Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming[1]

D.W. Welch, Y. Ishida, and K. Nagasawa

Abstract: Ocean surveys show that extremely sharp thermal boundaries have limited the distribution of sockeye salmon (*Oncorhynchus nerka*) in the Pacific Ocean and adjacent seas over the past 40 years. These limits are expressed as a step function, with the temperature defining the position of the thermal limit varying between months in an annual cycle. The sharpness of the edge, the different temperatures that define the position of the edge in different months of the year, and the subtle variations in temperature with area or decade for a given month probably all occur because temperature-dependent metabolic rates exceed energy intake from feeding over large regions of otherwise acceptable habitat in the North Pacific. At current rates of greenhouse gas emissions, predicted temperature increases under a doubled CO_2 climate are large enough to shift the position of the thermal limits into the Bering Sea by the middle of the next century. Such an increase would potentially exclude sockeye salmon from the entire Pacific Ocean and severely restrict the overall area of the marine environment that would support growth.

Résumé : Les campagnes d'évaluation océaniques révèlent que des limites thermiques très prononcées ont restreint la répartition du saumon rouge (*Oncorhynchus nerka*) dans l'océan Pacifique et dans ses mers bordières au cours des 40 dernières années. Ces limites sont exprimées comme une fonction échelon dont la température qui définit la position de la limite thermique varie mensuellement selon un cycle annuel. La netteté de la différence de température au bord limitrophe, les différentes températures qui définissent la position du bord limitrophe pendant l'année et les subtiles variations de température d'une zone ou une décennie pour un mois précis découlent probablement du fait que les taux métaboliques thermosensibles dépassent l'absorption d'énergie de la prise alimentaire sur de vastes régions de milieu autrement acceptables du Pacifique Nord. Si les émissions de gaz à effet de serre continuent au rythme actuel, les augmentations de température prévues dans un climat où la quantité de CO_2 est doublée seront suffisantes pour causer le déplacement des limites thermiques jusqu'à la mer de Béring d'ici le milieu du siècle prochain. Une telle augmentation pourrait complètement chasser le saumon rouge de l'océan Pacifique et restreindre considérablement les milieux marins propres à la croissance de la population.
[Traduit par la Rédaction]

Introduction

The ocean migration of Pacific salmon is generally believed to involve a counterclockwise movement south in winter and north in summer following the currents of large oceanic gyres (Neave 1964; Royce et al. 1968; Pearcy 1992). Neither temperature nor salinity has been found to be either a strong or consistent determinant of the ocean distribution of Pacific salmon (Burgner 1991), and the influence of oceanographic features on the distribution and migration of sockeye salmon (*Oncorhynchus nerka*) has not been clearly established (Bakkala 1971). The primary oceanographic factor influencing the southern limit to the distribution of Pacific salmon has in the past been variously identified as sea surface temperature (SST) (Ogura and Takagi 1987), subsurface temperatures (Fujii et al. 1965), and various oceanic frontal structures (e.g., Tabata 1983).

The first evidence for strong thermal limits was observed during a spring 1990 survey of Pacific salmon distributions in the Gulf of Alaska (Welch et al. 1995). To further examine possible limits on the distribution of Pacific salmon, a major survey effort involving a total of eleven 1-month surveys was conducted by the Japanese and Canadian governments during the spring, summer, and winter of 1992. These surveys covered all areas of the North Pacific, and a number were repeated in subsequent years. The final survey was a trans-Pacific survey in January 1996 that resurveyed the areas first examined in December 1992 (Fig. 1). These data were combined with historical data from Canadian and U.S. salmon longline surveys for the 1950s and 1960s (Turner and Aro 1968), archived Canadian gillnet surveys from the 1950s and 1960s, modern Canadian data collected in the 1980s and 1990s, and data from all Japanese ocean salmon gillnet surveys completed since 1972.

We report here the limits to the distribution and abundance

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[1] Figures of the differences in thermal limits between areas and decades for November–March, April, May, and September may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

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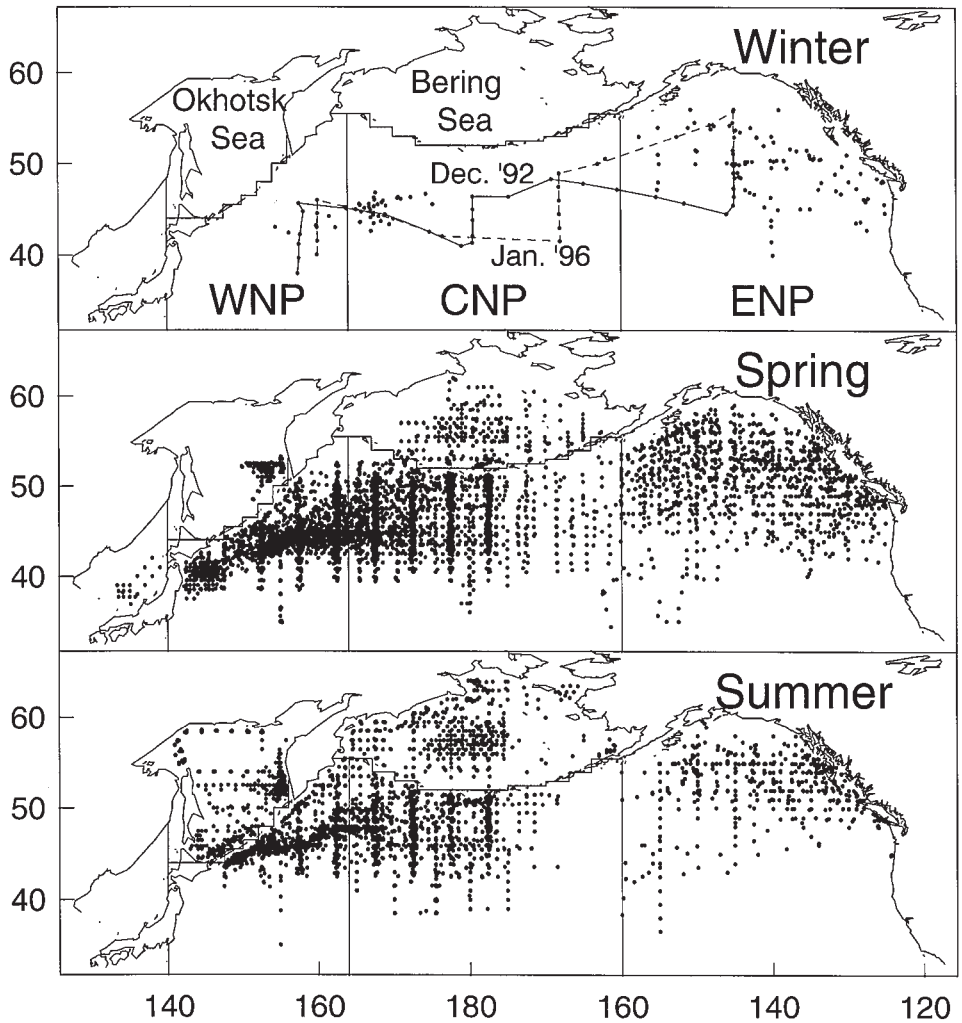
Fig. 1. Distribution of available observations on salmon abundance and temperature, 1956–1996 ($N = 20\,397$) and the geographic divisions of the North Pacific (eastern, ENP; central, CNP; western, WNP) used later. The true density of the data is poorly represented because many stations are overplotted dozens of times. Note that the December 1992 and January 1996 trans-Pacific surveys include observations from all three geographic areas. Winter, November–March; spring, April–June; summer, July–September.



of sockeye salmon using the entire data set ($N = 20\,397$). These data represent a remarkable sampling effort extending over the 40-year period 1956–1996 and covering the entire North Pacific Ocean and adjacent seas. They are the result of a total sampling effort equivalent to 29.1 years of continuous ship survey time, after excluding time lost to weather or in transit. Our results demonstrate that extremely sharp thermal limits to the oceanic distribution of Pacific salmon occur throughout the year. We also show that the temperature defining the thermal edge changes, primarily between months but secondarily between regions or decades examined, probably reflecting the balance between losses due to temperature-dependent basal metabolic processes and energy gained from foraging.

Methods and materials

At each location the catch of each species of salmon was recorded along with the level of fishing effort and a limited number of observations on simultaneously collected oceanographic variables, chiefly SST. Three fishing gears are used in ocean salmon surveys. We defined a unit of fishing effort as being 1 tan (50 m) of gill net, 1 hachi (138 m) of longline, and 1 km of distance towed for surface rope trawls. Catch per unit fishing effort (CPUE) observations were normalized by dividing by annual mean CPUE for each gear type separately to remove interannual variations in abundance and differences between gear types.

The majority of the observations on salmon abundance are based on 8-m-deep gill nets fished at the surface. The remainder of the observations are based on surface longlines (fished in the top 1.5 m of the water column) or surface trawls (0–40 m depth interval). Direct observations of acoustically tracked free-swimming sockeye in the open ocean show that sockeye, as with the other species of Pacific salmon, are strongly surface oriented (Manzer 1964; Ogura and Ishida 1995). Ogura and Ishida (1995) reported that sockeye in the open ocean spent 70% of their time in depths <10 m (mean swimming depth 9.9 m) and maintained an overall vertical distribution almost entirely confined to the upper 40 m of the water column, where nearly isothermal conditions prevail. Deep-diving behaviour was only observed for sockeye salmon (Ogura 1994), and only 1% of the total time was spent below the surface mixed layer by this species during rapid deep dives at near-maximum burst swimming speeds (4.4 body lengths/s). Ascents back to the surface mixed layer were nearly as

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rapid (2.8 body lengths/s), suggesting that this behaviour was probably an adaptation to escape predators and indicating the strong preference for remaining within the surface mixed layer.

Echosounding surveys carried out concurrently with the January 1996 trans-Pacific survey confirmed the strong surface orientation of Pacific salmon (Sakai et al. 1996). Acoustic targets were only identified within the surface mixed layer and at temperatures below the thermal limits observed in winter from the trawl survey (see below). As the mixed layer depth of the subarctic Pacific is >50 m in summer and 80–100 m in winter, the simultaneously collected surface measurements therefore provide a reasonable characterization of the thermal environment of near-surface (<40 m) conditions.

Limits to ocean distributions

The extensive data allow us to subdivide the data by species, month, decade, and geographic region in a set of trellis plots (Cleveland 1993) to examine interactions with oceanographic variables on a consistent set of axes. We concentrate here on analysing the distributional limits for one species, sockeye salmon (*O. nerka*). The sharp thermal limits we report below for sockeye are also evident for the other species of *Oncorhynchus* (which are also caught during the same fishery surveys), but the temperatures defining the upper thermal limits are species specific and generally higher, particularly in the spring and summer. Detailed analysis of the thermal limits for the other species will be reported elsewhere.

In Fig. 2, we plot the logarithm of the catch observations versus SST for all areas combined in the first column, partitioning the data by months. The transformation $\log_e$(CPUE + 1) preserves the zero catches as zero. With the exception of October, when there are no data, an upper thermal bound on the distribution is evident in all months and all regions where sampling extended into sufficiently warm ocean regions. For the "winter" months of November through March, sockeye are confined to regions ≤7°C. Thermal limits increase from April through August, when they reach a maximum of about 15°C. The limit then declines again until finally returning to the 7°C level by November.

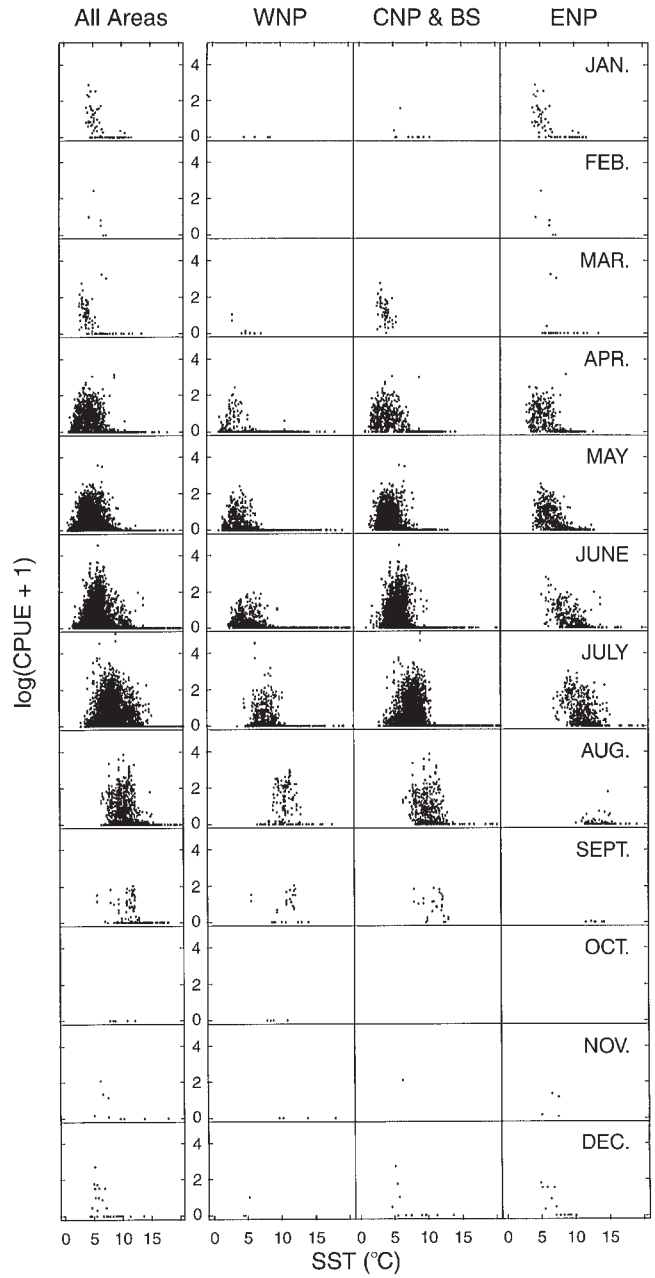
Although the sockeye distribution is clearly bounded to the south by higher temperatures, the thermal limits are not particularly sharp for the aggregated data. Subdividing the data into three regions (Fig. 2, right-hand columns) reveals a much sharper relationship in each month. The highest thermal limits are generally observed in the eastern Pacific, demonstrating that a single uniform response to temperature does not occur.

Further subdivision of the July data by decades and geographic areas shows an extremely sharp response to SST (Fig. 3). The same sharpness is also seen for the other months when similarly subdivided (e.g., Figs. 4 and 5); thus, earlier studies did not identify sharp thermal limits partly because combining data for different months and regions with different thermal limits blurs the response to temperature.

Two of the major limitations of the 40 years of data are the limited number of observations taken in winter or warmer regions where salmon are likely absent and the ambiguity of the available data for some months. For example, sampling always occurred within the sockeye distribution in February (Fig. 2), so the existence, sharpness, and location of the edge are unknown.

The December 1992 and January 1996 trans-Pacific surveys provide a specific opportunity to examine the sharpness

Fig. 2. Monthly comparison of $\log_e$(CPUE + 1) versus temperature. The first column shows the observed response for all areas and decades combined. The next three columns show the monthly changes in thermal limits defining the southern edge of the sockeye distribution for three separate geographic areas of the North Pacific (BS, Bering Sea). The seasonal cycle is similar in all areas, but monthly limits are sharper because they occur at different temperatures in different regions; for this reason, the aggregate response shown in the first column is blurred. A seasonal cycle is clearly evident and far below lethal temperatures (23–25°C; Coutant 1977).



of these thermal limits. The winter distribution of Pacific salmon had previously been described as extending south to about 40°N, to temperatures of about 10–11°C (Manzer et al. 1965). However, we caught no salmon at temperatures above 7.4°C in December 1992 or 7.3°C in January 1996. In

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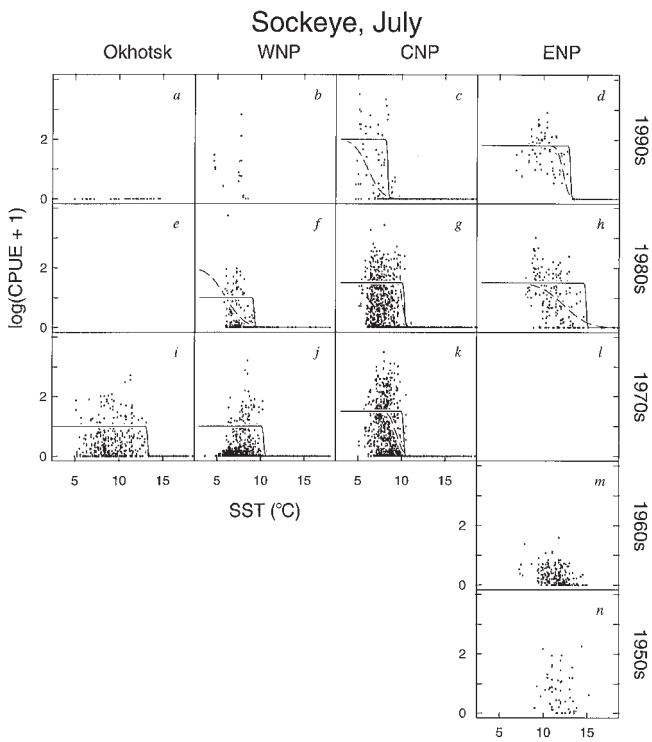
Fig. 3. Differences in thermal limits between areas (columns) and decades (rows) for July, the month with the greatest amount of available data. The thermal limits are now extremely sharply expressed, with abundance dropping to zero in a fraction of a degree Celsius. In three cases (Figs. 3*c*, 3*f*, and 3*h*) the ML estimate described in the text (broken line) indicates that a gradual decline in sockeye density with increasing SST provides the best description of the response, but fails to describe the thermal edge. We refit the model constraining $\sigma_T = 0.1°C$, equivalent to assuming that a sharp step function exists. The estimation problem then reduces to describing the position of the thermal limit. In these three cases the constrained model (solid line) captured the thermal edge; for the other possible comparisons the unconstrained and constrained estimates of the shape of the response are nearly identical. Results for other months are similar.



reexamining the data from the 1950s and 1960s, we found that records of salmon at warmer winter temperatures were primarily limited to a few coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*), which were caught at temperatures up to 10–11°C, near the subarctic boundary at 40°N. However, a clear upper thermal limit on the midwinter distribution of all species of salmon except coho was evident.

Generalized additive models

Lethal limits for Pacific salmon are generally well above 20°C (Coutant 1977), so the remarkably low thermal limits observed result in sockeye being excluded from vast areas of the North Pacific that are otherwise potentially habitable. The sharpness of the edge that results when the data for different months, areas, and decades are considered separately suggests that the primary response is often nearly a step function, with sockeye expressing strong avoidance behaviour within a relatively narrow range of temperatures, and temperature having relatively little influence on distribution below this threshold.

A step function implies that temperature has no influence on behaviour except at the limit, where essentially all individuals must simultaneously express strong avoidance behaviour. The surprising nature of this response has important implications for understanding why sockeye avoid exceeding these temperatures during their ocean migrations. We used a generalized additive model (GAM) to relate the distribution of sockeye to temperature, expressing the abundance as the logarithm of the number of individuals caught at the *i*th station per unit sampling effort, $\ln(n_i + 1)$. Specifically, the GAM model we used can be expressed as

$$(1) \qquad \ln(n_i + 1) = \mu + f_T(T_i) + \varepsilon_i$$

where μ represents the average abundance, $f_T(T_i)$ represents the loess smooth of temperature, and ε_i represents the error distribution for the *i*th observation.

GAMs were estimated assuming a negative binomial (NB) error distribution with known "shape parameter" (Venables and Ripley 1994). The shape parameter is equivalent to the degrees of freedom (df), *k*, on which each observation is based (Welch and Ishida 1993). We modified the definition of the NB family within the statistical analysis program S-Plus to allow the specification of a different number of df k_i for each observation, using $k_i = N_i/15$, where N_i is the number of metres of gill net or longline used, or distance trawled, at the *i*th station. As the sampling effort or df approaches infinity, the NB distribution approaches the Poisson. Thus, for finite df, the distribution we used has heavier tails and higher variance than the Poisson.

In GAMs, locally weighted fitting is used to calculate a nonparametric estimate of the relationship between sockeye abundance and potential explanatory variables using a realistic model of the observational error (Hastie 1992). In essence, the GAM method is the maximum likelihood equivalent of nonparametric smoothing techniques. The advantage of GAMs is that they do not require initial specification of the form of the functional relationship between SST and salmon abundance, and therefore permit a realistic evaluation of the appropriate form of the relationship that should be specified in our more detailed analyses (see below).

In our analysis, we used a loess curve with $\lambda = 1$ and generally chose a data window as narrow as possible in calculating the local response of sockeye abundance to SST, typically using 10–20% of the data points to measure the average response. The sharpness of the response is therefore limited by the smoothing specified; use of a narrower data window results in a more sharply defined response but greater statistical uncertainty in the estimated mean response. The observations on the ocean distribution of salmon are typically spread over a 15°C range of temperatures, with most observations at lower temperatures, so the transition width for even a perfect step function will be spread over roughly 3–6°C, depending on the exact width of the smoothing window chosen. The GAM analysis therefore permits an assessment of whether the change in sockeye abundance is "step-like," with the major drop in abundance occurring in 3°C or less.

Applying the GAM analysis to the sockeye data indicates that abundance is related to ambient temperature as a threshold in both winter and summer, with little measurable effect of SST on abundance away from the edge (Fig. 6). Because the GAM estimate of salmon abundance decreases with increasing

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Fig. 4. Differences in thermal limits for sockeye between areas (columns) and decades (rows) for June. Note that although the thermal limits are sharply expressed, the temperature at which the thermal limit occurs is lower than that evident in July. The fitted curve has been excluded for clarity.

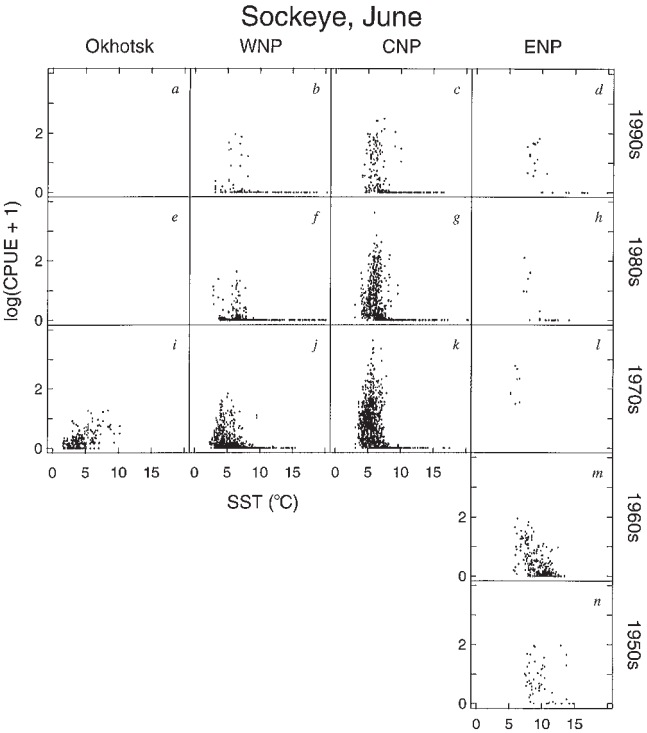
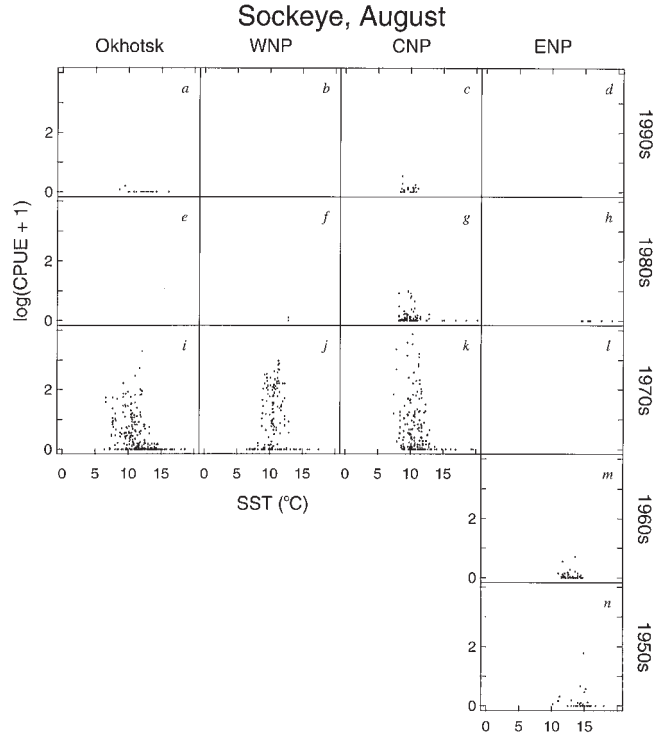


Fig. 5. Differences in thermal limits for sockeye between areas (columns) and decades (rows) for August. Note that although the thermal limits are sharply expressed, the thermal limit occurs at higher temperatures than in June or July. The fitted curve has been excluded for clarity.



temperature over a 2–3°C interval, it is unclear from this analysis alone whether abundance primarily decreases over this relatively narrow thermal interval, or even more sharply than the GAM analysis is capable of resolving (i.e., an extremely sharp step-function response to temperature). However, the analysis does make clear that the primary response to temperature does occur near the thermal limit in a 2–3°C interval and that relatively little change in abundance is evident far from the limit, particularly when sufficient data exist so that the analysis can be performed for a single month and a specific region of the North Pacific. As the maximum likelihood (ML) analysis in the following section makes clear, the response in most months and areas is a very sharp decline in abundance that takes place over only 1–2°C.

Influence of other oceanographic variables

Introducing salinity into the GAM analysis revealed no measurable influence, but the majority of the survey observations do not include information on any oceanographic variables other than SST. Using the World Ocean Atlas (WOA) database of oceanographic observations for the North Pacific (NODC 1994) from 40 to 60°N, we compared the relationship between 10-m SSTs with other simultaneously collected oceanographic variables. After splitting the WOA data into areas, months, and decades to match the previous analyses, we found no strongly coherent relationships between temperature and salinity, O_2, or major nutrients (nitrate, phosphate, silicate) (Fig. 7). The sharpness of the step-function relationship between temperature and sockeye abundance and the absence of a strong relationship between SST and other oceanographic properties therefore strongly suggest that other factors do not play a substantial role in determining the position of the southern edge of the distribution.

Maximum likelihood (ML) analysis

To more precisely measure the influence of temperature on the southern limit, we fit a parametric model that assumes an asymptotic level of sockeye abundance away from the thermal edge and allows estimating T_{crit} and σ_T, the critical temperature and rate of change in abundance near the critical temperature, respectively, by maximum liklihood (Appendix). We concentrate here on defining the variations in the upper thermal limit for different months and areas, since there is little evidence of a lower thermal limit for sockeye.

In most cases, fits of the parametric model provided a realistic description of the sharp thermal limit evident in the data. In three of the possible comparisons for July (Figs. 3*c*, 3*f*, and 3*h*) the ML estimate of the average response of abundance to SST indicated that abundance decreased steadily with SST over the entire range of temperatures. However, in these cases the fits failed to describe the visually evident edge. We therefore refit the model after constraining $\sigma_T = 0.1$°C, which is equivalent to assuming that a sharp edge to the distribution exists, and then estimating the temperature at which the edge is located. The constrained fits were identical to the unconstrained fits in most cases and provided a more realistic estimate of the position of the thermal limit in the other three cases.

Figure 8 summarizes the monthly changes in critical

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Fig. 6. GAM analysis of the estimated response of sockeye abundance to temperature in winter (November–March) and midsummer (July) and associated 95% confidence interval. Over a wide range of temperatures the estimated response is flat, indicating little influence of temperature on abundance within the distribution. Broken horizontal lines are included for reference.

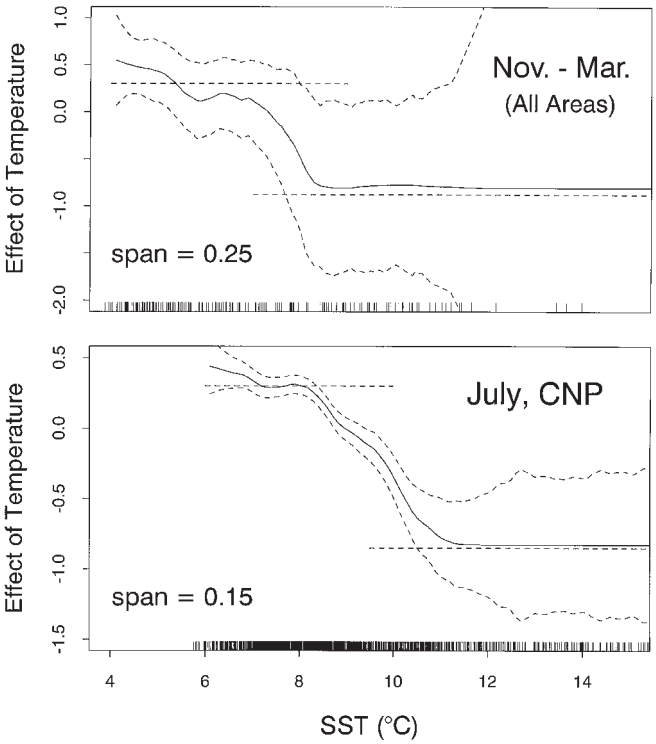
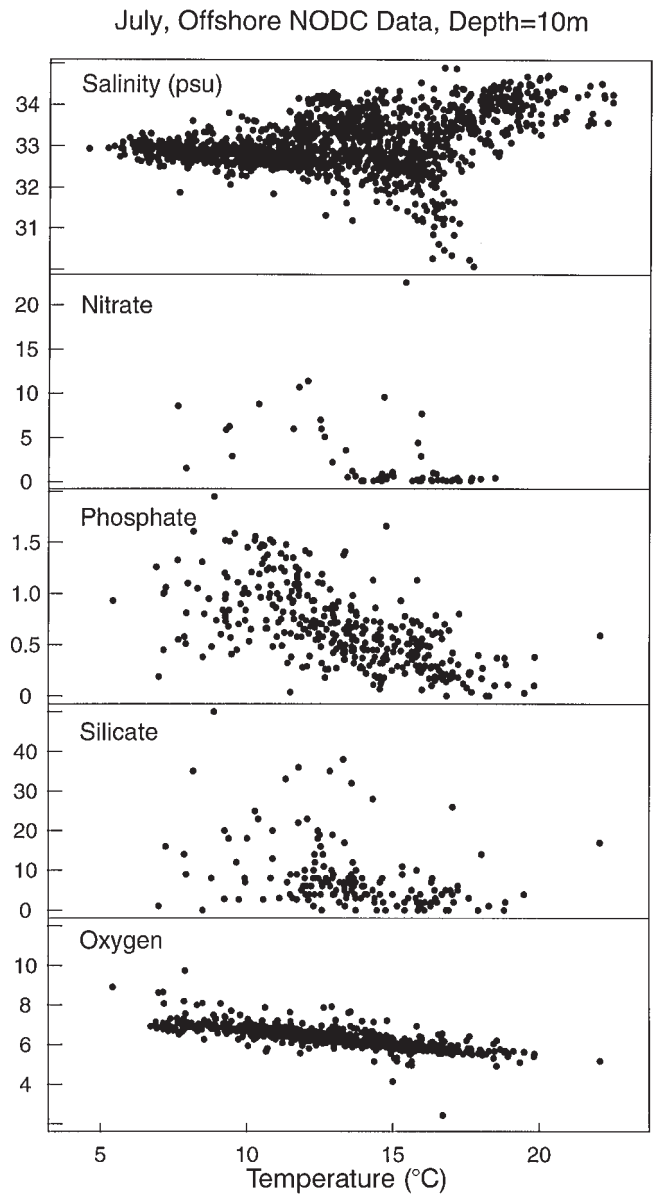


Fig. 7. Comparison of measured values of salinity, nitrate, phosphate, silicate, and O_2 with simultaneous measurements of ocean temperature in July (all data are for observations at 10 m depth). A similar lack of a consistent relationship with temperature is evident for the other months of the year (not shown). The sharp drop in sockeye abundance at the thermal boundaries shown in Fig. 3 makes it unlikely that the sockeye response is actually determined by these oceanographic variables because the observed level of correlation with temperature is insufficient to cause such a sharp drop. Measurements were based on all historical bottle data collected for offshore regions of the Pacific Ocean north of 40°N since 1932 (NODC 1994).



temperatures defining the thermal limits for three areas of the North Pacific after aggregating the data for all decades, and the temperature interval over which sockeye abundance drops by one order of magnitude. Despite the combination of data from different decades with slightly different thermal limits (see below), in most months and areas the thermal limits are sharply expressed, with abundance estimated to decline by an order of magnitude in ≤1°C in eight of 19 possible comparisons. Repeating the analysis after constraining $\sigma_T = 0.1$°C resulted in an almost identical pattern of change, with the thermal limit in the eastern North Pacific consistently found at a higher temperature than in the central or western North Pacific.

Depending on area, the temperature defining the position of the thermal limit varies cyclically from 7°C in winter months to about 13–15°C by late summer. This response is in direct contrast with past theories of salmon migration that suggested a southward movement in winter, but without a strong influence of temperature on distribution (cf. review by Burgner 1991). Within a given month, the thermal limits are also found at different temperatures in different areas of the Pacific; thus, previous studies overlooked the sharp limits because the aggregation of data for different months or regions with different thermal limits results in a blurred and less clearcut response to temperature.

Two alternative explanations for the existence of the extremely sharp thermal limits evident in Figs. 3–5 seem initially possible, but are inconsistent with key aspects of the data. First, sockeye may be orienting relative to the distribution of prey or predators, which are responding directly to temperature. However, the observed thermal limits differ between salmon species, and Pacific salmon have some trophic overlap and similar predators, so this explanation is unlikely.

A second possibility is that the sharp edge to the distribution

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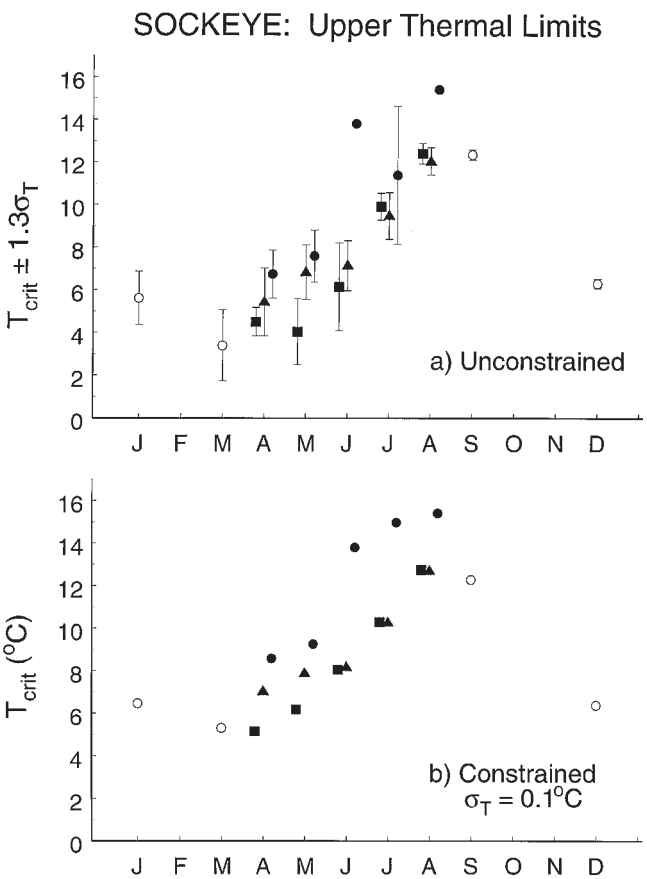
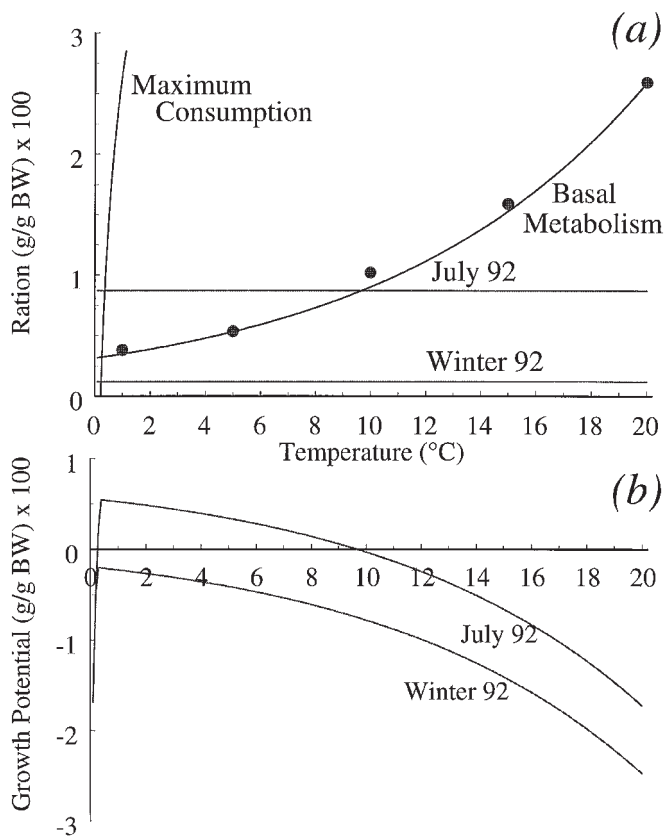
Fig. 8. Estimated critical temperatures defining the southern limit to the sockeye distribution, T_{crit}, in different months. (*a*) Unconstrained. (*b*) Constrained. Squares, WNP; triangles, CNP; solid circles, ENP; open circles, areas combined. The vertical bars in Fig. 8*a* represent the thermal range over which sockeye density drops by a factor of 10, $T_{crit} \pm 1.3\sigma_T$, not the statistical uncertainty in ML estimates of the critical temperature (differences in estimated thermal limits between months for a given region were statistically significant in all cases). In cases where no vertical bars are evident, the estimated thermal range is smaller than the size of the symbol. Figure 8*b* shows the constrained estimates of the monthly thermal limit after fixing $\sigma_T = 0.1°C$. For both Figs. 8*a* and 8*b*, thermal limits increase into the late summer and then decline; in months where sufficient data exist to permit separate estimation of area-specific thermal limits, the eastern North Pacific has significantly higher thermal limits for any given month. The only substantial difference between the results for the constrained and unconstrained estimations is for the eastern North Pacific in July, where the unconstrained estimation gave a substantially lower thermal limit and indicated a very gradual decline in abundance with increasing SST; the constrained estimate is more consistent with the data and the pattern seen for the other months (see Fig. 3).



is geographically fixed. Seasonal warming and cooling of the ocean could then cause the isotherms to move past the edge of the distribution in a predictable and cyclic fashion. However, despite the sharpness of the edge in all months, the geographic position is not fixed, with the greatest southern extent of the sockeye distribution occurring in the spring and very early summer (June) and the winter and summer thermal limits lying several hundred kilometres to the north.

Fig. 9. (*a*) Comparison of laboratory data on temperature effects with seasonally averaged sockeye stomach contents for the eastern North Pacific. Maximum consumption and basal metabolic rates are fitted curves of daily rates (% of body weight (BW)/day) for fingerling sockeye raised in freshwater and fed a high-energy artificial diet; symbols show the original measurements by Brett et al. (1969). Stomach contents are instantaneous observations (% of BW) for much larger ocean-caught sockeye in February, July, and December 1992. The vertical positions of the winter and summer feeding measurements are not directly comparable with metabolic rates because they are not corrected for digestion or repeated feeding throughout the day or possible metabolic differences between the two groups, but provide a conceptual guide to the balance between consumption and metabolism that may occur. (*b*) Potential growth, defined as the difference between food consumed and basal metabolic losses, declines to zero with increasing temperature. Both the maximum and the zero point shift to higher temperatures as food availability increases, but only orientation to avoid negative growth rates (i.e., starvation) is consistent with a step-function response to temperature. The distributional data are therefore most consistent with salmon avoiding thermal regions that result in starvation, i.e., regions where energy lost to metabolism exceeds the energy gained from foraging. The exact positions of the zero crossings in different seasons are dependent on daily rates of consumption and activity costs in the ocean, which have not been measured.



Bioenergetic control

The extreme sharpness of the thermal limits indicates that on evolutionary time scales the development of a strong behavioural response to temperature is very important to overall

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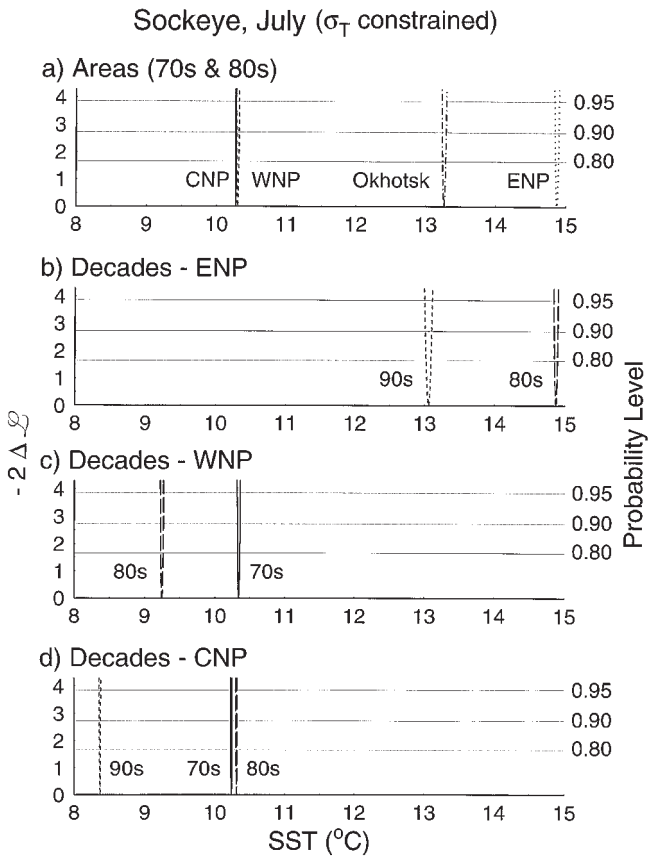
Fig. 10. Likelihood profiles comparing the differences in the estimated critical temperature defining the upper thermal limit for July between (*a*) areas and decades for (*b*) ENP, (*c*) WNP, and (*d*) CNP. Profile values show the relative likelihood that different temperatures define the actual position of the thermal limit, calculated as twice the difference in log-likelihoods from the ML estimate of T_{crit}, which occurs at $-2\Delta\mathscr{L} = 0$. The ML estimate of the critical temperature occurs where the likelihood profile touches the *x*-axis. Probability levels (right axis) are based on a $-2\Delta\chi^2_{1\ df}$ distribution, appropriate for testing differences in one parameter. For consistency, all critical temperatures were calculated using the constrained ML model assuming $\sigma_T = 0.1°C$. Results for the unconstrained model are similar.



fitness. The observed response also raises the question of what mechanism underlies this thermal avoidance behaviour.

Basal metabolic rates increase exponentially with temperature in cold-blooded animals (Fig. 9*a*), resulting in a growth maximum when the difference between maximum potential rates of food intake and basal metabolism plus activity costs is greatest (Brett et al. 1969). In laboratory studies, fish growth is maximized at lower temperatures as food is reduced. Fish, given the opportunity to choose, move to the environmental temperature yielding maximum growth when food is limited (Beitinger and Fitzpatrick 1979; Jobling 1981; Mac 1985). However, although qualitatively correct in predicting a migration to colder waters in times of reduced food availability, growth declines roughly symmetrically about the growth maximum (Weatherley and Gill 1995), so either a decrease or increase in temperature should have similar effects.

A step-function response to temperature is inconsistent with a strategy of growth maximization. This response is, however, consistent with behaviour where thermal avoidance is only expressed once metabolic losses due to increased temperature exceed the energy gained by feeding (Fig. 9*b*). Sockeye can maintain positive growth rates at higher ocean temperatures as food levels seasonally increase, consistent with the observed expansion into warmer waters in spring and summer. The observed distributional limits therefore likely reflect the boundary where growth rates become negative if exceeded, and starvation sets in even in the presence of significant levels of prey.

Although information on the relative abundance of lower trophic level prey is limited, a comparison of the position of the thermal limits shown in Figs. 3–5 and 8 generally supports the expectation of higher thermal limits in regions or decades with greater productivity. Thermal limits in July were 3–5°C higher in the Okhotsk Sea and eastern North Pacific (Fig. 10*a*), areas with enhanced nutrient levels due to estuarine recirculation and enhanced upwelling (Tully and Barber 1960). These areas presumably have correspondingly higher standing stocks of zooplankton than the central and western North Pacific.

Both zooplankton and salmon abundances approximately doubled between the 1960s and 1980s (Brodeur et al. 1996) in the eastern North Pacific. Unfortunately, little sampling effort was expended south of the thermal limit in the 1950s and 1960s (Figs. 3*m*, 3*n*, 4*m*, 4*n*, 5*m*, and 5*n*), so the distributional data are uninformative about the existence and position of a thermal limit. Only with the inclusion of data from the directed Canadian and Japanese cruises of the 1990s, which focussed much effort near this boundary, does the characterization of the thermal edge become substantially better (Fig. 10*b*).

A testable prediction for all regions of the North Pacific is that the ratio of zooplankton to salmon abundance fell following the 1977 (Beamish and Bouillon 1993; Hayward 1997) and 1990 climate shifts (Trenberth and Hoar 1996), since thermal limits were clearly lower in recent decades (Figs. 10*b*, 10*c*, and 10*d*). Unfortunately, the plankton data necessary to test this prediction are not readily available. However, taken as a whole, our results are consistent with the prediction that the highest thermal limits should be observed in those months, areas, and decades with the highest food levels. Productivity changes therefore shift the temperatures defining the thermal limits in predictable ways, with the greatest differences occurring between months and the finest scale differences between decades within a given month and region.

Climate change and ocean carrying capacity

Models of the world's climate predict significant warming in the next century as the CO_2 content of the atmosphere increases. The greatest warming is expected in winter and high latitudes (Watson et al. 1995). The Canadian Climate Centre's equilibrium climate model couples a simplified 50-m surface mixed layer representation of the ocean to a multilevel atmosphere and provides a midrange prediction of the amount of climate warming expected under a doubled CO_2 climate (Boer et al. 1992; McFarlane et al. 1992). Applying the predicted mean position of the isotherms limiting the seasonal distribution of sockeye under current and future climates provides a forecast of their possible future ocean distribution.

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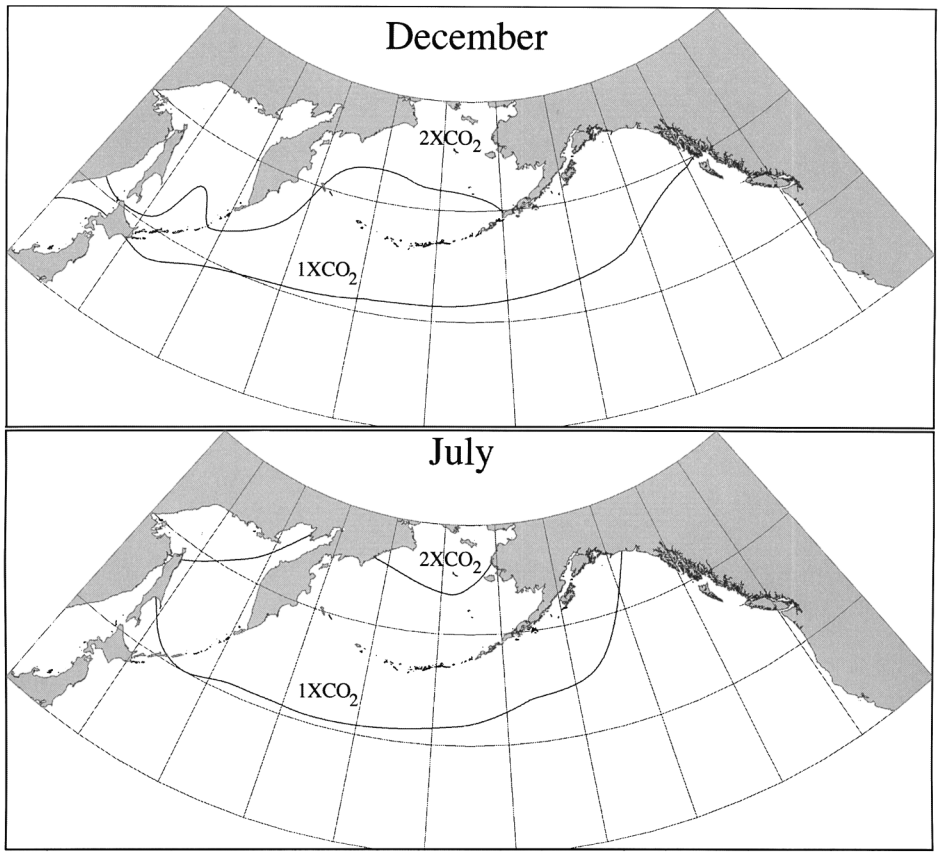
Fig. 11. Comparison of the predicted winter (7°C) and summer (12°C) positions of the sockeye salmon distribution under current and future climates (Albers equal area projection). Under a doubling of atmospheric CO_2 the area of acceptable thermal habitat in the North Pacific is predicted to decrease to zero in summer and decline sharply in winter. The predictions are based on the Canadian Climate Centre's coupled ocean–atmosphere general climate model (Boer et al. 1992; McFarlane et al. 1992).



Regions of thermally acceptable habitat are predicted to shrink dramatically under a doubled CO_2 climate, largely restricting the distribution to marginal seas in northern regions and presumably increasing the density of sockeye in the area remaining (Fig. 11). Thus, although much attention has been paid to the possibility that some stocks of salmon near the southern end of their distribution may be adversely affected by climate warming in freshwater (e.g., Francis and Sibley 1991; Levy 1992), events happening in the marine phase could be even more disruptive.

If the surface mixed layer does warm past currently maintained thermal limits, sockeye would appear to have three choices: (*i*) develop the ability to migrate into the Bering Sea (and return), (*ii*) begin to vertically migrate to stay below the thermocline for much of the day, migrating into surface waters to opportunistically forage for short periods of time, or (*iii*) incur the energetic or other penalties associated with thermal environments that they now strongly avoid.

Young sockeye are observed to vertically migrate in thermally stratified lakes prior to migration to the ocean when surface waters become very warm (Henderson et al. 1992), and adult chum salmon (*Oncorhynchus keta*) have been observed to migrate at depth to avoid the high temperatures of the Tsugaru current off Japan (Ueno 1992). However, as we have noted, there is excellent evidence that Pacific salmon are strongly surface oriented, so although the innate behaviour needed to permit vertical migration appears to exist, the costs associated with expressing new behaviour and avoiding the surface mixed layer are likely significant.

Unless prey abundances increase, the opposite of current predictions (Hsieh and Boer 1992; Hinch et al. 1995), sockeye remaining in the North Pacific may therefore incur significant energy deficits, reducing growth and consequently both their productivity and resulting population sizes. Irrespective of the degree of warming, the combination of decreasing prey abundance and shrinking thermal habitat due to climate warming will likely have negative effects on survival, growth, and size- and age-at-maturity that will reduce future productivity (Forbes and Peterman 1995).

Comparison with prior studies

A striking aspect of our findings is how sharp the thermal limits are when divided by months, regions, and decades. This suggests that salmon respond with extreme sensitivity to even slight changes in their thermal environment. However, the response evident in our analysis has not been previously noted, raising the question of why our extensive data and methods of analysis show such widespread evidence for sharp thermal limits when most earlier studies indicated a more ambiguous influence of temperature on the distribution of Pacific salmon (cf. review by Burgner 1991).

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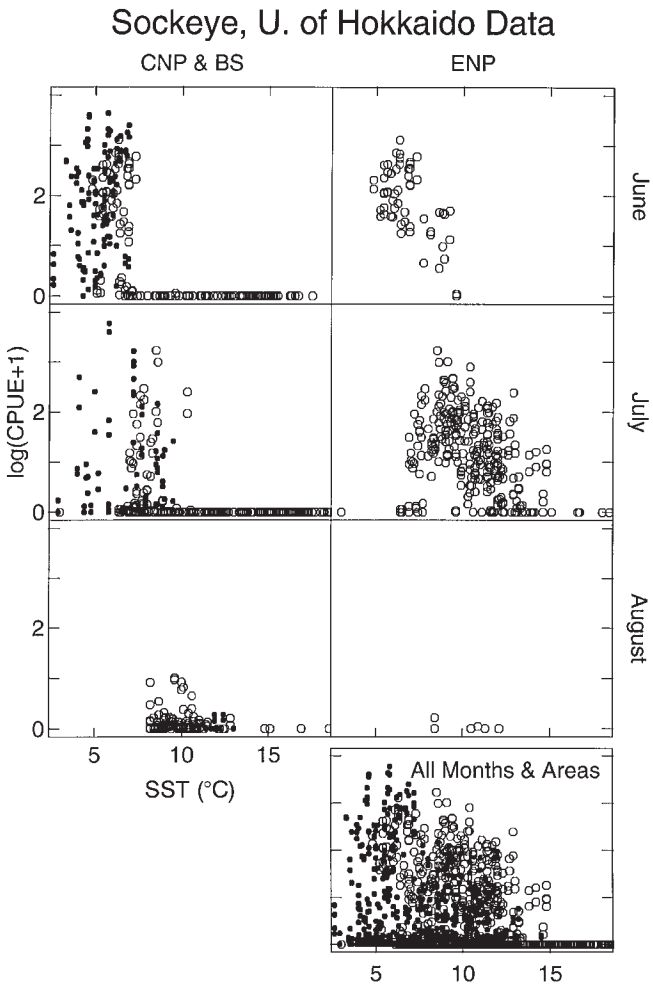
Fig. 12. Comparison of the sockeye response to SST for the University of Hokkaido data (1972–1993) divided by areas (columns) and months (rows) (the 1978–1993 subset is shown using open circles and earlier years using solid circles). The same sharp thermal limits shown in Figs. 3–5 are evident for this subset. Note that, as for the full data set, the aggregation of the data for all months and areas results in a more ambiguous relationship because combining data with differing thermal boundaries blurs the overall response.



A recent elegant and thorough statistical analysis by Pearcy et al. (1996) provides an excellent example. Pearcy et al. (1996) studied the relationship between the abundance of fish and squid measured by surface gill nets using the University of Hokkaido research vessels *Oshoro Maru* and *Hokusei Maru* and a range of simultaneously collected oceanographic data, including SST. As the authors noted, theirs "...is a unique study because it utilizes collections repeated every year for over a decade and a half, over a large region". The observations used in the Pearcy et al. (1996) paper are from 1978–1993 ($N = 513$ samples). The data forming the basis for our paper also contain the same data from Hokkaido University, but for a wider range of years, 1972–1993, and also include data for the Bering Sea ($N = 1924$ samples). Thus the Pearcy et al. (1996) analysis was based on 2.5% of the data used in the current paper. (The full Hokkaido University data set forms <10% of the total used here.)

Pearcy et al. (1996) reported that "...distinct boundaries between species groups and sample groups were lacking" but that "Interannual fluctuations...were most closely related with changes in SST," although "All the physical factors, and latitude, were very highly intercorrelated." These authors did not identify clear thermal limits on the distribution of salmon, but did demonstrate the existence of a northern (chiefly salmon) and southern group of species, thus explaining part of the reason for the association with temperature. They also described a number of other important aspects to the community structure of the North Pacific fauna and noted that the boundary between the species groups moved north or southward by several degrees of latitude in different years, equivalent to a spatial scale of several hundred kilometres.

Analysis of the sockeye salmon response to SST for the University of Hokkaido subset of our database shows that the same sharp thermal limits found for the entire 40-year database are also evident for this more restricted sample (Fig. 12). Pearcy et al.'s (1996) analysis of the aggregated data did not identify the presence of sharp thermal limits in this data set primarily because different temperatures define the thermal edge in June, July, and August. Unless the data are partitioned, the sharpness of the overall response is less clear, essentially because the data set is now a set of several overlapping step functions buried in noise.

Previous difficulties hampering the earlier identification of the thermal limits we report here by a wide range of investigations that used subsets of the same data (e.g., Fujii et al. 1965; Tabata 1983; Ogura and Takagi 1987) can therefore be attributed to two factors. First, there is a need to partition the data into aggregates (i.e., seasons, regions, or periods) with similar thermal limits to prevent the blurring or smearing of the response when data representing different thermal responses are aggregated. Second, standard statistical methods lead to inherent limitations in the analysis that need to be recognized. These methods implicitly require that a smooth and continuous relationship between abundance and temperature exists, rather than the discontinuous response that we have shown characterizes the data. The calculation of a correlation between abundance and SST, no matter how the data are partitioned, will only measure the linear contribution to the overall relationship between two variables. In the case of a step-function response to SST, this contribution can be quite small.

Ecological implications

As greenhouse gases increase and new climates develop, major losses in ocean habitat are likely to occur for all salmon species. Large areas of the North Pacific may warm past current thermal limits for much of the year, reducing ocean habitat. However, perhaps the most surprising prediction is that none of the Pacific Ocean may lie within the thermal limits that have sharply defined the distribution of sockeye salmon over the last 40 years.

In British Columbia alone, there are more than 9600 genetically separate stocks of Pacific salmon (Slaney et al. 1996). British Columbia formerly produced about 15% of Pacific salmon production, making for a rough estimate of >60 000 genetically separate populations in the North Pacific. Because salmon abundances drop so sharply with temperature, most

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populations of each species must be responding identically; otherwise, the sharpness of the response would be blurred. Whatever the specific causes, thermal influences on the long-term survival of each species must be very important, or such a uniform response to temperature would not be observed.

The sharpness of the boundaries that we have found in all months suggests that Pacific salmon evolved acute thermal sensitivities because factors influencing growth in the ocean have profound effects on survival over evolutionary time scales. The boundaries also imply that food is limiting growth in the ocean over virtually the entire year because thermal limits should otherwise be less sharply expressed and seasonally unchanging. The clear response seen consistently in all partitions of our data also raises the question of whether many other cold-blooded organisms may also express similar distributional responses to temperature that have so far gone unrecognized, for similar reasons.

The expression of strong avoidance behaviour over the range of temperatures observed might seem consistent with the large body of evidence that demonstrates temperature selection based on *optimizing growth* rather than avoiding growth deficit, as we had earlier suggested (Welch et al 1995). However, close examination of published growth curves (e.g., Shuter and Post 1990, fig. 3; Weatherley and Gill 1995) shows that the response of growth rate to temperature in fish tends to be relatively flat-topped and symmetrical near the optimum temperature. Neither property is consistent with an abrupt decline in abundance over a very narrow temperature range and relatively little change in salmon abundance away from the thermal limit.

In summary, the sharp ocean-wide response to temperature that we have demonstrated restricts the distribution of sockeye salmon to a relatively small area of the subarctic Pacific for much of the year. However, it is the strength of the response and the remarkably low temperatures at which it occurs that are of greater concern. With climate change, large areas of the North Pacific may be unable to support growth. Ironically, because the vast majority of salmon research has focussed on the freshwater phase of the life history (e.g., review by Magnuson et al. 1996), even the complete shift of open-ocean salmon distributions into the Bering and Okhotsk seas could be missed without ocean research to complement freshwater programs, and the consequent losses in productivity incorrectly attributed to freshwater habitat changes.

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Appendix

The southernmost edge of the salmon distribution can be defined by assuming an average critical temperature at which animals express avoidance behaviour, T_{crit}, and Gaussian variability between individual animals in the temperature at which this behaviour occurs, σ_T (Welch et al. 1995). Although the response of individual animals cannot be measured from the fisheries surveys, the population-level response is the proportion of the initial density of animals in the interior of the distribution, μ, that still remains at some temperature, T_i, or

$$\text{(A.1)}\quad n(T_i) = \mu(1 - \Phi(T_i|T_{\text{crit}}, \sigma_T))$$

where $\Phi(T_i|T_{\text{crit}}, \sigma_T)$ defines the cumulative Gaussian probability (or proportion) of all individuals that have responded by some temperature T_i. Estimates of the midpoint, T_{crit}, and the rate of change in abundance with temperature around this point, σ_T, define the rate at which abundance declines with increasing temperature at the thermal limit (Welch et al. 1995).

ML estimates of the mean density within the distribution, the critical temperature defining the edge, and the rate of decrease in abundance with SST at the edge, (μ, T_{crit}, σ_T), were obtained by minimizing the negative log-likelihood of the data with respect to the parameters, assuming that errors in the observations of catch were distributed negative binomially (Welch and Ishida 1993; Welch et al. 1995). Likelihood profiles of the response of sockeye abundance to SST allow us to objectively examine the effect of seasonal, regional, and decadal differences in the temperature defining the thermal limits. Profiles were calculated by taking twice the difference in log-likelihoods from the ML estimates for various alternative temperatures T_{alt} (allowing all other parameters to vary freely) and finding the relative likelihood

$$-2\Delta\mathscr{L} = -2[\mathscr{L}(T_{\text{alt}}, \sigma_T^*, \mu^*) - \mathscr{L}(T_{\text{crit}}^*, \sigma_T^*, \mu^*)].$$

Confidence intervals on estimates of T_{crit} can be calculated by setting $-2\Delta\mathscr{L}$ equal to a specific value from a $\chi^2_{1,1-\alpha}$ distribution. This is a large-sample test appropriate for testing differences in a single parameter.

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