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PARAMETER ESTIMATION FOR A CLASS OF MODELS DESCRIBING THE MIGRATORY TIMING OF CHINOOK SALMON (*Oncorhynchus tshawytscha*) IN THE LOWER YUKON RIVER, ALASKA

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Equation 41 and 42 were found to be incorrect. The correct derivation is as follows:

Since

$$\frac{N(t)}{N_T} = [B_0 + B_1\omega_t]\ [R_{t-1} + Y'(t)]$$

(equation 39) and

$C(t)$ is assumed to be proportional to $[N(t) - qf(t)N(t)]$

or $C(t) = \alpha\ [1 - qf(t)]N(t)$ where α is the constant of proportionality. Therefore

$$N(t) = \frac{C(t)}{\alpha\ [1-qf(t)]}$$

and $N_T = \sum_{t=1}^{n} N(t) = \frac{1}{\alpha} \sum_{t=1}^{n} \frac{C(t)}{[1-qf(t)]}$

which, upon substituting $\sum_{t=1}^{n} \frac{C(t)}{1-qf(t)}$ for C_T, results in the following correction:

Equation (41)

$$\frac{C(t)}{\sum_{t=1}^{n} \frac{c(t)}{(1-qf_t)}} = [1-\beta_2 f(t)]\ (\frac{N(t)}{N_T})$$

Equation (42)

$$\left[\frac{C(t)}{[1-\beta_2 f(t)]\ \sum_{t=1}^{n} \frac{C(t)}{[1-qf(t)]}}\right] = \frac{N(t)}{N_T} = (\beta_0+\beta_1\omega_t)[R_{t-1}/N_T + Y(t)]$$

The revision of equations 41 and 42 will result in small changes in parameter values of Tables 19 and 20. The differences in parameter values are not large enough to affect the results or conclusions of the report.

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ABSTRACT

The migratory timing of chinook salmon *(Oncorhynchus tshawytscha)* in the Yukon River delta is defined as a genetically based, environmentally mediated phenomenon. Fluctuations in abundance are often associated with environmental perturbation, removal by the commercial fleet, and the intrinsic character of the population comprising the migration. The effects of wind and commercial effort on test fishery catches are quantified by empirical time series analysis, least-squares fitting of mechanistic models, and maximum-likelihood estimation of a derived probability density function. The ability to resolve migratory timing of Yukon River chinook salmon into a mixture of two populations which are normally distributed over time and the relative contributions of wind and commercial effort to daily fluctuations in catch is evaluated. The results are interpreted in terms of the ability of each model to predict daily abundance and total abundance.

The fourteen years of available chinook migratory time densities could not consistently be resolved into a mixture of two populations. Abundance forecasts employing a two-population model were poorer than predictions from a one-population model. High daily wind speeds were consistently associated with large catches, while commercial effort depressed the test fishery catch. Daily errors of proportion in total abundance estimates employing a mechanistic model were comparable to the errors of an empirical time series model, although the empirical approach more accurately predicted total abundance. Both models provide a quantitative means of predicting test fishery catch.

A comparison of estimated annual parameter values and average April temperatures provides insight into the dynamics of the Yukon chinook migration. Cold spring temperatures delay the arrival of migrating salmon, shorten the time interval of migration, and reduce the effect of daily environmental changes on migratory behavior. Warms springs portend an early arrival, a more extended migration, a greater effect by a covariate of wind speed on migratory behavior. Trends in the effect of commercial effort suggest an increasing efficiency of the fishery.

KEY WORDS: chinook salmon, Yukon River, time series analysis, migratory timing, parameter estimation of mathematical models, wind speed and migration, temperature and migratory timing, quantitative description of test fishery catches, and catchability

INTRODUCTION

Abundance is preeminent among the biological attributes of a fish population which are of concern to fisheries biologists. The primary goal of fishery management is to control the exploitation of a population or assemblage of populations so as to obtain the maximum sustainable benefit. Maximum benefit is often synonymous with maximum sustained yield. In order to obtain an estimate of the optimum harvest of the resource, accurate assessment of total abundance is essential. Accurately forecasting the magnitude of harvestable surplus depends upon knowledge of future abundance.

The migratory behavior of adult salmonid populations precludes the use of classic closed-population estimation methods which ignore the time dimension. Management benefits little from accurate total abundance estimates once the population has migrated past the fishery. Predicted time of arrival and distribution of abundance over time are biological statistics which are also indispensable to salmon managers. Fortunately, migratory timing of salmon populations is a conservative and predictable phenomenon.

The concept of quantifying migration in terms of its time density distribution has been well developed by Mundy (1979). In summary, the time density is the relative abundance of migrating population as a function of time. The time density of the population is defined with respect to unidirectional movement through a fixed location by a single life-history stage of a population. Migratory behavior is measured in units of time, such that the probability of occurrence of any given interval of time is dependent upon the location of that interval relative to the center of the migration (mean) and upon the dispersion of migration through time (variance). When the probability assigned to each day of the migration is the proportion of the total population arriving on a given day, the mean and variance of the time density distribution can be defined by standard statistical procedures.

The advantage of the time-density approach is that migratory behavior may be characterized by its time-density distribution and associated statistics for any population. Describing migration in terms of its time-density distribution enables differences in migratory timing between populations (either interspecific or intraspecific populations) or changes in migratory timing within a population across generations to be readily quantified. Migratory time densities have been defined for populations as diverse as sockeye salmon *(Oncorhynchus nerka)* (Mundy 1979; Mundy and Mathisen 1981; Hornberger et al. 1979; Hornberger and Mathisen 1980; 1981; Brannian 1982), chinook salmon *(O. tshawytscha)* (Mundy 1982a; 1982b; Hornberger and Mathisen 1981), pink salmon *(O. gorbuscha)* (Merritt and Roberson 1981; Hornberger and Mathisen 1981), chum salmon *(O. keta)* (Hornberger and Mathisen 1981) and brown shrimp *(Penaeus aztecus)* (Babcock 1981).

As noted by Mundy (1979), expressing abundance or daily proportion of total abundance as a function of time (calendar date) is conceptually misleading. Migratory behavior is directly dependent upon the individual physiological state, which in turn is mediated by ambient physical factors. Time is merely a convenient covariant of ice break-up, wind direction and speed, water temperature, river discharge, and photoperiod (Favorite et al. 1976; Neibauer 1980; and Neibauer 1979; Ingraham et al. 1976; Dodimead et al. 1963), all of which may affect the character of the time-density distribution (Alabaster 1970; Barber 1979; Burgner 1978; Ingraham 1979; Lorz and Northcote 1966; and other; also see the review by Banks 1969; Leggett 1977). Mundy (1979) suggests that the next logical advance in modeling migratory behavior is to define, in lieu of time densities, 'temperature density' or 'photoperiod density' or a multivariate probability density which might be termed a 'migratory density'.

Intraannual variability associated with daily fluctuations in abundance is also a resultant of the stock (defined as a Mendelian population) composition of the migration. In a study of the migratory timing of Yukon River chinook salmon, Mundy (1982a) noted that variability in observed daily commercial catches limited useful forecasts to a function describing the cumulative migratory time density. Considering that the Yukon chinook salmon migration is a composite of many separate stocks distributed over thousands of river miles, the significant deviations from average values of the migratory time distribution should be expected, due to behavioral differences and intra and interseasonal changes in relative abundance of each stock.

The recognition of multiple stocks in an exploited migrating species is crucial. Ricker (1958; 1973) mathematically demonstrated that the maximum yield obtainable from a mixture of stocks of varying reproductive potential is realized only if each stock is harvested separately. Overexploitation of the most productive races can result in greatly diminished future yields. In North Pacific salmon fisheries, because of the multinational destination of groups of stocks, allocation of the resource to various user groups has international implications. Many studies have employed discriminant analysis to classify major spawning stocks of Pacific salmon, usually by scale patterns (e.g., Cook and Lord 1978; Anas and Murai 1969; Bilton and Messinger 1975; Major et al. 1975). The genetic foundation of migratory timing implies that migratory timing may serve as one objective criterion to separate stocks (Mundy 1979) and as an aid to management in optimally exploiting each stock.

Accurate knowledge of abundance and timing of commercially exploited fish populations which migrate into or through the fishery are the first priorities of management. Fortunately, when migratory behavior is conserved across generations, abundance and time are related by the characteristic time density of the population. As postulated, the apparent time density is a product of the stock composition, and environmental influences on that mixture of stocks. Knowledge of the seasonal distribution of the population enables management to forecast both daily and total catch from observed cumulative catch. Forecasts can be updated throughout the season, providing management with a dynamic method of in-season estimation.

Daily abundance is relevant to fisheries management only in the context of total abundance. The convention of describing migration in terms of proportions of total abundance over time has several advantages. The factors governing migratory behavior can more easily be discerned through the vagaries of yearly abundance since the units of relative abundance are dimensionless, confering an added flexibility to interannual and intraanual comparisons. Predictions of daily or cumulative proportion of total abundance are estimated by averaging previously observed proportions on the date of interest (Walters and Buckingham 1965; Mundy 1979; Hornberger et al. 1979), by averaging proportions across 'day or run' (Hornberger and Mathisen 1980; 1981; Brannian 1982), or by fitting functions which approximate the shape of the temporal distribution of proportions (Mundy and Mathisen 1981; Hornberger and Mathisen 1980). Studies of the Nushagak Bay salmon migrations (Hornberger et al. 1979; Hornberger and Mathisen 1980; Hornberger and Mathisen 1981) and the sockeye migration in Togiak Bay, Alaska (Brannian 1982) seem to indicate that the use of average proportions over day of run is an appropriate strategy in the pursuit of more accurate estimates of proportions.

Standard procedures used in fitting nonlinear equations to observed data minimize the sum of the square deviations from the expected value. The assumption that deviations from the expected values (residuals) are independent and normally distributed with mean zero and constant variance is usually implicit in the statistical inferences accompanying these procedures. Even in the absence of any assumptions about the joint distribution of the random variables under consideration, the method of least squares can still serve as a legitimate means of obtaining point estimates of the parameter values, although no objective judgment of the quality of the estimates can be made. The minimization of the sum of squared residuals is still the criterion which determines the values of the parameters of the equation.

The association of probabilities with proportions by Mundy (1979) was an important conceptual achievement. The presumption that proportions accurately reflect probabilities associated with daily migration enables the migratory behavior to be quantified in terms of its probability distribution. This is a subtle, yet fundamental distinction. Probability density functions are studied in relation to the 'strategy' of the population itself, availing new methods in point estimates of parameters of the function (Freund and Walpole 1980). The method of moments and the method of maximum likelihood are examples. The qualifying conditions in such approaches are that the function sums to unity and all probability values are greater than or equal to zero.

The objective of the present study is to quantify the effects of environmental factors, commercial fishery removal, and differential timing of upstream and downstream stocks on the relative abundance of chinook salmon in the lower Yukon River as estimated by test fishery catches. Several methods are proposed as means to achieve this objective. Data from the lower Yukon River test fishery are analyzed using the statistical techniques of linear time series analysis (Box and Jenkins 1976), and least-squares fitting of nonlinear functions is employed. The iterative technique of estimating the parameters of a mixture of normal populations by a maximum likelihood function (Hasselblad 1966) is regularly utilized in size frequency analysis (e.g., MacDonald and Pitcher 1979; McNew and Summerfelt 1978). This technique is evaluated as a means to separate the assumed populations on the basis of migratory timing. Results of the fitting procedures are compared in terms of the ability of each function to accurately predict the daily proportion of the total catch, and the total catch itself. Improvement in the predictive ability of each function over the normal distribution function, defined by a single mean and variance, or in comparison to an empirically-derived stochastic model serves as a criterion for the applicability of each model.

STUDY AREA AND DATA

Only a synopsis of the lower Yukon River commercial and test fishery methods will be presented here. More detailed descriptions are available in Mundy (1982a); in

Yukon Area Management Reports, and in Lower Yukon River Test Fishing Reports. The test fishery began in 1963 near the seaward boundary of the south mouth of the Yukon River delta at the location known as Flat Island (Figure 1, site A). Until 1968, test-net sites were chosen by Alaska Department of Fish and Game (ADF&G) personnel. In 1968 the practice of renting set-net sites from local residents was initiated and the success of the test fishery effort increased (the 1963-to-1967 8 1/2-inch mesh yearly average chinook salmon catch was 446 chinook, compared to a 1968-to-1978 yearly average of 708). For logistic reasons, the test fishery was relocated to 1979 approximately 20 miles upriver at Big Eddy (Figure 1, site B), and another test fishery operation, Middle Mouth, began. The Middle Mouth site is located near the confluence of the middle and north-mouth sloughs (Figure 1, site C).

For 20 years the test fishery has assisted management by providing a measure of relative daily abundance of chinook salmon, summer and fall chum salmon, and coho salmon. Recently, Brady (unpublished draft) demonstrated that, as management had suspected, a high correlation exists between test fishery and commercial catches, adjusted by one day to account for average travel time. The relation between Big Eddy catches and commercial catches was the strongest, with Middle Mouth being only slightly more variable. The use of test fishery catch data to study the migratory timing of chinook salmon minimizes problems of estimation relating to censorship and truncation which are inherent in commercial catch data.

Methods of data collection have been consistent for the last 14 years (1968-1981). Two 25-fathom gill nets of 8 1/2-inch mesh and one 25 fathom 5 1/2-inch mesh gill net were fished in locations judged to be productive and representative of the major river channels near the test fishery. Set nets were chosen to standardize the effort and avoid dependence on the ability of personnel. Except when circumstances prevented, each net fished 24 hours a day and was checked twice daily.

In the present study, observed daily catch is defined as the total recorded catch at the 3 net sites for the 24 hours fished. Catches were adjusted upward proportionally on days with less than 24 hours of fishing. In 1979, Middle Mouth test fishing did not begin until 18 June, which was half way through the chinook migration. Therefore, the 1979 Middle Mouth data are not included in this analysis. Calendar dates are coded relative to 11 June (coded day 1).

Weather observations recorded in Nome and Emmonak were obtained from the National Weather Service. When available, the Emmonak wind speed was used. In 1979 a lapse in weather recording required that Nome wind speeds be substituted from 2 July to the end of the migration. The rate of travel of chinook salmon in the Yukon River has been estimated at between 25 and 30 river-miles a day (Trasky 1973). If upriver migration is considered to commence immediately offshore of the Yukon River delta south mouth (Figure 1), fish would arrive at the Big Eddy test fishery approximately one day later. Chinook salmon beginning at the middle-mouth exit would also arrive at the Middle Mouth test fishery approximately one day later. Observed average wind speed is defined here as the arithmetic average of all observations on the given day.

Standard statistical techniques and tests of significance used throughout this study are described in Sokal and Rohlf (1969). The SPSS statistical package (Nie et al. 1975) was employed for standard Pearson's correlations, t-tests, some of the linear regression analyses, averages, and confidence limits. Preliminary

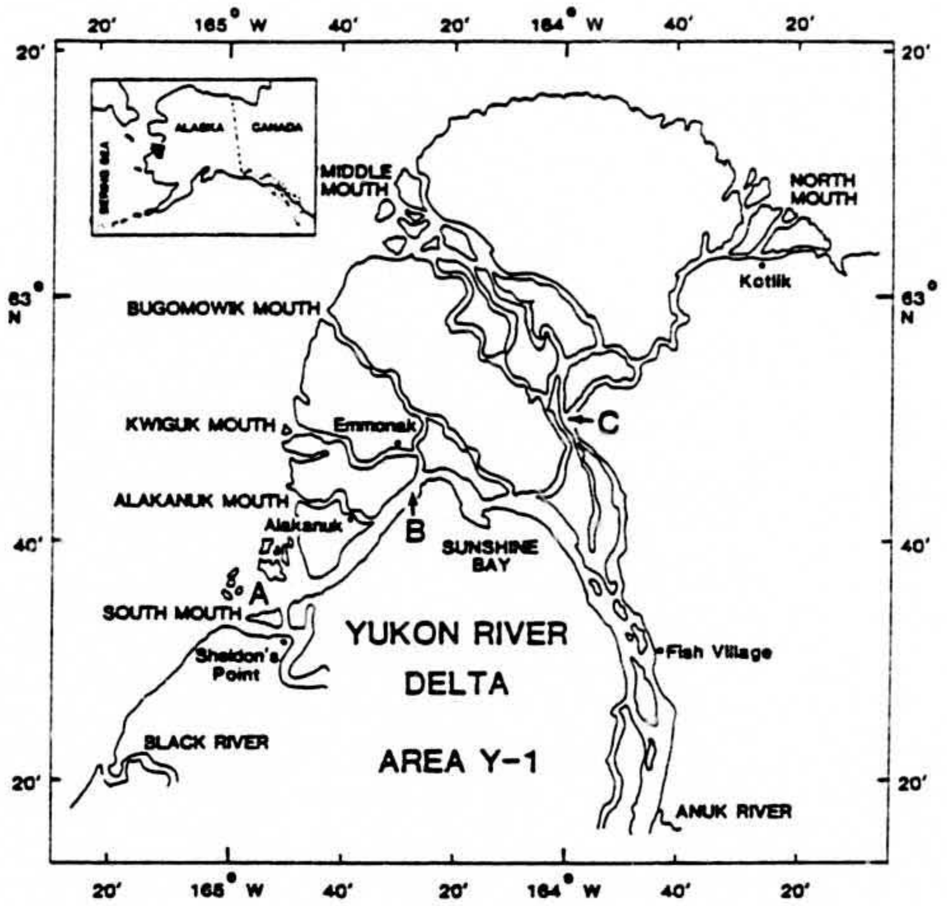

Figure 1. Detail of the Yukon River delta and fisheries statistical area Y-1. Site A is the location of the Flat Island test fishery, Site B the Big Eddy test fishery, and Site C the Middle Mouth test fishery.

time series analysis was performed with the BOXJ computer program package (University Computer Center, University of Massachusetts at Amherst) and the independence of residuals was also tested using the same package.

INTRODUCTION TO TIME SERIES METHODS

The use of conventional stock and recruitment models is common in the attempts of fisheries managers to predict the annual abundance of distinguishable stocks of Pacific salmon migrating through the fishery. The estimated abundance of the resource is assumed to be a function of past abundance, measured one or more years prior to the adult migration. Expectations of abundance and harvest guidelines are set prior to the fishing season. Intraseasonal adjustment of the estimation of total abundance is frequently an intuitive, subjective process, the accuracy of which depends on the expertise of the local resource manager. Developing an ability to estimate the magnitude of the migration involves comparing the magnitude of commercial or test catches by date of catch to the historical performance of the migration, environmental factors believed to affect migratory behavior, and numerous intangibles witnessed by the managerial staff over each migration.

Techniques to anticipate daily or total abundance by exploiting the conservative nature of migratory behavior have been developed for several populations of Pacific salmon (Walters and Buckingham 1975; Mundy 1979; Hornberger and Mathisen 1981; Brannian 1982) and populations of brown shrimp (Babcock 1981). A common method involves averaging cumulative proportions recorded on each calendar date of the migration for every year with reliable historical observations. Total abundance is estimated by the quotient of total catch to date over expected proportion on the given date. Variations on this strategy include defining the day of migration relative to the day a set cumulative proportion of total catch is realized (Brannian 1982; Hornberger and Mathisen 1981), or fitting a deterministic equation, usually the inverted exponential function, to the distribution (Mundy and Mathisen 1981; Matylewich 1982; see the Methods Section for a discussion of other appropriate deterministic functions).

Application of a migratory time density function to estimate the total run size has been successful in several salmon fisheries (Mundy and Mathisen 1981, for Bristol Bay sockeye salmon; Brannian 1982, for Togiak Bay salmon; Mundy 1982a, for Yukon River chinook salmon; and Hornberger and Mathisen 1981, for four species of Nushagak Bay salmon). Because deviations from expected catch are often associated with the physical environment of the salmon and, since physical factors are generally not independent, the accuracy of estimates made during the season can be enhanced by incorporating measures of the effect of environmental variables on migratory behavior, and the dependence of sequential daily observations into the model. The distribution of adult salmon catches over equally spaced intervals of time (days) is suited to time series analysis. The time series approach proposed by Box and Jenkins (1976) appears particularly appropriate.

Several studies have employed Box-Jenkins methods to forecast future abundance of commercially exploited marine organisms. Univariate models have been employed to forecast monthly rock lobster catch per unit effort (Saila et al. 1981), and yearly

Atlantic menhaden catch (Jensen 1976). Time series analyses which have incorporated univariate and multivariate transfer functions have been applied to the skipjack tuna fishery (Mendelssohn 1981) and lobster fishery (Boudreault et al. 1977) respectively.

Excellent summaries of the procedures involved in the Box-Jenkins method of time series analysis may be found in McMichael and Hunter (1972), Poole (1976b), and Mendelssohn (1981). Assuming that the series of observations is stationary, or can be made stationary by differencing or employing a suitable transformation, a model is proposed which describes an observation as a function of past observations (autoregressive terms) or of past errors of estimate (moving average terms). The exact terms in the model are tentatively identified by studying the autocorrelation and the partial autocorrelation function exhibited by the data. The parameters of the postulated model are estimated and the residuals examined to evaluate the adequacy to the model. The three-step process of model identification, model estimation, and diagnostic checking becomes an iterative routine designed to estimate the most parsimonious model.

The notation used in the present study is consistent with that of Box and Jenkins (1976). Autoregressive models of order n (AR_n), moving average models of order m (MA_m), and mixed autoregressive moving average models of order nm ($ARMA_{nm}$) are discussed. The symbol ϕ_n is reserved for the coefficient associated with the observation lagged n time intervals prior to the present observation. The symbol Θ_n is the parameter associated with the error of estimation n time intervals prior to the present observation. The residual error of the final model, a_t, are assumed to be independent and identically distributed with mean zero and variance σ^2.

DEVELOPMENT OF THE TIME SERIES MODEL

Catch data used in the study were obtained from the Big Eddy and Flat Island test fisheries. Procedures employed in the test fisheries have been outlined previously. The bias introduced by yearly differences in total abundance is minimized by transforming daily catch into the daily proportion of total annual catch. Daily proportions of total abundance, average daily wind speed recorded by the National Weather Service for Nome, and the proportion of the calendar day open to commercial fishing was analyzed for the years 1968 through 1981.

Mean dates of migration and variances were calculated by standard methods (see Mundy 1982; and others) and correlated with average monthly air temperatures for April and May, as recorded by the National Weather Service for Nome (Table 1). The high negative correlation between average April air temperature and mean date of migration (r = -.913) suggests that the ability of predictive schemes to estimate the lower Yukon River catch distribution by calendar date can be enhanced by adjusting the calendar dates of migration using average April air temperature. In the present study, the relative day of migration D_r, which corresponds to a calendar day of migration D_c, is defined as the difference between the estimated mean day of migration D_m, and coded day corresponding to each calendar day (1 = 1 June) (i.e., $D_r = D_m - D_c$). The estimated mean day of migration is assumed to be a linear function of April temperature (see Table 1):

$$D_m = 38.49 - 1.025 \text{ (April air temperature, °F)} \qquad (1)$$

Table 1. Relationship of mean day of migration for the years 1968 through 1981, and average April and May air temperatures.

Year	Mean Coded Day[1]	Variance	April Air Temperature (°F)	May Air Temperature (°F)	Predicted Mean Day
1968	17.53	51.56	14.4	29.1	23.74
1969	14.48	54.48	21.8	42.8	16.15
1970	21.15	49.81	15.1	36.5	23.02
1971	29.21	64.65	12.9	29.7	25.27
1972	26.36	86.56	11.9	35.4	26.30
1973	20.57	78.84	18.3	35.2	19.74
1974	13.57	64.84	20.9	38.2	17.07
1975	27.37	40.25	13.4	33.9	24.76
1976	30.37	25.03	9.7	33.1	28.55
1977	28.20	33.94	9.4	32.9	28.86
1978	12.61	95.15	24.9	42.1	12.96
1979	13.91	110.90	25.5	41.8	12.36
1980	14.88	62.48	23.8	43.2	14.10
1981	16.26	103.56	24.3	42.7	13.57

The Pearson Correlation coefficients are:

Mean day and April temperature: $r = -.9127$
Mean day and May temperature: $r = -.7454$
Mean day and Variance of Migration: $r = -.5709$

The regression of mean day on April air temperature yields the following equation:

Mean day = 38.49 - 1.025 (Mean April air temperatures, °F)

with an R^2 value of .833 and F-value of 59.84 ($P < .001$).

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[1] Number of days after 31 May.

Therefore, the pronounced shift of migratory timing due to previous environmental conditions can be compensated for by defining the day of migration with reference to a relevant measure of the earlier environment. The distribution of proportions of lower Yukon River test fishery catch averaged over the relative days for years 1968 to 1981 is presented in Figure 2.

The derivation of a predictive model which incorporates the conservative nature of the time distribution over generations (Mundy 1979), the dependent distribution of sequential daily proportions, and the effect of environmental and commercial factors on the test fishery catch is attempted. The model consists of two components: an average of observed proportions of total catch across the relative days of migration, and a stochastic component describing the daily deviations from the average values (e_t) as a function of average daily wind speed, surrounding commercial effort, the errors observed on prior days (e_{t-i}), and the difference between the estimated proportion and observed proportion of prior days (a_{t-i}). Mathematically the model is:

$$P = \frac{1}{n_T} \sum_{i=1}^{n_T} P_{D_r(i)} + e_i \qquad (2)$$

where the observed proportion P, observed on relative day D_r is the average of the proportions $P_{D_r(i)}$ over the relative days $D_r(i)$ $(i = 1 \text{ to } n_T; n_T$ being the number of years with recorded catch on day $D_r)$ plus an error term (e_i). The series of errors arranged sequentially by day of migration and by year $(e_{1,1968}, e_{2,1968}, \ldots, e_{k,1968}, e_{1,1969}, \ldots, e_{k,1981})$ where $e_{i,yr}$ is the error associated with day i of the migration $(i = 1 \text{ to } k)$ and year yr $(yr = 1968 \text{ to } 1981)$, forms a succession of data amenable to time series analysis. The parametric time series models proposed by Box and Jenkins (1976) are used to derive a predictive function of the e_t.

The change in location of test fishery sites in 1979 requires a separate analysis of the daily errors for the years prior to the 1979 relocation (Flat Island catch, 1968 - 1978) and subsequent to the move (Big Eddy catch, 1979 - 1981). The closer proximity of Flat Island to the seaward boundary of the Yukon River (approximately 1 day of travel time for chinook salmon (Trasky 1973), the more intense commercial fishery surrounding the Big Eddy test net sites, and differences in the physical regime of the Yukon River at each test fishery site imply that the relationship of test fishery catch to wind, commercial effort, and prior catches may be of a different character for each location.

Visual inspection of the distribution of errors about their mean of 0 revealed heteroscedasticity of the errors near the annual mean day of the migrations compared to the errors near the beginning or end of the migrations. The square root transformation (± square root of the absolute value of the error, the sign of the transformed error being identical to the sign of the original error) normalized the variances, as demonstrated by the nonsignificance of the F-values of the residuals of the quartiles. Due to the nature of the distribution in time and space of commercial effort, and the desire to avoid complicated transformations of effort data to correspond to its effect on the test fishery catch, a value of one was assigned to days of 0.75 or 1.00 days of commercial fishing, and a value of 0

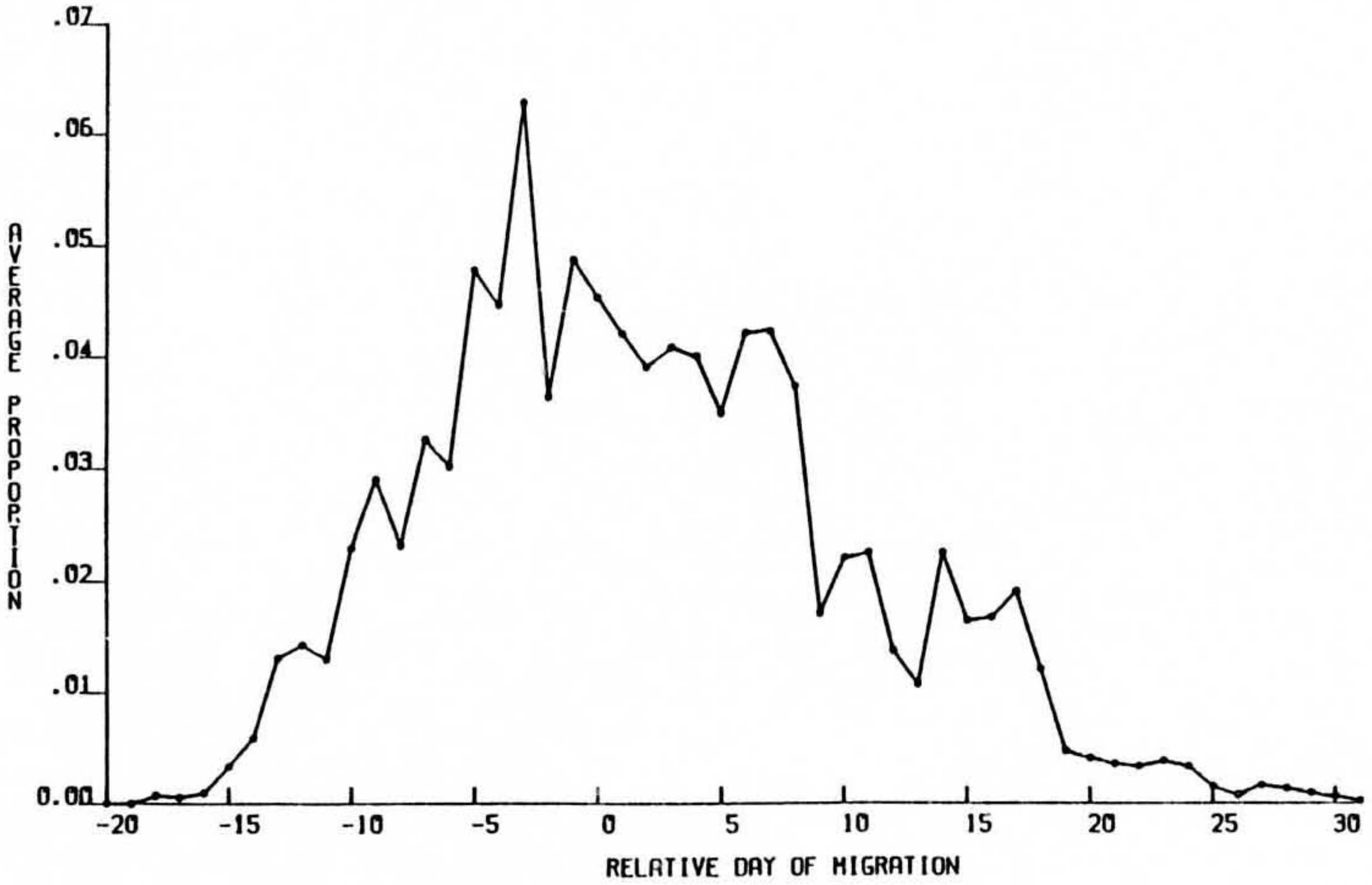

Figure 2. Average daily proportion of total annual catch in 1968 to 1981 test fishery catches. Day 0 is the mean day estimated as a linear function of average April air temperature in Nome.

assigned to days of 0 or 0.25 days of fishing. Although this transformation of commercial effort produced little change in the residual sum of squares or estimated parameter values, it did result in a slightly better fit of predicted to observed values and was retained in the following models.

The autocorrelations (ACF) and partial autocorrelations (PACF) of lag 1 to lag 20 days are presented graphically in Figure 3 for the years of the Flat Island test fishery catch. The large peak at lag 1 in both ACF and PACF and the absence of large peaks at other lags implies that the errors can be described as either an autoregressive process of lag 1 day (AR_1 model) or a moving average process of lag 1 day (MA_1 model). Fitting the MA_1 and AR_1 processes to the observed ε_i results in slightly lower residual sum of squares for the AR_1 model (Table 2). Therefore the AR_1 model is considered to be the more appropriate interim model for the errors. Inclusion of secondary peaks observed in the ACF and PACF (for example the positive peak at lag 3 days and negative peak at lag 13 days) into the time series models is deferred until incorporation of the average wind speed and commercial effort transfer function into the model has been accomplished.

Correlograms of the ACF and PACF of the observed daily commercial effort and the average daily wind speed (Figures 4 and 5) demonstrate the strong dependence of commercial effort on past values of effort and the presence of an autoregressive process of lag 1 in the distribution of daily wind speed. If the errors of the test fishery catch are strongly correlated with either variable, large peaks in the residual ACF and PACF of the AR_1 model (Figure 6) may be related to the statistical dependence of environmental factors on past measurements of these factors. The residuals of the fitted AR_1 model are compared to the average daily wind speed and commercial effort of 5 days after the date of recorded catch back to 14 days before the catch to discern the relationship between the three variables.

A very significant ($p<.001$) correlation was found between wind speed and commercial effort, and the errors on the day of recorded test fishery catch (Figures 7 and Table 2). Letting r_t ($t = 1,2,\ldots N$; N being the total number of observed deviations from the AR_1 model) represent the residuals from the AR model; the transfer function:

$$r_t = -.0052628 + .001197(w_t) - .016341(f_t) \tag{3}$$

is the fitted regression equation to the observed deviations (Table 2).

After including the effects of wind and commercial effort in the autoregressive model, the peaks in ACF and PACF at a 3 day lag were found to be significant and a lag-3 term was added to the model. The final procedure involves making small adjustments in the values of the parameters to minimize the sum of squared errors (a_t). Results are presented in Table 3. The $AR_{1,3}$ and alternate $ARMA_{1,3}$ models are considered. The parsimonious and minimum variance model which best describes the errors from the average daily proportion, ε_t, is the $ARMA_{1,3}$ model:

$$\varepsilon_t = -.0796 + .00936w_t - .0671f_t + .294e_{t-1} + .146a_{t-3} + a_t \tag{4}$$

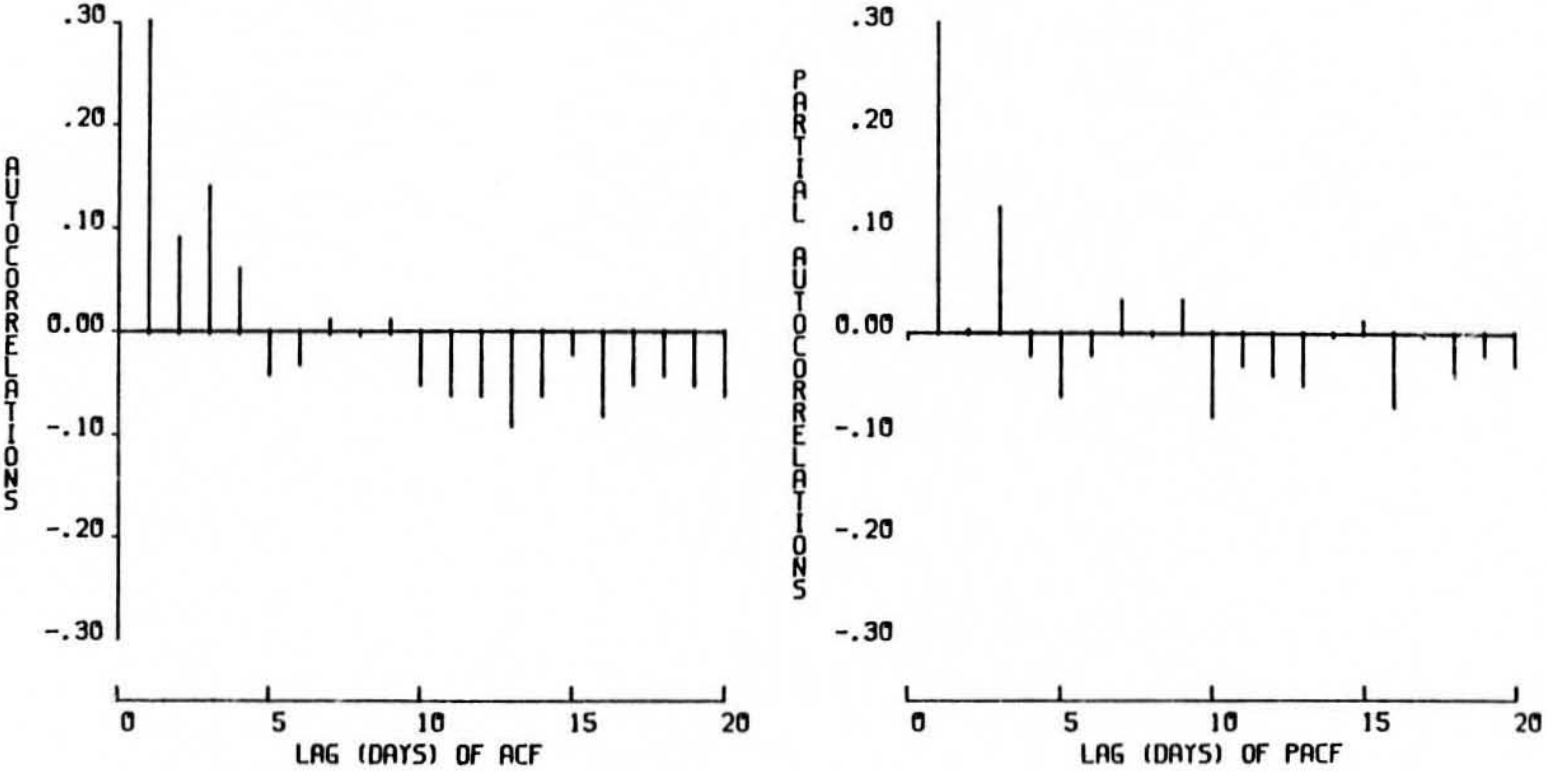

Figure 3. Autocorrelations and partial autocorrelations of transformed errors of expected proportions of Flat Island test fishery catches, 1968-1979.

Table 2. Statistics concerning the time series models and relationships discussed in the text for Flat Island test fishery catches, 1968-1978.

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1. The residual sum of squares (sum of all e_i^2 is .307897

2. The residual sum of squares of transformed e_i, where $\varepsilon_i = sign\ (e_i)|e_i|^{\frac{1}{2}}$ (sum of all ε^2) is 7.6337

3. Statistics regarding the fitted AR_1 model:

   Fitted model = $\varepsilon_t = -.013012 + .30418\varepsilon_{t-1} + a_t$

   Residual sum of squares = 6.8612; degrees of freedom = 418

4. Statistics regarding the fitted MA_1 model:

   Fitted model = $\varepsilon_t = -.012983 + .30688a_{t-1} + a_t$

   Residual sum of squares = 6.8769; degrees of freedom = 418

5. Statistics regarding the multiple linear regression of average wind speed (w_t) and the commercial effort (f_t) on errors.

   a. Correlation coefficients: Effort and errors: $r = -.2514$ ($p < .0001$)
   Wind and errors: $r = .2390$ ($p < .0001$)

   b. Fitted model: $\varepsilon_t = b_0 + b_1 w_t + b_2 f_t + a_t$

   where: $b_0 = -.0621903$

   $b_1 = .0087317$ (F-value = 23.27)

   $b_2 = -.0638786$ (F-value = 26.18)

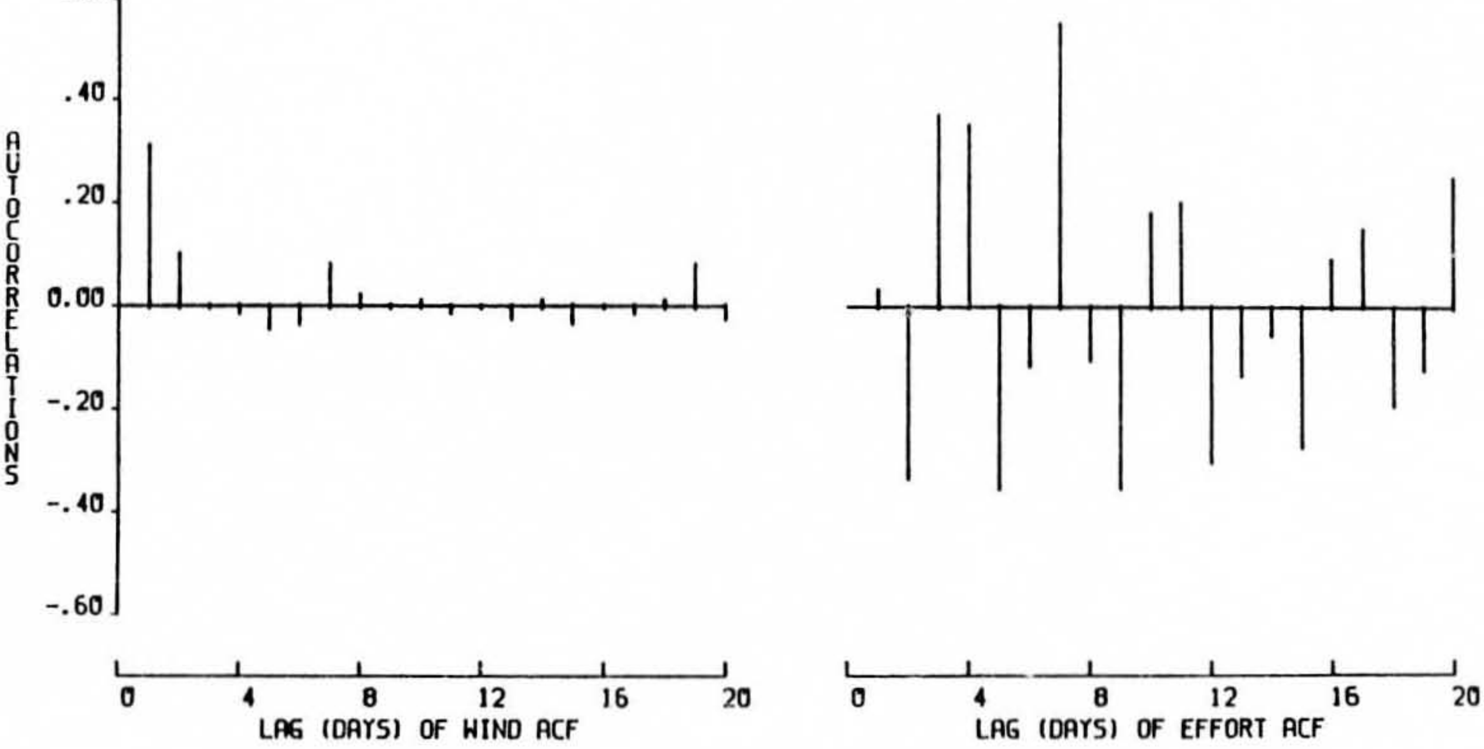

Figure 4. Autocorrelations of average daily wind speed and daily effort for all years of test fishery operations.

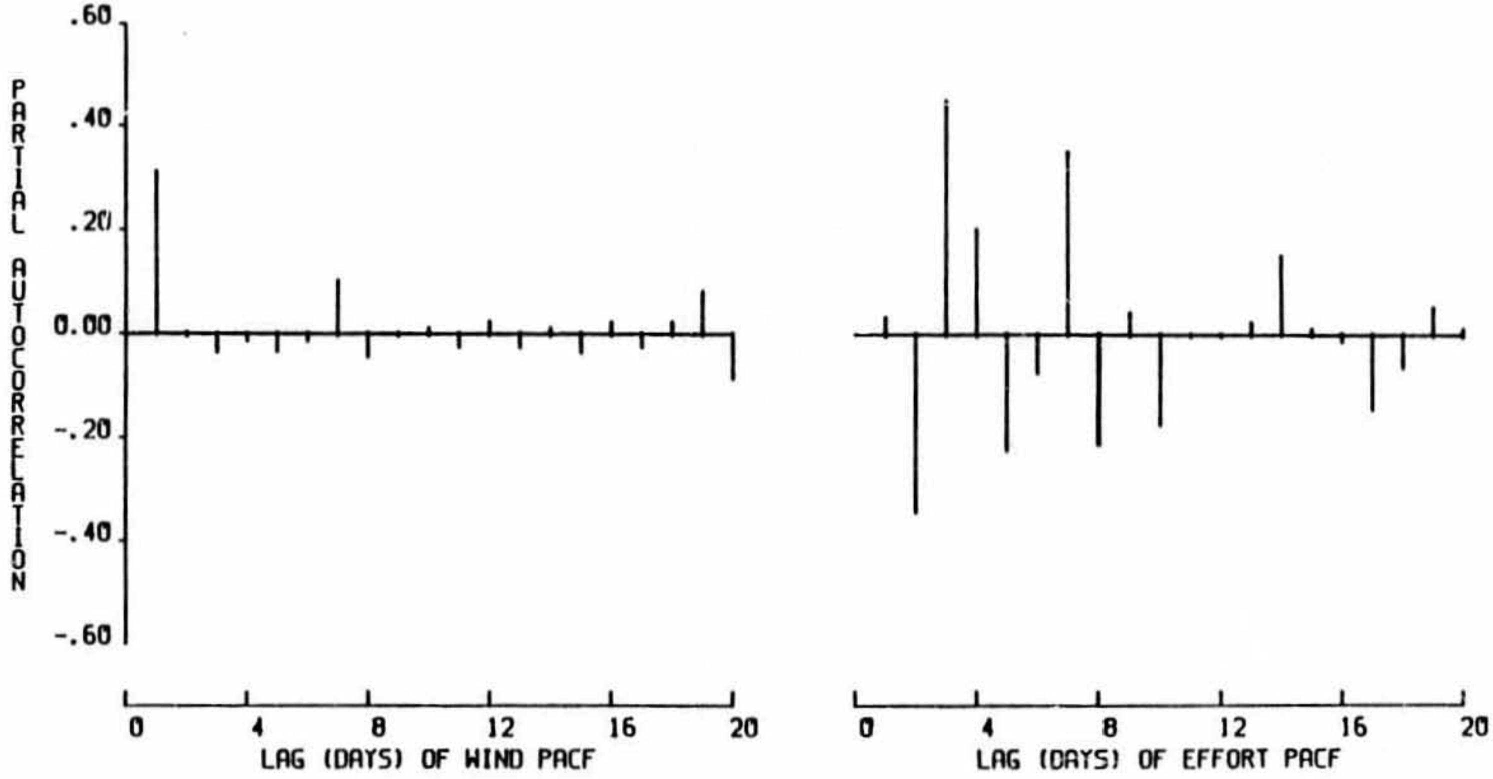

Figure 5. Partial autocorrelations of average daily wind speed and daily effort for all years of test fishery operations.

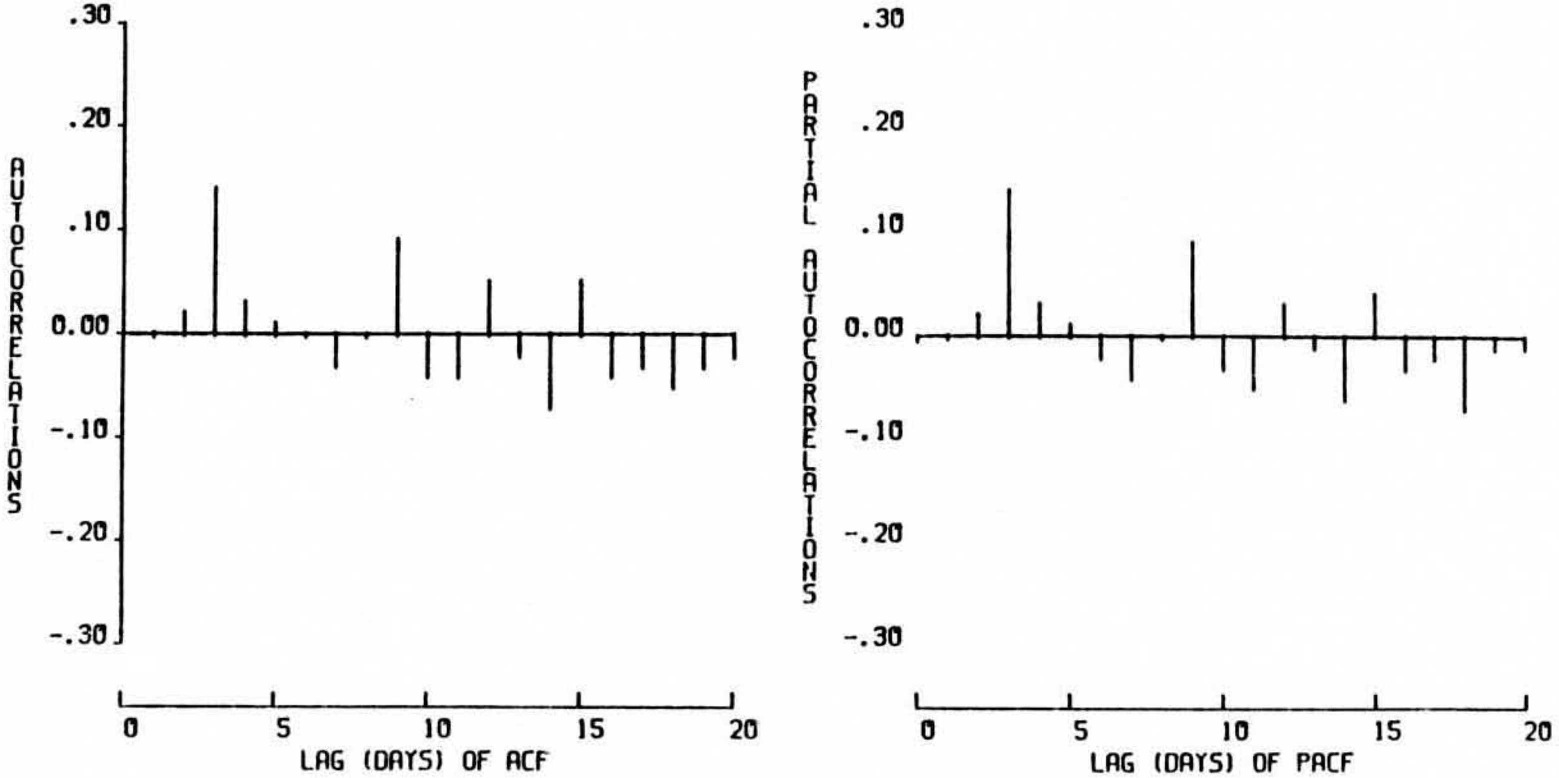

Figure 6. Autocorrelations and partial autocorrelations of residuals from the fitted autoregressive model of Flat Island test fishery catches, 1968-1979.

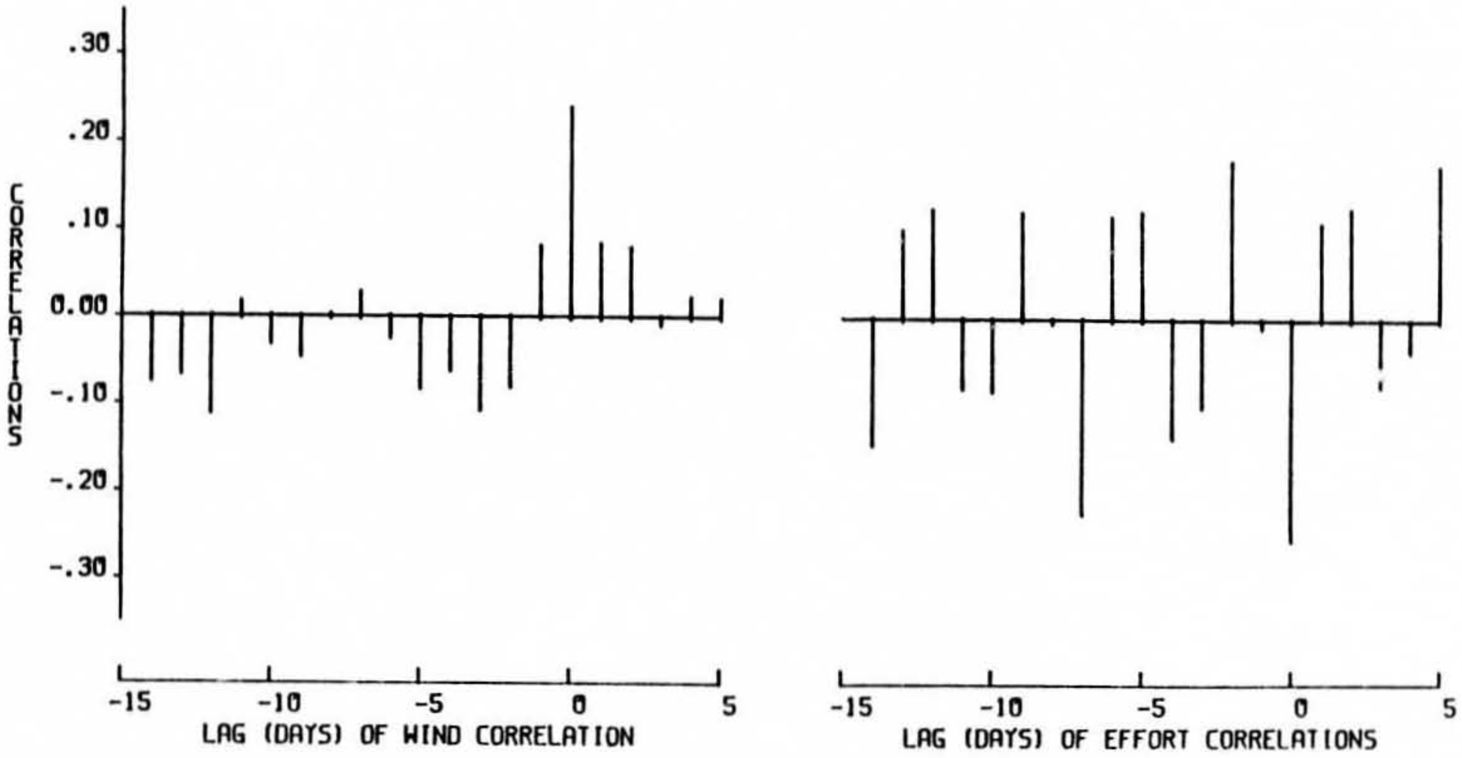

Figure 7. Correlations of average daily wind speed and daily effort with residuals from the autoregressive model for Flat Island test fishery catches, 1968-1978.

Table 3. Parameter values and goodness of fit for two functions proposed as possible models to describe the time series of the errors, ε_t, for test fishery catches from 1968 through 1978.

Statistics regarding the fitting of the $AR_{1,3}$ and $ARMA_{1,3}$ models.

Model: $AR_{1,3}$ $\quad \varepsilon_t = b_0 + b_1 w_t + b_2 f_t + \phi_1 \varepsilon_{t-1} + \phi_3 \varepsilon_{t-3} + a_t$

where $b_0 = -.075117$

$b_1 = .009005$

$b_2 = .066458$

$\phi_1 = .298321$

$\phi_3 = .101325$

Sum of squares = 5.9100; degrees of freedom = 394

Model: $ARMA_{1,3}$ $\quad \varepsilon_t = b_0 + b_1 w_t + b_2 f_t + \phi_1 \varepsilon_{t-1} + \theta_3 \varepsilon_{t-3} + a_t$

where $b_0 = -.079625$

$b_1 = .009357$

$b_2 = .067129$

$\phi_1 = .29418$

$\theta_3 = .14624$

Sum of squares = 5.8748; degrees of freedom = 394

Analysis of the residuals (a_t) of Equation 4 reveals no significant deviations from a white-noise model (Figure 8). The randomness of the ACF and PACF are indicative of a time series model which has sufficiently accounted for the dependence of values on preceding values. Correlation coefficients between the a_t, wind speed, and commercial effort are also nonsignificant for all lags (Figure 9). It is surmised that the multiple regression transfer function has adequately explained the dependence of catch on wind speed and the surrounding commercial fishery.

Deviations from expected daily proportions of 1979, 1980, and 1981 test fishery catches were subjected to the same analytical procedures described above for the Flat Island data (see Tables 4 and 5). The large peak in the ACF and PACF at a 1 day lag which characterized the Flat Island data also appeared in the Big Eddy ACF and PACF (Figure 10). A secondary peak at a 6 day lag was also present. MA_1 and AR_1 models were fitted to the errors ε_i. Although the fitted MA_1 model resulted in a lower value of sum of squared deviations (1.7898) than the AR_1 model (1.7912), the difference was small. In order to be consistent with the Flat Island analysis, an AR_1 model was employed as the interim model.

Correlations between the errors and average wind speed and commercial effort are presented in Figure 11. The average wind speed recorded the day before the test fishery catch produces the highest correlation, followed by the wind speed recorded the day of the test fishery catch. As was found for the Flat Island catch, there is a high negative correlation between the residuals of the AR_1 model and the commercial effort on the same day (Figure 11). The transfer function

$$r_t = -.041523 + .006072w_{t-1} - .08199f_t \tag{5}$$

is derived from the multiple regression of average wind speed recorded the day before recorded catch and commercial effort the same day as test fishery catch on the residuals of the AR_1 model.

Values of the parameters of the MA_1 and AR_1 models with a transfer function were refined by minimizing the sum of squared deviations (Table 5). The models yield almost identical results. The slightly lower sum of squares and choice of an AR_1 term for the data of the Flat Island catch suggest the selection of an AR_1 process for the Big Eddy data. Cursory inspection of the ACF and PACF of the residuals (Figure 12) and the correlation coefficients between the residuals and the wind speed and commercial effort (Figure 13) reveal no obvious deficiency in the model.

Autoregressive and partial autoregressive correlations for all years of the test fishery (1968-1981) are graphically presented in Figure 14 and Table 6 presents the statistics associated with fitting an AR_1 time series model with a transfer function for wind and commercial effort to the combined Flat Island and Big Eddy test fishery data. Analysis of the residuals (Figures 15 and 16) demonstrates the adequacy of this model. No pattern was observed in the ACF or PACF of the residuals, and the correlation coefficients were all small and nonsignificant. The residuals from the full model are presented in Figure 17. No deviations from the assumption of homogeneity of variance are observed in the distribution of the residuals.

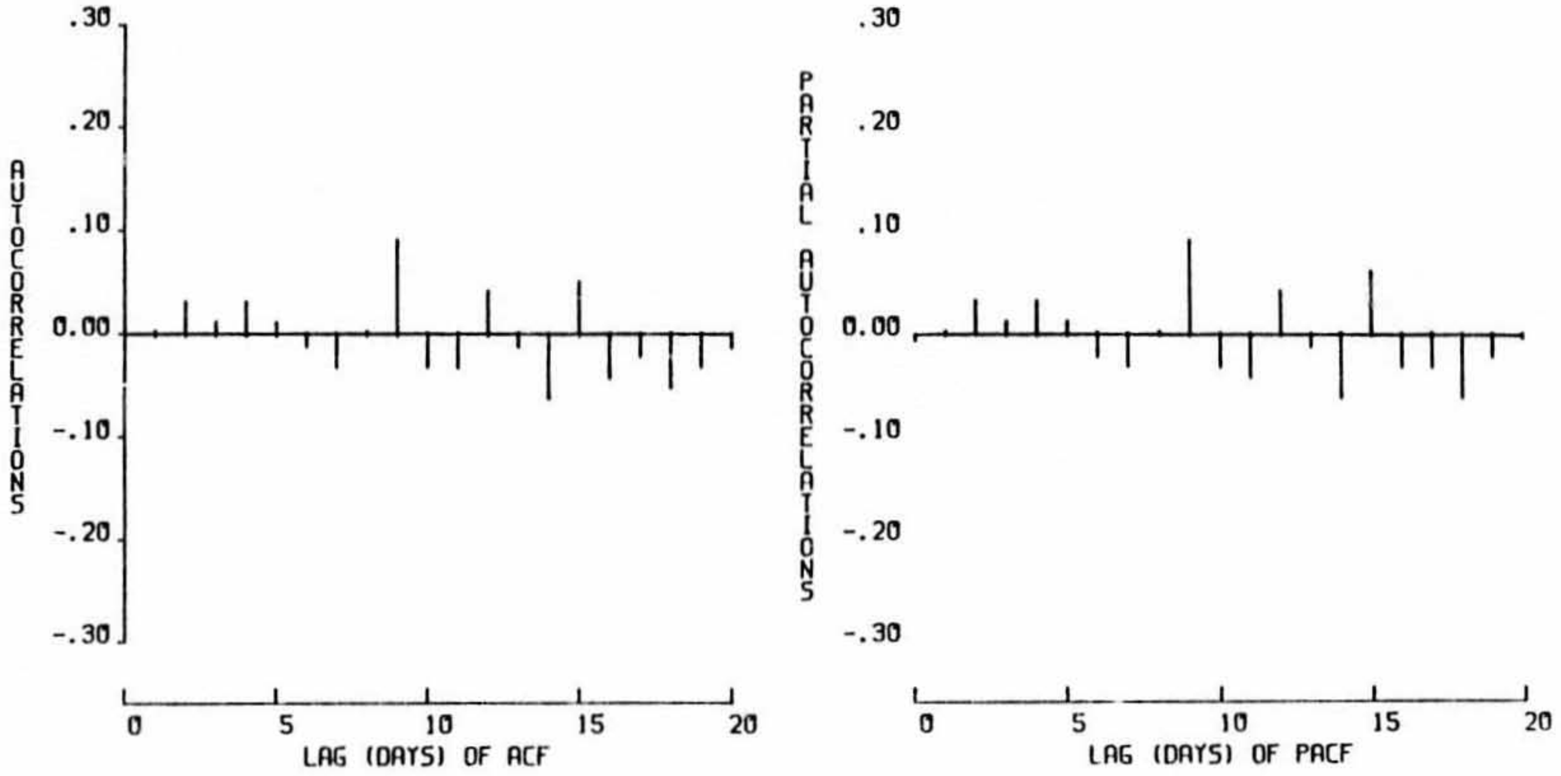

Figure 8. Autocorrelations and partial autocorrelations of residuals from the autoregressive model for Flat Island test fishery catches, 1968-1978.

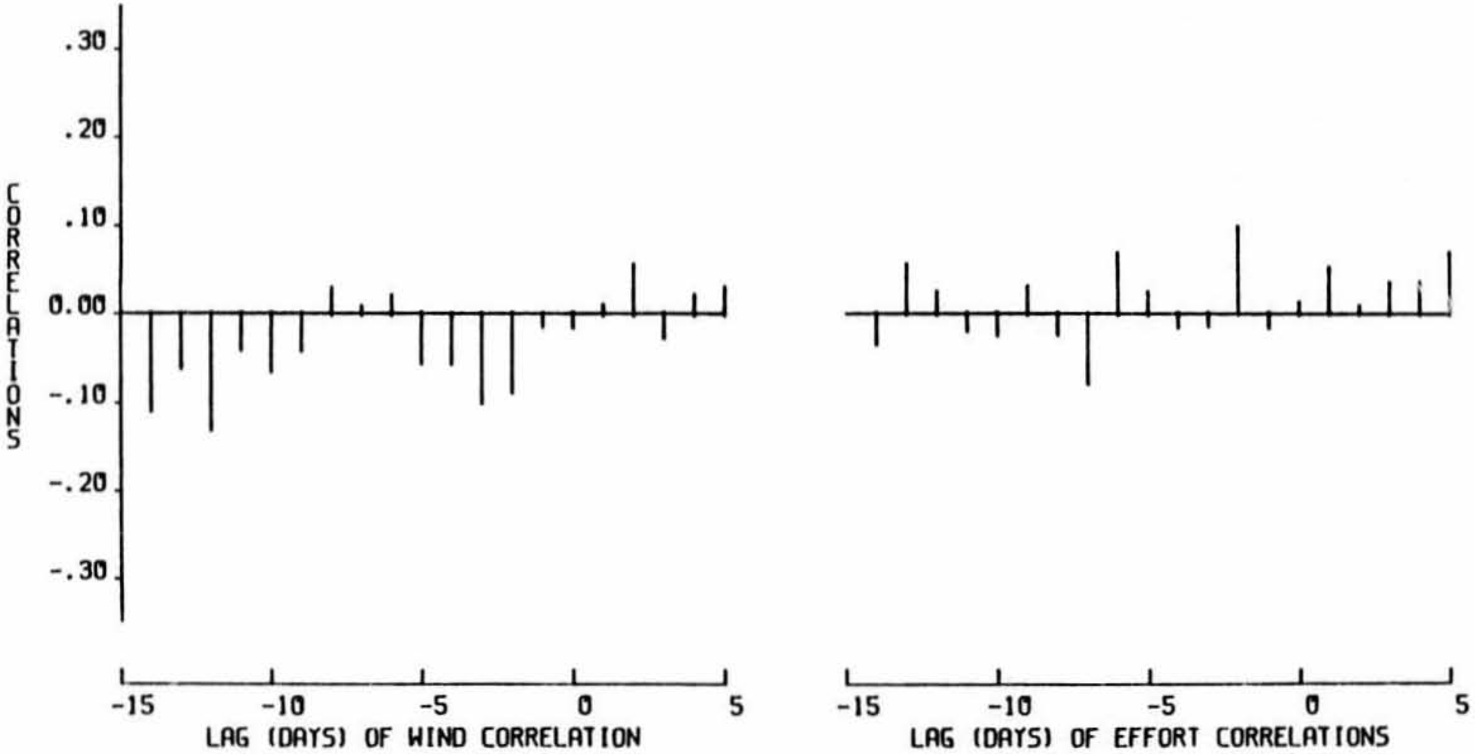

Figure 9. Correlation of average daily wind speed and daily effort with residuals from the autoregressive model with transfer function for Flat Island test fishery catches, 1968-1978.

Table 4. Statistics concerning the time series models and relationships discussed in the text for Big Eddy test fishery catches, 1979-1981.

1. The residual sum of squares (sum of all e_i^2's) is .058757

2. The residual sum of squares of transformed e_i, where $\varepsilon_i = sign\ (\varepsilon_i)|\varepsilon_i|^{\frac{1}{2}}$
The sum of ε^2 is 1.84703

3. Statistics from the fitted AR_1 model:

   Fitted model = $\varepsilon_t = -.002287 + .17115\varepsilon_{t-1} + a_t$

   Residual sum of squares = 1.7912; degrees of freedom = 143

4. Statistics from the fitted MA_1 model:

   Fitted model = $\varepsilon_t = -.002587 + .17930a_{t-1} + a_t$

   Residual sum of squares = 1.7898; degrees of freedom = 143

5. Statistics from the multiple linear regression of average wind speed (w_{t-1}) and commercial effort (f_t) on errors.

   a. Correlation coefficients: Effort and errors: $r = -.3116$ ($p < .001$)
   Wind and errors: $r = .1582$ ($p = .052$)

   b. Fitted model: $\varepsilon_t = b_0 + b_1w_t + b_2f_t + a_t$

   where $b_0 = -.041523$
   $b_1 = .006072$ (F value = 4.88)
   $b_2 = .08199$ (F value = 17.08)

Table 5. Parameter values and goodness of fit for two functions proposed as possible models to describe the time series of the errors, ε_t, for test fishery catches from 1979 through 1981.

Statistics regarding the fitting of the MA_1 and AR_1 models.

Model: MA_1 $\quad \varepsilon_t = b_0 + b_1 w_t + b_2 f_t + \phi_1 \varepsilon_{t-1} + a_t$

where $b_0 = -.039500$

$b_1 = .005826$

$b_2 = -.085630$

$\phi_1 = .261993$

Sum of squares = 1.5229; degrees of freedom = 144

Model: AR_1 $\quad \varepsilon_t = b_0 + b_1 w_t + b_2 f_t + \phi_1 \varepsilon_{t-1} + a_t$

where $b_0 = -.036719$

$b_1 = .005732$

$b_2 = -.090661$

$\phi_1 = .25574$

Sum of squares = 1.5225; degrees of freedom = 144

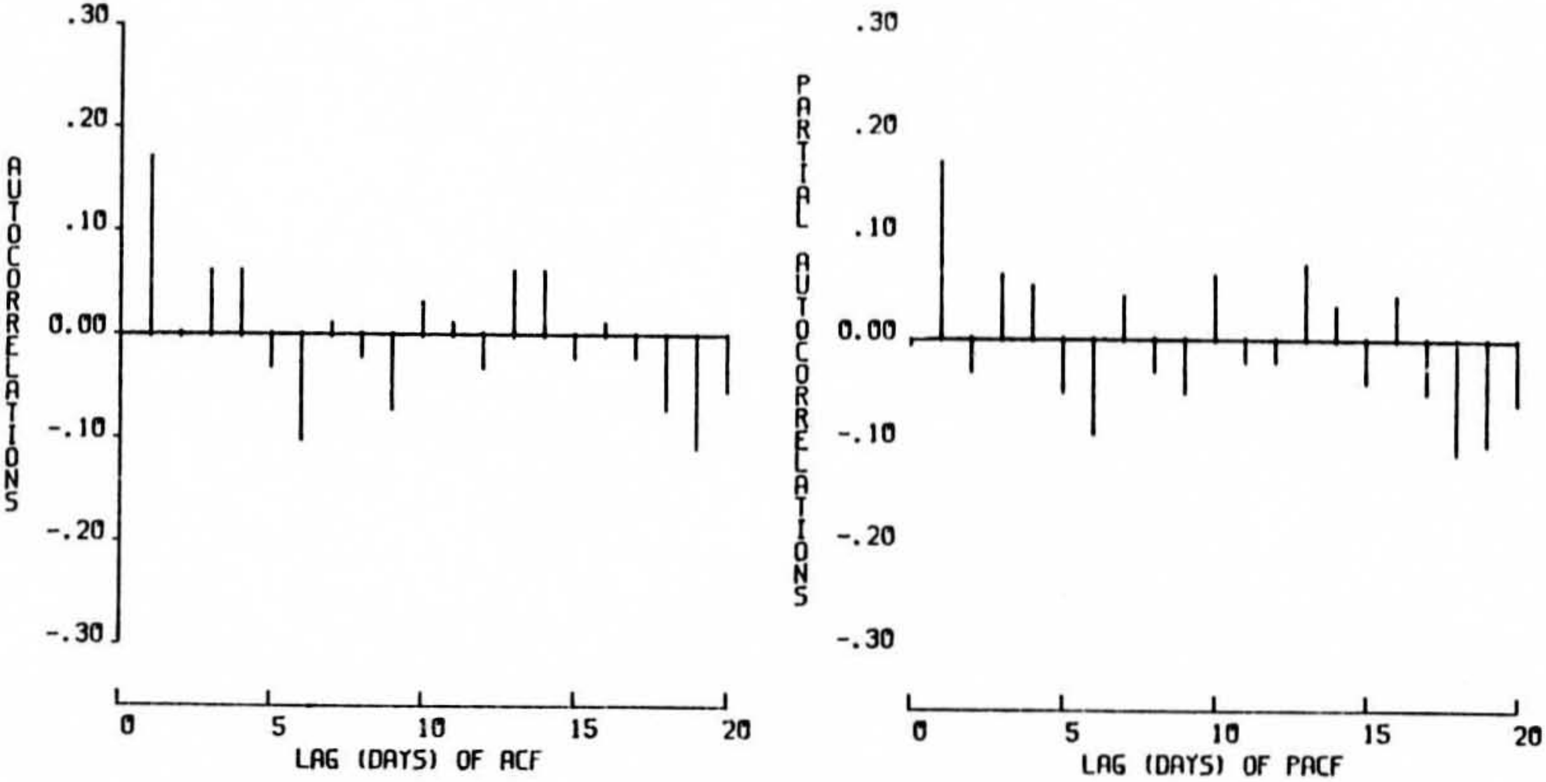

Figure 10. Autocorrelations and partial autocorrelations of transformed errors of expected proportions of Big Eddy test fishery catches, 1979-1981.

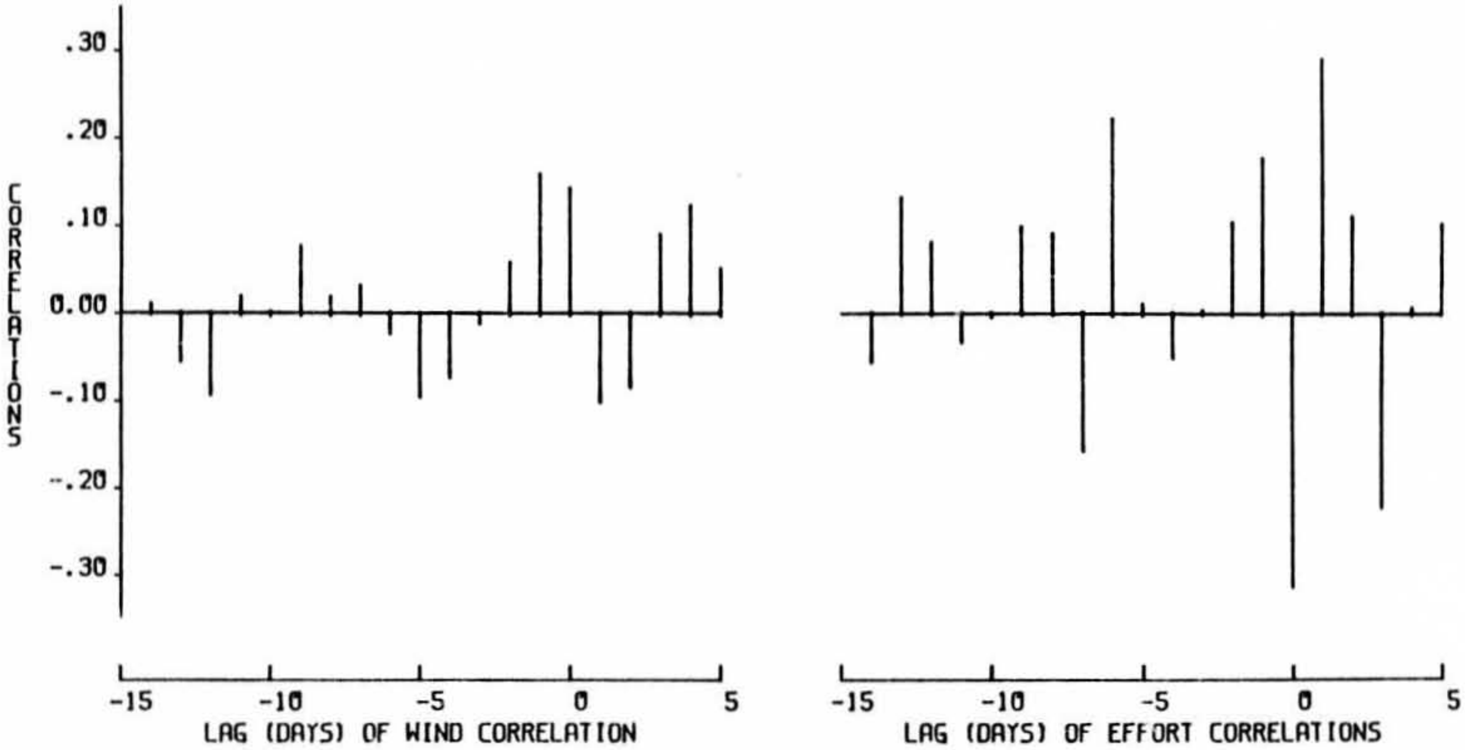

Figure 11. Correlations of average wind speed and daily effort with residuals from the autoregressive model for Big Eddy test fishery catches, 1979-1981.

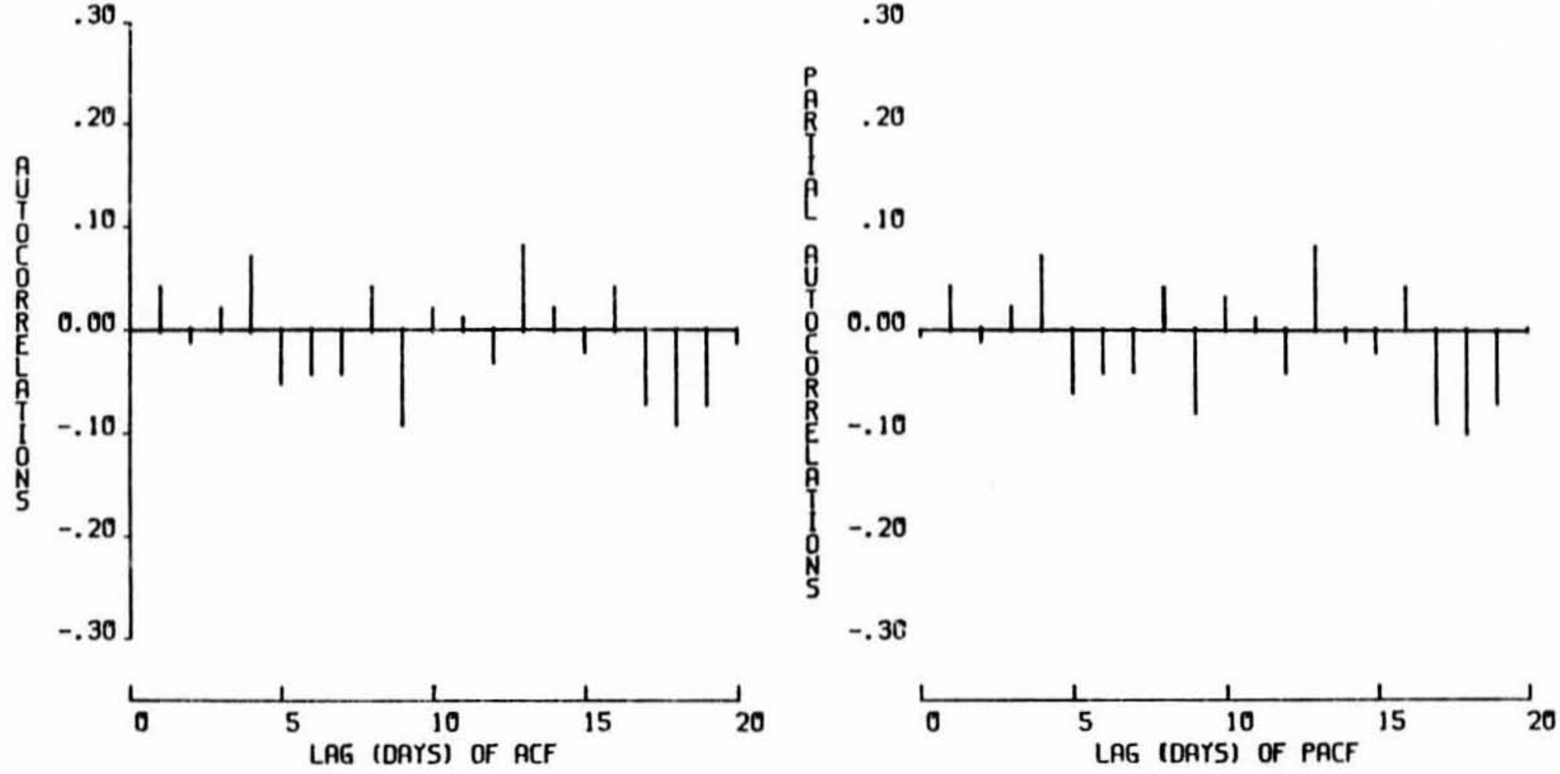

Figure 12. Autocorrelations and partial autocorrelations of residuals from the autoregressive model with the transfer function for Big Eddy test fishery catches, 1979-1981.

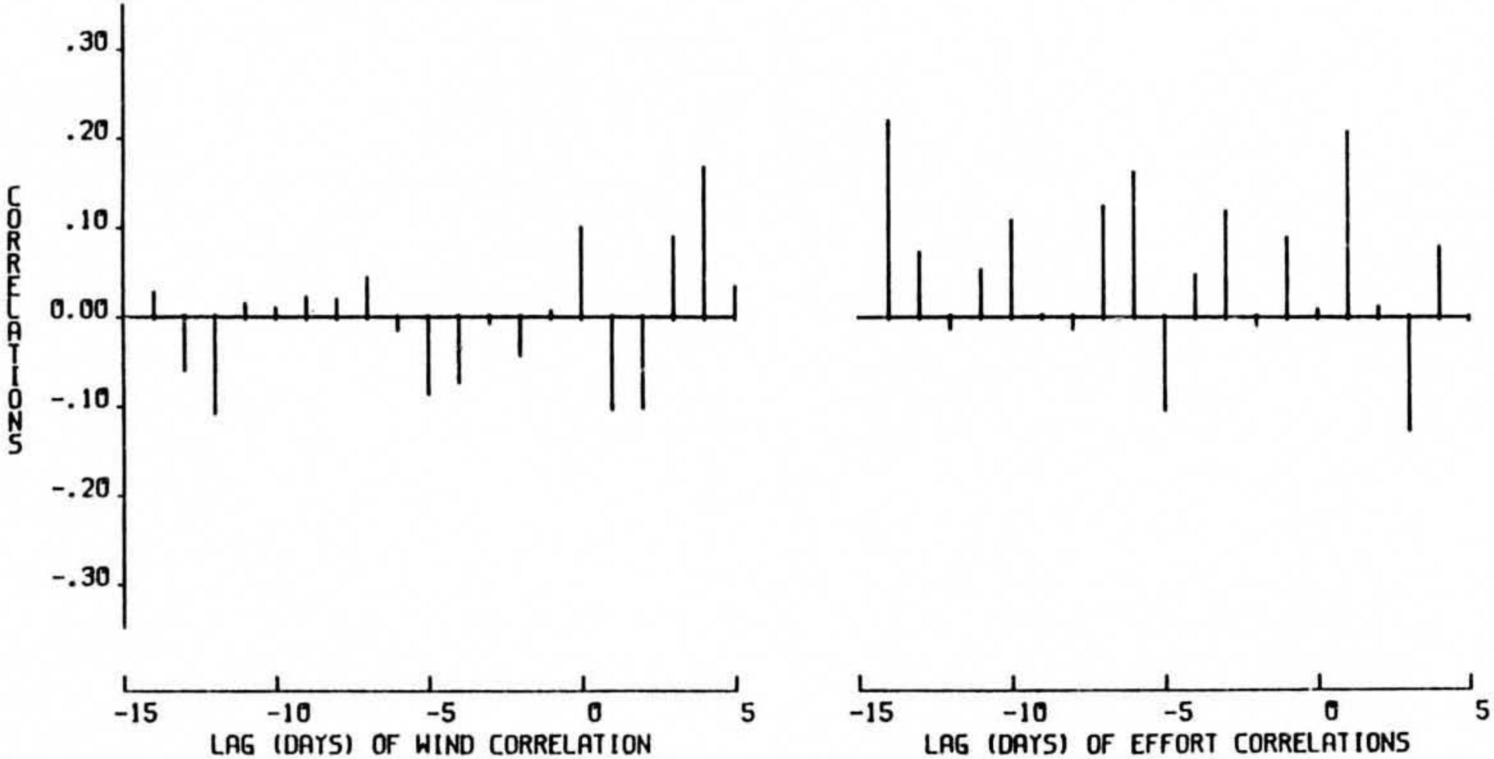

Figure 13. Correlations of average daily wind speed and daily effort with residuals from the autoregressive model with transfer function for Big Eddy test fishery catches, 1979-1981.

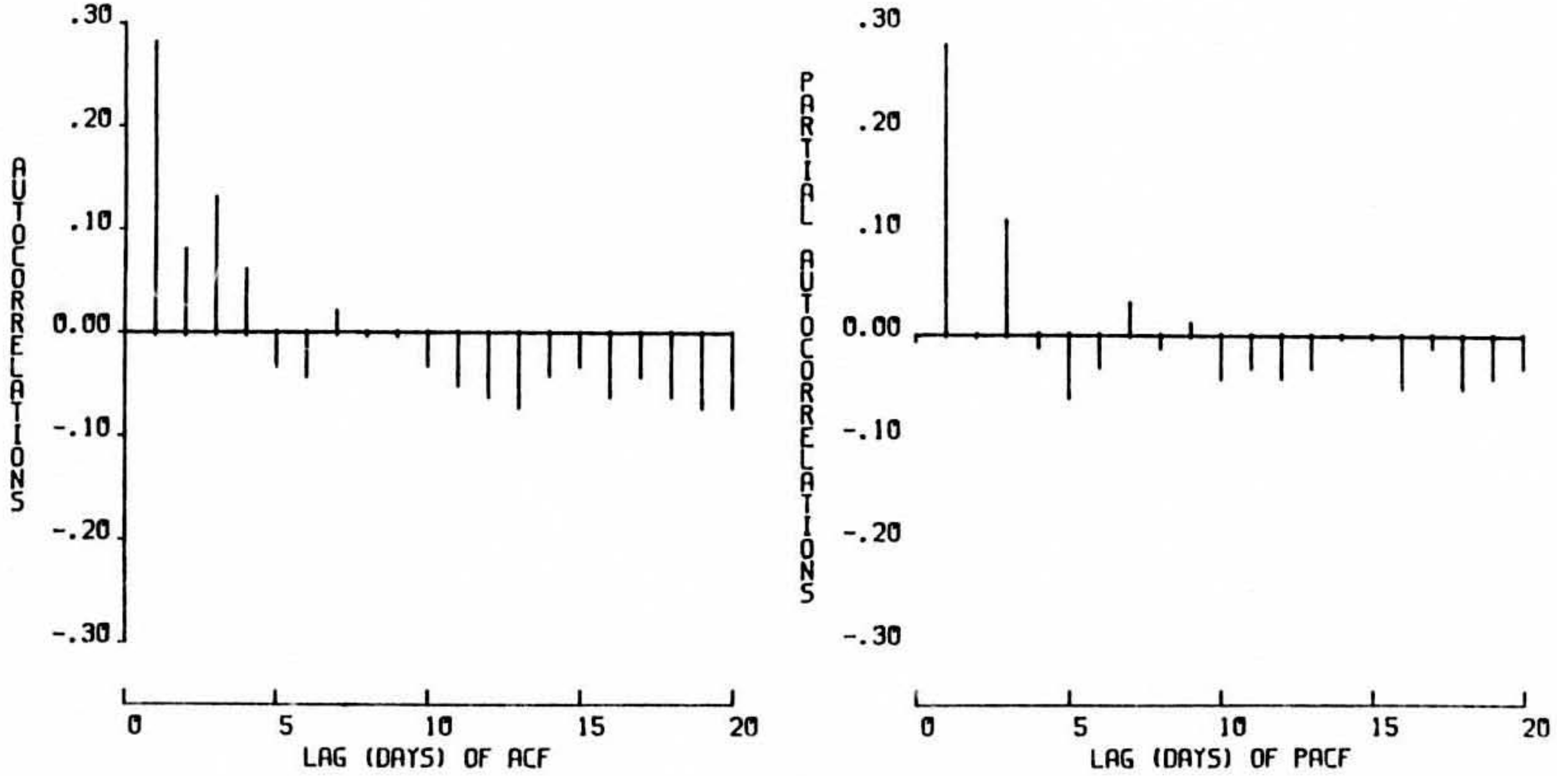

Figure 14. Autocorrelations and partial autocorrelations of transformed errors of expected proportions of combined test fishery catches, 1968-1981.

Table 6. Parameter values and goodness of fit for the function proposed as the model to describe the time series of errors, ε_t, for 1968-to-1981 test fishery catches.

Statistics from the fitting of the AR_1 model.

1. The residual sum of squares (sum of all e_i^2's) is .369689
2. The residual sum of squares of transformed e_i, where $\varepsilon_i = sign\ (e_i)|e_i|^{\frac{1}{2}}$ (sum of all ε^2) is 9.48072

Model: AR_1 $\quad \varepsilon_t = b_0 + b_1 w_t + b_2 f_t + \phi_1 \varepsilon_{t-1} + a_t$

where $b_0 = -.062750$

$b_1 = .007919$

$b_2 = .074693$

$\phi_1 = .29793$

Sum of squares = 7.5396; degrees of freedom = 569

Sum of squares for all years = .319193

Average error of estimated proportion = .0151179

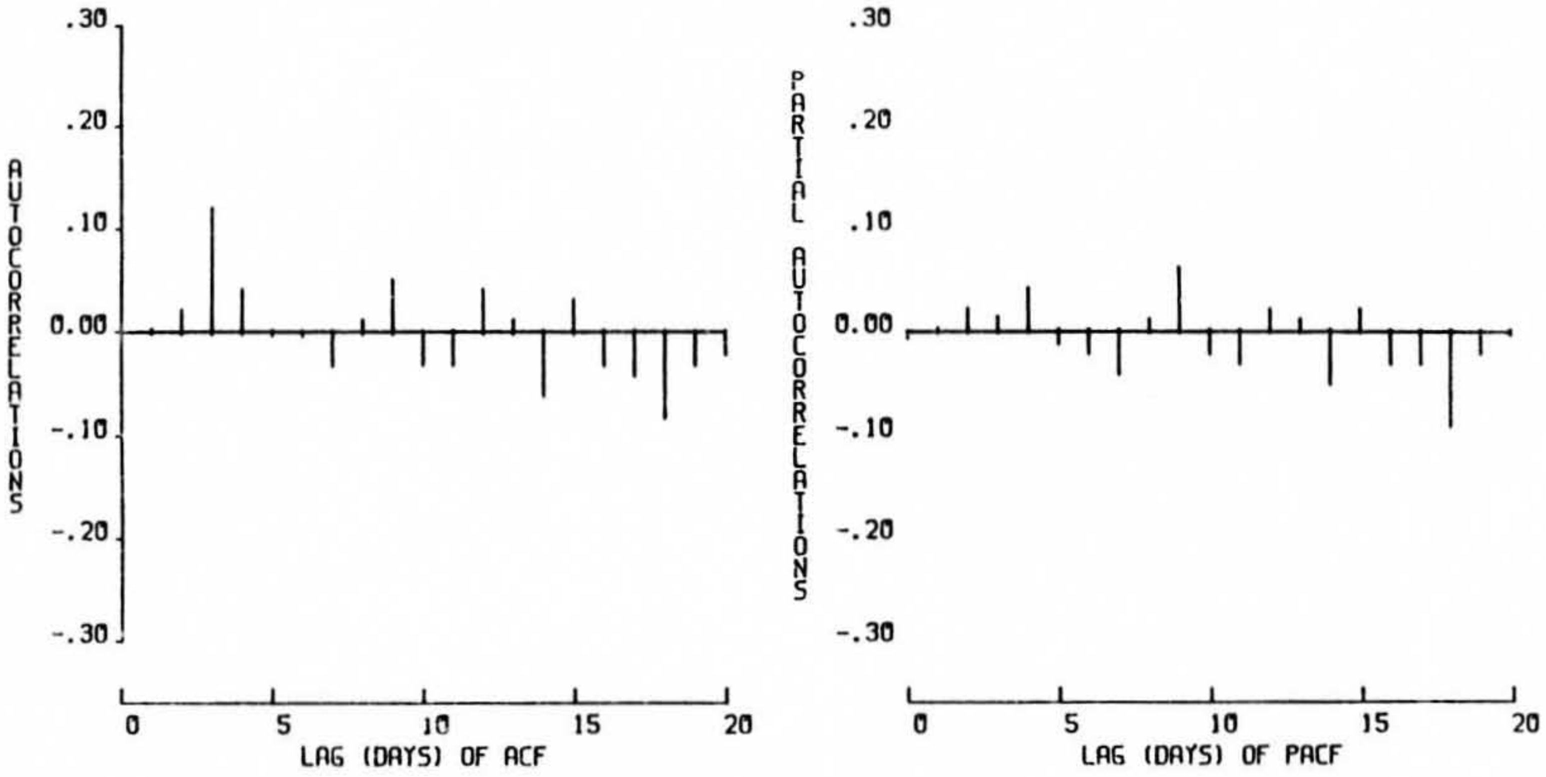

Figure 15. Autocorrelations and partial autocorrelations of residuals from the autoregressive model with transfer function for combined test fishery catches, 1968-1981.

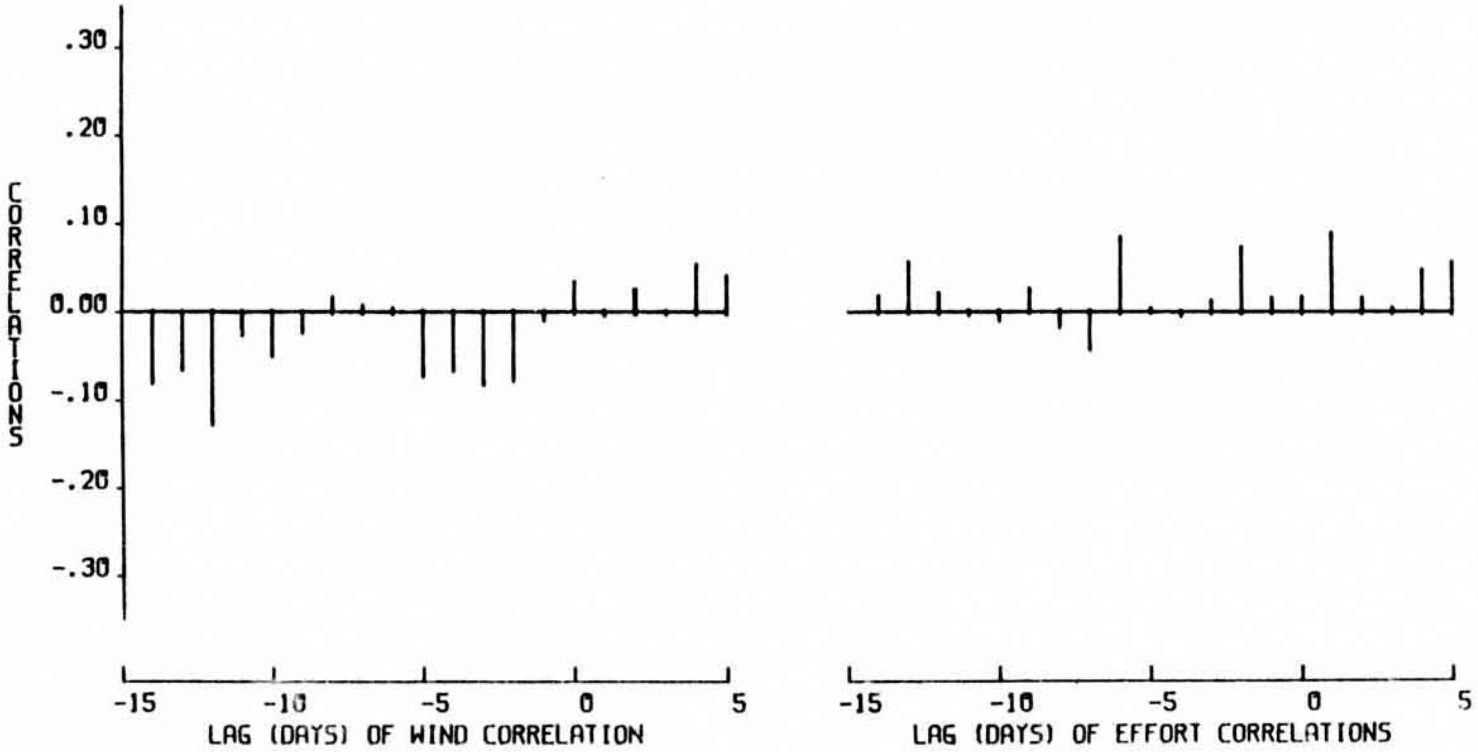

Figure 16. Correlations of average daily wind speed and daily effort with residuals of the autoregressive model with transfer function for combined test fishery catches, 1968-1981.

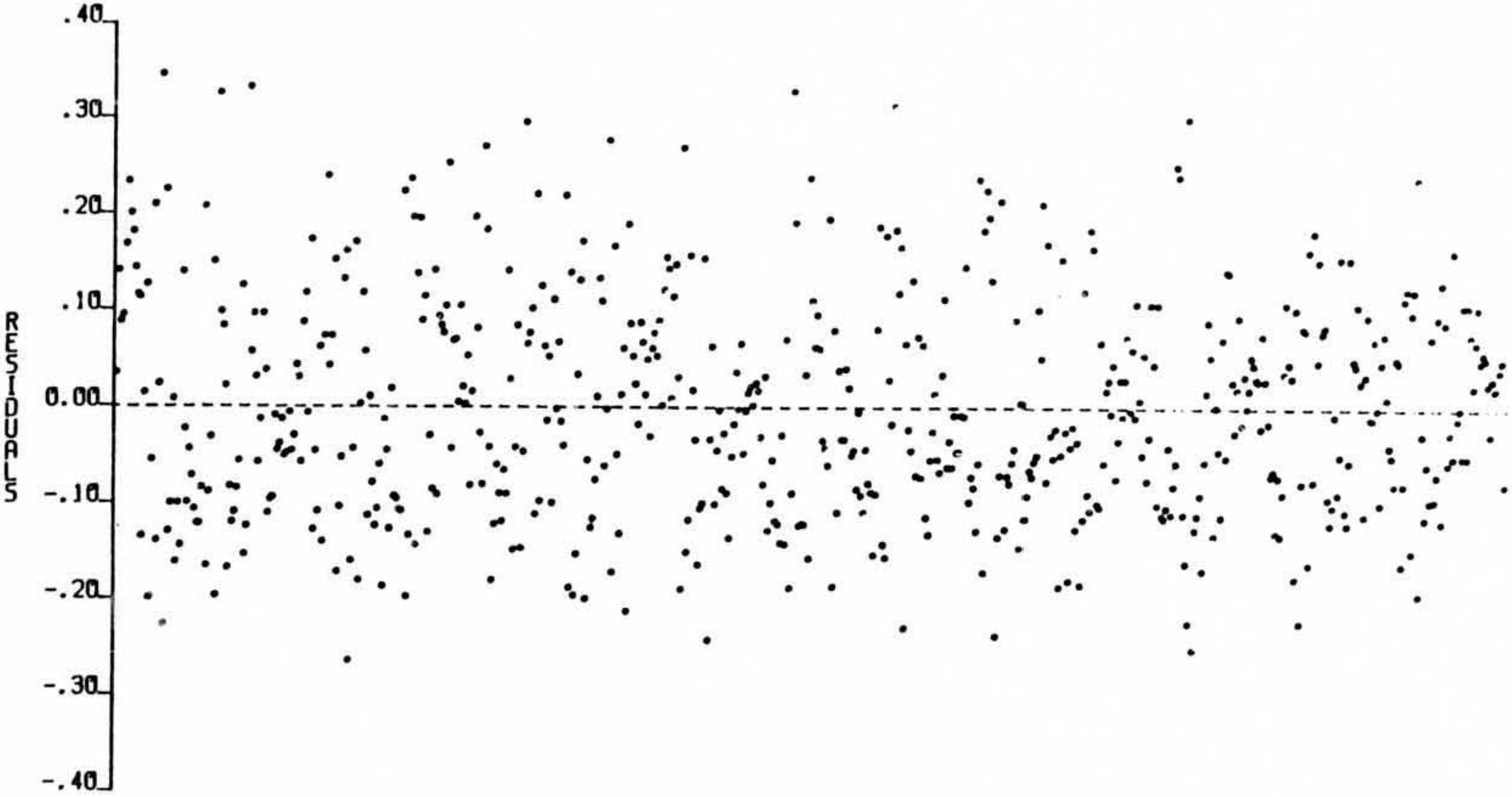

Figure 17. Residuals from the autoregressive model with transfer function for all years (1968-1981).

DISCUSSION OF TIME SERIES RESULTS

Time series analysis can benefit fisheries management in two ways. The resultant empirical model can be utilized as an aid in the prediction of future resource abundance, either by forecasting the catch or relative abundance of the resource (Mendelssohn 1981; Boudreault et al. 1977; Jensen 1976), or by estimating the deviation from average performance of seasonal fisheries (Saila et al. 1980; present study; also see Bulmer 1976, for similar results concerning Canadian populations of exploited fur resources). The dynamic nature of the Box-Jenkins approach allows regular updating of parameter values, increasing the reliability of resource forecasts. The variability found in most fisheries is well suited to the stochastic nature of the fitted models. The analysis is linear in nature but can describe fairly complex behavior. Nonstationary and seasonal time series can easily be adapted to analysis.

The second and potentially greater benefit to fisheries management is insight into the dynamics of the fishery. Mendelssohn (1981) concluded that variability in the skipjack fishery was more a function of unexpected changes in commercial effort than the behavior of the fish. Boudreault et al. (1977) discussed the possibility that lobster abundance is not only a function of past population levels, but the effect of temperature on larval survival as well. By including the environmental variables of rainfall and temperature in a time series model describing mosquito densities, new insights into the effects of the environment on life history stages of the mosquito were obtained (Hacker et al. 1975). Interaction between various species of *Drosophila* have been investigated by similar time series methods (Poole 1976a).

The effect of surface winds on the migratory behavior of salmon has been shown to be significant (Lorz and Northcote, 1965), yet the nonuniform nature of the distribution of migrants over time has precluded a quantitative description of the effects. Some authors (Hornberger and Mathisen 1980) have suggested that wind speed affects the interaction between commercial gear and fish. Others have attributed the correlations to the influence of wind on the spreading of home stream water (Lorz and Northcote 1965). Results of the present study indicate that wind, or a covariate of wind, promotes upriver migratory behavior in chinook salmon located near the mouth of the Yukon River. The highest correlation was obtained between deviations from expected catch and wind speed the same day as the catch for Flat Island test fishery observations. Big Eddy analysis found the highest correlation between the deviation and wind speed one day before the catch. The approximate one-day travel time of migrating chinook salmon from Flat Island to Big Eddy are in accord with these conclusions.

The relationship of catch and effort remains perplexing. There is strong evidence that competition between units of fishing gear is high in the lower Yukon chinook salmon fishery. The large negative correlation between the test fishery catch of Flat Island and Big Eddy and the commercial effort of the same day implies that a sizable proportion of the population vulnerable to the commercial fishery is harvested before it reaches the test fishery. Therefore daily catch per unit of effort is not solely a function of the initial daily chinook salmon abundance, but also a function of fishing mortality experienced by the population. In order to rely on catch per unit effort as an estimator of the relative abundance of the population, consideration must also be given to the magnitude and effectiveness of the commercial fishery.

The advantage that time series analysis has over the fitting of conceptual equations is that time-series models are constructed empirically, requiring few a priori assumptions. If the investigator has sufficient knowledge of the processes driving the phenomenon, conceptual models are much preferred over empirical models. However, in the absence of critical information, the empirical model can serve as a first step in the development of a conceptual model. Anderson (1977) extended the Box-Jenkins analysis to include interpreting the results rationally. Fortuitous autocorrelations 'for which no reasonable explanation can be found, should not have this effect reflected by the model'(Anderson 1977).

Reduction in the sum of squares is a standard measure of the ability of a model to estimate recorded observations. The objective of the present study is to reduce the squared deviations between observed daily proportions of total catch and corresponding average proportions (Figure 2). Time series models provided only a modest reduction in the sum of squares (14%, Table 6). Saila et al. (1981) found that monthly averages provided a model which had a lower sum of squares than the time series model, although the time series model forecast future values with somewhat higher accuracy. The importance of the present study is not an improved ability to predict future catch though obscure, by the time series model, but the demonstration of a relationship, between wind speed, surrounding commercial effort, and catch.

DISCUSSION OF MATHEMATICAL METHODS

The time distribution of abundance of a migrating population for a given locale is certainly a multivariate phenomenon. The ability of mathematics to accurately describe and forecast daily abundance of adult chinook salmon migrating through the lower Yukon River drainage depends on an understanding of genetic and environmental contributions to the distribution of abundance, or equivalently the proportion of total population abundance, over time. Unfortunately there is no concensus on the distribution function governing daily proportion of total catch. Normal, binomial, or multinomial distributions appear adequate considering the genetic nature of the migratory behavior. The recurrent, apparently Gaussian, distribution of daily abundance in diverse populations of migrating birds has been approximated by a cosine power function (Preston 1966). Frohne (unpublished manuscript) has suggested that the inverse gaussian distribution, which describes the passage of particles randomly dispersing in a flowing medium, may better describe the mechanics of migration. A two parameter inverted exponential function was first employed by Royce (1965) to describe the cumulative proportion of total abundance per unit time. Others have continued its use (Rothschild and Balsiger 1971; Mathisen and Berg 1968; Dahlberg 1968; Mundy 1979; Mundy and Mathisen 1981; Matylewich 1982). The derivative of this function with respect to time describes a bell-shaped curve of proportion as a function of time. Other functions which generate the familiar bell-shaped curve and have been fitted to the time distribution of proportions include functions from the general class of beta curves (Vaughan 1954; Hornberger 1980)

Migration has been characterized as a genetically controlled environmentally mediated event (Mundy 1979). Fluctuations of daily abundance in a given locale are principally a function of short term environmental changes, the commercial harvest below the reference area, and random variation. Daily peaks in salmon counts have been successfully correlated with changes in cloud cover (Ellis 1962), wind speed and direction (Lorz and Northcote 1965), barometric pressure (Ellis 1962), and rainfall and increased stream discharge (Alabaster 1970; Libosvarsky 1976; and others: see Banks' 1969 review of factors affecting the upstream migration of salmon). Results of preliminary comparisons of data from ADF&G test fishery catches and daily weather observations recorded in Nome suggest that a covariant of wind speed is the principal daily environmental parameter affecting the lower river migration of Yukon chinook salmon.

METHODS

The derivative of the inverted exponential function and the normal probability density function are used to quantify the time density of an assumed homogeneous population or subpopulation of chinook salmon. Both distributions describe a bell-shaped curve. However, there are advantages inherent in each model. The more conventional parameters, mean (μ) and variance (σ^2), of the equation describing the normal distribution of the proportions of total abundance, $Q(t)$, over day of the migration, t:

$$Q(t) = exp[-((t-\mu)^2/(2\sigma^2))]/(2\pi\sigma^2)^{1/2} \qquad (6)$$

can easily be related to the location and dispersion of migratory abundance over time. The derivative of the two-parameter logistic inverse exponential function, referred to subsequently as simply the inverse exponential function:

$$Y'(t) = b[exp(-(a+bt))]/[(1+exp(-(a+bt)))^2], \qquad (7)$$

where $Y'(t)$ is the daily proportion of total abundance on day t, is more prevalent in the literature (see Royce 1965; and others) and it can be integrated to yield an exact solution which describes the distribution of cumulative proportion $(Y(t))$ over time.

$$Y(t) = 1/[(1+exp(-(a+bt)))] \qquad (8)$$

The parameters defining the shape and location of the inverse exponential function, a and b, are related to the mean and variance of the distribution.

$$\mu = -a/b \qquad (9)$$

and

$$\sigma^2 = \pi^2/(3b^2) \qquad (10)$$

Local fishermen are of the opinion that the king salmon migration is composed of two distinct runs, a 'white nose race' and a 'black nose race'. Each race is supposed distinguishable according to morphological and migratory timing characteristics. Although a pilot study by U.S. Fish and Wildlife (Anon. 1960) did not discern any meristic differences in fish categorized as 'white nose' or 'black nose', the segregation of major spawning stocks in the Yukon River tributaries implies distinct races separable according to a yet-undiscovered set of characteristics. The possibility of temporally distinct races can be incorporated into the analysis. Assume that the time density distribution is composed of two groups of migrants (subpopulation 1, s_1, and subpopulation 2, s_2), each with a distinct mean (μ_1, μ_2) and variance (σ^2_1, σ^2_2) (or a_1, a_2, b_1, b_2 for the inverted exponential complement of the normal distribution equation). Let ρ_1 define the proportion of total migratory abundance apportioned to s_1, and $\rho_2 = 1 - \rho_1$ the proportion of s_2. Then the expected proportion of s_1 on day t ($q_1(t)$, or $y'_1(t)$) is

$$q_1(t) = \exp[-((t-\mu_1)^2/(2\sigma^2_1))]/(2\pi\sigma^2_1)^{1/2} \qquad (11)$$

for a normally distribution subpopulation, and

$$y'_1(t) = b_1[\exp(-(a_1+b_1t))]/[(1+\exp(-(a_1+b_1t)))^2] \qquad (12)$$

for a population temporally distributed according to the inverted exponential function. Likewise, the equations predicting the expected proportion of s_2 on day t is

$$q_2(t) = \exp[-((t-\mu_2)^2/(2\sigma^2_2))]/(2\pi\sigma^2_2)^{1/2} \qquad (13)$$

and

$$y'_2(t) = b_2[\exp(-(a_2+b_2t))]/[(1+\exp(-(a_2+b_2t)))^2] \qquad (14)$$

for the normal and inverted exponential function respectively. The expected proportion of total abundance can now be expressed as either

$$Q(t) = \rho_1 q_1(t) + \rho_2 q_2(t) \qquad (15)$$

or

$$Y'(t) = \rho_1 y'_1(t) + \rho_2 y'_2(t) \qquad (16)$$

The same concept can be extended to k subpopulations. The proportion of subpopulation j, where $j=1,2,\ldots, k$, on day t is:

$$q_j(t) = \exp[-((t-\mu_j)^2/(2\sigma^2_j))]/(2\pi\sigma^2_j)^{1/2} \qquad (17)$$

for a normally distributed migration, and

$$y'_j(t) = b_j[exp(-(a_j+b_jt))]/[1+exp(-(a_j+b_jt))]^2], \tag{18}$$

for an inverted exponentially distributed migration. The proportion of total abundance on day t is a sum of proportions of all subpopulations on day t:

$$Q(t) = \rho_1 q_1(t) + \rho_2 q_2(t) + \ldots + \rho_k q_k(t) \tag{19}$$

or

$$Y'(t) = \rho_1 y'_1(t) + \rho_2 y'_2(t) + \ldots + \rho_k y'_k(t) \tag{20}$$

If the number of subpopulations is one (Equation 6), the estimation procedure for the parameters μ and σ^2 reduces to classical mean and variance computations:

$$\bar{t} = \sum_{t=1}^{n} (t) \left[\frac{C(t)}{C_T} \right] \tag{21}$$

$$S^2 = \sum_{t=1}^{n} (t-\bar{t})^2 \left[\frac{C(t)}{C_T} \right] \tag{22}$$

where it is assumed that daily catch is proportional to daily average abundance at the test fishery site, C_T is the total catch, $C(t)$ is daily catch, and n is the last_day of effort. The constants a and b may be estimated by solving $S^2 = \pi^2/3b^2$) and $\bar{t} = a/b$. If the migration is believed to be composed of more than one population, the values of the parameters $\mu_1, \sigma^2_1, \rho_1, \ldots \mu_{k-1}, \sigma^2_{k-1}, \rho_{k-1}, \mu_k, \sigma^2_k$, or similarly, $a_1, b_1, q_1, \ldots a_{k-1}, b_{k-1}, q_{k-1}, a_k, b_k$ can be obtained using maximum likelihood procedures with steepest descent methods.

Hasselblad (1966) applied maximum likelihood techniques to mixtures of normal curves to compute the means, variances, and proportions of total abundance of each subpopulation. The equations derived by Hasselblad (1966) for a mixture of k normal subpopulations are:

$$\mu_j = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)} \right] \left[(t) q_j(t) \right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)} \right] \left[q_j(t) \right]} , \tag{23}$$

$$\sigma^2_j = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[q_j(t)(t-\mu_j)^2\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[q_j(t)\right]} \tag{24}$$

$$\rho_j = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[q_j(t)\rho_j\right]}{C_T} \tag{25}$$

The system of equations created has no closed-form solution. However, with the aid of high speed computers, iterative schemes can be devised to approximate the maximum likelihood estimates of the parameters.

Although minimization of the sum of squared deviations of the observed values from expected values is not the criterion used here to obtain optimal parameter values, the sum of squares is a standard measure of the ability of a function to describe observed data. Sums of squares are included below with tables of parameter values for comparative purposes.

The relationship of wind speed to migratory behavior is assumed to be linear. Attempts to assess the importance of environmental factors on in-season migration of adult salmonids have been confined to either reporting the coincidence of observed peaks in migration and weather anomalies, or univariate linear regression (Ellis 1962; Lorz and Northcote 1965). Functional dependence of more complexity has not been explored. It should be noted that the linear relationship used in the following analysis does not imply a direct dependence of migration on wind. Wind speed, like calendar day, is a convenient covariate of other factors responsible for the inhibition or stimulation of migration. The assumed linear dependence of decreases in catch on amount of fishing effort surrounding the test fishery site follows from classical catch models (Ricker 1975). The linear equation is:

$$\omega_t = \beta_0 + \beta_1 w_{t-1} + \beta_2 f_t + a_t \tag{26}$$

where ω_t is the proportion of the population potentially 'present and able' to begin migration into the river, w_{t-1} is the average wind speed on day $t-1$; f_t is the effort, in days fished, on day t, and a_t is random error.

Migration can now be quantified as a product of the inherent time-density distribution of the population (Eq. 19 and 20), and the effects of daily wind speed and commercial effort (Eq. 26).

The time density of the population characterizes the proportion of the total population that is 'present and able' to enter the lower river. The effects of wind speed and removal of fish down river from the test nets modify the distribution of catch realized by the test fishery. The proportion of total catch $(C(t)/C_T)$ realized on day t is expressed as:

$$C(t)/C_T = Q(t)\omega_t \tag{27}$$

or

$$C(t)/C_T = Y'(t)\omega_t \tag{28}$$

for a normally or inverse exponentially distributed mixture of subpopulations respectively. Under the assumption of a single homogeneous population, $Q(t)$ and $Y'(t)$ are defined by equations 6 and 7, and assuming two or more subpopulations, $Q(t)$ and $Y'(t)$ are defined by equations 19 and 20.

Standard statistical procedures used to find the values of μ_j, σ^2_j, ρ_j, β_0, β_1, and β_2 for Eq. 27 $(j = 1 \text{ to } k)$ by minimizing the sum of squares, are to differentiate the expression

$$\sum_{t=1}^{n} \Big[[(C(t)/C_T) - \omega_t Q(t)] \Big]^2 \tag{29}$$

with respect to each of the parameters to be estimated, equate the expression to zero and solve the 3_{k+2} equations in terms of each parameter. The equations describing a mixture of normally-distributed subpopulations generate the following set of implicit equations which produce converging estimates of the parameters using an iterative procedure:

$$\mu_j = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[\omega_t q_j(t) - \omega_t^2 Q(t) q_j(t) t\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[\omega_t q_j(t) - \omega_t^2 Q(t) q_j(t)\right]}, \tag{30}$$

$$\sigma^2_j = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[\omega_t q_j(t) - \omega_t^2 Q(t) q_j(t) (t-\mu_j)^2\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[\omega_t q_j(t) - \omega_t^2 Q(t) q_j(t)\right]}, \tag{31}$$

$$\sigma_j = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[\omega_t[q_j(t)-q_k(t)] - \omega_t^2[q_j(t)-q_k(t)]\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[\omega_t^2[q_j(t)-q_k(t)]^2\right]} , \tag{32}$$

$$\beta_0 = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[Q(t) - Q(t)^2[\beta_1 w_{t-1}+\beta_2 f_t]\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] Q(t)^2} , \tag{33}$$

$$\beta_1 = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[Q(t)w_{t-1} - Q(t)^2 w_{t-1}[\beta_0+\beta_2 f_t]\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] Q(t)^2 w_{t-1}} , \tag{34}$$

and

$$\beta_2 = \frac{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] \left[Q(t)f_t - Q(t)^2 f_t[\beta_0+\beta_1 w_{t-1}]\right]}{\sum_{t=1}^{n} \left[\frac{C(t)}{Q(t)}\right] Q(t)^2 f_t} , \tag{35}$$

where all constants and variables are as defined previously, $Q(t)$ is defined by Eq. 19, and $q_j(t)$ by Eq. 17; and ω_t by Eq. 26. Having obtained estimates for μ_j and σ^2, a_j and b_j can be approximated according to relationships previously defined (equations 9 and 10). It should be noted that this system of equations does not always converge, due to round off error in the computer or the character of the equations themselves.

Regretably, Eq. 27 and Eq. 28, which express the proportions of total abundance as a function of time, wind speed, and fishing effort, do not satisfy the conditions defining a probability density function. The proportions do not necessarily sum to one, and depending on the value of $(\beta_0 + \beta_1 w_{t-1} + \beta_2 f_t)$, the proportions can assume values greater than one or less than zero. In order to meet the requirements of a probability density function, the expression $(\beta_0 + \beta_1 w_{t-1} + \beta_2 f_t)$ must be limited to values between zero and one. The other modification of equations 27 and 28 necessary to equate the area under the distribution to one can be developed within the context of the dynamics of the migration.

Cursory inspection of the distribution of daily catch (Figures 18-33) substantiates the observations of commercial fishermen and managers that a large immigration of chinook salmon into the lower Yukon River is a one or two day phenomenon, usually followed by an exceptionally low abundance of migrants. It is hypothesized that the 'offshore pool' of chinook salmon physiologically ready to migrate up river is temporarily depleted after a peak in migratory activity. In more general terms, the number of chinook salmon, $N(t)$, that migrate into the lower river on any given day t can be expressed as a percent of the sum of the number remaining behind on day $t-1$ and the daily increase in offshore numbers from offshore arrivals and physiological maturation:

$$N(t) = \omega_t [R'_{t-1} + Y'(t) N_T] \quad , \tag{36}$$

where ω_t is the percent of the 'offshore pool' that does begin the upriver journey on day t, R'_{t-1} is the number of potential migrants remaining from day $t-1$, $Y'(t)$ is the proportion of the total population that becomes able to migrate into the river on day t, and N_T is the total abundance of the population. The proportional complement of Eq. 36 is derived on dividing Eq. 36 by N_T:

$$N(t)/N_T = \omega_t [R'_{t-1}/N_T + Y'(t)] \tag{37}$$

As discussed above, it is assumed that the percent of offshore fish that do migrate up river is a linear function of wind. Redefining ω_t as a linear function solely of wind speed

$$\omega_t = \beta_0 + \beta_1 w_{t-1} \tag{38}$$

and constraining by the condition that $0 < \omega_t < 1$, R'_{t-1} is equivalent to $1-\omega_{t-1})$ of the potential immigrants on day $t-1$. The expression quantifying the proportion of total abundance present in the lower Yukon delta on day t is:

$$N(t)/N_T = (\beta_0 + \beta_1 w_t)[R_{t-1} + Y'(t)] \tag{39}$$

where $Y'(t)$, assuming a single homogeneous population, is defined by Eq. 7, and

$$R_{t-1} = R'_{t-1}/N_T = (1-\omega_t)[N(t)/N_T] \tag{40}$$

Under the condition that $0 < \omega_t = \beta_0 + \beta_1 w_{t-1} < 1$, and since the integral of $\beta_0 + \beta_1 w_{t-1})[R_{t-1} + Y'(t)]$ equals one over the integral $-\infty$ to $+\infty$, Eq 39 does satisfy the requirement for a probability density function.

The test fishery catch $C(t)$ is a function of the number of fish migrating up the Yukon River and the commercial effort surrounding the test fishery sites on day t. Given that the test fishery catch is directly proportional to daily abundance in the lower river on days of no commercial effort, and directly proportional to a fraction of the total abundance of total abundance of total abundance on days of commercial effort, the fraction being a linear function of effort (f_t), the following relationship can be derived:

$$C(t)/C_T = [1-\beta_2 f(t)][N(t)/N_T] \tag{41}$$

where constants and variables have been previously defined. Equating Eq. 39 to Eq. 41,

$$[C(t)/C_T]/(1-\beta_2 f(t)) = N(t)/N_T = (\beta_0 + \beta_1 \omega_t)[R_{t-1}/N_T + Y'(t)] \tag{42}$$

As was the case for Eq. 19, the method of maximum likelihood can be utilized to obtain estimates for the parameter a, b, β_0, β_1, and β_2. Letting

$Z(t) = [C(t)/C_T]/(1-\beta_2 f(t))$, the natural logarithm of the likelihood function, $Ln\ L$, is:

$$\begin{aligned} Ln\ L = {} & Z(1)(\omega_1)(Y'(1) + R_0) + Z(2)(\omega_2)(Y'(2) + R_1) + \ldots + \\ & Z(t)(\omega_t)(Y't) + R_{t-1}) + \ldots. + Z(n)(\omega_n)(Y'(n) + R_{n-1}) \ , \end{aligned} \tag{43}$$

where n is the total number of observations.

To develop an expression for R_0, which is a function of the migratory history of the population before the test fishery begins, regressing backwards in time:

$$R_0 = (1-\omega_0)[Q(0) + R_{-1}] \ . \tag{44}$$

Since

$$R_{-1} = (1-\omega_1)[Q(-1) + R_{-2}] \tag{45}$$

the expression for R_{-1} can be substituted into Eq. 44, giving

$$R_0 = (1-\omega_0)[Q(0)] + (1-\omega_0)(1-\omega_{-1})[Q(-1) + R_{-2}] \ . \tag{46}$$

Therefore, if Eq. 35 is expanded backwards in time to $t = -\infty$, it follows by induction that:

$$R_0 = \sum_{t=-\infty}^{0} Y'(t) \prod_{k=t}^{0} (1-\omega_k) \tag{46}$$

Equation 47 can be simplified by either assuming that all the fish arriving offshore during time interval [$-\infty$, 0] which are physiologically able have immigrated the day before nets were set (day 1) (i.e., at t = 0, ω_t = 1, and R_0 = 0), or no fish have entered the lower Yukon delta prior to day 1 (i.e., at t = 0, $\omega_{-\infty}$ to ω_0 = 0, and

$$\prod_{k=t}^{0} (1-\omega_k) = 1 \tag{48}$$

Therefore, under the second assumption, the number of chinook salmon remaining in the 'offshore pool' on day 1 is

$$R_0 = \sum_{t=-\infty}^{0} Y'(t) \quad . \tag{49}$$

$Y'(t)$ can be integrated exactly over the interval of $-\infty$ to 0:

$$R_0 = 1/(1+\exp(-(a))) \tag{50}$$

The difference in parameter values assuming either total offshore depletion or total offshore retention is minimal. The latter assumption is considered to be more realistic in view of the observations of other investigators that many salmon populations mill offshore for various periods of time before ascending their home river, the supposed difficulty in entering the Yukon River during ice breakup, and the promptness of test net placement after breakup. Taking the partial derivative of Eq. 38 with respect to each of the parameters (a, b, β_0, and β_1), setting the resulting expressions equal to zero, and solving for each of the parameters, the following set of implicit equations are derived: for a

$$a = \frac{\displaystyle\sum_{t=1}^{n} \left[\frac{Z(t)}{Y'(t)+R_{t-1}}\right]\left[\frac{(a)(b)\exp(-(a+bt))}{(1+\exp(-(a+bt)))^2} + \frac{\partial R_{t-1}}{\partial a}\right]}{\displaystyle\sum_{t=1}^{n} \left[\frac{Z(t)}{Y'(t)+R_{t-1}}\right]\left[\frac{2(b)\exp(-2(a+bt))}{(1+\exp(-(a+bt)))^2}\right]} \quad , \tag{51}$$

where,

$$\partial R_t/\partial a = (1-\omega_t)\left[\frac{\partial Y'(t)}{\partial a} + \frac{\partial R_{t-1}}{\partial a}\right], \tag{52}$$

$$\frac{\partial Y'(t)}{\partial a} = \frac{2b\exp(-2(a+bt))}{(1+\exp(-(a+bt)))^2} - \frac{b\exp(-(a+bt))}{(1+\exp(-(a+bt)))^2} \tag{53}$$

and

$$\partial R_0/\partial a = \exp(-a)/(1+\exp(-a))^2 \ . \tag{54}$$

For b,

$$b = \frac{\sum_{t=1}^{n}\left[\frac{Z(t)}{Y'(t)+R_{t-1}}\right]\left[\frac{2(t)b\exp(-2(a+bt))}{(1+\exp(-(a+bt)))^2} + \frac{\exp(-(a+bt))}{(1+\exp(-(a+bt)))^2} + \frac{\partial R_{t-1}}{\partial_b}\right]}{\sum_{t=1}^{n}\left[\frac{Z(t)}{Y'(t)+R_{t-1}}\right]\left[\frac{t(\exp(-(a+b))}{(1+\exp(-(a+bt)))^2}\right]}, \tag{55}$$

where

$$\partial R_t/\partial b = (1-\omega_t)\left[\frac{\partial Y'(t)}{\partial b} + \frac{\partial R_{t-1}}{\partial b}\right] , \tag{56}$$

$$\frac{\partial Y'(t)}{\partial b} = \frac{2(t)(b)\exp(-2(a+bt))}{(1+\exp(-(a+bt)))^2} - \frac{(t)(b)\exp(-(a+bt))}{(1+\exp(-(a+bt)))^2} + \underline{\exp(-(a+bt))} ,$$

$$(1+\exp(-(a+bt)))^2 \tag{57}$$

and

$$\partial R_0/\partial b = 0 \ . \tag{58}$$

For β_0:

$$\beta_0 = \frac{\sum_{t=1}^{n}\left[\frac{Z(t)}{(\omega_t)(Y'(t)+R_{t-1}}\right]\left[(\beta_0)[Y'(t) + \partial R_{t-1}/\partial\beta_0]\right]}{\sum_{t=1}^{n}\left[\frac{Z(t)}{Y'(t)+R_{t-1}}\right]\left[-\partial R_{t-1}/\beta_0\right]}, \tag{59}$$

where

$$\partial R_t/\partial\beta_0 = (1-\omega_t)\left[\frac{\partial R_{t-1}}{\partial\beta_0}\right] - Y'(t-1) - R_{t-2} \ , \tag{60}$$

and

$$\partial R_0/\partial \beta_0 = 0 \quad , \tag{61}$$

and for β_1:

$$\beta_1 = \frac{\sum_{t=1}^{n} \left[\frac{Z(t)}{(\omega_t)(Y'(t)+R_{t-1})}\right] \left[(\beta_1 w_t)[Y'(t) + \partial R_{t-1}/\partial \beta_1]\right]}{\sum_{t=1}^{n} \left[\frac{Z(t)}{Y'(t)+R_{t-1}}\right] \left[-\partial R_{t-1}/\beta_1]\right]} \quad , \tag{62}$$

where

$$\partial R_t/\partial \beta_1 = (1-\omega_t)\left[\frac{\partial R_{t-1}}{\partial \beta_1}\right] - w_t\ [Y'(t-1) - R_{t-2}] \tag{63}$$

and

$$\partial R_0/\partial \beta_1 = 0 \quad . \tag{64}$$

The value of β_2 is not known but can be approximated by regressing the ratio of observed catch to expected catch ignoring the effect of commercial effort $[(C(t)/C_T)/Z(t)]$ against effort with a given intercept of one (when effort = 0, $C(t)/C_T = Z(t)$):

$$\beta_2 = \frac{\sum_{t=1}^{n} (ft) \left[\frac{C(t)/C_T}{\omega_t (C_T)(Y'(t)+R_{t-1})} - 1\right]}{\sum_{t=1}^{n} f_t^2} \tag{65}$$

At each iteration, a new β_2 was calculated for the new estimates of the parameters. Parameters a and b were estimated by substituting the normal equation into equations 51 and 54, solving for the mean and variance, and approximating a and b according to the relationships $a = (-b)\mu$ and $b = \pi^2/(3\sigma^2)$. Equations 58 and 61 were solved by bisection of the i^{th} and $i+1^{th}$ iteration values of β_0 and β_1.

Deciding which function to use for the intraseason prediction of daily and total abundance requires that several factors of quantitative importance be evaluated to assess the relative benefits to management. The following criteria are employed in the present study. The measure of fit of each model is defined as the sum of squared deviations. The ability to predict daily abundance for each year is expressed in terms of the relative daily error of prediction:

$$\text{Relative daily error} = \frac{1}{n} \sum_{t=1}^{n} (| \text{expected} - \text{observed} |) \tag{66}$$

Time of convergence is used to quantify the ability of each model to accurately predict total abundance from expected cumulative proportions of total abundance, where forecasted total abundance is the ratio of the cumulative catch on day t over the expected cumulative proportions on day t (Walters and Buckingham, 1965). The criteria comparing time of convergence is the earliest day that a posteriori predicted total catch remains within either 20%, or 50% of observed total catch.

RESULTS

Five equations expressing the daily proportion of total catch as either a function of calendar day or a function of daily average wind speed, fishing effort, and calendar day were fitted to observed 1979, 1980, and 1981 Big Eddy daily test fishery catch; 1980, and 1981 Middle Mouth daily test fishery catch; total 1980 and 1981 daily test fishery catch, and the 1968 to 1978 Flat Island test fishery catch. Estimates of the parameter values were obtained either by maximizing the likelihood function or minimizing the sum of squares. For conciseness, the five equations will be designated by number, as model one, M_1, to model five, M_5. The standard normal distribution equation (Eq. 6) will be referred to as M_1. The function describing a mixture of two subpopulations (Eq. 15), M_2, is fitted to the data by maximization of the likelihood function. Model three quantifies daily abundance at the test fishery sites as a product of the effects of removal of chinook salmon by commercial effort and daily wind speed on a single homogeneous population (Eq. 27, $Q(t)$ defined by Eq. 6). Model four describes the results of the same environmental perturbations on a mixture of two subpopulations (Eq. 27, $Q(t)$ defined by Eq. 15). Both M_3 and M_4 are fitted by minimization of the sum of squares. Model five (Eq. 42) is analogous to M_3 and fitted by maximization of the likelihood function.

An F-test comparison of the M_1 residuals of the first and fourth quartiles of the time density distributions with those of the central second and third quartiles demonstrates that the variance of the residuals near the mean day of the migration is significantly larger than the residual variance of the tails of the time distribution (Tables 7 and 9). Fourteen of the 18 time densities were characterized by significantly larger residual variances near the center of the distribution at the $P < .01$ level. The cube root transformation was found to be satisfactory for attaining homogeneity of variances. The results of fitting M_1 to transformed data are presented in Tables 8 and 10. Only the 1969 Flat Island and 1979 Big Eddy residuals remain heterogeneous. For consistency, the cube root transformation was retained for all minimizations of sum of squares calculations.

The fit of M_1 to daily catch is summarized in Tables 8 and 10, and depicted for the representative years of 1972, 1977, and 1981 (Figures 18 to 20). Although each distribution of observed catch over time can be described as somewhat bell-shaped, with a larger proportion of the observed catch concentrated near the mean of the migration (Figure 19), large daily deviations from expected values of catch occur. Several time densities manifest a bimodal (1968, 1969, and 1972 Flat Island catch (Figure 18), pronounced right skewed (1974 and 1978 Flat Island catch, and

Table 7. Estimated values of the mean and variance of the normal curve equation, F-values from the test of significance for differences in variances between the first and last quartile and the center quartile, and the resulting sum of squared deviations from the fitted model.

Year	Site	Mean	Variance	F-value	Probability	Sum of Squares
1979	Big Eddy	13.908	110.899	13.003	P < .01	.0428138
1980	Big Eddy	14.885	62.476	3.444	P < .01	.0107782
1980	Middle Mouth	19.366	79.650	6.012	P < .01	.0148250
1980	Total Test Fishery	17.825	78.273	5.433	P < .01	.0112911
1981	Big Eddy	16.264	103.561	1.646	NS	.0116698
1981	Middle Mouth	14.567	81.889	6.082	P < .01	.0115667
1981	Total Test Fishery	15.437	93.716	3.140	P < .01	.0104684
Average		16.036	87.208			.0162029

Table 8. Estimated values of the mean and variance of the normal curve equation, F -values from the test of significance for differences in variances between the first and last quartile and the center quartile, and the resulting sum of squared deviations from the fitted model. Data are the cube roots of reported test fishery catches for the years 1979 through 1981.

Year	**Site**	**Mean**	**Variance**	**F-value**	**Probability**	**Sum of Squares**
1979	**Big Eddy**	**16.435**	**162.666**	**2.701**	**P = .01**	**.0500352**
1980	**Big Eddy**	**17.681**	**121.066**	**1.205**	**N S**	**.0151434**
1980	**Middle Mouth**	**21.459**	**128.922**	**2.148**	**P = .05**	**.0231644**
1980	**Total Test Fishery**	**20.113**	**136.627**	**1.418**	**N S**	**.0180163**
1981	**Big Eddy**	**18.654**	**143.169**	**1.335**	**N S**	**.0224473**
1981	**Middle Mouth**	**18.136**	**133.840**	**1.661**	**N S**	**.0227938**
1981	**Total Test Fishery**	**18.590**	**143.158**	**1.041**	**N S**	**.0217933**
Average		**18.724**	**138.493**			**.0247703**

Table 9. Estimated values of the mean and variance of the normal curve equation, F-values from the test of significance for differences in variances between the first and last quartile and the center quartile, and the resulting sum of squared deviations from the fitted model. Data are the reported test fishery catches of Flat Island for the years 1968 through 1978.

Year	Site	Mean	Variance	F-value	Probability	Sum of Squares
1968	Flat Island	17.538	51.561	1.756	N S	.0213495
1969	Flat Island	14.482	54.484	10.389	P < .01	.0435148
1970	Flat Island	21.155	49.813	7.927	P < .01	.0248546
1971	Flat Island	29.213	64.653	1.348	N S	.0198836
1972	Flat Island	26.359	86.561	3.040	P = .01	.0324197
1973	Flat Island	20.568	78.843	5.021	P < .01	.0250178
1974	Flat Island	13.566	64.836	7.879	P < .01	.0154573
1975	Flat Island	27.366	40.246	10.467	P < .01	.0400488
1976	Flat Island	30.373	25.032	2.668	P = .04	.0247959
1977	Flat Island	28.205	33.941	4.903	P < .01	.0199380
1978	Flat Island	12.612	95.147	2.756	P = .01	.0176815
Average		23.295	89.137			.0055124

Table 10. Estimated values of the mean and variance of the normal curve equation, F-values from the test of significance for differences in variances between the first and last quartile and the center quartile, and the resulting sum of squared deviations from the fitted model. Data are the cube roots of reported Flat Island test fishery catches for the years 1968 through 1978.

Year	Site	Mean	Variance	F-value	Probability	Sum of Squares
1968	Flat Island	18.781	74.574	1.134	N S	.0299347
1969	Flat Island	16.990	84.974	4.972	P < .01	.0572191
1970	Flat Island	22.122	79.380	1.704	N S	.0285834
1971	Flat Island	28.855	82.078	1.419	N S	.0271098
1972	Flat Island	26.973	91.428	1.402	N S	.0482256
1973	Flat Island	22.066	105.390	1.183	N S	.0329826
1974	Flat Island	17.569	132.281	1.195	N S	.0280416
1975	Flat Island	27.591	64.343	1.526	N S	.0449112
1976	Flat Island	30.464	48.034	1.799	N S	.0238994
1977	Flat Island	28.007	69.563	1.550	N S	.0190051
1978	Flat Island	16.827	148.476	1.162	N S	.0279536
Average		23.295	89.137			.0334424

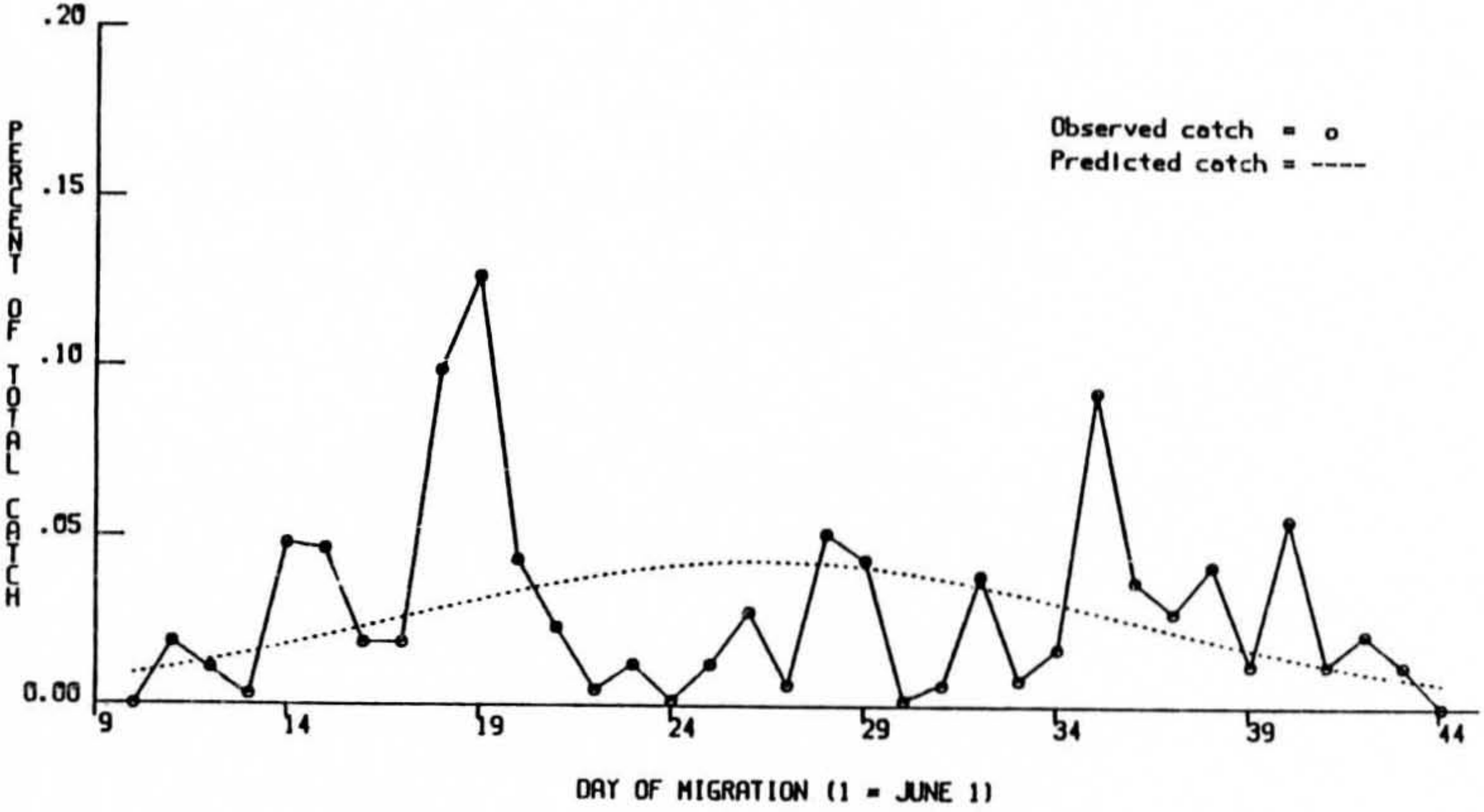

Figure 18. Observed daily proportions of total catch and expected proportions of total catch from model one for 1972 Flat Island catches.

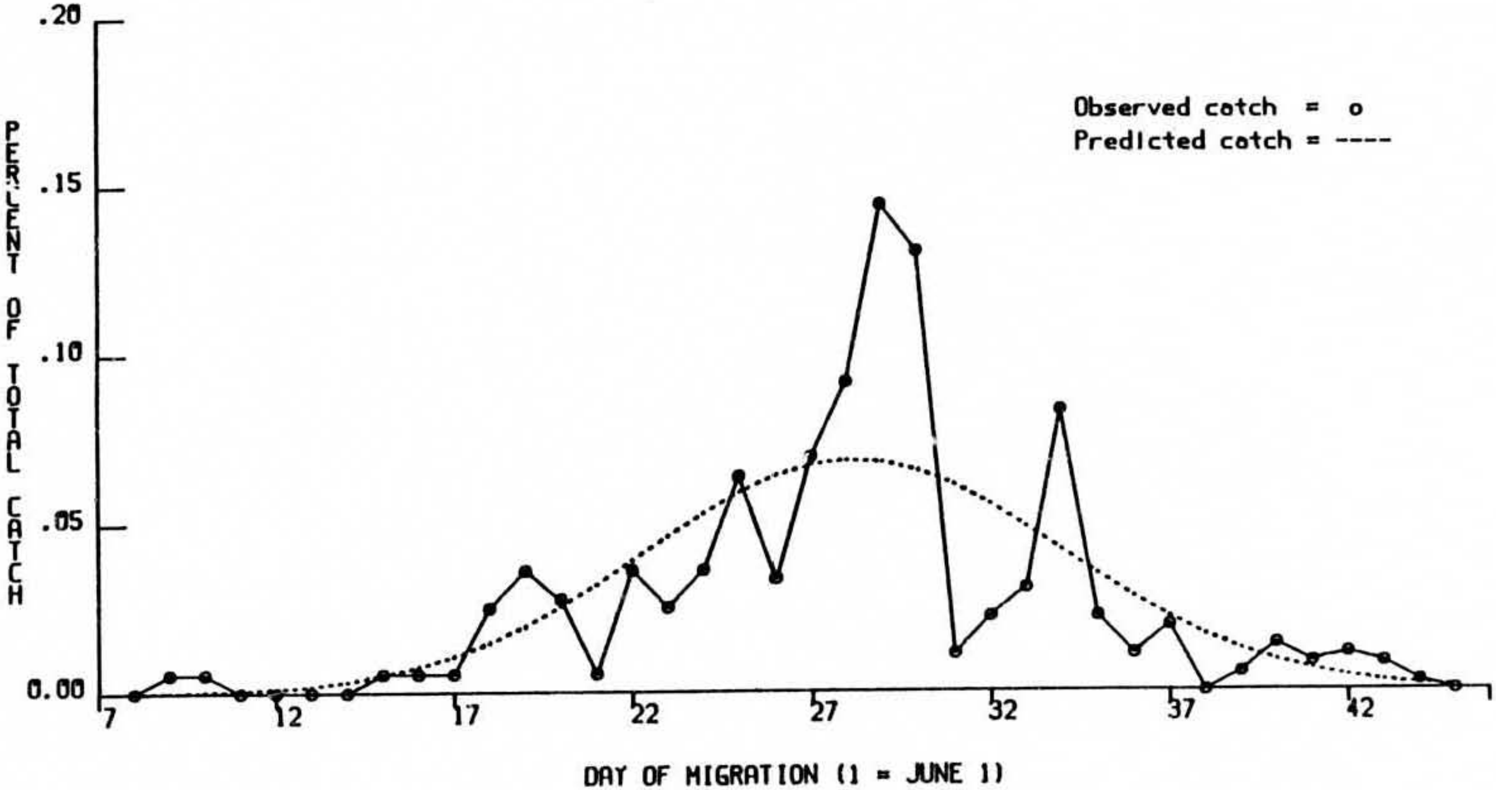

Figure 19. Observed daily proportions of total catch and expected proportions of total catch from model one for 1977 Flat Island catches.

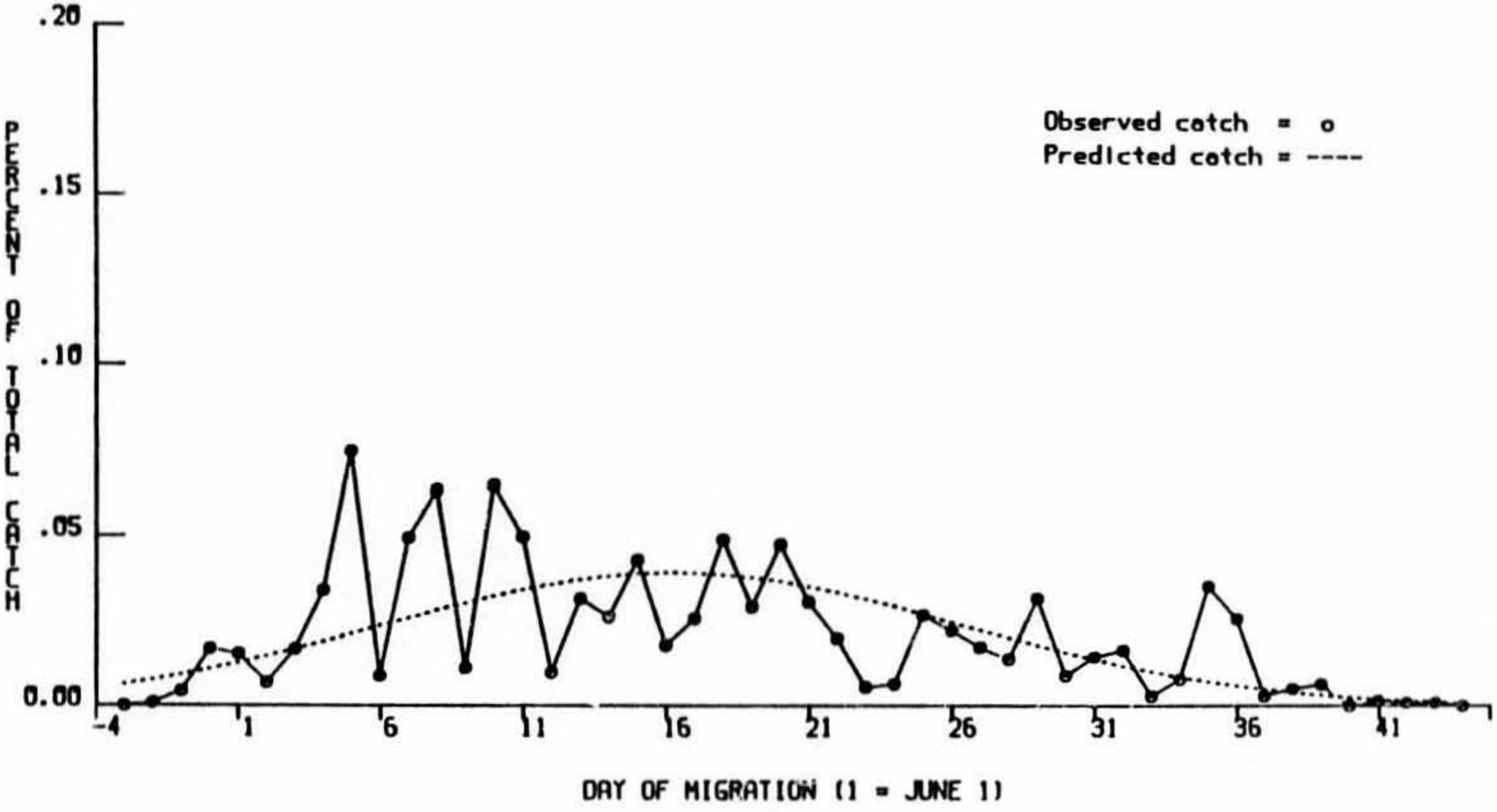

Figure 20. Observed daily proportions of totai catch and expected proportions of total catch from model one for 1981 Flat Island catches.

1981 Big Eddy [Figure 20] and Middle Mouth test fishery catch), or left skewed character (1971 Flat Island and 1980 Big Eddy catch).

The fluctuations of daily catch for 1972, 1977, and 1981 are portrayed in Figures 18-20. A peak catch of almost four times the expected catch was observed on 19 June 1972 (Figure 18). Large daily catches, over three times the expected daily catch, were recorded on 9 June 1969; 17 June 1973; 22 June 1975; and 7 June and 11 June 1979. Large peaks in chinook salmon abundance were generally a one-day phenomenon: (5 July 1972 [Figure 18]; 4 July 1977 [Figure 19]; and 5 June 1981 [Figure 20]; also 9 June 1969; 18 June 1970; 17 June 1973; 3 July 1976; 2 June and 4 June 1978; 7 June and 11 June at Big Eddy, 1979; 21 June at Middle Mouth, 1980; and 5 June at Big Eddy, 1981) or two days (18-19 June 1972 [Figure 18]; 29-30 June 1977 [Figure 19]); and 7-8 June, 10-11 June, and 5-6 July at Big Eddy, 1981 (Figure 20); also 22-23 June, 1975; 30 June - 1 July 1976; 14-15 June at Middle Mouth, 1980) followed by unusually poor catches. Smaller than expected catches near the midpoint of migration were a multi-day feature of several annual distributions (for example 21-27 June 1972 (Figure 18); also 14-18 June 1968; 12-18 June 1969; 18-23 June 1973; 24-28 June 1975; 12-18 June 1978; 12-16 June 1979; and 12-17 June 1981 Middle Mouth catch). The conventional bell-shaped curve generated by M_1 provides a relatively poor fit to such skewed and variable observations.

The mean and variance of the catch distribution do provide a uniform and computationally simple means to define the location and dispersion of the migration in time. Values are relatively consistent (means range from 13 June to 30 June; variances range from 25 days^2 to 111 days^2 (Tables 7 and 9) and comparable to Nushagak Bay chinook salmon catch data (means ranging from 16 June to 29 June; variances range from 42 days^2 to 147 days^2 [Mundy et al. 1979]) and the Bristol Bay sockeye salmon migrations (means range from 30 June to 9 July; variances range from 19 days^2 to 42 days^2 [Mundy 1979]). The means of the Flat Island test fishery catch are apparently later and the variances smaller than those of the Big Eddy and Middle Mouth test fisheries. This is a result of the warmer-than-average springs preceding the 1979, 1980, and 1981 chinook migrations and will be discussed later. The mean and variance of the Big Eddy test fishery catch does not appear to be predictably different from that of Middle Mouth. Big Eddy's 1980 mean date of catch was approximately 4 days earlier and the variance of catch 17 days^2 smaller than the mean date and variance of Middle Mouth catch. However, the 1981 results are reversed, with the mean date of Middle Mouth catch being two days earlier and variance 22 days^2 smaller than the mean date and variance of Big Eddy catch (Table 7). Although, based on only 2 years of observations, no large differences were found between the Big Eddy and Middle Mouth catch distributions; subtle differences in the time densities of the South Mouth and Middle Mouth may become apparent after several more years of data have been collected.

Although M_2, which quantifies the migratory timing of a mixture of two subpopulations, poorly predicts unexpectedly large or small daily test fishery catches, it adequately describes multi-day departures from a bell-shaped distribution (Tables 11-14). Migratory distributions which are ostensibly bimodal in character are well approximated by M_2 (for example the 1972 Flat Island test fishery (Figure 21). Skewed distributions are also better described by a two population model. Right-skewed time densities are best fitted by a model consisting of an early subpopulation with small variance and a late subpopulation of larger vari-

Table 11. The estimated values of the mean and variance of the earlier subpopulation, the proportion of the total population assigned to the earlier subpopulation, the mean and variance of the later subpopulation, and the proportion assigned to the later subpopulation. The model assumes a mixture of two subpopulations (model two, equation 15) and is fitted by maximization of its likelihood function. Untransformed data are used from the Big Eddy and Middle Mouth test fishery operations.

Year	Site	Earlier Mean	Earlier Variance	Later Mean	Later Variance	Proportions Early	Proportions Late	Sum of Squares
1979	Big Eddy	7.770	29.663	26.052	49.616	.664	.336	.0374620
1980	Big Eddy	4.669	2.313	16.319	54.217	.123	.877	.0095245
1980	Middle Mouth	15.370	32.651	31.746	22.526	.756	.244	.0128546
1980	Test Fishery	14.750	37.808	31.946	21.300	.821	.179	.0097846
1981	Big Eddy	7.193	14.065	21.507	80.240	.366	.634	.0091378
1981	Middle Mouth	6.712	12.280	20.029	57.554	.410	.590	.0082660
1981	Test Fishery	6.889	12.784	20.601	71.796	.377	.623	.0076375
Average		9.050	20.223	24.029	51.036	.498	.502	.0135229

Table 12. The estimated values of the mean and variance of the earlier subpopulation, the proportion of the total population assigned to the earlier subpopulation, the mean and variance of the later subpopulation, and the proportion assigned to the later subpopulation. The model assumes a mixture of two subpopulations (model two, equation 15) and is fitted by minimization of the sum of squared deviations. Data are cube roots of Big Eddy and Middle Mouth test fishery catches. * signifies that the variance of the residuals in the centered half of the distribution is significantly different from the variance in the tail quartiles.

Year	Site	Earlier Mean	Earlier Variance	Later Mean	Later Variance	Proportions		Sum of Squares
						Early	Late	
1979	Big Eddy	5.440	72.769	27.616	81.800	.539	.461	.0434110
1980	Big Eddy*	4.516	3.808	16.810	144.267	.071	.929	.0149022
1980	Middle Mouth	14.254	74.004	33.667	48.083	.659	.341	.0161843
1980	Test Fishery	13.981	92.445	34.376	40.745	.742	.258	.0139148
1981	Big Eddy	8.674	64.168	28.842	77.432	.543	.457	.0093344
1981	Middle Mouth	4.962	22.487	21.006	136.901	.226	.774	.0117835
1981	Test Fishery	5.452	26.696	22.311	149.944	.239	.761	.0106294
Average		8.181	50.910	26.377	97.024	.431	.569	.0171629

Table 13. The estimated values of the mean and variance of the earlier subpopulation, the proportion of the total population assigned to the earlier subpopulation, the mean and variance of the later subpopulation, and the proportion assigned to the later subpopulation. The model assumes a mixture of two subpopulations (model two, equation 15) and is fitted by minimization of the sum of squared deviations. Data are cube roots of Flat Island test fishery catches. * signifies that the variance of the residuals in the centered half of the distribution is significantly different from the variance in the tail quartiles.

Year	Site	Earlier	Earlier	Later	Later	Proportions		Sum of
		Mean	Variance	Mean	Variance	Early	Late	Squares
1968	Flat Isl.	8.948	6.922	21.447	73.478	.207	.793	.0179039
1969	Flat Isl.	7.982	14.793	22.947	49.237	.401	.599	.0381016
1970	Flat Isl.	19.971	78.165	35.403	6.011	.879	.121	.0271074
1971	Flat Isl.	24.526	69.209	39.938	9.216	.766	.234	.0173344
1972	Flat Isl.	17.521	20.927	35.146	40.045	.444	.556	.0232732
1973	Flat Isl.	10.677	31.406	27.250	87.639	.330	.670	.0256612
1974	Flat Isl.	9.063	40.571	26.067	127.688	.517	.483	.0172290
1975	Flat Isl.	23.104	33.969	34.110	37.503	.537	.463	.0408688
1976	Flat Isl.	21.301	5.698	31.365	45.534	.107	.893	.0323846
1977	Flat Isl.	26.516	56.264	29.554	44.035	.816	.184	.0279093
1978	Flat Isl.*	3.220	10.392	19.029	169.317	.199	.808	.0154996
Average		15.712	33.483	30.219	62.701	.472	.528	.0257509

Table 14. The estimated values of the mean and variance of the earlier subpopulation, the proportion of the total population assigned to the earlier subpopulation, the mean and variance of the later subpopulation, and the proportion assigned to the later subpopulation. The model assumes a mixture of two subpopulations (model two, equation 15) and is fitted by maximization of its likelihood function. Untransformed data are used, from Flat Island test fishery operations.

Year	Site	Earlier Mean	Earlier Variance	Later Mean	Later Variance	Proportions Early	Proportions Late	Sum of Squares
1968	Flat Isl.	9.827	4.507	21.688	27.659	.350	.650	.013398
1969	Flat Isl.	8.925	6.809	22.155	18.799	.580	.420	.025946
1970	Flat Isl.	19.875	34.820	34.947	3.493	.915	.085	.023396
1971	Flat Isl.	25.797	37.452	39.622	3.645	.753	.247	.013948
1972	Flat Isl.	17.519	7.582	34.197	25.862	.470	.530	.019908
1973	Flat Isl.	13.801	22.191	27.625	40.365	.510	.490	.023977
1974	Flat Isl.	10.039	19.394	22.435	69.138	.715	.285	.010045
1975	Flat Isl.	26.026	29.518	37.745	1.724	.886	.114	.037579
1976	Flat Isl.	23.760	0.189	31.091	22.466	.098	.902	.019317
1977	Flat Isl.	27.937	43.358	29.124	0.606	.774	.226	.007951
1978	Flat Isl.	3.516	5.171	17.223	77.554	.336	.664	.011282
Average		17.004	19.181	28.893	26.481	.581	.419	.018797

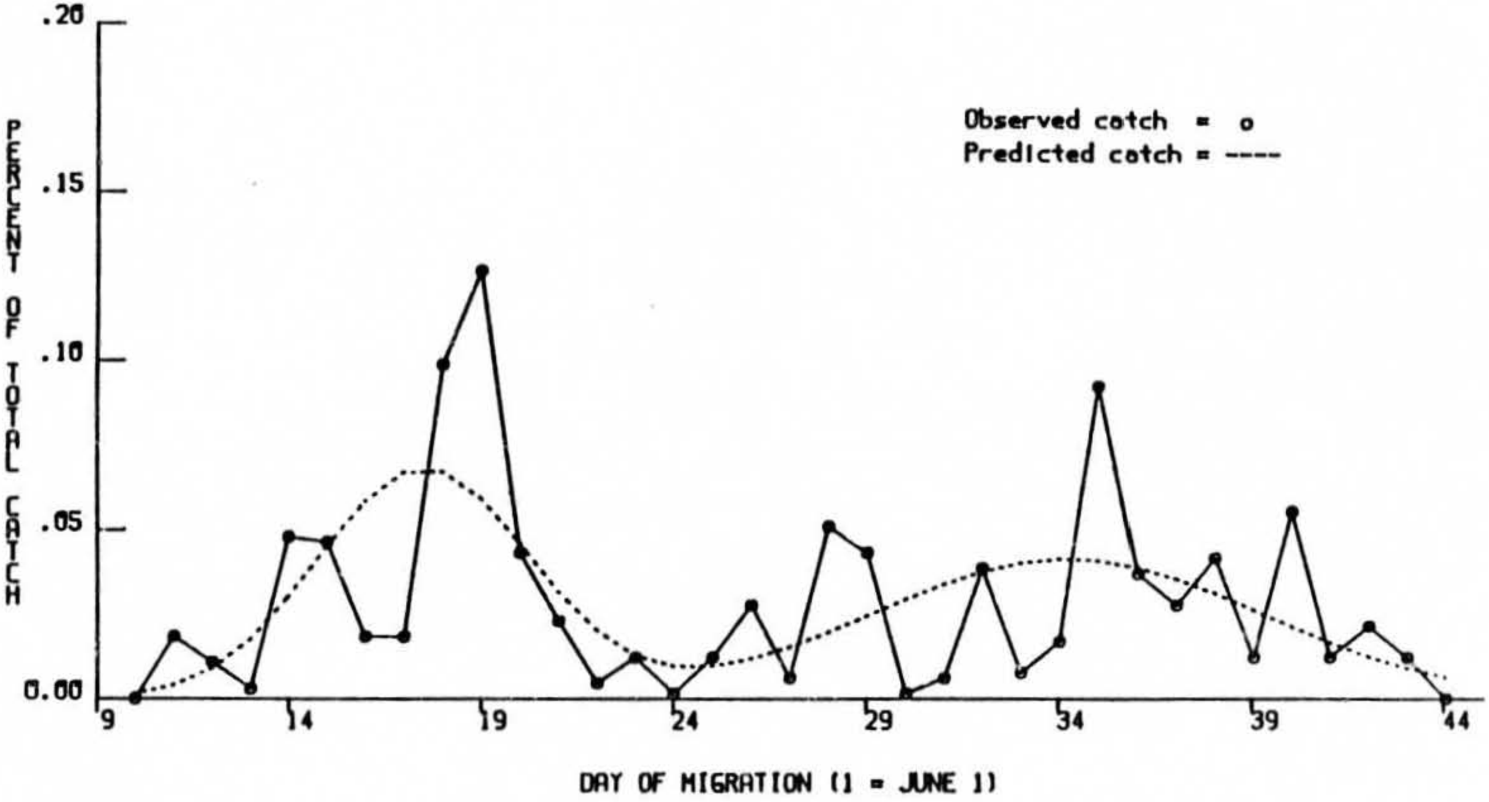

Figure 21. Observed daily proportions of total catch and expected proportions of total catch from model two for 1972 Flat Island catches.

ance (for example the 1981 Big Eddy test fishery catch [Figure 22]; also 1974 and 1978 Flat Island; and 1981 Middle Mouth test fishery catch) (Tables 11 - 14). Left skewed distributions are approximated by a model consisting of an early subpopulation with a relatively large variance and a later subpopulation with smaller variance (1971 Flat Island).

The most common pattern of the temporal distribution of catch and the resulting fit of M_2 is illustrated by the 1981 test fishery catch of Big Eddy (Figure 22), where large fluctuations in daily catch (4 June through 12 June) are followed by a relatively moderate and stable catch of 5 days, which in turn is succeeded by a week of higher and more variable catches. Model two defines both 1981 Big Eddy and Middle Mouth catch distributions as a composite of an early subpopulation comprising about 40% of the total population, and less dispersed about its mean date of 7 June; and a later more temporally dispersed population centered around the mean dates of 21 June to 22 June (Table 11). The two subpopulations correspond very closely to the more variable first two weeks of the migration, and the more consistent later four weeks of the migration. Similar temporal patterns were evident in the Big Eddy test fishery catch of 1979. Two large catches on 7 June and 11 June were allocated to the earlier subpopulation and a less-variable (30 days^2) series of catches from 13 June to 13 July corresponded to a later subpopulation of larger variance (50 days^2). The 9 June peak catch of 1969, 18 June and 21 June peak catches of 1979, 19 June peak catch of 1972 (Figure 21), 17 June peak catch of 1973, 10 June and 13 June peak catch of 1974, and 14, 15, and 21 June peak Middle Mouth catch of 1980 were allocated to the early and less dispersed subpopulation of the fitted model (see Tables 11-14). The 1968 and 1976 Flat Island and 1980 Big Eddy catch were also best approximated by a mixture of a less dispersed earlier subpopulation and a later subpopulation with a large variance although larger catches were apportioned to the later subpopulations (19, 22, and 24 June of the 1968 Flat Island catch; 30 June - 3 July of the 1976 Flat Island catch; and 10 June - 20 June of the 1980 Big Eddy catch). The distributions of 1971 and 1975 were characterized by a late peak in catch (10 July 1971 and 7 July 1975) which resulted in the best approximation to the distribution being a combination of an earlier subpopulation with a large variance and a later subpopulation with a smaller variance. Of the 14 years of test fishing catch, the leptokurtic distribution of 1977 (Figure 23) was unique in the small differences in means (28 June and 29 June). The form of a combined distribution of two populations with coincident means but different variances is well-illustrated by the 1977 time distribution of catch (Figure 23).

A comparison of the means, variances, and proportions of M_2 fitted to the data by maximization of the likelihood function (Tables 11 and 13) and by minimization of the square residuals of transformed data (Tables 12 and 14) reveals consistent differences in parameter values. The earlier means of the transformed data are smaller than corresponding earlier means of untransformed data. Considering the tendency of the cube root transformation to smooth at large fluctuations in catch, the fact that the variances of both early and late subpopulations of the transformed data are larger than those of the untransformed data is expected. The differences between late means and proportions of transformed and untransformed data demonstrated no obvious trend. The relationships between the fitted parameters of M_2 are as yet ambiguous. Tendencies are noted for the variances of the later subpopulations to be larger than those of earlier subpopulations. The relative abundance of each subpopulation is not consistently greater than 50%, although some individual proportions differ decidedly from 50% (see 1980 Big Eddy and 1980 total test fishery catch; Tables 11 and 13).

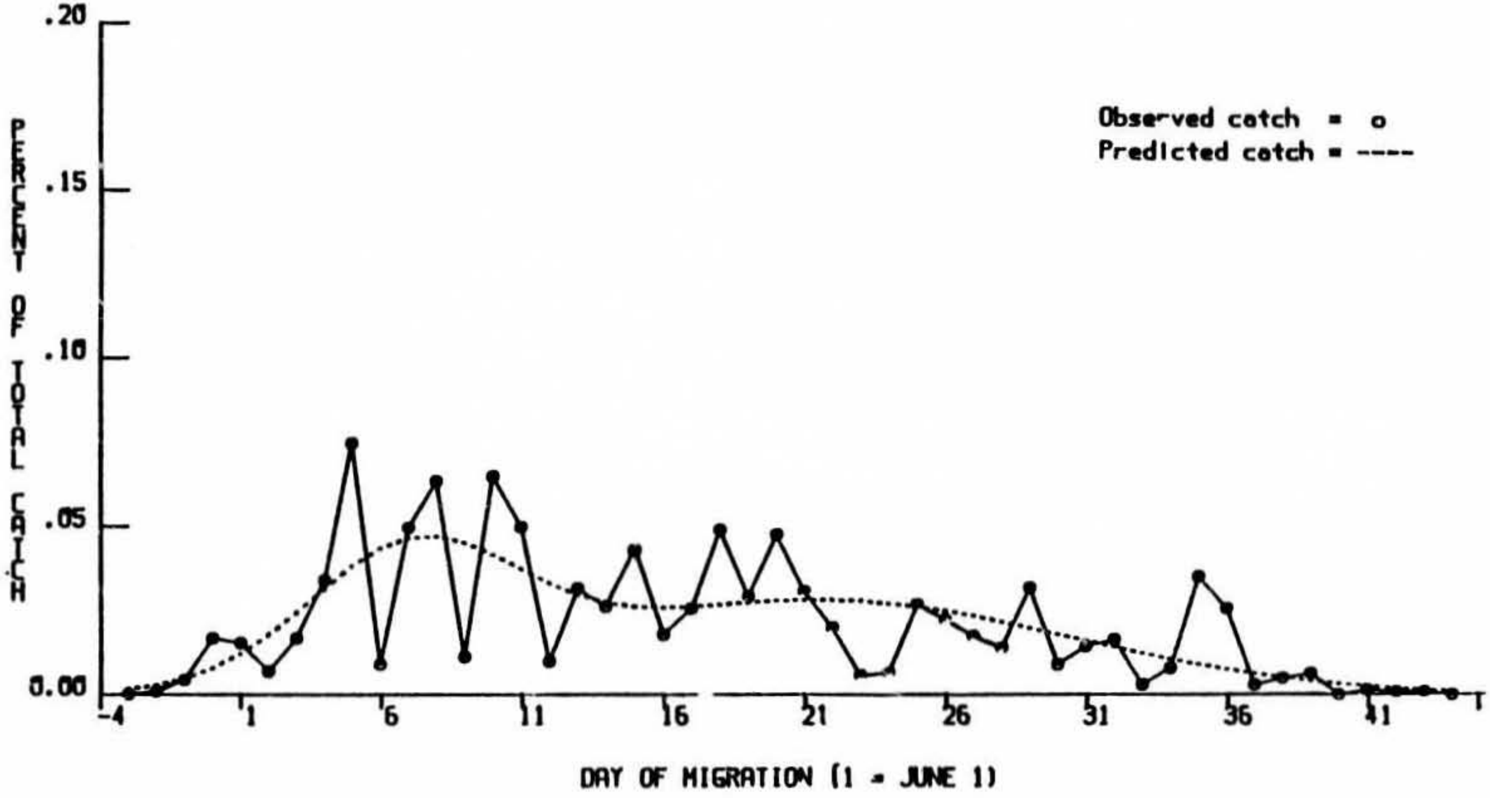

Figure 22. Observed daily proportions of total catch and expected proportions of total catch from model two for 1981 Flat Island catches.

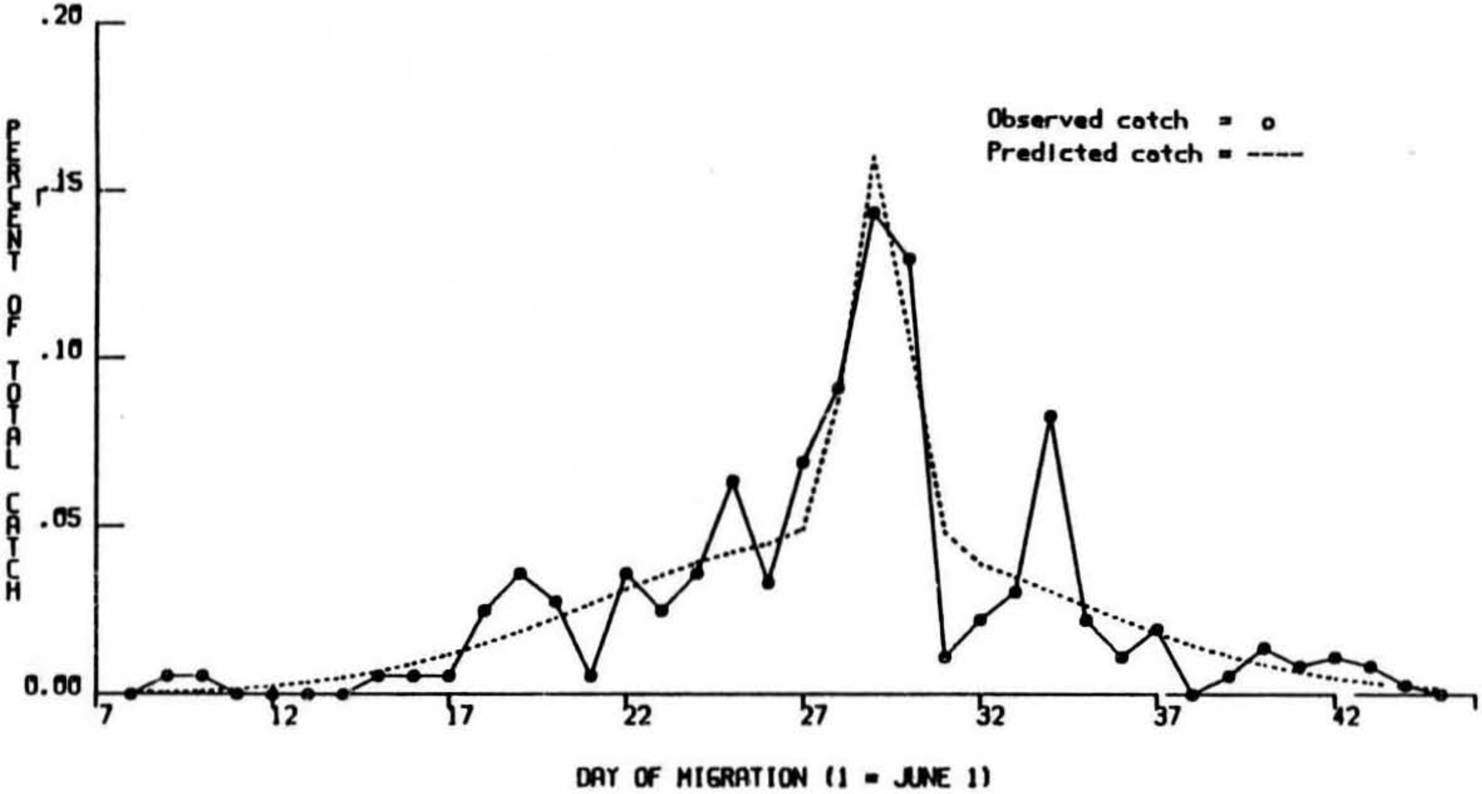

Figure 23. Observed daily proportions of total catch and expected proportions of total catch from model two for 1977 Flat Island catches.

The residuals of M_2 fitted by the likelihood function are consistently smaller than those fitted to the transformed data by minimizing the sum of squares. An average reduction in sum of squares by M_2 of 31% for the 1979-1981 test fishing catch, and 23% for 1968-1978 test fishing catch was achieved, compared to the sum of squares from M_1. The reduction in sum of squares was greatest for distribution with a bimodal (1972, 28%) or skewed Big Eddy, 58% and 1981 Middle Mouth, 48%) character. Given accurate estimates of the values of the parameters, M_2 offers few advantages over M_1 in the ability to predict daily fluctuations in abundance, although the general form of the distribution is approximated better by M_2 than M_1.

The vicissitudes of daily catch can to some degree be predicted by M_3. Major peaks in test fishery catch are paralleled by peaks in predicted catch, although the magnitude of the peaks differ (11, 14, 15, 18, 19, 25, 26, 28, 29 June and 2 July 1972 [Figure 24] and 5, 7, 10, 13-15, 25, and 29 June, 1981 Big Eddy [Figure 26]; also 9, 10, 16, and 19 June 1968; 9, 11, 15, 18, and 19 June 1969; 11, 15, 17, 21, 24, and 25 June 1979; 20, 21, 24, 27-30 June, and 4 July 1971; 7, 17, and 24 June 1973; 15, 17, 29, 30 June, and 1 July 1974; 19, 22, 28 June, and 7 July 1975; 24, 27, 28, 30 June, 1 and 3 July 1976; 10, 13, and 14 June 1978; 6, 11, 13, 17 June 1979; 11, 18, and 19 June 1980; and 7 and 10 June 1981 Middle Mouth). Reduced catches near the center of the migratory distribution were also accurately estimated (13, 16, 20, 23, 24, 27, 30 June and 1 July 1972; [Figure 24]; 1-2 July 1977 [Figure 25]; and 6, 9, 12, 16, 19, 22, and 23 June 1981 Big Eddy [Figure 26]; also 11, 14, 18, and 25 June 1968; 10, 13, 14, 20, and 21 June 1969; 16, 19, 20, and 23 June 1970; 22 June and 5 July 1971; 19 and 26 June 1973; 4, 11, 15, and 18 June 1974; 20, 24, and 30 June 1975; 25, 29 June 2 and 6 July 1976; 9, 13, and 20 June 1978; 8, 15, and 22 June 1979; 10 and 13 June 1980; and 6 and 16 June 1981 Middle Mouth). On several days, the predicted peak or depression in catch preceded the observed peak or depressions by one day (for example 25 June 1972; 3 July 1977; and 17 June 1981 [Figures 24-26]; also 8 June 1969; 17 June 1970; 9 and 12 June 1974; 26 and 27 June 1975; 7 July 1976; 21 June 1978). The predicted peak or depression followed the observed peak or depression on other occasions (3 July 1972 and 21 June 1981 [Figures 24 and 26]; also 21 June 1968; 11 June 1973; 23 June 1974; 15 June 1980 Middle Mouth; and 6, 9, and 10 June 1981 Middle Mouth).

No consistent pattern appears to exist between the errors of estimation near the mean of the migration and the errors of estimation at the beginning or end of the migration. No regular violation of the assumption of independence of observations was revealed in the autocorrelations of the residuals. Significant ($P <$ .05) positive autocorrelations of lag 1 were observed in 1970 and 1980, and a negative autocorrelation of -.29 was calculated for the 1975 residuals. Average wind speeds were highest in 1980 and 1970 respectively compared to wind speeds of other years. The high wind speeds in 1970 and 1980 could be responsible for sequences of positive or negative residuals, resulting in the observed positive autocorrelations. However, wind speeds in 1975 were also relatively strong. It is also possible that another factor which affects salmon migratory behavior and which is highly correlated with the number of salmon migrating through the lower river and also highly autocorrelated could be responsible for the anomalously high autocorrelations in 2 of 14 years.

The sum of squared deviations is reduced by an average of 43% over those of M_1 for the 1979-1981 test fishery catch, and by an average of 38% for the 1968-1978

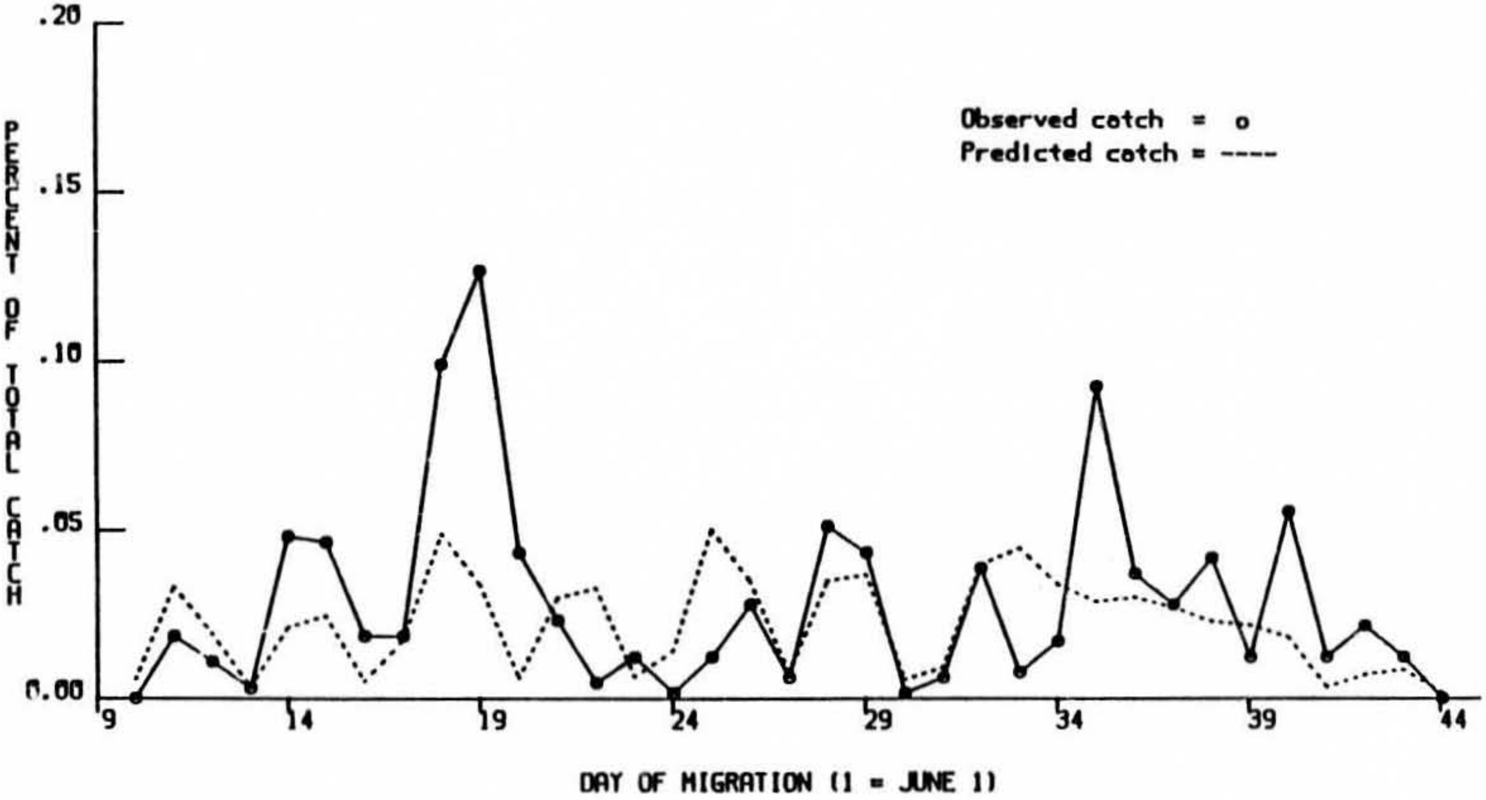

Figure 24. Observed daily proportions of total catch and expected proportions of total catch from model threee for 1972 Flat Island catches.

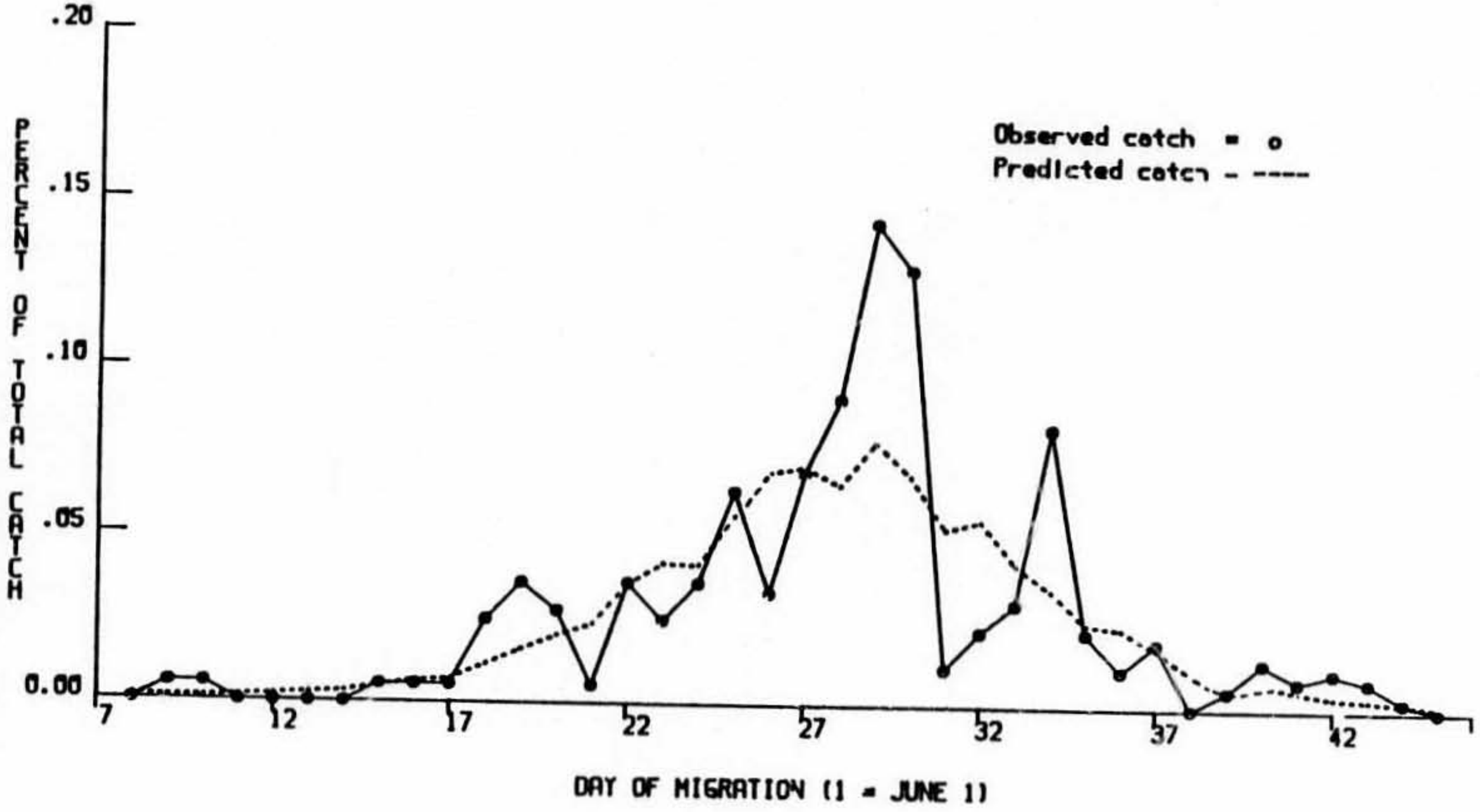

Figure 25. Observed daily proportions of total catch and expected proportions of total catch from model three for 1977 Flat Island catches.

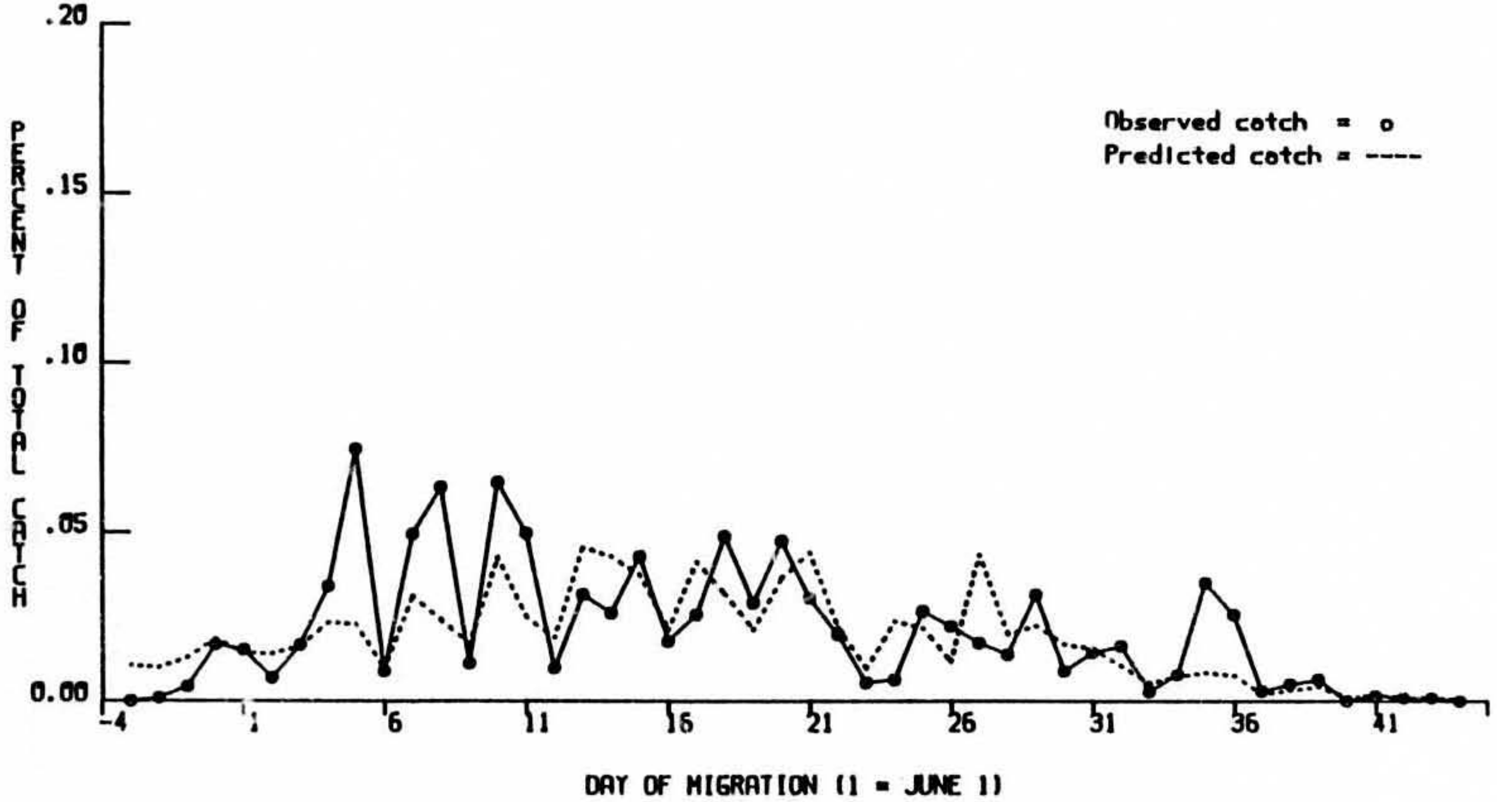

Figure 26. Observed daily proportions of total catch and expected proportions of total catch from model three for 1981 Flat Island catches.

test fishery catch (compare values of Tables 15 and 16 with values presented in Tables 22 and 24). The largest reductions in sums of squares were obtained for the 1974 (72%), 1981 (61%), 1972 (51%), and 1973 (51%) test fishery catches. Compared to M_2, M_3 reduced the sum of squared deviations by an average of 18% and 20% for Big Eddy and Middle Mouth and for Flat Island test fishery catches respectively (Tables 15, 16, 12, and 13). The ability of M_3 to reflect the daily variation in observed catch and the reduction in sums of squared deviations commend its use as a forecaster of daily abundance over that of M_1 or M_2.

Note the consistent positive correlation between wind speed and abundance (parameter β_1, Tables 15 and 16) and the consistent reduction of daily test fishery catch by commercial effort (parameter β_2). Large test fishery catches correspond to days of high wind speeds and periods of commercial closure. Exceptionally small catches occur on days of commercial fishing and relatively low average wind speeds. The high and consistently negative values of parameter β_2 indicates a high exploitation rate by the commercial fishery. Given an average wind speed of 10 mph, the Big Eddy and Middle Mouth test fishery catch is reduced by an average of 36% during a commercial fishing period. Flat Island catches are reduced by an average of 25%. The mean dates of migration are invariably earlier than those calculated for model 1, while the variances calculated for M_3 are larger than corresponding variances calculated for M_1. With accurate estimates of M_3 coefficients, the reduction in the errors of daily chinook catch predictions by M_3 relative to M_1 suggest that the temporal distribution of abundance can be accurately described as a function of time and environmental factors.

Fitting M_4 to observed catch results in good agreement between expected and observed values of test fishery catches (Figures 27-29; Tables 17 and 18). Unexpectedly large or small daily catches were accurately predicted by M_4 for a single-day or multi-day catch phenomena. As observed for M_3, exceptionally large or small catches were sometimes predicted the day before or day after the observed catch. Some exceptions to the goodness of fit should be noted. Some moderate peaks in abundance late in the migration (5 July 1972 [Figure 27]; also 22 June 1969; 5 and 10 July 1971; 28 June 1973; 22 June 1974; 22 and 23 June 1978; 27 and 28 June 1979) were not well predicted. The magnitude of large test fishery catches early or in mid-season were also poorly estimated by the model (29 and 30 June 1977 [Figure 28]; also 29 and 30 June; 9 June 1969; 18 June 1970; 17 June 1973; 22 and 23 June 1975; 30 June, 1 and 3 July 1976; 10 and 11 June 1978; 11 June 1979; and 18 June 1980). However, the deviations of observed catch from expected catch were apparently random throughout the migratory distribution and, except as noted previously, comparatively small.

The goodness of fit is reflected in the reduction of the sum of squares compared to previous models. The sum of squared residuals of Flat Island catch were reduced an average of 54% compared to M_1, 40% compared to M_2, and 25% compared to M_3. Middle Mouth and Big Eddy sums of squares were reduced an average of 69% over those of M_1, 55% over M_2, and 46% over M_3. Although the values of the parameters vary by year and test fishery site for M_4, some general qualitative conclusions can be made. The value of the wind speed parameter, β_1, lies between the values of -.43 and .59 and, with the exception of 1968, 1976, and 1977 is positive (Tables 17 and 18). The value of the effort parameter, β_2, is predictably negative, and lies between the values of -1.7, and -5.7, denoting a high exploitation rate. The variances corresponding to earlier means were, with the exception of the 1970 and 1977 Flat Island catches, smaller than the variances

Table 15. The estimated values of the mean and variance of a homogeneous population migrating past the test fisheries, and the values of the coefficients quantifying the effect of wind speed and commercial effort on the migration. Model three (equation 27) is fitted to observed data by minimizing the sum of squared deviations from the expected catches. Data are cube roots of Big Eddy and Middle Mouth test fishery catches. * signifies that the variance of the residuals in the centered half of the distribution is significantly different from the variance in the tail quartiles.

Year	Site	Mean	Variance	B_0	B_1	B_2	Sum of Squares
1979	Big Eddy*	13.925	524.908	13.56	.3064	−3.307	.043006
1980	Big Eddy	14.595	210.157	9.89	.3051	−3.556	.009052
1980	Middle Mouth	19.829	272.608	11.46	.2973	−4.121	.011147
1980	Total Test* Fishery	18.179	267.118	11.28	.3055	−3.994	.008574
1981	Big Eddy	15.123	307.408	12.759	.3753	−5.209	.009848
1981	Middle Mouth	14.252	282.205	14.527	.1464	−5.593	.008389
1981	Total Test Fishery	15.279	291.999	13.721	.2404	−5.216	.008500
Average		17.883	308.056	12.46	.2823	−4.428	.014073

Table 16. The estimated values of the mean and variance of a homogeneous population migrating past the test fisheries, and the values of the coefficients quantifying the effect of wind speed and commercial effort on the migration. Model three (equation 27) is fitted to observed data by minimizing the sum of squared deviations from the expected catches. Data are cube roots of Flat Island test fishery catches.

Year	Site	Mean	Variance	B_0	B_1	B_2	Sum of Squares
1968	Flat Island	17.562	142.180	14.80	-.3147	-2.961	.021341
1969	Flat Island	15.439	179.449	6.15	.5541	-2.534	.032005
1970	Flat Island	21.599	130.494	9.09	.1937	-2.257	.019940
1971	Flat Island	28.598	196.810	10.50	.2202	-1.715	.020614
1972	Flat Island	24.036	408.813	16.08	.2941	-8.790	.023560
1973	Flat Island	20.249	246.046	9.08	.4996	-2.746	.016241
1974	Flat Island	12.995	250.246	5.56	.8225	-1.973	.007973
1975	Flat Island	27.362	88.257	5.20	.4742	-4.426	.031073
1976	Flat Island	30.176	61.514	10.05	-.0557	-3.852	.019530
1977	Flat Island	28.671	77.735	11.72	-.1976	-2.406	.021300
1978	Flat Island	13.065	328.205	12.16	.3317	-6.534	.014085
Average		21.796	191.795	10.03	.2566	-3.654	.020694

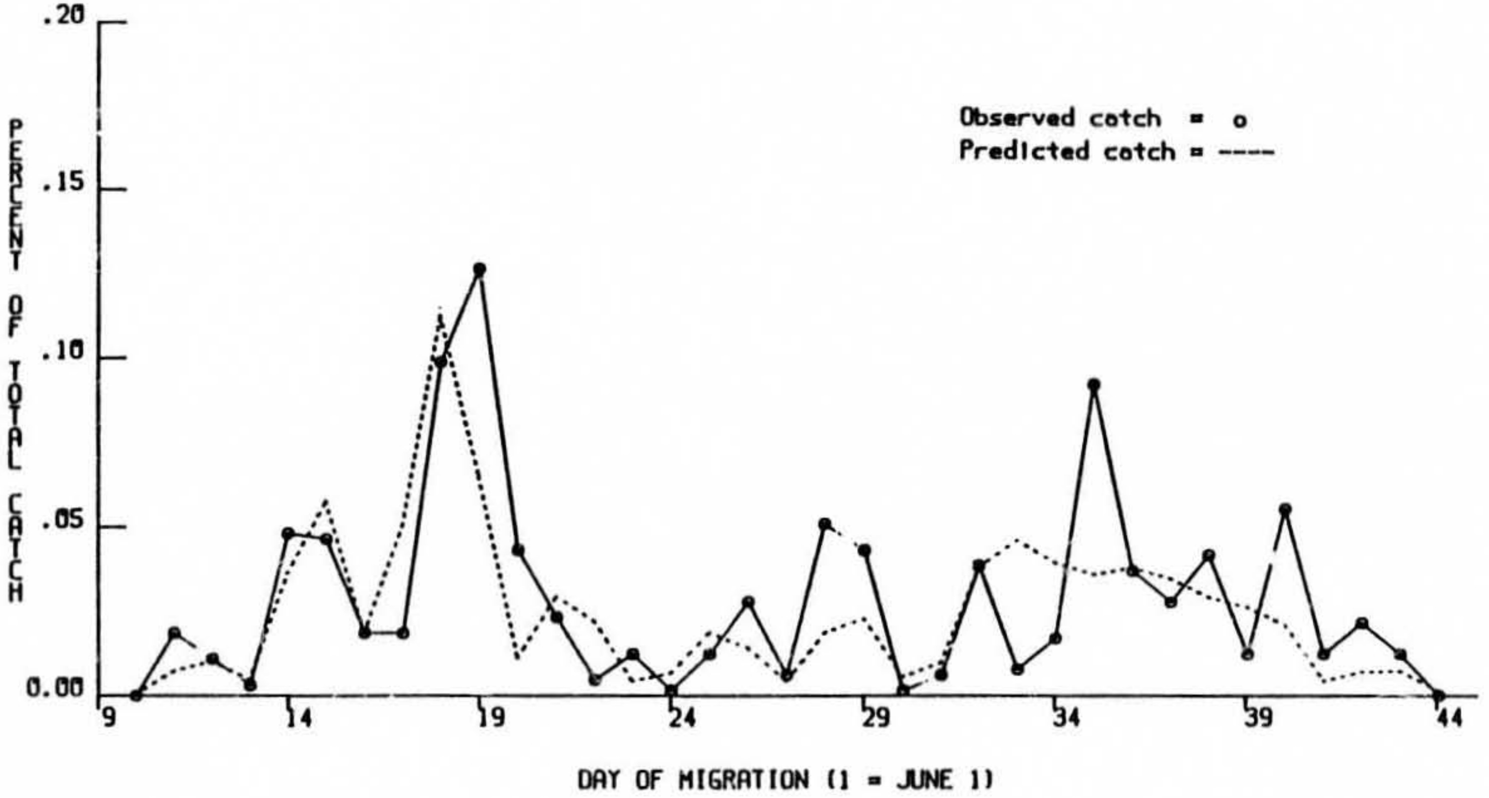

Figure 27. Observed daily proportions of total catch and expected proportions of total catch from model four for 1972 Flat Island catches.

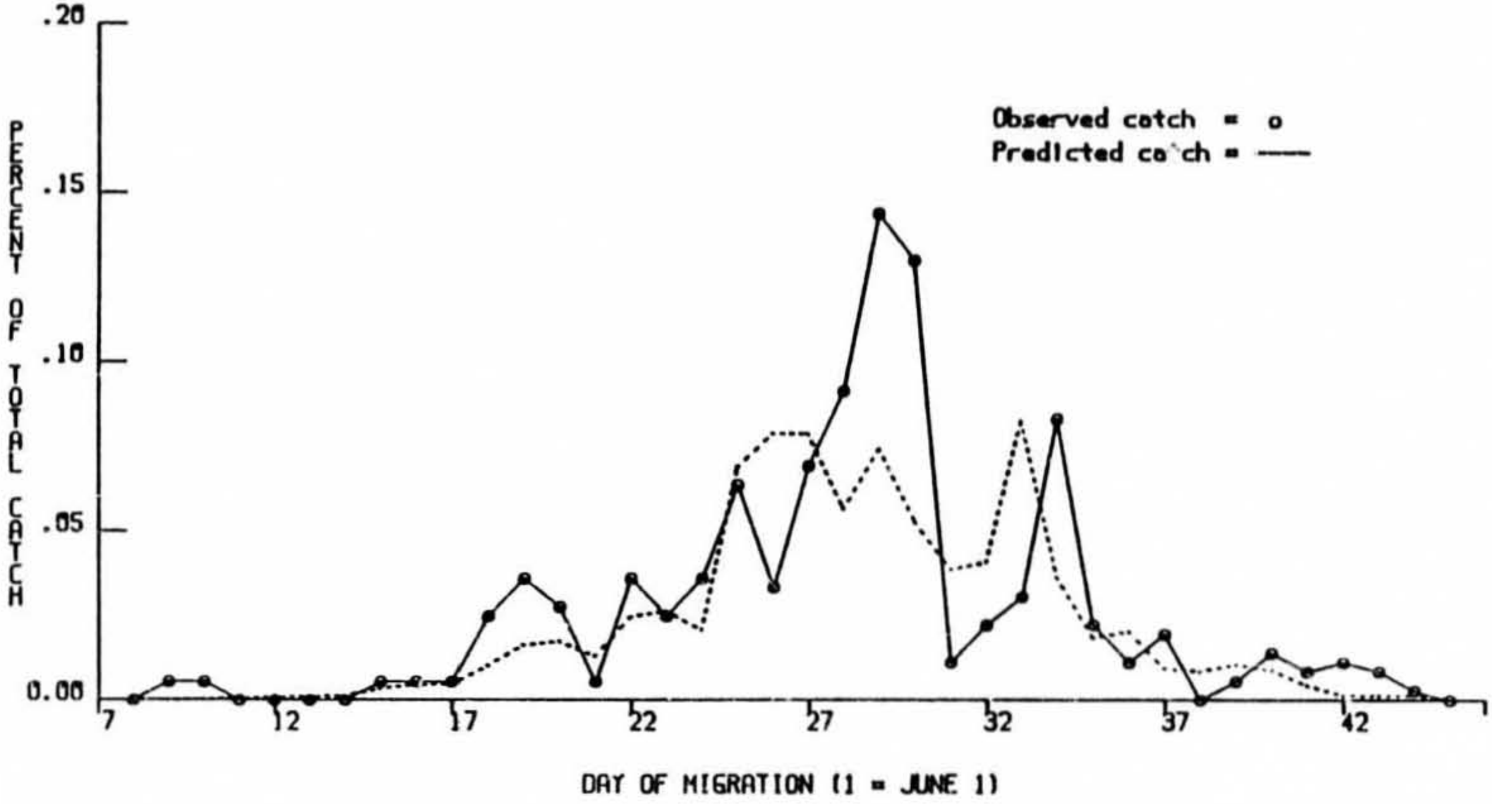

Figure 28. Observed daily proportions of total catch and expected proportions from model four for 1977 Flat Island catches.

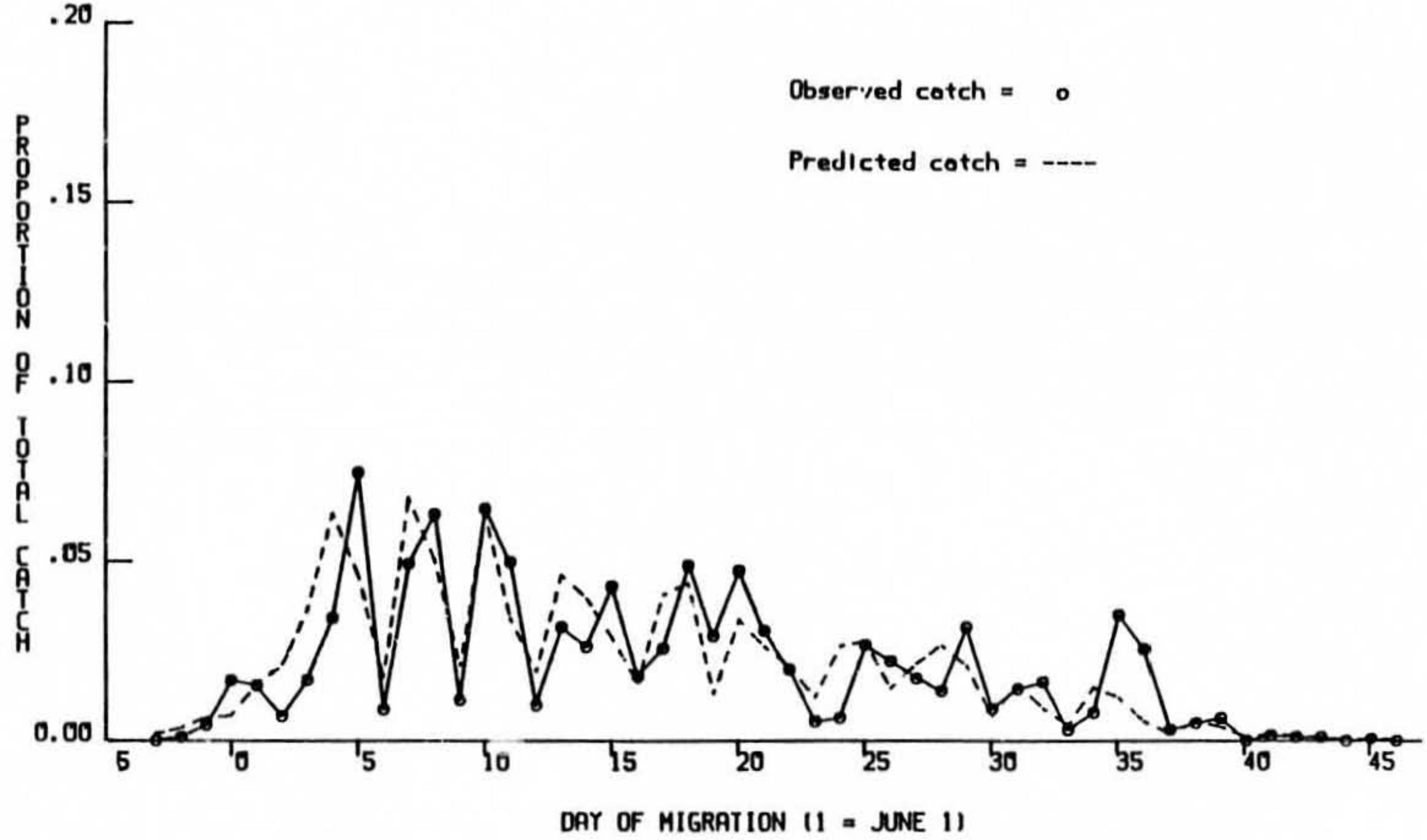

Figure 29. Observed daily proportions of total catch and expected proportions from model four for 1981 Flat Island catches.

Table 17. The estimated values of the mean and variance of the earlier subpopulation, the proportion of the total population assigned to the earlier subpopulation, the mean and variance of the later subpopulation, and the proportion assigned to the later subpopulation. The model assumes a mixture of two subpopulations affected by wind and commercial effort (model four, equation 27) and is fitted by minimization of the sum of squared deviations. Data are cube roots of Big Eddy and Middle Mouth test fishery catches.

Year	Site	Earlier Mean	Earlier Variance	Later Mean	Later Variance	Proportions	
						Early	Late
1979	Big Eddy	6.809	0.975	15.412	580.056	.049	.951
1980	Big Eddy	9.619	58.964	25.732	149.399	.485	.515
1980	Middle Mouth	10.701	32.452	27.545	158.461	.288	.712
1980	Test Fishery	13.179	81.870	33.816	47.442	.693	.307
1981	Big Eddy	6.387	16.259	19.332	247.927	.117	.883
1981	Middle Mouth	5.598	20.402	20.028	173.619	.176	.824
1981	Test Fishery	6.042	17.361	19.934	217.182	.138	.862
	Average	6.676	32.610	23.114	224.87	.278	.722

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Table 17. Estimated values of the wind, effort, and constant parameters and sum of squared deviations from model. The model assumes a mixture of two subpopulations affected by wind and commercial effort (model four, equation 27) and is fitted by minimization of the sum of squared deviations. Data are cube roots of Big Eddy and Middle Mouth test fishery catches (continued).

Year	Site	B_0	B_1	B_2	Sum of Squares
1979	Big Eddy	10.803	.59495	-4.7460	.0194351
1980	Big Eddy	8.105	.38872	-3.9471	.0077234
1980	Middle Mouth	8.929	.39402	-4.3586	.0065747
1980	Total Test Fishery	9.368	.33200	-4.0361	.0044401
1981	Big Eddy	11.570	.37480	-5.6378	.0065742
1981	Middle Mouth	12.391	.15209	-5.4817	.0043586
1981	Total Test Fishery	12.287	.24734	-5.5498	.0044718
Average		10.494	.35483	-4.8226	.0076529

Table 18. The estimated values of the mean and variance of the earlier subpopulation, the proportion of the total population assigned to the earlier subpopulation, the mean and variance of the later subpopulation, and the proportion assigned to the later subpopulation. The model assumes a mixture of two subpopulations affected by wind and commercial effort (model four, equation 27) and is fitted by minimization of the sum of squared deviations. Data are cube roots of Flat Island test fishery catches.

Year	**Site**	**Earlier Mean**	**Earlier Variance**	**Later Mean**	**Later Variance**	**Proportions Early**	**Late**
1968	**Flat Island**	**8.789**	**8.119**	**21.884**	**76.464**	**.205**	**.795**
1969	**Flat Island**	**7.880**	**17.790**	**23.153**	**44.944**	**.396**	**.604**
1970	**Flat Island**	**19.234**	**77.744**	**35.052**	**8.341**	**.858**	**.142**
1971	**Flat Island**	**22.730**	**46.863**	**39.115**	**48.885**	**.573**	**.427**
1972	**Flat Island**	**16.448**	**15.978**	**33.935**	**93.599**	**.331**	**.669**
1973	**Flat Island**	**9.956**	**22.134**	**26.431**	**94.029**	**.260**	**.740**
1974	**Flat Island**	**8.700**	**46.453**	**23.231**	**213.118**	**.374**	**.626**
1975	**Flat Island**	**21.968**	**25.919**	**33.721**	**32.279**	**.510**	**.490**
1976	**Flat Island**	**22.111**	**3.704**	**31.306**	**48.723**	**.095**	**.905**
1977	**Flat Island**	**28.768**	**87.933**	**29.906**	**4.691**	**.922**	**.078**
1978	**Flat Island**	**3.014**	**7.962**	**17.708**	**226.657**	**.103**	**.897**
Average		**11.418**	**32.781**	**24.675**	**81.066**	**.421**	**.579**

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Table 18. Estimated values of the wind, effort, and constant parameters and sum of squared deviations from model. The model assumes a mixture of two subpopulations affected by wind and commercial effort (model four, equation 27) and is fitted by minimization of the sum of squared deviations. Data are cube roots of Flat Island test fishery catches (continued).

Year	**Site**	B_0	B_1	B_2	**Sum of Squares**
1968	**Flat Island**	**14.359**	**-.43751**	**-2.3272**	**.0149271**
1969	**Flat Island**	**6.543**	**.33128**	**-2.1221**	**.0224319**
1970	**Flat Island**	**7.583**	**.27755**	**-2.3368**	**.0129419**
1971	**Flat Island**	**8.019**	**.32090**	**-1.7478**	**.0198892**
1972	**Flat Island**	**10.996**	**.16179**	**-5.1727**	**.0150231**
1973	**Flat Island**	**6.430**	**.52774**	**-2.0435**	**.0140535**
1974	**Flat Island**	**8.251**	**.43506**	**-2.7129**	**.0072566**
1975	**Flat Island**	**4.915**	**.45997**	**-4.7514**	**.0224506**
1976	**Flat Island**	**10.431**	**-.11567**	**-3.9336**	**.0153660**
1977	**Flat Island**	**13.142**	**-.33247**	**-2.2277**	**.0149221**
1978	**Flat Island**	**11.875**	**.14118**	**-4.6325**	**.0109367**
Average		**8.421**	**.16090**	**-3.0917**	**.0154726**

associated with later means. Early and late subpopulation proportions average close to one half of total abundance.

The results of fitting M_5 to the distribution of catch over time are similar to the results obtained in the fitting of M_3 (Tables 19 and 20; Figures 30-32). Large or small observed daily catches generally coincide with large or small estimated catches. Although exceptionally large or small daily chinook salmon abundances are generally underestimated or overestimated (18, 19 June and 5 July 1972 [Figure 30]; 29, 30 June and 1 July 1977 [Figure 31]; and 5 and 9 June 1981 Big Eddy [Figure 32]; also 9 June 1969; 18 and 23 June 1970; 1, 2, 3 July 1971; 17 June 1973; 22 and 23 June 1975; 30 June, 1 and 3 July 1976; 2 and 4 June 1978; 7 and 11 June 1979; 10 June 1980 Big Eddy), the more moderate peaks in catch are well represented by the estimates of M_5. It is observed that in M_5 there is a tendency for the catches on the extremities of the temporal distribution to be underestimated while catches near the mean day of distribution are generally overestimated. The skewness of the 1981 Big Eddy, 1980 Big Eddy, and 1974 Flat Island distribution is better approximated by the distribution function of M_5 than the skewness of the 1975 and 1978 Flat Island distributions, which are relatively poorly approximated.

The calculated mean day of catch is consistently earlier than the mean day of catch calculated by M_1, and the variance is smaller. The wind parameter β_1, is positive for all years and the effort parameter, β_2, is negative for all catch distributions. Although minimizing the sum of squared deviations is not the criterion used in estimating the parameters of the M_5, the values of sum of squares for each year compare favorably with corresponding values of M_3. The 1969, 1970, 1971, 1972, 1973, 1974, 1975, and 1977 Flat Island, the 1979 and 1980 Middle Mouth and Big Eddy, and the 1980 Big Eddy distributions all resulted in lower sum of squares for M_5 compared to M_3.

The relative ability of each model to accurately describe the distribution of daily catch can be summarized as follows. Models one and M_2 demonstrate the poorest predictive ability, followed by M_3 and M_5. Model four proved to be the most accurate estimator of daily catch. It can be concluded that models three, four, and five all accurately depict the time distribution of catch. Obviously, accurate estimation of the parameters is necessary to make these methods applicable to actual intraseason forecasts. The consistent positive value of the wind speed coefficient, β_1, and negative value of the commercial effort coefficient, β_2, are significant and consideration of these two effects would undoubtedly improve abundance estimates.

The statistics of the estimated values of the parameters of M_3, M_4, and M_5 are summarized in Tables 21, 22, and 23 respectively. The wind parameter, β_1, and the commercial effort parameter, β_2, are significantly different from 0 for all three models. Average April air temperatures were highly correlated with the fitted mean of M_3, the variance of M_3, the mean of S_1 and S_2 of M_4, the variance of S_2 of M_4, and the mean of M_5. Linear regression techniques were applied in the analysis of the relationship of the spring air temperatures and the means and the variances of M_3 and M_4, and the means of M_5. A logarithmic transformation was employed to stabilize the variance (σ^2). The statistics of the linear regression analysis are presented in Tables 21, 22, and 23.

Table 19. The estimated values of the mean and variance of a homogeneous population migrating past the test fisheries, and the values of the coefficients quantifying the effect of wind speed and commercial effort on the migration. Model five (equation 40) is fitted to observed data by maximization of the likelihood function. Data are from the Big Eddy and Middle Mouth test fishery operations.

Year	Site	Mean	Variance	B_0	B_1	B_2	Sum of Squares
1979	Big Eddy	5.247	20.923	0.0443	.00491	-0.3583	.0363204
1980	Big Eddy	13.115	50.602	0.0137	.02329	-0.4496	.0067951
1980	Middle Mouth	16.801	62.846	0.0292	.01726	-0.5957	.0101368
1980	Total Test Fishery	15.433	62.506	0.0268	.01856	-0.5313	.0067193
1981	Big Eddy	4.550	7.509	0.0048	.00936	-0.6332	.0069554
1981	Middle Mouth	13.627	74.399	0.2659	.01025	-0.6823	.0113025
1981	Total Test Fishery	4.964	8.829	0.0267	.00748	-0.6935	.0059759
Average		10.534	41.089	0.0588	.01302	-0.5634	.0120291

Table 20. The estimated values of the mean and variance of a homogeneous population migrating past the test fisheries, and the values of the coefficients quantifying the effect of wind speed and commercial effort on the migration. Data are from the Flat Island test fishery operations.

Year	**Site**	**Mean**	**Variance**	B_0	B_1	B_2	**Sum of Squares**
1968	**Flat Island**	**14.704**	**38.482**	**0.2434**	**.00000**	**−0.3524**	**.0223267**
1969	**Flat Island**	**7.302**	**7.116**	**0.0735**	**.00433**	**−0.2536**	**.0297612**
1970	**Flat Island**	**19.953**	**46.045**	**0.3688**	**.03752**	**−0.2394**	**.0143960**
1971	**Flat Island**	**27.653**	**59.287**	**0.1146**	**.03131**	**−0.1439**	**.0186809**
1972	**Flat Island**	**15.150**	**4.696**	**0.0320**	**.00590**	**−0.5347**	**.0213226**
1973	**Flat Island**	**18.185**	**62.721**	**0.0000**	**.02874**	**−0.3510**	**.0134308**
1974	**Flat Island**	**7.762**	**15.864**	**0.0145**	**.01242**	**−0.2526**	**.0068396**
1975	**Flat Island**	**25.703**	**37.293**	**0.0000**	**.03415**	**−0.4769**	**.0300980**
1976	**Flat Island**	**28.263**	**19.530**	**0.2618**	**.00773**	**−0.4167**	**.0220395**
1977	**Flat Island**	**27.206**	**32.399**	**0.4614**	**.00424**	**−0.2136**	**.0175581**
1978	**Flat Island**	**12.726**	**86.259**	**0.0597**	**.02354**	**−0.6942**	**.0173667**
Average		**18.601**	**37.245**	**0.1482**	**.01726**	**−0.3572**	**.0194383**

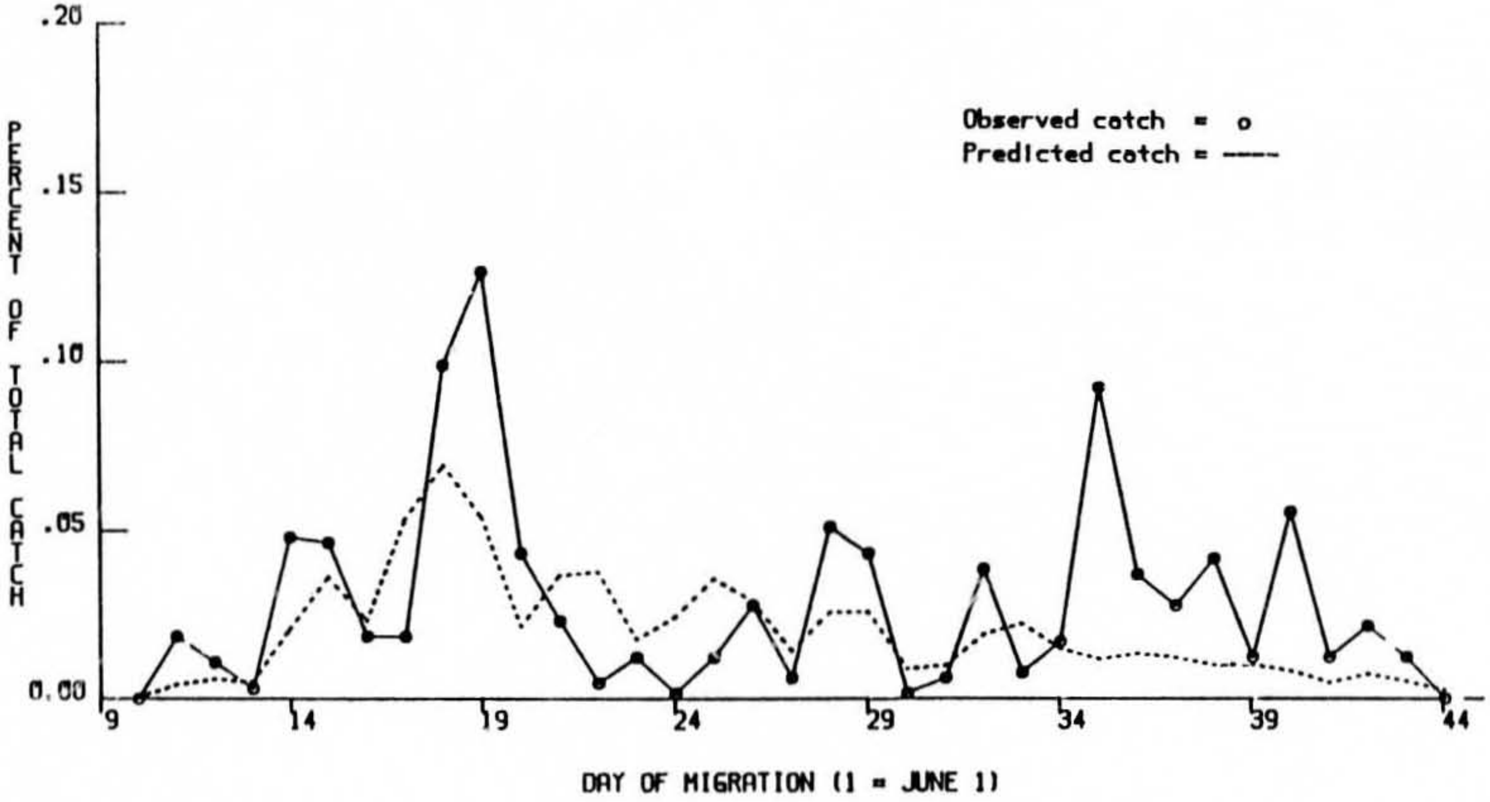

Figure 30. Observed daily proportio of total catch and expected proportions from model five for 1972 Flat Island catches.

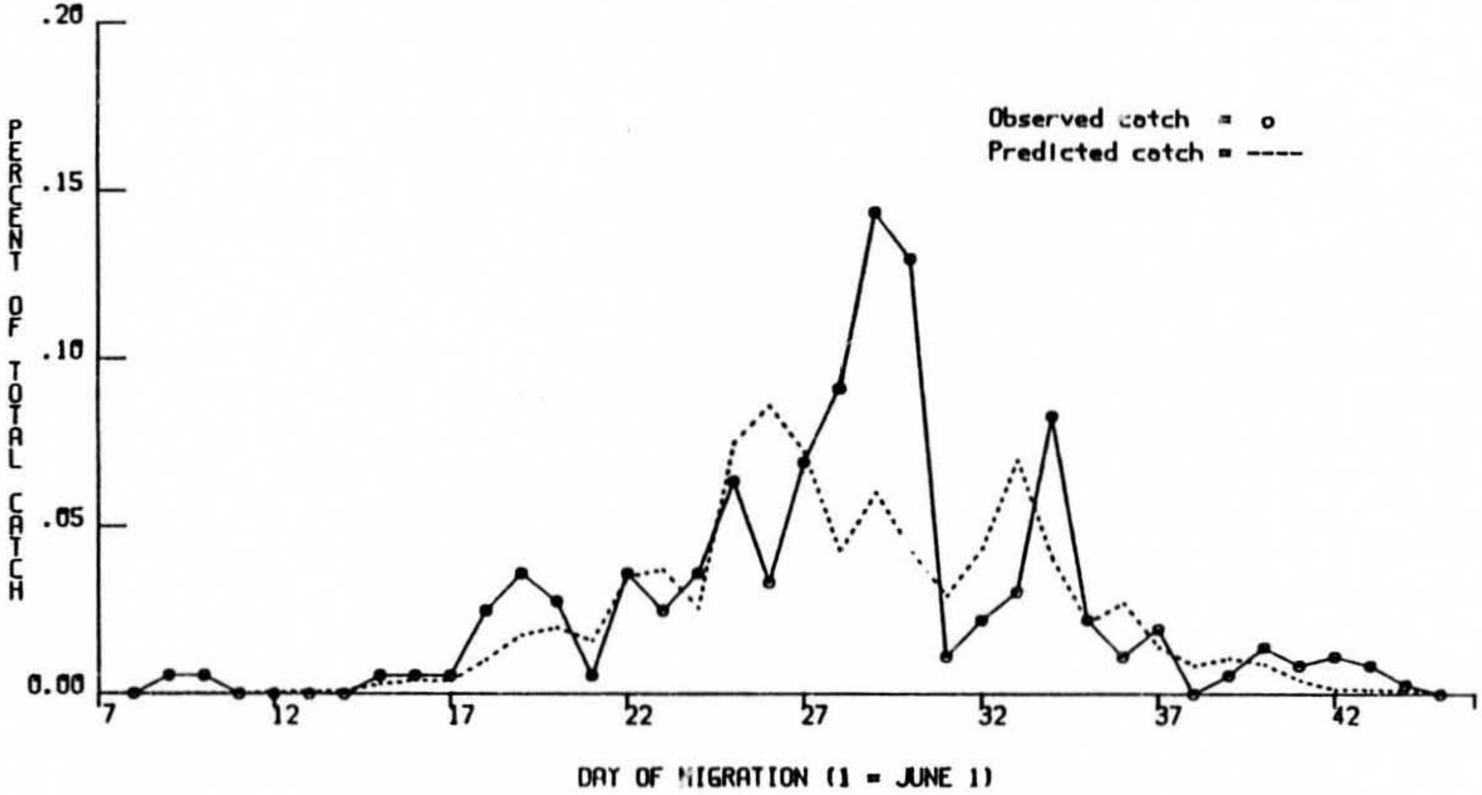

Figure 31. Observed daily proportions of total catch and expected proportions from model five for 1977 Flat Island catches.

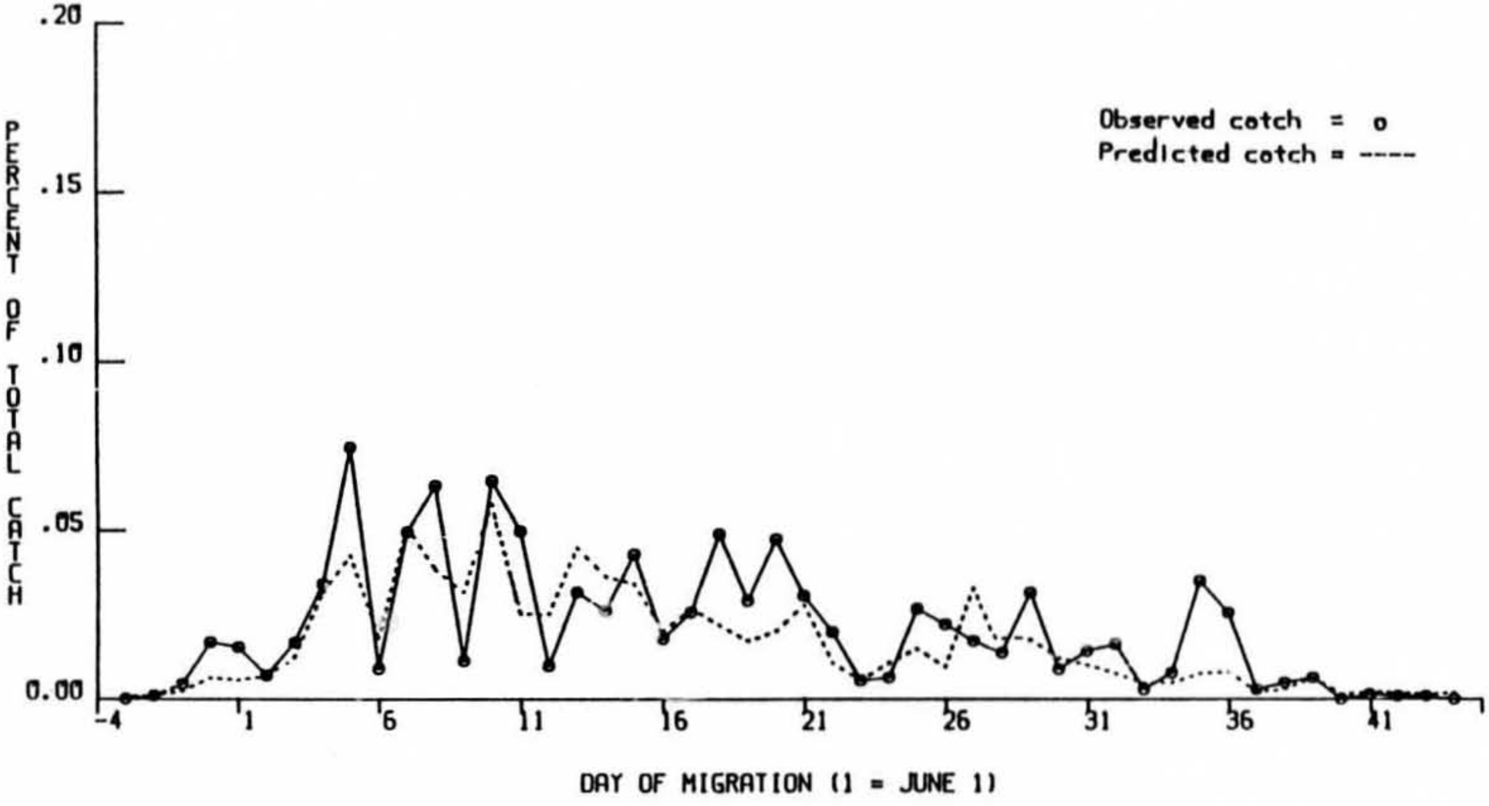

Figure 32. Observed daily proportions of total catch and expected proportions from model five for 1981 Flat Island catches.

Table 21. Mean parameter values, confidence limits, and the relation between mean and variance for model three and average April air temperature.

	Mean	Lower 95% limit	Upper 95% limit
Mean day of migration	20.243	16.526	23.960
Variance of migration	225.159	148.667	301.651
Constant	10.471	8.549	12.393
Wind parameter	0.272	0.099	0.445
Commercial effort parameter	-3.772	-4.887	-2.657

The Pearson Correlation Coefficients are:

Mean day and April temperature: $r = -.9154$ $P < .001$
Variance and April temperature: $r = .6092$ $P = .021$
Natural log of variance and April temperature: $r = .6961$ $P = .006$

$$\text{Mean day} = 37.933 - 1.0056\ (\text{Mean April air temperature, °F})$$

with an R^2 value of .838 and F-value of 62.01

$$\text{Variance} = e^{(3.9242 + .075763\ (\text{Mean April air temperature, °F})}$$

with an R^2 value of .485 and F-value of 11.28

Sum of squares for all years = .432103
Average error of estimated observation = .0169135

Table 22. Mean parameter values, confidence limits, and the relation between the means and variances for model three and average April air temperature.

	Mean	Lower 95% limit	Upper 95% limit
Early mean day of migration	13.744	9.173	18.315
Late mean day of migration	26.851	22.712	30.990
Early variance of migration	31.200	15.093	47.307
Late variance of migration	133.508	45.978	221.038
Proportion of early subpopulation	0.377	0.219	0.535
Proportion of late subpopulation	0.623	0.465	0.781
Constant	9.502	7.899	11.105
Wind parameter	0.223	0.042	0.404
Commercial effort parameter	-3.453	-4.241	-2.665

The Pearson correlation coefficients are:

Mean day of S_1 and April temperature: $r = -.8810$ $P < .001$
Mean day of S_2 and April temperature: $r = -.7946$ $P = .001$
Variance of S_2 and April temperature: $r = .7106$ $P = .004$
Natural log of variance and April temperature: $r = .7395$ $P = .003$

Mean day of S_1 = 34.681 - 1.1901 (Mean April air temperature, °F) with an R^2 value of .776 and F-value of 41.591

Mean day of S_2 = 43.952 - 0.9720 (Mean April air temperature, °F) with an R^2 value of .631 and F-value of 20.551

$$\text{Variance} = e^{(1.3628 + .165373 (\text{Mean April air temperature, °F})}$$

with an R^2 value of .5468 and F-value of 14.482

Sum of squares for all years = .511062
Average error of estimated proportion = .01800

Table 23. Mean parameter values, confidence limits, and the relation between mean and variance of model five and average April air temperature.

	Mean	Lower 95% limit	Upper 95% limit
Mean day of migration	16.251	11.350	21.152
Variance of migration	34.909	20.923	48.895
Constant	0.1210	0.0346	0.2074
Wind parameter	0.016	0.010	0.022
Commercial effort parameter	-0.384	-0.477	-0.291

The Pearson correlation coefficients are:

Mean day and April air temperature: $r = -.8516$ $P < .001$

Mean day = 37.958 - 1.2338 (Mean April air temperature, °F) with an R^2 value of .725 and F-value of 31.67

Comparisons of the ability of M_3, M_4, and M_5, and the time series model to accurately estimate both daily and total abundance are summarized in Tables 24, 25, and 26. Given accurate least squares estimates of the parameters of M_3 and M_4 (Tables 15-18) or maximum likelihood estimation of M_5 (Tables 19 and 20), the average daily error of estimation of 1968 to 1979 test fishery catches is smaller for both M_3 (averaging 0.01449) and M_4 (averaging 0.01318) than the average daily error of time series model (averaging 0.01666). The time series model more accurately predicts the daily proportion of 1980 and 1981 total Big Eddy catch compared to M_3, although less accurately than M_4. The ability of M_3 and M_4 to forecast total catch within a 50% error interval (predicted total catch equals the ratio of cumulative catch over estimated cumulative proportions of total catch) is not consistently better or worse than the ability of the time series model to predict total catch. Model 5 results in an average error of daily prediction of .01365 for the 1968 to 1981 proportions of total annual test fishery catch (Table 25), which is less than the average error of M_3 (6% less) but greater than the average error of M_4 (3% greater).

Total catch estimated by M_3 remained within a 50% error interval previous to the forecasts of the time series model for years 1968, 1971, 1974, 1976, 1979, 1980, and 1981, where as 1970, 1972, 1975, and 1977 total catch was more promptly estimated by the time series model. The time series model estimated total catch within a 50% error interval in advance of M_4 for 1969, 1970, 1971, 1972, 1973, and 1977 catch data. The time series model was superior to both M_3 and M_4 in the ability to predict total annual catch within a 20% error interval. Predicted total annual catches are greater than observed total catches. Total observed catch was not within 20% of final predicted catch of M_3 for the years 1969, 1971, 1972, 1975, 1979, and of M_4 for years 1971, 1975, and 1979.

Annual values of M_3's mean, variance, β_0, β_1, and β_2 were estimated according to the linear relationship or averages presented in Table 21 and substituted into M_3. In a similar manner the mean, variance, and proportion of S_1, the mean, variance, and proportion of S_2, β_0, β_1, and β_2 were estimated by a linear function of temperature $(\mu_1, \mu_2, \sigma^2_2)$ or as an average of the 14 estimated annual values of the parameters $(\sigma^2_1, \rho_1, \rho_2, \beta_0, \beta_1$, and $\beta_2)$. Estimates of both daily and total abundance of M_4 were more in error than estimates of the time series model (Table 25) or M_3. Estimates of daily abundance by the time series model were, on the average, 39% more accurate and those of M_3 were 36% closer to the observed daily catch than the corresponding estimates of M_4. Total abundance predictions did not converge to within 50% of observed abundance for 4 years (1972, 1975, 1976, 1977) and within 20% of observed abundance for 7 years (1970, 1971, 1972, 1975, 1976, 1977, 1981). The residuals of M_3 were tested for independence and found to be significantly correlated at lag 1 day. An autoregressive term of $\phi_1 = .39$ was added to M_3 to satisfy the conditions of independence. Both M_3 and the time series model resulted in differences of 0.01 to 0.02 between observed and forecasted daily proportion of total abundance. The time series model estimates were an average of 4% closer to the observed proportions than M_3 estimates for 14 years of observations. The time series model does anticipate total abundance with greater accuracy than M_3 (Table 26). Model three estimates of total catch failed to converge to within 20% of observed total catch for 8 years of test fishery catches (1969, 1974, and 1976-1981).

Table 24. Comparison of the ability of models three and four, fitted to the observed data by minimization of sum of squares, to predict daily proportion of total catch and total annual catch. Average daily error is defined by equation 66 in the text. NE signifies that the 20% error interval of predicted total catch did not include the observed total catch the last day of the test fishery.

	Fitted M_3			Fitted M_4		
Year	**Average daily error**	**total within**		**Average daily error**	**total within**	
		50%	**20%**		**50%**	**20%**
1968	.01776	June 11	June 17	.01590	June 10	June 13
1969	.01576	June 3	NE	.01386	June 5	June 25
1970	.01442	June 14	June 28	.01159	June 14	June 20
1971	.01694	June 13	NE	.01652	June 17	NE
1972	.01748	June 14	NE	.01438	June 12	June 15
1973	.01374	June 5	June 18	.01272	June 7	June 18
1974	.00891	June 1	June 12	.00830	May 31	June 8
1975	.01651	June 25	NE	.01599	June 20	NE
1976	.01515	June 25	July 4	.01315	June 20	July 4
1977	.01284	June 20	July 1	.01145	June 20	June 26
1978	.01020	May 31	July 15	.00992	May 30	June 3
1979	.01408	May 27	NE	.01036	May 31	NE
1980	.00970	June 3	June 21	.00871	June 2	June 8
1981	.00953	June 3	June 14	.00830	May 31	June 2

Table 25. Comparison of the ability of model four and the one population time density model to predict daily proportion of total catch and total annual catch. Parameters of model four are estimated by statistics presented in Tables 17 and 18. Parameters of model five are estimated by maximization of the likelihood function. Average daily error is defined by equation 66 in the text. NE signifies that the 50% or 20% error interval of predicted total catch did not include the observed total catch the last day of the test fishery,

	Estimated two-population model			**Fitted time density model, M_5**		
Year	**Average error daily predictions**	**Predicted total 50%**	**20%**	**Average error daily predictions**	**Predicted total 50%**	**20%**
1968	**.03348**	**June 24**	**July 30**	**.01819**	**June 12**	**June 16**
1969	**.01582**	**June 4**	**June 5**	**.01636**	**June 5**	**June 12**
1970	**.02016**	**June 16**	**NE**	**.01470**	**June 9**	**June 17**
1971	**.02982**	**July 10**	**NE**	**.01543**	**June 17**	**NE**
1972	**.04153**	**NE**	**NE**	**.01713**	**June 17**	**June 26**
1973	**.01499**	**June 11**	**June 13**	**.01389**	**June 11**	**June 20**
1974	**.00981**	**June 2**	**June 8**	**.00864**	**June 3**	**June 8**
1975	**.02811**	**NE**	**NE**	**.01615**	**June 18**	**June 28**
1976	**.04977**	**NE**	**NE**	**.01503**	**June 25**	**July 4**
1977	**.05478**	**NE**	**NE**	**.01244**	**June 12**	**June 21**
1978	**.01478**	**June 10**	**June 19**	**.01207**	**June 6**	**NE**
1979	**.01869**	**June 7**	**June 17**	**.01483**	**June 2**	**June 13**
1980	**.01554**	**June 15**	**June 18**	**.00802**	**June 4**	**June 18**
1981	**.01240**	**June 5**	**NE**	**.00819**	**June 3**	**NE**

Table 26. Comparison of the ability of model three and the time series model to predict daily proportion of total catch and total annual catch. Parameters of model three are estimated by statistics presented in Table 15 and 16. Average daily error is defined by equation 66 in the text. NE signifies that the 20% error interval of predicted total catch did not include the observed total catch the last day of the test fishery.

	Time Series Model			**Fitted one-population model**		
Year	**Average error**	**Predicted total**		**Average error**	**Predicted total**	
	daily predictions	**50%**	**20%**	**daily predictions**	**50%**	**20%**
1968	**.02188**	**June 18**	**July 3**	**.02279**	**June 25**	**June 30**
1969	**.01742**	**June 3**	**June 14**	**.01651**	**June 10**	**NE**
1970	**.01519**	**June 7**	**June 22**	**.01514**	**June 12**	**June 21**
1971	**.01770**	**June 16**	**June 28**	**.01932**	**June 24**	**July 7**
1972	**.01881**	**June 11**	**June 23**	**.02123**	**June 15**	**July 8**
1973	**.01599**	**June 5**	**June 13**	**.01573**	**June 5**	**June 19**
1974	**.01204**	**June 2**	**June 19**	**.01123**	**June 11**	**NE**
1975	**.02034**	**June 22**	**June 23**	**.01985**	**June 22**	**June 30**
1976	**.01902**	**June 28**	**June 30**	**.02162**	**June 30**	**NE**
1977	**.01503**	**June 18**	**July 1**	**.01814**	**June 11**	**NE**
1978	**.01103**	**May 31**	**June 7**	**.01155**	**June 5**	**NE**
1979	**.01542**	**June 7**	**June 8**	**.01489**	**May 28**	**NE**
1980	**.00912**	**June 6**	**June 16**	**.00968**	**June 5**	**NE**
1981	**.00946**	**June 5**	**June 6**	**.01105**	**June 1**	**NE**

DISCUSSION AND CONCLUSIONS ON MATHEMATICAL MODELS OF MIGRATORY TIMING

Two fundamentally different methods of intraseason estimation of abundance are evolving; the use of cumulative proportions averaged across defined days of historic data, and the adoption of hypothetical models which assume the general shape of the distribution of proportions over time. The first method was first formally quantified by Walters and Buckingham (1975) who suggested that total run size could be quantitatively anticipated by the ratio of catch plus escapement to date and the average cumulative proportion expected to have returned by that date. The average cumulative proportion on a given calendar date was defined as the arithmetic mean across years of the cumulative proportions recorded on that date. They concluded that the run size estimates were quite unreliable until over half of the run had past. Variation in average daily cumulative proportions can be reduced by standardizing the calendar date to day of the run, where the first day of the run is defined as the maximum of the second derivative of the normal equation defined by the mean and variance of each year (Hornberger and Mathisen 1980; Brannian 1982). Although the a posteriori assessment of average cumulative daily proportions is refined, the difficulties of objectively ascertaining the first day of the run during the season have yet to be resolved. Another means of synchronizing the calendar dates of migration is to objectively classify the years as early, average, or late according to mean day of migration (Mundy 1982a). The expected cumulative proportion is the average cumulative proportion across a calendar date for a subset of years, determined by spring temperatures.

The second technique developing as a method for intraseason abundance estimation assumes the existence of a probability density function which acurrately reflects the time distribution of proportions of total abundance for all years. Vaughan (1954) first recommended that temporal distributions of proportion could be modeled as probability distribution functions which best fit the data. For Southeastern Alaskan pink salmon migrations, beta curves were chosen the majority of times from the family of Pearson probability densities. In a study of Bristol Bay sockeye migrations, a two-parameter logistic function which asymptotically approaches one was chosen as an appropriate model of cumulative proportions over time (Mundy and Mathisen 1981). The parameters of the equation were estimated intraseason by least-squares fitting to early daily abundance estimates. Accurate estimates of total abundance were obtained well before the median day of migration in one of the two years. In contrast, Hornberger and Mathisen (1980) compared intraseason prediction performance of a normal curve function fitted to the average abundance distribution with the curve of the historical data average. They concluded that the historical average was the preferred means of intraseason prediction.

The results of the present study demonstrate that variations in the temporal distribution of abundance can be approximated by fitted probability density functions or by fitted analytical models; both of which employ equations used by previously-cited authors to express the daily proportion of total abundance as a function of time, environmental factors, and fishing effort. Errors of daily proportions estimated by empirical time series models are comparable to errors of daily proportions predicted by analytical models whose parameters are estimated by a function of average April temperatures or as an average of preiously determined parameter values. However, empirical methods remain superior to hypothetical models in their ability to forecast total abundance.

One advantage of the analytical approach is that the underlying mechanics of migratory behavior can be more easily incorporated into existing models without radically altering the model or the procedure for estimation of parameter values. The bell-shaped normal curve function is the nucleus of the models presented in the present study. The use of the normal curve is justified by virtue of the genetic nature of migratory timing (Mundy 1979); and the parameters of the normal curve function, mean and variance, are more readily related to the migratory time distribution than parameters of other bell-shaped curves. The assumption that catch is linearly dependent on wind and commercial effort is not contradicted by the results, but more directed studies may uncover a more complex nonlinear relationship. The ultimate objective of developing refinements in the quantitative description of migration should be a more complete conceptual model which explains the variation in migratory behavior as a function of intrinsic behavior of each major stock and the environmental parameters which directly affect the physiology of the animal.

A second advantage derives from the reduced number of parameters to be estimated in the analytical model. In the present study of chinook salmon migration, the problem of intraseason abundance forecasts is now reduced to the accurate estimation of the parameter values which characterize the analytical model. Mean day and variance of the Yukon River commercial catch have already been shown to be highly dependent on spring temperatures (Mundy 1982b). A similar relationship has been reported for Bristol Bay sockeye timing and May air temperatures (Burgner 1979). The mean and variance of the Yukon River test fishery catch is shown to be highly dependent on spring temperatures. Accurate forecasts of the constants which determine the distribution of predicted catches over time are essential for accurate catch estimates.

The results of the present study demonstrate that significant improvements in the ability to estimate daily proportions of total catch are achieved with the incorporation of wind speed and commercial effort measurements into the models. High wind speeds are often accompanied by larger-than-expected test fishery catches, intensive commercial effort reduces the test fishery catch, and the effects of both factors can be quantified. The time density of the migration is not readily and consistently divisible into two distinct migrations. Studies in progress confirm that the migrations of major upriver and downriver stocks of chinook salmon are not temporally separated at the Yukon River delta based on scale measurements (McBride and Wilcox, pers. comm.; pers. observ.). The inability to morphologically separate early and late migrants and the less accurate daily catch estimates of two population models presently restrict the class of analytical models describing the migratory timing of Yukon River chinook salmon to those models assuming only one population. However, fisheries of proven mixture of two or more populations (e.g., Lynn Canal in Southeastern Alaska) would be appropriate for such an analysis. Length frequencies of a mixture of age classes are routinely described by Hasselblad's (1966) iteration equations (MacDonald and Pitcher 1979).

As knowledge of migratory behavior continues to accumulate, quantitative descriptions will become more conceptual in nature. Yet interim analysis should not be restricted to the options of average proportional expectation of fitting nonlinear function to observed data. Statistical techniques of multiple regression analysis and time series analysis are relevant. Multivariate methods are regularly employed in quantifying bird migrations (e.g., Beason 1978; Blokpod 1978; and review by Richardson 1978). Time series analysis, utilizing the popular Box Jenkins Models (Box and Jenkins 1976) have been applied to yearly catch data of Atlantic Menhaden (Jensen 1976) and lobster landings (Boudreault et al. 1977) and monthly catch data of the New Zealand Rock Lobster (Saila et al. 1978) and the skipjack tuna fishery (Mendelssohn 1981). However, the danger of extrapolating false relationships is inherent in all statistically-based empirical models, and conceptual models should take precedence if acceptable accuracy is attainable.

Claims of the ability to foretell the abundance of a salmonid resource probably are as old as exploitation of the resource itself. Native Yukon Delta fishermen gage the magnitude of daily abundance by the speed and direction of wind at the river mouth. The track record of some old-timers is impressive, but the causal relation between wind and migratory behavior remains elusive, even though presently approximated by a linear function. Several authors have noted the difficulty of trying to statistically quantify the effects of atmospheric and water conditions on animal migrations. Banks (1969) comments that although there is an obvious correlation between stream flow and incoming Atlantic salmon migrants, it cannot be predicted accurately or reduced to a mathematical formula. Ellis (1962) reported that although correlations between river entry of sockeye salmon and six environmental measurements and changes of intensity of these measurements were not significant, upriver movement could be qualitatively predicted by observing changes from sunny weather to cloudy weather. Onshore wind speed was found to be more highly correlated with number of kokanee entering their spawning stream when the tails of the run were deleted (Lorz and Northcote 1965).

The relationship between wind speed and migratory behavior is elusive. Lorz and Northcote (1965) suggested that wind affects the spatial distribution of home stream water, broadcasting the chemical identity of the stream along a greater area of the shoreline. Reduction of light penetration was secondarily implicated. Barber (1979) speculated that some species of salmon may navigate bv Langmuir circulations in the open ocean. Hornberger and Mathisen (1981) noted that chinook salmon in Nushagak Bay are more susceptible to catch on windy days.

The present level of understanding limits the classification of analytical models developed in the present study and fitted to the lower Yukon test fishery data to an empirical set of relationships. The bridge from proxy data to the casual factor is either tentatively established (day or run, temperature and photoperiod; the negative commercial effort parameter and removal of chinook salmon by commercial fleet) or completely unknown (wind speed). To suggest that the proposed models represent conceptual or mechanistic models would be misleading (Austin and Ingham 1978). To some extent they approximate the true model. As noted by Brannian (1982), an empirical model many times is the predecessor of the conceptual or mechanistic model.

The mechanistic approach often provides new insights into the underlying dynamics and character of the migration. Figures 33-35 depict the relationship between April temperatures and annual mean, variance, and wind coefficients calculated by M_3. Chinook salmon returning to the Yukon River in years of warm springs arrive at an earlier date (Figure 33), the time interval of migration is prolonged,

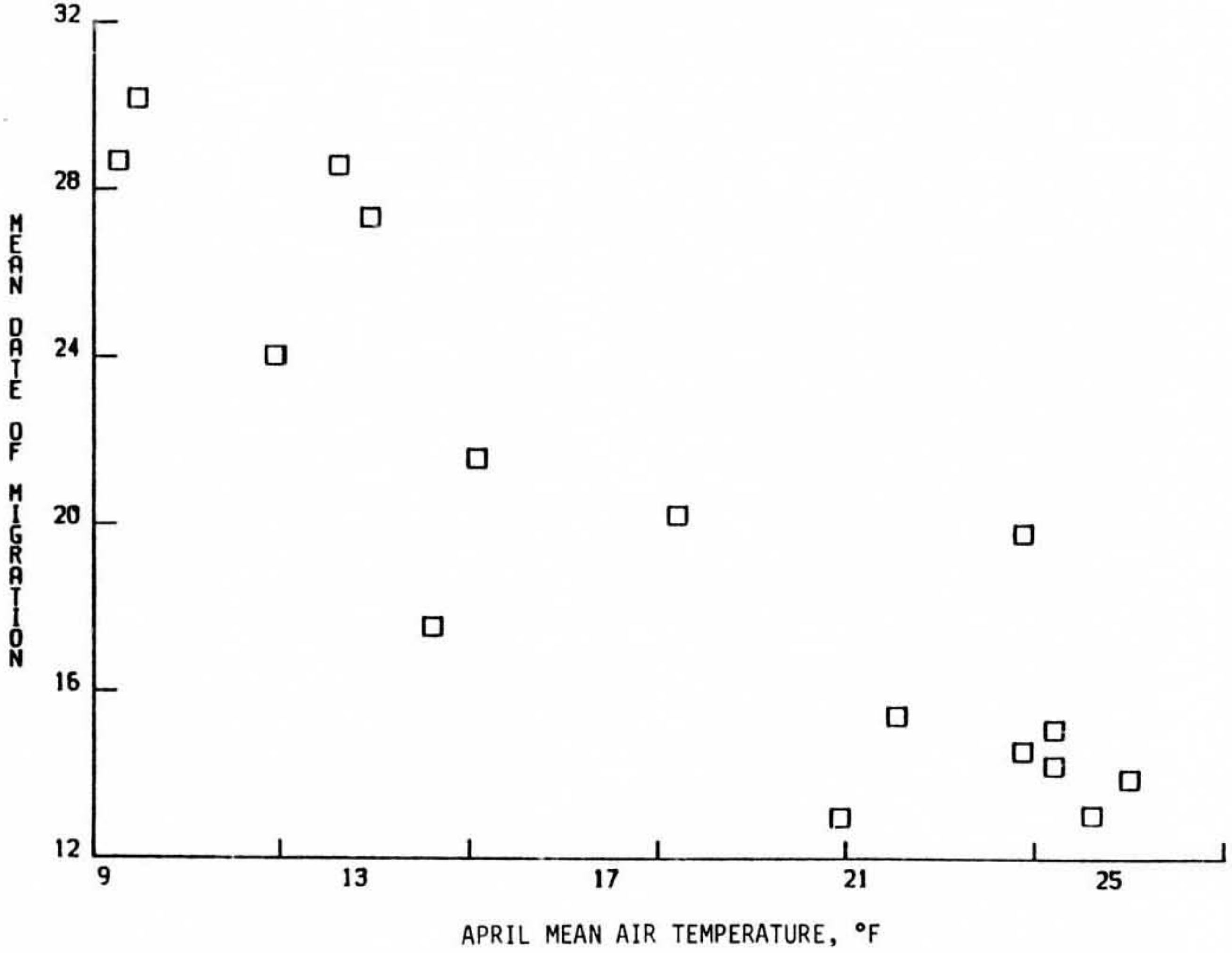

Figure 33. Relationship of April mean air temperature to the mean date of migration for model three.

as demonstrated by larger variances (Figure 34), and are more susceptible to the influence of wind (Figure 35). In contrast, the migration of chinook salmon whose arrival is retarded by a cool spring is characterized by a smaller time interval and reduced effect of wind. The physiological changes which accompany migratory behavior may become more insistent for fish arriving late. The parameter quantifying the effect of commercial effort on relative abundance has predictably become more negative in recent years (Figure 36). The increase in efficiency of the commercial fleet and its impact on chinook management is discussed by Mundy (1982a).

In order to avoid overharvesting or underharvesting the temporal components of a migratory population, managers need reliable estimates of abundance and time distribution of the resource. Increasing the accuracy of the yield estimates can result in substantial profit to the fishing community (Mathews 1967; Mundy and Mathisen 1981). To accomplish this objective, control systems have been proposed which incorporate long-range abundance estimation with intraseason modification (Walters and Buckingham 1965; Mundy and Mathisen 1981). Initially the estimation process uses escapement counts and the historical recruit-per-spawner relationship to forecast long range recruitment. Predicted yield is further refined at observable life history stages (fry, smolt, marine immature) when total yield is a function of the estimated abundance at the particular life history stage. Error in yield estimates tends to decrease for later life stages (Mundy and Mathisen 1981). The most accurate prediction of total abundance is expected to be the intraseason estimate which should deliver increasingly accurate forecasts of abundance as the run develops. Development of intraseason abundance estimation techniques should be viewed in the context of a complete abundance estimation system.

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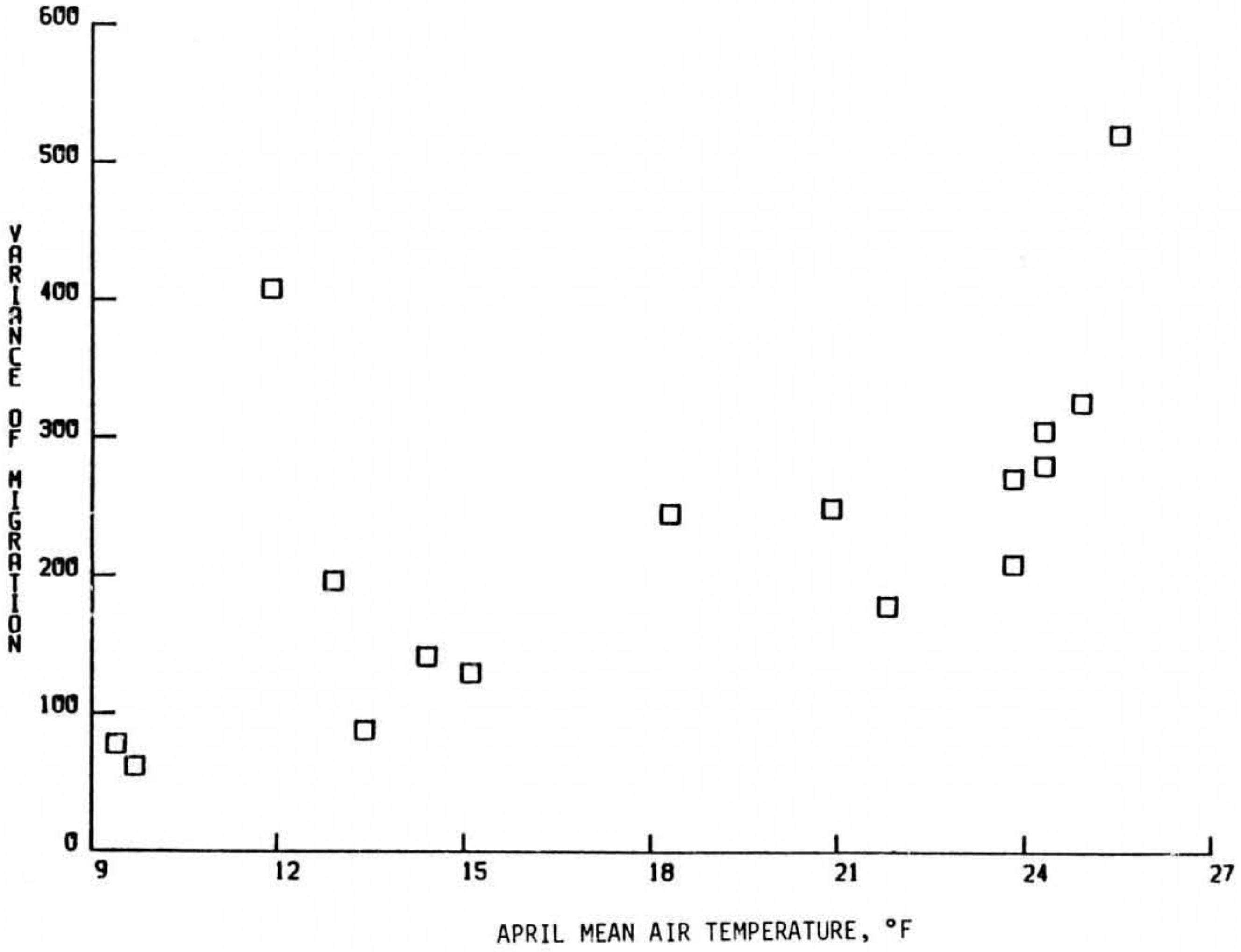

Figure 34. Relationship of April mean air temperature to the variance of migration for model three.

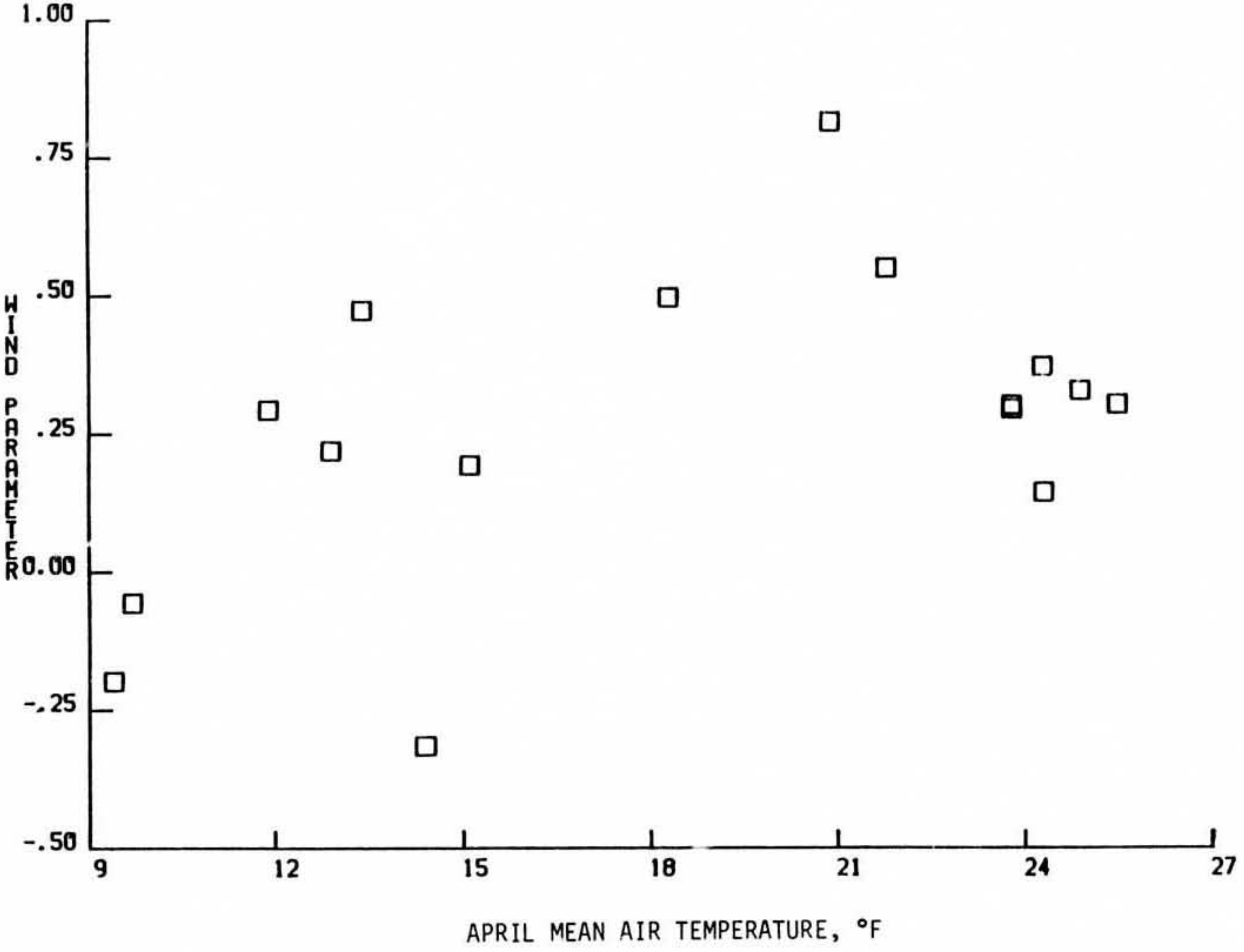

Figure 35. Relationship of April mean air temperature to the influence of wind on migratory behavior for model three.

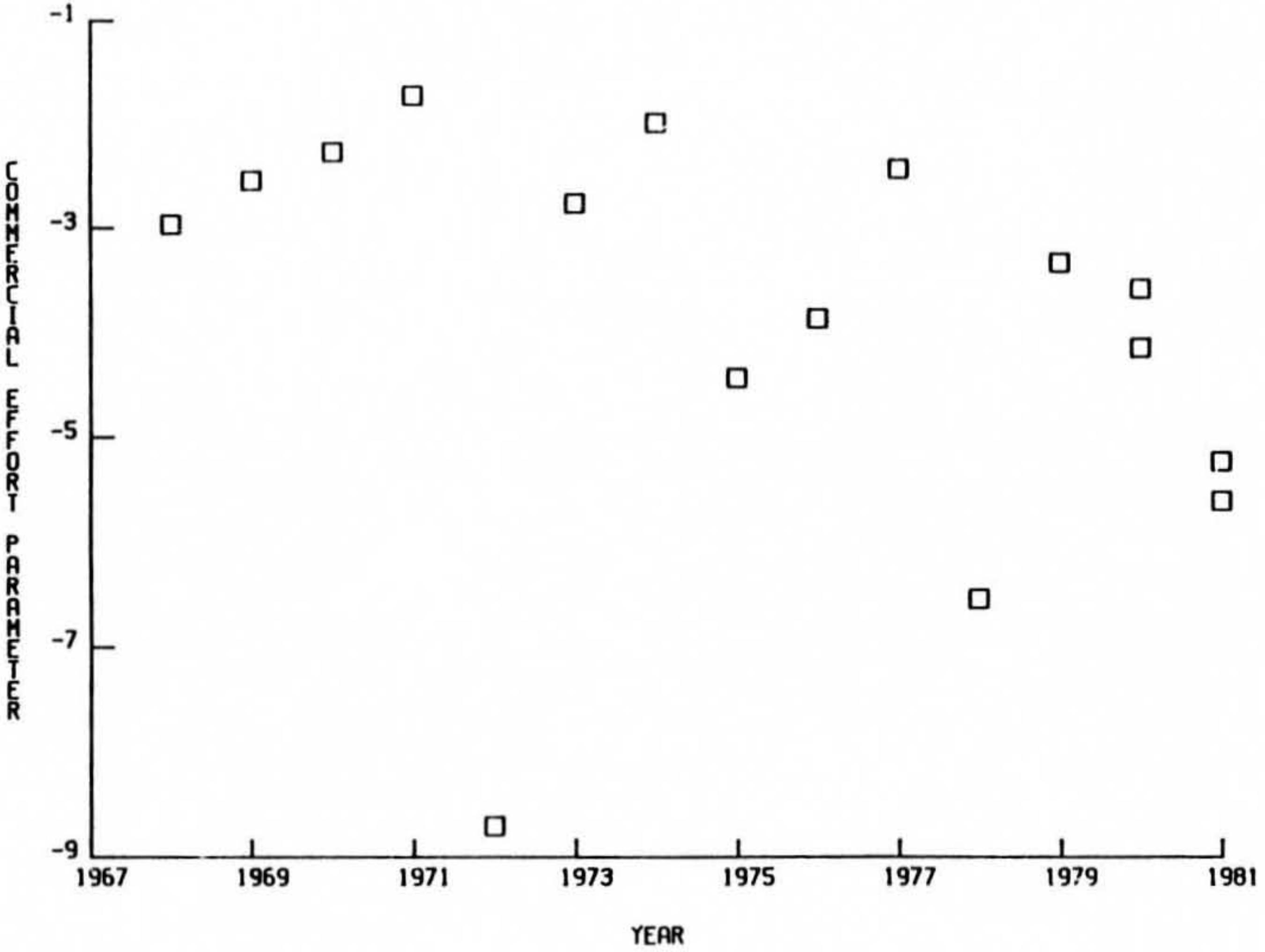

Figure 36. Relationship of year of test fishery catch to the effect of commercial effort on test fishery catch for model three.

chairman of the committee, was more than helpful in developing the concepts of this study. The foundations of many of the ideas expressed in this dissertation were introduced by Dr. Mundy in his 1979 dissertation. I also thank Ivan Frohne for revising this report and pointing out some of the areas which were not clear.

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LITERATURE CITED

Alabaster, J.S. 1970. River flow and upstream movement and catch of migratory salmonids. Journal of Fish Biology 2: 1-13.

Anas, R.E. and S. Murai. 1969. Use of scale characters and a discriminant function for classifying sockeye salmon *(Oncorhynchus nerka)* by continent of origin. International North Pacific Fisheries Commission Bulletin 26: 157 - 192.

Anderson, O.D. 1977. Time series analysis and forecasting: another look at the Box-Jenkins approach. Statistician 26: 285 - 303.

Anon. 1962. Racial study of king salmon. Fish and Wildlife, Yukon River Basin Progress Report 5, pp. 25 - 35.

Austin, H.M. and M.C. Ingham. 1978. Use of environmental data in the prediction of marine fisheries abundance. In Knauss, J. (chairman) Climate and fisheries. Proceedings from a workshop held at the Center for Ocean Management Studies, University of Rhode Island, Kingston, RI, pp. 93 - 105.

Babcock, A.M. 1981. A quantitative measure of migratory timing in the brown shrimp *(Penaeus aztecus)* with applications in fisheries management. M.S. Thesis, Old Dominion University, Norfolk, VA.

Banks, J.W. 1969. A review of the literature on the upstream migration of adult salmonids. Journal of Fish Biology 1: 85 - 136.

Barber, F.G. 1979. On ocean migration, speciation, cycle dominance, and density dependence in Pacific salmon. Fisheries and Marine Service Technical Report 872, Ocean and Aquatic Science Affairs Branch, Fisheries and Marine Service, Department of Fisheries and the Environment, Ottawa, Ontario. K1A 0E6. 7 pp.

Beason, R.C. 1978. The influence of weather and topography on water bird migration in the Southwestern United States. Oecologia (Berl.) 32: 153 - 169.

Blokpoel, H. 1978. Weather and spring migration of snow geese across southern Manitoba. Oikos 30: 350 - 363.

Bilton, H.T. and H.B. Messinger. 1975. Identification of major British Columbia and Alaska runs of age 1.2 and 1.3 sockeye from their scale characters. International North Pacific Fisheries Commission Bulletin 32: 109 - 129.

Boudreault, F.R., Dupont, J.N., and C. Sylvian. Models lineaires de prediction des debarquements de homard aux Iles-de-la-Madelaine (Golfe due Saint-Laurent). Journal of the Fishery Research Board of Canada 34: 379 - 383.

Box, G.E.P. and G.M. Jenkins. 1976. Time series analysis: forecasting and control. Rev. ed. Holden-Day, San Francisco. 575 pp.

LITERATURE CITED (Continued)

Brannian, L.K. 1982. The estimation of daily escapement and total abundance from catch per unit effort of the sockeye salmon fishery in Togiak Bay, Alaska. M.S. Thesis, University of Washington, Seattle, WA 173 pp.

Bulmer, M.G. 1974. A statistical analysis of the 10-year cycle in Canada. Journal of Animal Ecology 43: 701 - 718.

Burgner, R.L. 1978. Some features of ocean migrations and timing of Pacific salmon, Contrib. No. 448, College of Fisheries, University of Washington, Seattle, WA, pp. 153 - 164.

Cook, R.C. and G.E. Lord. 1978. Identification of stocks of Bristol Bay sockeye salmon *(Oncorhynchus nerka)* by evaluating scale patterns with a polynomial discriminant method. Fishery Bulletin 76: 415 - 423.

Dodimead, A.J., F. Favorite, and T. Hirano. 1963. Salmon of the North Pacific Ocean. Part II. Review of oceanography of the subarctic Pacific region. International North Pacific Fisheries Commission, Bulletin 13: 195 pp.

Ellis, D.V. 1962. Preliminary studies on the visible migration of adult salmon. Journal of the Fisheries Research Board of Canada 19: 137 - 148.

Dahlberg, M.L. 1968. Analysis of the dynamics of sockeye salmon returns to the Chignik Lakes, Alaska. Ph.D. Dissertation, University of Washington, Seattle. 337 pp.

Favorite, F., A.J. Dodimead, and K. Nasu. 1976. Oceanography of the subarctic Pacific regions, 1960-1971. International North Pacific Fisheries Commission, Bulletin 33: 187 pp.

Freund, J.E. and R.E. Walpole. 1980. Mathematical Statistics, 3rd Ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 548 pp.

Gray, R.H. and J.H. Haynes. 1979. Spawning migration of adult chinook salmon. Journal of the Fisheries Research Board of Canada 36: 1060 - 1064.

Hacker, C.S., D.W. Scott, and J.R. Thompson. 1975. A transfer function forecasting model for mosquito populations. The Canadian Entomologist 107: 243 - 249.

Hasselblad, V. 1966. Estimation of parameters for a mixture of normal distributions, Technometrics 8: 431 - 444.

Hornberger, M.L., P.R. Mundy, and O.A. Mathisen. 1979. Nushagak Bay salmon fishery model. Final Report, Fisheries Research Institute, University of Washington, Seattle, WA. 74 pp.

Hornberger, M.L. and O.A. Mathisen. 1980. Nushagak Bay salmon fishery model. Final Report, Fisheries Research Institute, University of Washington, Seattle, WA. 76 pp.

LITERATURE CITED (Continued)

Hornberger, M.L. and O.A. Mathisen. 1981. Nushagak Bay salmon fishery model. Final Report, Fisheries Research Institute, University of Washington, Seattle, WA. 63 pp.

Ingraham, W.J., Jr. 1979. The anomalous surface salinity minima area across the Northern Gulf of Alaska and its relation to fisheries. Marine Fisheries Review 1979: 8 - 19.

Ingraham, W.J., A.Bakun, and F. Favorite. 1976. Physical oceanography of the Gulf of Alaska. U.S. Department of Commerce, NOAA, NMFS, Northwest Fish. l Ctr. Seattle, Washington, Proc. Rep. 132.

Jensen, A.L. 1976. Time series analysis and forecasting of Atlantic menhaden catch. Chesapeake Science 17: 305 - 307.

Leggett, W.C. 1977. The ecology of fish migrations. Annual Review of Ecological Systems 8: 285 - 308.

Libosvarsky, J. 1976. On the ecology of spawning migration of brown trout. Zoologicke Listy. 25: 175 - 182.

Lorz, H.W. and T.G. Northcote. 1965. Factors affecting stream location and timing and intensity of entry by spawning kokanee *(Oncorhynchus nerka)* into an inlet of Nicola Lake, British Columbia. Journal of the Fisheries Research Board of Canada 22: 665 - 687.

Major, R.L., S. Murai, and J. Lyons. 1975. Scale studies to identify Asian and Western Alaskan chinook salmon. International North Pacific Fisheries Commission Annual Report 80 - 91.

Mathews, S.B. 1967. Economic evaluation of forecasts of sockeye salmon runs to Bristol Bay, Alaska. Ph.D. Dissertation, University of Washington.

MacDonald, P.D. and T.J. Pitcher. 1979. Age-groups from size-frequency data: A versatile and efficient method of analyzing distribution mixtures. Journal of the Fisheries Research Board of Canada 36: 987 - 1001.

Mathisen, O.A. and M. Berg. 1968. Growth rates of the char in the Vardnes River, Troms, northern Norway. Rep. 48, Inst. Freshw. Res., Drottningholm.

Matylewich, M.A. 1982. Environmental influence on the migratory behavior of the brown shrimp in Pamlico Sound, North Carolina. Master of Science Thesis, Old Dominion University, Norfolk, Virginia. 65 pp.

McMichael, F.C. and J.S. Hunter. 1972. Stochastic modeling of temperature and flow in rivers. Water Resources Research 8: 87 - 98.

McNew, R.A. and R.C. Summerfelt. 1978. Evaluation of a maximum likelihood estimator for analysis of length-frequency distributions. Transactions of the American Fisheries Society 107: 730 - 736.

Merritt, M.F. and K. Roberson. 1981. A quantitative measure of migratory timing in sixteen upper Copper River sockeye salmon stocks, and its management implications to the Prince William Sound commercial fishery. Draft of a report to Alaska Dept. Fish and Game, Division of Commercial Fisheries. 43 pp.

Mendelssohn, R. 1981. Using Box-Jenkins models to forecast fishery dynamics: identification, estimation, and checking. Fishery Bulletin 78: 887 - 896.

Mundy, P.R. 1979. A quantitative measure of migratory timing illustrated by application to the management of commercial salmon fisheries. Ph.D. dissertation, University of Washington, Seattle. 85 pp.

Mundy, P.R. 1982a. Migratory timing of adult chinook salmon *(Oncorhynchus tshawytscha)* in the lower Yukon, Alaska with respect to fisheries management. Department of Oceanography, Old Dominion University, Norfolk, VA. 23508. Technical Report No. 82-1.

Mundy, P.R. 1982b. Computation of migratory timing statistics for adult chinook salmon in the Yukon River, Alaska, and their relevance to fisheries management. North American Journal of Fisheries Management 4: 359 - 370.

Mundy, P.R. and O.A. Mathisen. 1981. Abundance estimation in a feedback control system applied to the management of a commercial salmon fishery, pp. 81-98 in K. Brian Haley (ed), Applied Operations Research in Fishing, Plenum Publ. Corp., New York.

Nie, N.H., C.H. Hull, J.G. Jenkins, and D.H. Bent. 1975. Statistical package for the social sciences, second edition. McGraw-Hill, Inc., New York. 675 pp.

Neibauer, H.J. 1979. Recent short period winter time climatic fluctuations and their effect on sea surface temperature in the eastern Bering Sea. In D.W. Hood, ed. Eastern Bering Sea Shelf: Oceanography and Resources. Vol. I, pp. 335 - 351.

Neibauer, H.J. 1980. Recent fluctuations in meteorlogical and oceanographic parameters in Alaska waters, Sea Grant Report 79-12 and IMS Report 79-2. 373 - 405.

Nishiyama, T. 1977. Food-energy requirements of Bristol Bay sockeye salmon, *Oncorhynchus nerka* (Walbaum) during the late marine life stage. Spec. vol. 1977: 289 - 320. Res. Inst. N. Pac. Fish., Faculty of Fisheries, Hokkaido Univ., Hakodate, Japan.

Poole, R.W. 1976a. Empirical multivariate autoregressive equation predictors of the fluctuation of interacting species. Mathematical Biosciences 28: 81 - 97.

Poole, R.W. 1976b. Stochastic difference equation predictors of population fluctuations. Theoretical Population Biology 9: 25 - 25.

Preston, F.W. 1966. The mathematical representation of migration. Ecology 47: 375 - 392.

Richardson, W.J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30: 224 - 272.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191: 382 pp.

Ricker, W.E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. Journal of the Fisheries Research Board of Canada 15: 991 - 1006.

Ricker, W.E. 1973. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. Journal of the Fisheries Research Board of Canada 30: 1275 - 1286.

Rothschild, B.J. and J.W. Balsiger. 1971. A linear programming solution to salmon management. Fishery Bulletin 69: 117 - 140.

Royce, W.F. 1965. Almanac of Bristol Bay sockeye salmon. University of Washington, Fish. Res. Inst. Circ. 235. 48 pp.

Saila, S.B., M. Wigbout, and R.J. Lermit. 1980. Comparison of some time series models for the analysis of fisheries data. J. Cons. Int. Explor. Mer 39 44 - 52.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, Second Edition. W.H. Freeman and Company. San Francisco, CA. 859 pp.

Trasky, L. 1973. Yukon River salmon tagging studies 1970 [illegible]2. Arctic-Yukon-Kuskokwim Region. Yukon stock separation report [illegible] Alaska Department of Fish and Game. Anchorage, Alaska.

Vaughan, E. 1954. The use of catch statistics for estimating [illegible]ters of the pink salmon migration pattern in Icy Strait. In: Science in Alaska 1952. Proceedings of the Third Alaska Academic Conference at Mt. McKinley National Park 1952. Alaska Div. AAAS.

Walters, C.J. and Buckingham. 1975. A control system for intraseason salmon management. Proceedings of a workshop on salmon management. International Institute for Applied Systems Analysis, Scholoss Laxenburg, 2361 Laxenburg, Austria.