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Climate change and abundance of the Atlantic-Iberian sardine (*Sardina pilchardus*)

C. GUISANDE,[1,]* A. R. VERGARA,[1]
I. RIVEIRO[1] AND J. M. CABANAS[2]

[1]*Facultad de Ciencias del Mar, Universidad de Vigo, Lagoas-Marcosende, 36200-Vigo, Spain*
[2]*Instituto Español de Oceanografía, Centro Costero de Vigo, Aptdo. 1552, Vigo, Spain*

ABSTRACT

Climatic warming is affecting oceanic circulation patterns in coastal upwelling areas, but the impact of this climatic change on pelagic fish populations remains unclear. From juvenile landings collected over 38 years, the thresholds of environmental factors were determined that limited the optimal environmental window (OEW) for sardine (*Sardina pilchardus* recruitment success in the northwestern Iberian peninsula. The environmental factors considered were: water column stability in February, offshore water transport in March–April (Q_xMA), upwelling intensity in the preceding year from May to August (Q_xMJJA), and the winter North Atlantic Oscillation (NAO) index. From 1875 to the mid-1920s, the mean number of years within the OEW was relatively constant. However, since the mid-1920s, there have been oscillations and alternating decades with high and low number of years within the OEW, which were related to oscillations in sardine landings. From 1906 to 2000, there were four record, low sardine catches in the 1920s, 1950s, 1970s and 1990s, related to a high number of successive years with prevailing conditions out of the OEW. From 1875 to the present, a high year-to-year variation of the NAO, Q_xMJJA and water stability in February was observed, although with mean values usually within the OEW. The collapse in the 1950s was related, partly, to successive years with low Q_xMJJA. Successive years with high NAO values may be related to the collapse of the sardine fishery in the 1990s. Q_xMA has been the most significant factor controlling SRS in this area, being the factor related to the low catches observed in the 1920s, 1950s and 1970s. Water stability was not responsible for any of the collapses observed, but since the 1920s, there has been a significant trend toward decreasing water column stability before the onset of the spring bloom.

Key words: climate change, optimal environmental window, recruitment, sardine

INTRODUCTION

There is strong evidence that year-to-year variations in the year-class strength of pelagic fishes in upwelling areas are governed mainly by oceanographic factors, i.e. upwelling intensity, offshore water transport and water column stability, whereas density-dependent processes are particularly likely to come into play after favourable environmental conditions have promoted a high year class (Cole and McGalde, 1998). Strong upwelling out of the spawning season favours larval survival because nutrient-rich, sub-surface waters are brought to the euphotic layers, thereby enhancing primary production (Mann and Lazier, 1991). Offshore water transport during the spawning season can have a negative effect on larval survival by carrying eggs and larvae to areas where there is not enough food to survive (Bailey, 1981; Parrish *et al.*, 1981). Water column stability favours spawning success, because turbulent conditions limit primary production, hence decreasing food availability for larvae (Lasker, 1975; Huntsman and Barber, 1977). Year-to-year fluctuations in recruitment variability are probably because of all these oceanographic factors which must combine favourably within an optimal environmental window (OEW; Cury and Roy, 1989) to achieve a high recruitment success. Because of the high intrinsic reproductive rate of pelagic fish species, population growth would be triggered by formation of one or a few powerful year classes, in those years that recruitment success is high due to optimal oceanographic conditions.

Upwelling intensity, turbulence and offshore water transport are all affected by the direction and strength of prevailing winds (climatic conditions) and, probably for this reason, many studies have shown that

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*Correspondence. e-mail: castor@uvigo.es
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climatic variation has a principal controlling influence on year-to-year recruitment success of some marine fish species (Alheit and Hagen, 1997; Daskalov, 1999; Guisande *et al.*, 2001; Parsons and Lear, 2001; Attrill and Power, 2002). In some zooplankton species of the North Atlantic sea, long-term variations in abundance (Planque and Fromentin, 1996; Reid *et al.*, 1998) and large-scale changes in biogeography (Beaugrand *et al.*, 2002) have been observed to be associated with climatic variation. These changes in zooplankton community assemblages reflect the adjustment of pelagic ecosystems to modifications in habitat conditions forced by climatic variation. Climate change could also drive prevailing oceanographic conditions in the spawning habitat of some pelagic fish species out of their OEW. That is why it is important to explain and predict climatic effects on interannual variations in recruitment, especially if habitat conditions of fish species are changing.

The sardine (*Sardina pilchardus*) is one of the most important species of pelagic fish off the northwest coast of the Iberian peninsula, although catches have been decreasing over the last decades (Guisande *et al.*, 2001). It has been observed that water column stability in February, offshore larval transport in March–April, input of nutrients in the preceding year from May to August, and the winter North Atlantic Oscillation (NAO) index explained 86% of year-to-year sardine recruitment variability off the northwest coast of the Iberian peninsula (Guisande *et al.*, 2001). In the present study, we examine long-term changes over the past 125 years in these environmental factors that affect sardine recruitment success (SRS) in this area. Our aim was to determine whether there is a trend in any of these environmental factors influencing the OEW for SRS.

MATERIAL AND METHODS

Recruitment estimation

Annual juvenile landings of the Atlantic-Iberian sardine (body length between 8 and 12 cm) at Vigo (northwest Spain) from 1980 to 1989 were shown to be significantly correlated with virtual population analysis recruitment estimates, calibrated by acoustic surveys and the catch per unit effort of the fishery (Robles *et al.*, 1992). Therefore, we used annual sardine juvenile landings at Vigo as an indicator of SRS for the northwest Iberian peninsula (Guisande *et al.*, 2001). Data are available since 1906, but until 1980 in most years, the proportion of landings composed of juveniles is unknown because the information is available only as combined adults and juveniles. In total, juvenile landing data are available for 38 years over the period 1906–1980 (Table 1). Adult and juvenile landings from 1980 to the present are shown in Guisande *et al.* (2001).

Ekman transport

Two independent time series of daily Ekman transport calculated for areas off the northwest Iberian peninsula were used. Series A is located at 43°N 11°W and series B at 42°N 10°W. Ekman transport from 1875 to 1997 and scalar wind and sea surface temperature (SST) data from 1924 to 1997 at station B were extracted from the Comprehensive Ocean Atmosphere Data Set

Table 1. North Atlantic Oscillation (NAO) winter index, the mean daily Ekman transport along the *x*-axis (in $m^3 s^{-1} km^{-1}$) in February (Q_xF) and March and April (Q_xMA) of the same year and from May to August (Q_xMJJA) of the prior year at station B (42°N 10°W), and annual landings of adults and juveniles of *Sardina pilchardus* (in metric tonnes) at Vigo.

Year	NAO	Q_xF	Q_xMA	Q_xMJJA	Adult landing	Juvenile landing
1926	0.11	100.8	−37.3	−80.4	6387.9	4425.0
1927	1.72	4.4	71.7	−29.9	9879.1	2157.0
1929	−1.03	13.6	−86.2	−96.7	1917.3	8467.3
1931	−0.16	−341.0	40.2	−14.6	12186.6	12779.3
1932	−0.5	−373.7	−128.2	−81.3	23074.2	810.4
1933	0.25	−43.1	9.4	−147.5	22666.6	2574.4
1934	0.86	−590.9	−16.6	−104.5	23886.0	5717.6
1935	0.97	−5.1	−26.7	152.2	33598.8	5918.4
1936	−3.89	63.7	42.5	−164.3	27736.9	1418.0
1937	0.72	281.9	35.7	−247.6	39378.3	2787.6
1938	1.79	−10.7	−444.1	−153.2	35770.8	2253.7
1939	0.37	13.8	−109.7	−196.8	10492.2	9095.1
1941	−2.31	−152.6	−55.3		977.8	5446.4
1962	−2.38	−497.7	−133.8	−506.6	5345.4	5109.5
1964	−2.86	183.0	−7.4	−196.0	5891.0	7355.5
1976	1.37	0.3	−318.9	−221.1	6556.6	668.5
1978	0.17	270.5	−50.2	−197.4	5235.9	3053.1

standard data set (http://www.cdc.noaa.gov/coads/products.html) (Woodruff *et al.*, 1987). At station A, Ekman transport data were calculated daily from 1954 to the present following Bakun (1973):

$$Q_x = \frac{\tau_y}{f\rho}1000 \quad Q_y = \frac{-\tau_x}{f\rho}1000 \tag{1}$$

where Q_x and Q_y are the Ekman transports along the x and y axes in $\mathrm{m}^3\ \mathrm{s}^{-1}\ \mathrm{km}^{-1}$, $f = 9.9410^{-5}\ \mathrm{s}^{-1}$ (Coriolis factor), $\rho = 1025\ \mathrm{kg\ m}^{-3}$ (water density) and τ_x and τ_y are the wind stress over the sea, calculated by the following equations:

$$\tau_x = \rho_a C_d u \sqrt{u^2 + v^2} \quad \tau_y = \rho_a C_d v \sqrt{u^2 + v^2} \tag{2}$$

where $\rho_a = 1.2\ \mathrm{kg\ m}^{-3}$ (air density), $C_d = 1.4\ 10^{-3}$ (drag coefficient) and u and v are the x and y components of the geostrophic wind in metre per second:

$$u = \frac{-\alpha}{f}\frac{\delta p}{\delta y} \quad v = \frac{\alpha}{f}\frac{\delta p}{\delta x} \tag{3}$$

where $\alpha = 1/\rho_a = 0.816\ \mathrm{m}^3\ \mathrm{kg}^{-1}$ and $\delta p/\delta x$ and $\delta p/\delta y$ are the mean pressure gradients between the opposite borders of a 1° × 1° cell centred at 43°N 11°W determined daily at 0, 6, 12 and 18 h.

It has been shown that series A is probably representative for the area of study (Vigo) because Ekman transport obtained from this series explained a high proportion of the variance observed in year-to-year sardine recruitment for the northwest Iberian peninsula (Guisande *et al.*, 2001). Series B is longer (from 1875 to 1997), so this series is better for examination of long-term changes in oceanographic conditions. Figure 1 shows that a good correlation between series A and B and, therefore, series B can also be used as an indicator of oceanographic conditions for this area.

The Atlantic northwestern coast of the Iberian peninsula shows a north-south orientation and, hence, winds from the north produce offshore transport. The magnitude of offshore transport in the upper layer is considered an indicator of the amount of water upwelled along the coast into the surface layers (Mann and Lazier, 1991). Therefore, for the northwestern coast of the Iberian peninsula, Ekman transport along the x-axis (Q_x) is a good indicator of both offshore larval drift and upwelling intensity (input of nutrients into the euphotic layers). Negative values of Q_x indicate offshore water transport, whereas positive Q_x values indicate onshore water transport. Figure 2 shows the monthly mean Q_x for station B from 1875 to 1997 and demonstrates that summer is the main upwelling season in this area. Therefore, Ekman transport from May to August in the preceding year (Q_xMJJA) is an indicator of nutrient input to surface waters available during the following spring bloom. The spawning season of sardine off the northwest Iberian peninsula is from January to June, but with a higher abundance of eggs and larvae in March–April (Riveiro *et al.*, 2000) and, hence, Ekman transport in March–April (Q_xMA) is an indicator of offshore larval transport. Finally, there is a dome shaped relationship between Q_x and water column stability in this area (Guisande *et al.*, 2001), which means that at both high and low Q_x values, stability of the water is low. Therefore, Ekman transport in February (Q_xF) is used

Figure 1. (a) Relationship between Q_x in February (slope significantly different from zero, $r^2 = 0.71$, $P < 0.001$) and (b) Q_x in March–April (slope significantly different from zero, $r^2 = 0.42$, $P < 0.001$) for stations A (43°N 11°W) and B (42°N 10°W).

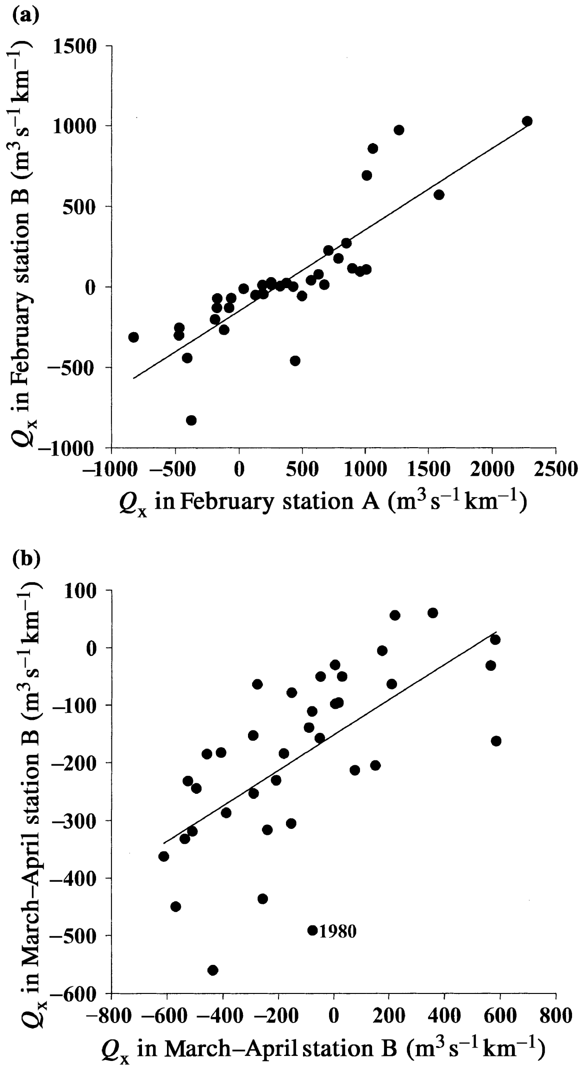


Figure 2. Mean (±SD) monthly Q_x at station B (42°N 10°W) from 1875 to 1997.

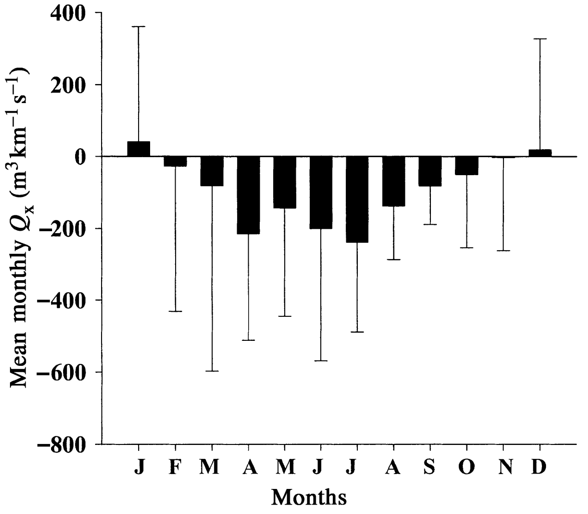
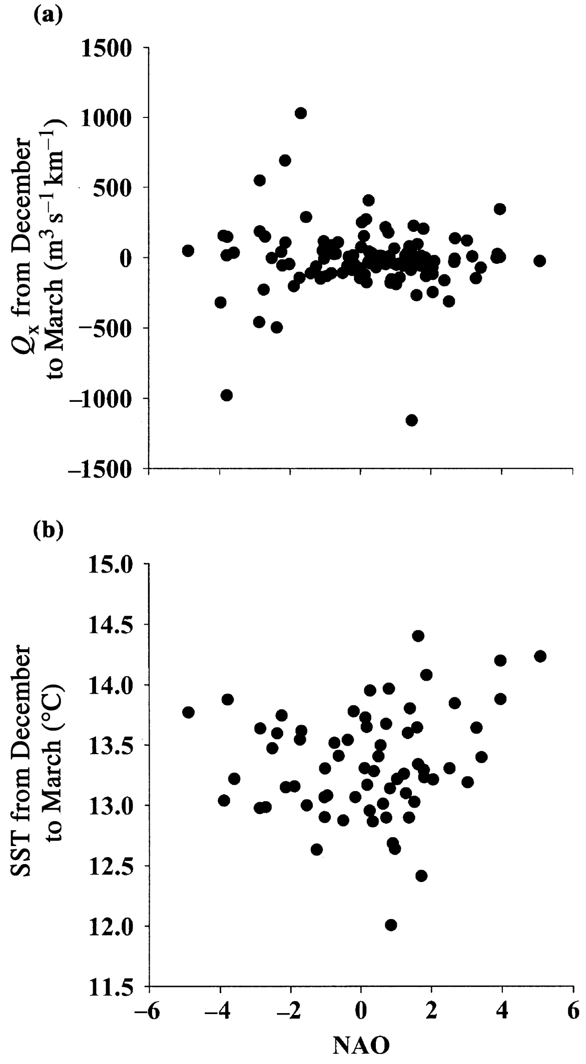


Figure 3. Relationship between NAO and (a) the mean Q_x from December to March and (b) the mean sea surface temperature (SST) from December to March, both at station B (42°N 10°W) from 1925 to 1997.



as an indicator of water column stability before the spring bloom.

North Atlantic oscillation winter index

The values of the NAO winter (December–March) index based on the difference of normalized sea level pressures between Lisbon (Portugal), and Stykkisholmur/Reykjavik (Iceland) were taken from the web page http://www.cgd.ucar.edu/~jhurrell/nao.html (Hurrell, 1995). NAO appears to be a good proxy for winter SST and wind strength in the North Sea, but the influence of NAO on the western coast of the Iberian peninsula is weak (Ottersen *et al.*, 2001). In fact, the lack of a linear relationship between the NAO with either the mean Q_x from December to March (Fig. 3a, slope not significantly different from zero, $r^2 = 0.001$, $P > 0.75$) or the mean SST from December to March (Fig. 3b, slope not significantly different from zero, $r^2 = 0.03$, $P > 0.19$) at station B, indicates that NAO has no relationship with either water transport direction or sea water temperature in this region.

Optimal environmental window

The OEW for SRS in this area is defined by four parameters (Guisande *et al.*, 2001): Q_xF, Q_xMA, Q_xMJJA, and the NAO. As there are more years of available data in series B, we used this series to calculate the long-term change of the OEW in this area from 1875 to the present. A 10-year period was chosen to minimize the effects of year-to-year variability. The number of years within the OEW (NYO) of 10 consecutive years (10-year moving average, e.g. 1975 plotted value is the NYO mean for the previous 10 years) was calculated using the following equation:

$$\mathrm{NYO} = \mathrm{NYO} \times Q_x\mathrm{MJJA} \times Q_x\mathrm{MA} \times Q_x\mathrm{F} \times N$$

where NAO is the mean number of years with a NAO value between −2.5 and +2.5 over the decade, Q_xMJJA is the mean number of years with a Q_xMJJA in each preceding year lower than −170 $m^3 s^{-1} km^{-1}$ over the decade, Q_xMA is the mean number of years with a Q_xMA higher than −70 $m^3 s^{-1} km^{-1}$ over the decade, Q_xF is the mean number of years with a Q_xF between −650 and +350 $m^3 s^{-1} km^{-1}$ over the decade, and N is 10 years. For some decades it was necessary to use the mean number of years within the

OEW for each parameter, because of some years of missing data. It was considered that if juvenile landings in 1 year were low, then one or several of the parameters that conditioned SRS in this area for that year must be out of the OEW. Therefore, the thresholds mentioned above that limited the OEW for SRS, were fixed by examining those years in which annual juvenile landings were low (<1500 t).

RESULTS

Figure 4 shows that for both series of Ekman transport data, SRS was high only in years when the NAO was within a range between −2.5 and +2.5, Q_xMJJA the preceding year was lower than −70 m^3 s^{-1} km^{-1}, Q_xMA was above a threshold (−100 m^3 s^{-1} km^{-1} for station A and −170 m^3 s^{-1} km^{-1} for station B) and Q_xF was within a specific range (between −300 and 500 m^3 s^{-1} km^{-1} for station A and between −650 and +350 m^3 s^{-1} km^{-1} for station B).

For series A (Fig. 4a), in 1981 SRS was high despite upwelling intensity from May to August being low in the preceding year. This might be explained by onshore water transport in March–April, 1981 being high (566.6 m^3 s^{-1} km^{-1} at station A), favouring larval retention in areas close to the coast. In 1983, SRS was also high despite the NAO also being high (3.42).

For series B, in 1980 a high SRS was observed out of OEW (Fig. 4b); this may be due to the Q_xMA of series B being below the threshold, according to the relationship observed for both series of data (Fig. 1). In 1938 there was also a high SRS out of the OEW and conversely, in 1985 and 1988, SRS was low under environmental conditions which were within the OEW.

Figure 4. Relationship between mean Ekman transport along the x-axis (Q_x) in February and March–April at the stations located at (a) 43°N 11°W and (b) 42°N 10°W in years with annual juvenile landings of *Sardina pilchardus* higher (Filled symbols) and lower (open symbols) than 1500 t from 1980 to 2000. Years with NAO values higher than 2.5 or lower than −2.5 and/or upwelling intensity the preceding year from May to August higher than −70 m^3 s^{-1} km^{-1}, are indicated by triangles; squares represent years with NAO values between +2.5 and −2.5 and upwelling intensity from May to August the preceding year <−70 m^3 s^{-1} km^{-1}. Dashed lines represent the thresholds of Q_x in February and March–April, which limited the OEW for SRS.

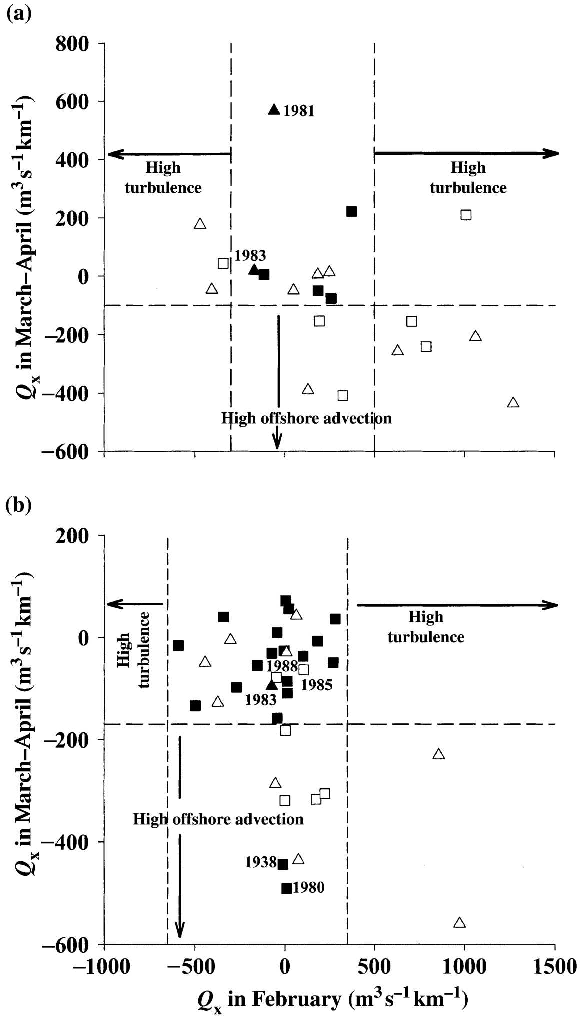
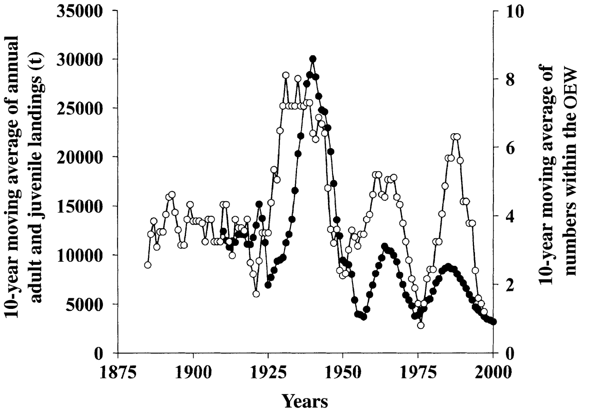


Figure 5 shows the mean annual adult and juvenile landings of sardine at Vigo, and the 10-year moving average of NYO. It is clear that catches were generally higher when the number of years within the OEW was higher. There were four periods of low catches of sardine, in the 1920s, 1950s, 1970s and 1990s, related to a high number of successive years with prevailing conditions out of the OEW. In decades with NYO values around 6–7 (i.e. during the 1930s), the mean annual landing for that decade was above 20 000 t; in decades with NYO values of around 3–4 (the 1900s, 1910s, 1960s and 1980s), the mean annual landings were between 5000 and 20 000 t, whereas in those decades with NYO values of less than around 2 (the 1920s, 1950s, 1970s and 1990s), annual landings were below 5000 t. Figure 5 also shows that from 1875 to the mid-1920s, the NYO was relatively constant with a mean of 3.5 and an SD of 0.6. However, since the mid-1920s, there have been oscillations, with alternating decades with high (>5) and low (<2) NYO values. NYO in the period from 1876 to 1900 (8.06) was similar to NYO in the period from 1976 to the present (8.21).

Figure 5. Ten-year moving averages of adult and juvenile landings of sardine at Vigo from 1906 to 2000 (solid circles) and number of years falling within the OEW (open circles).



Figures 6–9 show the long-term changes from 1875 to 1997 at station B of the NAO, Q_xMJJA, Q_xMA and Q_xF, the thresholds that limited the OEW for SRS for the northwestern Iberian peninsula, and the 10-year moving average.

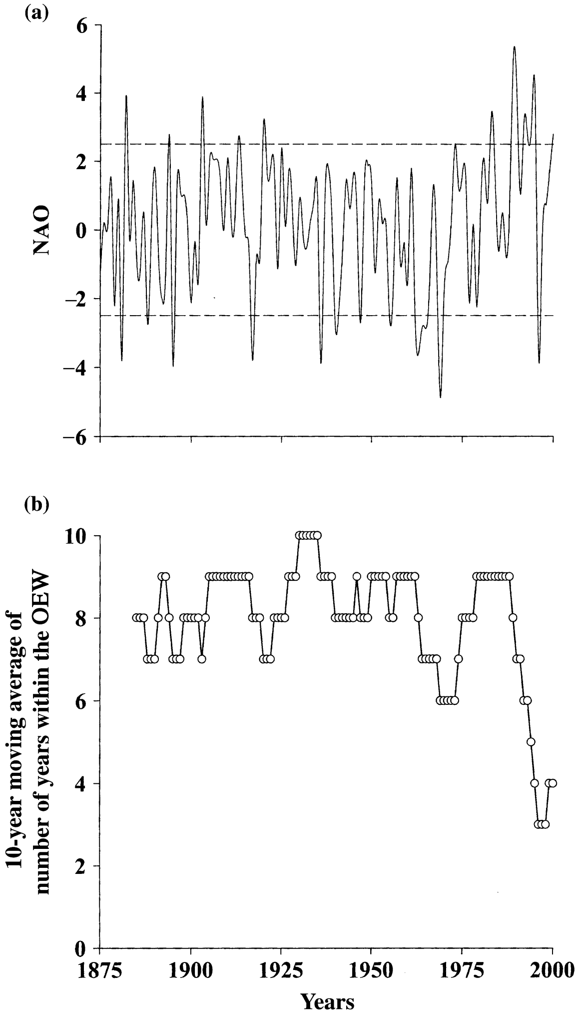
Since 1875, NAO values have usually been within the OEW (Fig. 6a) and, hence, the NAO has not been an important environmental factor affecting the SRS in this area. However, the reduced sardine landings in the 1990s coincided with successive years with high NAO values (Fig. 6b).

Ekman transport from May to August usually assures input of nutrients into surface waters (Fig. 7a) and, furthermore, from the mid-1920s to the present, offshore water transport was increasing (slope significantly different from zero, $r^2 = 0.25$, $P < 0.001$). Therefore, Q_xMJJA was not an important factor controlling SRS, although was partly related to the reduced catches in the 1950s (Fig. 7b).

The mean Q_xMA was consistently close to the threshold below which the SRS is low (Fig. 8a), indicating that offshore water transport has been an important factor related to the SRS. Offshore egg and larval transport was associated with the low catches observed in the 1920s, 1950s and 1970s (Fig. 8b).

From 1875 to the mid-1920s, Q_xF remained relatively constant and within the OEW (Fig. 9a), not being related to any of the reduced sardine catches observed (Fig. 9b). However, the slope of the linear trend toward increasing Q_xF from 1924 to the present is significantly different from zero ($r^2 = 0.06$, $P = 0.045$). The significant increasing SST corroborates this change in the oceanographic conditions in February (slope significantly different from zero, $r^2 = 0.27$, $P < 0.001$) (Fig. 10). SST increases with Q_x because increased Q_x gives higher onshore transport, resulting in reduced upwelling of cool water into surface layers.

Figure 6. (a) Long-term changes from 1875 to 2000 of the winter North Atlantic Oscillation (NAO) index. The horizontal dashed lines represent the thresholds that limited the OEW (−2.5 and +2.5). (b) Ten-year moving average of number of years with NAO values within the OEW (within −2.5 and +2.5).



DISCUSSION

This study shows that recruitment success of sardine of the north western Iberian peninsula is high when NAO, Q_xMJJA, Q_xMA and Q_xF combine within an OEW.

Both low and high values of the NAO affect SRS negatively in this area. The clearest and best-documented influence of the NAO on marine and

Figure 7. (a) Long-term changes from 1875 to 1997 of Q_x from May to August for station B (42°N 10°W). The horizontal dashed line represents the threshold that limited the OEW (-70 m^3 s^{-1} km^{-1}). The other dashed line indicates the linear trend fitted by least squares for the period 1925–1997. (b) Ten-year moving average of number of years with Q_xMJJA within the OEW (< -70 m^3 s^{-1} km^{-1}).

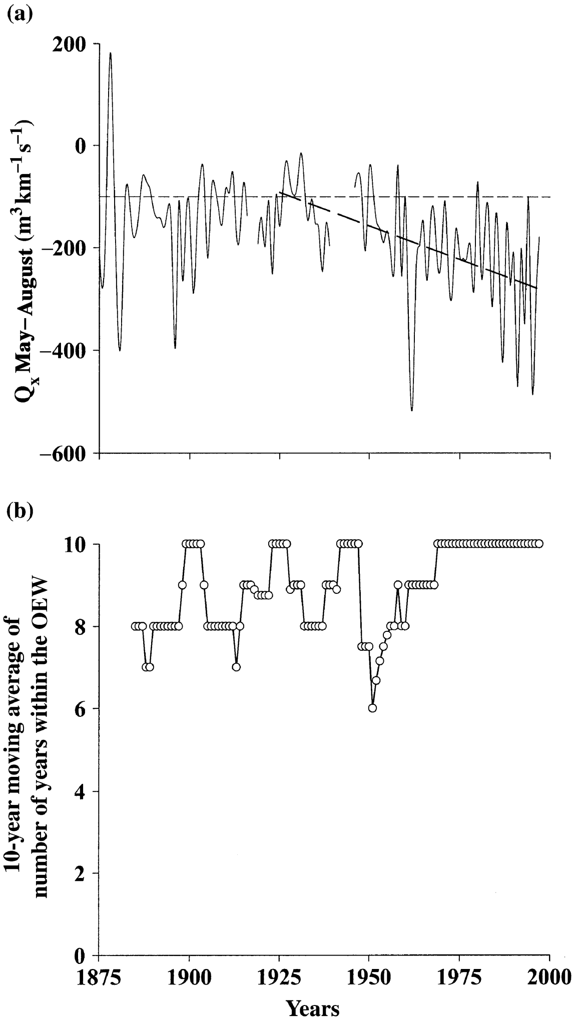
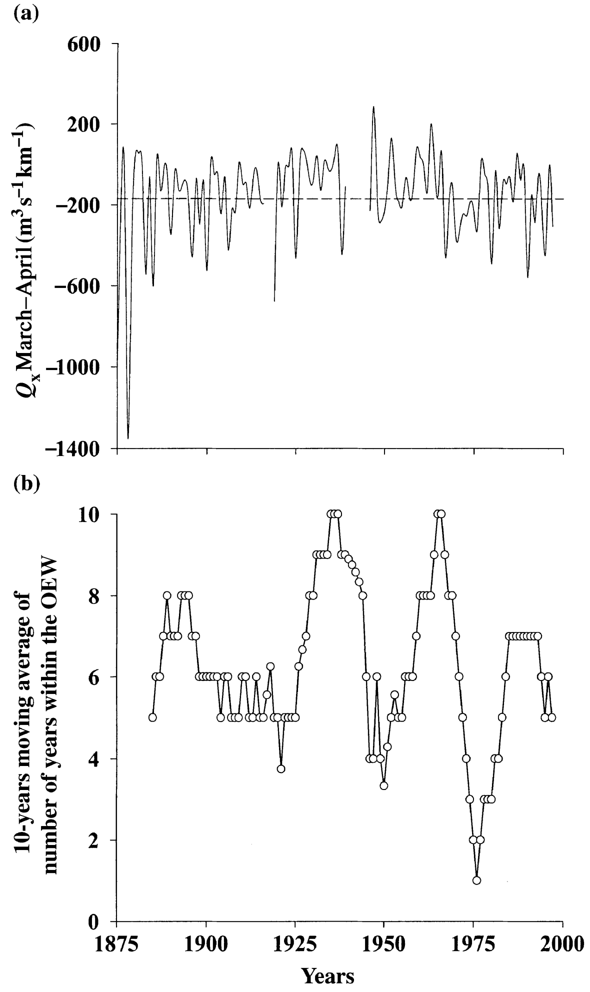


Figure 8. (a) Long-term changes from 1875 to 1997 of Q_x in March–April for station B (42°N 10°W). The dashed line represents the threshold that limited the OEW (-170 m^3 s^{-1} km^{-1}). (b) Ten-year moving average of number of years with Q_xMA within the OEW (>-170 m^3 s^{-1} km^{-1}).



terrestrial ecosystems is through temperature (Ottersen *et al.*, 2001). The effect of the NAO through temperature can be direct through its effect on the metabolic rates of the eggs and larvae, as has been shown for Arcto-Norwegian cod (*Gadus morhua*) (Loeng *et al.*, 1995). The effect of the NAO on marine fish species can also be due its effect on the temperature differential between estuarine and marine waters (Attrill and Power, 2002) and on water transport (Alheit and Hagen, 1997). The lack of relationship between the NAO and either Q_x or SST in the study area (Fig. 3a,b) indicates that the effect of the NAO on the SRS may not operate through water transport or temperature. The reduced SRS under both low and high NAO values could be due to strong winds delaying the onset of the spring bloom (Dickson *et al.*, 1988), total phytoplankton production for the season being reduced, and hence food quantity not being sufficient at the time of spawning to assure larval survival (Cushing, 1975). Moreover, a strong mixed layer could affect larval survival negatively because of the disruption of food aggregations (Lasker, 1981). However, as mentioned above, the influence of the NAO on the west coast of the Iberian peninsula is not clear and is, in any case, weak.

Figure 9. (a) Long-term changes from 1875 to 1997 of Q_x in February for station B (42°N 10°W). The horizontal dashed lines represent the thresholds that limited the OEW (−650 and +350 $m^3\ s^{-1}\ km^{-1}$). The other dashed line indicates the linear trend fitted by least squares for the period 1924–1997. (b) Ten-year moving average of number of years with Q_xF within the OEW (within −650 and 350 $m^3\ s^{-1}\ km^{-1}$).

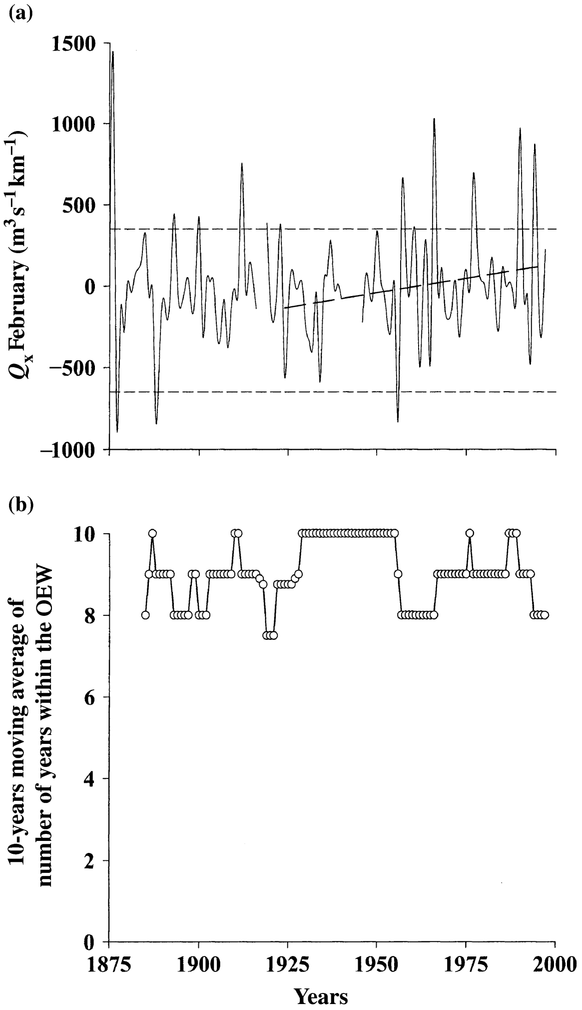
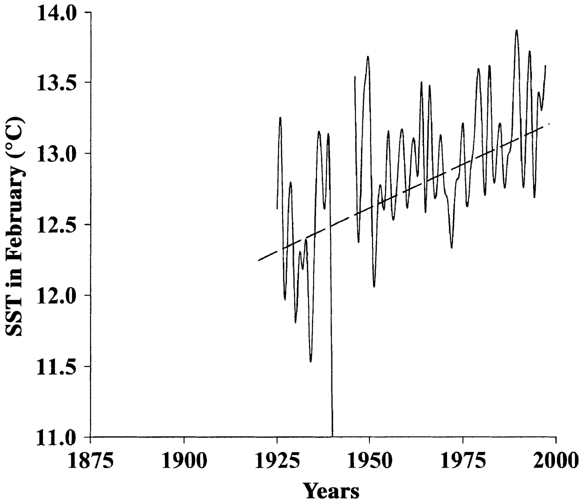


Figure 10. Long-term changes from 1924 to 1997 of sea surface temperature (SST) in February for station B (42°N 10°W). The dashed line indicates the linear trend fitted by least squares.



High upwelling intensity during May–August in the northwestern Iberian peninsula increases nutrient concentrations in surface water layers (Tenore *et al.*, 1995) and, hence, should favour primary production during the following spring. This would explain the reduced SRS when upwelling intensity was low in the preceding year. However, it is necessary to point out that there is no evidence that this input of nutrients could enhance primary production during the next spring bloom and, therefore favour SRS. Thus, the interpretation that low Q_xMJJA favours SRS because of the input of nutrients into surface waters should be taken with caution. In any case, Fig. 7a shows that the mean Q_xMJJA was usually below the OEW threshold, indicating that larval survival was not limited by upwelling intensity and, moreover, from the mid-1920s to the present, coastal upwelling has increased. This trend toward increasing intensity of upwelling in spring-summer has been shown in all major eastern upwelling systems (Bakun, 1990). As increased primary production promotes reproductive success and population growth of commercial fishes (Cury and Roy, 1989), this change in upwelling intensity in this area would, in any case, affect SRS positively.

The spawning season of sardine in the northwestern Iberian peninsula is from January to June, but with a higher abundance of eggs and larvae in March–April (Riveiro *et al.*, 2000). Therefore, the reduced SRS at low values of Q_xMA may be due to a high upwelling intensity during these months, which has a negative effect on SRS because of offshore transport of eggs and larvae (Bailey, 1981; Parrish *et al.*, 1981; Dickson *et al.*, 1988). Offshore egg and larval transport is postulated as having been an important factor controlling SRS in this area and being responsible for most of the periods of low sardine catch (Fig. 8b). The long-term change in the mean Q_xMA from 1875 to the present is similar to the pattern followed by the northern hemisphere seasonal temperature anomalies: (i) a warming trend from the 1910s to the 1940s, (ii) a cooling trend from the 1940s to the 1970s and (iii) another warming trend from the 1970s to the present time (Schneider, 1989; Jones *et al.*, 1999). In fact,

Figure 11. (a) Long-term changes from 1925 to 1997 of the mean annual atmospheric temperature for station B (42°N 10°W). (b) Long-term changes from 1925 to 1997 of Q_x in March–April for station B (42°N 10°W). The dashed lines indicate the linear trends fitted by least squares for the periods 1925–1940, 1940–1970 and 1970–1997.

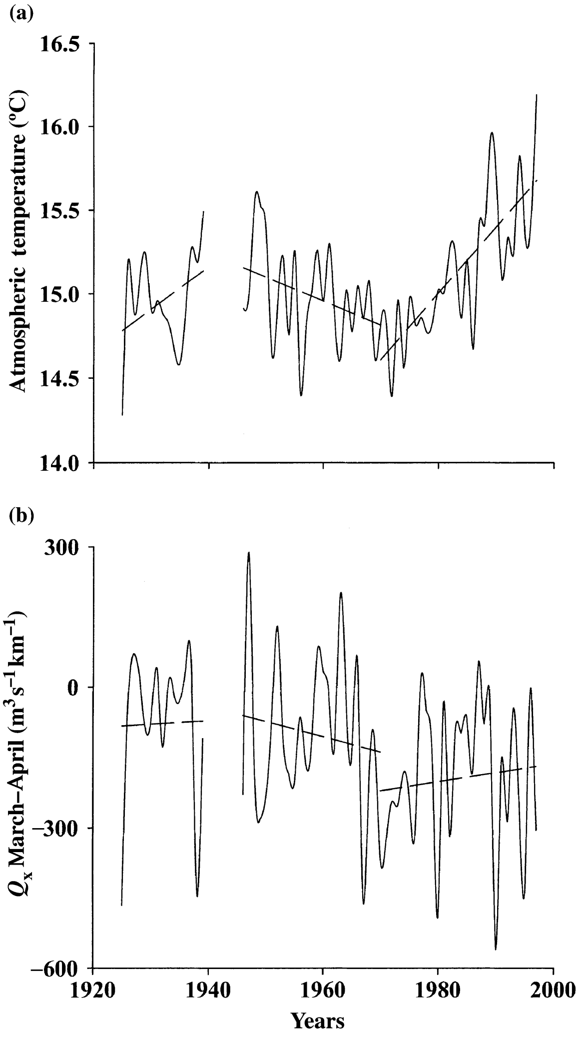


Fig. 11 shows that the long-term change at station B of atmospheric temperature follows a similar pattern to the long-term change of Q_xMA. This corroborates the observations that coastal upwelling in March–April increases during climate cooling and decreases during climate warming. As there is a trend toward increasing global temperature, this climate warming would lead to decreased coastal upwelling in March–April, which would benefit SRS.

The reduced SRS at low and high values of Q_xF could be explained because there is a dome-shaped relationship between Q_x and water column stability in February in this area (Guisande *et al.*, 2001), which means that at both high and low Q_x-values, stability of the water is low. A strong mixed layer before the onset of the spring bloom could have a negative effect on primary production because of light limitation and, hence, could negatively affect larval food availability (Lasker, 1975; Huntsman and Barber, 1977). It has been suggested (Dickson *et al.*, 1988) that increased strong-wind frequency in critical spring months was responsible for a progressive delay in the initiation of the spring phytoplankton bloom in certain areas of Europe. This resulted is a shortening of the growing season and reduced capacity for zooplankton, resulting in a long-term declining trend in zooplankton abundance from the 1950s to the 1980s. Moreover, strong mixing could affect larval survival negatively because of the disruption of food aggregations (Lasker, 1981). Therefore, both high and low Q_xF could have a detrimental effect on the year-class strength of sardine because they are associated with a strong mixed layer, resulting in decreased larval food availability. This study shows that there is a significant trend toward increasing Q_xF from 1924 to the present, with mean values generally out of the OEW. If this trend continues, it might negatively affect the abundance of the sardine in the area.

Most of the debate regarding the consequences of global climate change on pelagic fish recruitment has been focused on the effects of climate warming on the input of nutrients into surface waters (Bakun, 1990; Siegfried *et al.*, 1990; Hsieh and Bower, 1992; Mann, 1993), because larval food availability is conditioned, to large extend, by primary production. It has been suggested that climate warming increases the temperature contrast between the warmer continental landmasses and the oceans, which intensifies the thermal low-pressure cell over the coastal landmass. The result of this increased onshore-offshore temperature gradient would be a trend toward increasing equatorward alongshore wind stress in eastern areas of the ocean during spring-summer, which leads to enhanced upwelling intensity and, hence higher primary production (Bakun, 1990). However, other studies predict that climate warming will reduce the north-south temperature gradient and that there will probably be a significant reduction in average wind stress (Siegfried *et al.*, 1990; Hsieh and Bower, 1992; Mann, 1993). This should lead to a general weakening of coastal upwelling and, therefore, a decrease in primary production.

Our results show that the parameter that most affects the SRS in this area is not the input of nutrients into surface waters, but the offshore transport of eggs and larvae during the spawning season (responsible for the collapse of the stock in the 1920s, 1950s, and the 1970s). Furthermore, in the 1990s, there was a coincidence between high NAO values and low SRS. Our results show that, despite the climate changes, NYO was similar in recent years and 100 years ago, indicating that there has been no trend in habitat conditions toward values out of the OEW. However, it is necessary to stress that there is a significant trend toward decreasing water column stability before the onset of the spring bloom. The fact that different pelagic species have different OEWs for successful reproduction (Roy *et al.*, 1992) means that the relative dominance of the pelagic fish species that co-occur with the sardine in this area could be modified by this possible change in habitat conditions.

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