

Potential effects of climate change on marine growth and survival of Fraser River sockeye salmon

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Abstract: Simulation results from the Canadian Climate Centre's atmospheric general circulation model (CCC GCM) coupled to a simplified mixed-layer ocean model predict that doubled atmospheric CO₂ concentrations would increase northeast Pacific Ocean sea surface temperatures and weaken existing north-south air pressure gradients. On the basis of predicted changes to air pressure and an empirical relationship between wind-driven upwelling and zooplankton biomass, we calculate that production of food for sockeye salmon (*Oncorhynchus nerka*) may decrease by 5-9%. We developed empirical relationships between sea surface temperature, zooplankton biomass, adult recruitment, and terminal ocean weight for the early Stuart stock of Fraser River sockeye salmon. Our analyses show that warmer sea surface temperatures, larger adult recruitment, and lower zooplankton biomass are correlated with smaller adult sockeye. Bioenergetics modeling suggests that higher metabolic costs in warmer water coupled with lower food availability could cause the observed reductions in size. Warmer sea surface temperatures during coastal migration by juveniles were correlated with lower recruitment 2 yr later. Warmer sea surface temperatures may be a surrogate for increased levels of predation or decreased food during the juvenile stage. We speculate that Fraser sockeye will be less abundant and smaller if the climate changes as suggested by the Canadian Climate Centre's general circulation model.

Résumé : Les résultats obtenus par des simulations faites avec le modèle de circulation atmosphérique général du Centre climatologique canadien, et combinés à ceux d'un modèle simplifié à couche océanique mixte, nous amènent à prévoir que le doublement de la concentration atmosphérique du CO₂ conduirait à une hausse de la température en surface de l'eau dans le nord-est du Pacifique ainsi qu'à un affaiblissement des gradients de pression atmosphérique nord-sud. En nous appuyant sur les changements prévus de la pression atmosphérique et sur un rapport empirique entre les remontées des eaux sous l'effet du vent et la biomasse zooplanctonique, nous pouvons calculer que la production des ressources alimentaires exploitées par le saumon rouge (*Oncorhynchus nerka*) pourrait être réduite de 5 à 9%. Nous avons déterminé des rapports empiriques entre la température en surface de l'eau, la biomasse zooplanctonique, le recrutement chez les adultes et le poids au retour de la migration en mer des sujets qui constituent le stock hâtif de saumon rouge de la Stuart dans le Fraser. Nos analyses montrent que l'élévation de la température en surface de l'eau, le recrutement plus important chez les adultes et la baisse de la biomasse zooplanctonique sont en corrélation avec une taille inférieure des adultes du saumon rouge. Les modèles de bioénergétique paraissent montrer que le coût métabolique accru de la vie en eaux plus chaudes, lorsqu'il est combiné à une baisse des ressources alimentaires, pourrait expliquer la réduction observée de la taille. Une hausse de la température en surface de l'eau pourrait avoir le même effet que la prédation accrue ou qu'une

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diminution des ressources alimentaires pendant le stade juvénile. Nous croyons que le saumon rouge du Fraser sera moins abondant et plus petit si le changement climatique annoncé par le modèle de circulation atmosphérique général du Centre climatologique canadien se réalisait.

[Traduit par la Rédaction]

Introduction

Under present global energy- and land-use practices, carbon dioxide (CO₂) concentrations in the atmosphere will double within the next 100 years, and there is strong scientific consensus that global climate patterns will change as a result (Houghton et al. 1990). There is a growing belief that climate change will have profound effects on salmon stocks (Chatters et al. 1991; Francis and Sibley 1991; Neitzel et al. 1991; Levy 1992; Henderson et al. 1992; Mangel 1994; Hinch et al. 1994; Welch et al. 1995). Changes to the climates of British Columbia and the northeast Pacific Ocean may affect the production of Fraser River sockeye salmon (*Oncorhynchus nerka*), the most valuable salmon resource in British Columbia. Serious biological and economic consequences would arise if climate change negatively influences sockeye production.

As 1 yr olds in late spring, most Fraser River sockeye migrate to the ocean. During the summer, sockeye migrate northward along the coast of British Columbia and Alaska (Groot and Cooke 1987; International North Pacific Fisheries Commission 1986). Young fish are thought to enter the open Pacific Ocean in the fall (International North Pacific Fisheries Commission 1986) where they spend 1–4 yr foraging. Most Fraser sockeye begin to mature after 2 yr in the ocean and start homeward migration. Alterations to either freshwater or marine habitats resulting from climate change could thus affect sockeye production.

Using output from general circulation models (GCMs) in conjunction with empirical time-series analyses of hydrologic data, Moore (1991) and Levy (1992) suggested that in the Fraser River watershed, doubled atmospheric CO₂ will be associated with (i) an increase in river, lake, and groundwater temperatures of 1–4°C, (ii) an increase in river velocities in winter and spring, (iii) a decrease in river velocities in summer and fall, and (iv) earlier spring freshets. Altered runoff patterns are predicted to make the Fraser drainage more oligotrophic, resulting in a reduction in the abundance and availability of food for juvenile sockeye and hence a decrease in their growth and survival (Henderson et al. 1992). In-river and prespawning mortality of migrating adults is also predicted to increase with increasing temperature (Levy 1992; International Pacific Salmon Fisheries Commission 1990) as diseases become more prevalent and migration more energetically expensive. Henderson et al. (1992) and Levy (1992) both concluded that freshwater production of Fraser sockeye will be reduced if atmospheric CO₂ increases.

Fraser sockeye spend over half of their lives in the northeast Pacific Ocean. During this period, 99% of their growth is completed and all surplus energy needed for return migration and spawning is acquired. GCMs predict that doubled atmospheric CO₂ will increase the sea surface temperature (SST) in the northeast Pacific Ocean and weaken the north–south air pressure gradient over the northeast Pacific Ocean (McBean 1990; McBean et al.

1991). A weakening of westerly winds would result from the changes to the air pressure gradient, which could reduce secondary productivity owing to weaker open ocean upwelling (Hsieh and Boer 1992). The effects of climate change on the marine environment may have powerful influences on sockeye production. However, few studies have assessed the potential impact of increased atmospheric CO₂ on the growth and abundance of ocean-dwelling salmon.

Warmer northeast Pacific Ocean SSTs are correlated with poorer marine survival in Chilko Lake sockeye (Hsieh et al. 1991) and smaller adult weight in early Stuart sockeye (Hinch et al. 1994). These results imply that increasing atmospheric CO₂ may have negative effects on oceanic production of sockeye. Under constant food levels, SSTs higher than those at present will likely result in smaller adult sockeye (Hinch et al. 1994). This effect may be exacerbated by reductions in availability of food under future climates but has not been addressed. The relationship between ocean salmon production and both SST and food availability needs to be fully evaluated in the context of regional climate change projections for the northeast Pacific Ocean.

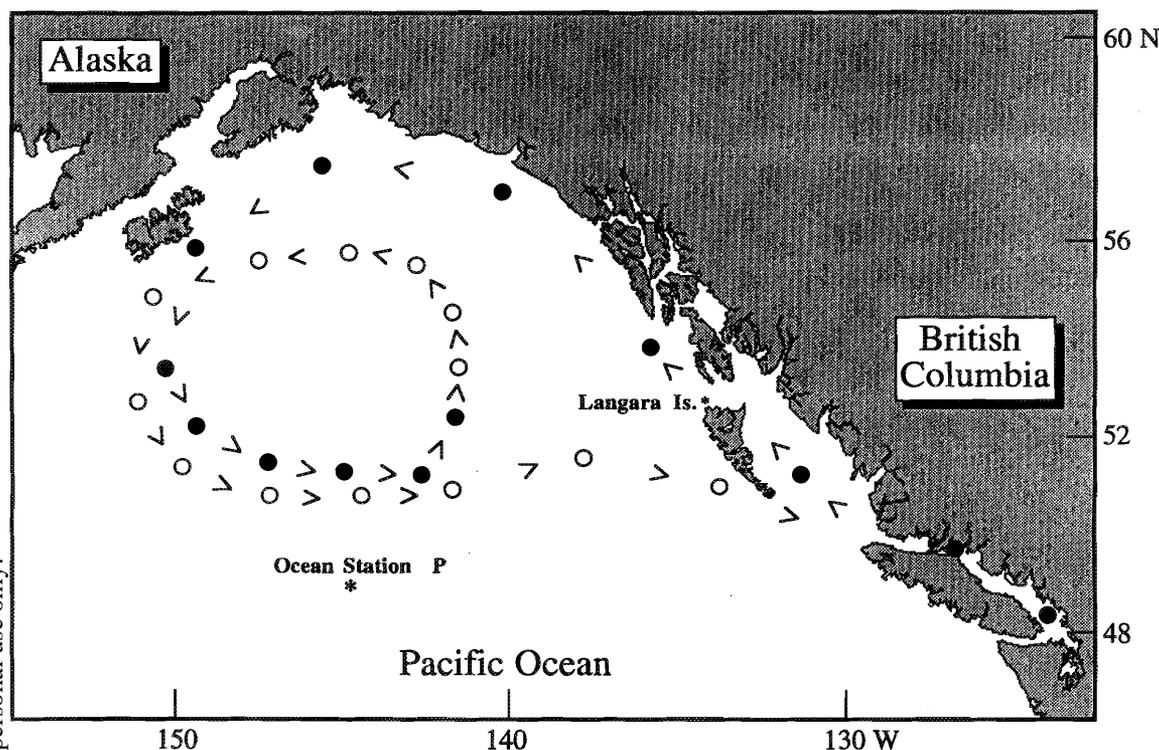
The objective of this paper is to evaluate the probable consequences of changes in SST and food availability, brought on by doubled atmospheric CO₂, to the adult recruitment and weight of Fraser sockeye. We develop empirical relationships between SST, an index of food abundance, adult recruitment, and mean weight for early Stuart sockeye, one of the Fraser stocks. We illustrate the potential effects on sockeye production of the changes in ocean climate forecasted by a GCM using these empirical relationships and a bioenergetics model to predict growth during the marine life-history period.

Materials and methods

Adult recruitment and spawning success estimates for 4-yr-old (age 4₂) early Stuart sockeye were available from 1952 to 1992. Recruitment data collection methodology was outlined in Woodey (1987) and Cass (1989). Recruitment data for 1952–1985, not partitioned by age, were presented in Cass (1989). Spawning success data from 1949 to 1987 were presented and described by the International Pacific Salmon Fisheries Commission (1990). Generally, over 90% of early Stuart sockeye return at age 4₂, and like most other Fraser sockeye stocks, exhibit 4-yr abundance cycles. Each of the four spawning years is referred to as a cycle line, with large cycle line spawning runs typically producing large adult recruitments and vice versa (Walters and Woodey 1992).

To assess the potential effect of SST on early Stuart sockeye survival_(t), we examined the regression relationship between an index of survival, $\ln(4_2 \text{ recruitment}_{(t)} / \text{female spawning success}_{(t-4)})$, and coastal SST_(t-2). Sockeye likely encountered these SSTs approximately 2 yr prior to reaching the river mouth when they were migrating

Fig. 1. Hypothetical monthly positions of Fraser River sockeye (adapted from Brett 1983). Solid and open circles represent first and second years of ocean residence, respectively. The first month of ocean life starts at the mouth of the Fraser River in late May (solid circle at 48°N); all other circles represent monthly midpoints. SST recording stations at Langara Island (54°N, 133°W) and ocean station P (50°N, 145°W) are indicated.



northward along the British Columbia coast as juveniles. We chose to examine SSTs experienced early in their ocean life because factors affecting interannual variability in marine salmon survival may have their largest influence during the first year of coastal life (reviewed by Peterman 1987).

Owing to the 4-yr abundance cycle, among-year variation in adult recruitment was large (Table 1) and this variation may obscure relationships between recruitment and SST. We therefore partitioned the data by cycle line and used analysis of covariance with SST as the covariate.

Average monthly SST was calculated from daily records of the Langara Island coastal temperature station (Fig. 1), for the years 1950–1990 (H. Freeland, Institute of Ocean Sciences, Department of Fisheries and Oceans, Sidney, BC V8L 4B2, Canada, personal communication). Average spring SSTs were calculated as the mean of monthly values in April to July inclusive.

Average annual weights of early Stuart sockeye were calculated from 1967 to 1993 using the Canadian Department of Fisheries and Oceans' salmon stock assessment catch data base for the lower Fraser River gill-net fishery. Early Stuart sockeye arrive at and migrate up the Fraser before other stocks. We assumed that sockeye intercepted between June 15 and July 15 were primarily early Stuart sockeye and accordingly based our calculations of average terminal weights using sockeye captured during this time period. While in operation, the fishery removes most of the sockeye from that portion of the Fraser River,

Table 1. Cycle-specific statistics of adult early Stuart sockeye recruitment, and spring coastal SSTs measured 2 yr prior to adult return.

	Cycle			
	1989	1990	1991	1992
No. of years	10	10	10	11
Recruitment ($\times 10^5$)				
Mean	8.40	1.18	2.02	0.96
Maximum	13.66	2.41	4.98	2.86
Minimum	2.52	0.27	0.15	0.10
SD	4.33	0.63	1.66	0.90
SST ($^{\circ}$ C)				
Mean	9.03	8.94	9.19	8.96
Maximum	10.63	10.03	10.73	9.58
Minimum	8.18	7.88	8.38	8.40
SD	0.62	0.37	0.43	0.17

suggesting that gillnetting is not strongly size selective in its removal of fish (J. Woodey, Pacific Salmon Commission, Vancouver, BC V6E 1B9, Canada, personal communication).

Sockeye bioenergetics models predict that growth is greatest during spring of the final ocean year. From mid-April to mid-June, sockeye may accumulate 20–30% of their terminal ocean weight (Brett 1983; Hinch et al. 1994),

Table 2. Pearson correlations (lower left diagonal) and associated probabilities (upper right diagonal) between adult recruitment, terminal weight, ocean station P May SST, and ocean station P spring zooplankton biomass.

	Recruitment	SST	Weight	Zooplankton
1967–1980				
Recruitment	—	0.858	0.200	0.165
SST	–0.053	—	0.292	0.899
Weight	–0.364	–0.303	—	0.019
Zooplankton	–0.393	–0.038	0.615	—
1967–1992				
Recruitment	—	0.968	0.050	
SST	0.008	—	0.056	
Weight	–0.389	–0.380	—	

so environmental factors could have large influences on growth during this time. We therefore chose to examine relationships between terminal ocean weight and features of sockeye habitat measured during their final spring.

Average May SSTs at ocean station P (Fig. 1) were determined, using daily SST records (H. Freeland, Institute of Ocean Sciences, Department of Fisheries and Oceans, Sidney, BC V8L 4B2, Canada, personal communication), for years that corresponded to the river entry weight data. Blackbourn (1987) suggested that maturing early Stuart sockeye may be distributed closer to ocean station P than other Fraser sockeye stocks. Thus, variability in ocean station P spring SSTs may be indicative of spring SST variability experienced by maturing early Stuart sockeye.

Zooplankton biomass was determined at ocean station P from 1958 to 1980 (June 15 – July 31) and the data were compiled by Brodeur and Ware (1992). Sockeye forage largely on euphausiids, occasionally eating small fish and squid (Brett 1983; Brodeur et al. 1987; Brodeur and Percy 1990). Although the zooplankton samples primarily consisted of smaller organisms (e.g., amphipods and copepods), it is reasonable to assume that annual changes in their productivity will be reflected in changes to euphausiids and micronekton.

We used multiple regression analyses to determine relationships between zooplankton abundance, SST, and terminal ocean weight. Sockeye abundance may contribute to variation in terminal ocean weight, so early Stuart adult recruitment was also used as a variable in these analyses.

We used a simple bioenergetics model to evaluate the effects of changes in temperature and food on terminal ocean weight. Predictions from the bioenergetics model complement the identified empirical relationships between temperature, food, and weight and suggest a functional explanation for the empirical results. The details of model parameters, equations, assumptions, sensitivity, and validation are discussed in previous papers (Beauchamp et al. 1989; Hinch et al. 1994), and will only be briefly described here. This model predicts monthly energy accumulation by an early Stuart sockeye during its 27-month ocean phase of life (Fig. 1). We used literature values for food consumption, metabolism, excretion, and egestion to estimate growth. Final ocean weights predicted from our model

under recent SST regimes fell within the range of empirical average terminal weights for early Stuart sockeye (Hinch et al. 1994). In this paper, we modify input into the bioenergetics model to account for changes in both SST and food abundance that could result from future changes to climate.

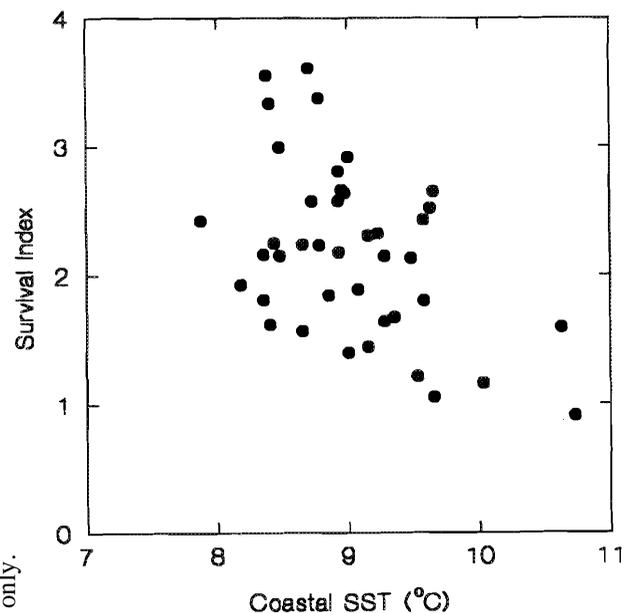
Simulation results from the Canadian Climate Centre's (CCC) atmospheric GCM coupled to a simplified mixed-layer ocean model were used to estimate SST and sockeye food biomass changes in the northeast Pacific Ocean resulting from the effects of climate change induced by greenhouse gases. The CCC GCM described by McFarlane et al. (1992) and Boer et al. (1992) provides a reasonable simulation of global climate (Gates et al. 1990). Future changes in SST and sea-level pressure (SLP) in the northeast Pacific Ocean were estimated by taking the difference between the 10-yr means of $1 \times \text{CO}_2$ and $2 \times \text{CO}_2$ climatologies. We assessed potential alterations to sockeye food biomass by (i) determining the percent change in a SLP index ($2 \times \text{CO}_2$ vs. $1 \times \text{CO}_2$), and (ii) imposing this change on an existing relationship between zooplankton biomass and SLP (Brodeur and Ware 1992).

Results

Analysis of covariance indicated that the main effect of spring $\text{SST}_{(t-2)}$, measured at the Langara Island coastal temperature station 2 yr prior to adult return, was able to predict \ln spawner-to-recruit survival_(t) ($P < 0.001$). No significant effects of cycle line ($P = 0.277$) or the interaction between cycle line and spring $\text{SST}_{(t-2)}$ ($P = 0.314$) were detected. The negative bivariate relationship between \ln survival_(t) and spring $\text{SST}_{(t-2)}$ is illustrated in Fig. 2.

On the basis of the 14-yr record of the zooplankton data (1967–1980), no correlations were evident among ocean station P May SST, ocean station P summer zooplankton biomass, and adult recruitment (Table 2). Therefore, these parameters were used as independent variables in a multiple regression to predict terminal ocean weight. The multiple regression model was marginally significant ($P = 0.077$). The partial correlations from this model indicated that zooplankton biomass contributed to variation in terminal weight ($P = 0.056$), whereas recruitment and

Fig. 2. Relationship between spawner-to-recruit survival ($\ln(4_2 \text{ recruitment}_{(t)})/\text{female spawning success}_{(t-4)}$) of early Stuart sockeye and coastal SST $_{(t-2)}$. The Pearson correlation was -0.471 ($P = 0.002$; $n = 41$, 1952–1992, inclusive).

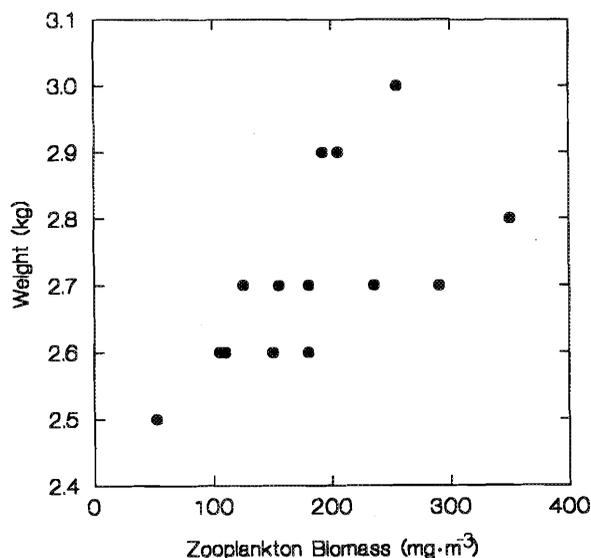


SST did not ($P = 0.513$ and 0.231 , respectively). Figure 3 illustrates the positive correlation between zooplankton biomass and terminal weight.

To examine interannual patterns in terminal weight across a longer time series (1967–1992), we excluded the zooplankton data and reconducted the analyses. No correlation was evident between recruitment and SST (Table 2); therefore, they were used as independent variables in a multiple regression to predict terminal weight. The multiple regression model was significant ($P = 0.019$). The partial correlations from this model indicated that recruitment and SST explained similar amounts of variation in terminal weight ($P = 0.038$ and 0.043 , respectively). Both variables were negatively correlated with terminal weight (Table 2).

GCM simulations suggest that SSTs will increase from 2 to 4°C in the northeast Pacific Ocean when atmospheric CO₂ doubles (Fig. 4). We used GCM simulations of SLP over the northeast Pacific Ocean to estimate how sockeye food may be affected by doubled atmospheric CO₂ (Fig. 5). To quantify the potential alteration in zooplankton biomass, we used the predicted changes in SLP between a Kodiak Island – Vancouver Island SLP index (hereafter KVI) for the winter 2× CO₂ and 1× CO₂ simulations. Winter values were used in order to make comparisons with a linear interannual relationship established between winter upwelling (Ekman transport) and summer zooplankton biomass in the northeast Pacific Ocean (Brodeur and Ware 1992). Surface wind stress and Ekman transport in the ocean surface layer are proportional to the square of KVI (Pond and Pickard 1983). Given the ratio of KVI for the 2× CO₂ case to the 1× CO₂ case, we estimated that

Fig. 3. Relationship between terminal ocean weight of early Stuart sockeye and June–July zooplankton biomass at ocean station P. The Pearson correlation was 0.615 ($P = 0.019$; $n = 14$, 1967–1980, inclusive).



winter surface winds under 2× CO₂ would be 0.942 times present values. Therefore, Ekman transport would be 0.942^2 (which is 0.89) times present values (Pond and Pickard 1983), an 11% reduction. To calculate the range of zooplankton biomass responses, we imposed this reduction on the lowest and highest observed upwelling values from the linear relationship reported by Brodeur and Ware (1992) and then estimated zooplankton biomass. Corresponding to an 11% reduction in the lowest and highest upwelling values, we calculated that zooplankton biomass would be reduced by 5 and 9%, respectively.

We modeled the effects on terminal weight of increases in SST and decreases in daily ration using a bioenergetics equation (Fig. 6). We assumed that a decrease in food biomass would result in a linear decrease in ration. Under present SSTs (1980s regime; Hourston 1992) and sockeye rations reported in Brett (1983), predicted average terminal weight was 2.65 kg. With an increase in SST of 2°C and a ration decrease of 5%, which we suggest are the minimum expected changes, weight was reduced by 10% to 2.39 kg. With an increase in SST of 4°C and a ration decrease of 9%, which we suggest are the maximum expected changes, weight was reduced by 30% to 2.05 kg.

Discussion

Empirical trends between sockeye and ocean habitat

The survival index that we use reflects spawner-to-recruit survival and thus does not solely consider ocean survival. An ocean survival index was not available for early Stuart sockeye. However, smolt-to-recruit (e.g., ocean) mortality in sockeye can be relatively high. McDonald and Hume (1984) examined the survival of Babine Lake sockeye salmon for 16 yr and found that egg-to-smolt survival was on average two to three times greater than smolt-to-recruit

Fig. 4. Predicted difference in sea surface temperature between current and future climates (based on 10-yr averages of CCC GCM, see text). (a) Winter (December, January, and February); (b) spring (March, April, and May); (c) summer (June, July, and August); and (d) fall (September, October, and November).

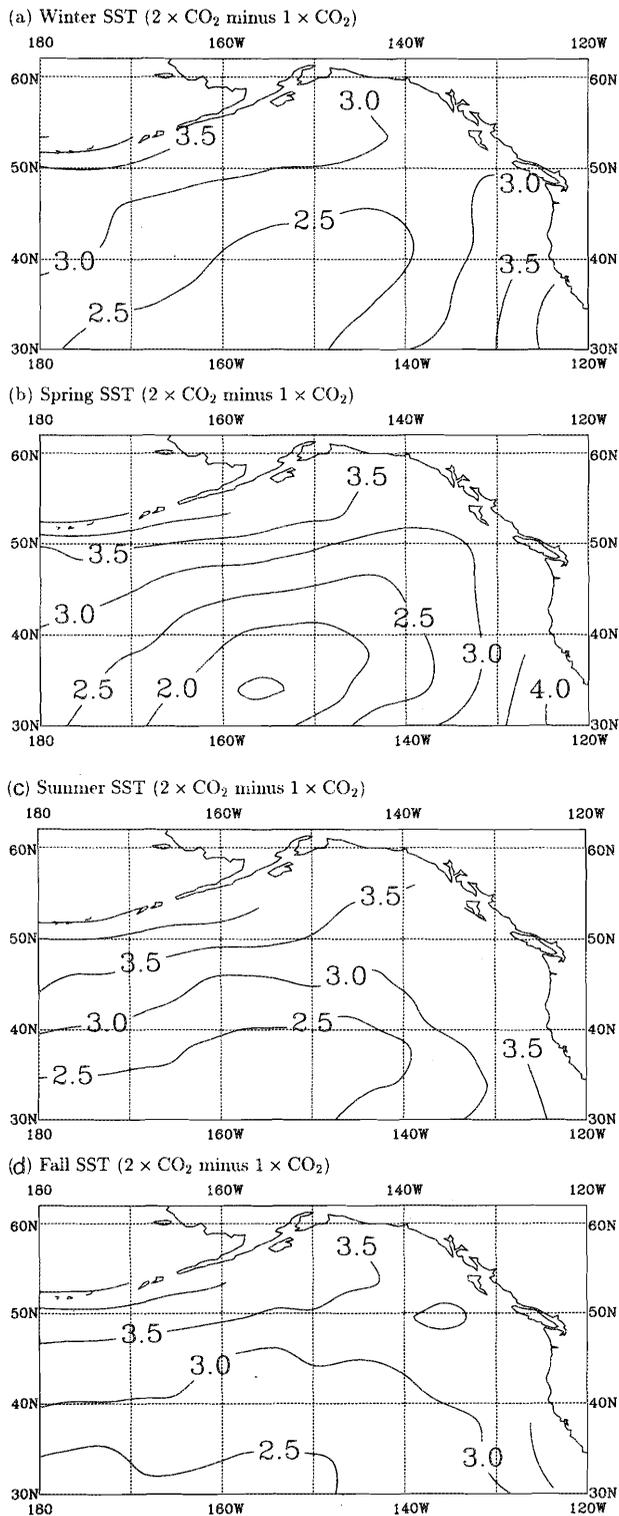
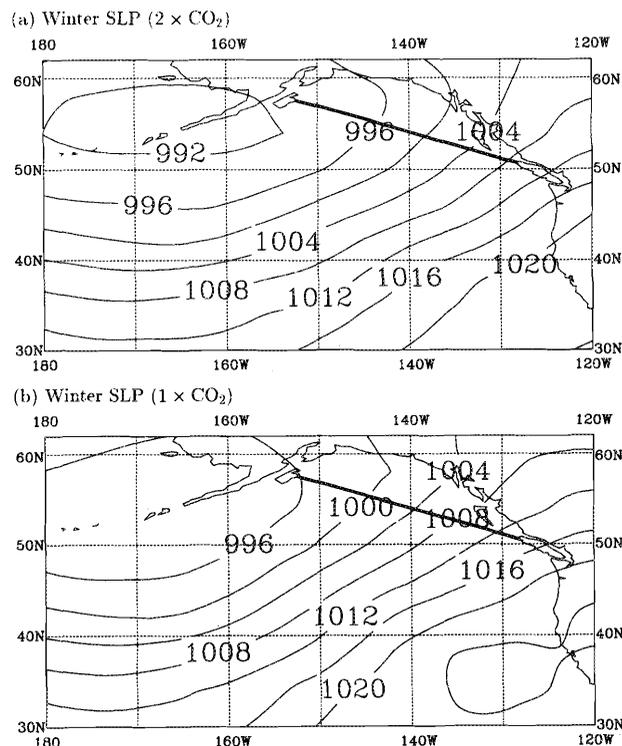


Fig. 5. Predicted current and future winter sea level pressures (mbar, 1 mbar = 100 Pa). The KVI sea level pressure index is defined as winter pressure at Kodiak Island minus winter pressure at Vancouver Island (thick solid line). The ratio of KVI for the $2 \times \text{CO}_2$ case (a) to the $1 \times \text{CO}_2$ case (b) is 0.942 (i.e., future mean winter surface winds would be 94% of present values).



survival. Therefore, ocean conditions may be a large determinant of spawner-to-recruit survival patterns.

During early ocean residence, mortality rates are extremely high for Pacific salmon (Pearcy 1992). Correlations have been identified between indices of Pacific salmon abundance and environmental factors experienced as juveniles (reviewed by Pearcy 1992). Furnell and Brett (1986) suggested that 90% of natural marine mortality in Babine Lake sockeye salmon occurs during the first 4 months at sea. We observed a significant negative correlation between survival and the SSTs likely encountered as coastal juveniles. The SSTs that sockeye experience as they migrate north along the British Columbia coast are within their tolerance range; therefore, SST variability is probably a surrogate for other processes causing interannual patterns in abundance. There are several reasons why SST may be an index of predation pressure. Nonresident predatory fish from more southern areas are known to migrate into southern British Columbia coastal waters during warm years and can be responsible for increased juvenile salmon mortality (B. Hargreaves, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada, personal communication). Resident predatory fish may need to increase foraging rates to offset increased metabolic expenditures incurred in warm water. In addition, juvenile sockeye may grow more slowly because of higher metabolic rates (Hinch

et al. 1994). Warmer coastal SSTs in southern British Columbia are associated with weak upwelling and poor plankton productivity (Percy 1992). As poorer food conditions could also reduce growth rates, predation rates on sockeye could be increased because smaller juveniles are more vulnerable to predators than larger juveniles (Hargreaves and LeBrasseur 1985).

Terminal ocean weight was negatively correlated with May SST at ocean station P and with adult recruitment (Table 2). Because SST and recruitment were not cross correlated, it is possible that more than one process affects sockeye growth, and they may be additive. The influence of SST may be explained by increased energetic costs, and hence slower growth, of swimming in warmer water (Hinch et al. 1994). Increased recruitment may limit food availability through density-dependent processes (i.e., increased competition). Density-dependent effects on terminal weight have been previously demonstrated for Gulf of Alaska sockeye. Peterman (1984) showed that over 50% of stock-specific final size in British Columbia and Alaska sockeye stocks could be explained by multiple regressions including both within- and between-stock sockeye abundances.

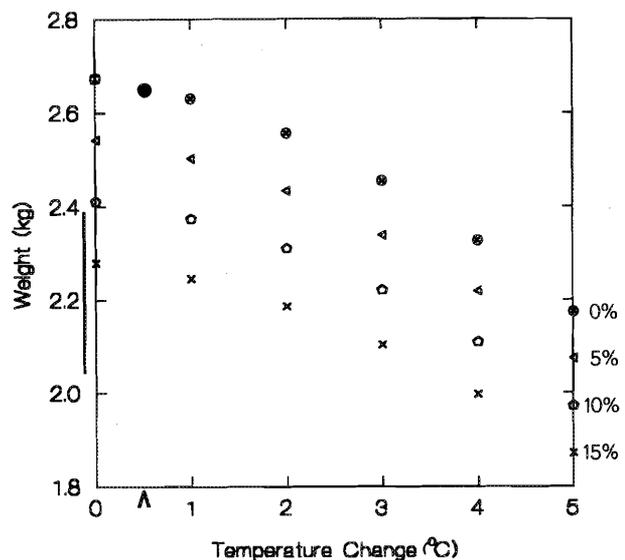
Food availability may also limit sockeye growth through density-independent processes (i.e., decreased secondary production); we uncovered a strong positive correlation between zooplankton biomass and terminal weight. However, over the relatively short time period that zooplankton data were available (1967–1980), significant effects of SST and adult recruitment on weight were not evident, as they were over the longer period (1967–1992). One explanation for this phenomenon may be that recent SST and recruitment regimes (during the 1980s and 1990s) are different from those in the past and their influences on terminal weight may now be greater. Relative to values in the 1960s and 1970s, northeast Pacific Ocean SSTs have increased by 0.5–1.0°C (Hourston 1992) and total salmon abundance has probably doubled (Beamish and Bouillon 1993).

Climate change and marine life history

Our analyses suggest a link between SST, food, and sockeye growth; warmer temperatures and lower food availability were associated with smaller sockeye. What might happen to ocean growth of sockeye in the future? Output from the CCC GCM suggests that within the next 100 yr, SSTs will increase by 2–4°C and will vary with season and locale (Fig. 4). On the basis of predicted changes in SLP, we suggest that sockeye food production will decrease by about 5–9%. Assuming SST increases and ration decreases within these ranges, the bioenergetics model predicts a reduction in terminal ocean weight, relative to present values, of 10–30% (Fig. 6).

Our empirical data suggest that as SSTs increase adult recruitment (e.g., survival) decreases. This relationship is based on contemporary summer SSTs with an inter-annual average of about 9°C and a range of 7.9–10.7°C (Table 1). If present SSTs approximate the long-term average, a 2–4°C increase above present values is entirely outside the current range of observations. The empirical data imply, however, that even relatively small temperature increases may cause declines in adult recruitment.

Fig. 6. Predictions of terminal sockeye weight, from a bioenergetics model, based on increases in temperature above 1960 average SSTs and ration reductions (0–15%). The arrowhead indicates approximate present (1980s) SST regime in the Northeast Pacific Ocean (which is approximately 0.5°C above 1960 values). The solid circle indicates predicted weight under present SSTs and rations. The thick vertical line illustrates the range in predicted weights resulting from SST and ration reductions suggested by the 2× CO₂ scenarios. Note that the average return weights from 1942 to 1992 have ranged from 2.5 to 3 kg. See text for further explanations.



Adult recruitment may also be affected by future changes in zooplankton spatial distribution in the northeast Pacific Ocean. Brodeur and Ware (1992) showed that as upwelling in the northeast Pacific Ocean increased, the spatial distribution of zooplankton changed. As advection of nutrient-rich water increased, so did coastal zooplankton biomass. Percy (1992) speculated that this change in distribution could be responsible for recent increases in salmonid survival in the northeast Pacific Ocean. The CCC GCM predicts that upwelling will decrease in the future. Therefore, distributional changes in zooplankton biomass could also lead to reduced juvenile survival and hence to reduced adult recruitment.

If climate changes as suggested, we speculate that Fraser River sockeye will be less abundant and smaller. Smaller sockeye will have fewer and smaller eggs and may therefore have lower reproductive value (Healey 1987). Smaller sockeye also run the risk of not having enough energy reserves to complete river migration and spawn because sockeye cease feeding prior to river migration and rely solely on energy reserves for their last month. Early Stuart sockeye, which must travel 1200 km upriver, arrive at spawning grounds with 90–95% of their fat reserves depleted (International Pacific Salmon Fisheries Commission 1959, 1980). It seems plausible that smaller early Stuart sockeye may have increased rates of in-river or prespawning mortality resulting from energy reserve depletion prior to arrival at spawning grounds.

Sockeye may be able to compensate for slower growth by increasing ocean residency from 2 to 3 yr. However, increasing their life cycle by 1 yr also increases the risk of predation and disease, and lowers reproductive potential by increasing generation length. Another possible strategy to increase terminal ocean weight would be to restrict the oceanic distribution to more northern areas where SSTs and food may be more favourable for growth. But this could also cause a reduction in growth because of increasing competitive interactions accompanying local increases in salmon density.

To summarize, if climate changes as predicted, the productivity of Fraser River sockeye will be reduced relative to present levels. This prediction is consistent with evidence that climate variation over the north Pacific Ocean is responsible for long-term (1925–1989) trends in salmon production (Beamish and Bouillon 1993).

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