

Model for stock-recruitment dynamics of the Peruvian anchoveta (*Eugraulis ringens*) off Peru

Ashneel A. Singh, Kazumi Sakuramoto*, Naoki Suzuki

Department of Ocean Science and Technology, Tokyo University of Marine Science and Technology, Tokyo, Japan;

*Corresponding Author: sakurak@kaiyodai.ac.jp

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ABSTRACT

This paper was aimed at re-examining the validity of the results from Cahuin *et al.* (Estuar. Coast. Shelf Sci. 84, 2009) and identify a model to describe the stock-recruitment relationship of the Peruvian anchoveta (*Eugraulis ringens*). Regression analysis was used to determine if density-dependent effects were present. The analysis did not show the existence of any density-dependent effects. It is important to use environmental factors and take observational and process errors into account when attempting to identify density-dependent effects in fish populations. Sea surface temperature (SST) and Southern Oscillation Index (SOI) were used as independent variables to fit the recruitment dynamics of the anchoveta. Both SST and SOI were found to be significantly important parameters in structuring anchoveta dynamics according to Akaike Information Criterion (AIC) and R^2 values. The results of this study do not correlate with the findings of Cahuin *et al.*, (2009), where density-dependent effects and the presence of regimes were detected. In conclusion, the recruitment R_t is essentially determined in proportion to spawning stock biomass S_t , and then environmental factors in year t further change the recruitments. This mechanism is completely same with that for Japanese sardine proposed by Sakuramoto (The Open Fish. Sci. 5, 2012).

KEYWORDS

Anchoveta; Density-Dependent; Recruitment; Regimes; Reproductive Success; Sea Surface Temperature; Southern Oscillation Index;

Spawning Stock Biomass

1. INTRODUCTION

Marine ecosystems are complex and are affected by numerous intrinsic and extrinsic environmental factors. Fish populations have a tendency to fluctuate over time and the mechanisms behind these fluctuation patterns can be understood by investigating relationship of the recruitment (R) to the spawning stock biomass (SSB) and environmental factors. Jacobson and MacCall [1] have shown that the recruitment of Pacific sardine in the coastal area of North America is significantly influenced by both the SSB and the sea surface temperature (SST). SST has been shown to be correlated to anchovy population dynamics previously [2-5]. The impact of sea surface temperature on the recruitment dynamics of other species of fish has also been identified [6,7]. Climatic conditions such as wind direction index, North Atlantic oscillation and Southern oscillation index (SOI) have also been correlated with the dynamics and regimes of anchovy as well as other fish species [7-11].

Cahuin *et al.* [11] examined the reproductive success (RPS) and SSB relationship of the Peruvian anchoveta (*Eugraulis ringens*) from 1963 to 2004 and discussed their fluctuation mechanisms. They explained the long-term fluctuations by the concept of “regime shift” and separating the data series into two periods of “favorable regimes” and one period of “unfavorable regime”. Separate regression lines of $\ln(RPS)$ against SSB were calculated for each regime. They stated that the long-term dynamics of the anchoveta are caused by regime shifts and the existence of different carrying capacities or density-dependent effects during these regimes.

Wada and Jacobson [12] identified the existence of regimes in the RPS dynamics of the Japanese sardine (*Sardinops melanotictus*) over a long time series from 1951

to 1995. The data for the time series was divided into two and separate regression lines were constructed and identified as regimes characterized as “favorable” and “unfavorable”. Based on the slope of the regression lines for the regimes the conclusion was drawn that density-dependent effects on recruitment does exist for *Sardinops* species. Density-dependent effects can only be measured for long-term data series if there is evidence of large (>1000-fold) difference between the maximum and minimum abundance in the data series [13]. Sakuramoto [14] discussed the validity of the results from Wada and Jacobson [13] and proposed a new concept for the stock-recruitment relationship of the *Sardinops* species. He reported that the false decreasing trend indicating the existence of density-dependent effects was due to observational error. When the data were adjusted for observational errors and regression analysis was applied to the full data series, the slope of the regression line did not differ significantly from unity indicating the absence of density-dependent effects as well as the absence of two different carrying capacities or regimes. Sakuramoto and Suzuki [15] provide a detailed report on the effect of observation and/or process error which in most cases results from environmental variables on recruitment and/or SSB in the selection of a stock-recruitment relationship.

Cahuin *et al.* [11] used the General Additive Model (GAM) to model the RPS of anchovy with SSB, SST, SOI and other environmental variables. They stressed the importance of the SST, however, they identified the SOI as the environmental variable to best explain the recruitment dynamics of the Peruvian anchoveta.

The purpose of this paper is to re-examine the assessment of the Peruvian anchoveta by Cahuin *et al.* [11]. The objectives are to: 1) re-examine the basis of separation of the anchovy data into the two regimes; 2) test the validity of the existence of density-dependent effects; 3) find out the best model for explaining the recruitment, by using SSB, SST and SOI as the environmental variables.

2. MATERIALS AND METHODS

2.1. Data

The data on the spawning stock biomass and recruitment of the North-Central stock of anchoveta (*E. ringens*), was obtained from Cahuin *et al.* [11] (Table 1). The stock distribution of the Peruvian anchoveta is shown in Figure 1. The recruitment (R) is the number of fish at age 0 and the spawning stock biomass (SSB) is the weight of reproductive adult fish at the initialization of the spawning season. The actual raw data for R and SSB was collected by the Instituto del Mar del Peru (IMARPE). More information regarding the landings of Peruvian anchovy is available from the IMARPE database (Table 1).

The data for monthly mean sea surface temperature

Table 1. Recruitment and spawning stock biomass of the North-Central stock of the Peruvian anchoveta *Eugraulis ringens* from 1963 to 2004 (source: Cahuin *et al.* [11]).

Year	Spawning biomass (10 ⁶) tons	Recruits (10 ⁹) fish	Year	Spawning biomass (10 ⁶) tons	Recruits (10 ⁹) fish
1963	7.997	1477	1984	2.741	563
1964	10.069	824	1985	5.703	57
1965	7.739	1304	1986	7.254	557
1966	9.998	1399	1987	5.751	929
1967	12.340	1083	1988	9.586	267
1968	11.124	1250	1989	6.544	556
1969	10.639	1681	1990	5.556	443
1970	13.644	1676	1991	5.530	990
1971	12.637	495	1992	9.232	1509
1972	5.665	461	1993	11.581	1430
1973	4.926	414	1994	15.792	1226
1974	5.877	151	1995	15.643	1039
1975	3.090	281	1996	14.227	317
1976	2.355	168	1997	6.525	677
1977	1.118	187	1998	4.986	521
1978	1.750	191	1999	8.670	910
1979	2.383	432	2000	11.581	746
1980	3.365	138	2001	8.517	1216
1981	3.179	27	2002	9.272	882
1982	1.539	10	2003	7.873	900
1983	0.561	266	2004	8.412	1294

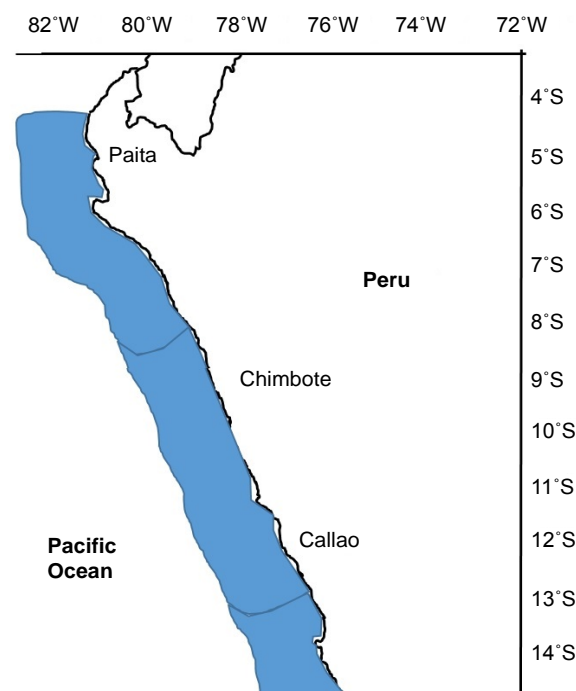


Figure 1. Map of Peru showing the stock distribution of the Peruvian anchoveta *Eugraulis ringens* off Peru (4° - 14° South). The shaded area (in blue) is the major anchovy fishing area to which the data used in this study belongs to, based on the information from Cahuin *et al.* [11] and IMARPE database. The fishing area is approximate and not to scale.

(SST) was obtained for the years ranging from 1963 to 2004 at Nino 1 + 2 (0° - 10° South) (90° West - 80° West), from the NOAA website. Data for the monthly Southern Oscillation Index (SOI) was also obtained from 1963 to 2004 and the annual averages were calculated from this. Both the SST and SOI data were calculated from this. The SST and SOI data as reported by the National Weather Service, Climate Prediction center were obtained from NOAA database (**Table 2**). The monthly anomalies from the standardized data series from 1963-2004 were used to calculate the annual means.

Descriptions of databases that were accessed for retrieving raw datasets used for this study are shown in **Table 2**.

2.2. Regimes and Density-Dependent Effects

Cahuin *et al.* [11] reported the existence of regimes and density-dependent effect in the anchovy population dynamics. To re-examine the validity of this, we began by plotting the log of recruitment, SSB and RPS of the anchovy for the data series from 1963-2004. The data were log transformed to reduce the effects of outliers and skewness. We replicated the method of Cahuin *et al.* [11] to separate the data into the “favorable” and “unfavorable” regimes. Linear regression was applied to $\ln(\text{RPS})$ against the SSB, for (a) recognizing the existence of the two regimes and (b) ignoring the regimes. In addition to this we carried out a reselection of the data based on the data points above and below the regression line for the graph of $\ln(\text{RPS})$ against (SSB) and applied linear regression analysis to it. The coefficients of all three regression analysis were reported.

For validation of the existence of density-dependent effects, we used simple regression with least squares method. We tested the slope of the regression line for the plot of $\ln(\text{RPS})$ against $\ln(\text{SSB})$ for zero. This method has some limitations as the RPS is sensitive to observational errors for short data series [14,16]. To confirm the results we applied regression analysis to $\ln(R)$ against

$\ln(\text{SSB})$ to test for unity as this method is more resistant to observational errors.

2.3. Recruitment Forecasting Model

The generalized additive model (GAM) was used to explain the recruitment dynamics of the Peruvian anchoveta. The basic model was

$$\ln(R/S) = \ln(\alpha) + \gamma \cdot (T) + \delta \cdot (I) + \varepsilon \quad (1)$$

where (R/S) is the reproductive success (RPS), α is the intercept parameter, T and I are the environmental variables for SST and SOI respectively, and ε is a normally distributed random variable. The other model for the RPS that was used, was derived from a linearized Ricker [17] model and it was modified to incorporate the environmental variable

$$\ln(R/S) = \ln(\alpha') + \beta'(\text{SSB}) + \gamma'(T) + \delta'(I) + \varepsilon' \quad (2)$$

where (R/S) is the reproductive success (RPS), and SSB is the spawning stock biomass. T and I represent the environmental variables for SST and SOI respectively. Different modifications of the two models were used for exploratory analysis to find out the best model for the recruitment fluctuations of anchoveta. The Akaike Information Criterion (AIC) was used to evaluate each model and form a basis for model selection [18]. The models exhibiting smallest AIC values and some of their parameters were reported. The actual recruitment dynamics from **Table 1** and the recruitment resulting from the model was plotted.

All statistical analysis for this study was carried out using the statistical software “R”, version 3.0.1 “Good Sport”.

3. RESULTS

3.1. Regimes and Density-Dependent Effects

The fluctuations patterns for $\ln(R)$, $\ln(\text{SSB})$ and $\ln(\text{RPS})$

Table 2. Table showing details about the sources of the different data used for this study.

Data	Source	Description
Spawning Stock Biomass (SSB)	http://dx.doi.org/10.1016/j.ecss.2009.07.027	SSB data was obtained from the article by Cahuin <i>et al.</i> [11], Table 1 .
Recruitment (R)	http://dx.doi.org/10.1016/j.ecss.2009.07.027	Recruitment data was obtained from the article by Cahuin <i>et al.</i> [11], Table 1 .
Sea surface Temperature (SST)	http://www.cpc.ncep.noaa.gov/data/indices	SST monthly data was obtained from the National Weather Service, Climate Prediction center NOAA website for the years ranging from 1963 to 2004 at Nino 1 + 2 (0° - 10° South) (90° West - 80° West).
Southern Oscillation Index (SOI)	http://www.cpc.ncep.noaa.gov/data/indices	SOI monthly data was obtained from the National Weather Service, Climate Prediction center NOAA website from 1963 to 2004.
Anchovy stock distribution	http://www.imarpe.pe	Information on the distribution of Anchovy stock was obtained from IMARPE database.

are shown in **Figures 2(a), (b)** and **(c)** respectively. The $\ln(R)$ shows a decreasing trend in the years 1970-1974, 1979-1982 and from 1992-1996. For the other years, the trend is either increasing or fluctuating with a decrease followed by an increase every following year. The fluctuation pattern for $\ln(R)$ is similar to $\ln(SSB)$. The pattern for $\ln(SSB)$ seems to be followed by $\ln(R)$ after a lag of one year. Cahuin *et al.* [11] identified regimes in the years 1963-1971, 1986-2004 for favorable regime and the years 1972-1985 for unfavorable regime. The plot of the $\ln(RPS)$ (**Figure 2(c)**) shows decreasing and increasing patterns to be randomly distributed for the range of year from 1963-2004 and does not show the regimes identified by Cahuin *et al.* [11].

The plots of $\ln(RPS)$ against SSB in **Figure 3** is replicated from Cahuin *et al.* [11]. It shows two regression lines for the data based on the favorable and unfavorable regime. We connected the data points for the two regimes following the year series. **Figure 3** also shows a single regression line for the whole data series without separation into regimes. We used the regression line for the whole data series to select the data points above and below the regression line and plot separate regression lines for each in **Figure 4**.

The model coefficients and other parameters for the plots in **Figure 3** and **Figure 4** are presented in **Table 3**. According to Cahuin *et al.* [11], the model recognizing the presence of the regimes is better than a model ignoring the regimes. The AIC selects the model with regime over a model without regimes (**Table 3**), however, it is unclear how the selection of the data points of regimes were made. The presence of regimes is unclear from **Figure 2(c)**, and in **Figure 3**, it can be observed that the RPS for the unfavorable regime does not remain continuously low for long periods of time (years). The fluctuations between low RPS and high RPS are too short to claim the existence of regimes.

The pattern is similar for the unfavorable regime. It is not clear what the basis of separation of the data into regimes really was.

If regimes do exist, then the method of separation of data by Cahuin *et al.* [11] in **Figure 3**, should be the best fit for the data points. This means that, any alternative way of separation of data should give a higher AIC value than the model of Cahuin *et al.* [11] (**Table 3 (Model 1)**). To test this, we performed an alternative selection of the data based on the data points above and below the regression line from the plot of $\ln(RPS)$ against SSB for the full data series and applied separate regression analysis to each (**Figure 4**).

When we compare the AIC value that was calculated for the single regression line without regimes with that of double regression lines which resulted from two different regimes, the latter AIC was smaller than the former one

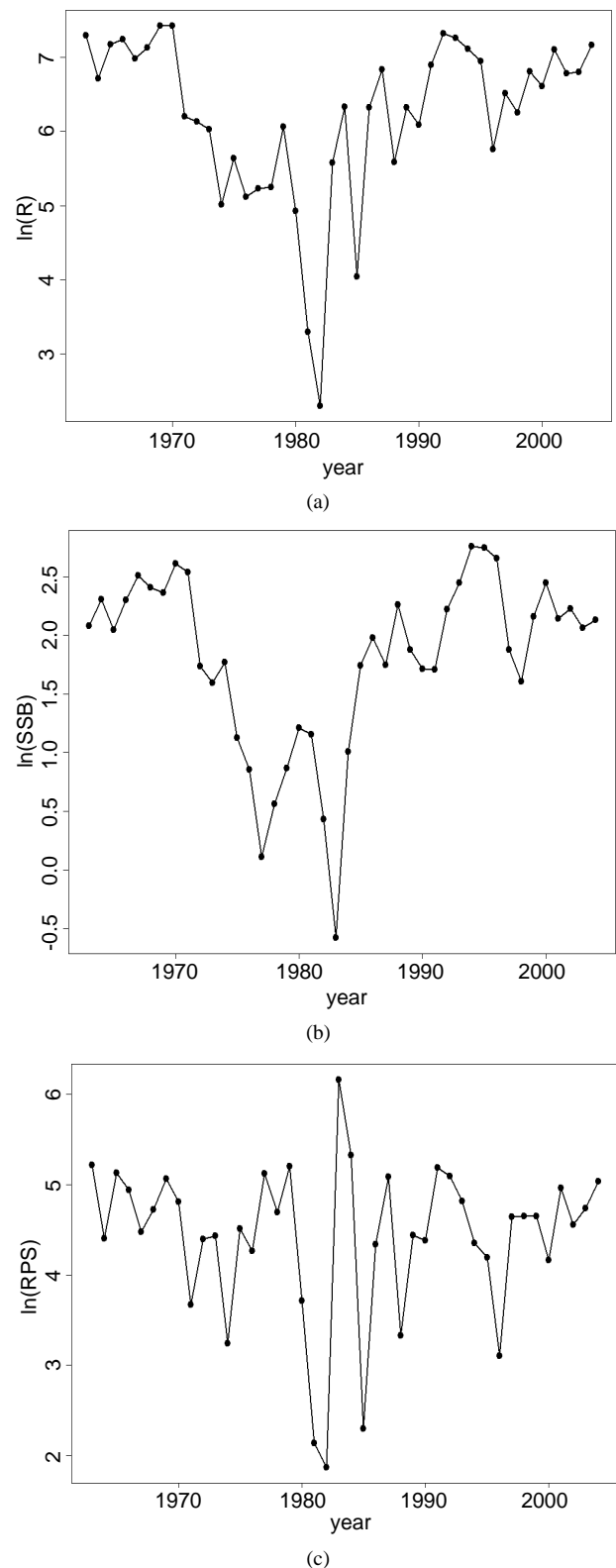


Figure 2. The dynamics of Peruvian anchoveta *Eugraulis ringens* from 1963-2004. (a) $\ln(R)$, (b) $\ln(SSB)$, (c) $\ln(RPS)$. The fluctuations patterns are similar for $\ln(R)$ and $\ln(SSB)$. The plot $\ln(RPS)$ does not show regimes identified by Cahuin *et al.* [11].

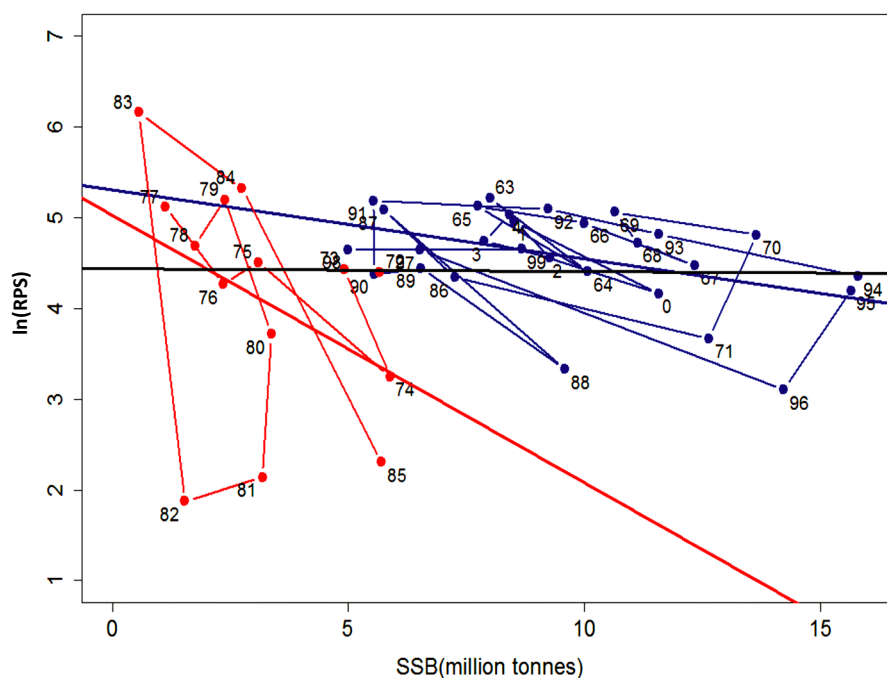


Figure 3. Graph of $\ln(RPS)$ plotted against the SSB of the Peruvian anchoveta *Eugraulis ringens* showing data selection based on the two regimes. The regression line in blue represents the favorable regime “F” and red represents the unfavorable regime “U” from Cahuin *et al.* [11]. The regression line in black represents the full data series. The lines connecting the data points for the favorable regime (in blue) and unfavorable regime (in red) show the annual variation of the data.

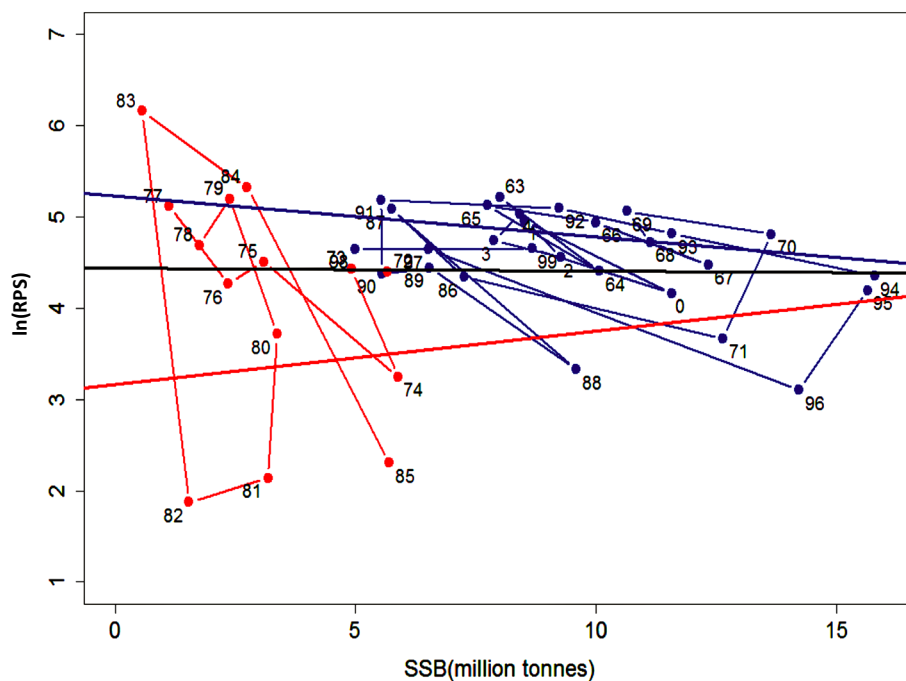


Figure 4. Graph of $\ln(RPS)$ plotted against the SSB of the Peruvian anchoveta *Eugraulis ringens* showing regression plots for two sets of data selected based on the data points above (regression line in blue) and below (regression line in red) the regression line for the full data series (in black). The lines connecting the data points for the favorable regime (in blue) and unfavorable regime (in red) show the annual variation of the data.

Table 3. Comparison of model coefficients for $\ln(\text{RPS})$ as a function of the SSB for the full model without regimes, with regimes and a model with two data sets having data points selection based on points above and below the regression line for the full data series.

Model	Coefficients	Estimate	Std. error	<i>t</i> value	Pr ($> t $)
(1) Two regimes ^a	Intercept	5.149	0.336	15.33	$<2 \times 10^{-16}$
	Slope (F) ^a	-0.061	0.035	-1.73	0.092
	Slope (U) ^a	-0.324	0.102	-3.19	0.003
	Null				
	Deviance	31.496	(41df)		
	Residual deviance	24.552	(39df)		
	AIC	104.64			
	Intercept	4.440	0.289	15.378	$<2 \times 10^{-16}$
	Slope	-0.003	0.034	-0.088	0.93
	Null				
(2) Without regimes ^a	Deviance	31.400	(41df)		
	Residual deviance	31.390	(40df)		
	AIC	112.97			
	Intercept	4.200	0.286	20.942	$<2 \times 10^{-16}$
	Slope (A) ^c	-0.045	0.019	-2.39	0.025
	Slope (B) ^d	0.058	0.046	1.264	0.227
	Null				
	Deviance	29.840	(40df)		
	Residual deviance	26.142	(38df)		
	AIC	66.25			
(3) Without regimes ^b	Intercept	4.200	0.286	20.942	$<2 \times 10^{-16}$
	Slope (A) ^c	-0.045	0.019	-2.39	0.025
	Slope (B) ^d	0.058	0.046	1.264	0.227
	Null				
	Deviance	29.840	(40df)		
	Residual deviance	26.142	(38df)		
	AIC	66.25			
	Intercept	4.200	0.286	20.942	$<2 \times 10^{-16}$
	Slope (A) ^c	-0.045	0.019	-2.39	0.025
	Slope (B) ^d	0.058	0.046	1.264	0.227

^aReplicated model from Cahuin *et al.* [11]. "F" represents the favorable regime and "U" represents the unfavorable regime. ^bModel based on separation of data points above and below the regression line for full data series. ^cRegression line for data points above the regression line for full data series in [Figure 4](#). ^dRegression line for data points below the regression line for full data series in [Figure 4](#).

(**Table 3**). However, this does not represent the validity of the latter model as being more optimal than the former one. In other words, it is not reasonable to compare the one line model with the two lines one. We should carry out comparisons between models which consist of two lines. One example of an alternative two lines model is shown in **Table 3** (**Model 3**). One group is constructed with the data points above the regression line for full data series in [Figure 4](#). The other group is constructed with the data points below the regression line. The former group indicates the years when $\ln(\text{RPS})$ was high, and the latter one indicates the years when $\ln(\text{RPS})$ was low. When we assumed this grouping method, and calculated the AIC, the AIC of this model (**Table 3** (**Model 3**)) was much lower than the model which considered the presence of regimes and adapted two lines (**Table 3** (**Model 1**)). This is evidence that the proposal of the existence of density-dependent effects in each regime is questionable.

To further elucidate whether density-dependent effects exist for the Peruvian anchovy data, we adopted the method employed by Sakuramoto [14]. Regression analysis was applied to $\ln(\text{RPS})$ against $\ln(\text{SSB})$ for the data separated into regimes from Cahuin *et al.* [11]. The slope for the favorable regime ([Figure 5](#)) was (slope = -0.673) and significantly negative ($p = 0.032$) and for the unfavorable regime the slope was (slope = -0.878) and significantly negative ($p = 0.097$) under the 10% significant level. When we applied a single linear regression to the whole data series from 1963-2004 for $\ln(\text{RPS})$ against $\ln(\text{SSB})$, the resulting regression line (slope = -0.067) did not differ significantly from zero ($p = 0.718$) and density-dependent effects could not be detected ([Figure 5](#)). The pattern in [Figure 5](#) coincided well with the simulations shown by Sakuramoto [14].

Same results can be obtained when the linear regression of $\ln(\text{R})$ against $\ln(\text{SSB})$ was conducted. For the plot of $\ln(\text{R})$ against $\ln(\text{SSB})$, the slope of the regression line

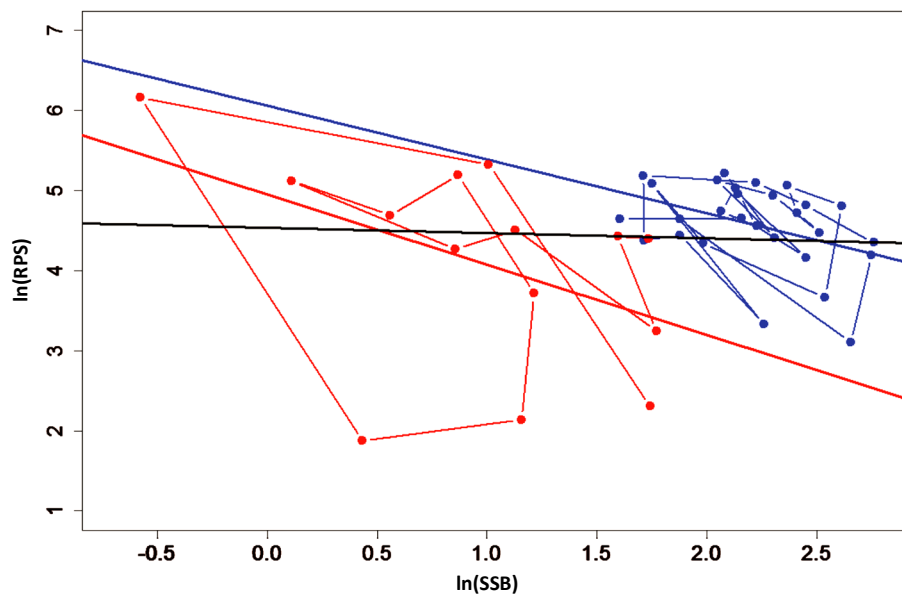


Figure 5. Graph of $\ln(RPS)$ plotted against the $\ln(SSB)$ of the Peruvian anchoveta *Eugraulis ringens*. The slope for the favorable regime (in blue) was (slope = -0.673) and significantly negative ($p = 0.032$). For the unfavorable regime (in red) the slope was (slope = -0.878) and significantly negative ($p = 0.097$) under 10% significant level. The slope of the regression line for full data series (in black) was (slope = -0.067) and not significantly different from zero ($p = 0.718$). Density-dependent effects and regime shift are not detected. The lines connecting the data points for the favorable regime (in blue) and unfavorable regime (in red) show the annual variation of the data.

for the favorable regime (slope = 0.327) was significantly different from zero and less than unity with a 95% confidence interval of $(-0.282, 0.936)$. The slope for the unfavorable regime (slope = 0.122) was not significantly different from zero and unity with a 95% confidence interval of $(-0.944, 1.188)$. When regression was applied to the full data set the slope for this regression was (slope = 0.923) with the 95% confidence limit of $(0.561, 1.305)$, which is not significantly different from unity (Figure 6). According to the results, the claim of the existence of density-dependent in each regime is highly questionable for the anchovy data series.

3.2. Recruitment Forecasting Model

Cahuin *et al.* [11] used the Generalized Additive Model (GAM) for modeling the anchovy dynamics with the SSB and having SOI and SST as the environmental parameters. They used the full time series from 1963-2004 in one approach and came up with the following model:

$$\log(R/S) = s(SSB) + s(I) \quad (3)$$

where (R/S) is the reproductive success (RPS), and SSB is the spawning stock biomass. I represent the environmental variable for SOI and s is a spline smoother parameter obtained using penalized regression splines analysis. Equation (3), when applied to full time series for anchovy data had a value of $R^2 = 0.251$. In another approach,

Cahuin *et al.* [11] used data only from the years 1963-1971 and 1986-2004 which were identified as the favorable regimes. The preferred model was produced with the years of the favorable regime and SOI and SSB as the independent parameters. The resulting model was the same as Equation (3), with a value of $R^2 = 0.494$. The difference between the two approaches is the proportion of data used for analysis. The best model by Cahuin *et al.* [11] was one with only the data from the favorable regimes that did not include the anchovy data for 14 years which is 33.33% of the total data. This is a major proportion of the stock-recruitment data series which was not incorporated for the modeling of the data, more importantly since the presence of regimes has now been put into question. The resulting model and the basis of selection of the best model are highly debatable.

In our approach, the fluctuation dynamics of the whole time series of the Peruvian anchovy was modeled through GAM and linearized Ricker model. We used various modifications of the models to incorporate the environmental variables of SOI and SST. In the study by Cahuin *et al.* [11], the SST at 4 different experimental stations across the coastal region of Peru was used. Since we did not have access to this data, in our study we used the SST from Nino 1 + 2 ($0^\circ - 10^\circ$ South) (90° West - 80° West) available from the NOAA website. We used

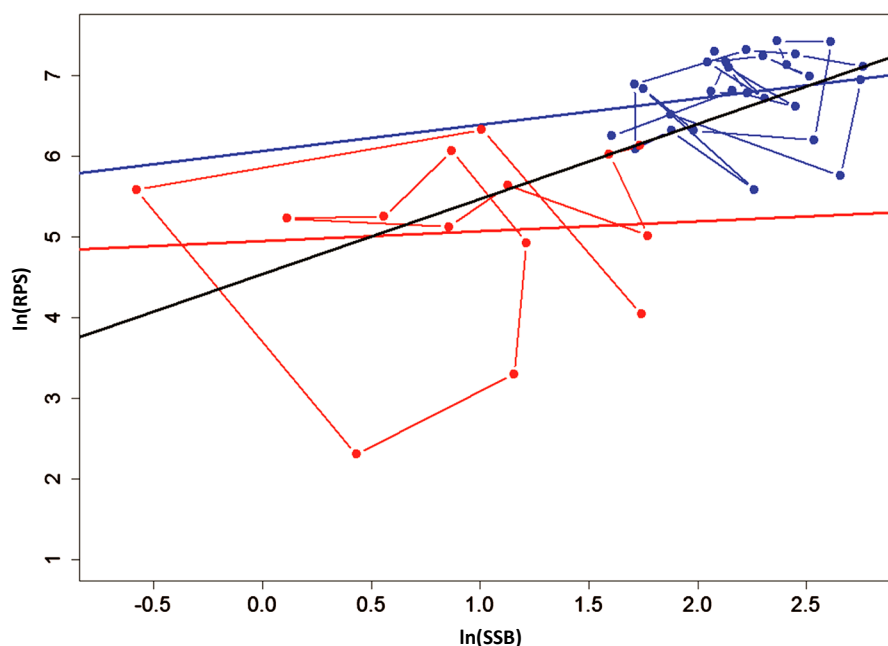


Figure 6. Graph of $\ln(R)$ plotted against $\ln(SSB)$ of the Peruvian anchoveta *Eugraulis ringens*. The slope of the regression line for the favorable regime (in blue) was (slope = 0.327) with a 95% confidence interval of (-0.282, 0.936). The slope for the unfavorable regime (in red) was (slope = 0.122) with a 95% confidence interval of (-0.944, 1.188). The regression line for the full data set had a slope of (slope = 0.923) with the 95% confidence limit (0.561, 1.305). This indicates the absence of density-dependent effects. The lines connecting the data points for the favorable regime (in blue) and unfavorable regime (in red) show the annual variation of the data.

the SST from the month of July as exploratory analysis showed July SST to be mostly strongly correlated to anchovy recruitment.

AIC values, R^2 and significant parameter estimates were used to determine the best model for explaining the dynamics of anchovy recruitment from 1963-2004. Some of the parameters and AIC values are shown for models that exhibited strong correlations and lowest AIC values in [Table 4](#). The table shows only the results expressed by Equation (1), as the AIC values for Equation (1) were much lower compared to Equation (2).

Models, (a), (b), (d) and (e) were the only models having significant parameter estimates with reference to their p -values. The difference in the AIC values between the models was <0.4 , which is not enough to select one model over the other. We selected model (d) as it had the highest R^2 value and incorporated both the SST and the SOI as the independent variables ([Table 4](#)). The best model by Cahuin *et al.* [11] had the SSB and SOI as the independent variables and in our case the selected model has SOI and SST as the independent variables.

The recruitment of the Peruvian anchovy was calculated from Model (d) and it was plotted against the actual recruitment from [Table 1](#) in [Figure 7](#). The actual recruit-

ment dynamics seem to fit well with the model recruitment dynamics. It seems that the reproductive success of the Peruvian anchoveta *Eugraulis ringens* from 1963 to 2004 can be explained well by the SST and SOI.

4. DISCUSSION

[Figures 3, 5](#) and [6](#) show the relationship between $\ln(RPS)$ and SSB, $\ln(RPS)$ and $\ln(SSB)$ and $\ln(R)$ and $\ln(SSB)$, respectively. In all these figures, the plots can be separated into two groups. One is the group plotted at the higher SSB or $\ln(SSB)$ and the other at the lower SSB or $\ln(SSB)$, which corresponds to Cahuin *et al.* [11] who defined favorable and unfavorable regimes. With reference to the SSB levels, the data can be separated into two regimes, however for the two regimes, the $\ln(R)$ and $\ln(RPS)$ fluctuated significantly above and below the regression line for the full data series. Particularly, when the SSB levels were low, the variation in the $\ln(RPS)$ levels were extremely high, which could have been produced by observational errors as was explained by Sakuramoto [14] in his simulations. On the contrary, with reference to [Figure 2\(c\)](#), it can be seen that the trajectory of $\ln(RPS)$ cannot be separated into the two regimes as the RPS levels fluctuate around average RPS except for the years 1981-1983 and 1985. Therefore, we agree that

Table 4. Table showing the different models used for modeling the recruitment dynamics of the Peruvian anchoveta *Eugraulis ringens* and the Akaike Information Criterion (AIC) values. The model with the lowest AIC value, significant parameter estimates, highest R^2 and incorporating most variables was selected. R is the recruitment, a_0 is the intercept, a_1 , b_1 and c_1 are the parameter estimates for the independent variables, S is the spawning stock biomass, T is the sea surface temperature and I is the Southern Oscillation Index.

Model	R^2	Parameter estimates	p -value	AIC value
(a) $\ln(R/S) = \ln(a_0) + a_1 \cdot T^2$	0.419	$a_0 = 2.084$ $a_1 = 0.005$	$a_0 = 0.067^f$ $a_1 = 0.040^e$	108.496
(b) $\ln(R/S) = \ln(a_0) + a_1 \cdot T^3$	0.413	$a_0 = 2.925$ $a_1 = 1.426 \times 10^{-04}$	$a_0 = 2.040 \times 10^{-04e}$ $a_1 = 0.040^e$	108.498
(c) $\ln(R/S) = \ln(a_0) + a_1 \cdot T$	0.426	$a_0 = -0.433$ $a_1 = 0.223$	$a_0 = 0.851$ $a_1 = 0.040^e$	108.508
(d) $\ln(R/S) = \ln(a_0) + c_1 \cdot T \cdot I$	0.557	$a_0 = 4.430$ $c_1 = -0.020$	$a_0 \leq 2.000 \times 10^{-16e}$ $c_1 = 0.047^e$	108.763
(e) $\ln(R/S) = \ln(a_0) + b_1 \cdot I$	0.555	$a_0 = 4.438$ $b_1 = -0.437$	$a_0 \leq 2.000 \times 10^{-16e}$ $b_1 = 0.050^e$	108.891
(f) $\ln(R/S) = \ln(a_0) + a_1 \cdot T^2 + b_1 \cdot I^2$	0.478	$a_0 = 2.195$ $a_1 = 4.963 \times 10^{-03}$ $b_1 = -0.394$	$a_0 = 0.054^f$ $a_1 = 0.037^e$ $b_1 = 0.242$	109.002
(g) $\ln(R/S) = \ln(a_0) + a_1 \cdot T + b_1 \cdot I^2$	0.483	$a_0 = -0.3477$ $a_1 = 0.2251$ $b_1 = -0.3910$	$a_0 = 0.880$ $a_1 = 0.038^e$ $b_1 = 0.245$	109.036
(h) $\ln(R/S) = \ln(a_0) + a_1 \cdot T^3 + b_1 \cdot I$	0.513	$a_0 = 3.416$ $a_1 = 9.690 \times 10^{-05}$ $b_1 = -0.267$	$a_0 = 2.840 \times 10^{-04e}$ $a_1 = 0.235$ $b_1 = 0.305$	109.349
(i) $\ln(R/S) = \ln(a_0) + a_1 \cdot T^3 + c_1 \cdot T \cdot I$	0.511	$a_0 = 3.441$ $a_1 = 9.399 \times 10^{-05}$ $c_1 = -1.231 \times 10^{-02}$	$a_0 = 3.310 \times 10^{-04e}$ $a_1 = 0.260$ $c_1 = 0.311$	109.377
(j) $\ln(R/S) = \ln(a_0) + a_1 \cdot T^2 + b_1 \cdot I$	0.516	$a_0 = 2.850$ $a_1 = 3.314 \times 10^{-03}$ $b_1 = -0.265$	$a_0 = 0.039^e$ $a_1 = 0.239$ $b_1 = 0.312$	109.381

^eStatistically significant at $p = 0.05$; ^fStatistically significant at $p = 0.10$.

the data can be separated into two different periods with high and low SSBs, however this does mean that these periods really indicate the existence of two regimes.

We did not detect the presence of density-dependent effects or regimes in our analysis of the Peruvian anchoveta through regression analysis. Sakuramoto [14] showed with simple deterministic relationships that RPS is quite sensitive to measurement errors even for small data series and can result in a false trend in the stock-recruitment relationship. For the short data series of the regimes identified by Cahuin *et al.* [11], we see a signif-

icant decreasing trend for $\ln(RPS)$ against $\ln(SSB)$ in **Figure 5**, but when the whole data series is used, there was no decreasing trend present. To confirm our results we applied regression analysis to recruitment. The results coincide well with regression analysis of the RPS and do not detect density-dependent effects. Sakuramoto [14] similarly used regression analysis on the recruitment of sardine to confirm the results of least squares regression for the RPS relationship.

Cahuin *et al.* [11] separated the anchovy data into two sets and applied separate regression analysis to the RPS.

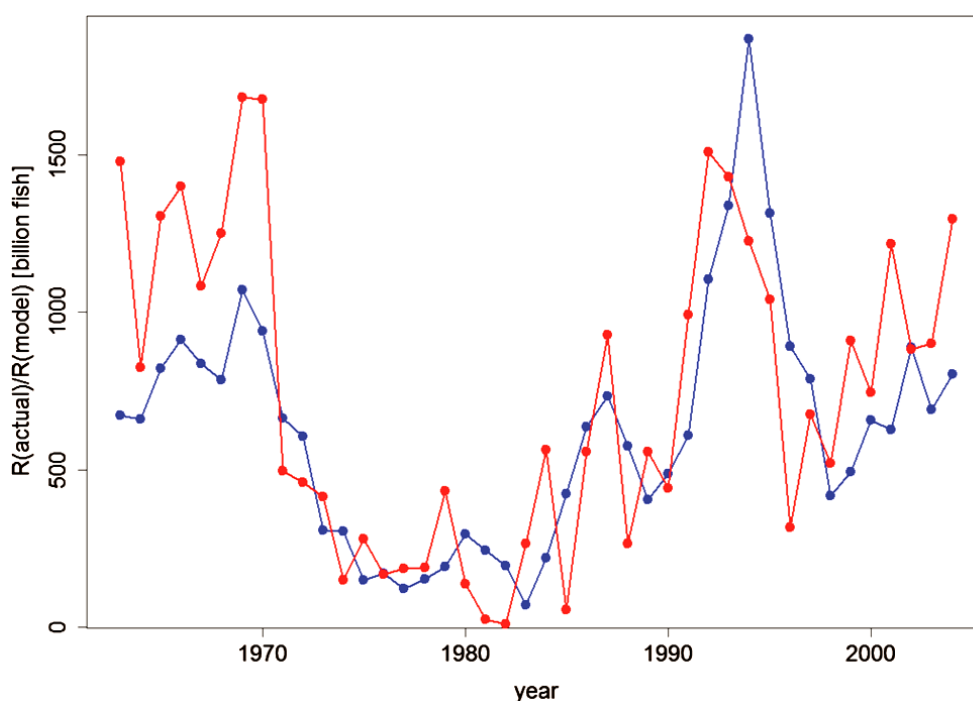


Figure 7. Graph showing the actual dynamics (in red) of the Peruvian anchoveta *Eugraulis ringens* from 1963 to 2004 and the dynamics resulting from model (d), (Table 4) shown in blue.

They showed that according to the AIC, the model recognizing the two regimes was better than a model with a single regression, without any separation of data (Table 3 (Models 1 and 2)). In our study, we separated the data into two sets based on the data points above and below the regression line for the RPS in Table 3 (Model 3) and Figure 4. When all three models were compared with AIC, our model was selected as the better model. In both cases, the superior model was a result of separation of the data into two sets. This may be due to the impact of the environmental factors and changes in the climatic conditions. This needs further investigation to verify why exactly this occurs and we should also be careful when using RPS to explain stock-recruitment relationships as previously stated, it is quite sensitive to observational errors [14].

Upon selection of the model with two regimes, Cahuin *et al.* [11] fit the RPS data with the model of Ricker. Sakuramoto and Suzuki [15] explain in detail that when the actual model for a stock-recruitment relationship is a proportional model, observational and/or process errors can result in the selection of a Ricker [17] or Beverton and Holt [19] model. On the contrary, when the actual model is a Ricker [17] or Beverton and Holt [19] model, observational and/or process errors seldom resulted in the selection of a proportional model. In this study, the expanded proportional model, which incorporated the environmental factors, SST and SOI, was selected as the optimal model, it strongly indicates a possibility that the

actual stock recruitment relationship is the proportional model and does not have a density dependent effect (Figure 6).

In this study we attempted to explain the recruitment dynamics of the Peruvian anchovy from 1963-2004 with modifications of the GAM and expanded proportional model to incorporate the environmental variables. In our analysis we based our model selection through the AIC, R^2 and significant parameter estimates. The R^2 value for our model was much higher ($R^2 = 0.557$) in comparison to the model with full data series (Equation (3)) by Cahuin *et al.* [11] ($R^2 = 0.251$). Our selected model incorporated both the SST and SOI as the independent variables (Table 4, Model (d)). Both SST and SOI have a strong influence in structuring the dynamics of the anchoveta.

Sea surface temperature has established its importance as an environmental factor in structuring the dynamics of various fish species [2-6,20-22]. Indeed, exploratory analysis showed strong negative correlation of SOI with SST. Funamoto *et al.* [7] and Funamoto [23] showed that SST and wind indexes had significant bivariate relationship with fish recruitment. The SST, Pacific Decadal Oscillation and Arctic Oscillation have been shown to have significant relationship with drastic reductions in fish populations in the Kuroshio Extension [20].

Cahuin *et al.* [11] showed the importance of SST and SOI in modeling the dynamics of the Peruvian anchoveta. Their overall best model had SOI as the independent variable and the model selection was based on the per-

centage deviance. Their model did not incorporate 33.33% of the data which was stated as belonging to the unfavorable regime. However, they did show that the resulting best model was still the same when the whole range of data were used (Equation (3)). Our model show both SST and SOI as important environmental variables for modeling the recruitment dynamics of the Peruvian anchoveta. We used numerous variations of the modifications of the GAM and expanded proportional model to reach our final models, whereas the analysis of Cahuin *et al.* [11] do not show much variation for model selection. Also, our SST data was different from theirs and this may have affected the outcome. The variation in the fit of the model with actual data may be due to the influence of other environmental factors not incorporated in this study and is subject to further investigation.

From 1979 to 1989 rapid changes can be observed in $\ln(R)$, $\ln(SSB)$ and $\ln(RPS)$ dynamics. According to Mysak [24], the catastrophic decline in the population of the Peruvian anchoveta is a result of strong El Niño events. Klyashtorin [25], shows that strong El Niño events are followed by a sharp decline in the population of the Peruvian anchoveta. In our study, we were able to generate a suitable model for explaining the dynamics of anchovy. However, we did not incorporate El Niño as one of the modeling variables, this needs further investigation to validate the influence of El Niño in structuring the dynamics of the Peruvian anchoveta.

In conclusion, the recruitment of the Peruvian anchoveta, *Engraulis ringens* off Peru R_t is essentially determined in proportion to spawning stock biomass S_t , and then environmental factors, SST and SOI, in year t further change the recruitments. That is, it can be written by

$$R_t = a \cdot S_t \cdot f(e_1, e_2, \dots, e_k) \quad (4)$$

where R_t is the recruitment in year t , S_t is the spawning stock biomass in year t and $f(\cdot)$ is the function determined by environmental factors e_i ($i = 1, 2, \dots, k$), where k is the number of environmental factors related to the recruitment. The mechanism shown by Equation (4) is completely same with that for Japanese sardine proposed by Sakuramoto [26,27].

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