THE EFFECTS OF PHYSICAL AND BIOLOGICAL OCEANOGRAPHIC FACTORS

ON MARINE GROWTH OF FRASER RIVER SOCKEYE SALMON

by

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Thesis Abstract

The average size at maturity of sockeye salmon (*Oncorhynchus nerka*) in the northeast Pacific Ocean varies considerably from year to year. It is generally accepted that the majority of variation in size at maturity of sockeye salmon is due to variation in marine growth. However, few studies have shown strong linkages between specific oceanographic factors such as temperature, ocean currents, zooplankton production, and salmon abundance and the ultimate size of returning Fraser River sockeye. Using size at maturity data specific for ten Fraser River sockeye stocks I demonstrate that i.) the amount of variation in size at maturity that is due to environment is detectable in spawning ground length samples and ii.) mean size at maturity declined in almost every stock over the period 1954-1993. I also show that variation in marine growth is strongly associated with changes in sockeye salmon abundance and sea surface temperature in the northeast Pacific Ocean. Marine growth was not correlated to sockeye salmon abundance over the period 1959-1975; however the two were strongly associated during the period 1978-1992. Annual scale growth increments support the assumption that critical periods for density dependent growth occur during the time when Early Stuart sockeye salmon are present in the Central Gulf of Alaska. If present levels of salmon abundance are maintained during future warmer climates, major declines in size at maturity of sockeye salmon are likely to result due to the combined effects of high temperature, high abundance, and possibly a reduction in the standing crop of prey.

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INTRODUCTION

The objective of this study was to identify physical and biological factors that potentially affect the marine growth of Fraser River sockeye salmon (*Oncorhynchus nerka*). The thesis proceeds from exploratory analyses of size at maturity data and temporal trends to tests of specific hypotheses that relate marine growth to biological factors on short time scales. The results from this study represent a significant contribution to the knowledge of marine life history of sockeye salmon and may be applied to both international and domestic salmon management as well as future high seas salmon research.

Chapter 1 synthesizes spawning ground length data specific for ten Fraser River sockeye stocks to demonstrate that size at maturity has generally declined over the past 40 years for females in all stocks and for males from eight stocks. Independent of this temporal trend, size at maturity of both sexes in all stocks was smaller in years when sea surface temperatures were relatively warm. The long-term declines in size at maturity that were identified in Chapter 1 have coincided with dramatic increases in the biomass of salmon in the North Pacific Ocean. The observation that punctuated decreases in size at maturity occurred at the same time as an equally abrupt increase in salmon abundance led to the hypothesis that size at maturity of Fraser River sockeye is related to sockeye salmon density in the Gulf of Alaska. Tests of this hypothesis in Chapter 2 first involved reconstructing, by ocean age, a time series of minimum sockeye abundance in the Gulf of Alaska, 1954-1992, inclusive. Results from Chapter 2 demonstrate that size at maturity of

Fraser River sockeye is significantly reduced when abundance estimates of sockeye in the Gulf of Alaska are high. This result was not surprising based on other studies performed for different stocks and time periods. The most important finding in Chapter 2 is that during the period 1958-1975 marine growth of age 1.2 Fraser River sockeye was not related to population size. In contrast, Gulf of Alaska sockeye abundance from 1978-1992 explained a significantly large amount (33-81%) of variation in growth of Fraser River sockeye. The fact that the associations were not significant until abundance surpassed 100 million sockeye suggests that Bristol Bay and Fraser River stocks begin to overlap in ocean distribution beyond this level.

Another important result gleaned from Chapter 2 is that tests for density-dependent growth that involve lagging abundance time series often have low power of detecting differences among the various hypotheses due to the large number of comparisons that are required. Because the conclusions from Chapter 2 rely on this type of analysis it was important to test these hypotheses using data more specific to the task. This was done in Chapter 3 by analysis of annual marine scale growth increments from the Early Stuart stock. Using the time-series of *age-specific* ocean abundance developed in the previous chapter, Chapter 3 demonstrates that marine growth was only reduced when sockeye abundance was high during the second year of ocean life; supporting the results obtained in Chapter 2. This result provides more direct evidence that density dependent growth occurs while Early Stuart sockeye are in the offshore regions of the Gulf of Alaska.

Chapter 1

Changes in size at maturity of Fraser River sockeye salmon (1952-1993) and associations with temperature

Chapter Abstract

Unlike other Canadian Pacific salmon (*Oncorhynchus* spp.) long-term declines in the size at maturity of Fraser River sockeye salmon (*O. nerka*) have not been reported in past studies. Using data specific for ten Fraser River sockeye stocks, I demonstrate that size at maturity has generally declined over the past 42 years for females in all stocks and for males from eight stocks. Independent of this temporal trend, I found that size at maturity of both sexes in all stocks was smaller in years when sea surface temperatures were relatively warm. Slower growth in warmer years may be caused directly by increased metabolic demand, or indirectly by oceanic changes that influence food acquisition. I speculate that fitness of Fraser River sockeye will be reduced in the future if sea surface temperature increases and salmon abundance remains near present levels.

Introduction

The size at maturity of Pacific salmon (*Oncorhynchus* spp.) has been decreasing in recent decades (Ricker 1982; Ogura et al. 1991; Helle and Hoffman 1995; Ishida et al. 1995; Ricker 1995; Bigler et al 1996). From 1951 to 1975, average weight of adult pink *(O. gorbuscha)*, coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon caught in coastal waters of British Columbia decreased by 5-25% (Ricker 1995). This reduction in weight has slowed somewhat for chinook salmon in recent years, however declines in weight of pink and coho salmon have continued (Ricker 1995). Declines of similar magnitudes have been observed for adult chum salmon (*O. keta*) captured in Asian and Alaskan waters (Ogura et al. 1991; Helle and Hoffman 1995).

Sockeye salmon (*O. nerka*) are the second most abundant salmon species in British Columbia waters and the most economically valuable (Healey 1993). Unlike other species, long-term declines in length or weight at maturity of Canadian sockeye salmon have not been detected (Ricker 1995). One reason may be that mixed-stock commercial catch data obscure individual stock trends. Age and size at maturity of Fraser River sockeye salmon can vary substantially among breeding populations (stocks), a result of both oceanic and genetic factors (Healey 1986; Blackbourn 1987; Burgner 1991). My first objective was to determine if stock-specific time trends exist for Fraser River sockeye salmon, and whether some or all of them are consistent with those of other Pacific salmon. I focus on Fraser River sockeye stocks.

The ocean life history of Fraser River sockeye salmon is typical of most British Columbia sockeye. In their second year of life, they enter the ocean and move northward along the coast between April and June (Groot et al. 1989; Burgner 1991). During autumn they move offshore into the open waters of the Gulf of Alaska where they typically remain for two years before maturing and returning to the Fraser River in their fourth year (French et al. 1976). Considerable among-year variation in size at maturity exists within most sockeye stocks (Healey 1986). Because size at maturity is not related to smolt size (Henderson and Cass 1991), oceanic environmental conditions must be largely responsible for variation in size at maturity.

One of the main factors that may be responsible for interannual changes in size at maturity is temperature. Temperature affects growth directly through changes to metabolic costs (Nikolsky 1963; Furnell and Brett 1986; Jobling 1994; Hinch et al. 1995a), or indirectly through alteration of features that affect food acquisition (e.g. high seas distribution, population density, or migration routes; Ricker 1982; Laevestu 1984; Blackbourn 1987; Hsieh et al. 1991; Ishida et al 1995; Welch et al 1995). Hinch et al. (1995a, 1995b) found a negative relationship between sea surface temperature (SST) and size at maturity of Early Stuart sockeye salmon, a relatively small Fraser stock, however, these results may be too specific to a single stock to be generally applicable to Fraser River sockeye as a whole. Ricker (1982) found associations between SST and size of Fraser River sockeye salmon using mixed-stock commercial catch data collected from 1951 to 1974. However, SST regimes in the north Pacific Ocean have changed dramatically since 1974 (Hourston 1992) so SST-size correlations may also have changed; another problem is that mixed-stock data

may obscure or bias general species relationships between size at maturity and environmental factors if a small number of stocks have a dominant influence. My second objective was to examine the associations between SST and size at maturity of Fraser River sockeye salmon using stock-specific information.

Methods

Size at Maturity and SST Data

As a measure of size at maturity, I used the average lengths of sockeye salmon measured on the major spawning grounds in the Fraser River drainage (Figure 1.1). Although weight may be the best measure of size, large losses in weight occur during the up-river spawning migrations. Length changes very little during this migration so it is a better measure of size when dealing with spawning ground data. Average standard lengths (SL) of male and female age 1.2 sockeye from the spawning grounds of the Adams, Horsefly, Chilko, Early Stuart, Late Stuart, Raft, Late Nadina, Stellako, Birkenhead and Gates stocks were obtained from the archives of the Canadian Department of Fisheries and Oceans and the Pacific Salmon Commission for the years 1952-1993, inclusive (*Appendix 1-10*). The 1.2 age class accounts for up to 95% of Fraser River sockeye production in most years (Gable and Cox-Rogers 1993). The ages of spawning ground samples were determined by scales from 1952 to 1968 and by otoliths from 1968-1993 (Mike Lapointe, Pacific Salmon Commission, Vancouver, BC, pers. comm.).

TAKLA
LAKE

MIDDLE RIVER

TREMBLEUR
LAKE

TACHIE RIVER

STUART
LAKE

STUART R.

NADINA
RIVER

STELLAKO
RIVER

FRASER
LAKE

FRANCOIS LAKE

NECHAKO RIVER

FRASER

BRITISH

COLUMBIA

QUESNEL RIVER

QUESNEL
LAKE

RIVER

FRASER

HORSEFLY
RIVER

CHILKO RIVER

CHILCOTIN
RIVER

RAFT
RIVER

UPPER ADAMS
RIVER

CHILKO
LAKE

RIVER

ADAMS
LAKE

SHUSWAP
LAKE

ANDERSON
LAKE

BIRKENHEAD
RIVER

THOMPSON

RIVER

LILLOOET
LAKE

VANCOUVER

HARRISON
LAKE

ISLAND

CANADA

UNITED STATES

PACIFIC

OCEAN

N

0   100   200 km

7A

Figure 1.1. Map of Fraser River watershed and major sockeye salmon production systems.

There was considerable variations, in the number of fish sampled for length on the spawning grounds. To ensure that average SL values from low sample years did not unduly affect results of analyses, I excluded years in which I did not have at least 20 SL values to create a mean for each combination of stock and sex. This criterion was chosen because of a natural gap in the data; in most years numbers of samples were well in excess of 20 but in a few years samples were less than 10. After excluding some data, annual sample sizes ranged from 72 to > 500, depending on the stock (Table 1.1). A summary of stock- and sex-specific mean SL is presented in Table 1.2.

SST data came from the Comprehensive Ocean-Atmospheric Dataset which is described in Woodruff et al. (1987). Annual SST values were calculated by averaging the mean monthly SSTs for the region bounded by 142° to 146°W and 52° to 56°N. This geographic region was selected because it reflects the general area of the Gulf of Alaska that Fraser River sockeye inhabit (French et al. 1976). I used only January to July monthly temperatures because this period represents a portion of sockeye's life history that is half-way through their ocean residency when they are probably largely in the area where SST was estimated. In order to assess associations between SSTs encountered during their high-seas residency and SL at maturity, SST data were lagged by one year before carrying out any statistical analyses.

Table 1.1. Mean and range of sample sizes used to determine within-year standard lengths for each stock over the period 1952-1993, inclusive. Mean square error (MSE; cm) of length at maturity and minimum detectable difference (MDD; cm) in among-year comparisons are based on data from 1984-1993, inclusive.

Stock	Females				Males			
	mean	range	MSE	MDD	mean	range	MSE	MDD
Adams	142	20 - 513	4.11	0.68	108	35 - 337	4.72	0.83
Birkenhead	229	39 - 543	5.25	0.57	102	20 - 314	16.32	1.56
Chilko	253	32 - 587	3.98	0.49	113	35 - 226	5.42	0.83
Early Stuart	106	28 - 203	4.25	0.78	72	24 - 145	5.16	1.01
Gates	141	29 - 236	4.81	0.73	103	22 - 229	7.47	1.09
Horsefly	134	21 - 408	4.59	0.73	105	22 - 254	3.96	0.91
Late Nadina	135	20 - 290	4.17	0.71	93	20 - 228	4.63	0.89
Late Stuart	98	20 - 200	4.31	0.88	91	20 - 420	6.54	1.12
Raft	143	20 - 491	4.29	0.71	78	20 - 118	4.56	0.87
Stellako	164	79 - 314	5.08	0.67	118	34 - 299	5.42	0.83
Stock Average	155		4.48	0.70	98		6.42	0.99

Statistical Analyses

Long-term trends in SL were determined by regressing SL on year (PROC REG; SAS Institute 1988). Among-stock regressions were compared using analysis of covariance (ANCOVA) with stock as the class variable (PROC GLM; SAS Institute 1988). ANCOVA was carried out separately for males and females. The presence of a long-term trend in sea surface temperature (SST) was assessed by regressing SST on year.

In order to examine the influence of within-year variability in SL on among-year trends I performed within-stock power analyses on each sex and determined among-year minimum detectable differences (MDD) in mean SL (Zar 1984). MDD reflect an estimate of measurement error. Stock- and sex-specific MDD were calculated using the mean sample size from each spawning area (1952 - 1993, inclusive) and the mean square errors (MSE) of length at maturity (1984 - 1993, inclusive). Only mean SL and sample size were available from the data archives prior to 1984. I used the MDD as a check on the statistical significance of sex- and stock-specific SL versus year relationships.

I removed existing linear time trends before relationships between SL and SST were determined, in order to reduce spurious correlations caused by similar underlying time trends. Residuals from the stock- and sex-specific regressions of SL and SST on year were then regressed on each other to examine potential effects of temperature on size at maturity. To assess the generality of these relationships, among-stock regressions were compared using ANCOVA separately for each sex.

Results and Discussion

Time Trends

The slopes of the regressions of SL on year did not differ among stocks for females (ANCOVA; $P = 0.17$). This interaction term was then removed from the ANCOVA revealing a significant effect of year ($P<0.01$) and stock ($P<0.01$). In all stocks, female SL declined in a similar fashion over time (Figure 1.2; Table 1.2). Females from Adams,

Gates, and Raft stocks tended to have relatively large SL at maturity whereas Late Nadina had a relatively small SL at maturity. The slopes of the regressions of SL on year differed among stocks for males (ANCOVA; $P < 0.01$); the differences were attributable to Birkenhead and Gates stocks where size at maturity showed no time trend (Figure 1.3; Table 1.2). After removing these two stocks from the analysis, the remaining regression slopes did not differ among stocks (ANCOVA; $P = 0.17$). This interaction term was then removed from the ANCOVA revealing a significant effect of year ($P < 0.01$) and stock ($P < 0.01$). Among the remaining eight stocks, male SL declined similarly over time (Figure 1.3; Table 1.2). Males from Adams and Raft stocks tended to have relatively large SL at maturity whereas the Late Nadina stock had a relatively small SL at maturity. With the exception of males from Birkenhead and Gates stocks, mean length at maturity of Fraser River sockeye salmon declined over time (Figures 1.2 and 1.3; Table 1.2) and the 1990's produced the smallest Fraser River sockeye salmon out of the previous five decades for both males and females.

Figure 1.2. Mean standard lengths (cm) of female Fraser River sockeye stocks over a 42 year period. Missing data points were either not available or excluded due to low sample size (n < 20). Dashed line represents linear time trend fitted by least squares. Correlation coefficients are reported in Table 2.1.

Standard Length (cm)

Adam
Birkenhead
Chilko
Early Stuart
Gate
Horsefly
Late Nadin
Late Stuart
Raft
Stellako

12A
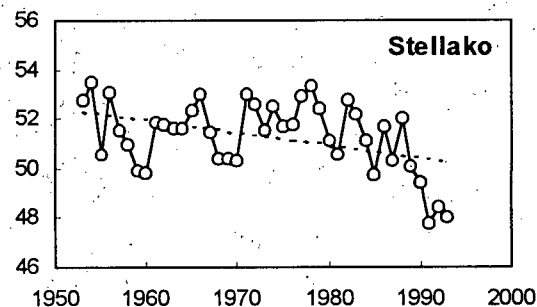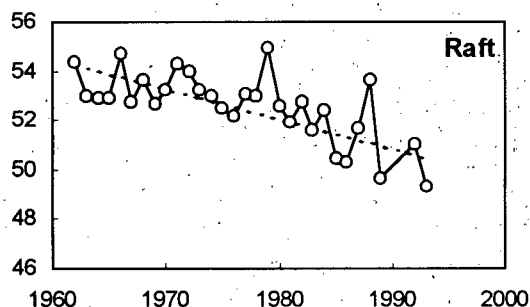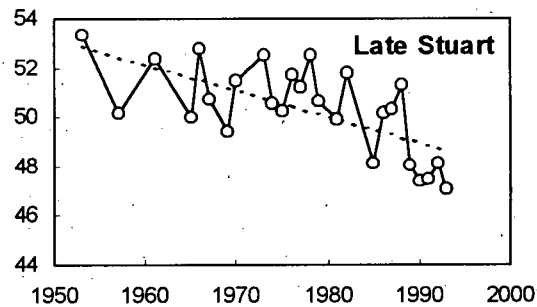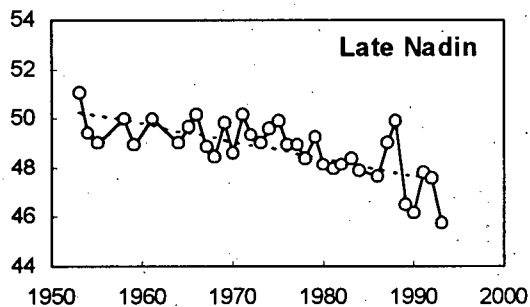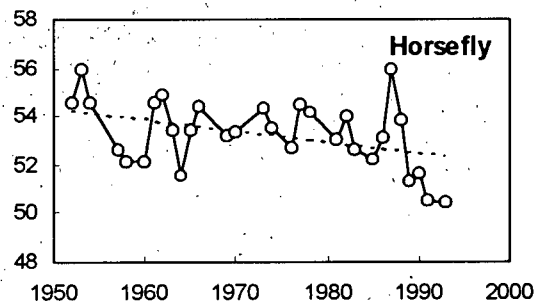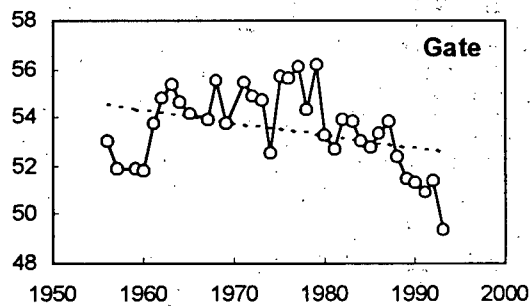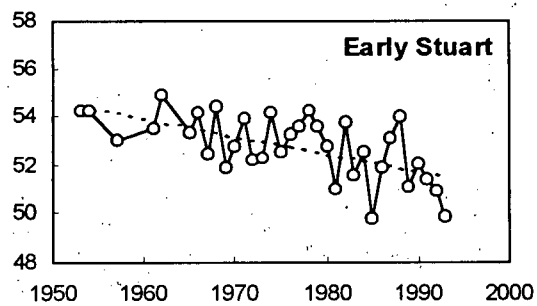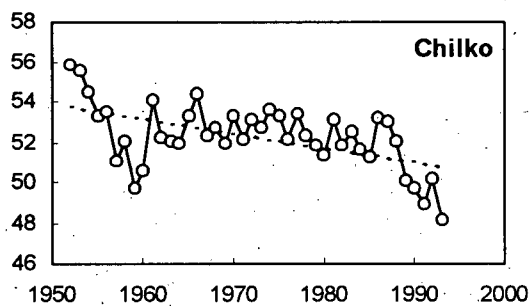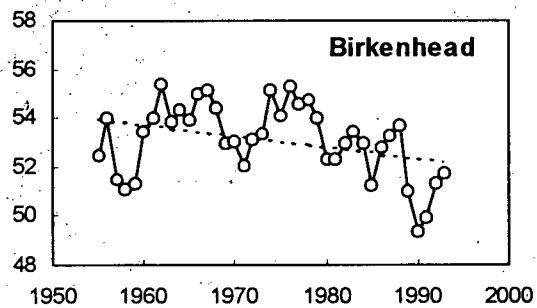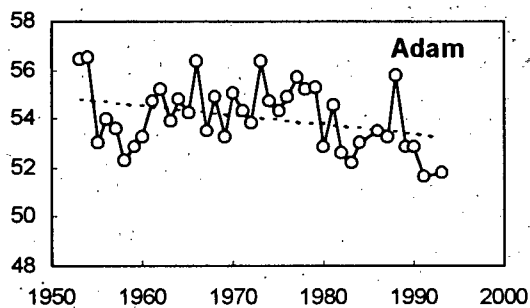
Figure 1.3. Mean standard lengths (cm) of male Fraser River sockeye stocks over a 42 year period. Missing data points were either not available or excluded due to low sample size. Dashed line represents linear time trend fitted by least squares. Correlation coefficients are reported in Table 2.

Standard Length (cm)

13A
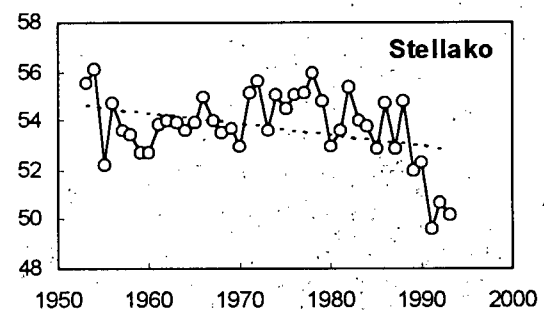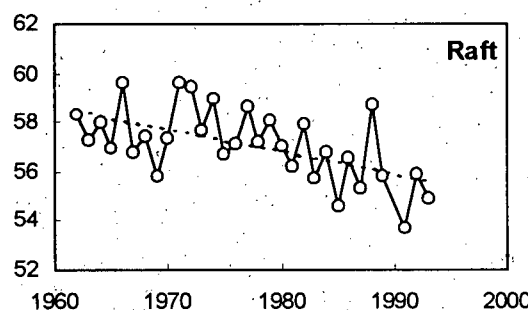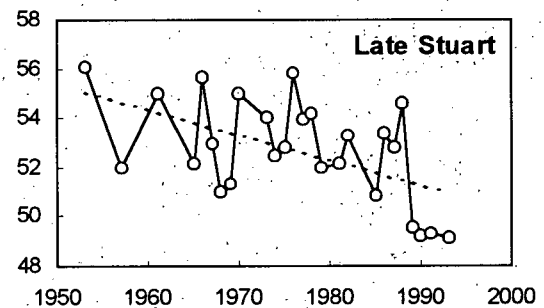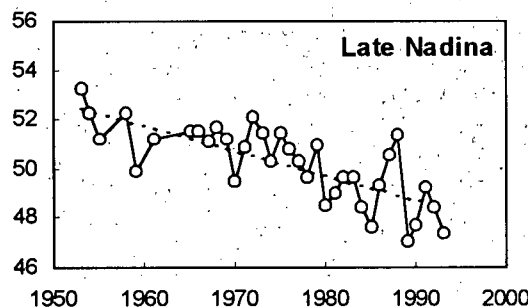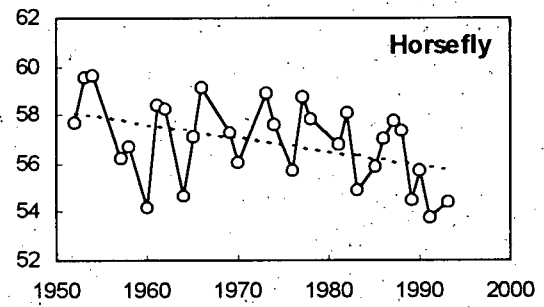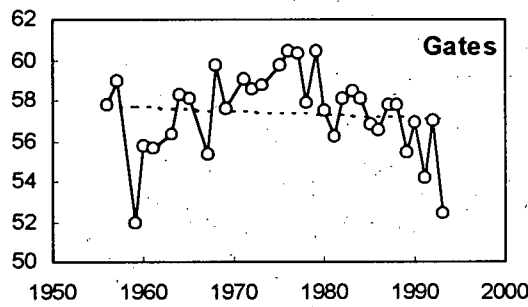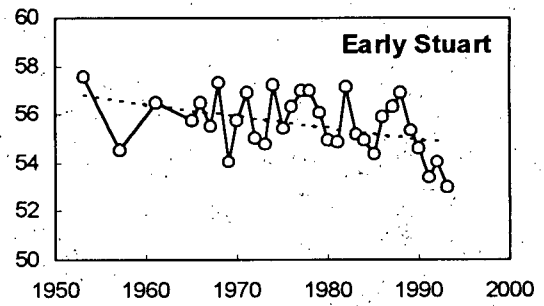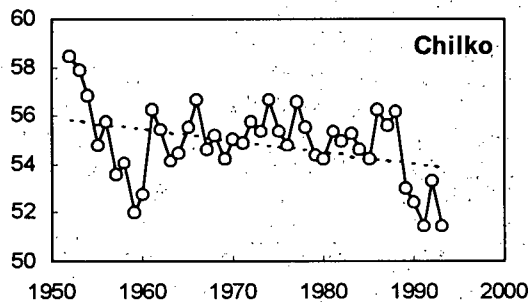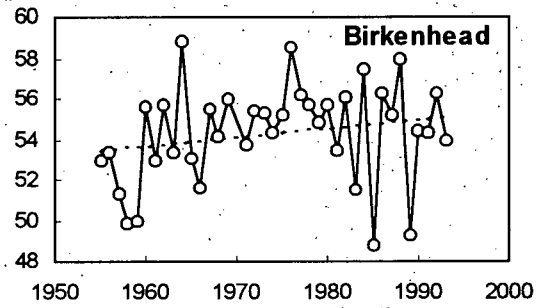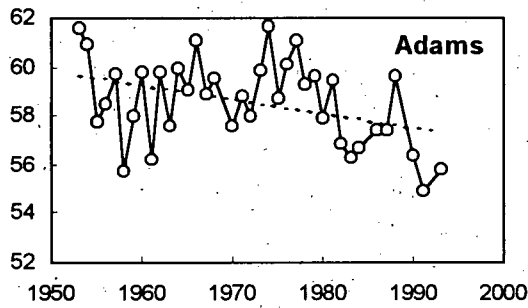
Table 1.2 Annual mean standard length at maturity (cm), standard deviation (SD), and number of years of data (n) for age 1.2 sockeye stocks of the Fraser River. Also shown are the correlation coefficients (and associated probabilities) between standard length and year.

Stock	Females					Males				
	Mean	SD	n	r	P	Mean	SD	n	r	P
Adams	54.12	1.32	38	-0.35	0.03	58.61	1.74	36	-0.39	0.02
Birkenhead	53.11	1.50	38	-0.35	0.03	54.32	2.44	37	0.20	0.21
Chilko	52.29	1.61	41	-0.55	<0.01	54.98	1.47	41	-0.37	0.01
Early Stuart	52.80	1.31	33	-0.62	<0.01	55.73	1.12	31	-0.41	0.01
Gates	53.61	1.63	34	-0.35	0.04	57.56	1.87	32	-0.10	0.60
Horsefly	53.22	1.31	29	-0.42	0.02	57.00	1.64	28	-0.42	0.02
Late Nadina	48.76	1.19	34	-0.71	<0.01	50.33	1.48	34	-0.75	<0.01
Late Stuart	50.57	1.81	25	-0.66	<0.01	48.94	1.96	25	-0.54	<0.01
Raft	52.44	1.59	30	-0.71	<0.01	57.11	1.48	30	-0.57	<0.01
Stellako	51.31	1.42	40	-0.42	<0.01	53.86	1.37	40	-0.37	0.02
Stock Average	52.22	1.47	34			54.84	1.66	33		

Power analyses indicated that minimum detectable differences (MDD) among-years in stock-specific size at maturity ranged from 0.83 - 1.56 cm for males , and 0.49 - 0.88 cm for females (Table 1.1). Each of the statistically significant stock- and sex-specific regression relationships between SL and year predicted a decline in size that exceeded the MDD (see Figures 1.2 and 1.3) suggesting that the declines are not the result of low sample size or measurement error in some years. The relatively larger MSE (and MDD; Table 1.1) of males implies that they varied more in size at maturity than females. This sex-specific difference in size variability has been found in other Pacific salmon species (Beacham and Murray 1985; Healey 1986). Greater within-stock variation in male size at maturity may be due to the presence of alternative mating strategies (e.g. satellite and dominant behaviours) which exist for male Pacific salmon (Hanson and Smith 1967). Size related variability in female sockeye salmon mating strategies is less well defined.

Mixed-stock commercial catch data have previously been used to examine trends in size at maturity of Canadian salmon (IPFSC 1963; Ricker 1982; Bigler et al 1996). With the exception of sockeye, Pacific salmon species have demonstrated a decline in size at maturity from the 1950's to the present (Ricker 1995). It is possible that variability in the relative abundance of sockeye salmon stocks could mask a general trend in size at maturity because size at maturity data will reflect the mean size at maturity of the most abundant stocks. This phenomenon is evident in sockeye salmon catch data (Ricker 1995); peaks in size at maturity of Fraser River sockeye caught in commercial fisheries coincide with peaks in the abundance of the Adams River stock which has one of the largest size at maturity (Table 1.2). Thus, their large size combined with relatively high abundance may

have resulted in a general species trend being obscured in past analyses that used mixed-stock catch data (i.e. Ricker 1995). I conclude that the size at maturity of Fraser River sockeye salmon has exhibited the same general decline over the past four decades that the other major Pacific salmon stocks have displayed.

Size at Maturity and SST Relationships

Average SST from January to July in the northeast Gulf of Alaska was positively associated with year; SST rose by almost 1°C from the early 1950's to the early 1990's. This temperature increase was first reported by Namias et al. (1988) who identified that a large-scale climate shift, resulting from changes to positions of the main high and low pressure areas, occurred over the northeast Pacific Ocean in 1976. The significant trend that I observed in the SST data indicates a similar punctuated change rather than linear increase (Figure 1.4). Since then, average annual SSTs have increased by 1°C in coastal areas and by 0.5°C in high seas areas. (Hourston 1992).

ANCOVA revealed that slopes of the regressions of residual SL on residual SST did not differ among the 10 stocks for males ($P = 0.07$) or females ($P = 0.18$). These interaction terms were removed and the ANCOVA recomputed. Regression intercepts did not differ among stocks for males ($P = 0.99$) or females ($P = 0.99$). However, slopes differed from zero for both males ($P = 0.01$) and females ($P < 0.01$). The common regression equation between residual SL and residual SST was, for males: residual $SL = -0.02 - 0.51$ residual SST; and for females: residual $SL = -0.01 - 0.32$ residual SST. The negative slopes associated with these relationships suggest that the growth of Fraser River sockeye salmon is reduced during relatively warm years of their high-seas residency. My multi-stock

Figure 1.4. Mean sea surface temperatures (SST) calculated from monthly averages (January - July, inclusive) over the period 1952-1992, inclusive, for a region in the northern Gulf of Alaska . See text.
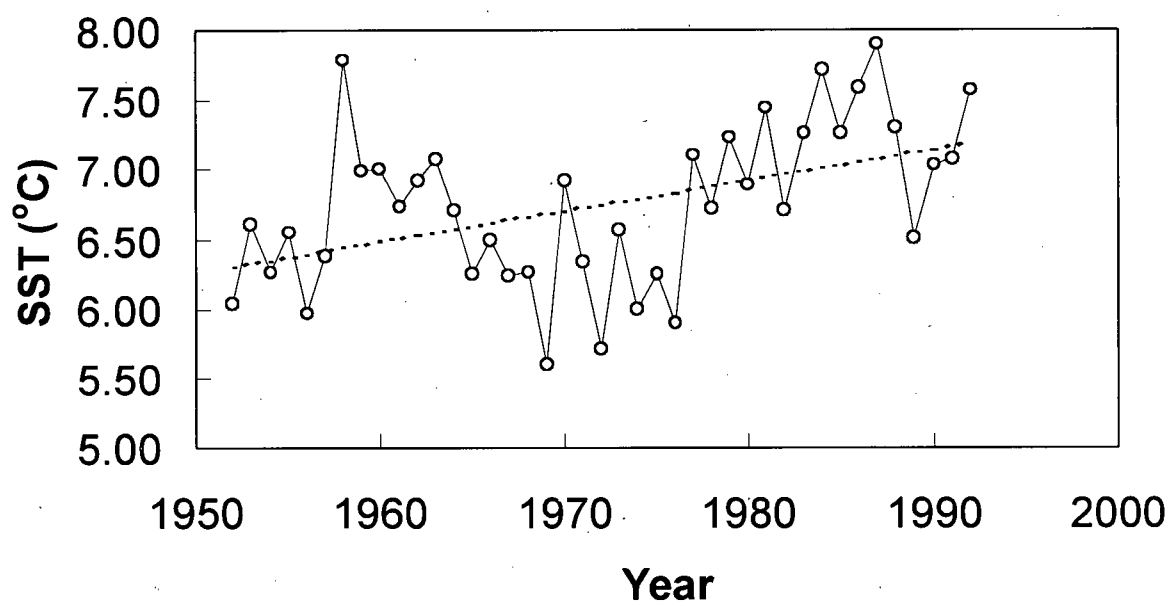
findings extend the single-stock results of Hinch et al. (1995a, 1995b) who found a negative association between SST and weight at maturity of the Early Stuart stock of Fraser River sockeye. Ricker (1982), using mixed-stock data collected from several British Columbia river systems before the climate shift of the late 1970s, also found that warmer SSTs were associated with smaller sockeye salmon. My results indicate that this relationship was consistently evident at the individual stock level, including the two stocks which did not show a decline in mean size with time, and that the relationship has continued in the two "warm" decades following the climate shift.

The slower growth of sockeye salmon may result from increased metabolic demand under warmer ocean conditions which reduces growth potential (Jobling 1994). Hinch et al. (1995a), concluded that increased metabolic costs associated with SST increases of the magnitude observed over the past several years could account for observed declines in weight at maturity of the Early Stuart stock. A complimentary hypothesis is that slower growth under warmer ocean conditions may result from reductions in the amount of ocean habitat available, thereby increasing competitive interactions (Welch et al 1995), because in warm years the southern limit of sockeye salmon distribution is situated farther north than in cool years.

Fraser River sockeye stocks vary in oceanic residence time (IPSFC 1990) and possibly in oceanic distribution (Blackbourn 1987; Welch and Parsons 1993). The fact that all stocks grew more slowly in warmer years indicates that SST may have powerful, broad-scale influences on sockeye salmon growth. However, size at maturity could be influenced by

environmental factors correlated with SST. When the abundance of salmon in the northeast Pacific Ocean is high, size at maturity may be reduced due to density-dependent growth (Peterman 1984, 1985, 1987; Ogura et al. 1991; Helle and Hoffman 1995; Ishida et al. 1995; Bigler et al 1996). Although the abundance of sockeye salmon in the Gulf of Alaska doubled over the past, relatively warm, 15 years (Beamish and Bouillon 1993), macrozooplankton biomass has approximately doubled during this same time (Brodeur and Ware 1995). Hinch et al. (1995b) showed that zooplankton biomass was correlated to size at maturity of Early Stuart sockeye in cool years, but stock abundance also helped explain variation in weight in warm years. The role of SST in mediating density dependent growth needs to be more fully explored.

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Chapter 2

Effects of abundance and thermal habitat on marine growth of Fraser River sockeye salmon

Chapter Abstract

Large increases in the abundance of Pacific salmon (*Oncorhynchus* spp.) over the past two decades have coincided with sharp declines in growth rates of many sockeye salmon (*Oncorhynchus nerka*) stocks. I use catch and escapement data from Bristol Bay and Fraser River sockeye stocks to reconstruct, by ocean age, a minimum ocean abundance time series of sockeye salmon in the Gulf of Alaska, 1952-1992. The role of ocean habitat was assessed by dividing the abundance estimates by an index of thermal habitat available to sockeye salmon in the northeast Pacific. I demonstrate that age-, sex-, and stock-specific size at maturity of Fraser River sockeye is significantly reduced when abundance and density estimates of sockeye in the Gulf of Alaska are high. I also show that during a period of generally low oceanic productivity (1958-1975) marine growth of age 1.2 Fraser River sockeye was not related to population size. In contrast, during a period of high productivity (1978-1992) sockeye abundance in the Gulf of Alaska explained 33-81% of variation in growth of females and 33-79% in males. My results suggest that under present climatalogical conditions and biological productivity, density dependent marine growth of Fraser River sockeye may occur if the abundance of age $x.2^+$ sockeye exceeds approximately 100 million.

Introduction

Since the mid-1970's, large changes have occurred to the physical characteristics, biological productivity, and salmon abundance in the North Pacific Ocean. For example, sea surface temperature rose approximately 1°C in coastal areas and 0.5°C in the open sea, presumably in response to global climate change (Hourston 1992). Also, the Aleutian Low Pressure system, which drives much of the surface current and nutrient upwelling in the Gulf of Alaska, was more intense during the 1980's compared to the period 1950-1970 (Namias et al. 1988; Beamish and Bouillon 1993). These and other changes in the physical characteristics of the north Pacific have coincided with large increases in biological productivity (Beamish and Bouillon 1993; Brodeur and Ware 1992; Polovina 1994). Between the 1960s and 1980s average summer biomass of zooplankton at Ocean Station P, located in the centre of the Gulf of Alaska, nearly doubled (Brodeur and Ware 1992). Substantial increases also occurred in the average biomass of other pelagic nekton such as neon flying squid, albacore, pomfret, salmon shark, and all species of Pacific salmon (Brodeur and Ware 1995). For Pacific salmon (*Oncorhynchus* spp.), larger increases in the abundance of the three species that migrate to the open sea (sockeye, pink, and chum) relative to species that are found in coastal areas (chinook and coho) suggests that changes in biological productivity were more prevalent in the open sea (Ware and McFarlane 1989; Brodeur and Ware 1995).

Coincident with the recent increase in salmon abundance has been a decrease in average size at maturity (Ishida et al 1993; Bigler et al 1996; Chapter 1; Cox and Hinch in press). This was particularly evident in most major Fraser River sockeye salmon stocks (*O. nerka*)

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which have declined 3-6 cm in average size during the past twenty years (1976-1993) relative to the period 1952-1975 (Chapter 1; Cox and Hinch in press).

Prior to the large changes in biological productivity that began in the mid 1970's, Rogers (1980) and Peterman (1984) examined interannual variation in growth of sockeye salmon from Alaska and British Columbia. Both showed that marine growth in the Gulf of Alaska of several sockeye stocks decreased linearly with increasing population size implying that growth was density dependent. Their results have been used by many authors (e.g. Chapter 1; Helle and Hoffman 1995; McKinnell 1995; Cox and Hinch in press; Bigler et al. 1996) as a basis for speculation that *recent* declines in size at maturity of all species of Pacific salmon are due to the large increases in salmon abundance that occurred over the past twenty years since Rogers' and Peterman's studies. Very few studies, however, have addressed this relationship directly (except see Ishida et al. 1993) and attempted to assess whether indeed, the recent declines in size of salmon are a density dependent phenomenon.

Present levels of sockeye salmon abundance in the Gulf of Alaska are at or near those that occurred prior to commercial exploitation (Welch and Parsons 1993). Thus, it is not surprising that many authors attribute recent declines in size to these increases by extrapolating the density-dependent relationships found by Rogers (1980) and Peterman (1984). However, increases in biological productivity in the North Pacific Ocean should have compensated for at least some of the increases in sockeye abundance resulting in a less severe loss in per capita ration size. This should, in turn, have resulted in less severe declines in size at maturity than those exhibited by many Fraser River sockeye stocks

(Chapter 1; Cox and Hinch in press). The rapid declines in size of Fraser River sockeye, which began in the relatively productive late-1970's and early-1980s, suggest that there is a need to examine density-dependent growth relationships from a more recent perspective. In particular, it is important to understand whether density dependent growth relationships still exist or have changed under different productivity regimes and levels of abundance.

My first objective is to examine the evidence for density-dependent marine growth using data from 1958-1992 of ten Fraser River sockeye salmon stocks. I accomplish this by reconstructing, by ocean age, the minimum annual abundance of sockeye salmon in the Gulf of Alaska. This time period also provides contrast in both oceanic productivity and total Gulf of Alaska sockeye salmon abundance, thus enabling me to assess potential differences in density-dependent growth relationships between the periods 1958-1975 (low productivity, low abundance) and 1976-1992 (high productivity, high abundance).

The decline in growth rates of sockeye during periods of increasing productivity could also be caused by physical factors such as increasing sea surface temperatures that limit the habitat available to salmon and thus exacerbate density-dependent growth (Welch et al 1995; Cox and Hinch 1997). The hypothesis that physical factors limit the distribution of salmon was first proposed by researchers from the *International North Pacific Fisheries Commission* (INPFC) during 1950's and 1960's. Much of this historical research on the high seas ecology of salmon centered on identifying migratory pathways and boundaries to the distribution of North American and Asian stocks of salmon (Hartt 1966; French 1976; Welch et al. 1995). The purpose of the research was to establish zones where North

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American salmon would be protected from high seas interception by Japanese fishing fleets. In performing this work the INPFC studies provided volumes of valuable information on the oceanic distribution of Pacific salmon.

It is now recognized that the distribution of North Amercian salmon within the region 128°W to 175°W is associated with certain physical oceanographic features such as thermal and saline fronts and current streams (Hartt 1966; French et al. 1976; Ignell and Murphy 1993). Of these physical oceanographic factors, temperature has been shown to be most important in delineating their southern limits; salmon seem to avoid certain regions where temperature is relatively high, but well below the lethal levels (Welch et al. 1995).

My second objective in this paper is to assess the role of thermal limits and its potential effects on density-dependent growth. I accomplish this by developing an annual index of sockeye salmon density that is based on recontructed ocean abundance and annual thermal habitat area.

Methods

Gulf of Alaska Sockeye Abundance

Most sockeye salmon that are found east of the North Pacific Convention (NPC) provisional line along 175°W are from either Western Alaska or British Columbia (Hartt 1966). Of these fish the Bristol Bay and Fraser River stock complexes are the most abundant (Peterman 1984). I use data on the escapement and commercial catch of Bristol

Bay and Fraser River sockeye salmon stocks to derive an estimate of minimum ocean abundance of sockeye in the Gulf of Alaska.

Bristol Bay sockeye abundance data from 1954-1994 inclusive, were obtained from the Alaska Department of Fish and Game (Steve Fried, AK Dept of Fish and Game, Anchorage, AK, pers. comm.). The stocks included in this analysis are Kvichak, Branch, Naknek, Egegik, Ugashik, Wood, Igushik, and Togiak. Age classes 1.2, 1.3, 2.2, and 2.3 were used because they comprise over 97% of the total sockeye returns from these rivers (Peterman 1984). Data collection methods for estimating Bristol Bay sockeye salmon catch and escapement are described in Peterman and Wong (1984).

Annual total return estimates (catch + escapement) of age 1.1, 1.2, and 1.3 sockeye from ten Fraser River sockeye stocks were obtained from *Pacific Salmon Commission* (PSC) and *Department of Fisheries and Oceans* (DFO) archives. Howard and Chapman (1948) provide a complete description of methods used to enumerate Fraser River sockeye escapements. Methods used to determine the stock and age composition of the commercial catch are described in Woodey (1987). The 1.2 (89.25%), 1.3 (6.9%), 1.1 (2.2%), and 2.2 (1.6%) age classes constitute the major portions of sockeye from the Fraser River (Killick and Clemens 1963).

I estimated, by ocean age, the minimum ocean abundance of sockeye in the Gulf of Alaska by applying virtual population analysis to catch and escapement data from Bristol Bay and Fraser River stocks. I use ocean age (winters at sea) as an age classification because it

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provides a better indication of the relative size of individual fish compared to total age (freshwater + winters at sea). Ocean age classes used in the reconstruction were $x.1$ (1 winter at sea), $x.2$ (two winters at sea), $x.2+$, $x.3$ (three winters at sea), and $x.3+$. Ocean age four ($x.4$) was the maximum age considered for this analysis because of the extremely small numbers of fish that spend greater than four winters at sea. A few Bristol Bay stocks have small numbers of these fish; however, their numbers were not large enough to justify separate age category.

I used the method of Fry (1949) as described in Peterman and Wong (1984) to calculate a minimum estimate of age-specific ocean abundance (Eq 1).

$$N_{i,t} = R_{i,t} + R_{i+1,t+1} + R_{i+2,t+2} \ldots\ldots R_{m,t+m-i}$$ (Eq. 1)

where $N_{i,t}$ = number of ocean age i fish in year t

$R_{i,t}$ = Returns (catch + escapement) of ocean age i fish in year t

m = maximum ocean age

Age-specific abundance ($N_{i,t}$) was then summed across Bristol Bay and Fraser River stocks for each year to arrive at the minimum ocean abundance for each ocean age.

The analyses that follow are based on the assumption that Gulf of Alaska abundance indices for all ages are representative of the true abundance of those ages during those time periods. As in Peterman (1984), I did not apply an annual survival rate to the VPA estimates of abundance. The reason for this is that information on annual marine survival rates of sockeye are not available. Therefore, this assumption is probably not valid for juveniles ($x.0$) because the VPA calculation does not account for variation in marine

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survival among-years and possibly among-stocks within-years. Variation in marine survival of Pacific salmon is log-normal and is assumed to occur mostly during early ocean life (Ricker 1962; Peterman 1981; Bradford 1995). Therefore, not adjusting abundance by a survival factor may have large effects on the interannual variation in $x.0$ abundance and to a lesser extent $x.1$ and older. It is for this reason that I do not include age $x.0$ in the following analyses.

Sockeye Density Index

As described earlier, I use regions of optimal temperature as an index of total habitat available to sockeye salmon in the northeast Pacific Ocean. I refer to this area throughout this paper as *thermal habitat area* (THA). Thermal habitat area (THA) is defined here as that area (km^2) of the north Pacific Ocean that is permanently bounded by the INPFC provisional line (175^OW) to the west and the Aleutian Island chain to the north. A month-specific isotherm, which determined the southern limit to the distribution of sockeye (David Welch, Pacific Biological Station, Nanaimo, BC pers. comm.), was used as a dynamic boundary to the south and east. For each combination of month and year I calculated the area of the north Pacific Ocean that fell within these boundaries. SST data used to estimate the monthly position of sea surface isotherms were obtained from the Comprehensive Ocean-Atmospheric Dataset which is described in Woodruff et al. (1987). Monthly averages were then averaged within-years to arrive at an annual thermal habitat index for sockeye in the Gulf of Alaska. Estimates of age-specific ocean abundance for each year were then divided by the thermal habitat index to arrive at the annual estimates of age-specific sockeye salmon density.

Marine growth data

Because over 98% of total somatic growth of sockeye salmon occurs in the ocean and because final size is not related to smolt size (Henderson and Cass 1991) I used spawning ground length (SL) as a measure of marine growth. Spawning ground lengths of age 1.1 and 1.2 sockeye from ten of the major Fraser River stocks were obtained from PSC and DFO archives. A full description of these data may be found in Chapter 1 and Cox and Hinch (in press). The Fraser River sockeye salmon stocks included in this study are Adams, Birkenhead, Chilko, Early Stuart, Gates, Horsefly, Late Nadina, Late Stuart, Raft, and Stellako. Because detailed data on size at maturity were not available, many of these stocks were not included in the original analyses of Peterman (1984).

Statistical Analysis

A correlation matrix was generated to examine the associations between abundance and density estimates and marine growth of Fraser River sockeye over the period 1961-1992, inclusive. Each stock-, age-, and sex-specific time series of SL was compared to five categories of abundance time series and five corresponding density time series. The abundance and density categories used were $x.1_{ry-2}$ ($dx.1_{ry-2}$), $x.1_{ry-1}$ ($dx.1_{ry-1}$), $x.2_{ry-1}$ ($dx.2_{ry-1}$), $x.2+_{ry-1}$ ($dx.2+_{ry-1}$), $x.2+_{ry}$ ($dx.2+_{ry}$), and $x.3_{ry}$ ($dx.3_{ry}$) where the subscript (ry) represents return year. Each category represents a hypothesis about the ocean age classes involved and timing of interactions that may lead to density-dependent ocean growth of sockeye salmon. For example, to test the hypothesis that abundance of $x.1$ sockeye (or density, $dx.1$) is associated with marine growth during the year of ocean entry, I examine correlations between SL_{ry} and $x.1_{ry-2}$ ($dx.1_{ry-2}$). Due to the large number of comparisons (10) for each stock-, age-, and sex-specific SL time series, Bonferroni adjustments were

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used to control the comparisonwise error rate. The abundance and density measures that were significantly correlated with stock-, age-, and sex-specific SL were recorded. Abundance-SL correlations were then compared to the corresponding density-SL correlations by Fisher's Z-test (Zar 1984, p.310) within each stock, sex, and age class in order to assess the utility of thermal habitat area information. Correlations were also compared among ocean age categories and lags in an attempt to identify key ocean age classes and time periods that may lead to density-dependent growth.

After identifying the most critical age class interactions and timing, I proceeded to test the hypothesis that these relationships have changed since the coincident increases in ocean productivity and salmon abundance. To accomplish this, SL and ocean abundance data were grouped into two time periods. The first period (1958-1975) represented low ocean productivity and low salmon abundance and the second (1976-1992) represented high productivity and high salmon abundance. After stratifying the data by period, I detected a significant increasing linear trend in ocean abundance from 1976 to 1992. I eliminated this trend by removing the low abundance years 1976 and 1977so that a fair comparison could be made between the two periods. I used analysis of covariance (ANCOVA) (PROC GLM; SAS Institute 1988) to test the hypothesis that the slopes of relationships between stock- and sex-specific SL of age 1.2 Fraser River sockeye and ocean abundance were the same for the two periods.

Results and Discussion

From the 1950's to 1990's the abundance of sockeye salmon more than doubled in the Gulf of Alaska. Average annual minimum ocean abundance of $x.2+$ sockeye was 46.6 million over the period 1954-1974 and increased to an average 95.1 million from 1976-1992. The doubling of abundance is due largely to increases in Bristol Bay stocks, which have apparently benefited from both a reduction in high-seas interception and increased ocean productivity (Eggers et al. 1984). The abundance of Fraser River sockeye, on the other hand, increased more gradually between the 1960's and the late-1980's and approximately doubled in abundance (Figure 2.1).

As a check on the data, I compared estimates of $x.2+$ abundance with similar estimates of ages 4 and 5 (total age) sockeye obtained (to the nearest million) from graphs found in Peterman and Wong (1984). Age classes 4 and 5 were selected because they most closely resemble my $x.2+$ age grouping. The two datasets were highly correlated; however, my data were biased high compared to Peterman and Wong (1984) (Figure 2.2). This was expected due to the addition of older ages in the $x.2+$ age group. The single outlier (1959) could not be explained without detailed knowledge of the ocean ages present in the data of Peterman and Wong (1984). Close examination of the influence of the 1959 data point showed that it had no affect on the final results. General agreement between the two datasets permits more meaningful comparisons between my results and those of Peterman (1984) and McKinnell (1995). Both of these studies used minimum ocean abundance data from Peterman and Wong (1984).

Estimated thermal habitat area for sockeye in the northeast Pacific followed what appears

to be a long-period fluctuation with little interannual variation (Figure 2.3) THA averaged

1.05 million km^2 from the early 1960's to the mid-1970's, with a maximum (1.35 million

km^2) occurring during the mid-1970's. THA reached lows in the early 1960's (856,000

km^2) and again in the early 1990's (90,000 km^2).

Figure 2.1. Minimum ocean abundance of age $x.1+$ Bristol Bay (upper panel) and Fraser
River sockeye (lower panel) in the Gulf of Alaska, 1954-1990.
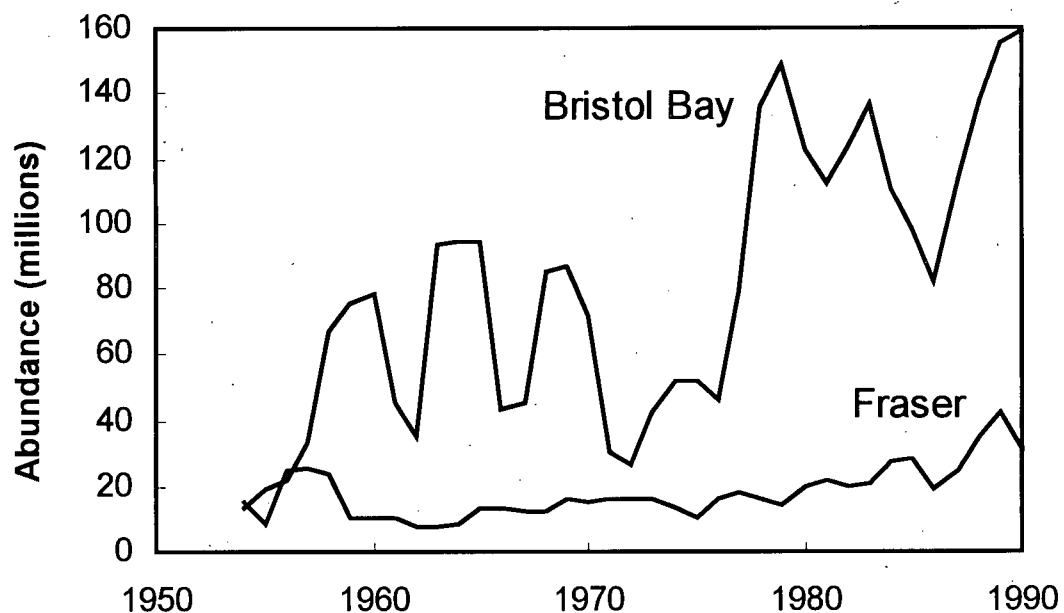
Figure 2.2. Comparison of ocean abundance estimates of age $x.2+$ Bristol Bay and Fraser River sockeye (1958-1973) with estimates of age 4 and 5 (total age) Gulf of Alaska sockeye from Peterman and Wong (1984). The dashed line represents the 1:1 relationship between the two datasets.
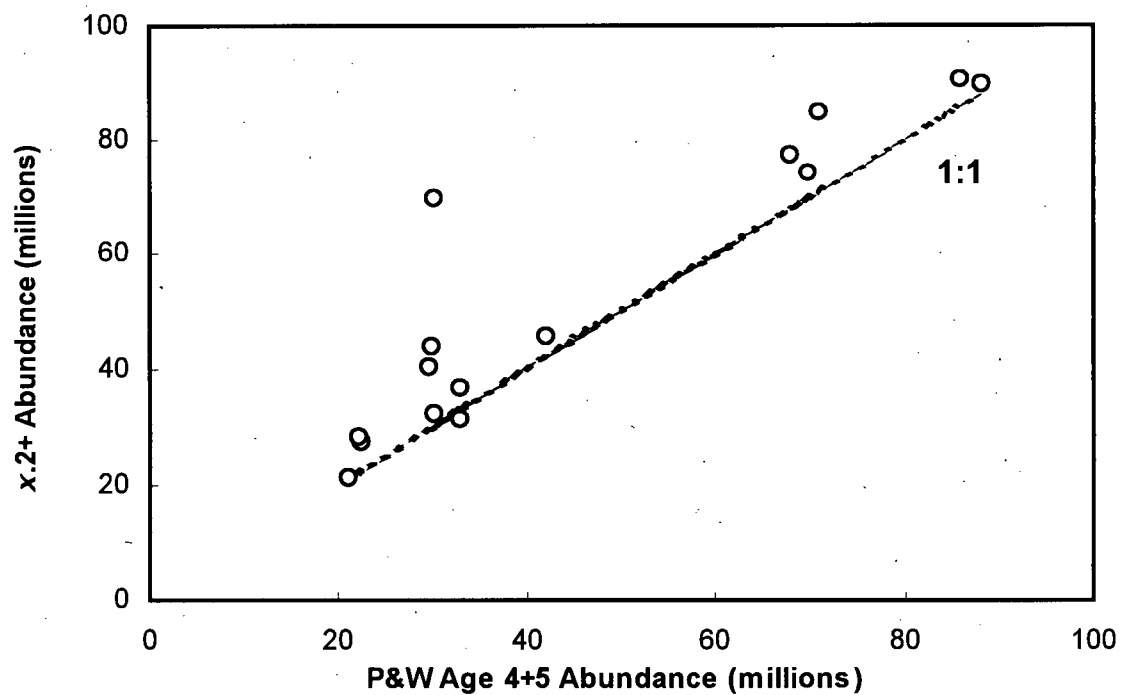
Figure 2.3. Estimated thermal habitat area for sockeye salmon in the northeast Pacific ocean, 1961-1992.

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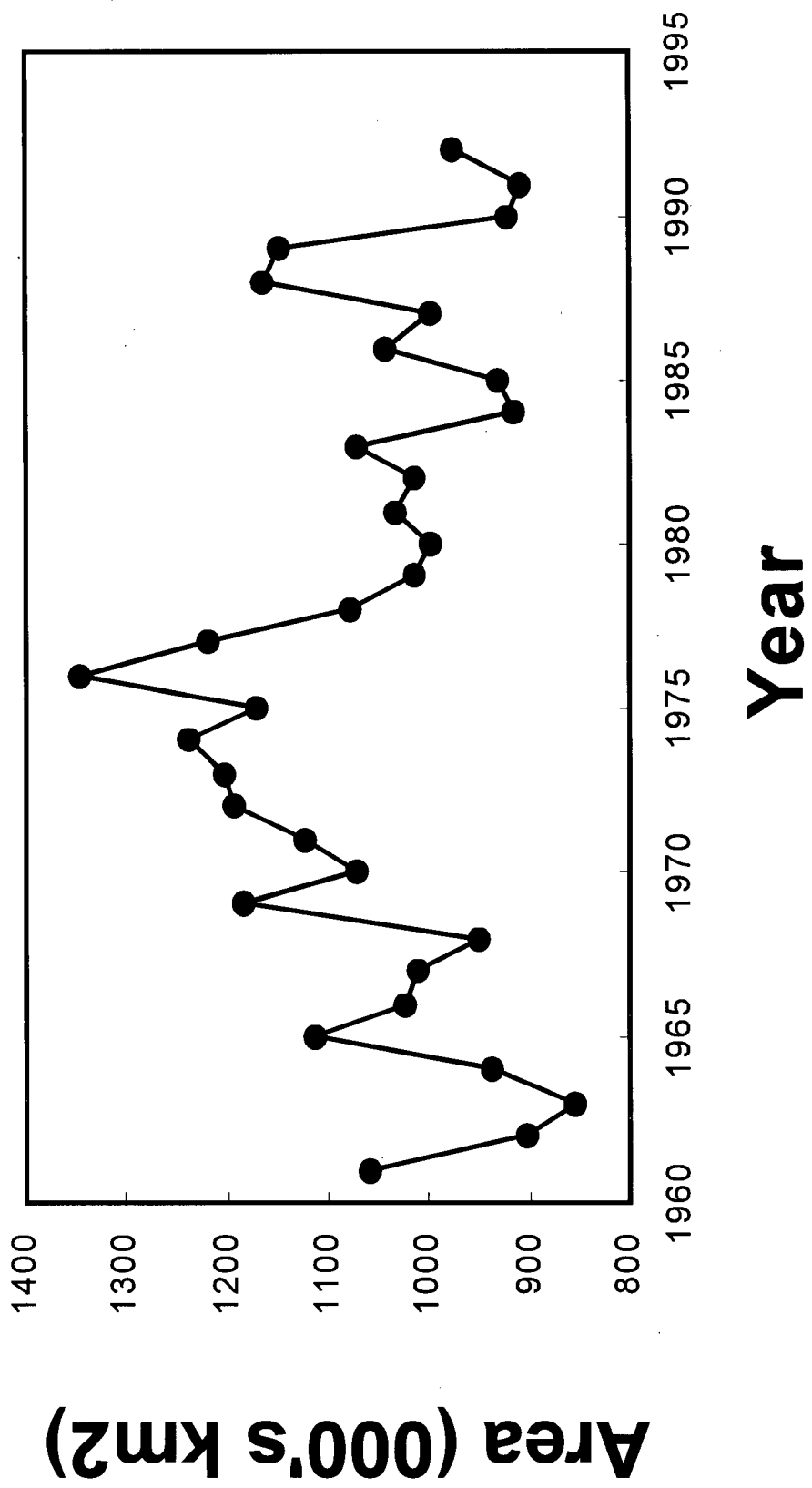
Gulf of Alaska abundance and density were both significantly correlated with age-, sex-, and stock-specific SL at maturity of Fraser River sockeye (Table 2.1). Although density-SL correlations (Table 2.2) were generally of greater magnitude, none were significantly different from their corresponding abundance-SL correlations (Fishers Z-test $P > 0.05$). An annual index of thermal habitat, therefore, does not appear to explain a significant amount of variation beyond that explained by Gulf of Alaska sockeye abundance. It is possible that my initial choice of an annual index does not reflect the true importance of thermal habitat in affecting sockeye salmon growth. If the majority of body growth occurs in short intervals (e.g., spring and summer) then my use of an annual index would be inappropriate. However, the limited amount of data that is available on seasonal growth patterns suggest that sockeye are able to find suitable conditions for growth throughout the year (Bilton and Ludwig 1966; French et al. 1976). More likely, the range of THA that I have observed is not representative of events that determine salmon density at the appropriate scale. Using THA to derive an index of density assumes that salmon are evenly distributed within the available habitat. In reality, salmon on the high seas are not distributed evenly and are often found in aggregations on spatial scales from 0-2000 km (Ignell and Murphy 1993; Welch et al. 1995; Hinch unpubl. data). Therefore, changes in THA on a large scale may not necessarily effect similar changes on small scale salmon density. THA may be important in describing the limits to the distribution of salmon, but its value for predicting actual salmon density within the distribution is probably limited, as was initially suggested by Welch et al (1995). Because of these limitations and the fact that abundance and density indices did not differ in their association with SL I will limit the following discussion to abundance-SL associations.

Female SL from ten stocks were significantly correlated with at least one category of ocean abundance. SL_{ry} were most highly correlated with the $x.2+_{ry-1}$ category (7 stocks) followed by $x.2+_{ry}$ (2 stocks), and $x.3_{ry}$ (1 stock). Although most maximum correlations occurred for the $x.2+_{ry-1}$ category, the correlation coefficients (within stocks) between SL_{ry} and each of the three categories ($x.2+_{ry-1}$, $x.2+_{ry}$, and $x.3_{ry}$) were not significantly different from each other (Fisher's Z-test; $P > 0.05$).

Male SL from eight stocks was significantly correlated with at least one category of ocean abundance. SL_{ry} were most highly correlated with the $x.2+_{ry-1}$ category (5 stocks) followed by $x.2+_{ry}$ (2 stocks) and $x.3+_{ry}$ (1 stock). Again, differences in correlation coefficients among the three categories were not significant (Fisher's Z-test; $P > 0.05$).

SL of age 1.1 male (jack) sockeye from only two stocks were significantly correlated with at least one category of ocean abundance. Birkenhead River and Gates Creek were the two stocks whose abundance-SL correlations (with $x.2+_{ry}$ and $x.2+_{ry-1}$, respectively) met the required adjusted significance level ($p = 0.05/10 = 0.005$). Five additional stocks were significantly correlated with at least one ocean abundance category at the 0.01 (3 stocks) and 0.05 (2 stocks) levels. As with age 1.2 males and females, differences in correlation coefficients among abundance categories were not significant (Fisher's Z-test; $P > 0.05$).

Table 2.1 Correlation coefficients between age-, sex-,and stock-specific spawning ground length and abundance indices for Bristol Bay and Fraser River sockeye. Correlations that meet the Bonferroni adjusted significance level ($P = 0.05/10 = 0.005$) are underlined.

Age, sex, and stock	n	$x.1_{ry-2}$	$x.1_{ry-1}$	$x.2_{ry-1}$	$x.2+_{ry}$	$x.2+_{ry-1}$	$x.3_{ry}$
1.1 Males							
Adams	26	-0.245	-0.329	-0.245	-0.398	-0.431	-0.245
Birkenhead	31	-0.571	-0.553	-0.571	-0.713	-0.614	-0.572
Chilko	29	-0.333	-0.389	-0.333	-0.447	-0.300	-0.333
Early Stuart	19	0.117	-0.136	0.117	-0.057	-0.179	0.115
Gates	28	-0.398	-0.315	-0.398	-0.497	-0.539	-0.399
Horsefly	9	0.124	-0.154	0.124	-0.111	-0.424	0.124
Late Nadina	16	-0.280	0.073	-0.280	-0.192	-0.434	-0.280
Late Stuart	10	-0.414	-0.566	-0.414	-0.638	-0.751	-0.417
Raft	12	0.150	-0.161	0.150	-0.042	0.021	0.150
Stellako	19	-0.473	-0.213	-0.473	-0.427	-0.563	-0.474
1.2 Males							
Adams	28	-0.457	-0.178	-0.457	-0.455	-0.585	-0.458
Birkenhead	31	-0.323	0.146	-0.323	-0.134	-0.312	-0.323
Chilko	32	-0.523	-0.414	-0.523	-0.594	-0.521	-0.524
Early Stuart	29	-0.476	-0.183	-0.476	-0.432	-0.515	-0.477
Gates	28	-0.280	-0.096	-0.280	-0.303	-0.462	-0.280
Horsefly	22	-0.604	-0.506	-0.604	-0.709	-0.468	-0.605
Late Nadina	29	-0.689	-0.456	-0.689	-0.721	-0.732	-0.689
Late Stuart	23	-0.595	-0.433	-0.595	-0.641	-0.490	-0.595
Raft	30	-0.550	-0.257	-0.550	-0.522	-0.508	-0.551
Stellako	32	-0.550	-0.230	-0.550	-0.525	-0.588	-0.551
1.2 Females							
Adams	30	-0.519	-0.288	-0.519	-0.518	-0.536	-0.519
Birkenhead	32	-0.621	-0.346	-0.621	-0.658	-0.762	-0.621
Chilko	32	-0.501	-0.566	-0.501	-0.676	-0.528	-0.501
Early Stuart	30	-0.479	-0.222	-0.479	-0.454	-0.524	-0.480
Gates	30	-0.580	-0.396	-0.580	-0.651	-0.706	-0.580
Horsefly	23	-0.514	-0.533	-0.514	-0.675	-0.471	-0.514
Late Nadina	29	-0.581	-0.401	-0.581	-0.633	-0.595	-0.581
Late Stuart	23	-0.710	-0.372	-0.710	-0.701	-0.674	-0.711
Raft	30	-0.475	-0.287	-0.475	-0.521	-0.544	-0.475
Stellako	32	-0.474	-0.224	-0.474	-0.476	-0.545	-0.475

Table 2.2 Correlation coefficients between age-, sex-, and stock-specific spawning ground length and Gulf of Alaska sockeye density indices. Correlations that meet the Bonferroni adjusted significance level ($P = 0.05/12 = 0.004$) are underlined. Sample sizes for some comparisons may vary by n-1 or n+1.

Age, sex, and stock	n	$dx.1_{ry\text{-}2}$	$dx.1_{ry\text{-}1}$	$dx.2_{ry\text{-}1}$	$dx.2\text{+}_{ry}$	$dx.2\text{+}_{ry\text{-}1}$	$dx.3_{ry}$
1.1 Males							
Adams	26	-0.218	-0.295	-0.233	-0.398	-0.426	-0.255
Birkenhead	30	-0.516	_-0.545_	_-0.588_	_-0.710_	_-0.633_	_-0.595_
Chilko	28	-0.243	-0.371	-0.337	-0.449	-0.373	-0.348
Early Stuart	18	0.129	-0.210	0.037	-0.108	-0.276	0.066
Gates	27	-0.432	-0.327	-0.444	-0.492	_-0.562_	-0.417
Horsefly	8	0.309	-0.086	0.225	-0.227	-0.421	0.040
Late Nadina	15	-0.298	0.115	-0.260	-0.224	-0.399	-0.286
Late Stuart	9	-0.498	-0.679	-0.511	-0.668	-0.805	-0.442
Raft	11	-0.072	-0.265	0.076	-0.128	0.021	0.083
Stellako	19	-0.517	-0.261	-0.537	-0.479	-0.615	-0.513
1.2 Males							
Adams	27	-0.482	-0.259	_-0.539_	-0.515	_-0.630_	-0.515
Birkenhead	30	-0.341	0.164	-0.338	-0.116	-0.297	-0.296
Chilko	31	-0.429	-0.412	_-0.520_	_-0.659_	_-0.544_	_-0.583_
Early Stuart	28	-0.435	-0.241	-0.515	-0.483	_-0.563_	_-0.523_
Gates	27	-0.345	-0.203	-0.381	-0.342	-0.530	-0.316
Horsefly	21	-0.498	-0.518	_-0.601_	_-0.725_	-0.505	_-0.623_
Late Nadina	28	_-0.616_	-0.421	_-0.645_	_-0.744_	_-0.694_	_-0.722_
Late Stuart	22	-0.493	-0.425	_-0.597_	_-0.687_	-0.524	_-0.643_
Raft	30	-0.513	-0.292	_-0.595_	_-0.561_	_-0.561_	_-0.590_
Stellako	31	_-0.556_	-0.287	_-0.599_	-0.588	-0.635	-0.603
1.2 Females							
Adams	29	-0.473	-0.299	_-0.549_	_-0.557_	_-0.581_	_-0.555_
Birkenhead	31	_-0.549_	-0.338	_-0.624_	_-0.696_	_-0.761_	-0.669
Chilko	31	-0.402	_-0.547_	-0.497	_-0.725_	_-0.565_	_-0.562_
Early Stuart	29	-0.428	-0.269	-0.511	-0.468	_-0.569_	-0.496
Gates	29	_-0.569_	-0.412	_-0.603_	_-0.660_	_-0.716_	_-0.607_
Horsefly	22	-0.380	-0.539	-0.515	_-0.709_	-0.510	-0.547
Late Nadina	28	-0.508	-0.315	-0.524	_-0.667_	_-0.571_	_-0.625_
Late Stuart	22	_-0.628_	-0.395	_-0.728_	_-0.735_	_-0.711_	_-0.752_
Raft	30	-0.435	-0.314	_-0.511_	_-0.543_	_-0.588_	-0.500
Stellako	31	-0.451	-0.268	_-0.506_	_-0.541_	_-0.590_	_-0.536_

My results indicate that in all cases where SL is significantly correlated with sockeye abundance I cannot distinguish between effects that occur in the year preceding return (ry-1) from those effects that may occur during the return year (ry). In most cases, I also cannot distinguish between the potential effects that different ocean age categories have on growth of Fraser River sockeye. Peterman (1984) defined the most critical ocean residence periods and age categories for density dependent effects on sockeye as those periods and ages that produced the greatest fraction of significant slopes of SL on Gulf of Alaska sockeye abundance. Although I have shown that this type of approach may suffer from an inability to distinguish among the various periods and age categories, the results may be suggestive. For example, 90% of the maximum age-, stock-, and sex-specific abundance-SL correlations occurred when $x.2+$ fish were used as an abundance index and 10% occurred with $x.3$. In addition, 65% of these maximum correlations occurred when abundance data from the year preceding return (ry-1) were used and 35% occurred using the return year data (ry). This is similar to the original findings of Peterman (1984) who suggested that the most critical period for Gulf of Alaska sockeye abundance to cause density-dependent growth effects on age 1.2 British Columbia sockeye was early in the penultimate year (ry-1). The results do not indicate a strong age class interaction with $x.1$ as was found by Peterman (1984). However, McKinnell (1995) found no significant relationships between mean length at maturity of age 1.2 Skeena, Nass, and Rivers Inlet sockeye and Bristol Bay sockeye catch. Peterman (1984) suggested that competition among similar sized sockeye may lead to density-dependent reductions in growth. However, I believe that the large volume of food consumed by maturing $x.2$ and $x.3$

sockeye (McKinnell 1995) is a more plausible mechanism that would explain slower growth of fish of all sizes. The significant cases that I reported for age 1.1 sockeye support this hypothesis. Age 1.1 "jacks" are relatively small during their 13-15 month (1-winter) existence in the ocean compared to $x.2$ and $x.3$ fish, yet still they exhibit significant decreases in growth when Gulf of Alaska abundance of $x.2$ and $x.3$ fish are high.

The results for age 1.1 fish also suggest that variation in marine growth may be more dependent upon state of maturity rather than size. Lander and Tanonaka (1964) examined marine growth of immature and maturing Western Alaskan sockeye that were captured by research vessels operating in the North Pacific Ocean during the period 1956 to 1960. Their results showed little variation in marine growth of immature sockeye taken from broadly separated geographical areas during the same ten day period each year. In contrast, average size of maturing fish differed significantly between areas of capture. Of course, the differences in growth rate shown for maturing fish may also be attributable to stock-specific differences that were not accounted for because the samples were not separated by area of origin.

Changes in density-dependent growth relationships
I chose to use $x.2+_{ry-1}$ for the following regression analyses for a number of reasons. First, it was most highly correlated to SL of most stocks. Second, Fraser River sockeye spend the entire penultimate year (ry-1) in the open sea; this would increase the likelihood of interaction with other Gulf of Alaska sockeye stocks (Chapter 1; Cox and Hinch in press). Third, Fraser River sockeye that are destined to mature after two winters at sea are

maturing during the latter portion of this period. Finally, growth in length is greatest

during the penultimate year (Lander and Tanonaka 1964).

Female sockeye from nine stocks and males from five stocks showed significant negative

SL-$x.2+_{ry-1}$ relationships during the 1978-1992 period. Differences between sexes in the

number of significant relationships could be partly due to the lower power of detecting

changes in size at maturity of males compared to females (Cox and Hinch in press;

Chapter 1). Significant stock- and sex-specific regressions of SL on $x.2+_{ry-1}$ during this

period explained 33-81% and 33-79% of variation in growth of females and males,

respectively (Table 2.3; Figure 2.4). In contrast, stock- and sex-specific regression slopes

were both positive and negative during the 1958-1975 period and all were non-significant.

ANCOVA revealed that, in most cases, relationships between SL and $x.2+_{ry-1}$ were

different during the periods 1958-1975 and 1978-1992 (Table 2.3). One could speculate

that the large increases in zooplankton biomass during the 1978-1992 period would have

offset the coincident increases in salmonid abundance resulting in no net change in growth

rate. Instead, strong density-dependent growth during the productive 1980s suggests that

sockeye abundance increased at a faster rate than the food supplies required to maintain

growth rates.

The fact that growth of age 1.2 sockeye was not density-dependent from 1958-1975

contradicts the results of Peterman (1984), although Peterman (1984) used ocean

abundance of ages 2 and 3 (total age; corresponds to $x.0$ and $x.1$) as explanatory variables.

On the other hand, my results support those of McKinnell (1995) who found no

relationship between mean length at maturity of age 1.2 Skeena sockeye and Gulf of

Alaska abundance during this period.

Table 2.3. Comparison of standardized slopes (b'), probabilities that slopes are equal to zero ($P_{b=0}$), coefficients of determination (r^2) and number of years of data (n) for relationships between mean spawning ground length of age 1.2 female and male Fraser River sockeye and abundance of age $x.2 + _{ry-1}$ Bristol Bay and Fraser River sockeye during the periods 1958-1975 and 1978-1992. The last column gives the probability from ANCOVA that slopes from the two periods are equal ($P_{b1=b2}$).

| | *1958 - 1975* | | | | *1978 - 1992* | | | | |
Stock	b_1'	$P_{b1=0}$	r^2	n	b_2'	$P_{b2=0}$	r^2	n	$P_{b1=b2}$
Females									
Adams	0.154	0.54	0.02	18	-0.580	0.03	0.35	13	0.04
Birkenhead	-0.003	0.99	0.00	18	-0.848	< 0.01	0.76	15	< 0.01
Chilko	0.342	0.16	0.12	18	-0.784	< 0.01	0.41	15	< 0.01
Early Stuart	0.217	0.48	0.05	13	-0.672	< 0.01	0.43	15	0.02
Gates	-0.136	0.63	0.02	15	-0.622	< 0.01	0.45	15	0.20
Horsefly	0.197	0.54	0.04	12	-0.885	< 0.01	0.58	11	0.01
Late Nadina	0.420	0.12	0.18	13	-0.623	< 0.01	0.44	14	< 0.01
Late Stuart	0.220	0.57	0.05	9	-0.975	< 0.01	0.81	12	< 0.01
Raft	0.346	0.22	0.12	14	-0.793	0.03	0.33	14	0.01
Stellako	0.217	0.38	0.05	18	-1.042	< 0.01	0.64	15	< 0.01
Males									
Adams	-0.066	0.800	0.00	17	-0.489	0.06	0.31	12	0.26
Birkenhead	-0.299	0.240	0.09	17	-0.183	0.48	0.04	15	0.77
Chilko	0.208	0.400	0.04	18	-0.898	< 0.01	0.55	15	< 0.01
Early Stuart	0.247	0.440	0.06	12	-1.045	< 0.01	0.79	15	< 0.01
Gates	-0.030	0.920	0.00	13	-0.493	0.05	0.27	15	0.42
Horsefly	0.026	0.940	0.00	11	-0.758	0.02	0.47	11	0.14
Late Nadina	-0.167	0.570	0.03	14	-0.608	0.01	0.42	15	0.09
Late Stuart	0.549	0.100	0.30	10	-0.843	< 0.01	0.75	11	< 0.01
Raft	0.189	0.520	0.04	14	-0.704	0.03	0.33	14	0.04
Stellako	0.051	0.840	0.00	18	-1.117	< 0.01	0.62	15	< 0.01

Figure 2.4. Relationships between mean spawning ground body length of females (abscissa) and abundance of age $x.2^+_{ry-1}$ sockeye (ordinate) in the Gulf of Alaska during 1958-1975 (solid line;closed circles) and 1978-1992 (dashed line; open circles). Regression relationships that were significantly different between periods are shown. See Table 2.3 for regression summary.

Standard Length (cm)

*x.2+*_{ry-1} Sockeye Abundance

49 A
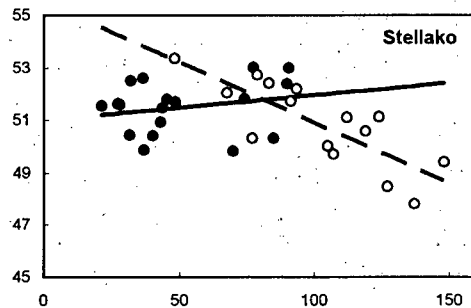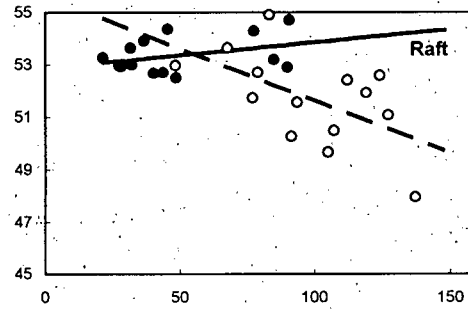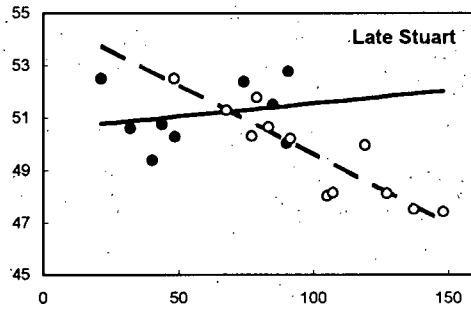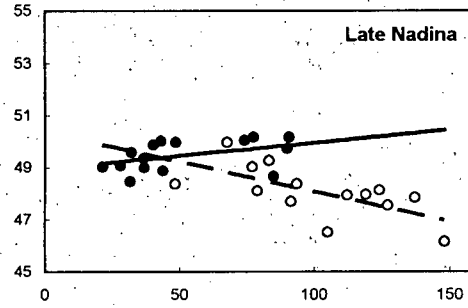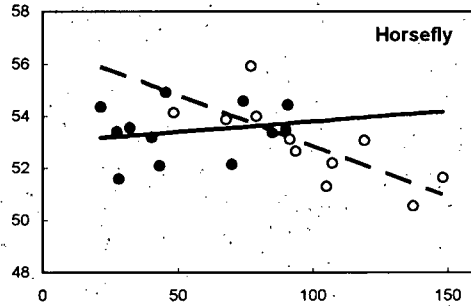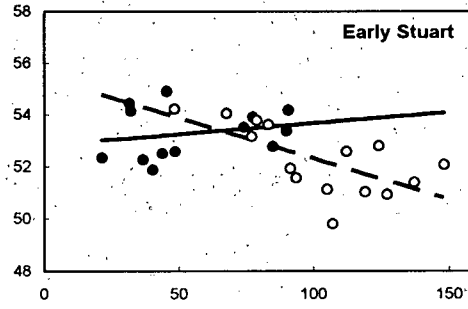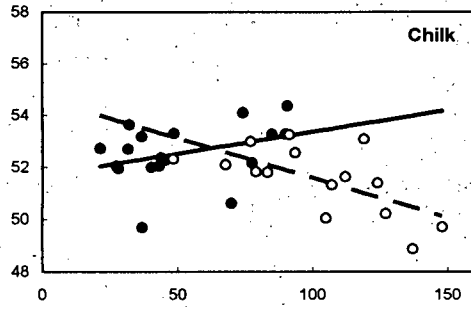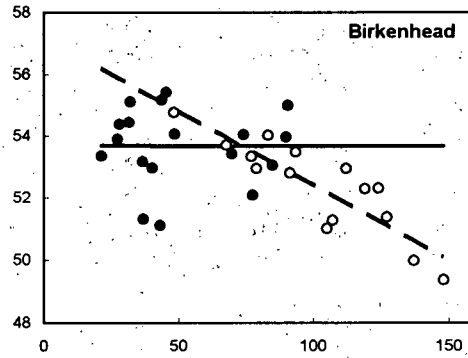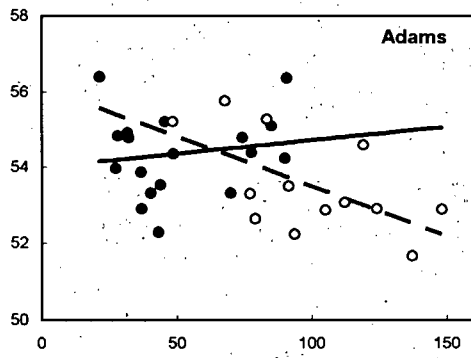
Figure 2.5. Relationships between mean spawning ground body length of males (abscissa) and abundance of age $x.2^{+}_{ry-1}$ sockeye (ordinate) in the Gulf of Alaska during 1958-1975 (solid line;closed circles) and 1978-1992 (dashed line; open circles). Regression relationships that were significantly different between periods are shown. See Table 2.3 for regression summary.

Standard Length (cm)

x.2+ry-1 Sockeye Abundance

50A
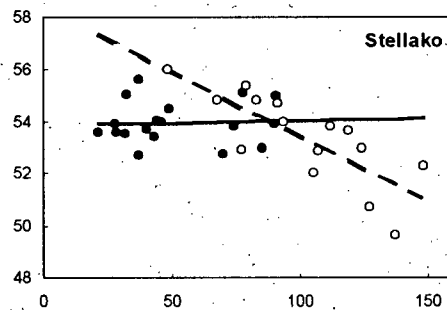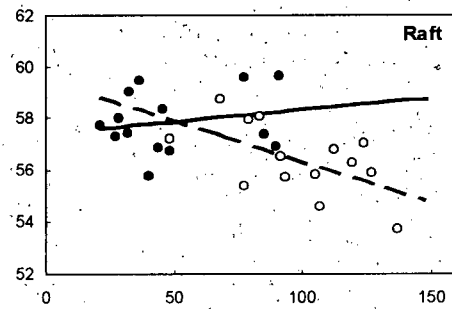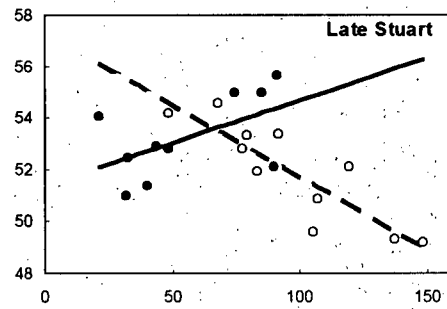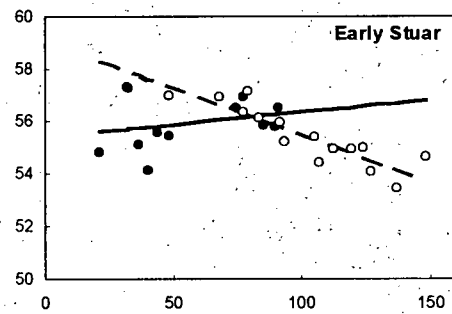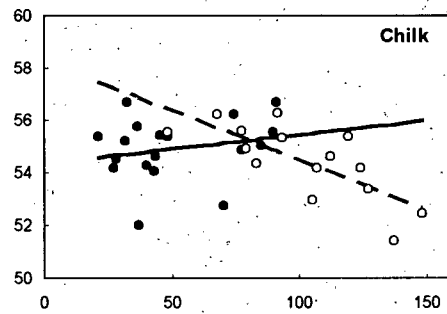
Detailed mechanistic explanations for the density-dependent growth of sockeye on the high-seas are not possible at this time. However, explanations for sudden changes in density-dependent growth relationships, as I present, are simpler to conjure. In a brief analysis of spatial distribution of British Columbia sockeye salmon stocks, McKinnell (1995) concluded that differences in density-dependent growth relationships among British Columbia sockeye stocks could be attributed to their relative proximity to the centers of abundance of Western Alaska sockeye. Although this would account for differences in density dependent growth relationships among stocks, it does not explain the changes in relationships over time that I observed.

The fluctuations in abundance of fish stocks are often associated with expansion and contraction of habitat area occupied by those stocks (MacCall 1990; McConnaughey 1995). If this relationship holds for Bristol Bay sockeye salmon, then the doubling of abundance during the late 1970s and early 1980s most likely caused an increase in their range in the northeast Pacific Ocean. Expansion of habitat occupied by Bristol Bay sockeye into regions commonly occupied by British Columbia fish would lead to an increase in competitive interactions between the two stocks. Increases in area occupied have been observed for Japanese chum (*O. keta*) salmon as hatchery populations increased during the 1980s and 1990s (Nagasawa 1992). Therefore, a doubling of the abundance of Bristol Bay sockeye could explain the significant changes in density-dependent growth relationships between the two time periods that I observed

The change in density-dependent growth relationships between the two periods that I observed may not be simply due to sockeye salmon abundance alone. Although it appears from a closer examination of Figures 4 and 5 that the density-dependent growth response occurs mainly beyond 100 million age $x.2+$ sockeye, some of this effect is confounded with oceanographic events that prevailed during the period in which these abundance levels were attained. During the 1980s, when sockeye abundance first approached record levels, the main prey species for sockeye were being advected towards the perimeter of the Gulf of Alaska (Brodeur and Ware 1992; Hinch unpubl. data), presumably in response to intensification of the gyre upwelling system. This advection is believed to be partly responsible for the increases in juvenile salmon survival observed during that period (Beamish and Bouillon 1993). The redistribution of prey away from the center of the gyre may have caused lower effective prey densities in offshore areas where maturing sockeye are believed to exist. This effect, combined with higher sea surface temperatures, increases in pink and chum salmon abundance and an expanding range of the dominant sockeye stocks probably all contributed to the severe drop in size at maturity of Fraser River sockeye during the late 1980s and early 1990s.

Conclusions

My results indicate that sockeye salmon have become abundant enough in recent decades to cause strong density-dependent reductions in growth of Fraser River sockeye. The record small sizes of Fraser River sockeye that occurred during the early 1990s (Chapter 1; Cox and Hinch in press) could have resulted from a combination of high Gulf of Alaska sockeye abundance and a shift back to a period of low biological productivity (Polovina et

al 1994).This evidence suggests that marine growth may be even more drastically reduced

if abundance is artificially maintained at high levels during periods of low productivity.

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Chapter 3

Density-dependent marine growth of Early Stuart sockeye salmon: evidence for a critical period

Chapter Abstract

Critical periods for density dependent marine growth have not been clearly identified for Fraser River sockeye salmon. Using annual marine scale growth and age-specific estimates of sockeye salmon abundance from 1954-1991, I show that Early Stuart sockeye salmon marine growth is negatively correlated to abundance during the penultimate year at sea. However, the correlations are only significant during the past fifteen years (1978-1991) compared to the earlier period 1954-1975. This suggests that critical periods for density dependent growth occur during the time when Early Stuart sockeye salmon are present in the Central Gulf of Alaska.

Introduction

Improvements in wild stock management and beneficial ocean conditions have resulted in dramatic increases in the abundance of many sockeye salmon (*Oncorhynchus* spp.) populations in recent years (Eggers et al. 1984; Beamish and Bouillon 1993). These increases are believed to be the major factor responsible for the significant declines in size at maturity of most Fraser River sockeye salmon stocks (Chapter 1 and 2; Cox and Hinch in press). Although it seems clear that marine growth is related to population size in the ocean (Rogers 1980; Peterman 1984; McKinnell 1995; Chapter 2), the timing of competitive interactions, sometimes refered to as critical periods, between stocks and age classes of sockeye from British Columbia and Alaska remains uncertain (Chapter 2).

The search for critical periods for marine growth of sockeye salmon has been of interest to biologists for many years (Killick and Clemens 1963). More recent studies of density dependent marine growth of Pacific salmon (*Oncorhynchus* spp.) continue to offer some speculation on the potential timing of competitve interactions (Rogers 1980; Peterman 1984; Ishida et al 1993; McKinnell 1995; Chapter 2). However, few studies relate salmon abundance to direct estimates of annual marine growth (Ogura 1991; Ishida et al 1993; McKinnell 1995). In most cases, size at maturity and abundance data are simply lined up to represent different hypotheses about the timing of competitive interactions (Rogers 1980; Peterman 1984; McKinnell 1995; Chapter 2). Lagging data in this way often results in low power of detecting differences among the various hypotheses due to the large number of comparisons that are required (see Chapter 2).

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British Columbia sockeye salmon typically spend 24-27 months (age 1.2; two winters) or 36-39 months (age 1.3; three winters) foraging in the Gulf of Alaska. The total body size increment achieved by an individual salmon from the time it enters the ocean as a juvenile until the time it re-enters freshwater as an adult, and thus stops growing, is referred to as *total marine growth*. It may be subdivided into individual marine growth phases that are assumed to each vary in response to changing physical and biological oceanographic conditions.

My objective in this chapter is to determine if specific marine growth phases tend to vary in response to changing levels of sockeye salmon abundance in the Gulf of Alaska. I base my analyses on an up to date time series of sockeye abundance in the Gulf of Alaska and annual marine scale growth increments from age 1.2 Early Stuart sockeye.

Methods

Marine Growth Data

Information on the amount of growth attained in each marine growth phase is obtained from returning adult fish by measuring the distance between successive ocean annuli on the scales. Each ocean annulus begins to form sometime in November or December and is completed by January (Bilton and Ludwig 1966). For age 1.2 fish that enter the ocean in May-June this leaves seven to eight months (June-December) of scale growth in the first marine growth stage (M1), approximately eleven months for the second phase (M2), and five to seven months for the final marine growth phase (M3) (Bilton and Ludwig 1966).

Average annual marine scale growth increments from the Early Stuart (1954-1991) stock

were estimated to the nearest micron from figures found in Welch (1994). Scale

measurements for each marine growth zone (M1, M2, and M3) are assumed to be

proportional to growth in either body length or body weight during that period.

Sockeye Abundance

Minimum age-specific ocean abundances of sockeye salmon for the period 1954-1991

inclusive, were calculated by applying virtual population analysis to catch and escapement

data from Bristol Bay and Fraser River sockeye salmon stocks (Chapter 2). These two

stock complexes make up a significant proportion (>50%) of sockeye salmon found in the

Gulf of Alaska (Peterman 1984).

Statistical Analysis

I used correlation analyses to detect the presence of critical periods for density-dependent

marine growth of age 1.2 Early Stuart sockeye. Each time series of marine scale growth

was correlated with time series of minimum ocean abundance of age $x.1$ and $x.2+$ sockeye

in the Gulf of Alaska. The $x.1$ and $x.2+$ age categories represent immature ($x.1$) and

maturing ($x.2+$) components of the sockeye population in the Gulf of Alaska. Because

there were two comparisons for each time series of marine growth, Bonferroni

adjustments were used to control the comparisonwise error rate.

Results and Discussion

Scale growth during each marine growth phase of Early Stuart sockeye salmon flucuated without trend from 1954-1991 (Figure 3.1). Growth during the first marine year (M1), which is spent largely within the continental shelf region, slowed for a period of five successive years from 1979-1983. This period follows the well documented climatological shift in the dominant weather system over the northeast Pacific Ocean (Namais et al 1988). The subsequent intensification of gyre upwelling and circulation is believed to have resulted in advection of standing crops of zooplankton toward the perimeter of the Gulf of Alaska (Brodeur and Ware 1992; Hinch unpubl. data) where juvenile sockeye may be found during their first year in the ocean (Hart and Dell 1986). The fact that growth was actually slower during this time suggests that either the zooplankton species preferred by juvenile sockeye were not advected onto the continental shelf region, or conditions were simply not optimal for taking advantage of increased food concentrations.

Figure 3.1. Marine growth of age 1.2 Early Stuart sockeye salmon over the years 1954-
1991, inclusive for ocean entry year (M1), penultimate year (M2), and return year (M3).
Growth stages of a single cohort may be found by subtracting one from the return year
for M2 and subtracting two for M1. For example, growth for the cohort returning in 1990
may be found under 1990 (M3), 1989 (M2), and 1988 (M1).
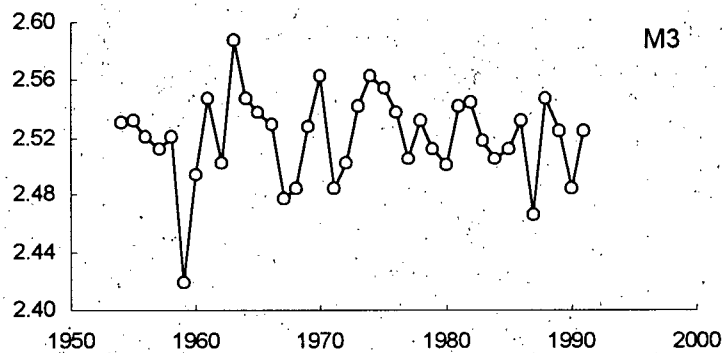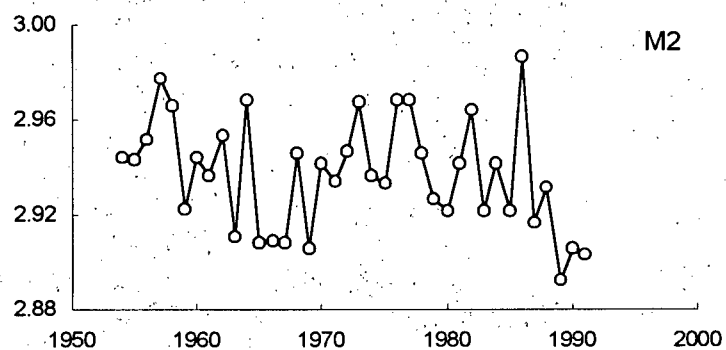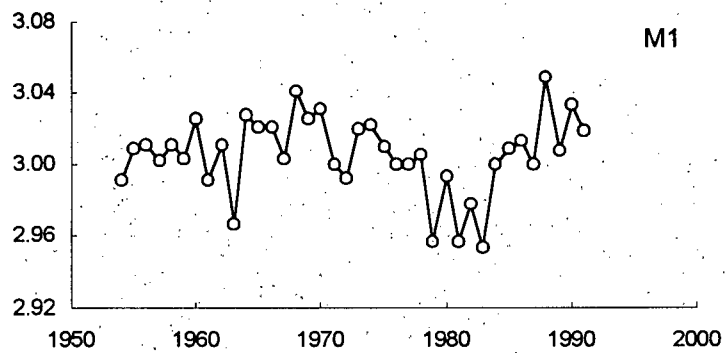
Marine growth during the second year at sea (M2), which is spent in the offshore waters of the Gulf of Alaska, also showed no long-term trend. However, aside from the single high growth rate year in 1986, M2 growth decreased from 1976 to 1991. Slower growth during the period spent in the Central Gulf of Alaska coincides with a period of higher biological productivity in the northeast Pacific Ocean (Brodeur and Ware 1995; Chapter 2). This suggests that effective prey densities were not, in fact high, possibly due to either advection of zooplankton toward the coast, increased predator/prey ratios due to increases in sockeye salmon abundance, or a combination of the two (Chapter 2).

Early Stuart marine scale growth was only correlated with sockeye abundance during the second ocean year (M2; Table 3.1), however the relationship is not statistically significant at the adjusted probability level (P > 0.025). If the relationships are examined by time periods 1954-1975 and 1978-1991 (e.g. Chapter 2), representing low ocean productivity-low salmon abundance and high ocean productivity-high salmon abundance, respectively, then Early Stuart M2 scale growth during the period 1978-1991 is significantly correlated to $x.2+$ sockeye abundance (r = -0.662, P < 0.025, n = 15) (Figure 3.2). In Chapter 2 I found that ocean abundance of sockeye during the second ocean year (M2) over the period 1978-1992 explained 79% and 43% of the variability in length at maturity of age 1.2 Early Stuart males and females, respectively.

Previous attempts to identify critical periods for density dependent growth of sockeye salmon have been limited by our inability to relate annual marine growth to annual estimates of sockeye abundance in the Gulf of Alaska. Using annual growth information

obtained from scales, I have shown that the second ocean year (M2) is the most likely

critical period for density-dependent growth of age 1.2 Early Stuart sockeye salmon. This

supports the conclusions of Chapter 2, where I proceeded under the assumption that

density dependent effects occurred during the penultimate year at sea.

Table 3.1. Age-specific correlations between marine growth estimated from scales (Mx) and age-specific ocean abundance of sockeye. Probabilities and number of data points are included below each r value. All probabilities are controlled for comparisonwise error rate (CER) by dividing $\alpha = 0.05$ by the number of comparisons for each stock/age group. The CER = (.05/2) = 0.025 in all cases. Significant correlation coefficients appear in bold type. Data obtained from 1954 - 1991, inclusive.

	x.1	*x.2+*
Early Stuart 1.2		
M1	-0.195	-0.033
	.284	0.858
	32	32
M2	-0.130	-0.347
	0.470	0.048
	33	33
M3	0.063	-0.083
	0.726	0.645
	33	33

Figure 3.2. Relationships between second year marine growth (M2) of Early Stuart sockeye (sexes combined) and minimum abundance of age $x.2+$ sockeye in the Gulf of Alaska during the period 1954-1975 (open circles;solid line) and 1978-1991 (closed circles; dashed line).
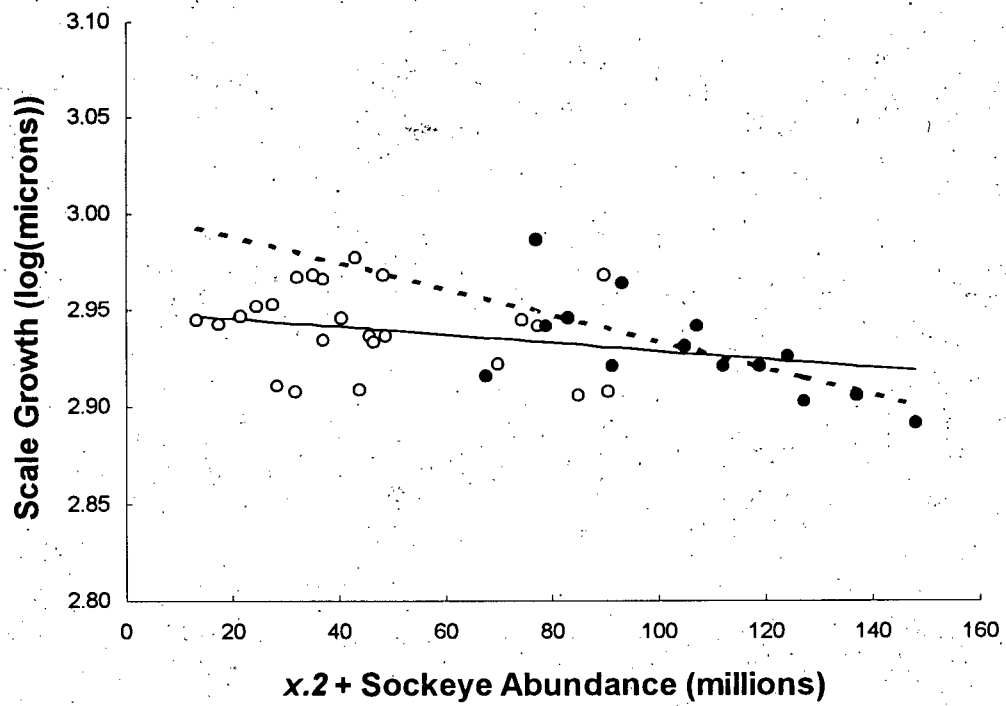
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CONCLUSIONS

Using data from several sockeye salmon stocks I have demonstrated that size at maturity has declined substantially over the past twenty years apparently in response to changing biotic *and* abiotic oceanographic conditions. During this time, these two factors appear to affect marine growth on different temporal and spatial scales. In general, physical oceanographic factors, such as temperature are associated with changes in size at maturity across many stocks during both the 1960s-1970s and 1980s-1990s climatic regimes; suggesting both large spatial (e.g. gyre) and temporal scale effects. Biotic processes, such as competitive interactions among sockeye salmon are more strongly associated with interannual variation in size at maturity, however these associations are restricted to relatively fewer stocks and predominate during the 1980-1990 climatic regime; indicating smaller spatial and temporal scale effects. Therefore, both large and small spatial and temporal scale phenomena appear to affect the marine growth of Fraser River sockeye salmon.

Potential effects of climate change: sockeye salmon may be in hot water
Current trends suggest that the northeast Pacific Ocean has been warming over the past decade; however, it remains uncertain whether the trend is due to global climate warming or a reversal of a regional cooling period which began in the late 1950s (Zebdi and Collie 1995). Realizing the appropriate scales of biotic and abiotic effects represents a positive step toward understanding the potential effects of global climate warming on the marine growth of sockeye salmon. For example, an increase in northeast Pacific Ocean sea surface

growth of most sockeye stocks if salmon abundance is low. If the same situation occurred, but salmon abundance remained at or near present levels, perhaps due to enhancement or increased survival, major declines in size at maturity are likely to result due to the combined effects of high temperature, high abundance, and possibly a reduction in the standing crop of prey (Hinch et al 1995). Large decreases in size at maturity may result in punctuated changes to the population dynamics of sockeye salmon. Decreases in body weight of mature fish will reduce egg production and the ability to migrate upstream and spawn (Healey 1986). To compensate, sockeye salmon may need to remain at sea for an additional year in order to aquire the size and energy reserves necessary to minimize pre-spawning mortality (Peterman 1985; Mangel 1994). However, this would reduce population productivity due to an increase in generation time (Forbes and Peterman 1994). Welch (1994) showed that an additional year at sea would result in a 20% decrease in productivity for populations that primarily mature at age 1.2. Increases in average age at maturity associated with increases in SST have been observed in other salmon species, but not sockeye (Ogura et al. 1991; Helle and Hoffman 1995). If salmon abundance were to decrease during extended periods of warming, then growth reductions may be less obvious because constraints imposed by density dependent growth processes could be alleviated. Even if abundance decreases, large changes in ocean temperature and circulation could result in a re-distribution of sockeye stocks in the northeast Pacific Ocean and, combined with a reduction in thermal habitat, may result in higher sockeye densities. Although it does not appear to be a critical factor in regulating competitive interactions at the present time, thermal habitat area could become very important if it is reduced to critical levels in the future. If the changes to climate are abrupt then sockeye salmon may not have the

capacity, nor the time, to compensate by altering their life history strategies and migrations.

Existing along the southernmost portion of the species range, Fraser River sockeye may also be vulnerable to anthropogenic impacts of climate change such as an increased need for irrigation and hydropower, as well as a possible redistribution of the human population to more inland areas where the major Fraser River sockeye populations are found. Regardless of climate change, communities in the interior of British Columbia will continue to grow in response to tourism and natural resource opportunities, as well as human population growth. Therefore, it is not improbable that the present priority to preserve salmon stocks will dwindle in response to increasing natural resource exploitation and development in the future.

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Appendix 1. Reconstructed ocean abundance of Fraser River, British Columbia sockeye salmon totaled over ten major stocks (Chapter 2; Methods; Sockeye Abundance Data).

Year	x.1	x.2	x.3	x.2+	x.3+	Total
1954	2358494	2146020	10860070	13006090		15364584
1955	3758744	2358494	2103601	4462095		8220839
1956	18121275	3758744	2323234	6081978		24203253
1957	3373515	18121275	3740694	21861969		25235484
1958	3137414	3373515	17378718	20752233		23889647
1959	3986743	3137414	3294798	6432212		10418955
1960	3058712	3986743	3101792	7088535		10147247
1961	3373098	3058712	3972652	7031364		10404462
1962	1483485	3373098	2912350	6285448		7768933
1963	2713997	1483485	3314348	4797833		7511830
1964	4633963	2713997	1447896	4161893		8795856
1965	5601728	4633963	2645294	7279257		12880985
1966	2636677	5601728	4511863	10113591		12750268
1967	3839566	2636677	5387639	8024316		11863882
1968	5590051	3839566	2581631	6421197		12011248
1969	6647483	5590051	3790842	9380893		16028376
1970	3104704	6647483	5408347	12055830		15160534
1971	6034608	3104704	6496469	9601173		15635781
1972	6994942	6034608	3032115	9066723		16061665
1973	2712868	6994942	5943391	12938333		15651201
1974	3475102	2712868	6700760	9413628		12888730
1975	4688802	3475102	2598427	6073529		10762331
1976	8334559	4688802	3386738	8075540		16410099
1977	5040149	8334559	4623458	12958017		17998166
1978	2604726	5040149	8129109	13169258		15773984
1979	6743796	2604726	5007207	7611933		14355729
1980	10567122	6743796	2551828	9295624		19862746
1981	4276185	10567122	6715052	17282174		21558359
1982	5159330	4276185	10405130	14681315		19840645
1983	11536838	5159330	4246959	9406289		20943127
1984	10893588	11536838	5136120	16672958		27566546
1985	5808919	10893588	11510940	22404528		28213447
1986	1996769	5808919	10725480	16534399		18531168
1987	16608458	1996769	5728556	7725325		24333783
1988	16482503	16608458	1984061	18592519		35075022
1989	9692233	16482503	16553180	33035683		42727916
1990	4679200	9692233	16391637	26083870		30763070
1991	70399	4679200	9659704	14338904		14409303

Appendix 2. Reconstructed ocean abundance of Bristol Bay, Alaska sockeye salmon totaled over eight major stocks (Chapter 2; Methods; Sockeye AbundanceData).

Year	x.1	x.2	x.3	x.2+	x.3+	Total
1954	12885449	74239		74239		12959688
1955	5576760	12885449	74239	12959688	74239	18536448
1956	3074815	5576760	12885449	18536448	12959688	21611263
1957	11348124	3074815	5576760	21283689	18208874	32631813
1958	50861056	11348124	3074815	16164706	4816582	67025762
1959	11624800	50861056	11348124	63551782	12690726	75176582
1960	11036399	11624800	50861056	67084882	55460082	78121281
1961	6574750	11036399	11624800	38613010	27576611	45187760
1962	13693680	6574750	11036399	21137058	14562308	34830738
1963	69784161	13693680	6574750	23334849	9641169	93119010
1964	8516429	69784161	13693680	85761347	15977186	94277776
1965	10562044	8516429	69784161	83394548	74878119	93956592
1966	9348154	10562044	8516429	33746542	23184498	43094696
1967	21431007	9348154	10562044	23590148	14241994	45021155
1968	50703621	21431007	9348154	33801824	12370817	84505445
1969	10731216	50703621	21431007	75624061	24920440	86355277
1970	5786658	10731216	50703621	65382861	54651645	71169519
1971	2782444	5786658	10731216	27218783	21432125	30001227
1972	14052785	2782444	5786658	12313070	9530626	26365855
1973	22863876	14052785	2782444	19318913	5266128	42182789
1974	12216522	22863876	14052785	39140056	16276180	51356578
1975	11148168	12216522	22863876	40200634	27984112	51348802
1976	19461300	11148168	12216522	27035451	15887283	46496751
1977	44058693	19461300	11148168	35466326	16005026	79525019
1978	65284516	44058693	19461300	69965779	25907086	135250295
1979	32265551	65284516	44058693	116612192	51327676	148877743
1980	12872166	32265551	65284516	109339337	77073786	122211503
1981	50097683	12872166	32265551	61712762	48840596	111810445
1982	45063156	50097683	12872166	78694752	28597069	123757908
1983	33886331	45063156	50097683	102190719	57127563	136077050
1984	19538582	33886331	45063156	90350966	56464635	109889548
1985	29130175	19538582	33886331	68957036	49418454	98087211
1986	21290496	29130175	19538582	60579470	31449295	81869966
1987	52734737	21290496	29130175	59955929	38665433	112690666
1988	51507473	52734737	21290496	86207787	33473050	137715260
1989	39772529	51507473	52734737	115182222	63674749	154954751
1990	48133836	39772529	51507473	110752357	70979828	158886193
1991	41671245	48133836	39772529	112344431	64210595	154015676
1992	33098800	41671245	48133836	112515097	70843852	145613897

Appendix 3. Minimum ocean abundance of sockeye salmon totaled over Fraser River and Bristol Bay stocks.

Year	x.1	x.2	x.3	x.2+	x.3+	Total
1954	15243943	2220259	10860070	13080329		28324272
1955	9335504	15243943	2177840	17421783	74239	26757287
1956	21196090	9335504	15208683	24618426	12959688	45814516
1957	14721639	21196090	9317454	43145658	18208874	57867297
1958	53998470	14721639	20453533	36916939	4816582	90915409
1959	15611543	53998470	14642922	69983994	12690726	85595537
1960	14095111	15611543	53962848	74173417	55460082	88268528
1961	9947848	14095111	15597452	45644374	27576611	55592222
1962	15177165	9947848	13948749	27422506	14562308	42599671
1963	72498158	15177165	9889098	28132682	9641169	100630840
1964	13150392	72498158	15141576	89923240	15977186	103073632
1965	16163772	13150392	72429455	90673805	74878119	106837577
1966	11984831	16163772	13028292	43860133	23184498	55844964
1967	25270573	11984831	15949683	31614464	14241994	56885037
1968	56293672	25270573	11929785	40223021	12370817	96516693
1969	17378699	56293672	25221849	85004954	24920440	102383653
1970	8891362	17378699	56111968	77438691	54651645	86330053
1971	8817052	8891362	17227685	36819956	21432125	45637008
1972	21047727	8817052	8818773	21379793	9530626	42427520
1973	25576744	21047727	8725835	32257246	5266128	57833990
1974	15691624	25576744	20753545	48553684	16276180	64245308
1975	15836970	15691624	25462303	46274163	27984112	62111133
1976	27795859	15836970	15603260	35110991	15887283	62906850
1977	49098842	27795859	15771626	48424343	16005026	97523185
1978	67889242	49098842	27590409	83135037	25907086	151024279
1979	39009347	67889242	49065900	124224125	51327676	163233472
1980	23439288	39009347	67836344	118634961	77073786	142074249
1981	54373868	23439288	38980603	78994936	48840596	133368804
1982	50222486	54373868	23277296	93376067	28597069	143598553
1983	45423169	50222486	54344642	111597008	57127563	157020177
1984	30432170	45423169	50199276	107023924	56464635	137456094
1985	34939094	30432170	45397271	91361564	49418454	126300658
1986	23287265	34939094	30264062	77113869	31449295	100401134
1987	69343195	23287265	34858731	67681254	38665433	137024449
1988	67989976	69343195	23274557	104800306	33473050	172790282
1989	49464762	67989976	69287917	148217905	63674749	197682667
1990	52813036	49464762	67899110	136836227	70979828	189649263
1991	41741644	52813036	49432233	126683335	64210595	168424979
1992	33098800	41671245	48133836	112515097	70843852	145613897