Temporal and Spatial Dynamics of a Coastal Pelagic Species, *Sardinella maderensis* off the Ivory Coast

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Variations of fortnightly catch-per-unit-effort (CPUE) of *Sardinella maderensis* off the Ivory Coast is studied both in time and in space–time. Using multivariate time series models, lagged values of coastal sea surface temperature (SST) and salinity explain 33% of the variation of CPUE during this period. When optimal transformations are estimated, 55% of the variance is explained. The optimal transformations suggest that good catch rates are associated with local upwelling or oceanic frontal structures. However, the model differs significantly from previous models that examine the CPUE for the combined catches of the fleet. The model is shown to produce reasonable forecasts for the next two years. In space–time, evidence is presented that suggests that the migration of the fish between areas is related to movement of structures in the ocean. The relationships between CPUE and the environment are again highly nonlinear, so that linear analysis, such as correlation analysis, will be of limited use in examining these questions.

On étudie dans le temps ainsi que dans l'espace et le temps les variations des prises par unité d'effort (PPUE) de *Sardinella maderensis* observées à tous les quinze jours au large de la Côte d'Ivoire. Quand on utilise des modèles de séries chronologiques à plusieurs variables, les valeurs décalées de la TMS et de la salinité près des côtes expliquent 33 % de la variation des PPUE observée pendant cette période. L'estimation des transformations optimales permet d'expliquer 55 % de la variance. Ces transformations donnent à penser que de bons taux de capture sont associés à une remontée locale ou à des fronts océaniques. Cependant, le modèle diffère sensiblement des modèles précédents qui étudient les PPUE en fonction des prises regroupées de la flottille. On montre que le modèle fournit des prévisions raisonnables pour les deux prochaines années. Sur le plan spatio-temporel, on présente des faits qui portent à croire que la migration de ce poisson entre les secteurs est liée au déplacement de structures dans l'océan. Les relations fonctionnelles entre les PPUE et l'environnement sont une fois de plus fortement non linéaires, de sorte que l'analyse linéaire, comme l'analyse de corrélation, sera d'une utilité restreinte pour l'étude de ces questions.

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In a previous paper (Mendelssohn and Cury 1987) we studied the temporal dynamics of the combined pelagic species of the fishes off the Ivory Coast and how environmental processes affected the combined species dynamics, ignoring any spatial dynamics. There is reason to believe, however, that the dynamics of the combined species, which is of the greatest importance to the fleet, may differ from the dynamics of any individual species. If the biology of the individual species differs significantly, only broad oceanographic processes may appear to be affecting the dynamics, while different, more local processes may be affecting a particular species. Therefore, in this paper, we focus our attention on the dynamics of the catch rates of the dominant pelagic species caught in this area, *Sardinella maderensis*.

Determining the factors that affect changes in pelagic fish abundance, availability, and distribution, is complicated since the fish show a preference both for certain contemporaneous environmental conditions as well as for a particular history of the water masses and their food content (Mendelssohn and Roy 1986; Cury and Roy 1987; Mendelssohn and Cury 1987). A purely spatial analysis would blur these features, suggesting little relationship with the environment. Thus a dynamic, temporal approach is required.

The continental shelf off the Ivory Coast is affected by two upwelling seasons: a main season that occurs around June to September and a weaker, shorter season around January and February (Morlière 1970; Picaut 1983). Both sea surface temperature and salinity in this area vary seasonally and the intra-year variability in fish availability has been shown to be influenced by this variability (Marchal 1967). Marchal and Picaut (1977) present evidence that the strength of the local upwelling off the Ivory Coast, which is partly influenced by the configuration of the continental shelf, induces differential pelagic fish distributions. These fish distributions will fluctuate in space due to the dynamics of the water masses (Marchal 1967; ORSTOM/FRU 1976). Thus a temporal approach by itself also is not sufficient to explain the variability in fish availability — a spatial approach is required.

Understanding intra-year variations in indices such as catch-per-unit effort (CPUE) that reflect availability or abundance of a fish species is important to fisheries management. Studies have suggested that environmental conditions affect availability and hence fishing success (see for example Belvèze and Erzini 1983). During any given year there are probably several environmental factors that may influence fish availability, such as: sea temperature, salinity, dissolved oxygen, water mass boundaries, color and turbidity of the water, river outflows etc. (Bakun and Parrish 1980; Laevastu and Hayes 1981). Robust forecasts for fisheries need to be based on an understanding of the processes involved and should also help to clarify and increase our understanding of how the climatic factors influence the fish population.

Our interest in this paper is to determine the environmental processes that are important to the dynamics of *S. maderensis*, the form of these relationships, and to see to what extent spatial aggregation of fisheries data distorts these relationships. We analyze, using catch rate data, the changes in CPUE of this species through time, treating the entire area in aggregate, as well as the spatial–temporal dynamics of the species, that is the changes in time as well as the simultaneous changes in the distribution in space. As indicators of the environment we use sea surface temperature (SST), the sea temperature at 5 m depth (SST5M) and salinity at 5 m depth (SAL5M). These variables are chosen because they are the most complete and readily available environmental series and because they tend to reflect broad changes in the ocean environment.

Our models lead us to the conclusion that the dynamics of an individual species may differ considerably from that of an assemblage of related species. The interpretation of possible causal mechanisms affecting the population dynamics also differs when we examine the species in space and time, rather than in either dimension alone. We also examine the ability of the spatially aggregated model to provide forecasts of future catch rates.

Methods

As in our previous paper, our main methods of analysis are multivariate time series techniques. We fill in missing data using an algorithm of Shumway and Stoffer (1982). This algorithm fits to the data an autoregressive (AR) model (in this case of lag 2) of the form:

$$(1)\quad x(t) = Ax(t-1) + w(t)$$

$$(2)\quad y(t) = Hx(t) + v(t),$$

where $x(t)$ is a p-dimensional vector of the underlying population at time t, $y(t)$ is a q-dimensional vector of the observed data, H is a $q \times p$ known matrix, A is a $p \times p$ matrix of parameters to be estimated, $w(t)$ is an independent, identically distributed random vector distributed as normal $(0,Q)$ and v is an independent, identically distributed random vector distributed as normal $(0,R)$. The algorithm uses a variant of the EM algorithm (Dempster et al. 1977) to find maximum likelihood estimates of A, Q, and R as well as minimum mean square estimates of the $x(t)$. A rationale for using AR(2) models is given in Mendelssohn and Cury (1987).

To find local trend lines in the data we use the LOWESS scatterplot smoother (Cleveland 1979). This smoother is a two pass algorithm. In the first pass, each point is estimated using a weighted regression of all points within a given neighborhood of the point to be estimated. The second step corrects the estimate for outliers.

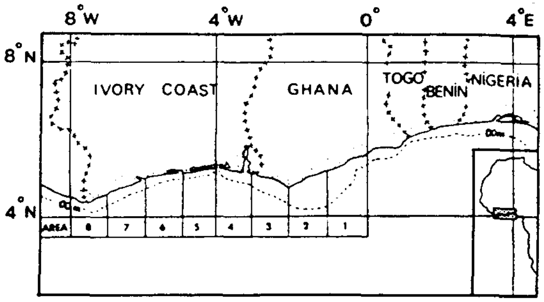

FIG. 1. Location of areas studied off the Ivory Coast.

Given data from a set of k time series, we consider a class of stochastic difference equations called vector autoregressive moving average models (or ARMA models for short) of the form (Tiao and Box 1981)

$$(3)\quad \Phi_p(B)z_t = \Theta_q(B)a_t,$$

where

$$(4)\quad \Phi_p(B) = I - \Phi_1 B - \ldots - \Phi_p B^p,$$

$$(5)\quad \Theta_q(B) = I - \Theta_1 B - \ldots - \Theta_q B^q$$

are matrix polynomials in B, the Φ's and Θ's are $k \times k$ matrices, $z_t = Z_t - \eta$ is the vector of deviations from some origin η that is the mean if the series is stationary, and $\{a_t\}$ with $a_t = (a_{1t}, \ldots, a_{kt})$ is a sequence of random shock vectors, identically, independently and normally distributed with zero mean and covariance matrix Σ. We follow the identification and estimation scheme described in Tiao and Box (1981) and Tiao et al. (1980), also used in our previous paper (Mendelssohn and Cury 1987).

We emphasize that throughout the paper we fit true multivariate models, not transfer-function or so called ARMAX models. There are some technical differences between the two models, which are most important when we are looking at space–time dynamics and are modeling both CPUE and the environment. Vector ARMA models, since they include the interaction between all the variables, tend to better take into account the intercorrelations between various different environmental series. These points are discussed further in Tiao and Box (1981, p. 804) and in Tiao et al. (1980).

At points in the paper we also use a subset autoregression procedure developed by Akaike (Akaike et al. 1979) to help identify the appropriate model form for estimation. This is a complicated procedure based on the Householder transformation and the AIC information measure and the reader is referred to the reference for a complete description of it.

Most techniques such as regression fit a linear, additive model to the data of the form

$$(6)\quad y(t) = u + \sum_{i=1}^{N} \beta_i x_i(t) + e(t).$$

A simple, natural extension is to fit additive models of the form

$$(7)\quad T(y(t)) = a + \sum_{i=1}^{N} s_i(x_i(t)) + h(t),$$

where $T(\ )$ and the $s_i(\ )$ are possible nonlinear transformations

TABLE 1. Values of the coefficients of the multivariate AR(2) model used to estimate missing values in the CPUE time series.

	Area 4 CPUE		Area 5 CPUE		Area 6 CPUE		Area 7 CPUE	
Area	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$	$(t-1)$	$(t-2)$
4	0.03	0.04	−0.05	0.04	−0.19	0.43	0.29	0.29
5	−0.05	0.02	0.03	0.02	0.02	0.27	0.05	0.13
6	0.04	0.02	0.02	0.13	0.36	0.22	0.04	−0.01
7	0.08	0.08	0.10	−0.19	−0.22	0.51	0.26	0.42

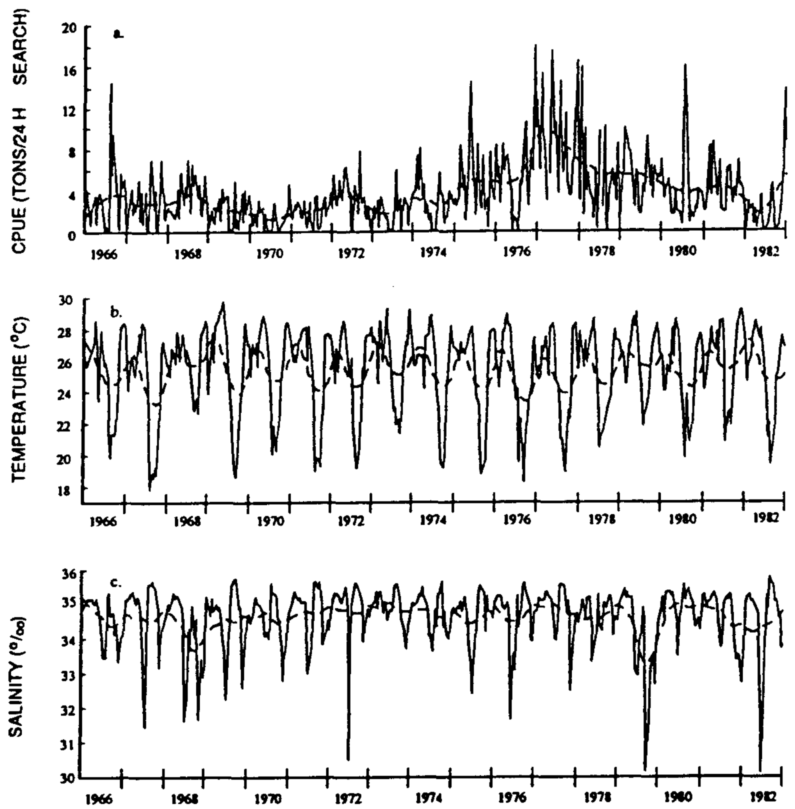

FIG. 2. Time series and estimated local trend for (a) aggregate CPUE, (b) SST, and (c) salinity.

of the data. In most problems, the form of these functions is not known a priori. The ACE (Alternating Conditional Expectations) algorithm of Breiman and Friedman (1985) empirically estimates the transformations that will have the smallest normalized residual error. In the bivariate case, this is equivalent to finding the transformations that produce the highest correlation. As the method is empirical, the form of each transformation is found by plotting the transformed data versus the original data. In the fisheries literature this algorithm has been used successfully by Mendelssohn and Cury (1987) and Mendelssohn and Mendo (1987).

Data

Biological Data

The pelagic fishery off the Ivory Coast has been described previously (Marchal 1967; FAO 1974, 1982), and Fonteneau and Marchal (1970) describe the data collection and data summarization procedures. *Sardinella maderensis* is the primary species exploited by the purse seiners based in Abidjan. The average annual landings of *S. maderensis* are about 10 000 t (mean for 1966–82); this is approximately 50% of the total Ivoirian catch of small pelagic species.

For purposes of our analysis, the Gulf of Guinea off the Ivory Coast was divided into eight areas each one degree in longitude and extending from 4°N of latitude to the coastline (Fig. 1). Measures of effort based on the time the boats spent searching for fish have been calculated using the method described in Fonteneau and Marchal (1970). CPUE for areas 4 to 7 was calculated for each fortnight from 1966 to 1982. (Fortnights in this context are periods of one-half month, not of 2 wk. Therefore each "fortnight" can vary in duration by up to several

TABLE 2. Parameters estimate and SE of the model using SST5M and SAL5M time series.

	Period 1966–1982		
Lag	Parameters	Estimate	SE
1	LNCPUE	0.304	0.049
	SST5M	−0.057	0.025
	SAL5M	0.028	0.012
2	LNCPUE	0.144	0.048
	SST5M		
	SAL5M		
4	LNCPUE		
	SST5M		
	SAL5M	−0.098	0.042
5	LNCPUE		
	SST5M	−0.078	0.026
	SAL5M	0.120	0.053
6	LNCPUE	0.192	0.046
	SST5M		
	SAL5M	0.073	
13	LNCPUE		
	SST5M	−0.062	0.014
	SAL5M		

days). Areas 4 to 7 are those where most of the catch of *S. maderensis* was taken. CPUE for each area was calculated by dividing the total catch in that area by the total search time for the boats in that area for the entire fortnight.

Mendelssohn and Cury (1987) discuss this measure of CPUE and possible problems that can arise when using it as a measure of local abundance. These problems are further compounded in this instance because it is not clear how to partition the measure of effort to reflect the effort expended only for *S. maderensis*. Using total effort as we do in this paper is not a completely satisfying alternative, because the fishermen fish for many species and for many periods, so the level of effort may be independent of the abundance of *S. maderensis* due to the presence of other species in the area.

The CPUE time series has missing data points, because an absence of fishing effort does not necessarily imply an absence of fish. Each of the areas 4–7 has about 10% of the data missing. The estimated parameters of the AR(2) model given in equations (1) and (2), used to fill in the data (Table 1), suggest a west to east migration and possible return. For example, CPUE in area 4 is significantly influenced by CPUE in areas 6 and 7 both 1 and 2 fortnight earlier (the last four values of the first row of the table) while area 7 is influenced by the past history of areas 6 and 7 and to some extent that of area 5 (the last row of the table).

Use of the completed data series in forming the space–time model will introduce more bias than in Mendelssohn and Cury (1987), due to some circularity in the process. The missing values of CPUE are estimated by an AR(2) model based on CPUE in all the areas during the surrounding time periods. Thus estimates of inter-area migrations might be affected by the filled-in data. Also, as only one species is being investigated, there are many more periods where there was effort but no catch of this particular species. This increases the likelihood that the form of the relationships is nonlinear, and that simple linear tools such as correlation studies or regression-like models will not be adequate. However, as only 10% of the data are missing, the filled-in data would have to have high leverage to greatly affect the final parameter estimates. As a further assurance that the filled-in values have not unduly influenced our results, we checked the stability of our parameter estimates to the inclusion or deletion of data and compared our results for consistency with independent observations on the fishery.

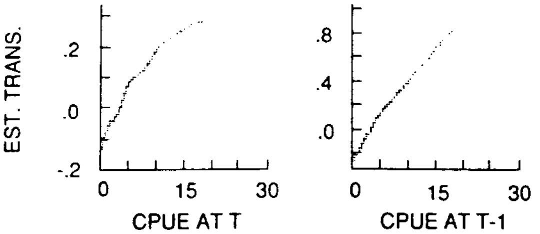

FIG. 3. Estimated optimal transformations of CPUE for predicting spatially aggregated CPUE.

The AR(2) model estimated by the missing data algorithm produces smoothed estimates of the data, including observation error. The smoothed values in each area (not shown) are close to the observed values when both exist and are consistent with other areas when one area has data and the second area does not. The completed time series of CPUE for each area were formed by substituting the smoothed estimate for each missing data point (see below).

A time series of CPUE aggregated across areas was calculated as the catch for all areas divided by the total effort (Fig. 2a). The localized trend, calculated using the LOWESS scatterplot smoother (Cleveland 1979), shows a slight dip in 1970, a slight rise and then a dip in 1972–73, and then a steady rise in CPUE to 1977. From mid-1977 onward, the trend has been downward until the start of an upturn in 1982.

Environmental Data

The environmental series consisted of SST data collected by merchant ships in the areas and SST5M and SAL5M collected by the Centre de Recherche Océanographique of Abidjan at a coastal station near Abidjan. Mean values were calculated for each fortnight to coincide with the fisheries data and missing data were filled in as in Mendelssohn and Cury (1987). SST aggregated across areas was calculated as the mean of the SST data by area.

The SST5M time series (Fig. 2b) shows a slight cooling trend until the end of 1967 followed by a slight warming trend until mid 1969. Since then there is no long-term trend in the data. The years 1969, 1973, 1978, and 1979 had noticeably warmer temperature minimums, while 1967 had a colder temperature minimum.

The SAL5M time series (Fig. 2c) also shows little long-term trend, except for sharp drops in 1968 and 1979. The years 1972, 1979, and 1982 also had significantly lower salinity minima.

Temporal Models of Aggregate Data

In this section we examine spatially aggregated CPUE for *S. maderensis* (actually we use LNCPUE = ln(CPUE + 0.5)) and the environment. The approach of this section closely parallels Mendelssohn and Cury (1987) so that we can illuminate the differences between the dynamics of the dominant, more coastal *S. maderensis* from the dynamics of the combined species, many of which are more oceanic.

Identification

Sardinella maderensis is a more coastal species than some of the other pelagic species, and SST averaged over such a wide area is not a very accurate reflection of the conditions faced by a stock which only is fished near the coast. Seemingly then, the coastal station data should better reflect the environmental conditions that affect the fish. However, the coastal station data were taken near a river estuary and thus also may have not reflected the actual temperatures that the fish experienced. For these reasons, two different models were examined: one using LNCPUE, SAL5M and average SST, and one using LNCPUE, SAL5M and SST5M.

We model the dynamics by identifying and estimating a vector ARMA model of the form (2). We simultaneously model LNCPUE and the environmental variables. This is especially important for our data as SST and salinity tend to be highly intercorrelated. To identify the proper form of the model (AR, MA, or ARMA) and the appropriate lags to be included in the model, we examined the cross-correlation matrices and the generalized partial-correlations (Tiao and Box 1981). The autocorrelation functions of SST and SST5M showed a strong annual seasonal cycle, while that of SAL5M showed a 6-mo cycle with perhaps a smaller annual seasonal term. The autocorrelation function of LNCPUE did not suggest a seasonal cycle; there were significant peaks around lags of 1, 6, and 12 fortnights.

The cross-correlation functions between LNCPUE with SST or SST5M showed persistent significant correlations at lags of roughly five to 15 fortnights. The partial-correlations were significant at only a few lags both for LNCPUE with itself and with the environmental series. The decaying behavior of the cross-correlations coupled with the spikes in the partial-correlations suggested that an AR model was appropriate (Tiao and Box 1981).

The lags suggested by the partial-correlations were then used in an exact maximum likelihood routine (Tiao et al. 1980) to estimate the AR parameters. Nonsignificant parameters were then removed from the models, and any additional parameters suggested by the residual covariance matrices were added to the models. In general, the model using SST5M tended to give both a better overall fit to the data as well as better behaved residual series. For this reason, we will concentrate on this model only. The estimated parameters to model LNCPUE are (see Table 2 for the complete model):

$$\begin{aligned}\mathrm{LNCPUE}(t) = {} & 0.304{*}\mathrm{LNCPUE}(t-1) + 0.144{*}\mathrm{LNCPUE}(t-2)\\ & + 0.191{*}\mathrm{LNCPUE}(t-6) - 0.057{*}\mathrm{SST5\ M}(2t-1)\\ & - 0.078{*}\mathrm{SST5M}(t-5) - 0.062{*}\mathrm{SST5M}(t-13)\\ & + 0.028{*}\mathrm{SAL5M}(t-1) - 0.098{*}\mathrm{SAL5M}(t-4)\\ & + 0.120{*}\mathrm{SAL5M}(t-5) - 0.073{*}\mathrm{SAL5M}(t-6).\end{aligned}$$

The residual cross-correlation matrices showed no lack of fit for this model, and the normalized residuals appeared to satisfy most of the Gaussian assumptions of the model. The model using SST5M explained 33% of the variance in LNCPUE. The model does a particularly good job at predicting the large peaks in LNCPUE.

Improving the Model Predictions

There are a priori reasons to believe that the relationships between CPUE and the environment are nonlinear or discontinuous in nature. For example, there is most likely a maximum temperature beyond which the fish are not found in abundance; a further increase in the temperature will not change the number of fish. Likewise, there probably is a minimum temperature below which the fish are not found; a further decrease in temperature will have no additional effect. Marchal (1967) notes that outside the optimum ranges for temperature or salinity the relationships may be very different in form than within the optimum ranges.

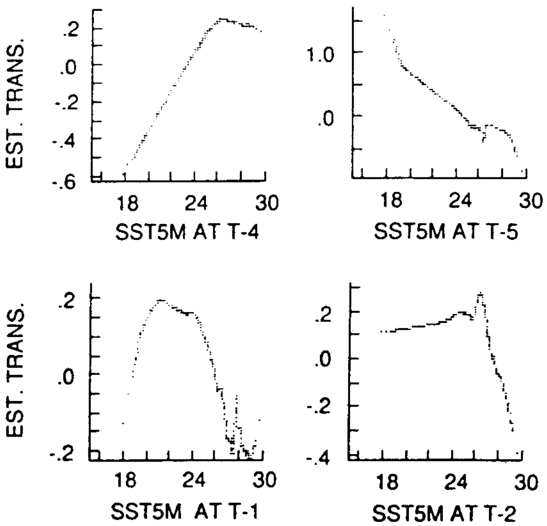

FIG. 4. Estimated optimal transformations of SST5M for predicting spatially aggregated CPUE.

The models we have estimated so far are all linear. To obtain a more realistic model, we used a technique due to Breiman and Friedman (1985) that calculates optimal transformations for a given dependent variable and a set of predictor variables, while preserving an additive structure to the model.

It is necessary to reidentify the proper model (i.e. what variables and what lags to use as predictors) for the transformed case, as it is possible that if the optimal transformations were known a priori, then variables that were not important predictors on a linear scale might become important predictors on the transformed scale. To this end, predictor variables to be included in the final model were selected by a stepwise procedure. First, all lag one variables were included in the model, entered in order of CPUE, SST5M, and SAL5M. (Some studies have shown that the order of the variables affects the transformations. We always enter CPUE first, so that any bias is conservative for environmental effects.) Any variable that was essentially transformed into a constant was removed.

Then models with lags 1 and 2, lags 1,2,3, etc. were used in the transformation algorithm, up to a lag of 15 fortnights. If the addition of the three variables in a new lag did not decrease the residual variance to a significant degree, then the entire lag was not included in the model. This stepwise procedure is highly nonoptimal and may well select a set of variables whose transformations do not explain as much variance as some other set of variables. Surprisingly, we ended up with a model very similar to the linear model in terms of the variables included in the model. However, the form and interpretation of the model differed substantially from the linear AR model.

The transformed model explained 55% of the variance of the transformed CPUE, a substantial increase over our original

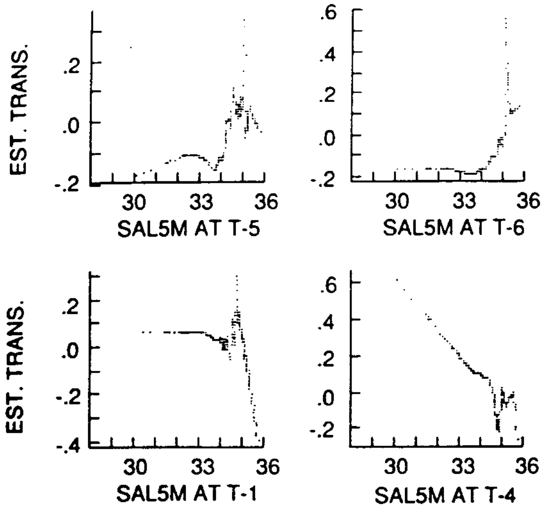

FIG. 5. Estimated optimal transformations of SAL5M for predicting spatially aggregated CPUE.

model. The transformations for CPUE at time *t* and at a lag of one fortnight are both very close to the natural log transformation selected a priori in our original models (Fig. 3). The estimated transformation for SST5M displays behavior consistent with our a priori reasoning (Fig. 4).

There is an increase in value between 18 and 20°C, a nearly constant value to 24°C, a sharp drop to 27.5°C, and a small rise to 28°C before dropping again. This suggests that at one period previous, conditions are most favorable between 20 and 24°C, dropping off sharply if the water is either colder or warmer. The small rise around 28°C may be water that is at the boundary of a frontal structure (Bakun 1978).

The estimated transformation for SST5M two fortnights earlier (Fig. 4) suggests that there is a slight preference for temperatures between 27–28°C, but mainly that temperatures greater than 28°C are not desirable. At four fortnights previous, the transformation of SST5M is linear with an asymptote around 26°C, while at five fortnights earlier the transformation is nearly linear with a preference for colder waters.

The transformation of SAL5M at one fortnight earlier (Fig. 5) suggests a preference for salinity at 35‰, with a strong avoidance of any greater density. The period from six to four fortnights prior shows a preference for a density in a narrow band centered at 35‰ at both six and five fortnights earlier, followed by a transition to relatively low densities of salinity. If this occurs at the same time that colder water is being replaced by warmer water, then CPUE should be particularly high.

Forecasting

The parameters for the linear model using LNCPUE, SST5M, and SAL5M were reestimated using data only from the years 1966–80. The new parameter estimates were close to the old ones, with no significant difference in the form of the estimated model. These parameter estimates were then used to calculate one-step ahead forecasts of CPUE, i.e., forecasts that assumed that at the start of each fortnight the data from the last fortnight were available. This would be equivalent to a real-time forecasting system.

The forecasts were transformed back to the original scale using the unbiased inverse transform (Granger and Newbold 1977):

(8) CPUE(t) = EXP(LNCPUE(t) + 0.5*(SE** 2)),

where SE is the standard error of the forecast on the transformed scale. The forecasted values for 1981 and 1982 (Fig. 6) describe quite well the increase of CPUE during the main upwelling season which began in fortnight 13 in 1981 and fortnight 14 in 1982. The model does not forecast as well during other parts of the year.

Implications of the Analysis

It is not surprising that our linear model explains only 33% of the variance in CPUE of *S. maderensis* and predicts only broad changes in CPUE. This is a multispecies fishery that is not targeted on any one species. There does not appear to be a good way to partition effort between the species, and thus our measure of CPUE is highly biased and may only roughly reflect availability or abundance of *S. maderensis*. A single species that is more coastal in its distribution is more likely to have different environmental features dominate its dynamics during different times of the year. That is, the problem is nonstationary while we have restricted ourselves to stationary models.

Nevertheless, our model has a biological interpretation that is consistent with previous studies, and the differences between this model and our previous model for all species combined (Mendelssohn and Cury 1987) reflect known differences between *S. maderensis* and most of the other species. Moreover, the improvement in fit when transformations were calculated suggests that much of the relationship with the environment is nonlinear and only roughly approximated by a linear model.

Mendelssohn (1990) examines the affects of the optimal transformations in the frequency domain, both for the combined species model and for the models of *S. maderensis* only. For the combined species, LNCPUE, as compared with CPUE, shifts the spectral peak from a period of approximately 1 mo to a peak centered at a period of 5 wk. The estimated transformations for SST5M and SAL5M also shift the spectral peaks to the same frequency band, thus aligning the spectral peaks in all three series.

Both transformed SST5M and transformed SAL5M are strongly coherent with LNCPUE for the combined species at this frequency band, but partial coherences (the frequency domain equivalent to partial correlations) show that only transformed SST5M is important. The coherence between LNCPUE with transformed SAL5M is due to the coherence between transformed SST5M and transformed SAL5M.

For *S. maderensis* only, Mendelssohn (1990) shows that while the coherences between LNCPUE for *S. maderensis* with transformed SST5M and transformed SAL5M are significant at the same frequency bands, the partial coherences are significant at different time scales. Transformed SST5M shows significant partial coherences at lower frequencies, while transformed SAL5M has significant partial coherences at higher frequencies.

Our analysis of CPUE for all species combined revealed no relationship with salinity (Mendelssohn and Cury 1987). Our present models, particularly after the transformations, indicate that salinity is a crucial variable in predicting the CPUE of *S. maderensis*. In addition, a coastal measure of SST5M provided a better fit than a more offshore measure of SST. This is con-

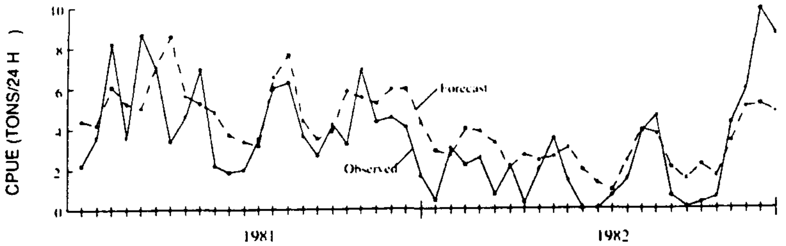

FIG. 6. One-step ahead forecast of CPUE for 1981–82 when only data through 1980 used to estimate the model.

sistent with the known fact that *S. maderensis* is a highly coastal species that is sensitive to salinity (FAO 1974). CPUE is predicted by CPUE lagged one, two, and six fortnights. The lags of one and two fortnights suggest that CPUE for *S. maderensis* is persistent. The lag at six fortnights may reflect environmental conditions occuring at that lag. Picaut (1983) shows that SST in the area has a spectral peak around a frequency of 45 d. The environment side of our model also suggests important behavior at this lag.

The lags of SST5M and SAL5M in the model, while open to interpretation, are not as immediately obvious. The model says that higher levels of CPUE will be found when starting six fortnights earlier, the waters make a transition from cooler, high-salinity waters to warmer, low salinity waters. This interpretation is strengthened by the estimated transformations, which show quite sharply the transitions from one type of water to another around four fortnights previous if CPUE is to be high. Why should a transition in the waters so much before the period of fishing affect CPUE so much? One possible answer is that at the beginning of the rainy season sudden and strong storms occur which decrease the salinity of the water. Upwelling usually starts about four fortnights later. The river outflows during this period bring terrigenous materials to the sea, and through a series of links, this improves the zooplankton productivity in the area (Binet 1976, 1983), the food of that species (Dia 1972). We emphasize that while this explanation has events occurring in the proper sequence, so might other explanations. Our model does not validate this explanation.

While a number of assumptions have been made, it appears that the enrichment in the food, which is triggered by environmental changes, plays an important role in the observed fluctuations in CPUE for *S. maderensis*. While the fish may be sensitive to salinity levels, salinity and temperature variables appear to reflect more a dynamic process that creates the proper conditions for the fish, rather than absolute measures of the conditions that are favorable to the fish. That the dynamics of the dominant species, *S. maderensis*, differs to a great extent from the dynamics of the combined species suggests that it may be preferable to aggregate forecasts of individual species rather than to forecast the aggregate behavior.

Space–Time Models

The general pattern of the seasonal migration for *S. aurita* off the Ivory Coast and Ghana has been described in ORSTOM/FRU (1976), and Binet (1983) has analysed the similarities between the migratory pattern of *S. aurita* and the spatial dynamics of zooplankton in the same area. For *S. madernesis*, Marchal (1967) briefly speculates on possible migratory patterns between the areas, but otherwise not much is known of the migratory behavior of *S. maderensis*. Since environmental factors play an important role in the migrations of *S. aurita* we expect that the same may be true for the migrations of *S. maderensis* off the Ivory Coast. In this section we analyze the fluctuations in the CPUE and environmental time series across areas to clarify the patterns of migration and their possible linkages with climatic factors.

The spatially disaggregated CPUE series (Fig. 7) were modeled with area specific SST as the environmental series (Fig. 8), making a simultaneous model with eight series in total. The results of the previous section suggest that a more coastal measure of temperature would be preferable, as well as an area specific measure of the salinity of the water. However, these series were only available from the one coastal station.

For an initial analysis of the data we used a subset autoregression procedure due to Akaike et al. (1979) with a maximum allowable lag of 12 fortnights to construct a simultaneous model of the eight series. (Hereafter, SST4 will denote SST in area 4, CPUE4 will denote CPUE in area 4 etc.) The results of the subset autoregression (Table 3) were mixed. While the parameters for the model did seem to indicate a migratory pattern (discussed below) the fit to the data is quite low with an r-squared no better than .15 in any of the areas.

Due to the lack of fit in the space–time model, optimal transformations were calculated to predict the CPUE in each area using the same stepwise selection process as in the previous section. The variables were always entered lower order lags before higher order lags and CPUE series before SST series.

The transformations greatly increased the predictability of the transformed CPUEs, with r-squared values of .47, .50, .58, and .53 for areas 4,5,6, and 7, respectively. For each area, lags of one, two, and four fortnights were found to be important in predicting CPUE for that area. The migratory pattern suggested by the transformed series qualitatively was the same as suggested by the linear AR model. We will discuss the suggested migratory pattern and then examine the transformations in areas 4 and 7 more closely.

Migration

The transformed variables suggest that migration between areas is associated with higher or lower levels of CPUE in given areas during the preceding periods as well as the relative temperature of the water in each area and its movement between areas during the preceding time periods.

The overall pattern suggested by the transformed model (Figs. 9 and 10) is that areas 6 and 7 vary together, area 4 varies separately from the other areas, and area 5 is a transition zone. A major fishing area is located in area 7 but often overlaps into

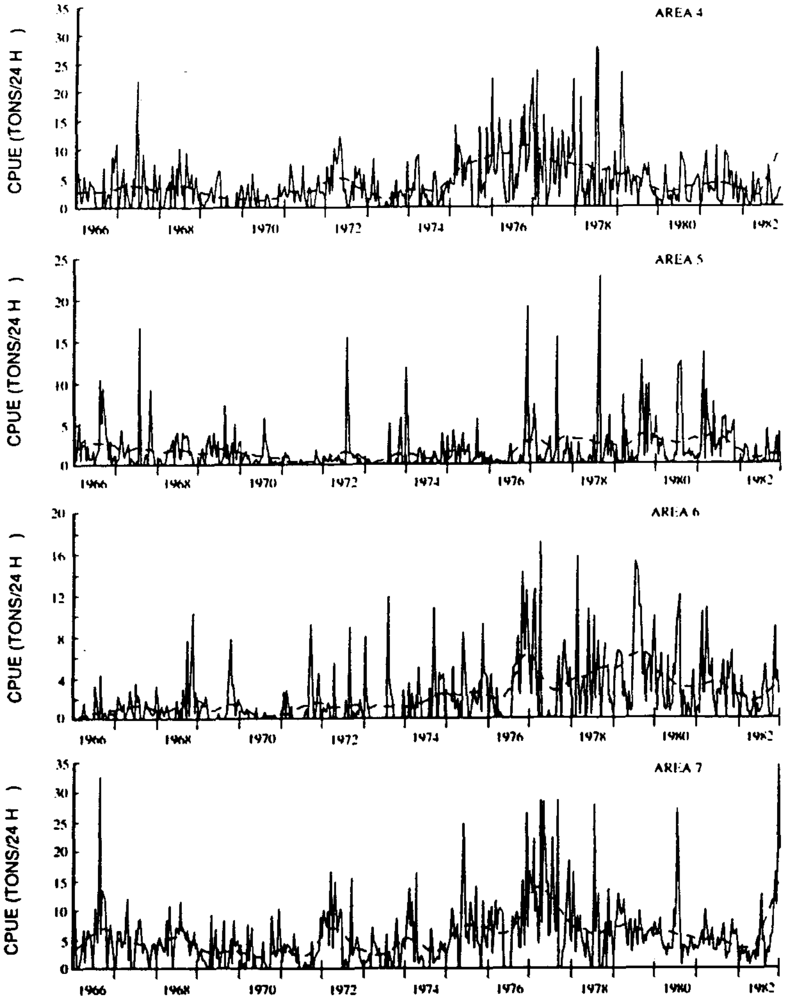

FIG. 7. Filled-in series of CPUE for *S. maderensis* by area. Solid lines are the data series while dashed lines are estimated local trend lines.

area 6. This probably explains why these two areas vary together.

In more detail, from the figures an east–west migration clearly appears in CPUE as shown in the one and two fortnight lags between areas 4 and 7. A reverse movement in CPUE is shown in the lags of one and four fortnights with area 4, indicated by the eastward pointing arrows in the figure.

A very similar pattern is seen for transformed SST (Fig. 10). An east–west migration, particularly from area 4 to areas 6 and 7 is seen, and at the same lags as with CPUE. A similar return migration is also seen, though the relationship with area 6 is not as clear as with CPUE.

The transformed SST suggests that CPUE4 is usually higher when area 6 and area 7 have environmental conditions that are associated with lower values of CPUE6 and CPUE7. Combining these observations, we suggest that the proposed migratory pattern may be due to the fish moving to the areas with the most favorable environmental conditions. The transformed SST (discussed below) appear to associate favorable conditions with frontal structure. The west-to-east movement probably reflects advection due to the Guinea Current while the east-to-west movement, reflects changes in upwelling (Bakum 1978; Picaut 1983).

Optimal Transformations

The main fishing areas are located in areas 4 and 7. Therefore we will only examine in detail the transformations for these two areas. The estimated transformation for CPUE7 (not shown) is very close to the log transformation that we have used throughout this paper for a priori reasons. The transformation of CPUE7 at time $t-1$ (not shown), however, suggests two regimes: a value of CPUE7 of 5 t per 24 h search or less and a value of CPUE7 of 10 t per 24 h search and greater. Generally, when CPUE7 has been high it tends to persist for two fortnights or longer at the high level. CPUE7 is generally higher when CPUE4 and CPUE6 were higher the previous fortnight. The

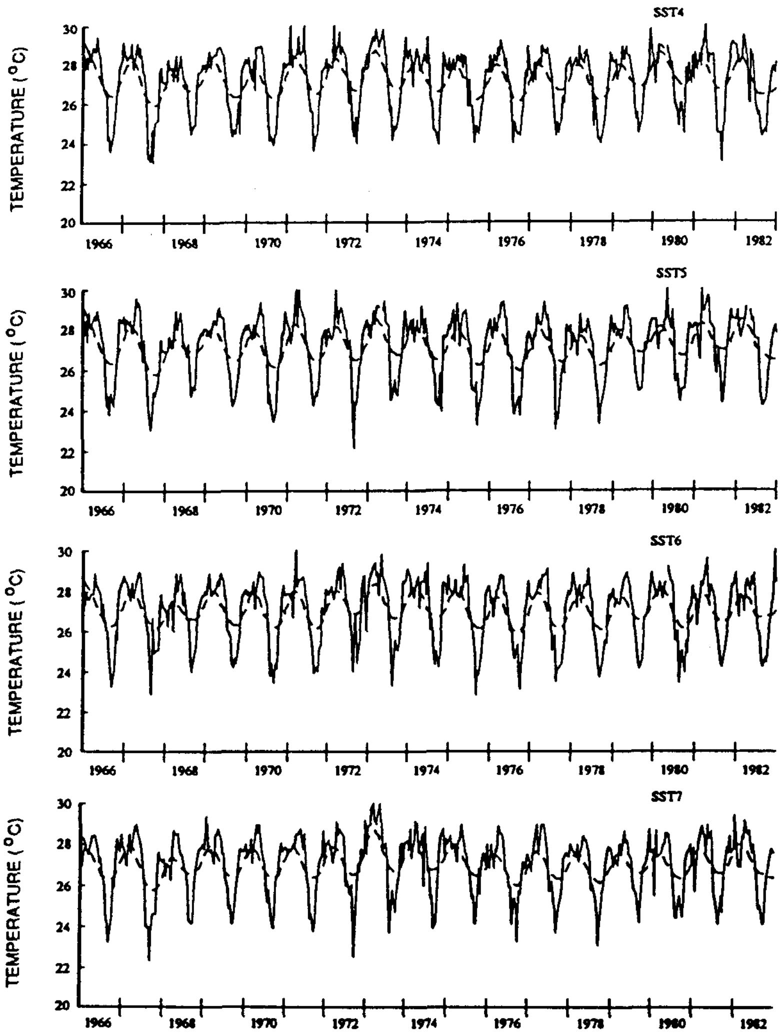

Fig. 8. Filled-in series of SST by area. Solid lines are the data series while dashed lines are estimated local trend lines.

transformations of CPUE at higher lags are similar in form, though they may be the inverse function.

The transformation of SST7 (Fig. 11) suggests three regimes: when the temperature is less than 24°C, when the temperature is between 24 and 28°C, and when the temperature is greater than 28°C. These values correspond with the isotherms used by Bakun (1978) to define the different oceanographic regimes in the area. Generally, CPUE7 is higher when SST7 two fortnights ago is less than 24°C, while SST7 one fortnight ago is greater than 25°C, preferably greater than 28°C. This suggests that the best fishing will occur in this area when there has been a transition in the water probably due to the passing through of a frontal structure.

A similar but not identical change in SST4 (Fig. 12) also leads to higher levels of CPUE7, though higher levels of CPUE4 occur when SST7 undergoes a change that causes lower levels of CPUE7. The transformed values of SST4 and SST7 one fortnight previous define to a large degree when there will be high levels of CPUE7 (greater than 10 t per 24 h search). If we plot SST4 one fortnight previous versus SST7 one fortnight previous and mark the points with high CPUE7 (not shown) the points with high CPUE7 show about the same distribution as the rest of the points. However, the same plot for the transformed variables (Fig. 13) shows that the points with a high CPUE7 are clustered in one region, to a large degree separated from the rest of the data.

The estimated transformations for area 4 (Figs. 14 and 15) have a similar interpretation. The transformation of the dependent variable CPUE4 (not shown) is also very close to a log transformation. Higher levels of CPUE4 will occur when SST4 makes a transition from colder waters two fortnights previous to warmer waters one fortnight previous (Fig. 14). At the same time SST7 should make a transition from warmer (but not too warm) to colder waters (Fig. 15).

TABLE 3. Model estimated by subset autoregression procedure due to Akaike for space–time model.

Lag		LNCPUE4	LNCPUE5	LNCPUE6	LNCPUE7	SST4	SST5	SST6	SST7
1	LNCPUE4	.115			.137				
	LNCPUE5	−.041	.109		.015				−.182
	LNCPUE6	.006	.023	.212	.021			−.151	.064
	LNCPUE7	.017	.020	.042	.226			.128	−0.13
2	LNCPUE4	.089		.132	.157				
	LNCPUE5	−.087	.212	.123			.135		
	LNCPUE6	−.007	.045	.140			.029		
	LNCPUE7	.003	.039	.070			.025	−.123	
3	LNCPUE4	.099							
	LNCPUE5	.011							
	LNCPUE6	.016		.103					
	LNCPUE7	.023		.021					
4	LNCPUE4								
	LNCPUE5								
	LNCPUE6				.086				
	LNCPUE7				.017				
Initial variance		1.177	.866	1.106	1.111				
Residual variance		1.051	.752	.881	.900				

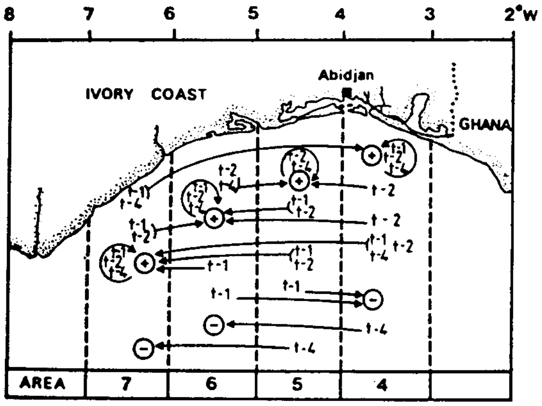

FIG. 9. Schematic representation of migration pattern in CPUE suggested by the transformed model. The plus or minus signs indicate the direction of the influence (higher or lower CPUE), the arrows show which areas affect other areas, and the time lags of the relationships are also shown.

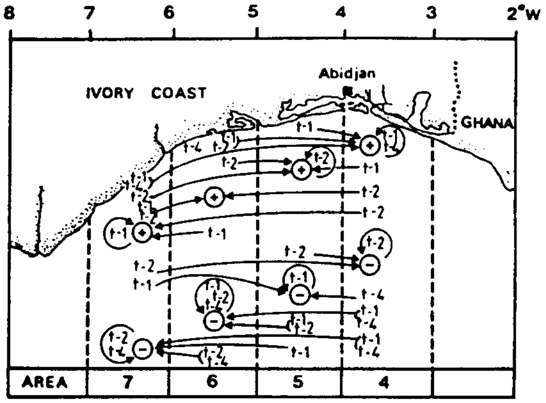

FIG. 10. Schematic representation of the propagation in SST suggested by the transformed model. The figure is interpreted as in Fig. 9.

Plots of transformed SST4 and SST7 through time (not shown) show that the ideal conditions in area 7 for high CPUE4 rarely occur at the same time as the ideal conditions in area 4. Thus CPUE4 tends to be higher either when conditions are favorable in area 4 but not too favorable in area 7 or when conditions are not unfavorable in area 4 but conditions in area 7 are very unfavorable. Unlike in area 7, SST4 and SST7 one fortnight previous are not sufficient to identify periods with high CPUE4. This suggests that the process in area 4 is more complicated, involving both what the fish are doing and more complicated behavior in the ocean.

Discussion and Conclusions

While there must be caution in making interpretations of our space–time analysis for reasons mentioned previously, the general pattern that emerges is that of a west-to-east migration followed by an east-to-west migration. The fish appear to migrate mainly between areas 7 and 4, perhaps avoiding the fishery in the central area by going too deep for the gear. Environmental processes, measured here by the dynamics in SST, appear to influence these migrations. Zooplankton are one of the major food sources for *S. maderensis*, and comparing this proposed migratory pattern with the dynamics of zooplankton in the same region provides a plausible rationale for the migration. During the main cold season there is a general enrichment of zooplankton with an eastern movement associated with the Guinea Current. The zooplankton then make a return migration to the west (area 7) around August, associated with an undercurrent (Binet 1976). During the warm season, the western part of the Ivoirian Gulf (area 7) is the area most favorable for zooplankton enrichment and fishing also usually is favorable during this period. Area 5 generally is the area poorest in zooplankton (Binet 1976) and also generally has the lowest levels in CPUE.

Fishermen in the area have observed a lack of fish in the central areas and an apparent rapid migration of fish from one area to another. It is difficult to compare two different biological processes, especially when the evidence is circumstantial, but there appears to be enough evidence to develop some ten-

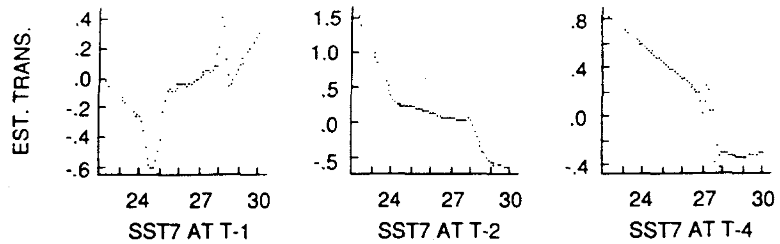

FIG. 11. Estimated optimal transformations of SST in area 7 for predicting CPUE in area 7.

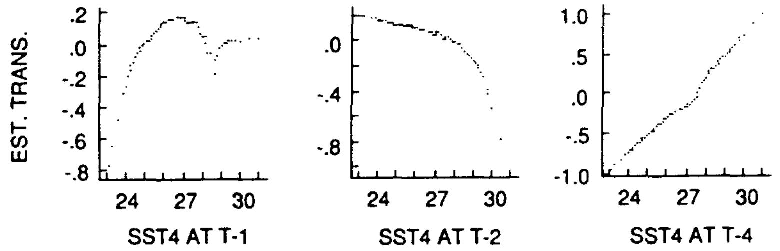

FIG. 12. Estimated optimal transformations of SST in area 4 for predicting CPUE in area 7.

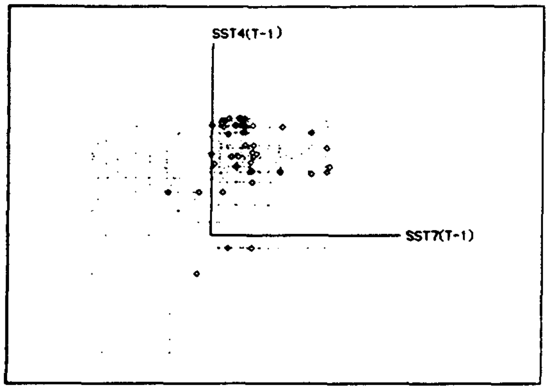

FIG. 13. Transformed SST7 versus transformed SST4. Diamonds mark time periods when CPUE in area 7 was high.

tative hypotheses and to point to the underlying environmental processes and fish behaviour that would have to be studied further to validate these hypotheses. The short (fortnight) time scales in which we find movement in the CPUE as well as the changes in the environment that lead to high levels of CPUE all seem to support the idea that the fish are migrating between areas where they can take advantage of sudden increases in zooplankton biomass caused by favorable environmental conditions (see Binet 1976). Further simultaneous studies of both zooplankton and *S. maderensis* in the same area would help to clarify some of these issues.

Our analysis has presented evidence that the dynamics of *S. maderensis*, both in space and time, appear to be influenced to a considerable degree by the environment. The space–time analysis suggests that the environment may be an indirect influence: favorable environmental conditions may be causing an increase in both the total biomass of the zooplankton as well as in the degree of aggregation of the zooplankton, as suggested by Binet (1976, 1983), and the fish move and take advantage of the increased biomass.

We have also shown that the relationships between CPUE and the environment most likely are highly nonlinear. If we are to better understand the dynamics, we must be careful to work on the appropriate functional scales. Simple linear methods will often obscure relationships that exist both in the data and in the real world. And finally, we have shown that the dynamics of an individual species, in this instance *S. maderensis*, can differ from the dynamics of the combined species of a fishery of which it is a part, both in terms of the behavior of the fish and in terms

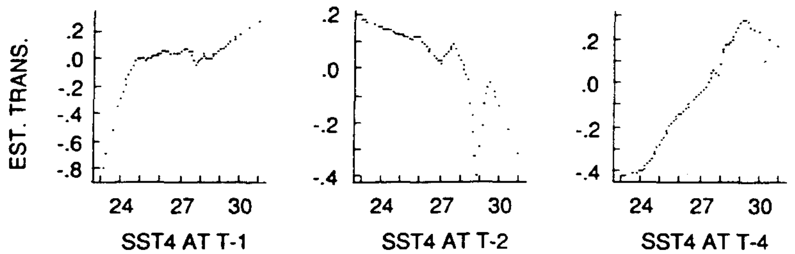

FIG. 14. Estimated optimal transformations of SST in area 4 for predicting CPUE in area 4.

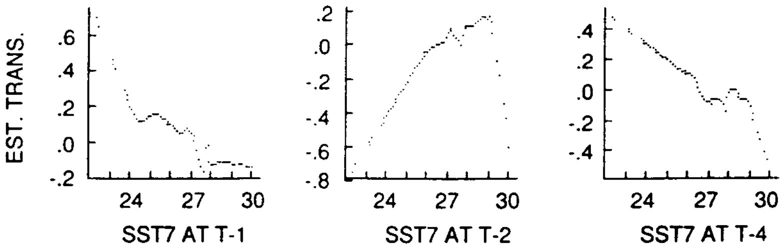

FIG. 15. Estimated optimal transformations of SST in area 7 for predicting CPUE in area 4.

of the oceanographic processes that influence the fish. Management based on the combined species dynamics could lead to unforseen changes in the dominant species. An open, but important question, is whether management plans or forecasts based on an aggregate of models for individual species would outperform models of the aggregate dynamics.

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