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250 years of sardine and anchovy scale deposition record in Mejillones Bay, northern Chile

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ABSTRACT

Marine oxygen-deficient environments with high sedimentation rates and high primary productivity can provide relevant information regarding variations of ocean-climatic conditions in the past. In the Humboldt current ecosystem, which now hosts huge populations of pelagic fishes (mainly anchovy and sardine), fish scale abundance in the sedimentary record may be useful indicators of environmental change. Here we assess such a proxy record in a 42 cm-long sedimentary core collected from 80 m in Mejillones Bay (23°S, northern Chile). We also analyse fish remains in surface sediment sampled along a bathymetric transect (from 10 to 110 m water depth) in the same bay. In the core-top record, the fluctuations of sardine and anchovy scale deposition rates (SDR) agreed with those of industrial catches for these two species in northern Chile, tending to validate the SDR as a proxy of local fish biomass when bottom anoxic conditions prevail. However, apparent SDR for records prior to 1820 have probably been influenced by dissolution processes linked to the oxygenation of the bottom environment of Mejillones Bay, as suggested by other proxy records. After 1820, the fluctuations in the relative abundance of sardine and anchovy scales point to alternating warm and cold conditions during about 30 years and then a progressively cooler period. Since ca. 1870, marked fluctuations of SDR of both species are observed, probably as a consequence of the onset of a different oceanographic regime characterized by intensified upwelling, stronger subsurface oxygen deficiency, higher primary productivity, and enhanced "ENSOlike" interdecadal variability. While anchovy SDR fluctuated in periods of 25-40 years, only two peak periods of sardine SDR occurred (late 19th century and late 20th century), suggesting that sardine abundance depends on other ocean-climatic factors.

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1. Introduction

Pelagic fish catches have exhibited large global fluctuations in the course of the last few decades. These fluctuations have been interpreted variously as depending upon fishing activity or upon natural variations in fish populations as a response to the environmental changes which operate at different time and space scales (Lluch-Belda et al., 1992; Yañez et al., 2001; Chavez et al., 2003; Gutierrez et al., 2007). Historical fluctuations in sardine and anchovy stocks in the Northern Hemisphere, for instance, were principally attributed to climatic changes at a large geographical scale (Lluch-Belda et al., 1989; Baumgartner et al., 1992). A similar situation occurs in the Southern Hemisphere in the Humboldt current ecosystem where the ENSO mode of climatic variability seems to strongly influence the fish stocks (Cañón, 1978, 1985; Cury, 1988; Yañez, 1989; Csirke et al., 1996; Yañez et al., 1998; Schwartzlose et al., 1999; Chavez et al., 2003; Bertrand et al., 2004; Escribano et al., 2004; Ñiquen and Bouchon, 2004).

Past fluctuations of pelagic fish populations and oceanographic conditions can be deduced from analyses of laminated marine sediment sequences when particular physico-chemical conditions are met, particularly in low-oxygen environments (Fitch, 1969; Soutar and Isaacs, 1969; DeVries, 1979; Schwartzlose et al., 1999; O'Connell and Tunnicliffe, 2001). In such environments, which are much less affected by bioturbation and other post-depositional processes, fish remains and particularly their scales are often well-preserved and can provide a record of former fish populations (Gallardo, 1963; Milessi et al., 2005). Relationships between fish remains in sediments and past fluctuations of pelagic populations





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have mainly been studied in the California Current ecosystem (e.g. Soutar, 1967; Fitch, 1969; Soutar and Isaacs, 1969; Baumgartner et al., 1992; Holmgren-Urba and Baumgartner, 1993; Tunnicliffe et al., 2001; Wright et al., 2005). In the Humboldt current ecosystem of northern Chile and Peru, few studies have examined fish scales as paleoenvironmental and paleoceanographic indicators (DeVries and Pearcy, 1982). Schwartzlose et al. (1999) stressed the need for more detailed studies on fish remains in sediments of the Humboldt current ecosystem to better understand the links between oceanic/climatic phenomena and fish fluctuations.

In northern Chile, a series of previous studies (Ortlieb et al., 2000; Valdés et al., 2000, 2004; Valdés and Ortlieb, 2001; Valdés, 2004; Vargas et al., 2004, 2007) pinpointed the high paleoceanographic potential of sediments accumulated in Mejillones Bay (23°S; Fig. 1). This bay is characterized by a coastal upwelling centered at nearby Punta Angamos, hydrodynamic stability behind a thermal front, high sedimentation rates, and occurrence of the oxygen minimum zone below 40–60 m depth depending on the season (Fig. 1; Zúñiga et al., 1983; Rodríguez et al., 1991; Marín et al., 1993; Valdés et al., 2003). These conditions, which prevail during non-El Niño years, favour the accumulation of abundant biogenic remains and the preservation of primary structure of bottom sediment. In this study we evaluate the quality of the sedimentary record of pelagic fish abundance in Mejillones Bay, with emphasis on the state of preservation of the fish remains, their taxonomic identification, and their potential significance for the reconstruction of former variations of pelagic fish populations.

2. Materials and methods

A 42 cm long sedimentary core (F98-1A) was recovered with a boxcore ("Fuchsia" type) from 80 m of water depth at the center of the Mejillones Bay (Fig. 1). This core was cut transversely every 0.5 cm immediately after sampling, and the samples were disaggregated and sieved through a 250 μ m mesh, under a constant flow of water. Fish scales were identified and counted using a microscope. Additionally, superficial modern sediment samples were taken along a bathymetric transect between 14 and 120 m of water depth in the central zone of the bay (Fig. 1) using a small box corer with a 225 cm² section. Surface sediment (0.5 cm thick) was taken from each sample and kept at low temperatures during transport and storage.

The identification of the fish scales was restricted to the socalled "typical scales" characteristic of each species; such scales



Fig. 1. Schematic geographic and oceanographic setting of the study area, Mejillones Bay, with localization of the sampling zones (bathymetric transects and F98-1A sediment core). Vertical distribution of dissolved oxygen in the water column of Mejillones Bay between 2001 and 2004 (below left) is also shown.



Fig. 2. Sardine (A) and anchovy scales (B). Modern (left) and fossil scales (right) found in the sedimentary core. Principal structures used for the taxonomic identification are indicated (see text).

are those more easily released from the fish body and are found in greater abundance in bottom sediments (Soutar, 1967; Soutar and Isaacs, 1974; DeVries and Pearcy, 1982; Shackleton, 1987; O'Connell and Tunnicliffe, 2001). Typical scales were defined by reference to a preliminary collection of the most important fishes present in the study area, and are characterized by shape, position and shape of scale focus, appearance of the anterior and posterior fields, and radii (Fig. 2).

The most typical scales of both species used in this study present the following characteristics:

 Order: Clupeiformes; Family: Clupeidae; Specie: Sardinops sagax (Jenyns, 1842) – sardine.

Scale type: cycloid (Fig. 2).

Shape: square, with relatively round edges.

Focus: diffused aspect, located in the middle part of the scale, close to the posterior field.

Radii: regular, well-defined and parallel grooves or channels present between the insertion zone and the focal point.

 Order: Clupeiformes; Family: Engraulidae; Specie: Engraulis ringens (Jenyns, 1842) – anchovy.

Scale type: cycloid (Fig. 2).

Shape: rectangular with oval borders in a shield-like form, and with prominent convex lateral borders around the stuffed area.

Focus: diffused aspect, located close to the posterior field. Radii: longitudinal and external (outer border) position which converge towards the focus, and ornamented with numerous circuli.

The sediment core scales were compared with modern scales from each of the species present in the study area. For the quantification of fish scale abundance in the sediment samples, the following rules were applied: (i) a scale was counted whenever the nucleus and more than one half of the scale were preserved; (ii) counts of 0.5 units were applied for incomplete half-scales which did not show the scale nucleus, provided that no other incomplete scale of the same species was found in the same sample; (iii) the smallest scale fragments were not counted. The chronological framework of the sediment core was determined through the combination of downcore excess ²¹⁰Pb activities and ¹⁴C ages, as detailed in Vargas (2002) and Vargas et al. (2007). The sedimentation rate was estimated to be 0.131 ± 0.07 cm y⁻¹, which is equivalent to a 2–4 year resolution for 0.5 cm slices obtained from this core. The accumulation of scales down the sediment core is expressed as a scale deposition rate (SDR), according the following formula: SDR = (N^*T)/A, in which N represents the number of scales in each sample, T the time interval of such sample, and A is the cross sectional area of the core (cm²).

3. Results and discussion

3.1. Preservation of fish remains and distribution of sardine and anchovy scales

In this paper we focus on sardine and anchovy scale records because fishery catch and ecological data are available for these two taxa in terms of geographic distribution, importance as fishing resources, and significance for teleconnection studies related to ocean–climatic interactions (Baumgartner et al., 1992; Schwartzlose et al., 1999; Yañez et al., 2001; Chavez et al., 2003;



Fig. 3. Dissolved oxygen (in mLL^{-1}) distribution in the water column of Mejillones Bay, in October 2004, along the studied transect (see Fig. 1).

Niquen and Bouchon, 2004; Miller et al., 2006). Off northern Chile, anchovy reaches a maximum length of 19 cm, has a short life span (4 years), and is distributed principally within the first 60 nm offshore, and most often the first 25 nm. The sardine is larger (to 40 cm long) and lives longer (25 years), and has a more offshore distribution (0–200 nm) (Gutierrez et al., 2007). Both species commonly live above the thermocline (Yañez et al., 2001). In the study area, the Punta Angamos upwelling center (Fig. 1) adjacent to the bay produces a high biological productivity which favours anchovy and sardine, particularly during their reproductive periods (Barbieri et al., 1995). The fish remains present in surface sediment and box-core samples correspond to scales, vertebrae, dental pieces, opercula and bones from the scapular zone and otoliths which generally exhibit a low degree of degradation by physical and/or chemical processes. The scales were the most abundant fish debris found in the sediments. Even though they present different degrees of fragmentation, their principal characteristics (shape, anterior and posterior field, head shapes, radii) are well-preserved and allow identification of anchovy, sardine, and mackerel (*Trachurus murphyi*). However, preservation of the fish debris is imperfect and depends on many factors, e.g. their chemical composition and surrounding



Fig. 4. Sardine and anchovy scale abundances in surface sediments (core top, 0–0.5 cm) along the studied transect (see Fig. 1). Abundance is expressed in number of scales per area of sampling (225 cm²).



Fig. 5. Anchovy and sardine SDR for the last two decades in Mejillones Bay. The chronology was taken from Vargas et al. (2007). Each point in the curve corresponds to 0.5 cm of sediment (\sim 3 year time range, according to sedimentation rate: see text). SDR is expressed in Number of scales 1000 cm⁻² y⁻¹. Most important dates cited in the text are highlighted.

sediments, mechanical abrasion, and the rate of bacterial degradation (O'Connell and Tunnicliffe, 2001). Fish bones are compounds of collagen that eventually harden with salts, while the scales are a mixture of microcrystalline apatite within a collagen matrix (Wright et al., 2005) and have greater susceptibility to degradation (Tunnicliffe et al., 2001). Schenau and De Lange (2000) indicate that in aerobic bottom sediments, the acidity generated during organic matter degradation can provoke the dissolution of biogenic apatite, a situation that is strongly reduced in anaerobic environments. The cited authors conclude that the presence of an intense oxygen minimum zone (OMZ) may account for the enhanced preservation of fish debris in sedimentary deposits of the continental margins. Therefore, in Mejillones Bay, the presence of an OMZ diminishes the potential chemical degradation of fish debris. Moreover, the quite limited mechanical abrasion observed in this material coincides with the general lack of benthic organism activity and of bacterial action. The preserved state of fish scales in the sediment of Mejillones Bay is comparable with others sedimentary records of northern Chile (Gallardo, 1963; Milessi et al., 2005); the continental margin of Peru (DeVries, 1979; DeVries and Pearcy, 1982); and the California current ecosystem (Soutar and Isaacs, 1974; Baumgartner et al., 1992; Wright et al., 2005).

To examine the effect of bottom water oxygen concentration on the preservation of fish debris (O'Connell and Tunnicliffe, 2001; Tunnicliffe et al., 2001), we assessed the abundance, composition and preservation state of scales as a function of the oxygenation of the depositional environment within Mejillones Bay. The distribution of dissolved oxygen across a south–north section of the water column in October 2004 is showed in Fig. 3. Based on the oxygenation scale of Bernhard and Sen Gupta (1999) (oxic, >1 mL L⁻¹; disoxic, 0.1–1 mL L⁻¹; microxic, <0.1 mL L⁻¹), most sediments of this bay appear to have been deposited under microxic conditions while, at shallow depth, the environment was more oxygenated.

A total of 2753 scales were counted in the modern core-top sediment samples obtained along the transect (Figs. 1 and 3), with 94% identified as anchovy and sardine. A greater abundance of sardine scales were found between 40 and 60 m, while anchovy scales were most abundant between 50 and 100 m (Fig. 4). One explanation could involve the selective degradation of scales of both species. If this were the case, the anchovy scales would be better preserved under oxygen-deficient conditions (less oxygen, more scales), while the preservation of sardine scales would be less influenced by oxygen (Figs. 3 and 4). Another possibility is that



Fig. 6. (A) Standardized SDR anomaly for anchovy and sardine (this work), (B) δ^{15} N and (C) organic carbon flux, in the F98-1A sedimentary record of Mejillones Bay (Vargas et al., 2007). Organic carbon flux is used as an indicator of primary export production and δ^{15} N is used as an indicator of denitrification and oxygen deficiency, according to Vargas et al. (2007).

these patterns of scales distribution result from the circulation of water inside the bay, and from the differences in size and form of the scales of each species, which probably influence their vertical transit through the water column. At present, our interpretation is that the observed distribution of scales of the two species along the bathymetric transect does not reflect the relative abundance of the two fish populations within the embayment, due to the mobility of the populations and the small dimensions of the bay.

In conclusion, this study of the present-day distribution of fish scales suggests that dissolution processes of fish scales are reduced below 50 m water depth and especially at maximal depths (in the center of the bay), characterized by oxygen-deficient conditions. Therefore if it can be assumed that the physical-chemical conditions observed nowadays were similar in a recent past, the down-core records of abundance of fish scales in the center of the bay may reflect fluctuations of fish scale fluxes and related environmental variations.

3.2. Downcore trends of fish scales and preservation issues

The chronology of the core (F98-1A) suggests that the base of the sedimentary sequence has an age of about 250 years, i.e. was deposited around 1740 AD. No indication of interruption of the sedimentation (or of post-depositional erosion) has been observed (more details concerning sedimentological characteristics of this core in Vargas et al. (2007)). The top of the core is assigned the date of extraction, 1998. Assuming a constant sedimentation rate (Vargas, 2002; Vargas et al., 2007), the 0.5 cm slices would yield a succession of time windows of 3 years each.

Sardine and anchovy SDR exhibited low values and variability from 1740 to 1820, when a slight increase in anchovy abundance is observed (Fig. 5). The anchovy SDR exhibited somewhat larger fluctuations from 1820 to 1860, and after 1870, the anchovy SDR increased. The sardine SDR also increased from ca. 1860 AD until 1900 relative to the former period.

Fish debris are susceptible to dissolution in the water column and in the upper part of the sediment column (Schenau and De Lange, 2000). For this reason eventual loss of fish remains due to dissolution is a factor which must be considered in the potential use of scales and bones in sedimentary records. O'Connell and Tunnicliffe, 2001 suggested that scales present in sediments older than 500 years are more susceptible to dissolution, while Wright et al. (2005) indicated that anchovy scales are more heavily mineralized than other species, and thus more resistant to dissolution. On the other hand, it is generally accepted that dissolution processes are much less efficient in depleted oxygen environments (Schenau and De Lange, 2000; O'Connell and Tunnicliffe, 2001; Tunnicliffe et al., 2001; Wright et al., 2005), as observed in the deepest part of Mejillones Bay at present (Fig. 4). However, the profile of δ^{15} N from the same core (Fig. 6) suggests that bottom waters of this bay were more oxygenated prior to 1820. If so, the preservation potential of the fish scale record after deposition may have been reduced, affecting the reliability of the scale deposition rates, as an estimator of true vertical fluxes to the seafloor.



Fig. 7. Anchovy and sardine catch in (A) the Antofagasta region (including Mejillones) and (B) in the whole country, according National Fishing Service, Chile (SERNAPESCA, 1995–2002).

In order to identify changes in SDR which deviate from the mean, we calculated the SDR anomalies (Fig. 6) by subtracting the record mean from each SDR value and normalized the differences by the standard deviation. Fig. 6 also shows the anomalies of organic carbon flux and δ^{15} N, as reported by Vargas et al. (2007) for the same core, which are interpreted to reflect, respectively, fluctuations in biological productivity and intensity of oxygen deficiency in the water column. Negative anomalies, such as those observed between ca. 1744 and ca. 1825 ($C_{\rm org}$), or ca. 1744 and 1844 (δ^{15} N), are interpreted to indicate lower surface productivity and lower denitrification in the water column (and hence less intense subsurface oxygen deficiency), respectively. Both anchovy and sardine SDR exhibit significant correlations with organic carbon flux and with δ^{15} N (anchovy: r = 0.551; p < 0.01; and r = 0.536; p < 0.01, respectively; sardine: r = 0.350; p < 0.01; r = 0.340; p < 0.01, respectively). However, when anchovy SDR are compared with both parameters before 1825 and after 1870, which mark two oxygenation regimes, as inferred by δ^{15} N values, no significant correlation was found. Within the transition period (1825-1870), anchovy SDR was significantly correlated with carbon flux (*r* = 0.609; *p* < 0.05) but not with δ^{15} N. For sardine SDR, no correlation was found with δ^{15} N for any period, and only with organic carbon flux after 1870 (r = 0.395; p < 0.01). All together these comparisons strongly suggest reduced preservation with higher oxygenation in the bay, as in the regime before 1825, but also indicate that within each regime, oxygenation is not a significant factor explaining SDR downcore variability.

3.3. Interdecadal variability of SDR in relation to climate and oceanographic changes

Geochemical, micropaleontological and mineralogical analyses of the core F98-1A (Vargas et al., 2007) suggest a high biological productivity, probably due to an intensification of the upwelling at Punta Angamos (Fig. 1) since 1820. After 1820 the anchovy SDR exhibited larger fluctuations, and after ca. 1870 a general increase is observed. These findings are consistent with the Vargas (2002) study, which depicts two regimes of organic carbon (Fig. 6) and minerals fluxes within the same core, with a transition period between 1820 and 1878. Prior to 1820 a limited biological productivity would have been linked to relatively low-intensity southwest winds, contrasting with an intensification of winds favourable to the upwelling. Time-series of $\delta^{15}N$ (Fig. 6), $\Delta^{14}C$, and alkenones-derived sea surface temperature in the same F98-1A core indicate a secular trend in coastal upwelling intensity since AD 1878, characterized by an enhanced influence of the nutrientrich Equatorial Subsurface Water and a decrease of 2 °C in SST in the zone, as well as enhanced ENSO-like interdecadal variability (Vargas et al., 2007). These oceanographic characteristics correspond to modern upwelling conditions in Mejillones Bay (Strub



Fig. 8. SDR (A) and catch of anchovy in the Antofagasta Region (B) and in Chile (C), between 1950 and 1998. The dashed bar corresponds to El Niño events.

et al., 1998; Marín et al., 2003). Thus the downcore studies on different proxies point to an interpretation of relatively stable oceanclimate conditions in northern Chile before 1820 unfavourable for anchovy and sardine populations and/or for preservation of fish debris in bottom sediments, either or both resulting in low SDRs, and a higher interdecadal variability overimposed with secular higher productivity since the second half of the 19th century.

Anchovy is generally considered a cool-water fish and sardine a warmer water fish (Chavez et al., 2003; Wright et al., 2005). It is the thermal dependence during the spawning period which may account for these classifications, the anchovy preferring temperatures of 16–18 °C, while sardines prefer temperatures of 19–21 °C (Chong et al., 1991). During strong El Niño events, which are characterized by warming, anchovies tend to disappear while sardine populations increase off Chile and Peru (Zuzunaga, 1985; Csirke et al., 1996; Chavez et al., 2003; Ñiquen and Bouchon, 2004). Bertrand et al. (2004) proposed that climatic variations lead to changes in the range of anchovy and sardine habitat, causing apparent shifts of dominance between anchovy and sardine populations.

The SDR measured in the Mejillones sediment record thus suggests alternating warm and cold periods since 1820 (Figs. 5 and 6). Sardine SDR increased during the second half of the 1800s until ca. 1900, dominating the scale record between ca. 1860 and 1880. Between 1875 and 1905 high values of SDR are recorded for anchovy and sardine and point to a similarity of oceanic regimes with those of 1980s decade (Fig. 7). In both cases, but at slightly different time-scales, high values of sardine SDR preceded peaks of anchovy SDR; for the latter period the SDR pattern followed that of landings (Fig. 7). If this comparison is correct, the lapse comprised between 1860 and 1880 (higher contribution of sardine SDR relative to anchovy SDR) would have been characterized by relatively warm water conditions, and would have been followed by cooler conditions until ca. 1900 as inferred from the replacement of sardine by anchovy. Afterwards an abrupt decline of both species SDR took place in less than a decade.

During the 1900s, the SDR (Figs. 6 and 7) shows variability associated with large-scale changes in the Pacific Ocean. Chavez et al. (2003) proposed an Ecosystem Index for the Southeastern Pacific based on sardine and anchovy landing and seabird abundance for the period 1940-2000. The authors postulated the occurrence of two oceanographic regimes, with a cool phase ("anchovy regime") from 1950 to 1975, followed by a warm phase ("sardine regime") from 1975 to the mid-1990s. Our results for the past 50 years agree with this pattern (Fig. 6). During the 1975-1990s period, an increase of sardine SDR (Fig. 5) and a predominance of sardine landings by the Chilean fishery (Fig. 7) between 1982 and 1988, might be interpreted as secondary effects of the 1982-83 El Niño event. The positive anomaly of anchovy SDR observed at the top of the record (1998, Fig. 6) might possibly be related to the shift to an "anchovy regime", during the 1990s as suggested by Chavez et al. (2003), even though sardines remained abundant.



Fig. 9. SDR (A) and catch of sardine in the Antofagasta Region (B) and in Chile (C), between 1978 and 1998. Dashed zone corresponds to El Niño 1982-1983 event.

On the other hand, based on a mineralogical study of the same core, Vargas et al (2007) determined an interdecadal climate variability that roughly follows the Pacific Decadal Oscillation (PDO). The authors deduced that warm interdecadal 'El Niño-like' conditions predominated 1925-1942, and 1976 onward. They propose that during interdecadal warm conditions an increased land-sea thermal contrast along the arid coast of northern Chile and Peru intensifies the equatorward wind stress due to reduced mean low-cloud cover, resulting in enhanced upwelling and primary and export production. According to the thermal preferences of sardine and anchovy, sardine would be better adapted to cope with 'El Niño-like' conditions (Chavez et al., 2003), while anchovies might also benefit from the presence of cold upwelled waters near the coast. Our downcore record shows a positive anomaly of anchovy SDR during the 1925-1942 El Niño-like period, but a positive anomaly of the sardine SDR during the 1976 - El Niño-like period. This apparent contradiction could result from differences between warm periods: the first one less intense than the second one and hence the coastal upwelling response being dominant over the oceanic warming signals.

3.4. SDR and population changes of anchovy and sardine in Northern Chile

The historical data of landing of sardine and anchovy show some correspondence with the respective SDR measured in the sedimentary column (Figs. 8 and 9). This is more evident for anchovy than sardine, probably because there is a longer anchovy landing time series. The strong increase of anchovy SDR in the 1960s coincides with an increase of anchovy catches (Fig. 8). After the fall of anchovy catches between 1975 and 80, the anchovy population recovered as shown by increases both in catches and SDR (Fig. 8). The parallel sequences of both time series are striking even if the magnitude of these fluctuations is different. The sedimentary record indicates that in Mejillones Bay there were more anchovy in the 1960s than in the 1990s, however catches were much greater in the 1990s (Fig. 8) probably due to greater numbers and capacity of fishing ships. The sediment core of this bay can be used to show the higher potential of sedimentary records with respect to landing statistics for an evaluation of pelagic fish populations, even for the last decades.

Anchovy and sardine scales in sediment from the Santa Barbara Basin, California current system, showed changes over the past two millennia (Soutar and Isaacs, 1969; Baumgartner et al., 1992). At time-scales less than 150 years, anchovy SDR appear to fluctuate with periodicities around 60, 70 and 100 years, while sardine SDR fluctuate in periods around 60 and 75 years (Baumgartner et al., 1992). The Mejillones record shows fluctuations in the anchovy SDR of the order of 25-40 years, while the only two observed peaks of sardine SDR were separated about one century one from another, differing to the Santa Barbara Basin records for both species. On the other hand, a positive correlation exists between both species SDR for the whole record (r = 0.470, p < 0.01), also in the transition period (r = 0.602, p < 0.05), despite the lag between both, and after 1870 (r = 0.450, p < 0.01), suggesting that the alternation observed in the late 20th century may not be typical. Baumgartner et al. (1992) noticed that the positive correlation between the California sardine and anchovy SDR is mostly explained by the low-frequency variance (>150 years), and that it vanished at higher frequencies. The sedimentary record of Mejillones Bay, though shorter and limited by preservation issues, suggests different mechanisms governing the population dynamics of the anchovies and sardines off northern Chile than those in California at decadal or longer time-scales, and also different ocean-climatic factors for each species.

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