



The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983 to 2005

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ABSTRACT

The Humboldt Current System (HCS) is dominated by two pelagic species; Peruvian anchovy or anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax*). Using data from 43 acoustic surveys conducted from 1983 through 2005 by the Peruvian Marine Institute (IMARPE), we examined the distribution of these two species relative to water masses. We tested the hypothesis that anchovy was found more frequently in upwelled cold coastal water (CCW) and mixed waters (MCW) than in other water types and that sardine was more associated with more offshore oceanic surface subtropical water (SSW). Surface temperature, salinity, latitude, season and distance to the coast data were used to define water masses. Results using generalized additive models (GAM), modelling sardine and anchovy presence-absence as a function of year, water body, bottom depth and latitude, showed that anchovy were primarily found in CCW and MCS, while sardine were more ubiquitous relative to water masses with some predilection for SSW. These results were supported by various indexes of anchovy and sardine distribution versus water mass as well as temporal and location variables.

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1. Introduction

The Humboldt Current System (HCS) off Peru is one of the most productive coastal upwelling systems in the world (Carr, 2002). It supports the world's largest tonnage fishery for Peruvian anchovy or anchoveta (*Engraulis ringens*) (Bouchón et al., 2000) and has in the past also supported a major sardine (*Sardinops sagax*) fishery (Csirke et al., 1996). The HCS experiences year-round upwelling (Thomas et al., 2001). The abundance of anchovy and sardine appears to be linked both to El Niño Southern Oscillation (ENSO) events (frequency of 2–7 years) and to decadal-length regime shifts (Lluch-Belda et al., 1992; McFarlane et al., 2002; Chavez et al., 2003; Alheit and Niquen, 2004). Additionally, the abundance of the anchovy population appears to fluctuate out of phase with sardine in the HCS (Lluch-Belda et al., 1989, 1992; Csirke et al., 1996; Schwartzlose et al., 1999; Bakun and Broad, 2003; Fréon et al., 2003). Chavez et al. (2003) proposed the term 'El Viejo' to define the warm, decadal 'sardine regimes' and 'La Vieja' to define the cold decadal 'anchovy regimes'. However, little is known about the processes underlying the functional response of these species to ENSO events and decadal regime (Bertrand et al., 2004).

It has been hypothesized that cold upwelling water, which supports elevated levels of phytoplankton (Thomas et al., 2001;

Chavez et al., 2003), provides overall favourable conditions, in particular for feeding, for anchovy while sardine appears to be favoured in warmer oceanic and frontal waters (Bertrand et al., 2004; Gutiérrez et al., 2007). Sardine is a more efficient filter feeder on phytoplankton and small zooplankton, while anchovy operates more efficiently preying on larger zooplankton (Konchina, 1991; van der Lingen et al., 2006, in press; Espinoza and Bertrand, 2008). Thus, more favourable feeding conditions for sardine may predominate in small and for anchovy in large-zooplankton areas, presumably corresponding to warmer oceanic water and cooler upwelling water, respectively (Mackas et al., 2001; Peterson et al., 2002; Zamon and Welch, 2005). Bertrand et al. (2004) hypothesized that variation in the range of favourable habitat leads to variation in spatial extent of the fish populations. In that sense, dramatic biomasses of anchovy can be concentrated in very small refuge areas when conditions are adverse, as occurred, for instance, during the El Niño event of 1997–1998 (Bertrand et al., 2004). When the range of favourable habitat increases very quickly (at the beginning of La Niña condition for instance) the fish range of distribution can increase drastically even if the population is still not very abundant (Bertrand et al., 2004; Gutiérrez et al., 2007). Gutiérrez et al. (2007) provide evidence that environmentally mediated alterations in habitat range can lead to population changes. In that paper habitat was defined using a very simple proxy, the coast-wide temperature anomaly (Gutiérrez et al., 2007) over a long time period, while the other paper used a more

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complex water mass definition but with a short time series (Bertrand et al., 2004).

Here we examine the hypothesized relationships using a complex water mass definition over a long time series. Within this context our objective is to describe the co-variation of water masses and fish spatial distributions and to test hypotheses concerning fish association with water masses. To this end, we used data from 43 acoustic surveys off the Peruvian coast from 1983 to 2005.

2. Data and methods

2.1. Acoustic survey data

Acoustic data were collected from 1983 to 2005 by the Peruvian Marine Institute (IMARPE), most commonly using the R/V Humboldt (76 m long), the R/V Olaya (41 m long) or the R/V SNP-1 (36 m long). At least two acoustic surveys were run in most years. Survey design was composed of parallel transects averaging 90 nautical miles (167 km) long with an inter-transect distance varying between 14 and 16 nautical miles (26–30 km) depending on the cruise.

The surveys intended to cover most of the range of anchovy distribution (transects shown in Fig. 1), which varied from survey to survey. Extensive midwater trawl sampling completed the acoustic surveys for species identification. The seasonal and temporal distributions of scientific acoustic surveys were: spring (1983, 1986, 1989, 1990, 1996–2005), summer (1990–1996, 1999–2005), autumn (1985, 1986, 1997, 2 surveys in 1998), and winter (1984, 1987–1989, 1991, 1998–2005 with 2 winter surveys in

1999, 2000 and 2001). The acoustic surveys deployed Simrad (Kongsberg Simrad AS, Kongsberg, Norway) scientific echosounders EK, EKS, EK400 before 1995, and EY500 and EK500 (the EK60 was also used 2001–2005 in one vessel) thereafter. After 1998 at least two vessels were used for each survey to reduce survey time and the bias from changes in distribution of studied species during the survey. Calibration and intercalibration of the echosounders were undertaken before each survey. Calibration up until 1992 used hydrophones and after 1992 sphere calibration followed a standard procedure (Foote et al., 1987). A bias may exist in acoustic backscatter over the years due to the use of different calibration methods, but more likely due to the use of different acoustic systems. The magnitude of this latter bias is unknown but is assumed to not be a major factor since some calibrations between the systems were made. Acoustic back-scattered energy by surface unit (s_A) was recorded in each geo-referenced elementary sampling distance unit (ESDU) of 2 n.mi. (1983–1993) or 1 n.mi. (1994–2005). Acoustic echo identification was performed using fishing trawl composition and echotrace characteristics. Biomass estimation based on both the trawls and acoustic backscatter for each species was carried out by IMARPE for each survey. There were between 55 and 660 trawls for each survey (average of 190 trawls). Surface temperature and salinity were measured and interpolated per ESDU for almost all surveys (exceptions are missing samples in summer 1990 for both temperature and salinity and additionally summer 1994 and spring 2000 for salinity), while surface oxygen levels were measured for about half the surveys but were not used because the coverage (number of surveys) was deemed insufficient.

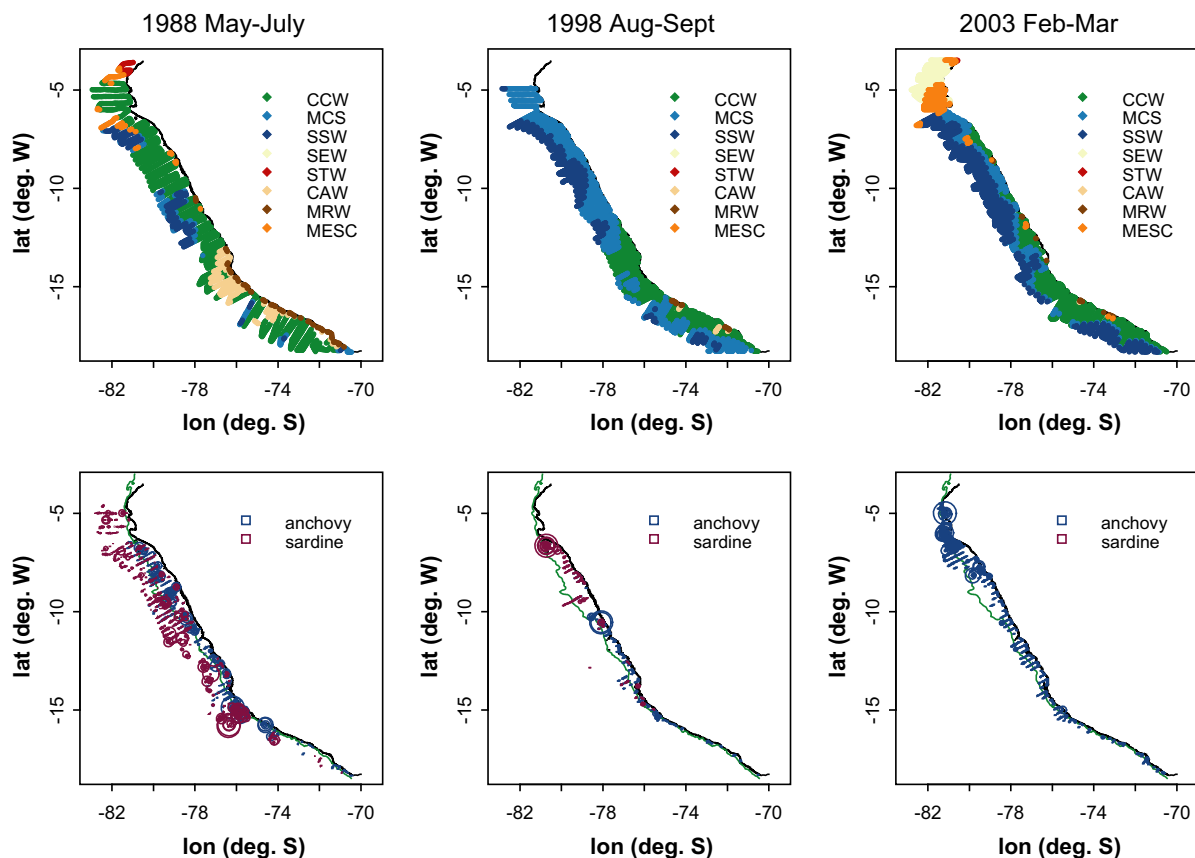


Fig. 1. Plots of the spatial distribution of anchovy (blue circles) and sardine (red circles) abundance (acoustic s_A ; lower panels) and of eight water mass categories (upper panels) from acoustic surveys off the coast of Peru in (left to right) 1988, 1998, and 2003. The 200 m isobath is shown on the lower panels.

2.2. Definition of water mass types

Since Peru is a strong upwelling area the water near the coast is generally dominated by upwelled cold coastal water (CCW) which is highly productive. However, over the years the location and extent of this water mass changes considerably and, during periods like El Niño it may completely disappear (Zuta, 1988). The northern region is frequently dominated by warmer water masses coming from the North (Zuta and Guillen, 1970). Offshore, subtropical (oceanic) water, more saline and warmer also mix with the coastal and the equatorial waters (Zuta et al., 1978). Occasionally, Antarctic generated waters reach the Peruvian coast and river water also enters the area. As such, the water masses off Peru are a labile mix of several water types of different temperature and salinity ranges (Urquiza et al., 1987; Strub et al., 1998). We developed in this work an algorithm for defining water masses in one of eight categories based mainly on temperature and salinity ranges but also on season and sometimes latitude ranges as well (Blanco et al., 2001). The algorithm was based on a method discussed in Bertrand et al. (2004) but extended by four additional water mass categories to accommodate the much larger number of survey conditions considered here. To produce an effective categorization, we expect the algorithm to produce contiguous ESDU having the same category (i.e. that the water masses did not appear to be randomly distributed, but represented reasonable sized spatial regions of similar water mass), and unique water mass by ESDU (each ESDU belonged to no more than one water mass type). Also, we intended the categorization to be complete in that very few ESDU would not fit into any category. Because environmental conditions (i.e. temperature and salinity) were highly variable between surveys and due to some missing data, it was not possible to meet these criteria all the time. However, the incidence of uncategorized ESDU was

less than 5% of all surveys and, for ESDU without missing temperature or salinity less than 1% was uncategorized. The parameter ranges for defining cold coastal (upwelling) water (CCW), mixed coastal-subtropical (oceanic) water (MCS), surface subtropical water (SSW), surface equatorial water (SEW), surface tropical water (STW), mixed equatorial, subtropical and coastal water (MESC), mixed coastal and river water (MRW) and cold Antarctic water (CAW) are given in Table 1 and were defined according to the literature (Zuta and Guillen, 1970; Morón, 2000). Examples of surveys with water mass distributions compared to sardine and anchovy distributions are given in Fig. 1. Graphs for all surveys are given in Appendix 1 in the web version.

The water masses defined in this paper are dominated by upwelling water (cold coastal water; CCW), this very productive water mass tends to be near the coast and has somewhat lower salinity than the local oceanic or surface subtropical water (SSW) south of 8°S, or lower temperature than the local surface equatorial water (SEW) north of 8°S, which has an intermediate temperature range (Table 1). In the northern region (north of 8°S) very low salinity and warm tropical water is also found (STW), while in the extreme south coast of Peru (south of 13°S and offshore (beyond 5 n.mi from the coast) low temperature and salinity surface Antarctic water (SAW) is found. This is distinguished from low salinity masses of water mixing upwelling water with riverine water (mixed riverine water; MRW) by the latter being closer to the coast (and possibly also farther north to 8°S). Two other masses of water represent mixtures between the primary water types. When spreading CCW mixes with SSW, mixed coastal-subtropical water (MCS) is formed. This water mass is distinguished from SSW by having lower salinities than SSW with potentially higher temperatures or a temperature range similar to CCW, but with higher salinity. North of 8°S CCW can mix both with equatorial

Table 1
Criteria in temperature, salinity, latitude and seasonal ranges used to categorize the eight water mass classes. STW: surface tropical waters; SEW: surface equatorial waters; SSW: surface subtropical waters; CCW: cold coastal water; MESC: mixed equatorial, subtropical and coastal water; MCS: mixed subtropical and coastal water; CAW: coastal Antarctic water; MRW: mixed river and coastal water.

Water mass	Temperature	Salinity	Latitude	Season	Special considerations
CCW	$14 < T < 18$	$34.8 \leq S \leq 35.0$	S of 8°S ^a	Spring	
	$14 < T < 19$			Summer	
	$14 < T < 18$			Autumn–winter	
	$13.5 < T < 17$		N of 8°S	Spring	
	$T \geq 18$			Summer	
	$T \geq 19$			Autumn–winter	
	$T \geq 18$				
$T \geq 17$					
SSW		$S > 35.1$			
SEW	$20 < T < 26$	$34.0 < S < 34.8$	N of 8°S	Winter–spring	
	$21 < T < 26$	Summer–autumn			
STW	$T > 21$	$S < 34.0$	N of 8°S	Spring	
	$T > 24$			Summer	
	$T > 22$			Autumn–winter	
	$T > 20$				
MCS ^b	$14 < T < 25$	$35.05 \leq S < 35.1$		Spring–autumn	
	$13.5 < T < 25$			Winter	
	$14 < T < 18$	$S \geq 35.05$		Spring	
	$14 < T < 19$			Summer	
	$14 < T < 18$			Autumn–winter	
	$13.5 < T < 17$				
MESC	$T \geq 18$	$34.8 < S < 35.05$	N of 8°S	Spring, autumn	
	$T \geq 19$			Summer	
	$T \geq 17$			Winter	
	$14 < T \leq 18$	$34.0 < S \leq 34.8$		Spring, autumn	
	$14 < T \leq 19$			Summer	
	$14 < T \leq 17$			winter	
MRW	$14 < T < 20$	$S < 34.8$	S of 8°S	Spring–autumn	≤ 5 nm of coast
	$13.5 < T < 20$		Winter		
CAW	$13 < T < 18$	$S < 34.8$	S of 13°S		> 5 nm of coast

^a Increase maximum by 1 °C north of 8°S and decrease minimum by 1 °C south of 15°S.

^b Temperature and salinity ranges are either the top group or second group of the MCS and MESC rows.

SEW and subtropical SSW resulting in a mixed equatorial, subtropical and coastal water (MESC). This water mass has either high temperatures and intermediate salinities or lower temperatures and lower salinities (Table 1). The temperature thresholds defining the ranges of temperature for the different water masses can change between seasons (higher in summer) and the boundary of 8°S between different water masses can shift south (during El Niño) and north (La Niña; Table 1).

2.3. Water mass and fish species centroids and correlation

In order to analyse the effect of water mass dynamic on fish spatial distribution we first examined the distribution of water masses over space and time. We computed the percentage of the survey area in each water mass type in each survey. We divided the coast into 1° latitude bins and computed the dominant water mass in each bin in the 1–10, 10–25 and 25–50 n.mi. distance ranges from the coast. To help the interpretation of water masses time series, we used a temperature anomaly time series from Chicama (8°S), Peru, which is a good surrogate for temperature anomaly (tA) for the entire Peruvian HCS (Gutiérrez et al., 2007). Strong positive anomalies of this index illustrate the El Niño events of 1987, 1992 and 1997–1998 (Fig. 2a; but; the very weak El Niño in 2002 was not detectable in the temperature anomaly data series).

We computed for each survey, fish species and water mass category, the centroid of the distance from the coast and tested for correlation between the fish and water mass centroids. When testing correlation between parameters we took into account autocorrelation (Pyper and Peterman, 1998; ACF procedure from S-PLUS) and multiple testing (Bonferroni correction, in Peres-Neto, 1999) potential bias.

To examine a survey-wide measure of the preference of anchovy and sardine for a particular water mass type we computed, for each survey, the ratio of (a) the fraction of the total s_A of anchovy or sardine contained in a particular water mass to (b) the fraction of ESDU of the survey in that water mass. For example, a ratio of 1 represents no preference for that water mass (i.e. the proportion of anchovy in a water mass in the survey is the same as that for the entire survey), while a ratio of 2 represents that the fish abun-

dance is twice as high in this water mass than if the fish had been distributed randomly among the water masses.

2.4. GAM modelling

We modelled the probability of anchovy and sardine presence in an ESDU as a function of latitude, year, bottom depth, and water mass using generalized additive models (GAM; Hastie and Tibshirani, 1990). Since the dependent variable was the probability of fish presence in an ESDU we assumed an underlying binomial distribution. Spline smoothers were used in all cases. Since water mass is a categorical variable ANOVA was used to model it. Thus the full analysis was a mixed model. Additionally, we used the Akaike information criterion to stepwise test whether a variable should be either removed from the GAM or included as a linear factor (rather than a smooth) by examining whether the elimination of a variable or changing from a GAM smooth to a linear factor would reduce the information criterion (or, in case both reduce it, which would most reduce it). This was affected through the S-PLUS function *step.gam*.

3. Results

3.1. Spatio-temporal dynamics of water masses

The percentage of CCW, SSW and MCS water for each survey (Fig. 2b) show that the CCW extent decreased during the El Niño events, while SSW increased and MCS decreased. This pattern was particularly clear during the 1992 and 1997–1998 El Niño (this pattern was not apparent for the 1987 El Niño event probably because there was no survey during the strong positive temperature anomaly part of this event; Fig. 2). The extent of CCW showed a seasonal pattern, more evident since 1998 (as the number of surveys increased from 1 or 2 per year to 2–4 after 1998) with increases during the winter and decreases during summer.

The spatial distribution of water masses north–south but also onshore-offshore (Fig. 3) shows an interesting contrast before and after 1999. During warmer periods (1992–1995 and 1997–1998) SSW dominated the coastal domain (to 25 n.mi.; Fig. 3a

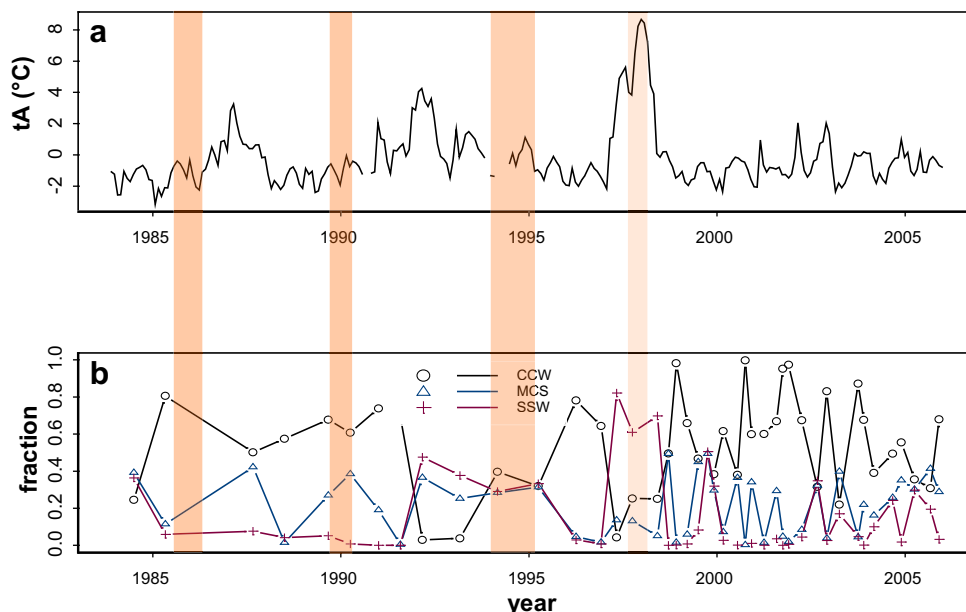


Fig. 2. (a) Temperature anomaly (tA) for surface temperature off the Peruvian coast near Chicama (8°S), Peru (b). Percentage of the survey area covered by CCW, SSW, and MCS from 1983 to 2005. El Niño periods are shown by salmon coloured bands with intensity proportional to opacity.

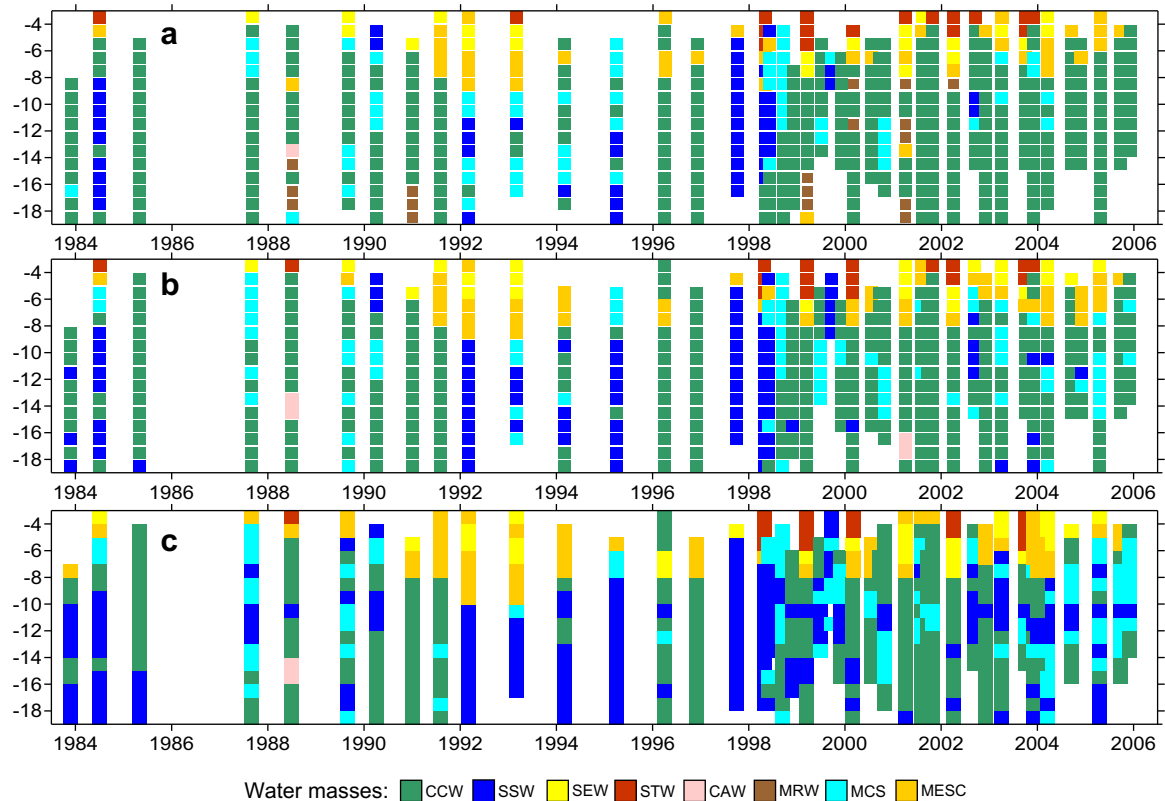


Fig. 3. Dominant water mass by degree of latitude along the Peruvian coast for each survey (a) between 0 and 10 n.mi. from the coast; (b) between 10 and 25 n.mi. from the coast; (c) between 25 and 50 n.mi. from the coast. Year markers refer to January 1. During some years survey results overlap due to intensive temporal coverage.

and b) over a large latitude range, and was even often prevalent close to shore (to 10 n.mi.; Fig. 3a). Since 1999 tropical waters were present in the north in many years. South of 6°S there was dominance by CCW coastward but also offshore to 25 n.mi. and even out to 50 n.mi. for much of the coast. This pattern was also observable for most surveys between 1987 and 1991 (Fig. 3).

3.2. Relating water masses, anchovy and sardine

Anchovy mean distance to the coast (Fig. 4) was significantly correlated with the distance to the coast of the CCW centroid ($r = 0.48$, $p = 0.003$) and the MCS centroid ($r = 0.44$, $p = 0.006$), but not with that of SSW. Sardine mean distance to the coast (Fig. 4) was correlated with the distance to the coast of the SSW centroid ($r = 0.40$, $p = 0.028$) and marginally non-significant with the MCS centroid ($r = 0.38$, $p = 0.058$). This suggests an association of anchovy CCW and MCS water masses and of sardine with SSW. As expected, anchovy was distributed closer to the coast than sardine. The position of the centroid of anchovy distribution was much more variable than that of sardine, which ranged between 40 and 60 km from the coast until the mid 1990s. Thereafter the position of the sardine coast distance centroid distribution showed wider variations. During El Niño periods (except the weak event of 2002), the centroid of anchovy distribution was very close to the coast in 1987, 1992–1993 and 1997–1998 (Fig. 4). The centroid for sardine distribution was also closer to the coast in 1997–1998 but not during the other El Niño periods. As expected, CCW was, on average, closer to the coast during El Niño periods though less so in 1987 (note, however that there was no spring or summer survey in 1987). Similarly, the centroids for SSW and MCS were found closer to the coast during El Niño periods, as they presumably extended their range to include the near coast (Fig. 3). There were no clear

patterns in the time series for coast distance of the other water mass categories (not graphed).

The analysis of the preference of anchovy (Fig. 5a) and sardine (Fig. 5b) for a particular water mass according to their availability (based on abundance ratios) shows contrasted results. Results for anchovy are clear with a strong preference for CCW (mean ratio >1.5) all along the time series with a peak during the 1997–98 El Niño. The relationship with MCS (mean ratio ~1) was neutral and negative with SSW (mean ratio <0.5). Results for sardine show three different periods. Until 1991 there was no clear pattern and sardine was distributed in each water mass in proportion to their availability (all mean ratios ~1). From 1992 to the end of 1996, sardine was proportionally more distributed in MCS (mean ratio >1.5) than in other water masses. Since 1997 sardine were usually found preferentially in SSW, although the ratio was quite variable.

3.3. GAM modelling

A GAM model with a binomial link function represented the probability of anchovy presence in any ESDU as a function of latitude, depth, water mass (because water mass is a categorical variable, it is included as an analysis of variance factor in the model) and time of the survey (Fig. 6). The probability of encountering anchovy increased over time, but was relatively constant between the El Niño of 1992 and 1997, followed by further increase after 1998. Relative to latitude, probability of encountering anchovy was highest between 6°S and 14°S and was significantly lower outside this range. There was a decrease in the probability of encounter with increasing water depth (generally fewer anchovy in deeper water). The water mass effect show that anchovy was much more prevalent in CCW (and MRW and CAW), had intermediate encounter probability in mixed waters (MCS and MESC) and was

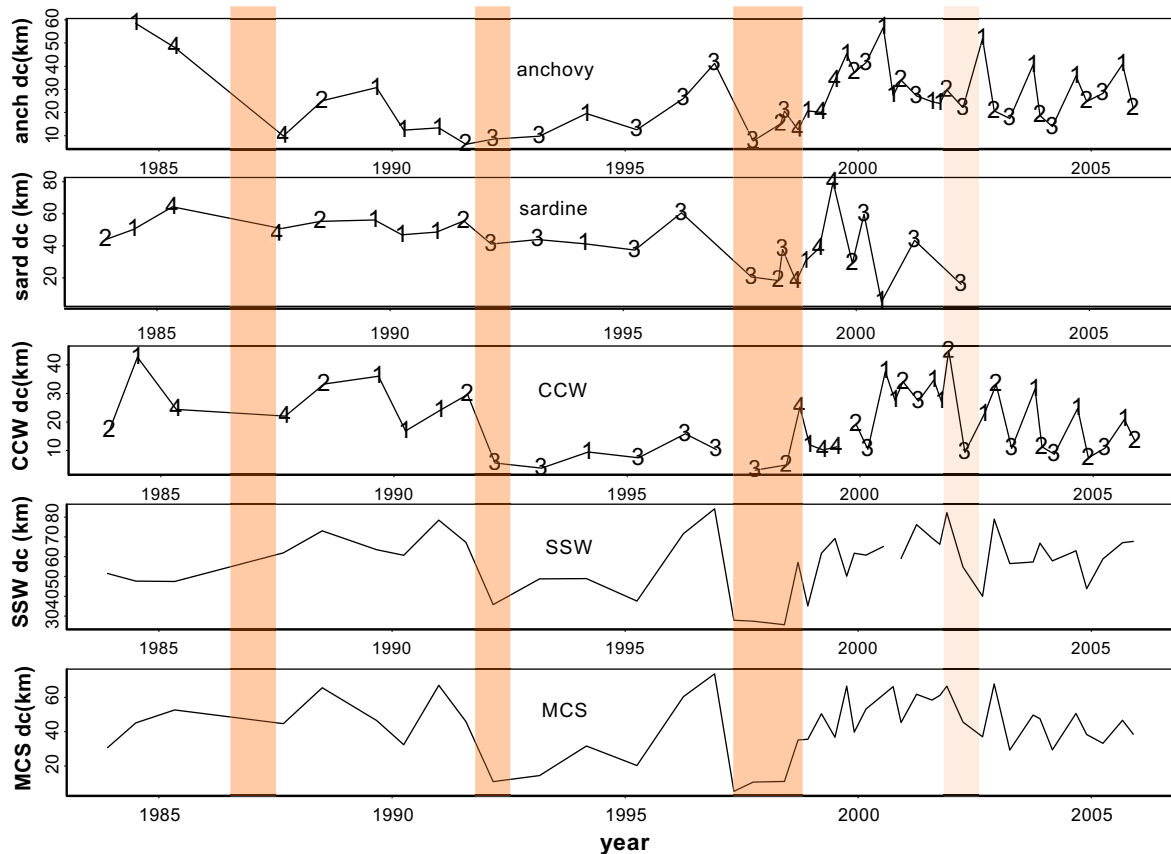


Fig. 4. Distance from the coast (dc; km) of the centroid of distribution of, top to bottom, anchovy s_A , sardine s_A , CCW, SSW and MCS water masses, based on acoustic survey data and concomitant surface temperature and salinity measurements taken from 1983 to 2005 off the coast of Peru. The season is noted by a number 1–4 for winter–spring–summer–autumn. Missing centroids reflect too small a sample size in that category for a survey. El Niño periods are shown by salmon coloured bands with intensity proportional to opacity.

lowest in warmer SSW, SEW and STW. All effects shown were highly significant with p -values near 0.

The sardine presence GAM model showed quite different responses to the covariates from those for anchovy (Fig. 7). The temporal effect was markedly different, with constant high probability of sardine ($s_A > 0$) before 1994 and a rapid decline thereafter. Unlike anchovy, sardine probability of encounter was not highest in shallow water, but increased with increasing depth up to 800 m and decreased thereafter. The water mass associations with sardine were weaker than for anchovy. Sardine showed a slight affinity for subtropical and warm waters (SSW, MESC and SEW, but not STW), a slight negative association with colder waters (MRW, CAW and CCW) and intermediate association with MCS and STW (Fig. 7). All GAM main effects were significant with p -values close to 0, except depth which had a p -value of 0.001. However, most of the water mass differences were not statistically significant (note the overlap in the error bars for the water mass effects). Several of the water mass effects had very wide error bars, reflecting the few data for these water mass types).

4. Discussion

4.1. Water mass dynamics

Inside our “window of observation”, the dominant water masses were CCW (highly productive, medium salinity, low temperature), SSW (oligotrophic, high salinity and temperature), and, generally south of 8°S, MCS (mesotrophic, low temperature and high salinity, or medium temperature and medium salinity). An

important feature of these water masses is their strong dependence on salinity (Table 1), which makes distinguishing them using satellite products alone problematical. Although the study of the seasonal dynamics of water masses is hampered by unequal seasonal sampling, particularly before 1998 (Figs. 2 and 3), there is a clear increase in the extent of CCW during winter and a reduction in summer. However, the La Niña of 1999–2000 seems to have initiated a period of stronger upwelling all along the coast most of the year (Fig. 3). This change affected the weather of the northern coast, and people complained of “cooler” summers and winters (Mariano Gutierrez, IMARPE, pers. com.). The earlier period, before the El Niño of 1997–1998, was characterised by consistently less cold coastal water and more subtropical water (Figs. 2 and 3). Another notable pattern was the higher percentage of SSW and lower percentages of CCW and MCS during 1992–1995 (note, however, that those surveys were performed in summer, which on average have lower percentages of CCW and MCS waters).

4.2. Anchovy and water masses

The methods we used demonstrated the strong relationship linking anchovy distribution to cold and highly productive water masses in general and CCW in particular. Thus, anchovy distance to the coast was correlated with the distance from the coast of the centroid of CCW and MCS, but not with that of SSW (Fig. 4). Anchovy distance from the coast was consistently lower during 1992–1995, when SSW dominated the Peruvian coast (Figs. 2 and 3); compressing CCW and anchovy distributions closer to the coast (see Gutiérrez et al., 2007 for detailed spatial patterns of anchovy

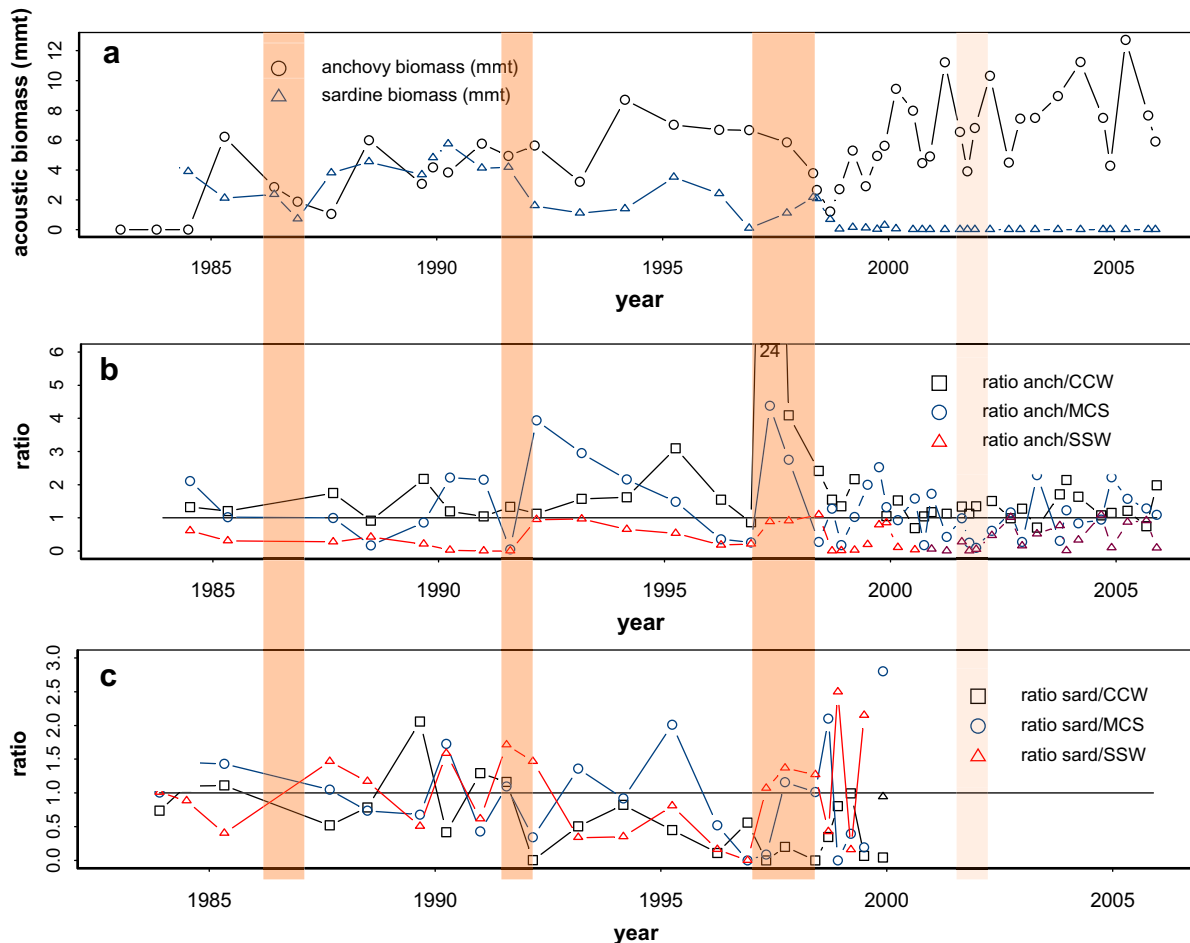


Fig. 5. Acoustic survey estimates for (a) anchovy and sardine biomass. Ratio of the fraction of total s_4 of anchovy (b) and sardine (c) in CCW, MCS and SSW respectively to the fraction of total survey ESDU in that water mass. A ratio of 1 (horizontal line shown) represents no preference for that water mass. El Niño periods are shown by salmon coloured bands with intensity proportional to opacity.

and sardine). This pattern was even more marked during the El Niño of 1997–1998. CCW almost disappeared and SSW dominated all along the coast (Fig. 3). Anchovy was then concentrated in few refuge areas (Bertrand et al., 2004) where productive CCW were still present. This affinity of anchovy for colder CCW and MCS is also illustrated by the very high abundance ratios for anchovy in CCW and to a lesser extent in MCS during the 1997–1998 El Niño (Fig. 5a). Anchovy distribution relative to the proportion of water mass available showed a clear and consistent association with CCW, whatever its availability. GAM results (Fig. 6) showed that the probability of anchovy presence in an ESDU was highest in cold and highly productive water masses (CCW, CAW and MRW) and lowest in oceanic and tropical water masses (SSW, SEW, STW). These results are in accordance with previous work (Ñiquen et al., 2000; Bertrand et al., 2004), and, as they are based on longer time series and more exhaustive analysis, they demonstrate with more confidence the affinity of anchovy for CCW. The anchovy range (probability of having anchovy in an ESDU) appears to depend both on water mass type and overall abundance. The relationship of range with abundance can be seen by comparing the year effect for the GAM (Fig. 6) with anchovy acoustic abundance estimates (Fig. 5a; based on the same surveys). The latter show much more variability, though the long-term pattern is similar. As average anchovy abundance increased over time their range also expanded. Because CCW increased particularly in the winter, the range of anchovy, directly associated with CCW, also increased during that season.

4.3. Sardine and water masses

Sardine association with water mass was weaker than anchovy. Sardine distance to the coast was significantly correlated with the distance from the coast of the centroid of SSW but not with that of CCW and MCS (Fig. 4). GAM results (Fig. 7) also illustrate that sardine had a slight (though not statistically significant) preference for SSW compared to CCW. These results seem to support (weakly) a relationship between sardine and SSW (e.g. Castillo et al., 1996; Bertrand et al., 2004). There is no apparent seasonal change in sardine range, possibly due to their lack of or weak association with water masses or possibly due to the insufficiency of seasonal coverage during the period of sardine dominance. Analysis of sardine distribution relative to the proportion of water mass available, suggested three different periods: before 1992; 1992–1997; and after the 1997–1998 El Niño (Fig. 5b). Interestingly, these periods are similar to the ones defined by Gutiérrez et al. (2007) based on fish spatial patterns of distribution (independent of water mass). Before 1992 (a period of mixed sardine and anchovy dominance, Fig. 5a; Gutiérrez et al., 2007), sardine did not have any consistent preference for any of the three dominant water masses (CCS, SSW and MCS) and was distributed between the water masses in proportion to their availability in the study area (i.e. abundance to water mass ratio about 1.0). During this period sardine was mainly distributed between 40 and 60 km from the coast (offshore part of the CCW), centred around the shelf break (GAM results by period not shown) and straddling CCW, SSW and MCS water masses.

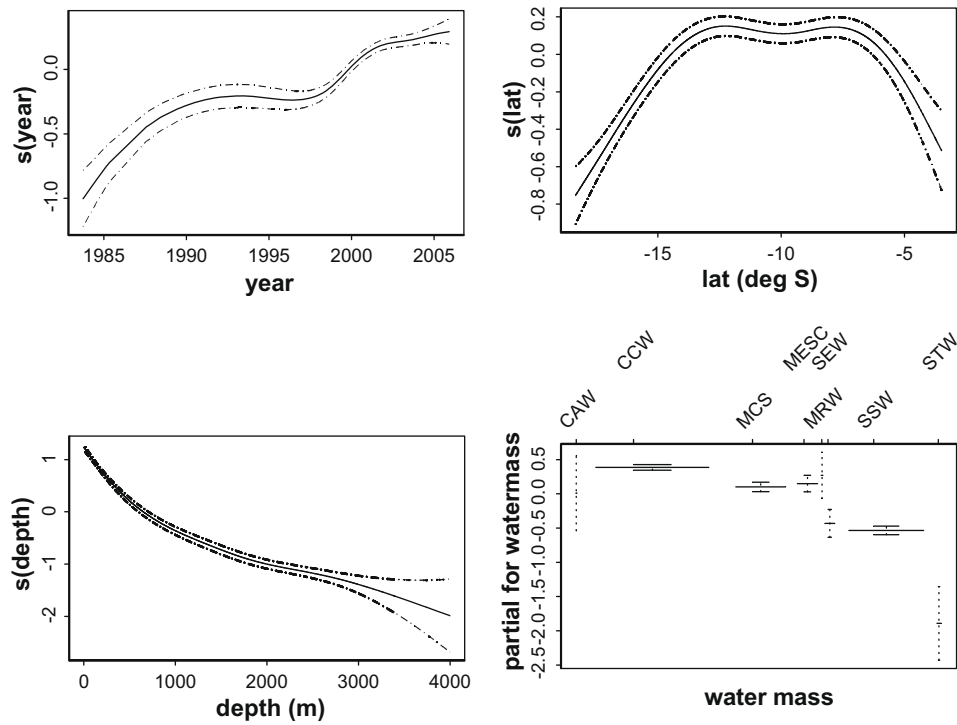


Fig. 6. GAM analysis of anchovy presence probability as a function of water mass, latitude, water column depth and year.

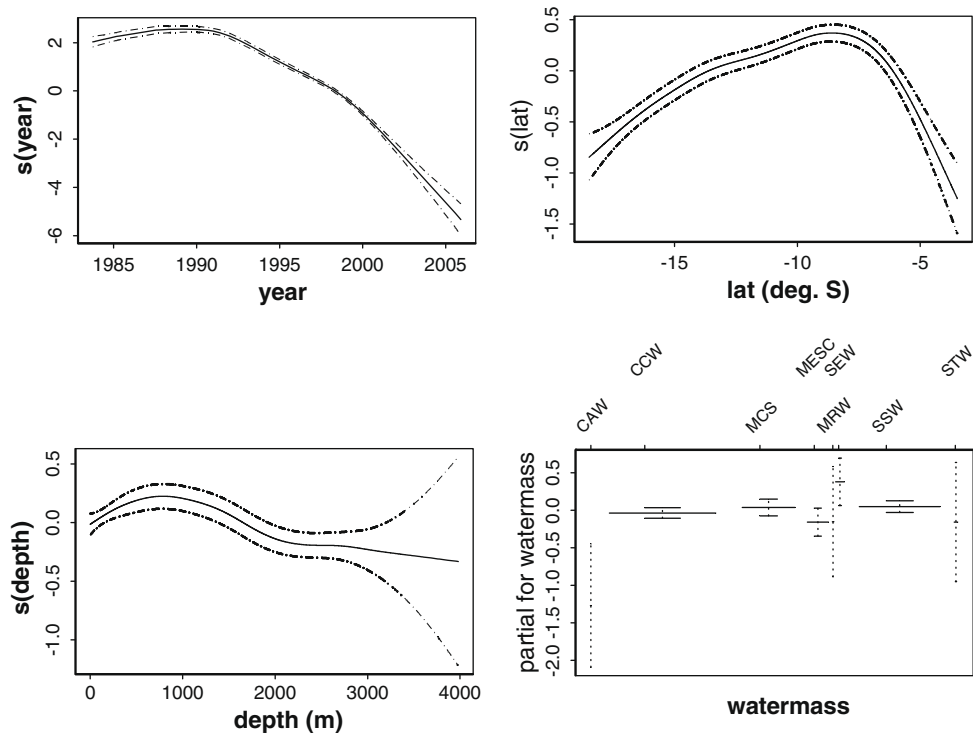


Fig. 7. GAM analysis of sardine presence probability as a function of water mass, latitude, water column depth and year.

The abundant sardine population during this period (Fig. 5a) probably benefited from the enhanced production and retention provided by the shelf break area. From 1992 to 1997 (a period of anchovy dominance; Gutiérrez et al., 2007) the reduced population of sardine (Fig. 5a) was distributed closer to the coast, perhaps

associated with the intrusion of SSW toward the coast (Fig. 3) and was found mainly on the shelf (GAM results by period not shown) in the frontal MCS waters between CCW and SSW. Finally, after the 1997–1998 El Niño (period of anchovy dominance; Gutiérrez et al., 2007), sardine was initially distributed preferentially

in SSW and then disappeared from the Peruvian coast. We do not know from available evidence whether the absence of sardine after 2000 was due to population depletion or to the migration of sardine out of the survey area. However, the lack of sardine capture by scientific or commercial vessels strongly suggest that sardine population off Peru was depleted (see Bertrand et al. (2004) and Gutiérrez et al. (2007) for more details). A more offshore distribution of sardine-favourable habitat, as found after 1997, should indeed disadvantage sardine since biological enrichment or larval retention and more generally recruitment success would likely be reduced by the offshore Ekman transport of their eggs and larvae which dilute them and diminish their chance of benefiting from aggregations of their most efficiently utilized food sources (see Bakun's triad; Bakun, 1996).

Sardine appears to have a different feeding strategy than anchovy, apparently moving more than anchovy to find large aggregations of small zooplankton and phytoplankton, which they can efficiently filter (van der Lingen et al., 2006). Thus, their presence in a particular water mass may depend more on the availability of small-sized food than on water mass per se, among SSW, MCS and CCW. While CCW is characterised by dominance by large plankton favouring the particulate feeding behaviour of anchovy, and SSW by smaller plankton more appropriate to sardine filter feeding (Mackas et al., 2001; Peterson et al., 2002; van der Lingen et al., 2006), sardine, a more migratory species, may find large aggregations of appropriate sized food in any of the water masses. The fact that sardine is a highly migratory species is supported by the existence of a single sardine species along both East and West Pacific Ocean coasts (Lluch-Belda et al., 1992). It is important to note that, unlike the case with anchovy, our study area may not include the entire range of sardine distribution. It is therefore possible that a proportion of sardine was distributed farther offshore than the survey (i.e. in SSW) and was not considered in our analysis. This problem limits the significance of our results for sardine.

4.4. Synthesis

Peruvian anchovy clearly preferentially inhabits the CCW and other associated cold and productive water masses (CAW and MRW and, to a lesser extent, MCS). Its range of distribution is intimately linked to the area covered by CCW independent of anchovy's abundance as suggested by the habitat-based model proposed by Bertrand et al. (2004). In contrast to previous studies, which suggested anchovy range should be linked primarily to the size of anchovy stock (e.g. Lluch-Belda et al., 1989) it appears that anchovy range of distribution is primarily related to the size of favourable habitat (determined by large scale oceanic forcing, e.g. Kelvin waves, see Bertrand et al. (2008b) and secondarily to the size of the fish stock. These conclusions are supported by our analysis and by examples such as when millions of tons of anchovy were distributed in a very small refuge area during the 1997–1998 El Niño (Bertrand et al., 2004) while a similar anchovy biomass occupied a much larger surface area (>3-fold) in April–May 1986 when CCW was more extensive.

For sardine, even though the results are limited by the fact that we may have only observed a part of the stock (the surveys were designed to focus on the distribution of anchovy, not sardine), the relationship with SSW was weak and varied over time, illustrating a more pervasive distribution.

Sardine and anchovy appear to be ecological neighbours but not ecological analogues (Bertrand et al., 2004; Gutiérrez et al., 2007). Their differences depend not only on differences in their trophic level (e.g. Konchina, 1991; Schwartzlose et al., 1999; van der Lingen et al., 2006), but also on the strength of their association with water mass and their migrating capacities (e.g. Rodríguez-Sánchez et al., 2002). Sardine showed a slight preference

for SSW (e.g. Castillo et al., 1996; Bertrand et al., 2004) while anchovy range significantly overlapped with CCW. Both species are able to feed directly on phytoplankton, although sardines are more efficient filter feeders (van der Lingen et al., 2006). Anchovy, which are bite feeders (Konchina, 1991; van der Lingen et al., 2006), are not able to sustain growth on a diet consisting entirely of phytoplankton (Espinoza et al., 2000; van der Lingen et al., 2006) and are mainly zooplanktivorous (98.0% of dietary carbon; Espinoza and Bertrand, 2008). We hypothesize that anchovy associates preferably with CCW because these areas are dominated by the larger zooplankton efficiently ingested by these predominantly predators (see Bertrand et al., 2008a for small scale association between anchovy and zooplankton patches); sardine may find better feeding conditions in areas containing abundant aggregations of small filterable zooplankton in their patchy environment, which may predominate in SSW and mixed water masses (e.g. MCS and MESC).

Sardine is a fish that appears well adapted to the Humboldt Current Ecosystem. It has the ability to perform long migrations, to utilize very small particles (van der Lingen, 2002; van der Lingen et al., 2006; Garrido et al., 2007), to feed and spawn in rather low productivity areas (Garrido et al., 2007), to grow to a size less susceptible to predation than anchovy, and to occupy more offshore environments less susceptible to predation on eggs, larvae and early juveniles (Bakun and Broad, 2003). Therefore, it is a challenge to explain why sardine is currently depleted in the HCS? The answer may be in the distribution of sardine habitat in relation to the shelf and the shelf break. When its preferred habitat moves further offshore (i.e. increased upwelling), as happens during cool periods, retention of eggs and larvae of sardine may be reduced, weakening larval feeding success and survival. Also, the depletion of the sardine during high upwelling periods may be due to reduction in its usable habitat through an extremely shallow oxycline associated with an expanded oxygen minimum zone (OMZ), which is known to affect the vertical and horizontal distribution of many marine organisms (Morales et al., 1999). Finally it is important to note that sardine depletion was probably aggravated by overfishing during the 1990s, in particular during El Niño 1997–98 (Csirke et al., 1996; Bertrand et al., 2004).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocan.2008.10.021.

References

- Alheit, J., Niquen, M., 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* 60, 201–222.
- Bakun, A., 1996. Patterns in the ocean: ocean process and marine population dynamics. Centro de Investigaciones biológicas del Nordeste, La Paz, México and University of California Sea Grant, San Diego, USA, 325 p.
- Bakun, A., Broad, K., 2003. Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Niño effects in the Pacific. *Fisheries Oceanography* 12, 458–473.

- Bertrand, A., Segura, M., Gutiérrez, M., Vásquez, L., 2004. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and Fisheries* 5, 296–316.
- Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., Díaz, E., Espinoza, P., Ledesma, L., Quesquén, R., Peraltila, S., Chavez, F., 2008a. Aggregation behaviour and environmental forcing as determinants of fish 3D spatiotemporal distribution across scales: the case for the anchoveta. *Progress in Oceanography*.
- Bertrand, S., Dewitte, B., Pasapera, J., Bertrand, A., 2008b. Spatial re-organisations in the Peru Humboldt Current system under Kelvin waves forcing: contrasting ecological scenarios from physics to fishers. *Progress in Oceanography*.
- Blanco, J.L., Thomas, A., Carr, M.-E., Strub, T., 2001. Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile. *Journal of Geophysical Research* 106 (C6), 11451–11467.
- Bouchón, M., Cahuín, S., Díaz, E., Niquen, M., 2000. Captura y esfuerzo pesquero de la pesquería de anchoveta peruana (*Engraulis ringens*). *Boletín del Instituto del Mar del Perú* 19, 109–115 (in Spanish, with English abstract).
- Carr, M.-E., 2002. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. *Deep-Sea Research II* 49, 59–80.
- Castillo, J., Barbieri, M.A., Gonzalez, A., 1996. Relationships between sea surface temperature, salinity, and pelagic fish distribution off northern Chile. *ICES Journal of Marine Science* 53, 139–146.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niquen, M., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299, 217–221.
- Csirke, J., Guevara-Carrasco, R., Cárdenas, G., Niquen, M., Chipollini, A., 1996. Situación de los recursos anchoveta (*Engraulis ringens*) y sardina (*Sardinops sagax*) a principios de 1994 y perspectivas para la pesca en el Perú, con particular referencia a las regiones norte y centro de la costa peruana. *Boletín del Instituto del Mar del Perú* 15, 1–23 (in Spanish, with English abstract).
- Espinoza, P., Bertrand, A., 2008. Revising anchovy's (*Engraulis ringens*) trophic niche and ecological role reveals its plasticity and lead to a new vision of the Humboldt Current system. *Progress in Oceanography*.
- Espinoza, P., Blascovic, V., Torriani, F., Navarro, I., 2000. Dieta de la anchoveta *Engraulis ringens* según intervalos de talla. *Crucero BIC José Olaya Balandra y BIC Humboldt*, 9906. Informe del Instituto del Mar del Perú No. 149.
- Foot, K.G., Knudsen, H.P., Vestnes, D.N., MacLennan, D.N., Simmonds, E.J., 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. *ICES Cooperative Research Report No. 144*, pp. 1–69.
- Fréon, P., Mullon, C., Voisin, B., 2003. Investigating remote synchronous patterns in fisheries. *Fisheries Oceanography* 12, 443–457.
- Garrido, S., Marçal, A., Zwolinski, J., van der Lingen, C.D., 2007. Laboratory investigations on the effect of prey size and concentration on the feeding behaviour of *Sardina pilchardus*. *Marine Ecology Progress Series* 330, 189–199.
- Gutiérrez, M., Swartzman, G., Bertrand, A., Bertrand, S., 2007. Anchovy and sardine spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. *Fisheries Oceanography* 16, 155–168.
- Hastie, T., Tibshirani, R., 1990. *Generalized Additive Models*. Chapman and Hall, London, UK.
- Konchina, Y.V., 1991. Trophic status of the Peruvian anchovy and sardine. *Journal of Ichthyology* 31, 59–72.
- Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., Smith, P.E., 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. *South African Journal of Marine Science* 8, 195–205.
- Lluch-Belda, D., Schwartzlose, R.A., Serra, R., Parrish, R., Kawasaki, T., Hedgecock, D., Crawford, R.J.M., 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fisheries Oceanography* 1, 339–347.
- Mackas, D.L., Thomson, R.E., Galbraith, M.D., 2001. Changes in the zooplankton community of the British Columbia continental margin, 1985–1999, and their covariation with oceanographic conditions. *Canadian Journal of Fisheries and Aquatic Science* 58, 685–702.
- McFarlane, G.A., Smith, P.E., Baumgartner, T.R., Hunter, J.R., 2002. Climate variability and Pacific sardine population and fisheries. *American Fisheries Society Symposium* 32, 195–214.
- Morales, C.E., Hormazabal, S.E., Blanco, J.L., 1999. Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off northern Chile (18–24°S). Implications for the pelagic system and biogeochemical cycling. *Journal of Marine Research* 57, 909–932.
- Morón, O., 2000. Características del ambiente marino frente a la costa peruana. *Boletín del Instituto del Mar del Perú* 19, 179–204 (in Spanish, with English abstract).
- Niquen, M., Bouchón, M., Cahuín, S., Díaz, E., 2000. Pesquería de anchoveta del mar Peruano 1950 – 1999. *Boletín del Instituto del Mar del Perú* 19, 117–123 (in Spanish, with English abstract).
- Peres-Neto, P.R., 1999. How many statistical tests are too many? The problem of conducting multiple ecological inferences revisited. *Marine Ecology Progress Series* 176, 303–306.
- Peterson, W.T., Keister, J.E., Feinberg, L.R., 2002. The effects of the 1997–99 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast. *Progress in Oceanography* 54, 381–398.
- Pyper, B.J., Peterman, R.M., 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 2127–2140.
- Rodríguez-Sánchez, R., Lluch-Belda, D., Villalobos, H., Ortega-García, S., 2002. Dynamic geography of small pelagic fish populations in the California Current System on the regime time scale (1931–1997). *Canadian Journal of Fisheries and Aquatic Sciences* 59, 1980–1988.
- Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura, Y., et al., 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science* 21, 289–347.
- Strub, T., Mesias, J., Montecino, V., Rutllant, J., Salinas, S., 1998. Coastal ocean circulation off Western South America. In: Robinson, A.R., Brink, K.H. (Eds.), *The Sea*, vol. II. John Wiley, New York, pp. 273–314.
- Thomas, A.C., Blanco, J.L., Carr, M.-E., Strub, P.T., Osses, J., 2001. Satellite-measured. Chlorophyll and temperature variability off northern Chile during the 1996–1998 La Niña and El Niño. *Journal of Geophysical Research* 106 (18), 899–915.
- Urquiza, W., Wosnitza-Mendo, C., Valdivia, E., Moreno, C., 1987. Catalogo de datos oceanográficos (T, S y O₂) por estaciones del año en diferentes profundidades frente a la costa peruana. Periodo: 1970–1985. Informe del Instituto del Mar del Perú (in Spanish, with English abstract).
- van der Lingen, C.D., 2002. Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *South African Journal of Marine Science* 24, 301–316.
- van der Lingen, C.D., Hutchings, L., Field, J.G., 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* 28, 465–477.
- van der Lingen, C.D., Bertrand, A., Bode, A., Brodeur, R., Cubillos, L., Espinoza, P., Friedland, K., Garrido, S., Irigoien, X., Möllman, C., Rodríguez-Sánchez, R., Tanaka, H., Temming, A., in press. Trophic dynamics of small pelagic fish. In: Checkley Jr., D.M., Roy, C., Alheit, J. (Eds.), *Climate Change and Small Pelagic Fish*.
- Zamon, J., Welch, D., 2005. Rapid shift in zooplankton community composition on the Northeast Pacific Shelf during the 1998–1999 El Niño–La Niña event. *Canadian Journal of Fisheries and Aquatic Sciences* 62, 133–144.
- Zuta, S., Guillen, O., 1970. Oceanografía de las Aguas Costeras del Perú. *Boletín del Instituto del Mar del Perú* 2, 157–324 (in Spanish, with English abstract).
- Zuta, S., Rivera, T., Bustamante, A., 1978. Hydrologic aspects of the main upwelling areas off Peru. In: Boje, R., Tomczak, M. (Eds.), *Upwelling Ecosystems*.
- Zuta, S., 1988. Variations of the mass field and currents off the Peru coast. In: *IOC. Time Series of Ocean measurements*, vol. 4. IOC Tech Ser. 33, UNESCO.