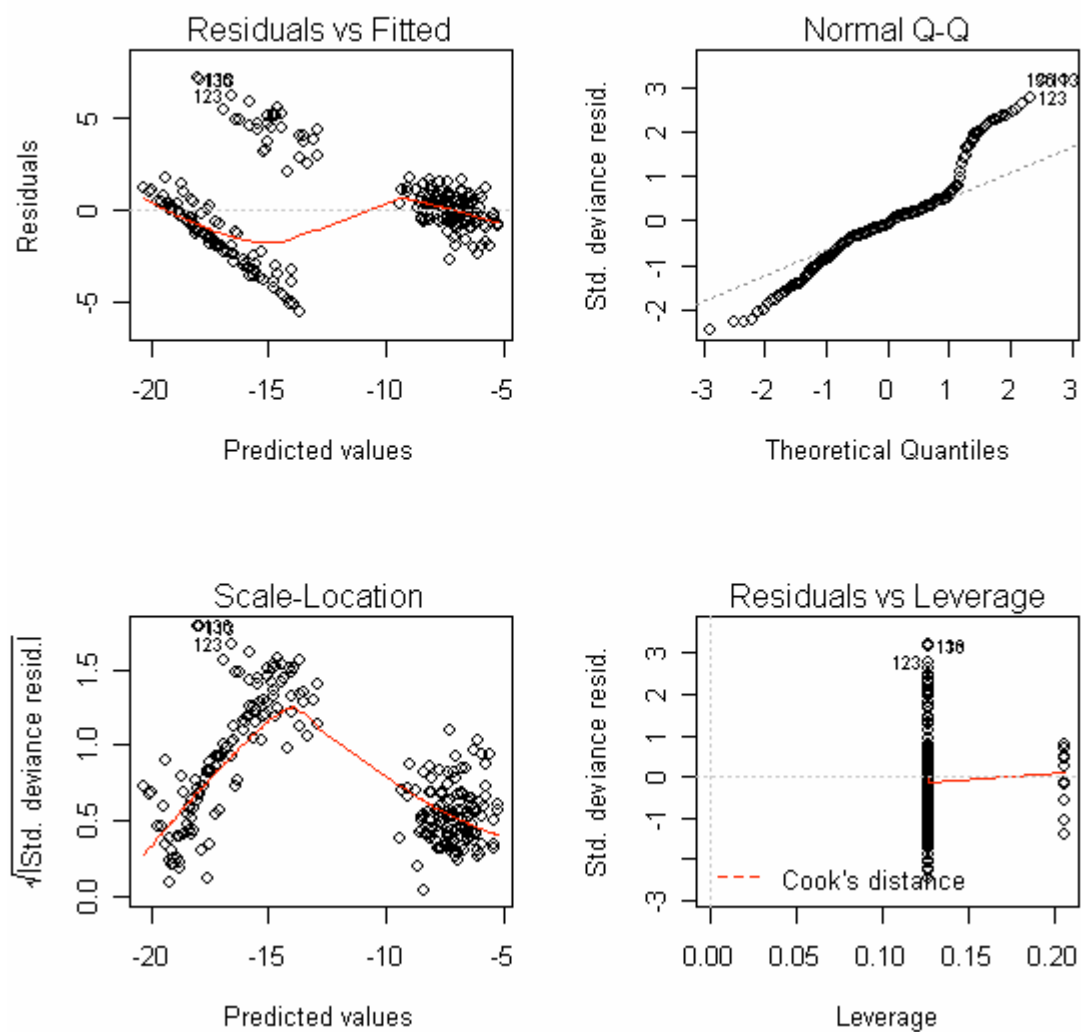


Figure 2.7A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for northern BC.

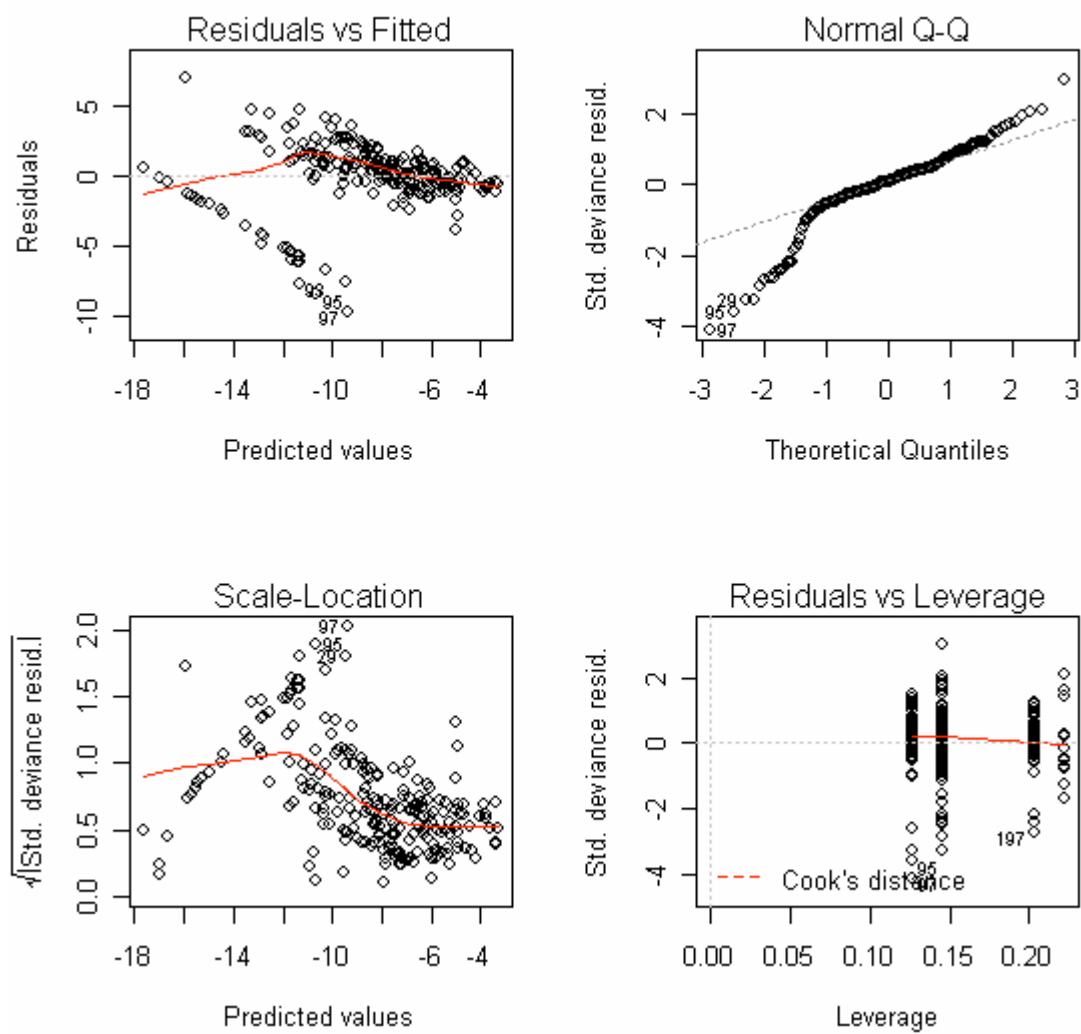


Figure 2.8A1: Residual Diagnostics of the Log-Linear Model (eq. 2.2) for the Oregon coast.

APPENDIX 2.2: RESIDUAL DIAGNOSTICS OF THE POISSON RESPONSE MODEL FIT BY AREA

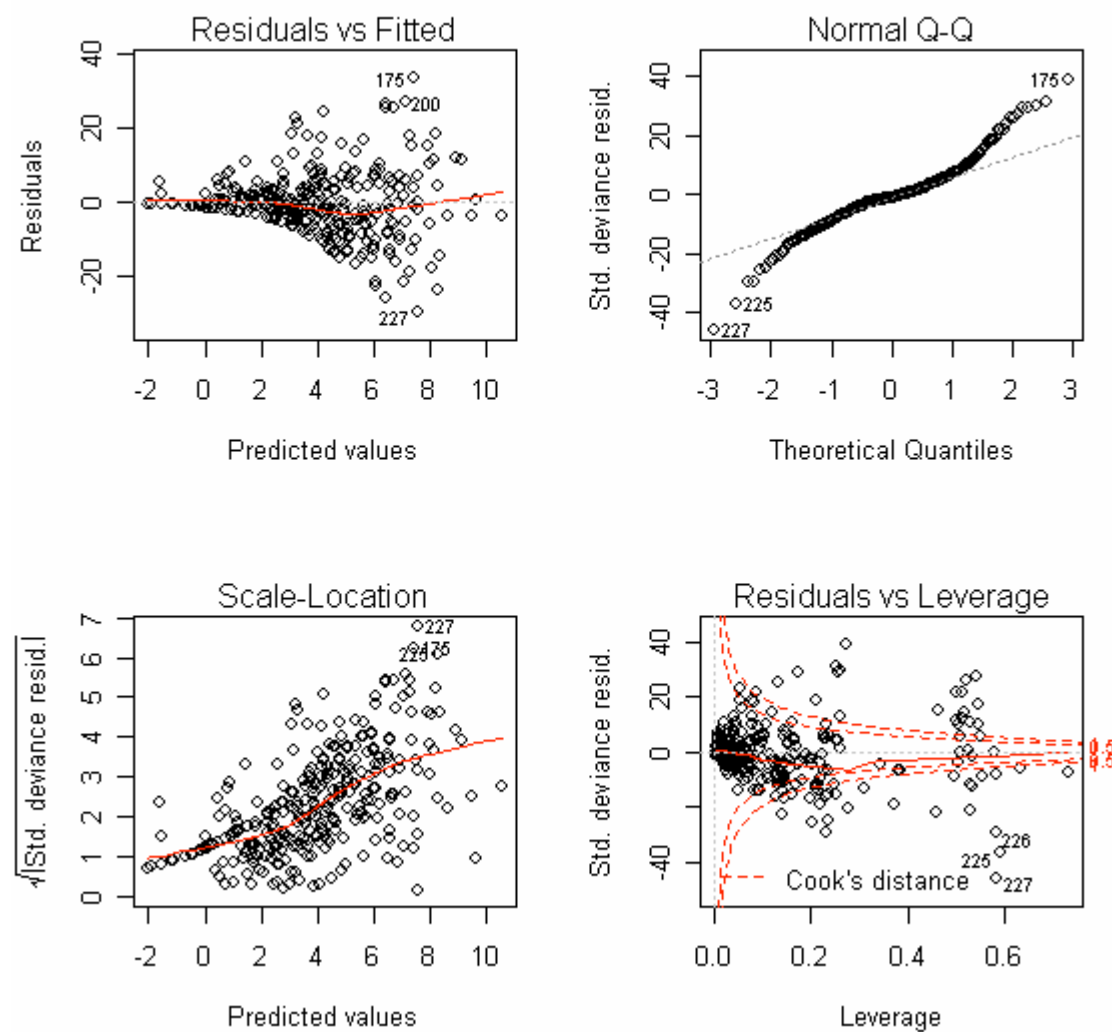


Figure 2.1A2: Residual Diagnostics for the Poisson Response Model for the Lower Columbia (WA Side)

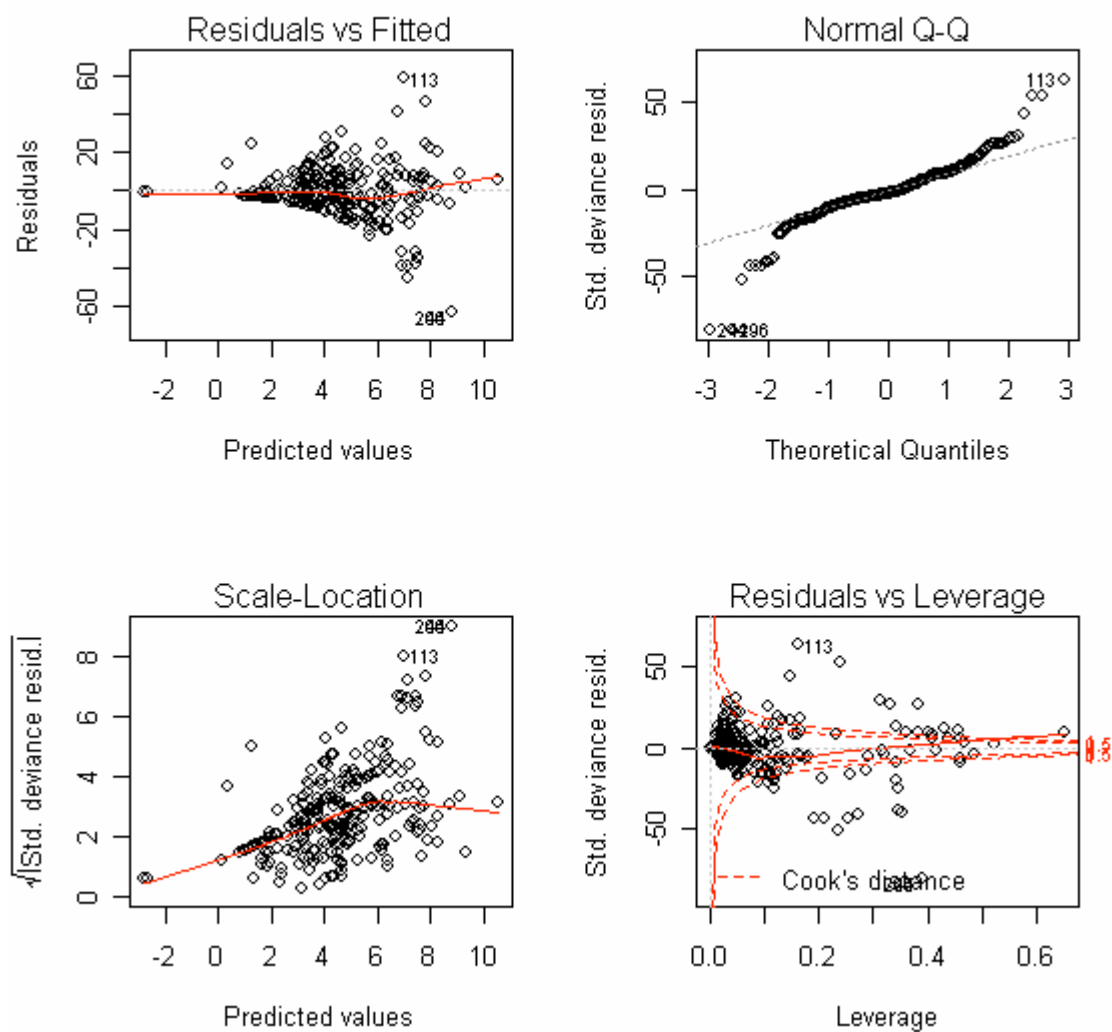


Figure 2.2A2: Residual Diagnostics for the Poisson Response Model for the Lower Columbia (OR Side)

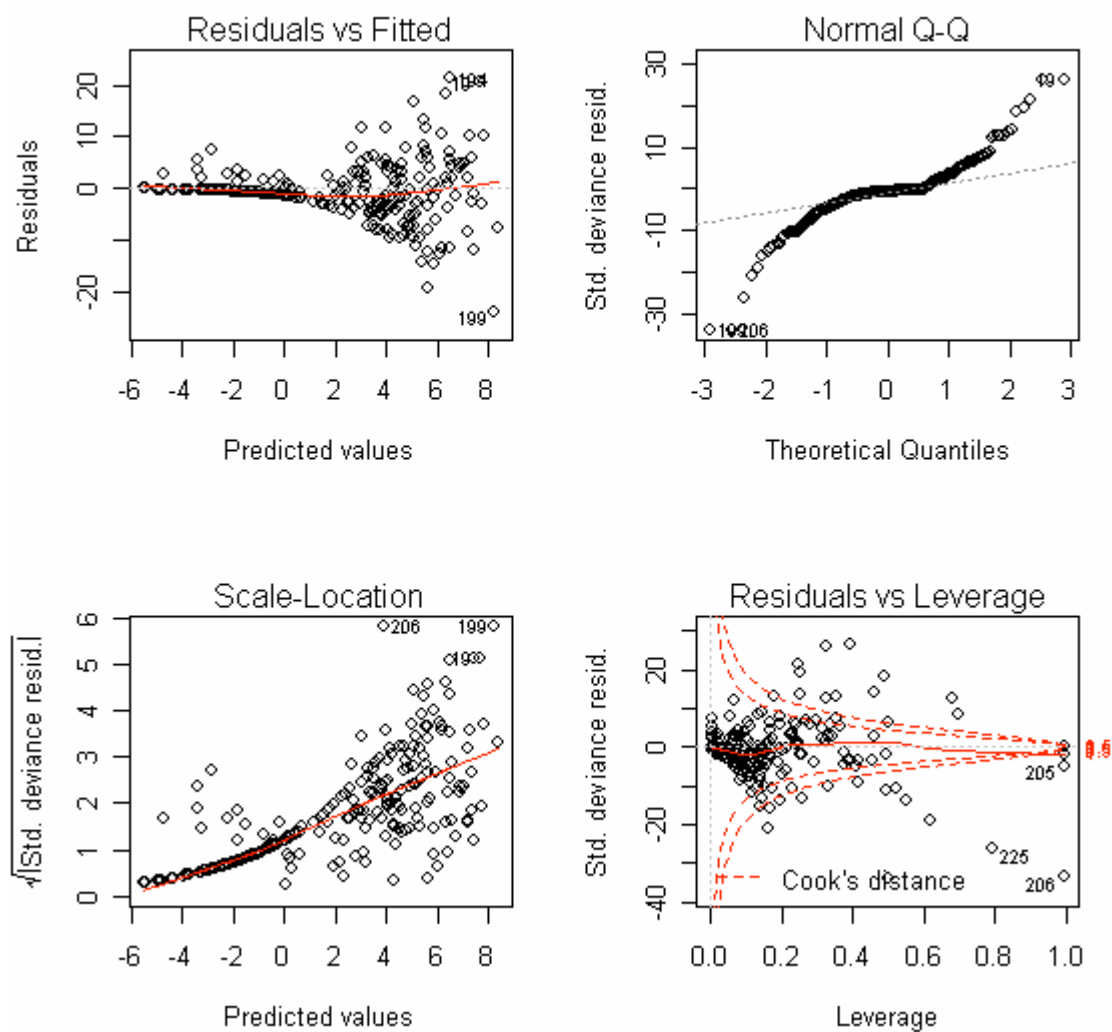


Figure 2.3A2: Residual Diagnostics for the Poisson Response Model for the Upper Columbia

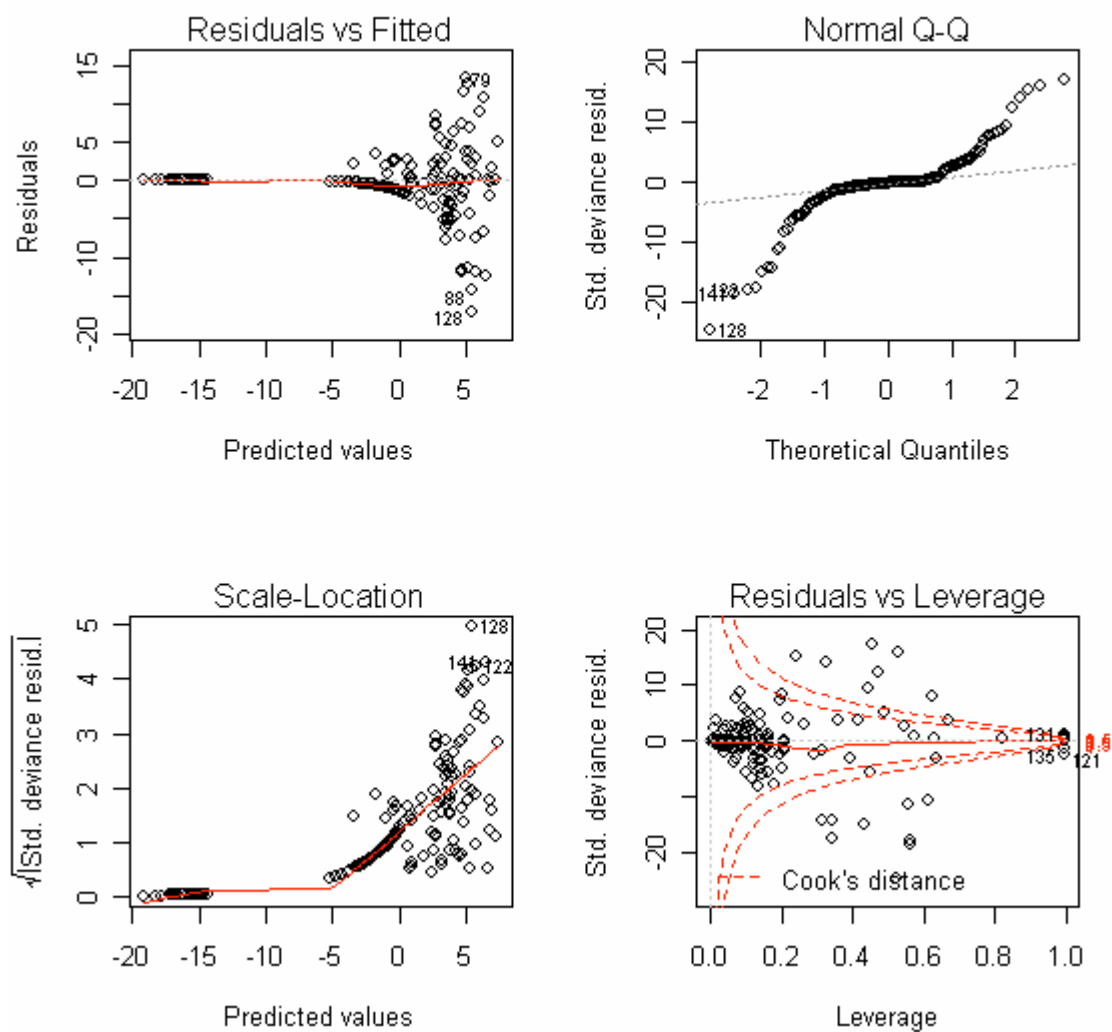


Figure 2.4A2: Residual Diagnostics for the Poisson Response Model for the Snake River

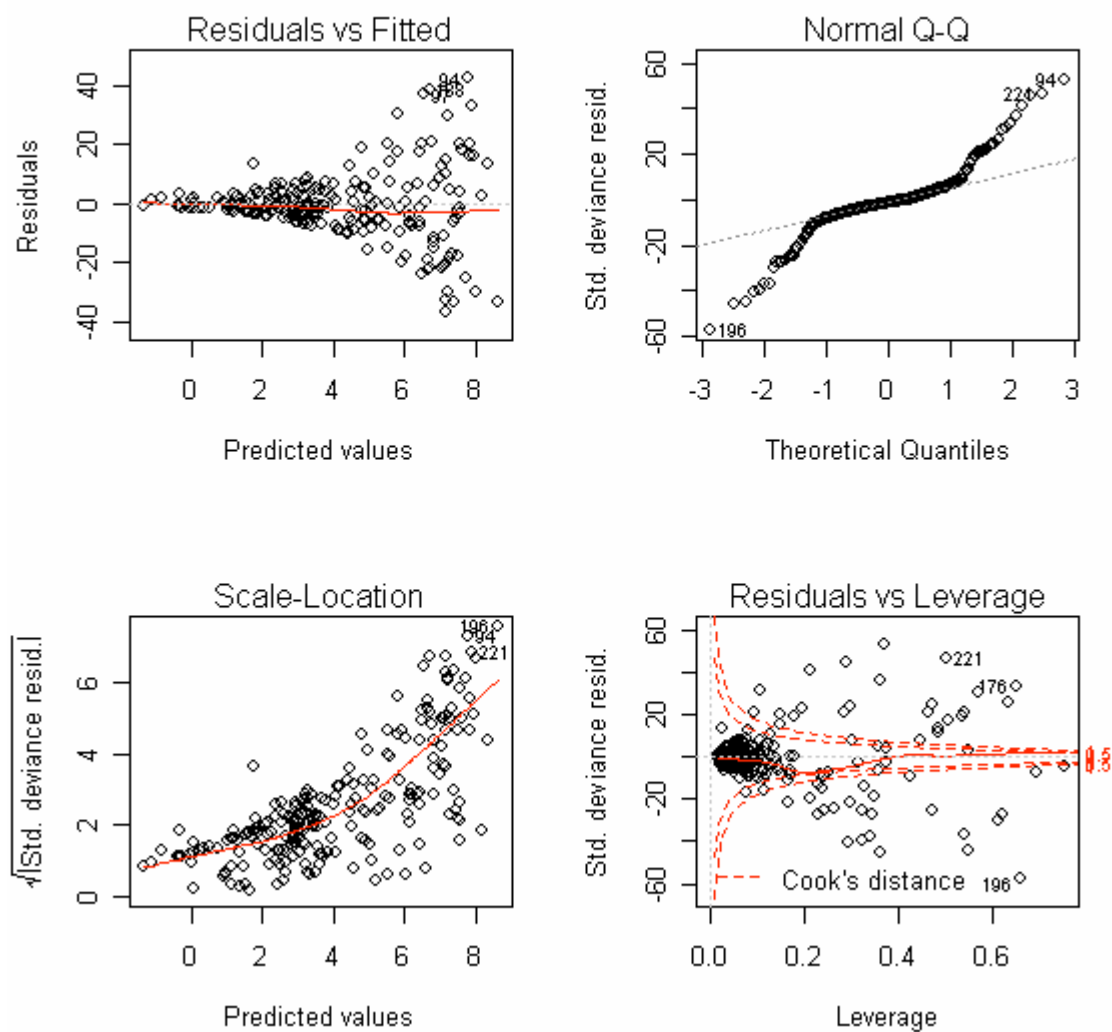


Figure 2.5A2: Residual Diagnostics for the Poisson Response Model for the lower Fraser

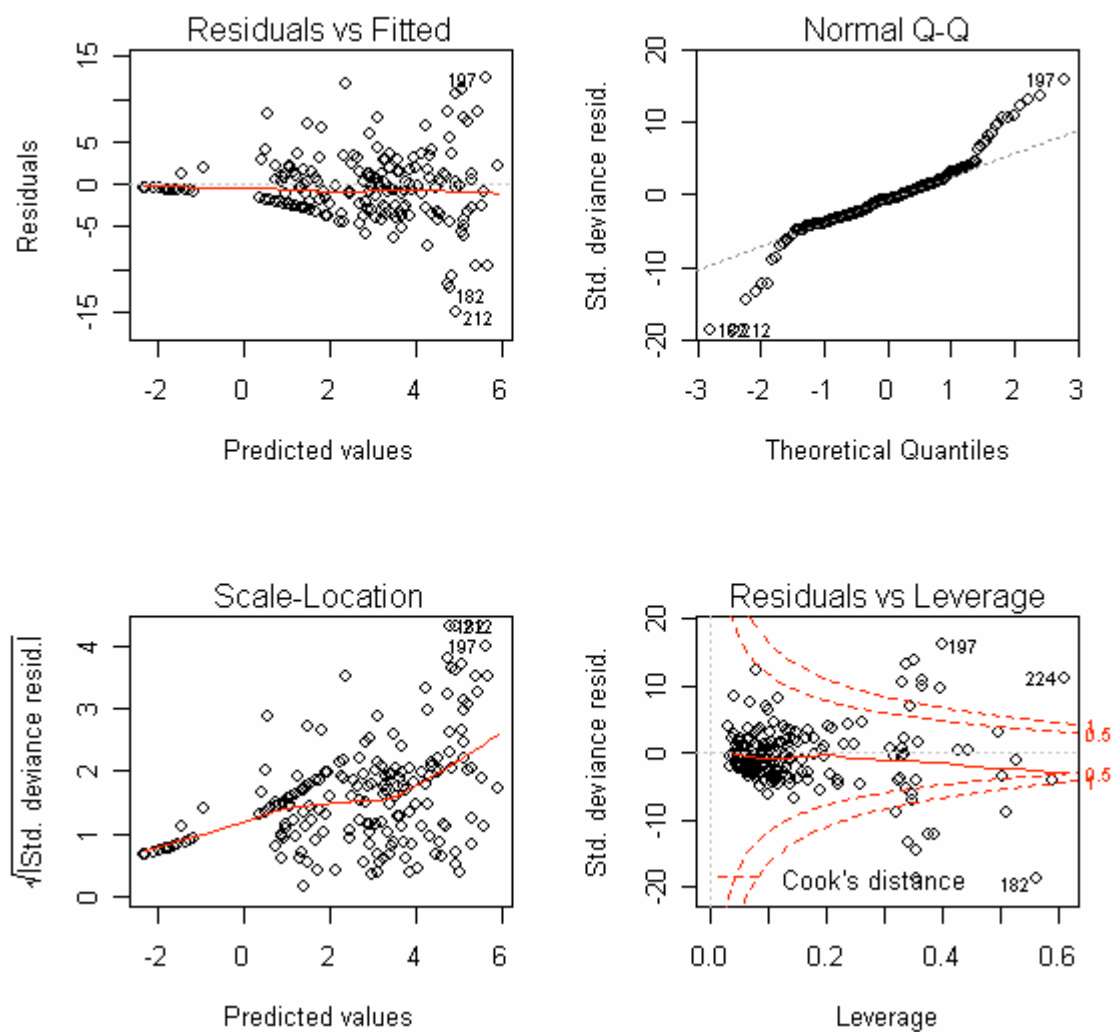


Figure 2.6A2: Residual Diagnostics for the Poisson Response Model for the upper Fraser

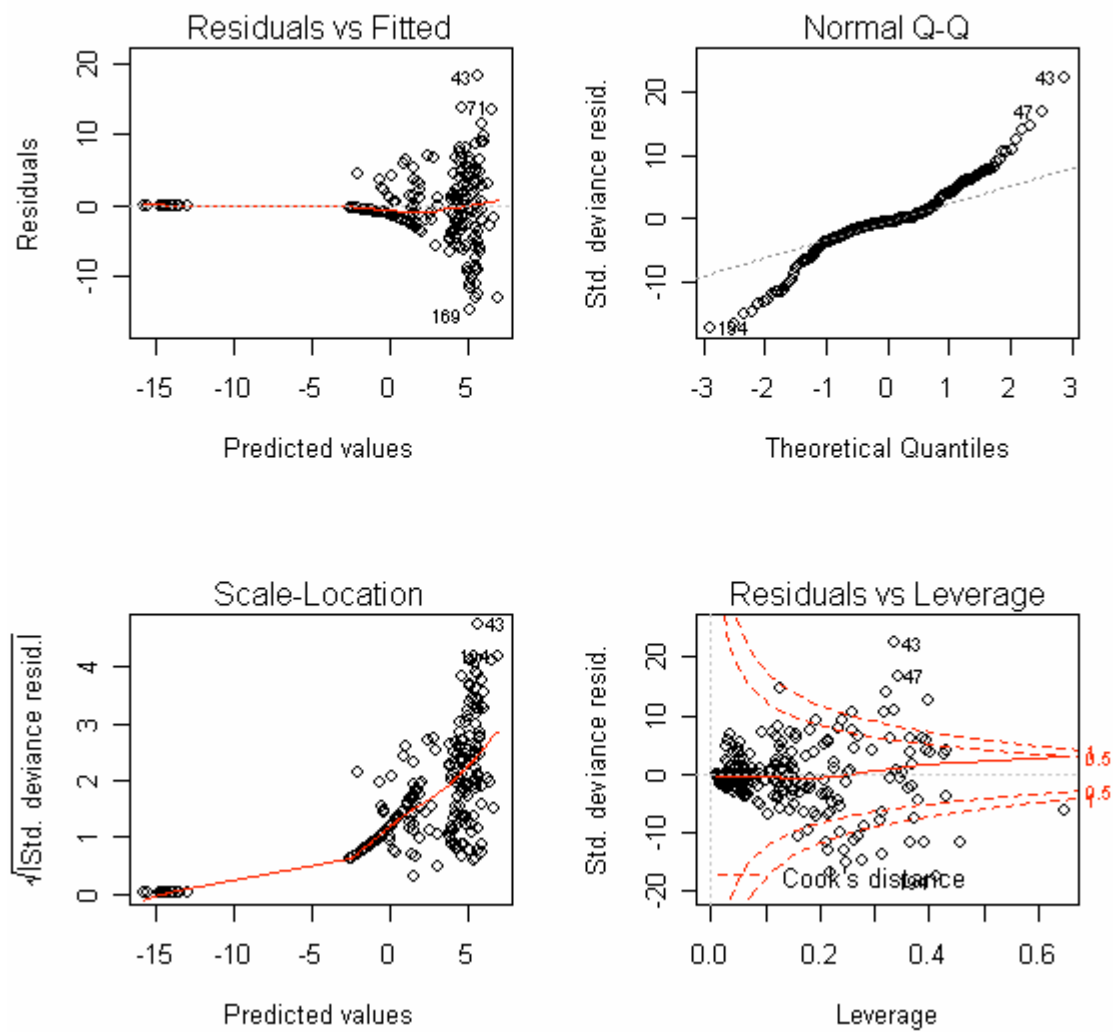


Figure 2.7A2: Residual Diagnostics for the Poisson Response Model for Northern BC

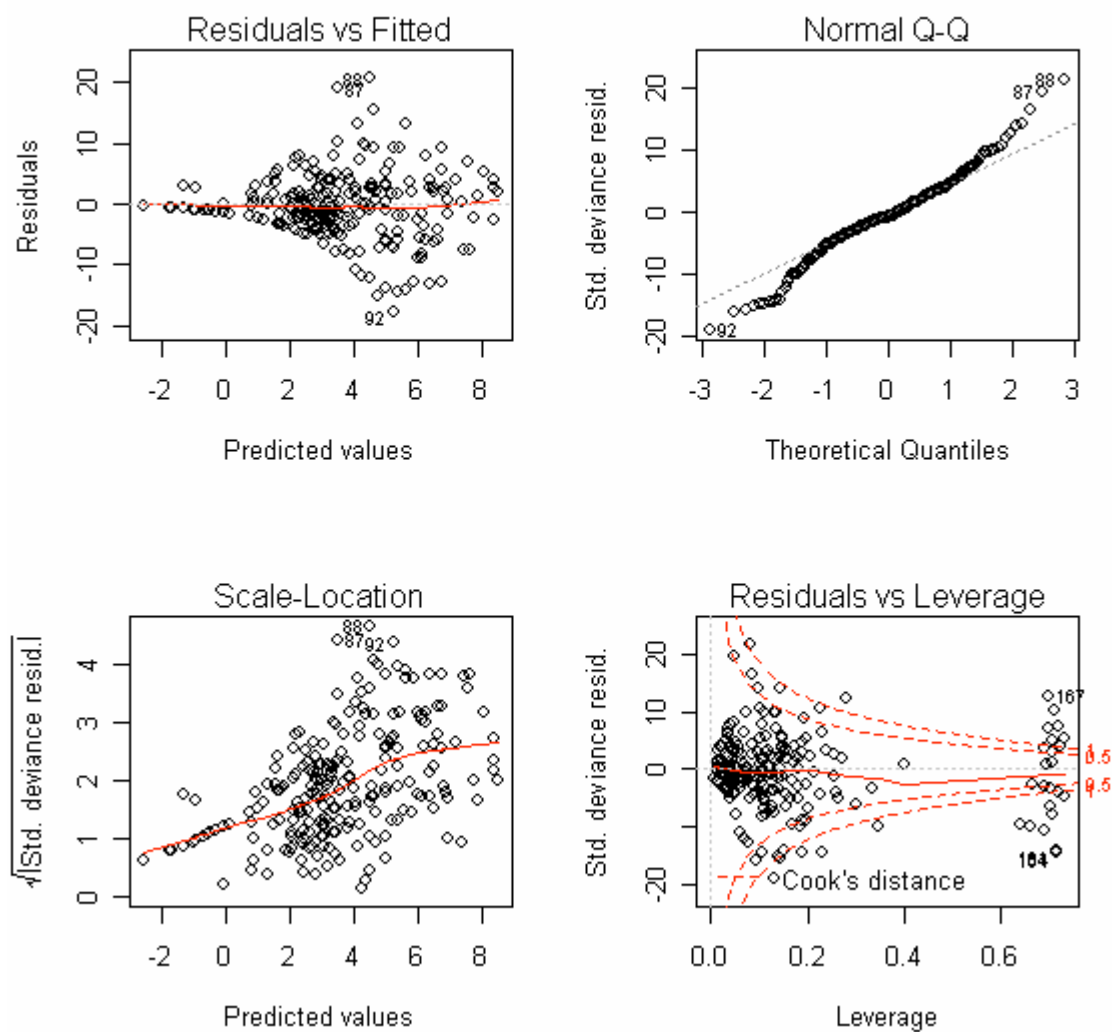


Figure 2.8A2: Residual Diagnostics for the Poisson Response Model for the Oregon coast

**CHAPTER 3: RELATING SPATIAL AND TEMPORAL SCALES
OF CLIMATE AND OCEAN CYCLES TO PACIFIC NORTHWEST
CHINOOK SURVIVAL AND MATURATION**

3.1 INTRODUCTION

The timing of Chinook salmon smolt migration varies among populations from southern Oregon to southeast Alaska. They either migrate as sub-yearlings in their first spring or summer after hatching (known as ocean-type), or as yearlings, migrating to sea after spending an additional winter in freshwater (stream-type). Most of the Chinook salmon caught in US-Canada jurisdictional waters governed by the Pacific Salmon Treaty (PST) are ocean-type fish. The life history strategies of the two types of fish are primarily determined by the temperature of the stream environment in which they rear (Brannon et al. 2004) but also by genetics (Clarke et al. 1992, 1994). Because temperature limits growth, Chinook in colder regions such as northern BC, southeast Alaska, and the upper Columbia (Snake River Basin) tend not to reach a threshold size for emigration into the ocean environment in their first freshwater year (Brannon et al. 2004), and therefore employ the stream-type life history strategy, waiting longer to undertake their ocean migration.

While the freshwater phase of these fishes' life history is undeniably important, they spend 50%-90% of their adult life in ocean environments (Healey 1991, Quinn 2005). Accordingly, the effect of ocean conditions on Chinook salmon ecology is extremely important. The relationship between ocean conditions and salmon ecology has been discussed for many decades; for example, the work of Pearcy (1992) and Francis and Hare (1994) showed that many major changes in salmonid abundance could be related to changes in ocean conditions. In recent years, research has indicated that ocean and freshwater conditions affect survival for coho salmon (Lawson et al. 2004, Logerwell et al. 2003, Ryding and Skalski 1999a, Coronado and Hilborn 1998).

For Chinook salmon, survival has been shown to be correlated to ocean and near-shore estuarine conditions (Magnusson 2002, Ryding and Skalski 1999b, Greene and Beechie 2004). Magnusson (2002) suggests a dome-shaped effect, with survival peaking at an optimal ocean temperature, whereas Green and Beechie (2004) suggest both estuarine and near-shore coastal processes are important for overall survival of Skagit River populations.

Environmental factors may impact species directly by affecting local conditions or indirectly by influencing conditions at another geographic scale. Levin (1992) discussed these issues of scale from both a spatial and temporal perspective for different marine and terrestrial species. He states:

“Two fundamental and interconnected themes in ecology are the development and maintenance of spatial and temporal pattern, and the consequence of that pattern for the dynamics of populations and ecosystems. Central to these questions is the issue of how the scale of observation influences the description of pattern; each individual and each species experiences the environment on a unique range of scales, and thus responds to variability individualistically. Thus, no description of the variability and predictability of the environment makes sense without reference to the particular range of scales that are relevant to the organisms or process being examined” (Levin 1992).

In the case of salmonids, spatial scales are important for both the freshwater and ocean phases of their life history (Scheurrell et al. 2006, Sharma et al. 2005). During the freshwater and oceanic phase of their lives, global circulation patterns can

play an important role. For example, ocean currents in the northeast Pacific are a function of larger ocean circulation patterns (Bakun 1996, Pearcy 1992). Bakun (1996) observed phenomena connected across different spatial scales, and demonstrated that transition zones are extremely important locations for a species in terms of reproduction, rearing, and overall persistence. He demonstrates these relationships using the example of how sardines persist across different areas in the world's oceans. Sardines migrate longer distances to find suitable areas to feed, but spawn in areas of local retention like the southern California Bight (Bakun 1996) thereby emphasizing how some zones are extremely important for local retention of larvae, and the overall persistence of sardines.

Variation occurs on different temporal and spatial scales in the Pacific Ocean that might affect local conditions experienced by Pacific Northwest (PNW) salmon. Large-scale global phenomena like the El Niño Southern Oscillation (ENSO) operate on different spatial scales in the equatorial, central, and northeast Pacific Ocean, and impact PNW Chinook on local scales by directly and indirectly affecting local environmental conditions. The effects on Chinook salmon could possibly be quantified by examining indicators such as survival and maturation rates for different stocks and areas in the region. In previous examinations of large-scale patterns in PNW salmon ecology, regionally aggregated stock abundance and survival have been shown to fluctuate on a decadal or inter-decadal scale for *Oncorhynchus* spp. (Francis and Hare 1994, Hare and Francis 1995, Hare et al. 1999). Mueter et al. (2002), Peterman et al. (2003), and Beamish et al. (2004) have shown that at the stock level, productivity is

related to climate change at a finer scale of resolution for pink salmon (*O. garbucha*) and sockeye salmon (*O. nerka*). For these species (*O. garbucha* & *O. nerka*) survival was correlated across regions on a spatial scale of less than 200 km (Peterman et al. 2003); this relationship diminished with greater distances. In addition, the Pacific Decadal Oscillation (PDO; Mantua et al. 1997), a basin scale process, could be related to changes in Fraser River sockeye productivity over time (Beamish et al. 2004). For Chinook salmon, however, such studies have been limited and have not been performed in an integrated manner for the entire Northwest. I attempt to relate different scales of environmental condition by tying the ENSO to intermediate basin scale signals like the Pacific Decadal Oscillation and finally to regional conditions that might be important to Chinook salmon survival and maturation.

Because near-shore coastal processes are important for overall survival of salmonid species (Beamish et al. 2004, Peterson et al. 2006), it is likely that most of the Chinook stocks examined here are influenced to some extent by the California Current, and to a lesser extent by the Alaskan current. Chapter 2 demonstrates that the primary area where these fish reside as juveniles is along the coastal shelf from coastal Oregon to southeast Alaska. The California Current system (CCS), like other eastern boundary systems (Bakun 1996), exhibits strong upwelling as a function of three components: i) northern wind stress; ii) offshore Ekman transport as a function of the wind stress along the shelf; and iii) strong circulation that brings deeper water to shallower depths to fill the void created by the offshore transport (Hickey 1978). Higher primary

production results from the transport of nutrient-rich water to shallower depths (Peterson et al. 2006).

I postulate that for Chinook salmon, the timing of the transition from freshwater to ocean environments with respect to the onset of spring upwelling is key for their survival, i.e. upwelling events of long duration during this transition phase create conditions favorable for growth and survival, while weaker upwelling conditions correspond to poor food availability, and therefore poor salmon survival. To determine upwelling strength, I used two indicators: Bakun Upwelling Indices (UPI) and sea surface temperature (SST) for the spring transition period (April through July) and related them to Chinook survival data collected in the same geographic areas. I chose only one of these indicators in my analysis (UPI for the broad spatial scale analysis across the PNW, and SST for the fine-scale analysis) because UPI and SST are highly correlated across the region examined. Further, I hypothesized that ocean conditions, as indicated by UPI (and SST) from previous years or the current year, affect maturation rates, i.e. a higher proportion of fish mature when UPI conditions are positive in the ocean, and vice versa.

In order to examine the above hypotheses, I analyzed Chinook tag data from populations tracked by the Pacific Salmon Commission as exploitation rate indicator stocks (TCChinook 08-1) and estimated their survival. In addition to analyzing large-scale patterns in Chinook survival and variation in the northeast Pacific, I also examined finer scale effects in terms of likelihoods (i.e. probability density functions) on overall survival and tied them to changes in SST.

3.2 MATERIALS AND METHODS

3.2.1 Coded Wire Tag Data

The Chinook Technical Committee (CTC) of the Pacific Salmon Commission tracks 36 indicator stocks using coded wire tags (CWT; Johnson 1990, Lapi et al. 1990) to evaluate exploitation rates in the ocean. I chose 22 of these stocks (see Table 3.1 and Figure 3.1) for which the tagging data had adequate escapement sampling and a sufficiently long time series. In addition, I also analyzed the Klamath River in southern Oregon/northern California. This stock is not managed under the jurisdiction of the Pacific Salmon Commission, but is important for management off the coast of Oregon and California, and has adequate sampling and tag data that fit the other stock criteria. With these data, abundances of age-2 cohorts were reconstructed using virtual population techniques (cohort analysis), similar to the approach used by Coronado and Hilborn (1998). I also calculated maturation rates for the time series available (eq 3.1, 3.2 and 3.3).

From the CWT data, age 2 ocean abundances were constructed using eq. 3.1:

$$O_{a,t} = \frac{OC_{a,t} + TC_{a,t} + E_{a,t} + O_{a+1,t+1}}{1 - NM_{a,t}} \quad (3.1)$$

Where O is the ocean cohort at age a; OC, TC and E are the ocean catch, terminal catch and escapement at age a and time t; and NM is natural mortality at age a. Note that equation 3.1 is used recursively starting at an assumed final age (in this case age 5).

Corresponding survival to age 2 is computed using equation 3.2:

$$S_{2,t} = \frac{O_{2,t}}{Rel_{t-2}} \quad (3.2)$$

where $S(2)$ is survival to age 2, associated with brood year releases (Rel) at time $t-2$ for the associated CWT group (In the case of yearling releases, this subscript on $S_{3,t}$ (1st ocean age) Release should be $(t-3)$).

Maturation rate is computed using equation 3.3:

$$MR_{a,t} = \frac{TC_{a,t} + E_{a,t}}{TC_{a,t} + E_{a,t} + O_{a+1,t+1}} \quad (3.3)$$

where MR is the maturity rate at age a and time t .

3.2.2 Ocean Environmental Data

I used sea surface temperature from April to July (SSTAMJJU), ocean upwelling indices from April to July (UpwellAMJJU), and sea level pressure (SLPAMJJU) for April to July. SSTAMJJU was calculated as the mean monthly sea surface temperature from April to July (the primary months of ocean entry for the smolts) in the smolt year, obtained from Comprehensive Ocean Atmospheric Data Set, COADS

(<http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.version2/.SST/>)

and standardized using the Smith and Reynolds approach (2004). Station locations were along the coastal shelf from 42 °N to 60 °N. Some SST for the region of interest

was taken from the National Data Bouy Center (NDBC,

http://www.ndbc.noaa.gov/historical_data.shtml) for US waters, and from BC

lighthouse data for Canadian waters (http://www-sci.pac.dfo.mpo.gc.ca/osap/data/SearchTools/Searchlighthouse_e.html).

Similarly, UpwellAMJJU was calculated as the monthly mean upwelling indices from April to July in the smolt year, obtained from the Pacific Fisheries Environmental Laboratory (PFEL: <http://www.pfeg.noaa.gov/pfel/>, Schwing et al. 1996). SSTAMJJU was collected for the Canadian stations using the BC lighthouse data set. US coastal Buoy data for SST had poor spatial coverage and were not available for the entire time period for most areas analyzed. Hence, I used COADS (<http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.version2/.SST/>) which had adequate coverage and resolution for the stocks analyzed here.

For convenience I used the standardized forms of the environmental variables throughout these analyses. Variables were standardized by subtracting the mean of all observed values of the variable from the observed value and then dividing the difference by the standard deviation.

3.2.3 Spatial Cluster Analysis Used on Survival and Maturation Data (Correlation Analysis) on a Large Spatial Scale

Two essential hypotheses were tested with spatial cluster analysis (correlation analysis) of survival and maturation data on a large spatial scale: 1) survival varies spatially across the PNW, but may be strongly influenced by regional phenomena, and 2) survival anomalies occur on the same temporal scales as anomalies in ocean conditions in the northeast Pacific, implying that survival variations are correlated with aspects of regular ocean/climate variation.

To explore these hypotheses, standard cluster analysis techniques based on hierarchical agglomeration algorithms (Gordon 1981) were employed. Local-scale environmental variables were chosen for the small-scale analysis by using a protocol similar to that of Mueter et al. (2002), which was used to find correlation among environmental variables at different spatial scales. This analysis was carried out separately for the survival data, the maturation data, and the ocean variables. I also performed a cross-correlation analysis for survival, maturation and ocean variables in order to look for patterns that might be explained by ocean environmental variation.

3.2.4 Relationships Between Physical Ocean Conditions and Chinook Survival

I constructed linear regressions between survival and ocean variables (like SST) from the stations closest to the river mouth in the year of smolt outmigration to examine the relationship between ocean conditions and survival (or maturation). Conditions in the years preceding or following outmigration were not expected to be essential to a parameter such as survival to age 2. The linear regressions are expressed as:

$$S_{2,t,s} = \alpha + \beta V_{t,s} + \varepsilon_s \quad (3.4)$$

where $S_{2,t,s}$ is parameter survival (to age 2) for stock (s) at time (t), $V_{t,s}$ is the independent ocean variable (SST, UPI, SLP etc.) at time t, α is a constant, β is the slope parameter of the variable ($V_{t,s}$) and ε is the normal additive error.

Likelihood profiles (Hilborn and Mangel 1997, Sharma and Hilborn 2001) were generated on the slope parameter using equation 3.5:

$$L(S_{2,t,s} | \alpha, \beta) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left[-\frac{(S_{2,t,s} - \hat{S}_{2,t,s})^2}{2\sigma^2} \right] \quad (3.5)$$

Because on a local scale the physical variables (upwelling, and SST) are highly correlated, the analysis was performed only with SST. Rather than using a traditional approach of statistical inference, i.e, testing for significance of a particular variable (in this case the value of the β parameter in equation 3.5), a likelihood profile analysis on SST was performed (Hilborn and Mangel 1997) to quantify the uncertainty of the effect.

Finally, the fit of the data to non-linear models was also examined for each stock using the functional form in equation 3.6:

$$S_{2,t,s} = \alpha e^{\beta V_{t,s}} e^{\varepsilon_s} \quad (3.6)$$

Where α is now a constant multiplier, β is the exponential slope parameter of the variable ($V_{t,s}$), and ε is now the multiplicative error term.

3.2.5 Building Time and Space Lag-Based Models for Understanding Survival and Maturation Dynamics

Based on results obtained in the SST local scale analysis, I performed time series lag-based analyses tying ENSO, a global-scale phenomenon, to large basin-scale phenomena (i.e., the PDO), and then tying the PDO to local effects (SST) that might impact Chinook salmon survival in the near-term. The ENSO and PDO were chosen because numerous studies (Mantua et al. 1997, Beamish et al. 2004, Hollowed et al.

2001, Francis et al. 1998) have shown how large-scale forcing impacts these coupled systems in the tropical and northeast Pacific. These relationships were incorporated into a model to determine how phenomena occurring on different spatial scales affect local ocean conditions and therefore the survival of a particular stock of Chinook salmon. The models are built on equations 3.7-3.10:

$$PDO_t = \alpha_1 + \beta_1 ENSO_{t-a} + \varepsilon_s \quad (3.7)$$

where PDO is Pacific Decadal Oscillation (Mantua et al. 1997) estimated at time (t) and ENSO is El Niño Southern Oscillation Index as estimated through multivariate techniques (Wolter and Timlin 1998) measured at time (t-a). α_1 and β_1 are the slope and intercept parameters in eq. 3.7.

$$PCSST_t = \alpha_2 + \beta_2 PDO_{t-a} + \varepsilon_s \quad (3.8)$$

where PCSST is the first principal component (PC) of local sea surface temperatures at the river mouth for a particular stock (s) influenced by the PDO measured at time (t-a). α_2 and β_2 are the slope and intercept parameters in eq. 3.8.

Finally, equation 3.9 relates PCSST to SST, which has the largest effect on survival:

$$SST_t = \alpha_3 + \beta_3 PCSST_{t-a} + \varepsilon_s \quad (3.9)$$

Where SST is the sea surface temperature at a station that is important for Chinook survival and influenced by PCSST at some time (t-a).

Outputs from this set of equations are then used to understand what might be affecting survival. Equation 3.10 extends this analysis to the species level by relating survival, $S_{2,t,s}$ linearly to SST:

$$S_{2,t,s} = \alpha_4 + \beta_4 SST_{t,s} + \varepsilon_s \quad (3.10)$$

I tested this approach for one stock in each of the distinct regions resulting from the cluster analysis on survival described in a previous section.

3.3 RESULTS

3.3.1 Chinook Salmon Survival in Relation to the Environment in the Pacific Northwest

After standardizing the estimated survival data using equations 3.1 and 3.2, I examined spatial and temporal patterns of PNW Chinook survival over a 30-year period (Figure 3.2). Using standard cluster analysis techniques in R (R Development Core Team 2007) I determined eight distinct clusters based on survival rates (Figure 3.3): northern BC and Alaska, Georgia Straits, lower Fraser River and west coast of Vancouver Island, Puget Sound and Hood Canal, lower Columbia Tules, Columbia Brights and Cowlitz, Oregon and Washington coasts, and the Klamath River (which is, interestingly, clustered with the Columbia River Summers). Survival to age 2 ocean

recruits (using absolute measures of survival) is shown for these broad geographical clusters (Figure 3.4).

In order to test whether Chinook salmon populations in the Northwest respond to ocean anomalies, I performed cluster analysis on the normalized Chinook survival data on years between 1978 and 2004 (Figure 3.5, left panel). The ocean upwelling data for the spring and summer transition periods (from April through July) across this broad area (From 42°N 125°W to 60 °N 149°W, Schwing et al. 1996) were examined in a similar manner (Figure 3.5, right panel) for the same set of years. Finally, a cross-correlation analysis was carried out across years using the two data sets, with like years shown in highlighted cells ($\rho > 0.4$, Table 3.2). Based on these results, there is only a weak relationship between ocean conditions and Chinook survival coastwide (Table 3.2 and Figure 3.5). Although the relationship is weak, the ocean does appear to have some effect in anomalous years of high survival (mid 1980s and late 1990s) and low survival (early 1990s), as displayed by the clusters (Figure 3.5). This relationship in anomalous years is supported by the correlations in survival shown by the highlighted cells for survival anomalies (Table 3.2a) and upwelling anomalies (Table 3.2b), especially for the latter years.

A broad scale spatial analysis indicates how upwelling is positively correlated with survival of stocks across different regions (Table 3.3), and how local SSTs are also related to survival in different areas. In general, higher SSTs correlate with poor survival, and large prolonged upwelling events relate in a positive manner with survival (Table 3.3).

A Principal Component Analysis was then used to evaluate the relationship between the environment (as indicated by ocean upwelling from stations along the coast from Oregon to southeast Alaska for the months of April, May, June, and July) and survival (Figure 3.6). The data set was narrowed to 1981-2004 as there were fewer stocks with missing data for that time series (as opposed to the previous analysis that was from 1978 to 2004). Average conditions for the entire time series were applied for stocks with missing data for the 1981-2004 period analyzed. While an initial examination of the overall results does not appear to reveal a relationship between the environment and survival (Figure 3.6), an examination of the relationship on the third principle component (loadings) reveals that for both data sets this component appears to be correlated ($\rho=0.42$, Figure 3.7). Thus there is weak evidence from both the cluster analysis (Figure 3.5) and the PCA (Figure 3.6) indicating that extremes in survival (poor survival through most of the 1990s, and high survival in 1980 and 1999-2001) correspond to extremes in the ocean environment that either favor or depress fish survival. The years 1983 and 1984 to 1986 are also interesting, in that there is an overlap with survival and the ocean environment (Figure 3.5). An ANOVA carried out on the rotated components (Figure 3.7) indicated that ocean variables had a significant relationship with survival ($p<0.05$, two-tailed test).

3.3.2 The Effect of Environment on Chinook Maturation in the Pacific Northwest

For a subset of the stocks used in Table 3.1, I estimated maturation and tested hypotheses regarding spatial and temporal changes in maturation similar to those tested for survival. Figures 3.8, 3.9, and 3.10 show maturation anomalies by age and time for each stock. For southeast Alaska (AKS), northern BC (KLM), and Willamette River

(WSH) stocks, fish first reach maturation at age 3 (indicated in Figure 3.8), age 4 (indicated in Figure 3.9), and age 5 (indicated in Figure 3.10); fish from these stocks are one year older than other stocks when they first enter the ocean because of their stream-type life history.

For Chinook in their first year of ocean residence (first ocean age), years of good ocean conditions, indicated by low sea surface temperatures coastwide, have a positive effect on maturation (these are years prior to the years indicated in Figure 3.8 as that denotes the calendar year in which the fish matured). In the late 1970s, some of the stocks that migrate to northern waters (Oregon coastal, Columbia Upriver Brights, and the west coast of Vancouver Island) exhibited some of the highest maturation rates on record. These patterns were apparent in the mid 1980s as well. Through most of the 1990s, maturation rates were below average, probably corresponding with poor ocean conditions, but maturation rates returned to higher than average values in the late 1990s.

In general, it appears that anomalously cold oceans that have strong upwelling signals affect maturation rates positively and to a greater degree than do average conditions. However, extremely poor ocean conditions (for example, the prolonged El Niño of 1991-1992) seem to have a positive effect on some stocks like the Lower Columbia Tules. This result implies that fish might mature at a higher rate if conditions are so bad that food availability is extremely poor and odds of survival are better if a fish matures in the current year rather than stays another year in the ocean. Conditions like those experienced by the Tules in the early 1990s are rare, and in general La Niña-

like conditions such as those of 1983-1984, 1993, and 1997-1998 appear to have the highest positive effect on maturation rates (Figure 3.8). In contrast, the northern stocks (spring stocks of southeast Alaska and northern BC) appear to have some of highest age 3 maturation rates in the early 1980s.

For Chinook in their second year of ocean residence (second ocean age), the trends appear to be the same as the first ocean age, i.e. years of positive ocean conditions like the La Niña-like conditions of 1983-84 and 1997-98 (Figure 3.9) appear to have the biggest positive impact on maturation rates. For Chinook in their third year of ocean residence (the third ocean age, namely age 4 for ocean-type Chinook and age 5 for stream-type Chinook), the patterns of maturation rates appear to be fairly stable over time (Figure 3.10) without much inter-annual variation. One exception is El Niño years (1982-83 and 1992-93), which seem to be associated with a lower than average maturation as shown in Figure 3.10. Some of the coastal Chinook stocks (like Oregon (ORC) and Washington (QUE)), seem to have generally lower maturation rates as these two stocks tend to mature at older ages (age 4 and 5 primarily, except for some anomalous years in the early 1980s; Figure 3.10), but even for these stocks, higher maturation rates are associated with positive ocean conditions (Figure 3.10).

Using clustering techniques similar to those used for survival, I found regional patterns that could be explained by rearing areas (Figures 3.11 and 3.12). These clusters were quite different from the survival clusters shown in Figure 3.3. Figure 3.11 indicates regional anomalies in maturation rates by age, and Figure 3.12 displays

anomalies in maturation rates by year. PCA analysis similar to that carried out for maturation anomalies and ocean conditions was also performed.

There appear to be five distinct clusters in each of the three ages (Figure 3.11). However, these clusters change by age and region. For the first ocean age the return rates of the far northern stocks, namely Upriver Bright, Oregon coast and west coast of Vancouver Island, seem to be affected by the same anomalies. The only stock that doesn't seem to respond similarly is the Queets on the Washington coast. For the second ocean age, clustering appears to be random, with no distinct regional or migration-based pattern. For the third age, the pattern is again random, although some stocks like the Lewis on the Columbia and Queets on the Washington coast exhibit similar anomalies, as do the Oregon coastal and Willamette stocks (indicating some regional anomalies). Finally, there is an apparent random effect on the fish in the ocean for the third year, implying a large scale mixing of these stocks in the northeast Pacific.

In terms of a common year effect on Chinook maturation rates coastwide, no years appear to have a strong signal with maturation anomalies by age (Figure 3.12). However, for all three ages there appear to be some years that cluster together: the mid 1980s, the early 1990s, and the later 1990s and early 2000s (other than 2004). The actual years that make up the cluster may vary (Figure 3.12), but the general trend of clusters in the mid 1980s, early 1990s, and late 1990s and early 2000s remains. If survival (Figure 3.4) was overlaid on these clusters, a pattern is discernible, i.e. in years of high survival (mid 1980s and late 1990s and 2000s), maturation anomalies seem to cluster together. In years of poor survival (e.g., early 1990s) these anomalies appear to

cluster as well. These results indicate that some common effect might be influencing survival and maturation rates for PNW Chinook. When survival is high, maturation rates tend to be higher than average (Figures 3.8, 3.9, and 3.10), implying that a coastwide ocean effect causes these fish to survive and mature at higher rates than average.

Since maturation rates are affected by food availability, a productive ocean (in which there is positive upwelling coastwide) would have a positive impact on maturation rates. Ocean effects on maturation rates were tested using the same upwelling data that were used to create Figure 3.5, but data for the entire year was used (in contrast with only using spring and summer data). I tested whether ocean conditions affected maturation rates within a given year and whether ocean conditions affected maturation rates one year later (indicating a one-year lag effect).

There appears to be no lagged (Figures 3.13 and 3.14) or within-year (Figures 3.15 and 3.16) relationship between ocean conditions and maturation anomalies. When testing for significance across the rotated data (using the first, second and third principal components on the maturation and UPI data with and without a lag effect), the relationships between maturation anomalies and the ocean environment were not significant when performing an ANOVA. This result is different than what I observed with survival (Figure 3.7 above).

3.3.3 Localized Effects on Survival

I tested for localized SST effects on survival by using data for one stock from each cluster shown in Figure 3.4. The stocks examined were Alaska Spring, Big

Qualicum River, Columbia Upriver Bright, Salmon River (Oregon Coast), west coast Vancouver Island, Spring Creek, south Puget Sound and the Klamath. This analysis was carried out for the months of April through September (to test the hypothesis that the ocean conditions during the spring transition are important to Chinook survival), the spring transition when fish move out of the freshwater into the ocean environment. SST data for each of these stocks (regions) were collected primarily from <http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.ERSST/.version2/.SST/> and the BC lighthouse data were used for Big Qualicum River, west coast Vancouver Island, southeast Alaska spring Chinook, and Puget Sound.

Summer upwelling conditions appear to play an important role in overall survival of PNW Chinook. For most systems there is a statistically significant effect of SST at a certain time and area on survival. These effects are local in nature (Figure 3.17 and 3.18), and even though the relationships may not have a high r^2 , they are significant for six out of the eight stocks (Table 3.4; For $p < 0.1$ six stocks are significant; for $p < 0.05$ five stocks are significant). The significance of the relationships between SST and survival (Figure 3.19) is further emphasized by the uncertainty in the slope parameters (converted into a meaningful measure by multiplying by SST change). The figures indicate that the effect of a one-degree change in SST in either the positive or negative direction could have a significant effect on survival. For example, a 1°C increase in SST in July at 44°N 124°W would lead to a 0-4% decrease in survival for Oregon coastal Chinook, with the most likely decrease at around 2%.

Table 3.4 shows results of these models using both a linear and non-linear fit (equations 3.4 and 3.6). In five of the eight stocks, there is a statistically significant ($p < 0.05$) fit. In most cases, the non-linear model exhibits a better fit. The Klamath and Puget Sound stocks are marginally significant if $p < 0.1$ is used as the basis for testing significance (depending on the model chosen). For stocks for which this relationship is not significant, i.e. Klamath, south Puget Sound and Alaska spring, likelihood profiles (Figure 3.19) indicate a likely increase or decrease in survival corresponding with a decrease or increase in SST, although the distribution overlaps zero (no effect). Thus, even though Table 3.4 indicates that there is no effect from a theoretical statistical point of view, the likelihood profile still indicates a probable effect of SST on these stocks. Based on residual diagnostics, both models appear to fit the data well.

3.3.4 Building Lagged Models of Survival by Region

I investigated whether survival for two stocks, the Columbia Upriver Brights and the Oregon Coastal Chinook, was related to local conditions in a lagged fashion, using the data shown in Figure 3.17.

Using data on the ENSO (Wolter and Timlin 1998) and PDO (Mantua et al. 1997), I built a lagged model in which ENSO conditions in the tropical Pacific in May-June are used to predict PDO conditions in the following year in June. This model is statistically significant (Table 3.5). Then the June PDO results were used to predict July ocean conditions, represented by SST, in the same year at the $44^{\circ}\text{N } 124^{\circ}\text{W}$ and $48^{\circ}\text{N } 124^{\circ}\text{W}$. An intermediate step that related PDO in June to conditions between $44^{\circ}\text{N } 124^{\circ}\text{W}$ and $48^{\circ}\text{N } 124^{\circ}\text{W}$ was carried out via an analysis on the lead PCA based on COADS data (Smith and Reynolds 2004) at $42^{\circ}\text{N } 124^{\circ}\text{W}$, $44^{\circ}\text{W } 124^{\circ}\text{W}$, 46°W

N124 °W and 48 °W N 124 °W W (Table 3.5). The leading principal component (July) is regressed on PDO conditions in June (eq 3.8). Finally, the principal component (July) is related to SST in July for 44°N 124°W and 48°N124°W (Table 3.4), the two stations that are important for survival for the Oregon Coastal Chinook and Columbia Upriver Bright Chinook. Based on these models, I can forecast expected survival for spawning Chinook that outmigrate the following year based on ENSO conditions in the tropical Pacific in the year that they spawn. The relationships used are shown in Figure 3.20, and the results of a positive or negative ENSO is shown for Oregon coastal Chinook (Figure 3.21) using bootstrap techniques on parameter estimates obtained in each of the steps described in equations 3.7 through 3.10.

3.4 DISCUSSION

3.4.1 Survival and Scale

Studies similar to this one have examined the effect of large-scale phenomena on sockeye and pink salmon (Peterman et al. 2003, Mueter et al. 2002). Bradford et al. (1997) found that large-scale factors affect coho smolt survival. In addition, catch data analyzed by Hare et al. (1999) indicated a north-south regime shift in terms of salmon catches from Alaska to Oregon that oscillated in concordance with the PDO. My study employs many of the same general techniques used in these studies, but applies them to the case of Chinook salmon survival and maturation.

This study's results indicate that there is a positive correlation among survival rates in stocks that are less than 500 km apart (Figure 3.22), the strength of which decreases as distance between stocks increases. This relationship is not as strong as the one Mueter et al. (2002) observed for sockeye salmon.

In addition, survival appears to cluster regionally (Figure 3.3), and exhibits a weak relationship with ocean conditions (Figure 3.5). Local ocean conditions appear to have a large influence on survival for some stocks; juveniles are particularly affected by local conditions when they move from a freshwater to an ocean environment (Figures 3.17 and 3.18).

Finally, I demonstrate how this information could be used on various spatial scales to forecast survival (Figures 3.20 and 3.21). Thus this study attempts to relate issues of spatial and temporal scales to survival for Chinook in the way that Levin (1992) and Mackas et al. (1985) did for other marine organisms. This information could also be integrated with other biological indicators (Peterson et al. 2006, Trudel et al. 2005) to understand the ecosystem interactions that affect survival of salmon across these scales. Survival of PNW Chinook is strongly linked to global climate patterns, and this study demonstrates these connections empirically by relating a derived species-scale parameter (survival) to processes that occur on a variety of scales.

3.4.2 Maturation and Scale

Maturation appears to be linked only weakly to ocean conditions (Figure 3.12), and seems to have no geographic relationships across the regions analyzed (Figure 3.11). Figures 3.8, 3.9, and 3.10 indicate that anomalously high maturation rates tend to occur over all ages in the same years, implying that maturation is triggered by size or rate of growth (Quinn 2005). Thus, in years of good ocean conditions characterized by positive upwelling patterns year round, a higher rate of maturation than normal is observed.

An analysis of fish size, using 1997-2004 data for the upper Columbia Brights reveals similar results: in years when maturation rates are higher than average, fish are larger than average (Appendix 3.1 Figure 1), implying that maturation is a function of a critical size or growth rate for these fish in their initial ocean years. At older ages (age 4 and above, Appendix 3.1, Figure 1) this rate changes marginally. This is clearly evident for the younger fish which responded to positive ocean conditions in 1998-1999 and came back as larger fish with a higher maturation rate for that age (Appendix 3.1, Figure 3.1).

Finally, while Figure 3.12 indicates some relationship between maturation and ocean conditions, these relationships do not appear to be statistically strong (Figures 3.13, 3.14, 3.15, and 3.16).

3.4.3 Large-scale Environmental Conditions in the PNW

Figures 3.2 and 3.4 indicate that survival of stocks coastwide has oscillated over time across the entire PNW. An examination of four years (1983, 1985, 1992, and 1999) provides more evidence for this pattern. In these years, the Pacific exhibited anomalous patterns that were either detrimental (1983 and 1992, Figure 3.23) or beneficial (1985 and 1999, Figure 3.23) to survival. The right-hand panels of this figure depict more favorable conditions and the left-hand panels depict less favorable conditions. Both 1983 and 1992 exhibited lingering effects of a prolonged El Niño which brought warm water to the coastal shelf, leading to low productivity and shifts in species composition at lower trophic levels, e.g., euphausiid species with lower caloric and fat content than the typical north Pacific species (Peterson et al. 2006).

Further evidence of this is provided in Figure 3.24. Poor ocean conditions in 2005 had an adverse effect coastwide on Chinook survival (CTC 08-01). Based on the results obtained here, forecasts should predict higher than average survival for 2008 outmigrants with larger than average runs possible in 2010, 2011 and 2012 (for the 3, 4, and 5 year olds for ocean-type Chinook, and 4, 5, and 6 year olds for stream-type Chinook). These are the types of spatial and temporal patterns that can be used to infer trends in survival over the near-term.

This analysis could be taken a step further by examining the multivariate ENSO (Figure 3.20). ENSO is directly related to the PDO, which in turn affects conditions on the shelf and survival of Chinook coastwide. Thus an ENSO value in May-June would relate to a PDO value in June of the following year that could be related to local effects for the region in question. In the example displayed for the Oregon coastal and Columbia River Chinook stock, temperatures at stations north and south of the Columbia are key to survival of the Brights and Oregon coastal stock. This effect and its uncertainty can be quantified with an ENSO value for Oregon coastal Chinook (Figure 3.21).

3.5 OVERALL CONCLUSIONS

This study attempts to relate phenomena that occur across different temporal and spatial scales, and tie them to derived parameters (survival and maturation) for Chinook salmon in the Northwest. This information could be of vital importance to the overall viability of the species as it could be used to formulate early predictions of Chinook survival coastwide and incorporated into an adaptive management framework based on these projections. Principles of precautionary management (FAO 1996,

Richards and Maguire 1998) could be used as guidelines, and risk to the resource could be minimized by setting lower fishing targets when conditions are poor, so that spawning biomass would not be threatened across all areas being impacted by the ocean fisheries. These measures would remain in place until ocean conditions appeared to indicate that survival and maturation rates would be better than average. Such measures would need to include a decision analysis to assess long-term benefits to the resource, similar to what is done for numerous groundfish (*Sebastes* spp.) on the West Coast and Alaska (PFMC 2005).

List of Tables

Table 3.1: Exploitation rate indicator stocks, location, run type, and age of smolt at release.

Table 3.2: Correlations over time for survival data anomalies and ocean data anomalies for the Pacific Northwest.

Table 3.3: Correlation of stock survival with environmental station ($>|0.4|$) showing a positive (blue) or negative (yellow) relationship

Table 3.4: ANOVAs using equation (3.4) and log-transformed equation (3.6) indicating significance of ocean variable SST in months indicated in Figures 3.17 and 3.18. Each SST effect is different although for simplicity it is referred to as SST in the Table.

Table 3.5: ANOVAs using equation (3.7), equation (3.8) and equation (3.9) demonstrating significance of ENSO in predicting PDO, then the PDO in predicting conditions of the Columbia, Washington and Oregon coasts, and the then relating the PCA off the Columbia to the Oregon coast station at 44°N 124°W

Table 3.1: Exploitation rate indicator stocks, location, run type, and age of smolt at release

Origin	Stock Name	Location	Stock Acronym	Run Type	Smolt Age
S.E. Alaska	Alaska Spring	Southeast Alaska	AKS	Spring	Age 1
British Columbia	Kitsumkalum	North/Central BC	KLM	Summer	Age 1
	Robertson Creek	WCVI	RBT	Fall	Age 0
	Quinsam	Georgia Strait	QNSAM	Fall	Age 0
	Puntledge	Georgia Strait	PUNTL	Summer	Age 0
	Big Qualicum	Georgia Strait	BQR	Fall	Age 0
	Chilliwack (Harrison Stock)	Lower Fraser River	CHILLIWAC/CHI	Fall	Age 0
Puget Sound	Stillaguamish Fall Fingerling	Central Puget Sound	STL	Summer/Fall	Age 0
	George Adams Fall Fingerling	Hood Canal	GAD	Summer/Fall	Age 0
	South Puget Sound Fall Fingerling	South Puget Sound	SPSF	Summer/Fall	Age 0
	Nisqually Fall Fingerling	South Puget Sound	NIS	Summer/Fall	Age 0
	White River Spring Yearling	South Puget Sound	WSY	Spring	Age 1
Washington Coast	Queets Fall Fingerling	North Wash. Coast	QTS	Fall	Age 0
Columbia River	Cowlitz Tule	Columbia Rvr. (Lower WA)	CWF	Fall Tule	Age 0
	Spring Creek Tule	Columbia Rvr. (Mid)	SPR	Fall Tule	Age 0
	Columbia Lower River Hatchery	Columbia River (Lower OR)	LRH(Big Creek Hatchery)	Fall Tule	Age 0
	Upriver Bright	Upper Columbia Rvr. (Hanford)	URB	Fall Bright	Age 0
	Lewis River Wild Lyons Ferry ³	Lower Columbia Rvr. Snake River	LRW LYF	Fall Bright Fall Bright	Age 0 Age 0

	Willamette Spring Summers	Willamette Columbia Rvr. (Upper WA)- Wells Dam	WSH SUM	Spring Summer	Age 1 Age 1
Oregon Coast	Salmon River	North Oregon Coast	SRH (ORC)	Fall	Age 0
Southern Oregon/CA	Klamath River	Southern OR coast/ Northern CA coast	KLAM	Fall	Age 1

Table 3.2: Correlations over time for survival data anomalies and ocean data anomalies for the Pacific Northwest

a) Correlations over time using Chinook stock outmigration year as the basis

Year	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
1978	1.00																										
1979	0.00	1.00																									
1980	-0.11	-0.08	1.00																								
1981	0.09	0.44	-0.18	1.00																							
1982	0.29	0.16	-0.22	0.23	1.00																						
1983	0.08	0.20	-0.43	0.29	0.23	1.00																					
1984	-0.18	-0.13	0.03	0.38	0.07	0.39	1.00																				
1985	-0.19	0.31	0.08	0.28	0.03	0.07	0.47	1.00																			
1986	-0.20	-0.19	-0.10	0.02	-0.27	0.40	0.39	-0.02	1.00																		
1987	0.02	0.19	0.10	-0.05	0.30	-0.30	-0.45	-0.26	-0.17	1.00																	
1988	0.03	0.17	-0.14	0.18	-0.05	0.14	-0.16	-0.07	0.23	0.21	1.00																
1989	0.23	-0.08	-0.21	-0.04	0.28	-0.01	-0.38	-0.27	0.00	0.47	0.18	1.00															
1990	-0.02	-0.03	0.08	-0.08	-0.19	-0.33	-0.29	0.05	-0.07	0.33	0.35	0.53	1.00														
1991	-0.16	0.28	0.26	-0.04	-0.34	-0.32	0.09	0.17	-0.21	0.10	0.09	-0.35	0.24	1.00													
1992	-0.07	0.08	0.14	0.07	-0.51	-0.13	-0.03	0.01	0.44	-0.21	-0.02	-0.24	-0.09	-0.16	1.00												
1993	-0.29	-0.17	0.25	-0.25	-0.06	-0.23	0.09	-0.12	0.02	-0.01	-0.55	-0.33	-0.55	0.18	0.12	1.00											
1994	-0.19	-0.31	-0.05	-0.18	-0.21	0.06	0.32	0.15	-0.08	-0.13	-0.25	-0.37	-0.04	0.43	-0.41	0.10	1.00										
1995	0.16	-0.45	-0.01	-0.32	-0.03	-0.44	-0.22	-0.14	-0.25	0.26	-0.18	0.40	0.61	0.19	-0.20	-0.01	0.28	1.00									
1996	0.14	-0.20	-0.41	-0.05	-0.04	0.41	0.23	0.10	0.06	-0.52	-0.49	-0.05	-0.35	-0.34	0.03	0.11	0.13	-0.09	1.00								
1997	-0.14	-0.22	-0.12	-0.32	0.31	-0.23	-0.24	-0.16	-0.29	0.10	-0.32	-0.15	-0.22	-0.29	-0.04	0.39	-0.09	0.16	0.21	1.00							
1998	-0.11	-0.28	0.00	-0.06	-0.21	-0.13	0.21	-0.06	0.20	-0.53	-0.11	-0.31	-0.35	0.15	0.04	0.39	0.16	-0.19	0.06	-0.18	1.00						
1999	-0.28	-0.52	-0.05	-0.64	-0.23	-0.16	-0.25	-0.18	0.05	0.00	-0.24	0.02	-0.07	-0.19	-0.18	0.21	0.42	0.13	0.08	0.19	0.30	1.00					
2000	-0.31	0.52	0.12	-0.06	-0.07	-0.03	-0.20	0.11	0.04	0.46	0.31	0.17	0.33	0.38	-0.07	-0.10	-0.10	-0.17	-0.52	-0.35	-0.12	0.10	1.00				
2001	-0.41	-0.16	-0.15	-0.43	-0.20	-0.23	-0.32	-0.11	-0.04	0.01	-0.06	0.00	0.11	0.11	-0.23	0.22	0.20	0.13	-0.15	0.12	0.42	0.71	0.38	1.00			
2002	-0.20	-0.37	0.27	-0.32	-0.49	-0.29	-0.15	-0.18	0.09	-0.12	0.36	-0.02	0.42	0.12	-0.04	-0.33	0.07	0.03	-0.34	-0.22	0.23	0.41	0.25	0.44	1.00		
2003	-0.19	-0.41	-0.18	-0.07	0.03	-0.17	-0.05	-0.30	0.20	-0.11	-0.17	-0.16	-0.44	-0.45	0.19	0.43	-0.17	-0.11	0.15	0.58	0.31	0.27	-0.51	0.25	-0.05	1.00	
2004	0.12	-0.20	0.10	-0.06	0.25	-0.36	-0.22	-0.26	-0.26	0.31	-0.22	-0.05	-0.23	-0.18	0.12	0.49	-0.31	0.22	-0.02	0.72	-0.24	-0.14	-0.40	-0.13	-0.31	0.57	1.00

b) Correlations over time using Ocean spring transition year as the basis

Year	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
1978	1.00																										
1979	0.05	1.00																									
1980	0.16	-0.39	1.00																								
1981	0.18	-0.58	-0.11	1.00																							
1982	-0.13	0.31	0.41	-0.44	1.00																						
1983	-0.08	0.53	-0.43	-0.22	0.24	1.00																					
1984	0.00	0.20	-0.07	-0.03	-0.41	-0.23	1.00																				
1985	-0.43	0.03	-0.13	0.04	-0.02	0.03	0.19	1.00																			
1986	-0.08	-0.31	-0.21	0.59	-0.41	-0.25	0.08	0.31	1.00																		
1987	-0.57	-0.29	0.15	0.11	0.25	-0.15	-0.35	0.44	0.22	1.00																	
1988	-0.10	-0.02	-0.48	0.40	-0.52	-0.08	0.38	0.24	0.59	-0.12	1.00																
1989	-0.39	0.29	-0.33	-0.44	0.23	0.58	-0.15	0.33	-0.22	-0.01	-0.12	1.00															
1990	0.02	-0.37	-0.19	0.51	-0.57	0.03	0.24	0.32	0.46	-0.17	0.48	0.20	1.00														
1991	-0.09	0.04	0.48	-0.55	0.47	0.01	-0.27	-0.24	-0.51	-0.11	-0.34	0.01	-0.39	1.00													
1992	0.00	-0.09	0.38	-0.05	0.46	-0.16	-0.17	0.03	-0.35	0.07	-0.29	-0.08	-0.19	0.47	1.00												
1993	0.19	-0.57	0.29	0.36	-0.19	-0.42	-0.07	-0.04	0.07	0.07	-0.25	-0.13	0.17	-0.19	0.30	1.00											
1994	0.18	-0.16	-0.23	0.48	-0.51	0.08	0.29	-0.11	0.16	-0.20	0.44	-0.49	0.21	-0.21	-0.19	-0.09	1.00										
1995	-0.30	-0.39	0.18	0.10	0.29	0.19	-0.59	0.05	-0.18	0.44	-0.35	0.22	0.10	0.23	0.47	0.17	-0.17	1.00									
1996	-0.08	-0.50	0.43	0.11	-0.03	-0.54	0.16	0.07	-0.30	0.12	-0.27	-0.15	0.03	0.10	0.54	0.71	-0.07	0.25	1.00								
1997	0.01	0.09	-0.16	-0.31	-0.45	0.08	0.46	-0.07	-0.12	-0.53	0.21	0.35	0.43	-0.01	-0.31	-0.11	-0.05	-0.23	-0.08	1.00							
1998	0.12	0.22	0.16	-0.61	0.07	-0.10	0.12	-0.04	-0.14	-0.22	-0.34	0.31	-0.12	0.19	-0.04	0.11	-0.49	-0.23	0.02	0.37	1.00						
1999	-0.20	-0.20	-0.23	0.31	-0.23	-0.03	-0.16	-0.12	0.27	0.35	0.14	-0.38	-0.13	-0.20	-0.31	-0.32	0.40	0.07	-0.29	-0.20	-0.39	1.00					
2000	-0.17	-0.25	0.03	-0.01	-0.18	-0.16	-0.18	-0.15	0.07	0.03	0.15	0.01	0.07	0.21	0.01	0.29	0.06	0.04	0.10	0.11	0.10	-0.21	1.00				
2001	0.00	-0.17	-0.15	0.33	-0.13	-0.24	0.08	-0.24	0.12	0.14	0.28	-0.49	-0.29	-0.28	-0.19	-0.15	0.52	-0.20	-0.01	-0.27	-0.44	0.64	-0.16	1.00			
2002	-0.27	0.10	-0.59	0.12	-0.53	0.12	0.42	-0.06	0.16	-0.18	0.63	0.02	0.29	-0.31	-0.53	-0.44	0.45	-0.34	-0.32	0.49	-0.29	0.45	0.02	0.42	1.00		
2003	-0.18	0.05	-0.25	-0.18	-0.08	-0.21	0.13	-0.31	-0.25	-0.11	0.14	-0.01	-0.36	0.01	-0.07	0.12	0.10	-0.31	0.24	0.08	-0.01	-0.09	0.41	0.46	0.33	1.00	
2004	-0.40	-0.08	-0.06	-0.42	-0.05	0.13	-0.10	0.25	-0.24	0.01	-0.14	0.63	0.27	0.31	0.22	0.12	-0.35	0.40	0.20	0.51	0.42	-0.27	0.37	-0.55	-0.02	-0.02	1.00

Table 3.3: Correlation of stock survival with environmental station (>10.4l) showing a positive (blue) or negative (yellow) relationship

	AKSP	KLM	RBT	NSAM	PUNTI	BQR	ILLIM	GAD	SPSF	NIS	WRY	QTS	WSH	CWF	SPR	LRH	LRW	URB	SUM	SRH	KLAM
A42N125W	-0.06	0.08	0.12	-0.08	0.28	-0.09	0.01	0.11	0.11	-0.11	0.17	0.57	0.06	0.03	0.49	0.13	0.01	0.04	0.57	0.18	-0.01
A45N125W	0.08	0.07	0.38	0.14	0.27	0.17	0.23	0.24	0.04	-0.22	0.21	0.51	0.32	0.09	0.38	0.21	0.09	0.00	0.28	0.22	-0.13
A48N125W	0.17	0.03	0.41	0.23	0.25	0.22	0.27	0.27	0.03	-0.21	0.20	0.39	0.36	0.12	0.31	0.26	0.07	-0.02	0.18	0.21	-0.12
A51N131W	0.18	0.02	0.31	0.16	0.25	0.10	0.13	0.22	-0.25	-0.33	0.13	0.20	0.30	0.01	0.35	0.24	-0.08	-0.06	0.30	0.10	-0.19
A54N134W	0.21	-0.02	0.03	-0.02	0.10	0.08	-0.11	-0.05	-0.55	-0.38	0.11	-0.02	0.08	-0.06	0.30	0.06	-0.28	0.00	0.15	-0.07	-0.18
A57N137W	0.23	-0.06	-0.08	-0.12	0.08	0.08	-0.29	-0.14	-0.48	-0.40	-0.22	0.00	-0.12	-0.01	0.20	0.01	-0.41	0.12	0.12	-0.12	-0.11
A60N146W	0.35	0.37	-0.06	0.24	0.38	0.29	0.08	0.16	0.05	-0.18	0.26	0.27	-0.02	0.23	0.49	0.31	-0.11	0.31	0.55	0.22	0.06
A60N149W	0.25	0.39	0.09	0.13	0.42	0.30	0.15	0.12	0.02	-0.15	0.23	0.29	0.11	-0.01	0.56	0.09	-0.12	0.13	0.60	0.26	-0.06
M42N125W	-0.21	0.07	-0.01	0.13	0.05	-0.01	0.19	0.03	0.08	0.14	-0.29	-0.13	-0.15	-0.28	0.23	-0.05	-0.16	-0.21	0.32	-0.01	-0.28
M45N125W	-0.23	0.12	-0.08	0.20	-0.06	0.07	0.14	-0.15	0.00	-0.06	-0.31	-0.32	-0.14	-0.25	-0.03	-0.08	-0.20	-0.14	-0.02	-0.04	-0.31
M48N125W	0.02	0.42	0.12	0.50	0.07	0.42	0.37	-0.03	0.15	-0.09	-0.14	-0.35	0.12	-0.06	0.07	0.06	-0.04	0.08	-0.11	0.00	-0.28
M51N131W	-0.40	-0.03	0.02	0.09	0.05	0.03	0.13	-0.41	0.00	0.12	-0.51	-0.41	-0.17	-0.24	-0.08	-0.01	-0.33	-0.18	-0.17	-0.17	-0.17
M54N134W	-0.05	-0.24	-0.13	0.07	-0.09	0.07	-0.08	-0.38	-0.26	-0.08	-0.28	-0.43	-0.24	0.04	-0.37	-0.07	-0.31	0.05	-0.54	-0.27	0.09
M57N137W	0.02	-0.27	-0.14	0.04	-0.08	0.10	-0.12	-0.38	-0.27	-0.11	-0.18	-0.36	-0.27	0.10	-0.44	-0.13	-0.28	0.09	-0.59	-0.30	0.16
M60N146W	-0.10	-0.16	-0.07	0.05	0.23	-0.15	0.10	-0.20	-0.24	0.05	-0.34	-0.27	-0.33	-0.04	-0.27	0.06	-0.28	-0.21	0.07	-0.42	0.30
M60N149W	-0.08	-0.09	-0.13	0.04	0.35	-0.12	-0.03	-0.15	-0.25	-0.04	-0.23	-0.20	-0.27	-0.13	-0.23	0.01	-0.32	-0.20	0.28	-0.28	0.35
J42N125W	-0.09	0.00	-0.19	0.09	0.14	-0.08	-0.08	-0.13	-0.03	0.04	-0.28	-0.20	-0.17	0.00	-0.21	0.03	0.10	-0.06	0.16	0.01	0.31
J45N125W	0.27	0.27	-0.10	0.54	0.17	0.25	0.18	0.20	0.19	-0.05	-0.05	-0.13	0.05	0.25	-0.20	0.21	0.24	0.13	0.09	0.15	0.44
J48N125W	-0.06	0.01	-0.21	0.07	0.38	-0.03	-0.13	-0.18	-0.10	-0.11	-0.21	-0.09	-0.08	-0.14	-0.21	-0.11	-0.13	-0.22	0.29	0.09	0.47
J51N131W	-0.01	0.04	-0.41	0.05	0.30	0.02	-0.22	-0.24	-0.28	-0.16	-0.10	-0.20	-0.21	-0.13	-0.21	-0.14	-0.33	-0.14	0.19	0.01	0.45
J54N134W	0.00	0.04	-0.54	-0.04	0.28	-0.03	-0.36	-0.29	-0.39	-0.20	-0.08	-0.20	-0.32	-0.13	-0.11	-0.13	-0.46	-0.07	0.28	0.01	0.38
J57N137W	-0.10	-0.22	-0.59	-0.19	0.13	-0.21	-0.46	-0.36	-0.46	-0.23	-0.19	-0.21	-0.43	-0.13	-0.19	-0.11	-0.52	-0.06	0.13	-0.02	0.31
J60N146W	-0.11	-0.24	-0.53	-0.15	0.11	-0.21	-0.36	-0.32	-0.46	-0.23	-0.24	-0.21	-0.38	-0.14	-0.18	-0.11	-0.53	-0.09	0.09	-0.02	0.28
J60N149W	-0.54	-0.29	-0.09	-0.45	-0.09	-0.44	-0.14	-0.13	-0.13	0.46	-0.38	0.02	-0.26	-0.47	0.33	-0.14	-0.29	-0.47	0.45	-0.20	-0.03
JU42N125W	-0.10	-0.14	-0.21	-0.35	0.15	-0.35	-0.14	-0.02	-0.19	0.14	-0.09	0.17	-0.21	-0.21	0.34	-0.06	-0.09	-0.18	0.65	0.13	0.13
JU45N125W	-0.02	-0.26	-0.27	-0.30	0.03	-0.33	-0.27	-0.27	-0.28	-0.23	-0.07	0.25	-0.46	0.10	-0.06	0.09	-0.12	0.20	0.19	0.13	0.03
JU48N125W	0.31	-0.12	-0.04	0.01	0.10	-0.17	-0.10	-0.06	-0.08	-0.36	0.18	0.28	-0.18	0.47	-0.21	0.40	0.16	0.37	-0.05	0.14	0.06
JU51N131W	-0.24	-0.15	-0.23	-0.30	0.21	-0.40	-0.20	-0.49	-0.04	-0.05	-0.14	-0.12	-0.28	-0.13	-0.15	-0.09	-0.13	-0.20	0.03	-0.19	-0.11
JU54N134W	-0.17	0.13	0.00	-0.09	0.27	-0.26	0.05	-0.40	0.28	0.09	-0.10	-0.20	-0.08	-0.01	-0.17	0.08	0.10	-0.16	0.03	-0.08	-0.01
JU57N137W	-0.32	0.21	0.21	-0.09	0.17	-0.36	0.16	-0.25	0.33	0.18	-0.18	-0.33	0.11	-0.12	-0.13	0.22	0.14	-0.25	0.03	-0.14	-0.20
JU60N146W	-0.17	0.09	0.16	-0.16	0.16	-0.36	0.19	-0.16	0.07	0.08	0.07	-0.15	0.06	-0.16	-0.16	-0.02	0.13	-0.37	0.06	-0.21	0.01
JU60N149W	-0.08	-0.03	0.18	-0.12	0.35	-0.40	0.30	0.02	-0.03	-0.01	-0.03	0.00	0.19	-0.19	0.18	0.02	0.16	-0.34	0.30	-0.10	-0.16
40N124WSSTSEP	0.04	0.02	-0.26	0.20	-0.03	0.34	0.04	-0.07	0.03	0.08	-0.02	-0.22	-0.31	0.05	0.03	0.03	-0.36	0.29	-0.27	-0.07	-0.20
44N124WSSTJUL	-0.19	0.02	-0.04	-0.03	-0.35	0.08	-0.02	-0.03	-0.20	0.10	-0.09	-0.41	-0.02	-0.27	0.00	-0.12	-0.36	-0.28	-0.28	-0.44	-0.24
46N124WSSTAPR	-0.16	-0.08	-0.25	-0.19	-0.03	0.05	-0.36	-0.32	-0.25	-0.05	0.00	-0.42	-0.12	-0.35	-0.33	-0.42	-0.23	-0.29	-0.28	-0.36	-0.14
48N124WJUL	-0.41	0.07	-0.08	-0.15	-0.29	0.04	0.02	-0.19	-0.16	0.20	-0.23	-0.40	0.01	-0.46	0.13	-0.28	-0.36	-0.40	-0.18	-0.33	-0.27
RR-June	-0.14	0.30	-0.10	0.00	-0.07	0.05	0.00	0.15	-0.09	0.18	0.14	-0.18	0.12	-0.25	0.13	-0.04	-0.03	-0.27	0.15	-0.26	0.04
Amphitrite Pt-June	0.06	-0.13	-0.34	-0.08	-0.11	0.17	-0.39	-0.25	-0.10	0.06	-0.01	-0.51	-0.08	-0.13	-0.28	-0.28	-0.25	0.03	-0.45	-0.17	-0.09
Chrome Island-August	-0.14	-0.17	-0.24	-0.04	0.24	-0.01	-0.23	-0.02	0.11	0.26	-0.01	-0.09	-0.28	-0.25	-0.11	-0.30	-0.28	-0.18	0.17	-0.30	0.27
Langara Island-Sep	-0.10	-0.36	-0.15	-0.11	0.34	-0.06	0.02	-0.17	-0.14	-0.01	-0.33	-0.25	-0.37	-0.39	-0.08	-0.38	-0.57	-0.18	0.05	-0.12	-0.42

Table 3.4: ANOVAs using equation (3.4) and log-transformed equation (3.6) indicating significance of ocean variable SST in months indicated in Figures 3.17 and 3.18 Each SST effect is different although for simplicity it is referred to as SST in the Table.

LINEAR MODELS (eq. 3.4)						NON-LINEAR MODELS (eq. 3.6)					
Klamath						Klamath					
	Df	SS	MSE	F	Pr(>F)		Df	SS	MSE	F	Pr(>F)
SST	1	0.0006	0.0006	1.43	0.25	SST	1	4.61	4.61	2.86	0.11
Residuals	20	0.0086	0.0004			Residuals	20	32.23	1.61		
Oregon Coast						Oregon Coast					
	Df	SS	MSE	F	Pr(>F)		Df	SS	MSE	F	Pr(>F)
SST	1	0.0058	0.0058	7.9	0.01	SST	1	3.92	3.92	6.77	0.02
Residuals	26	0.0192	0.0007			Residuals	26	15.08	0.58		
Spring Creek (Lower Columbia Tules)						Spring Creek (Lower Columbia Tules)					
	Df	SS	MSE	F	Pr(>F)		Df	SS	MSE	F	Pr(>F)
SST	1	0.003	0.003	8.35	0.01	SST	1	7.59	7.59	6.79	0.01
Residuals	30	0.011	0.000			Residuals	30	33.54	1.12		
Upriver Brights						Upriver Brights					
	Df	SS	MSE	F	Pr(>F)		Df	SS	MSE	F	Pr(>F)
SST	1	0.001	0.001	6.02	0.02	SST	1	8.09	8.09	9.26	0.01
Residuals	26	0.006	0.000			Residuals	26	22.72	0.87		
South Puget Sound						South Puget Sound					
	Df	SS	MSE	F	Pr(>F)		Df	SS	MSE	F	Pr(>F)

SST	1	0.001	0.001	3.07	0.09
Residuals	29	0.010	0.000		
West Coast of Vancouver Island					
	Df	SS	MSE	F	Pr(>F)
SST	1	0.009	0.009	4.44	0.04
Residuals	29	0.060	0.002		
Georgia Straits (Big Qualicum River)					
	Df	SS	MSE	F	Pr(>F)
SST	1	0.016	0.016	8.65	0.01
Residuals	29	0.053	0.002		
Alaska Spring Chinook					
	Df	SS	MSE	F	Pr(>F)
SST	1	0.004	0.004	1.51	0.23
Residuals	22	0.063	0.003		

SST	1	0.58	0.58	0.96	0.34
Residuals	29	17.49	0.60		
West Coast of Vancouver Island					
	Df	SS	MSE	F	Pr(>F)
SST	1	19.80	19.80	9.47	0.00
Residuals	29	60.60	2.09		
Georgia Straits (Big Qualicum River)					
	Df	SS	MSE	F	Pr(>F)
SST	1	13.94	13.94	6.08	0.02
Residuals	29	66.45	2.29		
Alaska Spring Chinook					
	Df	SS	MSE	F	Pr(>F)
SST	1	0.69	0.69	2.04	0.17
Residuals	22	7.46	0.34		

Table 3.5: ANOVAs using equation (3.7), equation (3.8) and equation (3.9) demonstrating significance of ENSO in predicting PDO, then the PDO in predicting conditions of the Columbia, Washington and Oregon coasts, and the then relating the PCA off the Columbia to the Oregon coast station at 44°N 124°W

ANOVA on equation (3.7)					
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Pr(>F)</i>
ENSO(t-1)	1	13.67	13.67	12.94	0.001
Residual	53	56.00	1.06		
ANOVA on equation (3.8)					
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Pr(>F)</i>
PDO(t)	1	6.47	6.47	20.24	3.67E-05
Residual	54	17.27	0.32		
ANOVA on equation (3.9)					
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Pr(>F)</i>
Columbia (t)	1	13.00	13.00	1515.84	2.93E-25
Residual	27	0.23	0.01		

List of Figures

Figure 3.1: Chinook Populations tracked with coded wire tags. Some locations (such as Puget Sound or Columbia) have multiple tag codes.

Figure 3.2: Survival rescaled to survival anomalies by area. Red indicates lesser than average survival and a blue denotes higher than average survival for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1. White areas denote missing data.

Figure 3.3: Cluster Analysis exploring survival anomalies by region. Refer to Table 3.1 for stock and region acronyms. Each circle denotes a broad scale region where survival anomalies seem to correspond to numerous stocks.

Figure 3.4: Absolute survival for clustered regions shown in Figure 3.3.

Figure 3.5: CWT survival data and ocean upwelling data clusters by time period. Arrows indicate similarities across ocean conditions and Chinook survival.

Figure 3.6: Spring upwelling (green) and fish survival (red) across the Pacific Northwest between 1981 and 2004.

Figure 3.7: Significant relationship between the third principal component loadings on survival and ocean conditions.

Figure 3.8: Maturation for age 2 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.

Figure 3.9: Maturation for age 3 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.

Figure 3.10: Maturation for age 4 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.

Figure 3.11: Regional based cluster analysis on maturation rates by ocean age. Stocks are identified by the three-letter acronym shown in Table 3.1.

Figure 3.12: Yearly clusters based on maturation rates by ocean age. Arrows indicate similarity across ages.

Figure 3.13: Lag 1 effects on maturation anomalies using PCA (displaying only the 1st PC).

Figure 3.14: Lag 1 effects on maturation anomalies using PCA (displaying the first three PCs). The upwelling data (green) and maturation by age (red) is shown for each age separately.

Figure 3.15: Same-year effects on maturation anomalies using PCA (displaying only the first PC).

Figure 3.16: Same-year effects on maturation anomalies using PCA (displaying the first three PCs). The upwelling data (green) and maturation by age (red) is shown for each age separately.

Figure 3.17: Relationship between survival and SST for Klamath, Salmon River (Oregon Coastal Chinook), Spring Creek Tules (Columbia) and the Columbia Upriver Brights. The SST was obtained from COADS database for locations near the coastal shelf and were the most highly correlated with survival during the first few months after smolts emigrate into the ocean. Stations reported are 40°N 124°W, 44°N 124°W, 46°N 124°W and 48°N 124°W. Linear fits (solid) and non-linear fits (dashed line) are shown for each set of data.

Figure 3.18: Relationship between survival and SST for Puget Sound, West Coast of Vancouver Island (WCVI), Georgia Straits and South East Alaska (SEAK). The SST was obtained from BC lighthouse database for nearest locations that could be used as surrogates for these systems. Linear fits (solid) and non-linear fits (dashed line) are shown for each set of data.

Figure 3.19: Rescaled likelihood profiles of the Beta parameter as a function of a one-degree change in SST at each of the locations specified in Figures 3.17 and 3.18. A 1°C increase in SST (solid line) indicates the absolute amount of decrease in overall survival might be expected for the stock, whereas a 1°C decrease in SST (dashed line) indicates the absolute increase in survival that might be expected for a particular stock. These figures assume a linear fit.

Figure 3.20: Lag time effects from different scales affecting survival at the local scale for the Columbia and Oregon coast Chinook stocks. The top left panel relates ENSO conditions the previous year to PDO conditions in the current year, the top right panel relates June PDO conditions in the NE Pacific to conditions off the Washington and Oregon coast in the vicinity of the Columbia, and the bottom two panels relate conditions off the Columbia to sea surface temperatures that are related to survival of Columbia Bright and Oregon coastal Chinook.

Figure 3.21: The effect of a positive or negative ENSO on Oregon Coastal Chinook survival.

Figure 3.22: Correlation analysis displaying correlation between stocks and regions as a function of distance.

Figure 3.23: Four distinct patterns of environmental conditions that may have consequential impacts on PNW Chinook survival during the spring transition period (April through July). The upper and lower left hand panel shows warmer than average conditions indicating poor upwelling in 1983 and 1992 impacting survival coast-wide (Figures 3.2 and 3.4). The right hand panels indicate cooler than average conditions in 1985 and 1999 that had a positive effect on survival coast-wide (Figure 3.4).

Figure 3.24: Conditions in 2005 to 2008 during spring transition.

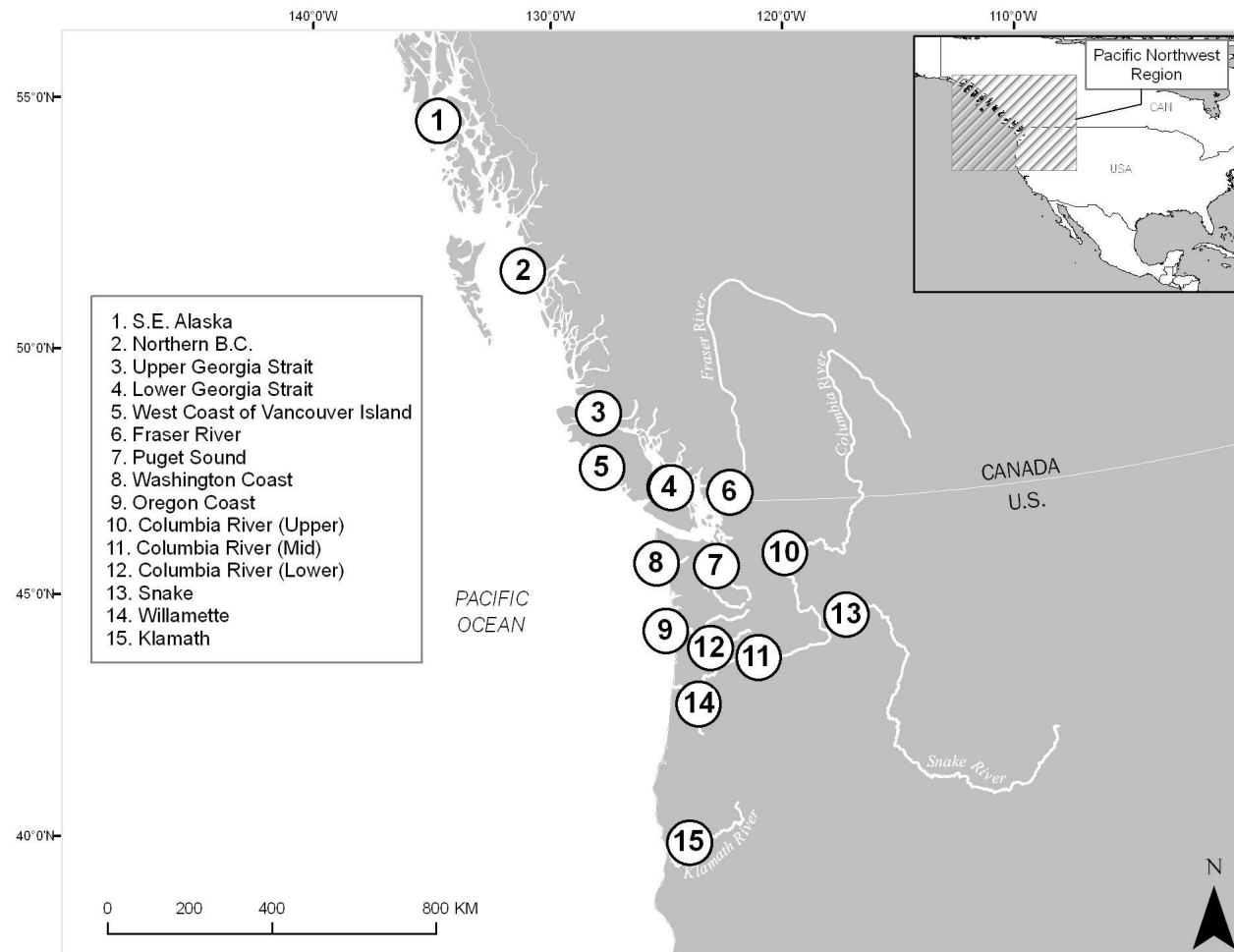


Figure 3.1: Chinook Populations tracked with coded wire tags. Some locations (such as Puget Sound or Columbia) have multiple tag codes.

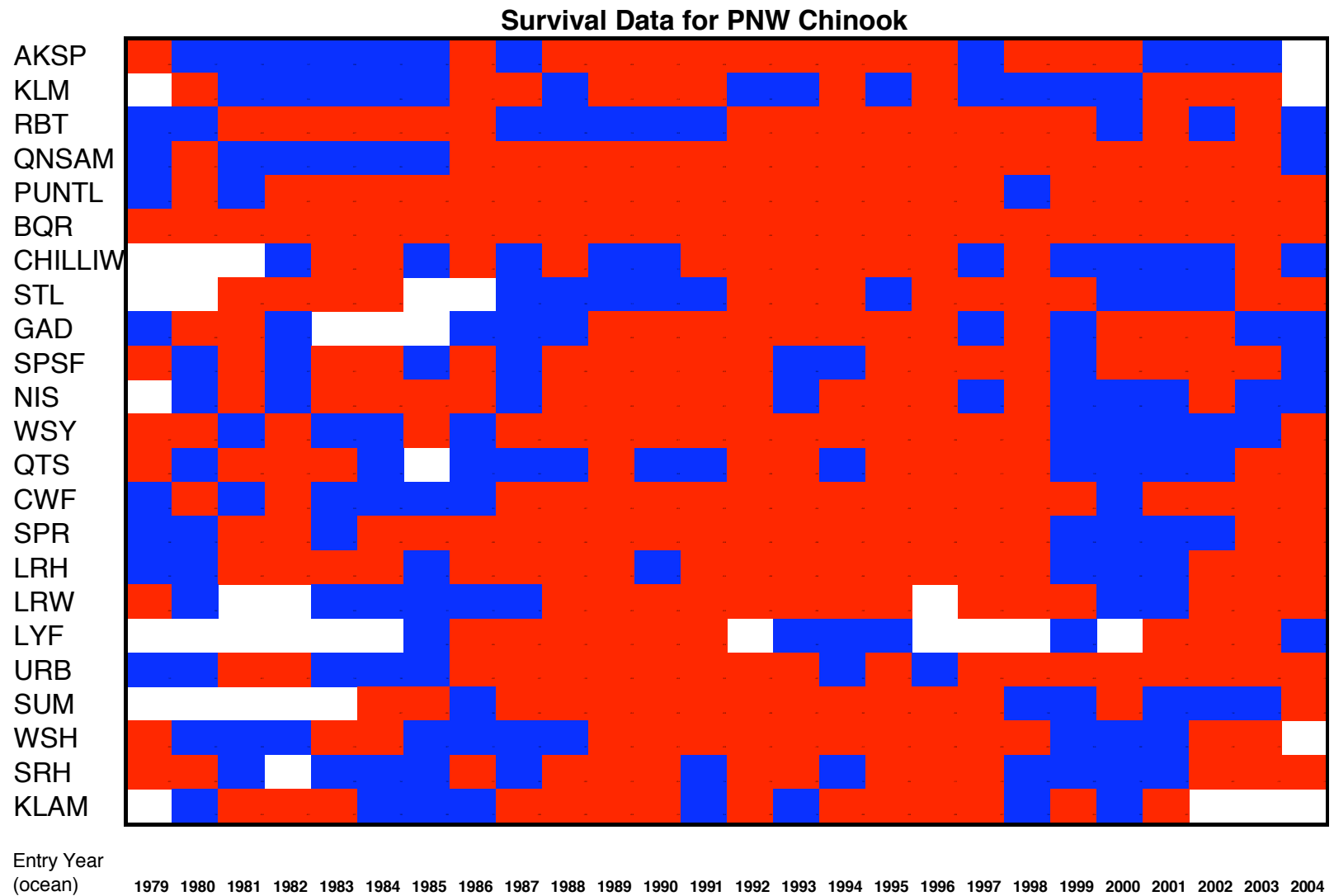


Figure 3.2: Survival rescaled to survival anomalies by area. Red indicates lesser than average survival and a blue denotes higher than average survival for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3,1. White areas denote missing data

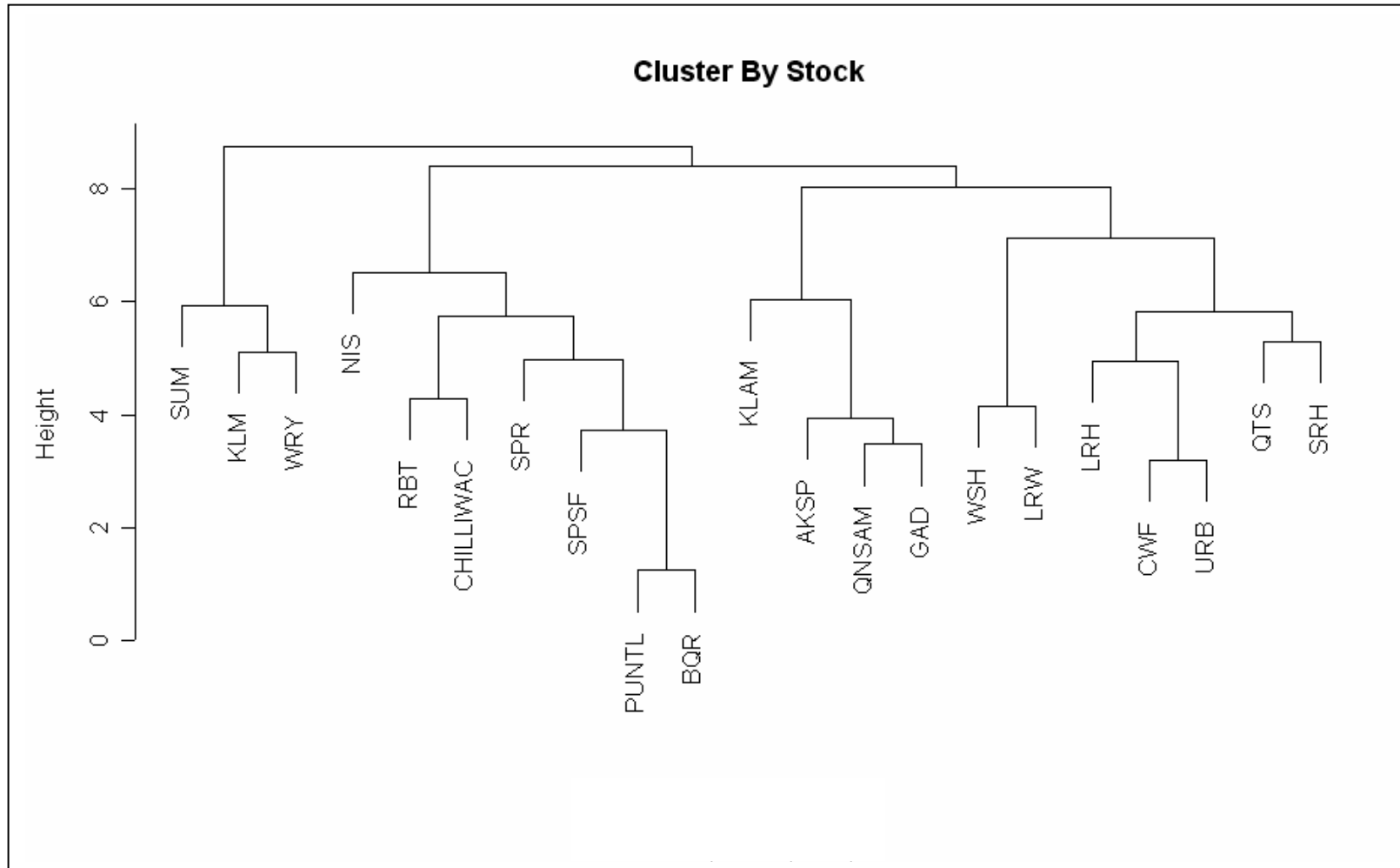


Figure 3.3: Cluster Analysis exploring survival anomalies by region. Refer to Table 3.1 for stock and region acronyms. Each circle denotes a broad scale region where survival anomalies seem to correspond to numerous stocks.

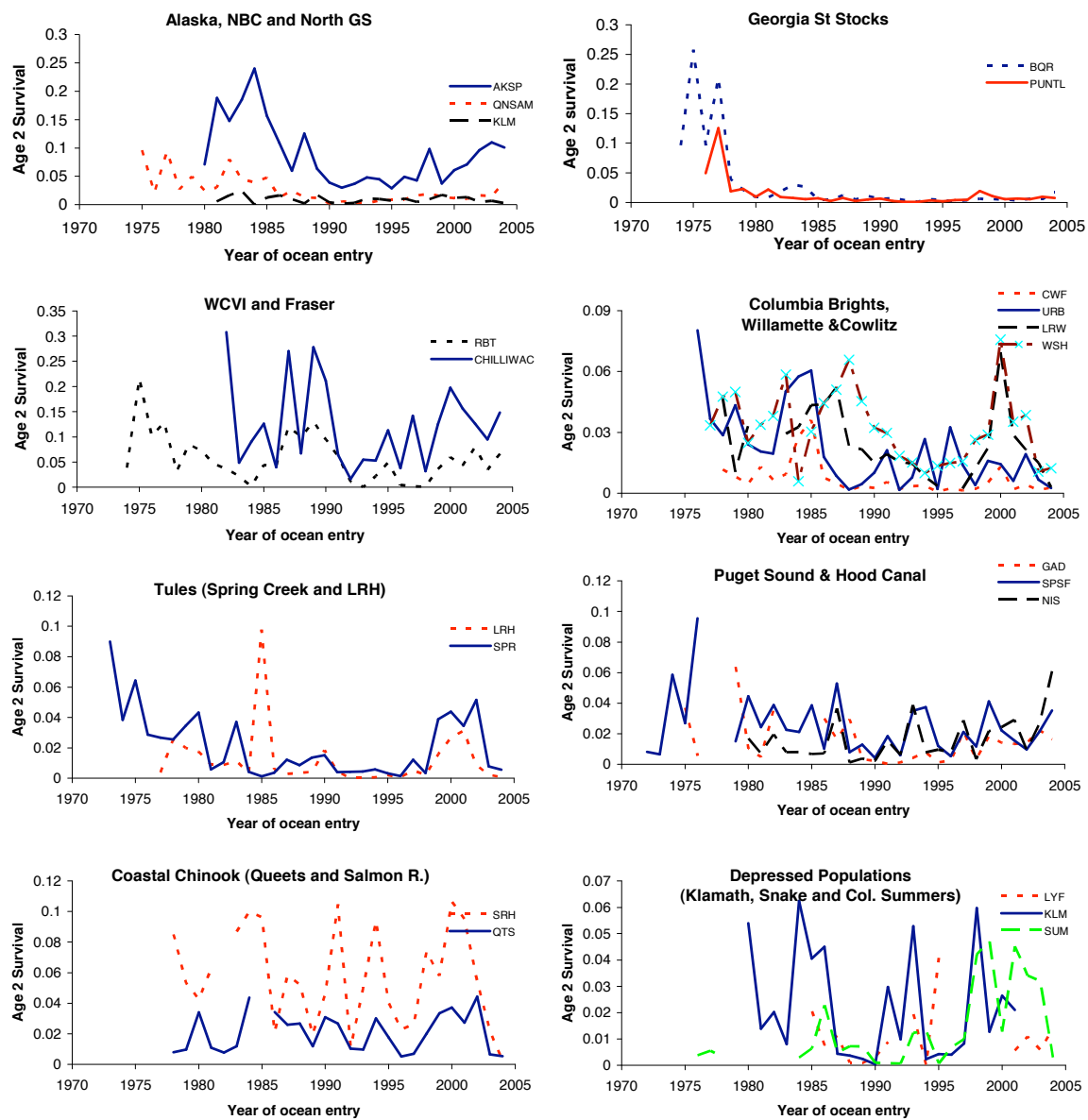


Figure 3.4: Absolute survival for clustered regions shown in Figure 3.3.

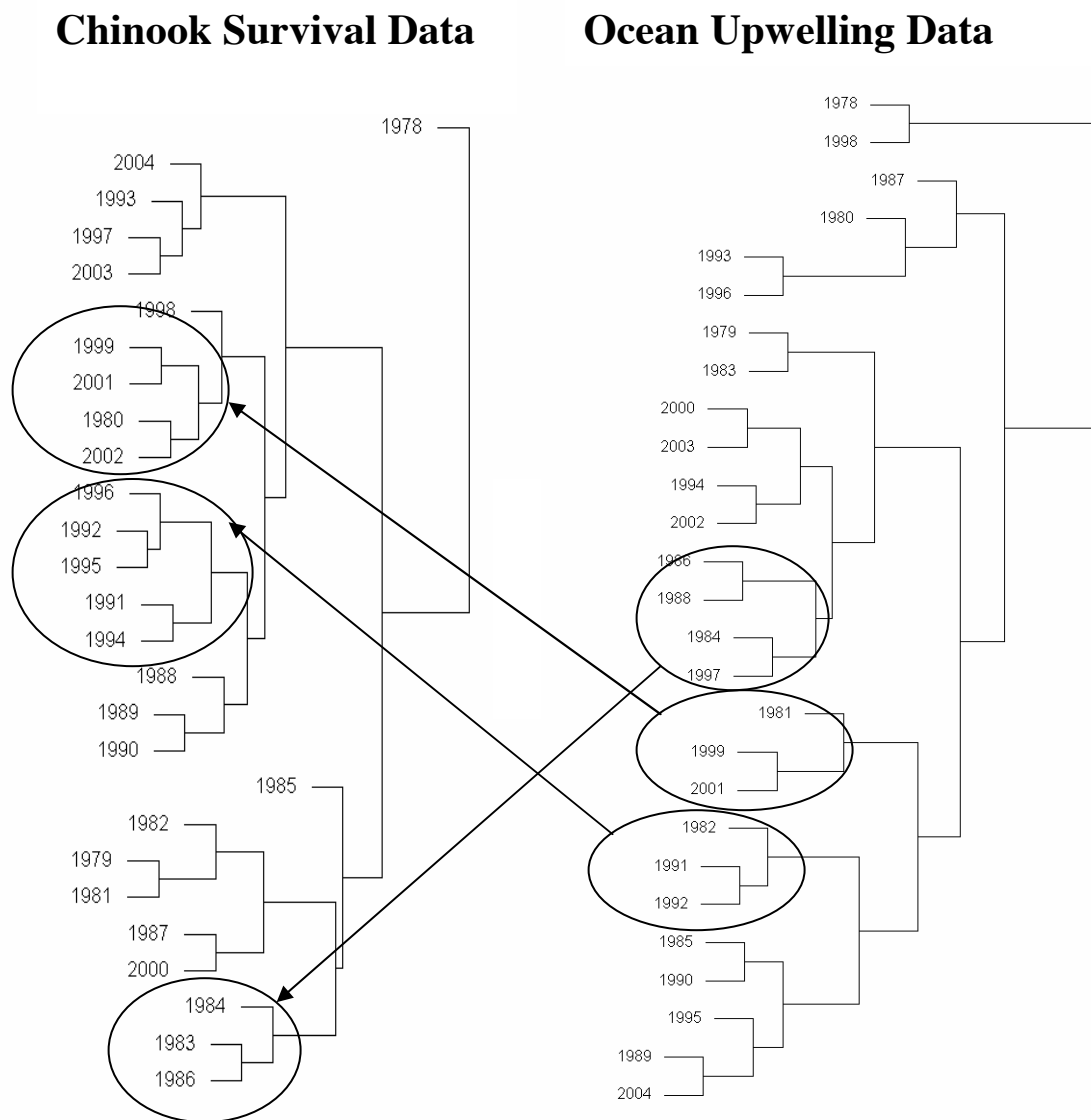


Figure 3.5: CWT survival data and ocean upwelling data clusters by time period. Arrows indicate similarities across ocean conditions and Chinook survival.

Ocean and Survival Data on 1st 3 Principle Components

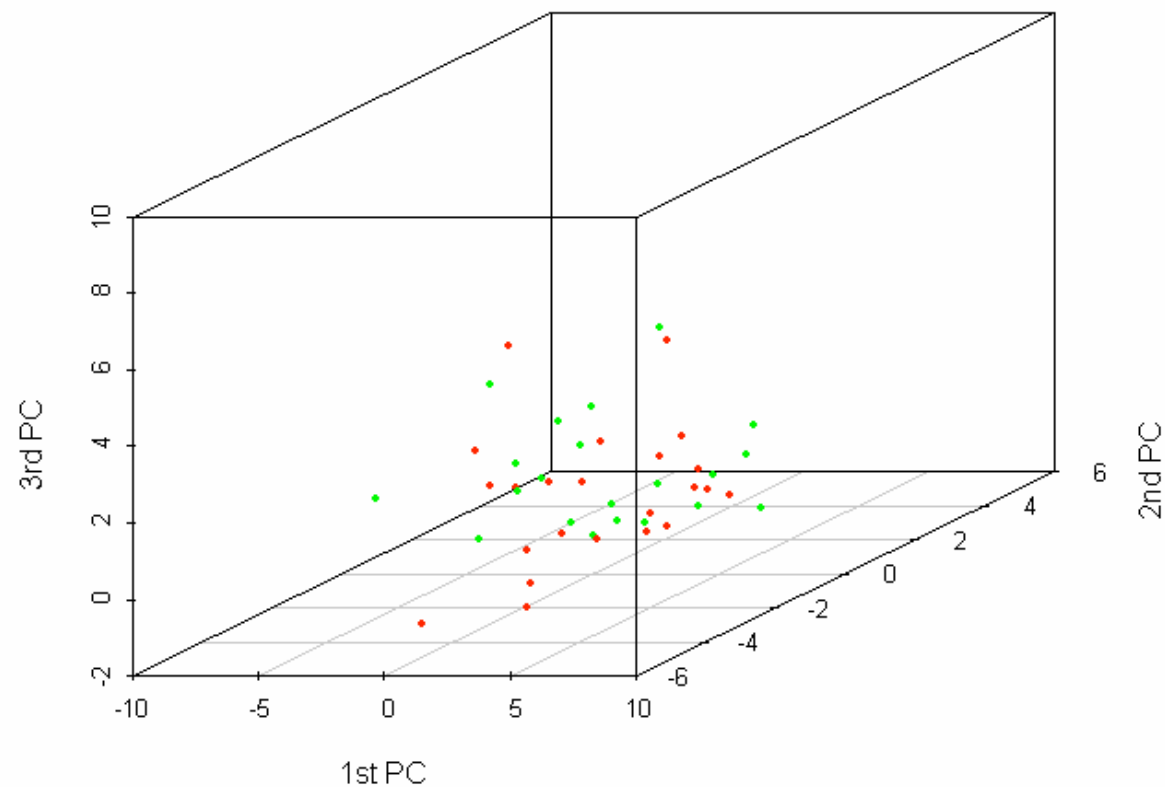


Figure 3.6: Spring upwelling (green) and fish survival (red) across the Pacific Northwest between 1981 and 2004 using the PC loadings.

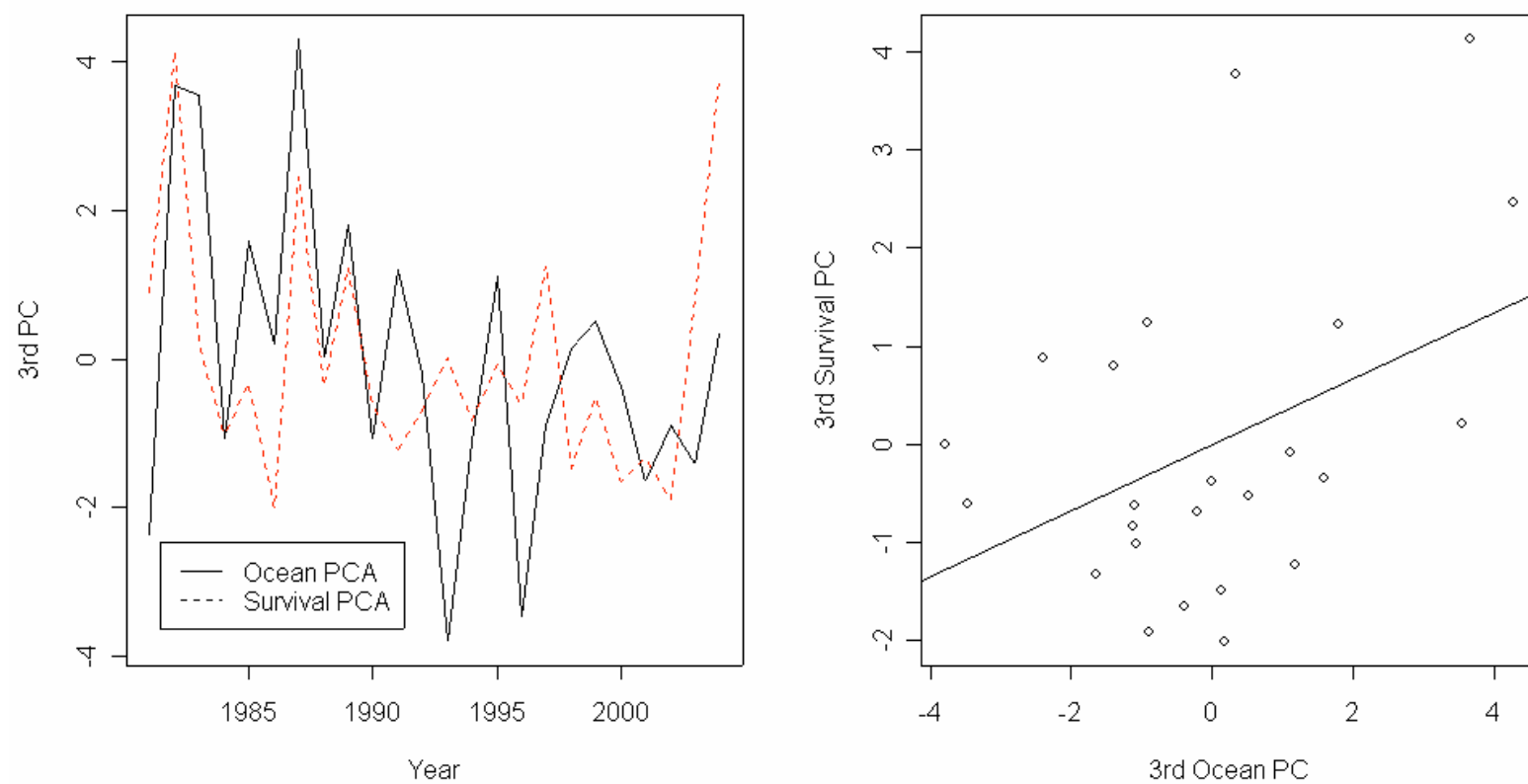


Figure 3.7: Significant relationship between the third principal component loadings on survival and ocean conditions

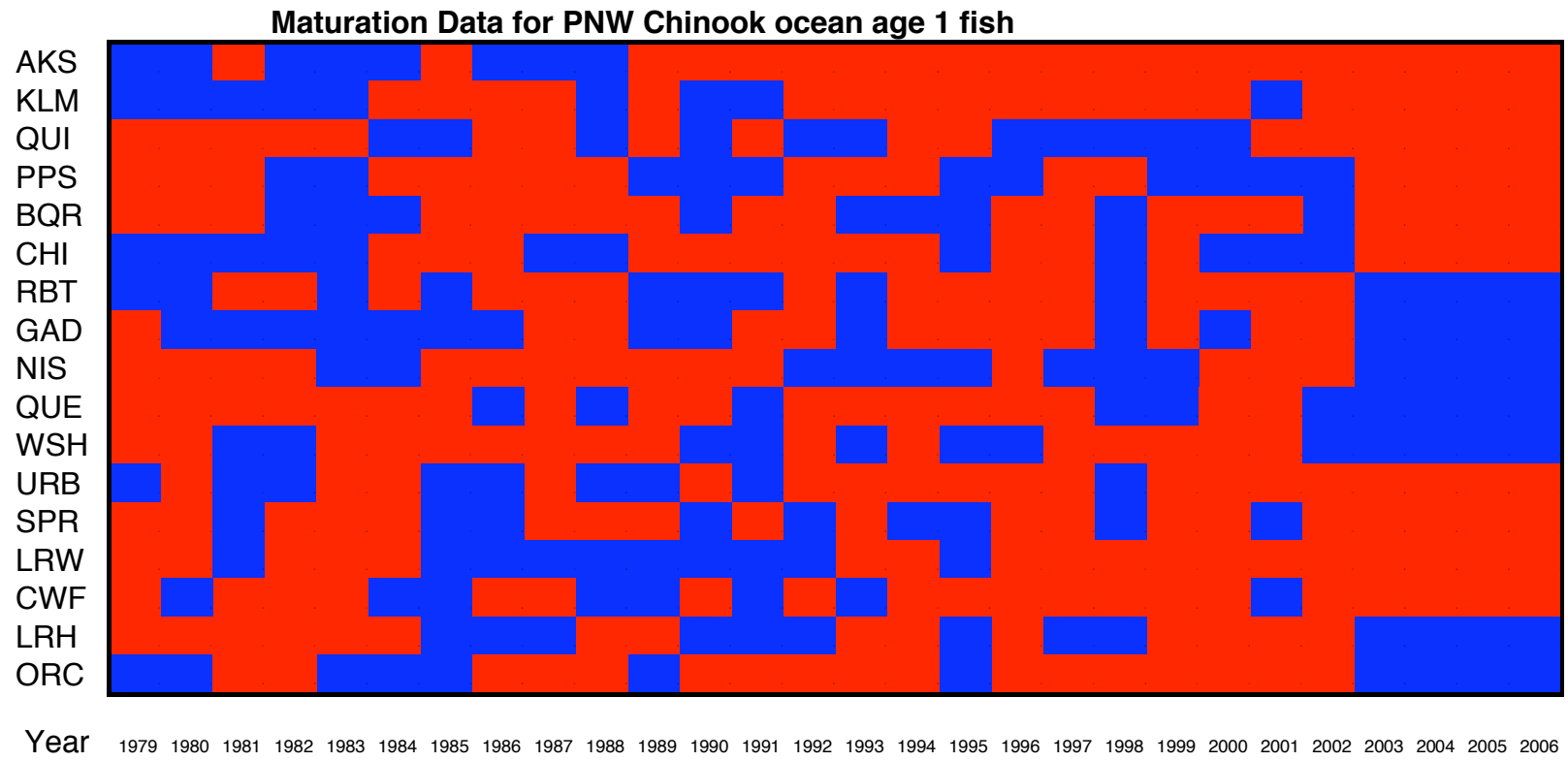


Figure 3.8: Maturation for age 2 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.

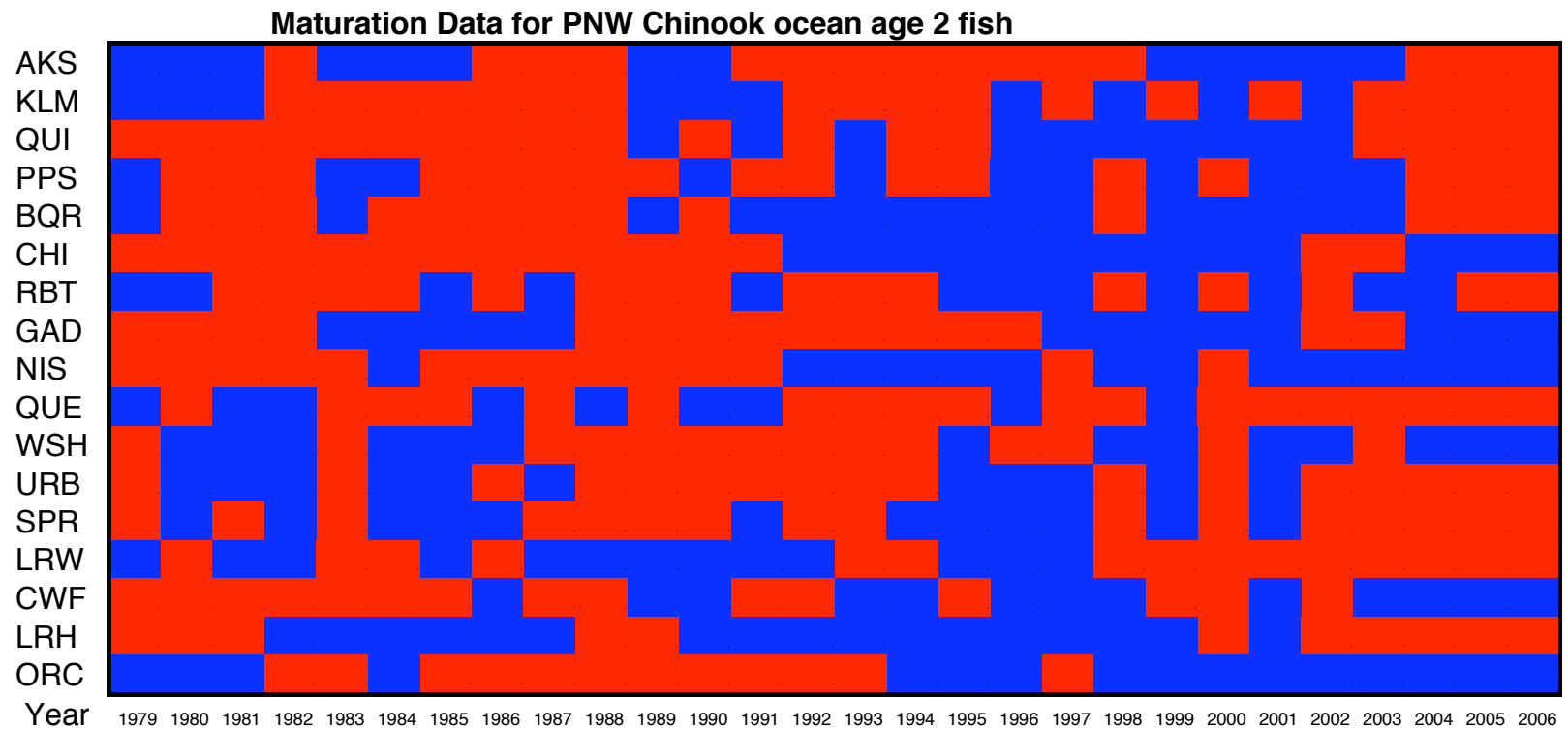


Figure 3.9: Maturation for age 3 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.

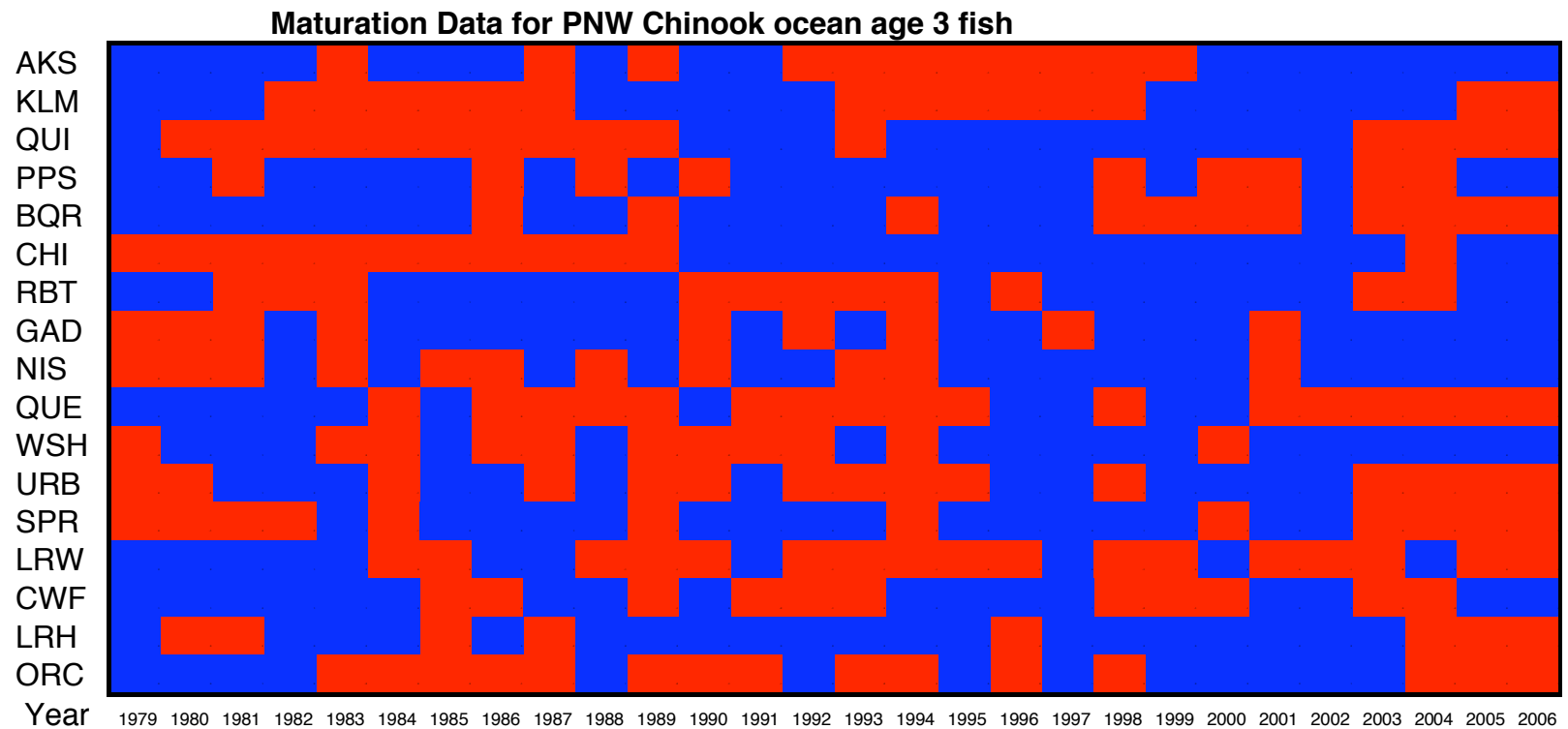


Figure 3.10: Maturation for age 4 rescaled for each area. A red indicates lower than average maturation for age 2 for the time period observed and a blue denotes higher than average maturation for age ever observed for the stock. Stocks are denoted by the three-letter acronym as shown in Table 3.1.

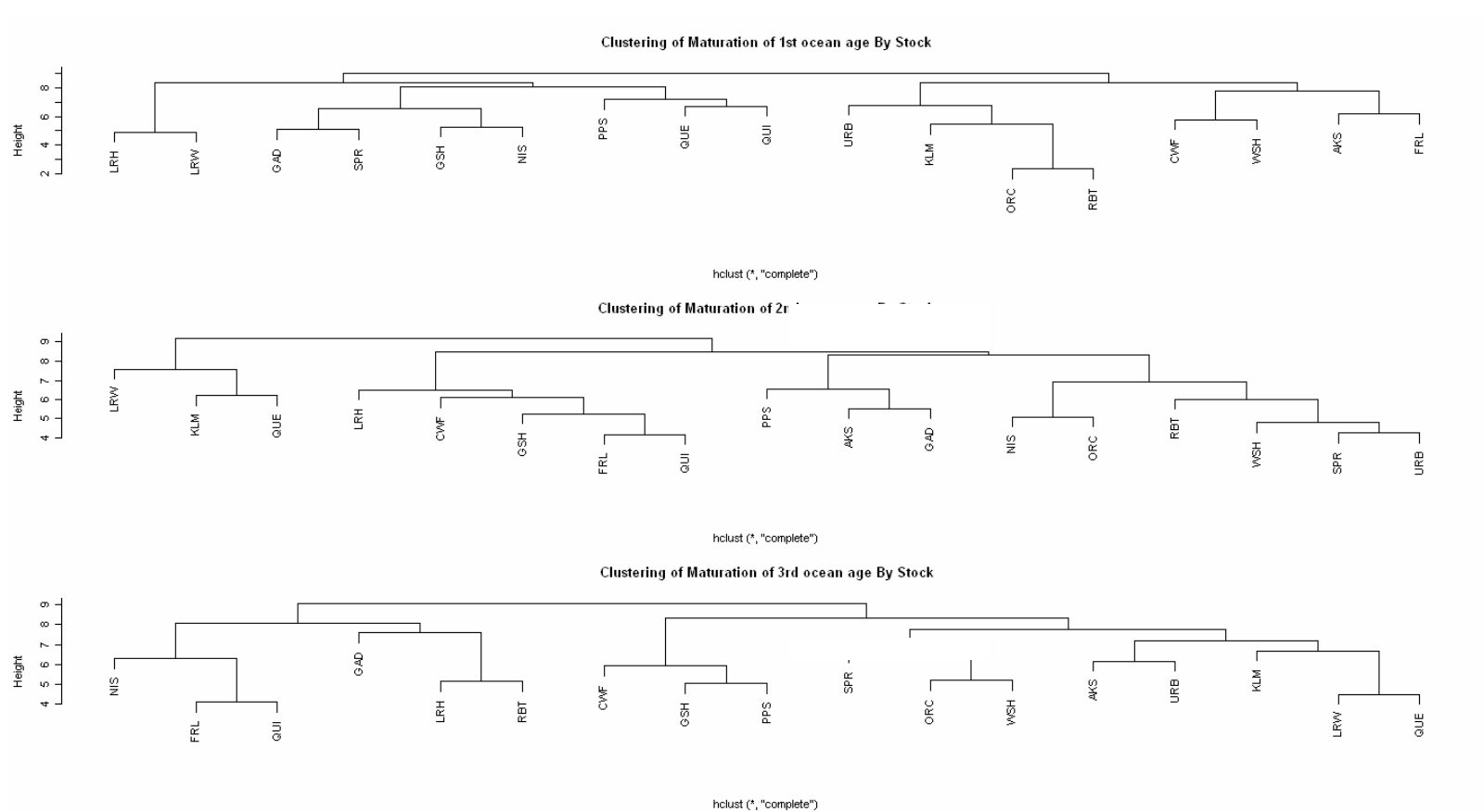


Figure 3.11: Regional based cluster analysis on maturation rates by ocean age. Stocks are identified by the three-letter acronym shown in Table 3.1.

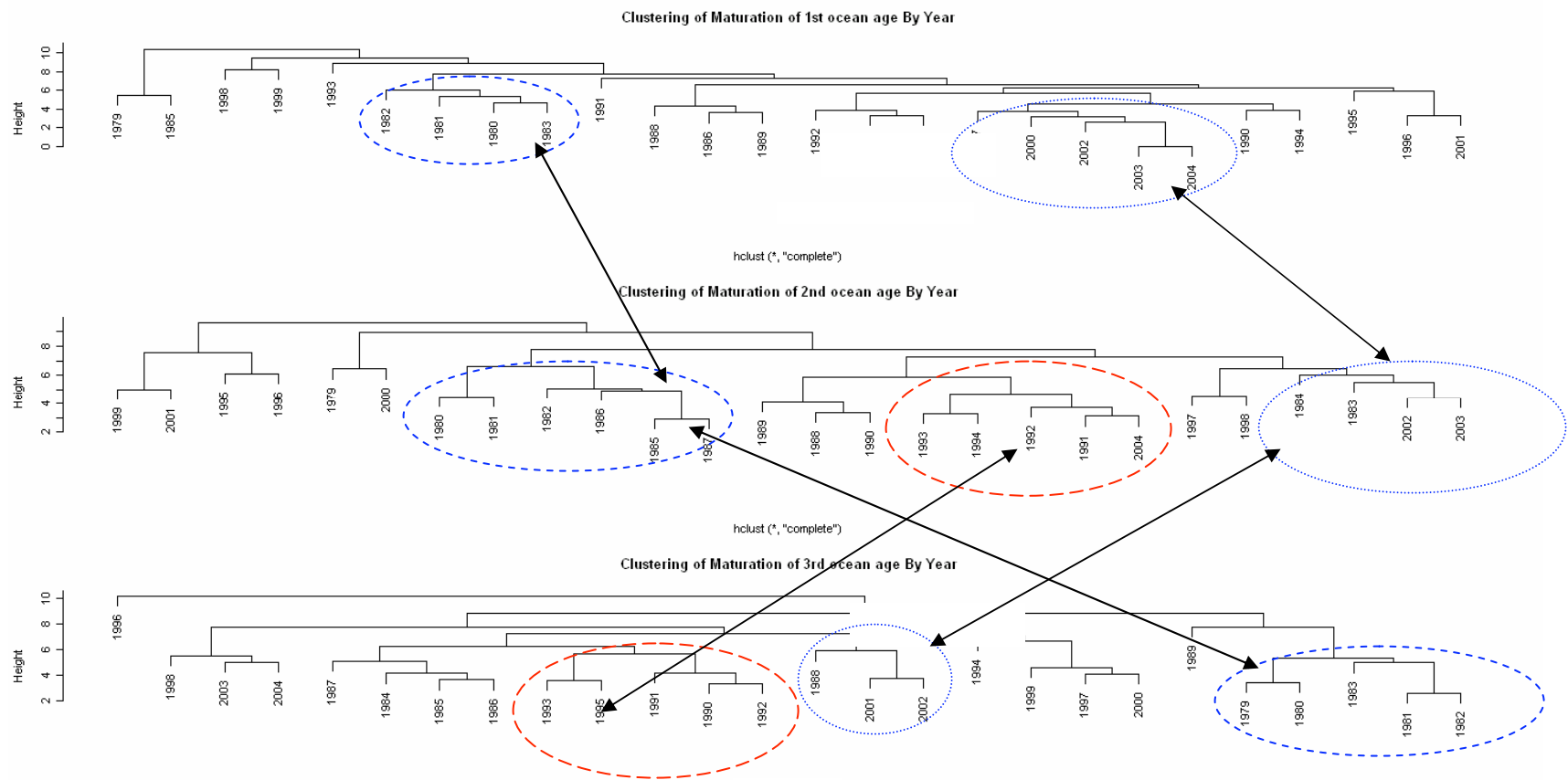


Figure 3.12: Yearly clusters based on maturation rates by ocean age. Arrows indicate similarity across ages.

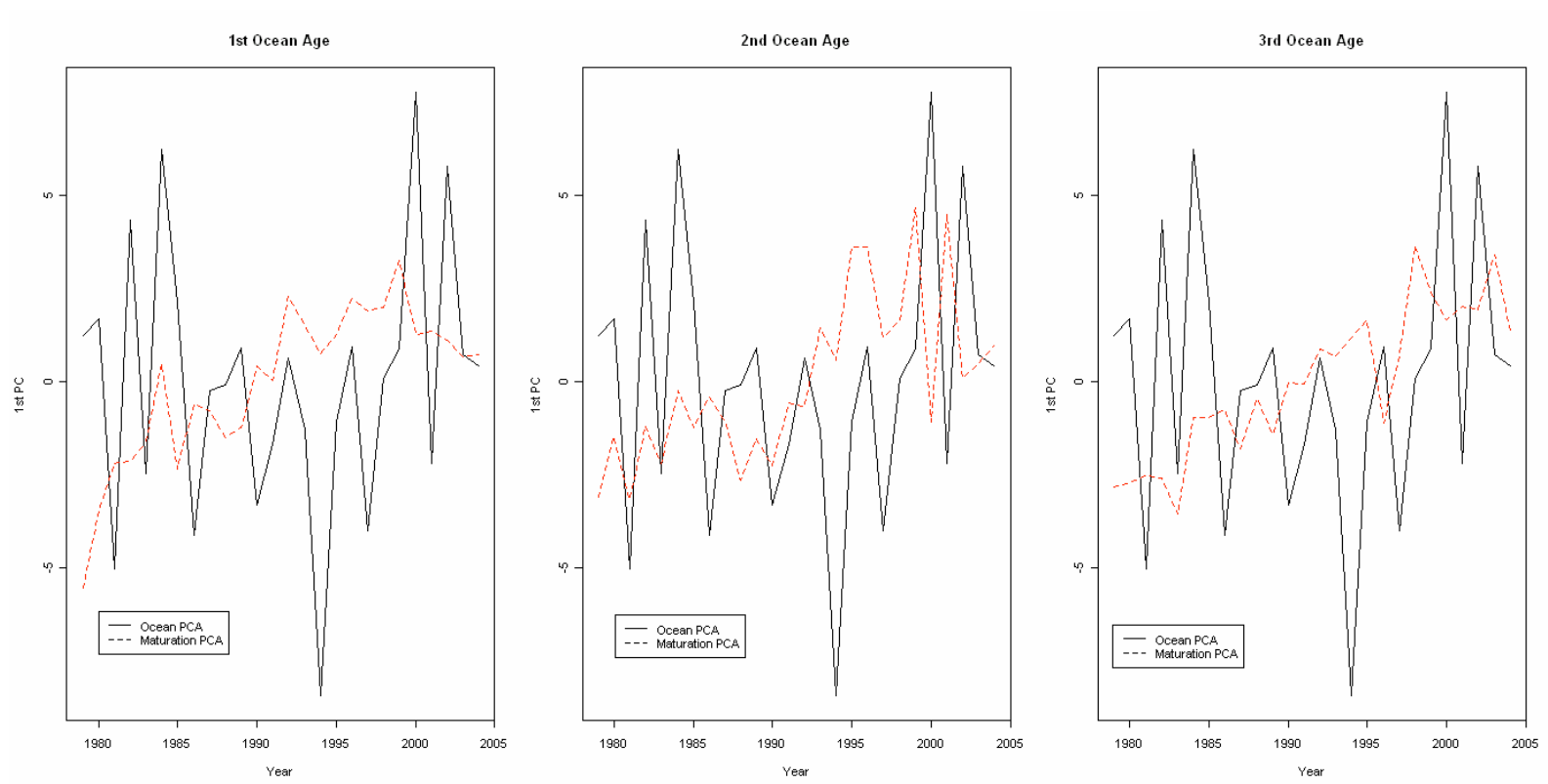


Figure 3.13: Lag 1 effects on maturation anomalies using PCA (displaying only the 1st PC).

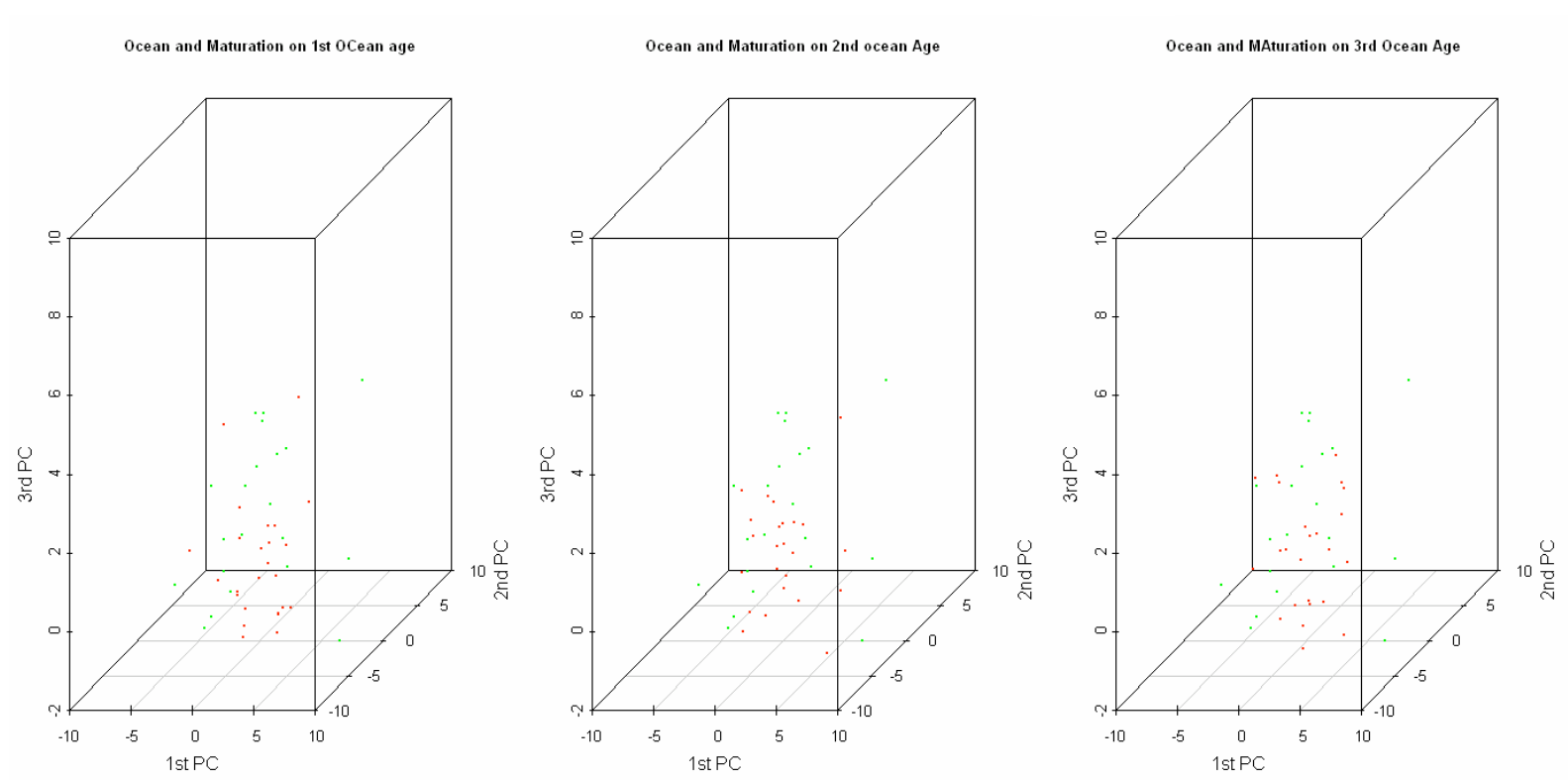


Figure 3.14: Lag 1 effects on maturation anomalies using PCA (displaying the first three PCs). The upwelling data (green) and maturation by age (red) is shown for each age separately

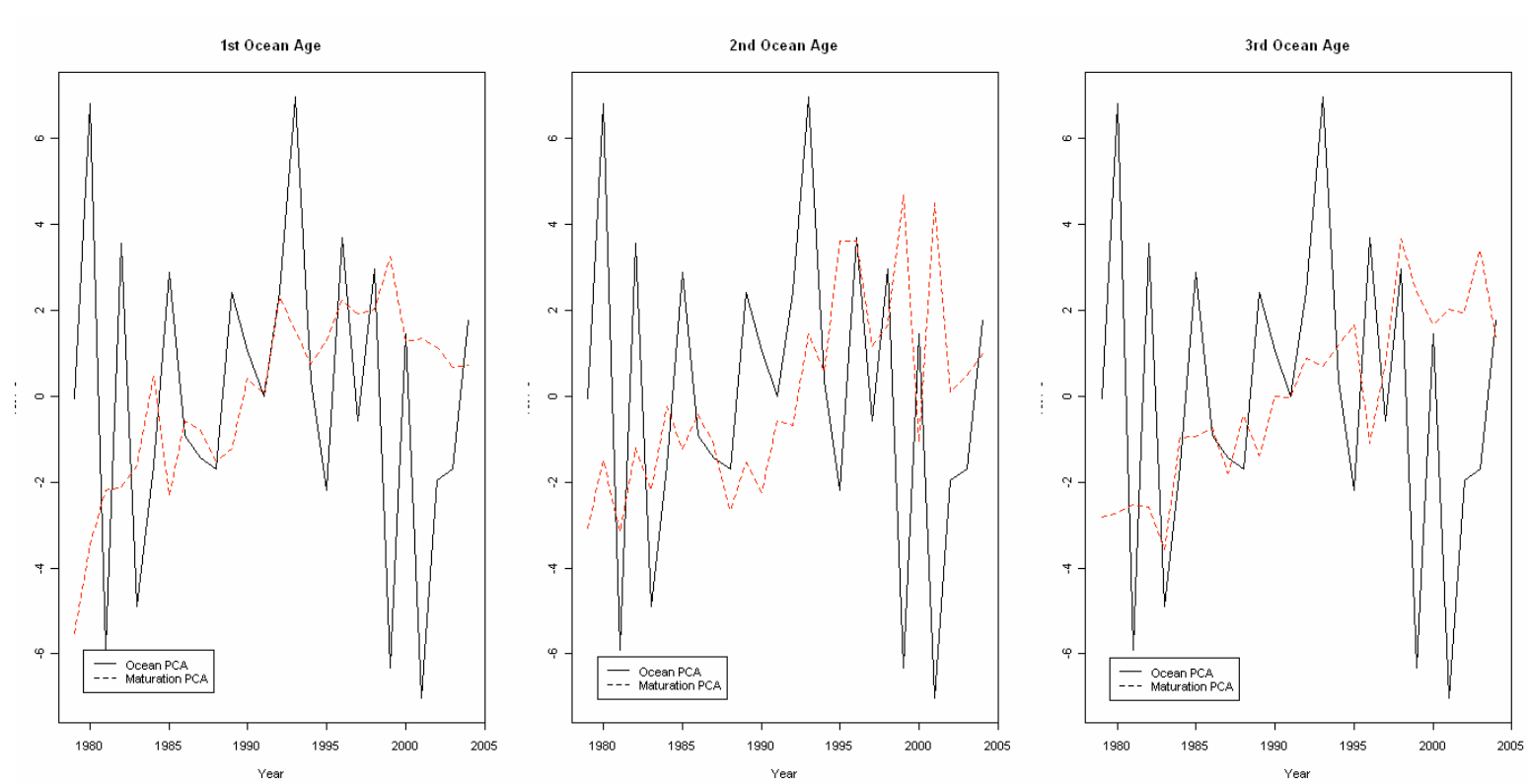


Figure 3.15: Same-year effects on maturation anomalies using PCA (displaying only the first PC)

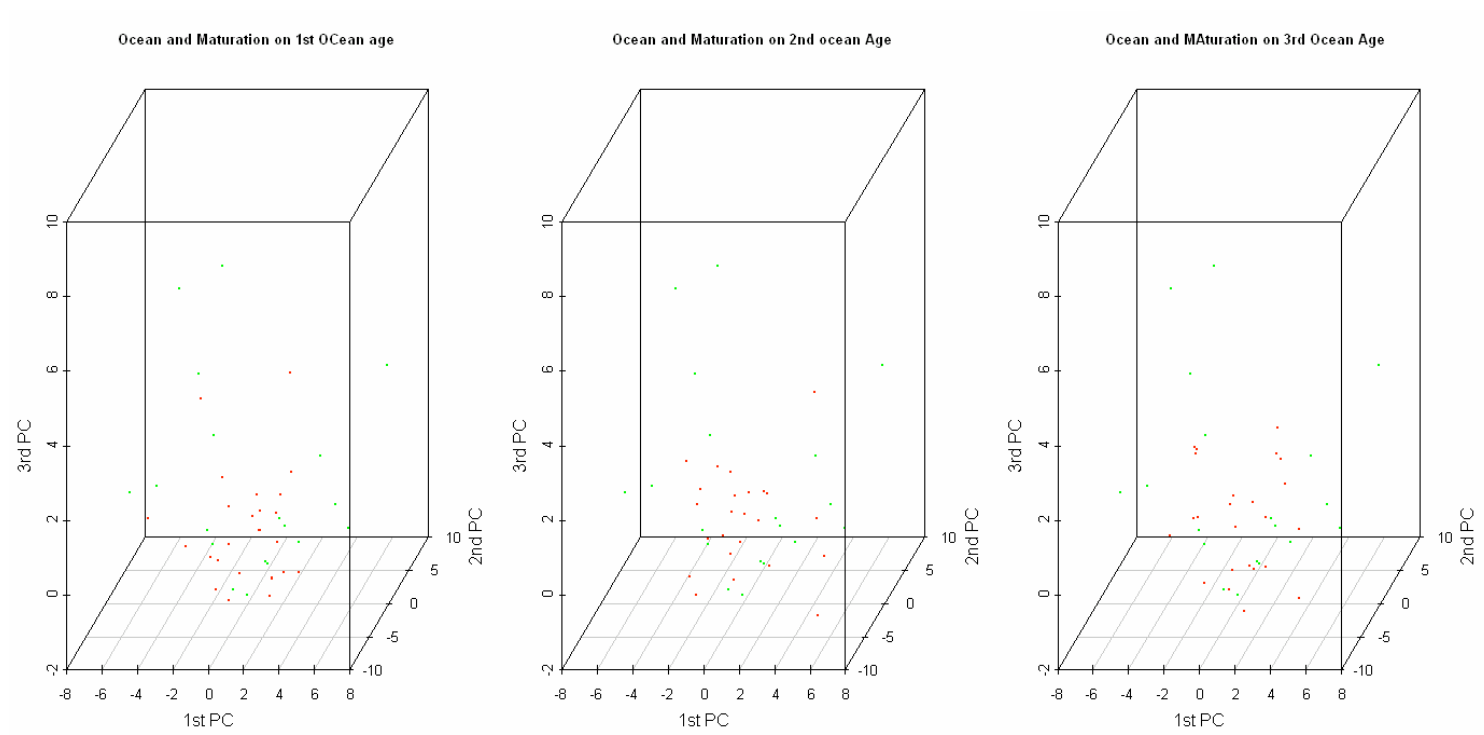


Figure 3.16: Same-year effects on maturation anomalies using PCA (displaying the first three PCs). The upwelling data (green) and maturation by age (red) is shown for each age separately.

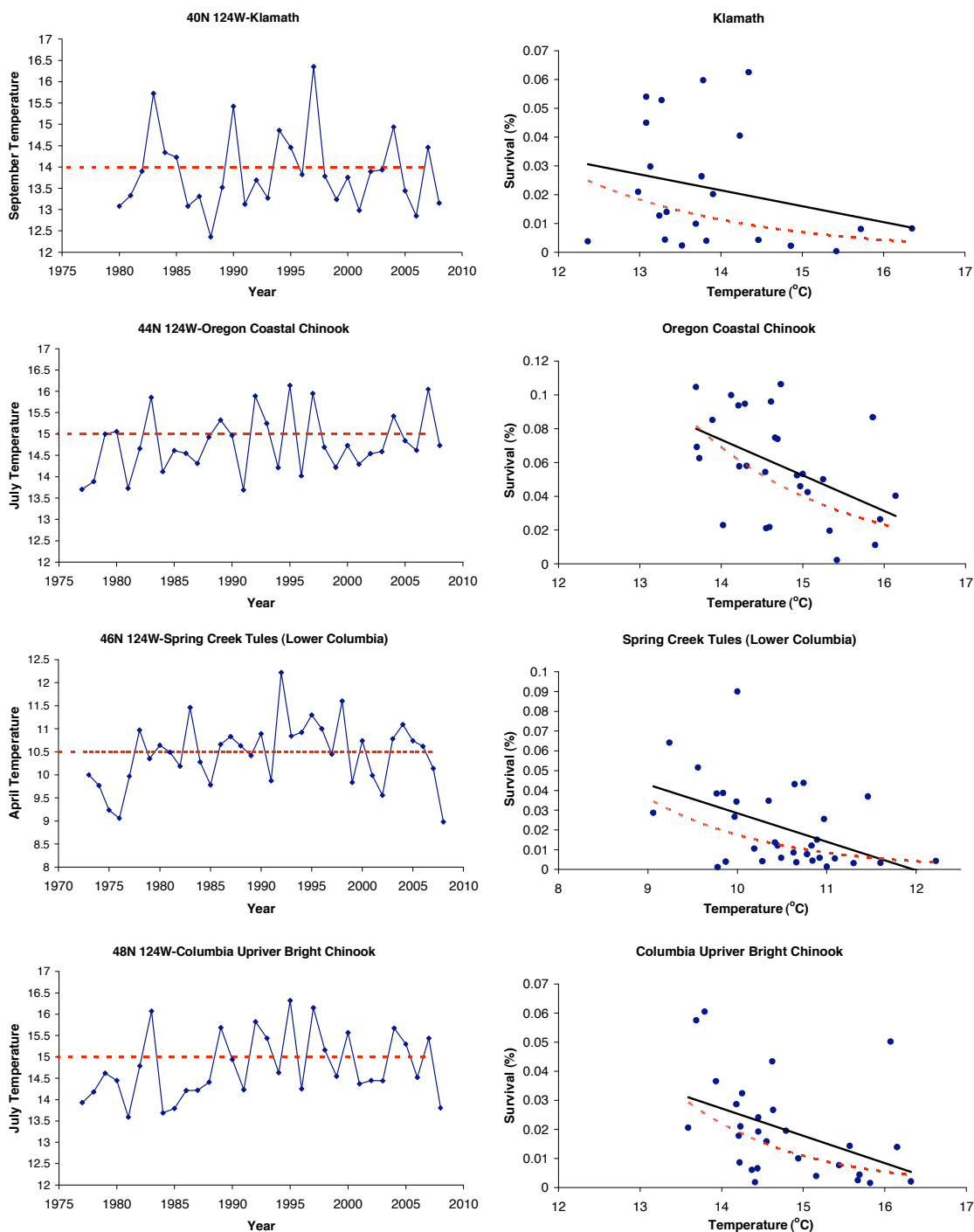


Figure 3.17: Relationship between survival and SST for Klamath, Salmon River (Oregon Coastal Chinook), Spring Creek Tules (Columbia) and the Columbia Upriver Brights. The SST was obtained from COADS database for locations near the coastal shelf and were the most highly correlated with survival during the first few months after smolts emigrate into the ocean. Stations reported are 40°N 124°W, 44°N 124°W, 46°N 124°W and 48°N 124°W. Liner fits (solid) and non-linear fits (dashed line) are shown for each set of data.

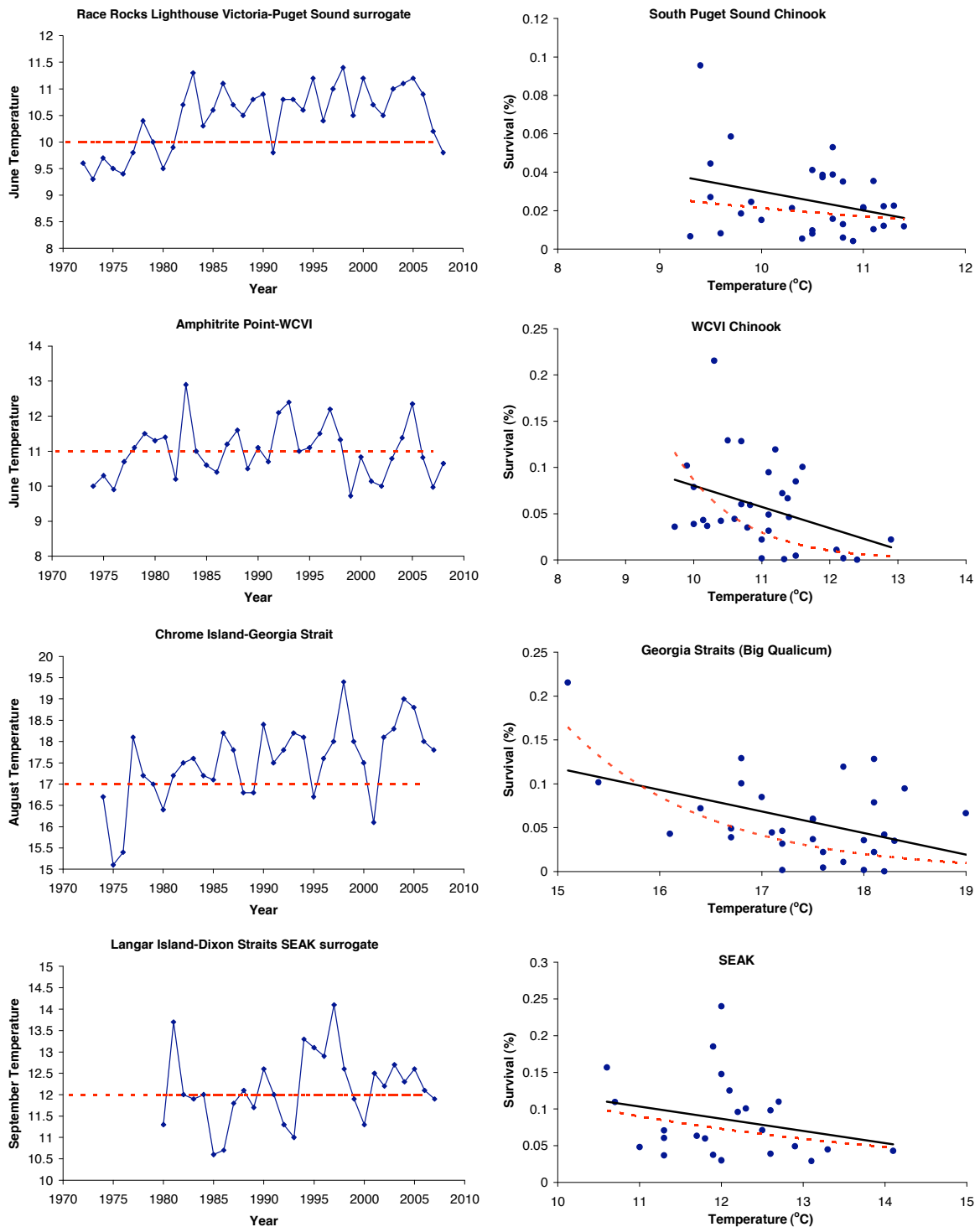


Figure 3.18: Relationship between survival and SST for Puget Sound, West Coast of Vancouver Island (WCVI), Georgia Straits and South East Alaska (SEAK). The SST was obtained from BC lighthouse database for nearest locations that could be used as surrogates for these systems. Linear fits (solid) and non-linear fits (dashed line) are shown for each set of data.

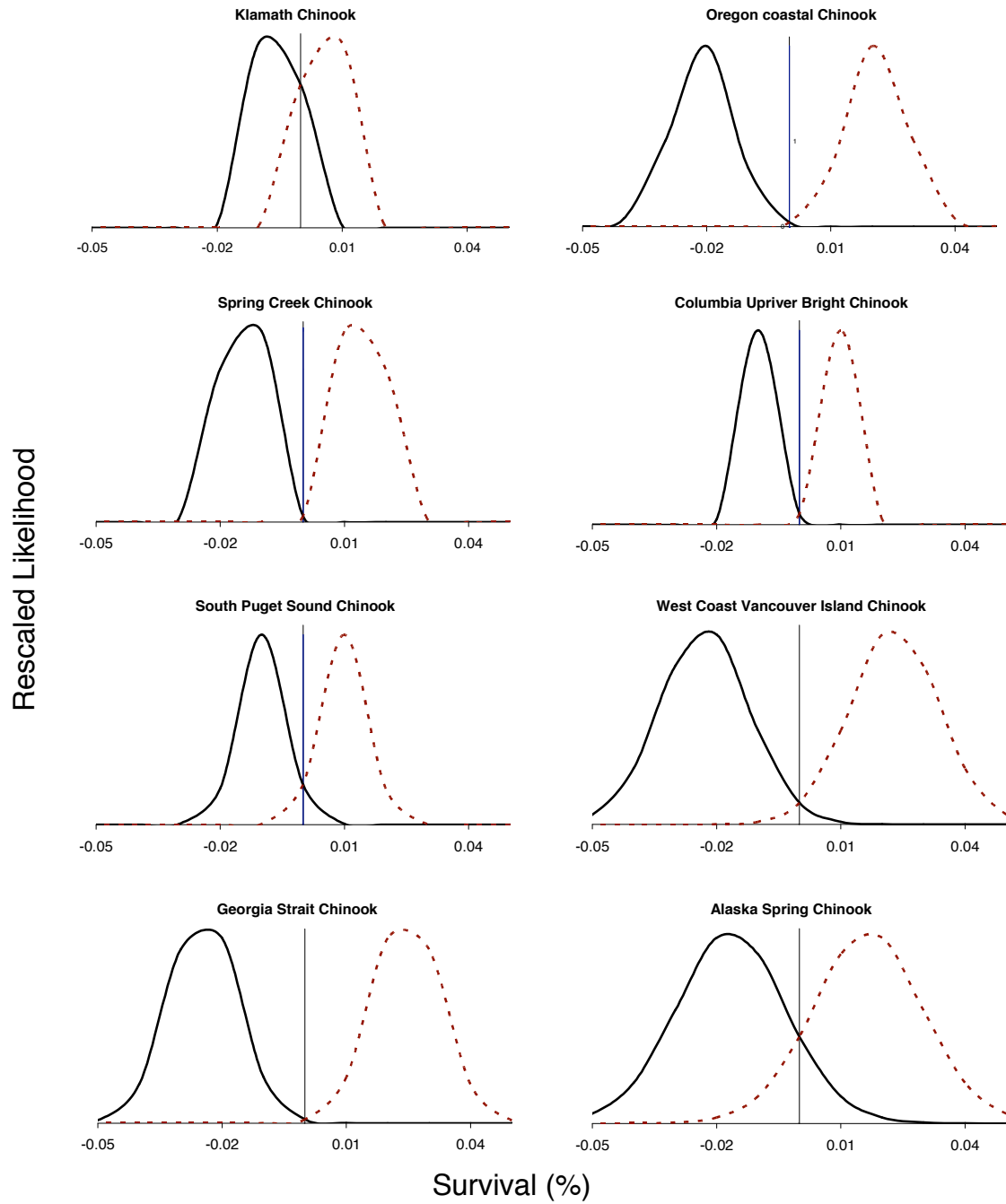


Figure 3.19: Rescaled likelihood profiles of the Beta parameter as a function of a one-degree change in SST at each of the locations specified in Figures 3.17 and 3.18. A 1°C increase in SST (solid line) indicates the absolute amount of decrease in overall survival might be expected for the stock, whereas a 1°C decrease in SST (dashed line) indicates the absolute increase in survival that might be expected for a particular stock. These figures assume a linear fit

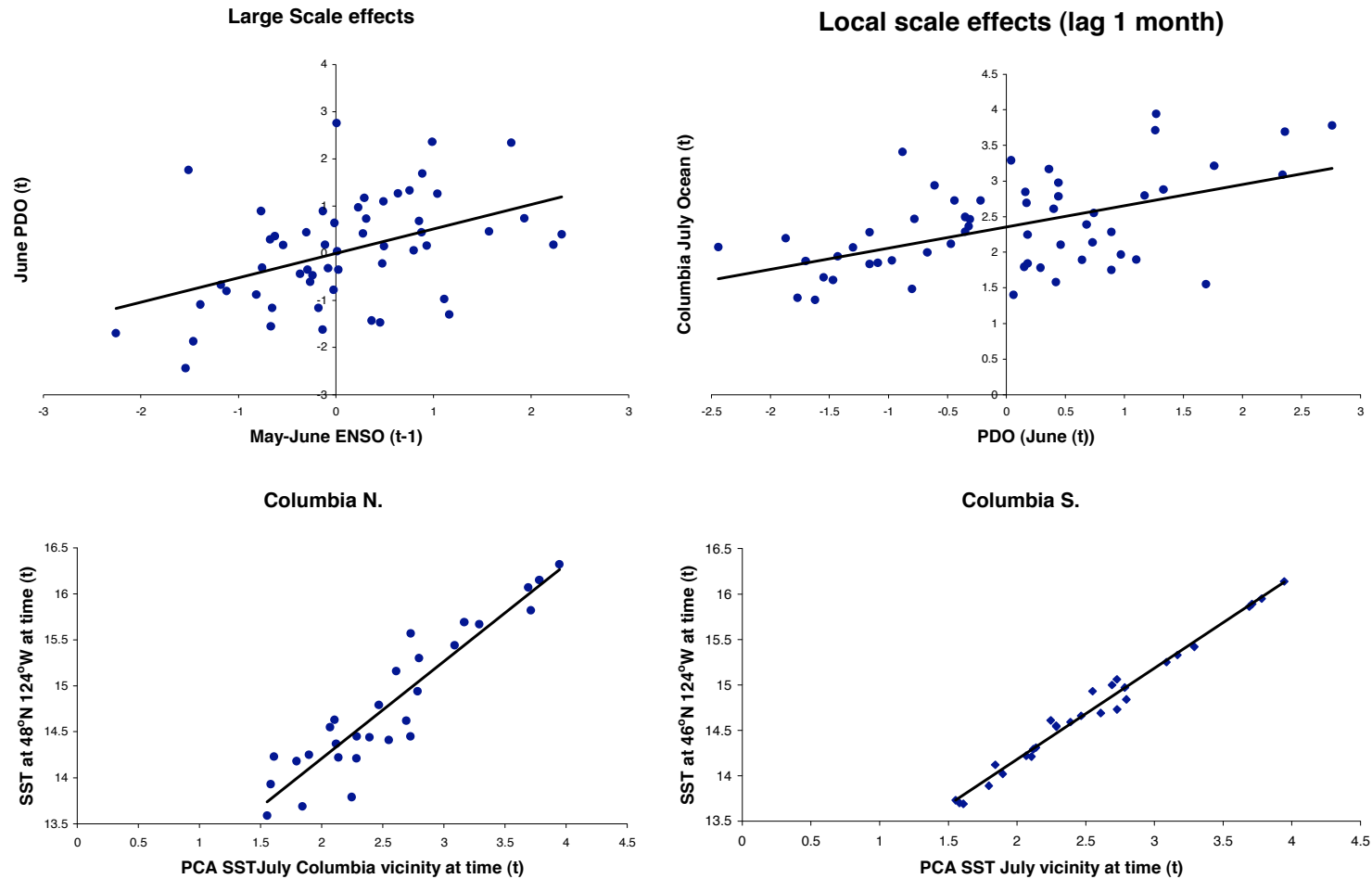


Figure 3.20: Lag time effects from different scales affecting survival at the local scale for the Columbia and Oregon coast Chinook stocks. The top left panel relates ENSO conditions the previous year to PDO conditions in the current year, the top right panel relates June PDO conditions in the NE Pacific to conditions off the Washington and Oregon coast in the vicinity of the Columbia, and the bottom two panels relate conditions off the Columbia to sea surface temperatures that are related to survival of Columbia Bright and Oregon coastal Chinook.

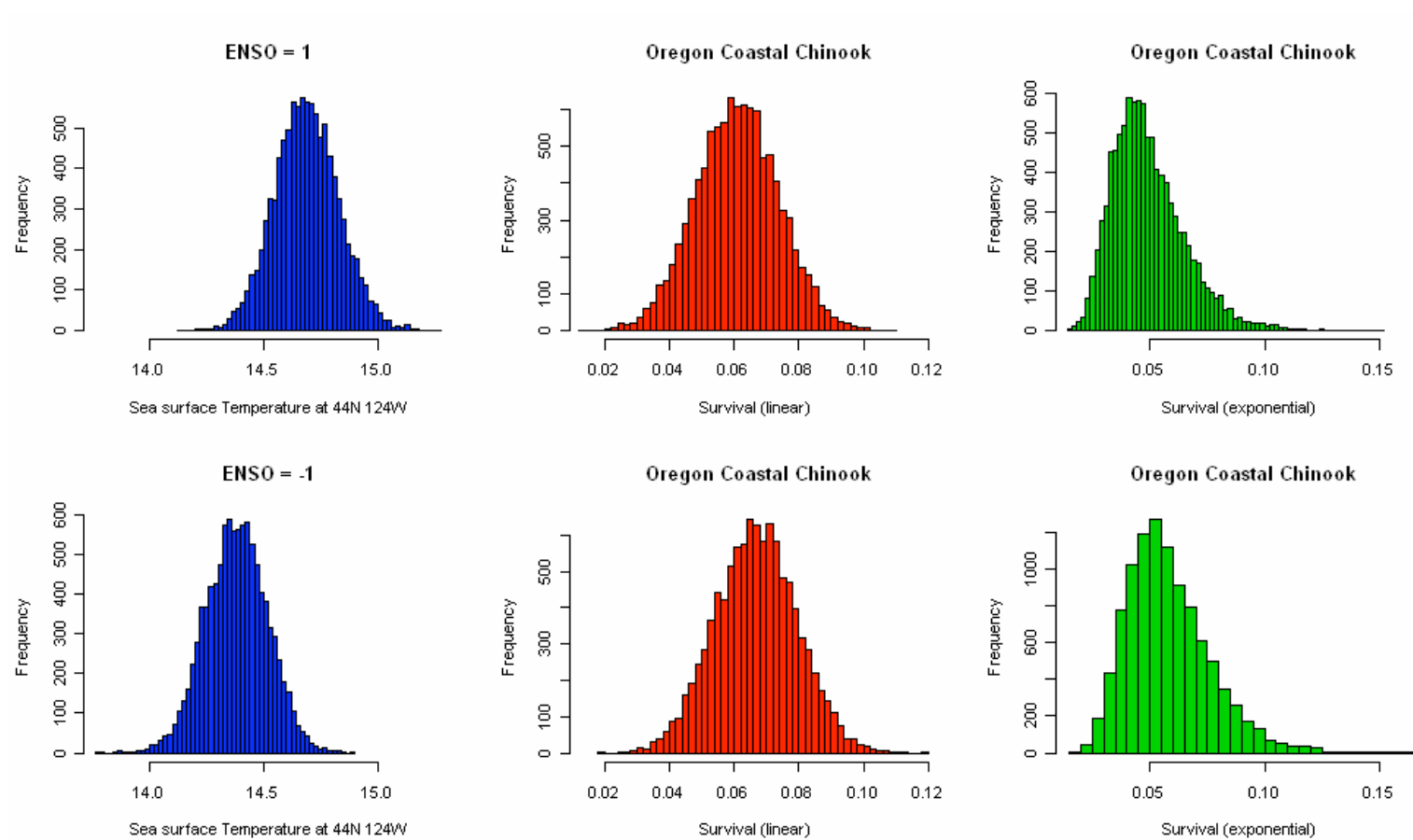


Figure 3.21: The effect of a positive or negative ENSO on Oregon Coastal Chinook survival

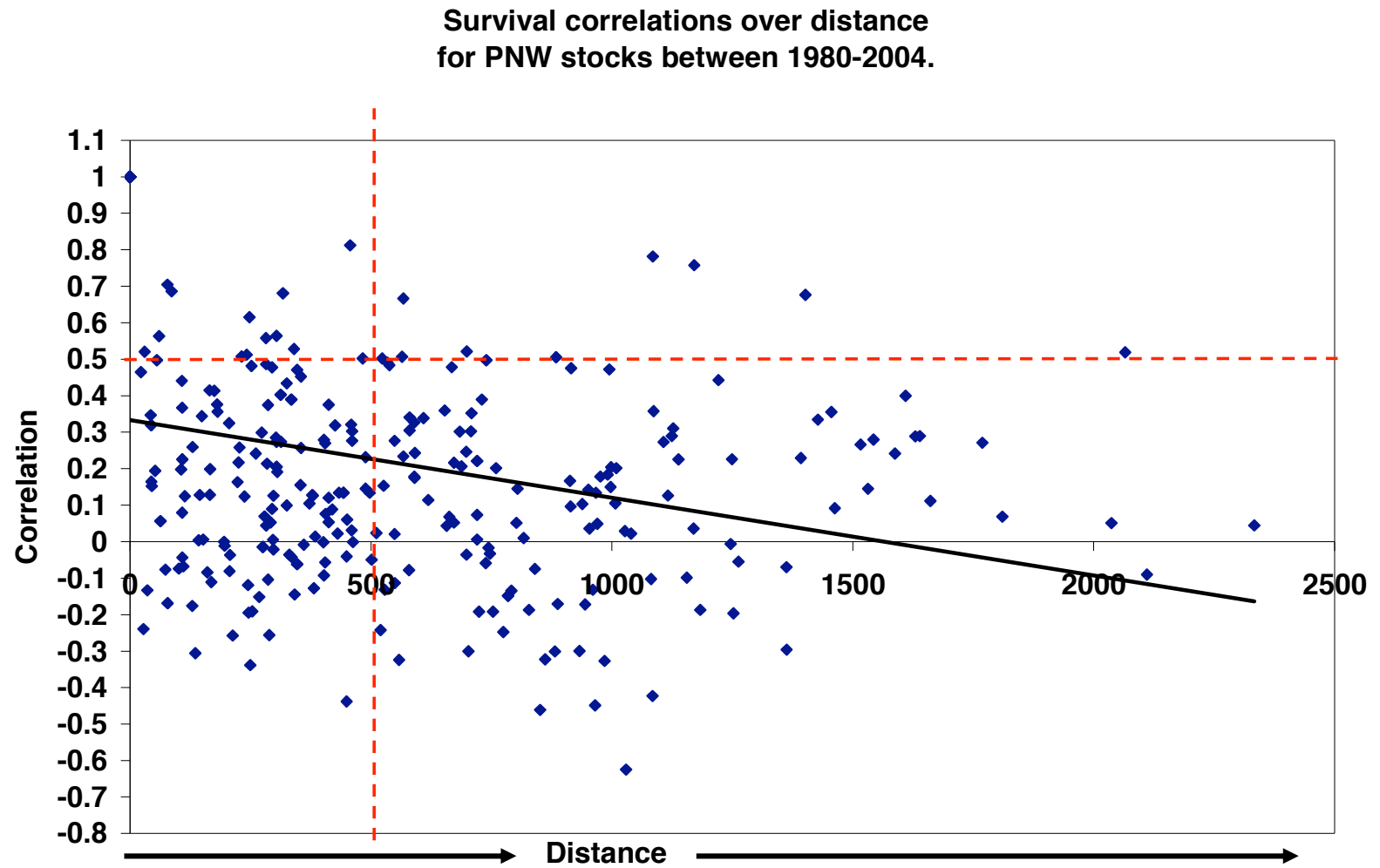


Figure 3.22: Correlation analysis displaying correlation between stocks and regions as a function of distance

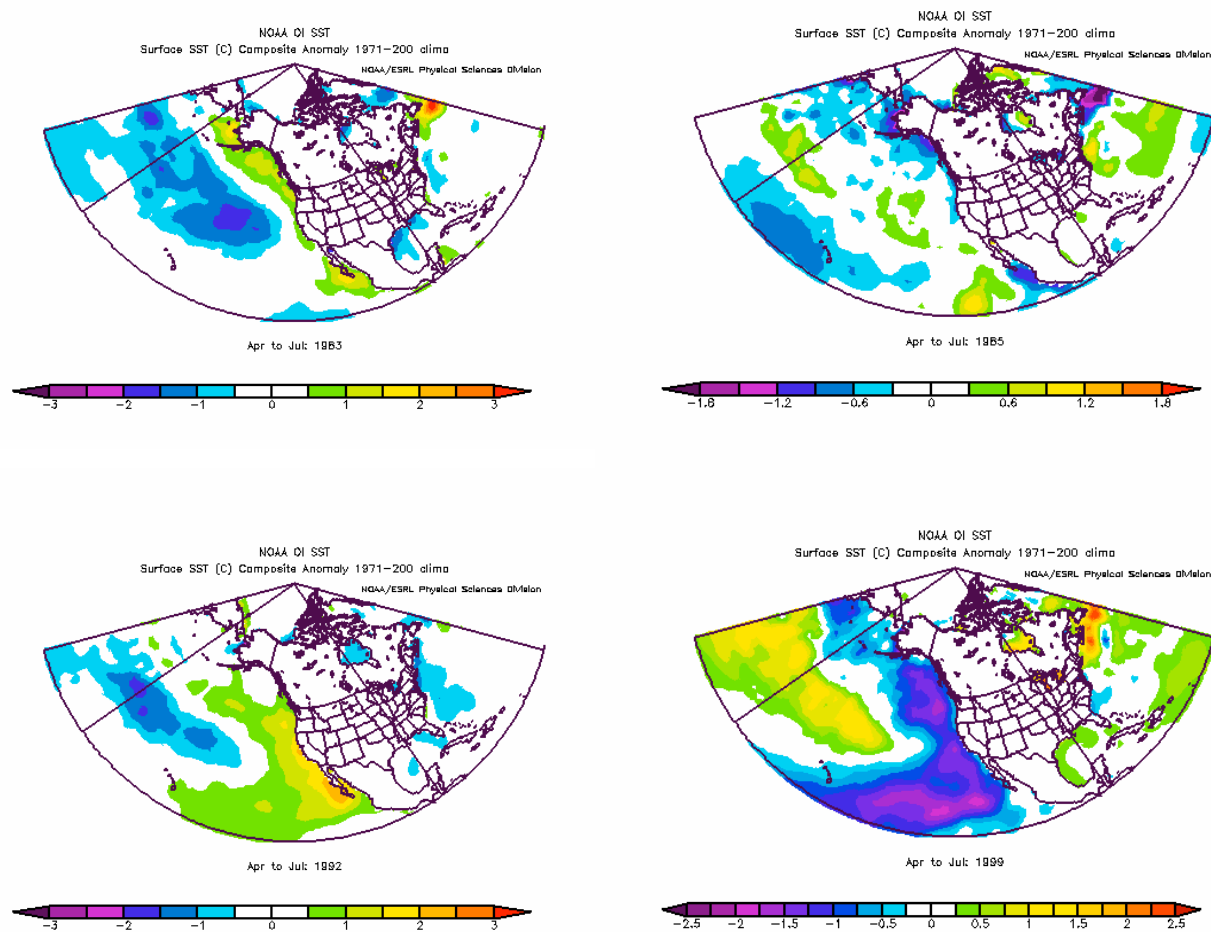


Figure 3.23: Four distinct patterns of environmental conditions that may have consequential impacts on PNW Chinook survival during the spring transition period (April through July). The upper and lower left hand panel shows warmer than average conditions indicating poor upwelling in 1983 and 1992 impacting survival coast-wide (Figures 3.2 and 3.4). The right hand panels indicate cooler than average conditions in 1985 and 1999 that had a positive effect on survival coast-wide (Figure 3.4).

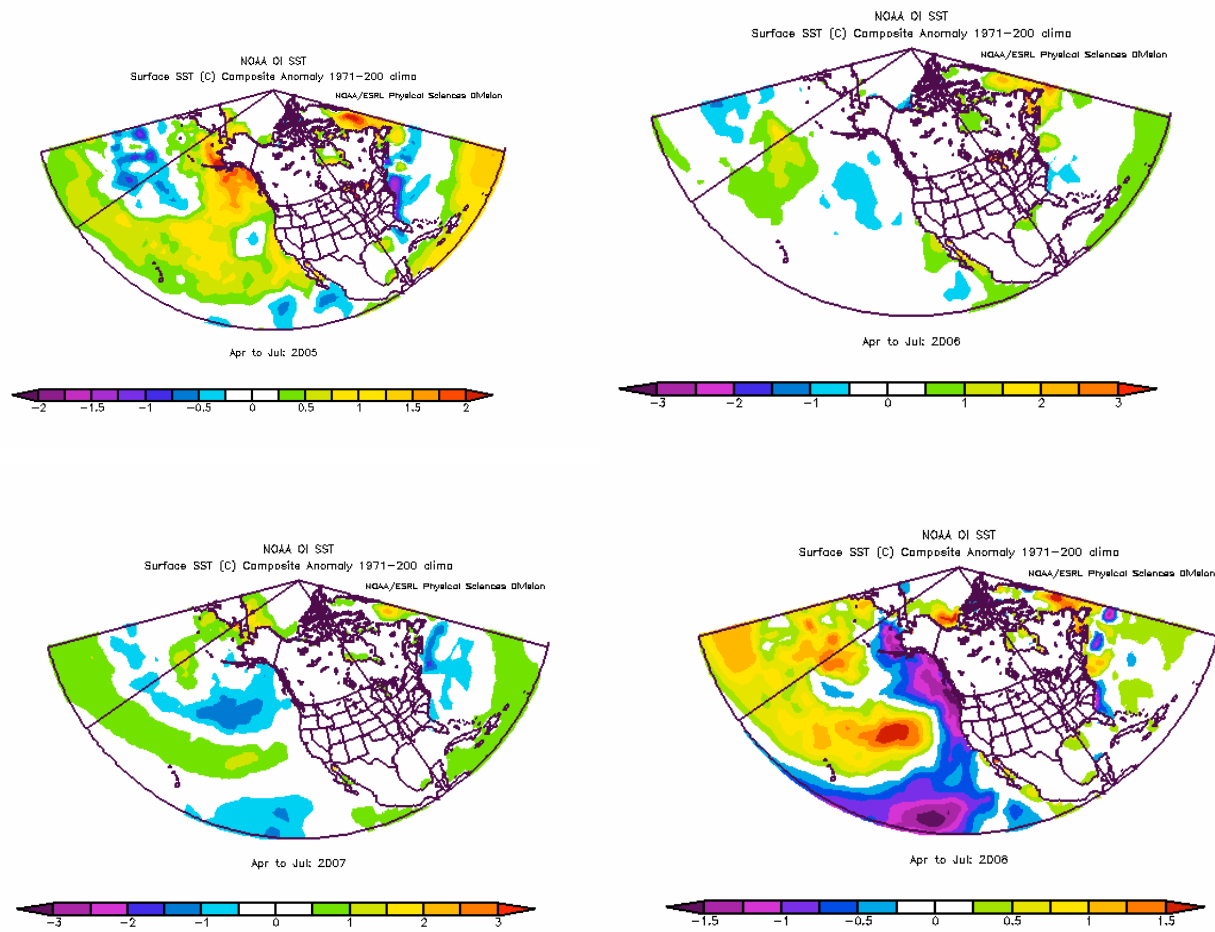


Figure 3.24: Conditions in 2005 to 2008 during spring transition

Appendix 3.1: Maturation at age and length relationship for Columbia Upriver Brights between 1997 and 2004.

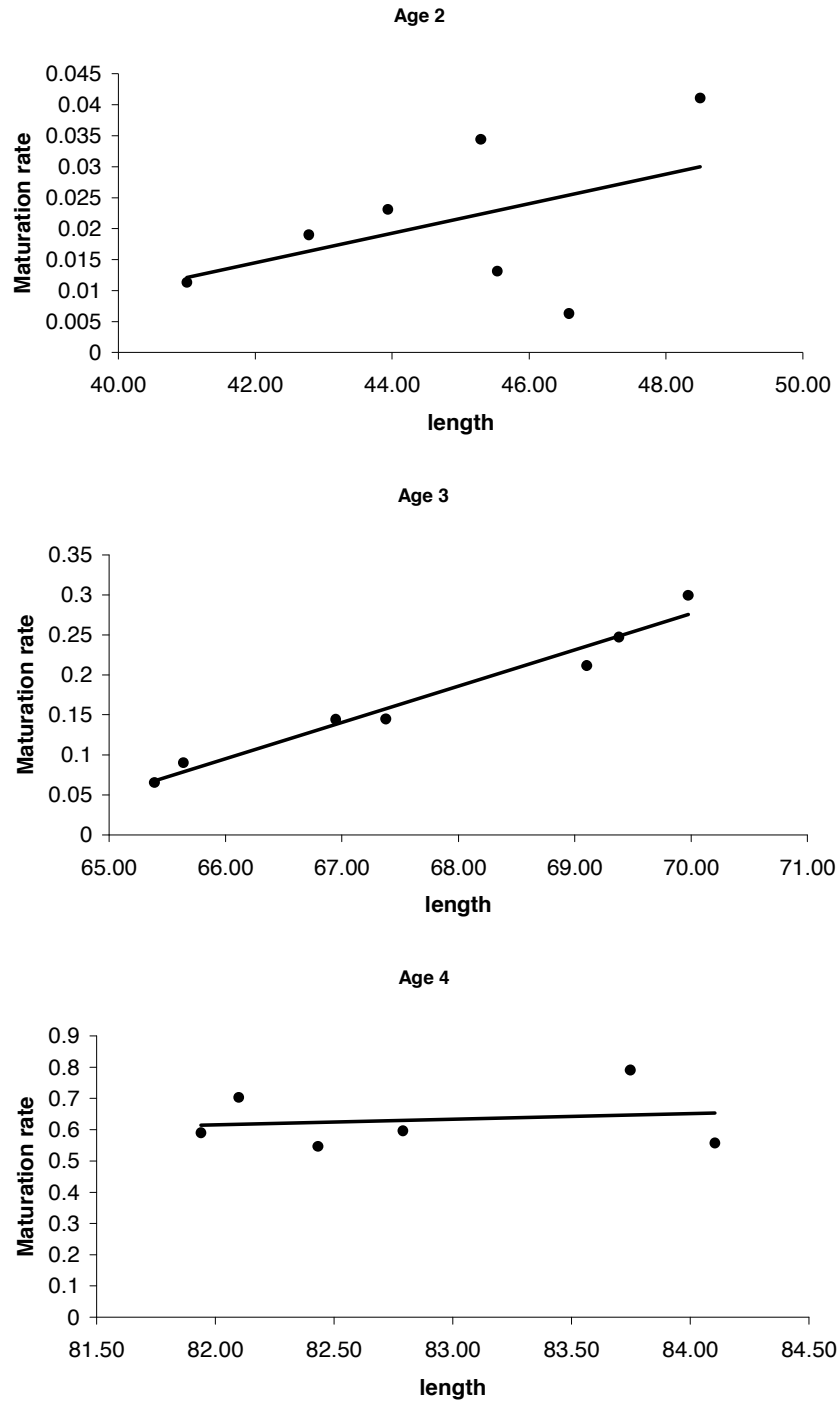


Figure.1: Relationship between maturation rate at age (proportion mature) and length (cms) of the fish in terminal areas (sampled at Bonneville Dam)

**CHAPTER 4: DEVELOPING STATISTICAL CATCH-AT-AGE
MODELS FOR CHINOOK SALMON: AN ALTERNATIVE
MODELING TOOL FOR CHINOOK SALMON STOCK
ASSESSMENT**

4.1 INTRODUCTION

The Pacific Salmon Commission (PSC) was established in 1985 to ensure the conservation of Pacific salmon in Alaska, Canada, Oregon, and Washington. One of the more valuable species managed by the PSC, both commercially and recreationally, is Chinook salmon (*Oncorhynchus tshawytscha*). An appendix to the Pacific Salmon Treaty (PST), signed in 1999, describes the principles behind the management of this species (PSC 2000). Under the PST's Aggregate Abundance Based Management (AABM) approach for Chinook, the annual allowable harvest level in specific ocean fisheries is determined based on corresponding changes in the abundance of the individual Chinook stock aggregates that contribute to that fishery. This management approach also includes provisions for additional adjustments if there are declines in specific weak stock groups. Under this management system, the more abundant stocks have a greater influence on the abundance index and the resulting harvest level, and changes in the productivity of these so-called "driver stocks" largely determine the catch levels in these fisheries. The Columbia Upriver Bright fall Chinook salmon stock, which spawns in Hanford Reach, tends to be far north-migrating (these stocks tend to be ocean-type Chinook that migrate thousands of miles from their natal streams to waters off southeast Alaska and northern British Columbia) and contributes heavily to ocean fisheries in southeast Alaska (SEAK) and northern British Columbia (NBC), making them driver stocks for those fisheries.

Currently the PSC uses a cohort analysis algorithm (TCChinook 08-1) that compares current abundance to a historic base period abundance (1979-1982). It projects terminal run size or escapements for thirty different stocks by estimating

environmental variability parameters to adjust Ricker stock-recruitment functions that fit to the observed data for each stock (terminal run or escapement). The algorithm does not fit to fishery specific catches, but uses assumptions about vulnerability schedules based on size regulations (size-based selectivity) and harvest rate scalars (based on effort or harvest rate ratios) to estimate (and predict) catches across fisheries. The current model has two phases. The first phase uses coded wire tag (CWT) data and terminal abundance for each stock to estimate ocean abundance of that stock through a ratio-estimator in a certain set of years (1979-1982 were used for the PSC model). The second phase is an estimation phase using standard cohort analysis techniques (TCChinook 08-01) to fit to the observed terminal run and escapement data by age. Fishery-specific mortalities are based on estimates of exploitation by fishery and age for the base period (the phase one estimates), adjusting for size-based regulations and/or effort scalars. There is no uncertainty presented in the current model estimates, nor are all available tag or abundance data used in the current approach as it relies on the historic estimates obtained from the first phase.

The techniques used in the PSC model are over two decades old. Over the past few decades, numerous age-structured models have been developed to manage long-lived species such as cod and halibut (Clark 2003, Sullivan et al. 1999). These models simultaneously estimate numerous parameters to give the best fit to observed data (Patterson et al. 2001, Deriso and Parma 1987, Fournier and Archibald 1982). Algorithms such as the generic age-structured algorithm developed by Fournier and Archibald (1982) are adapted in numerous ways to model the species being managed.

Coleraine (Hilborn et al. 2003) and Stock Synthesis (Methot 1989), two modelling tools that adapt these algorithms, are being used to manage commercial fisheries in New Zealand and the West Coast of the United States. For Pacific salmon, however, simple models of this type have been developed only recently (Lessard et. Al. 2008, Savereide and Quinn 2004) and still have not been used for complex fishery and stock structures.

I developed a catch-at-age model using the life history of Chinook salmon, a time series of CWT data recoveries (Johnson 1990, Lapi et al. 1990), and a time series of terminal run sizes to forecast ocean catches, terminal catches, and terminal escapement. I compare this model and the parameter estimates it generated to the approach currently being used by the PSC for one of the driver stocks in the PSC model (Columbia Upriver Brights), and propose an alternative assessment tool for Chinook management. The model is then tested for bias and robustness through simulation testing (Shnute and Richards 1995), allowing for both process (environmental variation) and sampling (observational) error. The techniques employed in preparation of this model are evaluated by comparing its associated uncertainty and precision with previous models. The improved model outputs presented here have demonstrable Chinook salmon management benefits.

4.2 MATERIALS AND METHODS

4.2.1 Data Sources

The data used for this analysis, shown in Table 4.2, are the estimates of natural production at Hanford reach, the last free flowing segment of the upper Columbia below Priest Rapids Dam at river mile 397. Although there is a hatchery at Priest

Rapids Dam, it is estimated that less than an average of 10% of the overall population over twenty years is hatchery fish (data from Evenson et al. 2002). Upriver Bright tag data (TC Chinook 05-2) were used to estimate ocean and in-river harvests of this stock. For simplification and estimation purposes the fine-resolution stock structure used in the PSC model (25 fisheries) was scaled to two fisheries, namely ocean and terminal (or freshwater).

Notation used for describing the model dynamics is shown in Table 4.1. The stock-specific catches in ocean fisheries were computed as:

$$CO_{a,f,t} = \frac{CT_{a,f,t}}{CWTT_{a,f,t}} CWTO_{a,f,t} \quad (4.1)$$

where $CO_{a,f,t}$ is the catch in the ocean fishery by age (a) and time (t), and $CT_{a,f,t}$ is the catch in the terminal area by age (a) and at time (t). $CWTT_{a,f,t}$ and $CWTO_{a,f,t}$ are the CWT recoveries by age in terminal (T) and ocean fishery (O) by age and time respectively.

Because the terminal net catch data were the most reliable information available (sample rates were greater than 25% in terminal net fisheries), the ratio of the terminal catch to terminal CWT recoveries was used to expand the ocean CWT recoveries into landings. Implicit in this formulation is the assumption that the terminal to ocean catch ratios are equal across both the tagged and natural components of this stock. I did not use the ratio of escapement to CWT recoveries because escapement is often sampled at lower rates. Data from southeast Alaska, northern and central BC, west coast of

Vancouver Island, and Washington/Oregon were collapsed into a single ocean fishery.

For the terminal fisheries, the terminal net and sport fisheries were combined (Table 4.2, Figure 4.1).

4.2.2 Estimations of Variance

Each fishery (ocean and terminal) and escapement has a catch (escapement estimate) and sample size associated with it, and thus an error term. Estimates of the variability around these point estimates were all calculated using equations below.

For the terminal fishery, the variance in catch was calculated and considered equal to the CWT sample variance, as estimates of total catch by age are based on these samples. Because $CWTT_{a,f,t} \sim \text{Bin}(R_{t-a}, pT_{a,f,t})$, where R_{t-a} is the number of fish released from the hatchery for a particular brood year associated with the recovery for the terminal fishery at that year, and $pT_{a,f,t}$ is the proportion of the fish that are recovered in the terminal fishery at that age for a particular brood and time, t , therefore

$$E(CWTT_{a,f,t}) = pT_{a,f,t} R_{t-a}$$

and $Var(CWTT_{a,f,t}) = R_{t-a} pT_{a,f,t} (1 - pT_{a,f,t})$ (4.2)

Thus, the CV for this fishery's catch by age can be calculated based on the CV for the tagged sample by age.

For the purposes of calculating variances in the ocean fishery, I assumed that the catch in terminal areas was a constant (and not a random variable for calculation of variance, i.e. it was known without any error), and both the numerator and denominator were random variables (from equation 4.1 above), and are independent (ocean fisheries versus terminal fisheries).

Thus,

$$Var(CO_{a,f,t}) = (CT_{a,f,t})^2 \left(\frac{R_{t-a} pO_{a,f,t}}{R_{t-a} pT_{a,f,t}} \right)^2 \left(\frac{R_{t-a} (pO_{a,f,t})(1 - pO_{a,f,t})}{(R_{t-a} pO_{a,f,t})^2} + \frac{R_{t-a} (pT_{a,f,t})(1 - pT_{a,f,t})}{(R_{t-a} pT_{a,f,t})^2} \right)$$

Simplified, this is:

$$Var(CO_{a,f,t}) = (CT_{a,f,t})^2 \left(\frac{pO_{a,f,t}}{pT_{a,f,t}} \right)^2 \left(\frac{(1 - pO_{a,f,t})}{(R_{t-a} pO_{a,f,t})} + \frac{(1 - pT_{a,f,t})}{(R_{t-a} pT_{a,f,t})} \right) \quad (4.3)$$

For escapement, variance is calculated as a function of the variability in redd surveys:

$$Var(S) = K^2 \frac{\sum_{i=1}^n (RC_i - \overline{RC})^2}{n} \quad (4.4)$$

where K is the constant by which the redd count is expanded, and RC is the peak redd count in strata (i) and \overline{RC} is the average RC over all strata, with a total of n strata. All escapement data (Table 4.2) are based on redd surveys expanded for sampling area and an expansion factor that takes into account a fish per redd estimate.

4.2.3 Effort Data

An index of ocean catch effort data (Table 4.3) was calculated from the annual ocean catch of all ages in all ocean fisheries, and standardized by the overall ocean catch data observed for 1979-2005 in those fisheries for N years, as per equation 4.5:

$$EO_t = \frac{\sum_{a=2}^5 \sum_{f=1}^n CO_{a,f,t}}{\left(\frac{\sum_{t=1979}^{t=2005} \sum_{a=2}^5 \sum_{f=1}^n CO_{a,f,t}}{N} \right)} \quad (4.5)$$

This calculation was carried out for two reasons: 1) ocean effort data were missing or difficult to obtain for some years, and 2) there were no standardized methods of collecting data in ocean fisheries. For terminal areas I used the sum of fishing days below and above Bonneville Dam as the index of effort for the terminal fisheries (TAC 2008).

4.2.4 Model Formulation

A slight modification of the Fournier and Archibald (1982) statistical catch-at-age model was used to model Chinook salmon. This approach uses ocean and terminal catch data by stock and age in conjunction with escapement data to estimate parameters such as recruitment to age 2, fishing mortality by fishery, stock and age, and maturation and vulnerability schedules by age for fisheries. This method can be extremely useful in cases where escapement data may not meet data standards (e.g., some of the Puget Sound, and north central British Columbia escapement data).

The method uses a forward projection algorithm based on estimation of certain key parameters determined by fitting the parameters to the observed (or derived) data. An optimization function is used to find the parameters that minimize the difference between model projections and observed ocean catches (Deriso et al. 1985, Press et. al.

1988) by maximizing the likelihood functions between observed and predicted catches in the two fisheries and escapements (Figure 4.2).

Age-2 recruitment is estimated by using a spawner-recruit function with a recruitment deviate. Catches in ocean and terminal fisheries are a function of effort, catchability, and selectivity, parameters estimated by age. The catches based on these estimates are then projected by age and fit to the observed data. Finally, escapement is the difference between terminal run and terminal catch. Within the optimization framework, the variance-covariance matrix is estimated and this is the basis for projecting the uncertainty in both the estimated parameters (age 2 recruitment, catchability, etc.) as well as the derived parameters (catch by age and fishery, and escapement by age).

The prototype model developed here is fitted to ocean catches, terminal catches and escapement. The equations describing the ocean component of the fishes' life history are shown below:

$$NO_{2,t} = S_{t-2} e^{\alpha \left(1 - \frac{S_{t-2}}{\beta} \right)} \varepsilon_t \quad (4.6)$$

where $NO_{2,t}$ is the ocean recruitment to age 2 and time (t), and is estimated as a function of the observed number of spawners (S) at time period (t-2). The number of age-2 fish is predicted using a Ricker stock-recruitment relationship with a density independent parameter (α), and a density dependent parameter (β) using the number of spawners (S) two years before. This function deviates with error ε_t by year to best fit the observed catch and escapement data. In effect the entire Chinook freshwater life history is captured in this relationship and the ε represents differential freshwater and early ocean survival based on environmental conditions.

$$NO_{a+1,t+1} = NO_{a,t} e^{-(FO_{a,t} + M_a)} (1 - MR_{a,t}) \quad (4.7)$$

where NO is the numbers of Chinook in the ocean at age (a) and time (t), and is a function of population size at time ($t-1$), ocean fishing mortality (FO) at the previous age and time, and natural mortality (M) at that age as well as the fraction of the population that matured (MR) at the previous age and entered the terminal area (Equation 4.7).

In order to project catch, ocean fishing mortality rate (FO) is estimated as a function of the ocean catchability coefficient (qO) and ocean effort, EO :

$$FO_t = (qO)EO_t \quad (4.8)$$

Ocean fishing mortality (FO) at age is then estimated as a function of age-specific ocean vulnerability (VO) and ocean fishing mortality rate:

$$FO_{a,t} = VO_{a,t} FO_t \quad (4.9)$$

Ocean vulnerability (VO) was modeled as a function of age:

$$VO_{a,t} = \frac{1}{(1 + e^{(-r \cdot (a - K))}) \cdot \eta_{a,t}} \quad (4.10)$$

where r and K are shape function of the logistic curve, a is the age of Chinook, and ($\eta_{a,t}$) is the age-specific deviation from the logistic function by time ($\eta_{a,t}$).

Ocean catch-at-age and time were then projected as a function of the ocean abundance at a particular age, fishing mortality, and natural mortality at that age:

$$CO_{a,t} = NO_{a,t} \left[1 - e^{-(FO_{a,t} + M_a)} \right] \left[\frac{FO_{a,t}}{FO_{a,t} + M_a} \right] \quad (4.11)$$

The terminal fishery equations are similar to the ocean equations, with the added component of estimating maturation rates (MR) of the ocean cohort after the removal of the ocean catch CO .

$$NT_{a,t} = (NO_{a,t} - CO_{a,t})MR_{a,t} \quad (4.12)$$

where NT is the terminal run at age that is calculated after the ocean fisheries take place followed by maturation (MR). Maturity rates were modeled as a function of age (a) and were described by a logistic curve (Equation 4.13):

$$MR_{a,t} = \frac{1}{(1 + e^{(-r_m \cdot (a - K_m)) \cdot \nabla_{a,t}})} \quad (4.13)$$

where r_m and K_m are the shape parameters of the logistic function for maturation, and $\nabla_{a,t}$ is the age- and time-specific deviates in maturation.

Equations similar to Equations 4.8 to 4.11 were used to project terminal catch (Equations 4.14, 4.15, 4.16, and 4.17):

$$FT_t = (qT)ET_t \quad (4.14)$$

where F is fishing mortality in terminal areas, the subscript T indicates terminal effort (ET) and catchability (qT).

$$FT_{a,t} = VT_{a,t} FT_t \quad (4.15)$$

where $FT_{a,t}$ is fishery-specific mortality by age and is a function of vulnerability by age. Vulnerability (Equation 4.16) in the terminal fishery (VT) is a function of the shape functions (r_T and K_T) of the logistic curve, and $\gamma_{a,t}$ is the deviate from the original curve for a particular year and age:

$$VT_{a,t} = \frac{1}{(1 + e^{(-r_T \cdot (a - K_T))}) \cdot \gamma_{a,t}} \quad (4.16)$$

Terminal catch (CT) is determined using Equation 4.17:

$$CT_{a,t} = NT_{a,t} (1 - e^{-(FT_{a,t})}) \quad (4.17)$$

where $CT_{a,t}$ is the projected catch in the terminal area (loss due to natural mortality is assumed to be zero). Finally, escapement (S) at age was then calculated as terminal run minus terminal catch (equation 4.18)

$$S_{a,t} = NT_{a,t} - CT_{a,t} \quad (4.18)$$

The Likelihood equations could have either a normal error structure:

$$L(\theta | C_{a,t,f}) = \prod_{f=1}^n \frac{1}{\sqrt{2\pi\sigma_f^2}} \exp \left[-\frac{(C_{a,t,f}) - (\hat{C}_{a,t,f})^2}{2\sigma_f^2} \right] \quad (4.19)$$

or a log-normal error structure in log space:

$$-\ln(L(\theta | C_{a,t,f})) = \sum_{i=1}^n \ln(\sigma_f) + \frac{\ln(C_{a,t,f}) - \ln(\hat{C}_{a,t,f})^2}{2\sigma_f^2} \quad (4.20)$$

Note that escapement (S) is part of the likelihood as well and is added to the overall likelihood using Equation 4.21 for the normal likelihood (a similar form of equation 4.20 with S instead of C would be used for the log-normal likelihood and added as well (since independence is assumed in all cases)):

$$L(\theta | S_{a,t,f}) = \prod_{f=1}^n \frac{1}{\sqrt{2\pi\sigma_E^2}} \exp \left[-\frac{(S_{a,t,f}) - (\hat{S}_{a,t,f})^2}{2\sigma_s^2} \right] \quad (4.21)$$

The fishery-specific likelihoods could be weighted by external estimates of fishery specific σ_f or σ_s . This would be analogous to some of the new techniques developed for groundfish such as the Stock Synthesis approach (Methot 1989) and the Coleraine approach (Hilborn et al. 2003).

4.2.5 Model Selection

Many different models were built, some including more parameters (more time-specific parameters on deviations of vulnerability, and maturation by year), resulting in better fits than the others. If the simple likelihood (or log likelihood) of the fit is examined, a model with more parameters may appear to fit the data better, but the likelihood does not indicate whether the model is over-parameterized. I used a measure known as Akaike Information Criteria (AIC) which penalizes the likelihood by adding twice the number of parameters to the overall likelihood value (Equation 4.22, Akaike 1992):

$$AIC = -2\text{Log}(L) + 2n \quad (4.22)$$

where n is the number of parameters in the model and L is the likelihood of the fit of the model (sum of equations 4.19 and 4.21). If this equation is transformed, the penalty in likelihood space is:

$$e^{\frac{-AIC}{2}} = Le^{-n}$$

so the likelihood is modified by a factor of e^{-n} which is essentially the number of parameters used. To determine the best model structure, the model with the lowest AIC value is used.

4.2.6 Model Diagnostics

I compared results obtained from the current PSC assessment program with the age-structured approach developed here. The new age structured modelling approach also provides information on uncertainty that is missing from the current PSC

modelling approach. Estimates of recruitment based on the current exploitation rate analysis were evaluated, and the catch and escapement projections generated by the two models were compared using root mean square error (RMSE) calculations, and residual diagnostics.

4.2.7 Parameter Uncertainty

To test whether the model parameters converged to an optimal solution, I tested the model using Markov Chain Monte Carlo (MCMC) techniques with ADMB software package (Fournier 2000). Implicit in this approach is that I am now using a Bayesian framework (Gelman et al. 1995) with uniform priors across numerous parameters in order to test whether the model converges. In order to insure that the model does not deviate by large amounts from an optimal solution, priors were used on three different parameter sets shown in Table 4.4.

4.2.8 Simulation Model

In order to test the robustness of the model, a simulation algorithm was developed in which recruitment data were simulated using a Ricker spawner-recruit curve where the α and β parameters were sampled from its joint distribution in a manner similar to McCallister et al. (1999; Figure 4.3; adapted from McCallister et al. 1999). Process error was then applied to the simulated recruitment from the parameters of the spawner-recruit curve. Random variation was then applied to the catchability, vulnerability, and maturity rates prior to simulating the catch and escapement projections. Finally, sampling error was applied to the catch and escapement data to generate the data set to which I fit my model. Random variation in the recruitment

process occurs as a function of process error and is assumed (in the depiction of log-normal error structure, see Figure 4.3) while running the simulation.

4.3 RESULTS

4.3.1 Model Selection

After testing the models described above, I determined that model seven (Table 4.5 AIC values) was the best. This model's log-likelihood was equivalent to the others; although it wasn't the lowest value, this model captured the PSC's management intent, as it varied catchability over different time periods, reflecting changes in fishing practices mandated by the Pacific Salmon Treaty. In addition, this model also captured the effects of ocean productivity on maturation rates of these fish in response to changes in the ocean environment.

The models increased in complexity sequentially from model one to model seven. The first model estimates maturation by year and age, age two recruitment over time, and includes one estimate of catchability and selectivity over all years by gear type. The second model structures estimated maturation by decade (i.e., the maturation schedule was assumed to be constant by decade), but is otherwise identical to model 1. The third model includes a decadal structure for estimating catchability as well as maturation. The fourth includes decadal structures for estimating maturation, catchability, and selectivity by fishery. The fifth model includes an estimate of constant recruitment, but estimates of catchability change by year, and estimates of selectivity and maturation change by decade. The sixth model estimates recruitment variability by year, and estimates catchability, selectivity and maturation by decade.

The seventh model has the same structure as the sixth, except that it estimates maturation decadal by changes in ocean productivity (1977-1987, 1987-1997 and 1998 onwards), and catchability and selectivity vary with fishing regimes (pre-1985, the pre-treaty period; 1986-1995, the first treaty period; and 1996 onwards, a new treaty period of abundance-based management).

For maturation (Figure 4.4), time period 1 was the years before 1988, time period 2 was the years between 1988 and 1997, and time period 3 was the years from 1998 and later. These periods corresponded to changes in ocean condition regime (Hare et al. 1999), which was assumed to impact growth and maturity schedules (Quinn 2005). Fits of model seven to the data are shown in Figure 4.4. In general, trends in escapement and terminal catches are captured relatively well, and ocean fishery trends are captured poorly. This is largely a function of the precision in the data, which is very important in model fitting (Deriso et al. 2007).

4.3.2 Simulation Model Results

After determining the best model structure to use, I tested the robustness of the model via simulation techniques. As described in the Materials and Methods section, I created 10,000 data sets through bootstrapping, first without and then with sampling variability, and fit the model to each of those sets. In general the model tends to capture the dynamics of age-2 recruitment variability (Figure 4.5). The figure extends only to 1999, as it was created simply to provide a sense of the robustness of the model's algorithms and fits. This figure assumes that sampling error is zero in the observed data.

Although sample variability changes, the relationship between simulated and estimated data changes only marginally (Appendix 4.1 Figure 1). Given the inherent uncertainty in natural systems and the ability to make inference with observational data, the age structured modelling method is reliable even with a small amount of sampling error ($CV=0.1$). However, when CVs are greater than 0.5, the relationship does not work well (note: only in rare cases are the tag data CVs greater than 0.5 for the aggregated fisheries). Other results such as relative error distributions, correlation plots of fits to ocean catch, and terminal catch and escapement data with and without sample error are shown in Appendix 4.1. Although some of the plots might appear to demonstrate a slight bias (because the data points do not lie on the one-to-one line), these graphs only plot point estimates. If the uncertainty (confidence intervals or credible intervals) of the point estimate is taken into account, then confidence intervals for simulated values will overlap in most instances. These diagnostic checks imply that the model is robust in estimating recruitment, fishing mortality, catches, and escapement provided the model structure is correct.

4.3.3 Uncertainty in Derived Parameters

A major advantage of this approach is that it provides estimates of parameter uncertainty. Currently, management systems in both international (Pacific Salmon Commission) and domestic forums (e.g., US vs. Oregon process in the Columbia River, or Pacific Fishery Management Council) do not incorporate uncertainty in their assessment framework and manage according to point estimates of harvest or exploitation rates. Targets set for management should include all sources of uncertainty as shown in Figures 4.7 and 4.8 for harvest rates, for which the CV varies between 0.28

and 0.5 in ocean fisheries, and 0.15 to 0.28 in terminal fisheries. This variability largely reflects the number of fish caught of each stock group in these fisheries. In general terminal fisheries have a lower sampling error (CV) than ocean fisheries.

Age-2 recruitment is much less precise (CV between 0.26 and 0.52 from 1980 to 2004) as is evident from Figure 4.6. General trends indicate that age-2 recruitment was high in the mid-1980s and declined from 1987 to 1999 with spikes in recruitment again in the early 2000s.

Estimates of maturation (Figure 4.9) show precise estimates by age and little variation by time period. The figure indicates that uncertainty in maturation is highest at age 2 (CV = 0.28), and diminishes for ages 3 and 4 (CVs of 0.18 and 0.08, respectively). In addition, the results indicate that maturation rates in earlier (period 1) and later years (period 3) of age-2 fish appear to be low compared to the mid-years (period 2).

Vulnerability appears to have dropped over time (from period 1 to period 3) in ocean fisheries, while in terminal fisheries it remained constant for ages 3 and 4 but declined in age-2 fish (probably due to a change in mesh sizes; Figure 4.10). In ocean fisheries there is a drop in vulnerability across all ages in each time period. This trend is probably due to a succession of catch reductions and time-area closures from period 1 (largest effort) to period 2 (the first phase of the Pacific Salmon Treaty) to period 3 (the later PSC management phase characterized by abundance-based management and a new treaty for 1999-2009; PSC 2000).

Catchability in the ocean (Figure 4.11) showed similar trends with declines across each of three time periods, although for terminal areas period 2 showed a marginal increase in catchability as opposed to the ocean fisheries.

4.3.4 Model Convergence Monte Carlo Markov Chain Diagnostics (Appendix 4.2)

Smith (2007) describes the concept of characterizing uncertainty, and the use of Model Convergence Monte Carlo (MCMC) techniques to display distributions of parameter values. In contrast to techniques that look at convergence in terms of converging to a single point, checking for convergence of a distribution is also required. The chains appear to converge based on inspection (Appendix 4.2 Figures 1 through 9), autocorrelation statistics, and Geweke's statistics (Gelman et al. 1995) with the exception of vulnerability in the terminal fisheries for age 2, and period 1. Cross-correlation between parameters was negligible. While there is no guarantee that the chain did in fact converge to the posterior distribution, because the ADMB model package starts with values that are equivalent to the maximum likelihood solution (close to the posterior mode), and the chain was run for over 1 million iterations, I am confident that the chain converged.

4.4 DISCUSSION

Although age-structured models have been extensively described in the literature for numerous species (e.g., cod, Clark 2003, and halibut, Sullivan et al. 1999), their use in salmon management is only just emerging. Standard cohort analysis or virtual population models are largely used for salmon without any explicit incorporation of uncertainty (Morishima and Henry 2000). The statistical catch-at-age (SCAA) model described here explicitly incorporates uncertainty into the assessment

procedure. This approach has been attempted before (Lessard et al. 2008, Sæveride and Quinn 2004) although not on the scale that is being attempted here. The SCAA model can progressively refine the spatial scale and incorporate external data in the fitting structure as well as in describing recruitment variability. For Atlantic salmon (*Salmo salar*) state-space approaches conceptually similar to this one have shown promise (Michielsens et al. 2006), and although this model is not state-space, it successfully attempts to fit data simultaneously to numerous fisheries using a likelihood-based framework. Thus, this model has the capability to move salmon models into the 21st century by implicitly incorporating uncertainty through the MCMC framework and using it retrospectively as well as for forecasting purposes.

The approach described here has been tested through simulation techniques and then practically applied for a particular stock. More complicated models using the general framework here have also been developed and work equally well, although as uncertainty increases with decline in catches in particular fisheries, precision of the exploitation rates tends to get worse (higher CV).

The real advantage of this approach is that it can produce forecasts by extending the chain out for another year or a number of years (Appendix 4.3). In addition, it can be used to explore components of recruitment variation by adding additional variables like environmental factors.

4.4.1 Understanding Recruitment Variation in an Environmental Context

Recent approaches in salmon management have modelled the species within a life-cycle framework. Lawson et al. (2004) and Logerwell et al. (2003) demonstrated how using Generalized Additive Models (GAMs), fitting data with non-linear

techniques, appears to capture inter-annual variation in coho. A similar approach is used here, determining the impact of covariates that are hypothesized to be of key importance in survival for Columbia Chinook salmon, namely flow and sea surface temperature (SST, Scheuerell and Williams. 2005, Magnusson 2002) on age-2 recruitment for the Columbia Upriver Bright population.

The method takes estimates of age-2 recruitment derived from Equation 4.6 above and adds covariates to it:

$$N_{2,t} = S_{t-2} e^{\alpha \left(1 - \frac{S_{t-2}}{\beta}\right)} e^{\varepsilon_t} \quad (4.23)$$

Rearranging some terms in the equation, Equation 4.23 can be rewritten to include additional covariates (such as SST and/or flow; note α and β are re-parameterized here):

$$\ln\left(\frac{N_{2,t}}{S_{t-2}}\right) = \ln(\alpha) - \beta S_{t-2} + \phi_i X_{i(t+1)} + er_t \quad (4.24)$$

$X_{(i)t}$ is the value of the i^{th} covariate related to recruitment in year (t+1). In this case the covariates are flow and SST in the year preceding age-2 recruitment (i.e., the year the fish move from freshwater to the ocean environment). er is the new error term. This formulation assumes that covariates exhibit no density dependence in the production relationship.

Flow (Table 4.6), measured at the time of juvenile Chinook outmigration at Priest Rapids Dam on the upper Columbia, is expressed as the seasonal average between April and June for that station (Table 4.6 has standardized values). SSTJ is the

SST in July (when these fish are hypothesized to be in the ocean at station 48°N and 124°W off the Washington coast, Table 4.6 has standardized values). In this framework, age-2 recruitment was estimated rather than directly observed, using the age structured catch-at-age model described previously.

I fit a linear model (Table 4.7) after estimating recruitment from the age structured model (in the previous section) that indicates that SST is highly significant in explaining variation in both recruitment over time and spawning stock size (Table 4.7). As indicated in Table 4.7, spawners (S) and SST (July) are both highly significant. Adding flow (normalized over time) improves the fit using a non-linear fitting function (GAM) and captures variation such as the 1990 brood year (shown in Figure 4.12), when a prolonged El Niño in 1991-1992 probably led to poor survival for the 1991 outmigrants (Peterson et al. 2006). Fits are similarly improved in the El Niño of 1997 (1996 brood year, Figure 4.12) and positive conditions of brood year 2000 which had higher than average survival. The GLMs do not capture these trends as well as GAM-based techniques (Logerwell et al. 2003, Lawson et al. 2004), but using GAMs in forecasting can be complicated, and they are more useful in explaining processes.

It is apparent (Figure 4.13) that conditions were more favorable for the Upriver Brights between 1982 and 1988, declined between 1989 and 1998, and were positive from 2000 to 2004 (Peterson et al. 2006). Forecasts in 2005 indicated poor survival conditions, and poor returns were observed in 2007 (TAC 2008), although my incomplete data could not be extended to those years.

To understand how each of these variables affect recruitment, an independent variable analysis was conducted using Equation 4.24 which calculated the effect on recruitment of changes in flow and SST (Figure 4.14) assuming a known spawning stock size. The uncertainty in the relationship between age-2 recruitment and SST (Figure 4.14 (b)) means that when temperatures off the coast of WA in July are lower by one standard deviation than the average conditions of 1977-2007 (14.02 °C vs. 14.79 °C), the age-2 recruitment potential ranges from 65,000 to 95,000 with a peak around 80,000 Chinook. The opposite case occurs if temperatures are higher by one standard deviation. This situation produces conditions where the recruitment could be anywhere from 65,000 to 72,000 Chinook with a peak around 68,000 Chinook. The uncertainty in recruitment estimation as a function of SST is clearly displayed in the figure and illustrates that in general colder seas, corresponding to upwelling conditions, are better for survival and recruitment than average conditions. This study further strengthens the hypothesis of Peterson et al. (2006) who suggest prey availability and primary production during upwelling conditions (which correspond to lower SST off the coast of Washington in July) are beneficial to overall recruitment and survival for Columbia Upriver Bright Chinook. However, flow has a marginal or no effect on recruitment as shown in Figure 4.14 (a), although substantially larger flows have a positive effect. Lawson et al. (2004) demonstrate that good flow years correspond to good ocean years. Consequently there is a positive effect of both flow and ocean conditions in those years, which provides a tremendous boost to recruitment. Such was the case in 1985 through 1988 (1983 to 1986 brood years) and 2002 and 2004,

respectively (or brood year 2000 and 2002 respectively). These events led to some of the strongest runs in recent history in the Columbia River (TAC 2008).

4.4.2 Forecasting Model with Hindcasting Test (2005)

In-river management and terminal run forecasts currently use sibling regression relationships (TAC 2008) and almost never account for structural or model uncertainty. Given the results described above, it is possible to incorporate indicators of ocean conditions encountered by the outmigrating brood in order to refine forecasts. Methods to generate and correct forecasts are shown in Appendix 4.3. The MCMC chain that is used to test model convergence was also used to project future ocean and terminal runs by extending the chain out for a number of years.

Forecasts were generated only for terminal areas, as ocean abundance is back-calculated from terminal area data (TCChinook 2008-01). It is apparent from Figure 4.15 that applying this technique to 2005 data is problematic, although this calculation does not correct for ocean conditions. Based on Table 4.8, I used a weighting mechanism that is highly weighted to SST anomalies (unless flow anomalies' standard deviations are greater than 1.5, in which case the weighting structure is reversed). Arbitrary weights were chosen (namely 10 for the SST effect and 1 for the flow effect). The results shown in Figure 4.12 and Figure 4.14 indicate that the SST effect is greater than the flow effect. They also indicate that the lower SSTs are correlated with higher survivals, and vice versa. Similarly, larger flows correspond with higher survival. Thus the sign of the weight will be negative for SST and positive for flow when calculating a standard deviation away from the median to use in projecting a forecast. This weighted standard deviation correction is applied to the median forecast shown in the table,

resulting in a risk-averse forecast (as shown in Table 4.8). Note that these factors are ad hoc, and are used here just for demonstration purposes; a more thorough examination, using a hind-casting approach for multiple years, should be used to estimate the weights, rather than specify them.

The age-2 forecast was ignored for management purposes as jacks are not believed to spawn in large numbers. Once uncertainty has been explicitly incorporated into the projections (Figure 4.15) and I have established how environmental conditions might affect the dynamics of the stock (Figures 4.12 and 4.14), I could use a variance correction factor that might indicate what the new forecast would be, as indicated in Table 4.9. This method could then be used to downsize the regression-based forecast in order to utilize a precautionary management approach (FAO 1996).

Other approaches could use a qualitative decision, based on the percentiles of the forecast (Table 4.9). If conditions based on the variance correction (Table 4.8) seem to be arbitrary, a conservative or optimistic projection could be used based on the forecast distributions (Table 4.9). Thus, based on the results, if there is a colder than average SST for the brood year returning (as with age 5s) we would provide a forecast towards the higher percentile, versus the subsequent ages 4 and ages 5 would indicate a lower forecast, towards a lower percentile (Table 4.9).

For example, using these criteria for the age-3 fish, implementing a big correction based on ocean conditions would lead to using a forecast based on the 10th percentile (74,284), age 4s could use the 25th percentile (210,540), and age 5s a positive correction with the 90th percentile (44,358) for a total of approximately

329,000. These are the kinds of approaches that agencies should investigate when setting a forecast for in-river harvest targets.

4.4.3 Comparisons with the Current Pacific Salmon Commission (PSC) Chinook Model

The model currently used for Chinook management has worked remarkably well given that it relies on weak assumptions about harvest rates estimated during the base period years of 1979 to 1982; based on these rates, the PSC model uses a standard spawner-recruit function, terminal area estimates of post-season run size, and forecasts for the current year. The PSC model estimates recruitment deviates and fits data directly to terminal catch (Figure 4.16, Appendix 4.4 for ocean and escapement fits by age) and escapement. The PSC model does better than the SCAA estimate for age-2 fish, primarily because there are very few age-2 recoveries to which the SCAA can be fit. The PSC model generates some estimates of shaker mortality (these are fish that are too small to be landed and recorded, but nonetheless get encountered in the fisheries, are “shaken” off, and consequentially suffer some mortality) based on size limits, and proportion of a stock vulnerable to a fishery, but unlike the SCAA model, it has no ability to compute uncertainty in recruitment (Figure 4.6) or in harvest rates by age (Figures 4.7 and 4.8).

It is not entirely appropriate to compare the SCAA and PSC models, given that the PSC model has a finer scale of resolution for both fisheries and stocks (the PSC model is multi-fishery and multi-stock in nature), and that it computes a relative index of abundance for a variety of fisheries, while the SCAA model presented here is for a single stock and two aggregated fisheries. While the SCAA model is capable of

calculating estimates at a finer resolution (provided effort and CWT tag-recovery data are available at that resolution), the precision of data decreases at finer scales of resolution, increasing the uncertainty in harvest estimates. Regardless, if the PSC model is scaled to the same level of resolution of the SCAA model (i.e. two fisheries, ocean and terminal), the SCAA model performs better according to a mean square error criterion (Table 4.10) for every age, fishery, and escapement (except age 2 for terminal fisheries and escapement) when compared to the observed catch and escapement (based on CWT tag expansions for ocean fisheries, and observed catches and escapement in terminal fisheries proportioned by age according to CWT tags).

4.5 CONCLUSION

Finally, as summarized in Table 4.11, this model makes no assumptions with respect to parameter choices other than natural mortality. Variance can be estimated for each of the parameters. The SCAA method demonstrates the inherent uncertainty in the stock assessment using MCMC, and can forecast using extensions of the Markov chain into the future. This approach could also be used in management (Punt and Hilborn 1997) to determine optimal harvest strategies for long-term yield and sustainability of populations. In addition, environmental effects could be quantified and precautionary approaches to management could be determined by managing to the quartiles in the distributions of the forecast (Figure 4.15, Table 4.8 and Table 4.9) based on environmental conditions (Figures 4.12 and Figure 4.14). Finally, given the likelihood structure of the model, when used in a multi-stock, multi-fishery framework, the model could also be tuned to either CWT or genetic stock identification (GSI) age and stock composition data. These advantages over the current model framework used by the

PSC could eventually lead to management based on harvest rate schedules on a stock and area basis.

Acknowledgements

This project was funded under NOAA grant NFFP5000-7-13358. The code development benefited substantially from ADMB code guidance from Dr. Mark Maunder (Inter American Tropical Tuna Commission), and from Dr. Bob Lessard (University of Washington).

List of Tables

Table 4.1: Notation used for the modeling approach used

Table 4.2: Harvest data in numbers of fish used in the assessment

Table 4.3: Effort data used for the model. Ocean data is an index based on equation 4, and terminal data is obtained using boat days (number) as a measure for the commercial in-river fishery

Table 4.4: Priors used on recruitment deviates and maturation to enable model convergence. These were primarily based on tag data for maturation, and recruitment variation for Chinook.

Table 4. 5: Model selection procedures using negative log-likelihoods and AIC criteria. The models were sequentially developed from one to six with varying levels of complexity. The first model estimates maturation by year and age, age recruitment over time, and has one estimate of catchability and selectivity over all years by gear type (fishery). The second has a decadal structure on maturation, and everything else is the same as model 1. The third has a decadal structure for maturation, as well as catchability. The fourth has decadal structures for maturation, catchability and selectivity by fishery. The fifth has constant recruitment, but catchability changes by year, and selectivity and maturation changes by decade. The sixth model has recruitment vary by year, and catchability, selectivity and maturation changes by decade. The seventh model has the same structure as the previous model but has decadal structures with maturation that worked by ocean changes in productivity, and catchability and selectivity changes by different fishing regimes.

Table 4.6: Data on Upriver Bright age-2 recruitment, spawning stock size and environmental covariates

Table 4.7: ANOVA on the linear model fit using Equation 22, and flow and SST as covariates

Table 4.8: Incorporating environmental signals and corrections into forecasts based on weighting factors, and standard deviations of environmental conditions

Table 4.9: Percentiles of terminal forecasts based on distributions on Figure 14.

Table 4.10: MSE calculations on the PSC Model (TC-Chinook 08-01 *in prep*) and SCAA model

Table 4.11: SCAA comparisons with current model

Table 4.1: Notation used for the modeling approach used

	Description
A	Age
F	Fishery
T	Year
CO	Ocean catch
CT	Terminal Catch
$CWTO$	Coded Wire Tag fish in Ocean fishery
$CWTT$	Coded wire Tag fish in terminal fishery
R	Coded Wire Tag (CWT) hatchery releases
pT	Proportion of CWT releases recovered in terminal fishery
pO	Proportion of CWT releases recovered in ocean fishery
NO	Numbers (abundance) in th ocean
NT	Numbers abundance in the terminal areas
S	Spawners
A	Density independent parameter of the spawner-recruit curve
B	Density dependent parameter of ths spawner recruit curve
K	Observed escapement expansion parameter
RC	Observed redd count
EO	Ocean effort index
ET	Terminal effort index
qO	Ocean catchability coefficient
qT	Terminal catchability coefficient
FO	Fishing mortality in the ocean
FT	Fishing mortality in the terminal area
M	Natural Mortality
MR	Maturation Rate
VO	Ocean vulnerability
VT	Terminal Vulnerability
Σ	Model process error (standard error)

Table 4.2: Harvest data in numbers of fish used in the assessment

Year	Ocean Harvest					Terminal Harvest					Escapement				
	age 2	age 3	age 4	age 5	total	age 2	age 3	age 4	age 5	total	age 2	age 3	age 4	age 5	total
1978															44,783
1979															48,033
1980		21,549	43,716				2,286	6,125			19,564	8,783	20,781	16,556	65,684
1981		15,919	80,343	31,530			1,682	10,088	3,403		14,575	3,956	31,019	9,052	58,602
1982		28,550	36,554	17,486			4,012	4,794	1,809		15,225	25,340	21,745	11,392	73,702
1983	4,931	39,017	44,926	3,108	91,982	852	7,097	11,425	2,001	21,375	45,593	16,178	30,004	6,930	98,705
1984	5,379	14,787	124,266	27,984	172,416	7,092	14,375	27,840	4,377	53,684	77,588	9,894	28,955	9,500	125,937
1985	10,976	19,128	41,329	57,498	128,931	21,753	25,561	35,884	25,681	108,879	100,312	23,170	33,880	19,625	176,987
1986	3,929	46,516	69,516	17,636	137,597	23,302	37,450	80,845	22,794	164,391	149,658	34,714	46,405	14,055	244,832
1987	-	28,875	146,683	76,488	252,046	3,527	34,546	114,613	56,143	208,829	63,860	47,694	62,603	31,850	206,007
1988	804	2,622	76,698	87,827	167,951	5,995	12,789	120,471	63,004	202,259	62,232	17,428	46,727	37,028	163,415
1989	-	3,340	20,985	114,802	139,127	1,188	12,056	35,359	95,474	144,077	29,748	14,132	22,089	58,400	124,369
1990	-	1,000	41,110	38,236	80,346	1,451	3,260	36,203	38,266	79,180	31,253	4,293	26,149	29,242	90,937
1991	117	3,226	13,057	34,527	50,927	1,853	3,336	9,996	25,693	40,878	33,717	3,648	13,544	31,165	82,074
1992	3,365	1,352	24,291	6,654	35,662	2,542	3,821	8,423	6,223	21,009	24,700	7,127	21,242	17,078	70,147
1993	-	2,493	44,204	23,250	69,947	1,084	1,880	15,136	9,310	27,410	12,265	5,816	37,911	16,175	72,167
1994	4,414	-	14,604	20,656	39,674	2,051	4,806	8,999	11,047	26,903	26,343	6,706	37,003	41,499	111,551
1995	1,251	1,864	2,180	31,715	37,010	1,861	3,520	3,733	12,998	22,112	33,190	14,598	13,581	40,639	102,008
1996	-	1,484	3,292	3,727	8,503	967	9,217	18,685	5,167	34,036	13,427	22,341	43,201	12,744	91,713
1997	-	-	23,774	10,128	33,902	1,031	6,750	30,858	8,586	47,225	17,269	12,661	55,284	20,968	106,182
1998	-	2,315	1,881	37,986	42,182	1,560	4,340	5,996	23,533	35,429	18,873	17,765	11,617	44,981	93,236
1999	-	2,150	29,727	8,858	40,735	1,269	1,782	26,842	3,997	33,890	18,961	9,166	47,939	10,767	86,833
2000	-	1,774	10,829	31,593	44,196	1,046	3,955	17,965	19,837	42,803	44,079	8,491	36,536	46,917	136,023
2001	-	3,706	13,730	6,853	24,289	3,513	7,241	27,981	11,178	49,913	56,614	43,982	71,147	27,375	199,118
2002	-	6,840	50,624	22,873	80,337	1,341	11,466	50,435	16,235	79,477	32,543	32,919	99,012	33,228	197,702
2003	257	13,837	48,819	40,709	103,622	2,962	11,463	43,017	28,824	86,266	36,948	27,373	157,196	79,816	301,333
2004	255	5,718	35,136	39,961	81,070	2,466	16,778	25,007	33,478	77,729	30,156	51,484	59,270	123,483	264,393

Table 4.3: Effort data used for the model. Ocean data is an index based on equation 4, and terminal data is obtained using boat days (number) as a measure for the commercial in-river fishery

Year	ocean	terminal
1980	2.21	68
1981	2.1	50
1982	2.11	18
1983	1.88	33
1984	1.7	41.5
1985	1.56	19.5
1986	1.55	67
1987	1.46	68
1988	1.47	84
1989	1.64	84
1990	1.65	76.5
1991	1.59	85
1992	1.97	70
1993	1.88	56
1994	1.03	54.5
1995	1.22	43
1996	1.24	14
1997	1.58	11
1998	0.81	37
1999	0.89	41
2000	0.54	31
2001	0.88	47
2002	1.31	41
2003	1.22	58
2004	1.22	58

Table 4.4: Priors used on recruitment deviates and maturation to enable model convergence. These were primarily based on tag data for maturation, and recruitment variation for Chinook.

Parameters	Priors values
μ MR (2)	0.03
σ MR (2)	0.02
μ MR (3)	0.16
σ MR (3)	0.07
μ MR (4)	0.59
σ MR (4)	0.13
SR deviate (σ_r)	0.87

Table 4. 5: Model selection procedures using negative log-likelihoods and AIC criteria. The models were sequentially developed from one to six with varying levels of complexity. The first model estimates maturation by year and age, age recruitment over time, and has one estimate of catchability and selectivity over all years by gear type (fishery). The second has a decadal structure on maturation, and everything else is the same as model 1. The third has a decadal structure for maturation, as well as catchability. The fourth has decadal structures for maturation, catchability and selectivity by fishery. The fifth has constant recruitment, but catchability changes by year, and selectivity and maturation changes by decade. The sixth model has recruitment vary by year, and catchability, selectivity and maturation changes by decade. The seventh model has the same structure as the previous model but has decadal structures with maturation that worked by ocean changes in productivity, and catchability and selectivity changes by different fishing regimes.

Parameters	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
initial age 3 4 5	3	3	3	3	3	3	3
vuln_ocean	3	3	3	9	9	9	9
vuln_terminal	3	3	3	9	9	9	9
q_ocean	1	1	3	3	25	25	3
q_terminal	1	1	3	3	25	25	3
maturity rates	75	9	9	9	9	9	9
age 2 recruits	25	25	25	25	1	25	25
Total parameters	111	45	49	61	81	105	61
-log(likelihood)	276	279	276	272	271	256	273
AIC	773	649	649	666	703	722	669

Table 4.6: Data on Upriver Bright age-2 recruitment, spawning stock size and environmental covariates

Year(t)	Out Migration year(t-1)	Age2(t) Recruitment	S(t-2)	dev	SSTJ(t+1)	Flow(t+1)	Rs	ln(rS)
1980	1979	374591	44783	0.83	-0.22	-0.81	8.36	0.92
1981	1980	648412	48033	1.38	-0.44	-0.34	13.50	1.13
1982	1981	911964	46120	1.99	-1.55	0.55	19.77	1.30
1983	1982	707686	44027	1.60	0.00	1.12	16.07	1.21
1984	1983	1284968	58477	2.40	1.65	0.46	21.97	1.34
1985	1984	1713310	98705	2.47	-1.42	0.02	17.36	1.24
1986	1985	1743198	125937	2.36	-1.29	-0.73	13.84	1.14
1987	1986	768649	176987	1.04	-0.75	-0.01	4.34	0.64
1988	1987	803364	244832	1.22	-0.74	-0.47	3.28	0.52
1989	1988	368092	206007	0.52	-0.49	-1.05	1.79	0.25
1990	1989	454836	163415	0.61	1.16	-0.50	2.78	0.44
1991	1990	634622	124369	0.86	0.19	0.76	5.10	0.71
1992	1991	594914	90937	0.88	-0.73	1.12	6.54	0.82
1993	1992	242427	82074	0.38	1.33	-0.40	2.95	0.47
1994	1993	618443	70147	1.04	0.84	-0.94	8.82	0.95
1995	1994	938710	72167	1.55	-0.21	-0.55	13.01	1.11
1996	1995	251337	111551	0.35	1.98	-0.34	2.25	0.35
1997	1996	858193	102008	1.22	-0.70	1.91	8.41	0.92
1998	1997	578135	91713	0.86	1.76	3.08	6.30	0.80
1999	1998	794558	106182	1.12	0.48	0.04	7.48	0.87
2000	1999	1257117	93236	1.85	-0.31	0.64	13.48	1.13
2001	2000	1421331	86833	2.15	1.01	0.26	16.37	1.21
2002	2001	1023139	136023	1.37	-0.54	-1.83	7.52	0.88
2003	2002	1540974	199118	2.13	-0.44	0.56	7.74	0.89
2004	2003	1394271	197702	1.93	-0.45	-0.23	7.05	0.85

Table 4.7: ANOVA on the linear model fit using Equation 22, and flow and SST as covariates

	Df	Deviance	Resid. Df	Resid. Dev.	F	Pr(>F)
NULL			24	2.25168		
S	1	0.84979	23	1.40189	17.9669	0.000367
Flow	1	0.0125	22	1.38939	0.2642	0.612614
SSTJ	1	0.39614	21	0.99325	8.3754	0.008681

Table 4.8: Incorporating environmental signals and corrections into forecasts based on weighting factors, and standard deviations of environmental conditions

Age	SST dev (-effect)	SST Wt	Flow dev (+ive effect)	Flow Wt	SD Correction	Median	Std Dev	Corrected Forecast	TAC Forecast	Actual
age 5	-0.31	10	0.64	1	0.34	28,865	9,549	32,112	73,200	64,800
Age 4	1.01	10	0.26	1	-0.89	244,215	64,718	186,322	231,800	155,100
Age 3	-0.54	1	-1.83	10	-1.61	108,285	44,370	36,648	47,200	58,600
TOTAL						381,365		255,081	352,200	278,500

Table 4.9: Percentiles of terminal forecasts based on distributions on Figure 14.

Age	10%	25%	50%	75%	90%
Age 5	20101	23801	28866	36288	44358
Age 4	183843	210540	244216	290070	334185
Age 3	74284	89425	108285	138696	172924
TOTAL	278228	323765	381366	465053	551467

Table 4.10: MSE calculations on the PSC Model (TC-Chinook 08-01 *in prep*) and SCAA model

root(MSE) Ocean Catch			
AGE	SCAA	PSC	% PSC
Age 2	3643	3704	98%
Age 3	13820	15541	89%
Age 4	26984	27002	100%
Age 5	23684	32067	74%
root(MSE) Terminal catch			
AGE	SCAA	PSC	% PSC
Age 2	5003	3091	162%
Age 3	4183	15202	28%
Age 4	9363	30735	30%
Age 5	9629	21309	45%
root(MSE) Escapement			
AGE	SCAA	PSC	% PSC
Age 2	42338	16457	257%
Age 3	20572	21285	97%
Age 4	25273	27856	91%
Age 5	14312	20516	70%

Table 4.11: SCAA comparisons with current model

Attribute	Existing model	SCAA model
Tuning	Tuned to observed escapements for the stock of concern	Tuned to a combination of CWT and GSI based estimates of observed ocean recoveries, observed terminal catch, and observed escapement for the stock of concern.
Objective function	Minimize difference between successive estimates of Environmental Variability (EV). EV is the annual error term in the spawner recruit curve.	Minimize $-\log$ likelihood. Weighting between fishery likelihoods is possible with external estimate of σ and can be a function of perceived data quality.
Parameters estimated for forward projection	RT, EV. RT is the ratio of observed to base period harvest rates. This model accounts for changes in effort or gear selectivity. Maturation based on CWT's.	Recruitment, catchability, vulnerability, maturity/
Variance estimates for parameters or derived parameters	No	Yes
Source of age and stock composition	CWT for base years only (first 4 years on the model)	CWT, GSI

List of Figures

Figure 4.1: Ocean fisheries and geographical areas encountering Upriver Bright Chinook Stocks

Figure 4.2: Schematic used to estimate age 2 recruitment, catchability, vulnerability, and maturation using statistical catch-at-age techniques for a simple two-area model (ocean and terminal)

Figure 4.3: The simulation and estimation process

Figure 4.4: Age 2 recruitment, observed versus estimated catches for each fishery and escapement

Figure 4.5: Simulated and estimated age 2 recruitment over time

Figure 4.6: Age 2 recruitment over time

Figure 4.7: Simple ERs (Catch of ages 3 and greater divided by Cohort of age 3s and over) over time for ocean fisheries for ages 3 and over

Figure 4.8: Simple ERs over time for terminal fisheries

Figure 4.9: Maturation uncertainty

Figure 4.10: Vulnerability uncertainty

Figure 4.11: Catchability uncertainty

Figure 4.12: GLM and GAM fits to observed variation in data using SST and flow as covariates

Figure 4.13: Deviations from the spawner-recruit fit (> 1 indicates greater than S-R model projection and < 1 indicates lesser than S-R model projection)

Figure 4.14: Likelihood profiles as a function of flow and SST (independently)

Figure 4.15: Age specific forecast distributions with the observed values in 2004 (the red line indicates observed values and the green line indicates current forecasting techniques)

Figure 4.16: Comparisons of this approach with existing model for terminal fisheries by age



Figure 4.1: Ocean fisheries and geographical areas encountering Upriver Bright Chinook Stocks

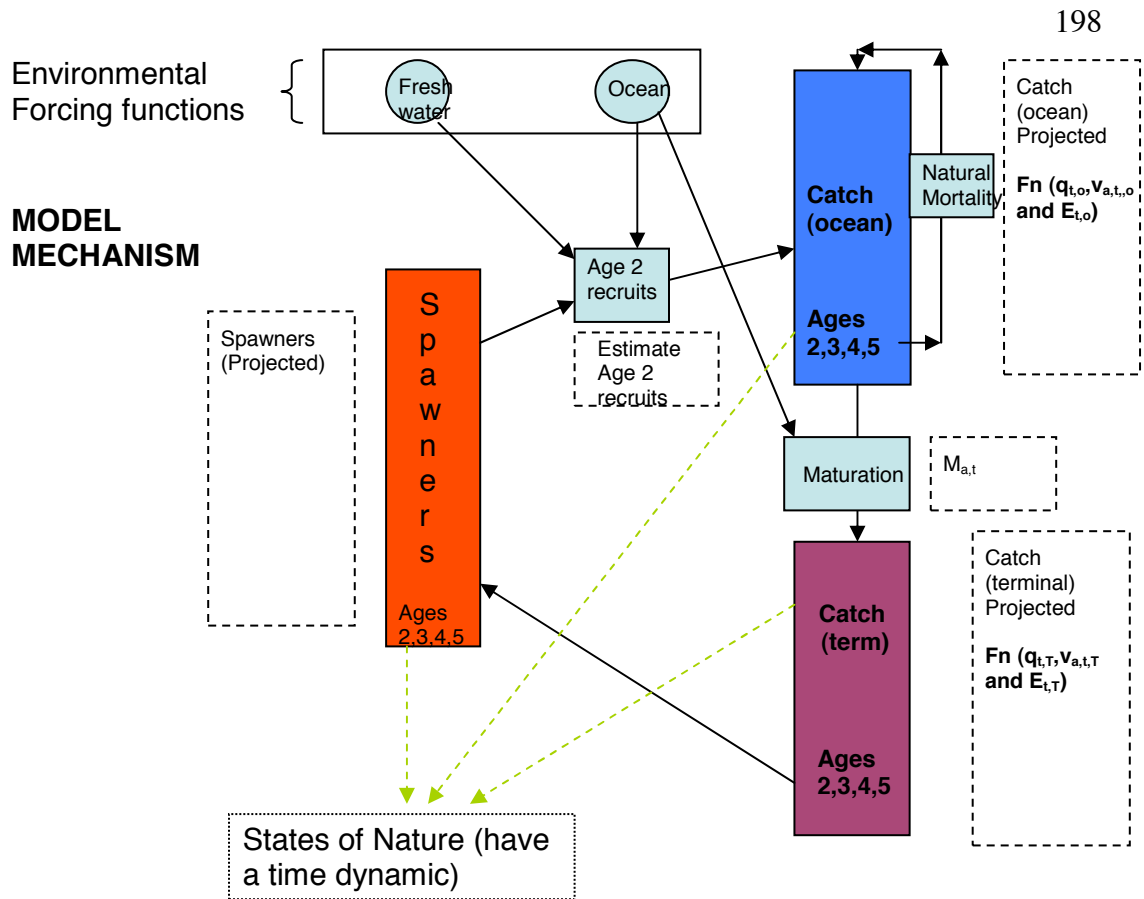


Figure 4.2: Schematic used to estimate age 2 recruitment, catchability, vulnerability, and maturation using statistical catch-at-age techniques for a simple two-area model (ocean and terminal)

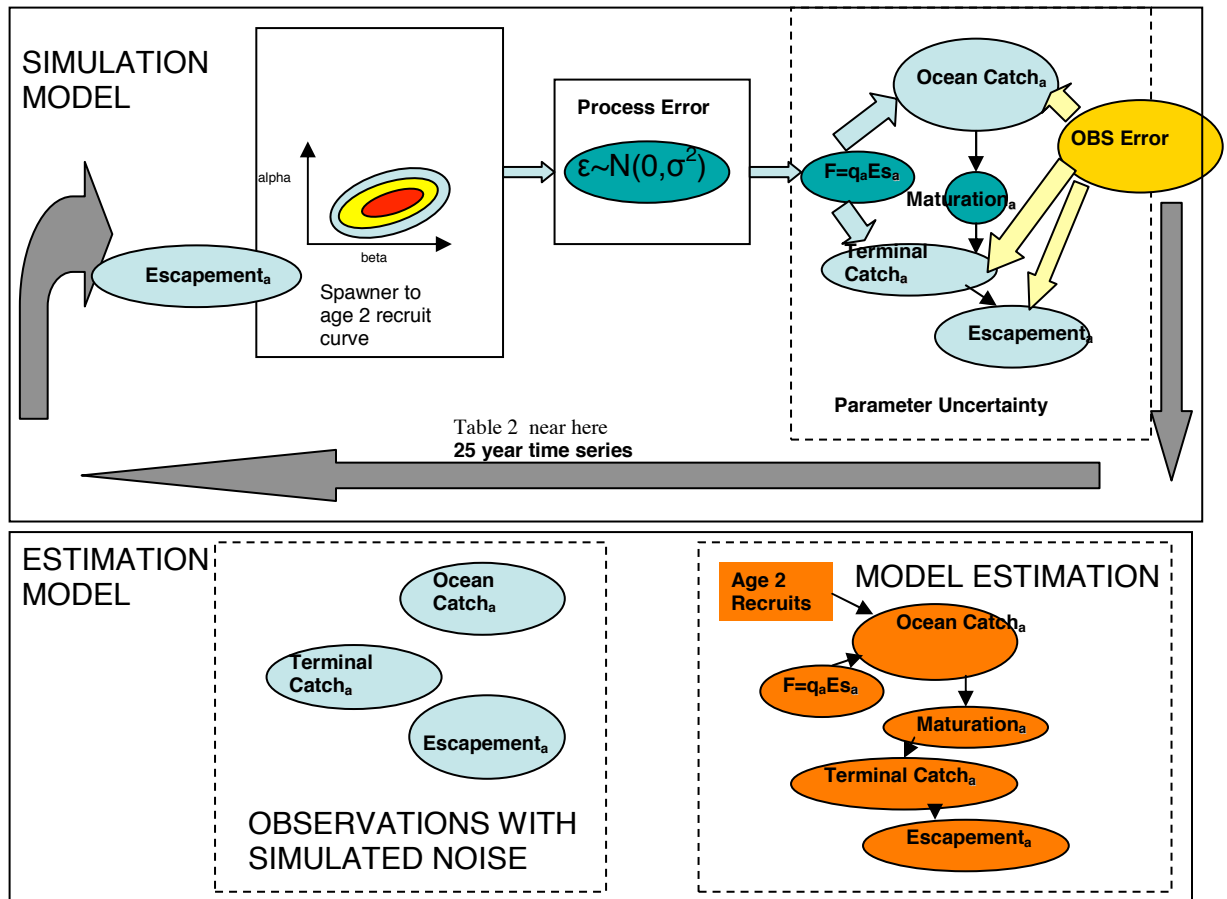


Figure 4.3: The simulation and estimation process

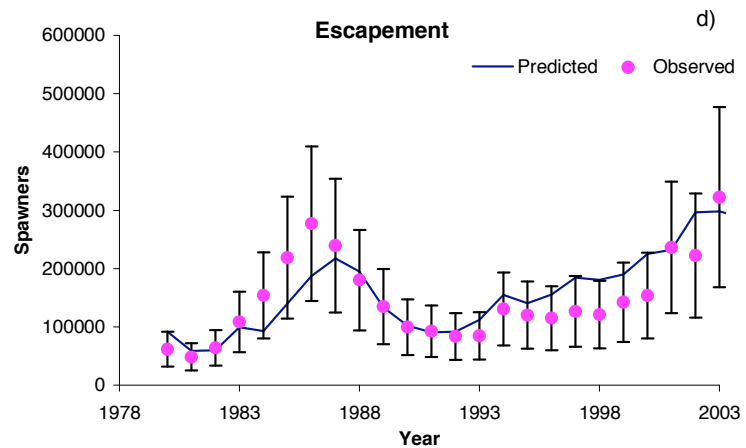
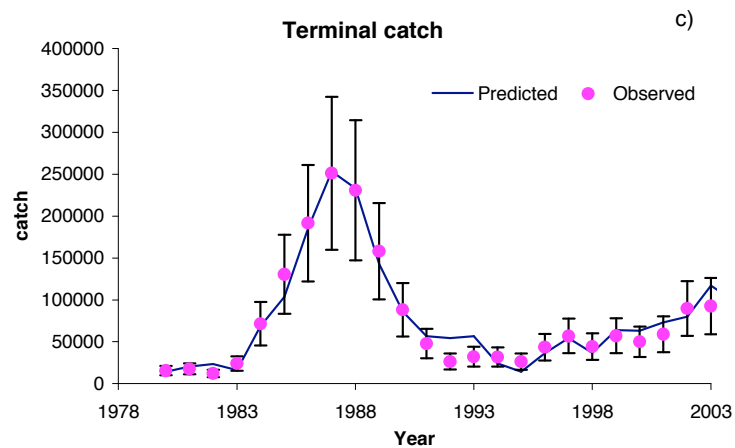
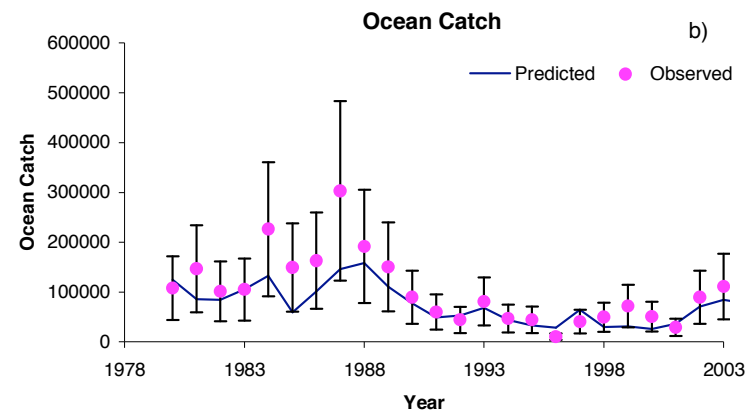
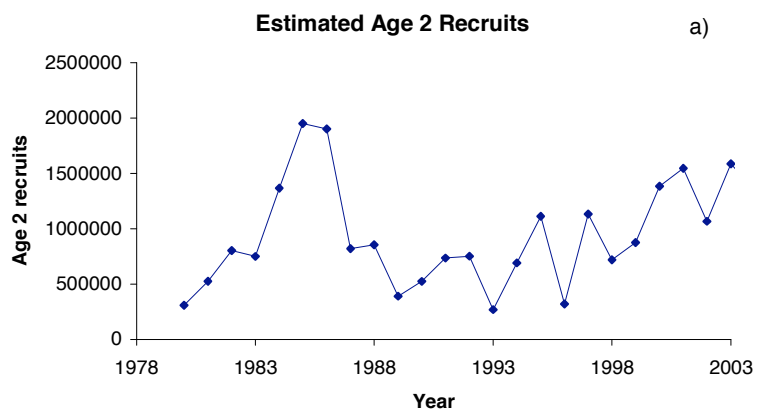


Figure 4.4: Age 2 recruitment, observed versus estimated catches for each fishery and escapement

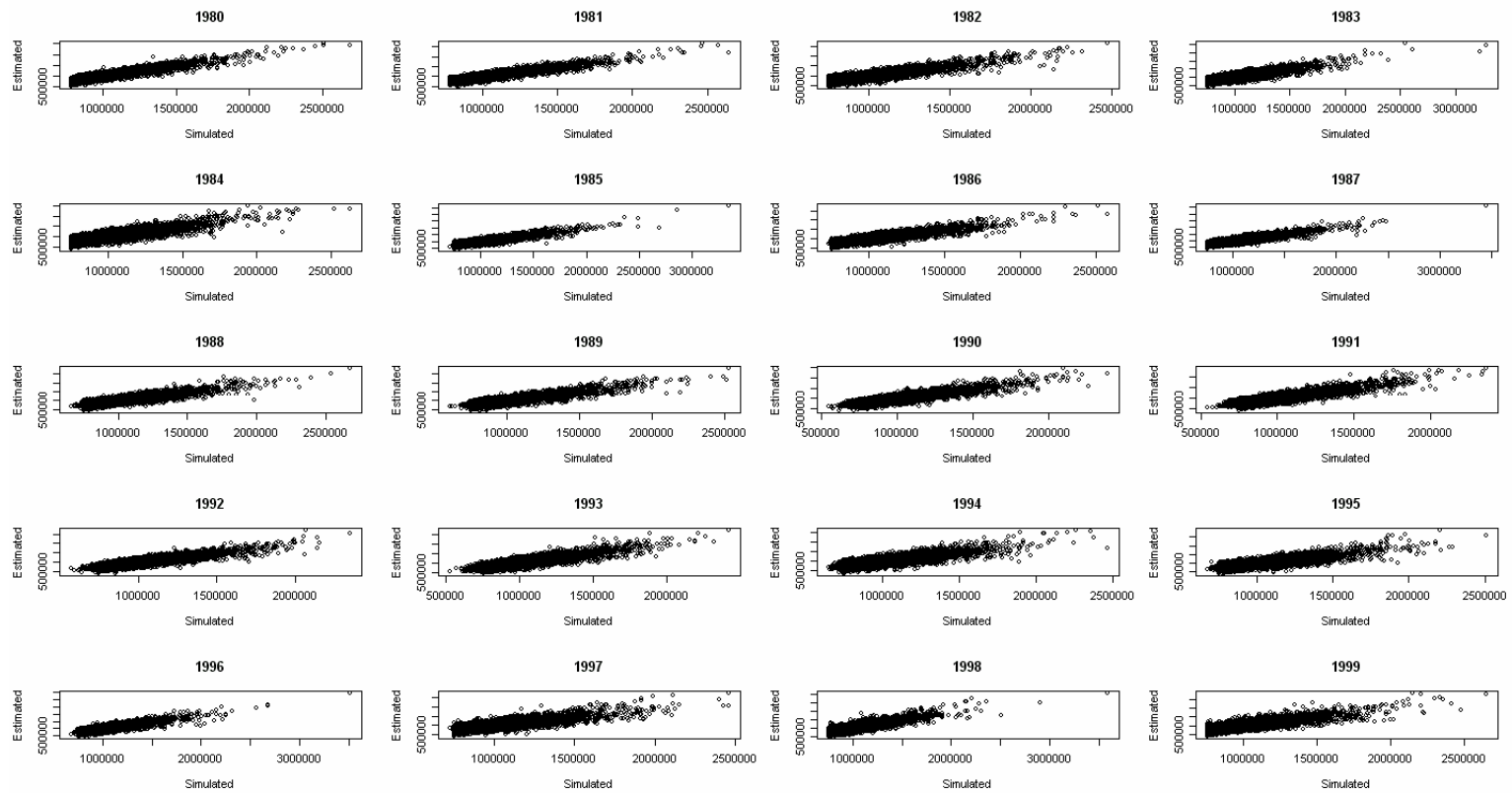


Figure 4.5: Simulated and estimated age 2 recruitment over time

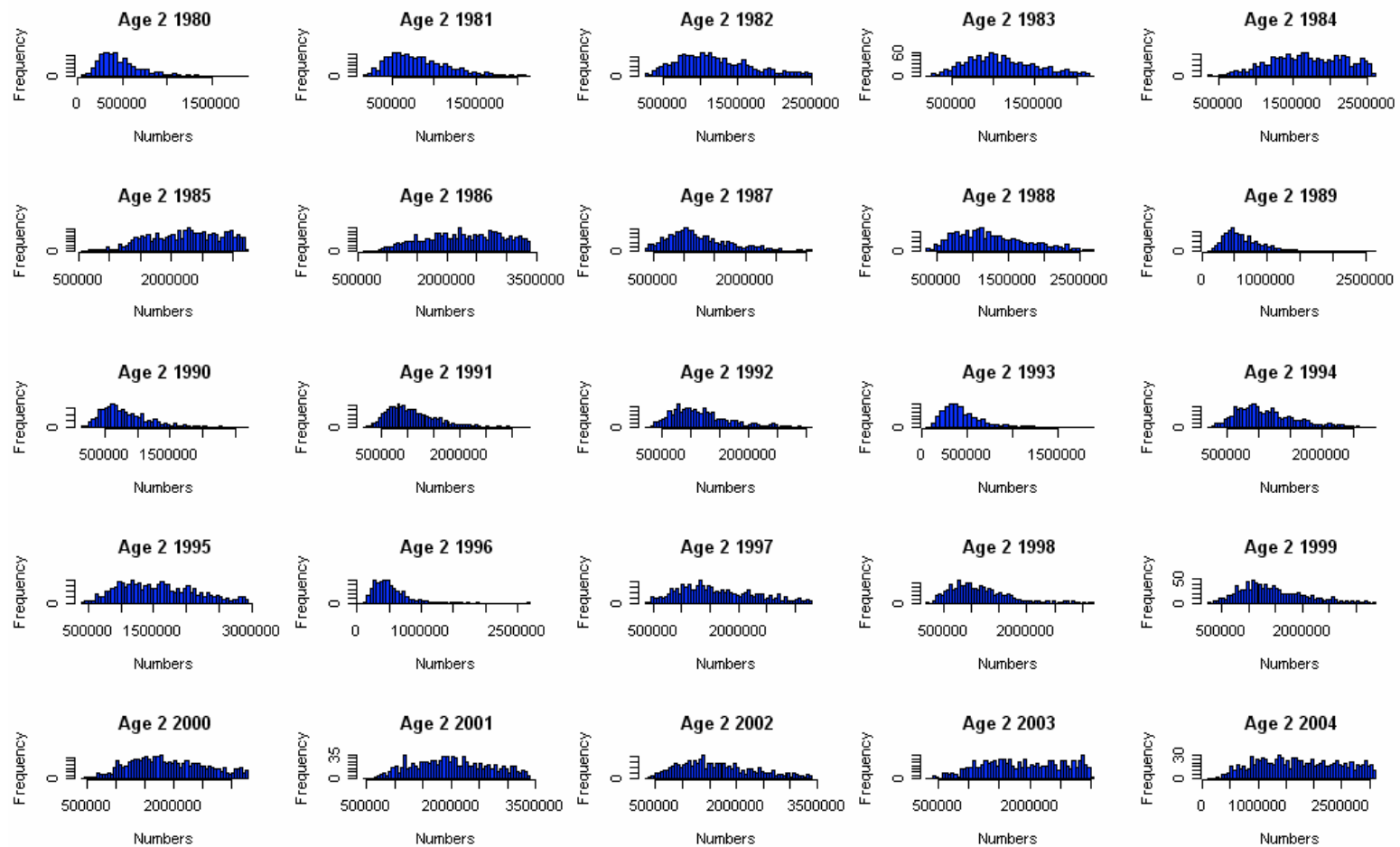


Figure 4.6: Age 2 recruitment over time

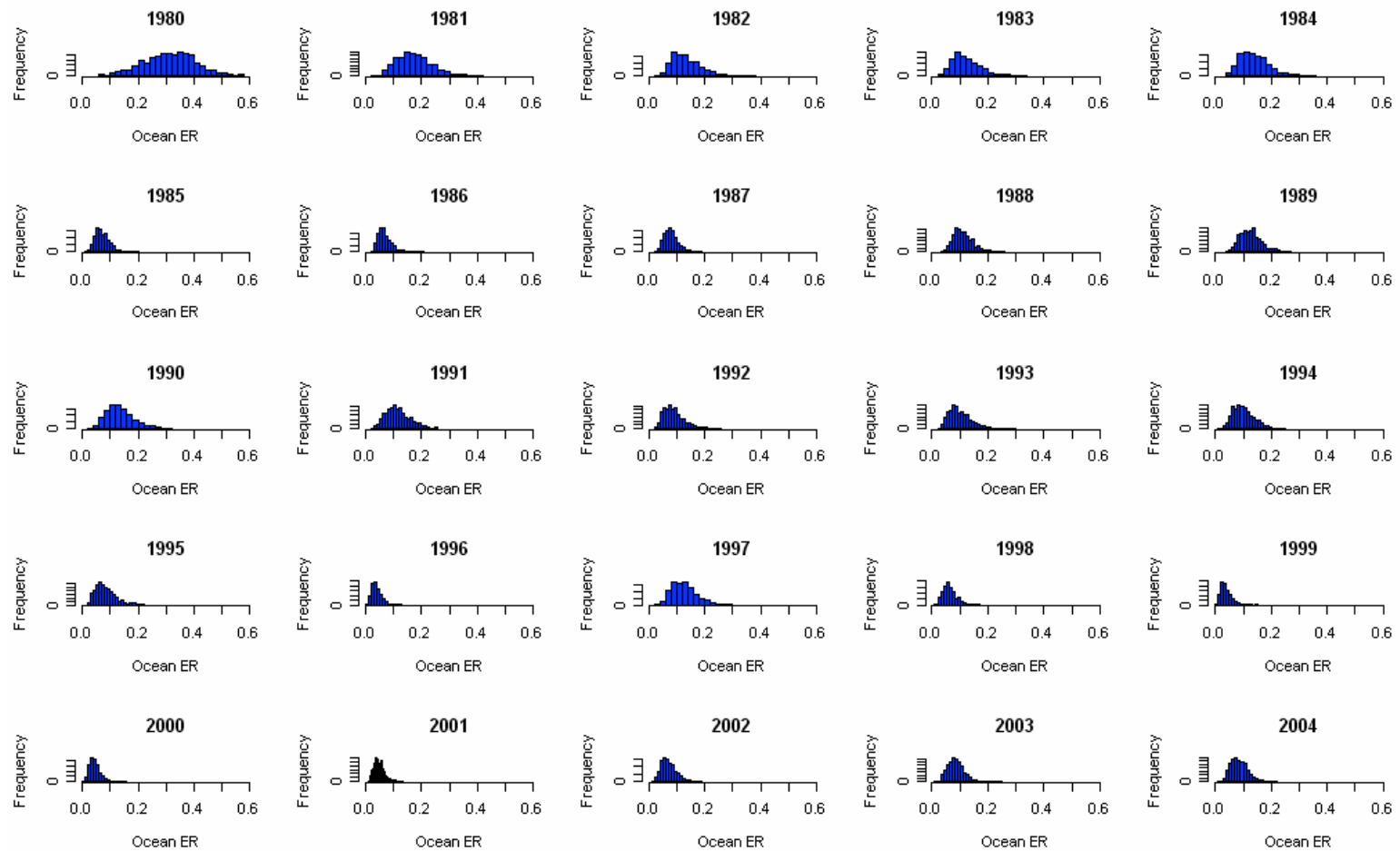


Figure 4.7: Simple ERs (Catch of ages 3 and greater divided by Cohort of age 3s and over) over time for ocean fisheries for ages 3 and over

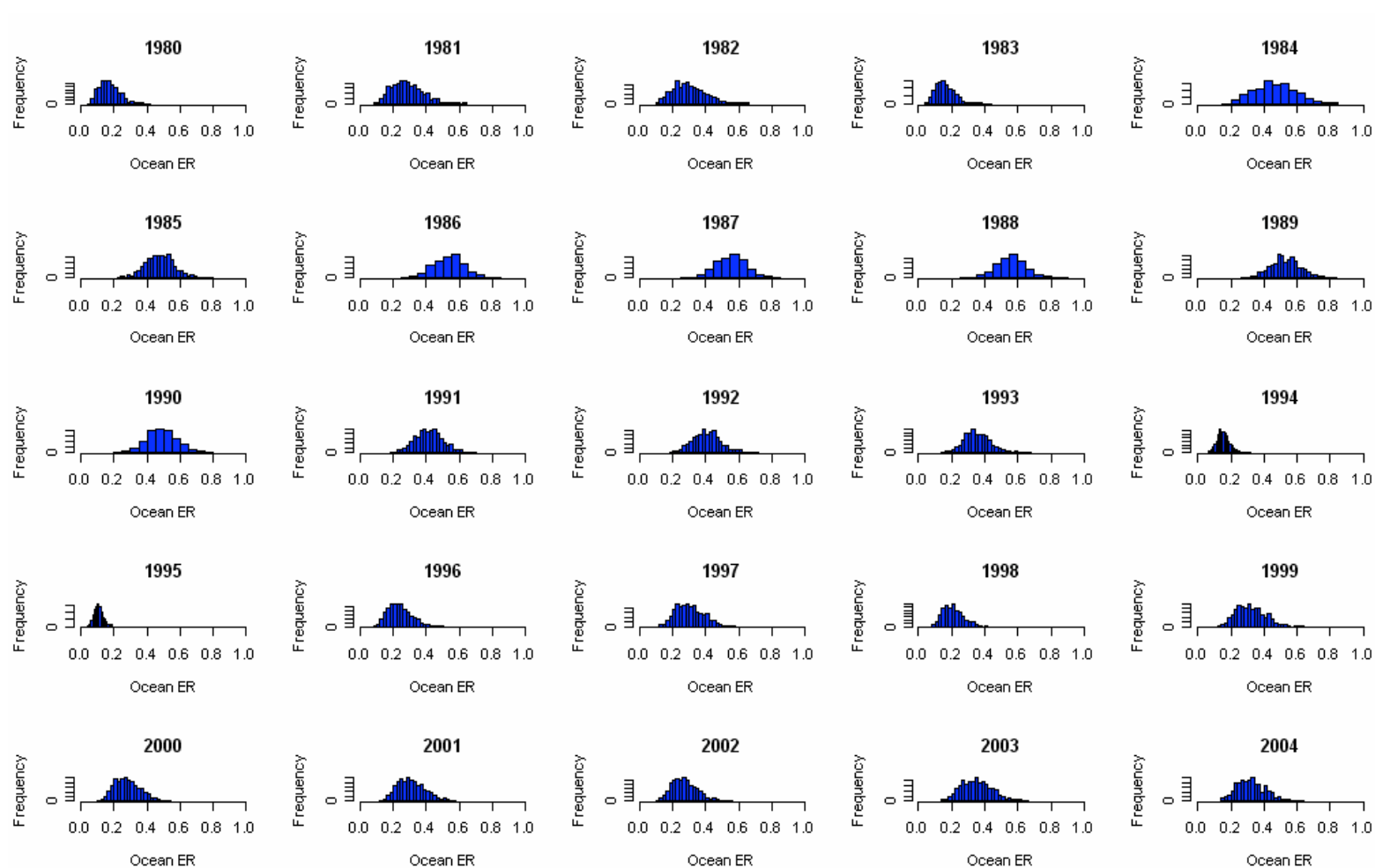


Figure 4.8: Simple ERs over time for terminal fisheries

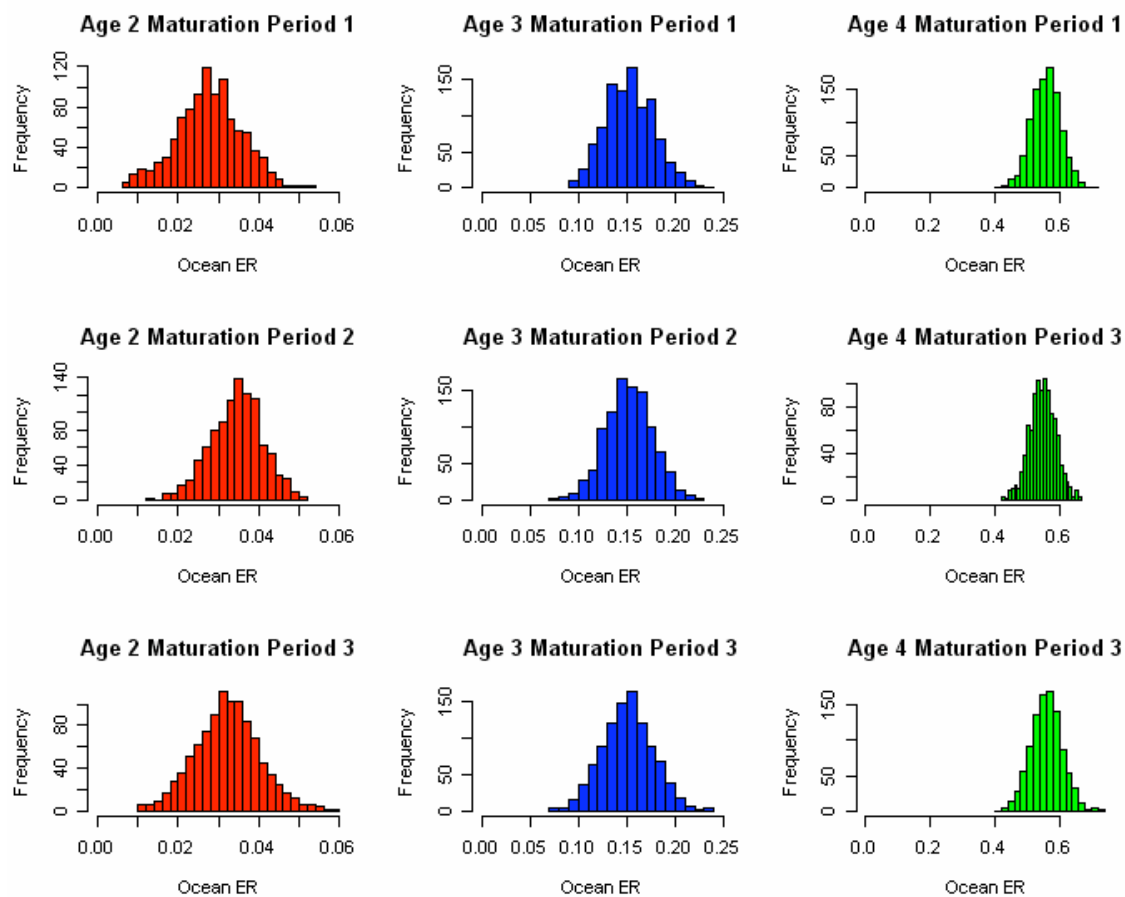


Figure 4.9: Maturation uncertainty

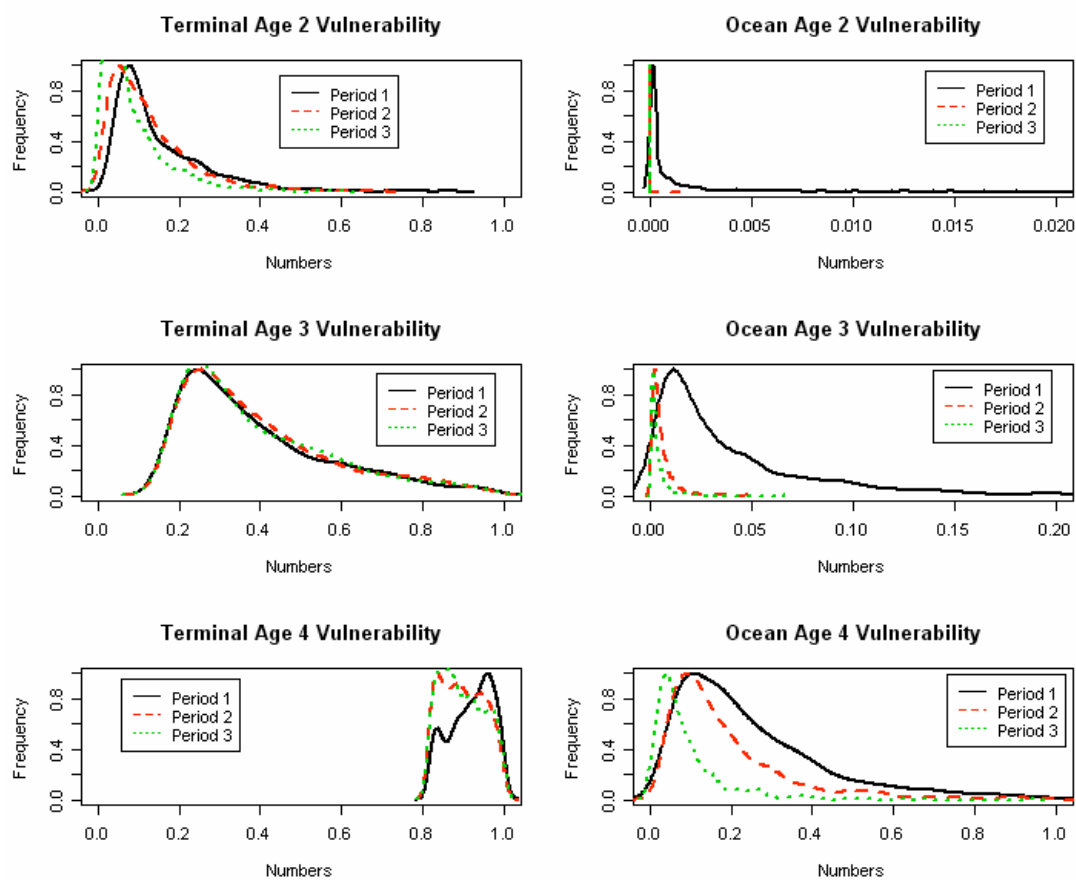
**F**

figure 4.10: Vulnerability uncertainty

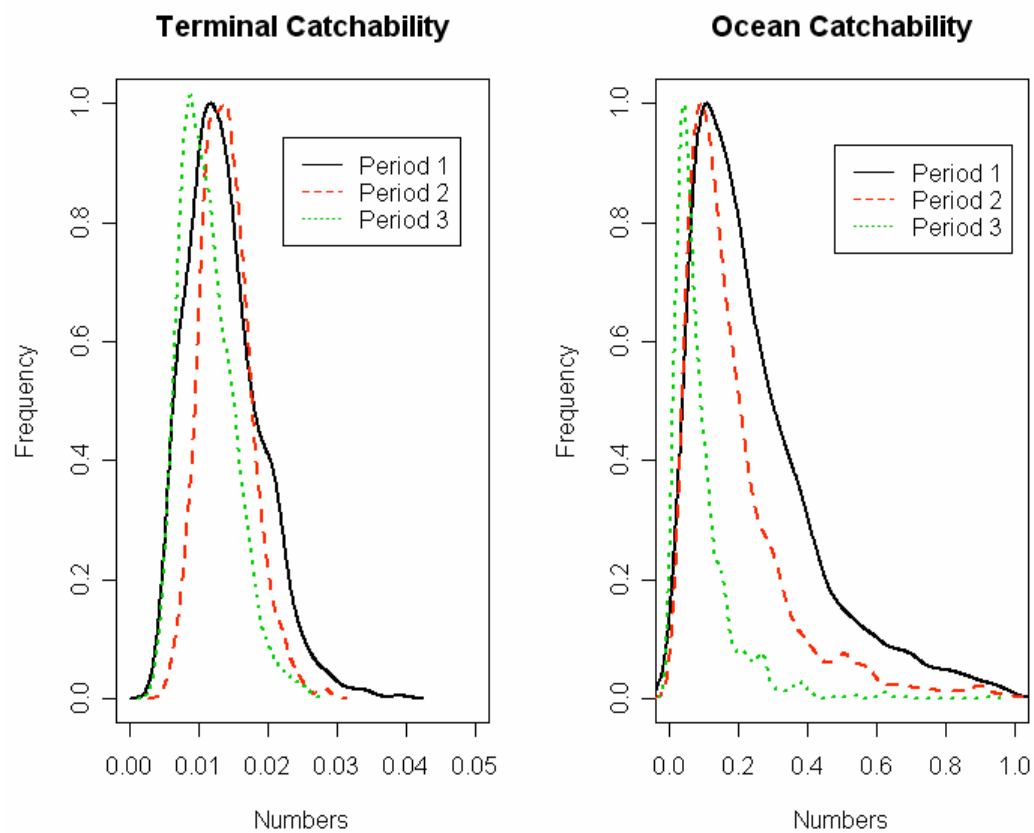


Figure 4.11: Catchability uncertainty

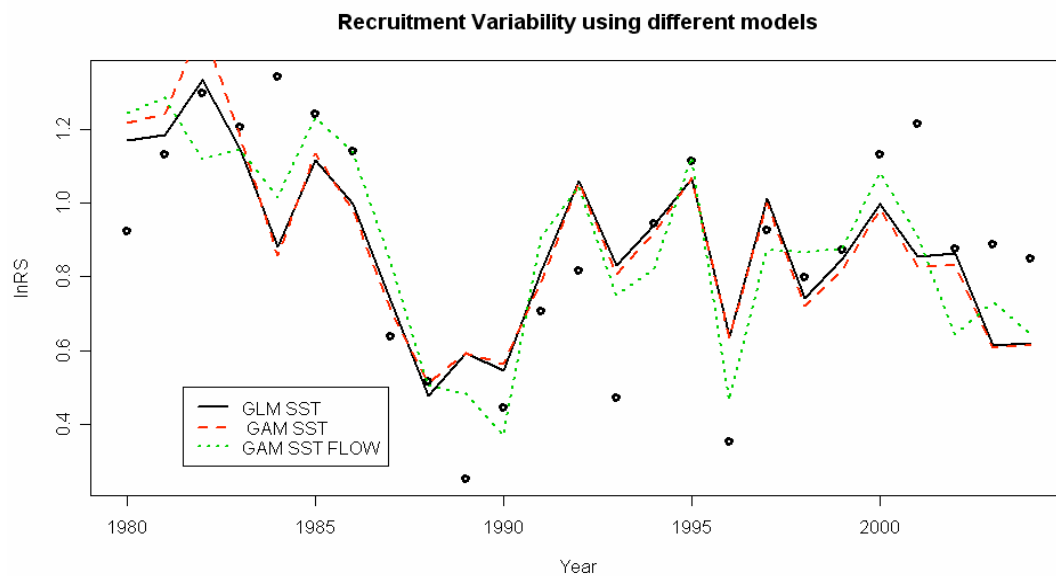


Figure 4.12: GLM and GAM fits to observed variation in data using SST and flow as covariates

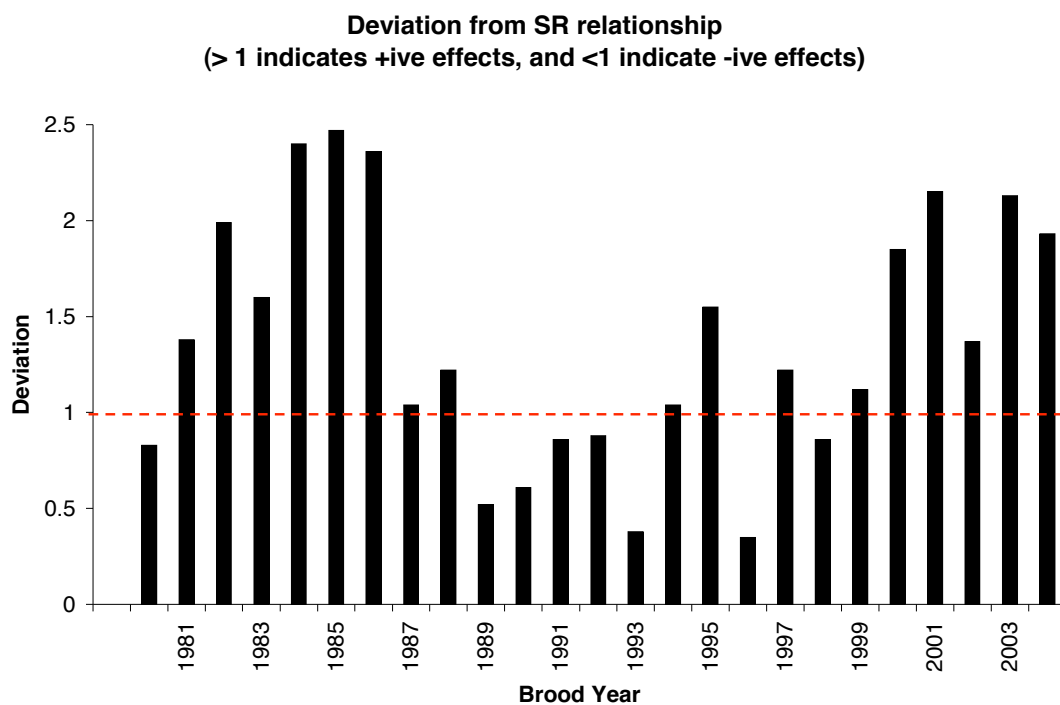


Figure 4.13: Deviations from the spawner-recruit fit (> 1 indicates greater than S-R model projection and <1 indicates lesser than S-R model projection)

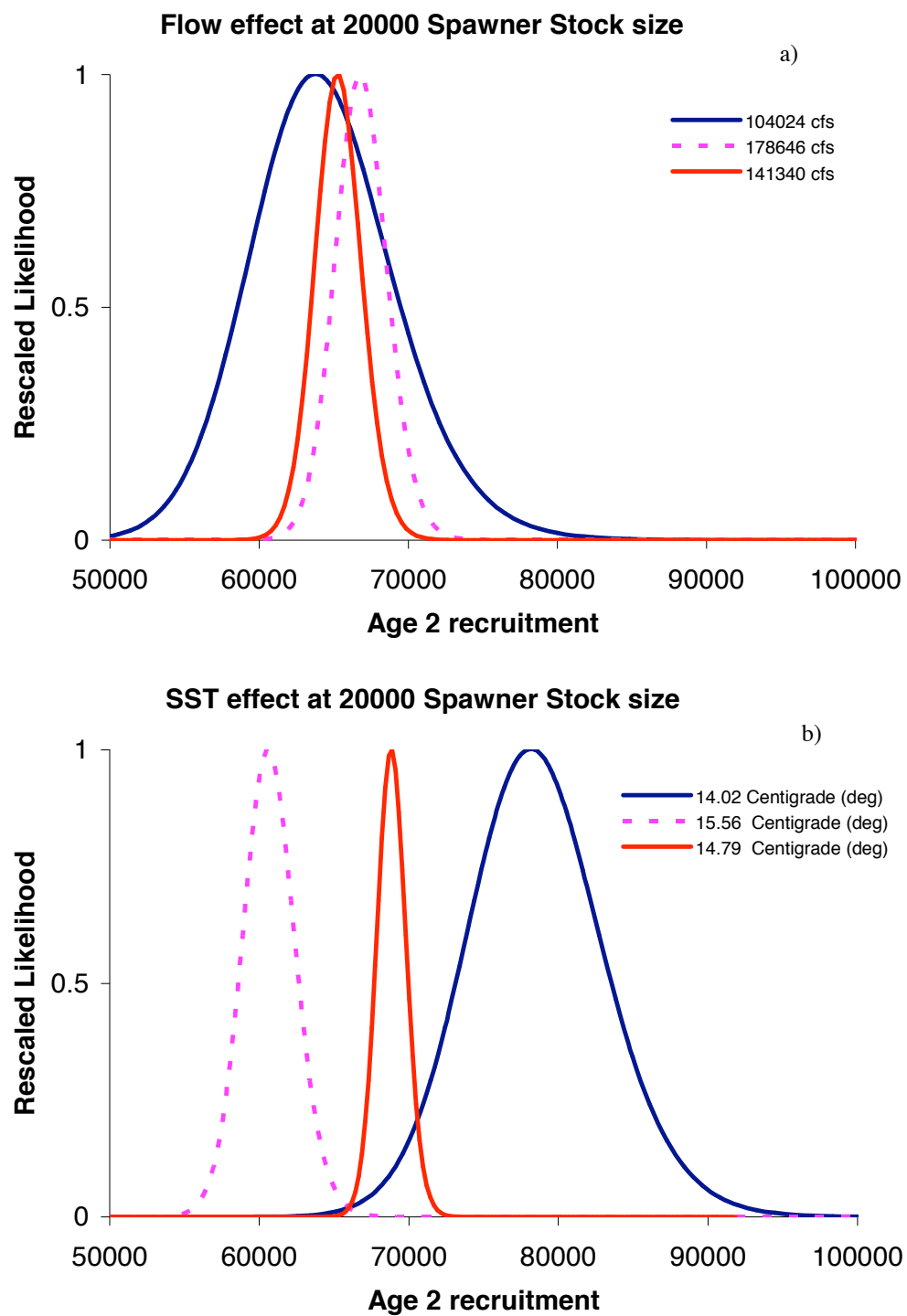


Figure 4.14: Likelihood profiles as a function of flow and SST (independently)

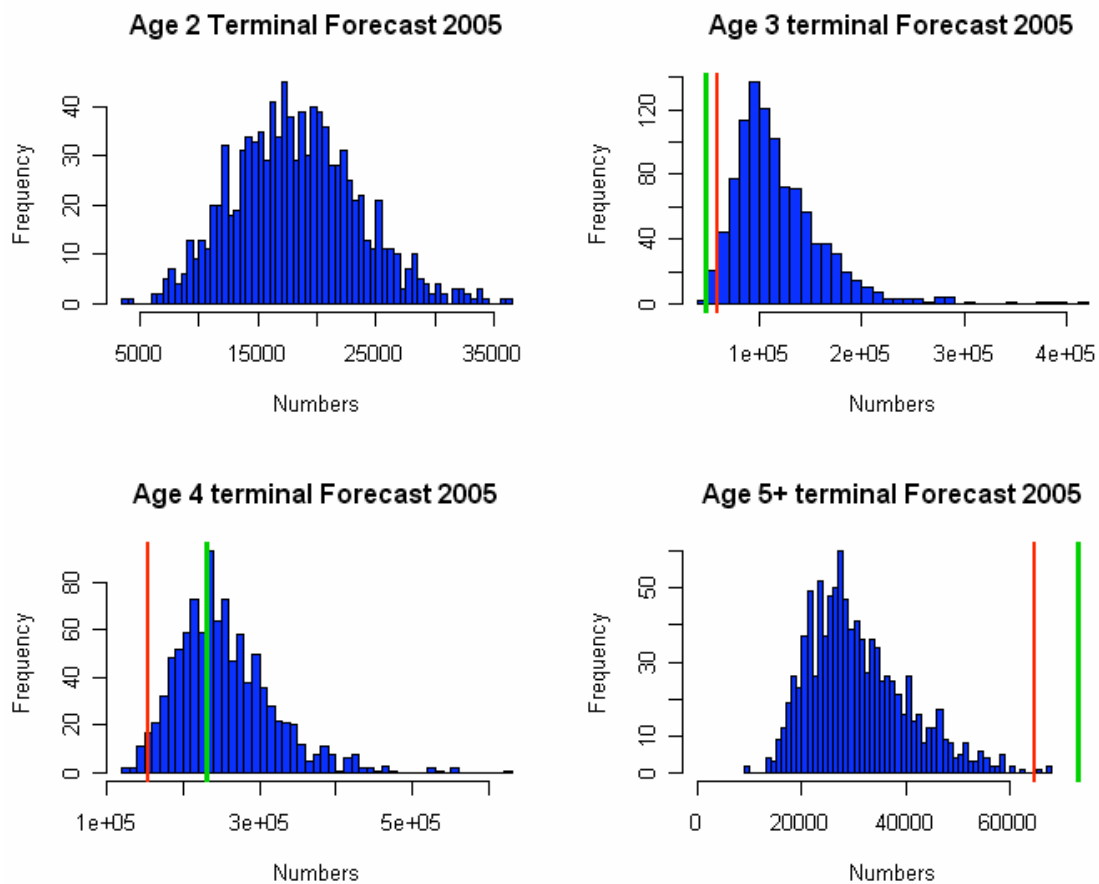


Figure 4.15: Age specific forecast distributions with the observed values in 2004 (the red line indicates observed values and the green line indicates current forecasting techniques)

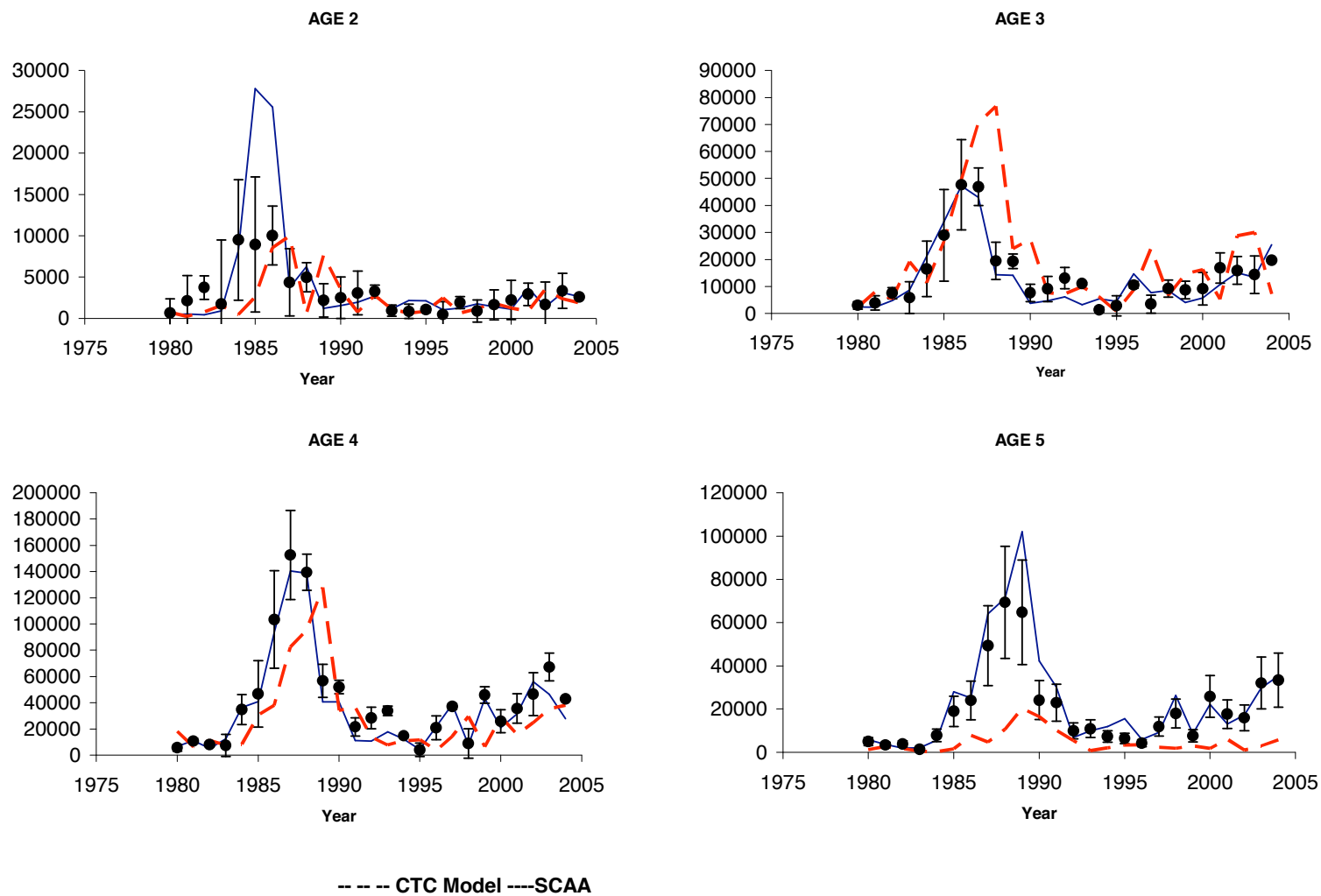


Figure 4.16: Comparisons of this approach with existing model for terminal fisheries by age

APPENDIX 4.1: SIMULATION MODEL RESULTS

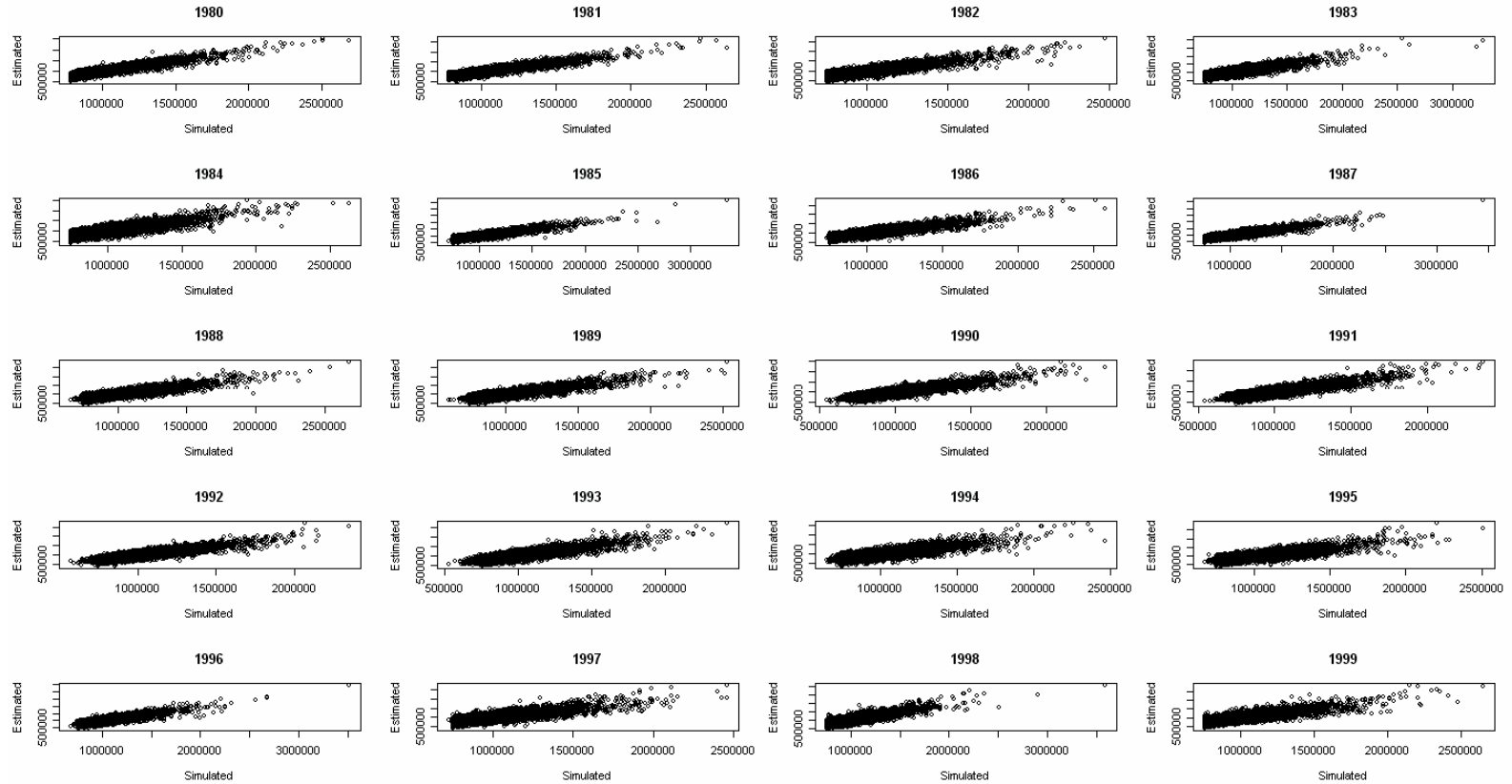


Figure 1: Estimated versus simulated age 2 data with CV of 0.1 in observed data.

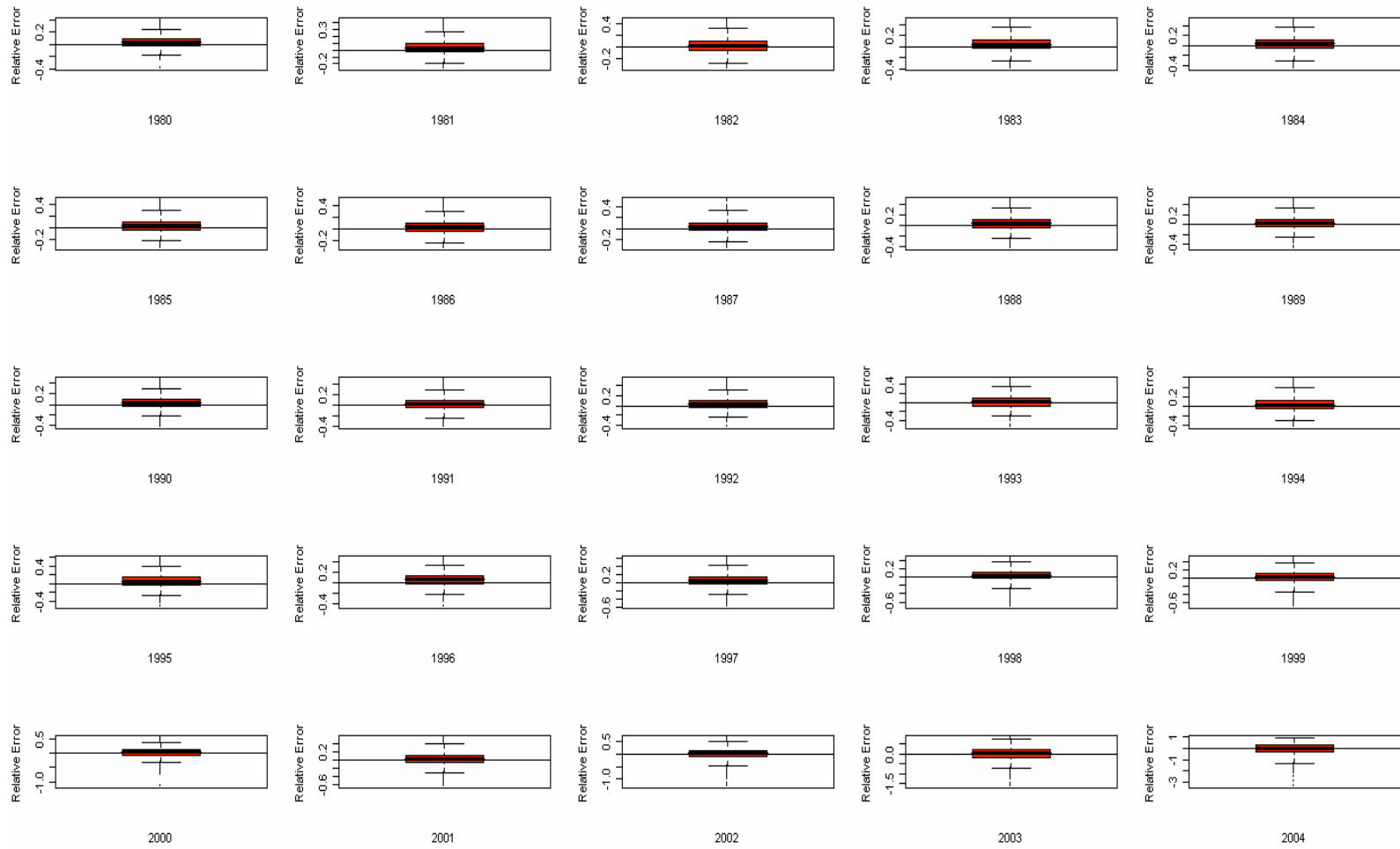


Figure 2: Relative error distributions for age 2 recruitment estimates using the model structure without sampling error

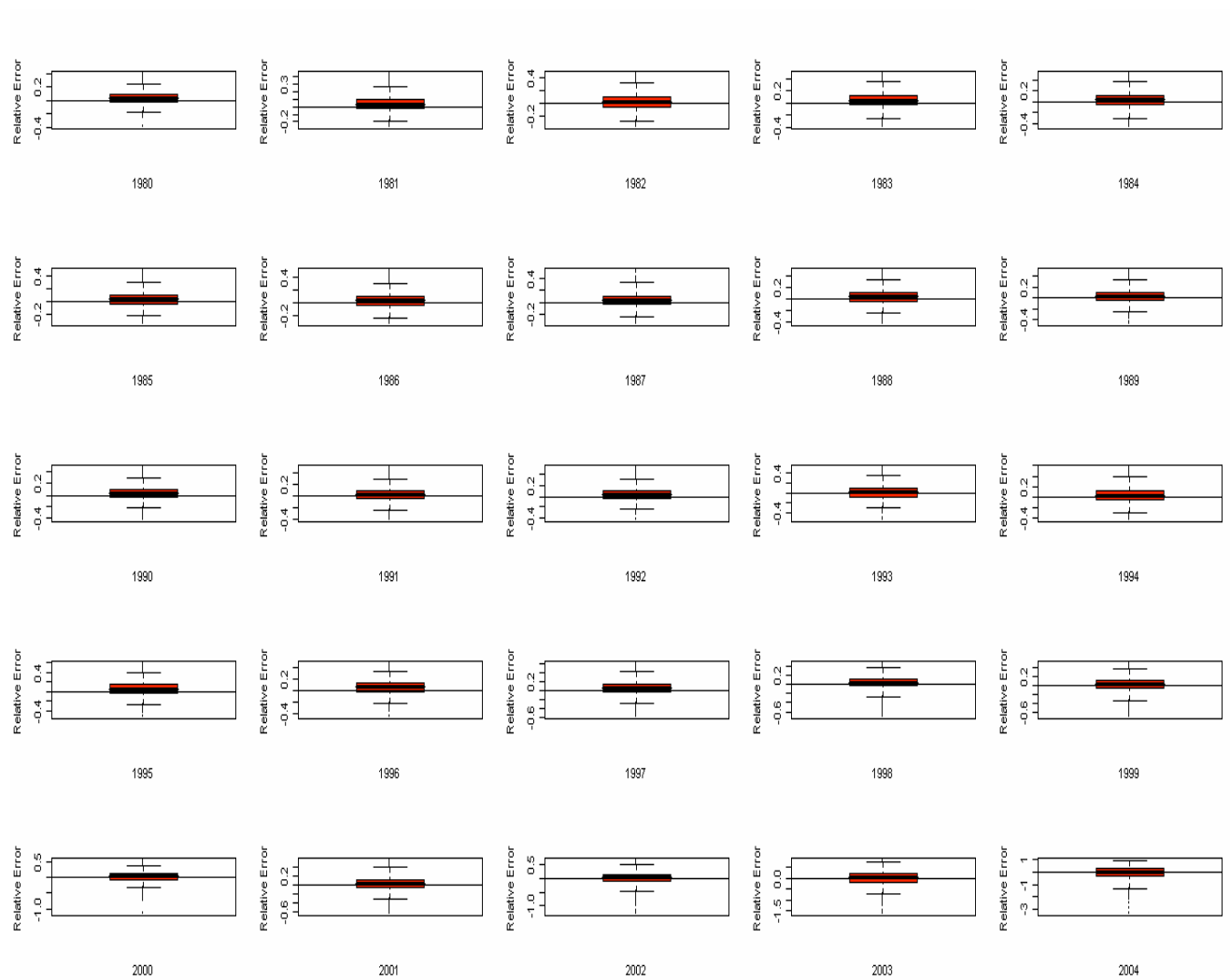


Figure 3: Relative error distributions for age 2 recruitment estimates using the model structure with sampling error

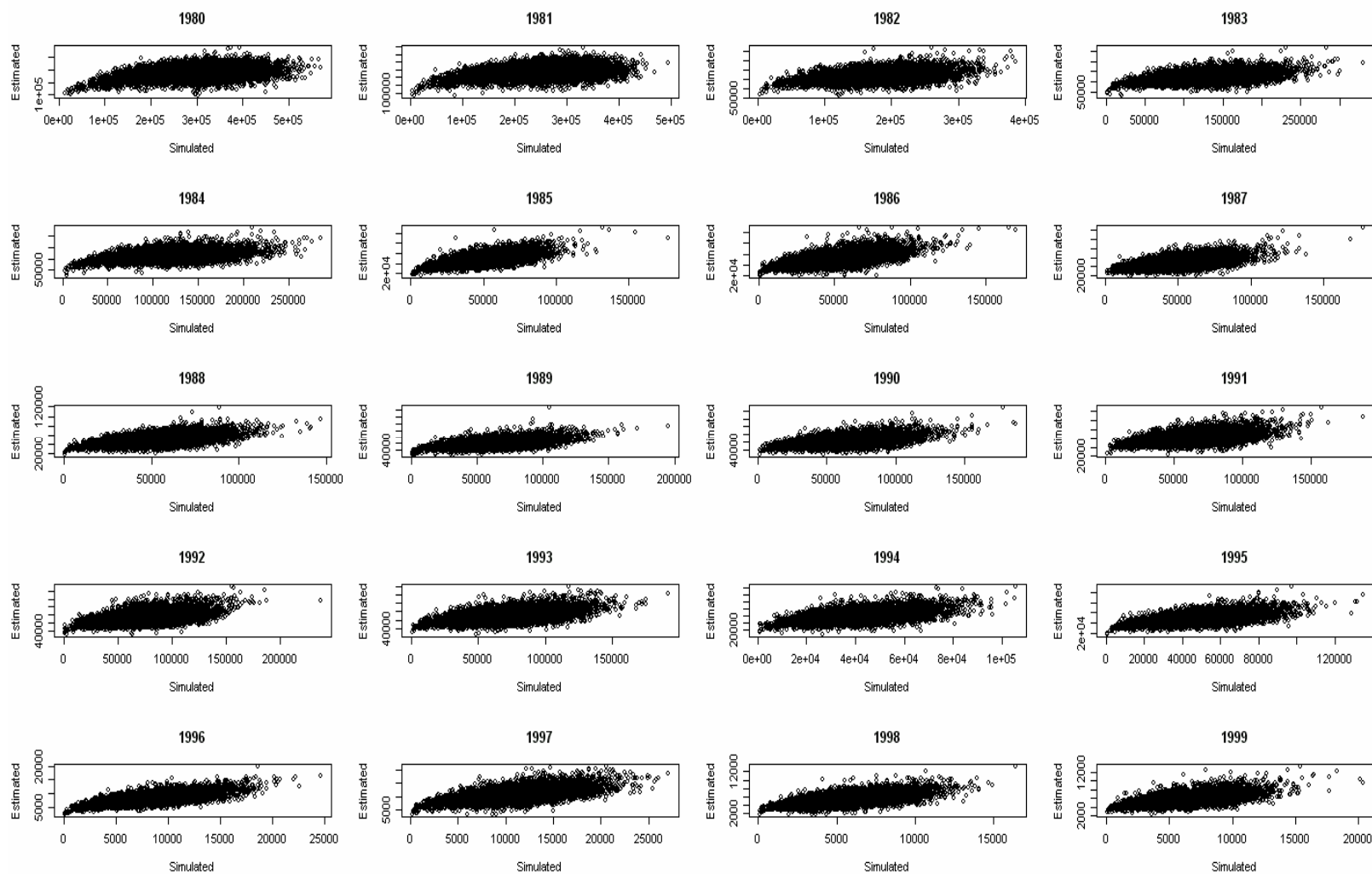


Figure 4: Estimated versus simulated ocean catch data with no sampling error (only till 1999).

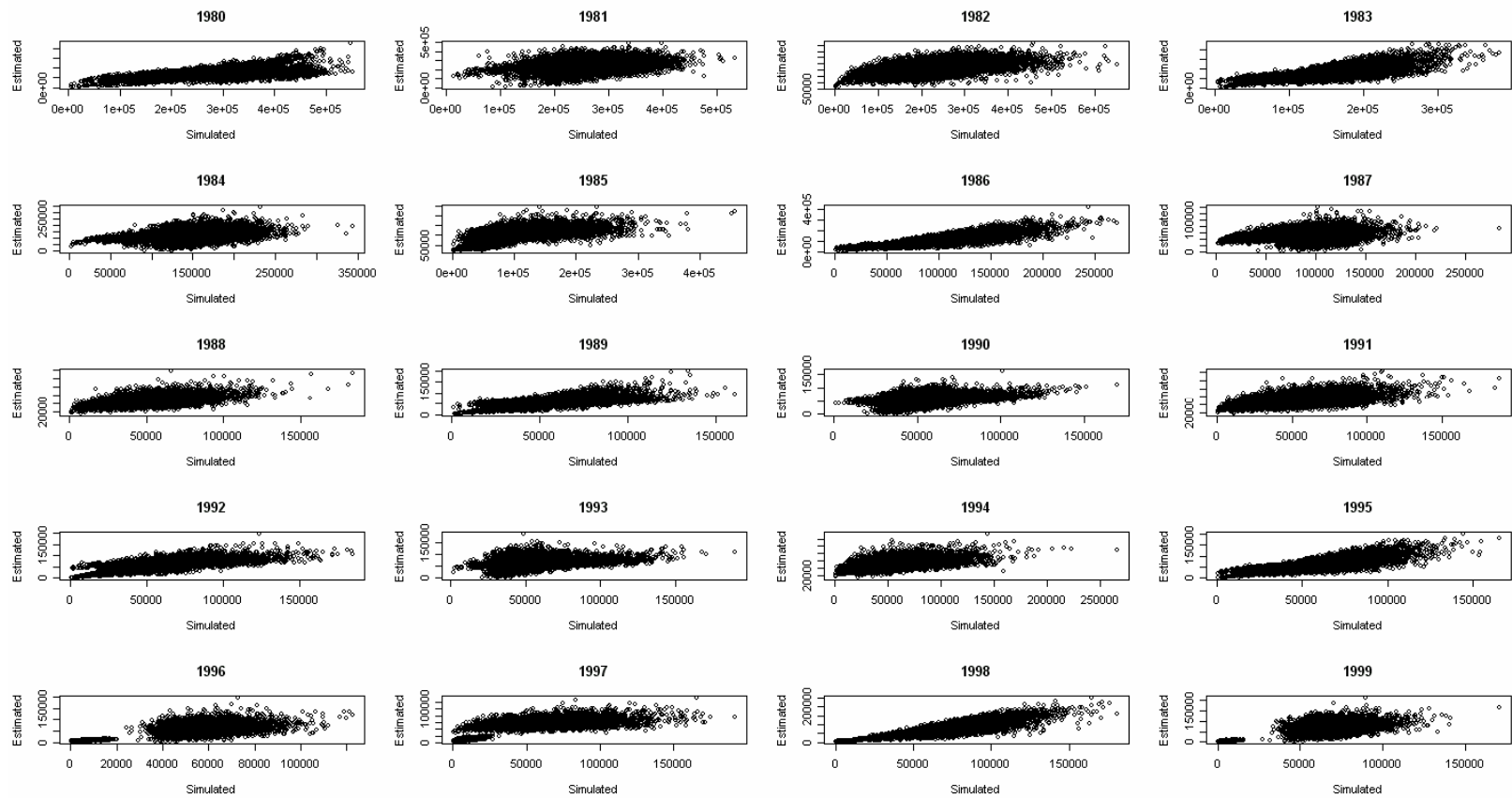


Figure 5: Estimated versus simulated ocean catch data with sampling error (only till 1999).

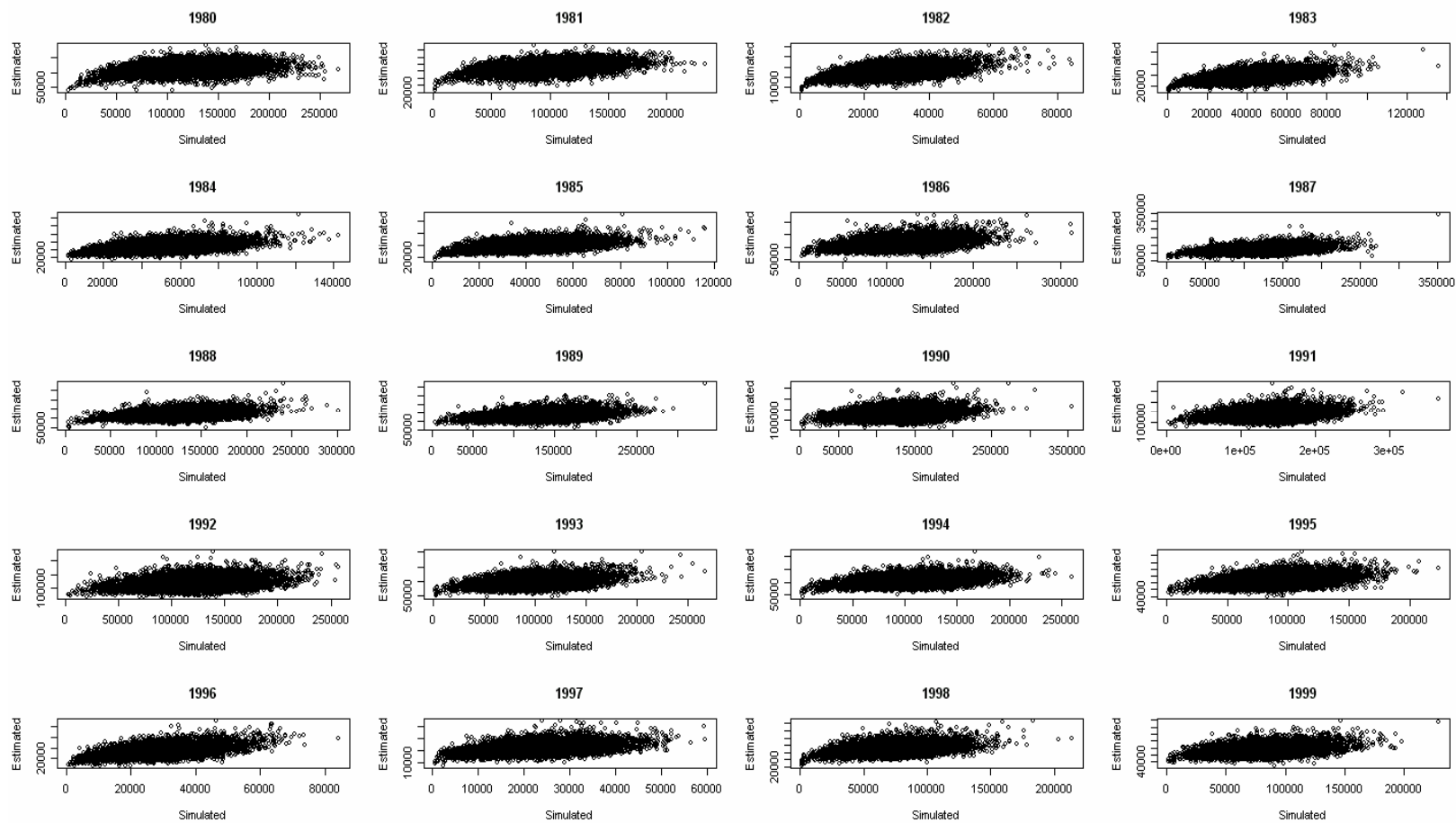


Figure 6: Estimated versus simulated terminal catch data with no sampling error (only till 1999).

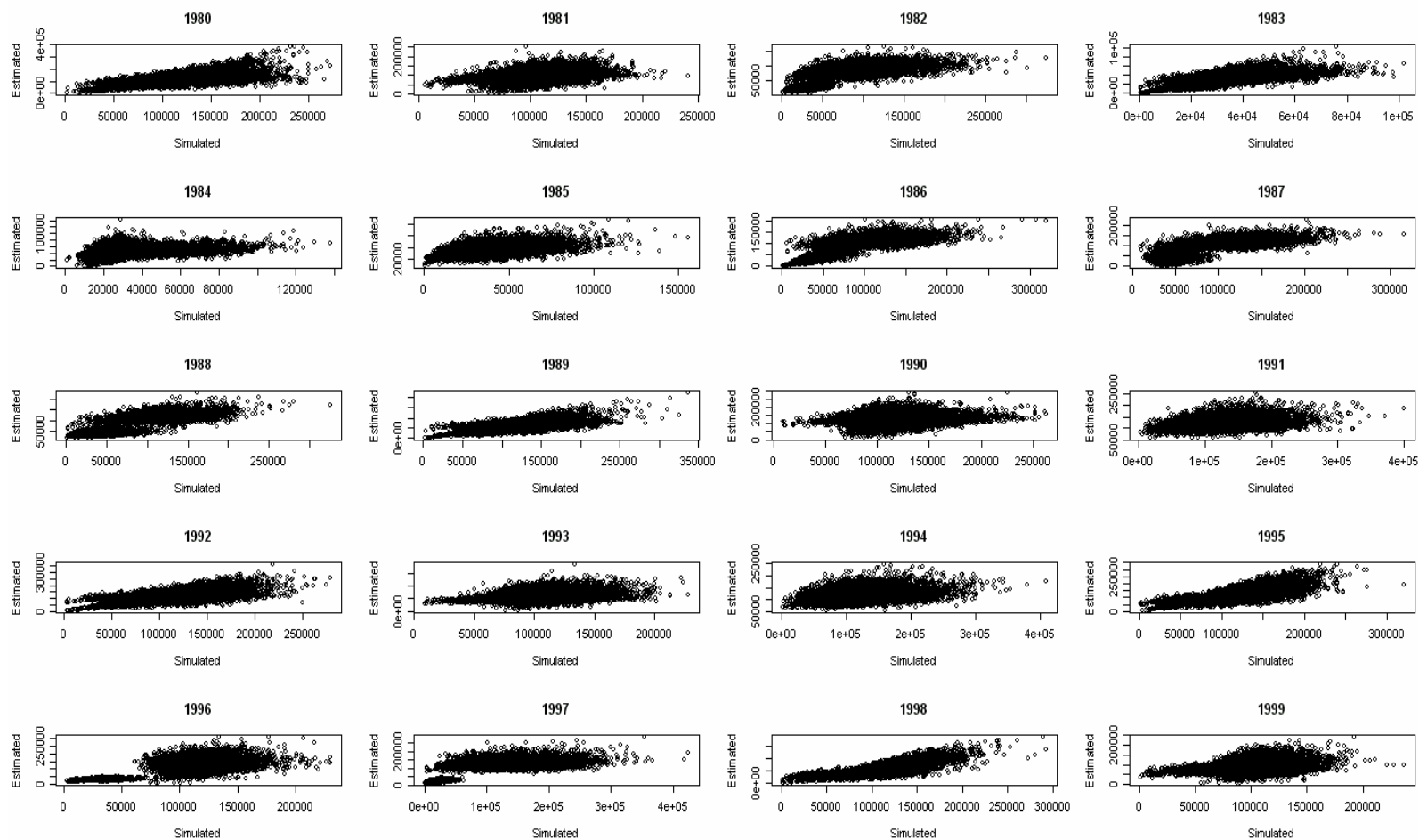


Figure 7: Estimated versus simulated terminal catch data with sampling error (only till 1999).

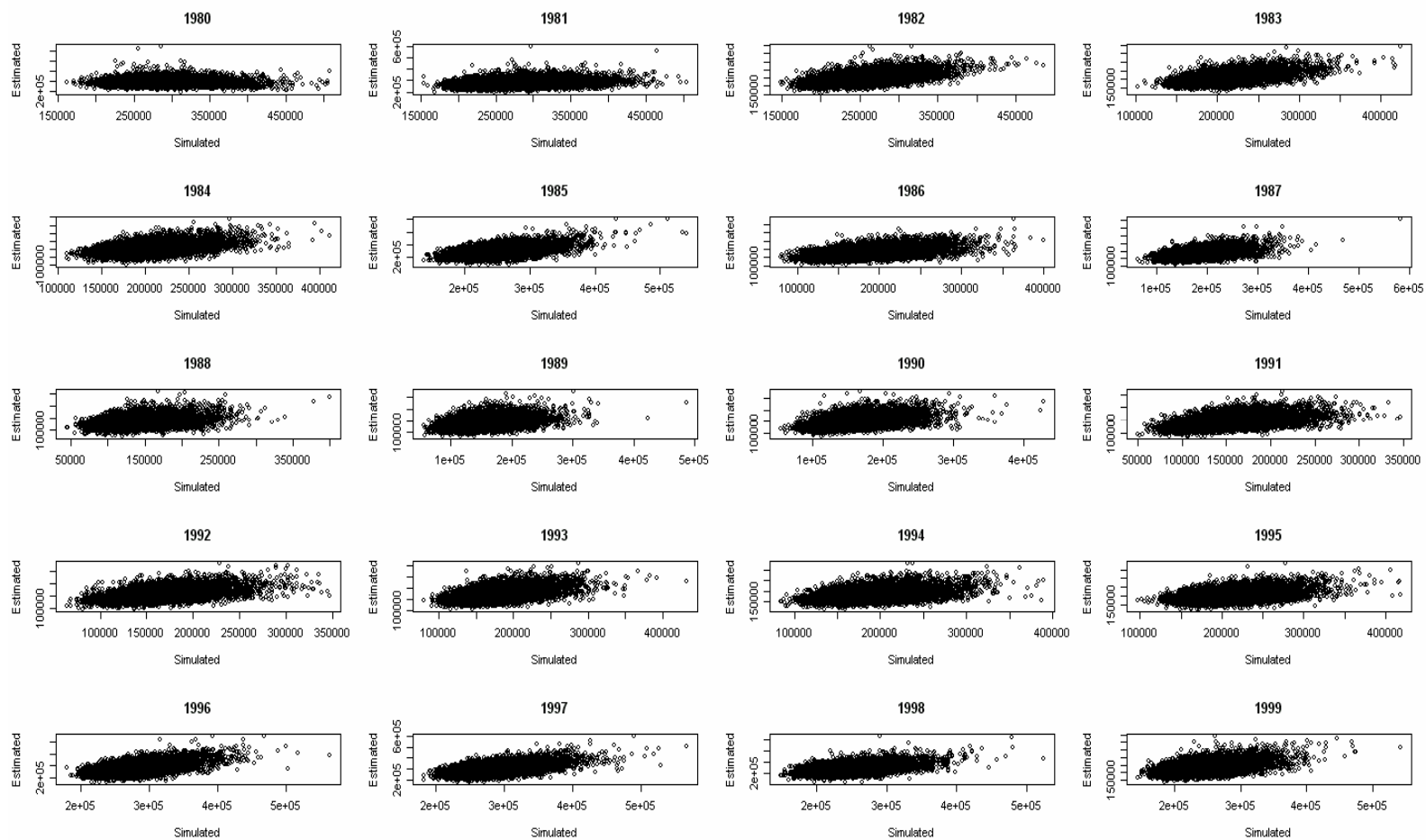


Figure 8: Estimated versus simulated escapement with no sampling error (only till 1999).

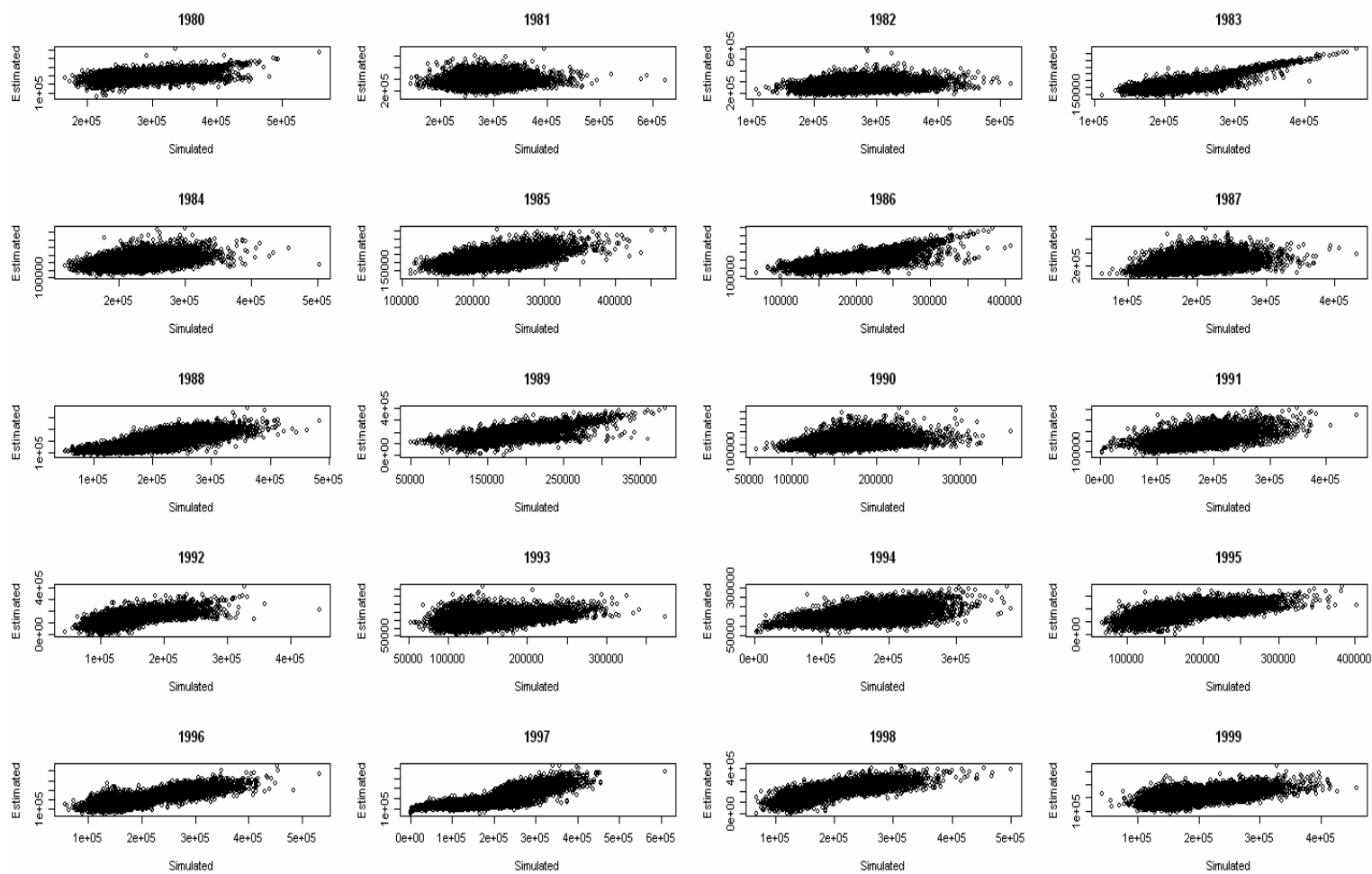


Figure 9: Estimated versus simulated escapement with sampling error (only till 1999).

APPENDIX 4.2: MONTE CARLO MARKOV CHAIN CONVERGENCE DIAGNOSTICS

Geweke Convergence Diagnostic

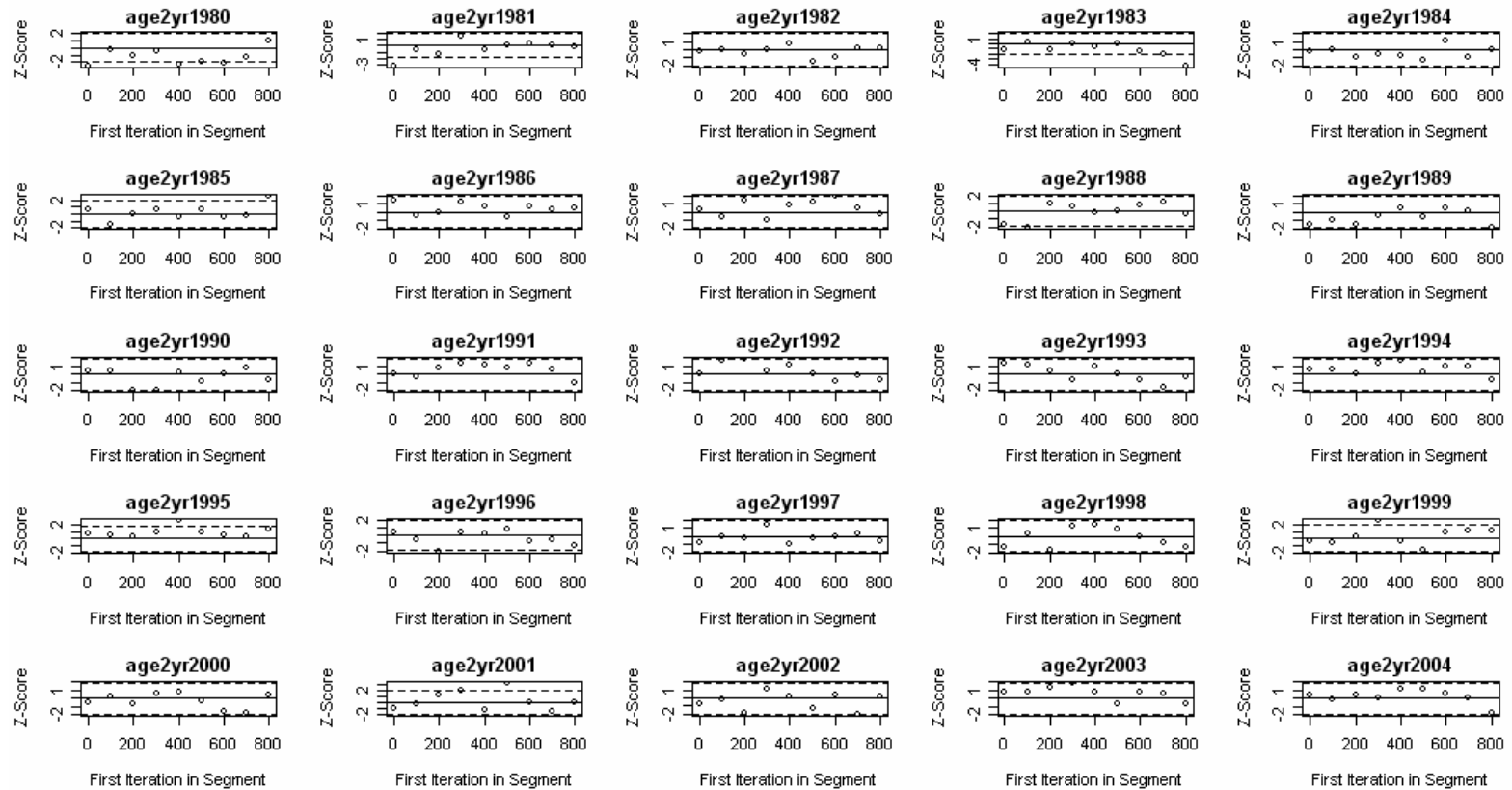


Figure1: Gweke Convergence Diagnostic for age 2 recruitment

Sampler Running Mean

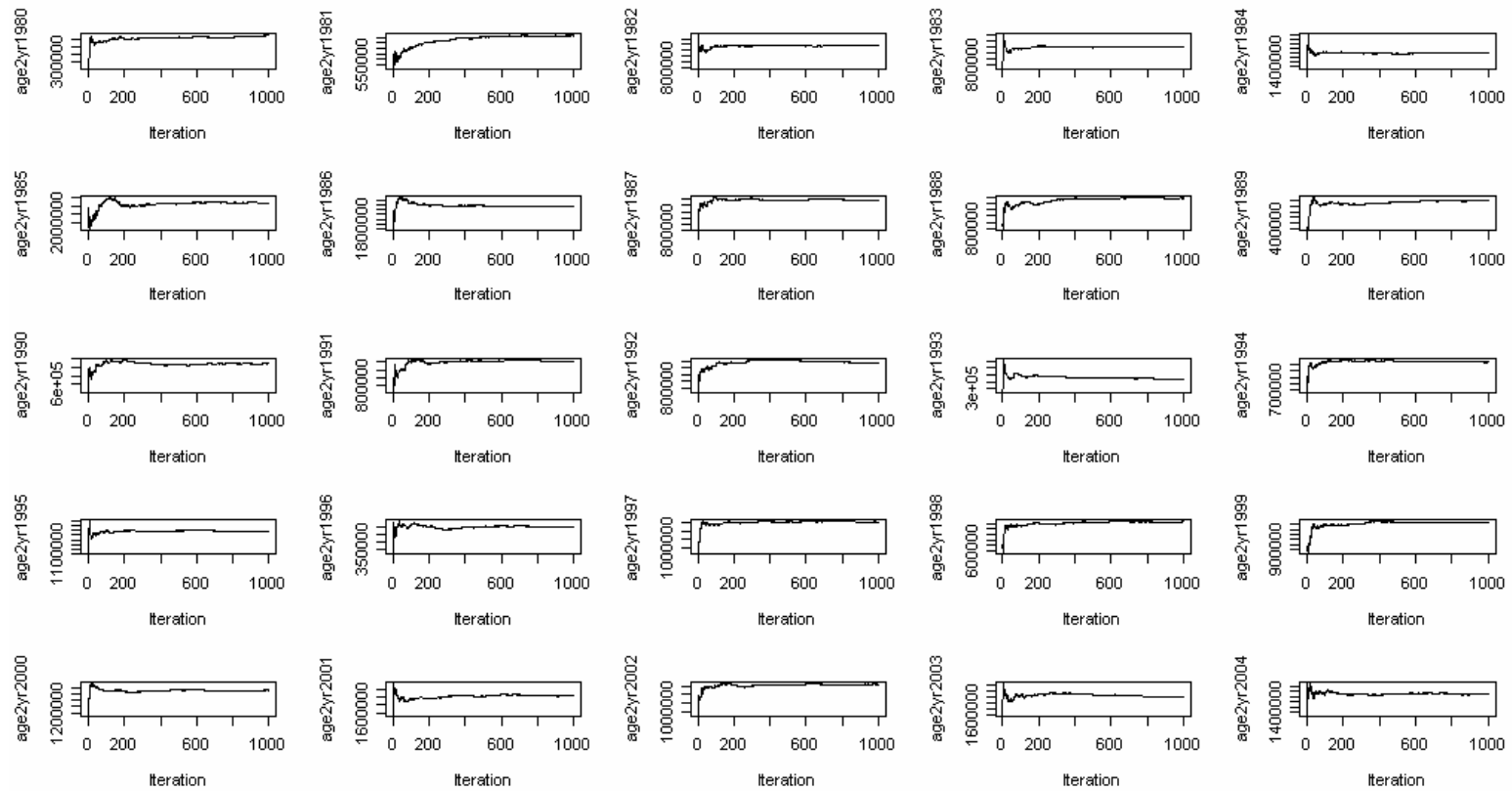


Figure 2: Running Mean plots for age 2 recruitment

Geweke Convergence Diagnostic

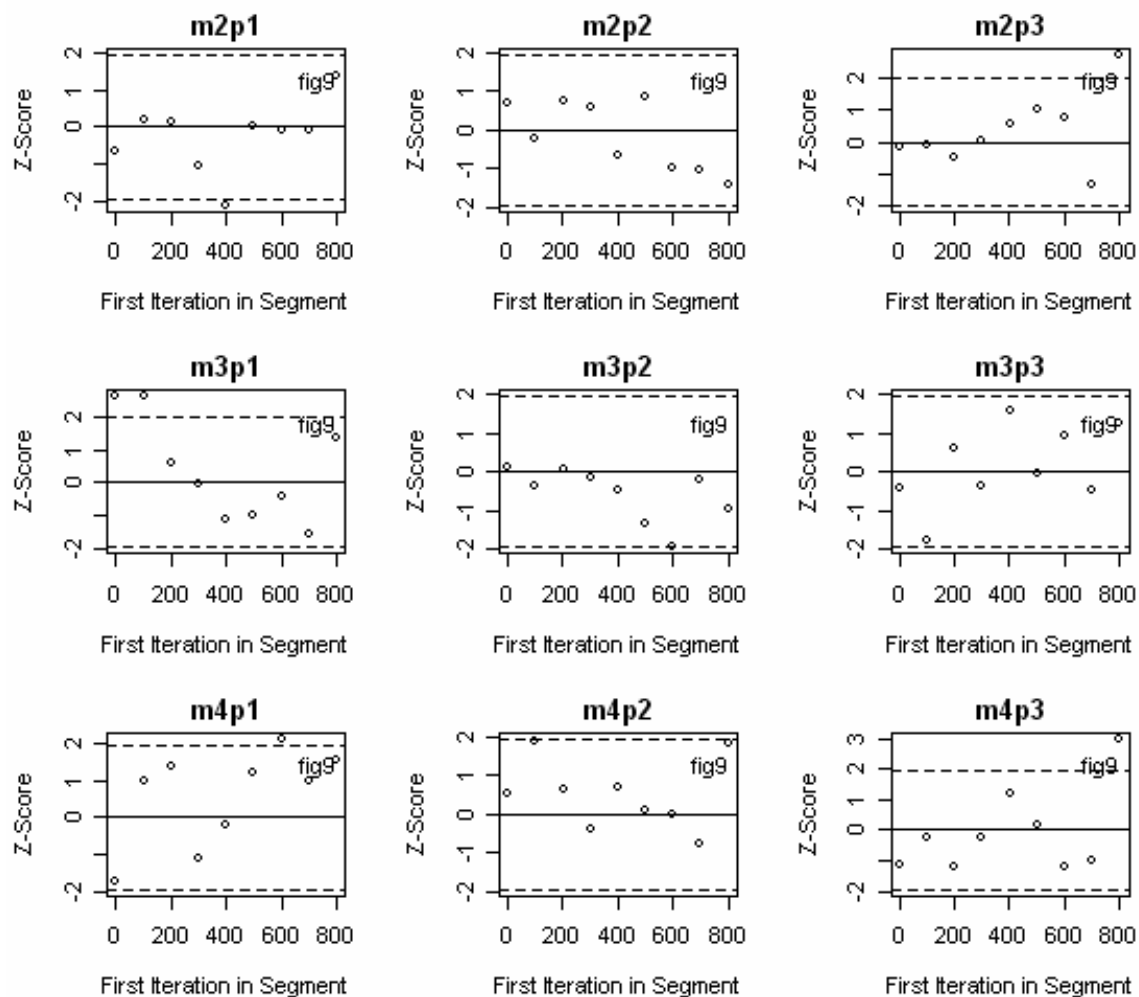


Figure 3: Gweke convergence plots for maturation

Sampler Running Mean

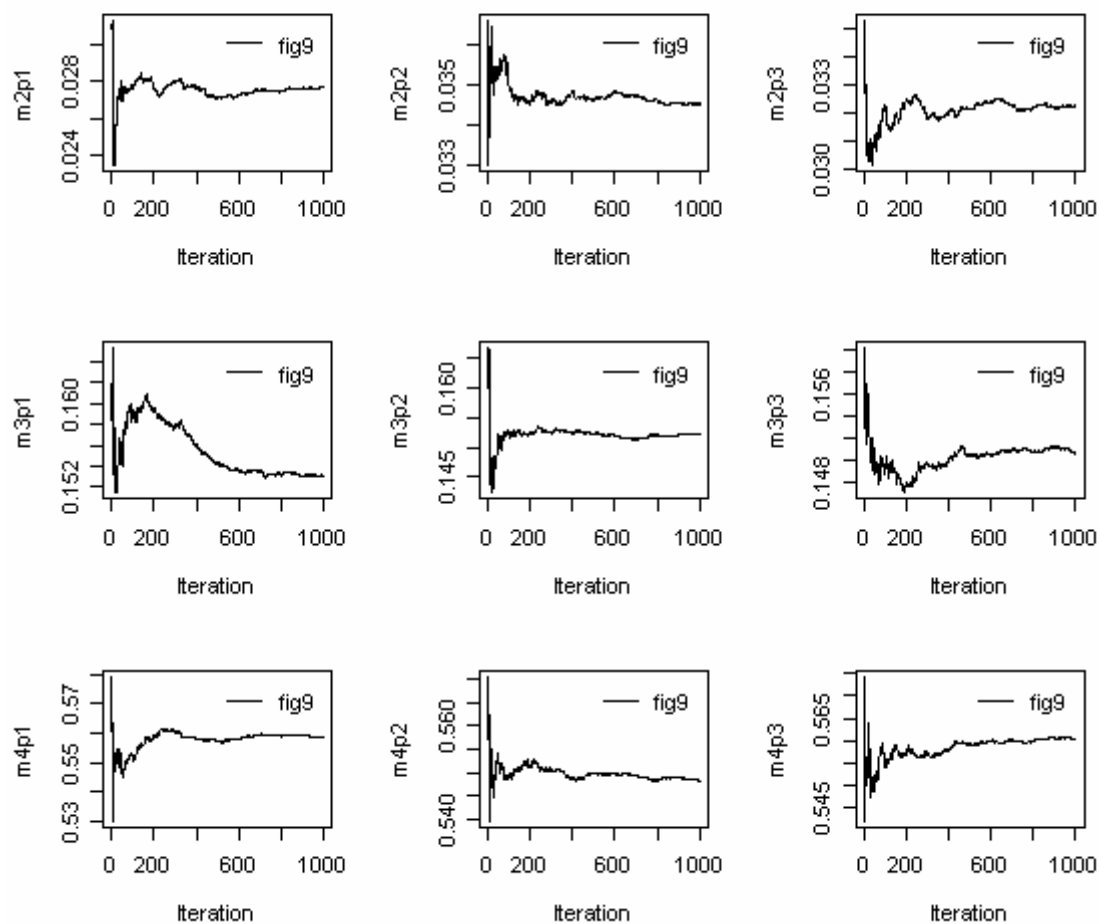


Figure 4: Running mean plots for maturation

Geweke Convergence Diagnostic

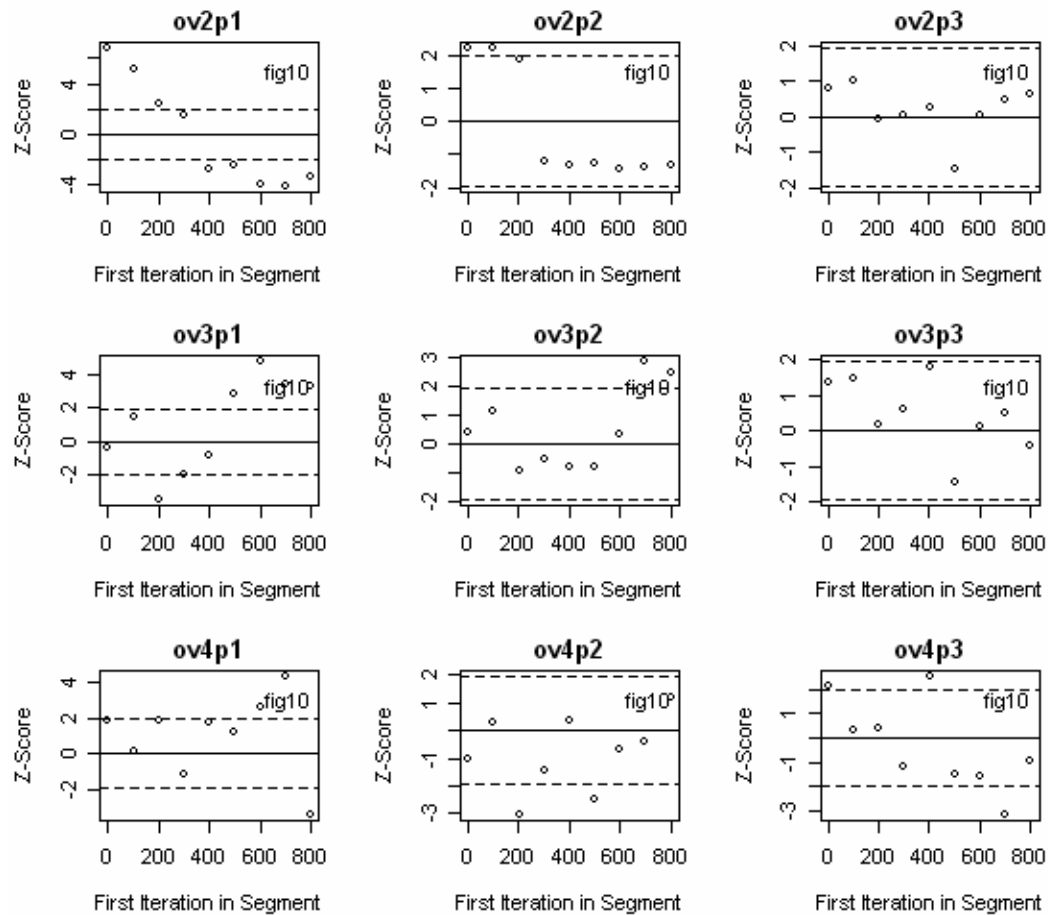


Figure 5: Gweke convergence plots for Ocean vulnerability by age

Sampler Running Mean

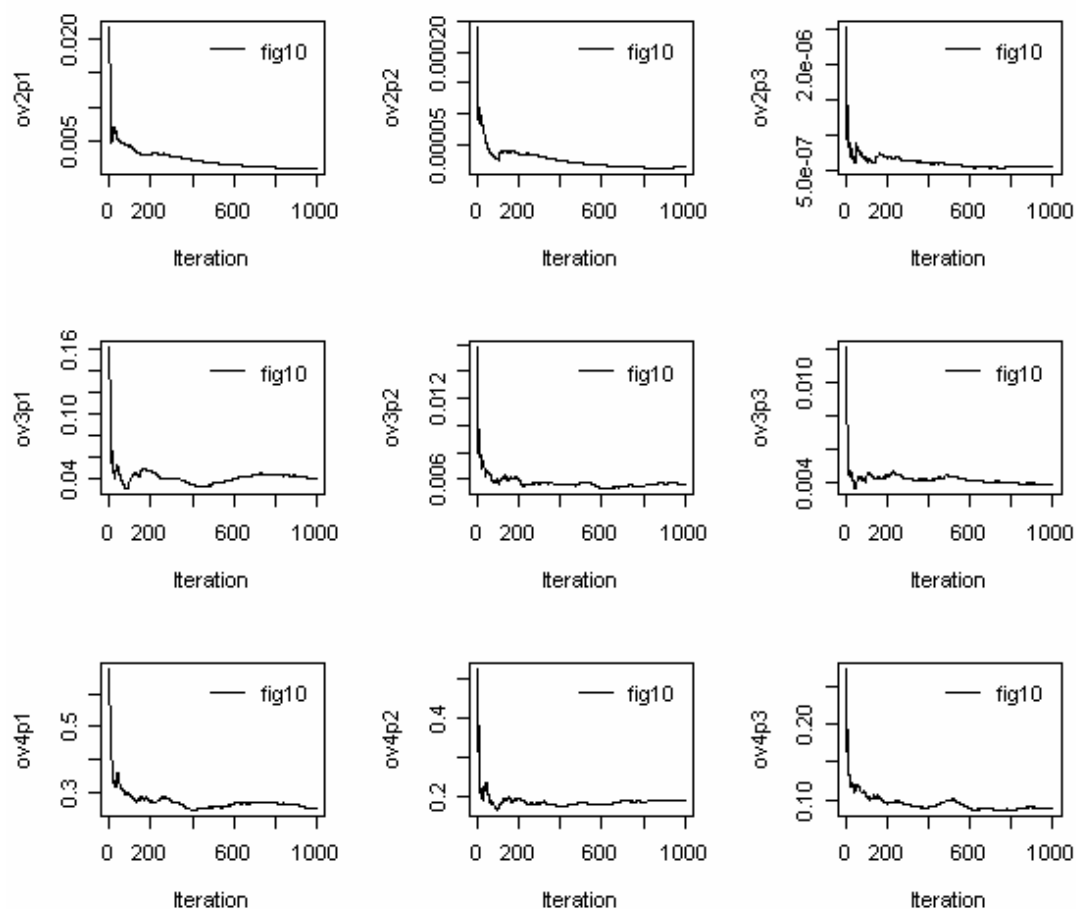


Figure 6: Running Mean plots for ocean vulnerability by age

Sampler Running Mean

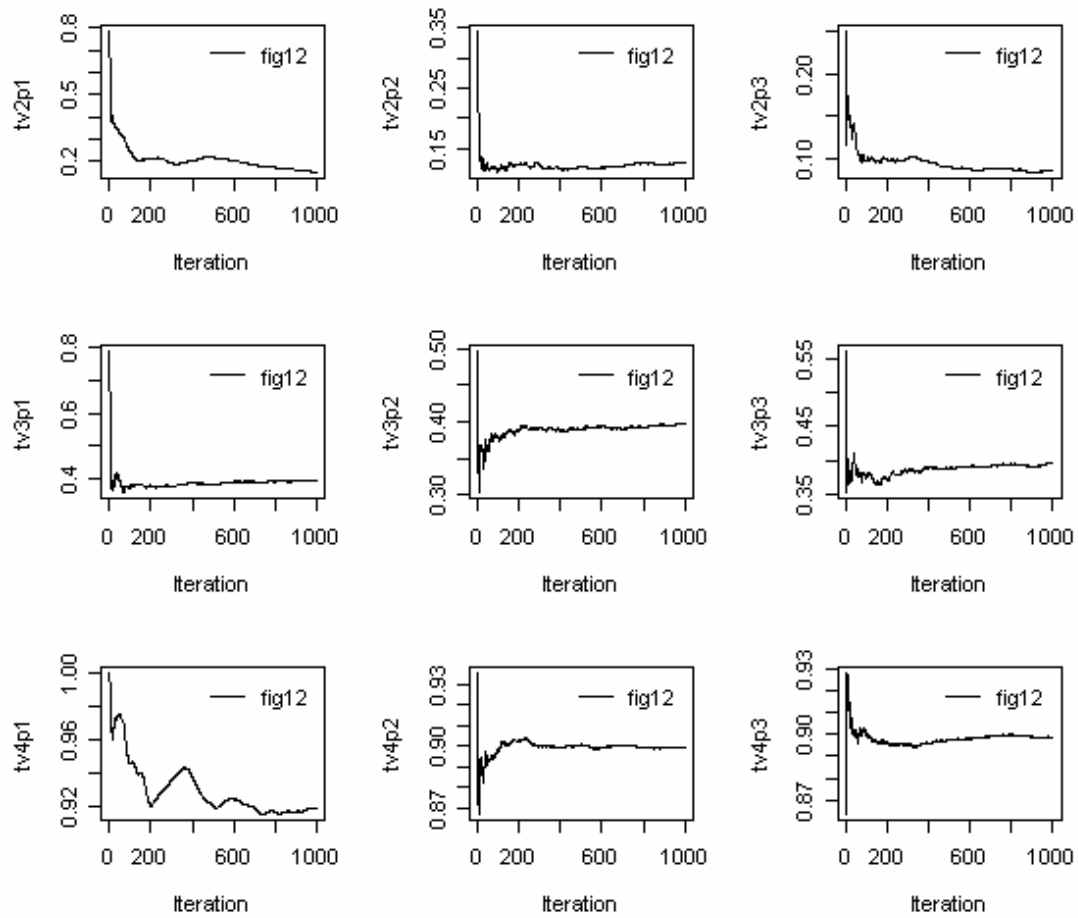


Figure 7: Running Mean plots for terminal vulnerability by age

Geweke Convergence Diagnostic

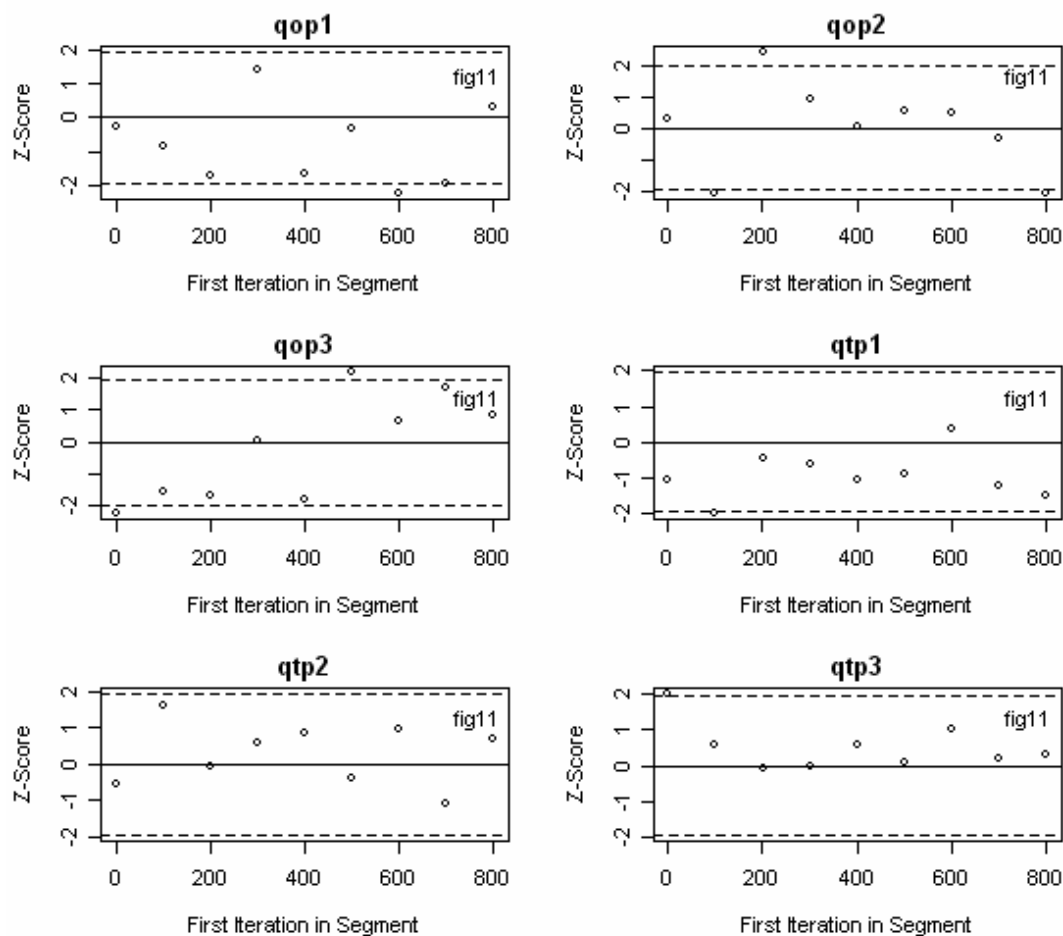


Figure 8: Gweke convergence plots for catchability

Sampler Running Mean

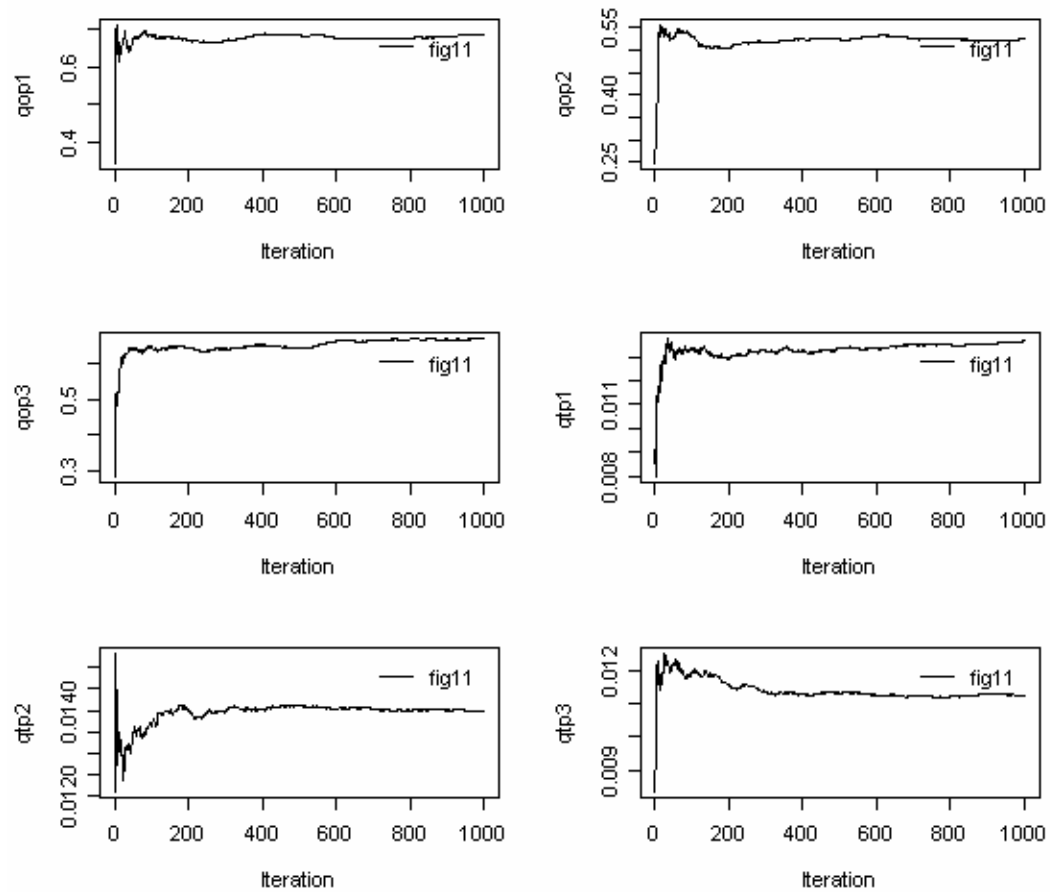


Figure 9: Running Mean plots for catchability

APPENDIX 4.3: CHINOOK SALMON TERMINAL FORECAST MODEL

Based on the retrospective analysis, I will be able to project age 2 recruitment from the equation below:

$$A_2 = f(S, W, UPI, SST) \quad (1)$$

where age(2) recruitment is a function of Spawning stocks size (S), flow (W), UPI (upwelling Index) and sea-surface temperature (SST).

$$\hat{T}_2 = A_2(1 - \bar{\mu}_2)\bar{M}_2 \quad (2)$$

where \hat{T}_2 (is Terminal run of age 2's), $\bar{\mu}_2$ is the average harvest rate (from CWT data for recent years), and \bar{M}_2 is the maturation rate for age 2's (also from CWT data or from the model) for recent years, Figure 6 above).

Now, we will have an expectation from equation 2, and we will have an observation of T_2 based on the data, so we can apply a correction based on what happened and what we predicted for age 3's using equation 3.

$$B_2 = \frac{T_2}{\hat{T}_2} \quad (3)$$

Where T_2 is the observed run.

Now, the age 3 (\hat{T}_3) prediction will apply B_2 and the forecast based on equation (4).

$$\hat{T}_3 = [A_2(1 - \bar{\mu}_2)(1 - \bar{M}_2)S_2(1 - \mu_3)\bar{M}_3]B_2 \quad (4)$$

Where S_2 and \bar{M}_3 are survival of fish from age 2 to 3 and maturation of age 3 fish. Normally rates are assumed for survival from age 2 to age 3 (0.7 TCChinook 05-2), and we estimate \bar{M}_3 and μ_3 from recent trends based on CWT data.

Age 4 will have similar corrections based on equations 5 and 6.

$$B_3 = \frac{T_3}{\hat{T}_3} \quad (5)$$

Now, the age 4 (\hat{T}_4) prediction will apply B_2 and B_3 to the forecast based on equation (6).

$$\hat{T}_4 = [A_2(1 - \bar{\mu}_2)(1 - \bar{M}_2)S_2(1 - \mu_3)(1 - \bar{M}_3)(S_3)(1 - \mu_4)\bar{M}_4] \frac{B_2 + B_3}{2} \quad (6)$$

where S_3 is the survival of age 3 to 4 fish, \bar{M}_4 is the maturation of age 4 fish and μ_4 is the ocean harvest of age 4's and are estimated from recent trends based on CWT data.

For simplicity, I will assume all fish return at age 5 and the equations used are shown below:

$$B_4 = \frac{T_4}{\hat{T}_4} \quad (7)$$

Now, the age 5 prediction (\hat{T}_5) will apply B_2 , B_3 and B_4 to the forecast based on equation (8).

$$\hat{T}_5 = \left[A_2 (1 - \bar{\mu}_2) (1 - \bar{M}_2) S_2 (1 - \mu_3) (1 - \bar{M}_3) (S_3) (1 - \mu_4) (1 - \bar{M}_4) S_4 (1 - \mu_5) \right] \frac{B_2 + B_3 + B_4}{3} \quad (8)$$

where S_4 is the survival of age 4 to 5 fish, \bar{M}_5 , i.e. the maturation of age 5 fish=1, and μ_5 is the ocean harvest of age 5's and are estimated from recent trends based on CWT data. In all the above cases, B_i are biases observed in the forecasts by age. Note, survival rate has to be assumed as maturation and survival are confounded, and one has to be fixed while the other is estimated.

APPENDIX 4.4: AGE STRUCTURED FITS FOR OCEAN FISHERIES AND ESCAPEMENT

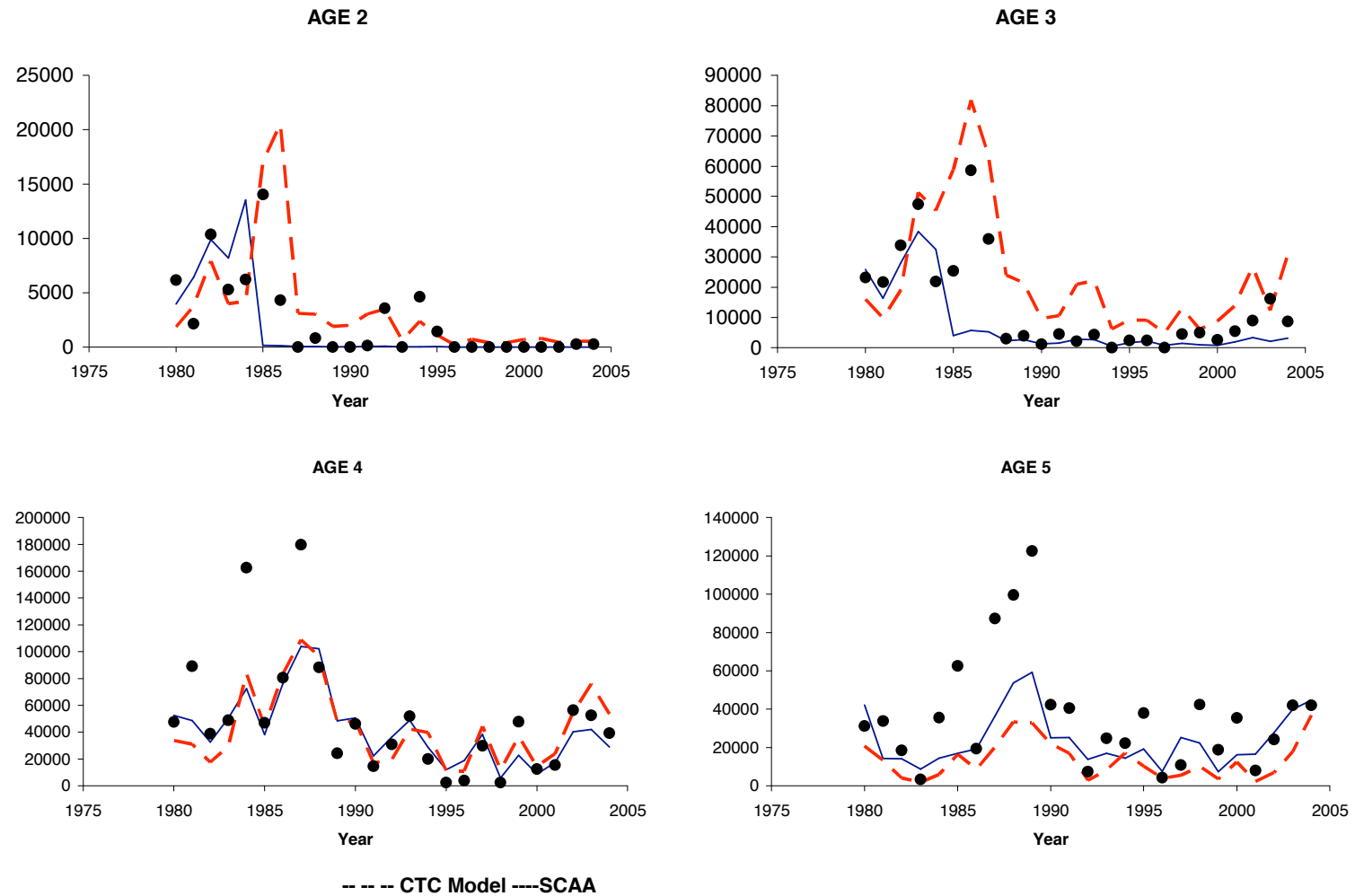


Figure 1: Ocean catches by age using the Catch-at-age model compared to the PSC Chinook Model

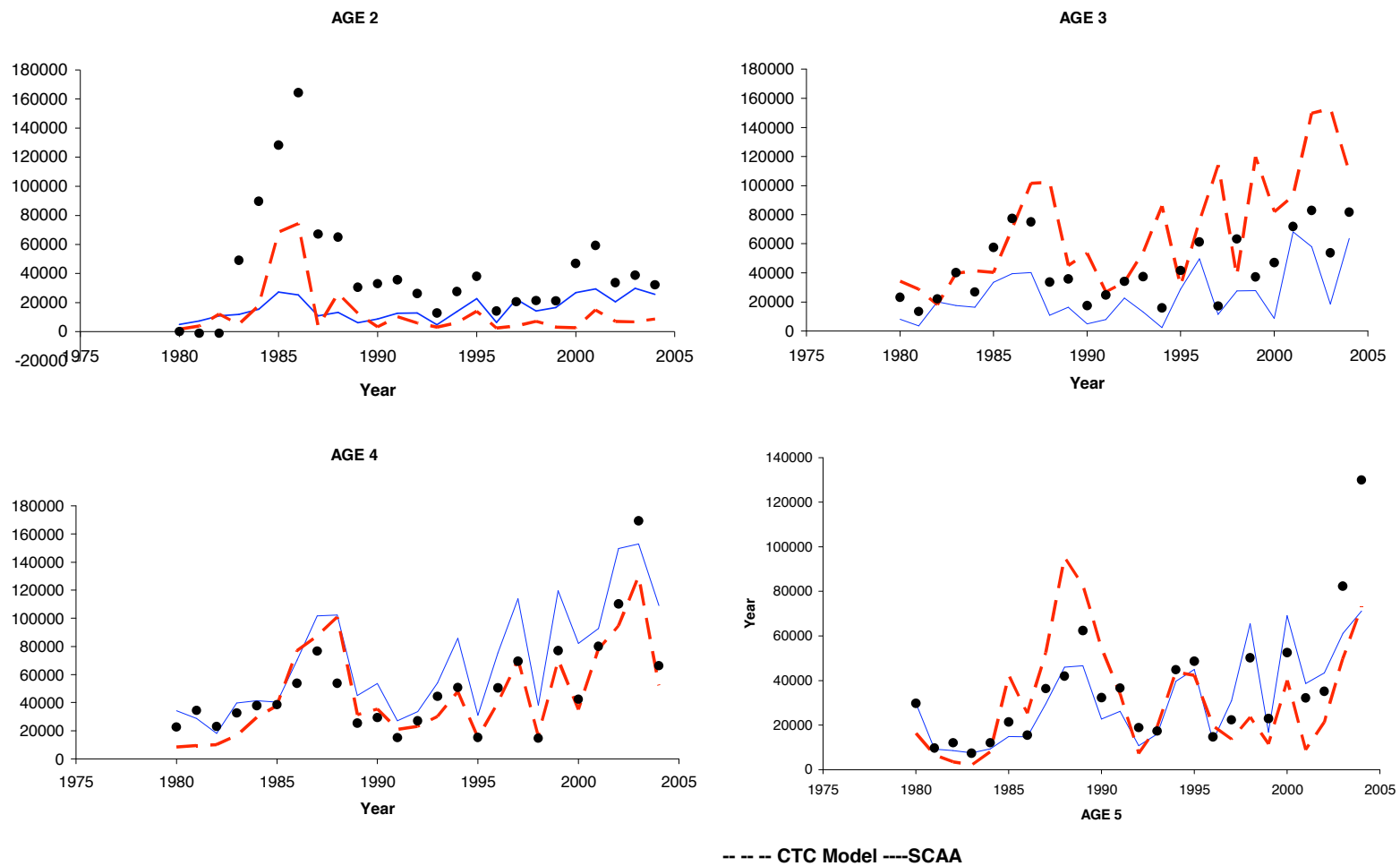


Figure 2: Escapement by age using the Catch-at-age model compared to the PSC Chinook Model

**CHAPTER 5: WHERE WE ARE AND WHERE WE SHOULD GO
WITH RESPECT TO CHINOOK SALMON STOCK ASSESSMENT**

5.1 INTRODUCTION

This dissertation has discussed three facets of Pacific Northwest (PNW) Chinook salmon ecology that are relevant to current management models: 1) life history, 2) the impacts of spatial and temporal variability on PNW Chinook survival, maturation, and migration pathways as determined using coded wire tags, and 3) the relationship between recruitment variability and environmental variation, explored via development of a new age-structured model.

To address the first objective, I used coded wire tag (CWT) data to test Healey's (1983) hypothesis that ocean-type Chinook salmon are distributed primarily along the continental shelf during their marine residence while stream-type Chinook salmon are more common off the shelf and on the open ocean. I demonstrated regional and life history based differences in migration pathways in the Pacific Northwest, supporting Healey's hypothesis for some, but not all, regions and stocks. In some cases, the ocean distributions of stream-type and ocean-type Chinook exhibited significant overlap, suggesting gene flow between populations. The findings of this study have important management implications, especially in cases where there is inadequate representation of some stocks (particularly stream-type Chinook) in the assessment models used by the Pacific Salmon Council (PSC) and the Pacific Fisheries Management Council (PFMC). Healey (1983) hypothesized that stream-type fish were rarely caught in ocean mixed-stock fisheries on the coastal shelf, but as demonstrated in Chapter 2, this is not the case. This chapter asserts that conservation of some depressed PNW Chinook stocks cannot be achieved without understanding their life history and marine distribution pathways.

The second objective of this dissertation was to understand how environmental variables relate to ocean survival and maturation of Chinook (estimated using CWT data) across the Pacific Northwest. As reported in the analysis, PNW Chinook respond only weakly to changes in ocean conditions, as measured by upwelling indices and sea surface temperatures. However, broad-scale ocean-atmospheric signals were found to translate into local signals like SST that do affect Chinook survival on a local scale (as demonstrated for Oregon coastal Chinook in Chapter 3). With respect to maturation, although it appears that larger fish tend to mature faster, it is not possible to detect effects of coastal ocean conditions on maturation with the broad-scale data examined here. Because these fish are highly migratory and range over areas that span thousands of kilometers, it is difficult to identify the appropriate scale on which to examine data in order to infer causation. However, it is important to understand issues of scale (Levin 1992) and how phenomena occurring on a range of spatial scales impact the resource being studied (Wallace and Gutzler 1981). Building mechanistic models of these interactions (Peterson et al. 2006) is critical for understanding these complex ecosystem processes.

The final objective of the dissertation was to demonstrate how direct measures of environmental conditions could be integrated into Chinook salmon stock assessments. The results shown in Chapter 4 for the Upriver Bright population on the Columbia River provide a better understanding of the mechanisms governing the relationships between environmental variability and Chinook salmon abundance and variability in the PNW. This knowledge could be used to increase pre-season

management precision by improving ocean abundance forecasts or to initiate in-season management as Peterson et al. (2006) suggest. In addition, the model quantifies uncertainty so that managers can use precautionary approaches to managing their stocks (FAO 1996) that would help protect the resource in the long run.

The following sections provide an overview of PNW stock exploitation over the last 25 years, outline possible reasons for the overexploitation of these stocks, and provide realistic solutions to management problems that would support a precautionary management framework.

5.2 THE CURRENT STATUS OF PNW CHINOOK EXPLOITATION RATES

In 1995, Endangered Species Act litigation had a positive effect on numerous Chinook salmon stocks (NMFS 1997). At the same time Canada was complaining that Alaskan fishermen were overfishing some of their key sockeye stocks, including the Skeena River stocks in Northern BC, and coastal and Fraser Chinook and coho populations. Despite their efforts to resolve this issue using science, politics eventually took over, and Canadians fished heavily on depressed Washington and Oregon Chinook and coho stocks, causing a decline in these populations between 1991 and 1994. Finally, as a last straw when the Pacific Salmon Treaty was being renegotiated, Canadian fisherman blockaded a US ferry at Prince Rupert in the Queen Charlotte Islands. A new treaty was eventually reached in 1999 with an interim agreement in 1996 that dramatically reduced catches and moved from a catch-ceiling (constant catch) based management system to a system based on overall abundance and harvest rates (Brown 2005, Harris 1999). The 1999 agreement was a new paradigm of Chinook salmon ocean fisheries management that was supposed to respond to changes in

Chinook ocean abundance. However, for many stocks decreased exploitation rates in the ocean fisheries did not lead to recovery. After ten years of management under the 1999 PSC regime, the treaty is currently being ratified again but only minor changes are being discussed, rather than a full evaluation of long-term sustainability of depressed PNW Chinook (e.g. west coast of Vancouver Island Chinook, Georgia Strait Chinook, Fraser Chinook, Puget Sound Chinook and Columbia/Snake River Chinook).

Here I synthesize some of the data that has been collected over the past twenty years to assess optimal harvest rates for Chinook populations, and evaluate whether optimal rates for maintaining healthy stocks have been met. Implicit in this approach is that it is necessary to determine appropriate target reference points (i.e. sustainable exploitation rate targets) for Chinook, and to evaluate the status of Chinook stocks with respect to these exploitation rate targets.

The target reference point for Chinook populations is currently estimated using a meta-analysis (Appendix 5.2). This approach relies on spawner-recruit relationships that tend to be highly uncertain due to environmental variability and measurement error (Shnute and Kronlund 2002). In the traditional management approach, each population is analyzed separately. Information from other stocks may be used informally, for example in model selection, but parameter estimates are based solely on the data from the population being managed. Here I use a hierarchical model analysis to assess uncertainty in target reference points (optimal spawning stock size, optimal harvest rates, etc.; Appendix 5.2). This approach allows estimation of an overall distribution of density-independent productivity and target reference points for PNW Chinook. I used

data on numerous stocks of Chinook (26 stocks from Oregon to Alaska, Parken et al. 2006, Liermann et al. in prep Appendix 5.2) to derive a distribution of productivity values, and to then determine the optimal harvest rate for Chinook across the Northwest (Figure 5.1, Table 5.1, to get more specifics of the approach refer to Appendix 5.2).

Credible intervals (Table 5.1) indicate that the optimal harvest rate should be between 55% and 77%, with a median harvest rate between 61% and 66%. In numerous areas in Washington, Oregon (Good et al. 2005), and Canada (<http://www-ops2.pac.dfo-mpo.gc.ca/xnet/content/salmon/webdocs/SalmonStockOutlook2009.htm?>), Chinook populations are depressed. In such cases, managers should drop overall exploitation rates below the estimated optimal rate of between 61-66% (Appendix 5.2) to rebuild these stocks in the near-term.

However, these exploitation rates have not been mandated over the past decade. Prior to 1999 stocks were fished at or over the optimal rates for many years (Figure 5.2). The management regime negotiated by the Pacific Salmon Treaty (PST) in 1999 (PSC 2000) was a vast improvement over the previous treaty, and dropped exploitation on numerous stocks. However there are still a number of stocks (14 out of 32 stocks, Table 5.2) that are approaching (or above) the median optimal exploitation rate. For example, the exploitation rate of two depressed Canadian stocks, Robertson Creek, an indicator for the west coast of Vancouver Island, and Cowichan, an indicator for the lower Georgia Strait Chinook, are above the sustainable exploitation rate (Figure 5.2)

determined through the hierarchical analysis. Some US ESA-listed stocks, namely the Cowlitz, Nisqually, and Lower Columbia River stocks, are exploited at or above sustainable rates. The 2000 brood year of the Snake River (Lyons Ferry) stock, now listed as endangered, was exploited at a high rate (62%) between 2002 and 2006. Exploitation rates for other broods of the stock encountered in the same years were lower (Figure 5.2).

Finally, healthy stocks, including the Oregon coast, Washington coast, and the Columbia River Summer stocks, are being over-harvested, but are meeting their escapement objectives, and so may not be of concern. However, if a catastrophic event impacting salmon juveniles occurs in these regions (for example, the development of an anoxic “dead zone” in the coastal upwelling regions along the Oregon and Washington coasts (Grantham et al. 2004)), then these exploitation rates may pose a risk to the overall sustainability of the stocks. One problem with the current management regime is that high exploitation rates do not allow depressed stocks to rebuild. Hence, a further improvement in management of these stocks, including a decrease in exploitation rates, is required.

From Figure 5.2, it appears that the management approach negotiated in the PST has, for the most part, met the conservation goals for four out of nine ESA-listed stocks (Nooksack, Skagit fall and springs, and Willamette springs). Some stocks, including the Nisqually, Cowlitz (lower Columbia River Tules), Hood Canal, and south Puget Sound stocks, are still being fished at rates between 50% and 60%. The Snake River population has been fished below optimal harvest rates for a number of years,

although fishing on this stock approached rates as high as 62% in one brood year (2000).

Depressed stocks in Canada (Cowichan for lower Georgia Strait, and Robertsohn for the west coast Vancouver Island) are fished at optimal rates, but these rates generally result in keeping stocks at low abundances. Finally, depressed stocks that were rebuilt during the 1990s, such as the Columbia River summers, tend to be fished at rates of 70-80% that would lead to stock collapse in case of events that reduce productivity for successive broods.

While there has been an overall decline in most exploitation rates of stocks managed by the Pacific Salmon Commission (Appendix 5.1), exploitation rates still approach 60% in most cases, and have been increasing over the past few brood years. This trend might be problematic in light of the depressed status of numerous PNW stocks, the inherent interannual variability in survival (as shown in Chapter 3), and the intent to rebuild stocks over the long run.

5.3 WHY DO WE TEND TO OVER HARVEST CHINOOK SALMON?

As stated in Chapter 1, both the PFMC and the PSC use management approaches that rely heavily on pre-season forecasts. The entire management process is completed by the end of March and the fisheries are prosecuted simultaneously coastwide starting in April. Thus, most forecasts have to be completed by February for ocean-type Chinook that return primarily in the fall between August and November of the same year. Because the assessment must be completed so early, often the only indication of terminal abundance is what happened the previous year. As shown in Chapter 3, Chinook dynamics can change quite rapidly and using indicators from past

years can often be misleading (Peterson et al. 2006) unless the environmental effects on salmon survival are examined at the appropriate scale. This is the primary reason that pre-season management approaches do not work (Mantua and Francis 2004). Ocean fisheries coastwide begin in early April and continue until August before the in-river fisheries begin. In some cases, like the Port Albion test fishery (Parken et al. 2008) or at the Bonneville Dam (TAC 2008) there is an index of abundance in terminal areas that is used to regulate fisheries in order to meet escapement goals. However, this is not the case for most Puget Sound or coastal Washington, Oregon, or British Columbia stocks, nor is this the case for most ocean fisheries. Thus, the combined effect of ocean and in-river fisheries when ocean abundance of particular stocks is low is often over-harvesting some of these stocks.

This problem is exacerbated when there is systematic bias in a forecast that tends to overpredict the abundance of PNW Chinook, or when environmental conditions change radically causing changes in survival of PNW Chinook. In the former case, the model will always tend to make forecasts that lead to over-harvesting fish, while in the latter case the model will correct itself after a year or two when the data sets are corrected to the actual postseason run, and then used in the predictive process (normally through sibling regressions). However, in the latter case the over-harvesting would have already occurred if the environmental change caused a decline in PNW Chinook survival.

Mantua and Francis (2004) state that it is necessary to de-emphasize the importance of pre-season forecasts; their particular solution is three fold: “i) De-

emphasize the role of preseason run-size predictions in management activities, ii)

Emphasize preseason and in-season monitoring of both the resource and its

environment, and iii) Focus on strategies that minimize the importance of uncertain

climate variability and change scenarios to increase the resilience of short and long-

term planning decisions.” In order to implement such a plan, management entities need

to emphasize monitoring of in-season indicators of ecosystem health and plan a fishery

accordingly for the desired returns. The next few sections will focus on Mantua and

Francis’ points two and three with respect to PNW Chinook salmon.

5.4 BUILDING A RISK-AVERSE FRAMEWORK FOR HARVEST INCORPORATING ECOSYSTEM INDICATORS

Chapter 3 focused on the inherent temporal variability in Chinook survival rates, and tried to correlate it with ocean conditions. In most cases, there is weak correlation between survival and ocean conditions, but it might be possible to use a covariate such as sea surface temperatures (SST) to determine near-term trends in survival. The next section will present four criteria for management that would build on points two and three emphasized by Mantua and Francis (2004).

The precautionary approach presented here aims to ensure sustainability of stock productivity and diversity as reflected by four indicators: 1) survival rates (as a surrogate for a particular Chinook’s productivity); 2) abundance; 3) exploitation rates; and 4) ecosystem indicators connected to the stock being managed. The first three of these criteria are evaluated by the Chinook Technical Committee (CTC) in its annual Escapement and Exploitation Rate report (TCChinook (08)-1); the fourth criterion is a set of ecosystem measures that are proposed by Peterson et al. (2006).

5.4.1 CRITERIA USED IN THE PRECAUTIONARY FRAMEWORK

During recent negotiations between the US and Canada, the first three indicators in a framework for precautionary management were presented (US South 2008), though never formally adopted. Some facets of the approach being presented here are from an analysis done by Morishima and Sharma (US South 2008).

5.4.1.1 Survival Rates

Substantial variability in survival rates has been observed for many stocks (Chapter 3). Here I consider survival rates for a subset of the stocks used in the analyses of Chapter 3. Figure 5.3(a) illustrates a stock with survival rates that have dropped substantially over time. Figure 5.3(b) illustrates highly variable survival rates with no discernable trend. Figures 5.3(c)-(d) illustrate stocks with extremely variable, periodic survival patterns. Of these stocks, the ones shown in Figures 5.3(c)-(d) are at the greatest risk of becoming conservation concerns because stocks with significantly below-average survival rates in consecutive brood years can exhibit decreased productivity and reduced abundance. The steep declines in survival toward the end of the time series indicate that both productivity and abundance will be depressed in the near term for some PNW Chinook stocks, increasing the difficulty of achieving spawning abundance management goals. Thus, the approach developed needs to be responsive to changes in survival.

The first principle of the proposed approach would be the necessity of accounting for trends in survival. For example, if most (>50%) of the stocks managed for escapement by the PSC decline or fall below a stock-specific threshold survival level, managers would be required to take particular management actions.

5.4.1.2 Escapements Trends

Trends in escapements for the stock groups represented by Figures 5.3(c) and 5.3(d) provide evidence for the relationship between depressed productivity and abundance (Figure 5.4). Anomalous patterns have been observed in run timing and survival for several salmon stocks coastwide (for example, Fraser sockeye runs in 2007 and 2008 and Columbia River spring Chinook runs in 2007 and 2008). Unprecedented downward trends in escapement are being observed for stocks like the Oregon Coast and the west coast of Vancouver Island (Figure 5.4). This approach will become particularly important when, over the next ten years, increased uncertainty of the impact of global warming and climate change on the resource can be expected (Mantua and Francis 2004, Peterson et al. 2006).

The second principle to be incorporated into this framework would be the importance of escapement levels for the stock groups being managed under the PSC. If data indicate that more than some specified percent (25%, 50% etc.) of the stocks being managed are below their escapement goal, then managers would be required take particular management actions.

5.4.1.3 Pre-Terminal Exploitation Rates

If runs are lower in terminal areas, management entities normally take severe management actions to restrict fisheries in near-terminal or terminal areas. For example, fishing was shut down on the Sacramento Chinook stock for most of southern Oregon and California in 2008, and the Klamath run was shut down for most of southern Oregon and the Klamath basin in 2007 (PFMC 2008). In the face of depressed survivals and declining escapements, pre-terminal total mortality rates can increase. Figure 5.5

illustrates that pre-terminal total mortality rates have been increasing for the west coast of Vancouver Island (WCVI) and Oregon coastal (ORC) stocks while these stocks have shown declines in spawning abundance (Figure 5.4).

The third criterion to be used in determining harvest levels would be a target exploitation rate for a particular stock and fishery (or group of fisheries). If these targets are exceeded on a group of fisheries, then an explicit management action would be taken in the fishery (fisheries) to reduce catch.

5.4.1.4 Ecosystem Indicators

A number of environmental indicators measured by Peterson et al. (2006) could be used along with the criteria described above, or could be used independently.

Mantua and Francis (2004) emphasize the role of in-season management and monitoring of ecosystem indicators to evaluate the health of the system (Table 5.3 from Peterson et al. 2006). Numerous indicators related to survival of juvenile Chinook could be used to evaluate whether the Chinook runs would be better than average or worse than average. Fisheries coastwide could plan on different harvest levels as function of these indicators.

The fourth criterion would be if ecosystem indicators corresponding to the juvenile out-migration for a majority of stocks being managed by the PSC (for e.g. >50%) indicate worse conditions than normal, management actions should be taken to reduce the catch.

5.5 DEVELOPING A DECISION MATRIX THAT WOULD GOVERN FISHING LEVELS AS A FUNCTION OF THE FOUR CRITERIA

Based on the four criteria, a rule-based system should be developed that would govern harvest control (Restrepo and Powers 1999). An example of how this might work is shown in Table 5.4. The first step would be to populate a matrix of n stocks and four criteria using a binary control rule. In this example, if the target criterion is met for a given stock, the matrix cell is colored green, and if not, it is red.

The second step would be to evaluate these criteria over all stocks encountered in a fishery using the decision rules (Table 5.4). Thus, in this example if 50% of stocks are below a target survival rate, the matrix cell is red, if between 25% and 50% are below the target survival rate, the cell is yellow, and if less than 25% of stocks are below target survival the cell is colored green.

Based on these evaluations across multiple criteria, the stocks are divided into three categories: all green cells (best case), all red (worst case), or intermediate (yellow). The intermediate category occurs only if two or more criteria are evaluated as yellow or red. Thus, if one category is red or yellow and all other three are greens, fishing should take place at the green level. There are 81 possible outcomes using the three indicators for the four criteria, not all of which are presented here. Of course, this matrix is open to policy interpretations and is just being used here for illustrative purposes. Based on the outcomes, a possible fishing level could be associated with the estimated abundance in the fishery (Figure 5.6).

5.6 INCORPORATING UNCERTAINTY IN THE FORECASTS: THE BACKUP APPROACH

Chapter 4 develops a complex catch-at-age model that is capable of calculating uncertainty associated with a variety of fishery parameters (e.g., survival, maturation).

If the management system is unable to de-emphasize the pre-season aspects of the process, an alternative approach based on this model could be used.

Using the model developed in Chapter 4, I presented a forecast across all ages which included measures of uncertainty (quartiles were demonstrated for a particular year's forecast). These quartiles could be used in order to be risk-averse. This approach could be used by the PSC and PFMC to estimate ocean abundance and set risk-averse harvest limits that would err on the side of benefiting stocks.

An example of the use of this technique begins with an examination of Table 5.3. If indicators imply that juveniles will be exposed to poor ocean conditions, managers would use the 25th quartile of the forecast interval rather than the median or mode. This approach would provide a risk buffer that would, in the worst case, under-predict the run, resulting in a recommendation of a lower ocean catch than that determined in the pre-season management scheme used by both the PSC and the PFMC.

5.7 OVERALL CONCLUSIONS

Based on these results I've presented, I propose an integrated management approach that would account for changes in the environment based on post-season and in-season indicators, as well as physical environmental indicators as suggested by Mantua and Francis (2004). This approach could be integral to the long term viability of Chinook in the PNW, and could help manage these stocks in a sustainable manner in the long run. This approach is important as recent trends in physical ocean conditions, ocean ecosystem indicators, Chinook escapement, and survival data for Chinook stocks

(Chapter 3) indicate that lower survival can be expected in the short term. Poor ocean conditions in 2005 through 2007 might impact outmigrating smolts from preceding brood year significantly, resulting in large changes in Chinook abundance, but these changes will not be detected until at least 2008 and 2009 when these ocean migrants enter the fishery. Preliminary ocean indicators in 2008 indicate these outmigrants will have higher than average survival, but again these changes will not be detected until at least 2010 when the 2008 ocean migrants enter the fishery in substantial numbers.

Finally, while the conditions in the marine environment have largely favored high recruitment events over the recent years analyzed here (1999-2003 from Chapter 3); these large year classes have not contributed to correspondingly large escapements for depressed stocks due to the high levels of ocean fishing that occurred between 2002 and 2006. Southeast Alaska trollers fished at record rates between 2003 and 2006, and both northern British Columbia and west coast Vancouver Island fisheries have seen increasing catch trends for those years (Note: 2004 had one of the highest ocean catches over the past 25 years, with over 1 million Chinook caught (TCChinook 08-01)). Such catch levels are not sustainable in the long run. Thus, the time is right to introduce the precautionary management approach outlined here. A Management Strategy Evaluation should also be undertaken for the stocks in order to provide a better understanding of how the stocks would perform under different sets of fishing rules and targets over the short and long term (Punt and Hilborn 1997, McAllister et al. 1999). This would be the basis of determining the harvest control rules as shown in the

preceding sections of this chapter that would account for rebuilding depressed PNW

Chinook populations, and guarantee long-term viability of these stocks.

List of Tables

Table 5.1: Quartiles on optimal harvest rates for Chinook

Table 5.2: Current brood year harvest rates

Table 5.3 (taken from Peterson et al. 2006): Ocean and ecosystem conditions in the Northern California Current. Colored dots indicate whether the index was positive (green), neutral (yellow), or negative in the year salmon entered the ocean. The last two columns forecast adult returns based on ocean conditions in 2005. The year 2000 is included as an example of conditions during a "good" year, in contrast to the "poor" conditions observed in recent years, 2004-2006.

Table 5.4: Decision matrix for determining fishing levels

Table 5.1: Quartiles on optimal harvest rates for Chinook

Credible Intervals	Optimal HR for Chinook
0.05	49%
0.25	55%
0.5	61%
0.75	68%
0.95	77%

Table 5.2: Current brood year harvest rates

Stock	BY	Ocn HR	Total HR	Stock	BY	Ocn HR	Total HR	Stock	BY	Ocn HR	Total HR	Stock	BY	Ocn HR	Total HR
Alaska Springs	1998	31%	41%	Cowlitz	1999	50%	60%	Kitsumkalum	1998	25%	31%	Nisqually	1999	30%	72%
	1999	27%	41%		2000	36%	60%		1999	28%	41%		2000	31%	70%
	2000	40%	54%		2001	31%	55%		2000	27%	31%		2001	24%	52%
	2001	57%	79%		2002	36%	36%		2001	22%	47%		2002	25%	35%
Bbig Qualicum	1999	53%	54%	George Adams	1999	39%	57%	Lower Col. River	1999	44%	58%	Nooksack F	1999	34%	35%
	2000	38%	41%		2000	40%	55%		2000	50%	66%		2000	31%	31%
	2001	43%	44%		2001	40%	55%		2001	51%	66%		2001	50%	50%
	2002	37%	39%		2002	36%	46%		2002	50%	69%		2002	47%	48%
Chilliwac	1998	22%	27%	Hanford	1999	27%	52%	Lewis River Wild	1999	20%	26%	Puntledge	1999	22%	22%
	1999	29%	34%		2000	34%	59%		2000	17%	26%		2000	38%	38%
	2000	19%	24%		2001	34%	72%		2001	17%	44%		2001	35%	35%
	2001	23%	31%		2002	15%	40%		2002	25%	40%		2002	26%	26%
Cowichan	1999	54%	63%	Hoko	1999	31%	31%	Lyons Ferry Hatchery				Queets	1998	47%	68%
	2000	69%	72%		2000	34%	34%		2000	36%	63%		1999	59%	82%
	2001	70%	74%		2001	28%	28%		2001	9%	18%		2000	58%	82%
	2002	55%	62%		2002	32%	32%		2002	10%	14%		2001	49%	89%
Robertson Creek	1999	32%	63%	Samish	1999	37%	74%	Skagit	1999	41%	41%	Skagit Sprin	1998	3%	40%
	2000	30%	67%		2000	37%	63%		2000	31%	33%		1999	0%	46%
	2001	35%	66%		2001	45%	84%		2001	31%	34%		2000	4%	39%
	2002	24%	57%		2002	38%	70%		2002	36%	42%		2001	7%	34%
Soos	1998	31%	36%	Spring Cr	1999	33%	58%	South Puget Sound Fingerling	1999	41%	53%	South Puget Sound Yearling	1999	82%	85%
	1999	35%	51%		2000	33%	58%		2000	49%	62%		2000	95%	95%
	2000	38%	42%		2001	28%	48%		2001	49%	55%		2002	52%	63%
	2001	54%	54%		2002	22%	48%		2002	39%	44%				
Salmon River Hatchery	1999	29%	60%	SSF	1999	41%	42%	Stilliguamish	1999	25%	25%	Columbia Summers	1999	55%	73%
	2000	34%	64%		2000	23%	24%		2002	30%	32%		2000	49%	69%
	2001	40%	67%		2001	27%	29%						2001	61%	77%
	2002	36%	70%		2002	41%	51%								
URB	1999	24%	47%	White Riv	1997	72%	75%	Willamette	1998	8%	29%	Quinsam	1999	40%	52%
	2000	35%	56%						1999	11%	36%		2000	45%	53%
	2001	31%	54%						2000	12%	36%		2001	51%	54%
	2002	16%	39%						2001	17%	35%		2002	40%	40%

* Queets escapement may be missing thus biasing overall rates

Table 5.3 (taken from Peterson et al. 2006): Ocean and ecosystem conditions in the Northern California Current. Colored dots indicate whether the index was positive (green), neutral (yellow), or negative in the year salmon entered the ocean. The last two columns forecast adult returns based on ocean conditions in 2005. The year 2000 is included as an example of conditions during a "good" year, in contrast to the "poor" conditions observed in recent years, 2004-2006.

	Juvenile migration year				Forecast of adult returns	
	2000	2004	2005	2006	Coho 2006	Chinook 2007
Large-scale ocean and atmospheric indicators						
PDO	■	■	■	■	●	●
MEI	■	■	■	■	●	●
Local and regional physical indicators						
Sea surface temperature	■	■	■	■	●	●
Coastal upwelling	■	■	■	■	●	●
Physical spring transition	■	■	■	■	●	●
Deep water temp. & salinity	■	■	■	■		
Local biological indicators						
Copepod biodiversity	■	■	■	■	●	●
Northern copepod anomalies	■	■	■	■	●	●
Biological spring transition	■	■	■	■	●	●
Spring Chinook--June	■	■	■	■	●	●
Coho--September	■	■	■	■	●	●

Key

■ good conditions for salmon marine survival
 ■ intermediate conditions for salmon marine survival
 ■ poor conditions for salmon marine survival

● good returns expected
 ● poor returns expected

Table 5.4: Decision matrix for determining fishing levels

Category	Stock 1	Stock 2.....Stock n
Survival			
Escapement			
Exploitation			
Ecosystem			

DECISION RULES

Survival Criteria	Escapement Criteria	Exploitation Criteria	Ecosystem Criteria
If $\geq 50\%$ of stocks survival is lesser than threshold then red	If $\geq 50\%$ of stocks escapement is lesser than threshold then red	If $\geq 50\%$ of stocks ocean exploitation is lesser than threshold then green	If $\geq 50\%$ of stocks ecosystem is good then green
If 25 to 50% of stocks lesser than threshold then yellow	If 25 to 50% lesser than threshold then yellow	If 25 to 50% lesser than threshold then yellow	If 25-50% of stocks ecosystem is good then yellow
if $< 25\%$ of stocks lesser than threshold then green	if $< 25\%$ of stocks lesser than threshold then green	if $< 25\%$ of stocks lesser than threshold then red	if $< 25\%$ of stocks lesser than threshold then red

Overall Stocks	Category 1	Category 2	Category 3
Survival Escapement Exploitation Ecosystem		2 or more criteria are yellow or red	

List of Figures

Figure 5.1: Optimal harvest rate based on the watershed area SMSY relationship (using hierarchical models)

5.2: Simple Exploitation Rates (SER) on ESA-listed and depressed stocks in the US and Canada

Figure 5.3: Survival rate patterns for four exploitation rate indicator stocks

Figure 5.4: Escapement trends for WCVI and Oregon Coastal Chinook (TC-Chinook (08)-1)

Figure 5.5: Total mortality pre-terminal exploitation rates for WCVI and Oregon Coastal fall Chinook indicator stocks (Data from Appendix E, TCChinook (08)-1)

Figure 5.6: Total allowable catches in a mixed-stock ocean fishery based on overall aggregate abundance of all stocks encountered in the fishery. Best case, intermediate case, and worst case catch levels are depicted

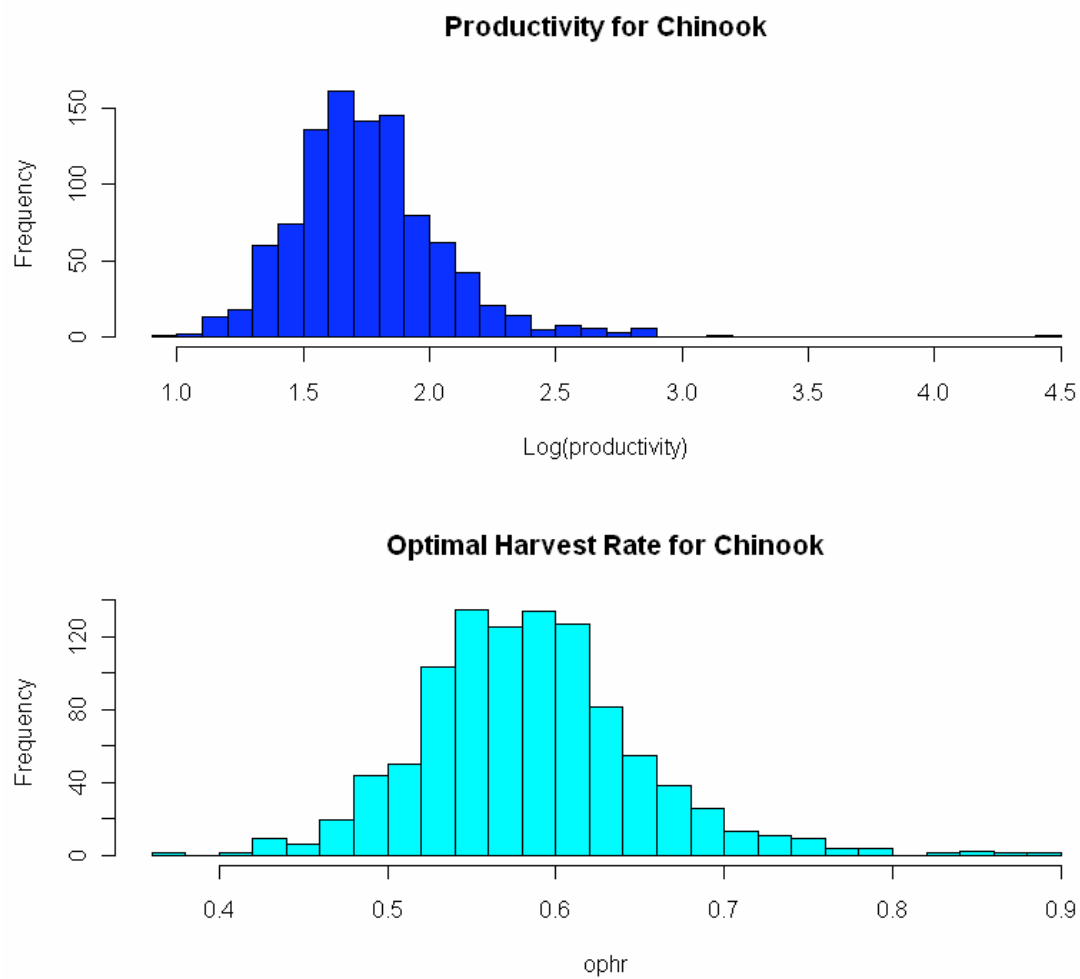


Figure 5.1: Optimal harvest rate based on the watershed area SMSY relationship (using hierarchical models)

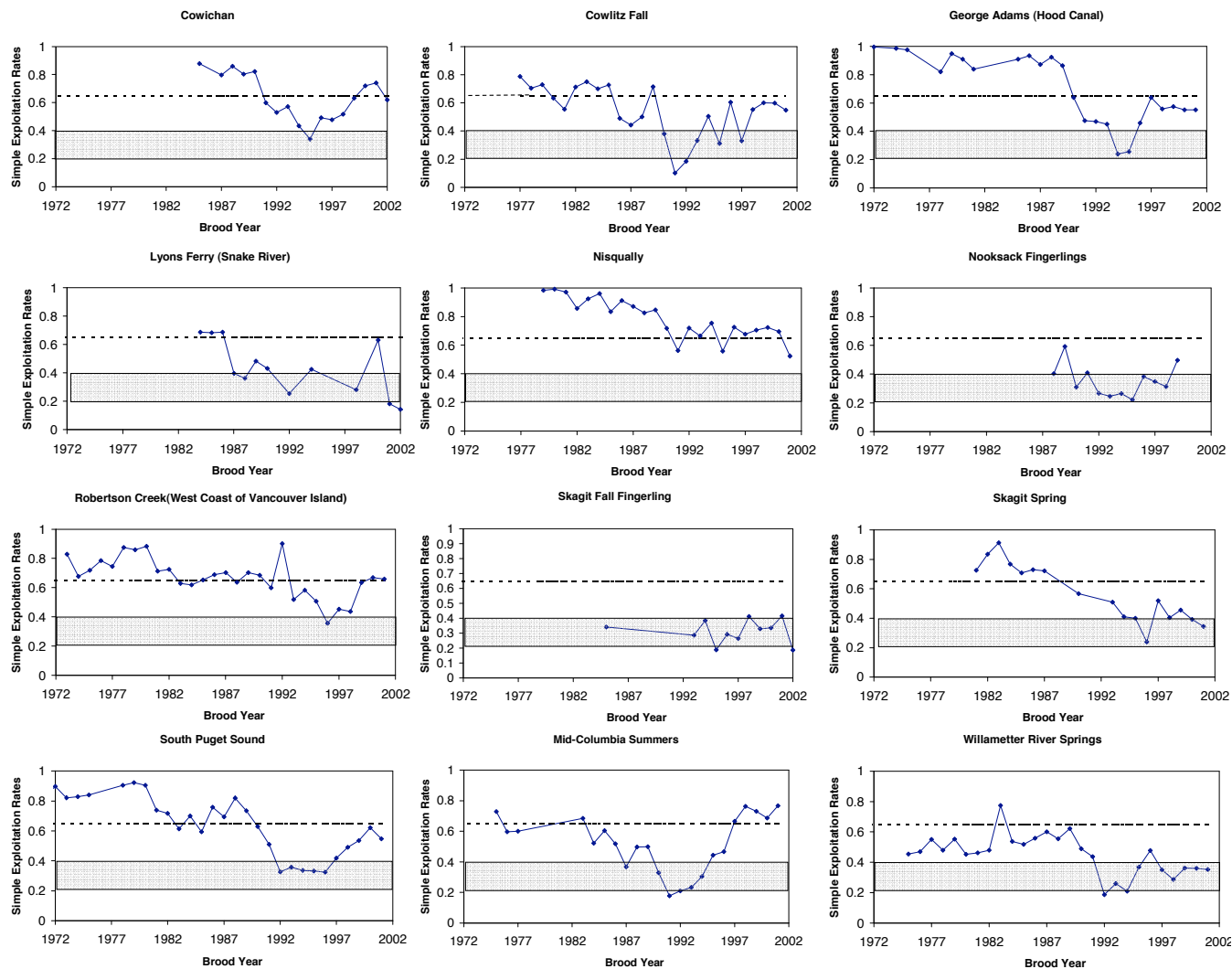


Figure 5.2: Simple Exploitation Rates (SER) on ESA-listed and depressed stocks in the US and Canada

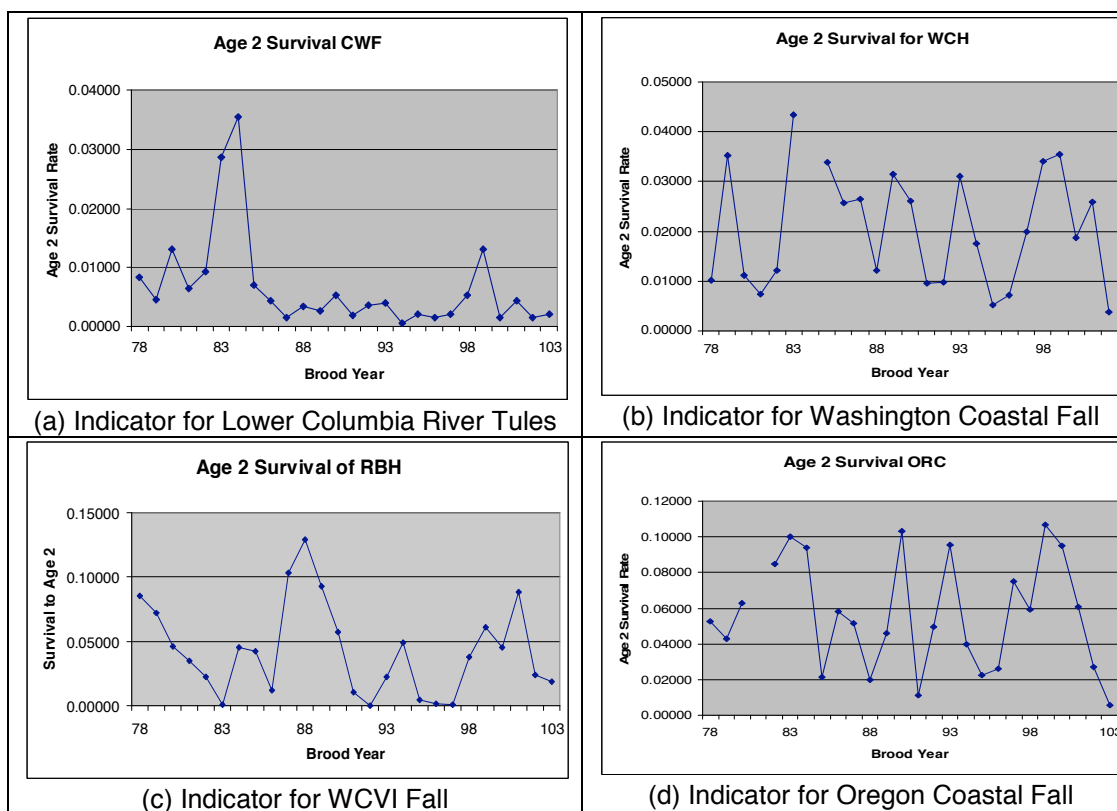


Figure 5.3: Survival rate patterns for four exploitation rate indicator stocks

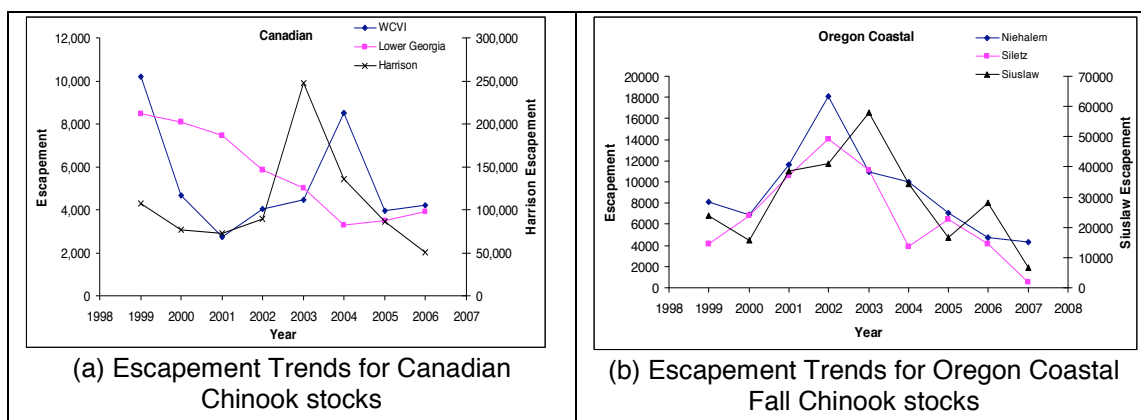


Figure 5.4: Escapement trends for WCVI and Oregon Coastal Chinook (TC-Chinook (08)-1)

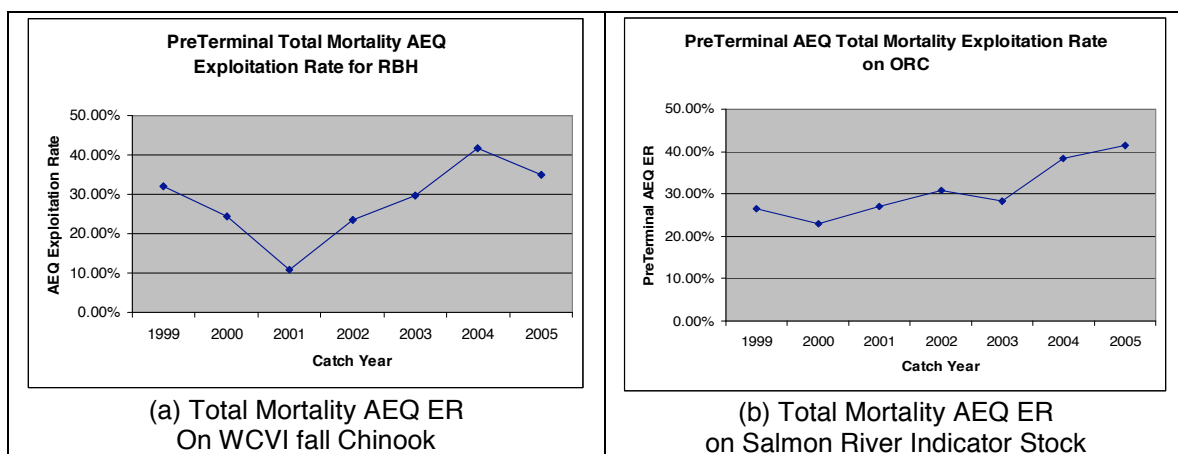


Figure 5.5: Total mortality pre-terminal exploitation rates for WCVI and Oregon Coastal fall Chinook indicator stocks (Data from Appendix E, TCChinook (08)-1)

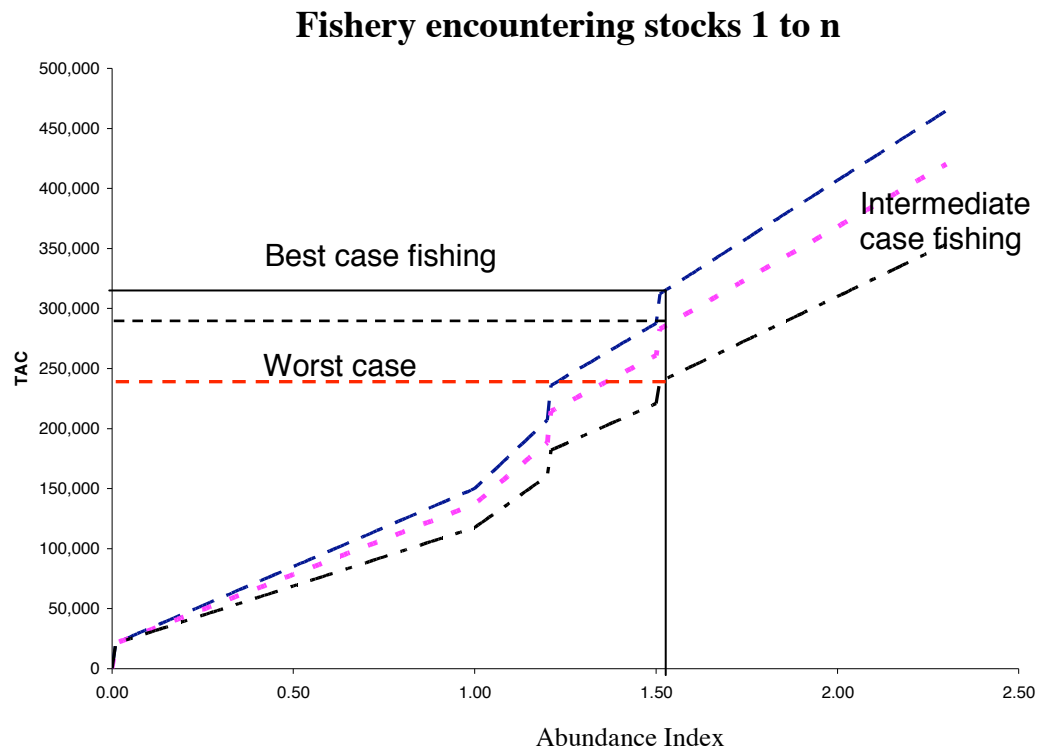


Figure 5.6: Total allowable catches in a mixed-stock ocean fishery based on overall aggregate abundance of all stocks encountered in the fishery. Best case, intermediate case, and worst case catch levels are depicted

APPENDIX 5.1: EXPLOITATION RATES ON INDICATOR STOCKS USED BY THE CHINOOK TECHNICAL COMMITTEE

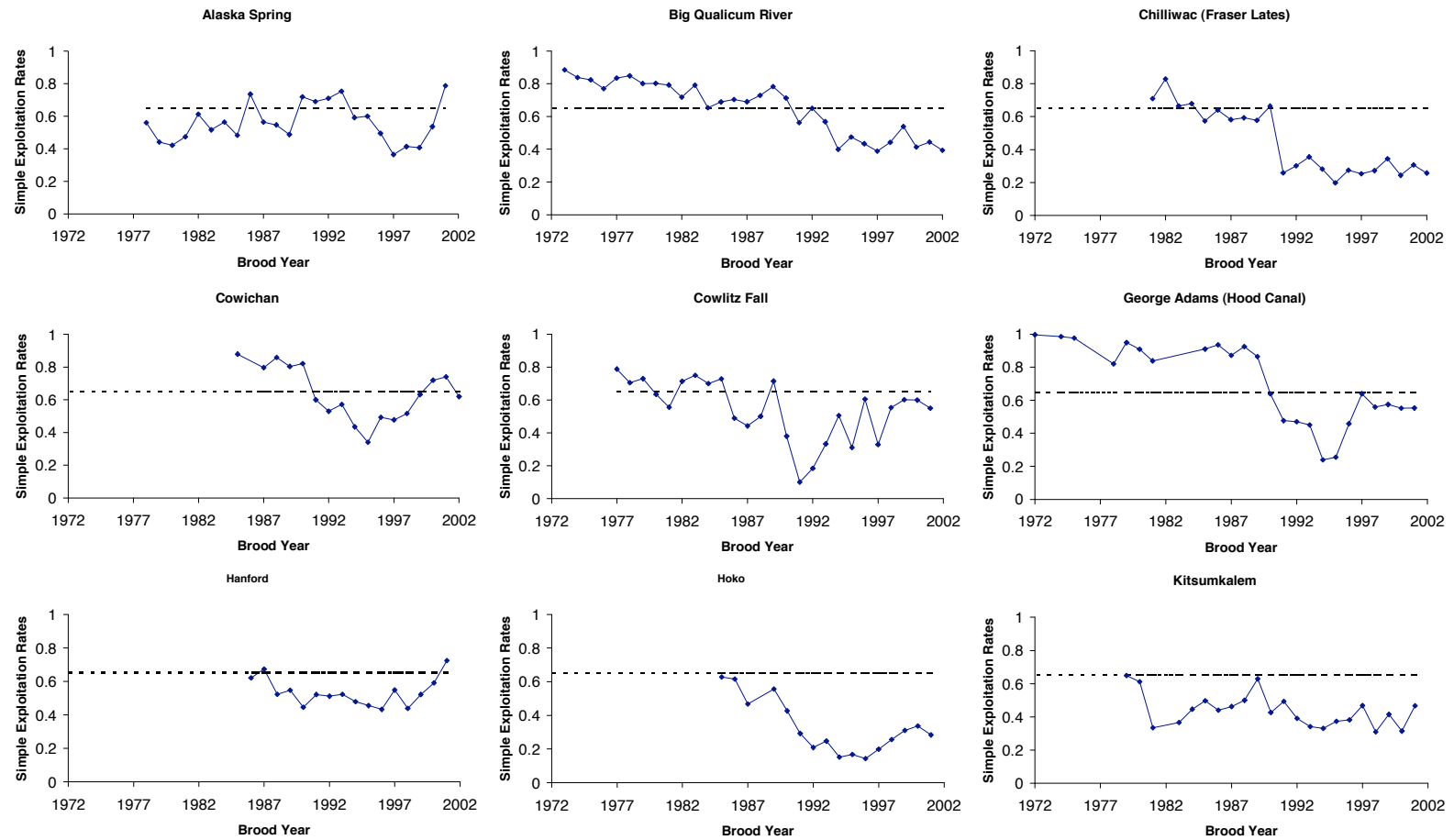


Figure 1: Simple Exploitation Rates (SER) on the CTC indicator tag program with comparisons to optimal Exploitation rates

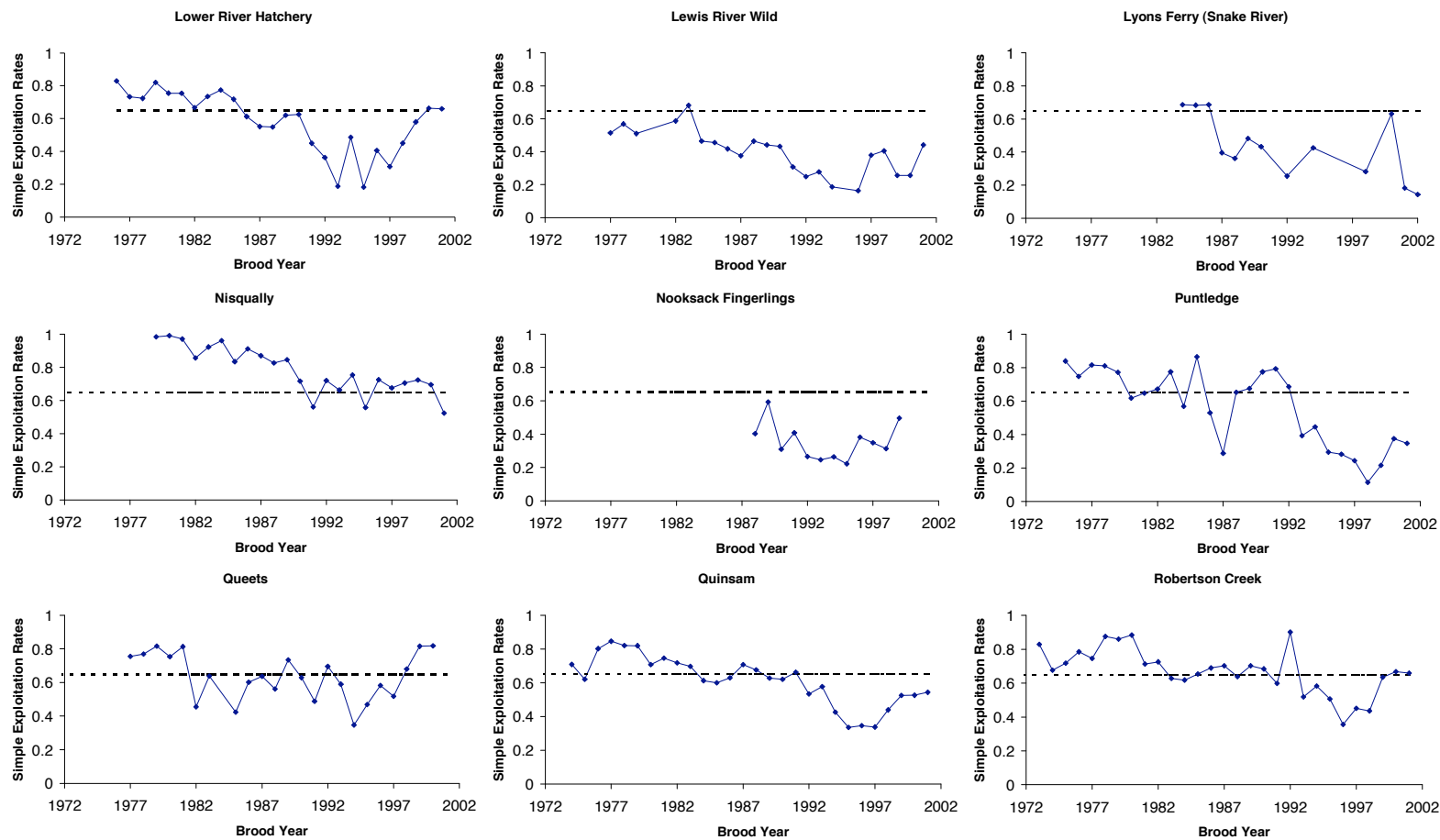


Figure 2: Simple Exploitation Rates (SER) on the CTC indicator tag program with comparisons to optimal Exploitation rates

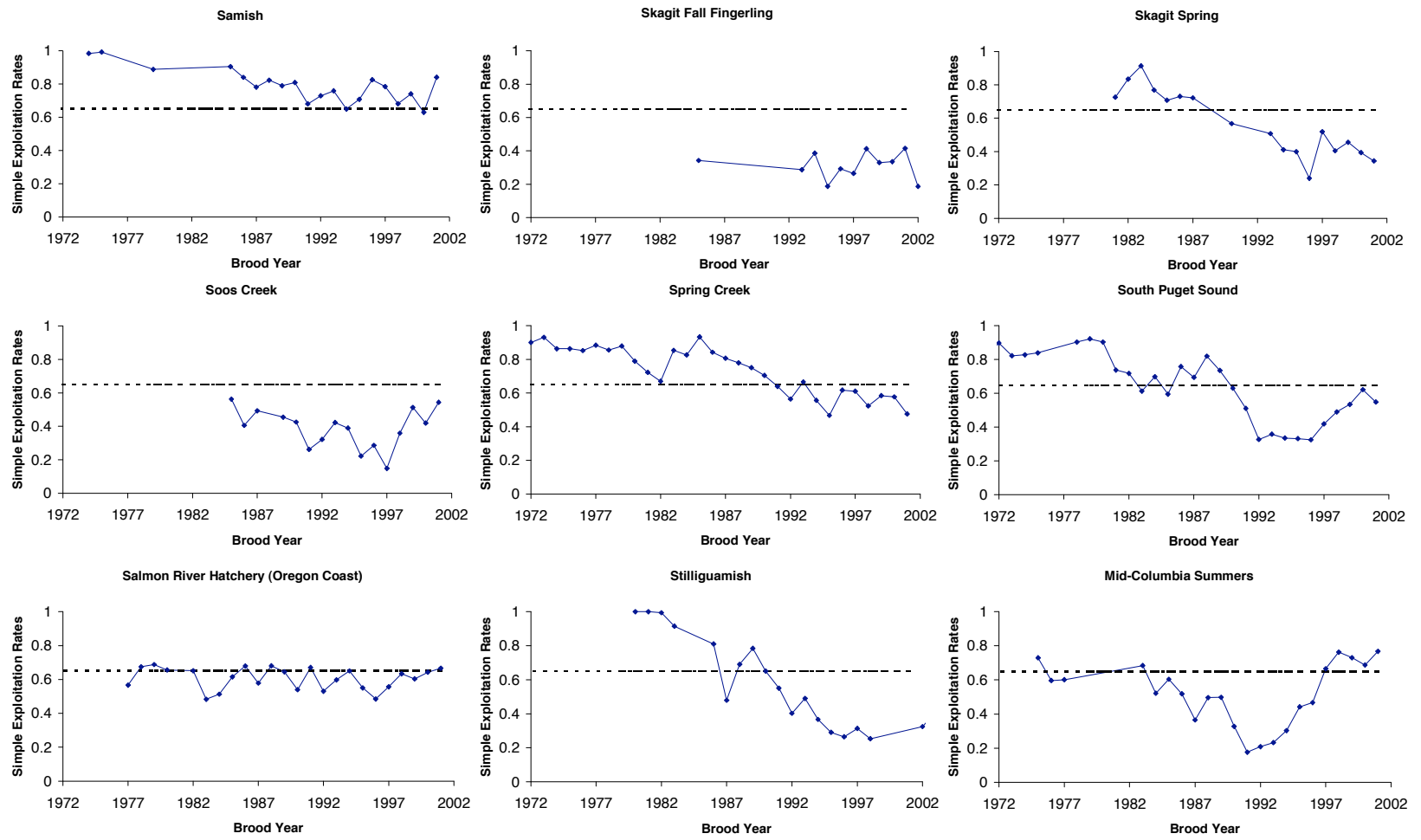


Figure 3: Simple Exploitation Rates (SER) on the CTC indicator tag program with comparisons to optimal Exploitation rates

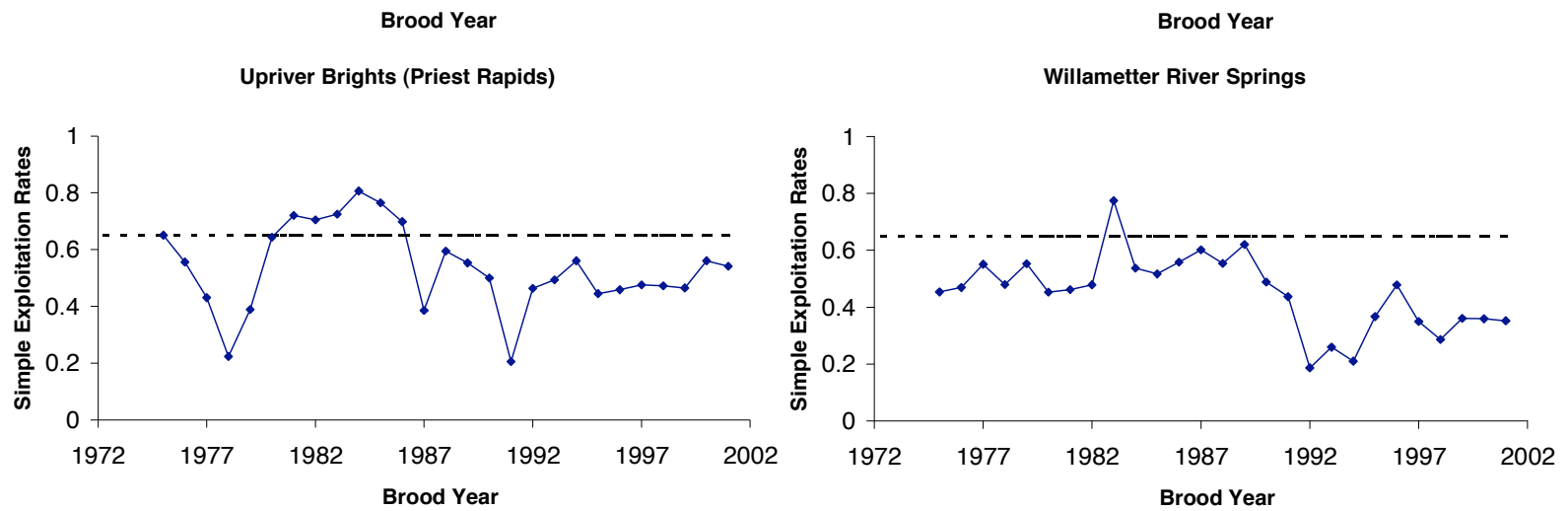


Figure 4: Simple Exploitation Rates (SER) on the CTC indicator tag program with comparisons to optimal Exploitation rates

APPENDIX 5.2: SUPPLEMENTING SPAWNER-RECRUIT DATA WITH WATERSHED SIZE TO IMPROVE ESTIMATION OF S_{MSY} : A BAYESIAN HIERARCHICAL MODELING APPROACH.

Martin Liermann,
Northwest Fisheries Science Center,
NOAA Fisheries,
2725 Montlake Blvd E.
Seattle, WA 98112.

Rishi Sharma,
Columbia River Intertribal Fisheries Commission,
729 NE Oregon St., Suite 200,
Portland , OR 97232

Charles K. Parken,
Pacific Biological Station, Fisheries and Oceans Canada,
3190 Hammond Bay Road,
Nanaimo, BC V9T 6N7 Abstract

Escapement goals for Pacific salmon (*Oncorhynchus* sp.) are used to prepare advice on the status of populations and to help plan fisheries on healthy populations. Escapement goals for Chinook salmon (*O. tshawytscha*) populations tend to be highly uncertain due to variability in and in some cases complete absence of spawner-recruit data. Using spawner-recruit data from 25 Chinook salmon populations from Oregon to Alaska, Parken et al. (2006) demonstrated that watershed size is a good predictor of spawners at maximum sustainable yield and therefore a useful surrogate for spawner-recruit data when it is unavailable. We used hierarchical modeling to combine these two sources of data in a single analysis where an allometric relationship between equilibrium stock size and watershed size is assumed. This approach provides a number of benefits: 1) it accounts for variability in quality and quantity of spawner-recruit data across populations, naturally weighting the different sources of data, 2) the distribution of productivity across populations can be modeled within the analysis to improve estimates for individual populations, 3) when available, both spawner-recruit data and watershed size can be used in inference for a population, and 4) this modeling structure can easily be expanded to incorporate other sources of information affecting production, such as temporal patterns in ocean conditions. Our results demonstrate that using a hierarchical model that incorporates both watershed size with spawner-recruit data, provides a simple yet logical framework for combining these two sources of informative data to estimate management parameters.

Introduction

Spawner-recruit relationships for Pacific salmon (*Oncorhynchus* sp.) tend to be highly uncertain due to unexplained environmental variability, little or no available data, and measurement error introduced through estimation of maturation rates, harvest rates and spawner abundance (Schnute and Kronlund 2002). Management based on spawner-recruit relationships is therefore also often very uncertain. In the traditional management approach, each population is analyzed separately. Information from other populations may be used informally, for example in model selection, but parameter estimates are based solely on the data from that population. Although we would not expect populations to share exactly the same demographic parameters (e.g. productivity and capacity), we would expect populations of the same species and life-history type to have demographic parameters that are more similar to each other than to populations of other species or from other regions. It is therefore intuitive that for situations where demographic parameters are very uncertain, as is the case with most spawner-recruit models, (Schnute and Kronlund 2002, Hilborn 2001), that using the parameter values from other similar populations can lead to better estimates (Hilborn and Liermann 1998).

In the past decade fisheries scientists have begun to implement this approach using hierarchical or random effects modeling (Myers et. al. 1999, Myers 2001, Liermann & Hilborn 1997, Chen & Holtby 2002, Minte-Vera 2004). These types of models assume that one or more of the parameters describing the population dynamics of each stock are random variables which follow a common distribution. This generally results in “shrinkage” of the individual parameter values (estimated in isolation) towards the central tendency of this common distribution (Gelman et. al. 1995). Hierarchical modeling provides several advantages; i) it provides higher precision for model or model-derived parameters of interest if the data are less informative (Rivit and Prevost 2002) or as in our case the spawner-recruit fit is extremely poor, ii) it provides reasonable estimates of model and model-derived parameters when the model solely based on one set of data provides nonsensical results (Myers et. al. 2001), and iii) it discerns patterns or structure in data sets that might not be discernible otherwise (Myers 2001). The mixed-population character of Chinook salmon (*O. tshawytscha*) fisheries along western North America has led to an abundance-based management approach for population-aggregates and harvest regimes intended to achieve goals, such as maximum sustained yield, for many populations (PSC 2004; PFMC 2003). Because spawner-recruit data is not available for many of these populations, there is a critical need for approaches that include other sources of population information. Parken et al. (2006) showed that for 25 west coast Chinook salmon populations, the spawner level at maximum sustainable yield³ (S_{MSY}) was closely related to the size of the available watershed. Using this relationship they proposed a simple regression based approach of estimating S_{MSY} for populations without spawner-recruit data. The advantages of this approach is that it is simple to apply, easy to explain and is based on a well-understood robust statistical procedure. There are, however, several advantages to using hierarchical modeling for this problem. First, the model can easily accommodate spawner-recruit and watershed data when both are available, second productivity for the different populations can be assumed to come from a common distribution, reducing uncertainty in this parameter, and finally, the influence of data from individual populations on the results is inherently weighted by the population information content. In this paper we apply hierarchical modeling to the relationship found in Parken et al. (2006). We assume an allometric relationship between watershed size and capacity, and further assume that the productivity parameters for the different populations come from a common distribution. This approach allows us to incorporate all of the data into a single analysis which naturally weights the different sources of information.

Methods

The data

³ Here MSY refers to the the maximum vertical difference between the function describing median recruitment (e.g. the Ricker 1973), and the one to one line, or roughly (assuming deterministic dynamics), the maximum constant harvest that results in a non-declining population.

Spawner-recruit data and watershed size were compiled for 25 populations of Chinook salmon in Oregon, Washington, British Columbia, and Alaska (Table 1). Recruitment was defined as the number of adults from the same cohort that would have survived to maturity without harvest, and spawners calculated as the number of 2-ocean age and older fish (stream-type Chinook salmon implies an age 3 fish and ocean-type an age 2 fish). Watershed size was defined as the total drainage area (km²) minus the area upstream of man-made barriers and natural barriers on 4th order or 5th order stream segments (Strahler 1957) for respective stream-type or ocean-type Chinook salmon populations (Healey 1991). A complete description of the data can be found in Parken et al. (2006) (some of the data has been updated since this publication).

The model

As in Parken et al. (2006), we assume an allometric relationship between a population parameter, E_j , and watershed size (W_j) for populations $j = 1$ to m ,

$$(1) \quad E_j = e^a W_j^b,$$

for each of the $j = 1$ to m populations, where this relationship is different for stream and ocean-type life histories (L),

$$(2) \quad E_j = e^{(a+a_D L_j)} W_j^{(b+b_D L_j)}.$$

Here we are able to use the more biologically motivated parameter equilibrium population size, E_j , instead of S_{MSY} (used by Parken), because we use a single step analysis. Life history type is designated with the indicator variable L , where L is 0 for stream-type and 1 for ocean-type.

We assume an allometric relationship between the equilibrium population size and watershed size because of the structural relationships between freshwater habitats (i.e. total channel length and total stream area) and drainage area. Total channel length, total stream area, or drainage area are habitat quantity indices commonly used to model the standing crop of stream fish (Fausch et al. 1988). Watershed size is a useful index of habitat area that corresponds to the productive capacity of Chinook salmon because of its relationship to total stream channel length and stream area (Parken et al. 2006). There is an allometric relationship between drainage area and cumulative channel length that exists over 11 stream orders (Horton analysis: Horton 1945), with variation in the relationship's coefficients among regions as drainage densities vary (Leopold et al. 1992). Total stream area is the product of channel length and mean channel width summed over all channels in the drainage. Total stream area follows an allometric relationship with drainage area, since mean channel width increases downstream as an allometric relationship with mean annual discharge (Leopold and Maddock 1953) and mean annual discharge is directly proportional to the drainage area (Rodriguez-Irtube and Rinaldo 1997). As both total channel length and total stream area have allometric relationships with drainage area, the population parameters are assumed to have an allometric relationship with watershed size.

In log-log space equation 2 translates to a linear relationship:

$$(3) \quad \log E_j = a + a_D L_j + (b + b_D L_j) \log W_j,$$

where the intercept and slope are a and b for stream-type and $(a + a_D)$ and $(b + b_D)$ for ocean-type. We incorporate population specific variability from these linear relationships with the variables k_j (Figure 1):

$$(4) \quad \log E_j = a + a_D L_j + (b + b_D L_j) \log W_j + k_j.$$

We centered $\log W_j$ (subtracted the mean) to improve estimation performance.

This relationship between equilibrium population size and watershed size is linked to the spawner-recruit data through a series of spawner-recruit functions:

$$(5) \quad R_{i,j} = S_{i,j} \exp \left[r_j \left(1 - \frac{S_{i,j}}{E_j} \right) + w_{i,j} \right].$$

Here $R_{i,j}$ and $S_{i,j}$ are the i^{th} year's recruits and spawners for population j . The parameter r_j is the log of the slope at zero and E_j (the equilibrium) is the non-zero value where $R_{i,j}$ is equal to $S_{i,j}$. The $w_{i,j}$ are

normally distributed independent random variables with mean 0 and population specific standard deviations σ_j . Intrinsic in this parameterization is the assumption that an equilibrium exists, or in other words the initial slope, r_j , is greater than 0. We check this assumption by looking for effects of this constraint on the posterior distributions for the r_j parameters. The Ricker (1973) spawner-recruit function was chosen as the default spawner-recruit relationship because it tends to give more realistic parameter estimates (Myers et al. 1999) and has been used extensively with Chinook salmon data (PSC 1999). To enforce non-zero r_j , r_j is assumed to follow a lognormal distribution.

$$(6) \quad r_j \sim \text{lognormal}(r_M, r_{SD})$$

Since the k_j is a residual, by definition it has mean zero. We assume a normal distribution.

$$(7) \quad k_j \sim \text{normal}(0, k_{SD})$$

The priors on the two standard deviation hyper-parameters (r_{SD} , and k_{SD}) are assumed to have uniform distributions (Gelman et.al. 1995),

$$(8) \quad r_{SD} \sim \text{uniform}(0, 100) ,$$

$$(9) \quad k_{SD} \sim \text{uniform}(0, 100) .$$

And the mean for lognormal distribution of the r_j parameters (r_M) is assigned a normal prior.

$$(10) \quad r_M \sim \text{normal}(0.6, 0.45)$$

The mean of 0.6 produces a median of approximately 1.8 for the lognormal distribution of r_j which corresponds to approximately 6 recruits per spawner, a typical value for healthy Chinook salmon populations (PSC 1999). The 25th and 75th percent quantiles are 3.8 and 11.8 recruits per spawner respectively. We assessed the sensitivity of the results to the choice of priors (see below).

The priors for the parameters defining the relationship between equilibrium population size and watershed size (equation 4) are all defined using the normal distribution. Because the natural log of watershed size, $\log W_j$, is centered (the mean is subtracted from all values), the intercepts (a and $a + aD$) should be approximately equal to the mean log Equilibrium, $\text{mean}(\log E_j)$. The mean for the prior on a was therefore set to 10 which is approximately the average of log recruitment across all 25 populations. While this use of the same data in both the prior and likelihood is not technically correct, we use a large standard deviation (31.6) and test for sensitivity to prior assumptions (see below).

$$(11) \quad a \sim \text{normal}(10, 31.6)$$

For the other regression parameters, a plausible null hypothesis would be that there is no life history effect and the slope is 0. The means are therefore all set to 0 with large standard deviations (31.6).

$$(12) \quad a_D \sim \text{normal}(0, 31.6)$$

$$(13) \quad b \sim \text{normal}(0, 31.6)$$

$$(14) \quad b_D \sim \text{normal}(0, 31.6)$$

Notice that a standard deviation of 31.6 corresponds to a precision (inverse of the variance) of 0.001.

Finally the prior on the population specific precisions for the spawner-recruit process error is assigned a diffuse gamma distribution (Gelman et al. 1995).

$$(15) \quad \frac{1}{\sigma_j^2} \sim \text{gamma}(0.0001, 0.0001)$$

This results in 25 r_j , k_j , and σ_j parameters, as well as a , a_D , b , b_D , r_{SD} , k_{SD} and r_M for a total of 82 parameters. The full posterior distribution⁴ is proportional to the product of the two likelihoods for the spawner-recruit and watershed size data, the densities defining the distribution of the r_j and k_j parameters, and the priors:

$$(16)$$

⁴ The posterior distribution is the probability density function of the model parameters given the observed data, and is derived using Bayes formula (for example see Gelman et al. 1995).

$$P(\bar{r}, \bar{k}, \bar{\sigma}, r_M, r_{SD}, a, a_D, b, b_D, k_{SD} | data) \propto P(data | \bar{r}, \bar{k}, \bar{\sigma}) P(\bar{r} | r_M, r_{SD}) P(\bar{k} | a, a_D, b, b_D, k_{SD}) P(r_M) P(r_{SD}) \\ \times P(a) P(a_D) P(b) P(b_D) P(k_{SD}) P(\sigma)$$

Here we assume that the populations are exchangeable when conditioned on the watershed size. The likelihood for the spawner-recruit data is therefore simply the product of the individual population likelihoods.

The posterior probabilities of r and k for populations without data (the induced priors on r and k) can be easily calculated as

$$(17) P(r_I | data) = \int P(r_I | r_M, r_{SD}, data) P(r_M, r_{SD} | data) dr_M dr_{SD}$$

$$(18) P(k_I | data) = \int P(k_I | k_{SD}, data) P(k_{SD} | data) dk_{SD}.$$

Finally, given a watershed size and life-history type, we can calculate the induced prior for management parameters derived from the original parameters. For example, the induced prior for S_{MSY} is

$$(19) P(S_{MSY} | WS, LH, data) = \int P(S_{MSY} | WS, LH, r_I, k_I, data) P(r_I, k_I | data) dr_I dk_I.$$

The spawner-recruit only model

We also applied a standard spawner-recruit analysis to each population without the watershed information or common distribution of r 's. To speed computation we used the simpler parameterization:

$$(20) R_{i,j} = S_{i,j} \exp \left[r_j - \frac{S_{i,j}}{b_j} + w_{i,j} \right].$$

The parameter r_j is assumed to have a uniform prior.

$$(21) r_j \sim \text{uniform}(0.0001, 4)$$

The natural logarithm of b_j (S at maximum recruits), is assumed to have a uniform distribution between 0 and 17 (note, $\exp(17) > 24$ million).

$$(22) \log(b_j) \sim \text{uniform}(0, 17)$$

We used the same prior for precision as we used for the full hierarchical model described above.

These results are compared to the full hierarchical model to assess the degree to which the watershed size relationship and common distribution for r_j parameters affect the posterior distributions on the parameters of interest.

Monte Carlo Markov Chain (MCMC) analysis

We used Monte Carlo Markov Chain (MCMC) integration to estimate posterior distributions for the parameters of interest (e.g. Gelman et al. 1995). Briefly, this involves generating a large sample from the full posterior distribution, and then using this sample for inference about the parameters of interest. The WinBUGS (Spiegelhalter et al. 1999), R (R Development Core Team 2007), and R2WinBUGS (Sturtz et al. 2005) software environments were used. We used the two-step regression approach of Parken et al. (2006) to assign initial values, and ran the chain for 11 million iterations, with a 1 million iteration burn in and thinning to every 1000th draw. The resulting chains were analyzed for convergence by inspecting the parameter traces, autocorrelation plots, and plots of the parameters against each other to assess cross correlation. We also applied Geweke's (Geweke 1992), and Heidelberger and Welch's (Heidelberger and Welch 1981) convergence diagnostics as implemented in the R package CODA (Plummer et al. 2007).

Sensitivity to Prior Choice

While we attempted to use priors that were non-informative (i.e. let the data speak for themselves), or based on well established prior information (e.g. other data or previous analyses), we assessed posterior sensitivity to prior choice by, one at a time, exchanging each base prior with an alternate prior substantially different from the base prior (Table 2). If changing the prior for any parameter resulted in a large change in the posterior distributions of interest, this was noted in the results.

Model evaluation

We examined model fit at both levels of the hierarchical structure 1) the level describing the relationship between watershed size and equilibrium population size (equation 4), and 2) the level describing the relationship between spawners and recruits (equation 5). For the equilibrium – watershed size relationship we plotted the posterior distribution of the k 's against the watershed size and looked for patterns as in a standard regression (i.e. increasing variance, runs). Similarly for the spawner–recruit relationship (the Ricker model) we examined the residuals for patterns.

To check the performance of the modeling approach and compare it to the simple two-step regression approach of Parken et al. (2006), we simulated 1000 data sets and analyzed each of these with the two approaches. We evaluated their performance by calculating 80% S_{MSY} prediction intervals for populations without spawner-recruit data and comparing the coverage frequency to the true coverage probability (based on the parameters used to simulate the data).

For each of the 1000 simulations we used the following procedure:

Simulate spawner-recruit data for 25 populations by first generating a random set of 25 r , k , and σ values (based on distributions fit to the estimated values from the original data set), and then combining these values with the original watershed sizes, life history types, and spawner values to generate new simulated recruits.

Apply the full hierarchical model, and the two-step regression approach to the data.

Calculate 80% prediction intervals based on each of the two approaches for 100 hypothetical populations without spawner-recruit data where the watershed sizes and life history types are randomly generated from distributions fit to the watershed sizes and life history types from the original data set. This is simulating the process of making inference about S_{MSY} for populations without spawner-recruit data where we know the watershed size and life-history type. The prediction intervals for the full hierarchical model are high posterior density (HPD) intervals (for example see Gelman et al. 1995).

Estimate the true coverage probability for the two sets of 100 prediction intervals by generating r , k , and σ values (as in step 1), 1000 times for each of the 100 hypothetical populations without data, calculating the corresponding S_{MSY} values, and noting the proportion of the 1000 S_{MSY} values that fell in each of the 100 x 2 prediction intervals (i.e. an estimate of the coverage probabilities).

This process produces 1000 x 100, or 100,000 estimates of the coverage probabilities for the two methods. We calculate the median estimated coverage probability for the two approaches (full hierarchical model and two-step regression) as well as plotting histograms. These values and histograms are used to compare the two approaches and determine how they performed relative to the expected 80% coverage.

Results

The posterior distribution for the slope, b , of the relationship between watershed size and equilibrium has no observed probability to the left of 0, supporting the hypothesis that there is a positive relationship between the two quantities (Figure 2). In addition, the posteriors for both a_D and b_D are well to the right of zero suggesting that the relationship varies for the two life-history types. Using the medians of these distributions, the estimated relationship between equilibrium and watershed size is $E = 10.0WS^{0.97}$, and $E = 8.94WS^{0.69}$ for the ocean-type and spring type life histories respectively. The joint posterior distribution of r and k for a population with no spawner-recruit data (the induced prior) shows no sign of correlation. The induced prior for k is centred approximately at zero (as specified in the model). The induced prior for log-productivity, r , is centered on 1.7 with 95% of the probability falling between 1.2 and 2.2 (Figure 3). Thus, assuming the 25 Chinook salmon populations in this analysis are representative of West Coast Chinook salmon populations in general, in the absence of other population specific information we would assume the maximum productivity would fall between $\exp(1.2) = 3.3$ recruits per spawner (RPS) and $\exp(2.2) = 9$ RPS with 95% confidence, with a median value of approximately $\exp(1.7) = 5.5$ RPS.

To illustrate how these models can be applied to individual populations we calculated three different S_{MSY} posterior distributions for the Klukshu and Skagit populations (Figure 4). These are: 1) the posterior distribution based on the full hierarchical model, 2) the posterior distributions based on independent fits to the populations without including watershed size, and 3) the induced prior (equation 19), where only the population specific life-history and watershed size are used. The second and third distributions exclude population specific information about watershed size, and spawner-recruit data

respectively. In the Klukshu River, the spawner-recruit data precisely defines the equilibrium population size, and therefore has a strong influence on the posterior distribution of the full hierarchical model. For the Skagit, however, there is no spawner-recruit data close to the equilibrium population size, resulting in a very diffuse posterior distribution for the model with only spawner-recruit data. Therefore, the Skagit full hierarchical model posterior is much more influenced by the watershed size relationship. Looking at all of the 25 populations (Figure 5), there are several examples similar to the Skagit River, where the posterior distribution for S_{MSY} based on just the spawner-recruit data is very broad, increasing the influence of watershed size. This illustrates the advantage of incorporating watershed size into the analysis even when spawner-recruit data is available. In general the posterior distributions based on watershed size alone, and spawner-recruit data alone, tended to agree with a few exceptions like the Kitsumkalum, and Taku rivers. However, in all cases the 90% HPD intervals overlap.

We also compared prediction intervals generated from the full hierarchical model and the two-step regression approach (Parken et al. 2006), for four hypothetical watersheds with watershed sizes of 100, 1000, 10000, and 100000 Km² (Figure 6). We assumed that all populations were ocean-type and that there was no spawner-recruit data available. While the intervals overlapped substantially for all watershed sizes, the intervals for the hierarchical model were consistently narrower than those of the two-step regression approach, a result which is reinforced by the simulation results described below. The narrower intervals show that some shrinkage occurred towards the mean for the hierarchical model estimates.

MCMC Diagnostics

The MCMC chains appear to converge based on inspection (Figure 7a), autocorrelation statistics, and Geweke's, and Heidelberger and Welch's convergence statistics. The autocorrelation, lags 1 to 50, were between -0.05 and 0.05 for all parameter chains. With the exception of a and aD , cross-correlation between parameters was negligible (Figure 7b). While there is no guarantee based on these results that the chain did in fact converge to the posterior distribution, we are relatively confident that the chain converged because we carefully chose initial values that were likely to be close to the posterior mode and we ran the chain for over 10 million iterations. In addition, the simulation study produced S_{MSY} intervals with correct coverage frequency, although it was based on much shorter chains.

Sensitivity to Prior Choice

The posterior distributions of the model parameters showed very little sensitivity to the choice of priors (Figure 8). The model was run for each parameter with the alternate prior (Table 2) and the resulting posterior distributions were superimposed to look for sensitivity to prior choice. It is difficult to distinguish the different posterior distributions.

Model evaluation

There did not appear to be any patterns in the residuals for the equilibrium – watershed size relationship that would suggest departure from model assumptions of equal variance and independence (Figure 9). However, the spawner-recruit residuals for several of the populations showed signs of positive autocorrelation. To assess the potential impact of ignoring this in the model, we simulated 2000 sets of residuals for the 25 populations, half with autocorrelation and half without (parametric bootstrap). We then estimated r , E , and S_{MSY} , and compared the distributions with and without assumed autocorrelation. We found no appreciable differences in central tendencies and only moderate differences in variability for two of the populations. Based on these results and the fact that the time series were all relatively short (9 to 31 years with an average of 20 years) we did not attempt to model this autocorrelation. The results of the simulation study (described in the methods) showed that the full hierarchical model produced approximately correct HPD prediction intervals while the prediction intervals from the two-step regression approach tended to be slightly more conservative (Figure 10). The median coverage probabilities for the full hierarchical model and the two-step regression were 0.81 and 0.86 respectively. The higher accuracy of the prediction interval from two step regression approach than the hierarchical model was due, at least partially, to the wider prediction intervals produced by the two step regression over four orders of watershed sizes (Figure 6).

Discussion

Our analysis showed a strong relationship between watershed size and population specific parameters, as in Parken et al (2006). The full hierarchical model provides a straight forward approach to estimating management parameters for populations with little or no spawner-recruit data. By directly incorporating all of the data into a single hierarchical analysis, we accounted for population to population differences in parameter uncertainty, shared demographic information among populations, and provided a straight forward framework in which additional sources of information can easily be added. The validity of the results was supported by the simulation study in which both the full hierarchical model and the two-step regression approach were applied to data generated from a known model.

While life history based differences in equilibrium population size were supported by the hierarchical analysis, as Parken et. al. (2006) noted, the life history based differences might have been an artifact of the location since all the stream-type data (except the Columbia upriver spring population) are from Northern latitudes. Taylor (1990) indicated that Chinook salmon populations north of 56° N latitude are virtually all stream-type and that most ocean-type populations are from southern latitudes. As such, it may be possible to explain these watershed based differences as a function of latitude. While Parken et al. (2006) found that including life history type provided a better fit than latitude; with the current data it is difficult to determine which covariate is more biologically justified. If life history type is substantially influenced by environmental conditions (temperature in particular) as Brannon et al. (2004), for example, suggest, then from a predictive perspective there may be little difference between the two approaches. As with all observational studies, any inference about causality should be approached cautiously.

Parken et al. (2006) developed their two step regression approach in order to provide estimates for the many Chinook salmon populations that do not have spawner-recruit data and therefore no straight forward method of developing S_{MSY} targets. However, even for populations with spawner-recruit data, there can be serious concerns about the validity of the S_{MSY} estimates. For example, Kope (2006) used simulations to show that observation error combined with overfishing will likely lead to underestimates of S_{MSY} for Chinook salmon populations. Incorporating independent sources of informative data, such as watershed size in our case, is therefore advisable even when spawner-recruit data is available.

Hierarchical modeling provides a natural framework on which to add additional sources of information. For example, there are other watershed scale habitat variables that could explain variability in capacity (pool area for example, see Sharma and Hilborn 2001), and the model can be easily extended to include a time varying productivity parameter linked to environmental variables, as demonstrated by Mueter et al. (2005) and Pyper et al. (2005) for sockeye (*O. nerka*) and pink (*O. gorbuscha*) salmon. While collection and compilation of this type of data is difficult, it provides an exciting avenue for learning more about how the environment affects population dynamics which in turn will allow for more informed management.

While the flow of information between populations in the full hierarchical model will tend to provide more robust results that are less easily swayed by errant individual pieces of data, it is not a panacea. There are a number of problems that can lead to poor inference. First, the model assumes that the group of populations is representative of the larger population of interest. The 25 populations used for this analysis cover most of the geographic range of Chinook salmon populations, exhibit both stream and ocean life-history types, and inhabit a wide range of watershed sizes. However, the group of populations for which good quality spawner-recruit data was available was determined by the management history of these regions and is therefore not necessarily representative of west coast Chinook populations. Therefore, when using the model to infer demographic characteristics for other Chinook populations, interpretation of the results should include consideration of how these populations compare to the 25 populations of this analysis. For example, while examination of the 25 posteriors for the log productivity parameter, r , suggested that the constraint $r > 0$ did not effect the results, using these results to make predictions for a population where log productivity is thought to be close to or less than 0, would likely lead to an overoptimistic result. A second potential problem relates to the way the model combines the data across populations. One of the advantages of the hierarchical model is that it naturally weights the data from the different populations. However, this assumes that the uncertainty in the spawner-recruit

relationship is accurately captured by the model. Because spawner observation error is not accounted for in the model and likely varies considerably between populations, the relative weighting for the different populations may not always be optimal. Finally, interpreting the results requires an understanding of how the population estimates are affected by the hierarchical structure. The model shrinks the individual r and k values towards the mean (for all populations). While this reduces the mean square error of the estimates it also introduces systematic bias, especially for values far from the mean or for populations with uninformative spawner-recruit data. This should be understood when providing management advice.

Parken et al. (2006) provide convincing evidence that watershed size provides a good first estimate of S_{MSY} when Chinook salmon population data is not available. Their two-step regression approach is straight forward, easy to motivate, and requires few statistical assumptions. However, supplementing the spawner-recruit model with watershed size data in a Bayesian hierarchical analysis provides some additional opportunities. Variation in uncertainty across populations, due to varying quality and quantity of spawner-recruit data, is accounted for by weighting the different sources based on their uncertainty. The production parameter, r , can be modeled as a random effect, combining information across populations to improve the precision of the individual estimates. Watershed size can be regressed with a more biologically motivated parameter such as equilibrium population size. Inference for an individual population can include both sources of data (watershed size and spawner-recruit). And finally, the model provides a natural framework to incorporate additional environmental information as it becomes available. There is immense societal and monetary value to accurately manage the mixed-population fisheries, while considering the status of Chinook salmon populations along the west coasts of Canada and the United States. While substantial resources have been applied towards constructing spawner-recruit series to achieve this goal, spawner-recruit data are notoriously noisy, vary considerably in quality and quantity between populations, and are often unavailable for populations of Pacific salmon. It is therefore only logical that decisions be informed by methods such as hierarchical modeling that more fully exploit the available data.

References

- Brannon, E., Powell, M., Quinn, T., and Talbot, A. 2004. Population structure of Columbia River basin Chinook salmon and steelhead In *Reviews in Fisheries Science* Ed Robert Stickney. Taylor And Francis. 221 p.
- Chen, D. and Holtby, B. 2002. A regional meta-model for stock recruitment analysis using an empirical Bayesian Approach. *Can. J. Fish. Aquat. Sci.* 59:1503-1514.
- Fausch, K.D., C.L. Hawkes, and M.G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-213. Portland.
- Gelman A., Carlin JB, Stern HS, Rubin DB. 1995. Bayesian data analysis. Chapman & Hall, London, UK.
- Geweke, J. 1992. Evaluating the accuracy of sampling-based approaches to calculating posterior moments. In *Bayesian Statistics 4* (ed JM Bernardo, JO Berger, AP Dawid and AFM Smith). Clarendon Press, Oxford, UK.
- Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). P. 311-394. In C. Groot and L. Margolis [ed.]. *Pacific Salmon Life Histories*. UBC Press, Vancouver, B.C.
- Heidelberger, P. and Welch P. 1981. A spectral method for confidence interval generation and run length control in simulations. *Comm. ACM.* 24, 233-245
- Hilborn, R. and M. Liermann. 1998. Standing on the shoulders of giants: learning from experience. *Reviews in Fish Biology and Fisheries* 8:273-283
- Hilborn, R. 2001. Risk Analysis for salmon spawning reference levels. In E. Provost and G. Chaput [ed]. *Stock, recruitment and reference points: Assessment and management of Atlantic salmon*. INRA, Paris 2001.
- Horton, R.E. 1945. Erosional developments of streams and their drainage basins; hydrophysical approach to quantitative morphology. *Geological Society of America Bulletin* 56:275-370.
- Kope, R. 2006. Cumulative effects of multiple sources of bias in estimating spawner–recruit parameters with application to harvested stocks of Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Research* 82:101–110
- Leopold, L.B., and T. Maddock. 1953. The hydraulic geometry of stream channels and some physiographic implications. U.S. Geol. Surv. Prof. Paper 252.
- Leopold, L.B., M.G. Wolman, and J.P. Miller. 1992. *Fluvial Processes in Geomorphology*. Dover Publications Inc. Mineola, NY.
- Liermann, M. and Hilborn, R. 1997. Depensation in fish stocks: A hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* 54: 1976-1984.
- Minte-Vera, C. 2004. Meta-analysis of density-dependent somatic growth. Ph. D. Thesis. University of Washington, Seattle.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low populations sizes. *Can. J. Fish. Aquat. Sci.* 56: 2404-2419..
- Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. – *ICES Journal of Marine Science*, 58: 937-951.
- Myers, R.A., Mackenzie, B.R., Bowen, K.G., Barrowman, N.J. 2001. What is the carrying capacity of fish in the ocean? A meta analysis of population dynamics of North Atlantic cod. *Can. J. Fish. Aquat. Sci.* 58: 1464-1476.
- Mueter, F. J., B. J. Pyper, and R. M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of salmon in the Northeast Pacific Ocean at multiple lags. *Transactions of the American Fisheries Society* 134:105-119.
- Pacific Fishery Management Council (PFMC). 2003. Pacific coast salmon plan. Fishery management plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon and California as revised through Amendment 14. Pacific Fisheries Management Council, Portland OR. 78 p plus appendices.
- Pacific Salmon Commission [PSC]. 1999. PSC Joint Chinook Technical Committee Report. Maximum Sustainable Yield or Biology Based Escapement Goals for Selected Chinook Salmon Stocks used by the

- Pacific Salmon Commission's Chinook Technical Committee for Escapement Assessment. Volume 1. Pacific Salmon Commission, Vancouver British Columbia, Canada.
- PSC. 2004. Pacific Salmon Treaty including; Yukon River Agreement Revisions to December 2002, Memorandum of Understanding (1985), Exchanges of Notes – 1985, 1999 & 2002. Vancouver, B.C.
- Parken, C. K., R. E. McNicol, J.R. and Irvine. 2006. Habitat based methods to estimate escapement goals for Chinook salmon stocks in British Columbia, 2004. Canadian Science Advisory Secretariat Research Document 2006/083, Ottawa. Available: www.dfo-mpo.gc.ca/csas/csas/Publications/Pub_Index_e.htm.
- Pyper, B. J., F. J. Mueter, and R. M. Peterman. 2005. Across species comparisons of spatial scales of environmental effects on survival rates of Northeast Pacific salmon. *Transactions of the American Fisheries Society* 134:86-104.
- Plummer, M., N. Best, K. Cowles and K. Vines. 2007. coda: Output analysis and diagnostics for MCMC.
- R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. <http://www.R-project.org>
- Ricker, W.E. 1973. Critical statistics from two reproduction curves. *Journal of the Fisheries Research Board of Canada* 160:333-340.
- Rivet, E. and Prevost, E. 2002. Hierarchical Bayesian analysis of capture mark-recapture based data. *Can. J. Fish. Aquat. Sci.* 59: 1768-1784.
- Rodriguez-Iturbe, I., and A. Rinaldo. 1997. *Fractal River Basins Chance and Self-Organization*. Cambridge University Press. NY.
- Schnute, J.T. and Kronlund, A.R. 2002. Estimating salmon stock-recruit relationships from catch and escapement data. *Can. J. Fish. Aquat. Sci.* 59: 433-449.
- Sharma, R., and Hilborn, R. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. *Can. J. Fish. Aquat. Sci.* 58: 1453-1463.
- Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. *Am. Geophys. Union Trans.* 38:913-920.
- Sturtz, S., U. Ligges and A. Gelman. 2005. R2WinBUGS: A Package for Running WinBUGS from R. *Journal of Statistical Software.* 3:1-16
- Spiegelhalter, D. J., A. Thomas and N. G. Best. 1999. WinBUGS Version 1.2 User Manual. MRC Biostatistics Unit
- Taylor, E. B. 1990. Environmental correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *J. Fish Biol.* 37:1-17.

List of Figures

Figure 1: Illustrates the assumed linear relationship between watershed size and equilibrium for the two different life-history types. The k s represent the deviations from the relationship for the individual populations.

Figure 2: Posterior distributions of parameters used in Eq 4 (describing the relationship between the Equilibrium, and watershed size and life history type).

Figure 3: The joint posterior distribution of r and k for a population with no spawner-recruit data (i.e. the joint induced prior).

Figure 4: The data and posterior distributions for two populations. Plotted on the left are the spawner-recruit data and MLE fits (solid line), and replacement lines (dashed line). On the Right are the three posterior distributions corresponding to the full model, the model with only watershed size (for that population), and the model with only spawner-recruit data (for that stock).

Figure 5. The 90% high posterior density (HPD) intervals for all of the populations with spawner-recruit data. The top bar (light gray) is the HPD interval for the model with only watershed size data (for that stock), the middle bar (medium gray) is the HPD interval for the model with both watershed size and spawner-recruit data for each stock, and the lower bar (black) is the HPD interval for the model with just spawner-recruit data for that stock.

Figure 6: A comparison of estimates and prediction intervals for S_{MSY} based on the full hierarchical model (black), and the two-step approach (gray) described in Parken et al. (2006). Prediction intervals for the two approaches were calculated for populations with watershed sizes of 100, 1000, 10000, 100000, and ocean-type life history.

Figure 7a: The traces of four key parameters.

Figure 7b: Cross correlation plot for the main model parameters.

Figure 8: Superimposed posteriors for the eight runs where each of the eight priors was changed one at a time (Table 2). The eight posteriors are difficult to differentiate because they overlap almost completely.

Figure 9: Residuals for the relationship between log equilibrium and log watershed size.

Figure 10: Coverage distributions of the spawner-recruit data in comparison with the prediction intervals. The vertical dashed line corresponds to the median coverage.

Table 1: Chinook salmon populations used in the analysis with life-history type^A, watershed size, latitude, number of years of spawner-recruit data, contrast ($\max(S)/\min(S)$), the maximum likelihood estimate (MLE) for S_{MSY} , and the S_{MSY} posterior median for the full hierarchical model. The spawner-recruit and watershed size data is from Parken et al. (2006) (with some minor updates).

Population	Life history type ^A	Watershed size (Km ²)	Latitude	Years	Contrast	S_{MSY} MLE	S_{MSY} Posterior median
Chena	S	4515	64.8	10	5	3508	4570
Salcha	S	5620	64.5	9	6	3875	4855
Klukshu River	S	260	60.1	16	3	890	957
Situk River	O	176	59.4	18	5	586	890
Taku River	S	15539	58.4	19	5	25460	21181
King Salmon River	S	93	58.0	21	6	136	236
Andrew Creek	S	126	56.7	24	7	626	668
Stikine	S	15337	56.6	22	9	15340	13983
Unuk River	S	2213	56.1	22	4	3630	3467
Chickamin	S	1696	55.8	22	7	1930	2181
Blossom River	S	176	55.4	22	25	737	731
Keta River	S	192	55.3	22	8	905	844
Kitsumkalum	S	2255	54.5	14	4	7826	7107
Harrison	O	7611	49.2	15	8	57919	52939
Cowichan	O	1227	48.8	19	8	3744	6045
Skagit	O	4198	48.4	28	5	54723	27271
Quillayute	O	1313	47.9	11	5	4289	5863
Queets	O	1164	47.5	18	5	3691	4004
Humptulips	O	635	47.0	18	19	3535	4699
Chehalis	O	4390	47.0	20	19	9451	18533
Lewis R. Falls	O	816	45.9	28	6	5791	6318
Nehalem	O	1728	45.7	25	13	7108	7818
U. Columbia-Sp.	S	114434	45.6	31	8	49044	52558
Siletz	O	523	44.9	25	10	3455	3878
Siuslaw	S	2010	44.0	27	47	13918	13202

^A O = ocean-type; S = stream-type

Table 2: Base priors used in the full hierarchical model, and alternate priors used to assess the sensitivity of the results to prior choice. Normal distributions are expressed using both standard deviation (sd) and precision (prec = $1/\text{sd}^2$). Here the gamma distribution is parameterized with the shape and rate parameter.

parameter	Base prior	Alternate prior
r_M	Normal(0.6, sd=0.45 or prec=5)	Normal(0, sd=0.71 or prec=2)
r_{SD}	Uniform(0,100)	Uniform(0,20)
k_{SD}	Uniform(0,100)	Uniform(0,20)
a	Normal(10, sd=31.6 or prec=0.001)	Normal(7, sd=31.6 or prec=0.001)
aD	Normal(0, sd=31.6 or prec=0.001)	Normal(0, sd=10 or prec=0.01)
b	Normal(0, sd=31.6 or prec=0.001)	Normal(0, sd=10 or prec=0.01)
bD	Normal(0, sd=31.6 or prec=0.001)	Normal(0, sd=10 or prec=0.01)
$1/\sigma^2$	Gamma(0.001,0.001)	Gamma(0.0001,0.0001)

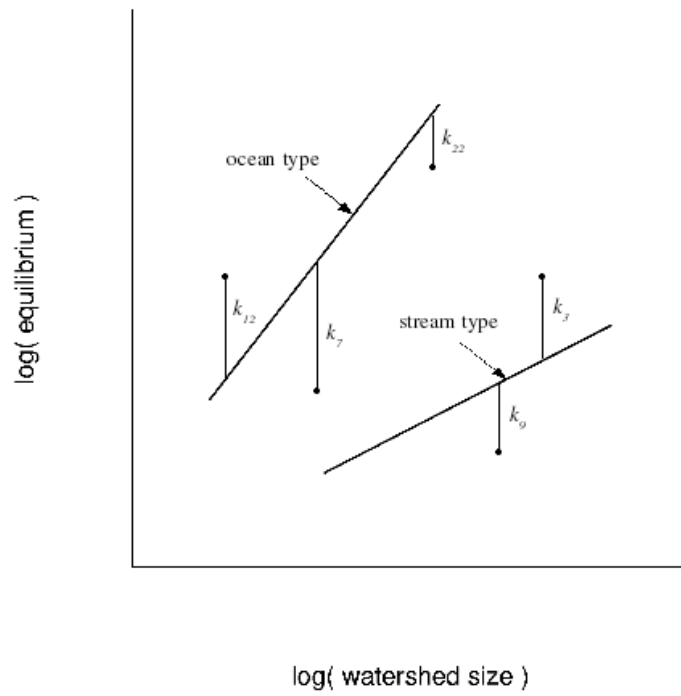


Figure 1: Illustrates the assumed linear relationship between accessible watershed area and equilibrium for the two different life-history types. The k s represent the deviations from the relationship for the individual stocks.

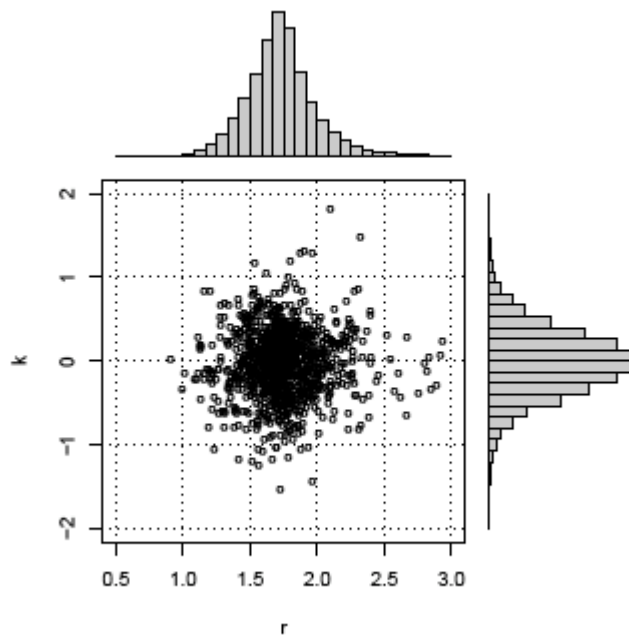


Figure 2: The joint posterior distribution of r and k for a population with no spawner-recruit data (i.e. the joint induced prior).

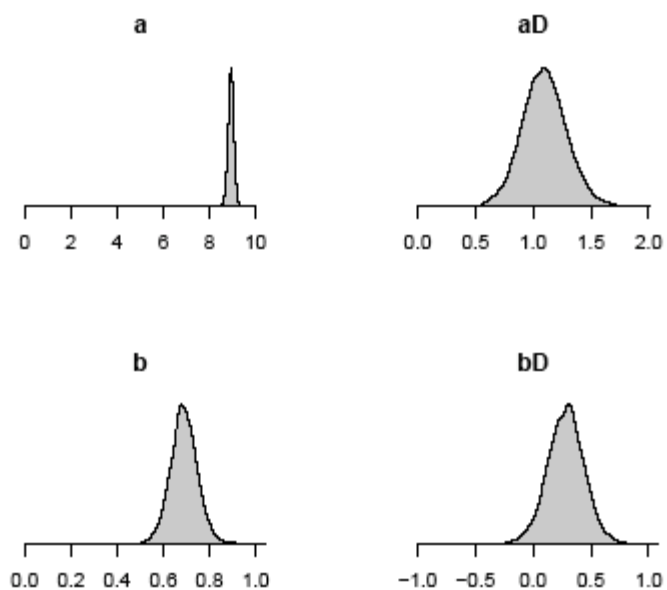


Figure 3: Posterior distributions of parameters used in Eq 4 (describing the relationship between the Equilibrium, and accessible watershed size and life history type).

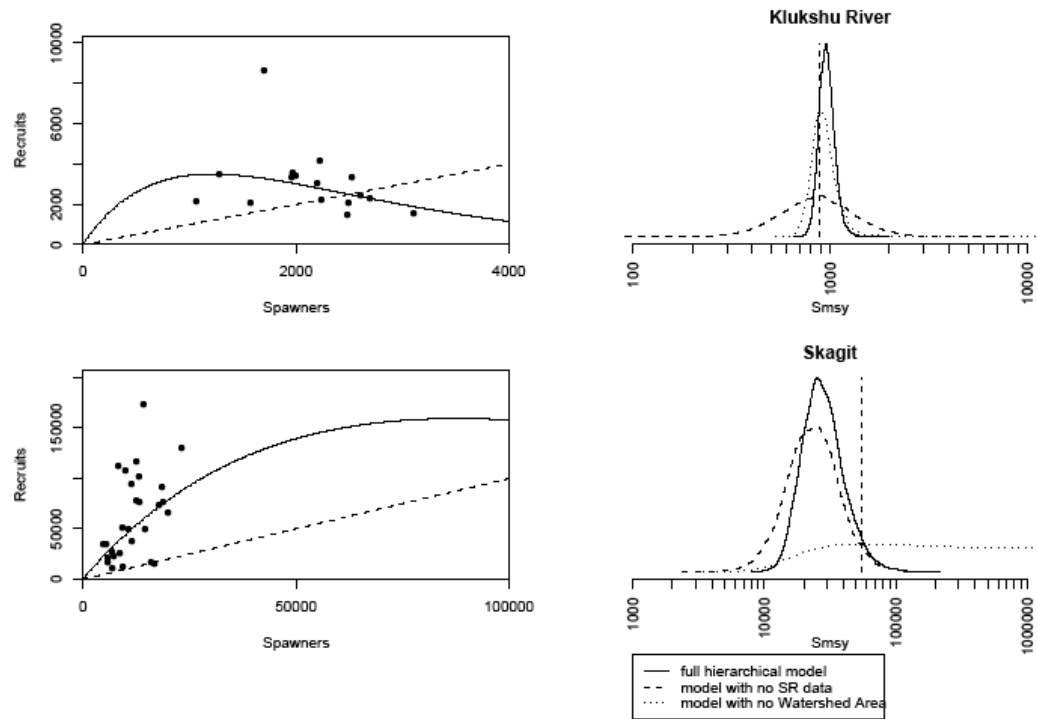


Figure 4: The data and posterior distributions for two stocks. Plotted on the left are the spawner-recruit data and MLE fits (solid line), and replacement lines (dashed line). On the Right are the three posterior distributions corresponding to the full model, the model with only watershed area (for that stock), and the model with only spawner-recruit data (for that stock).

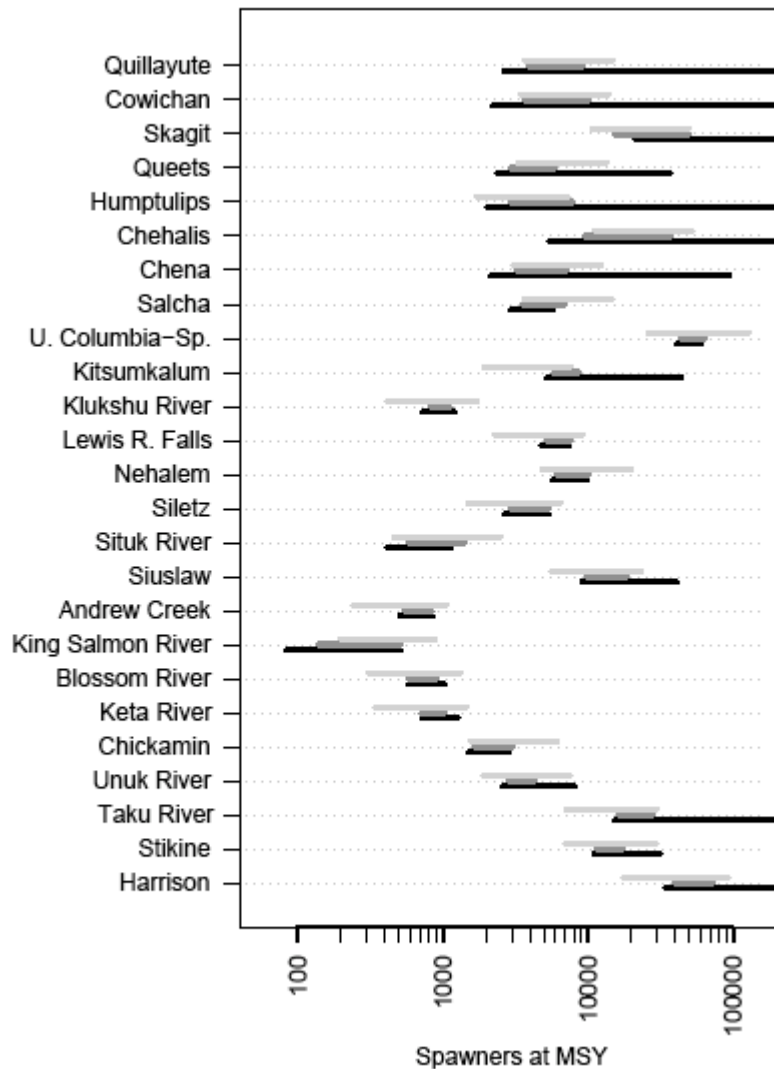


Figure 5. High posterior density (HPD) intervals for all of the stocks with spawner-recruit data. The top bar (light gray) is the HPD interval for the model with only watershed area data (for that stock), the middle bar (medium gray) is the HPD interval for the model with both watershed area and spawner-recruit data for each stock, and the lower bar (black) is the HPD interval for the model with just spawner-recruit data for that stock.

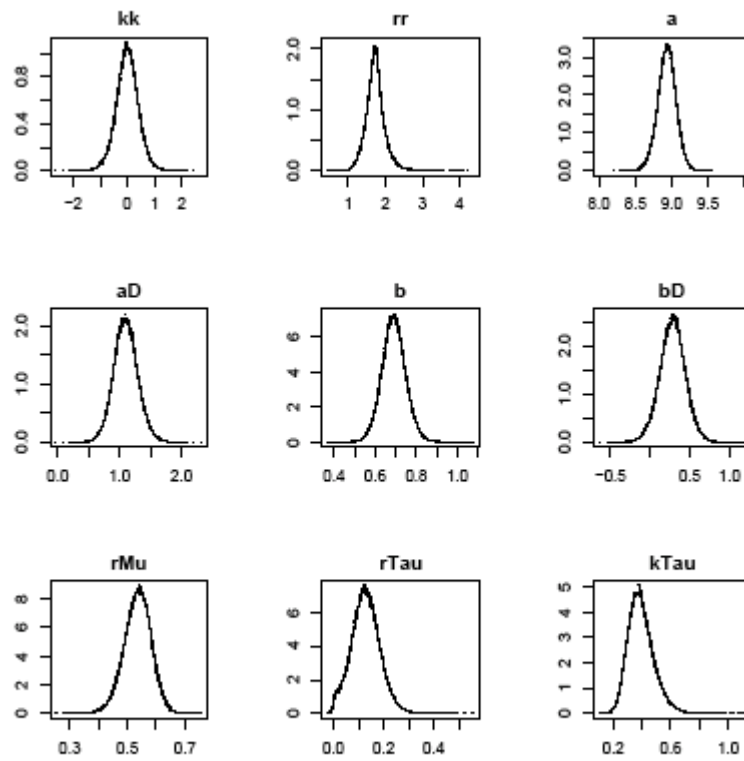


Figure 6: Superimposed posteriors for the eight runs where each of the eight priors were changed one at a time (Table 2). The 8 posteriors are difficult to differentiate because they overlap almost completely.

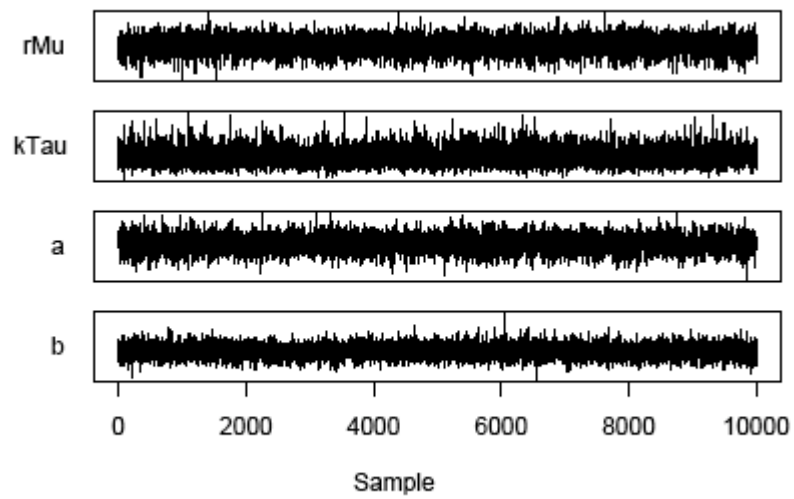


Figure 7a: The traces of four key parameters.

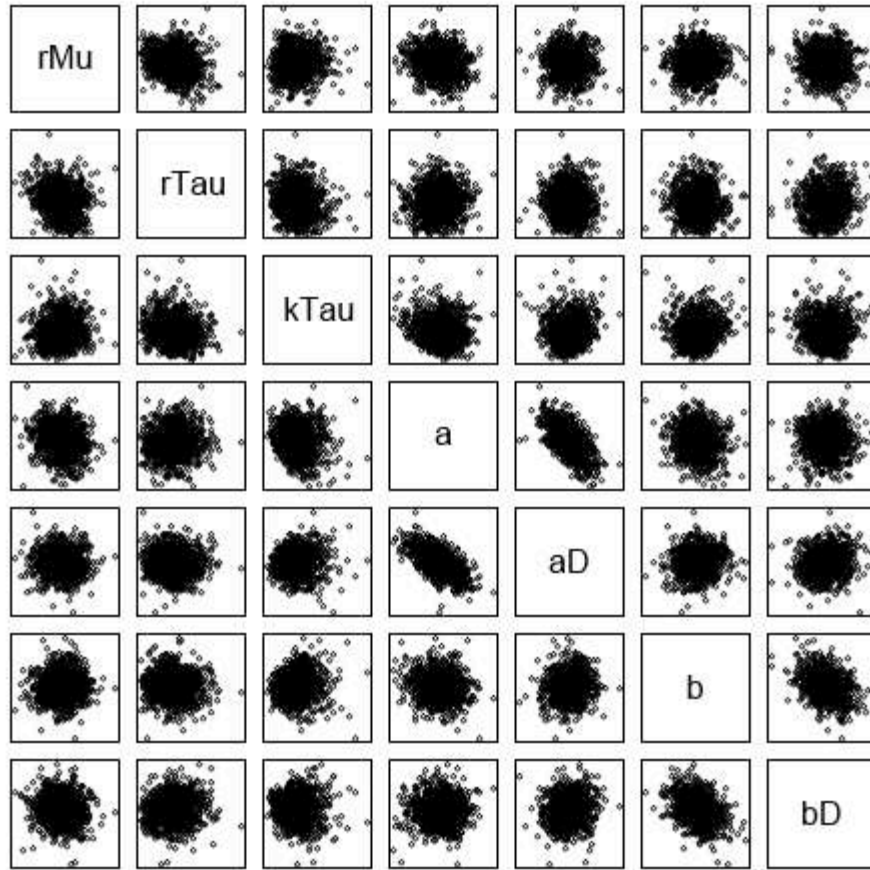


Figure 7b: Cross correlation plot for the main model parameters.

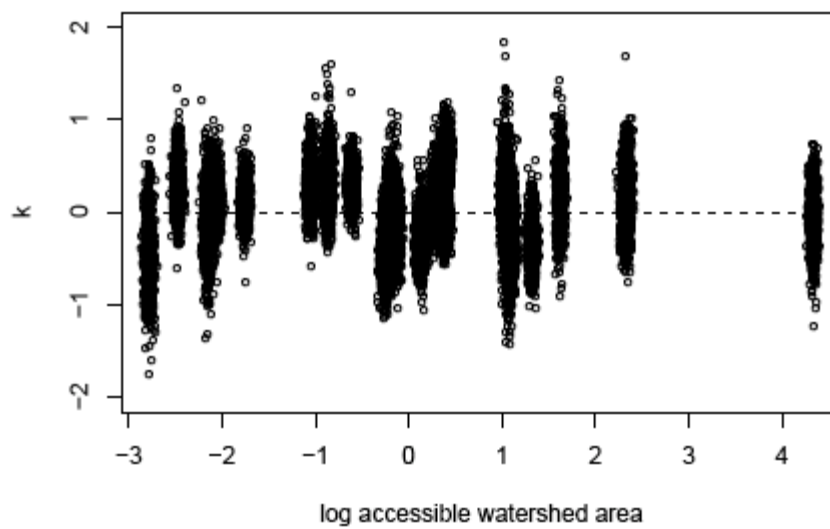


Figure 8: Residuals for the relationship between log equilibrium and log accessible watershed size.

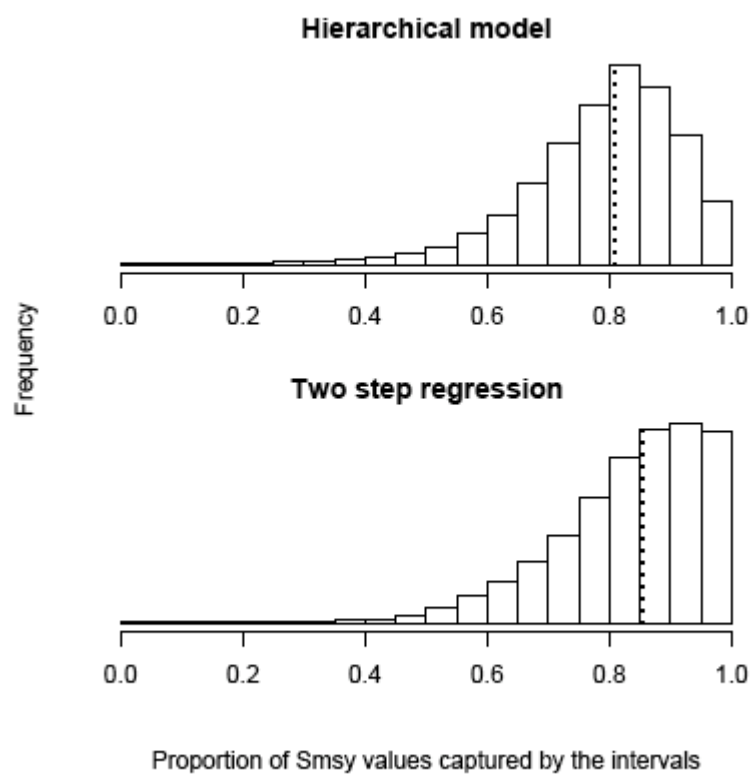


Figure 9: Coverage distributions of the spawner-recruit data in comparison with the prediction intervals. The vertical dashed line corresponds to the median coverage.

BIBLIOGRAPHY

- Agostini, V. N., Francis, R.C., Hollowed, A. B. , Pierce, S. D. , Wilson, C. and Hendrix, A. N. 2006. The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current System. Can. J. Fish. Aquat. Sci. 63:2648-2659.
- Akaiki, H. 1992. Information theory and an extension of the maximum likelihood principle. In Kotz, S. and Johnson, N. [ed]. Breakthroughs in Statistics. pp 610-624. Springer Verlag, New York.
- Aro, K.V. 1972. Recoveries of salmon tagged offshore in the North Pacific Ocean by Japan and the United States in 1970 and 1971, and additional recoveries from earlier taggings by Canada, Japan and the United States. Fish Res. Board Can. MS Rep. Ser. 1186:31 p
- Aro, K.V. 1973. Recoveries of salmon tagged offshore in the North Pacific Ocean by Japan and the United States in 1972 and 1973, and additional recoveries from earlier taggings by Canada, Japan and the United States. Fish Res. Board Can. MS Rep. Ser. 1328:20 p
- Bakun, A. 1996. Patterns in the Ocean. California Sea Grant. 323 pp.
- Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–71. U.S. Department of Commerce, NOAA Technical Report NMFS-SSRF-671.
- Beamish, R.J. and Neville, C. M.. 1995. Pacific salmon and Pacific herring mortalities in the Fraser River plume caused by river lamprey (*Lampetra ayresi*). Can. J. Fish. Aquat. Sci. 52:644-650.
- Beamish, R., Schnute, J. T., Cass, A., Neville, C. and Sweeting, R. 2004. The influence of climate on the stock and recruitment of pink and sockeye salmon from the Fraser River, British Columbia, Canada. Trans. Am. Fish. Soc. 133: 1396-1412.
- Beamish, R.J, Thompson, B. L. and McFarlane, G. A. 1992. Spiny dogfish predation on juvenile Chinook and coho salmon and the potential effects on hatchery-produced salmon. Trans. Am Fish Soc. 121: 444-455.

- Bradford, M., Taylor, G. and Allen, J. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Trans. Am. Fish. Soc. 126 :59-64.
- Brannon, E., Powell, M., Quinn, T. and Talbot, A. 2004. Population Structure of Columbia River Basin Chinook Salmon and Steelhead. In Reviews in Fisheries Science, Ed Robert Stickney. Taylor And Francis. 232 pp.
- Brown, D. 2005. Salmon Wars: The battle of the west coast salmon fishery. Harbour Publishing. Madeira Park, BC. 408 p.
- Clark, W.G. 2003. A Model for the world: 80 years of model development and application at the International Pacific Halibut Commission. Natural Res. Modeling 16: 491-503.
- Clarke, W.C., Withler, R.E., and Shelbourn, J.E. 1994. Inheritance of smolting phenotypes in backcrosses of hybrid stream type x ocean-type chinook salmon (*Oncorhynchus tshawytscha*). Estuaries 17(1A): 13-25.
- Clarke, W.C., Withler, R.E., and Shelbourn, J.E. 1992. Genetic control of juvenile life history pattern in chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 49: 2300-2306.
- Cormack, R. and Skalski, J. 1992. Analysis of coded wire tag returns from commercial catches. Can. J. Fish. Aquat. Sci. 49: 1816-1825.
- Coronado, C. and Hilborn, R. 1998. Spatial and temporal factors affecting survival in coho salmon (*O. kisutch*) in the Pacific northwest. Can. J. Fish. Aquat. Sci. 55: 2067-2077.
- Dawley, E. M., Ledgerwood, R. D., Blahm, T. H., Sims, C. W., Durkin, J. T., Kirn, R. A., Rankis, A. E., Monan, G. E., and Ossiander, F. J. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Report 81-102 to Bonneville Power Administration, Portland.
- Deriso, R.B. and Parma, A.M. 1987. Dynamics of Age and Size for a Stochastic Population Model. Can. J. Fish. Aquat. Sci. 45: 1054 1068.

- Deriso, R.B., Maunder, M. N., and Skalski, J.R. 2007. Variance estimation in integrated assessment models and its importance for hypothesis testing. *Can. J. Fish. Aquat. Sci.* 64: 187-197.
- Deriso, R.B., Quinn II, T.J., and Neal, P.R. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* 42: 815-824.
- Evenson, D.F., Hatch, D.R., Talbot, A.J. 2002. Hatchery Contribution to a Natural Population of Fall Chinook in the Hanford Reach of the Columbia River, WA. *In* E. Brannon and D. McKinlay (Eds). *Hatchery Reform: The Science and the Practice* (pp 93-105). International Congress on the Biology of Fish. UBC, Vancouver, CA.
- Food and Agriculture Organization (FAO). 1996. Precautionary Approach to Capture Fisheries: Part 1. Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Rome, 1996.
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S. and Balcomb, K. C. I. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76:1456-1471.
- Fournier D.A.. 2000. *An introduction to AD Model Builder version 4 for use in nonlinear modeling and statistics*. Otter Research Ltd., Sidney, BC, Canada.
- Fournier, D. and Archibald, C.P. 1982. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* 39: 1195-1207.
- Field, J.C., Francis, R.C., and Aydin, K. 2006. Top down modeling and bottom up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Prog. in Oceanography*:68-238-270.
- Francis, R.C., Hare, S.R., Hollowed, A.B, Wooster, W.S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr*: 7: 1-21.
- Francis, R.C., Little, J.E., and Bloeser, J. 2008. Matching Spatial Scales of Ecology, Economy and Management for Groundfish of the U.S. West Coast Marine

- Ecosystem: A State of the Science Review. A report to the Lenfest Ocean Program at the Pew Charitable Trust 131 p.
- Francis, R.C. and Hare, S.R. 1994. Decadal-scale regime shifts in the large marine ecosystems of the Northeast Pacific: A case for historical science. *Fisheries and Oceanography* 3: 279-291.
- Francis, R.C. and Sibley, T.H. 1991. Climate change and fisheries: What are the real issues? *Northwest Envir. J.* 7:295-307.
- Gelman A., Carlin, J. B., Stern, H. S., and Rubin, D. B. 1995. Bayesian data analysis. Chapman & Hall, London, UK.
- Good, T.P., Waples, R.S. and Adams, P. (eds.). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-66, 598 p.
- Gordon, A. D. 1981. Classification: Methods for the exploratory analysis of multivariate data. London. Chapman & Hall. 193pp.
- Grantham, B.A. Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenco, J. and Menge, B.A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429: 749-753.
- Green, P. and McDonald, P. 1987. Analysis of mark-recapture data from hatchery-raised salmon using log-linear models. *Can. J. Fish. Aquat. Sci.* 44: 316-326.
- Greene, C. and Beechie, T. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 61: 590-602.
- Gross, M. R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14-25.
- Hare, S. R., Mantua, N. J., and Francis, R. C. 1999. Inverse production regimes: Alaskan and West Coast Salmon. *Fisheries*, 24, 6–14.
- Hare, S. R., and Francis, R. C. 1995. Climate change and Salmon production in the Northeast Pacific Ocean. In R. J. Beamish (Ed.), *Ocean climate and northern*

- fish populations (pp. 357–372). Canadian Special Publication of Fisheries and Aquatic Science, 121.
- Harris, M. 1999. Lament for an Ocean: The collapse of the Atlantic Cod Fishery: A True Crime Story. McClelland and Stewart Inc. 389 pp.
- Hartt, A.C. 1966. Migrations of salmon in the North Pacific Ocean and Bering Sea as determined by seining and tagging, 1959-1960. Int. North Pac. Fish. Comm. Bull. 191:141 p
- Hartt, A.C. and Dell, M.B. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. Int. N. Pac. Fish. Comm. Bull. 46:1-105.
- Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*) In Pacific Salmon Life Histories Ed. Groot, C. and Margolis, L. 1991. UBC, Vancouver, Ca.
- Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type Chinook salmon, *Oncorhynchus tshawytscha*. Can. Field-Nat. 97:427-433.
- Healey, M. C. and Groot, C. 1987. Marine migration and orientation of ocean-type Chinook and sockeye salmon. Am. Fish. Soc. Symp. 1:298-312.
- Hickey, B. M. 1998. Coastal oceanography of western North America from the tip of Baja California to Vancouver island. in A. R. Robinson and K. H. Brink, editors. *The sea. Vol. 11, the global coastal ocean*. Wiley, New York; Chichester.
- Hickey, B.M. 1989. Patterns and processes of shelf and slope circulation. Pp. 41-115 in *Coastal Oceanography of Washington and Oregon*, M. R. Landry and B. M. Hickey (eds.), Elsevier Science, Amsterdam, The Netherlands.
- Hickey, B.M. 1978. The California Current System-hypothesis and facts. Prog Oceanog. 8: 191-279.
- Hilborn, R. 1992. Current and Future Trends in Fisheries Stock Assessment and Management. S. African J. Mar. Sci. 12: 975-988.
- Hilborn, R., Maunder, M. , Parma, A., Ernst, B., Payne, J., and Starr, P. 2003. Coleraine: A Generalized Age structured stock assessment model. User's

- Manual Version 2.0. School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2002. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Science* 100: 6564-6568.
- Hilborn, R and Mangel, M.1997.*The Ecological Detective*. Princeton University Press. 315 pp.
- Holling, C.S. 2001. Understanding the complexity of economic, ecological and social systems. *Ecosystems* 4:390-405.
- Hollowed, A., Hare, S.R., and Wooster, W.S. 2001. Pacific basin climate variability and patterns of northeast Pacific marine fish production. *Progress In Oceanography*. Vol 49: 257-282.
- Hunn, E.S. 1990. Nch'i-Wana, "the big river": Mid-Columbia Indians and their land. University of Washington Press. 378 p.
- Johnson, J.K. 1990. Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. *Am. Fish. Soc. Symp.* 7. 782-816.
- Johnson, S. W., J. F. Thedinga, and K V. Koski. 1992. Life history of juvenile ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the Situk River, Alaska. *Can. J. Fish. Aquat. Sci.* 49:2621-2629.
- Kallio-Nyberg, I. and M.-L. Koljonen. 1999. Sea migration patterns in the Atlantic salmon: a comparative study of two stocks and their hybrids. *Boreal Environment Research* 4: 163-174.
- Kallio-Nyberg, I., M.-L. Koljonen, and I. Saloniemi. 2000. Effect of maternal and paternal line on spatial and temporal marine distribution in Atlantic salmon. *Animal Behaviour* 60: 377-384.
- Kallio-Nyberg, I., H. Peltonen, and H. Rita. 1999. Effects of stock-specific and environmental factors on the feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 853-861.

- Kondo, H., Hirano, Y., Nakayama, N., and Miyake, M. 1965. Offshore distribution and migration of Pacific salmon (genus *Oncorhynchus*) based on tagging studies (1958-1961). Int. North Pac. Fish. Comm. Bull. 17:213 p
- Koslow, J.A., Hobday, A.J., and Boehlert, G.W. 2002. Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. Fish Oceanogr. 11:65-77
- Landry, M.R., Postel, J.R., Peterson, W.K. and Newman, J. 1989 Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. Pp. 1–40 in *Coastal Oceanography of Washington and Oregon*, M. Landry and B. M. Hickey (eds.), Elsevier, Amsterdam.
- Lapi, L. Hamer, M. and Johnson, B. 1990. Data organization and coding for a coastwide mark-recovery data system. Am. Fish. Soc. Symp. 7. 720-724.
- Lawson, P., Logerwell, L., Mantua, N. Francis, R. and Agostini, V. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 61: 360-373.
- Ledgerwood, R. D., Thrower, F. P. and Dawley, E. M. 1991. Diel sampling of migratory juvenile salmonids in the Columbia River estuary. Fishery Bulletin 89:69-78.
- Lee, K. N. 1993. Compass and gyroscope: Integrating science and politics for the environment. Island Press, Washington DC. 243 p.
- Lessard, R. B., Hilborn, R., and Chasco, B. E. 2008. Escapement goal analysis and stock reconstruction of sockeye salmon populations (*Oncorhynchus nerka*) using life-history models. Can. J. Fish. Aquat. Sci. 65: 2269-2278.
- Levin, S.A. 1992. The problem of pattern and scale in Ecology. Ecology 73: 1943-1967.
- Lichatowich, J. 1999. Salmon without rivers- a history of the Pacific Salmon Crisis. Island Press. Washington DC. 317 p.

- Liermann, M., Sharma, R. and Parken, C. *in prep.* Supplementing Spawner-Recruit data with watershed size to improve estimation of S_{MSY} : A Bayesian hierarchical modeling approach.
- Logerwell, L., Mantua, N., Lawson, P., Francis, R. and Agostini, V. 2003. Tracking environmental process in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography Vol. 12 (6).
- Mackas, D., Denman, K.L., and Abbot, M.R. 1985. Plankton Patchiness: Biology in the Physical Vernacular. Bull. Of Mr. Sc. 37:652-674.
- Magnusson, A. 2002. Survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) released from hatcheries on the U.S. and Canadian Pacific coast 1972–1998, with respect to climate and habitat effects. Master Thesis. University of Washington, Seattle, WA.
- Major, R.L., J. Ito, S. Ito, and H. Godfrey. 1978. Distribution and origin of Chinook salmon (*Oncorhynchus tshawytscha*) in offshore waters of the North Pacific Ocean. Int. N. Pacific Fish. Comm. Bull. 38. 54 p.
- Mantua, N. J and R.C. Francis. 2004. Natural Climate Insurance for Pacific Northwest Salmon and Salmon Fisheries: Finding Our Way Through the Entangled Bank. American Fisheries Society Symposium 43.
- Mantua, N., S. Hare, Y. Zhang, J. Wallace, and R. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production, Bull. Am. Meteorol. Soc., 78: 1069–1079.
- McCallister M.K.; Starr P.J.; Restrepo V.R.; Kirkwood G.P. 1999. Formulating quantitative methods to evaluate fishery-management systems: what fishery processes should be modelled and what trade-offs should be made? ICES Journal of Marine Science. 56: 900-916.
- McDowall, R. M. 1988. Diadromy in Fishes. Timber Press, Portland, Oregon.
- McEvoy, A.F. 1996. Historical interdependence between ecology, production, and management in California fisheries. pp 45-53 in D. Bottom, G. Reeves and M.

- Brookes (eds.) Sustainability Issues for Resource Managers. USDA Forest Service Tech Rep. PNW-GTR-370.
- Methot, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. *In* Mathematical analysis of fish stock dynamics: reviews, evaluations, and current applications, E. F. Edwards and B. A. Megrey, eds. *Ap. Fish. Soc. Symp. Ser. 6*, pp. 66-82.
- Michielsens, C.G.J., McAllister, M.K., Kuikka, S., Pakarinen, T., Karlsson, L., Romakkaniemi, A., Perä, I., and Mäntyniemi, S. 2006. A Bayesian state-space mark-recapture model to estimate exploitation rates in mixed-stock fisheries. *Can. J. Fish. Aquat. Sci.* 63: 321-334.
- Morishima, G.S., and Henry, K.A. 2000. The History and Status of Pacific Northwest Chinook and Coho Salmon Ocean Fisheries and Prospects for Sustainability in *Ed Knudsen, E.E., Steward, C.R., MacDonald, D.D., Williams, J.E., and Resiser, D.W. Sustainable Fisheries Management: Pacific Salmon*. Pp 219-235. Lewis Publishers, New York.
- Mueter, F., Ware, D., and Peterman, R. 2002. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the northeast Pacific Ocean. *Fish. Oceanogr.* 11:4, 205-218.
- Myers, J. M., Kope, R. G., Bryant, G. J., Teel, D., Lierheimer, L. J., Wainwright, T. C., Grant, W. S., Waknitz, F. W., Neely, K., Lindley, S. T. and Waples, R. S. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon and California. National Marine Fisheries Service, NOAA Tech. Memo. NMFS-NWFSC-35. Seattle.
- Myers, K. W., K. Y. Aydin, R. V. Walker, S. Fowler, and M. L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956-1995. Univ. Washington School of Fisheries, Fish. Res. Inst. FRI-UW-9614. Seattle.

- Narum, S. R., Powell, M.S., and Talbot, A.J. 2004. A distinctive microsatellite locus that differentiates ocean-type from stream-type Chinook salmon in the interior Columbia River Basin. *Trans. of Am. Fish. Society* 133: 1051-1055
- National Marine Fisheries Service (NMFS). 1997. Review of the status of Chinook Salmon (*Oncorhynchus Tshawytscha*) from Washington, Oregon, California and Idaho under the US Endangered Species Act. Tech Memorandum NMFS-NWFSC-35.
- National Research Council (NRC). 1996. Upstream: Salmon and society in the Pacific Northwest. National academy Press. Washington DC.
- Nicholas, J. W. and Hankin, D. G. 1989. Chinook salmon populations in Oregon's coastal river basins. Oregon Dept. Fish Wildl., Portland. 359 p.
- Pacific Fishery Management Council (PFMC). 2008. Fisheries Regulation Assessment Model (FRAM) An Overview for Coho and Chinook v 3.0 . (Document prepared for the Council and its advisory entities.) Portland, Oregon.
- Pacific Fishery Management Council (PFMC). 2005. Stock Assessments and rebuilding Analysis for 2007-2008 Groundfish Fisheries. Agenda Item H.2 November 2005. Portland, OR.
- Pacific Salmon Commission (PSC). 2000. Pacific Salmon Treaty. Vancouver, BC.
- Parken, C., K. Candy, J. R., Irvine, J.R., and Beacham, T.D. 2008. Genetic and coded wire tag results combine to allow more precise management of a complex Chinook salmon aggregate. *North Am. Jr. of Fish Mgt.* 28: 328-340.
- Parken, C. K., R. E. McNicol, J.R. and Irvine. 2006. Habitat based methods to estimate escapement goals for Chinook salmon stocks in British Columbia, 2004. Canadian Science Advisory Secretariat Research Document 2006/083, Ottawa. Available: www.dfo-mpo.gc.ca/csas/csas/Publications/Pub_Index_e.htm.
- Pascual, M. A. and Quinn, T. P. 1994. Geographical patterns of straying of fall chinook salmon (*Oncorhynchus tshawytscha*) from Columbia River (U.S.A.) hatcheries. *Aquaculture and Fisheries Management* 25 (Suppl. 2): 17-30.
- Patterson, K., Cook, R., Darby, C., Gavaris, S., Kell, L., Lewy, P., Mesnil, B., Punt, A., Restrepo, V., Skagen, D.W., and Stefánsson, G. 2001. Estimating

- uncertainty in fish stock assessment and forecasting. *Fish and Fisheries* 2: 125-157.
- Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program. Seattle, WA.
- Peterman, R.M., Pyper, B.J. and MacGregor, B.W. 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 60 :809-824.
- Peterson, W.T. Hooff, R.C., Morgan, C.A., Hunter, K.L. Casillas, E. and Ferguson, J.W. 2006. Unpublished Manuscript. Ocean Conditions and Salmon Survival in the Northern California Current.
- Peterson, W. T. and Schwing, F.B. 2003. A New Climate Regime in Northeast Pacific Ecosystems. *Geophys. Res. Letters* 30: 6-1:6-4.
- Pielke, R.A. 2003. The Role of Models in Prediction for Decision. *In* Canham, C.D., Cole, J.J., and Lauenroth, W.K.(eds). *Models in Ecosystem Science*. Pp 111-135. Princeton University Press, New Jersey.
- Press, W.H., Flannery, B. P., Teukolsky, S. A. and Vetterling, W. T. 1988. *Numerical Recipes in C : The Art of Scientific Computing*. Second Edition. Cambridge University Press.
- Punt, A. and Hilborn, R. 1997. Fisheries Stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* 7: 35-63.
- Quinn, T. P. 2005. *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press, Seattle.
- Quinn, T. J. 2003. Ruminations on the development and future of population dynamics models in fisheries. *Nat. Res. Modelling* 16: 341-391.
- Quinn, T. P., Doctor, K. , Kendall, N. and Rich, Jr. H. B. 2009. Diadromy and the life history of sockeye salmon: nature, nurture, and the hand of man. *American Fisheries Society Symposium* 69: 23-42.
- Quinn, T. P. and Myers, K. W. 2004. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. *Reviews in Fish Biology and Fisheries* 14: 421-442.

- Quinn, T.P., Kinnison, M.T., and Unwin, M.J. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112/113: 493-513.
- R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. <http://www.R-project.org>
- Restrepo, V.R. and Powers, J.E. 1999. Precautionary control rules in US fisheries management: specification and management. *ICES Jr. of Mar. Sc.* 56: 846-852.
- Richards, L.J. and Maguire, J.J. 1998. Recent international agreements and the precautionary approach: new directions for fisheries management science. *Can J Fish Aquat Sci* 55:1545-1552.
- Roni, P. and Quinn, T.P. 1995. Geographic variation in size and age of North American Chinook salmon (*Oncorhynchus tshawytscha*). *North American Journal of Fisheries Management* 15: 325-345.
- Ryding, K. E., and Skalski, J.R. 1999a. Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*) *Can. J. Fish. Aquat. Sci.* 56: 2374-2384.
- Ryding, K. E., and Skalski, J.R.. 1999b. A multinomial model for estimating ocean survival from salmonid coded wire-tag data. Volume XII in the BPA Technical Report Series, the Design and Analysis of Salmonid Tagging Studies in the Columbia Basin. Technical report to Bonneville Power Administration, Portland, OR, Contract 96-BI-91572, Project 91-051-00, 174 p.
- Savereide, J.W. and Quinn, T.J. 2004. An age-structured assessment model for Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 61: 974-985.
- Scheuerell, M. D., R. Hilborn, M. H. Ruckelshaus, K. K. Bartz, K. M. Lagueux, A. D. Haas, and K. Rawson. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat relationships in conservation planning. *Can. J. Fish. Aquat. Sci.* 63:1596-1607.

- Scheuerell, M.D. and Williams, J.G. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon. *Fisheries Oceanography* 14: 448-457.
- Schnute, J.T. and Kronlund, A.R. 2002. Estimating salmon stock-recruit relationships from catch and escapement data. *Can. J. Fish. Aquat. Sci.* 59: 433-449.
- Schnute, J.T. and Richards, L.J. 1995. The influence of error on population estimates from catch-age models. *Can. J. Fish. Aquat. Sci.* 52: 2063-2077.
- Schwing, F.B., O'Farrell, M., Steger, J.M., and Baltz, K. 1996. Coastal Upwelling Indices West Coast of North America 1946-95. NOAA-TM-NMFS-SWFSC-231. PFEL, Pacific Grove, CA.
- Sharma, R., Morishima, G., Wang, Z., Talbot, A. and Gilbertson, L. 2006. An evaluation of the Clearwater River Supplemnetation Program in Western Washington. *Can. J. Fish. Aquat. Sci.* 63:423-437.
- Sharma, R., Cooper, A.B. and Hilborn, R. 2005. A quantitative framework for the analysis of habitat and hatchery practices on Pacific salmon. *Ecological Modeling*. 183: 231-250.
- Sharma, R. and Hilborn, R. 2001. Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. *Can. J. Fish. Aquat. Sci.* 58: 1453-1463.
- Smith, B.J. 2007. boa: Bayesian Output Analysis Program (BOA) for MCMC. R
- Smith, Tim D. 1994. *Scaling Fisheries : The Science of Measuring the Effects of Fishing, 1855-1955* (Cambridge Studies in Applied Ecology and Resource Management). Cambridge University Press. 392 pp.
- Smith, T.M. and Reynolds, R.W. 2004. Improved Extended reconstruction of SST (1854-1997). *Journal of Climate* 17: 2466-2477.
- Sullivan, P.M., Parma, A.M. and Clark, W.G. 1999. The Pacific Halibut Stock Assessment of 1997, *Int. Pac. Halibut Comm. Sci. Rep.* 79.
- Taylor, E. B. 1990a. Environmental correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *J. Fish Biol.* 37:1-17.

- Taylor, E. B. 1990b. Phenotypic correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha*. J. Anim. Ecol. 59:455-468.
- Taylor, E.B. 1989. Precocial male maturation in laboratory-reared populations of chinook salmon, *Oncorhynchus tshawytscha*. Can. J. Zool. 67: 1665-1669.
- Taylor, J.E. 2001. Seeking the entangled bank: ecologically and economically sustainable salmon recovery. Unpublished manuscript. Presentation to the NW Salmon Crisis Lecture Series, University of Washington, Seattle.
- Taylor, J.E. 1999. Making Salmon. An Environmental History of the Northwest Fisheries Crisis. University of Washington, Seattle, WA. 419 p.
- TC-Chinook (08)-1. 2008. Pacific Salmon Commission Joint Chinook technical Committee Report. Annual Exploitation Rate Analysis and Model Calibration. PSC Office, Vancouver, BC.
- TC-Chinook (05)-2. 2005. Pacific Salmon Commission Joint Chinook technical Committee Report. Annual Exploitation Rate Analysis And Model Calibration. PSC Office, Vancouver, BC.
- Technical Advisory Committee (TAC). 2008. Technical Advisory Committee: US vs Oregon Minutes to Compact.
- Titmus, C. 2001. The Buddhas book of daily meditations: A year of wisdom, compassion and happiness. Three Rivers Press. 416 p.
- Trudel, M., Tucker, S., Morris, J.F.T., Higgs, D.A. and Welch, D.W. 2005. Indicators of Energetic Status in Juvenile Coho Salmon and Chinook Salmon. North Am. Jr. Fish Mgmt. 25: 374-390.
- US South (unpublished document). 2008. Adaptive (Precautionary) Management Approach For PST Chinook Fisheries.
- Wallace, J.M., and Gutzler, D.S. 1981. Teleconnections in the Geopotential Height Field during the Northern Hemisphere Winter. Monthly Weather Review 109: 784-812
- Waples, R. S., Teel, D. J. , Myers, J. M. and Marshall, A. R. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution. 58:386-403.

- Ware, D.M. and McFarlane, G.A. 1989. Fisheries production domains in the Northeast Pacific Ocean, p. 359-379 In R.J. Beamish and G.A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Ca. Spec. Publ. Fish. Aquat. Sci. 108.
- Ware, B. 1995. A century and a half of change in the climate of the NE Pacific. Fish. Oceanogr. 4: 267-277.
- Willette, T.M. 2001. Foraging behavior of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. Fish Oceanogr. 10 (Suppl.1):14-41.
- Wolter, K., and Timlin, M. S. 1998: Measuring the strength of ENSO events - how does 1997/98 rank? Weather 53: 315-324.
- Zar, J.H. 1995. Biostatistical Analysis. Prentice-Hall, Inc. New Jersey.

VITA

Rishi Sharma was born in Calcutta, India in 1972 to Jitendra Nath and Lakshmi Sharma. After attending High School in India, Rishi came to the United States for pursuing Higher Education on a scholarship to Mount Saint Mary's College, Maryland, in 1992. He graduated in 1995 with a Bachelors degree in Mathematics, and minors in Computer Science and Economics. After this, he went on to complete a Masters degree in Quantitative Ecology and Resource Management in 1998, from University of Washington, Seattle, with a focus on quantifying habitat effects on salmon productivity and capacity. While pursuing his Masters, he also completed a certification in Environmental Management from the Business School at University of Washington, during the same period. Between 1998 and 2004, he worked on natural resource issues on salmon in the Olympic Peninsula, Washington; and thereafter on the Columbia River (Washington, Oregon, Idaho and British Columbia). He earned his Doctor of Philosophy in Quantitative Ecology and Resource Management in 2009. Currently, he calls Portland, Oregon his home, continues to work on Columbia River salmon issues, and has a loving family (wife Richa and daughter Uma).