Upper Thermal Limits on the Oceanic Distribution of Pacific Salmon
(Oncorhynchus spp.) in the Spring

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ABSTRACT

Pacific salmon are normally thought to be distributed throughout the Subarctic Pacific, an area where they form the dominant fish fauna. We use a series of generalized additive models to show that salmon exhibit strong species-specific threshold responses to temperature in the oceanic north Pacific in spring, with temperature having no measurable influence on abundance away from the southern edge of the distribution. The critical temperature defining the southern boundary varied by species: 10.4°C for pink and chum salmon, 9.4°C for coho salmon, and 8.9°C for sockeye salmon. These limits occur well to the north of the southern boundary of the subarctic Pacific. The sharp decline in abundance with temperature, and the remarkably low temperatures at which the response occurs, suggests that thermal barriers form an effective limit to the offshore distribution of salmon in spring, and can limit the distribution of Pacific salmon to a relatively small area of the Subarctic Pacific. The strength of this response is presumably the direct result of strong evolutionary selection. Future temperature changes in the North Pacific could therefore have a direct impact on the production dynamics of Pacific salmon.

(188 words)

INTRODUCTION

Despite some 40 years of research. the reasons why Pacific salmon undertake their vast ocean migrations are still only poorly understood. The reasons are presumably closely related to their evolutionary biology and production dynamics. Some two-thirds or more of the life history of Pacific salmon (Oncorhynchus) is normally spent in the pelagic environment of the open Pacific Ocean, a behavioural choice that is under evolutionary control. During this time most somatic growth is completed (Ricker 1962, 1976), and a significant fraction of total cohort mortality also occurs (Parker 1962; Ricker 1962, 1976). However. despite the length of this period in the life cycle, relatively little is known about the biological dynamics underlying the pelagic period of the life history.

Salmon are widely distributed on the high seas. One relatively tractable aspect of the study of the high seas biology of salmon involves the relationship between the distribution of salmon and physical and biological factors. A better understanding of the factors that restrict the pelagic distribution of Pacific salmon could provide insight into the interaction of Pacific salmon with their environment, and particularly with regards to understanding how predictions of climate change could influence the salmon resources of the North Pacific. Because the behaviour of salmon on the high seas is the result of evolutionary selection, oceanographic factors that influence the distributional response of Pacific salmon should therefore also influence their production dynamics, because the same selective forces that lead to dominance of genotypes with high fitness also lead to maximization of population growth rates (Caswell 1989).

Most published work on the high seas biology of salmon dates from the late 1950's and early 1960's, a period when the extensive ocean migrations of Pacific salmon were first documented. These studies established the widespread occurrence of salmon in the surface layer of the central subarctic region, a region now referred to

5   as the Subarctic Domain (Ware and McFarlane 1989). This region is bounded to the south by a vertical 34‰ isohaline structure (Dodimead et al. 1963), with cooler less saline water lying to the north. The vertical 34‰ isohaline structure is also viewed as defining the southern limit to the distribution of Pacific salmon (Favorite et al. 1976; Blackbourn 1987; Quinn 1990).

10   The fish fauna of the Subarctic Domain is dominated by Pacific salmon, despite their need to return to freshwater to reproduce (Ware and McFarlane 1989). Pacific salmon are therefore the dominant fauna of a cool lens of relatively fresh ocean water that forms the mixed layer above the more saline (>34‰) deep waters of the North Pacific. However, even within the Subarctic Domain salmon are differentially

15   distributed, by species (Birman 1985; French et al 1976; Major et al. 1978; Neave et al. 1976; Takagi et al. 1981), temperature (Birman 1985; Blackbourn 1987; Erokhin 1991; Favorite 1969a; Favorite et al. 1976; Quinn 1990), and possibly salinity (Favorite 1969b).

A descriptive understanding of the distribution and general migratory routes of

20   salmon on the high seas is now generally agreed upon. Manzer et al. (1964) reported that there was an apparent difference in temperature preferences between species, with different thermal ranges evident, and preferences seeming to increase over the spring and summer. Manzer et al. suggested that temperature preferences dropped again in

September although ambient temperatures remained high. Birman (1985), Erokhin (1991), and Ishida (1962) suggested that the offshore migration of pink salmon was a seasonal migration "following the movement of waters with temperatures of 4-11°C".

However, mechanistic questions concerning why salmon are distributed as they are, and the direct experimental measurement at sea of the factors influencing the distribution, have rarely been addressed. General statements about the oceanic distribution of Pacific salmon are useful, but they give little insight as to whether and why specific environmental variables are important to salmon, or how significant they really are.

Whatever the proximate response to physical or biological factors, the mechanisms underlying any distributional patterns are likely to have been strongly shaped by evolutionary selection. Establishing why Pacific salmon exhibit specific distributional patterns may help to predict their population response to climatic change, as well as understanding the evolutionary factors that cause Pacific salmon to undertake their remarkable oceanic migrations.

The study reported here was designed to re-examine the relationship between the physical distribution of salmon and a range of oceanographic factors, as a first step towards developing a better understanding of the effects of climate change on Pacific salmon, and the potential impact of the increasing abundance of Pacific salmon on their own production (Pearcy 1992). In particular, we examine the question of whether or not salmon are truly distributed throughout the Subarctic Pacific. We show that there is evidence of a sharp barrier limiting the distribution of salmon in the North Pacific Ocean in the spring. However, although the results of high seas surveys clearly show

evidence of a sharp barrier, satisfactory analysis of the data depends on three factors:
(i) establishing a satisfactory means of statistically discriminating between a number
of possible factors that can simultaneously influence distribution in complicated
nonlinear ways, (ii) developing a reasonable model of the uncertainty or error inherent
in the individual fishing observations made at sea, and (iii) providing a parsimonious
biological model of the results. We discuss each of these issues in turn.

EQUIPMENT, METHODS, AND DATA SOURCES

USSR-Canadian Surveys

A joint USSR-Canadian research cruise aboard the USSR research vessel TINRO examined the southern limits to the offshore distribution of Pacific salmon during late

5 spring, 1990. The results reported here are based on data from two cruises, the first occurring from 29 March to 21 April, and involving 20 trawl stations taken along a line between 55°N 145°W and 47°N 131°W (Morris *et al.* 1992). The second cruise, involving 42 trawl stations, occurred between 27 April and 14 May within a rectangle bounded by the co-ordinates 52°N 129°W and 39°N 150°W (Fig. 1).

10 Individual north-south transects near the observed southern limit to the salmon distribution were spaced 3° longitude apart, and usually involved three stations sampled during daylight hours with a rope trawl. Movement to the next transect was completed overnight. The original cruise plan was intended to extend south of the northern boundary of the Japanese squid driftnet fishing zone in June, at 40°N. However,

15 because of the rapid decline in salmon abundance evident during the first southern transect at 150°W latitude, the southern extent of each planned north-south transect was reduced in order to increase the east-west coverage.

All sampling used a rope trawl, with mouth dimensions 40 m (height) x 60 m (width), and length of 108 m. The net was towed at 5 knots, generally for two

20 contiguous 30-minute periods at depths of 20 and 40 m (depth to top of head rope), for a total sampling time of 1 hr. However, in cases where echosounding indicated that fish were located at a particular depth, trawling was restricted to these strata. This protocol

followed standard USSR survey practice. Results presented later are in units of numbers caught per trawl hour.

Vertical profiles to 300 m were made using a Neil Brown CTD probe to record temperature, salinity, O_2, and chlorophyll levels. At all stations the mixed layer depth

5 exceeded 100 m, and the vertical 34‰ isohaline denoting the limit of the subarctic domain lay well beyond the southern-most extent of the survey area (see below).

We used sea surface temperature and salinity as the physical variables to relate to the salmon distribution at each station. Pacific salmon are largely confined to the upper 50 m in the open ocean (Manzer 1964), and all sampling occurred in regions

10 where the mixed layer depth exceeded one hundred meters, thus justifying the use of single measurements of sea temperature and salinity. Oxygen and chlorophyll measurements showed significant variability with depth and between stations, but a preliminary analysis showed no clear relationship with salmon density, so we did not pursue the analysis of these variables further.

15

Canadian Surveys

During 1987, 1988, and 1990 the Canadian research vessel R/V W.E. RICKER collected salmon in southern regions of the NE Pacific using gillnets and surface longlines. Details of these cruises are described elsewhere (LeBrasseur et al. 1987,

20 1988; McKinnell et al. 1990). Additional data on the distribution of salmon in the NE Pacific conducted between 1961-67 by Canadian and American vessels using surface longline gear is also compiled in Turner and Aro (1968). None of these studies were designed to specifically examine the physical factors limiting the distribution of

salmonids on the high seas. However, we use these data to examine the replicability

of the results from the R/V TINRO cruise.

STATISTICAL METHODS

Error Model

The sampling distribution for Pacific salmon caught on the high seas is closely

described by a negative binomial distribution with parameters μ, the true mean

5 abundance or density, and k, the number of degrees of freedom on which the sample

is based (Welch and Ishida 1993). This distribution has long tails and at low densities

or limited sampling effort is highly asymmetric, probably because of the heterogeneous

distribution of salmon into small schools of varying sizes. At large sampling efforts

the distribution approaches the Poisson.

10 Welch and Ishida (1993) found that the spatial coherence of Pacific salmon on

the high seas disappeared at separations of ca. 15m. Samples taken at greater spatial

separations are therefore statistically independent, and contribute additional degrees of

freedom (df) on which observations of salmon abundance or density can be based.

This estimate provides a basis for estimating the uncertainty in the trawl survey

15 estimates.

Each one hour tow using the Russian rope trawl results in a single observed

catch that is collected over a transect 5 nautical miles (9.26 km) long. The trawl gear

therefore provides a single catch equivalent to a set of k = 9,260/15 = 617 statistically

independent samples taken under similar conditions. For sampling efforts involving

20 large degrees of freedom precise estimates of the exact df obtained are unnecessary

because the negative binomial distribution is nearly identical to the Poisson distribution,

but with slightly heavier tails. However, at the low densities that occur near the limits

to the salmon distribution the sampling distribution is still highly skewed, and it is

important to correctly weight the uncertainty in the different catch distributions as accurately as possible. We use this estimate of $k = 617$ d.f. in the statistical analysis described later.

5   *GAM Analysis*

Given an acceptable error model, the question remains of assessing how multiple factors contribute to determining the distribution of Pacific salmon. This issue is particularly important because observations collected at sea cannot be collected 10   according to a pre-planned experimental design, and are invariably inter-correlated. In addition, some or all of these influences may be non-linear, and it is important that the nature of this relationship not be distorted by a poor initial choice of a functional model to relate to the observations.

We therefore conducted a preliminary analysis of the relationship between the 15   distribution of Pacific salmon and physical factors using a series of generalized additive models (Hastie and Tibshirani 1990, Hastie 1992, Swartzman et al. 1992, StatSci 1993). We define the distribution of salmon in terms of their abundance, expressed as the number of individuals caught at the i-th station per trawl-hour, n_i. In general, a GAM model is defined as

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(1) $n_i = \alpha + f_T(T_i) + f_S(S_i) + \ldots + \epsilon_i$

where $f_T(T_i)$, $f_S(S_i)$, ... represent arbitrary smooth univariate functions of temperature, salinity, ... α represents the mean response, and ϵ_i represents the error distribution for the i-th observation. In GAMs, locally weighted fitting is used to calculate a non-parametric estimate of the functional relationship between salmon abundance and potentially significant explanatory variables. The advantage of this approach is that it does not require the prior specification of a series of satisfactory mathematical relationships, and instead allows the data to more clearly indicate the important variables and their functional responses.

As negative binomial distributions are not available in current GAM software, we used the Poisson distribution as our error model instead; this assumption is slightly conservative, and results in underestimating the true width of confidence limits on potentially important factors (i.e., overestimating the true number of significant factors; McCullagh and Nelder 1989). However, we use the generalized linear model framework chiefly as a means of identifying candidate factors influencing the salmon distribution, and for determining the nature of their influence. The parametric analysis discussed next uses the negative binomial distribution to more accurately calculate the uncertainty in the parameter estimates.

For ease of interpretation, we expressed our abundance observations as $\log_{10}(n_i+1)$, and used b-splines to form our non-parametric smoothing functions to describe the local influence of salinity and temperature on salmon abundance (Hastie and Tibshirani 1990; Hastie 1992). This model was fit to the $\log_{10}(n_i + 1)$ observations using the statistical modelling language S-Plus (StatSci, 1993).

An Edge Model for the Salmon Distribution

The GAM analysis presented later indicates that salmon density is related to ambient temperature. but not to other measured factors. This relationship appears as a threshold, with no discernable influence below a specific value and a strong negative influence above. In order to better define the influence of temperature on the southern limit to the distribution of salmon, and to provide a biological interpretation of our observations, we now describe a parametric mathematical model. We concentrate on defining the southern boundary, where the effect of temperature is most pronounced.

Regression analysis when Poisson or Negative Binomially distributed errors occur has been discussed by Lawless (1987). We limit our presentation to the derivation of the likelihood equations necessary for our parameter estimation. A simple functional form relating the observed salmon abundance at the i-th station to temperature, $n(T_i)$, is

(2)
$$n(T_i) = \bar{\mu} \, (\, 1 - \Phi(T_i \mid \bar{T}, \sigma_T) \,)$$

where $\Phi(T_i \mid \bar{T}, \sigma_T)$ is the value of the cumulative normal probability distribution with parameters $\bar{T}$ and σ_T at temperature T_i, and $\bar{\mu}$ is the mean salmon density in the interior of the geographic distribution.

Equation (2) posits that there is some mean threshold temperature level $\bar{T}$ which salmon actively avoid exceeding, and some normally distributed variance in the response of individual salmon to this temperature threshold. σ_T. The average population response is then obtained by integrating over the behaviour of all

5   individuals, which results in the cumulative distribution (Fig. 2). The mean temperature therefore defines the threshold value at which the <u>location</u> of the edge of the salmon distribution is fixed, while the variance will influence the <u>rate</u> at which abundance declines near the edge of the distribution. For example, if $\sigma_T = 0$, and all individuals respond exactly alike, then the edge will be a step function located at $\bar{T}$, with

10   abundance dropping to zero instantaneously. In general, 95% of the decline in abundance will occur over an interval of $\pm 2 \sigma_T$ centered on this mean, or roughly a two order-of-magnitude decline in abundance.

The third parameter. $\bar{\mu}$, describes the mean abundance in interior regions, away from the edge of the salmon distribution. This value is affected by both gear efficiency

15   and year-to-year fluctuations in abundance. As we are primarily interested in describing the limits to the salmon distribution, and the GAM analysis indicates that the effect of temperature is most reasonably modelled as a threshold, we treat the mean abundance in the interior as a nuisance parameter, and concentrate on the estimation of the parameters $\bar{T}$ and σ_T.

20   Equation (2) is a biologically based parametric model of the salmon distribution. However, it still lacks a firm statistical basis for estimation. As discussed above, the

uncertainty in the salmon catches can be described by the negative binomial distribution. We therefore calculated final parameter estimates and associated confidence intervals for the effect of temperature initially identified in the GAM analysis using maximum likelihood estimation.

5   Assuming the negative binomial distribution holds, the exact likelihood equation is derived as follows. The probability of observing n_i fish at the i-th station when the true abundance is μ_i and the sampling effort is $k_i=617$ df is:

$$(3) \qquad P(n_i \mid \mu_i, k_i) = \frac{\Gamma(n_i + k_i)}{\Gamma(n_i + 1)\ \Gamma(k_i)} \left(\frac{k_i}{\mu_i + k_i}\right)^{k_i} \left(\frac{\mu_i}{\mu_i + k_i}\right)^{n_i}$$

10   where the Γ function is the analytic continuation of the factorial function for non-integer real numbers and, for integer x, $\Gamma(x+1) = x!$.

The likelihood of observing a set of n_i catches at the i=1,....m stations when the true abundances are μ_i is therefore

$$(4) \qquad \mathcal{L}(n_i \mid \mu_i, k_i) = \prod_{i=1}^{m} \frac{\Gamma(n_i + k_i)}{\Gamma(n_i + 1)\ \Gamma(k_i)} \left(\frac{k_i}{\mu_i + k_i}\right)^{k_i} \left(\frac{\mu_i}{\mu_i + k_i}\right)^{n_i}$$

15

The likelihood is therefore dependent on the observations n_i, the sampling efforts k_i, and the temperature controlling the true abundance at the ith location,

$\mu_i(T)$. Maximum likelihood estimates of the parameters ($\bar{\mu}$, $\bar{T}$, σ_T) can be obtained by minimizing the negative log-likelihood of the data with respect to the parameters. Substituting the functional form for the parametric temperature-density relationship (2) into the theoretical likelihood (3) and taking the negative of the logarithm.

$$-\ln(\mathcal{L}(n_i \mid n(T_i), k_i = 617 \, d.f.)) =$$

(5)

$$\sum_{i=1}^{m} (n_i + k_i) \ln(n(T_i) + k_i) - n_i \ln(n(T_i))$$

where we neglect the contribution of an additive constant and n_i and $n(T_i)$ are the observed and predicted salmon abundances. We used the simplex algorithm (Press et al. 1986) as implemented by Mittertreiner and Schnute (1985), to estimate the maximum likelihood values of the parameters $\bar{T}$, σ_T using eqn (5), and their associated uncertainty.

A critical upper or lower level for some physical factor can be defined as that value at which the decline in density is most rapid. These values correspond to the mean responses $\bar{T}$ within our edge model. We calculate 95% confidence intervals on individual estimates of $\bar{T}$ and σ_T by finding the limits such that twice the difference in log-likelihoods from the maximum likelihood estimates (allowing all other parameters to vary freely) is less than or equal to a $\chi_1^2 = 3.81$ distribution. This calculation is asymptotically correct for large sample sizes (Kendall and Stuart 1979),

and is satisfactory for all but very small sample sizes (Lawless 1987). Alternatively, these limits can be thought of in terms of relative plausibility (Edwards, 1972). A difference of 3.84 log-likelihood units is equivalent to a difference in relative likelihood of $e^{-3.84}$=0.02, so parameter values outside the stated range may be thought of as being only $1/50^{th}$ as likely to describe the true value of a factor determining the limits of the distribution.

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RESULTS

USSR-Canadian Surveys

A total of 1.912 salmon were caught at 62 trawl stations. Chum (*Oncorhynchus keta* 749) and pink (*O. gorbuscha* 725) salmon predominated, particularly in southern

5   regions, but smaller numbers of sockeye (*O. nerka* 150), coho (*O. kisutch*, 283), and chinook (*O. tshawytscha*, 5) were also taken. The data are reported in Welch *et al.* (1990).

A vertical section through 150°W and surface maps of temperature and salinity show the major oceanographic features of the region. To the south, isohalines become

10   progressively steeper as the vertical 34‰ boundary defining the southern limit to the Subarctic Domain is approached (Fig. 3). This oceanographic boundary is also normally considered the limit to the distribution of Pacific salmon (Favorite *et al.* 1976; Blackbourn 1987; Quinn 1990) but, as results reported below show, the observed southern limit to the salmon distribution occurred well to the north of the vertical 34‰

15   boundary. Contour maps of surface temperature and salinity (Fig. 4) show that temperature and salinity isoclines were oriented approximately orthogonally, with temperature increasing to the NE as the coast is approached.

The results of our GAM analyses on the logarithm of salmon abundance are shown in Fig. 5. At ocean temperatures exceeding ca. 10°C a significant negative

20   effect of temperature on total salmon abundance is evident; however, at lower temperatures the estimated value of the non-parametric function fluctuates around zero and the two standard error bands always include zero. Temperature therefore has a negligible affect on the distribution of salmon until a threshold is passed, at which point

a pronounced negative influence on abundance is indicated. A similar result is evident when the catch by species is analyzed. Here the temperature at which the threshold is expressed clearly differs by species. Some evidence for a lower thermal limit is also evident, but the measured effect is only statistically significant for pink salmon.

Repeating the analysis to simultaneously consider both temperature and salinity gives similar results (Fig. 6A). The twice standard error curves about the calculated influence of salinity on abundance almost always include zero. and over most of the range of observed salinities the calculated influence is in fact zero. (Two near-coastal stations taken in low salinity waters suggest a weak effect of salinity, but the number of observations is too low to allow discriminating between a direct effect of salinity. and an indirect effect caused by proximity to the coast or some other geographic variable). In contrast, the strong negative influence of temperature on abundance shows little change when salinity is considered. An analysis of variance on these results, including a third analysis using surface density (σ_t) as a proxy for water mass origin (Fig. 6B), confirms these observations, and shows that only temperature has a statistically significant influence on salmon abundance (Table 1).

These results indicate that salmon exhibit a behavioural response to a threshold temperature that varies by species, and actively avoid entering warmer waters. A parametric analysis, assuming a negative binomial error structure and using maximum likelihood estimation allows us to more precisely estimate the response to temperature. By calculating the likelihood profile with respect to the model parameters we can also obtain an evaluation of the parameter uncertainty, by allowing all other parameters to

vary while we examine the effects of temperature and individual variability on the likelihood.

The results show that the influence of temperature is statistically well-defined with uncertainty in the estimates of the threshold temperature generally less than

5   ±0.1°C (Table 2.A). Based on the estimates of σ_T, our measure of the variation in the behavioural response to temperature. total salmon abundance falls by 95% (or nearly two orders of magnitude) in ± $2\sigma_T$. corresponding to a temperature interval of 0.68°C. At 150°W longitude, this sudden decline in abundance occurs in roughly 60 nautical miles (Fig. 4).

10   Plots of salmon abundance by species demonstrate the same statistically well-defined relationship between distribution and temperature. but with the maximum likelihood estimates of the upper thermal limit varying between species (Table 2B; Fig. 7). For the R/V TINRO data, the upper thermal limit are at ca. 10.4°C for pink and chum salmon, at 9.4°C for coho, and at ca. 9°C for sockeye (note, however, that the latter

15   estimate is dependent on a single large catch of sockeye salmon at 8.9°C).

Coho and pink salmon also show evidence of a lower thermal limit of 7-8°C (Fig. 7), an effect only strongly supported by the GAM analysis for pink salmon. We calculated the significance of the lower thermal limit by replacing our single-edged model of the salmon distribution by the two-edged model

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$$(6) \qquad n(T_i) = \bar{\mu} \, \Phi\left(\frac{T_i - \bar{T}_{Lo}}{\sigma_{Lo}}\right)\left[1 - \Phi\left(\frac{T_i - \bar{T}_{Hi}}{\sigma_{Hi}}\right)\right]$$

Interpretation of the parameters remains largely unchanged, but in this case we substitute eqn (8) instead of eqn (2) in the likelihood equation, and estimate both low and high critical temperatures. The abundance parameter $\bar{\mu}$ now reflects the mean abundance between the edges of the distribution.

5   Only the pink salmon abundance data could be satisfactorily fit by this model (Table 3).

Canadian Surveys

During annual research cruises on the R/V W.E. RICKER in 1987, 1988, and 1990,

10   salmon were caught during surface driftnet and longlining operations in southern regions of the subarctic North Pacific (LeBrasseur et al. 1987, 1988; McKinnell et al. 1990). These sampling locations were located west of where the R/V TINRO operated, and were occupied in June-July rather than April-May. However, if the relationship between temperature and salmon distribution is not an artifact, then it should hold for

15   different gears, and at different times or areas.

An examination of the relationship between abundance (all species) per unit effort (tans (~50 m panels) of gillnet, and hachi (120m, 49 hooks) of longlines) and temperature again shows a significant relationship (Fig. 8). Calculating the critical temperature shows a somewhat lower upper thermal limit for these two gear types than

20   that observed using trawl gear (Table 2A). A single anomalous data point is evident, consisting of 10 pink salmon caught with 10 hachi of longline, at 48°N, 134°W. This was the final set, taken on the return leg of the 1990 cruise, closest to the coastal zone (Fig. 1).

1961-67 High Seas Data

One further source of data on the relationship between salmon abundance and surface temperature lies in the extensive exploratory salmon surveys done by Canada and the United States between 1961-67 using surface longline gear (Turner and Aro

5   1968). Apparently only sea surface temperature data were collected during this period, so a comparison of salmon catches with other physical variables is not possible.

In contrast to the results obtained using data for the 1987-90 period, analysis of all available data shows no relationship between temperature and salmon abundance (Fig. 9). However, most data were collected during summer months, and included

10   samples taken in coastal regions. Maturing salmon must travel through coastal regions with substantially higher temperatures than the critical values estimated from the R/V TINRO data in order to return to their spawning grounds in the summer and fall.

A plot of all stations sampled in the winter and spring in the offshore region (defined for current purposes as those stations west of 135°W and south of 52°N)

15   shows that no fishing occurred in regions warmer than 11°C; thus, no data are available for those areas and times comparable to the more recent studies. This omission is perhaps not surprising, since the 1960's work was primarily concerned with determining where salmon went on the high seas, and not with establishing where the distribution stopped.

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DISCUSSION

Our results demonstrate that the high seas distribution of salmon can show extremely sharp species-specific thermal limits in the spring and early summer, a result not previously noted (cf. Burgner 1991). Although salmon are occasionally caught in

5   warmer waters, especially in the coastal zone, the abundance of Pacific salmon appears to drop by one to two orders of magnitude at 10.4°C, with somewhat lower species-specific thermal limits (sockeye: 8.9°C. coho: 9.4°C, pink and chum: 10.4°C). At least in spring and early summer, this thermal barrier confines Pacific salmon to a region much smaller than the total area of the Subarctic domain, which extends south

10   to roughly 39°N (Fig. 10). Pacific salmon thus do not always occupy the entire Subarctic Pacific, as they have traditionally been assumed to (Favorite et al. 1976; Blackbourn 1987; Quinn 1990; Ware and McFarlane 1989).

However, examination of distributional data collected during the late 1950's and early 1960's (Turner and Aro 1968), demonstrates that the specific thermal limits we

15   find in the offshore either do not hold in coastal regions, or at times other than the spring, early summer, and (possibly) winter. Asian studies of high seas salmon distributions in spring (Erokhin 1991, Mishima 1974) report upper thermal limits similar to those that we find, but do not demonstrate that these limits are either sharp, or that the limit is expressed as a threshold.

20   The sharpness of the limits, and their expression as a threshold, are clearly demonstrated through our use of generalized additive modelling techniques, and our earlier findings concerning the nature of the uncertainty in estimates of salmon catch on the high seas (Welch and Ishida 1993). GAMs have been used before in spatial

analysis of groundfish data (Swartzman *et al.* 1992). The distinguishing characteristics of our application are (1) the very clear demonstration that the response of salmon to temperature is expressed as a threshold, with no measurable influence below a specific temperature, and a very sharp population response at the threshold, and (2) the demonstration that other measured factors play little if any role in determining the southern limit to the distribution of salmon in the spring. Making these conclusions would be much more difficult without the use of GAMs, with their ability to incorporate realistic assumptions concerning the nature of the observational errors, or their lack of *a priori* assumptions about the nature of the functional response between variables. The comparison of cumulative distribution functions of measures of habitat and abundance (D'Amours 1993: Perry and Smith, *in press*) provide an alternative approach to GAMs, but lack an obvious way to incorporate the uncertainty of the catch observations into the analysis.

Our current understanding of the factors controlling salmon distributions on the high seas is still too limited to provide a clear understanding of why salmon apparently choose not to occupy the entire subarctic North Pacific, or why their distribution should change with season or region. However, some speculation is possible.

Brett et al. (1969), in a classic study of thermal physiology, demonstrated that the temperature for optimal growth decreased in juvenile sockeye as ration size decreased. Sockeye fed to satiation had a growth optimum at their final thermal preferendum (15°C); however, ration sizes of 1.5, 3.0, 4.5, and 6.0% body weight day^{-1} had respective temperature optima for growth of 5°, 8°, 10°, and 12°C, respectively (Brett et al 1969). An analogous relationship between increasing ration size and

preferred temperature was also found experimentally for lake charr, Salvelinus namaycush (Mac 1985).

Brett (1971) concluded that restricted ration dictated much of the energetic physiology of young sockeye in nature. As a result they were rarely found at the 15°C thermal optimum found in the laboratory. As fish exposed to thermal gradients under laboratory conditions demonstrate distinct thermal preferences, and the ability to discriminate temperature differences as small as 0.03°C (Beitinger and Fitzpatrick 1979), immature salmon maximizing their growth rate under food limiting conditions may therefore have both the ability and the evolutionary selective pressure needed to ensure that they can respond to the fine temperature gradients found on the high seas. Experimental data on behavioural thermoregulation by fish generally indicate that the preferred temperature selected by fish is similar to the temperature yielding optimal growth rates (McCauley and Casselman 1981; Jobling 1981).

Temperature optima for juvenile sockeye fed rations of 1.5-3% of body weight day^{-1} are similar to the temperatures at which adult sockeye were distributed in the spring in this study. A testable hypothesis is therefore that upper thermal limits for salmon in the North Pacific should vary with food intake, and therefore season.

Parsons and LeBrasseur (1968) showed that the progression of the spring bloom in the Northeast Pacific occurred in an arc that started first in southern regions of the Coastal domain, and then moved north up and around the coast surrounding the Gulf of Alaska, before finally progressing south offshore into the central Gulf. Following the spring bloom there is presumably a similar temporal progression in the amount of food available (Parsons and Lalli 1988). If salmon are behaviourally thermoregulating

to optimize growth, then the thermal optimum should vary with position within the Gulf, as well as with season.

In broad outline, this conjecture is consistent with the limited information available for coastal and high seas regions. Sockeye caught in coastal waters have

5 greater stomach content volumes than those caught in the offshore (Burgner 1991). Pacific salmon are found in much warmer waters in the productive coastal regions, and in fact are almost always exposed to substantially higher temperatures than the upper limits found in our study during their inshore spawning migrations. However, even in summer behavioural thermoregulation allows them to reduce their body temperature

10 below ambient temperatures in streams (Berman and Quinn 1991).

Defining the limits to distribution can depend on the gear used, because more efficient gear may capture salmon in areas where none are captured with another gear. However, the good agreement between data obtained using gillnet, longline, and trawl gear suggests that the very sharp drop in abundance at 10°-11°C is unlikely to be an

15 artifact. Salmon are occasionally encountered at high temperatures in offshore regions of the western North Pacific (particularly in summer, when most high seas salmon research takes place). This has raised concerns about the possible impact of high seas driftnet fisheries for squid on salmon (Burgner et al. 1982; Burgner and Meyer 1983; Dahlberg and Sigler 1987; Harris and Kautsky 1987; Takagi 1983; Walker and Burgner

20 1985). However, in large part these studies focused on identifying the occasional catch of salmon in anomalous conditions. As these incidents are by definition sporadic or rare, it is important that a statistical model be used to correctly take into account the occurrence of such observations. The use of the thermal range is a poor choice for

defining the distribution of salmon because it is dependent on sample size and is influenced by rare excursions into extreme temperatures (Magnuson et al. 1979).

Nevertheless, both juvenile and maturing salmon are clearly found at higher temperatures in coastal and offshore waters than were observed during our surveys, and

5   lethal limits for Pacific salmon exceed 20°C, irrespective of acclimation temperature (Brett 1956). Thus it is clear that temperature alone does not always determine the southern limit of the salmon distribution. However, the remarkably sharp response to temperature, and the low temperature at which this response occurs, suggest that the life history factors controlling the oceanic distribution of Pacific salmon probably play

10   important roles in shaping the evolution of Pacific salmon.

CONCLUSIONS

The reasons Pacific salmon undertake their vast migrations are still in large part unclear, but the central role this migration plays in the life history of Pacific salmon suggests that it will have been strongly shaped by evolutionary selection. Understanding the factors shaping the high seas distribution of salmon may therefore lead to better insight into the factors affecting salmon production on the high seas and the sustainability of commercial fishing operations in coastal waters. Improved understanding could also be crucial to understanding the response of Pacific salmon to climate change, or to changes in the total abundance of salmon populations on the high seas as a result of efforts to enhance salmon populations.

The extremely sharp threshold response to temperature that we have identified in the North Pacific suggests that changes in ocean temperatures could have a profound effect on the dynamics of salmon production. A clearer insight into the influence of temperature on distribution will be important to understanding the impact of either physical oceanographic changes that may occur as a result of climate change or biological changes that may occur as the result of ongoing efforts to further increase salmon populations.

We know very little of the extended period of life in the open ocean when the majority of growth occurs (Ricker 1962, 1975). If regions of optimal temperature were to shrink because of climate warming, or if increasing salmon population sizes were to result in reduced per capita rations, behavioural thermoregulation could lead to salmon being restricted to a smaller part of the subarctic Pacific. Any existing trophic competition for food on the high seas would then be exacerbated by the higher densities

that would result and lead to further contraction - a positive feedback. The potential for trophic competition has been examine elsewhere (Brodeur 1990; Welch and Parsons 1993), and some empirical evidence for density-dependent growth rates or species interactions on the high seas already exists (Ishida *et al.*, 1993; Krogius 1960, Ogura *et al.* 1990, Sano 1963).

Conversely, if the forage base was to change, salmon distributions could shift relative to the thermal regime in response to increased or decreased ration sizes. Brett et al's (1969) studies indicate that behavioural thermoregulation could shift the upper thermal limit for juvenile sockeye from 8°C to 12°C in response to a doubling of ration size from 3% to 6% of body weight day^{-1}. A doubling of zooplankton and salmon biomass levels between the 1950's and 1980's in the Gulf of Alaska has been reported by Brodeur and Ware (1992, submitted). The effect of such changes in the forage base on salmon growth are now currently under study.

Our results do not yet allow us a complete understanding of the factors controlling the distribution of salmon on the high seas. However, they do provide some surprising predictions. If salmon are thermoregulating to maximize growth, then they should move into colder waters in the winter, when food resources decline, and then move south into warmer waters in the summer. A full mechanistic explanation of the high seas migrations and distribution of Pacific salmon is still premature; we believe, however, that such information will be essential to informed management of these resources in the future.

ACKNOWLEDGMENTS

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Table 1. Analysis of variance for the generalized additive model analysis. The three nonparametric models listed in the table were fit sequentially assuming a Poisson error model.

5

	df	χ^2	$Pr(\chi^2)$
Intercept	1		
s(T)	3	25.1	0.00001[**]
s(S)	2.9	5.6	0.12
s(q)	2.9	4.9	0.17

10

Table 2. Maximum likelihood parameter estimates for the threshold temperature. Parenthetical values are approximate 95% confidence intervals on the parameter estimates (see text). Rope trawl results are for the 1990 R/V TINRO cruise: gillnet and longline results are for the R/V W.E. RICKER cruises. Species-specific estimates are based on the TINRO data. Degrees of freedom for the three sampling gears were calculated as k=617 df/trawl-hour, 3.3df/tan of gillnet and 8 df/hachi of longline.

	$\bar{\mu}$	$\bar{T}$	σ_T
A. Total Salmon Catch			
Rope Trawl	42.0	10.34°	0.17°
	(40.0, 44.0)	(10.3°, 10.4°)	(0.15°, 0.19°)
Gillnet	192.7	9.4°	0.92°
	(175.0, 213.9)	(. [1])	(0.83°, 1.01°)
Longline	105.9	8.2°	2.20°
	(95.9, 117.3)	(7.4°, 9.0°)	(1.99°, 2.43°)
B. Species			
Chum	16.2	10.4°	0.18°
	(15.1, 17.5)	(10.4°, 10.4°)	(0.16°, 0.20°)
Pink	15.8	10.4°	0.16°
	(14.7, 17.0)	(10.4°, 10.4°)	(0.14°, 0.18°)
Coho	8.4	9.4°	0.46°
	(7.5, 9.2)	(9.2°, 9.5°)	(0.41°, 0.50°)
Sockeye	5.0	8.9°	0.01°
	(4.2, 5.8)	(8.8°, 9.0°)	(0.0°, 0.1°)

[1] Confidence interval could not be calculated.

Table 3. Maximum likelihood parameter estimates for the two-edged distributional model applied to the pink salmon data. Parenthetical values show approximate 95% confidence intervals on the parameter estimates (see text).

$\bar{\mu}$	$\bar{T}_{Lo}$	$\sigma_{T,Lo}$	$\bar{T}_{Hi}$	$\sigma_{T,Hi}$
42.1	8.1°	0.49°	10.1°	0.28°
(32.1, 73.8)	(7.9°, 8.5°)	(0.38°, 0.66°)	(9.7°, 10.2°)	(0.18°, 0.49°)

5

FIGURE 1. Cruise track of the R/V TINRO in 1990. Filled circles indicate location of trawl fishing operations between 29 March and 21 April, and filled squares locations between 27 April and 14 May. Gillnet (□) and longline (Δ) samples

5   taken during opportunistic sampling by the W.E. Ricker in 1987-1990 are also shown.

FIGURE 2. A behavioural model of the edge of the salmon distribution. Individual salmon actively avoid temperatures greater than some threshold; individual variation in the temperature at which this response is expressed results in a

10   range of temperatures over which abundance changes. As temperature increases, a greater fraction of the total population will avoid any given temperature level, leading to a decrease in population density. The rapidity of the decline depends on the degree of individual variation.

FIGURE 3. Vertical sections of salinity and temperature along 150°W in May 1990.

15   A progressive steepening of the isohalines is evident to the south. R/V TINRO stations approached but did not reach the vertical 34‰ isohaline marking the southern boundary of the Subarctic Domain.

FIGURE 4. Contour plots of surface temperature and salinity, May 1990. The second leg of the R/V TINRO cruise track is superimposed

FIGURE 5. Generalized additive model fits for total salmon abundance and individual species: the point at which temperature has an influence varies by species. The non-parametric effect of temperature has been calculated using b-splines, and is shown along with the twice standard error bands about the estimates (shaded area) and the partial residuals (•). The y-axis shows the additive effect of temperature on log-abundance.

FIGURE 6. GAM fits of total salmon abundance as functions of (A) temperature and salinity. and (B) temperature. salinity, and density (σ_t).

FIGURE 7. Salmonid catch vs. temperature. Non-zero catches are expressed in terms of the logarithm of numbers trawled. after normalizing by the fishing time (t). Zero catches are plotted as log(1). Under this transformation the vertical range of positive catches is compressed to emphasize the sudden drop in density at the threshold temperature. Vertical bars indicate the 95% confidence limits on the individual catch estimates. calculated using the negative binomial distribution with $k = 617$ df and assuming equal probability tails. Lines show the predicted salmon abundance as a function of temperature based on the maximum likelihood analysis.

FIGURE 8. Comparison of total salmonid catch vs. temperature for the R/V TINRO and the 1987, 1988, and 1990 W.E. RICKER cruises. Confidence intervals on the R/V W.E. RICKER catches were calculated as in figure 7. but dividing the gear length (in meters) by 15 to calculate the degrees of freedom k.

FIGURE 9. Salmonid catch vs. temperature for the 1961-67 Canadian and U.S. High Seas salmon research cruises (Turner and Aro. 1968). CPUE is numbers caught per unit hachi of surface longline. (A) Total data (all stations). (B) January to May only. (C) Jan-May stations taken in the offshore (west of

5   135°W). and (D) Jan-May offshore stations taken in the south-central Gulf of Alaska (defined as south of 52°N).

FIGURE 10. The predicted geographic distribution of salmon in April 1990, based on the R/V TINRO data. Contour plots show the predicted temperature field, while the surface plot shows the predicted mean response of salmon

10   abundance to temperature. using the parameter estimates reported in Tables 2 and 3. Note the sharp drop in abundance well to the north of the subarctic boundary. which lay south of 40°N. Fine details in the abundance surfaces are dependent on the accuracy of the interpolation of the temperature field.
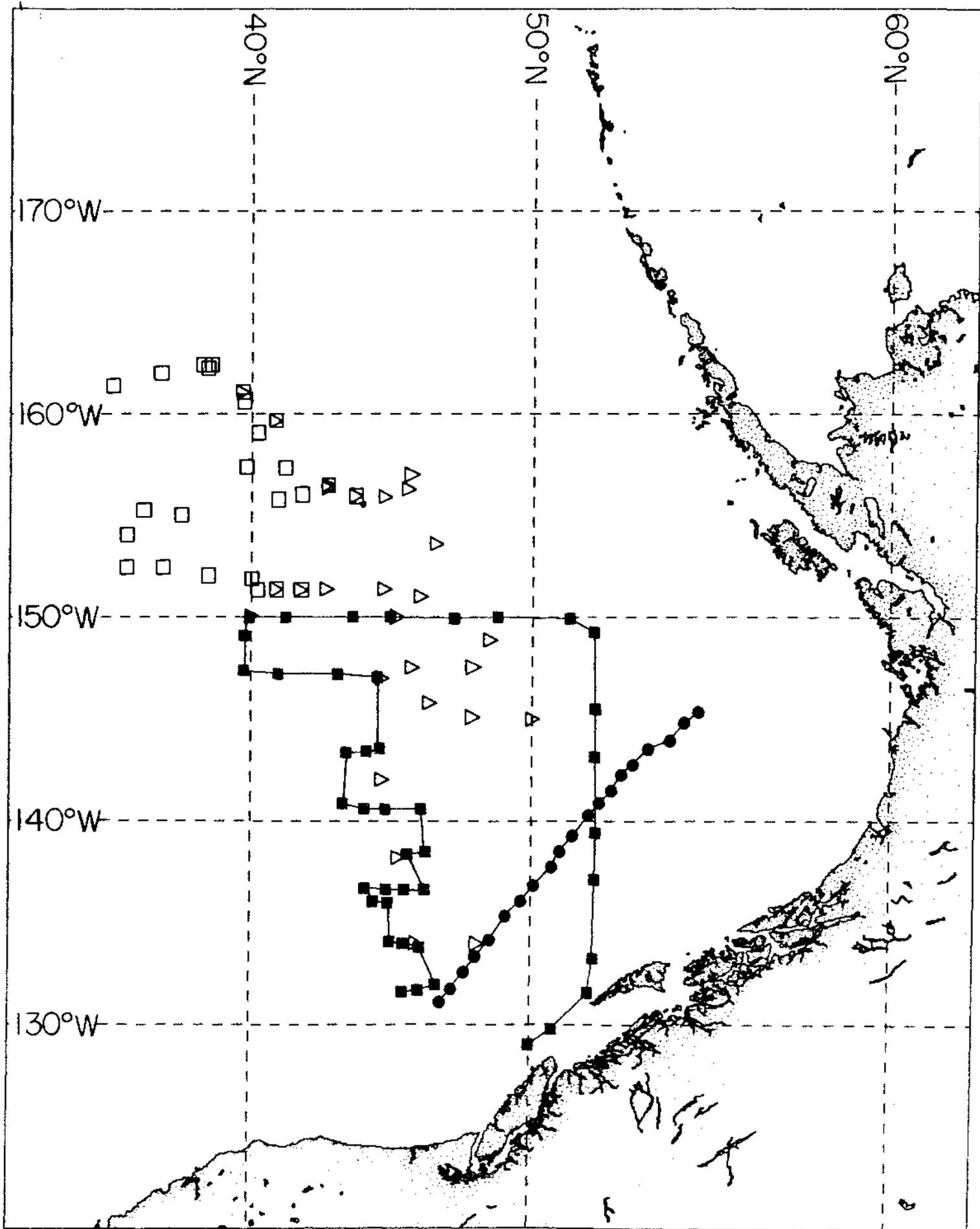
Behavioural Response to Temperature
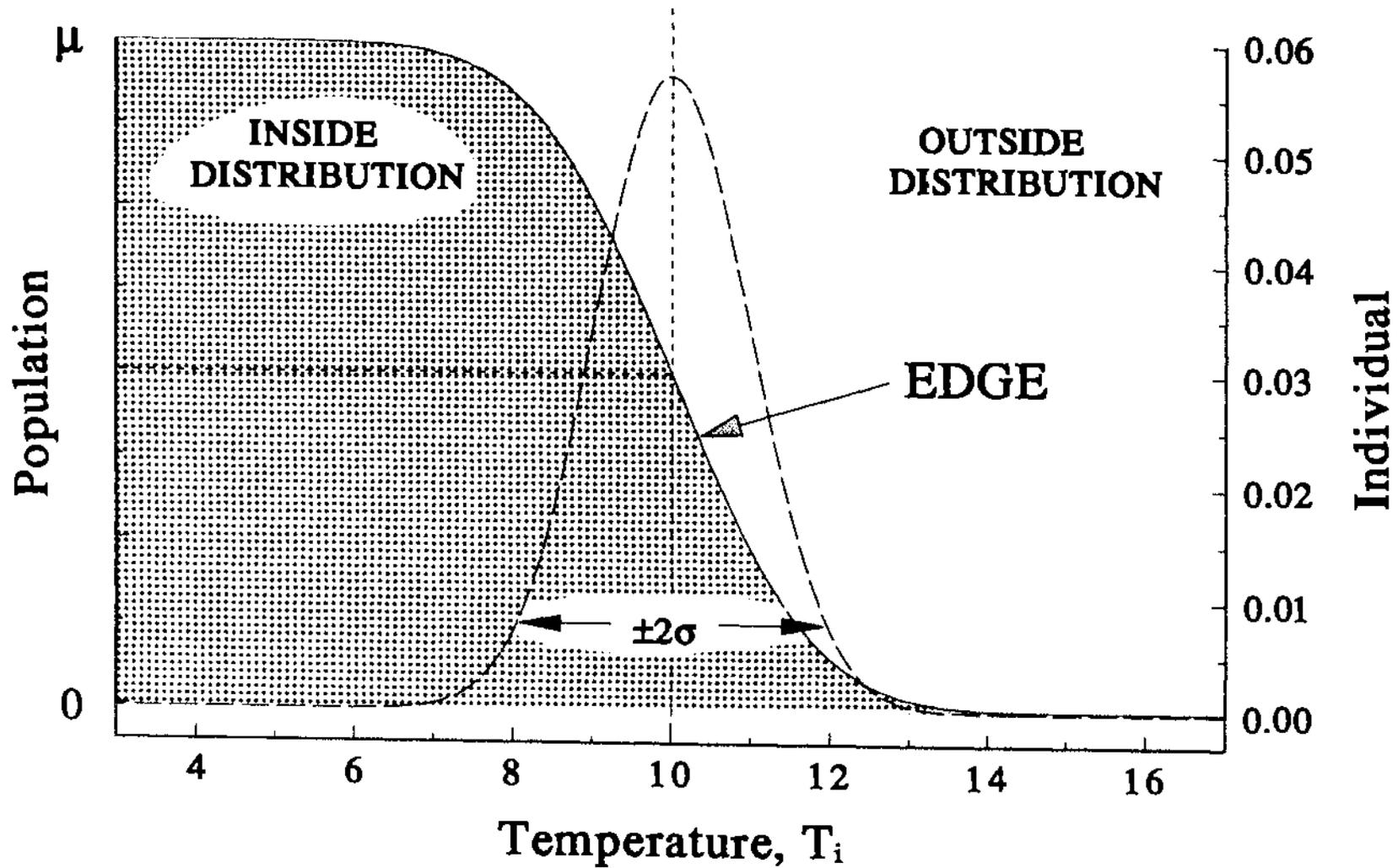
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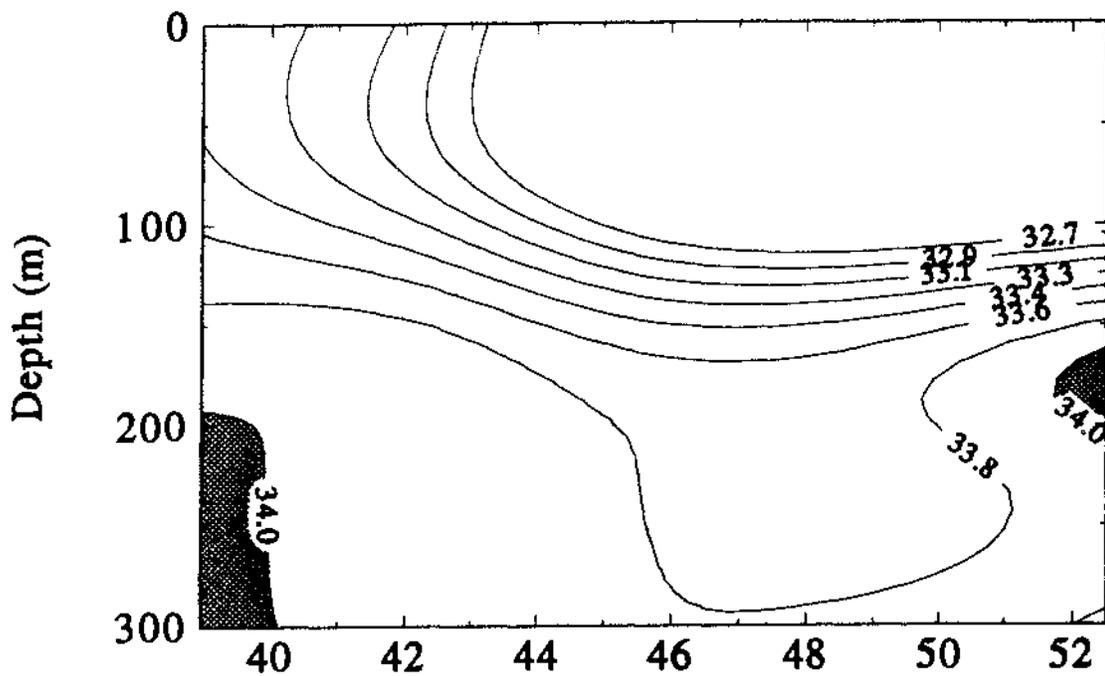
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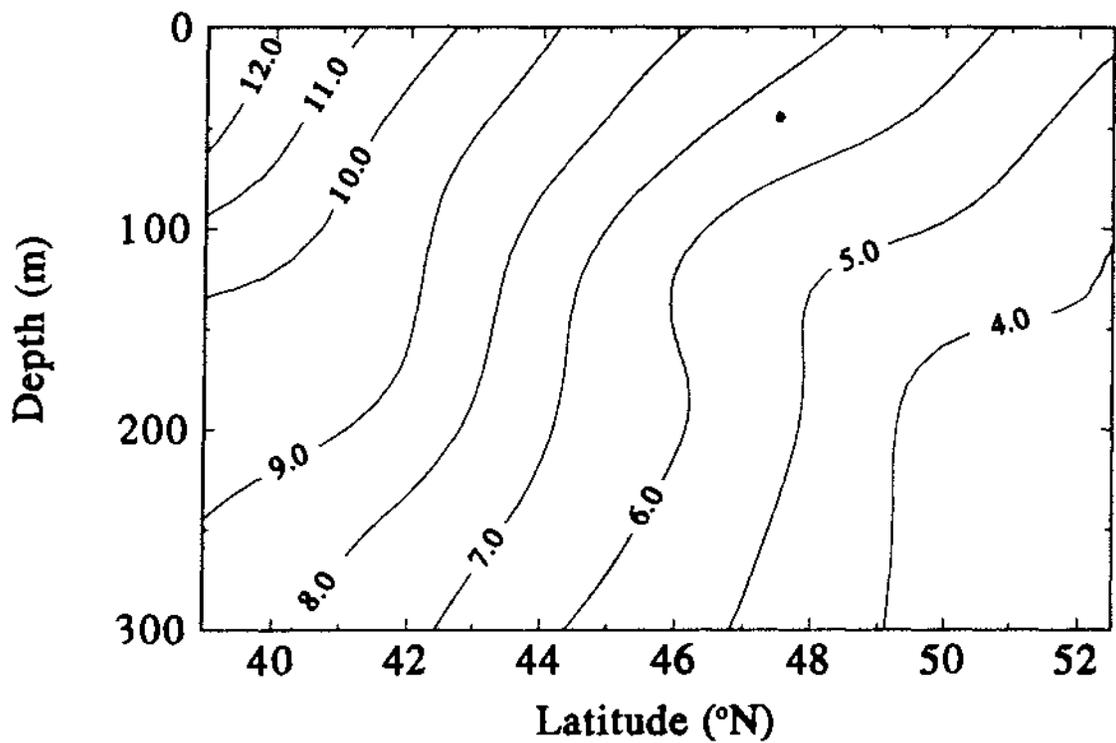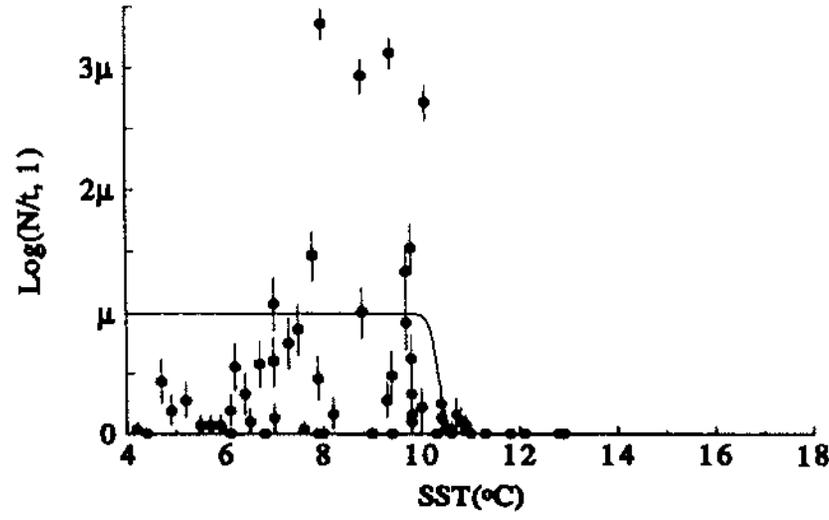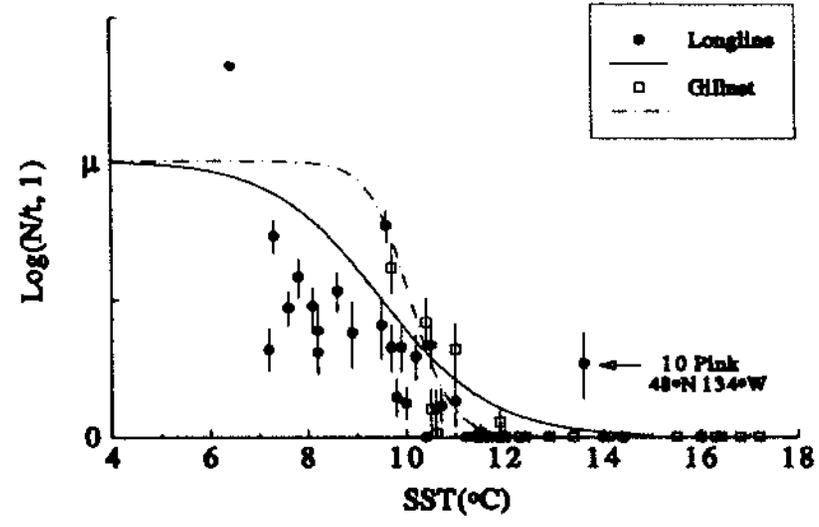
Surface Salinity

Surface Temperature

Longitude (°W)

SST(ºC)
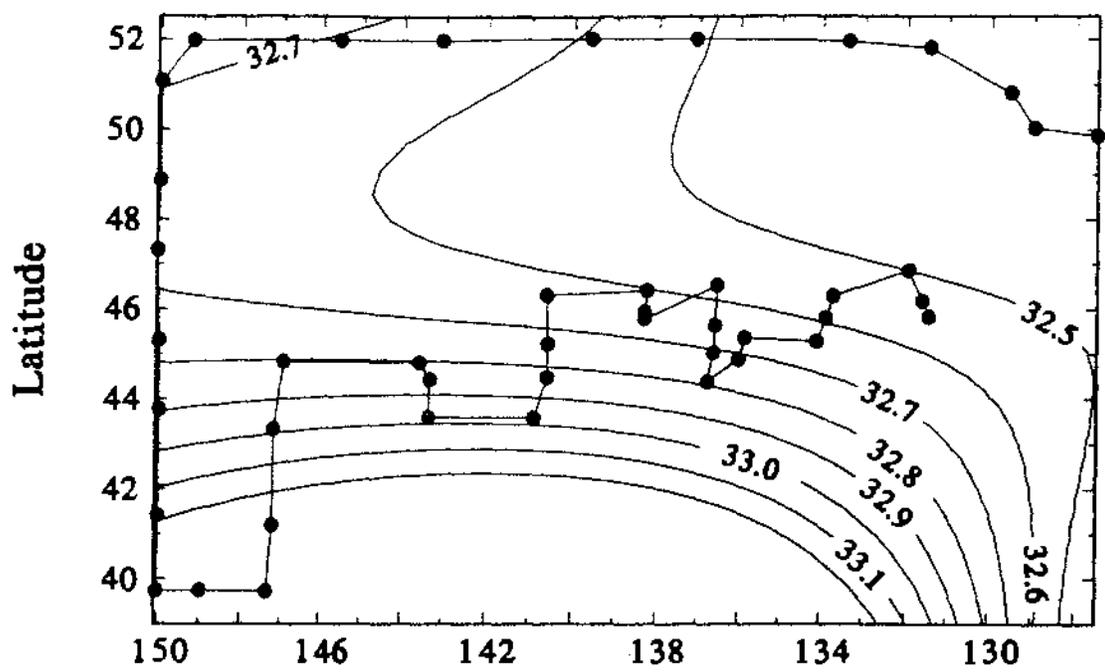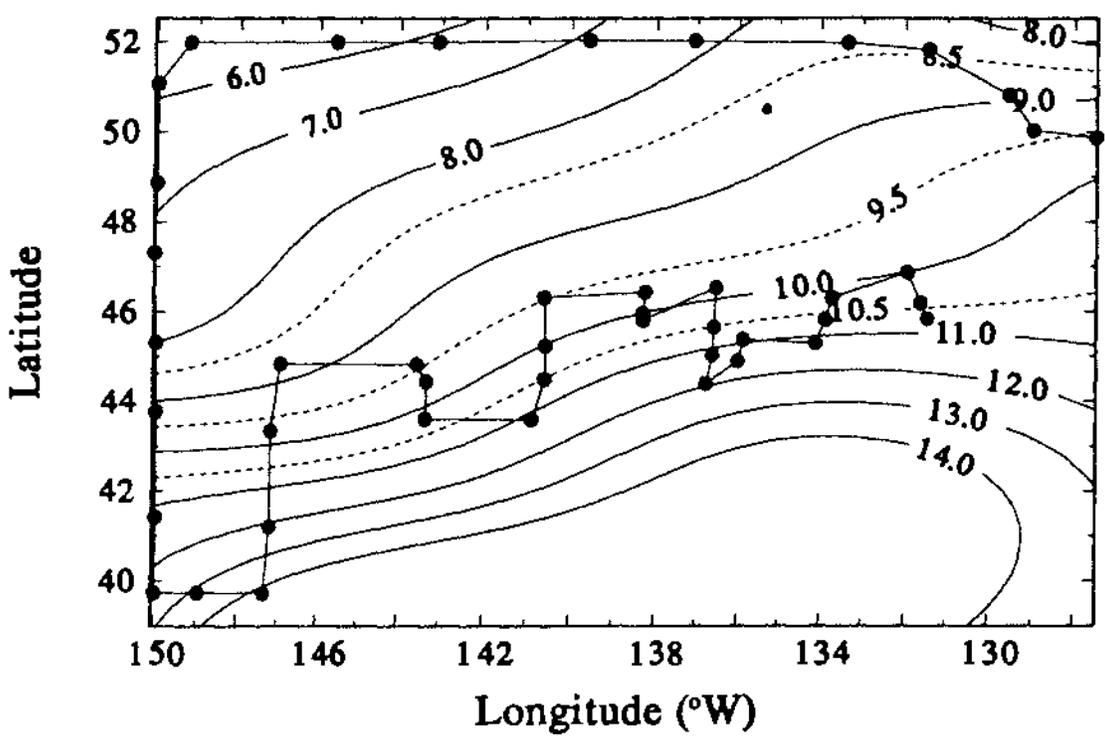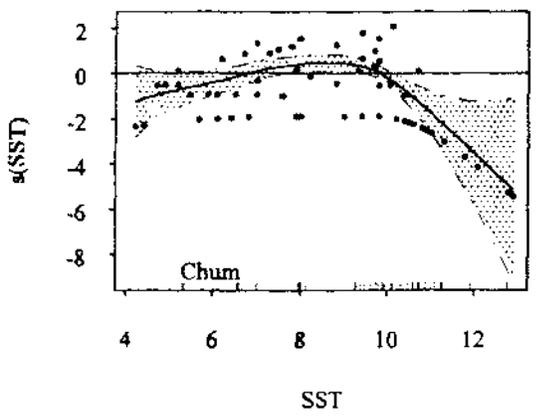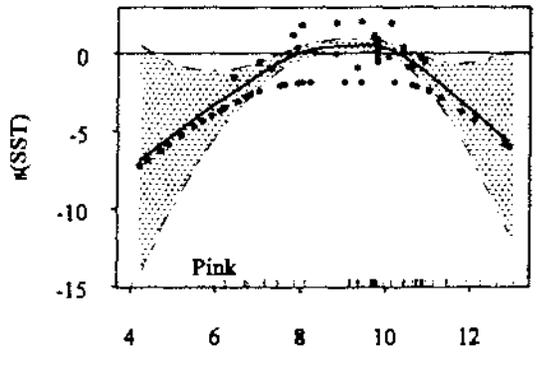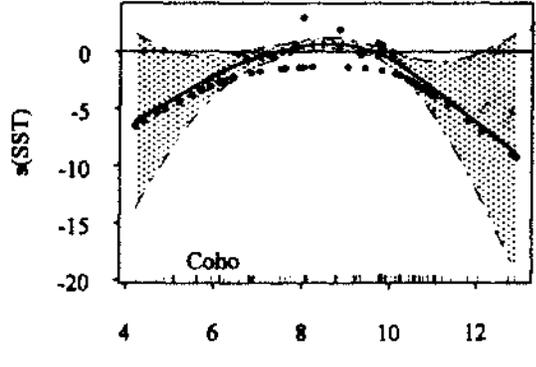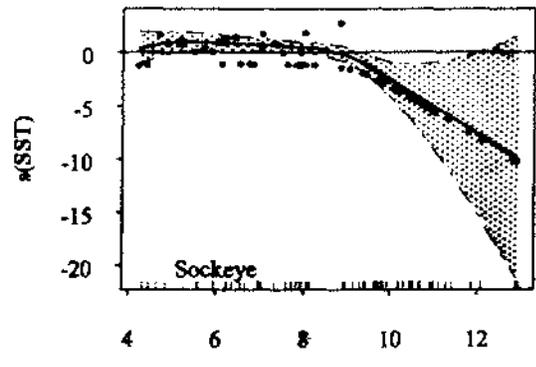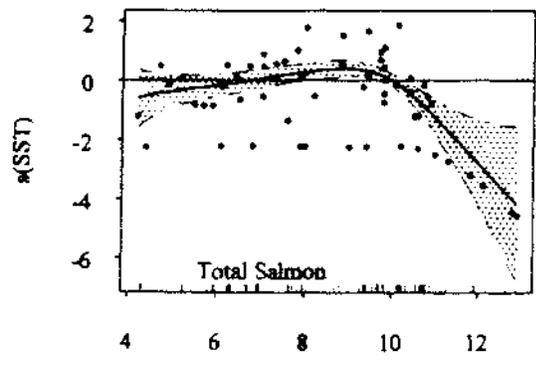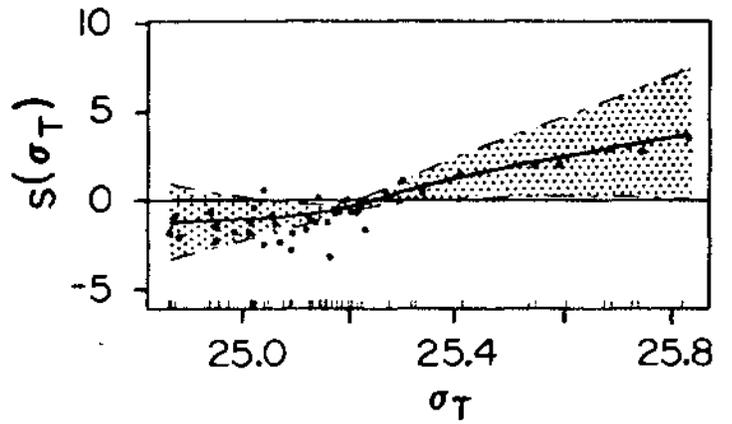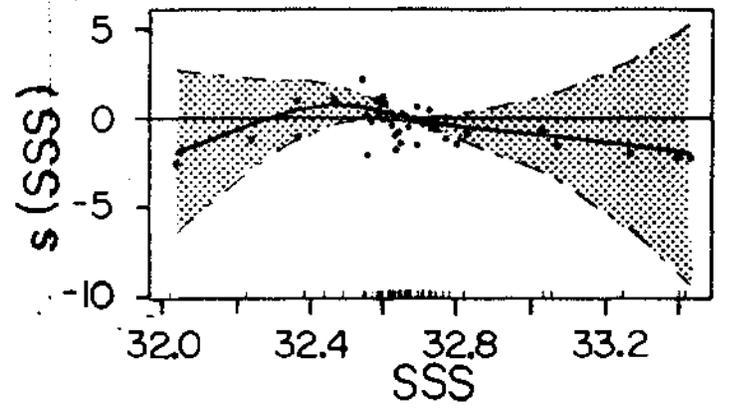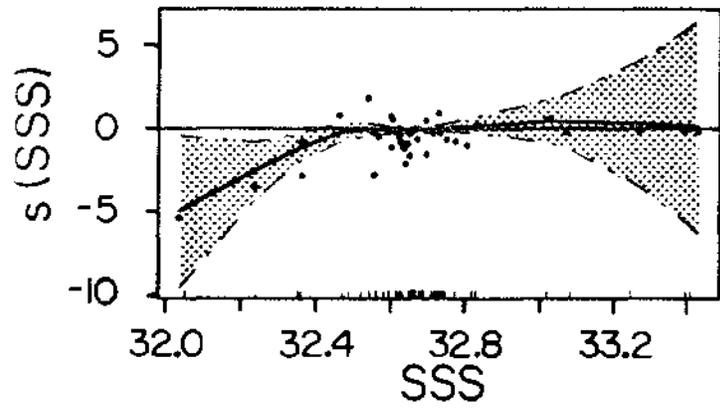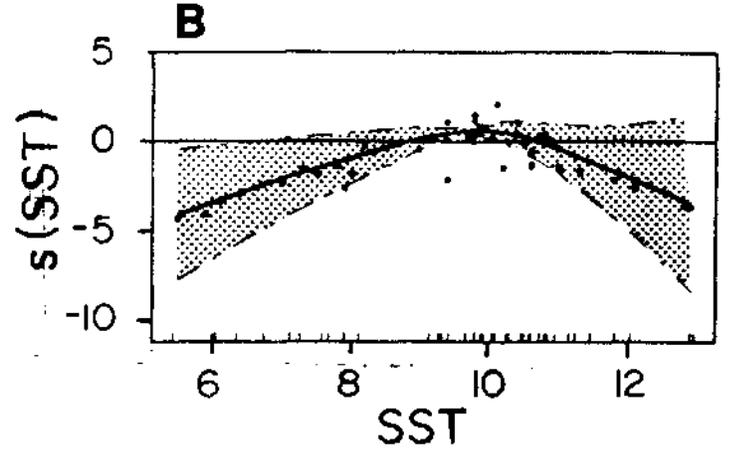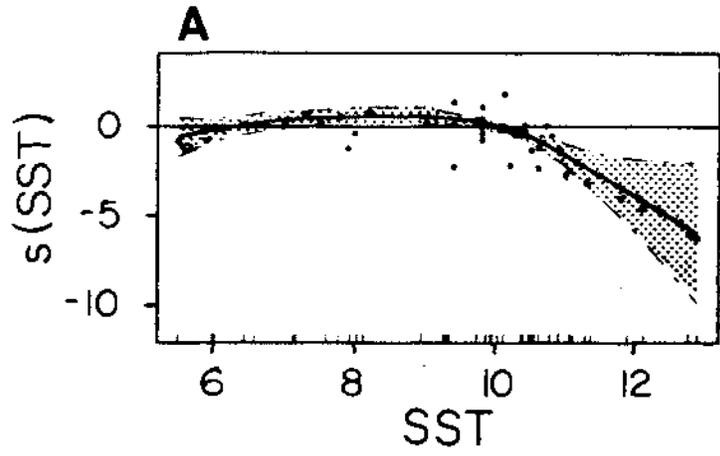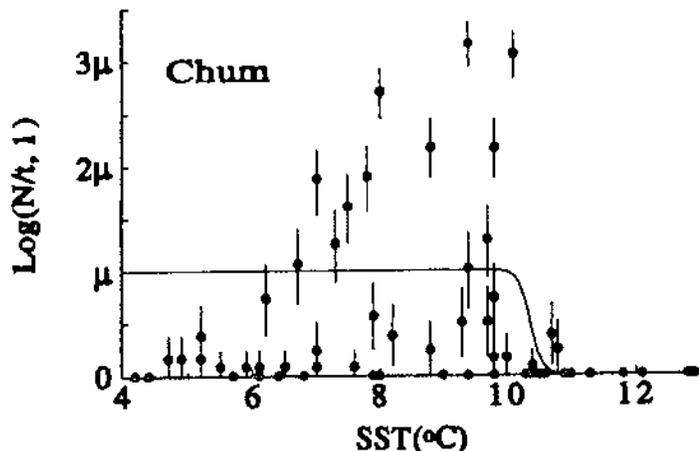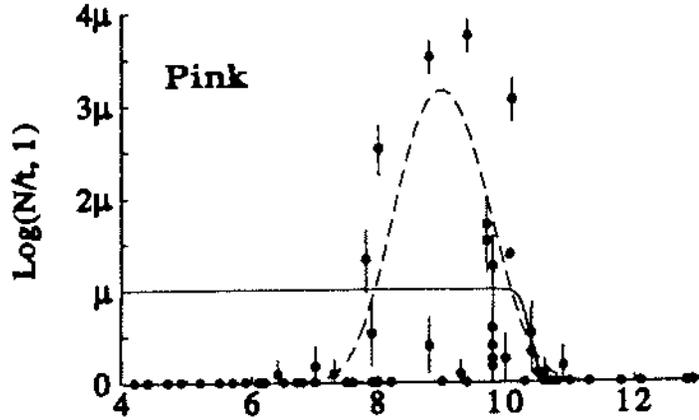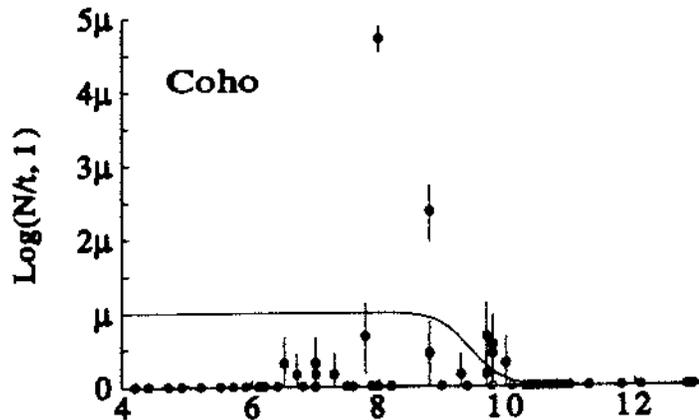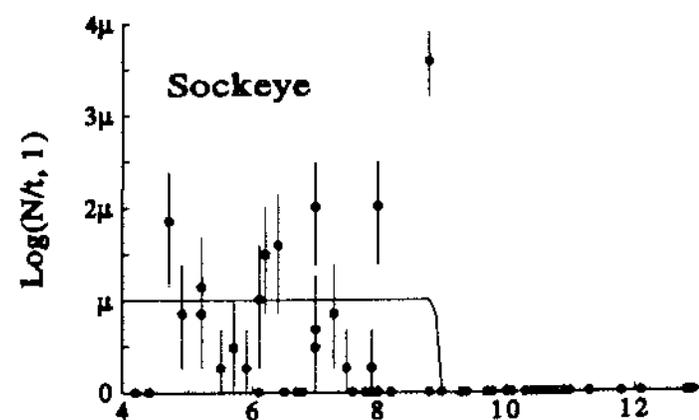
r/v TINRO
Total Salmon Catches

r/v Ricker
Total Salmon Catches

Fig. 7
Welch et al.

1961-67 High Seas Data

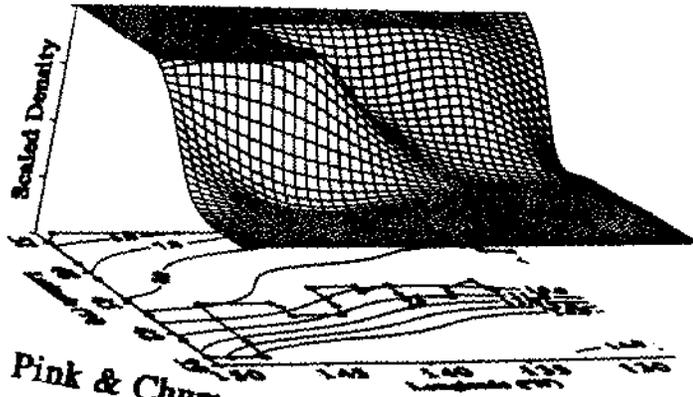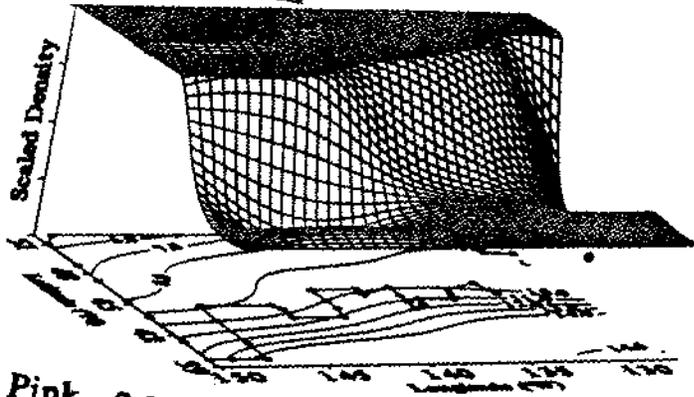Jan-May, Long. ≥ 135°W

Jan. - May Only

Jan - May, Long. ≥ 135°W, Lat. ≤ 52°N
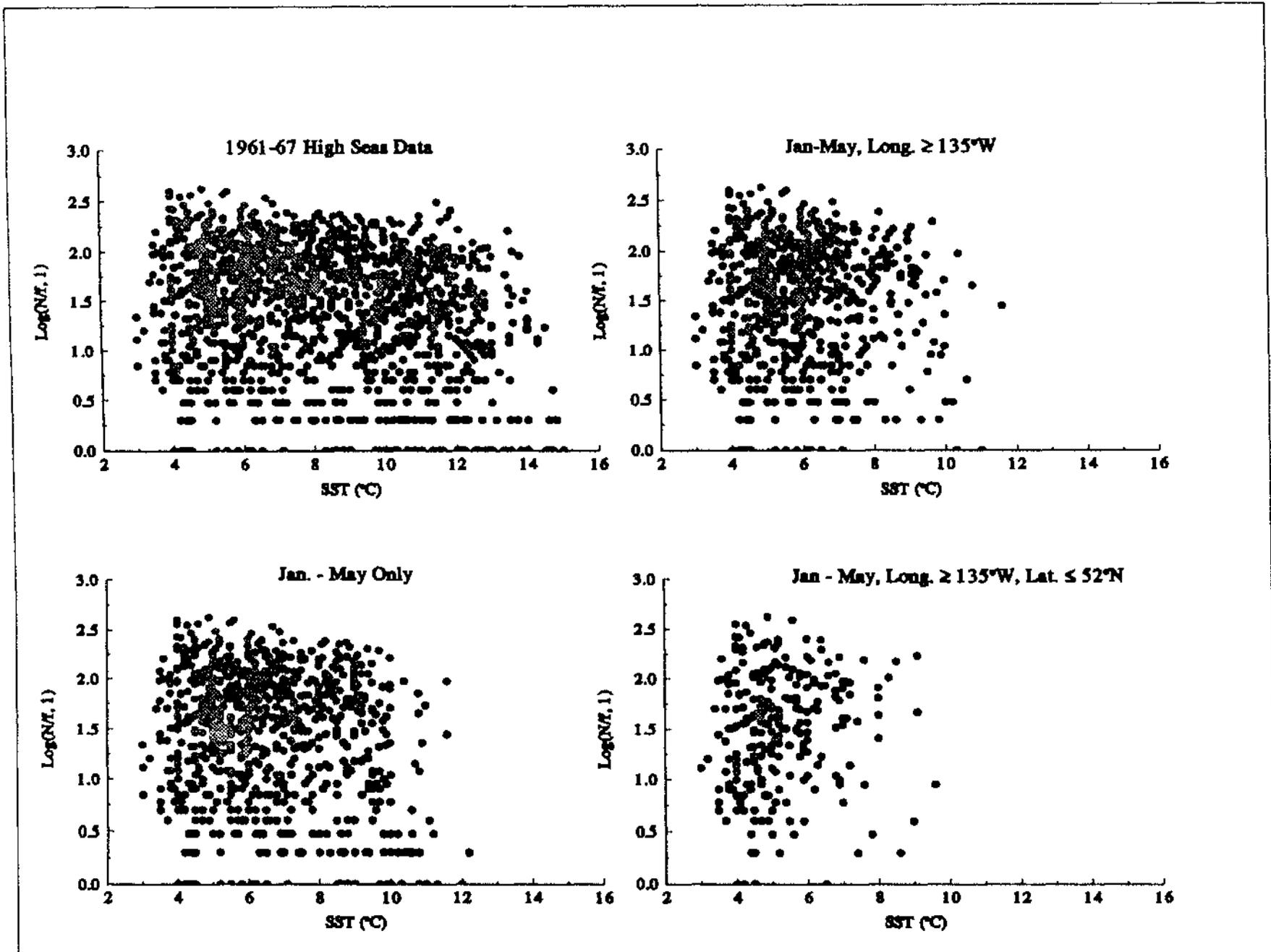
Sockeye
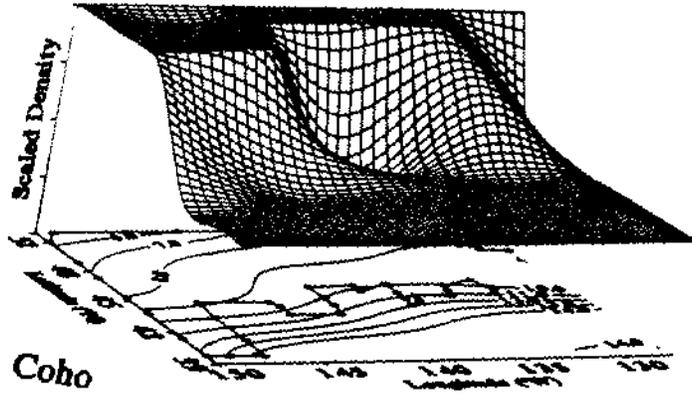
Coho

Pink & Chum

Pink - 2 Edged Distribution