Sardinella aurita Population Dynamics Related to Environmental Parameters in the Southern Caribbean (Venezuela)[1]

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ABSTRACT

In this study the population dynamics of *Sardinella aurita* in eastern Venezuela and its relation to upwelling is analyzed using a surplus-production approach and a length-based, analytical approach, implemented with the CLIMPROD and ELEFAN software, respectively. Due to underexploitation of the stock, the model retained by CLIMPROD was not validated by the jackknife method. Nonetheless, a multiple regression of catch as a function of effort and upwelling index permitted to establish the statistical significance of upwelling. In the later years of the study period, there is an increasing trend in recruitment and exploited biomass, and a decreasing trend in exploited parental biomass. Finally, relationships between catch-effort data, population parameter estimates and upwelling indices are explored by standard statistical techniques and the ACE algorithm.

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RÉSUMÉ

Dans cette étude, la dynamique de population de *Sardinella aurita* dans la partie est du Venezuela et sa relation avec l'upwelling est analysée à partir d'un modèle global de production (utilisant le logiciel CLIMPROD) et une approche analytique utilisant les longueurs (logiciel ELEFAN). A cause de la sous-exploitation du stock, le modèle retenu par CLIMPROD n'est pas validé par le méthode du « jackknife ». Cependant une régression mutiple des captures en fonction de l'effort et d'un indice d'upwelling permet d'établir la signification statistique de l'upwelling. Durant les dernières années de l'étude, il existe une tendance positive dans le recrutement et la biomasse exploitée ainsi qu'une tendance négative dans la biomasse parentale exploitée. Enfin, les relations entre les données de captures et d'efforts de pêche, les estimations des paramètres de population et les indices d'upwelling sont explorées par les analyses statistiques classiques et l'algorithme ACE.

INTRODUCTION

The regional climate in the southeastern Caribbean is determined by the seasonal migrations of the Inter-Tropical Convergence Zone (ITCZ). The dry season, from November to May, occurs when the ITCZ migrates towards the Equator, reaching its southernmost position during February and March. The rainy season is determined by the northwards migration of the ITCZ, which reaches its northernmost position during the months of July through September. Correspondingly, in a yearly cycle, the temporal variations in wind speed provide a well defined seasonal signal. During the dry season, from January through May, the northeast trade winds are dominant. During this season, average wind speed is above 4 $m.s^{-1}$ and attains maximum average values of about 5 $m.s^{-1}$ in March. From June through December, average monthly values are below 4 $m.s^{-1}$ and minima under 3 $m.s^{-1}$ are observed in September (Aparicio, 1986).

The Northeastern Venezuela shelf is the site of the most important fishing grounds in the Caribbean Sea. This shelf is oriented East-West along the southeastern boundary of the Caribbean Sea (Fig. 1). The study area covers approximately 240 miles in the East-West axis and reaches a maximum of 60 miles in the North-South axis. Shelf topography is rather complex with numerous islands (Margarita, Coche, Cubagua, Los Testigos, La Tortuga, etc.), embayments (the Gulf of Cariaco and Gulf of Santa Fe, among others), capes (Tres Puntas, Chacopata, Puerto Santo, etc.), submarine valleys (Araya and Carupano), offshore banks (Cumberland) and, especially, the largely anoxic Cariaco Basin, located within the shelf and reaching depths of around 1 400m. The trade wind regime, shelf topography and coastline orientation favor the occurrence of upwelling events during the dry season (Herrera and Febres, 1975).

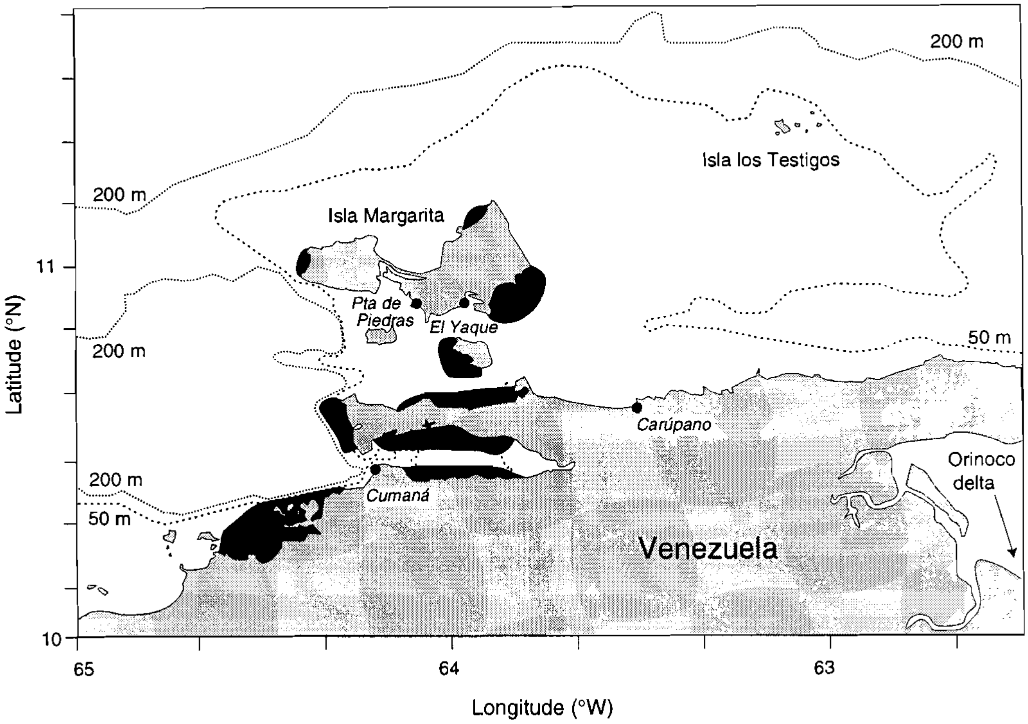

Fig. 1: The northeastern Venezuela shelf.

Another important feature of the study area is the relatively high input of low salinity water from river discharge. The Orinoco River has an estimated annual discharge of 36 000 $m^3.s^{-1}$ (Monente, 1990) with maximum output during August and September. Recent analysis of satellite data (Muller-Karger *et al.*, 1989) indicates that, during the rainy season, the influence of Amazon River water in the Caribbean is less important than that of the Orinoco.

The combined effect of wind-induced coastal upwelling in the dry season and river runoff in the rainy season generate relatively high levels of biological productivity. Primary production estimates are highly variable in space and time. Maximum values over 3 $gC.m^2.day^{-1}$ have been recorded in coastal upwelling areas and minimum values around 200 $mgC.m^2.day^{-1}$ have been measured offshore of main upwelling sources (Varela *et al.*, in prep.). Mendoza (1993) estimated that total annual primary production on the northeastern Venezuela shelf averaged 3 300 t km^{-2} (wet weight).

Sardinella aurita represents the most important finfish biomass on the northeastern Venezuela shelf. The main area occupied by this population is apparently limited to the east by the low salinity Orinoco waters and to the west by reduced upwelling and the narrow shelf west of Tortuga Island.

The fishery for *S. aurita* in this region started in the 1930s and is still strictly artisanal and labor-intensive, using small boats and seines known locally as 'peñeros' and 'chinchorros', respectively. The nature of the fishery limits fishing operations to a narrow band which rarely exceeds 5 nautical miles, covering a small area relative to known stock distribution. Most of the catch is canned; however small amounts are iced for direct human consumption and as bait for pelagic and demersal fisheries. After a period of increase, total estimated catch (Fig. 2) remained relatively stable around 40 000 t between 1964 and 1974, followed by a period of strong fluctuations up to 1983. Total catch has increased significantly in recent years to a level of around 60 000 t (Anon., 1990).

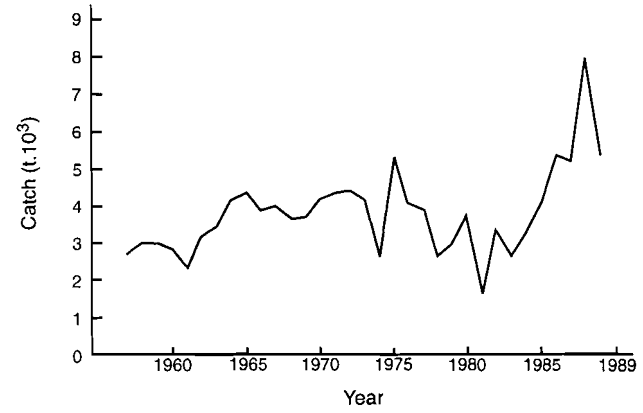

Fig. 2: Total catch of *Sardinella aurita* in eastern Venezuela, 1957-1989.

In this paper we analyze existing data on catch, effort, CPUE, length frequencies and environmental variables in order to study exploitation, population parameters and interactions between the resource and its environment.

1. MATERIAL AND METHODS

1.1. Environmental series

Sea surface temperature recorded at tidal gauges along the northeastern Venezuela coast lack adequate spatial and temporal coverage. The same situation occurs for wind data obtained at sea from ships of opportunity. Therefore, monthly mean values of wind speed and direction from coastal meteorological stations in the area are used as basic data for generating upwelling indices.

Four coastal meteorological stations are located within the study area: Cumaná (time series: 1969-1990) and Carúpano (1979-1989) on the mainland, and El Yaque (1976-1989) and Punta de Piedras (1973-1989 for wind speed and 1975-1989 for wind direction) in Margarita Island. However, considering the short series recorded at Carúpano, this station was not used for further analyses.

Two upwelling indexes were calculated using the above data :

1) A coastal upwelling index (CUE1) computed from wind stress (Bakun, 1973) and expressed as offshore Ekman transport in $m^3.s^{-1}$ per 100 m of coastline; and
2) An upwelling index (CUE2) based on mean yearly integrated wind speed values above 3.5 $m.s^{-1}$ at Cumaná and 4.8 $m.s^{-1}$ at Punta de Piedras (data from the nearby station of El Yaque were not available at the time of the study). Due to seasonality in the data series, each year i extended from November in the year i-1 to October of year i. This index was calculated to account for the complex topography of the area, which may generate upwelling events even when wind direction is not oriented along the East-West axis (Senior, in prep.).

1.2. Catch and effort analysis

Catch and effort data were obtained from industry reports to the Ministry of Agriculture and Husbandry (MAC). The only available fishing effort unit is the number of successful sets. Therefore CPUE is expressed in t per successful set.

These data and the environmental series were analyzed using the CLIMPROD expert system (Fréon *et al.*, 1993) and the ACE (Alternating Conditional Expectation) algorithm (Breiman and Friedman, 1985) in its latest version, which allows to force a monotonic transformation of the dependent variable. The contribution of each independent variable to total explained variance is estimated according to the range of its transformed values. As far as possible, the limitations of the algorithm for a short data series were taken into account by applying a jackknife-like approach (Fréon *et al.*, 1992).

The CLIMPROD expert system permits to select a surplus production model including the effect of an environmental variable. Due to the low number of annual observations (17) and the absence of independence between CPUE and effort or between catch and effort, the coefficient of determination is always high (between 78% and 95%) and hence its absolute value was not taken into account.

1.3. Analysis of length-frequency data

The data base consists of monthly catch and length frequency data extending for the period 1967-1989, which have been collected by personnel of MAC. However, due to variability in data, quality estimates of fishing mortality are based essentially on information for the period 1976-1989 and growth, recruitment and biomass estimates on data for the period 1967-1989. The Compleat ELEFAN software package (Gayanilo *et al.*, 1989) was used for parameter estimates:

- Growth parameters from the von Bertalanffy equation were obtained through modal progression analysis. Length frequency distribution decomposition was carried out using Battacharya's (1967) method. Estimates of L_∞ and K were initially obtained using the Gulland and Holt (1959) plot. Finally, the ELEFAN I method was used in order to improve these preliminary estimates;
- Pauly's (1980) empirical relation allowed to obtain an approximate value of natural mortality (M). Following Pauly's (op. cit.) suggestion concerning schooling pelagic fish, the estimates were corrected using a factor of 0.8;
- Biomass and fishing mortality were obtained from a virtual population analysis (VPA) for unequal time intervals as developed by J.G. Pope (see Pauly and Tsukayama, 1983), and implemented in the Compleat ELEFAN.

Monthly length-frequency and catch data were used in this application of the model. 'Cohorts' are obtained from monthly growth curves which 'cut' through the length frequency distributions. In this analysis, a unique non-seasonal growth curve obtained from the average values for the period 1976-1989 was used. In all cases a moderate level of terminal fishing mortality (Exploitation rate, $E = F/(F+M)=0.33$, with $F = 0.7$ and $M = 1.4$ year^{-1}) was assumed, based on auxiliary information (acoustic and associated trawling surveys). The transformation of length data into weight was based on the relationship established by González (1985). The estimates of parental biomass were obtained assuming knife-edge maturation at $L_m=19.5$ cm (Fréon *et al.*, in press).

Finally, bivariate and multiple relationships between exploitation, population parameters and environmental series were explored by standard statistical methods and the ACE algorithm.

2. RESULTS

2.1. Environmental series

Figs. 3a and 3b show the time series of monthly anomalies of CUE1 for the coastal meteorological stations of Cumaná and El Yaque, respectively. Both series reflect the strong seasonal component of trade wind intensity with maxima during March-April and minima during September-October. In the series generated from the Cumaná meteorological station, a strong negative anomaly is observed during a 16 month period from April 1971 to July 1972. A long term trend of decreasing CUE1 can also be seen in the Cumaná series. The series generated from the El Yaque meteorological station shows a protracted negative anomaly from mid 1980 to the end of 1982. The long-term decreasing trend is also present, but is not as evident as in the Cumaná series.

The yearly CUE2 series (Fig. 4) presents a decreasing trend during the study period, which mainly reflects the trend observed in the Cumaná CUE1 series. A marked negative anomaly is observed in the year 1981, corresponding to the observed anomaly in the CUE1 series for the El Yaque meteorological station. The 1971-1972 anomalies observed in CUE1 from Cumaná is not reflected in CUE2 because its is only due to a change in wind direction.

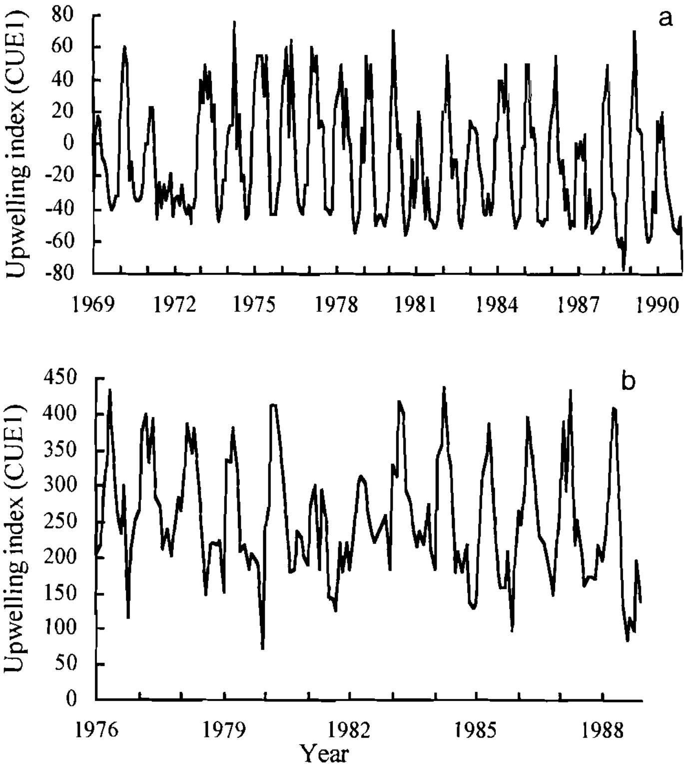

Fig. 3: Upwelling indices
(a) CUE1 time series (Ekman transport in m^3 per 100 m of coastline) estimated from Cumaná meteorological station data;
(b) CUE1 time series estimated from El Yaque meteorological station data.

Fig. 4: CUE2 time yearly time series (average integrated wind speed above 3.5 $m.s^{-1}$ at Cumaná meteorological station and 4.8 $m.s^{-1}$ at El Yaque meteorological station).

2.2. Surplus production approach

In the application of the CLIMPROD expert system, we have used catch per set as an index of abundance, and assumed that the number of exploited age classes as three, that recruitment occurs before the end of the first year and that upwelling influences the stock over a 4-year period (from maturity at year 0 and on to the exploited classes the three following years). We also considered that its influence acts simultaneously on catchability and abundance.

The four variables used in model adjustments (catch, effort, CPUE or CUE2) show a distribution that is not far from normal, except for CPUE, which presents an asymmetrical distribution (Fig. 5). The relationship between CPUE and effort appears linear or at least monotone (Fig. 6a). The model selected by CLIMPROD combined a conventional exponential surplus production model with an exponential effect of the environment:

$$CPUE = aV^b \exp(c\,V^b E)$$

where V represents the upwelling index averaged over four years and E represents fishing effort weighted over three fishing years. Fits were made both with CUE1 and CUE2, providing slightly better results for the first index. This was mainly due to the lack of response of the stock to the 1971-1972 Ekman transport anomaly. Moreover, the CUE2 series is longer. Therefore, in the rest of the paper we only present results obtained with the latter index, especially since we determined that differences were negligible compared to those obtained with CUE1. The R^2 coefficient was equal to 65% but was not validated by the jackknife method. The non-biased R^2 estimate was equal to 43%, and all regression coefficients, except c, were significantly different from zero, which suggests that fishing effort has no major effect on CPUE as opposed to the upwelling index (Fig. 6b).

The ACE algorithm applied to the variables Log $CPUE_i$ (dependent variable year i), E_i and V_i (independent variables year i) shows positive linear transformations for $CPUE_i$ and V_i and negative non-linear for E_i, which approaches a function of the type $1/E_i$ (Fig. 7). The form $1/E_i$ may imply a total independence between catch and effort ($C/E = f(1/E)$) or that the relation is not parabolic, but linear with an origin different from zero. To verify this, the algorithm was applied to the dependent variable C_i (catches year i) and E_i and V_i as independent variables (Fig. 8). In this case, all transformations are positive and linear, with an R^2 value of 95% and a strong contribution of E_i. Finally, an exploratory analysis of the relation between C_i and lagged values of E and V (results not presented) shows that the major effects of environmental variables on catch occurs without lags.

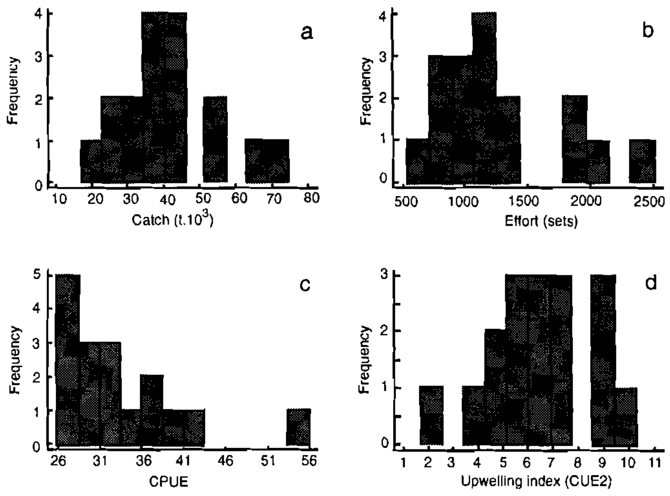

Fig. 5: Univariate distributions of a) Catch; b) Effort; c) CPUE; and d) CUE2.

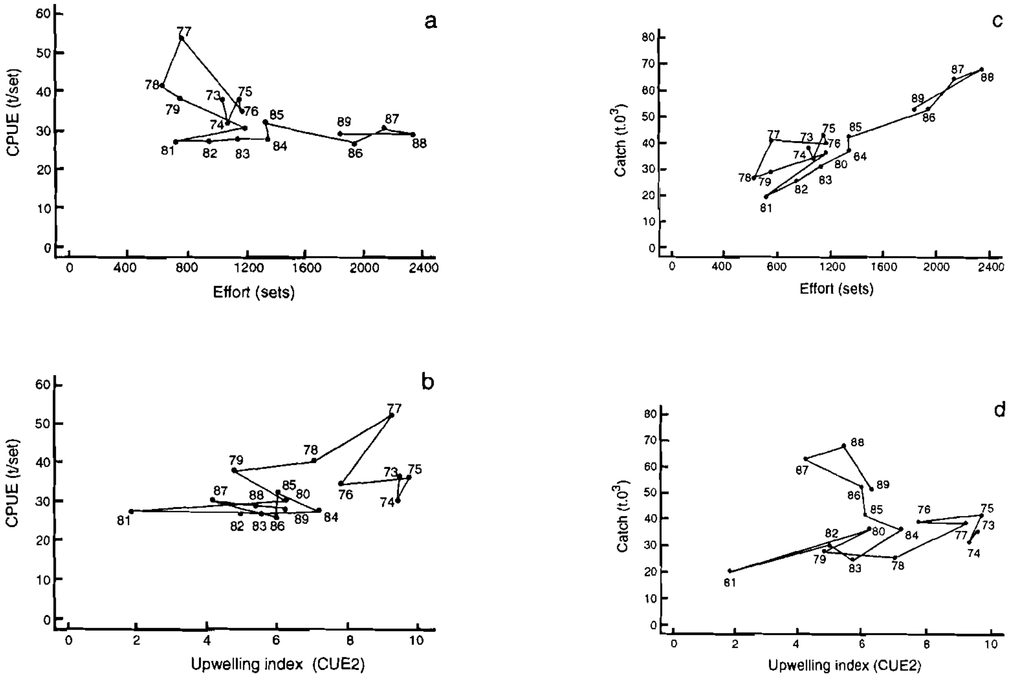

Fig. 6: Bivariate relations between: a) CPUE and effort; b) CPUE and CUE2; c) Catch and effort; and d) Catch and CUE2.

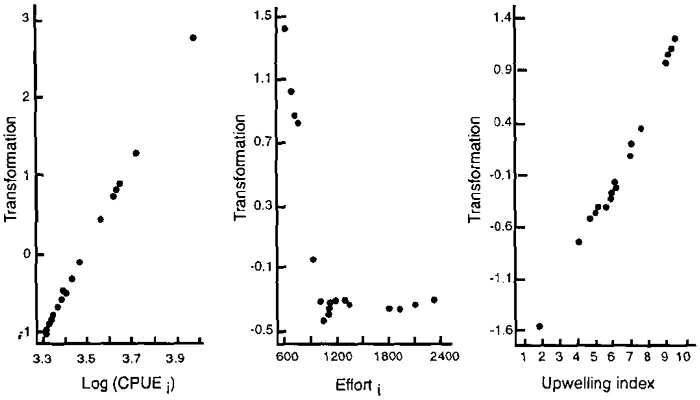

Fig. 7: Optimal unlagged transformations obtained by ACE for Log CPUE (dependent variable), fishing effort and CUE2 (independent variables).

In view of these results, instead of a surplus production model, we estimated a multiple linear regression of the form:

$$C_i = a + bE_i + cV_i$$

The coefficient of determination of this regression was 90% and all regression coefficients were significantly different from zero ($P<0.05$). Several statistical tests indicate that the regression is valid (ANOVA, residual analysis; see Fig. 9). However, this regression is not a model and it cannot be used for stock assessment, nor for predictions outside the observed range of E and V.

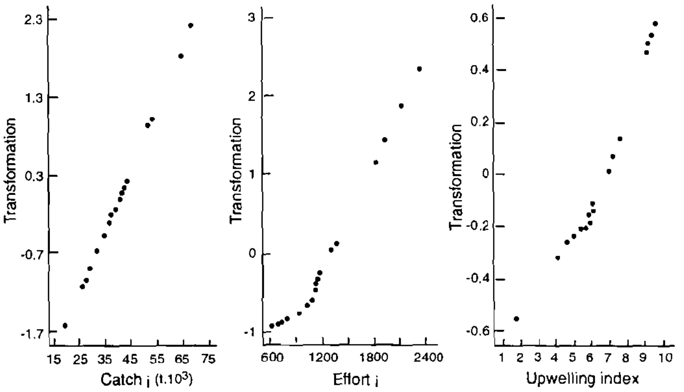

Fig. 8: Optimal unlagged transformations obtained by ACE for catch (dependent variable), fishing effort and CUE2 (independent variables).

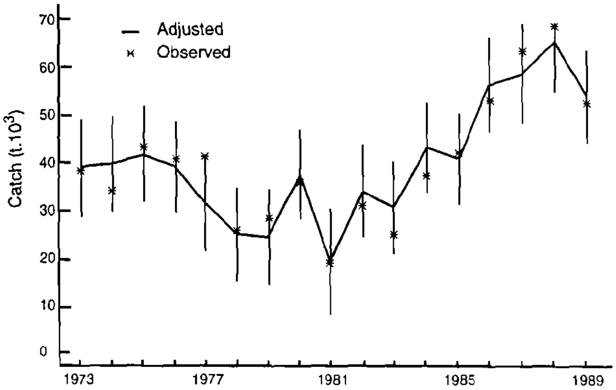

Fig. 9: Temporal series of catch observed and adjusted by a multiple regression using fishing effort and CUE2 as independent variables; vertical bars represent 95% confidence intervals of predicted values.

2.3. Analytical approach

Table 1 shows the growth parameter estimates (L_∞, K and Ø') for the study period. The yearly values correspond to average growth observed for the different cohorts present in any year. The average values for the study period were L_∞ = 266 mm total length and K = 1.26 year^{-1}. This average growth curve is depicted in Figure 10.

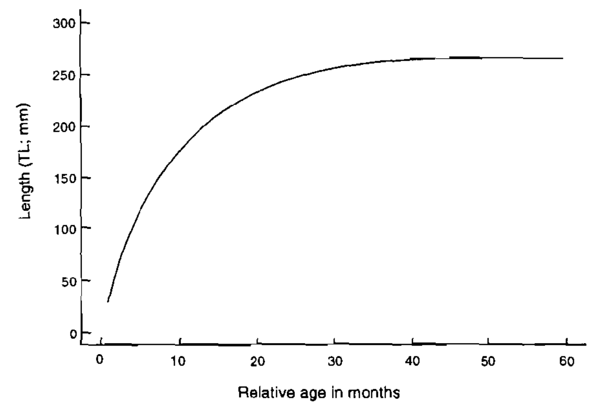

Fig. 10: Average *Sardinella aurita* growth curve for 1967 to 1989, based on L_∞ = 266 mm (TL) and K = 1.26 year^{-1}.

Year	1967	1968	1971	1972	1973	1975	1976	1977	1978	1979	1981	1982	1983	1984	1985	1986	1987	1988	1989	Mean
L_∞ (TL;mm)	240	243	275	273	266	285	262	274	240	278	238	290	252	285	288	266	260	272	260	266
K (year^{-1})	1.05	1.29	1.20	1.50	1.40	1.75	1.45	1.02	1.40	1.04	1.04	1.25	1.20	1.10	1.10	1.35	1.40	1.68	1.10	1.26
Ø*	4.78	4.88	4.96	5.05	5.00	5.15	5.00	4.88	4.91	4.90	4.77	5.02	4.88	4.95	4.96	4.98	4.98	5.09	4.87	4.94

* Values of Ø' were calculated from Ø' = log K + 2 * log L_∞ (Munro and Pauly, 1983).

Table 1: Growth parameter estimates for *Sardinella aurita* from eastern Venezuela (1967-1989).

Figure 11 presents the time series of number of 100 mm recruits into the fishing area during the period 1976-1988. In a general way, we may observe relatively low values, between 40 million and less than 200 million individuals (which correspond to 400 and 2000 t respectively) with a decreasing tendency between 1976 and 1982. This trend is reversed in the following years, until maximum values (around 700 million individuals) are observed at the end of the series. The analysis of the seasonal signal (results not presented) shows that between 1976 and 1983, higher recruitments occur from October to February and between 1984 and 1988 maximum values are observed from June to October.

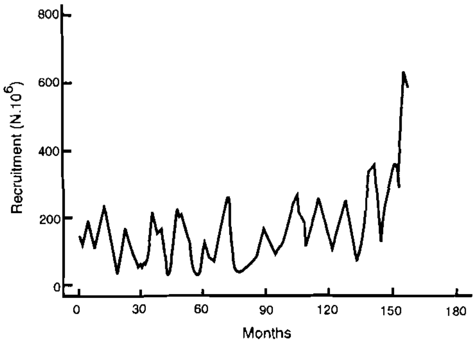

Fig. 11: Time series (1976-1988) of recruitment estimates of *Sardinella aurita* in eastern Venezuela, in millions of 100 mm individuals.

Figure 12 presents the time series of total exploited biomass, parental exploited biomass and catches for the period 1976-1988. As may be expected, the trend in biomass is similar to that of recruitment (Fig. 11). Exploited biomass maximum values (around 60 000 t) are observed at the end of the study period. Parental biomass estimates present minimum values during the period 1978-1980 and a marked decreasing trend in the years following the peak period (about 34 000 t in 1985). The catch series permits to infer that the exploitation ratio was relatively high during the years 1976-1980. However the increase in total biomass, which after 1986 was composed mainly of juveniles, has reduced the impact of exploitation. This effect may be observed in Figure 13, which shows the general decreasing trend of fishing mortality maxima over time.

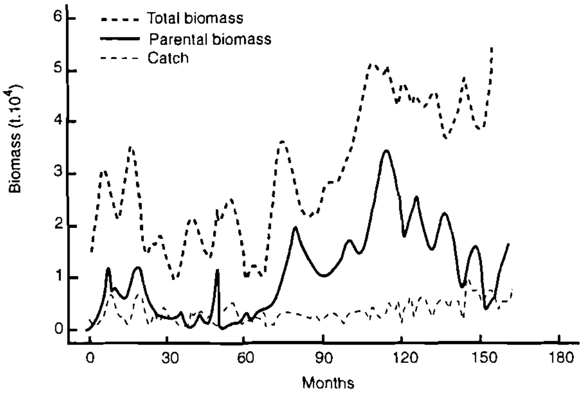

Fig. 12: Time series (1976-1988) of exploited biomass, exploited parental biomass and total catch.

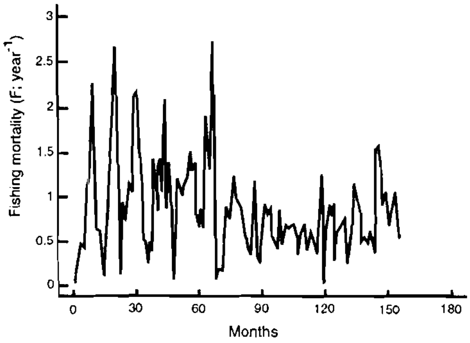

Fig. 13: Time series (1976-1988) of fishing mortality (F) estimates for *Sardinella aurita* in eastern Venezuela.

2.4. Exploratory data analysis of interactions between resource and environment

As a first approach, we attempted to establish relationships between variables used in the surplus production approach and estimates obtained through the analytical approach (i.e., VPA). There was no apparent relationship between average annual CPUE and yearly exploited biomass estimates or between fishing mortality estimates and fishing effort in number of sets. As might be expected, given the structure of VPA, there is a positive relationship between catches and exploited biomass. However, the relationship between exploited biomass and fishing effort is much closer (Fig. 14). A stepwise multiple regression of catch as a function of biomass and effort did not retain biomass as a significant explanatory variable (F=0.23; df=12) due to colinearity between effort and exploited biomass. Furthermore, there is a clear negative exponential relation, as expected on theoretical grounds, between catchability (q = F/f) and exploited biomass (R^2=0.34, P<0.001, n=156 months; Fig. 15).

As a second approach we searched for relationships between population estimates obtained from length frequency analysis and environmental variables. The growth performance index (Ø') is positively correlated with catch (Fig. 16), effort and, to a lesser degree, CUE2. A multiple regression of catch as a function of effort and growth index explains 79% of sample variance and both independent variables are highly significant (P<0.01). However, a stepwise multiple regression

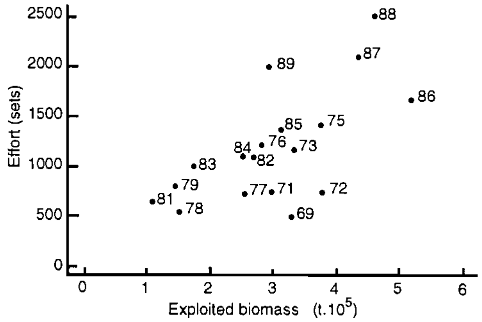

Fig. 14: Relation between fishing effort and exploited biomass of *Sardinella aurita* off eastern Venezuela.

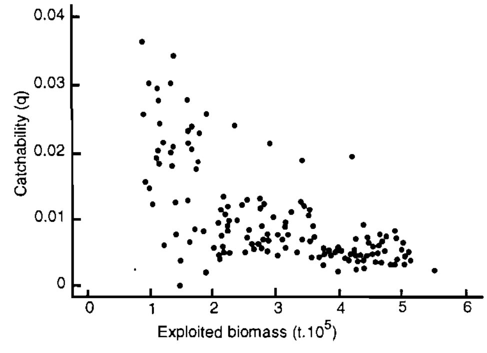

Fig. 15: Relation between catchability and exploited biomass of *Sardinella aurita* off eastern Venezuela.

in which catch is explained by the three above mentioned variables (effort, CUE2 and Ø') fails to incorporate the growth coefficient as a significant component (F= 0.024). This effect is probably due to colinearity between effort and growth performance index.

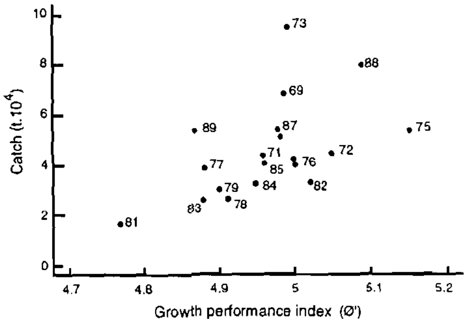

Fig. 16: Relationship between growth performance index and catch.

The ACE algorithm (Breiman and Friedman, 1985) and multiple regression were used to further explore relationships between recruitment in year i, parental biomass (years i and i-1) and environmental conditions during years i and i-1 (i.e., $CUE2_i$ and $CUE2_{i-1}$). This first pass permitted to establish that most of the explained variance of recruitment in year i (R^2= 0.78) was associated with the year i for parental biomass (PB_i) and $CUE2_{i-1}$ and weakly with $CUE2_i$. We therefore eliminated $CUE2_i$ and obtained similar transforms for the remaining variables, with the same amount of explained variance (Fig. 17). However, the transformation for parental biomass is non-monotone and difficult to interpret from a biological perspective. In order to introduce linearity or at least monotonicity into our data set, we used separately Ricker's (Log R/PB) and Beverton and Holt's (PB/R) transformations for establishing stock-recruitment relationships. In both cases, linear or monotone transformations were obtained between recruitment and PB/R and Log (R/PB): also a dome-shaped relationship between recruitment and $CUE2_{i-1}$ was obtained (Fig. 18). That is low, yearly integrated wind speed in year i-1 may have a positive effect on recruitment, at least until a threshold is reached beyond which accumulated wind effects become negative. However, considering the possible influence of the single outlier associated with the low accumulated wind speed anomaly in 1981, we tested the robustness of the transformations by eliminating this data point. The results

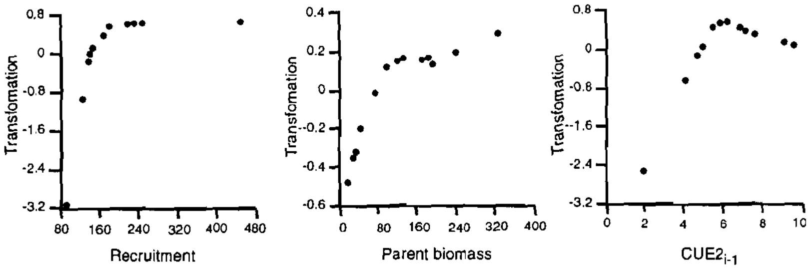

Fig. 17: Optimal transformations estimated by the ACE algorithm: PB/R (dependent variable), parental biomass, and CUE2 year i-1 (independent variables).

show that the transformations are extremely sensitive to this outlier. Under this set of conditions recruitment is inversely related to $CUE2_{i-1}$ in the case of the Ricker S/R relation and presents a sharp break (from negative to positive) in the Beverton and Holt relation (this abrupt change is also present in the Ricker case with CUE_{i-1} when Log R/S is explained by parental biomass, CUE_{2i} and $CUE2_{i-1}$). Moreover, the contribution of CUE2 $_{i-1}$ to total explained variance in both cases is considerably reduced when compared to the data set containing the year 1981.

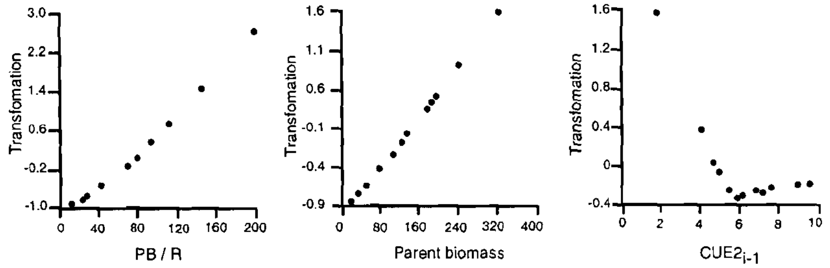

Fig. 18: Optimal transformations estimated by the ACE algorithm: PB/R (dependent variable), parental biomass and CUE2 year i-1 (independent variables).

Finally, a Stock-Recruitment relationship incorporating an environmental variable (Parrish and MacCall, 1978) was fitted to the different data sets by multiple regression. The transformations for $CUE2_{i-1}$ for the whole data set were approximated by a parabolic function and a negative exponential function for the Ricker and Beverton and Holt S/R relationships, respectively. In the case of the Ricker function the contribution of $CUE2_{i-1}$ was not statistically significant ($P<0.5$) with most of the explained variance ($R^2=0.64$) attributable to parental biomass ($P<0.001$). For the Beverton and Holt function, the environmental variable and parental biomass were statistically significant ($P<0.001$; $R^2=0.90$). However, the contribution of $CUE2_{i-1}$ to the relation depended almost exclusively on the data point representing the negative anomaly observed in 1981 (Fig. 19). The exclusion of the year 1981 did not permit to incorporate an environmental variable into a Stock-Recruitment relationship and the Y-axis transformation was explained by parental biomass only in both the Ricker ($R^2=0.69$, $P<0.001$), and Beverton and Holt ($R^2=0.59$, $P<0.003$) functions.

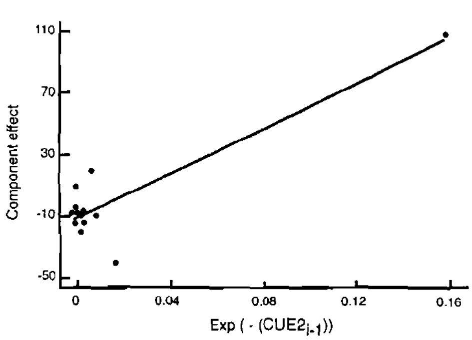

Fig. 19: Component effect of CUE2 $year_{i-1}$ in multiple regression of Log (R/PB) as a function of parental biomass and CUE2 $year_{i-1}$, showing spurious correlation due to a leverage effect.

DISCUSSION

If the *S. aurita* stock in Northeastern Venezuela is underexploited, linear positive relation between catch and effort can be expected, because we are on the left hand side of the production curve. In this case, the surplus production models will tend to underestimate the inflection point (i.e., MSY), and this problem remains in production models incorporating environmental variables (Fréon, 1988). This may explain the non-significant values of c in the model chosen by CLIMPROD. The high coefficient of determination (90%) of the multiple regression between catch, effort and upwelling index cannot be considered as proof of the validity of the regression, because the relation between catch and effort in an underexploited stock is trivial. Furthermore, as opposed to more conventional units, the measure of fishing effort used here does not allow us to observe effort without catches. However, the regression confirms the influence of the upwelling index. There is no temporal lag in the relation between mean CPUE in a fishing year and mean upwelling index in an environmental year. This does not necessarily mean that the environmental influence affects only catchability, for there is a 5-month lag between the environmental year and the fishing year, which allows for an influence of the upwelling on natural mortality and growth. This last point is very likely, considering the high estimates of growth rate obtained in this study. As a matter of fact, a relationship between biomass and Ø' was found (Fig. 16).

This positive effect of wind on CPUE may reflect a response of school size to prey abundance through a reduction in intra-school competition. Under conditions of high prey abundance, associated with stronger upwelling events, individuals located in the posterior margin of schools would be less affected by prey scarcity. This should result in increased occurrence of larger schools under the above mentioned conditions.

It is important to underline the uncertainty of catch per set as an index of abundance. The weakness of the relation between effort and CPUE may be related to biological factors, such as the absence of a relationship between school size (weight) and abundance. Several technical factors, such as the preferential selection of certain school sizes by fishers or the partial capture of large schools, may also explain the weakness of the relationship. In this context, notwithstanding possible biases due to estimation procedures, it is interesting to recall the relationship between exploited biomass and fishing effort (Fig. 14). Fishing effort may represent exploited stock abundance more closely than CPUE if the assumption is made that abundance varies as a function of school number and not school size. In this case, the effort unit retained would act as a school counter and would be, within certain limits, proportional to stock size (Laurec and Le Guen, 1981).

The nature of the eastern Venezuela fishery imposes certain limitations on the application of length-structured VPA. Catch series compared to hydroacoustic surveys (mean biomass 800 000 t; Anon., 1989) indicate that the exploitation level is low. Under these circumstances the uncertainty associated with levels of natural mortality and different sources of variability in this parameter have considerable weight on the degree of confidence which may be placed on quantitative results. This will also depend on the level of interchange (i.e., movement) between the exploited fraction and the rest of the population at any time. The assumption of a moderate exploitation level (E = 0.33) for all cohorts implies that this interchange occurs at an intermediate rate. Moreover, the enlargement of the fishing area from 1981 towards the northern fishing grounds where large fishes are more abundant could explain the increase in biomass presently being observed.

Despite the above mentioned limitations, our results are largely compatible with existing knowledge on this resource. For example, biomass estimates from VPA suggest that from 7% to 15% of total standing stock estimated from hydroacoustics was available in the restricted fishing area at the end of the study period. These values, probably underestimates would be reduced by reducing the terminal F value. Further research and more intensive sampling is required to tune VPA with independent biomass estimates from within the fishing area. In any case, assuming no major temporal changes in natural mortality, the yearly observed trends in recruitment to the fishery and exploited total and parental biomass would remain essentially the same.

The analysis of the relationship between recruitment, parental stock and environmental conditions is not conclusive. A dome-shaped transform was observed between accumulated wind in the year i-1 and recruitment in the year i, which is compatible with the Lasker (1975) hypothesis of wind effects on larval survival (Peterman and Bradford, 1987; Cury and Roy, 1989). Nevertheless, wind appears to have a monotonic effect on condition and perhaps maturation in the adult component (Fréon *et al.*, in press) and/or postlarval and early juvenile growth. However, the data set is extremely sensitive to an outlier. As a matter of fact, this outlier represents the lowest observed cumulative wind speed in the series, in the year 1981, which resulted in the lowest observed recruitment in the year 1982 (see Fig. 3,4 and 11). Obviously this result is possible from a biological perspective, but the exclusion of this point changes considerably (in fact reverses) the interpretation of possible upwelling effect upon recruitment. Therefore, we feel that a longer data series (hopefully including more cases with extreme conditions) is necessary in order to obtain a more robust representation of the underlying relationship.

REFERENCES CITED

Anon. 1989. *Surveys of the fish resources in the shelf areas between Surinam and Colombia 1988.* Inst. Mar. Res., Bergen, Norway.

Anon. 1990. *Resultados de los talleres sobre la pesca en Venezuela*. Ministerio de Agricultura y Cría, Dirección General Sectorial de Pesca y Acuicultura, Caracas, 60 p.

Aparicio R. 1986. *Upwelling along the southern coastal boundary of the Caribbean Sea: physical characterization, variability and regional implications*. Master Thesis, Oceanography Dept, Florida Institute of Technology,183p.

Bakun A. 1973. Coastal upwelling indexes, west coast of North America, 1946-1971. U.S. Dept. Commer. *NOAA Tech. Rep. NMFS SSRF*, 671, 103 p.

Battacharya C.G. 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics*, 23: 115-35.

Breiman L. and J. Friedman. 1985. Estimating optimal transformation for multiple regression and correlation. *J. Am. Stat. Assoc.* 80: 580-619.

Cury P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46: 670-680.

Fréon P. 1988. *Réponses et adaptations des stocks de clupéidés d'Afrique de l'ouest à la variabilité du milieu et de l'exploitation: analyse et réflexion à partir de l'exemple du Sénégal*. ORSTOM, Etudes et Thèses, Paris, 287 p.

Fréon P., B. Kiewcinski and D. López. 1992. Utilité du système expert CLIMPROD pour la connaissance du déterminisme du recrutement. *Bull. Inst. océanogr.* Paris, 68: 193-210.

Fréon P., C. Mullon and G. Pichon. 1993. CLIMPROD: Experimental interactive software for choosing and fitting surplus production models including environmental variables. *FAO Computerized Information Series (Fisheries)*, 5, 76 p.

Fréon P., M. Khattabi, J. Mendoza and R. Guzmán. In press. An original reproductive strategy: the case of *Sardinella aurita* life cycle in the southern Caribbean, Venezuela. *Marine Biology*.

Gayanilo F.C., Jr., M. Soriano and D. Pauly. 1989. A draft guide to the compleat ELEFAN. *ICLARM Software*, 2, 70 p.

González L.W. 1985. Determinación de edad y crecimiento de la sardina *Sardinella aurita* de la región nororiental de Venezuela. *Bol. Inst. Oceanogr. Venezuela*, UDO 24 (1-2): 111-128.

Gulland J. and S. Holt 1959. Estimation of growth parameters for data at unequal time intervals. *J. Cons.*, Cons. int. Expl. Mer, 25 (1): 47-49.

Herrera L. and G. Febres. 1975. Kinematics of the wind generated velocity field in the surface waters off eastern Venezuela, Caribbean Sea, *Bol. Inst. Oceanogr. Univ. Oriente*, 14(2): 165-186.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relationship between chlorophyll maximum layers and successful first feeding. U.S. *Fish. Bull.*, 73 :453-462.

Laurec A. and J. Le Guen. 1981. Dynamique des populations marines exploitées. Tome I. Concepts et modeles. *CNEXO Rapp. Sci. Tech.*, 45, 118 p.

Mendoza J. 1993. A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. *In*: V. Christensen and D. Pauly (eds.). Trophic models of aquatic ecosystems. *ICLARM Conf. Proc.*, 26.

Monente J. A. 1990. Influencia del río Orinoco. Materia en suspensión. *Mem. Soc. Cienc. Nat. La Salle*, 49-50 (131-134): 347-360.

Muller-Karger F., C. McClain, T. Fisher, W. Saias and R. Varela. 1989. Pigment distribution in the Caribbean Sea: observations from space. *Prog. Oceanog.*, 23 : 23-64.

Munro J. and D. Pauly. 1983. A simple method of comparing growth of fishes and invertebrates. *ICLARM Fishbyte*, 1 (1): 5-6.

Parrish R. and A. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. *Calif. Dept. Fish. Game, Fish Bull.*, 167: 110 p.

Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons.*, Cons. int. Expl. Mer, 39 (2): 175-192.

Pauly D. and I. Tsukayama. 1983. On the seasonal growth, monthly recruitment and monthly biomass of the Peruvian anchoveta from 1961 to 1979. *In*: G.D. Sharp and J. Csirke (eds.). Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 Abril 1983. *FAO Fish. Rep.*, 291, 3: 987-1004.

Peterman M. and M. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science*, 235: 354-356.

Senior W. (in preparation). Variabilidad estacional e interanual de parámetros físico-químicos en el Golfo de Cariaco (Período 1971-1975).

Varela R., F. Carvajal and F. Muller-Karger. (in preparation). El Fitoplancton de la plataforma nororiental de Venezuela.