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INDIRECT EVIDENCE FOR BIOENERGETIC CONTROL
OF SALMONID SPATIAL DISTRIBUTIONS IN THE
CENTRAL NORTH PACIFIC

by

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Abstract

In an attempt to understand the factors which lead to the bycatch of salmon within the driftnet fishery for flying squid, *Ommastrephes bartrami*, I quantify the spatial distribution of salmon, *Oncorhynchus* spp., bycatch at large- and meso-scales and use a bioenergetic hypothesis to explain the distribution of salmon. The bioenergetic hypothesis assumes that salmon are distributed in a manner which maximizes growth and that growth is dependent on both sea surface temperature and available forages. I identify two spatial patterns in forage which are important in the spatial distribution of salmon. 1) Changes in the biological productivity associated with water mass types produce large-scale spatial pattern in the encounter probability of salmon. 2) Mesoscale enhancement in biological productivity over the Northern Emperor Seamount Chain results in the formation of dense clusters of salmon above the seamounts. these spatial patterns in forage account for the varying response of salmon to temperature.

Introduction

The spatial distribution of salmon on the high seas has been an area of interest since they were first found to undertake their phenomenal circular migration between natal streams and the high seas of the Central North Pacific. Interest by all nations along the North Pacific rim led to a massive effort by the International North Pacific Fisheries Commission (INPFC) in the 1950's and 1960's to uncover the components of salmon migration and to determine what factors limit salmon distribution (Manzer, et al., 1965; French, et al. 1975). Recent concern on salmon carrying capacity (Pearcy, 1992) and on the avoidance of salmon in the squid driftnet fisheries (Burgner and Meyer, 1983; Ogura and Takagi, 1987; Ito and Murata, 1989) have stimulated a renewed interest in factors influencing the spatial distribution of salmon on the high seas.

Bioenergetic regulation of spatial distribution

If bioenergetic costs (respiration) and bioenergetic gains (assimilation) are modeled along environmental gradients, net energy (potential growth) can be modeled spatially and temporally using the spatial and temporal relationships of the environmental gradients. The degree to which the actual distribution of a species matches the distribution of potential growth, provides insight into the degree to which the growth of a species (the energetic balance between assimilation and respiration) forms the basis of the distribution and abundance of the species. If a species is distributed in such a manner which maximizes growth, models of net energy balance with respect

to environmental gradients can provide a useful means of predicting the spatial distribution and abundance of a species.

Due to the poikilothermic nature of salmon, temperature plays a major factor in the bioenergetics of salmon. Temperature can either control growth of salmon by influencing appetite or by altering metabolic rate (Fry, 1947). Data show that both of these factors, standard metabolic rate and food consumption, increase in poikilothermic animals over most non-lethal temperatures (Warren and Davis, 1967) (Fig. 1). However, these two properties do not increase at the same rate; the different slopes form the basis for optimum growth conditions and temperature preferences in many poikilothermic animals (Hall et. al., 1992). The pivotal difference is that the rate of food consumption reaches its maximum value prior to the maximum standard metabolic rate. This occurs because appetite is often influenced by environmental stress prior to metabolic function. Since metabolic rate continues to increase after food consumption has reached its maximum rate, optimum growth conditions (maximum energy available for growth) occur near the temperature of maximum food consumption when food is in unlimited supply. As food availability decreases, the temperature of optimum growth conditions decreases (Fig. 1). Optimum growth conditions in sockeye salmon (Brett, et al., 1969) and chum salmon (Averett, 1969) appear to follow this general pattern. Temperatures yielding optimum growth in sockeye ranged from 15°C at satiation to 12°, 10°, 8°, and 5°C for ration sizes of 6%, 4.5%, 3% and 1.5% of body weight per day, respectively (Brett, et al., 1969; Brett, 1971). In chum salmon maximum growth conditions occurred near 17°C, however growth was still observed at 23°C (Averett, 1969).

Using the above bioenergetic principles, a number of authors have shown that species are distributed in such a manner which maximizes the conversion of available energy into growth (Hall, et al., 1992; and references therein). In this paper, I argue that this behavior of energy conservation may be particularly suited for habitat selection of salmon on the high seas where predation is minimal and the availability of food is limited.

Salmon abundance data

Salmon bycatch data from the 1990 Japanese squid driftnet fishery (Pella, et al., 1993) are used to describe the spatial distribution of salmon on the high seas. This fishery covered much of the Central North Pacific (Fig. 2), but occurred in sea surface temperatures (SST) near or exceeding the upper temperature preferences of salmon (Ignell, 1991b; Ignell and Murphy, 1993). Subsequently, this paper only addresses the distribution of salmon near their upper temperature tolerance (the southern limit of their range in the North Pacific).

Observers aboard the driftnet vessels recorded numbers of all species captured by the drift gillnets, fishing effort (amount of gillnet deployed), SST, fishing location, and time for each fishing operation. A fishing operation forms the basic sampling unit in this study and is defined as all gillnets deployed and retrieved in a single day of fishing. Observers typically monitored six of an average of eight sections of gillnet set consecutively along an east-west axis. Gillnet sections have approximately 150 tans of net sewn together; a tan is a continuous piece of gillnet, which can vary in length between 35 to 50 meters from vessel to vessel.

All salmon species caught in a fishing operation were pooled together since it was decided that the observer data were inadequate for addressing species specific spatial distributions. Over 50% of all salmon captured in the squid fishery were unidentified. Of the identified salmon, chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*) were the most numerous species captured in 1990, accounting for 59% and 40% of the total identified salmon. The higher abundances of chum and coho salmon in the fishery is likely due to their higher temperature tolerances (Ogura and Takagi, 1987; Tabata, 1984).

Methods

To describe the large scale spatial distribution of salmon the n ($i = 1, 2, 3, \dots, n$) catches recorded by the observers were converted to a binary response, y_i , ($y_i = 1$ if salmon were encountered in the gillnet operation, and $y_i = 0$ if salmon were not encountered). A binary random variable was used, has the advantage of a simple error structure (a binomial error structure) and may be better suited for describing large scale patterns in salmon bycatch than a continuous variable such as catch per unit of effort (CPUE).

Encounter rates of salmon were modeled with a generalized additive model (GAM), which assumes that the explanatory terms are additive but not necessarily linear (Hastie and Tibshirani, 1990; Hastie, 1992). The GAM model can be written as a sum of a systematic component (μ_i , the mean or expectation of y_i) and a random component (ϵ_i , where the distribution of ϵ_i is a member

of an exponential family):

$$y_i = \mu_i + \varepsilon_i \quad (1)$$

The explanatory variables enter in as the sum of their effects, η_i ,

$$\eta_i = \alpha + f_1(x_{i1}) + f_2(x_{i2}) + \dots + f_j(x_{ij}). \quad (2)$$

and are related to μ_i through a logit link function,

$$\eta_i = g(\mu_i) = \text{logit}(\mu_i) = \log\left(\frac{\mu_i}{1-\mu_i}\right). \quad (3)$$

which is the canonical link for a binomial error distribution. The observed values, y_i , enter into the model through the binomial likelihood function,

$$L(\mathcal{Y}; \boldsymbol{\mu}) = \prod_{i=1}^n p_{Y_i}(\mathcal{Y}_i; \mu_i) = \prod_{i=1}^n \left\{ \mu_i^{y_i} (1 - \mu_i)^{1-y_i} \right\} \quad (4)$$

which is used to solve for μ_i by minimizing the log-likelihood-ratio, $-2[l_1 - l_0]$, where l_1 is the log of the likelihood function, L , maximized over μ_i and l_0 is the log-likelihood for the full model with n parameters.

The power behind GAMs is their ability to incorporate nonlinear relationships between the predicted and explanatory variables by including smooth functions in (2). The smoothness of the function can be controlled by its equivalent degrees of freedom (e.g. A smooth function with one degree of freedom results in a linear term.). Smooth terms are extremely useful if a "functional" (cause and effect) relationship between the observed and predicted variables can not be assumed (e.g. spatial relationships), or if the "functional" relationship between the two is unknown.

Three explanatory variables were used in the GAM model: latitude, longitude, and SST. The significance of these variables was determined by an analysis of deviance in a stepwise variable selection design and by the C_p statistic (Draper and Smith, 1981). Latitude and longitude were modeled with smooth functions containing four degrees of freedom (cubic spline fitting was chosen as the smoothing algorithm, see Hastie and Tibshirani (1990:300-304) for details), and SST was assumed to be linear in the logit scale. The assumed linear form was tested by first modeling SST as a smooth function. The resulting smooth fit was found to agreed well with the linear fit.

Only the months of June, July, and August were used in the analysis to avoid a seasonal effect. In addition, only data east of 175° E were used. Coverage west of 170° E was not adequate (fig. 2). Data between 170° E and 175° E were not used due to the large influence of the Emperor Seamount Chain near 170° E (seamounts occurring within the dataset are shown in figure 4). Dense clusters of salmon were present over the seamount chain which accounted for over 85% of all the salmon observed in the fishery (Ignell and Murphy, 1993; Fig. 3).

The approach taken to evaluate mesoscale distribution patterns of salmon is as follows. The fishery was stratified into 2° latitude x 5° longitude strata, and within each strata containing at least 5 observed fishing operations, the encounter rate, mean catch rate, and mean surface temperature were estimated. Both the encounter rate and the mean catch rate were modeled as a function of SST using a General Linear Model (GLM) with a logit transformation (3). The residuals from the fitted models were then evaluated in a spatial context.

Results

In the GAM model the relative merit of both the latitudinal and longitudinal effects was determined by an analysis of deviance in a stepwise variable selection design. Within this framework, as each variable is added, the reduction in the overall variance is compared to the number of degrees of freedom the variable adds to the model. The tradeoff between variance reduction and added degrees of freedom can be computed by the C_p statistic (Draper and Smith, 1981). The analysis of deviance and C_p statistics for the GAM model are given in Table 1 and indicate that both latitude and longitude add significantly to the model (lower C_p values indicate a more parsimonious model). The GAM model results show that the encounter rate of salmon is higher at latitudes North of 41.5° N than latitudes south of 41.5° N (Fig. 4b). It is also important to note that this latitude effect in the encounter rate is present in the fishery after the effects of SST have been accounted for. This indicates that there is a significant latitude pattern in the response of salmon (in terms of abundance) to temperature within the fishery. Similarly, the GAM model also identifies a significant longitude pattern in the encounter rate after the effects of SST have been accounted for. Encounter probabilities were higher in the western region of the fishery than the eastern region (Fig. 4a).

The most obvious mesoscale pattern in the catch rates of salmon is the dense clusters of salmon found above the seamount chain. Catch rates in the two strata above the seamount chain are considerably higher than all other strata in the fishery (Fig. 5). In addition, the catches of salmon above the seamounts occurred at temperatures near 15° C, which is thought to be the

upper temperature tolerance for salmon on the high seas (Ogura and Takagi, 1987). Of the seamounts occurring within the fishery, the highest salmon catch rates were above the Nintoku Complex which has several seamounts, including the Nintoku Seamount. The clusters of salmon above the seamounts may be due to topographic upwelling and bioaccumulation above the seamount chain. Interactions between topography and impinging flow have been shown to create mesoscale increases in productivity above seamounts (Shomura and Barkley, 1980; Boehlert, 1984).

The effect of the seamounts are not as large when encounter rates are considered (Fig. 6). However, encounter rates are less likely to be affected by the seamounts due to the aggregated nature of salmon above the seamount chain. Again, the encounter rates identify the Nintoku Complex as having a much larger influence on the distribution of salmon (The strata above the Nintoku Complex is farther from the regression line than the strata above the Suiko Seamount).

Discussion

Latitude pattern in encounter rates of salmon

Several studies have recognized that the preferred temperature ranges for salmon species is not consistent over time or between different regions of the North Pacific (Tabata, 1984 and references therein). The dynamic nature of the response of salmon to temperature may be due to varying forage conditions. Welsh, et al. (in press) argues that the seasonal progression of a spring bloom in the Gulf of Alaska could potentially cause spatial and temporal shifts in the optimum

temperatures for salmon species in the North Pacific. In the central North Pacific, a spring bloom is not thought to occur (Miller et al. 1988); however there are spatial patterns in forage abundance associated with water mass types that may alter the response of salmon to temperature. In the subarctic domain, major nutrients such as phosphates, nitrate, and silicate are not usually limiting because of the intense upwelling and mixing above the halocline (Anderson, 1969). In the subtropical domain, nutrient levels and phytoplankton production are limited year-round by weak mixing in the euphotic zone and strong vertical stability of the water column (Hayward et al., 1983; Percy, 1991). As a result of this nutrient gradient, the biomass of phytoplankton and zooplankton is higher in the subarctic domain (McGowan and Williams, 1973; Barnes and Mann, 1980; Hayward et al., 1983). The differences in production dynamics between the subarctic and subtropic water masses is clearly seen in ocean color data (Fig. 7).

If salmon are distributed in a manner which maximizes the conversion of available forage into growth, we would expect higher densities (or encounter rates) of salmon within the Subarctic Domain due to its higher productivity. Results of the GAM model indicate that after accounting for the effect of SST on encounter probabilities of salmon, a significant latitude gradient persisted in the spatial distribution of salmon. This latitude gradient in the encounter probabilities of salmon appear to agree quite well with the mean summer position of the Subarctic Boundary (Fig. 8), which is the front defining the southern limit of the subarctic water mass (Fig. 9). The close agreement between encounter probabilities of salmon and water mass types suggest that the latitude gradient found in the encounter probabilities of salmon is the result of different production levels found within the fishery; and supports a bioenergetic basis for the spatial distribution of salmon. I argue that the southern limit of the distribution of salmon in the squid

fishery may be determined by an energetic optimization of growth. This is similar to the conclusion of Welsh, et al. (in press), who identified preferred temperature ranges of salmon species which were consistent with temperatures of optimum growth estimated by bioenergetic models.

Longitude pattern in encounter rates of salmon

It is possible that the northward displacement of the SFZ when moving from the western Pacific to the eastern Pacific (Levine and White, 1981) could produce a longitude trend in the production levels within the fishery. This shift in the latitudinal position of the SFZ was suggested by Ignell (1991a) in his analysis of Japanese research vessel data as the basis for the higher salmon abundances west of 180° longitude than east of 180° longitude which was not explained by SST's. Species composition is known to vary between the Eastern and Western Pacific Basins. This could lead to differing abundance levels abundance of competitors and subsequently available forage densities between the two Pacific basins.

Alternatively, it is also possible that energy costs associated with dispersal may explain the longitude pattern in encounter rates of salmon. Asian and North American stocks are thought to occur in the eastern region of the fishery (Walker, 1993). The absence of Asian coho may be related to the energy costs required to disperse across the entire North Pacific. Similarly, the large hatchery production of chum salmon in Japan (Isakasson, 1988) may result in higher numbers of salmon occurring in the western Pacific than the eastern Pacific due to the energy costs required

to disperse across the entire North Pacific. This migratory constraint on the habitat selection of salmon could potentially produce a longitude pattern in the response of salmon to SST.

Another migratory constraint on habitat selection involves the migratory life-history stages. The degree to which salmon adhere to genetically determined shoreward and seaward migratory routes will greatly influence habitat selection irrespective of habitat quality. In the squid fishery, however, the influence of genetically determined migration routes may not be a large factor in the spatial distribution of salmon due to the mixing of numerous salmon stocks.

It is quite possible that the longitude pattern in encounter probabilities of salmon in the fishery is based on forage availability, however it is equally likely that this interpretation of encounter probabilities is confounded with migratory constraints associated with dispersal of salmon across the North Pacific. Nevertheless, the close agreement of the latitude pattern with expected productivity levels suggest that, at some level, salmon are distributed in a manner which provides the most efficient conversion of available food into growth.

Mesoscale Pattern

The most apparent mesoscale pattern in the catch rates of salmon were the clusters of salmon above the seamounts. The unusually high densities and encounter rates of salmon above the seamounts may be due to the formation of Taylor columns above the seamounts which are known to be associated with increased productivity (Boehlert and Genin, 1987; Shomura and Barkley, 1980).

The interaction of topography and impinging flow give rise to trapped columns of water which rotate counter-clockwise (anti-cyclonic) above seamounts. These trapped columns of water are known as Taylor columns. Topographic upwelling gives brings nutrient rich water up into the photic zone and is retained within the vicinity of the seamount through closed circulation of the Taylor column.

Taylor columns and eddies which spin off of the Taylor column are known to shed from the seamount and advect the nutrient rich water away from the seamount. Therefore, the persistence of a Taylor column will have a substantial affect on the ability of a seamount to influence species at higher trophic levels. It is thought that residence times, on the order of days, would only affect primary producers; a longer residence time, on the order of several weeks, may affect local growth and abundance of zooplankton, but residence times approaching months may be necessary to affect the abundance levels of nekton (Boehlert 1984; Pudyakov and Tseitlin, 1986). Actual residence times of Taylor columns are largely unknown, but the presence of seamount based fisheries for the pelagic armorhead, *Pseudopentaceros wheeleri*, on the Southern Emperor Seamount Chain (Wetherall and Yong, 1986; Sasaki, 1986) and seamount based seasonal feeding rounds for tuna, squid and marine mammals (Inoue, 1983; Yasui, 1984; Hui, 1985) suggest that residence times of Taylor columns for some seamounts can be large enough to attract and sustain populations of large nektonic species.

Data suggest that Taylor columns form over the Nintoku Complex and Suiko Seamount and their residence times appear to be large enough to influence nekton. Based on dynamic height calculations, Roden (1986) identified a Taylor column above the Suiko seamount (Fig. 10). In the summer of 1992 several drifting buoys were deployed along the Northern Emperor Seamount

Chain which overlapped the fishery to determine the presence and residence times of Taylor columns above the Northern Emperor Seamount Chain. One of the drifting buoys became trapped above the Nintoku Complex in an anticyclonic circulation pattern characteristic of a Taylor column and remained above the Nintoku Complex for over two months (Fig. 11). This suggests that Taylor columns form above the Nintoku Complex and have residence times large enough to influence species such as salmon which are typically top-level predators. If a Taylor columns were present above the Nintoku Complex and Suiko during the time in which the observer data were collected in 1990, the dense clusters of salmon above the seamounts may be due to elevated productivity associated with a Taylor column.

Summary

Although temperature is an important factor in determining salmon habitat during their oceanic life-history stage, forage patterns are also an important component of salmon habitat. I suggest that both temperature and forage can be combined to define salmon habitat during their oceanic life-history stage based on the energetic requirements for growth.

I identify two spatial patterns of forage important in the spatial dynamics of salmon captured in the squid fishery: topographic upwelling and bioaccumulation properties of Taylor columns over the Northern Emperor Seamount Chain, and changes in forage properties associated with the water masses occurring in the North Pacific. These two spatial patterns in forage appear to account for much of the variability associated with the distribution of salmon with respect to SST.

Terms	Df (Resid)	Deviance (Resid)	Test	Df (Added)	Deviance (Reduced)	C _p
SST	2574.0	1131.0				1132.6
s(Lat) + SST	2570.0	1066.0	+ s(Lat)	4.0	65.0	1070.7
s(Lon) + SST	2570.0	1062.3	2 vs. 3	0.0	3.7	1067.0
s(Lat) + s(Lon) + SST	2566.1	1001.3	+ s(Lat)	4.0	61.0	1009.0

Table 1. Analysis of deviance table from the Generalized Additive Model.

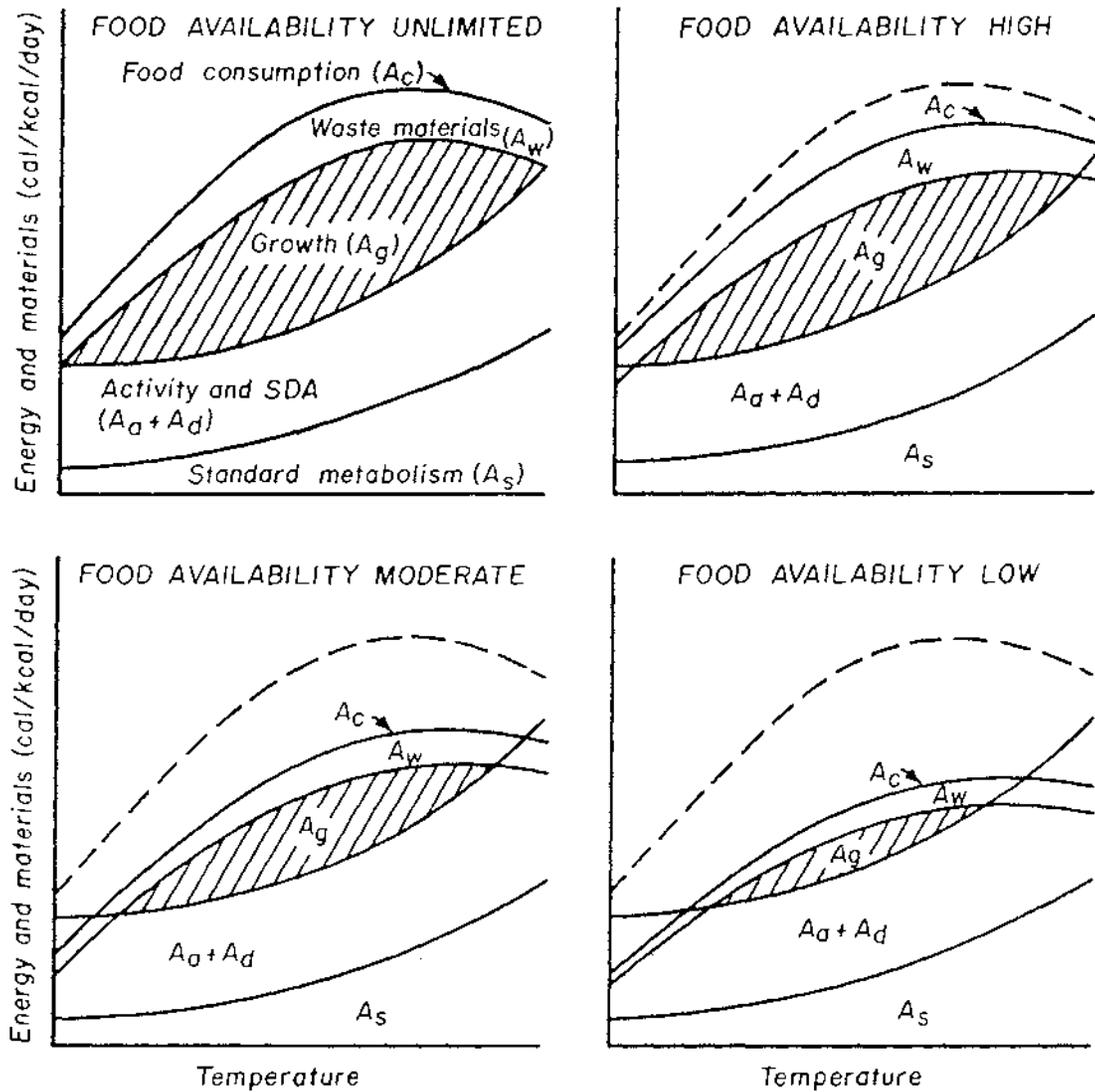


Figure 1. Theoretical effects of temperature change on the food consumption, energy budget, and scope for growth of a hypothetical poikilothermic animal having food available in different amounts (in Warren (1971:149)).

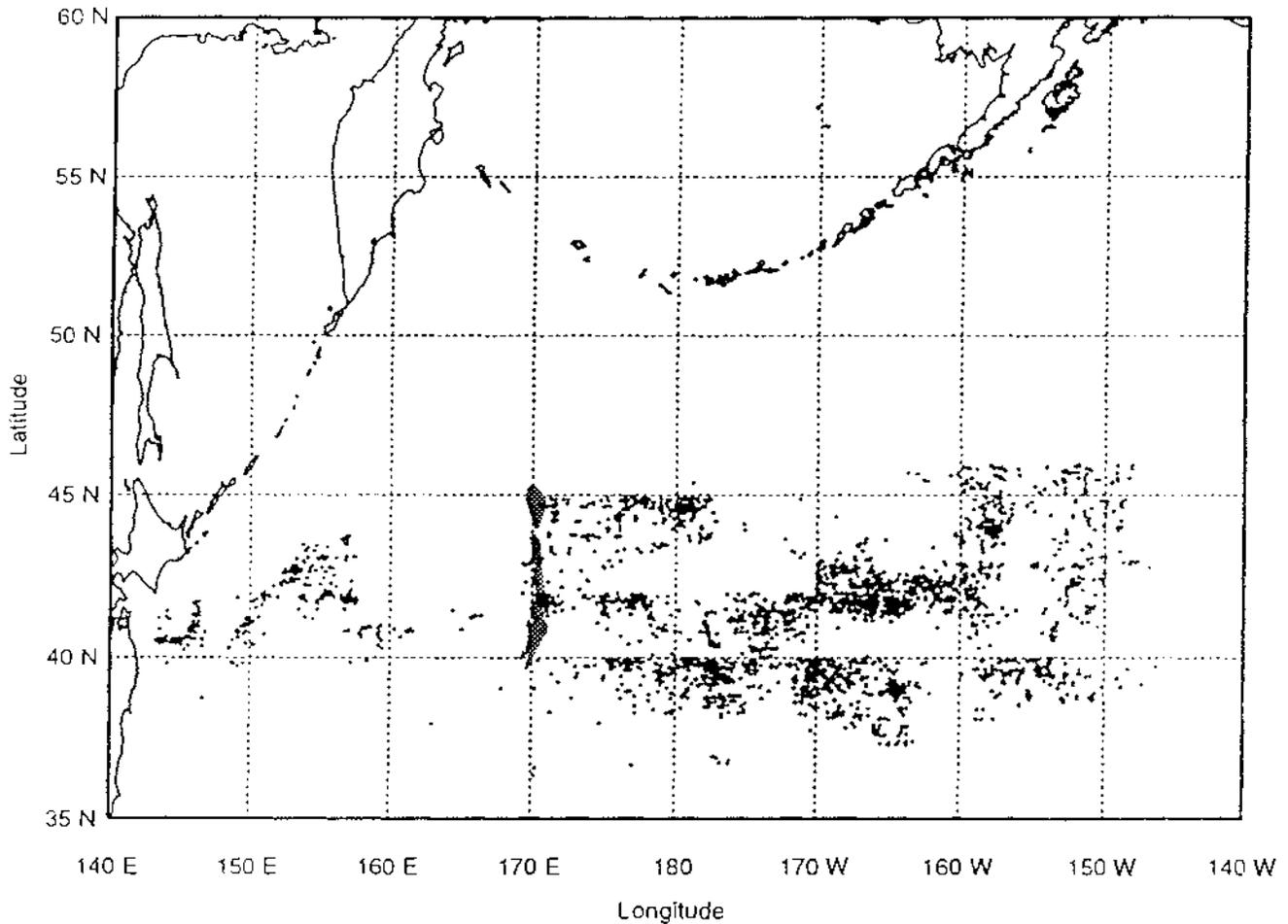


Figure 2. Sampling locations at the operational level for the months of June, July, and August. Each dot indicates the location of an observed fishing operation which was estimated by averaging the beginning and end positions of the gillnet deployment and retrieval. Polygons near 170° E longitude are seamounts belonging to the Northern Emperor Seamount Chain which occur in the area fished by the gillnet fishery.

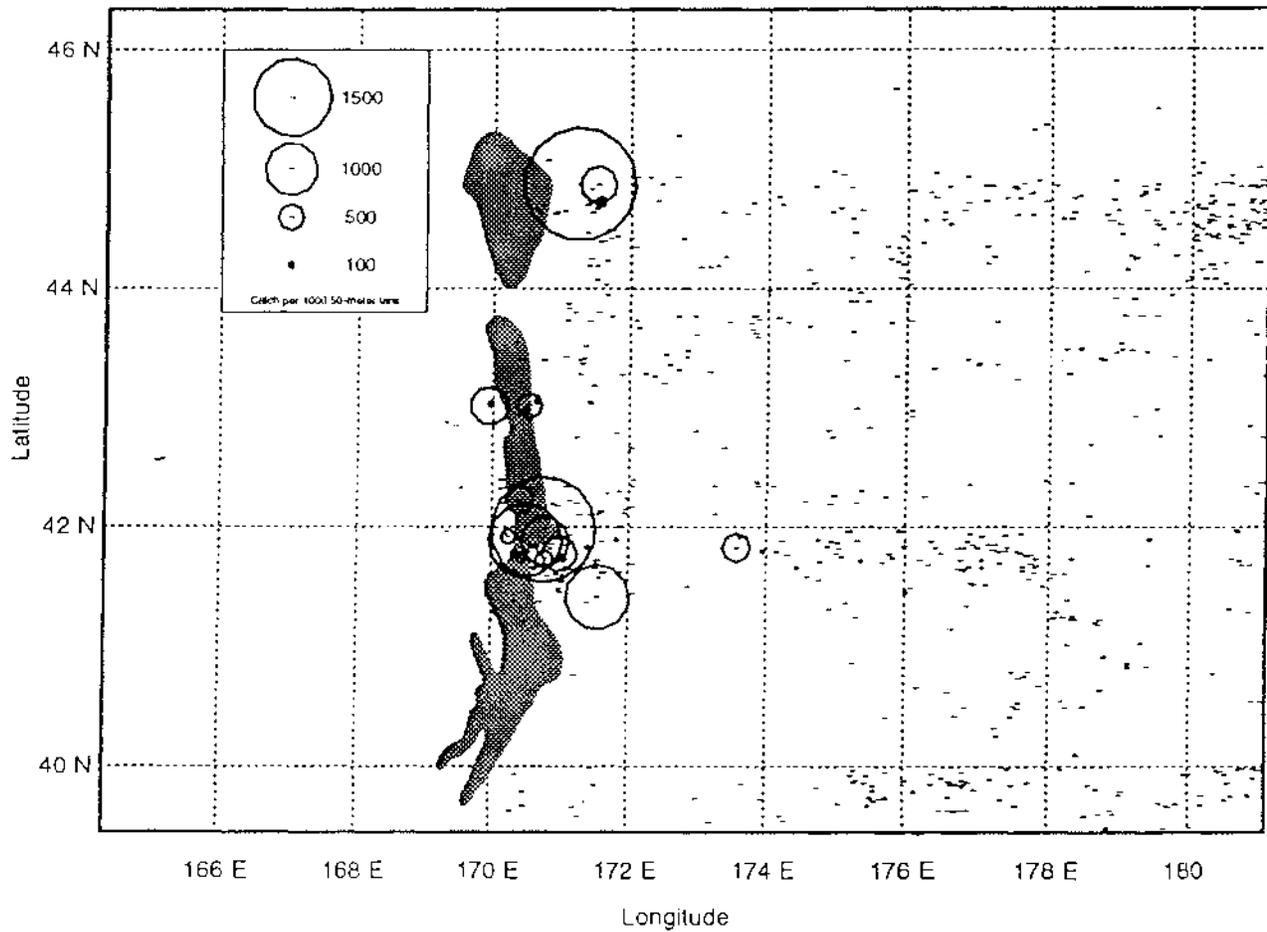


Figure 3. Salmon catch per unit of effort for fishing operations in the Japanese squid fishery over the Northern Emperor Seamount Chain. The standard unit of effort used was 1000 50-meter tans. Line segments indicate the position of observed fishing vessels and circles are scaled to the density of observed salmon catch. Polygons near 170° E are seamounts occurring in the squid fishery.

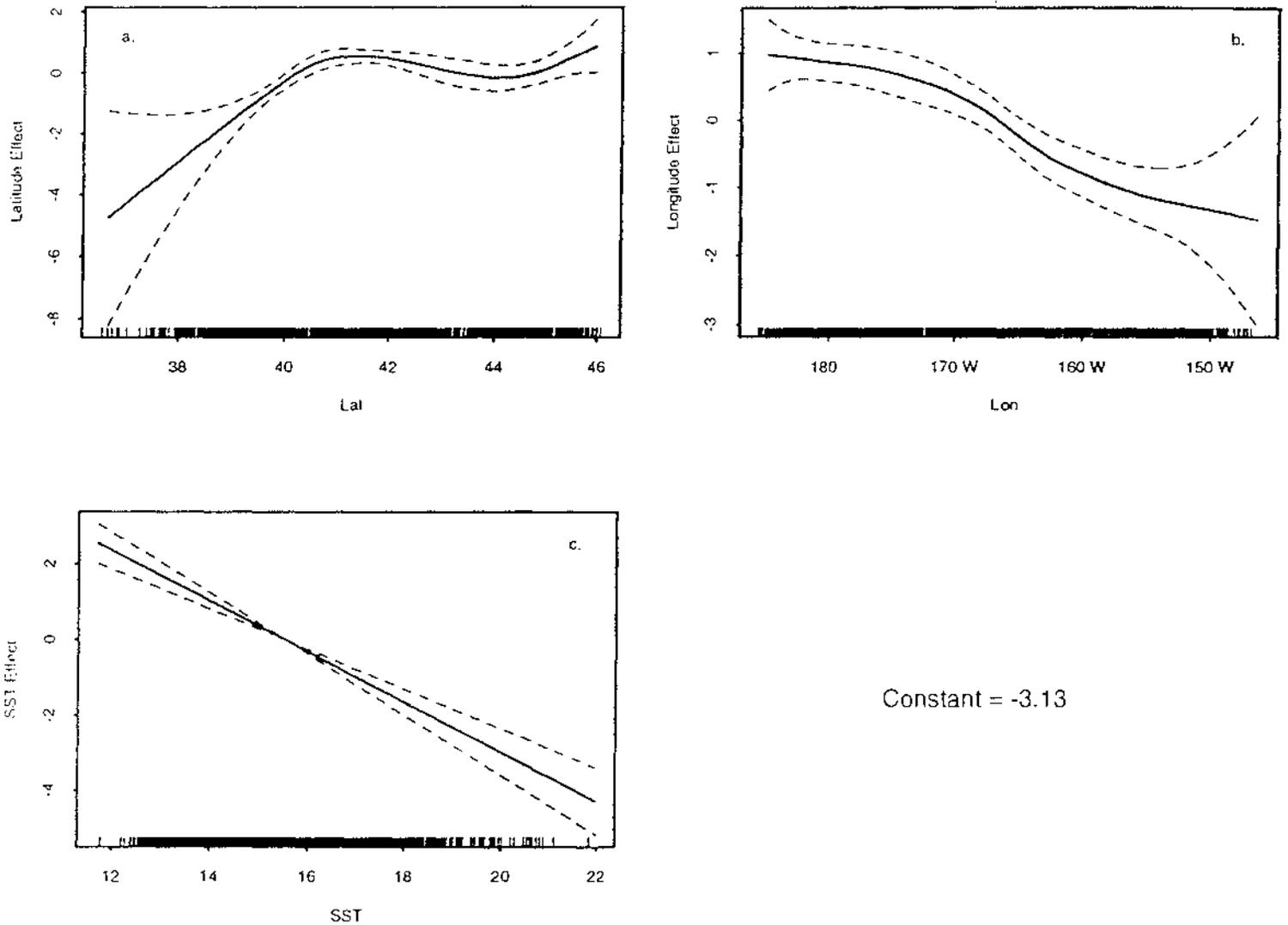


Figure 4. Generalized additive model results. Figure 5.a and 5.b are the nonlinear spatial effects and figure 5.c is the estimated sea surface temperature effect. All data are given in logit transformed probabilities. The standard error of the partial residuals (computed as outlined in Hastie (1992)) is provided and plotted as dashes above and below each of the fitted curves.

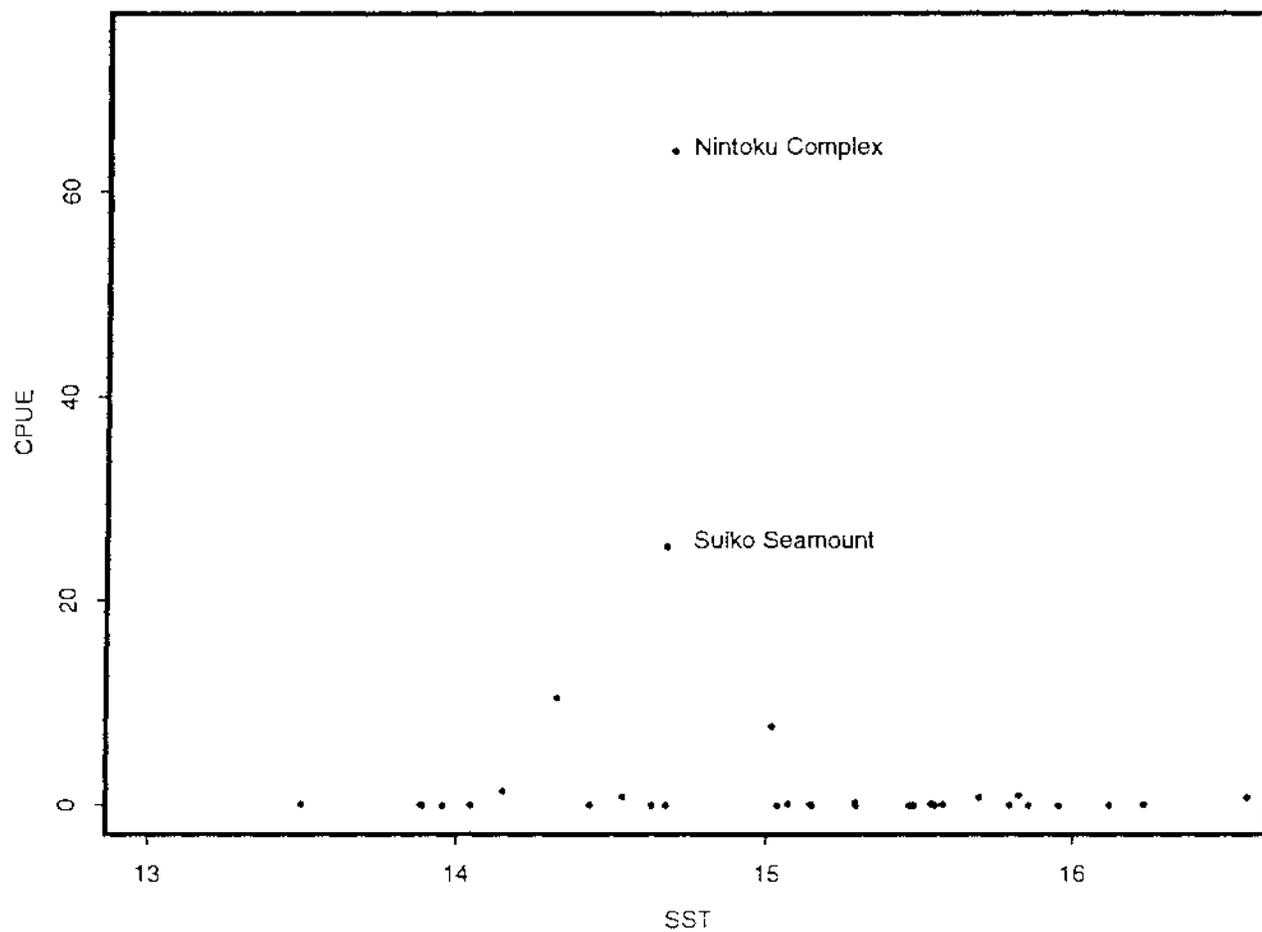


Figure 5. Salmon catch per unit of effort in the 1990 Japanese squid fishery for 2° latitude by 5° longitude strata expressed as a function of mean sea surface temperature. The standard unit of effort is 1000 50-meter tows.

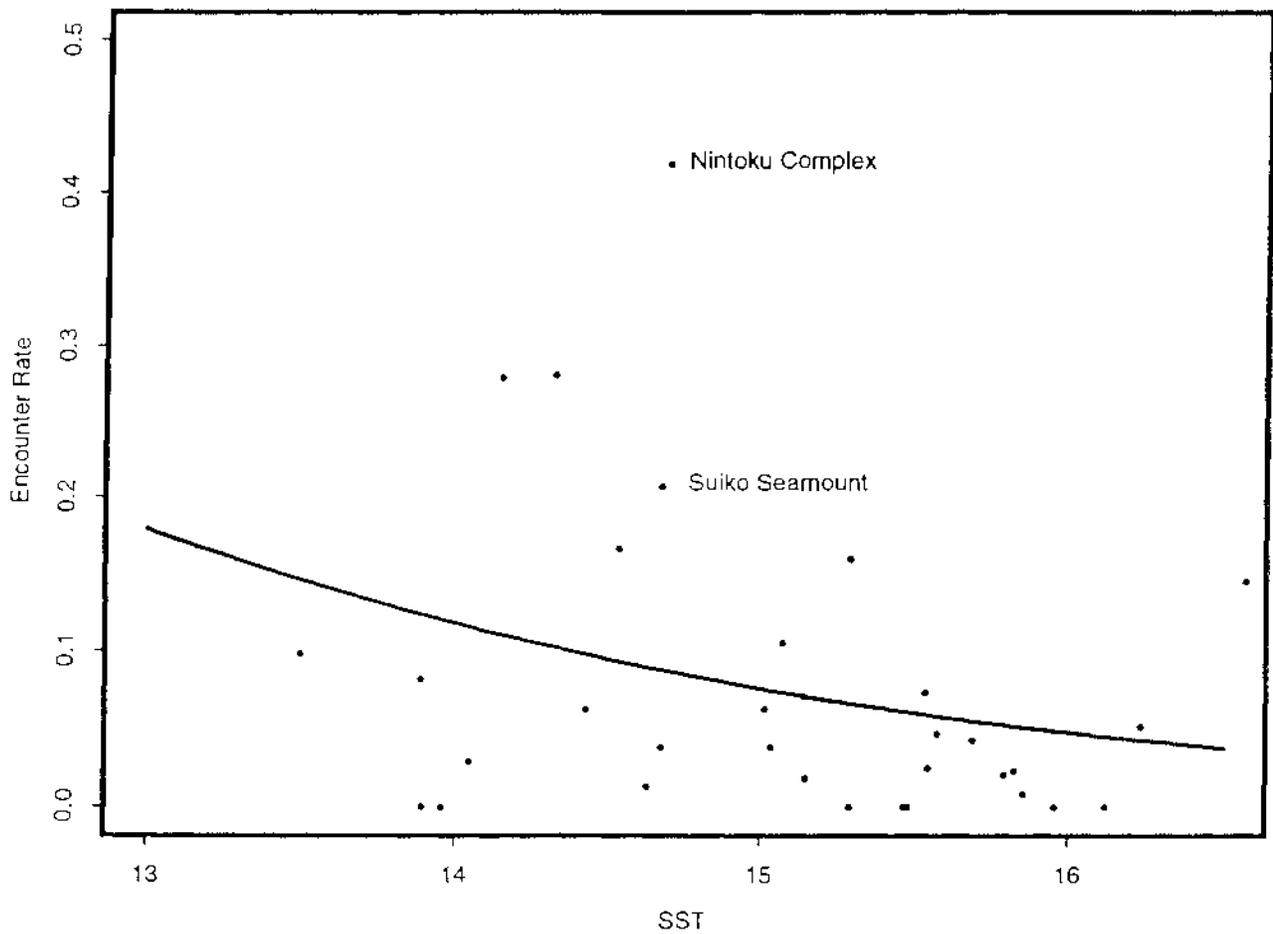
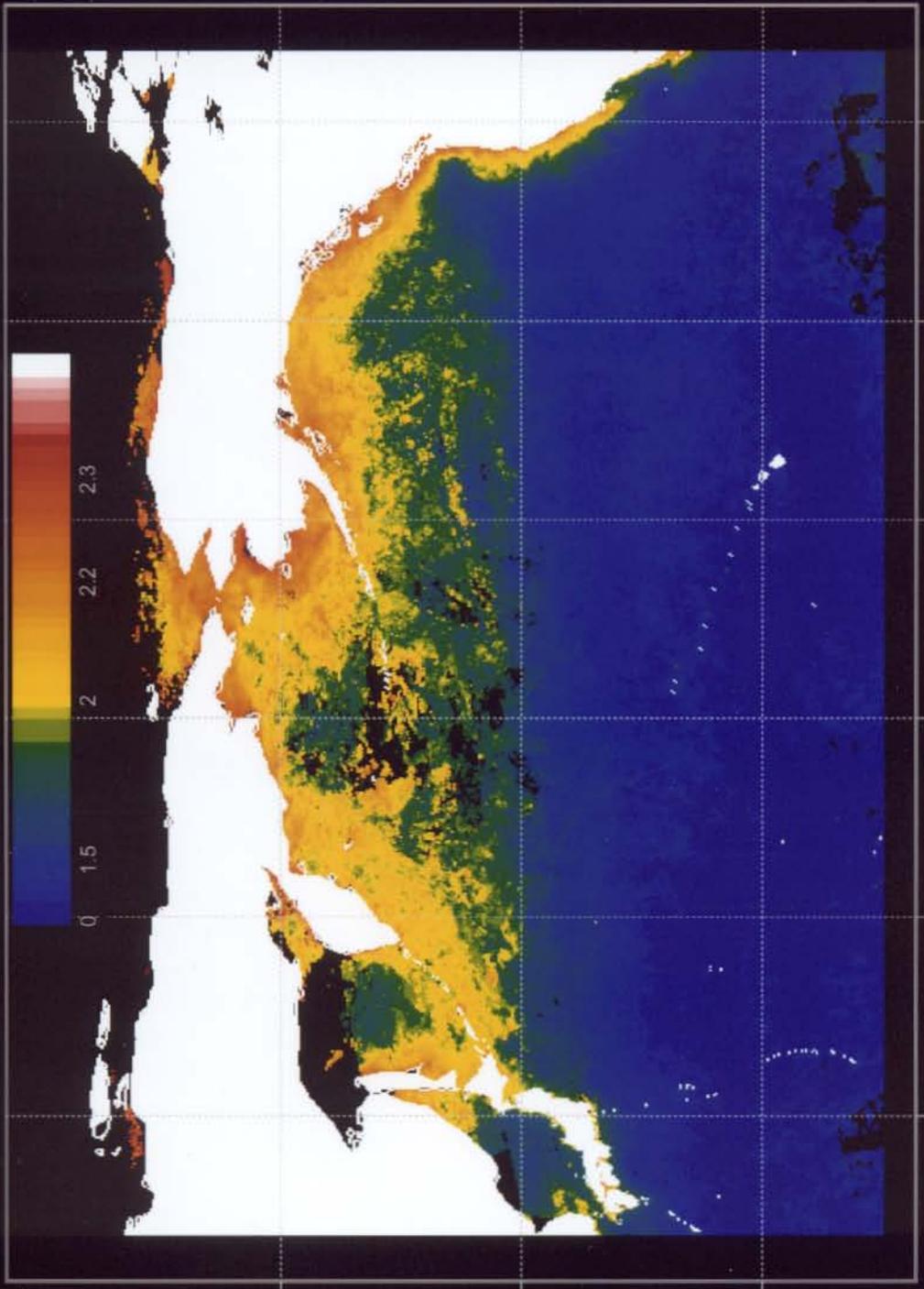


Figure 6. Fraction of 1990 Japanese fishing operations encountering salmon in 2° latitude by 5° longitude strata expressed as a function of mean sea surface temperature. The fitted line is the expected probability estimated from a logistic regression in a General Linear Model format.

Figure 7. Ocean color data from the Nimbus-7 Coastal Zone Color Scanner (CZCS). Data are mean chlorophyll (mg/m^3) for the months of July, August, and September during 1978-1986. Data were provided by the National Oceanic Data Center (NODC).



Latitude
20 N
40 N
60 N

Longitude
140 W
160 W
180
160 E
140 E
120 E

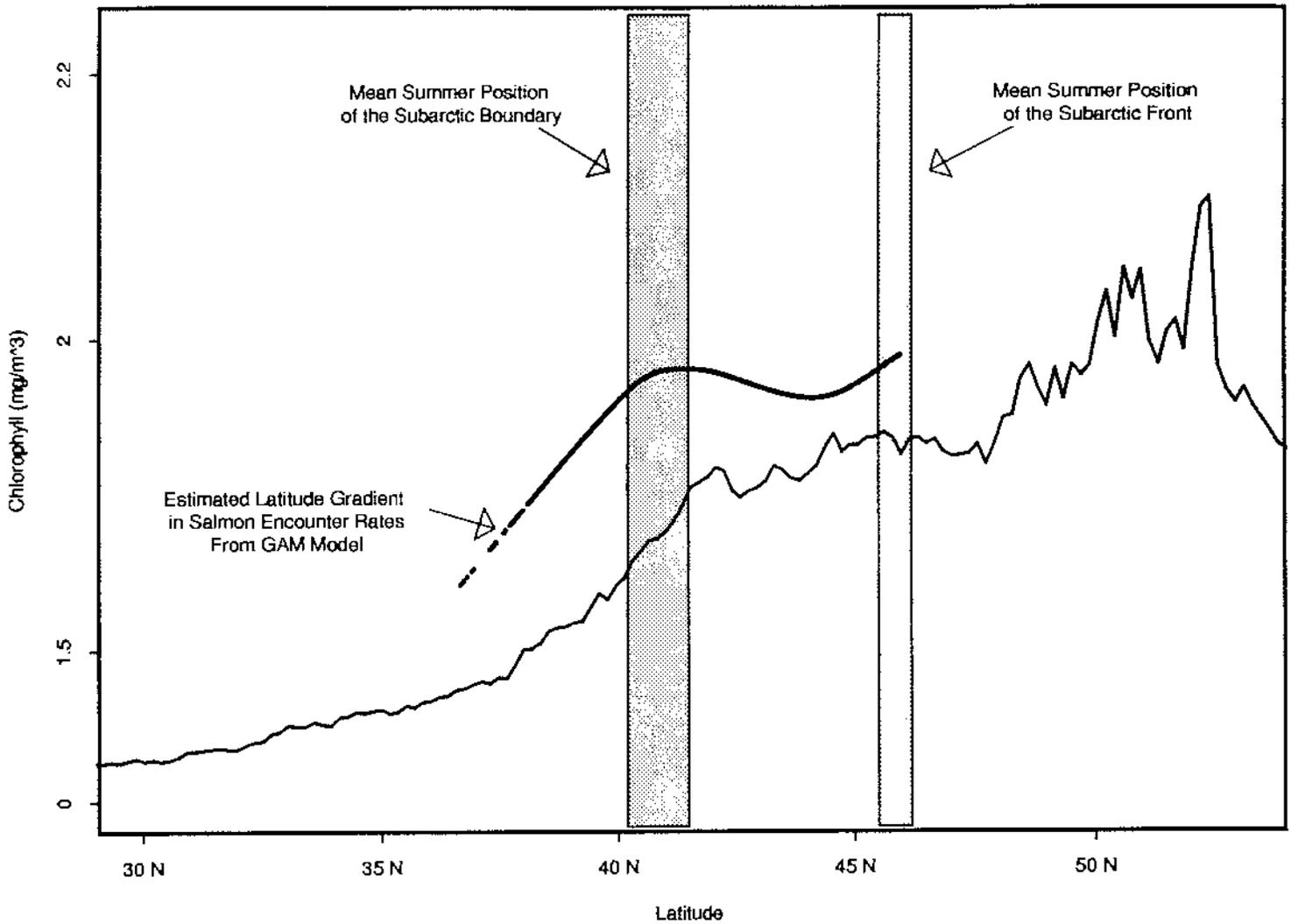


Figure 8. Mean chlorophyll levels (mg/m^3) along the 180° meridian for the month of July, August, and September during 1981-1986. Chlorophyll levels are shown in relation to the mean summer position of the Subarctic Boundary and Subarctic Front along the 180° meridian (Anma, et al., 1990) and the latitude effect on encounter rates of salmon identified by the GAM model.

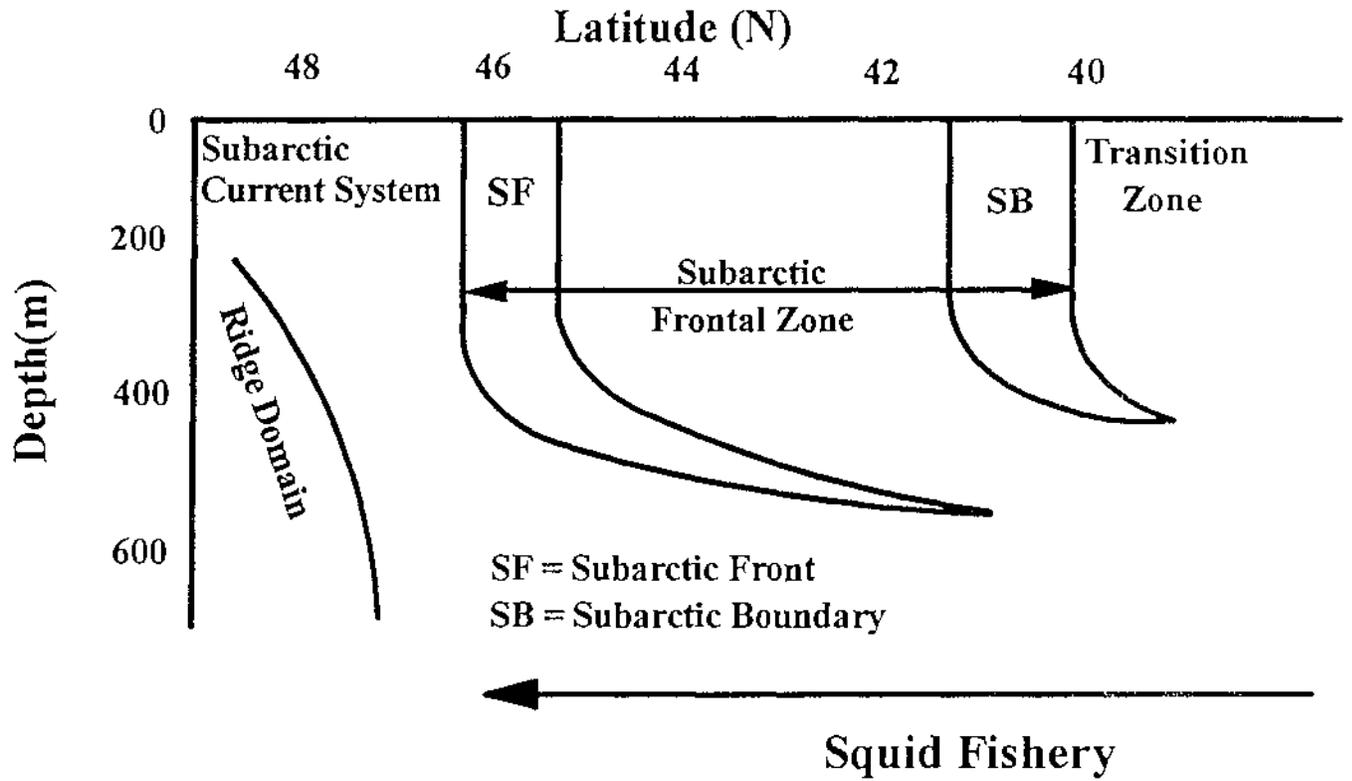


Figure 9. Mean summer positions of the different water masses occurring in the squid driftnet fishery. Mean latitude positions were estimated from a time series of meridional transects along 180° (modified from Anna, et al., 1990).

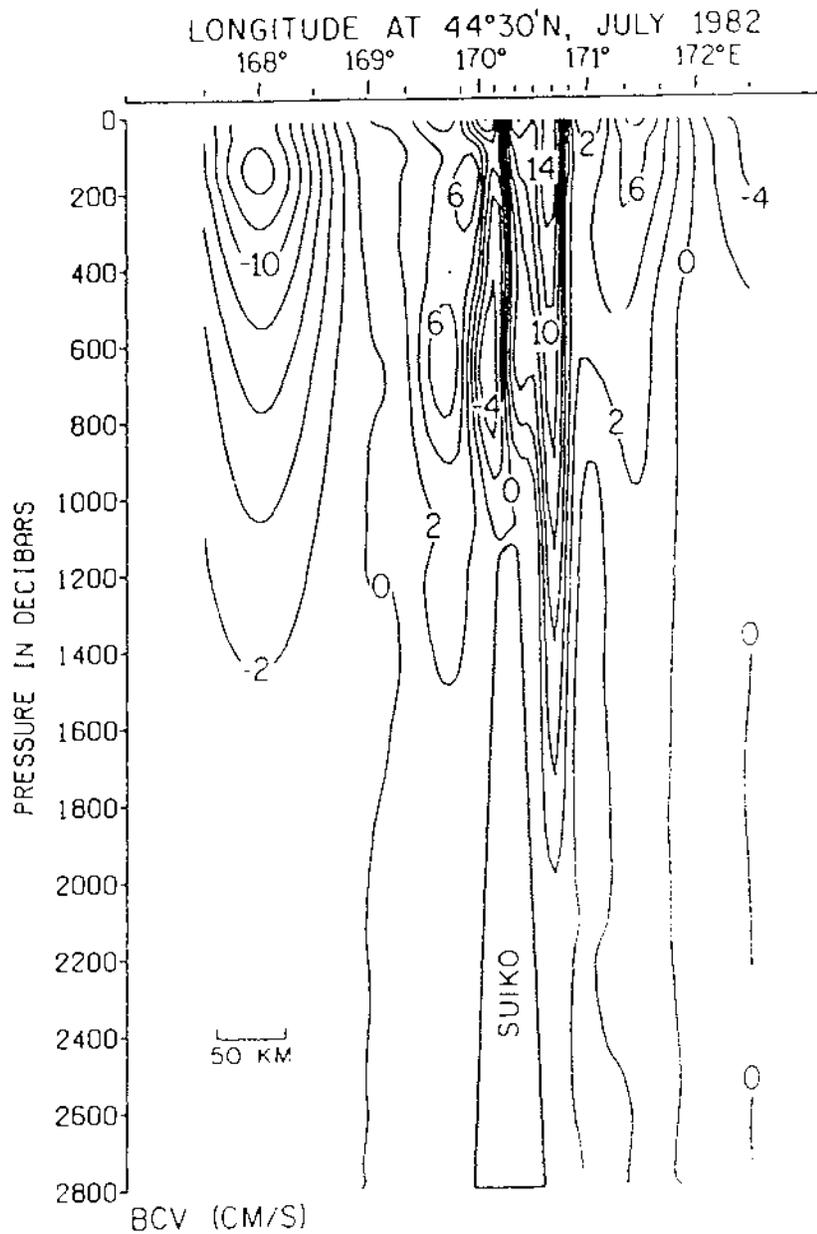


Figure 10. Meridional component of baroclinic flow relative to 28,000 dB, in the vicinity of the Suiko Seamount in July, 1982. Negative values are northward baroclinic velocities (BCV's) in cm/sec, positive values are southward baroclinic velocities (from Roden, 1986).

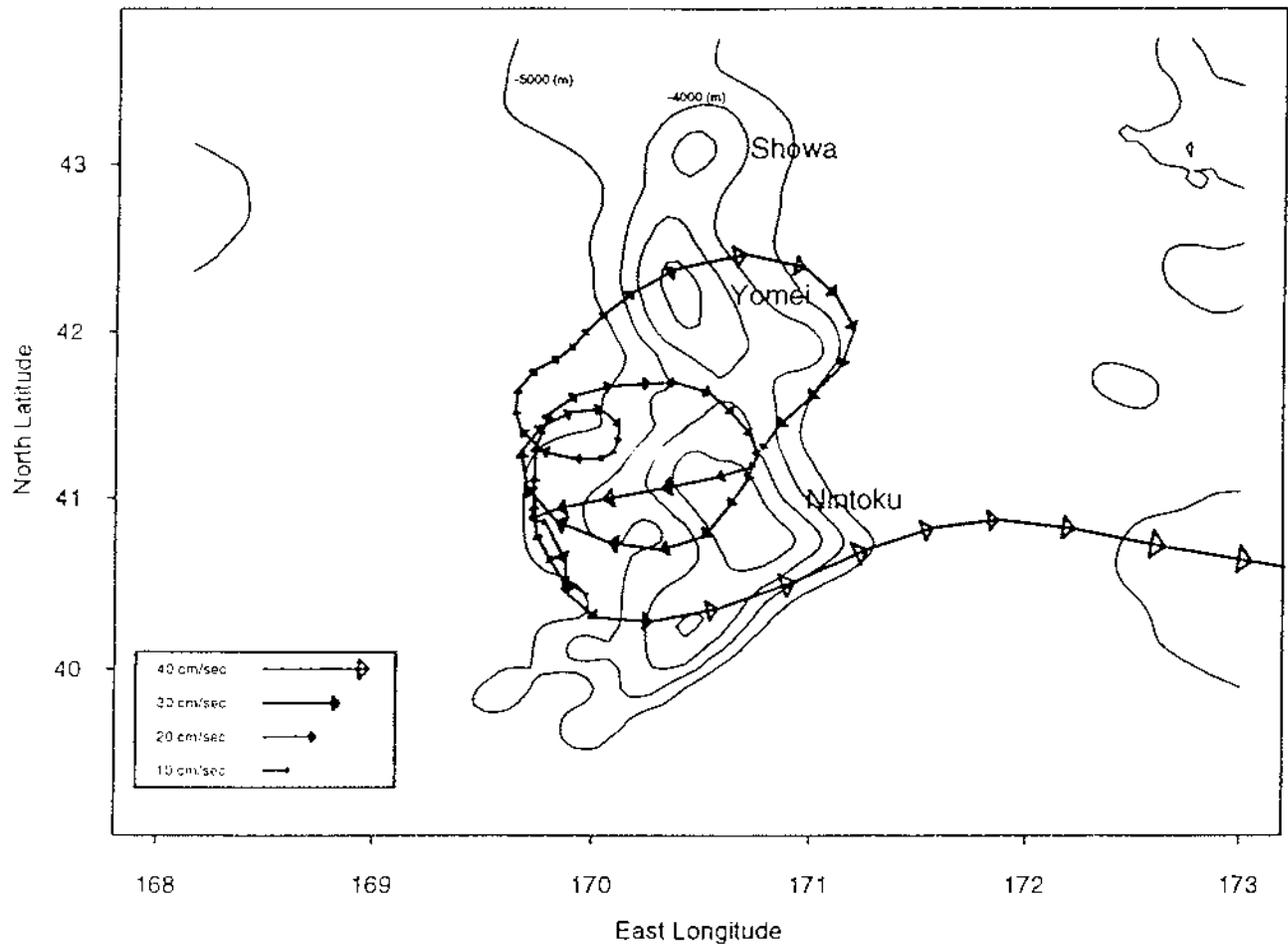


Figure 11. Anticyclonic rotation of a surface drifting buoy over the Nintoku Complex which includes the Nintoku, Showa, and Yomei Seamounts. Each arrow indicates the distance traveled by the drifting buoy in a single day.

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