

# Climatic regimes and the recruitment rate of anchoveta, *Engraulis ringens*, off Peru

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## ABSTRACT

The recruitment rate of Peruvian anchoveta, *Engraulis ringens*, was studied to test the hypothesis that long-term environmental variation (regime shifts) had a significant impact on density-dependent processes governing the anchovy recruitment during the period 1963–2004. On the basis of previous defined regimes and turning points for the Humboldt Current System, we identified two groups of years for increased recruitment of anchoveta (1963–1971 and 1986–2004), and one unfavorable period (1972–1985). A common intercept and significantly different slopes were found when the recruitment rate was plotted as a function of the spawning stock biomass during those groups of years, suggesting that density-dependent effects on recruitment were affected during different climate regimes. The favorable (unfavorable) regime was characterized by higher (lower) zooplankton volumes, and with a higher frequency of colder (warmer) waters. Dome-shaped relationships between recruitment rate, spawning stock biomass and SST, were detected with a Generalized Additive Model for the favorable regime. Thus, recruitment could be explained by non-linear effects of environmental variables. Ultimately, climatic regimes are affecting the density-dependent effects on recruitment of anchoveta and the mechanisms involved may be associated with changes in the carrying capacity of the spawning habitat of anchoveta off Peru, which in turn are related with the effects of cold and warm regimes.

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## 1. Introduction

The understanding of natural variability of marine ecosystems at different time scales is essential for an adequate management of marine resources. One of the approaches to explore how marine ecosystems will react to global changes is the search for causal relationships of natural variability patterns in fish populations. At present, there is much evidence suggesting that large marine ecosystems are driven by decadal fluctuations associated with climatic forcing (Stenseth et al., 2002), as suggested for the North Atlantic (Alheit and Hagen, 1997, 2002; Beaugrand, 2004; Beaugrand et al., 2002; Fromentin and Planque, 1996), for the North Pacific (Beamish, 1995; Hare and Mantua, 2000; Mantua, 2004; Wooster and Zhang, 2004), and for eastern boundary systems (Alheit and Hagen, 2001; Chavez et al., 2003). The climatic regime shifts can reorganize the marine communities and the trophic

relationships, with resulting changes in the dominance and mixing of species over decadal time scales (Steele, 2004; Collie et al., 2004).

In the Humboldt Current System (HCS), regimes characterizing either a dominant-anchovy or dominant-sardine system, have been described on the basis of annual catch time-series, zooplankton volume time-series, and physical environmental parameters, such as sea surface temperature, upwelling indexes, southern oscillation indices, thermocline depths and others (Chavez et al., 2003; Alheit and Ñiquen, 2004; Montecinos et al., 2003; Pizarro and Montecinos, 2004; Cubillos et al., 2007; Alheit and Bakun, 2009). According to Alheit and Ñiquen (2004), the long-term dynamics of the HCS is controlled by shifts between alternating anchovy and sardine regimes, restructuring the entire ecosystem. These regime shifts are caused by lasting periods of warm or cold temperature anomalies related to the intrusion or retreat of warm subtropical oceanic waters to the coast of Peru and Chile (Swartzman et al., 2009). Phases with predominant negative temperature anomalies parallel anchovy regimes (1950–1970, 1985–2004), and a relatively warm period from 1970 to 1985 characterized by a sardine dominance (Alheit and Ñiquen, 2004). Instead, Chavez et al. (2003)

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suggested that the Pacific changed from a cool “anchovy regime” to a warm “sardine regime” in the mid-1970s, and back to an “anchovy regime” in the middle to 1990s. Although the exact turning points defining the change from one regime to another are often subjective and questionable, we have chosen the regimes defined by Alheit and Niquen (2004) to analyze the impact of climate regimes on density-dependent processes on the recruitment of anchoveta off Peru.

Indeed, when looking for climatic changes, McFarlane et al. (2000) suggested that one method of measuring climate change is to observe the dynamics of species that could be affected. They suggested that a regime shift occurred in the late 1990s in the North Pacific marine ecosystem, and this was revealed in the dynamics of key commercial fish that indicated changes in their environment. Wada and Jacobson (1998) demonstrated that the reproductive success of a population was related to the productive cycle of the population, which was in turn controlled by the environment. Also, Mueter et al. (2007) demonstrated decadal-scale variability by studying recruitment and stock–recruitment residuals for fish stocks within Gulf of Alaska and eastern Bering Sea–Aleutian Islands. On this ground, it may be possible to use stock–recruitment relationships in order to account for the state of the environment for a given period. However, the objective of this paper is to elucidate the relationships between recruitment, spawning stock biomass and environmental forcing in the North-Central stock of the Peruvian anchoveta (*E. ringens*) during favorable and unfavorable regimes. We hypothesize that decadal to inter-decadal environmental variation (regimes) has a significant impact on density-dependent effects on recruitment of anchoveta.

## 2. Material and methods

### 2.1. Data sources

Recruitment and spawning stock biomass data of the North-Central stock of anchoveta off Peru (4°–14°S), from 1963 to 2004, have been provided by the Instituto del Mar del Peru (IMARPE). These estimates were obtained after virtual population analysis techniques by considering total catch biomass, length–frequency data, and acoustic survey methods for biomasses, and further methods described by Csirke et al. (1996). Recruitment ( $R$ ) is the number at age 0 and the spawning stock biomass ( $S$ ) represents the adult biomass, defined as all mature specimens at the beginning of the spawning season (Table 1).

In addition, time-series data of zooplankton volume, as an index of zooplankton biomass, were provided by the Plankton Laboratory of IMARPE (Ayón et al., 2004). Zooplankton samples were collected with Hensen nets (0.33 m<sup>2</sup> diameters, 300 µm mesh size) vertical tows from a depth of 50 m to surface in 57 surveys along the Peruvian coast during winter and summer from 1961 to 2001. Zooplankton volume (ml<sup>−3</sup>) was determined by using the displacement method (Kramer et al., 1972). Further details of sampling and analysis of zooplankton volume time-series can be found in Ayón et al. (2004).

Monthly mean sea surface temperature (SST) data covered the time period between 1963 and 2004 at four coastal stations along the Peruvian coast, i.e. Paíta (05°S), Chicama (07°S), Chimbote (09°S) and Callao (12°S). The mean annual of SST was obtained as to construct a time-series from 1963 to 2004. Also, the Southern Oscillation Index (SOI) reported by the Center for Climate Prediction, was obtained from NOAA (<http://www.cpc.noaa.gov/data/indices/soi>). We used the standardized data series, from which annual averages were computed from monthly anomalies for the period 1963–2004.

**Table 1**

Spawning stock biomass and recruitment of the Peruvian anchoveta (*Engraulis ringens*) in the North-Central stock (source: IMARPE).

Year	Spawning biomass (10 <sup>6</sup> tons)	No of recruits (10 <sup>9</sup> fish)	Year	Spawning biomass (10 <sup>6</sup> tons)	No of recruits (10 <sup>9</sup> 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

### 2.2. Recruitment rate and regimes

It has been assumed that density-dependent effects on recruitment exist for anchoveta off Peru, but they are usually masked in long data sets by climatic regimes and probably by measurement errors (Hilborn and Walters, 1992). In this context, stock–recruitment relationships were used to test the hypothesis about regime effects on reproductive success of anchoveta off Peru, namely: (a) two favorable groups of years (1963–1971; 1986–2004), and (b) one unfavorable group of years (1972–1985). The groups of years here used are consistent with previous defined regimes suggested by Alheit and Niquen (2004), but the year 1971 was included as part of the first favorable regime, and 1985 was included in the unfavorable regime. We decided those groups of year by considering that some transition (1–3 years) between regimes exists, in which the response of a fish population can take place. The lag effects on recruitment of anchovy were evaluated through the Akaike Information Criterion (AIC) by applying a lag of 1–4 years after the regime shift suggested by Alheit and Niquen (2004). The AIC for each model was obtained by fitting a stock–recruitment model to the data, trying to explain the changes in the recruitment of anchoveta during favorable and unfavorable regimes. The model was fitted through a Generalized Linear Model, i.e.

$$\log R_{i,t} = \text{offset}(\log S_{i,t}) + \alpha + \beta_i \times r_i \times S_t + \varepsilon_{i,t}$$

where  $R_{i,t}$  is the recruitment of anchoveta in the year  $t$  and  $i$ -th regime,  $\text{offset}(\log S_{i,t})$  is a term used to be added to a linear predictor, with known coefficient 1 rather than an estimated coefficient (Venables and Ripley, 2002);  $\alpha$  is the intercept (density-independent effects),  $\beta_i$  are the slopes for the  $i$ -th regime (density-dependent effects),  $r_i$  is a factor representing a particular regime (groups of years coded as F = favorable, and U = unfavorable), and  $S_t$  is the spawning stock biomass. We used Gaussian family and link identity for log-transformed recruitment. The coefficients associated to each regime represent density-dependent effects of spawning stock biomass on recruitment rate. The full model was compared with a model that does not ignore the existence of two regimes. Finally, to characterize each regime (favorable and

unfavorable), the SST and zooplankton volumes were compared among regimes through analysis of variance.

### 2.3. Exploratory analysis of non-linear relationship

Generalized Additive Model (GAM) techniques were used to explore the effects of environmental variables because usually non-linear relationships have been observed between recruitment and environmental indices. The 'mgcv' package (Wood and Augustin, 2002; Wood, 2003) was used. This is a library available for the software and language R (Ihaka and Gentleman, 1996). The recruitment rate was considered the dependent variable as a function of the spawning stock biomass; we then added to this model the environmental variables, such as zooplankton volumes, sea surface temperatures, and the Southern Oscillation Index. For the smooth function we used penalized regression splines. We used the 'mgcv' library because it implements an automatic selection of the smoothing parameters associated with each smooth term on the basis of generalized cross-validation (GCV). Roughly, cross-validation involves leaving one of the data-points out, fitting the model to the remaining data, and then computing the squared difference between those points. This procedure is repeated for all data-points and for several amounts of smoothing, and then the smaller squared differences yield a better model.

## 3. Results

### 3.1. Recruitment rate and regimes

The stock–recruitment data of the Peruvian anchoveta revealed a very scattered distribution, typically found in most fish populations (Fig. 1). According with the Akaike Information Criterion (AIC), a lag of one year after the regime shifts suggested by Alheit and Ñiquen (2004) was selected as the best model describing the recruitment changes of anchoveta as a function of the spawning stock biomass (Table 2). Indeed, when the recruitment rate is plotted against the spawning stock biomass it can be clearly observed two different linear relationships (Fig. 2a). These relationships have a similar intercept and two different slopes, and are characterizing two different stock–recruitment relationships, and described by the stock–recruitment model of Ricker (Fig. 2b). Also, only a stock–recruitment model that takes into account the presence of two different regimes as a factor (coded F for the favorable years and U for the unfavorable years) was better than a single model ignoring the presence of these regimes (Table 3). The best model has a single intercept and the deviance explained was equal to 22.1%. Because the slopes were significantly different ( $F_{2-39} = 5.515$ ,  $p < 0.01$ ), this model represents the effects of regime shifts

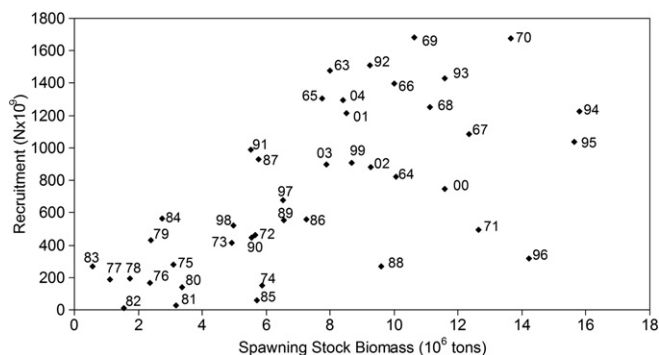


Fig. 1. Stock–recruitment data of the Peruvian anchoveta between 1963 and 2004, North-Central stock (see Table 1).

Table 2

Summary of the performance of different models for the stock–recruitment relationships fitted through Generalized Linear Models. The lags are in relation with the regime shifts suggested by Alheit and Ñiquen (2004), by lagging 1–4 years after 1970 and 1985. The best model is in bold.

Regimes	Group of years		Residual deviance	AIC
	Favorable	Unfavorable		
Without regimes	–	–	31.491	113.10
Alheit and Ñiquen (2004)	1963–1970 1985–2004	1971–1984	29.148	111.85
<b>Lag 1</b>	<b>1963–1971</b> <b>1986–2004</b>	<b>1972–1985</b>	<b>24.552</b>	<b>104.64</b>
Lag 2	1963–1972 1987–2004	1973–1986	25.553	106.32
Lag 3	1963–1973 1988–2004	1974–1987	27.375	109.21
Lag 4	1963–1974 1989–2004	1975–1988	27.759	109.80

on density-dependent effects on the recruitment rate of anchoveta for the whole study period (1963–2004,  $n = 42$ ).

The groups of years which we have separated through the analysis of the recruitment rate of anchoveta are shown in Fig. 3a. The first climate regime identified by Alheit and Ñiquen occurred from 1950 to 1970, but the recruitment rate of anchovy started to be affected by density-dependent processes one year later, in 1971. Similarly, the unfavorable regime affected the recruitment rate until 1985 (Figs. 1 and 2). The delay of anchoveta in responding to the first regime shift is also recorded in the zooplankton volume time-series (Fig. 3b), where it can be observed that after the first favorable regime zooplankton volumes started to decline until 1974. However, for the last favorable regime of anchovy recruitment (1985–2004) zooplankton volume remained lower, without evidence of a recovery. Nevertheless, there were significant differences in zooplankton volumes among regimes (ANOVA,  $F_{1,31} = 7.75$ ,  $p < 0.01$ ). In the case of sea surface temperature it can be observed

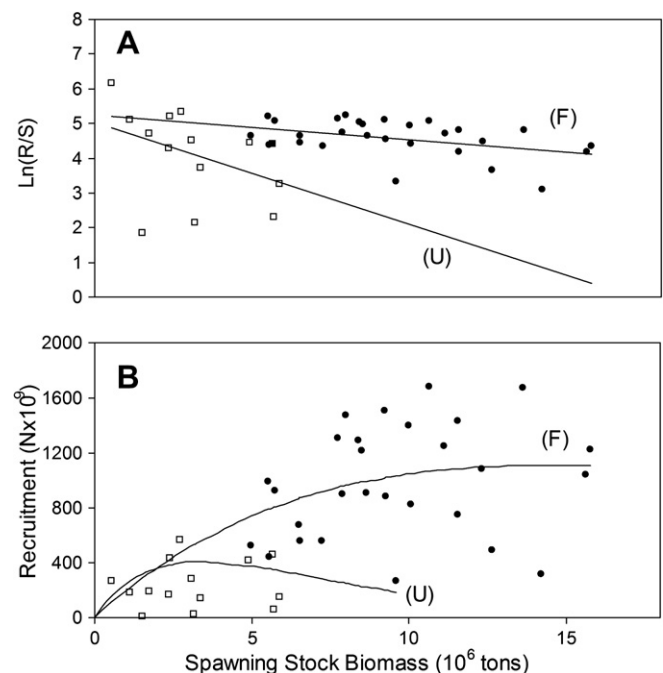


Fig. 2. Recruitment rate,  $\log_e(R/S)$ , on spawning stock biomass (A), and Ricker stock–recruitment relationships (B) obtained for the Peruvian anchoveta. Each curve is labeled with U for unfavorable regime and F for the favorable regime.

**Table 3**

Coefficients for the full model of the anchoveta log-recruitment (dependent variable) as a function of the spawning stock biomass at each of the identified regimes, and compared with a model ignoring the presence of climatic regimes.

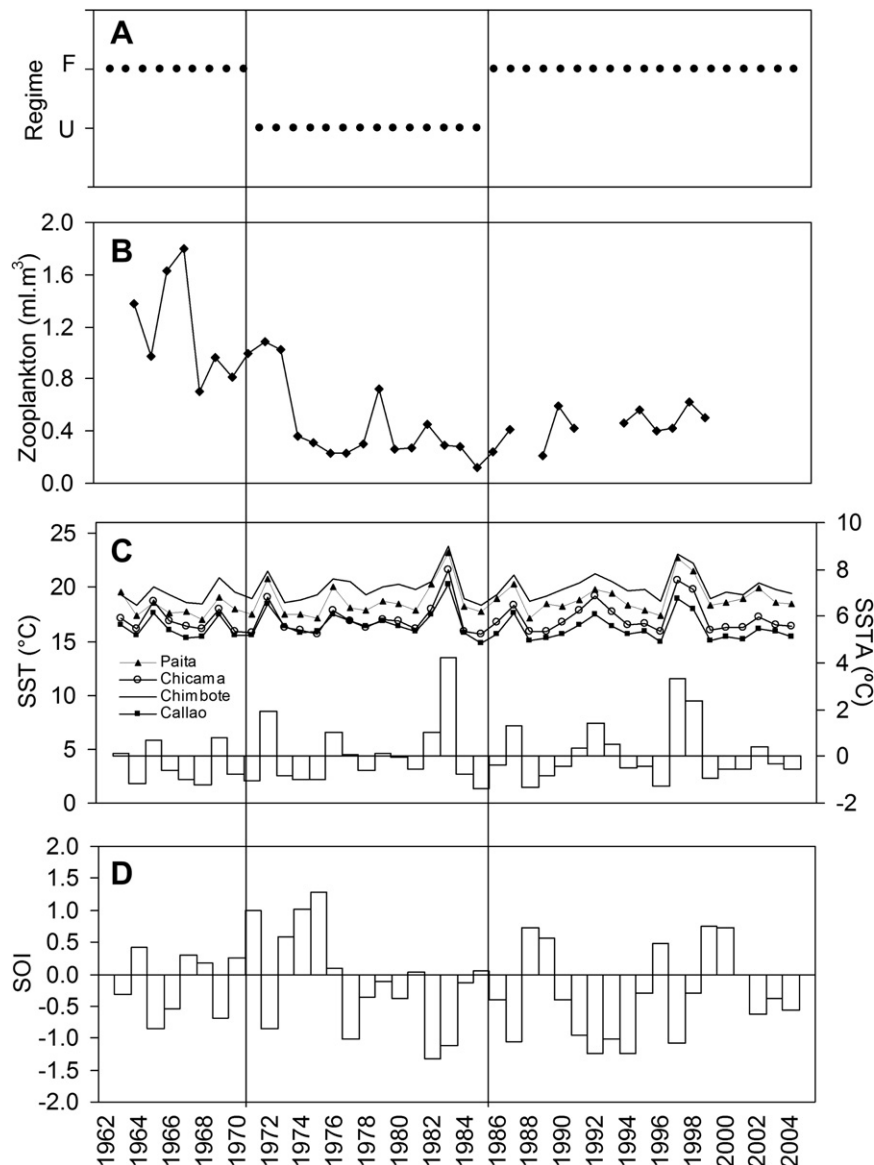
Model	Coefficients:	Estimate	Std. error	t value	Pr (> t )
Two regimes	Intercept	5.149	0.336	15.33	$<2 \times 10^{-16}$
	S*Regime F	-0.061	0.035	-1.73	0.092
	S*Regime U	-0.324	0.102	-3.19	0.003
	Null deviance	31.496	(41 df)		
	Residual deviance	24.552	(39 df)		
	AIC	104.64			
Without regimes	Intercept	4.437	0.289	15.344	$<2 \times 10^{-16}$
	Slope	-0.003	0.034	-0.076	0.94
	Null deviance	31.496	(41 df)		
	Residual deviance	31.491	(40 df)		
	AIC	113.10			

that the two favorable groups of years (1963–1971 and 1986–2004) have more frequent colder years. Instead, the unfavorable regime (1972–1985) was characterized with few colder years (Fig. 3c). The warmer years are related with El Niño events. In fact, in the

Southern Oscillation Index the presence of El Niño in 1972–1973, 1982–1983, 1987, 1992–1993, and 1997–1998 is evident and related with strong negative values. Also, a period with persistent negative anomalies between 1976 and 1984 can be observed. The former characterizes the unfavorable regime detected for the recruitment of anchoveta, but not in sea surface temperature (ANOVA,  $p > 0.01$ ).

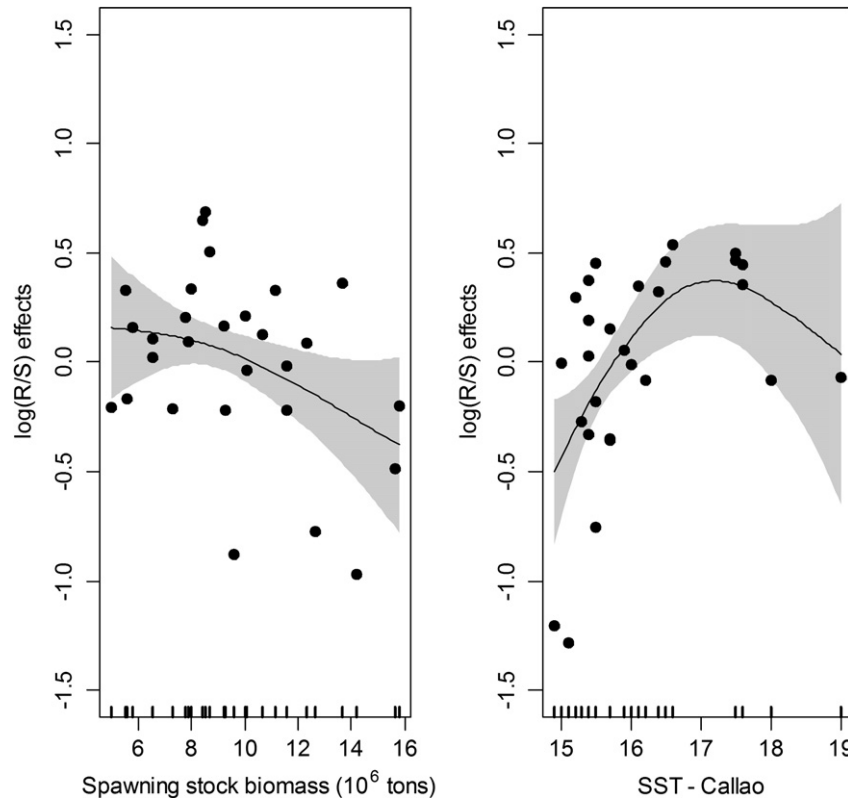
### 3.2. Recruitment rate and environmental variables: non-linear exploratory relationships

When looking for a probable existence of non-linear relationships effects through Generalized Additive Models, we cannot apply this methodology for the unfavorable regime because the low number of data-points available ( $n = 14$ ). For the favorable regime, the best models were described by a non-linear dome-shape effects of the sea surface temperature and negative effects of SOI (Figs. 4 and 5, respectively). However, the deviance explained was nearly 50% for those models (Table 4). When the complete time-series was explored the results were unsatisfactory (Table 4).



**Fig. 3.** Regime time-series showing the groups of years associated with the two stock-recruitment curves (A), zooplankton volume time-series (B), sea surface temperature (C), and Southern Oscillation Index time-series (D). The vertical lines are indicating the regime shifts according with Alheit and Niquen (2004).





**Fig. 4.** Relationship between the anchoveta recruitment rate,  $\log(R/S)$  as a function of spawning stock biomass ( $10^6$  tons) and SST at Callao ( $^{\circ}\text{C}$ ) for favorable regimes. The shaded area represents the 95% confidence limit.

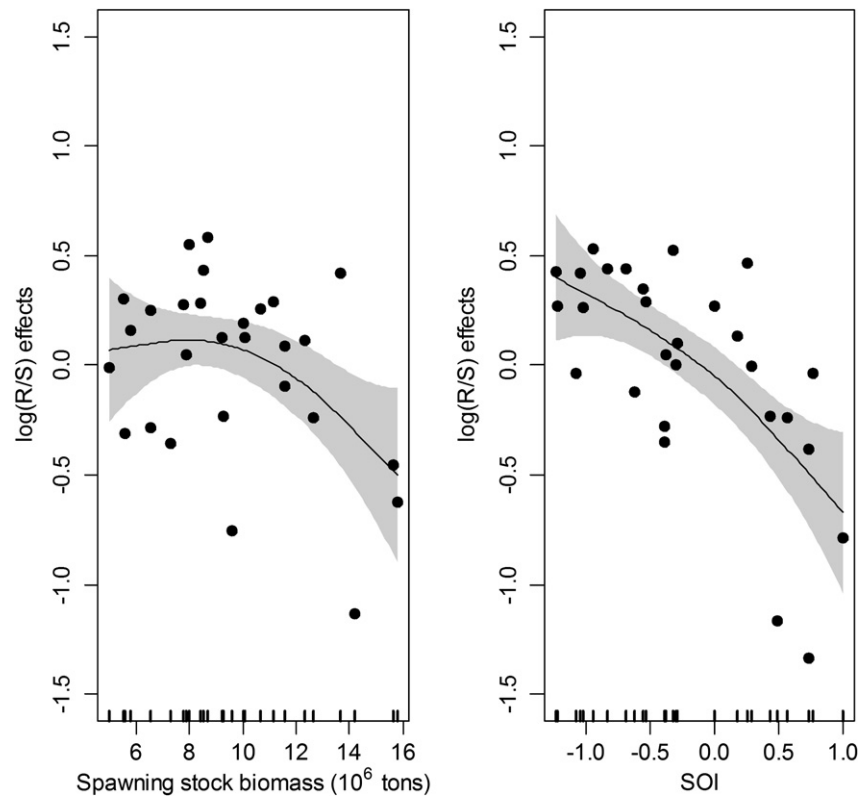
#### 4. Discussion

One of the objectives of this work was to identify whether climate regimes affected significantly the rate of production of recruits of anchoveta. Under this view, we found significant effects on the density-dependent effects of the spawning stock biomass on recruitment rate of anchoveta off Peru, but with a delayed response when compared with previous defined regime shifts, as suggested by Alheit and Niquen (2004). An unfavorable climatic regime for anchoveta generates a stronger density-dependent effect of spawning stock biomass on the recruitment rate than under a condition of a favorable regime. Unfortunately, the range of spawning biomass was not the same to avoid the potential time-series bias identified by Walters (1985). We cannot test if regime shift effects would have different recruitment over the same range of spawning stock biomass because the 'time-series' bias might be reflected in a steeper slope for spawning biomass lower than 6 million tons. Nevertheless, it would be difficult to test such 'time-series' bias for anchoveta because unfavorable regimes in the HCS are associated with lower abundance of this species. This meant that the survival of recruits is lower when biomass reaches 4–6 million tons during the unfavorable regime, probably due to the contraction of the spawning habitat. Instead, during a favorable regime and for spawning biomass ranging between 4 and 6 million tons, recruits have a better survival because density-dependent effects are reduced and probably due to that the spawning habitat is unconstrained spatially or trophically. Indeed, a positive correlation between anchovy biomass and the area of its distribution has been observed, as well as a negative correlation between anchovy density and distributional area (Gutiérrez et al., 2001). Changes in the area of the cold water habitat also influence anchoveta recruitment. Csirke (1980) added an "anchoveta concentration

index" to the standard stock–recruitment model of Ricker, and found that an increase in the concentration of the parent stock during spawning resulted in less recruits in the next year which suggests a density-dependent egg and larvae cannibalism.

For the Peruvian coast, the climatic regimes have been very well characterized in terms of sea surface temperature, zooplankton volume, and other environmental variables (Chavez et al., 2003). For example, in the Humboldt Current System decreases in primary production are associated with warmer periods. A warm period would increase (decrease) feeding and spawning potential habitat of sardine (anchovy). Indeed, sardine would take advantage when the associated decrease in primary production (and consequently zooplankton) because sardine can feed on both small zooplankton and phytoplankton. Therefore, a warm period is a disadvantage for anchovies that feed mainly on zooplankton. In addition, predation on all life stages of anchovies in their reduced habitat is enhanced during these warmer phases (Alheit and Niquen, 2004). The opposite changes occur during cold year phases. This meant that cold waters (warm waters) would increase (decrease) feeding and spawning potential habitats of anchoveta (sardine) (Swartzman et al., 2009). Increases in zooplankton abundance would benefit anchovies that can take advantage of their faster turn over and earlier maturity than sardines, thereby thriving and dominating the system. They would also increase the predation on sardine eggs.

In the HCS, a cold regime is associated with an anchovy dominating system and a warm regime is associated with a sardine dominating system (Chavez et al., 2003; Alheit and Niquen, 2004). Also, a cold regime is characterized by intensified upwelling which could explain the preferred feeding and spawning habitat of anchoveta. In turn, anchoveta seems better adapted to the higher production in cold coastal upwelled waters (e.g. Niquen et al., 2000; Bertrand et al., 2004; Niquen and Bouchon, 2004). During



**Fig. 5.** Relationship between the anchoveta recruitment rate,  $\log(R/S)$  as a function of spawning stock biomass ( $10^6$  tons) and SOI for favorable regimes. The shaded area represents the 95% confidence limit.

cold and favorable regimes the effects of the spawning biomass on recruitment rate, through density-dependent regulation, are less than during warmer unfavorable regimes. Density-dependent processes are probably related with expansion and contraction of favorable or preferable cold habitat, which could be associated with waters with temperatures less than  $17^\circ\text{C}$  (Muck et al., 1987). Changes in alongshore, extent and onshore–offshore distance of cold and warm waters are controlling – or at least influencing – the migration and concentration patterns of anchoveta off Peru. When the warm waters intrude into the coast, an increase in vulnerability of anchoveta to predation, egg and larval cannibalism, and to the

fishery tends to occur (Muck et al., 1987, 1989). Concentration and clustering are expected to be high during warm periods because favorable habitat in terms of hydrologic and trophic conditions would be restricted to the shore where fish will concentrate (Gutiérrez et al., 1999, 2007). Conversely, distribution and dispersion are expected to be higher during cold periods because upwelling and mixed waters extend farther from the coast.

In terms of the interannual environmental variability effects on the recruitment rate of anchoveta, we were only able to provide some evidences during a favorable regime because for the unfavorable regime few data-points were available for the GAM

**Table 4**

Generalized Additive Model analysis of the anchoveta recruitment rate (dependent variable:  $\log(R/S)$ ) as a function of spawning stock biomass and environmental variables. Spline smoother is represented by  $s(\bullet)$ ,  $S$ : spawning stock biomass, Zoop: zooplankton volume, SST: sea surface temperature, GCV: general cross-validation, SOI: Southern Oscillation Index.

GAM models	$R^2$ (adj.)	GCV score	Scale est.	$n$	Deviance explained (%)
<b>Regime favorable:</b>					
$\log(R/S) = s(S) + s(\text{Zoop})$	0.228	0.238	0.201	19	31.4
$\log(R/S) = s(S) + s(\text{SST-Paita})$	0.345	0.216	0.183	28	42.3
$\log(R/S) = s(S) + s(\text{SST-Chicama})$	0.409	0.197	0.166	28	48.6
$\log(R/S) = s(S) + s(\text{SST-Chimbote})$	0.323	0.227	0.190	28	41.3
$\log(R/S) = s(S) + s(\text{SST-Callao})$	0.420	0.195	0.162	28	49.9
$\log(R/S) = s(S) + s(\text{SOI})$	0.494	0.168	0.142	28	55.8
<b>All time-series:</b>					
$\log(R/S) = s(S) + s(\text{Zoop})$	0	0.965	0.877	33	6.2
$\log(R/S) = s(S) + s(\text{SST-Paita})$	0.146	0.755	0.656	42	23.9
$\log(R/S) = s(S) + s(\text{SST-Chicama})$	0.105	0.740	0.687	42	14.9
$\log(R/S) = s(S) + s(\text{SST-Chimbote})$	0.087	0.761	0.701	42	13.8
$\log(R/S) = s(S) + s(\text{SST-Callao})$	0.237	0.708	0.586	42	35.3
$\log(R/S) = s(S) + s(\text{SOI})$	0.251	0.776	0.576	42	43.1

analysis. Dome-shaped relationships between recruitment rate and sea surface temperature were detected, suggesting that moderate increments in water temperature are favorable for anchoveta but extreme warm waters are unfavorable. These warmer years are probably associated to El Niño events of great magnitude occurring during favorable regimes, such as the 1972–1973 or 1997–1998 El Niño events. Nevertheless, a negative effect of the Southern Oscillation Index on the recruitment rate was detected suggesting that warmer years are favorable for anchoveta during a favorable regime. Probably further analysis is required for modelling the interannual variability in recruitment of anchoveta because other factors different than sea surface temperature at coastal stations could be more important, such as upwelling, stratification, dispersion (Lett et al., 2007). In this paper, our attempt was only to compare the contribution relative to some environmental indices on the recruitment rate as compared with density-dependent process. It is therefore concluded that climatic regimes are affecting the density-dependent effects on recruitment of anchoveta, and that interannual environmental changes are also contributing in explaining the recruitment success in a non-linear fashion. El Niño events are the main cause for destabilizing the population during a favorable regime (higher spawning stock biomass), and a quickly recovery once the El Niño conditions are finished. However, if a long-term unfavorable El Niño-like regime is established in the HCS an increase in density-dependent effects causes the anchovy to remain in a low population biomass state.

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