


Multifarious anchovy and sardine regimes in the Humboldt Current System during the last 150 years

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Abstract

The Humboldt Current System (HCS) has the highest production of forage fish in the world, although it is highly variable and the future of the primary component, anchovy, is uncertain in the context of global warming. Paradigms based on late 20th century observations suggest that large-scale forcing controls decadal-scale fluctuations of anchovy and sardine across different boundary currents of the Pacific. We develop records of anchovy and sardine fluctuations since 1860 AD using fish scales from multiple sites containing laminated sediments and compare them with Pacific basin-scale and regional indices of ocean climate variability. Our records reveal two main anchovy and sardine phases with a timescale that is not consistent with previously proposed periodicities. Rather, the regime shifts in the HCS are related to 3D habitat changes driven by changes in upwelling intensity from both regional and large-scale forcing. Moreover, we show that a long-term increase in coastal upwelling translates via a bottom-up mechanism to top predators suggesting that the warming climate, at least up to the start of the 21st century, was favorable for fishery productivity in the HCS.

KEYWORDS

3D habitat, anchovy and sardine abundance fluctuations, climate change, Humboldt Current System, Pacific Decadal Oscillation, Peru–Chile, regime shifts, small pelagic fishes, upwelling

1 | INTRODUCTION

The Humboldt Current System (HCS) off Peru yields about 10% of the global fish catch, producing more fish per unit area than any other region in the world (Bakun & Weeks, 2008; Chavez, Bertrand, Guevara-Carrasco, Soler, & Csirke, 2008). The high productivity is maintained by the upwelling of cold, nutrient-rich, low-oxygen, sub-surface waters sustained by weaker winds than other upwelling systems due to the low latitude of the region and hence greater

Coriolis factor per given amount of turbulence (Bakun & Weeks, 2008). Currently, the fishery is based almost exclusively on anchovy (*Engraulis ringens*), fueling large parts of the global food supply based on fishmeal, for example, aquaculture and pig and poultry farming (Fréon et al., 2010). While a great abundance of anchovy in the 1950s stimulated the rapid development of the largest fishery in the world, it later collapsed in the 1970s and recovered in the late 1980s. It has been hypothesized that the HCS is currently in a “sweet spot” with regard to global warming resulting in greater upwelling, which is ideal for anchovy development (Bakun & Weeks, 2008). However, some of the interannual to decadal variations in

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recent anchovy catches apparently alternate with sardine catches (*Sardinops sagax*; Alheit & Ñiquen, 2004; Chavez, Ryan, Lluch-Cota, & Ñiquen, 2003), which produce a much lower yield when they dominate the ecosystem (Figure 1a,b). The underlying mechanisms driving decadal fluctuations of anchovy and sardine populations as well as the middle- to long-term trends of anchovy biomass are not well understood. This is particularly vital in view of the changing oceanographic conditions under global warming, putting a global business and local economies at stake.

The current paradigm based on late 20th century fish landings posits that anchovy and sardine alternate periodically and that fluctuations are associated with large-scale changes in the Pacific Ocean dynamics (Figure 1; Chavez et al., 2003; Schwartzlose et al., 1999). Since the beginning of the industrial fishery (late 1950s), there were two anchovy-dominated regimes (based on high landings from ~1960 to 1970 and late 1990s–present) generally associated with a cooler-than-average eastern Pacific and higher primary production. There was a sardine regime (~1975–2000), associated with a warmer-than-average eastern Pacific and lower primary production (Chavez et al., 2003) between the two anchovy regimes. These historical anchovy and sardine fluctuations have been characterized as oscillating with an approximate periodicity of 50–60 years in response to changes in the Pacific Ocean dynamics captured by ocean climate indices, such as the Pacific Decadal Oscillation (PDO; Chavez et al., 2003; Schwartzlose et al., 1999). Although the paradigm has been questioned (Field et al., 2009; Fréon, Bouchon, Mullon, García, & Ñiquen, 2008; Gutiérrez et al., 2009; McClatchie, Hendy, Thompson, & Watson, 2017; Valdés et al., 2008), it is still widely accepted and used in research and education.

In the present study, we question this paradigm for various reasons. First, the timing of changes in fish populations does not match that of the PDO and temperature changes at the interannual timescale

(Figure 1). Second, there are many years of overlap as sardine decline and anchovy increase in the 1990s (Figure 1; Gutiérrez, Swartzman, Bertrand, & Bertrand, 2007). Third, the fish landing time series is at most only a few years longer than the inferred periodicity. Fourth, the use of fish landings to understand relationships between environmental conditions and fish abundance fluctuations is limited and potentially biased due to a variety of factors inherent to human activity (Bertrand, Segura, Gutiérrez, & Vásquez, 2004; Finney et al., 2010). Finally, the Humboldt Current does not change linearly and uniformly with PDO indices, suggesting that other processes are also important. Isaacs (1976) originally proposed that a great deal of multifarious regimes involving biology, climate, oceanography, migration, temperature, weather, or combinations of these were likely to exist.

Apart from multidecadal anchovy fluctuations, there is an ongoing debate about the potential impact of climate change on upwelling dynamics and oceanographic conditions and hence on the trend of anchovy biomass in the near- and long-term future. On the one hand, it has been postulated that greenhouse warming will enhance the alongshore wind stress and coastal upwelling (Bakun, 1990), likely favoring marine productivity and thus anchovy populations in the HCS. Several works suggest that winds have intensified at least in parts of the California, Benguela, and Humboldt upwelling systems over the last decades (e.g., Sydeman et al., 2014). Moreover, a negative trend in coastal SST off northern Chile since at least 1979 (Falvey & Garreaud, 2009) and off central Peru since the mid-20th century associated with an increase in marine productivity (Gutiérrez et al., 2011) has been recorded. On the other hand, sardine dominate in other eastern boundary upwelling systems that are currently subject to relatively stronger winds and hence more turbulence (Bakun & Weeks, 2008). It is thus not clear if changes in oceanographic conditions lead to regime shifts in the HCS and, moreover, it

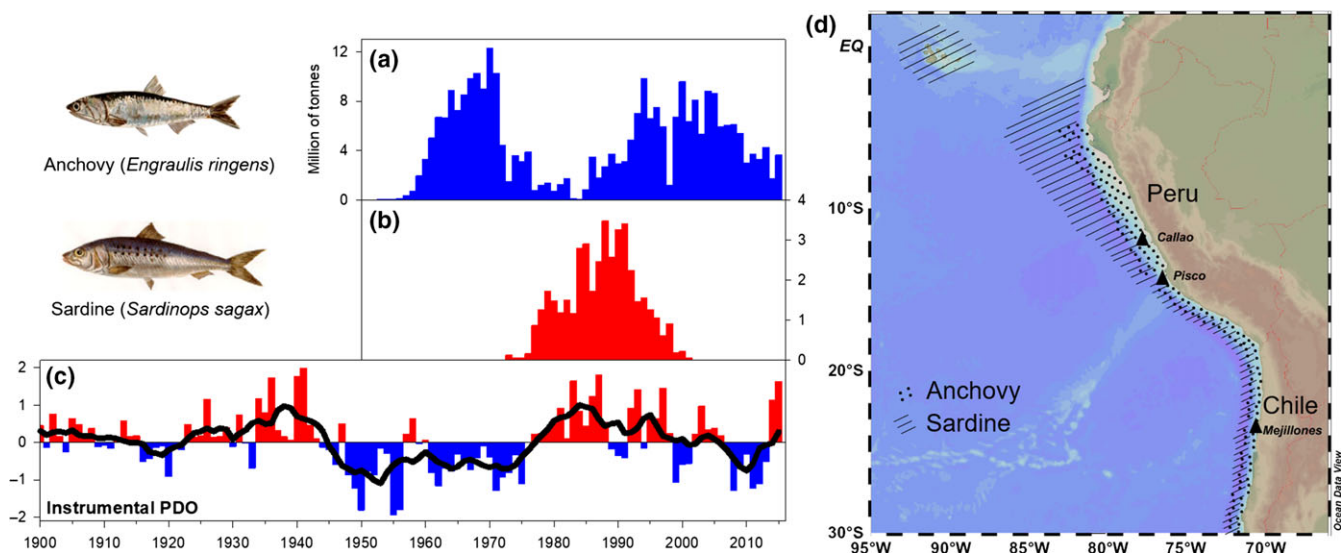


FIGURE 1 Anchovy and sardine landings in the Northern Humboldt Current System and their distribution range. (a) Anchovy (*Engraulis ringens*) landings in Peru. (b) Sardine (*Sardinops sagax*) landings in Peru. Note the different scales of the y-axes. (c) Annual and 7-year smoothed (black line) Pacific Decadal Oscillation (PDO), derived from principal component analysis of North Pacific Sea surface temperatures (Mantua & Hare, 2002). (d) Maximal range of distribution for anchovy (black dots) and sardine (black lines) and position of the sediment cores used in the present work (black triangles) (redrawn from Checkley et al., 2009) [Colour figure can be viewed at wileyonlinelibrary.com]

is hitherto unknown whether an intensification of upwelling winds translates into changes in productivity across intermediate (e.g., pelagic fishes) and higher (e.g., marine birds) trophic levels (Sydeman et al., 2014). The range and impacts of historical and present-day trends and variations of marine productivity for pelagic fishes and higher trophic levels remain to be established.

Fish scales accumulating in marine-laminated sediments provide long-term records of population variability (Baumgartner, Soutar, & Ferreira-Bartrina, 1992; Soutar & Isaacs, 1974). Over time, fish scales and bones fall to the ocean floor, bury, and accumulate. Variation in fish scale deposition rates (SDRs) as an indicator of fish population size is attributable to scale shedding (Field et al., 2009; Salvattec, Field, Baumgartner, Ferreira, & Gutiérrez, 2012). Under favorable conditions (that is, low bottom-water oxygenation and high sedimentation rates), a preserved record provides a history of the pelagic fish populations that inhabited the water column of the area.

To understand the natural variability and middle- to long-term trends of small-pelagic populations related to climatic conditions, we analyze fish scale deposition records from a wide spatial range (11 latitudinal degrees) and over a 100-year period (since 1860 AD) before the commercial fishery. We reconstruct marine productivity and anchovy and sardine biomass fluctuations at high resolution from two laminated sediment cores from Pisco and compare them with other previously published records in the HCS (Gutiérrez et al., 2009; Valdés et al., 2008). The new cores provide a more continuous record with better preservation of scales than other cores (Gutiérrez et al., 2009; Salvattec et al., 2012); Salvattec, Field, et al., 2014. In our study area, fish scale preservation indices revealed that the degradation of fish scales occurred prior to mid-19th century due to lower productivity and higher oxygenation of the water column and sediments, whereas for the past 150 years, the preservation is good (Salvattec et al., 2012). Due to high temporal resolution of the fish scale records developed in this work, it was possible to reliably relate the reconstructed fish abundances to indices of ocean-atmosphere variability like the PDO, the Tripole Interdecadal Pacific Oscillation (TPI; Henley et al., 2015), Tropical Pacific zonal wind stress (Compo et al., 2011), coastal and offshore SST from the COADS database (National Climatic Data Center/NESDIS/NOAA/U.S. Department of Commerce, 1984), and guano bird abundance (Barbraud et al., 2017; Tovar, Guillen, & Nakama, 1987) to determine the relative influence of basin-scale and regional forcings on anchovy and sardine dynamics and higher trophic levels. The expectation according to the paradigm would be that a warmer eastern Tropical Pacific (ETP) is conducive to sardine development while anchovy thrive in a cooler ETP. However, regional forcings could be as important, or more, as basin-scale dynamics.

2 | MATERIALS AND METHODS

2.1 | Sediment core locations

The location of the cores was congruent with the spatial distribution range of anchovy and sardine, with sediment cores spanning a range

of the preferred water masses. In the HCS, anchovy is more adapted to productive, cold coastal waters, while sardine, which need more oxygenated waters, prefers the oceanic waters and the front between oceanic and coastal waters (Figure 1d; Bertrand et al., 2011; Gutiérrez et al., 2007). The southernmost Mejillones core was retrieved at 9 km from the coast, in a small and shallow marine sedimentary basin, near the present nucleus of the southern fishing stock of anchovy and sardine (Figure 1d). The Pisco cores were located at ~15 km from the coast near the main upwelling center (Figure 1d). The site lies south of the present nucleus of the northern fishing stock of anchovy, and that of sardine during the 1980s when sardine fully dominated the HCS while sardine distribution shifted northward during the 1990s (Gutiérrez, Castillo, Segura, Peraltilla, & Flores, 2012). The northernmost Callao core was located farthest from the coast (~60 km) and lies within the nucleus of the northern fishing stock of anchovy and that of sardine during the 1990s (Figure 1d; Checkley et al., 2009; Gutiérrez et al., 2012). Therefore, high sardine SDRs in Pisco indicate the period of maximal sardine expansion in the HCS.

2.2 | Chronology

Unlike other settings like the Santa Barbara Basin, where varves can be counted downcore to determine the age of the sediment records, sediment cores from the Peruvian sediment margin show multiple discontinuities and the addition of previously deposited material from upslope (Salvattec, Field, et al., 2014). Thus, we developed independent chronostratigraphies based on multiple sediment cores to construct accurate age models to reliably reconstruct past changes at the highest possible temporal resolution (Salvattec, Field, et al., 2014; Salvattec, Gutiérrez, et al., 2014). Chronostratigraphies for cores B05-13 and B05-14 were determined by means of ^{210}Pb , ^{241}Am , and laminae correlations to detect missing sections (Salvattec, Field, et al., 2014; more details provided in the Supporting Information). The subsampling procedure for radionuclide measurements, fish scale identification, and export production quantification is described in detail in the Supporting Information. The time step of the sediment samples from 1860 to 1964 (best resolved in B05-13 and B05-14) is 1 year, while the time step from 1964 to 2005 (best resolved in B04-6 and B04-13) is 2.9 and 3.1 years, respectively.

2.3 | Sediment records

For the regional comparison of fish SDRs and export production, we used one record for Mejillones (Valdés et al., 2008) and one for Callao for both fish SDR and export production. In Pisco, we used three cores: for the fish scale record, we used cores B05-13 from 1860 to 1964 and B04-6 from 1964 to 2005 and for export production, B05-14 from 1860 to 1964 and B04-6 from 1964 to 2005. The stacked records from Pisco were assembled using the most complete sediment sequences of each core. Since these cores show a clear peak in Americium-241 associated with the peak in atomic bomb testing in the South Pacific in 1964, this feature can be used to correlate cores

and assemble a stacked record (Salvatteci, Field, et al., 2014). More details are available in the Supporting Information.

For the comparison of fish SDR and export production with indices of ocean–atmosphere variability, we used the following cores: for fish SDR, we used B05-13 (Pisco) from ~1860 to 1964 and B04-13 (Callao) from ~1964 to 2005. For export production, we used the stacked record from Pisco as explained above since no high resolution export production data is available for B04-13. The less disturbed sedimentary sequences in the first centimeters of B04-13 (Callao) indicated that this part of the core is the best section for assembling a stacked record (more detailed explanation in the Supporting Information). To assemble the stacked record of both fish SDR and export production, we normalized the data as percent of the maximum value in each series.

2.4 | Indices of ocean–atmosphere variability

To better understand the relationship of export production, anchovy, and sardine with environmental conditions, we compared the reconstructed fish SDR and a productivity record with tropical and regional indices of ocean and atmosphere variability. The PDO is a climate index of a dipole pattern of variation in sea surface temperature (SST) of the extratropical (poleward of 20°N) North Pacific (Mantua & Hare, 2002), although it also reflects aspects of tropical dynamics. The Walker circulation is an ocean–atmosphere system in the Pacific Ocean that is a result of a difference in surface pressure and temperature over the western and ETP (Bjerknes, 1969). The tropical Pacific zonal wind stress record (Compo et al., 2011) serves as an indicator of the Walker circulation strength, with stronger (lighter) winds toward the west indicating a stronger (weaker) Walker circulation. The TPI is based on the difference between sea surface temperature anomalies (SSTA) averaged over the central and eastern equatorial Pacific and the average SSTA in the Northwest and Southwest (Henley et al., 2015). By contrast, the PDO does not take into account the South Pacific region. The TPI resembles a multidecadal “El Niño-like” pattern of climate variability. During its positive phase, the tropical Pacific is warm and trade winds are weak, whereas during its negative phase, the tropical Pacific is cool and the trade winds are strong. Finally, for the regional area, we show coastal and offshore SST anomalies from the ICOADS dataset, and a temperature difference between the offshore and coastal area that we refer to as a cross-shore temperature gradient. One characteristic of coastal upwelling regions is that the coastal SST is colder than offshore SST as a response of wind forcing (Nykjær & Van Camp, 1994). Thus, we use this SST gradient as a proxy to infer upwelling intensity since no other upwelling indices are available for the time period considered in this work.

The indices of ocean–atmosphere variability were obtained from online databases. The Pacific zonal wind stress data at 1,000 mb were downloaded from the NOAA/ESRL PSD webpage (<http://www.esrl.noaa.gov/psd/data/timeseries/>), from the 20th century reanalysis project (Compo et al., 2011); the selected region (6°N to 6°S and 180° to 150°W) corresponds to where the Interdecadal

Pacific Oscillation exhibits maximum regression onto Pacific Ocean winds (*sensu* England et al., 2014). The PDO values (Mantua & Hare, 2002) since 1860 were taken from <https://www.ncdc.noaa.gov/teleconnections/pdo/>. This PDO time series was developed by the National Centers for Environmental Information (NCEI) based on NOAA's extended reconstruction of SSTs (ERSST v4). The Interdecadal Pacific Oscillation Tripole Index (TPI unfiltered; Henley et al., 2015) was taken from the ERSST v4 dataset (<http://www.esrl.noaa.gov/psd/data/timeseries/IPOTPI/>). SSTs from the offshore (11–21°S; 80–90°W) and coastal area (12–17°S; 73–78°W) off Peru were taken from the ICOADS database (<http://www.rda.ucar.edu>). To estimate the SST from the coastal area, only the 1°×1° boxes nearest to the coastline were selected. More detailed information is available in the Supporting Information.

2.5 | Statistics

To seek for multiscale temporal coherency between time series, we applied a wavelet approach (Torrence & Compo, 1998). Wavelet analyses are well adapted to noisy, nonlinear, and nonstationary data (Cazelles & Stone, 2003). We resampled the time series from the composite record at a regular time step (3.7 years), based on the longest time step of the samples, and then used a cross-wavelet analysis that provide local information on the covariance of two processes at any scale (Ménard, Marsac, Bellier, & Cazelles, 2007). Wavelet was processed using the R package WaveletComp (Roschhand & Schmidbauer, 2014). More detailed information is available in the Supporting Information.

3 | RESULTS

3.1 | Major patterns in anchovy and sardine fluctuations

The primary downcore fluctuations in anchovy and sardine scales show broad coherent decadal to multidecadal-scale variability along the three different core locations in the HCS (Figure 2), but with some marked local differences. The records show two anchovy regimes (~1910–mid-1970s, and from the late 1990s to the date) and two sardine regimes (~1890–1910, and mid-1970s–late 1990s), although the temporal range of each regime is slightly different among cores (Figure 2). The two sardine periods are separated by ~70 years and last about ~20 years each, while the longest anchovy period is ~3 times longer than the sardine periods (Figure 2). These regimes are defined based on the relative persistence of sardine scales both within and between cores and taking into account that high sardine SDRs in Pisco indicate the period of maximal sardine expansion in the HCS. During the first multidecadal sardine regime (1890–1910), anchovy regimes are greatly reduced off Callao and Pisco but abundant in Mejillones Bay, which suggests that anchovy move further south in times of lower biomass. However, the transition from the sardine to the anchovy regime is not abrupt; anchovy SDRs increase before sardine scale SDRs diminish (Figure 2).

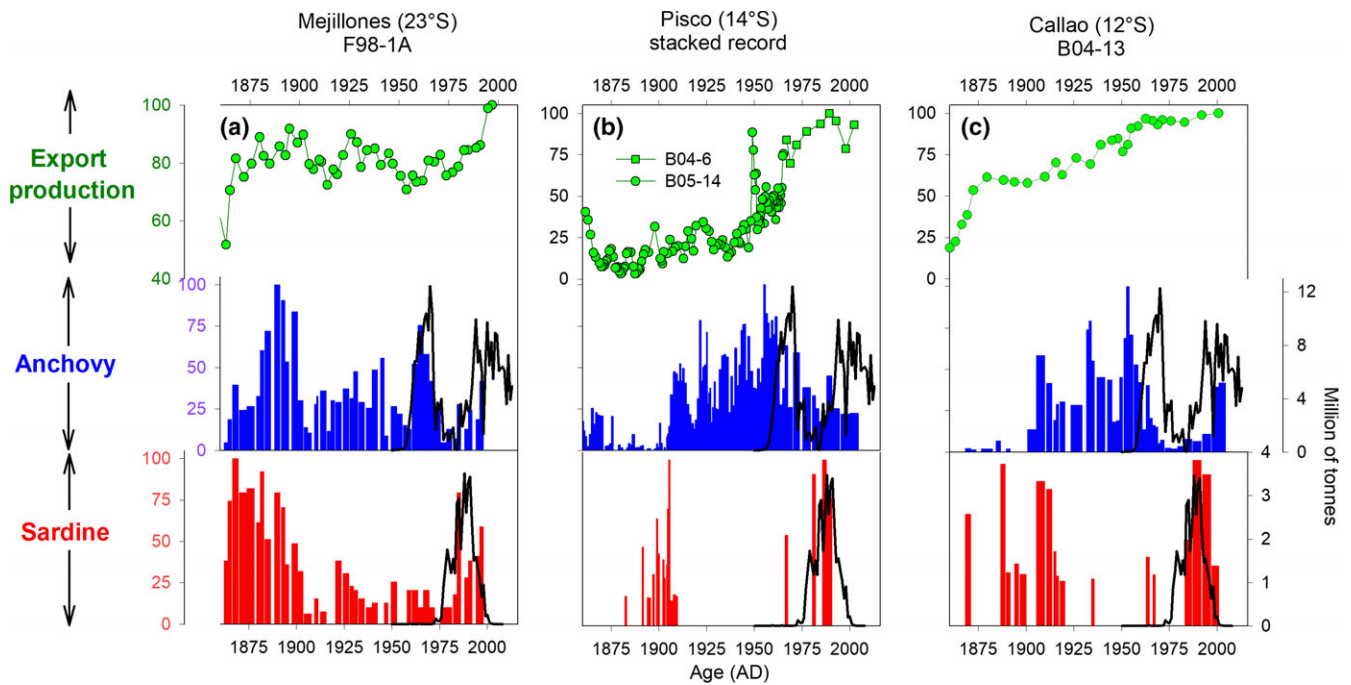


FIGURE 2 Paleo reconstructions of export production and fish abundance along the Humboldt Current System from south to north. (a) Mejillones (23°S), (b) Pisco (14°S), and (c) Callao (12°S). In green: Total organic carbon (TOC) fluxes ($\text{mg cm}^{-2} \text{y}^{-1}$) as a proxy for export production. In blue: Anchovy scale deposition rates (SDR) ($\#\text{scales cm}^{-2} \text{y}^{-1}$) along with anchovy landings (millions of tons, black bold line). In red: Sardine SDR ($\#\text{scales cm}^{-2} \text{y}^{-1}$) along with sardine landings (millions of tons, black bold line). The Mejillones record was taken from Valdés et al. (2008) and the Callao record from Gutiérrez et al. (2009). The records for export production and fish SDR are expressed as percentages of the maximum value in each time series for a better comparison among sites. The original data (fluxes) can be found in the Supporting information [Colour figure can be viewed at wileyonlinelibrary.com]

Multiple combinations of anchovy and sardine abundances are apparent in the HCS at decadal to multidecadal time scales, rather than simple sardine and anchovy alternations (Figure 2). The fish scale records show that there are decades of both high anchovy and high sardine abundances in Mejillones from 1870 to 1900 (Figure 2a), and considerable overlap in relatively high SDR of both species in Mejillones from 1900 to 1960 and in Callao from 1905 to 1921 (Figure 2c). The fish landings suggest an anchovy and sardine overlap of 11 years (from ~1986 to ~1997) since 1950 (Figure 1a,b), indicating that the anchovy and sardine overlap in the previous sardine regime is longer than during the fishery period (Figure 2). The fish scale records also show that from 1920 to 1960, anchovy are abundant and sardine scarce off the Central Peruvian coast but are present off Chile (Mejillones Bay), while anchovy are less abundant when high sardine SDR occurred from 1890 to 1910 (Figure 2). Additionally, low SDRs of both anchovy and sardine occur in Pisco and Callao from 1870 to 1880 (Figure 2b).

While the broad patterns of high and low abundance are mostly shared among sites, anchovy and sardine SDRs show different patterns of shared variability at each different sites. In Mejillones, anchovy and sardine SDRs show a positive and a significant correlation (Pearson correlation, $r = .41$, $n = 60$, $p = .001$), while in Callao and off Pisco, there is no correlation between the two species (Callao: $r = -.06$, $n = 54$, $p = .68$; Pisco: $r = -.03$, $n = 45$, $p = .85$). The different relationships suggest that part of the observed multidecadal variability at a given site may be due to shifts in the spatial distribution

and not entirely to changes in population size. Specifically the Mejillones site seems to be less reflective of total population sizes than the central Peruvian margin.

3.2 | Anchovy and sardine variability decoupled from marine productivity

The multidecadal anchovy and sardine fluctuations seem to be decoupled from marine productivity because the export production records do not follow the multidecadal fluctuation pattern observed in the fish SDR records (Figure 2). Instead, both, the Pisco and Callao records, show a positive trend in export production (Figure 2b,c), with values of more than 3 (Pisco) and 1.5 (Callao) times higher from ~1960 to 2005 compared to the rest of the record. Nevertheless, export production is positively correlated with both anchovy and sardine SDRs. Export production is low off Pisco and Callao from ~1860 to the first decades of the 20th century and increases since then (Figure 2b,c). Anchovy SDR and the export production record show a positive correlation in Mejillones (Pearson correlation, $r = .41$, $n = 60$, $p = .001$), while in Callao ($r = .34$, $n = 54$, $p = .012$) and off Pisco ($r = .28$, $n = 45$, $p = .06$), the correlations are also positive but weaker. In the three sites, the correlations of export production and anchovy SDR from 1860 to 1960 are higher than for the entire record (record shown in Figure 3, correlations not shown). There is a positive correlation of export production with sardine in Pisco ($r = .39$, $n = 44$, $p < .01$) and Mejillones ($r = .28$, $n = 60$, $p = .03$),

while in Callao, no correlation was observed (Callao, $r = .1$, $n = 54$, $p = .51$). The multiple modes of variability in anchovy, sardine, and export production highlight the multidimensionality of the HCS.

3.3 | Decadal to multidecadal changes of tropical and regional climate indices

The comparisons of the selected climate indices (Figure 3a–f) with our composite records of anchovy SDR, sardine SDR, and export production (Figure 3g–i) reveal the relative roles of regional and

large-scale climate on the HCS. The wavelet analyses provide evidence about the covariance between the multidecadal fluctuations of anchovy (Figure 4) and sardine (Figure 5) vs. the climate indices at multiple timescales.

Anchovy regimes (Figure 3h) are more associated with stronger zonal Pacific wind stress (Figure 3a), indicative of stronger Walker Circulation, and a cooler ETP (Figure 3c). Significant periods of variability (>32 years) occur for anchovy and these basin-scale indices since ca. 1950, but more consistent phase coherency (period of ca. 10 years) occurs only from 1920 to 1950 (Figure 4a,c). PDO and

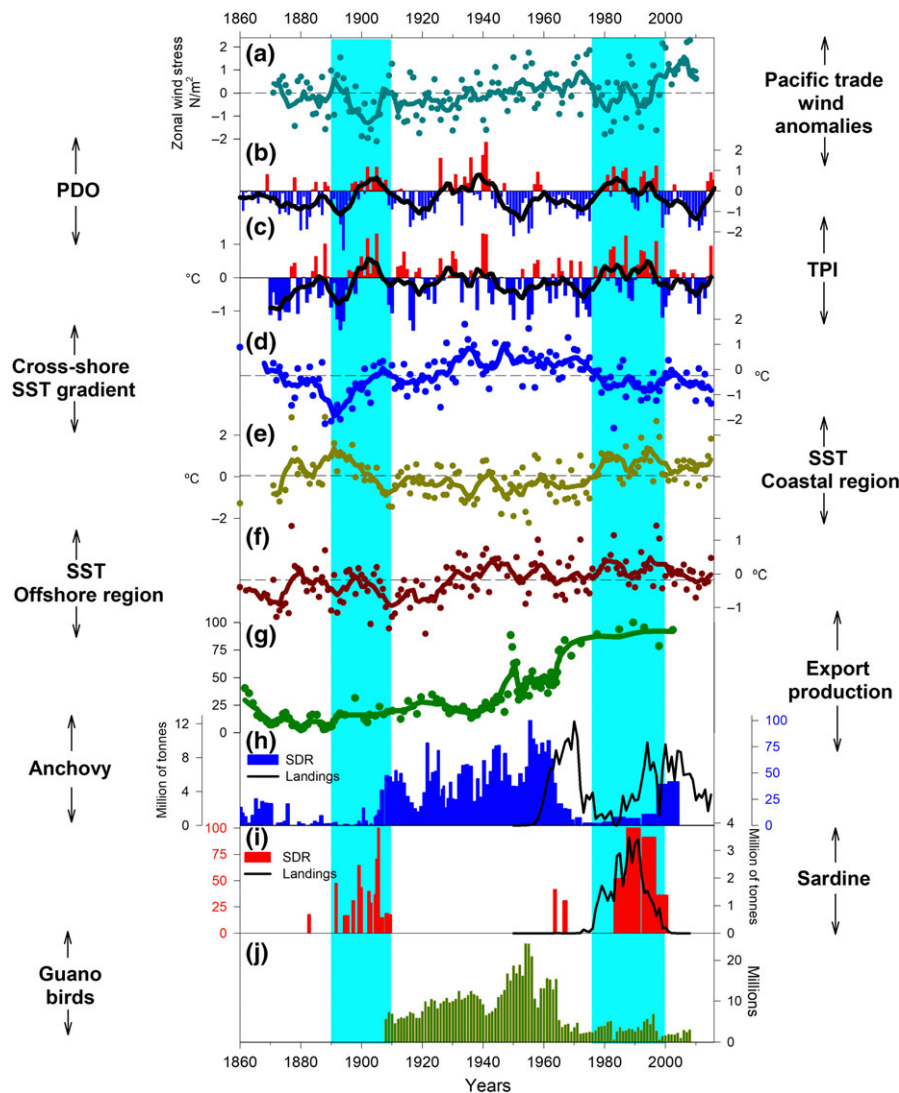


FIGURE 3 Physical indices of ocean–atmosphere variability in the tropical Pacific and off Peru and records of marine productivity. (a) Pacific zonal wind stress (Compo et al., 2011). (b) PDO index based on the NOAA's extended reconstruction of SSTs (ERSST Version 4). (c) Interdecadal Pacific Oscillation Tripole Index (TPI; Henley et al., 2015). (d) Cross-shore SST gradient calculated from the difference of the SST anomalies between the offshore and coastal areas off Peru. (e) SST anomalies from the coastal area (12° to 17° S; 73° to 78° W). (f) SST anomalies from the offshore area (11 to 21° S; 80 to 90° W). (g) Total organic carbon (TOC) fluxes as a proxy for export production off Pisco. (h) Anchovy scale deposition rates (SDR) and anchovy landings (bold line). (i) Sardine SDR and sardine landings (bold line). The records shown in h and i are based on a composite record (for more detail see Supporting Information). The records shown in export production and anchovy and sardine SDR are expressed as percentages of the maximum value in each time series (with the highest value of each time series assigned 100%); the original data (fluxes) can be found in the Supporting Information. (j) Number of guano producing birds: Guanay cormorant (*Leucocarbo bougainvillii*), Peruvian booby (*Sula variegata*), and Peruvian pelican (*Pelecanus thagus*), between 6° S and 14° S (data from IMARPE). In e, f, and g, the horizontal-dashed lines indicate the average of the dataset. In a–g, the thick-colored lines represent a 7-year running mean of the selected variable. The cyan boxes across the panels highlight the sardine periods (1890–1910 and 1976–1999) [Colour figure can be viewed at wileyonlinelibrary.com]

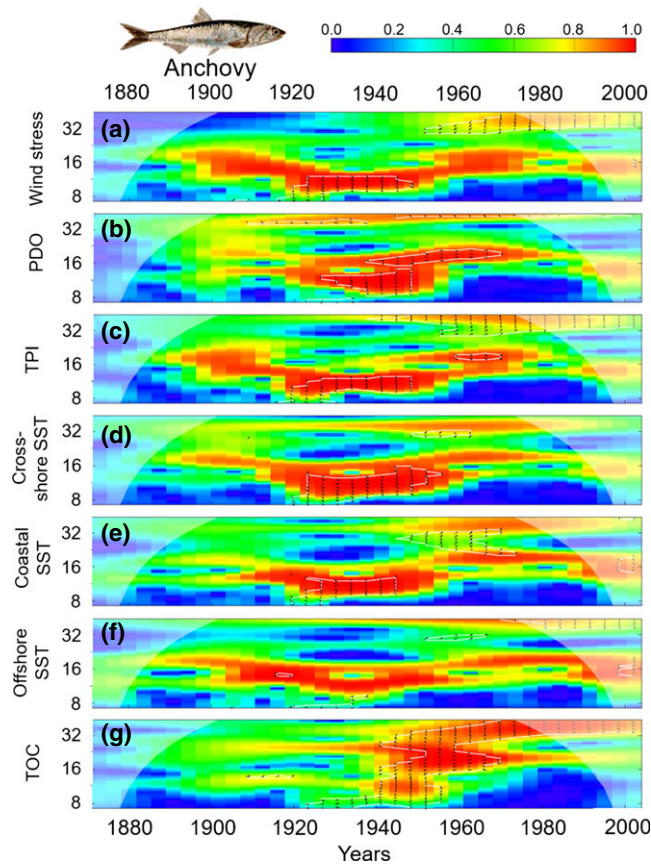


FIGURE 4 Wavelet analysis between anchovy SDR and proxies for environmental changes and export production. (a) Pacific zonal wind stress. (b) PDO index based on the NOAA's extended reconstruction of SSTs (ERSST Version 4). (c) Interdecadal Pacific Oscillation Tripole Index. (d) Cross-shore SST gradient. (e) SST anomalies from the coastal area. (f) SST anomalies from the offshore area. (g) Total organic carbon (TOC) fluxes. Arrows pointing to the right (left) indicate that the two series are in phase (out of phase). Arrows plotted within the white contour lines indicate significance (with respect to white noise processes) at the 10% level. Colors indicate significance levels. Y-axes (periods) are expressed in years [Colour figure can be viewed at wileyonlinelibrary.com]

anchovy present weak but significant phase opposition at a multi-decadal scale (period >32 years) during 1910–1940 and 1950–1990 (Figures 3b,h and 4b). On the contrary, the significant decadal variations observed at shorter periods (~8–20 years) in PDO during 1930–1970 are in some intervals in phase and in other intervals out of phase with anchovy fluctuation illustrating nonlinear relationships (Figure 4).

Regional temperature records, like the cross-shore temperature gradient (Figure 3d) and the coastal SST (Figure 3e), are more consistently related to anchovy fluctuations (Figures 3h and 4d–f) than the basin-scale indices. The gradient is weaker (suggesting weaker upwelling) from ~1885 to ~1900 and from ~1976 to ~1998, consistent with a decline in anchovy abundance, and stronger (suggesting stronger upwelling) from ~1900 to ~1970 and from ~1998 to ~2003, consistent with high anchovy abundance (Figure 3h). Accordingly, anchovy SDR and the cross-shore SST gradient show significant

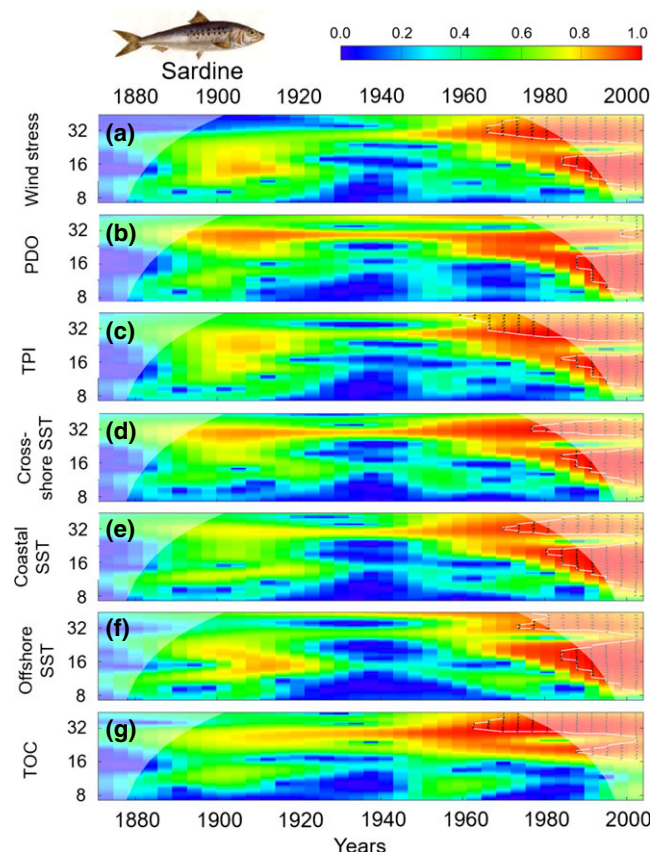


FIGURE 5 Wavelet analysis between sardine SDR and proxies for environmental changes and export production. (a) Pacific zonal wind stress. (b) PDO index based on the NOAA's extended reconstruction of SSTs (ERSST Version 4). (c) Interdecadal Pacific Oscillation Tripole Index. (d) Cross-shore SST gradient. (e) SST anomalies from the coastal area. (f) SST anomalies from the offshore area. (g) Total organic carbon (TOC) fluxes. Arrows pointing to the right (left) indicate that the two series are in phase (out of phase). Arrows plotted within the white contour lines indicate significance (with respect to white noise processes) at the 10% level. Colors indicate significance levels. Y-axes (periods) are expressed in years [Colour figure can be viewed at wileyonlinelibrary.com]

periods of variability (period <16 years) from 1920 to 1955, with an expected in phase relationship (Figure 4d). Anchovy SDR and the coastal SST also present significant periods of variability (period <16 years) from 1920 to 1945, with an expected out of phase relationship. Finally, offshore SST and anchovy patterns of variability do not present any clear relationships (Figure 4f). The last years of the record suggest a declining trend in upwelling intensity (Figure 3d), associated with a decline in anchovy landings (Figure 3h). An important observation is that the decrease in upwelling intensity from ~1977 to ~1999 is associated with a decrease in wind stress in the tropical Pacific (Figure 3a,d). However, during the first multidecadal sardine period (1890–1910), the decrease in upwelling intensity occurred 10 years before the decrease in Pacific zonal wind stress. This suggests a decoupling of regional and basin-scale forcings at the end of the 19th century and indicates an important role for regional forcing.

In the case of sardine, the two regimes (highlighted areas in Figure 3) are generally contemporaneous with periods of weaker zonal Pacific wind stress (Figure 3a), indicative of a weak Walker Circulation, and with the two warmest multidecadal TPI periods (Figure 3c). However, no sardine regime occurs during ~1920–1940 when warm TPI and PDO phases are also observed. Among the two sardine regimes (highlighted areas in Figure 3), only the most recent one presents a significant and expected covariation with the environmental proxies (Figure 5). Sardine SDR is then in significant phase opposition with the Tropical Pacific wind stress and in phase with the TPI (Figure 5a,c). In the same way, only the last sardine regime is significantly in phase with PDO variability (Figures 3b,i and 5b).

As also observed in the case of anchovy regimes, regional temperature records (Figure 3d–f) are more consistently related to sardine fluctuations (Figure 3i) than the basin-scale indices. Particularly, the two sardine regimes have strongest correspondence with the coastal SST record, which displays a first warm period from ~1870 to ~1900, and a second from the mid-1970s to the late 1990s (Figure 3e). Accordingly, the wavelet analyses (at multiple time scales of variability) show that sardine SDR was in a significant phase opposition with the cross-shore gradient and in phase with the coastal and offshore SST during the last decades (Figure 5d,e,f).

The multidecadal-scale anchovy and sardine fluctuations do not show the same multidecadal pattern as export production (Figure 3g, h,i), which suggests that, at these timescales, anchovy and sardine are not driven by productivity nor do they strongly control export production. Accordingly, anchovy SDR and TOC show multiple significant periods of variability (<8 to >32 years) from 1920 to 2005 (Figure 4g). However, these time series show both weak in-phase relationships from 1920 to 1935 (<8 years) and strong out of phase relationship from 1950 to 1970 at longer timescales (>16 years). In the case of sardine (Figure 5g), only the most recent sardine regime presents a significant covariation with TOC at longer timescales (>30 years).

The increase in upwelling from ~1905 to 1971 (Figure 3d) is associated with an increase in export production (Figure 3g) as well as an increase in abundances of intermediate (i.e., anchovy; Figure 3h) and higher (i.e., guano birds; Figure 3j) trophic levels. The positive trend toward strong upwelling, high abundance of anchovy and guano birds is interrupted from ~1971 to the mid-1990s, associated with a weaker tropical Pacific zonal wind stress (Figure 3a), triggering a sardine regime but not reducing export production (Figure 3g). Export production and the offshore SST record show a similar increasing trend from the start of the 20th century (Figure 3f, g). The record of SST anomalies offshore off Peru (Figure 3f) indicate a warm period between ~1880 and 1900, associated with the first sardine period, and then a warming trend from 1905 to the end of the record. From ~1900 to the mid-1970s, however, the coastal region do not exhibit a warming trend like the offshore area (and global average). The decrease in guano bird abundance after the start of the fishery (~1960) has been attributed to a combination of fishing pressure, prey accessibility, and the effect of El Niño in 1965

(Duffy, 1994; Jahncke, Checkley, & Hunt, 2004; Tovar et al., 1987). The increase in anchovy productivity resumes in the late 1990s and continues to ~2002, after which a slight decline in upwelling intensity and anchovy landings is observed during the last years of the record (Figure 3d,h).

4 | DISCUSSION

The modes and timescales of variability observed in our records demonstrate that the range of variations observed in the second half of the 20th century represent only part of the multiple responses of the HCS to climatic and oceanographic changes. In particular, our results provide evidence for asynchronous, regional fluctuations in fish distribution at decadal timescales, for multiple modes and timescales of variability in anchovy and sardine regimes, for a weak coupling between export production and fish fluctuations, and that regional dynamics are at least as important as basin-scale dynamics controlling fish population sizes and displacements, likely through modulations of the amount of habitat.

4.1 | Regional, asynchronous fluctuations in fish distribution at decadal timescales

In the HCS, anchovy and sardine modify their distribution (both along and cross-shore) at seasonal to interannual timescales according to the oceanographic conditions (Bertrand et al., 2004, 2011; Gutiérrez et al., 2007). Our results suggest that modifications in population distribution occur in response to oceanographic changes also at longer timescales. For example, the persistence of anchovy in the southern part of their range (Mejillones) for several decades from ~1880 to ~1905, when upwelling and anchovy were dramatically reduced in the northern part of their range off Peru, is concordant with the observation that during strong El Niño events anchovy tend to move coast and southward (Alheit & Ñiquen, 2004). Moreover, in Mejillones and Callao, sardine prevailed during a more extended time interval than in Pisco, which is also in accordance with the observed sardine distribution in the HCS (Gutiérrez et al., 2012). During the first half of the last sardine period in the 1980s, sardine regimes were distributed along the entire HCS, while during the declining phase of the sardine period (late 1990s), sardine regimes were distributed in the northern (around Callao) and southern (around Mejillones) parts of their range (Gutiérrez et al., 2012). The latter appears to be a permanent sardine habitat (Checkley et al., 2009). Our results emphasize the importance of regional population displacements at multidecadal time scales, and that they must be taken into account for the reconstruction of past fish abundance fluctuations. Furthermore, the high resolution records from multiple locations reiterate the belief that scale records from a single location can reflect many of the primary downcore changes observed at multiple sites, but regional differences due to population dynamics and shifts in distribution occur in patterns expected based on modern observations (Field et al., 2009).

4.2 | Multiple modes of variability in anchovy and sardine regimes

The different combinations of anchovy and sardine abundances are consistent with nonalternating fluctuations documented in the HCS at centennial time scales (Gutiérrez et al., 2009), but do not support the paradigm of regular anchovy and sardine alternations (Chavez et al., 2003; Schwartzlose et al., 1999). During the Little Ice Age (LIA), a global cold period that lasted from 1500 to 1850 AD, not only anchovy biomass was greatly reduced but also sardine was absent from the Peruvian coast (Gutiérrez et al., 2009; Salvattecí et al., 2012). Moreover, other types of variability involving high abundances of both species and also low abundance of both species observed in our records (Figure 2) make the multidimensionality of the system evident. Alternations between sardine and anchovy seem to be circumstantial and do not follow a consistent pattern in the HCS (McCall, 2009).

4.3 | Multiple timescales of variability in anchovy and sardine regimes

The observation of an anchovy regime that lasted ~65 years and a sardine regime of ~20 years adds to a growing body of evidence indicating that sardine and anchovy have a wide range of timescales at which they persist, as opposed to the suggested 50–60 years periodicity derived from fishery landings (Chavez et al., 2003; Schwartzlose et al., 1999). In the Santa Barbara Basin off California, both anchovy and sardine periods sometimes fluctuated at a period of approximately 60 years, but periods of persistence occurred at much shorter and longer timescales (Baumgartner et al., 1992; Lindgren, Checkley, Rouyer, MacCall, & Stenseth, 2013). The multiple timescales regarding anchovy and sardine fluctuations observed in the paleorecords indicate a wider range of long-term variability compared to the late 20th century observations. Past periodicities should be interpreted with caution for predicting future changes in anchovy and sardine temporal fluctuations, particularly with the advent of anthropogenic global warming (Field et al., 2009).

4.4 | Weak coupling between export production and fish fluctuations

The weak relationship between export production and anchovy and sardine fluctuations suggests that in the HCS, food abundance is not the limiting factor for anchovy and sardine population growth, at least during a time period of medium to high productivity that occurred after the LIA (Gutiérrez et al., 2009). While the earliest sardine period had relatively low export production, the export production in the most recent period was relatively high, although the warmer ocean conditions would be expected to coincide with a low-production regime (Chavez et al., 2003). Several authors have suggested that food quality (e.g., zooplankton size) plays a major role driving anchovy and sardine fluctuations (Espinoza & Bertrand, 2008; Espinoza, Bertrand, van der Lingen, Garrido, & Rojas de Mendiola,

2009; van der Lingen et al., 2009), rather than food abundance, which would better explain the observed patterns. The size structure of zooplankton also exhibited multidecadal fluctuations during the last 50 years; euphausiids and large copepods were associated with the anchovy regimes while small zooplankton dominated when sardine was abundant (Ayón, Swartzman, Espinoza, & Bertrand, 2011).

The mechanism behind the similar trends in export production and offshore SST records (Figure 3f,g) can be explained taking into account the seasonal variation in productivity. During spring–summer, when upwelling is less frequent and less intense than in winter, upwelling relaxation is followed by onshore pulses of stratified waters that promote phytoplankton blooms until nutrients are depleted (Echevin, Aumont, Ledesma, & Flores, 2008; Gutiérrez et al., 2011). In addition, an increase in water column stratification as a result of increased warming would result in less mixing and light limitation promoting primary production. Thus, a multidecadal trend of increasing spring–summer upwelling, as revealed by an alkenone record off Pisco (Gutiérrez et al., 2011), combined with an increase in offshore SST could be triggering the increase in export production observed in our records.

4.5 | Regional dynamics as important as basin-scale dynamics

Regional dynamics inferred from the cross-shore temperature gradient (Figure 3d) are more consistently related to anchovy fluctuations than basin-scale indices (Figure 3b,c), suggesting an important role of regional processes underlying anchovy–sardine fluctuations. The increase in upwelling, associated with the anchovy regimes, probably also increased the spatial extent of the habitat favorable for anchovy leading to an increase in anchovy biomass. This observation is consistent with the hypothesis that anchovy concentration increases in a favorable habitat when habitat quality increases (Barange et al., 2009; Bertrand et al., 2004), while it does not seem to spatially expand into and cope with less favorable habitats. Anchovy regimes require habitat to become available for population to grow (Barange et al., 2009; Bertrand et al., 2004); therefore, the change in the extent of the favorable habitat may be a driving mechanism for anchovy and sardine fluctuations.

4.6 | Changes in the regional 3D habitat as a driver of anchovy and sardine fluctuations

Identifying causality between environment and resources is difficult since nonlinearity is ubiquitous in nature and some processes are stochastic (Sugihara et al., 2012). Moreover, fish populations are dependent both on density-dependent processes (e.g., species-specific life history) and density-independent processes (e.g., ocean–atmosphere dynamics). It is, therefore, important to combine several factors to understand anchovy and sardine fluctuations (Jacobson & MacCall, 1995; Jacobson & McClatchie, 2013; Lindgren et al., 2013; McCall, 2009). In the California Current, for example, sardine SDR and PDO alone are not correlated (McClatchie, 2012), but the

multidecadal variability in anchovy and sardine fluctuations since 1661 AD was successfully modelled by a combination of density-dependent processes and climate forcing (including the PDO; Lindgren et al., 2013). In the HCS, the interaction of climate indices and density-dependent processes could also play a role in anchovy and sardine fluctuations, but the relatively short time series do not provide robust results from tests of causation like convergent cross mapping (Sugihara et al., 2012) or nonlinear dependence using generalized additive models (data not shown). Nonetheless, our results along with studies from the last several decades (e.g., Ayón et al., 2011; Bertrand et al., 2011; Gutiérrez et al., 2007; Swartzman, Bertrand, Gutiérrez, Bertrand, & Vasquez, 2008) allow for a synthesis of the most favorable conditions for each species and help understanding the multidimensionality of the changing conditions of anchovy and sardine habitat.

Changes in the vertical and horizontal extent of the local 3D habitat can trigger anchovy and sardine regimes, because they induce, among other factors, important changes in prey and recruitment conditions. A key characteristic of the HCS is the presence of an intense and shallow oxygen minimum zone (OMZ) limiting the vertical range of habitat of most species (Bertrand, Ballon, & Chaigneau, 2010; Bertrand et al., 2011). In the HCS, pelagic habitats are bounded vertically by the oxycline, so they should be regarded in 3D (Bertrand et al., 2010). Separate conditions and areas of optimal habitat for sardine and anchovy result in their generally different periods of greatest abundance. However, temporal and spatial variability in anchovy and sardine habitat allow them to coexist for periods of many years to decades (Bertrand et al., 2011; Field et al., 2009; Gutiérrez et al., 2009; Valdés et al., 2008).

The ideal conditions favorable for anchovy development seem relatively clear. To flourish anchovy need enough food and an access to large vertically migrating zooplankton that distribute mainly offshore, that is, the cold coastal waters need to extend offshore (Ballón et al., 2011; Bertrand et al., 2011; Espinoza & Bertrand, 2008). During a great part of the record (from ~1905 to 1970), there was an efficient upwelling of cold and nutrient-rich waters probably in combination with a shallower thermocline and larger zooplankton; characteristics that are favorable for the development of anchovy (Bertrand et al., 2011). A shallow-oxygenated habitat, promoted by the increase in upwelling, concentrates the prey near the surface enhancing anchovy foraging and leading to a reproductive advantage over sardine (Bertrand et al., 2011, 2014). On the opposite, anchovy are less abundant when the productivity is very low (Figure 3g) and/or when the horizontal extent of the cold coastal waters is reduced and the oxycline deepen as was observed from the 1970s–mid-1990s (Figure 3; Bertrand et al., 2011). In this last case, anchovy is confined close to the coast limiting its access to large zooplankton in particular the euphausiids (Bertrand et al., 2011; Espinoza & Bertrand, 2008). The highest anchovy abundance in the coastal area of Mejillones occurred (Figure 2a) during a dramatic upwelling reduction as evidenced by the lowest cross-shore SST values around 1890 AD (Figure 3f). This reinforces the idea that upwelling decline associated with a reduction in

horizontal habitat led anchovy to concentrate in coastal refuge areas (Bertrand et al., 2004).

By contrast, to flourish sardine require a complex set of conditions in terms of productivity, oxygen content, and plankton size structure. Indeed, from the 1970s to mid-1990s, the HCS was characterized by a deeper thermocline and a shift to smaller-sized zooplankton (Ayón et al., 2011; Bertrand et al., 2011). Sardine is physiologically well adapted to filter-feed on small zooplankton (van der Lingen, 1995), whereas for anchovy, it is energetically very expensive (James & Probyn, 1989). In addition, the HCS was more oxygenated and the front between coastal low-oxygen waters and the high-oxygen (and warmer) water moved closer to the coast (Bertrand et al., 2011). Consequently, sardine could distribute closer to the coast (Bertrand et al., 2011) and benefit from the coastal production and retention (Brochier, Lett, & Fréon, 2011), enhancing their recruitment. During the last 150 years, sardine were more consistently present off Mejillones (Figure 2) where the oxycline is deeper than the central Peruvian coast (Fuenzalida, Schneider, Garcés-Vargas, Bravo, & Lange, 2009). Moreover, both sardine periods were characterized by weaker winds, and thus a weak Walker Circulation, and a warmer Tropical Pacific (Figure 3a,c,i), while a high number of strong and very strong El Niño events likely oxygenated the system (Gergis & Fowler, 2006). Warmer coastal SST generally corresponds to a reduced upwelling of cold and nutrient-rich water, a coastward incursion of oceanic waters characterized by a deeper oxycline and thermocline, and smaller zooplankton, favoring sardine (Bertrand et al., 2011). It is thus probable that these conditions, during decadal-scale periods, characterized by a weaker Walker Circulation and reduced coastal upwelling are conducive to sardine development. These complex processes could not be completely disentangled with our proxies.

While our results support bottom-up forcing driven by regional climate modifying the 3D habitat, it could be hypothesized that interactions between sardine and anchovy or other mechanisms might trigger a shift in their respective abundance through trophic competition or behavioral processes. However, our results and other long-term studies (Field et al., 2009; Gutiérrez et al., 2009) show periods of low and high abundance of both species as well as periods with one species dominating. The thermal range of anchovy and sardine is very large (Bertrand et al., 2004; Swartzman et al., 2008) and except during strong extraordinary El Niño events, both species are well adapted to local thermal conditions. Sardine is rather ubiquitous relative to water masses (Swartzman et al., 2008) but need a deeper oxycline (Bertrand et al., 2011), so it is always distributed further offshore than anchovy in the northern HCS. This explain why the spatial overlap between sardine and anchovy is not that high even when both species are present in the system (Gutiérrez et al., 2007; Swartzman et al., 2008). Furthermore, the feeding capabilities of anchovy and sardine are different, so they can exploit different trophic niches (Espinoza & Bertrand, 2008; Espinoza et al., 2009; van der Lingen et al., 2009). Sardine and anchovy are thus ecological neighbors but not direct competitors (Gutiérrez et al., 2007).

The combined evidence of the present study clearly refutes a linear driving effect of Pacific basin interdecadal changes in fish fluctuations in the HCS. Based on the paradigm, we would have expected sardine to flourish during positive PDO periods (Chavez et al., 2003), but this was not the case during the warm PDO phase of 1920–1940 (Figure 3b); when a strong coastal gradient persisted, indicating sustained upwelling. Only in the late 20th century, records of tropical Pacific variability (e.g., Figure 3a) largely follow the PDO, indicating a strong role of the tropical Pacific dynamics in the North Pacific area resulting in a strong coherence of physical and biological forcing in both the tropical and extratropical Pacific (Deser & Phillips, 2006; Deser, Phillips, & Hurrell, 2004; Graham, 1994). This strong coupling of tropical forcing and local upwelling intensity off Peru from ~1960 to 2000 (Figure 3a,d,e) might explain the apparent synchronization of anchovy and sardine in the Pacific during the last decades (Schwartzlose et al., 1999). However, in the late 19th century and the start of the 20th century, this relationship is not evident, and there must have been different mechanisms driving the North Pacific variability (D'Arrigo et al., 2005).

4.7 | Anchovy in a warmer world

The collective evidence from this study and others indicates that there is a trend toward higher marine productivity during most of the 20th century and that anchovy biomass may be up to eight times higher than the last 500 years (Gutiérrez et al., 2009), although with superimposed variability (Figure 3). The increase in upwelling intensity translated via a bottom-up mechanism to higher trophic levels, increasing their populations. For example, in the 1950s, the number of guano birds doubled compared to the first decades of the 20th century (Figure 3j). In the HCS, bottom-up processes structure the faunal distribution from zooplankton to guano birds (Bertrand et al., 2014). Climate warming was favorable for anchovy productivity in the HCS until the start of the 21st century. Models of future climate scenarios predict a weakening of upwelling-favorable winds off Peru and southern Chile and a strengthening south of 35°S (Belmadani, Echevin, Codron, Takahashi, & Junquas, 2013; Brochier et al., 2013; Echevin, Goubanova, Belmadani, & Dewitte, 2011). These conditions will probably cause a potential southward shift of anchovy distribution in the next decades, opposed to the northward distribution pattern observed from the 1960s to the date (Gutiérrez et al., 2012). The interactions among climate, oceanographic conditions, and small pelagic fishes are complex and highly sensitive. Thus, the future of the HCS and the productivity predictions remain uncertain and should be treated as such in future management strategies.

In conclusion, our paleo records challenge the current paradigms of climate forcing and ecosystem response, particularly the idea that anchovy and sardine alternate according to large-scale changes across the Pacific. We show that fishery-independent paleo data from at least several well-dated sediment records along a latitudinal gradient are needed to unravel the complexity of underlying mechanisms of small pelagic fish fluctuations. Proposed mechanisms of

change must be consistent with paleo-record observations if they are to be predictive and helpful in understanding future changes. In the HCS, complex and variable bottom-up modifications of the 3D habitat, driven by regional or basin-scale mechanisms, seem to be the major driver of anchovy and sardine population expansion and contraction.

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SUPPORTING INFORMATION

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