

## SHORT COMMUNICATION

**Somatic energy of sockeye salmon *Oncorhynchus nerka* at the onset of upriver migration: a comparison among ocean climate regimes**

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**ABSTRACT**

We examined somatic energy patterns in two stocks (Chilko and Early Stuart) of adult Fraser River (British Columbia, Canada) sockeye salmon (*Oncorhynchus nerka*), collected at the end of their ocean residency, spanning years across different climate regimes. Both stocks had high levels of somatic energy in years with high open ocean productivity (1956, 1957, 2001 and 2002), and relatively low levels in years with poor open ocean productivity (1999 and 2000). For Early Stuart sockeye, energy levels in 1999 and 2000 were approximately 15% lower ( $\sim 1.5 \text{ MJ kg}^{-1}$ ) than that in the 1950s, an amount of energy equivalent to that necessary for migrating 600 km upriver. In recent years (2001 and 2002), energy levels have increased by about 9% for both stocks. Low energy levels at the onset of upriver migration, particularly in years of energetically demanding in-river conditions, such as high flows or temperatures, are likely to contribute to respawning and *en route* mortality in Fraser sockeye.

**Key words:** body energy, climate change, energetics, ocean climate, *Oncorhynchus*, Pacific salmon, regime shift, sockeye

**INTRODUCTION**

Climate has a strong effect on the growth and survival of ocean-dwelling Pacific salmon (*Oncorhynchus* spp.) (Welch *et al.*, 1998; Beamish *et al.*, 1999; McFarlane *et al.*, 2000). While the mechanisms are not completely clear, thermal habitat, food abundance, and food consumption are key features that are directly affected by climate. For instance, in years with relatively high sea surface temperatures (SST), and in years with relatively low zooplankton production (an index of prey abundance), ocean dwelling salmonids tend to mature at relatively small sizes (Hinch *et al.*, 1995; Bigler *et al.*, 1996; Cox and Hinch, 1997; Welch *et al.*, 2000). Although they can interact, temperature and food abundance can also have independent influences on size at maturity (Hinch *et al.*, 1995). Salmonid survival in marine environments is generally correlated with body size and growth rate (Koenings and Burkett, 1987), and thus survival rates. Hence, ocean abundance of salmonids should be high in years with high per capita food consumption (e.g., Peterman, 1984).

Pacific salmon stop feeding just before the onset of their freshwater spawning migrations and must rely on stored energy to power upriver migration, complete reproductive maturation, and spawn. Although relationships between salmonid growth patterns and ocean conditions such as temperature and food abundance have been examined (as mentioned above), there has been no consideration given to how ocean conditions may affect the ability of salmon to store energy. Because there is no relationship, within a given stock and year, between mature size and energy density (Hendry and Berg, 1999; Crossin *et al.*, in press), ocean growth rates may not be a good measure of a salmon's ability to accrue and store energy needed for the homeward migration. Upriver migrations typically utilize a large fraction of stored somatic energy (50–70%; reviewed in Brett, 1995), and in years when river conditions are energetically demanding due to high discharge rates, migrants can exhaust energy stores and die before spawning (Macdonald, 2000). Thus,

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understanding how oceanic factors affect energy accrual in salmon is critical if we are to better understand river migration and spawning success.

The climate of the North Pacific Ocean oscillates on a decadal time frame influencing ocean upwelling rates, SST, and production of phytoplankton, zooplankton, and fish (Brodeur and Ware, 1992; Beamish *et al.*, 1999; McFarlane *et al.*, 2000). Since the 1950s, two significant climatologic shifts have occurred in the North Pacific Ocean (in 1977 and 1989; McFarlane *et al.*, 2000; Welch *et al.*, 2000) and, from marine survival estimates of a Fraser coho (*O. kisutch*, Pacific Fisheries Resource Conservation Counsel, 2002) stock, and from physical and biological oceanographic data, there is good evidence that a third shift may have recently occurred, beginning in 1999 (Pacific Scientific Advice Review Committee, Fisheries and Oceans Canada, 1999–2001–2001). There have been no studies conducted to examine how broad changes to ocean conditions affect the energy content of mature adult salmon.

In this paper, we compare river entry energy levels in two stocks of Fraser River sockeye collected during three time-periods: 1956–57, 1999–2000, and 2001–2002. These periods represent three different oceanic states (or climate regimes). From 1977 to 2000, the north-east Pacific was characterized by relatively warm SST, low open-ocean primary production, and high coastal primary production, which contrasts with the pre-1977 period (Rand and Hinch, 1998a; Beamish *et al.*, 1999; Pacific Fisheries Resource Conservation Counsel, 2002). Beginning with a shift in 1989, the 1990s were characterized by several years of anomalously strong El Niño-like conditions. Year 1999 signaled the beginnings of change in the biological and physical conditions that characterized the poor productivity regime of the 1990s, suggesting a shift toward a cooler, more productive ocean regime. However, in year 2000, many of those same indicators shifted again back toward the poorer 1990s conditions. By 2001–2002, productivity levels improved and temperatures cooled slightly relative to 1999–2000, making conditions in the North Pacific comparable with those reported in the 1950s (Pacific Scientific Advice Review Committee, Fisheries and Oceans Canada, 1999–2001). Thus, years 1999 and 2000 may be viewed as transitional years between two distinct ocean regimes. If ocean climate plays a large role in energy status of salmon at the onset of upriver migration, we would predict energy densities to be highest during the cooler, pre-1977 period relative to the 1999–2000 period. We would also expect

energy densities to show some improvement in the relatively cooler and more productive period of 2001–2002 relative to 1999–2000.

## METHODS

Sockeye salmon bound for Chilko (~650 km) and Early Stuart (~1100 km) spawning grounds were collected from the mouth of the Fraser River, British Columbia, Canada, between July and early August in 1956, 1957, 1999, 2000, 2001, and 2002. At least 10 males and 10 females were sampled in each year. Somatic energy data (somatic lipid and protein percentages derived from proximate analyses) from 1956 were from Idler and Clemens (1959), data for 1957 were from Gilhousen (1980) (only means were available), data from 1999 were from Crossin *et al.* (in press), and data for 2000, 2001, and 2002 are unpublished. Lipid and protein percentages (by wet mass) were converted to MJ kg<sup>-1</sup> through their energetic equivalents (lipid 0.03954 and protein 0.02364; Higgs *et al.*, 1979). All river-entry energy data were collected at peak migration times. Analyses were confined to age 4<sub>2</sub> sockeye.

The only methodological difference between proximate analyses in 1956 and 1957 and of those in more recent years was the method of solvent extraction of total somatic lipids (acetone-methylene chloride in 1956–1957, and methanol-chloroform in all other years). As the sum of all proximate constituent percentages (lipid, protein, water, and ash) theoretically equals 100%, analysis of summed constituent percentages would indicate a difference between methods.

To quantify the relationship between somatic energy and measures of ocean climate, we searched for correlations of energy with a physiologically relevant ocean climate parameter, SST, and with a regional climatologic index, the North Pacific Index (NPI, an area-weighted sea level pressure measure within the zone 30–65°N, 160°E–140°W, and a surrogate for the Aleutian Low Pressure Index). SST and NPI values were averaged from January to June for each year, representing the last 6 months of ocean residency prior to upriver migration, when sockeye acquire > 50% of their final mature mass (Brett, 1983). SST is measured daily at several BC coast lighthouse stations and data are freely available from the Fisheries and Oceans Canada website ([http://www.pac.dfo-mpo.gc.ca/sci/osap/data/default\\_e.htm](http://www.pac.dfo-mpo.gc.ca/sci/osap/data/default_e.htm)). We analyzed data from the Langara Island lighthouse station on the Queen Charlotte Islands, BC, as this site provides a good surrogate for the temperature variability that

Fraser River sockeye experience during their last 6 months of ocean residency, and is within the general region where homeward bound adult Fraser River sockeye typically make landfall (i.e. enter continental shelf waters). NPI values are available from the National Center for Atmospheric Research's Climate and Global Dynamics section web page (<http://www.cgd.ucar.edu/~jhurrell/np.html>).

## RESULTS

ANOVA revealed no significant differences in proximate constituent totals among 1956 and 1999–2002 samples (i.e. all proximate constituents summed to  $100 \pm 1\%$ ;  $P > 0.05$ ). Thus we feel confident that the two lipid extraction methods employed between time periods are comparable.

Analysis of covariance (type III sums-of-squares, SAS proc glm, SAS Institute Inc., Carey, NC, USA), which corrected within-stock energy density for allometric differences associated with fish length (post-orbital to hypural), was used to compare energy density among years. There was no stock-by-length interaction, thus the interaction term was removed from the ANCOVA model. We found no significant inter-stock differences among years, nor were there significant sex differences within stock and year (all  $P > 0.05$ ), thus, within year, we pooled sexes for subsequent analyses. Least square means revealed that, for both stocks, energy densities were lowest in 1999

and 2000, and higher in 1956, 2001, and 2002 (ANCOVA, all  $P < 0.05$ ; Fig. 1). For Early Stuart sockeye, energy densities did not differ between 1999 and 2000 ( $P > 0.05$ ), but 1999–2000 differed from both 1956 and 2001–2002 (both  $P < 0.05$ ). Early Stuart energy also differed between 1956 and 2001–2002 ( $P < 0.05$ ). The 1957 Early Stuart mean was within 3% of the 1956 mean. Chilko sockeye, 1999–2000 energy densities differed from both 1956 and 2002 ( $P < 0.05$ ), but 1956 and 2002 did not differ ( $P > 0.05$ ).

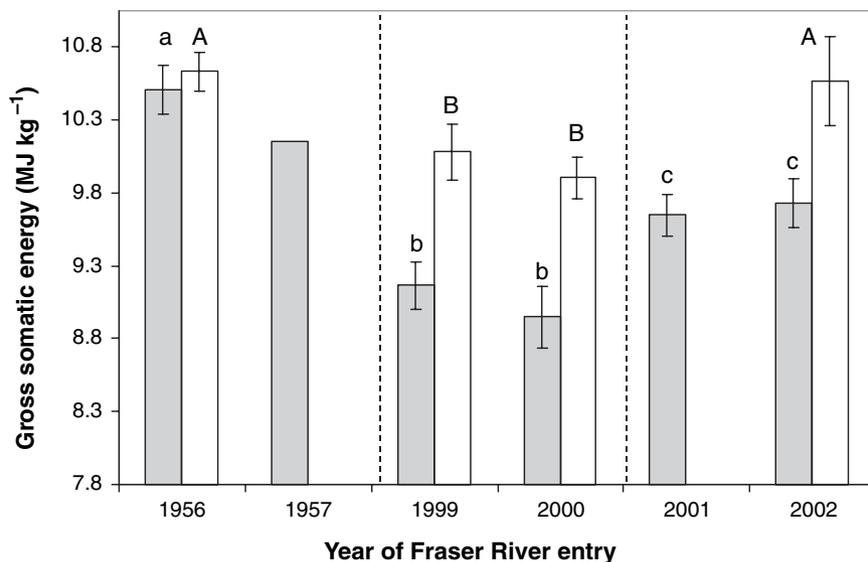
Between stocks, 1956 energy densities in Early Stuart and Chilko did not differ ( $P > 0.05$ ), but were different in all other years (1999, 2000, 2002) ( $P < 0.05$ ).

A Pearson correlation matrix revealed that gross somatic energy at river entry was significantly associated with both SST (Pearson's  $r = -0.775$ ,  $P = 0.012$ ) and NPI (Pearson's  $r = 0.678$ ,  $P = 0.031$ ). SST and NPI trends are plotted against body energy in Fig. 2a,b.

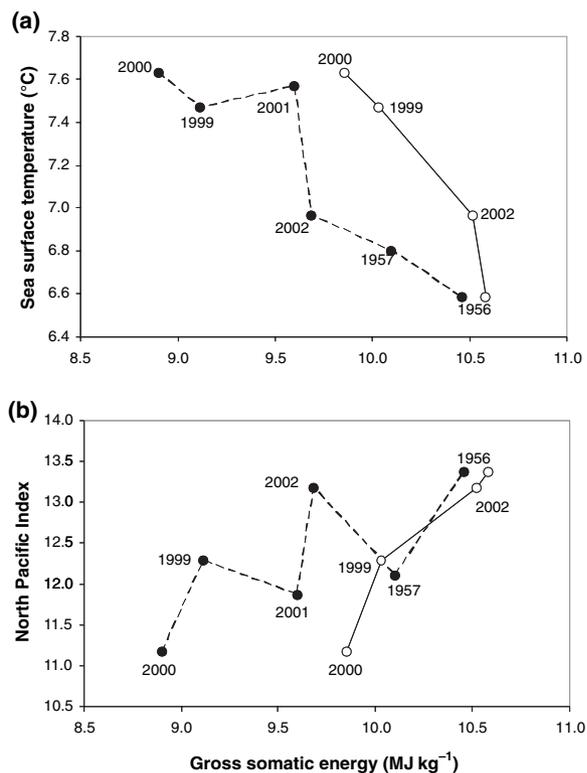
## DISCUSSION

Our results are consistent with the hypothesis that ocean climate regimes influence the river entry energy states of mature salmon. We found that, within both stocks of sockeye salmon, somatic energy densities were high during regimes characterized by good growing conditions and low during a regime with poorer, transitional growing conditions. We also found significant correlations between somatic energy and

**Figure 1.** Mean ( $\pm 1$  SE) gross somatic energy concentrations in Early Stuart (gray bars) and Chilko (white bars) sockeye at Fraser River entry. Dashed vertical lines delineate ocean regime periods. Lower case letters signify Early Stuart among-year contrasts, upper case letters for Chilko. Within stock, bars with different letters indicate significant differences ( $P < 0.05$ ).



**Figure 2.** Body energy of Early Stuart (dark circles) and Chilko (open circles) sockeye at the onset of upriver migration in relation to sea surface temperatures (a) and North Pacific Index values (b) averaged over the last 6 months of ocean residence.



two indicators of ocean climate: SST and the North Pacific Index. Low somatic energy levels during the 1999–2000 regime period may be attributable to both reduced food availability (low zooplankton production coupled with high salmon densities) and high costs of foraging (high metabolic rates at higher SST). Although 1999–2000 may be viewed as transitional years between two distinct ocean regimes, salmon from 1999–2000 spent part of their 2 yr of ocean residency in the warm El Niño like conditions prior to 1999. It is possible that there exists a link between the relatively low energy states and the poor ocean survival of Fraser sockeye observed during the 1977–99 period (Hinch *et al.*, 1995; Welch *et al.*, 2000). There is evidence that ocean climate influences the energy states and survival of other northeast Pacific marine species, most notably seabirds. In 1997, short-tailed shearwaters (*Puffinus tenuirostris*), which, like sockeye, forage primarily on euphausiids (*Thysanoessa* spp.), suffered massive mortality, primarily in the south-eastern Bering sea but also along a broad arc extending across the northern Gulf of Alaska. Post-mortem examination

revealed that this mortality was attributable to starvation (Baduini *et al.*, 2001).

Although both the Early Stuart and Chilko stocks examined in this study showed similar among-regime patterns, energy levels in Chilko sockeye were not as negatively affected by the poor productivity regime as were Early Stuart sockeye. Fraser River sockeye may have stock-specific locales in the northeast Pacific Ocean in which they grow. Using correlations between return times and SST (Blackbourn, 1987) and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios (Welch and Parsons, 1993), it has been suggested that Chilko sockeye rear and mature near the center of the Alaska Gyre, an area where strong upwelling of nutrients occurs. Thus, even during less productive regimes, food and growth conditions in the central Gyre may be better for energy accrual relative to peripheral areas in the northeast Pacific Ocean.

A reduction in river entry energy levels could have serious fitness consequences for salmon. Between the mid-1950s to 1999–2000, Early Stuart sockeye experienced a 15% reduction in river entry somatic energy, equaling roughly  $1.5 \text{ MJ kg}^{-1}$ . This is an equivalent density of energy used to migrate (with concomitant gonad development) 600 km up the Fraser River [based on energy expenditure rates calculated for 1997 and 1999 (P. Rand, unpublished data, Wild Salmon Center, Portland, OR, USA)]. How important might such a reduction in energy be? In 1997, about 50% of the Early Stuart run (approximately 500 000 sockeye) perished *en route* to spawning areas (Macdonald, 2000). During that year, record high river flows slowed migrations and caused high rates of energy depletion as well as stress (Macdonald, 2000). It is possible that low somatic energy levels at the onset of river migration, a consequence of warm SST and poor zooplankton productivity, may have been a significant additional factor: setting the stage for energy exhaustion prior to reaching the spawning grounds. We have previously documented that risk of *en route* mortality in sockeye salmon is considerable when river flow rates are high (Rand and Hinch, 1998b), and when fish swimming speeds are fast (Hinch and Bratty, 2000). As Early Stuart sockeye have been arriving on spawning areas in recent years with energy levels just above  $4 \text{ MJ kg}^{-1}$ , further reductions in energy at the onset of migration might push them dangerously close to the  $4 \text{ MJ kg}^{-1}$  threshold needed to sustain life (Crossin *et al.*, 2003; Crossin *et al.*, in press).

From a management perspective, an assessment of energy states in returning adult salmon as they approach coastal waters could generate valuable information when making fisheries harvest decisions. If salmon have relatively low somatic energy densities, and river conditions are expected to make upriver

migrations difficult, risk averse decisions, such as limiting some harvest to ensure adequate escapement, may have to be made.

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