# Climate change and ocean energetics of Fraser River sockeye (*Oncorhynchus nerka*)

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Hinch, S.G., M.C. Healey, R.E. Diewert, and M.A. Henderson. 1995. Climate change and ocean energetics of Fraser River sockeye (*Oncorhynchus nerka*), p. 439–445. *In* R.J. Beamish [ed.] Climate change and northern fish populations.Can. Spec. Publ. Can. Fish. Aquat. Sci. 121.

**Abstract:** We constructed a spatially explicit bioenergetics model to predict final ocean weight of Fraser River sockeye salmon (*Oncorhynchus nerka*), and to estimate the effects of climate warming on oceanic sockeye growth. The bioenergetics model successfully predicted average final ocean weight of the early Stuart stock under recent sea-surface temperature (SST) regimes. To assess the potential impact of climate warming on final ocean weight, we imposed a series of SST increases on the model. We found that predicted final ocean weights declined steadily as SSTs warmed above current values. An empirical correlation ($r = -0.433$, $P = 0.024$, n = 27 yr) between average final ocean weight of early Stuart sockeye and average SST at Station P (50°N, 145°W) during the month prior to migrating upriver also suggests that warm SSTs are associated with poorer growth. Global climate models predict that if atmospheric $CO_2$ doubles, Northeast Pacific Ocean SSTs will increase by about 3.5°C above present values. The bioenergetics model suggests that this increase will result in a 14% reduction in average final ocean weight. As a consequence, Fraser River sockeye would have fewer and smaller eggs, and they may have insufficient energy reserves to complete their river migration and spawn.

**Résumé :** Nous avons créé un modèle bioénergétique spatialement explicite pour prédire le poids final dans l'océan du saumon sockeye (*Oncorhynchus nerka*) du fleuve Fraser, ainsi que pour estimer les effets du réchauffement climatique sur la croissance du sockeye océanique. Le modèle bioénergétique a réussi à prédire le poids final océanique moyen du stock de la rivière Stuart à montée hâtive sous les récents régimes de température de surface de la mer (TSM). Pour évaluer les répercussions éventuelles du réchauffement climatique sur le poids final dans l'océan, nous avons appliqué au modèle une série d'augmentations de la TSM. Nous avons constaté que les poids finals prévus dans l'océan déclinaient de façon régulière à mesure que les TSM montaient au-dessus des valeurs courantes. Une corrélation empirique ($r = -0{,}433$, $P = 0{,}024$, n = 27 ans) entre le poids final moyen dans l'océan des sockeyes de la rivière Stuart à montée hâtive et la TSM moyenne à la station P (50° N, 145° O) durant le mois précédant la remontée migratoire donne également à croire que les TSM chaudes sont associées à une croissance plus faible. Les modèles climatiques globaux permettent de prévoir que si la teneur en $CO_2$ de l'atmosphère double, les TSM du nord-est du Pacifique monteront d'environ 3,5° C au-dessus des valeurs actuelles. Le modèle bioénergétique donne à croire que cette hausse se traduira par une réduction de 14 % du poids final moyen dans l'océan. En conséquence, le sockeye du fleuve Fraser aura moins d'oeufs et des oeufs plus petits, et risque de manquer de réserves énergétiques pour terminer sa migration et son frai dans le fleuve.

## Introduction

Over the next 50–100 yr, $CO_2$ concentration in the atmosphere is predicted to double and there is strong scientific consensus that climate will change as a result (Houghton et al. 1990). Global climate models have been developed to help understand changes in climate systems and they predict that a doubling of atmospheric $CO_2$ will be associated with a 2–4°C increase in air temperature over the Northeast Pacific Ocean (Boer et al. 1992). Although regional predictions made by global climate models may not be as reliable as global predictions because of the models' coarse spatial resolution and highly simplified representations of heat transport within oceans (McBean 1990), they present compelling scenarios that could have serious consequences for oceanic fishes.

Of all the fish species in the Northeast Pacific, salmon (*Oncorhynchus* spp.) are likely to be the first affected by increases in water temperature because they spend the majority of their lives in surface waters and the ocean surface

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will probably warm more quickly than deeper waters (McBean et al. 1991). Among the salmon species, sockeye salmon (*O. nerka*) may be most affected by changes in SSTs because of its long ocean migrations (Hartt 1966). Models have been developed to examine and predict the influence of SSTs on the distribution, abundance, production and migratory behaviour of sockeye salmon (Burgner 1980; Rogers 1984; Tabata 1984; Chelton 1984; Mysak 1986; Blackbourn 1987; Quinn and terHart 1987; Hsieh et al. 1991; Beamish and Bouillon 1993). Only a few, however, have explored the effects of temperature variation on oceanic growth rates of sockeye (Rogers 1980, 1984; Eggers et al. 1984). Because body size is an important determinant of migratory success and fecundity in sockeye (IPSFC 1959, 1980; Healey 1987), the relationship between temperature and growth rate should be examined in the context of a 3–4°C increase in SST in the Northeast Pacific Ocean.

We constructed an energetics model to explore the rate of energy accumulation (e.g., growth) that occurred each month during the oceanic phase of life for an "average" Fraser River sockeye salmon. Fraser River sockeye should be highly susceptible to the effects of climate warming because they are at the southern range of distribution of sockeye in North America. The validity of model predictions was assessed by comparing empirical measurements of mature adult river entry weight to model estimates of river entry weight using historical and current water temperature data. To examine the potential impact of climate change on sockeye growth, we imposed a series of temperature changes on the model. Although the model was run using weight and timing data on only one sockeye stock, the early Stuart, it should be generally applicable to other Fraser River sockeye stocks.

## Methods

### Model of oceanic sockeye distribution

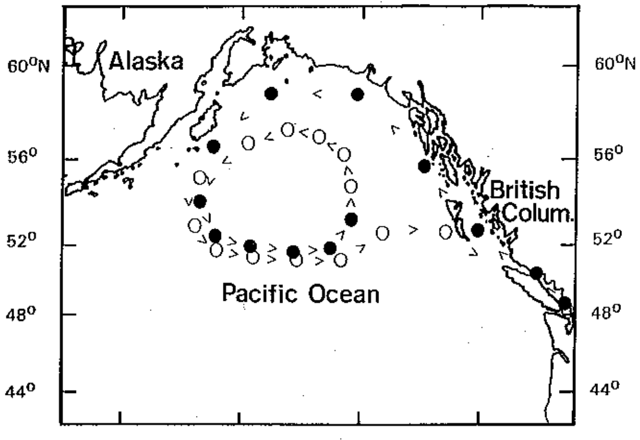

**Fig. 1.** Map of the Northeast Pacific Ocean showing average monthly locations of early Stuart sockeye (adapted from Brett (1983)). Closed and open circles represent the first and second year of ocean residency respectively. Arrowheads depict the monthly direction of movement. The first month of ocean life starts on May 25 at the mouth of the Fraser River (closed circle at 48°N); all other circles represent the 15th of each month.

After rearing for 1 yr in the Stuart Lake system, early Stuart sockeye smolts migrate to the ocean via the Fraser River. Once in the ocean, they migrate northward along the British Columbia and Alaska coasts and spend the next 2 yrs making two counterclockwise circuits in a region of the Northeast Pacific Ocean bounded by 50–58°N and 135–155°W (Fig. 1) (Brett 1983). A distribution model was developed by Brett (1983) to illustrate the monthly sea positions of an "average" British Columbia sockeye. Brett reported that monthly shifts in sockeye position were supported by mark–recapture and catch per unit effort studies (Neave 1964; Hartt 1966; French and McAlister 1970; French et al. 1976; Hartt and Dell 1978). Brett's model dealt with fish leaving and returning to the Skeena River, which is located on the north coast of British Columbia. We used general information on migration rates of Fraser River juveniles and mature adults (Groot and Cooke 1987; Healey 1989) to suggest monthly coastal positions for early Stuart sockeye that migrate along the south coast of British Columbia (Fig. 1). SST data from 1945 to 1987 that corresponded to these monthly positions were obtained from different sources (Fulton et al. 1968; Brett 1983; Slutz et al. 1985; Woodruff et al. 1987). We obtained more recent SST data from updates of the Comprehensive Ocean-Atmosphere Data Set (see Woodruff et al. 1987 for details).

### Description of bioenergetic model

The bioenergetic model was based on the thermodynamic principle that food consumed (energy input) equals the amount of energy placed into growth, plus that used for metabolism, plus that lost through excretion and egestion. We obtained information for each of these processes from the literature, with the exception of growth, which was estimated using the model. Brett (1983) determined size-specific rates of food consumption (measured in units of energy) for sockeye which he presumed to correspond to the monthly locations of sockeye in his distribution model. We incorporated these values into our energetics model. Brett (1983) reported that empirical measurements of monthly growth were very similar to predicted monthly growth calculated from a general salmonid growth model that assumed maximum daily ration. Thus, growth rate in the ocean approximated maximum capacity, and consequently, Brett (1983) argued that feeding rate also approximated maximum daily intake. For the purposes of our model, we assumed that sockeye could obtain maximum ration so that ration was only constrained by temperature. Brett and Groves (1979) determined that over a temperature range that encompassed our data (2.5–15°C), a 1°C increase in temperature increased maximum ration for sockeye between 5 and 8%. We used an intermediate value of 6.5% as a factor by which food consumption changed corresponding to a 1°C change in temperature.

The weight- and temperature-dependent equations and parameters describing standard metabolic costs and costs of swimming were taken from Beauchamp et al. (1989). They based their equations on a model of optimum sockeye swimming speed in which a hydrodynamics approach was linked with optimal foraging theory. These equations are not, however, based on assessments of metabolic rates in nature so they do not consider energy expenditures associated with attack–avoid–escape patterns or that of direction-oriented migration. These additional costs are probably substantive for sockeye that face a gauntlet of predators and competitors in the ocean and that migrate over 12 000 km (Brett 1983). Brett (1983) showed that feeding metabolic rate for sockeye approximates one half of their active (constant swimming) metabolic rate. To assess total swimming metabolism, we thus doubled the influence of swimming speed in the equations that assessed temperature- and weight-dependent optimum swimming metabolism.

Apparent heat increment (also called apparent specific dynamic action), the metabolic cost associated with chewing and swallowing food and with postabsorptive processes, was set to equal 17% of the difference between energy consumed and energy egested (Stewart et al. 1983; Beauchamp et al. 1989). Apparent heat increment may not remain constant over the life of a sockeye (Beamish and Trippel 1990), but is probably fairly constant during the ocean phase of life when the diet is composed primarily of a single food, euphausiids (Brett 1983). An increase in omnivorous feeding will, however, increase apparent heat increment and could represent an additional energetic cost. Monthly specific levels of excretion–egestion were set to equal 30% of the monthly energy consumed (Brett 1983).

The temperatures of each monthly sea location and the average fish weight at the first site (i.e., the mouth of the Fraser River) were inputted to the model. Growth (in energy units) was calculated at each month by subtracting the amount of energy used for metabolism and excretion–egestion from the amount of energy consumed that month. Weight (in energy units) at month$_{t+1}$ was determined by adding the estimated growth between month$_t$ and month$_{t+1}$ to the weight at month$_t$. We used equations in Brett (1983) to convert fish weights to energy equivalents.

The model operated under the following assumptions. (1) Monthly positions as presented in Fig. 1 were fixed. (2) Sockeye existed within the upper mixed layer of the ocean; thus, SSTs were representative of temperatures that the fish encountered. (3) Maximum daily ration was attainable. (4) Energetic costs associated with directed migration (e.g., energy used to move between monthly locations) and with biotic interactions were approximately equal to the costs arising from feeding. We will discuss the validity of these assumptions and the ramifications of violating them later in the manuscript.

### Running the model

To test the performance of the model, we compared empirical measurements of river entry weights (e.g., final oceanic size) to river entry weights predicted by the model. The Fraser River gillnet fishery collected early Stuart sockeye from the lower Fraser River over a 4-wk period (June 15 to July 15) from 1967 to 1992 (Fig. 2). During the fishery, there is a complete lack of movement of sockeye in the Fraser River likely as a result of the fisheries' intensity, suggesting that gillnetting was not size selective in its removal of fish (J. Woodey, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C. V6E 1B5, personal communication). In two separate runs of the model, we used site-specific temperature data that were based on among-year averages of data from 1960 to 1976 (1960s conditions), and on among-year averages from 1977 to 1992 (1980s conditions). This dichotomy was selected because a large-scale change occurred to northeast Pacific SSTs starting in 1976 (Namias et al. 1988). From 1976 to 1988, the Northeast Pacific Ocean (Fig. 1) experienced an increase in average annual SSTs of about 1°C at coastal sites and an increase of approximately 0.5°C at the high-sea sites (Hourston 1992). We did not have SST data from 1989 to 1992 that corresponded to the monthly positions illustrated in Fig. 1. However, an examination of unpublished monthly temperature data (provided by H. Freeland, Institute of Ocean Sciences, Sydney, B.C. V8L 4B2) collected from Amphitrite Point (49°N, 128.5°W) located on the west coast of Vancouver Island and from Station P (50°N, 145°W) located in the Northeast Pacific Ocean confirmed that the temperature patterns reported by Hourston (1992) were maintained from 1988 to 1992 at a coastal and a high-sea site.

To assess the effects of different temperature scenarios on river entry weights, we ran the model with temperatures that ranged from 3°C below average 1960s values to 5°C above 1960s values. This temperature range was chosen because, in particular years since 1945 in the Northeast Pacific Ocean, SSTs have been 2–3°C cooler than 1960s values (Slutz et al. 1985; Woodruff 1987), and global climate models predict a 2–4°C temperature increase from present temperatures over the next 100 yr (McBean et al. 1991).

In all model runs, the initial weight of sockeye juveniles at the Fraser River mouth was 5 g, an average value that is representative of smolt size for most Fraser River sockeye stocks (Henderson and Cass 1991). (However, results of preliminary model runs using different initial weights suggest that initial weight has only a small bearing on final ocean weight; final weights differed by less than 1% with initial weights ranging from 2.5 to 10 g.) The date of arrival at the mouth of the Fraser River was set to May 25, which corresponds to the peak arrival time for early Stuart sockeye (J. Woodey, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C. V6E 1B5, personal communication). The model was allowed to run for 27 consecutive mo of ocean life, the amount of time it takes for average early Stuart sockeye to leave the mouth of the Fraser River as juveniles and return as mature adults. We concluded each model run on July 15, which is approximately 1 wk after the peak number of mature adults arrive at the Fraser River mouth (J. Woodey, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, B.C. V6E 1B5, personal communication) and is a date that corresponds with our final date of sampling for early Stuart sockeye in the lower Fraser River (Fig. 2).

We used output from the Canadian Climate Centre's global climate model (Boer et al. 1992), which is a comprehensive atmospheric model coupled to a simplified mixed layer ocean model, to generate SST scenarios under a doubling of atmospheric $CO_2$. The Canadian Climate Centre modelled the annual cycle of sea-surface temperature and sea-level pressure based on a 20-year climatology of the two times $CO_2$ scenario (i.e., double the present amount of atmospheric carbon dioxide) and the one times $CO_2$ "control" scenario.

### Empirical relationship between SST and weight

Using daily sea-surface temperature records from Station P, average May SSTs were determined for years that corresponded with the river entry weight data. Among-year variability in

Station P SST is probably indicative of SST variability experienced by adult early Stuart sockeye that are migrating in the highseas. To assess a possible relationship between sockeye growth rate and SST, we correlated annual sockeye weights at return with annual May SSTs. We chose May of the final year of ocean life over other months for this analysis because output from the bioenergetics model shows that absolute growth is greatest during this time period so SST may have its greatest influence on growth during this month, and because the model suggests that SST has its greatest impact on final ocean size during the last spring in the ocean. The latter will be discussed below in more detail.

## Results and discussion

### Bioenergetics model

When temperature conditions characteristic of the 1960s were imposed on the model, the predicted weight at river entry was 2.67 kg, a value that was only 1.5% smaller than the overall average river weight (2.71 kg) calculated during the 10-yr period, 1967–76 (Fig. 2). When 1980s temperatures were imposed on the model, the weight at river entry was predicted to be 2.53 kg. This is slightly less than the model estimate for the 1960s and was only 5.9% smaller than the overall average river weight (2.68 kg) calculated from 1977 to 1992. This value was well within the range of average empirical river entry weights calculated from 1977 to 1992 (Fig. 2). The empirical data and model output suggest that the warmer time period (the 1980s) was associated with lighter sockeye, although the differences were small. We also concluded that the model should be useful for exploring the potential effects of alternative temperature scenarios on sockeye weights because it produced realistic estimates of river entry weights when recent temperature scenarios were employed.

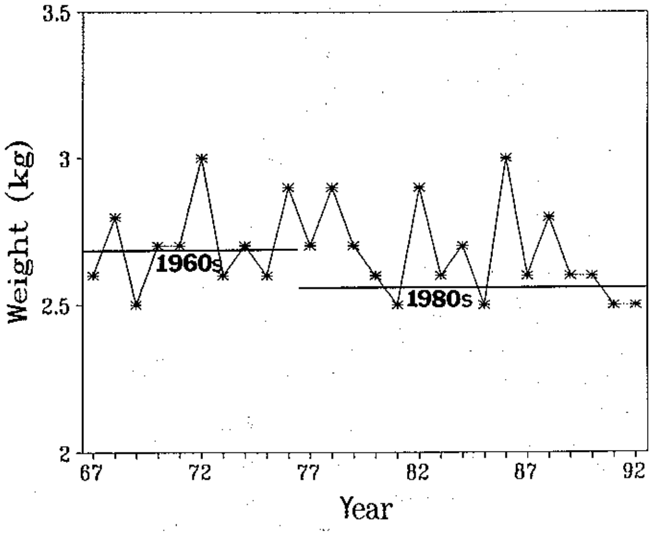

**Fig. 2.** Average annual weight (1967–92) of early Stuart sockeye caught in the lower Fraser River from June 15 to July 15 by the Fraser River gillnet fishery (from the Canadian Department of Fisheries and Oceans' catch statistic data base). Within-year sample size ranged from a low of 386 in 1968 to a high of 2.8′ $10^5$ in 1977. The solid lines represent predicted river entry weight based on our model for 1960s (left line) and 1980s (right line) SSTs.

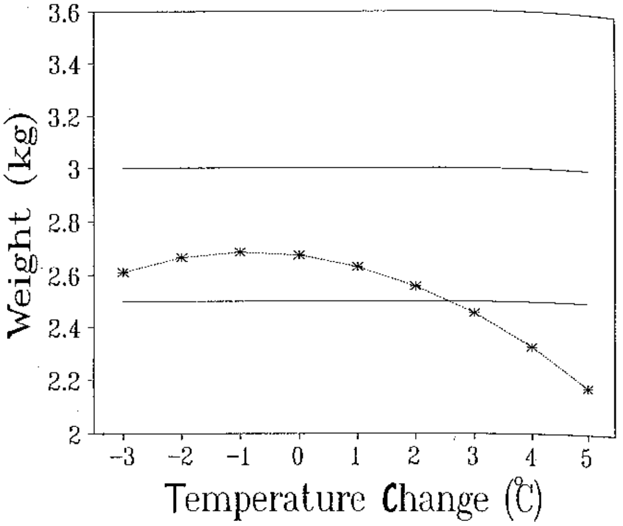

**Fig. 3.** Modeled relationship between weights of adult early Stuart sockeye when they enter the mouth of the Fraser River and SST change in the northeast Pacific Ocean. SST changes are relative to 1960s SSTs. A 1°C SST increase approximates the SST regime observed during the 1980s. Parallel lines represent the 26-yr minimum and maximum average annual river entry weight of adult early Stuart sockeye salmon (from Fig. 2).

We ran the model under oceanic temperatures 3°C below to 5°C above those observed during the 1960s (Fig. 3). For temperatures up to 3°C colder than the 1960s values, all predicted weights fell near the middle of the range of observed river entry weights during the 1960s. At 3°C below 1960s temperatures, average river entry weight was only 2.5% less than the predicted 1960s value. Maximum predicted river entry weight occurred when ocean temperatures were 1°C cooler than 1960s temperatures (approximately 2°C cooler than 1980s temperatures); however, this weight was only 0.4% greater than the predicted weight under 1960s temperatures. Thus, SSTs cooler than 1960s values appear to have little effect on growth and final adult size.

When SSTs were increased above 1960s values, the model predicted a steady decline in average river entry weight (Fig. 3). A 1°C increase (which approximated 1980s temperatures) decreased predicted river entry weight by 1.6% and a 2°C increase decreased predicted river entry weight by 4.4%. This latter value approached the smallest empirically observed, average river entry weight measured over the past 26 yr. SST increases of more than 2.5°C from 1960s values resulted in predicted river entry weights that were smaller than any empirical measure of average river entry weight. Therefore, temperature increases above 1960s values had more profound effects on river entry weight than temperature decreases. Because energetic costs of excretion–egestion were constant with respect to temperature, the energetic costs of metabolism apparently increased faster than the energy gained through

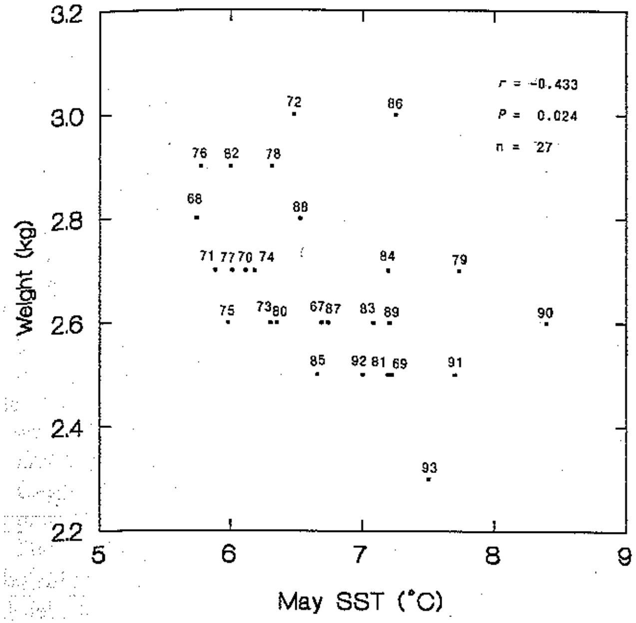

**Fig. 4.** The relationship from 1967 to 1993 between average river entry weight of early Stuart sockeye and May SST at Station P in the Northeast Pacific Ocean. Years are indicated on top of data points. Fish were captured and weights assessed in July, 2 mo after SST was determined. The Pearson correlation and associated probability are presented.

increased consumption rates in warmer waters. Thus, the balance between energy input and energy output that existed in cool temperatures broke down when temperatures increased modestly.

There appears to be a link between SSTs (1967 to 1993) and river entry weight with warmer years being correlated with lighter river entry weights (Fig. 4). Results of our bioenergetics modelling corroborates this by suggesting that once SSTs are greater than 1960s values, relatively warm temperatures will cause a reduction in growth rate.

The Canadian Climate Centre global climate model predicts that a doubling of atmospheric $CO_2$ will result in a 2–4°C increase in SSTs above present values in the Northeast Pacific (Boer et al. 1992). SSTs are predicted to increase by about 3.5°C at the sites that correspond with monthly sockeye locations in Fig. 1. If we assume that the past 30 years reflect "present" climate conditions, 3.5°C increase from a midpoint between 1960s and 1980s temperatures on Fig. 3 translates into a predicted river entry weight of 2.35 kg (Fig. 3). This value is 14% lighter than predicted weights under "present" climate conditions and 6.4% lighter than the smallest observed average river entry weight for early Stuart sockeye over the 26-yr period from 1967 to 1992 (Fig. 2).

## Robustness of model predictions

How might violations of our bioenergetic model assumptions alter predictions about river entry weights of sockeye? The first assumption is that monthly positions in Fig. 1 are fixed. It has recently been demonstrated that the southern boundary for Pacific Ocean sockeye in the spring is determined by the position of the 8.9°C isothermal (D. Welch, Department of Fisheries and Oceans, Nanaimo, B.C. V9R 5K6, personal communication). Brett's (1983) distribution model may thus underestimate the southern extent of Fraser River sockeye in the northeast Pacific Ocean, so we needed to assess how a more southern distribution would affect predicted river entry weight. To do this, we initialized the model with the 1980 scenario SSTs that were modified by increasing the November to March average monthly SSTs to 8°C from their original 5–6°C. From a spatial perspective, these SST changes mean that we stretched the southwestern monthly locations in Fig. 1 farther south. Under this scenario, predicted river entry weight was 2.56 kg. Although this weight was 4.4% lighter than the 26-yr average, it was still within the 26-yr range of mean river entry weights. We examined several other ocean distributions and found that their influence on predicted river entry weight were also relatively small (unpublished data); therefore, it is unlikely that violating assumption 1 would seriously affect model predictions. However, we found that changes in the locations (i.e., SSTs) of the last 2 mo of ocean life could alter predicted river entry weights enough to make them fall out of the empirical range. This suggests that variation in river entry weight is largely caused during the last few months of ocean life. Thus, variation in SSTs may primarily influence river entry weights during the homeward ocean migration phase. We are currently conducting research to assess migration and growth patterns in Fraser River sockeye during their final few months in the ocean.

The second assumption is that SSTs are representative of temperatures that sockeye encounter. If sockeye can vertically migrate to depths below the upper mixed layer, then the SSTs we used would be overestimates. The magnitude of influence of colder SSTs on predicted river entry weights depends on monthly location and sockeye weight. For instance, during the final months of ocean migration, a large fish will accumulate more weight if it experiences slightly cooler than normal SSTs. However, there is no evidence to suggest that sockeye in the high seas migrate below the upper mixed layer.

The third assumption is that maximum temperature-dependent ration was attainable. Brett (1983) suggested maximum ration was attainable during the 1960s. Food availability (e.g., zooplankton biomass) in the Northeast Pacific Ocean has more than doubled since then (Brodeur and Ware 1992) so it is possible that sockeye were able to obtain a maximum temperature-dependent ration during the 1980s. The recent doubling of zooplankton biomass in the Northeast Pacific is correlated with changes in nutrient transport, not changes in temperature (Brodeur and Ware 1992), so it is difficult to speculate on how patterns of zooplankton production will change in response to future increases in SSTs. Because sockeye obtain a maximum ration in our model, the only way climate change can affect ration is by inhibiting food intake. If food availability was decreased and maximum ration was not attainable, perhaps as a result of increased inter- or intra-specific competition for food or because of a decline in food production, then our present estimates of weight loss are conservative. Sockeye could become lighter than we have suggested as temperatures warm.

The fourth assumption is that energetic costs of directed migration and biotic interactions approximate the energetic costs of foraging. Because the predicted final ocean weights from the bioenergetics models fell within the empirical long-term average final ocean weight, our estimates of total swimming metabolic expenditure may be reasonable. However, in the future if the strength of Northeast Pacific ocean currents is affected by doubling atmospheric $CO_2$ as some have suggested (McBean 1991; Hsieh and Boer 1992), then migration costs could be affected. For instance, intensified coastal currents would mean that less energy would be needed by juveniles to migrate with the surface currents in a northwest direction to the high seas, but more energy may be needed by maturing adults for the final months of homing migration, which is against the surface coastal currents in a southeast direction. The converse situation may arise if coastal currents weaken. It is possible that, regardless of the magnitude of change in currents, the energetic savings of migration by one ocean life-history stage may trade-off against energetic costs of migration by another stage. Predator–competitor regimes in the northeast Pacific Ocean may be altered by climate changes (McBean et al. 1991) which could affect the amount of energy that sockeye expend with biotic interactions. To resolve these complex issues, further research into the present and predicted future energetic costs associated with directed swimming and biotic interactions are needed.

## Conclusions

Our study suggests that as ocean temperatures warm in response to increasing concentrations of atmospheric $CO_2$, Fraser River sockeye will become lighter. Lighter sockeye will have fewer and smaller eggs, and may therefore have lower reproductive value (Healey 1987). In addition, smaller sockeye run the risk of not having enough energy reserves to complete their river migration and spawning. For instance, early Stuart sockeye arrive at the spawning grounds with 90–95% of their fat reserves depleted (IPSFC 1959, 1980) and it seems plausible that smaller early Stuart sockeye may not be able to meet the energetic costs of river migration. Sockeye may be able to compensate for slower growth by increasing their ocean residency from 2 to 3 yr. However, by increasing their life cycle by 1 yr they put themselves at greater risk to predation and disease, and also lower their reproductive potential by increasing their generation time. As another strategy to increase their river entry weights, sockeye could compress their oceanic distribution into more northern areas thereby reducing the direct effects of warm SSTs. But this could cause a reduction in average growth rate as competitive interactions would probably increase in response to higher salmon densities in the northern portions of the northeast Pacific Ocean.

## Acknowledgements

We are grateful to Keith Thomson and Roy Hourston for their comments and suggestions throughout this project. Insights provided by David Welch and Jim Woodey are appreciated. We thank Howard Freeland for providing unpublished SST data. Comments from two anonymous reviewers helped us to clarify several aspects of this paper. S.G.H. was supported by a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada.

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