

Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature

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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 10 Fraser River sockeye stocks, we demonstrate that size at maturity has generally declined over the past 42 yr for females in all stocks and for males from eight stocks. Independent of this temporal trend, we 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. We 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.

Résumé : Contrairement à d'autres saumons du Pacifique (*Oncorhynchus* spp.) canadiens, on n'a pas signalé dans les études antérieures de déclin à long terme de la taille à maturité du saumon sockeye (*O. nerka*) du fleuve Fraser. Nous avons démontré, à l'aide des données spécifiques de 10 stocks de saumon sockeye du fleuve Fraser, que la taille à maturité a décliné de façon générale au cours des 42 dernières années dans tous les stocks pour ce qui est des femelles et dans huit stocks pour ce qui est des mâles. Indépendamment de cette tendance temporelle, nous avons constaté que la taille à maturité des deux sexes dans tous les stocks était plus faible au cours des années où la température de la surface de la mer était relativement chaude. Une croissance plus lente au cours des années plus chaudes peut être causée directement par une augmentation de la demande métabolique ou indirectement par des changements dans l'océan qui influent sur l'acquisition des aliments. Nous estimons que l'aptitude physique du saumon sockeye du fleuve Fraser sera réduite dans l'avenir si la température de la surface de la mer augmente et si l'abondance du saumon reste proche des valeurs actuelles.

[Traduit par la Rédaction]

Introduction

The size at maturity of Pacific salmon (*Oncorhynchus* spp.) has been decreasing in recent decades (Ricker 1982, 1995; Ogura et al. 1991; Helle and Hoffman 1995; Ishida et al. 1995). From 1951 to 1975, average weight of adult pink (*O. gorbuscha*), coho (*O. kisutch*), and chinook salmon (*O. tshawytscha*) 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). Our 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. We 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 2 yr 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 inter-annual 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; Laevastu 1984; Blackbourn 1987; Hsieh et al. 1991; Ishida et al. 1995; Welch

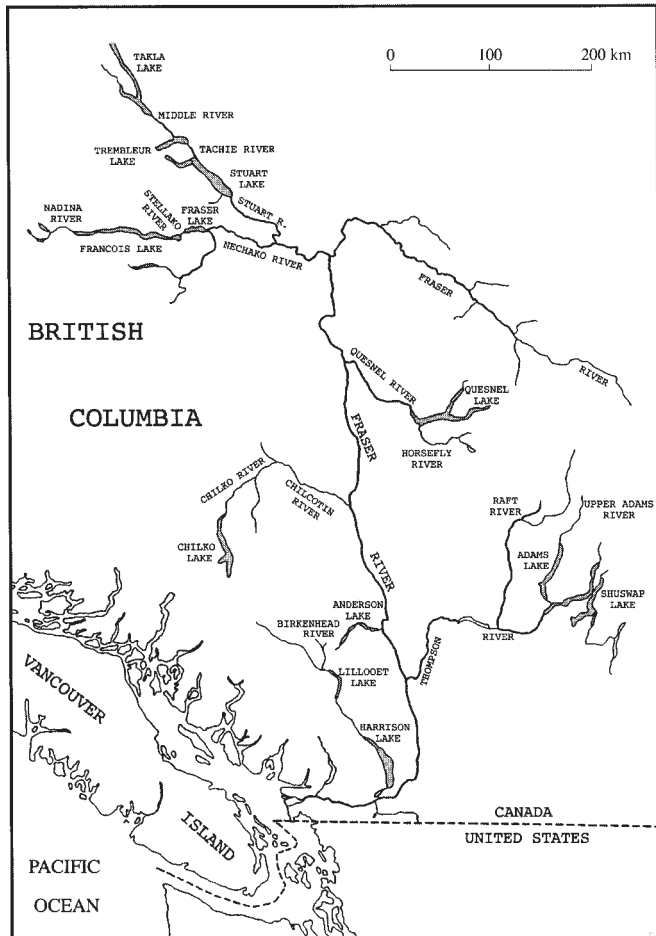
Received January 30, 1996. Accepted October 7, 1996.
J13279

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Fig. 1. Map of the major sockeye salmon spawning rivers and rearing lakes of the Fraser River watershed (adapted from Killick and Clemens 1963).



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. Our 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, we used the average lengths of sockeye salmon measured on the major spawning grounds in the Fraser River drainage (Fig. 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 4₂ 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. The 4₂ 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 to 1993 (M. Lapointe, Pacific Salmon Commission, Vancouver, B.C., personal communication).

There was considerable variation 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, we excluded years in which we 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 the samples were less than 10. After excluding some data, annual sample sizes ranged from 72 to >500, depending on the stock (Table 1). A summary of stock- and sex-specific mean SL is presented in Table 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 142–146°W and 52–56°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). We used only January–July monthly temperatures because this period represents a portion of sockeye's life history that is halfway through their ocean residency when they are probably largely in the area where SST was estimated. In order to assess associations between SST encountered during their high-seas residency and SL at maturity, SST data were lagged by 1 yr before carrying out any statistical analyses.

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 SST was assessed by regressing SST on year.

In order to examine the influence of within-year variability in SL on among-year trends, we 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. We used the MDD as a check on the statistical significance of sex- and stock-specific SL versus year relationships.

We 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

Table 1. Mean and range of sample sizes used to determine within-year standard lengths for each stock over the period 1952–1993, inclusive.

Stock	Females				Males			
	Mean	Range	MSE	MDD	Mean	Range	MSE	MDD
Adams	142	20–513	4.11	0.68	108	35–337	4.82	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
Gate	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

Note: Mean square error (MSE, cm²) of length at maturity and minimum detectable difference (MDD, cm) in among-year comparisons are based on data from 1984 to 1993, inclusive.

Table 2. Annual mean standard length at maturity (cm), SD, and number of years of data (*n*) for age 4₂ sockeye salmon stocks of the Fraser River.

Stock	Females					Males				
	Mean	SD	<i>n</i>	<i>r</i>	<i>P</i>	Mean	SD	<i>n</i>	<i>r</i>	<i>P</i>
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

Note: Also shown are the correlation coefficients (and associated probabilities) between standard length and year.

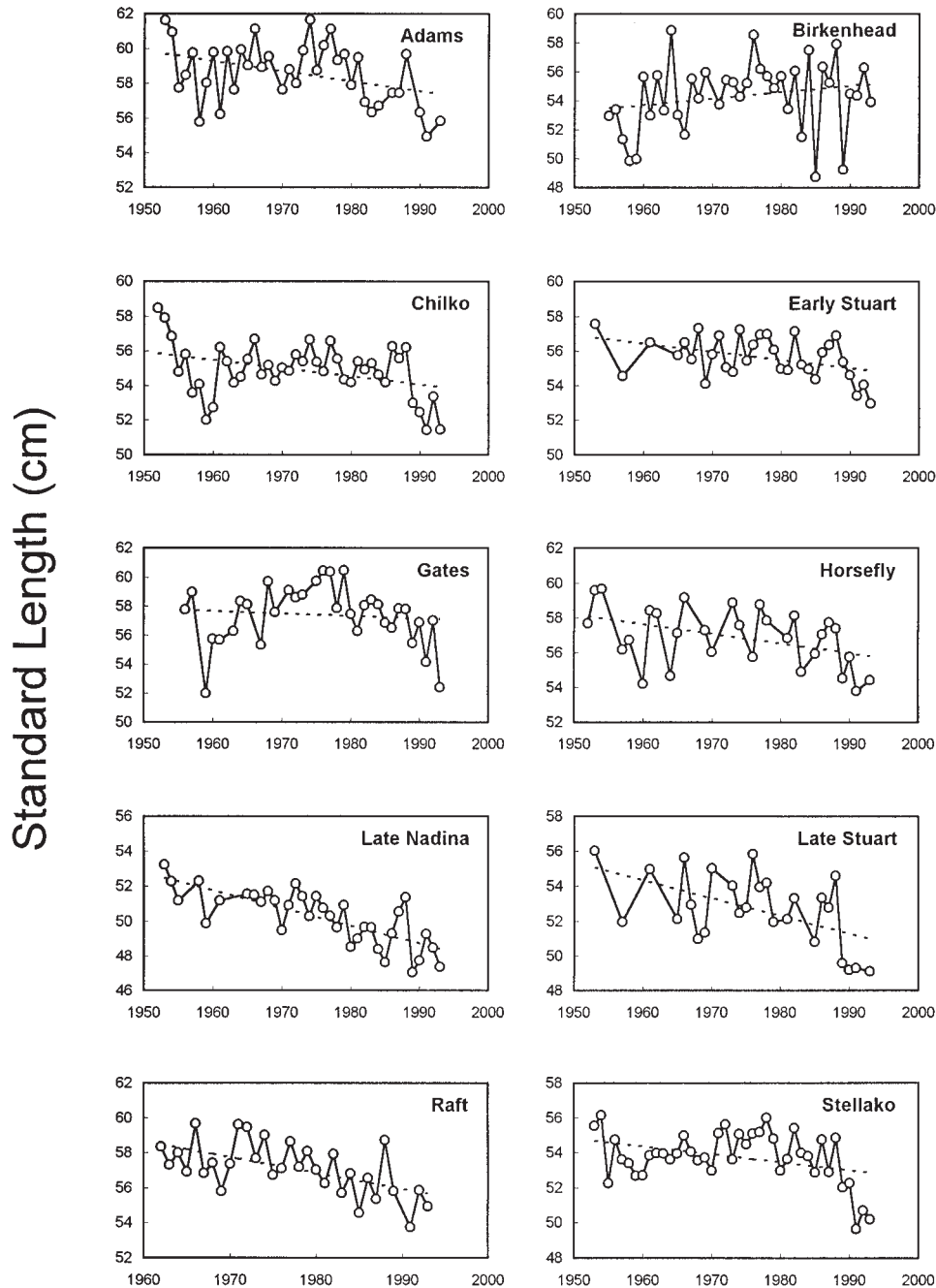
among stocks for females (ANCOVA; $P = 0.17$). This interaction term was then removed from the ANCOVA, revealing a significant effect of year ($P < 0.01$) and stock ($P < 0.01$). In all stocks, female SL declined in a similar fashion over time (Fig. 2; Table 2). Females from Adams, Gates, and Raft stocks 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 (Fig. 3; Table 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 (Fig. 2; Table 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 (Figs. 1 and 3; Table 2) and the 1990's produced the smallest Fraser River sockeye salmon out of the previous five decades for both males and females.

Power analyses indicated that MDD among years in stock-specific size at maturity ranged from 0.83 to 1.56 cm for males and from 0.49 to 0.88 cm for females (Table 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 Figs. 1 and 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) 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) that 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 (Killick and Clemens 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

Fig. 2. Mean standard lengths of male Fraser River sockeye stocks over a 42-yr period. Missing data points were either not available or excluded due to low sample size ($n < 20$). The broken line represents linear time trend fitted by least squares. Correlation coefficients are reported in Table 2.



largest sizes at maturity (Table 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). We 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.

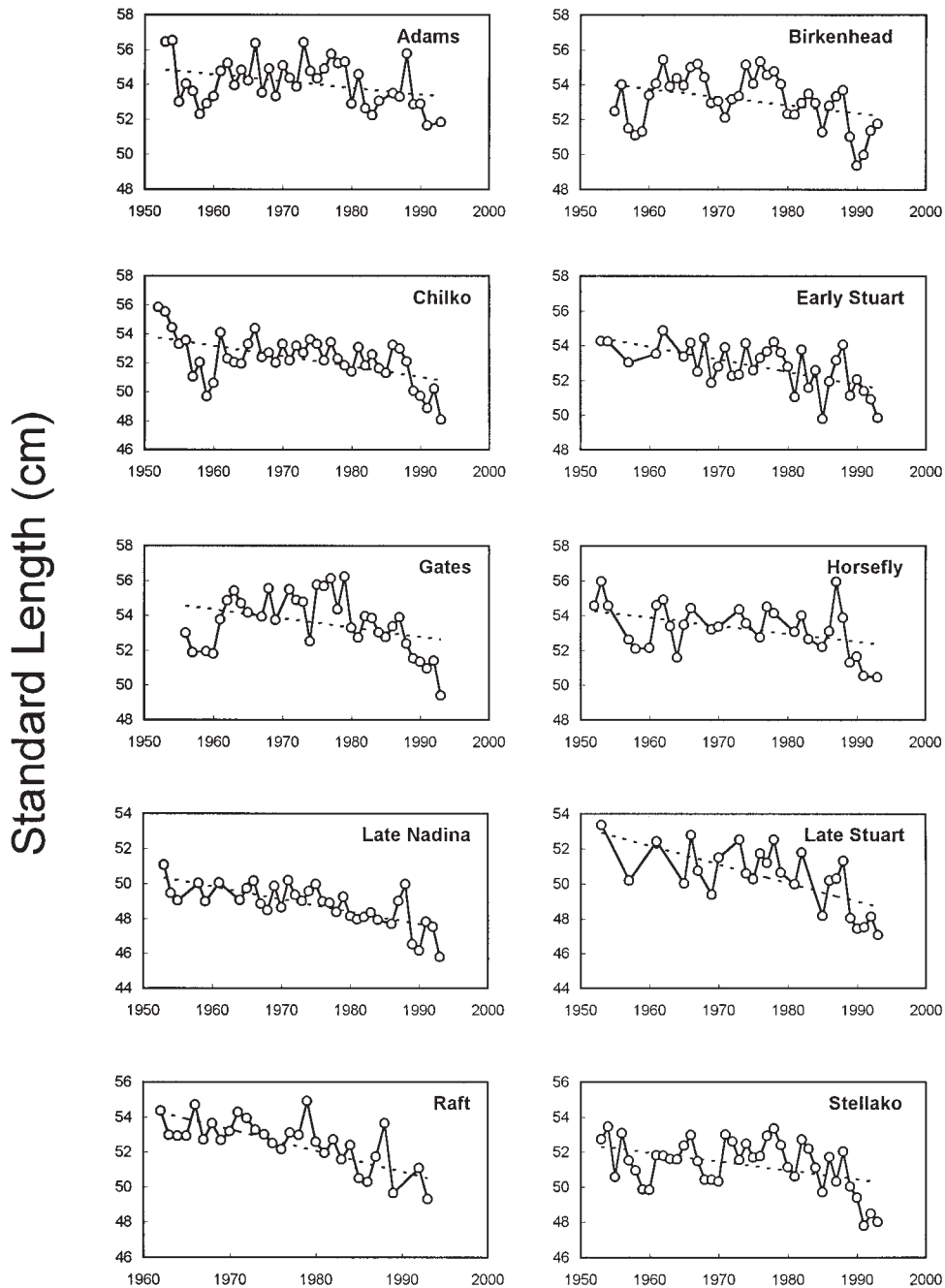
Size at maturity and SST relationships

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 we observed in the SST data indicates a similar punctuated change rather than linear increase (Fig. 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

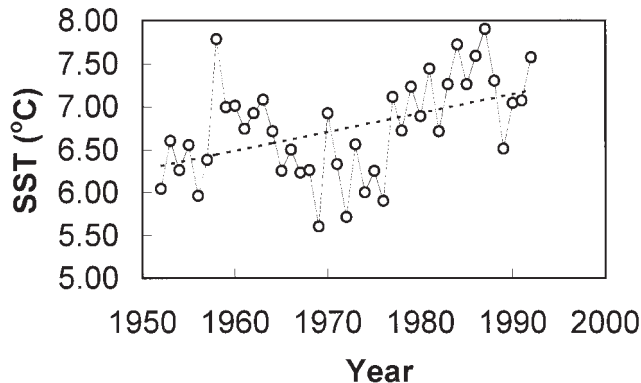
Fig. 3. Mean standard lengths of female Fraser River sockeye stocks over a 42-yr period. Missing data points were either not available or excluded due to low sample size ($n < 20$). The broken line represents linear time trend fitted by least squares. Correlation coefficients are reported in Table 2.



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. Our multistock

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 1970's, also found that warmer SST were associated with smaller sockeye salmon. Our results indicate that this relationship was consistently evident at the individual stock level, including the two stocks that 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.

Fig. 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).



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 (Gilhousen 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 has doubled over the past, relatively warm 15 yr (Beamish and Bouillon 1993), macrozooplankton biomass has more than doubled during this same time (Brodeur and Ware 1995). Hinch et al. (1995b) showed that zooplankton biomass was correlated with 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.

Potential impacts of climate warming: sockeye salmon may be in hot water

If we assume that SST is linked with changes in size of sockeye salmon, we can speculate on the potential effects of future climate warming. Global climate models predict that, over the century, the northeast Pacific will experience a 2–4°C increase in SST (Boer et al. 1992). 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 that began in 1958 (Zebdi and Collie 1995). In future years, if SST continue to increase and sockeye salmon abundance stays at or near present levels, sockeye salmon may continue to get smaller. 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 attain the necessary size and energy reserves to spawn successfully (Peterman 1985; Mangel 1994). However, an older age at maturity would decrease reproductive potential due to an increase in generation time. 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). Hinch et al. (1995b) speculated that changes in sea level pressure gradients over the North Pacific associated with global climate warming will cause a decline in upwelling-induced nutrients. Thus, growth could be negatively affected by increases in SST and decreases in prey availability. However, 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.

Acknowledgments

We thank Jim Woodey and Mike Lapointe from the Pacific Salmon Commission for providing the spawning ground data. Ian Jardine provided assistance with the SST data and Fraser River map. Insights from David Welch, Mike Healey, and Mike Lapointe are also appreciated. S.P. Cox was supported a Natural Sciences and Engineering Research Council of Canada strategic grant.

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