

# Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003

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## ABSTRACT

Three indexes of spatial aggregation are developed and used to examine the aggregation pattern of sardine (*Sardinops sagax*) and anchovy (*Engraulis ringens*) in the Peruvian Humboldt Current System, determined from 36 acoustic surveys conducted from 1983 through 2003 by the Peruvian Marine Institute (IMARPE). Each index assesses a different aspect of aggregation: the concentration, the percent occupancy of space and the clustering of high-fish abundance. Both time-series correlation and tree-based clustering-regression method, classification and regression trees (CART), were used to relate each of the indexes to environmental variables (season, temperature anomaly and year). Additionally, a measure of onshore–offshore distribution, the average distance from the coast, and abundance variables (the average acoustic backscatter per occupied sampling unit, and the acoustically estimated total abundance of sardine and anchovy from IMARPE) were related to environmental factors by using CART. We show that the 1983–2003 time series can be divided into three different periods: with shifts in 1992 and in 1997–98. Sardine and anchovy showed large differences in both abundance and aggregation among these periods. Although upwelling ecosystems support dramatic and sudden changes in environmental conditions, fish responses are sometimes

smoother than usually suggested and there are transition periods with concomitant high biomasses of anchovy and sardine, but with different spatial aggregation patterns. Observed relationships between environmental proxies and aggregation patterns support the habitat-based hypothesis that environmentally mediated alterations in range lead to population changes.

**Key words:** anchovy, El Niño Southern Oscillation, pelagic fish spatial aggregation, Peru-Humboldt Current System, sardine, time series

## 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 anchovy *Engraulis ringens*, (Bouchón *et al.*, 2000) and experiences year-round upwelling. In this region, the abundance of anchovy appears to be linked to El Niño Southern Oscillation (ENSO) events with a frequency of 2–7 yr 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 somewhat out of phase with that of the other major pelagic fish species in the HCS, the sardine (*Sardinops sagax*) (Lluch-Belda *et al.*, 1989, 1992; Csirke *et al.*, 1996; Schwartzlose *et al.*, 1999; Bakun and Broad, 2003; Fréon *et al.*, 2003), which at times has also sustained a large-tonnage Peruvian fishery (Csirke *et al.*, 1996). Chavez *et al.* (2003) proposed the term 'El Viejo' to define the warm, 'sardine regimes' and 'La Vieja' to define the cold 'anchovy regimes'. The exact timing of regime shifts (see de Young *et al.*, 2004 for definition) is debatable. In the case of the most recent regime shift in the Pacific, several periods were proposed: the mid-1980s (e.g. Csirke *et al.*, 1996; Yáñez *et al.*, 2001; Alheit and Niquen, 2004), the mid-1990s (e.g. Chavez *et al.*, 2003) and possibly 1998–99 (Fiedler, 2002).

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Although the large fluctuations in abundance of anchovy and sardine off Peru have been well documented (Csirke *et al.*, 1996; Gutiérrez, 2000; Bakun and Broad, 2003; Chavez *et al.*, 2003; Alheit and Niquen, 2004; Bertrand *et al.*, 2004a), little is known about the processes underlying the dynamics of the functional response of these species to ENSO events and decadal regime shifts (Bertrand *et al.*, 2004a).

In this paper, our objective is neither to propose a new definition of regime shifts nor to decide on their exact timing; rather we record the long-term changes in the dominant fish species in the HCS. Using a 20-yr acoustic survey time series (1983–2003), we follow the evolution of fish biomass, distance to the coast, and indices of fish density and aggregation. Looking at the fish descriptors (see McFarlane *et al.*, 2000), we empirically analyse the dynamics and the changes in fish population patterns.

For that purpose, we first specify what we mean by aggregation and then describe the indices we developed to quantify this aggregation. We identified three aspects of aggregation: (1) the index of surface occupation (ISO) over a defined area (i.e. the percentage of the surveyed space occupied by the species of interest), (2) the degree of concentration of abundance relative to habitat area (i.e. what proportion of abundance occupies what proportion of occupied space), and (3) the degree of clustering of high-density biomass samples close to each other.

Each of these features represents a different aspect of what we term aggregation. The first two indices look only at the relative abundance distribution, irrespective of location. The third index looks at the clustering of high-density sample units around each other (high-density patchiness).

Why is aggregation important? Firstly, changes in aggregation patterns of fish can help in predicting major changes in fish abundance because the aggregation response to changing environmental conditions may affect feeding, predation, and spawning and thus future population abundance (Perry *et al.*, 2002). Secondly, changes in aggregation may change the susceptibility of fish to fishing pressure, as observed with the continued high aggregation of the Newfoundland cod stock under low abundance conditions (Rose and Kulka, 1999) and the sustained high catch of Peruvian anchovy during El Niño events as the population range was restricted close to shore (e.g. Csirke, 1989). Thirdly, changing aggregation in response to changing feeding conditions can also change the susceptibility of a species to natural predation (Perry *et al.*, 2002).

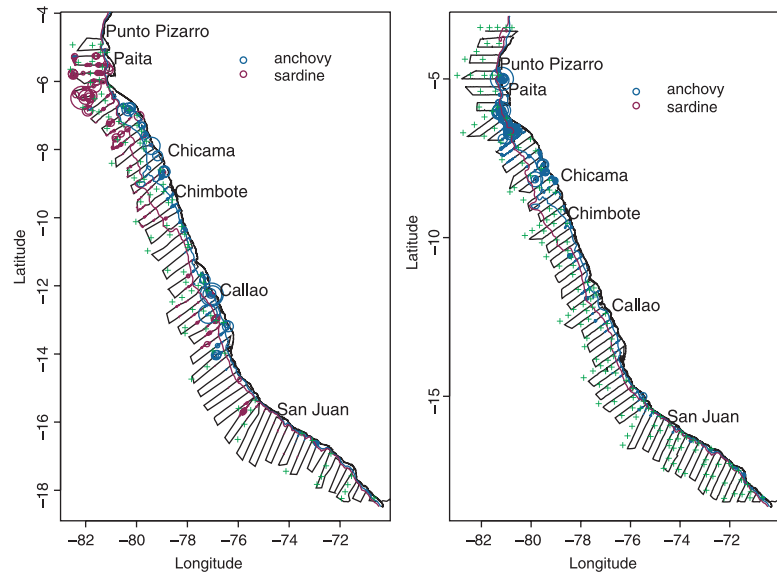
## DATA AND METHODS

### *Acoustic survey data*

Acoustic data were collected from 1983 to 2003 by the Instituto del Mar del Peru (IMARPE) on a variety of vessels, most commonly the R/V Humboldt (76-m long), the R/V Olaya (41-m long) and the R/V SNP-1 (36-m long). At least two acoustic surveys were run each year. 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 entire observable range of anchovy distribution was covered (transects shown in Fig. 1 are typical of almost all surveys). Extensive midwater trawl sampling accompanied the acoustic surveys for species identification (Fig. 1). The seasonal and temporal distributions of scientific acoustic surveys are: spring (1983, 1996–2003), summer (1990–96, 1999–2003), autumn (1985, 2 surveys in 1998) and winter (1984, 1987–89, 1991, 1998–2003 with two winter surveys in 1999, 2000 and 2001). The acoustic surveys deployed Simrad (Kongsberg Simrad AS, Kongsberg, Norway) scientific echosounders EK, EKS, EK400, EY500, EK500 and EK60 (2001–2003 in one vessel). The surveys from 1983 to 1991 and after 1996 used 120 kHz for abundance determination, while 38 kHz was used between 1992 and 1996. Calibration of the echosounders occurred before surveys. Until 1992, calibration was done by using hydrophones; after 1992, a standard procedure of calibration with a sphere (Foote *et al.*, 1987) was used. A review of calibration methods (Ken Foote; Woods Hole Oceanographic Institute, Woods Hole, MA, USA, unpubl. data) suggested that there is no bias in  $s_A$  (acoustic biomass) values because of differences in calibration methods. However, considering the large number of systems used over the years it is likely that there was bias in  $s_A$ , although we do not know the magnitude or direction of the bias, nor is there any known method for retrospectively correcting for it. We presume bias to be small relative to the overall patterns discernible in our analysis. Acoustic back-scattered energy by surface unit ( $s_A$ ) was recorded in each geo-referenced elementary sampling distance unit (ESDU) of 1 n.mi. (1994–2003) or 2 n.mi. (1983–1993). Acoustic echo identification was performed by using fishing trawl results and echotrace characteristics. Biomass estimation based on the acoustic backscatter for each species was carried out by IMARPE for each survey. A noise threshold of –65 dB was used.

**Figure 1.** Peruvian coastline showing the acoustic transects and the distribution of anchovy and sardine with circles proportional to acoustic abundance for a survey in summer 1990 (left panel) and 2003 (right panel). Anchovy and sardine are each scaled to their own maximum abundance. The 100- and 200-m isobaths are shown with a green and black line, respectively. Major ports are identified along the coast. Locations of net trawls are shown with a green +.



#### *Temperature anomaly as a proxy of environmental conditions*

Temperature data have been collected at Chicama by a moored temperature recorder since 1927 and serves as a surrogate for temperature anomaly ( $tA$ ) calculations for the entire Peruvian HCS (Dirección de Hidrografía y Navegación, Peru). The  $tA$  was calculated on a monthly basis by differencing the current temperature and the average for that month over the 1966–2003 time period. The choice of Chicama as a time series rather than an index of temperature, such as used by Ayon *et al.* (2004), is based on (1) the desire to have a univariate data series for the temperature covariate; (2) the high correlation of Chicama data with temperature records from 1976 to 2003 at Callao (south-central Peru;  $r = 0.930$ ) and Ilo (southern Peru;  $r = 0.791$ ); and (3) the fact that Chicama is the most complete time series available.

#### *Correction for unequal sampling effort*

The survey design (Fig. 1) sampling protocol was neither identical for all surveys nor did it have equal sampling over the entire area. For instance, the area close to the coast was more intensively sampled. This was, in part, because there was often more than one ship doing the survey and the nearshore ship moved between transects (the cross-transect lines) more frequently than the offshore ship. In any case, all cross-transect lines, which were included in the analysis, resulted in more effort at the distance from the coast where they occurred (which was often the same from transect to transect). To correct for this, we first

limited the analysis to survey points within 100 km of the coast. This also corrected in part for unequal coverage from survey to survey. Then, we divided each survey into 5-km bands based on the distance from the coast (20 bands in all). We weighted each data value by the ratio of 0.05 (the fraction of data expected in each band if each band was equally sampled) to the actual fraction in that band. Thus, bands having a larger sample fraction had their points down-weighted in the further analysis, and vice-versa.

#### *Concentration index*

Following the proposal of Petitgas (1998) and Bertrand *et al.* (2004b), we computed an index of concentration ( $S_s$ ) based on the cumulative distribution of  $s_A$  (used as a surrogate for biomass) by ESDU. A measure of concentration is obtained by plotting the fraction of total cumulative acoustic  $s_A$  in ESDU's in descending order (i.e. the first point is the fraction of total  $s_A$  in the largest biomass ESDU, the second, the fraction in the two largest  $s_A$  ESDUs, etc.) against the  $s_A$  rank of the ESDU (i.e. largest to smallest biomass). If the biomass in all the ESDU is equal (i.e. no concentration), then the curve will follow the 1 : 1 line. Otherwise, the curve lies below that line. A measure of concentration is thus the area between the 1 : 1 line and the cumulative biomass curve. The larger that area, the more the concentration departs from uniformity (see Bertrand *et al.*, 2004b for more details). In almost all surveys, a large amount of the total biomass was included in a relatively small fraction of the ESDU, in other words most ESDU contributed no

biomass or only a small fraction of the total. We therefore limited the index to those ESDU contributing the highest 90% of the total biomass and eliminated all null ESDUs from this index. The resulting index is a number between 0 and 0.45 (half of 0.9, the 90% biomass quantile) and is larger the greater the concentration.

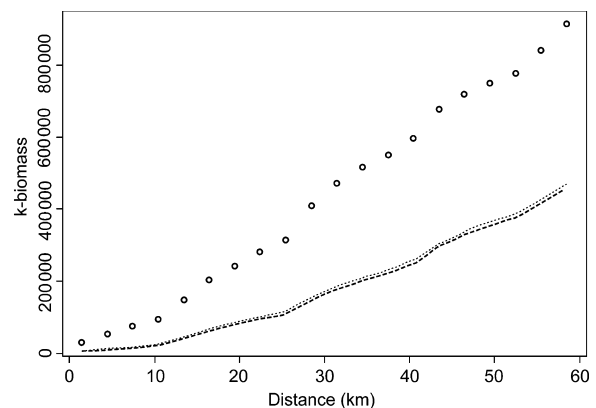
#### Clustering index

RIPLEY'S-K is a statistic developed for spatial point processes (Venables and Ripley, 1994), which is used to test whether a distribution of points is random, clustered (patchy) or inhibited (more regular than random). Because acoustic surveys are not random point processes (i.e. they are systematic surveys) and also because each sampling point (ESDU) has a biomass value or 'mark' (i.e. it is not the point location but the biomass value at each point whose randomness is under consideration), we modified RIPLEY'S-K to examine the randomness of the acoustic biomass distribution. We introduce our modified  $K$  by first describing the original RIPLEY'S-K statistic. The  $K$  distribution is the distribution of the number of points that are at different distances from any point in the sample. It is estimated in 2-D space by putting circles of increasing radii around each point (up to some maximum distance, say 100 km) and computing the number of points within each radius. The  $K$  value is the mean, for each bin size (radius range) of the number of points within the circle of that radius calculated for all the points in the sample. Corrections are often made for edges of the survey area (Venables and Ripley, 1994). To test this empirical  $K$  distribution for randomness, a Monte-Carlo simulation process is used where the total number of sample points are randomly distributed, say  $N = 100$  times, and for each randomization  $K$  is computed. These simulations represent what the distribution of  $K$  would be for cases having a random distribution of points. The 2.5th and 97.5th quantile curves for the distribution of  $K$  as a function of distance from the 100 random simulations are then drawn. Empirical values above the 97.5th quantile are considered to be clustered (i.e. more points are at that distance than expected under a random distribution of points), and those below the 2.5th quantile are considered to be regular or inhibited at that distance (i.e. fewer points within that distance than expected for a random distribution of points).

Our surveys were not random but systematic and we are interested in the distribution of  $s_A$  not of the sample points. Thus, we modified  $K$  to compute the sum of the biomass of all points within a given radius

from all sampled points (Swartzman *et al.*, 2002). Additionally, as we are primarily interested in the clustering of high acoustic density samples, we compute the  $K$  only for points of high acoustic density (i.e. the ESDU having  $s_A$  in the top 25% of all non-zero ESDU for all surveys). Thus, we only examined the clustering around high biomass values. A test for randomness or degree of clustering is performed by permuting the biomass marks (values) among the existing sample points (the non-zero biomass points) say  $N = 100$  times and computing the revised  $K$  for each permutation. As the permutations are random, we have a test for randomness equivalent to the spatial point process  $K$  test. Having more points farther above or more consistently above (i.e. over the whole distance range), the maximum  $K$  curve from the random permutations suggests a higher degree of clustering (Fig. 2) of  $s_A$  around high  $s_A$  ESDU than would be expected from a random distribution of acoustic biomass among ESDU. An index of clustering was developed by taking the area between the empirical ' $K$ ' and the 97.5th quantile ' $K$ ' from the permuted simulations. The higher the value of this index, the more overall clustering there is in a given survey. This approach is equivalent to taking the sum of the difference between the empirical ' $K$ ' curve and 97.5th quantile for the Monte-Carlo simulated  $K$  curves. This area is then divided by the maximum empirical  $K$  value to normalize the index (otherwise the index would depend directly on the total biomass). We corrected for edge effect by increasing the  $s_A$  sums for

**Figure 2.** Empirical clustering index (open circles) for anchovy from a survey in summer 2002. The clustering index is compared with the 2.5th (lower dashed line) and 97.5th (upper, dotted line) percentile curves based on 40 randomizations of the distribution of biomass among the survey locations. The degree of clustering is the area between the 97.5th percentile and empirical clustering curves.



points close to the edge by the ratio of total circle area to the part of the circle area inside the survey area (Besag, 1977). The choice of only the top 25th percentile biomass ESDU (for non-zero ESDU) was made based on empirical, fishery and biological grounds. Focusing on the higher density ESDU limits the clustering to fishable aggregations and thus provides information on the closeness of fishable aggregations, which has important implications for the viability and strategy of the fishery (Bertrand *et al.*, 2004b).

#### *Biomass and density*

For each survey and species, we computed the average  $s_A$  per ESDU for all occupied ESDU, (termed  $s_{A+}$ ) as a measure of average acoustic density in the occupied area. We also measured the fraction of the ESDU that have non-zero  $s_A$  for the species of interest. This index provides a measure of the fraction of the survey area occupied by the target species or ISO. It may be seen as a binary concentration index (i.e. presence–absence), but is different from the concentration index  $S_s$ , which does not consider the zero abundance ESDU. Concentration is thus considered to consist of two factors, the probability of finding fish (or percent occupancy, estimated by the fraction of non-zero ESDU) and the distribution of fish in the non-zero ESDU (i.e. conditional upon finding fish). We also computed the average distance from the coast for both sardine and anchovy, this being the acoustic biomass ( $s_A$ ) centroid of distance from the coast, corrected, as the other indexes, for unequal sampling effort at different distances from the coast. While not an index of aggregation *per se*, the average distance from the coast gives an indication of the degree of compression of the stock close to the coastline. Finally, we tabulated the IMARPE anchovy and sardine acoustic abundance estimates for each year (Csirke *et al.*, 1996; Gutiérrez, 2000; IMARPE, unpubl. data) as a measure of overall abundance.

#### *Time series and correlations*

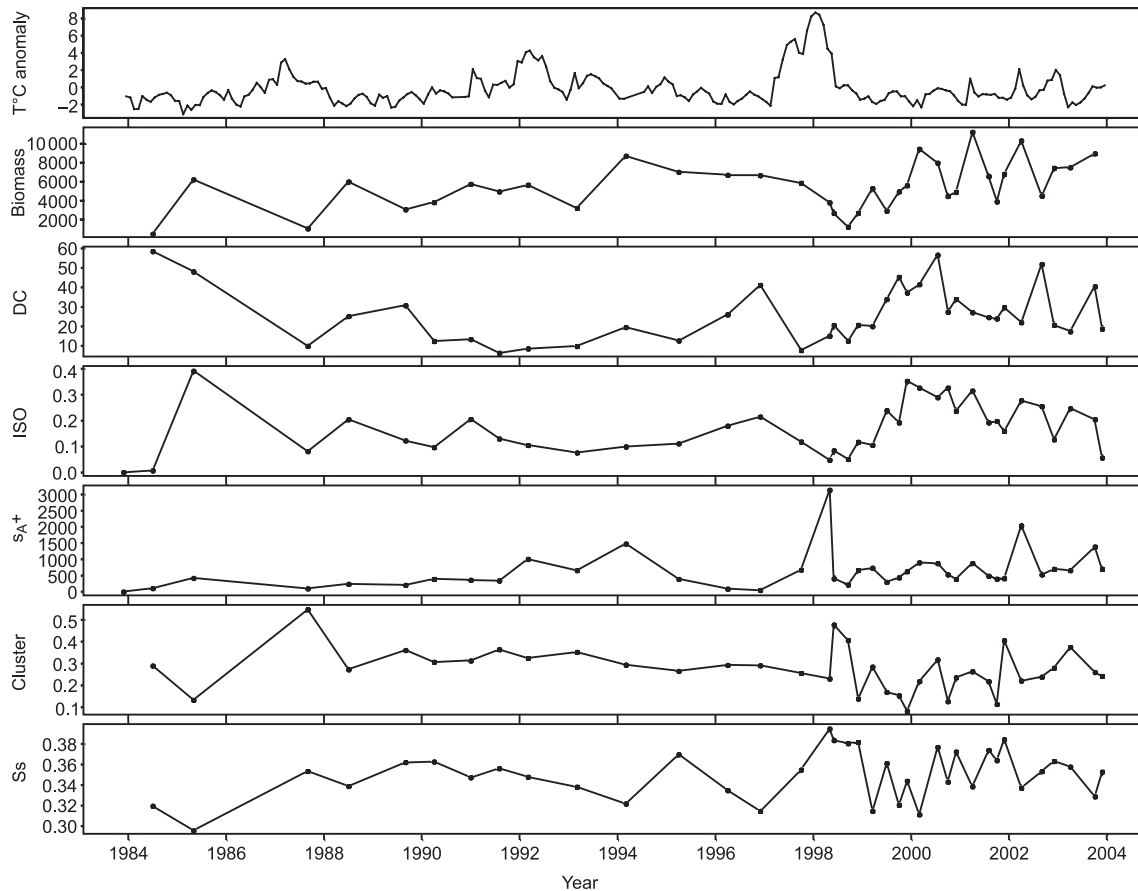
After calculating the three measures of anchovy and sardine aggregation (ISO, clustering index and  $S_s$ ) for all selected surveys between 1983 and 2003, we graphically and statistically compared their time series with the  $t_A$  over the time of all surveys, the overall acoustic abundance estimated from the survey data, the average distance from the coast and the mean backscatter acoustic energy ( $s_{A+}$ ) per occupied ESDU (Figs 3 and 4). When testing the correlations 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) bias. Significance of the resulting correlations is assessed using an *F*-test.

#### *Tree-based models of aggregation*

To examine the relationship between abundance, density, mean distance from the coast, and aggregation indexes for both sardine and anchovy on the one hand and environmental covariates on the other, we used a tree-based classification/regression algorithm CART (Classification and Regression Trees, Brieman *et al.*, 1984). In CART, the dependent variable is modelled as a function of covariates. CART proceeds to divide the data set by a sequence (tree) of binary splits on the values of one of the covariates at a time. The splits are chosen such that a regression (for an ordinal dependent variable as we have here) of the dependent variable on all the covariates within each split subset gives the best (in terms of level of significance) relationship. The splits continue down the tree until the sample size in each node gets below some preset threshold number of points. The CART tree is usually pruned to fewer nodes for clarity of explanation. For pruning the tree and validating the robustness of the CART results, we used the recursive partitioning method (rpart; De'ath and Fabricius, 2000). This method divides the data set into a number of subgroups (10 groups are used by De'ath and Fabricius, 2000) and then repeats the CART analysis sequentially, removing one subgroup each time. This replication provides a measure of robustness in the node splits in CART. Recursive partitioning provides a graph of the relative performance – the total model variance plus the number of nodes multiplied by a weighting factor – against the weighting factor. This provides a justification for choosing a particular weighting factor, which in turn determines the number of nodes in the 'best' tree. The best tree is determined from this graph as the tree with the fewest nodes such that adding additional nodes does not significantly improve the relative performance. The rule for choosing the 'best' number of nodes for the pruned tree in rpart is thus that adding additional nodes does not further reduce in a significant way the overall variance compared with the penalty incurred by having more nodes (the penalty depending on the weighting factor). The covariates used in our CART model were the year, the season and the  $t_A$  for each survey. Because there were so few non-zero ESDU for sardine after late 1999, we eliminated all surveys in the CART (but not time series, Figs 3 and 4) having  $0 < \text{EDSU} < 10$  (except for the CART having total acoustic biomass as a dependent variable, for which we used the entire data set). This resulted in omitting all surveys after late 1999 from CART analysis.

**Figure 3.** Time series from 1983 to 2003 acoustic surveys for temperature anomaly and indexes calculated for anchovy: acoustic biomass (in  $10^3$  tonnes), average distance from the coast (DC, in km), index of spatial occupation, average acoustic density in occupied elementary sampling distance unit ( $s_{A+}$  in  $m^2 \text{ mni}^{-2}$ ), index of clustering and concentration index (Ss).



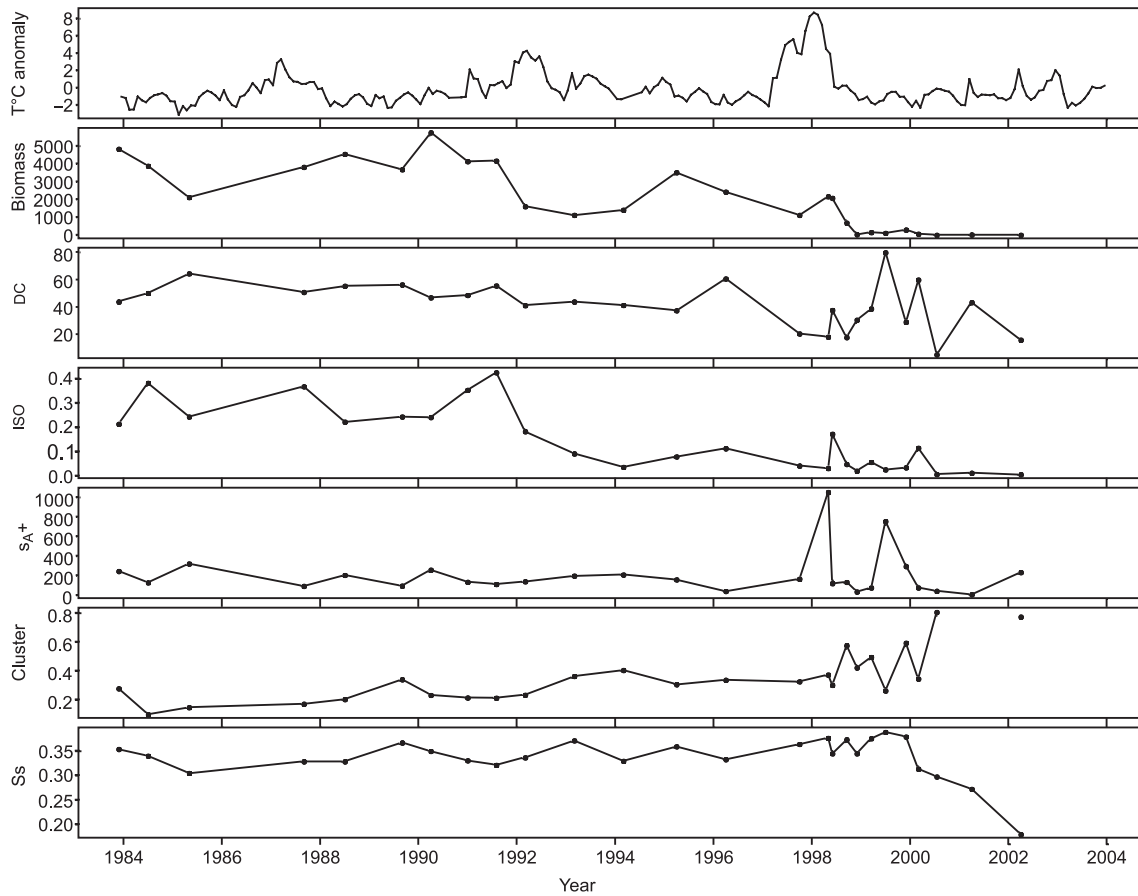
## RESULTS

### Anchovy

The tA data time series exhibits strong positive values from the El Niño events in 1987, 1992–93 and 1997–98 (Fig. 3) but not 1982–83 as our time series began just after this event. Anchovy acoustic biomass estimates were clearly reduced in 1987 and 1997–98 relative to the long-term mean, but the global trend shows an increasing of anchovy biomass along the time series, with, after 1999, a fluctuation around high values (about 8 million tonnes). The mean distance to the coast was negatively correlated with tA ( $F_{[1,35]} = 10.44$ ,  $P = 0.0027$ ). This relation was particularly clear during El Niño periods with anchovy distributed very close to the coast. The ISO (fraction of non-zero ESDU) was positively correlated with the biomass ( $F_{[1,35]} = 19.73$ ,  $P = 0.0001$ ) and distance to the coast ( $F_{[1,35]} = 11.42$ ,  $P = 0.0018$ ). The ISO index was low during El Niño events and it was lower before

than after the El Niño of 1997–98, when anchovy biomass was highest. The mean  $s_{A+}$  was correlated with the tA ( $F_{[1,36]} = 11.05$ ,  $P = 0.0020$ ). This index was particularly high in April 1998 during the 1997–98 El Niño (Fig. 3). Furthermore, the  $s_{A+}$  and ISO seem to be in phase (correlated) before 1990 and after 1999, and out of phase during the interim period. The cluster index had a significant negative correlation with the ISO ( $F_{[1,35]} = 13.00$ ,  $P = 0.0010$ ). It also appears positively correlated (not significant) with the concentration index Ss, particularly before 1997. Both Ss and the cluster index appeared to increase during El Niño periods (Fig. 3). The Ss was also negatively correlated with the distance to the coast ( $F_{[1,35]} = 5.33$ ,  $P = 0.0270$ ) and the ISO ( $F_{[1,35]} = 4.45$ ,  $P = 0.0421$ ) but did not pass the Bonferroni correction test. All parameters appeared more variable after 1998, but it is difficult to determine if this pattern is an artifact related to the higher sampling frequency during this period or illustrates an actual higher variability.

**Figure 4.** Time series from 1983 to 2003 acoustic surveys for temperature anomaly and indexes calculated for sardine: acoustic biomass (in  $10^3$  tonnes), average distance from the coast (DC, in km), index of spatial occupation, average acoustic density in occupied elementary sampling distance unit ( $s_{A+}$  in  $m^2 mni^{-2}$ ), index of clustering and concentration index (Ss).



Results from CART showed the relative effect of each of the independent variables (year, season and  $tA$ ) on the indexes of abundance, coast distance and aggregation for anchovy (Table 1). Seasonal patterns were difficult to check with the data as temporal sampling was not standard. For instance, no summer surveys were performed before 1990 while most of the surveys were performed in summer during the first part of the 90s. Therefore, CART results on seasons have to be taken advisedly. The results (Table 1) supported the observations from the time series in Fig. 3, but also extended them and provided covariate thresholds for different groupings of the dependent variable.

Classification and regression trees on the anchovy acoustic biomass estimates (Table 1) show that anchovy was significantly more abundant after 2000. Before this date, the acoustic index of fish biomass was lowest during surveys performed in autumn and winter. The mean distance from the coast was low for positive  $tA$  years and generally in summer for all years. The

ISO was highest during the period from early 1999 to mid-2001 (0.285), corresponding to a La Niña period, and very low earlier, except during other strong negative  $tA$  periods ( $tA < -1.16$ ; or temperature anomalies more negative than  $1.16^\circ C$ ). Average  $s_{A+}$  was highest for very positive temperature anomalies i.e. El Niño 1997–98 (Fig. 3). It was lowest before 1992 and higher after 1992, except for warm periods as mentioned above. The clustering index, or propensity of high-density anchovy ESDU to be close together, was globally higher before late 1998, particularly during periods of positive  $tA$  (Table 1; 0.364). The smallest values for clustering were observed during the La Niña period between late 1998 and 2000, when ISO was increasing (Fig. 3). Later, (after late 2001) the clustering index increased to average 0.288. Finally, the average anchovy concentration index Ss was lowest during strong negative temperature anomalies (La Niña;  $tA < -1.42$ , 0.323) and highest in years without strong negative temperature anomalies

**Table 1.** Results of classification and regression trees analysis of anchovy abundance and aggregation indexes as a function of year, temperature anomaly (tA) and season. Only values for terminal nodes are indicated.

Variable/covariate	Year	tA	Season	Value
Acoustic biomass estimate	Before 2000		Autumn, winter	3,342,000 (11)
	"		Summer, spring	5,579,000 (12)
	2000 and later		Winter, spring	6,161,107 (9)
	"		Summer	9,617,335 (4)
Mean coast distance		tA ≥ 0.02		14.8 (13)
		tA < 0.02	Summer	21.4 (7)
		tA < -1.12	Other seasons	38.5 (8)
		-1.12 < tA < -0.82	"	25.0 (4)
		0.02 < tA < -0.82	"	44.4 (5)
Index of surface occupation	Before 1999	tA < -1.16		0.172 (7)
	"	tA > -1.16		0.04 (13)
	1999–mid-2001			0.285 (8)
	After mid-2001			0.191 (9)
s <sub>A+</sub>		tA ≥ 0.93		1328 (6)
	Before 1992	tA < 0.93		273 (8)
	1992 and later			601 (23)
Cluster index	Before 1999	tA < -0.09		0.279 (9)
	"	tA ≥ -0.09		0.364 (9)
	1999–2002			0.194 (12)
	2002 and later			0.288 (7)
S <sub>s</sub>		tA < -1.42		0.323 (6)
		tA ≥ -1.42	Summer	0.344 (9)
		"	Other seasons	0.360 (22)

The numbers in parenthesis indicate the number of data points at each terminal node.

throughout the year except for summer (0.360). Anchovy aggregation appeared to be particularly sensitive to strong negative (cold) temperature anomalies.

#### Sardine

Before describing results on sardine (Fig. 4), it is important to recall that due to the very low number of non-null data after late 1999, indexes on sardine were unstable in this period. In the study area, the sardine acoustic biomass estimates fluctuated between 2.1 and 5.7 million tonnes until 1990. Then, sardine abundance began declining and was dramatically lower in the survey area off Peru after the El Niño of 1997–98. Two peaks of abundance were nevertheless observed after 1990, one in summer 1995, the other during the El Niño event in 1998. As with anchovy, the mean distance to the coast was significantly and negatively correlated with tA ( $F_{[1,18]} = 9.34$ ,  $P = 0.0068$ ). Sardine coast distance generally declined from 1985 to 1998, except for increases during cold years. Sardines were distributed very close to the coast during the El Niño of 1997–98. The residual population then spread offshore in 1999. Both the fraction of positive ESDU (ISO) and the average sardine s<sub>A+</sub> had a general

declining trend from 1985 to 1997 (Fig. 4). However, the s<sub>A+</sub> index showed two very high peaks: during the El Niño event in 1998 and at the end of 1999, when the population was greatly reduced (i.e. although fewer non-zero sardine ESDU were observed, they on average had higher sardine densities). The other two aggregation indexes also showed time trends; the cluster index generally increasing from 1984 to 2000 coincident with the reduction of sardine biomass, and a sharp increase from 1999 when almost no sardine were present. S<sub>s</sub> had a significant negative correlation with the distance to the coast ( $F_{[1,18]} = 15.99$ ,  $P = 0.0008$ ) and was slowly increasing over the period 1984–1998. Then, it decreased sharply after 1998 when the sardine population diminished off the Peruvian coast.

From CART results (Table 2), it appears that the sardine Peruvian acoustic biomass estimate had three different phases. The first was a high abundance phase (about 4 million tonnes) before 1992, a medium abundance phase (about 1.9 million tonnes) between 1992 and mid-1998, followed by a very low abundance phase. The mean distance from the coast for sardine was greater than that for anchovy (Tables 1 and 2). As



**Table 2.** Results of classification and regression trees analysis of sardine abundance and aggregation indexes as a function of year, temperature anomaly (tA) and season.

Variable/covariate	Year	tA	Season	Value
Biomass estimate	Before 1992			4,097,000 (8)
	1992–1999			1,917,609 (8)
	1999 and after			1,403,320 (9)
Mean coast distance			Winter	75.2 (4)
		tA ≥ 1.37	Other seasons	29.4 (4)
		tA < 1.37		48.3 (13)
Index of surface occupation	Before mid-1992			0.287 (10)
	After mid 1992			0.066 (11)
s <sub>A+</sub>		tA ≥ 1.37		367 (4)
		tA < 1.37		159 (17)
Cluster index	Before mid-1992			0.237 (10)
	After mid-1992		Summer–autumn	0.381 (7)
	"		Spring	0.476 (4)
S <sub>s</sub>	Before 1997	tA < -1.13		0.327 (5)
	"	tA ≥ -1.13		0.346 (9)
	From 1997			0.365 (7)

with anchovy, there was a season effect for sardine, with sardine being farther from the coast in winter, highest before mid-1992, and lower thereafter. The s<sub>A+</sub> was high for strong positive temperature anomalies (warm years). The smallest degree of clustering of high sardine abundance ESDU occurred before mid-1992 and was high thereafter, particularly during spring surveys. The concentration index S<sub>s</sub> was highest from 1997 while before 1997 it was lowest for strong negative temperature anomalies (tA < -1.13). The reduced concentration of sardine biomass after the El Niño of 1997–98, when the Peruvian coastal popula-

tion was low, contrasts with the results for the sardine cluster index (Fig. 4).

## DISCUSSION

### *Anchovy and sardine: ecological neighbours but not ecological analogues*

Anchovy and sardine are not ecological analogues despite their co-occurrence in the HCS pelagic zone and they do not share the same ecological niche in terms of water masses, tolerance to abiotic factors and migrating and feeding capacities (Table 3). Sardines

**Table 3.** Life history and migration summary for anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) in the Humboldt Current System. Source: Arnaud Bertrand, IRD and Mariano Gutierrez Instituto del Mar del Perú, unpubl. data.

Parameter	<i>Engraulis ringens</i>	<i>Sardinops sagax</i>
T °C range	13–23°C	9–25°C
First maturity	12 cm (1 yr)	20 cm (2 yr)
Max length (cm)	20	40
Max longevity (years)	4	25
Distribution	3.30°–43°S	59°N – 57°S
Main fishing zone	5°–14°S; 16°–24°S	5°–14°S; 16°–24°S; 29°–35°S
Fecundity	Batch fecundity: ~15000 (size dependant)	Batch fecundity: ~60000
Vertical range (m)	0–100	0–200
Diel migration	Very little	Yes
Longitudinal migration	Very coastal distribution in warm conditions	Migrate inshore in warm conditions
Latitudinal migration	According to hydrological conditions [El Niño Southern Oscillation (ENSO) events, etc.]	According to hydrological conditions (ENSO events, etc.)
Main spawning area	Coastal	Frontal zones
Main nursery area	Coastal	Frontal zones
Feeding	Planktivorous (mainly particle feeding)	Planktivorous (mainly filter feeding)

prefer oceanic waters and the frontal zone between these waters and more coastal waters (e.g. Castillo *et al.*, 1996; Bertrand *et al.*, 2004a), while anchovy are better adapted to the higher production in cold coastal upwelled waters (e.g. Niquen *et al.*, 2000; Bertrand *et al.*, 2004a). Both species are able to feed directly on phytoplankton, although sardines are filter feeders and appear to feed more exclusively on phytoplankton (van der Lingen, 1994) than anchovy. Anchovy, which are bite feeders (Konchina, 1991; van der Lingen, 2002), are mainly zooplanktivorous (Pepe Espinosa, IMARPE, Callao, Peru, unpubl. data) and may not be able to sustain growth on a diet consisting entirely of phytoplankton (Espinosa *et al.*, 2000).

#### The habitat-based hypothesis

These ecological differences are one of the bases of the habitat-based hypothesis proposed by Bertrand *et al.* (2004a) to explain fluctuations in pelagic fish populations in upwelling ecosystems. According to this hypothesis, climatic changes at different temporal scales (El Viejo-La Vieja, El Niño-La Niña) lead to changes in the range of anchovy and sardine habitat, and then to shifting of dominance between anchovy and sardine populations throughout the upwelling system. Aggregation and coast distance are important parameters in this regard because they reflect how the fish distribution responds to changing environmental conditions. Are the patterns we found in accordance with this hypothesis and, more generally, with our present knowledge of fish ecology and spatio-temporal dynamics? Anchovy biomass and mean distance to the coast are expected to be higher during cold periods such as La Vieja or La Niña conditions because upwelling and mixed water masses extend farther from the coast. However, dispersion of anchovy, when cold conditions prevail even if fish biomass is high, can lead to a downward bias in the acoustic biomass estimation (i.e. the higher biomass is not as easily detected; Gutiérrez *et al.*, 1999). Concentration and clustering are expected to be higher during warm periods, whatever the temporal scale (i.e. regime, ENSO event or season), because favourable habitat in terms of hydrologic and trophic conditions would be restricted close to the shore where fish will concentrate. Finally, a parameter such as the fraction of non-zero ESDU (ISO) depends both on global abundance and fish distribution. For a constant biomass, ISO is expected to be higher when fish distribution spreads offshore in cold conditions and lower when anchovy concentrate close to the coast when its habitat is reduced during warm periods. In the case of sardine, the trend should be the opposite for biomass; higher during warm years

when conditions are more favourable and the warmer oceanic waters which are suitable sardine habitat spread towards the coast. As with anchovy, the mean distances to the coast are expected to increase with decreasing temperature (while remaining greater than the anchovy distances). Sardine can even migrate out of the Peruvian coastal region during cold periods. These predictions were well supported by the data (see Results) and will be discussed over the studied period.

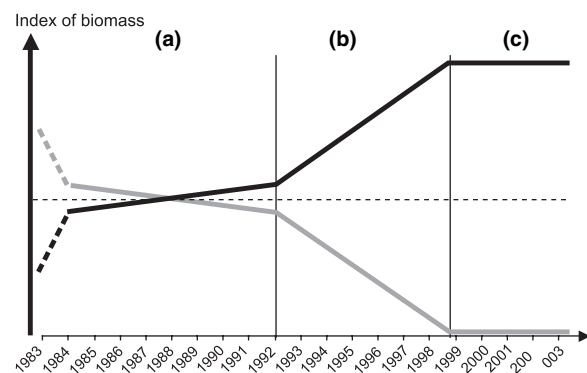
#### Long-term dynamics of Peruvian sardine and anchovy

As already described by other studies (Bakun and Broad, 2003; Chavez *et al.*, 2003; Alheit and Niquen, 2004; Bertrand *et al.*, 2004a), anchovy biomass increased and sardine biomass decreased during the study period. This trend, which was related to a global change towards cooler conditions in the ecosystem, was perturbed by the El Niño events of 1987 and 1997–98. Based on the time series and CART results (Figs 3 and 4, Tables 1 and 2), three different periods and two shifts, in 1992 and 1997–1999 (Fig. 5), clearly appeared in sardine and anchovy dynamics off Peru.

#### From late 1983 to 1992

The first period, before 1992, was characterized by a high sardine acoustic biomass (4 million tonnes), a high ISO (about 30 % of the study area) and a low index of clustering, indicating that sardine were distributed rather evenly in their habitat. At the same time anchovy had a low ISO (13%) and a low  $s_{A+}$  (compared with the rest of the time series, but higher than for sardine), indicating that anchovy distribution

**Figure 5.** Schematic diagram of relative dominance in the Peruvian water of anchovy (black line) versus sardine (grey line) from 1983 to 2003 with the periods defined from acoustic biomass and aggregation indexes: (a) mixed sardine-anchovy dominance; (b) anchovy dominance and sardine collapse; (c) full anchovy era.



was more restricted to specific areas. Clustering of anchovy during this period was also generally higher because of the predominance of warmer years (Fig. 3, Table 1). This period corresponds to the end of the sardine regime and the recovery of the anchovy population in the HCS (Lluch-Belda *et al.*, 1992; Csirke *et al.*, 1996; Alheit and Niquen, 2004). Between 1984 and 1992, sardine and anchovy co-existed in the HCS with quite similar acoustic biomass – around 4 million tonnes – but in different zones (Massé and Gerlotto, 2003) and having different aggregation patterns.

#### From 1992 to 1999

From 1991–92 to 1999, sardine biomass declined in Peruvian coastal waters (mean acoustic biomass of 1.9 million tonnes) as well as its ISO (about 7 % of the study area). Sardine habitat range reduction was accompanied by a higher clustering of the residual population. In contrast, anchovy acoustic biomass increased to about 6 million tonnes; however, anchovy was still rather aggregated as indicated by a quite high  $s_{A+}$ , a low ISO and a rather high degree of clustering. This period corresponds to a transition towards anchovy dominance in the ecosystem. This period ends with the El Niño of 1997–98.

#### 1997–98 El Niño

The impact of the El Niño of 1997–98 on the ecosystem was studied in detail by several authors (Alheit and Niquen, 2004; Bertrand *et al.*, 2004a). This event, one of the two largest of the twentieth century, was characterized by the persistence of local coastal efficient upwelling (see Barber and Chavez, 1983) providing refuge areas where anchovy concentrated. As already stated, the very coastal anchovy distribution led to a strong biomass underestimation (Bertrand *et al.*, 2004a). This pattern was clearly supported in our results by a very low anchovy distance to the coast, the highest values of  $s_{A+}$  and concentration index (Ss, parameter was negatively correlated to the mean distance to the coast) of the time series, but also a very high clustering. Anchovy adapted its spatial strategy to the conditions by dramatically reducing its distribution range to fit with the available refuge areas and increasing its density. Actually anchovy, generally protected from overfishing during this period by government regulations, found a ‘loophole’ (see Bakun and Broad, 2003) inside the generally unfavourable conditions (Bertrand *et al.*, 2004a). The short-term El Niño warm period of 1997–98 during an otherwise cool regime provided an opportunity for sardine abundance increase because of better feeding conditions for the residual population. Sardine, as with

anchovy, migrated towards the coast (Fig. 4) and was more concentrated, as indicated by very high  $s_{A+}$  and Ss values. At the end of this event, the sardine population was greatly reduced in the HCS. This may be due to a combination of overfishing on recruits, environmental stress caused by the abrupt shift between El Niño and La Niña, the long-term La Vieja regime that had previously reduced the sardine population and sardine migrating out of the study area to more northern refugia (Bertrand *et al.*, 2004a).

#### From 1999

During this latter period, there was a drastic reduction of the sardine population in Peruvian waters and the beginning of a period of anchovy dominance. From the end of 1998, all anchovy parameters reflect the prevailing favourable conditions for this species. High biomass, greater distance to the coast and high ISO illustrate the extension of anchovy favourable habitat. The average  $s_{A+}$ , Ss and low clustering index reflect the spatial strategy of anchovy for cooler periods of dispersion somewhat uniformly over a large area.

Just after the 1997–98, El Niño sardine abundance and ISO were very low (0–4%) and the residual population ranged further offshore. Sardine clustering increased dramatically while their concentration index was dramatically reduced. Because of a very low number of non-null ESDU, sardine statistical results are not reliable after mid-1999. However, these results appear to confirm the assumption that sardine cannot effectively utilize the increased production during a cooler regime (Schwartzlose *et al.*, 1999; Chavez *et al.*, 2003; Bertrand *et al.*, 2004a) and that their association with more offshore waters reduces the total area of acceptable habitat for them during a cool regime (Bertrand *et al.*, 2004a). Also, sardine may respond to cooler conditions by moving offshore and equatorward as occurred with sardine in the Northeast Pacific coastal region (Rodríguez-Sánchez *et al.*, 2002), thus reducing their overall abundance in the study region. A remaining and reduced stock of sardine was observed far offshore and in specific areas such as the Galapagos (Bertrand *et al.*, 2004a). Most aggregations of sardine encountered after El Niño 1997–98 off Peru were likely high-density migrating schools. Thus, lacking a preponderance of low-density ESDU, concentration remained low while clustering was high.

#### Species range, abundance and aggregation

Our results showed that for the same levels of biomass, anchovy may exhibit high density–low range and low density–high range combinations. Comparing cases having similar biomass (e.g. 1 million tonnes in winter

spring 1987 and 1997; 3 million tonnes in summer 1993 and winter 1999; 5 million tonnes in summer 1999 and spring 2000) could be either high ISO-low density or high-density low ISO. Similar results obtain for sardine although less frequently (e.g. similar biomass, 2 million tonnes, was observed in autumn surveys in 1985 with high ISO and low density and 1998 with low ISO and high density). The fact that sardine biomass was generally spread more evenly among ESDU than anchovy can be related to the more pervasive and migratory nature of sardine.

*Synthesis*

This work is only a first step in examining the long-term spatial dynamics of Peruvian Humboldt System pelagic fish. Here, we identified large-scale spatio-temporal patterns in both abundance and aggregation and suggested that differences in life history patterns of anchovy and sardine are reflected in their differing responses (Table 4) to changing environmental condition, including long-term, large-scale environmental condition shifts and ENSO signals, which play out over a tapestry of seasonal and annual distribution changes. Analysing anchovy and sardine abundance and aggregation pattern dynamics over this time series suggested or supported several conceptual ideas concerning HCS sardine and anchovy populations:

- 1) These species displayed a kind of anti-symmetry with regard to population change relative to long-term environmental patterns and ENSO conditions. The 1984–2003 time series could be divided into three different periods. Before 1992, the Peruvian coast was shared by sardine and anchovy. After 1992, the HCS became dominated by anchovy when the sardine population declined. Finally since 1999 (and at least until mid-2005), we have been in a ‘full anchovy era’ with dramatically low levels of sardine in the HCS. Changes in aggregation patterns occurred over these same three periods.
- 2) However, fish response is sometimes smoother than usually suggested and there are transition periods with concomitant high biomasses of anchovy and sardine; but with different spatial aggregation patterns, upwelling ecosystems support dramatic and sudden changes. This appears to be an important feature of the Peruvian HCS.
- 3) The habitat-based hypothesis, that population changes follow expansion or contraction of favourable habitats (Bertrand *et al.*, 2004a), reflected by changes in aggregation patterns, was supported for anchovy and sardine by the observed relationships between environmental proxies and aggregation patterns. The differing response of the two species appears to be forced

**Table 4.** Synthesis of the comparison of Peruvian sardine and anchovy abundance and aggregation indices evolution during 1983–2003.

Species/index	Acoustic biomass	Distance to the coast	ISO	s <sub>A+</sub>	Clustering	S <sub>s</sub>
Anchovy	↗ during time series but ↘ during El Niños 1987 and 1997–98	↘ with ↗ t°C anom. and in summer	↗ with ↘ distance to the coast and for cold years	↗ with ↗ t°C anom.	↘ during warm years	↗ during warm years with ↗ distance to the coast. Lowest in cool years
Sardine	↘ during time series but ↗ during El Niño 1987 and 1997–98	↘ with ↗ t°C anom. except in winter (high)	↘ with ↘ biomass during time series	↗ with ↗ t°C anom.	↗ during time series following ↘ in biomass. Highest in spring after mid-1992	↗ during time series along with ↘ in biomass. Lowest in cool years before 1997

by the biological requirements of each species and may reflect their adaptation to highly variable ecosystem conditions (Bertrand *et al.*, 2004b).

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