Sea Surface Temperature and the Subsequent Freshwater Survival Rate of Some Salmon Stocks: A Surprising Link Between the Climate of Land and Sea

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ABSTRACT: Previous consideration of the relationship between climate and the survival rate of Pacific salmon eggs and fry has been confined to effects of large variation in the ambient freshwater environment; *eg*, stream discharge, temperature, turbidity. This analysis shows sea surface temperatures during the last year of life of maturing adult salmon are also strongly associated with the subsequent survival rate of salmon eggs and fry in fresh water, presumably through development of the future eggs or sperm. In several stocks of three species of North American salmon, the association between the "marine" climate and egg survival is stronger than, or additive to, any estimated climatic association in fresh water. This apparent and surprising link between fresh water and the distant ocean has some interesting and complex implications for management of future salmon production.

The various species of Pacific salmon (*Oncorhynchus* sp.) spend from 6 months to several years of the early part of their lives in fresh water before they leave for the ocean. The first 3 to 6 months of this period are spent as eggs "incubating" in the gravel of the spawning area in cold, well-oxygenated water. Fewer than 10 percent, and often fewer than 1 percent, of the eggs laid by an adult female salmon develop and leave fresh water as juveniles, and much of the mortality occurs during spawning and incubation (Salo 1991).

When attempting to account for this annual variation early in the life cycle, it is natural that local and contiguous biological and physical processes are usually assumed to be the main agents of mortality. Therefore, in previous studies most attention has been focused on effects of unusually large numbers of spawners and/or on flooding of incubation sites by heavy rain and high river discharge. Both of these factors tend to disturb spawners, move gravel after spawning, and increase the silt content of the gravel; all to the detriment of the developing eggs, some of which may also be exposed or buried in less than optimum locations. Eggs laid in very shallow water are subsequently vulnerable to another physical factor during incubation, extremely cold water.

During a study of the migration timing of pink salmon back to the Fraser River, it was noted that, over several years the subsequent fresh water survival (FWS) rate of the eggs was strongly and surprisingly correlated with the speed of passage of the adult salmon into the terminal fisheries. Also, both of these phenomena were strongly correlated with coastal marine sea surface temperatures (SST) a few months before spawning.

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These results implied that SST, migration behavior, or both, had some effect on the quality of salmon eggs or sperm, and/or on adult spawning behavior. Simple models of statistical relationships between SST and the migration timing behavior and terminal pre-spawning mortality of adult salmon have been described elsewhere (Blackbourn 1987, In Prep).

This paper describes an attempt to test the generality of the apparent relationship between FWS for Fraser River pink salmon and SST. I report comparisons between FWS rate in some stocks of Pacific salmon and environmental data from various periods in the final adult year:

- Early in the year and far out in the Gulf of Alaska,
- From periods a month or two prior to spawning, and
- During incubation.

A measure of competitive or "crowding" factors on FWS, such as number of spawners or eggs is also included in the analyses.

Recent trends in near-shore SST and in spawner number for many North American salmon stocks have been similar and increasing. Therefore, to avoid the confounding effect of autocorrelation between these factors, I also examine the extents to which SST data account for significant variation in FWS rate in addition to that accounted for by spawner/egg number and other environmental data.

Fresh-water survival data from four salmon stocks from British Columbia are analyzed from two pink and two sockeye stocks. One stock of each species uses natural spawning conditions and the other stocks spawn under conditions of controlled flow and optimal gravel size in spawning channels. Data from both types of incubation are analyzed to investigate the possible existence of a partial, "universal", pre-spawning SST effort on egg or sperm quality, with and without the confounding effects of other potential agents of annual variation in FWS rate, such as river discharge or inter-gravel particle (silt) size.

Data Sources

The salmon data in this paper come from unpublished sources (see Acknowledgments).

The fresh-water survival (FWS) rate data cover various periods in the life history of the stocks. An estimate of numbers of eggs laid is calculated by extrapolation from estimates of average fecundity (number of eggs per female) and is known as the potential egg deposition (PED) in common to all four salmon stocks. In the case of (wild) Atnarko River pinks, the FWS rate is short-term and is based on the percentage of live, of the total of live plus dead eggs and recently hatched juveniles (fry), in the gravel in January, or about 4 months after spawning.

A slightly longer period is covered by FWS rate in the two stocks from spawning channels, Seton Creek pinks and Weaver Creek sockeye. Here FWS rate refers to the number of fry estimated as migrating out of the spawning channel in March as a percentage of the PED in October (in both cases), about 6 months earlier. FWS rate data covering a much longer period are the only kind available for Great Central Lake (GCL) sockeye. In this stock, the number of juveniles in the lake in September about 1 year after spawning is taken as a percentage of the PED.

Some of the British Columbia shore SST data used here have been published in Canadian Data Reports of Hydrography and Ocean Sciences; for example in Giovando (1983). Offshore SST data from the Bering Sea and Gulf of Alaska up to 1982 were obtained from unpublished records of Dr. D. McLain of the Pacific Environmental Group, NMFS, Monterey, California. Since 1982 most of the offshore SST data originates from reports (the "Oceanographic Monthly Summary" and the "15-Day SST Mean") published by the U.S. National Weather Service, NOAA, Washington DC, USA.

British Columbia rainfall and air temperature data are published in the series "Monthly Record-Meteorological Observations in Western Canada" by the Canadian Atmospheric Environment Service, Downsview, Ontario, and in the "British Columbia Climate Summary" from the regional office of the same service.

Analyses

Simple and multiple least squares regressions were used to identify associations among environmental data, spawner or egg number, and measures of FWS rate from four stocks of wild or enhanced pink and sockeye salmon. Results are considered significant where $P \leq 0.05$. Percentages of the FWS rates are not transformed, as this parameter for stocks of each "incubation type" has fairly low variance in most cases, with little overlap between types. Thus, the data do not greatly violate the assumption of normality in distribution.

Fresh water environmental variables in the analyses are the closest available in time and space to the spawning grounds or channels. Coastal SST data are mean monthly values from stations and periods close to the final marine migration areas of the stocks and also, where appropriate, from the outer coastal areas.

Gulf of Alaska SST data from the brood year are mean monthly values from "Marsden" squares of 5° latitude by 5° longitude and are included in the analyses as follows:

- Time: Data from every month from November (adult return year minus one) to June (return year) are considered as potentially appropriate from the inferred location of the stocks according to models of return timing in pink and sockeye salmon (Blackbourn 1984, 1987). Within these limits, those months or combinations of months of SST data with the highest single regression coefficients versus the FWS rate for each stock are shown in the results.

- Place: The stock-specific distribution of North American salmon at sea early in their last year is unknown, although it has been inferred for some stocks, particularly for Fraser River pinks and sockeye (Blackbourn 1984, 1987; Takagi *et al* 1981). From models in the latter papers, it is assumed that pink salmon stocks would be distributed in the southeastern Gulf of Alaska between 40° and 50° N and between 125° and 150° W. Therefore, monthly SST data from this area are used in primary analyses with pink FWS rate data. Similarly, SST data from a large area across the central Gulf between 45° and 55° N and between 135° and 160° W are used in initial comparisons with sockeye FWS rate data.

SST data showing the strongest coefficients when compared to FWS rate data were used in multiple regression analyses with all other factors, including: coastal SST; fresh water environmental data just before, during, or after spawning; and spawner or egg number. In some of the time series there are fairly strong time-series trends and, thus, strong cross-correlation between them, particularly between coastal SST and spawner or egg number in some stocks. In the absence of any model that fits the spawner/egg data with low variance, the best evidence for a real or potential effect of brood-year SST on FWS rate in such cases is taken to be significant additional variation accounted for when SST data are also used. In all analyses the variation is that proportion adjusted for the total degrees of freedom in each combination. A more extensive analysis of these relationships in a larger number of salmon stocks has been described by Blackbourn (1991).

To maximize the degree of biological insight gained, no formal protocol for dealing with successive correlation analyses (Walters 1990) is followed in this study or in Blackbourn (1991). In such a protocol it is recommended that the degrees of freedom be decreased for each successive "case" (here, stock, month or SST "area") investigated. To do so would rapidly exhaust the number of stocks for which it could be used, especially in those stocks with relatively short data records (see Blackbourn 1991).

Results

In all four stocks of salmon discussed here, the effect of SST alone in accounting for variation in FWS rate is significant (Table 1). This is also true for 16 of 18 stocks in a larger study (Blackbourn 1991). In addition, in all four cases the negative relationship between SST and FWS rate is stronger than that between FWS rate and (a) spawner or egg number or (b) local environmental data during incubation.

Table 1
FACTORS FROM THE FINAL ADULT YEAR OF SALMON THAT ACCOUNT FOR VARIATION IN FRESH-WATER SURVIVAL RATE OF STOCKS OF WILD AND SPAWNING-CHANNEL SALMON

				% of Adjusted Variance of FWS Rate Accounted for in: Simple Regression			Multiple Regression		
Data Period	N	Area	FWS Rate	Factor	Sign	% AR^2	Factor	% AR^2	P
Atnarko River Pinks (Wild)									
1974-1989	10	Central Coastal British Columbia	P.E.D. to live eggs and fry in January	1. Number of spawners	Neg	48	1 + 4	74	0.004
				2. Incub air temps	Pos	0	1 + 5	64	0.012
				3. Incub river disch	Pos	0	1 + 4 + 5	77	0.007
				4. Coastal SST July (Central BC)	Pos	10	1 + 2 + 5	59	0.040
				5. Gulf of Alaska SST Jan-Mar 45-50°N, 145-150°W Feb-Apr 45-50°N, 140-145°W	Neg	59			
Seton Creek (Fraser River) Pinks (Spawning Channel)									
1967-1989	12	South-Central Interior British Columbia	P.E.D. to outmigrant fry	1. Number of eggs laid		0	3 + 4	77	0.001
				2. Incub air temp	Pos	12	2 + 3	72	0.002
				3. Coastal SST July-Aug W. Vancouver Island	Neg	27	2 + 3 + 4	86	0.000
							1 + 3 + 4	85	0.000
				4. Gulf of Alaska SST May-Jun 45-50°N, 140-150°W	Neg	72	1 + 2 + 3 + 4	91	0.000
Great Central Lake Sockeye (Wild)									
1978-1988	11	Southwestern Vancouver Island (BC)	P.E.D. to lake juveniles	1. Number of spawners	Neg	21	4 + 5	51	0.023
				2. Incub air temps	Neg	0	3 + 5	49	0.029
				3. Near-coastal SST June	Neg	38	2 + 4 + 5	58	0.028
				4. Coastal SST July W. Vancouver Island	Neg	36	3 + 4 + 5	53	0.043
				5. Gulf of Alaska SST Mar-Apr 50-55°N, 145-155°W	Neg 38				
Weaver Creek (Fraser River) Sockeye (Spawning Channel)									
1965-1989	25	Southwestern British Columbia	P.E.D. to outmigrant fry	1. Number of eggs	Neg	46	5 + 6	74	0.000
				2. Female length	0	0	1 + 6	72	0.000
				3. Incub air temp	Neg	0	1 + 5 + 6	83	0.000
				4. Coastal SST Aug-Oct E. Vancouver Island	Neg	15	1 + 4 + 5 + 6	82	
				5. Coastal SST Aug W. Vancouver Island	Neg	47			
				6. Gulf of Alaska SST Jan-Feb 45-50°N, 130-145°W	Neg	61			

For three stocks, SST data from the Gulf of Alaska early in the final year account for more variation in FWS rate than do the later coastal data. In GCL sockeye the effect is of similar power for both types of SST data (Table 1). However, the comparisons are not balanced in that SST data from only one or two coastal locations along the migration routes are considered in each case and there is no search for strongest coefficients, whereas only those Gulf of Alaska SST data with the highest coefficients with FWS rate are used in the final comparisons.

Factor combinations from multiple regression analyses result in significant added variation in all four stocks (Table 1). In three stocks, the combination of two or three factors accounts for more than 70 percent of adjusted total variation ($P<0.01$); in GCL sockeye, three-factor combinations account for more than 50 percent of past variation in FWS rate ($P=0.028$).

Boundaries of SST areas with the strongest coefficients with FWS data for stocks of three salmon species show some, but not complete, separation (Blackbourn 1991), and distribution of "best" SST areas for each species shows an interesting parallel feature. Despite large differences in period of data record and location of spawning stream, several stocks of the same species have very similar "best" areas and times in the Gulf of Alaska (Figures 1 and 2).

Results for Seton Creek pinks confirm the earlier work with data for pinks from the whole Fraser River watershed in that there is a strong relationship between coastal SST data and FWS rate (Table 1) and, in this case, in that there is a still stronger relationship with earlier SST data from the Gulf of Alaska.

There appears to be little or no difference in the partial effect of early SST on FWS rate whether salmon stocks use natural or controlled spawning areas (Table 1).

Discussion

These comparative analyses include data from diverse physical and biological variables. The underlying precision and accuracy of the methods used to produce these salmon data are fairly well known except for Atnarko River pinks. For example, those used for Weaver Creek sockeye are described by Woodey (1984). Paradoxically, it may be a strength in that the expected outcome of analysis of heterogeneous biological and physical data might be expected to reveal few, if any, significant associations between SST and FWS. It is probable that the consistent statistically significant associations among these data reflect some real underlying connection (see Blackbourn 1991).

The hypothesis of a previous effect of brood-year SST on FWS rate in two incubation types is supported by these analyses. The overall additive

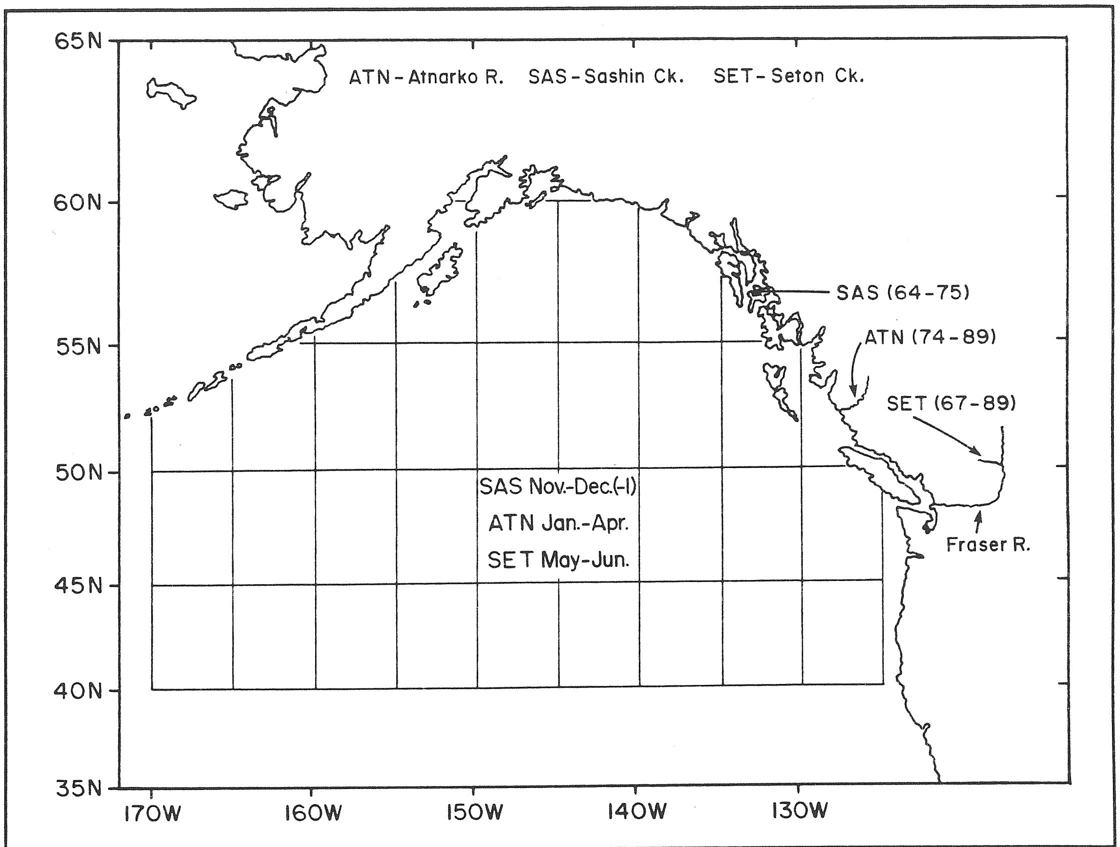

Figure 1. Sources of SST data that show the strongest correlation with the fresh-water survival rate of three stocks of pink salmon.

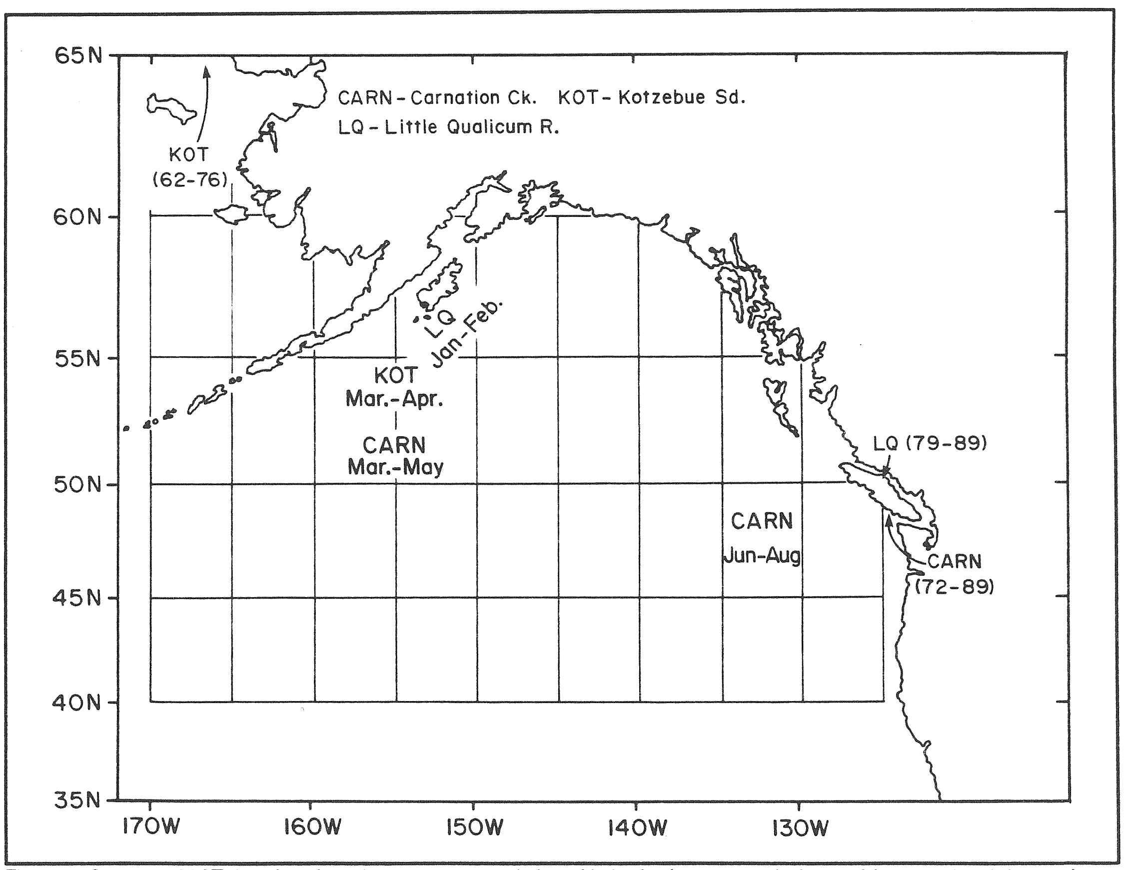

Figure 2. Sources of SST data that show the strongest correlation with the fresh-water survival rate of three stocks of chum salmon.

effect of SST on FWS rate in the multiple regression analyses is demonstrated by its occurrence in all four of these stocks and in all of which more than one factor is related to FWS rate. The particular effect of brood-year SST should be further tested by more intensive studies, particularly in those stocks for which detailed data on spawner and egg number and from the incubation environment can be readily measured. The effect of SST could be partially and experimentally investigated on fish held well before spawning at various sites along the migration path or perhaps held at fish farms with laboratory facilities.

These salmon stocks are of great economic importance. Therefore, in addition to more research, some consideration should be given in the management of such stocks to the application of:

- Final-year oceanic SST data when setting pre-season goals for spawner number.
- Coastal SST data when adjusting those goals during, or perhaps even before, the fishing season.

If these effects are real, and whether or not SST is an index for some other environmental effect on gamete quality, the short-term effect of SST may be predictable. For example, in a year that is warmer than average, a larger than average number of spawners may be necessary to obtain an average number of fry the following spring. However, because the FWS rate for a stock may also be negatively related to spawner or egg number (Table 1), the specific relationship between all these factors must be carefully considered for each stock before changes in goals for spawner number can be recommended.

Although results of the multiple regression analyses are statistically more noteworthy, from an ecological point of view results of the simple regression analyses of the effect of SST data are extremely interesting. First, in three of the four stocks, coastal SST data from locations and places thought, or in some cases known, to be appropriate to particular stocks do show moderate to strong relationships with FWS rate data for those stocks; *eg*, data from Amphitrite Point (western Vancouver Island) in July for the (very early) GCL sockeye and, for the late-summer returning Weaver Creek sockeye, data from Amphitrite Point in August and from Chrome Island (Georgia Strait) from August to October (Table 1).

Results of simple regression analyses of Gulf of Alaska SST data months before spawning are also intriguing. Areas from which SST data show the strongest relationship with FWS rates of pink and sockeye stocks are generally within the boundaries originally thought likely to show such results; *ie*, the southeastern and central Gulf of Alaska. Perhaps the most interesting result of all is that stocks of pinks and chums from widely separated spawning locations and different time-periods have very similar locations and periods for their "best" Gulf of Alaska SST data. These results give some credence to the idea that subtle effects of the ocean environment on the freshwater survival rate of salmon via gamete development may be real and, in some cases, as important or much more important than the more obvious local fresh water environmental factors. This type of transfer of the oceanic "history" of the salmon into fresh water represents a new form of link between two completely different environments.

The possible warming of the ocean and rivers in the next 50 years due to increased amounts of "greenhouse" gases is already of concern to salmon biologists. The potential warming has been considered important to both freshwater and marine phases of the life cycle of salmon; and present and potential fresh water and ocean temperatures are investigated for each phase respectively, particularly for vulnerable stocks in the southern part of the range for each species.

Consideration of data such as those discussed in this paper add a further concern. The time and place of future changes in ocean climate may be important not only to such salmon parameters as marine survival rates, marine growth rates, fecundity, migration timing and routes, *etc*, but also to the subsequent fresh water survival rates of the eggs of returning adults. In this respect it may be important to remember that, in the recent past, SST anomalies have been of different strengths and even of the opposite sign in various parts of the northeastern Pacific and the Gulf of Alaska. If the future ocean climate contains a similar amount of temporal and spatial heterogeneity, then the future fresh water survival rate of a particular stock may not be entirely directed by environmental trends at or near the spawning location. Also, to judge by these results, future trends in fresh water survival rate of stocks of different species (*eg*, pinks and chums) at the same spawning locations could be environmentally mediated to a different degree or even in a different direction.

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