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# THE OPTIMAL ENVIRONMENTAL WINDOW HYPOTHESIS : A NON LINEAR ENVIRONMENTAL PROCESS AFFECTING RECRUITMENT SUCCESS

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## ABSTRACT

In upwelling areas, the relationship between upwelling intensity and pelagic fish recruitment success appears to be sometimes positively and sometimes negatively correlated. The Optimal Environmental Window (OEW) hypothesis offers an interpretation for these apparently contradictory results. The OEW hypothesis suggests that a dome shaped relationship exists between recruitment success and upwelling intensity : recruitment success increases with upwelling intensity in areas where wind speed is low or moderate, food availability is then the limiting factor; recruitment success decreases with upwelling intensity in areas of strong wind where physical constraints are the main determinants of larvae mortality rates. Several studies have shown that the relationship between recruitment success of small pelagic fish stocks located in upwelling areas is dome shaped and in agreement with the OEW hypothesis. The limiting factors defined by the OEW hypothesis are also able to account for apparent contradictory patterns observed between reproductive strategies of related species located in geographically distinct areas.

The OEW hypothesis applies to eastern boundary current ecosystems located in tropical or subtropical areas where trade winds are responsible for the upwelling process. The applicability of the OEW to higher latitude areas like the ICES regions is discussed and example of an ICES region where upwelling events take place is presented.

## INTRODUCTION

Many attempts have been made to correlate environmental fluctuations to recruitment indices. For the pilchard *(Sardinops ocellatus)*, a relationship between year-class strength and sea-surface temperature is found to be positive in the southern Benguela (Shelton *et al.*, 1985) but for the same species a negative one is found in the northern Benguela (Shannon *et al.*, 1988). For the Iberian sardine (*Sardina pilchardus*), Dickson *et al.* (1988) found a negative correlation between catch and upwelling indices (Fig. 1). In a nearby area, Belvèze and Erzini (1983) found a positive relationship between the catch of the Moroccan sardine *(Sardina pilchardus)* and upwelling (Fig. 1).

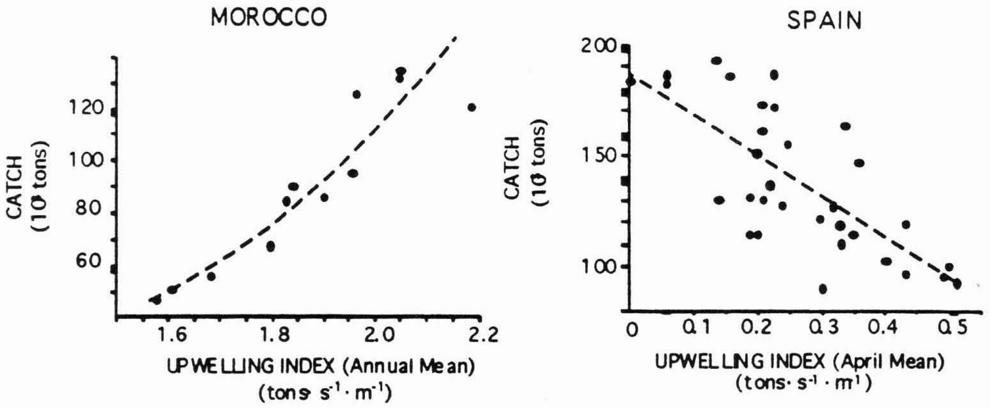


Figure 1: An example of positive and negative correlations between catch and upwelling index obtained for the same species *(Sardina pilchardus)* at two different locations : the sardine off Morocco (from Belvèze and Erzini, 1983) and the sardine off Spain (From Dickson *et al.*, 1988).

These results question the existence of a unified theory relating recruitment with the environment in upwelling areas. However, positive and negative correlations may both be valid if the relationship between recruitment and upwelling intensity is dome shaped as suggested by the "Optimal Environmental Window" (OEW) hypothesis (Cury and Roy, 1989). The applicability of the OEW to temperate latitude areas is discussed and the Iberian sardine is presented as an example of an ICES region where upwelling events take place.

## AN OPTIMAL ENVIRONMENTAL WINDOW FOR RECRUITMENT SUCCESS IN UPWELLING AREAS.

Food availability and physical constraints such as wind mixing or offshore transport are considered important factors that affect larval survival and pelagic fish recruitment. Acceptable food concentrations associated with stable ocean conditions must be present in the larvae's environment for survival (Lasker, 1981). Small-scale turbulence that increases the encounter rate between food particles and larvae (Rothschild and Osborn, 1988; MacKenzie and Leggett, 1991) may also be beneficial to larval survival. Strong mixing generated by high wind speed has a negative effect on larval survival by desaggregating food and larvae patches (Saville, 1965; Peterman and Bradford, 1987) and may affect recruitment (Lasker, 1981). In an upwelling ecosystem, vertical advection, new inputs of nutrients and mixing are generally closely related to the magnitude of the wind speed (Fig. 2). Increasing upwelling intensity from weak to moderate should have a positive effect on recruitment since increased primary production would enhance food availability with wind mixing remaining low. Strong upwelling should have a negative effect on recruitment because wind mixing is high even if primary production increases.

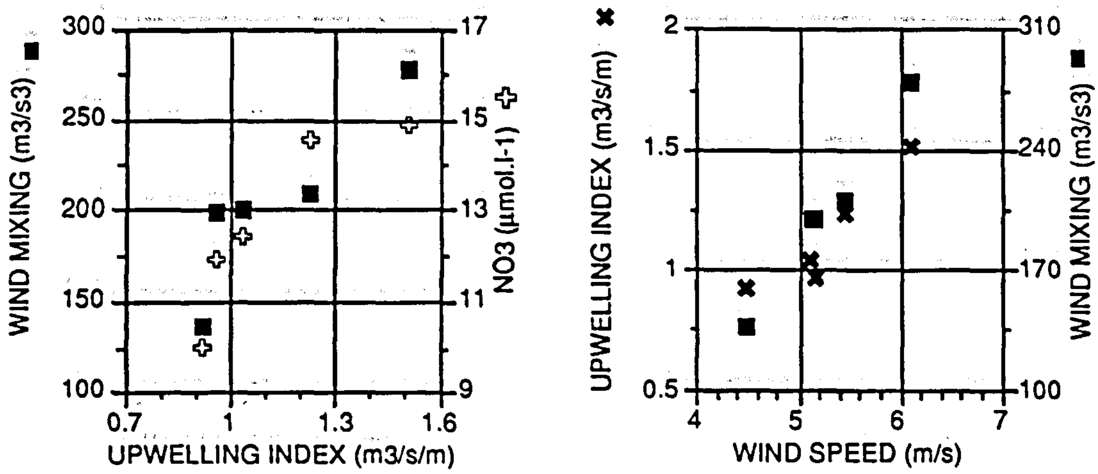


Figure 2: Relation between monthly values of : a) upwelling index and wind mixing or Nitrate concentration; b) wind speed and upwelling index or wind mixing.
Data from 1985 to 1989 at the Cap-Vert coastal stations (Sénégal). Mean calculated during the upwelling season from January through May (See Oudot et Roy, 1991 for details).

The Optimal Environmental Window (OEW) hypothesis (Cury and Roy, 1989) assumes that the relation between recruitment and upwelling indices is dome shaped (Fig. 3). The non linearity of the curve is explained by considering the positive or negative effects of several environmental factors. On the left side of the curve wind is weak or moderate; an increase in the wind speed may enhance food production or the encounter rate between larvae and food. On the right side of the curve the upwelling is strong so that wind-mixing and offshore transport are then detrimental factors. There is an "Optimal Environmental Window" for recruitment success in moderate upwellings where the effects of the limiting factors are minimized (Fig. 3).

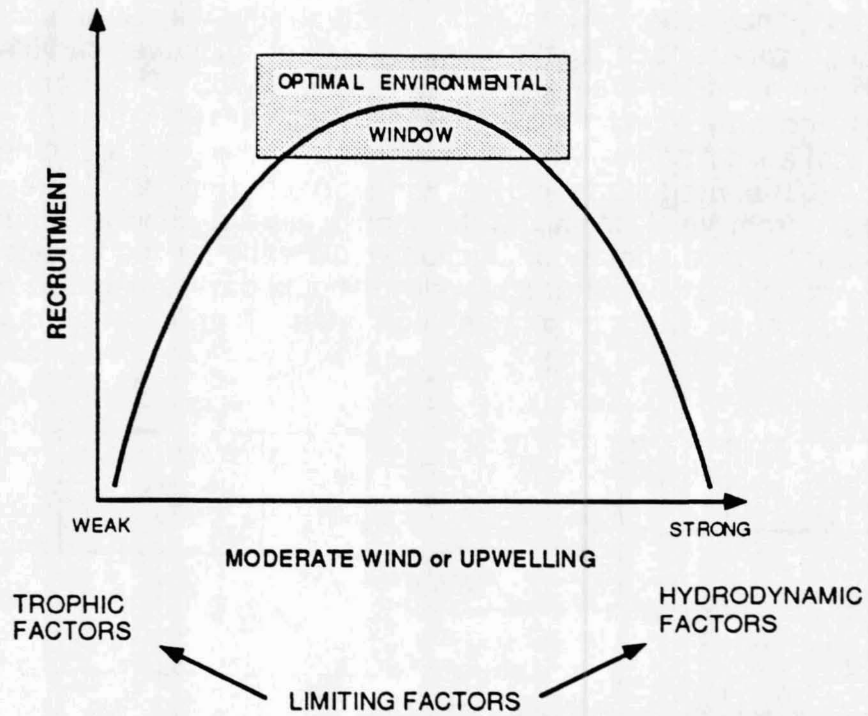


Figure 3 : Theoretical relationship between recruitment and environmental factors in upwelling areas (adapted from Cury and Roy, 1989).

## ECOLOGICAL VALIDATIONS OF THE OEW

### RECRUITMENT VARIABILITY

Four of the main pelagic fish stocks, all located in tropical or subtropical upwelling areas, were analyzed using an exploratory statistical method (Cury and Roy, 1989). For the Peruvian anchovy, the Californian sardine, the Moroccan sardine and the Senegalese sardinella, this comparative analysis shows that a dome shaped relation exists between recruitment and upwelling intensity (Fig. 4). The non-linearity always appears for values of wind speed around 5-6 m/sec (Fig. 4). This suggests that for different upwelling ecosystems there is a common and "optimum" wind mixing level in the stable layers of the upper ocean.

Using new estimates of recruitment for the Peruvian anchoveta, Mendelssohn (1989) found similar results. Using extended time series for the Pacific sardine, Ware and Thompson (1991) supported the existence of an optimal environmental window but at a wind speed value of around 7-8 $m.s^{-1}$. Roy *et al.* (1992) show new evidence of a non-linear relationship between recruitment and upwelling for the Moroccan sardine. Recently, an analysis of the Californian anchovy larvae data also supported the existence of a dome-shaped relationship between larvae abundance and upwelling intensity (Cury *et al.*, in press).

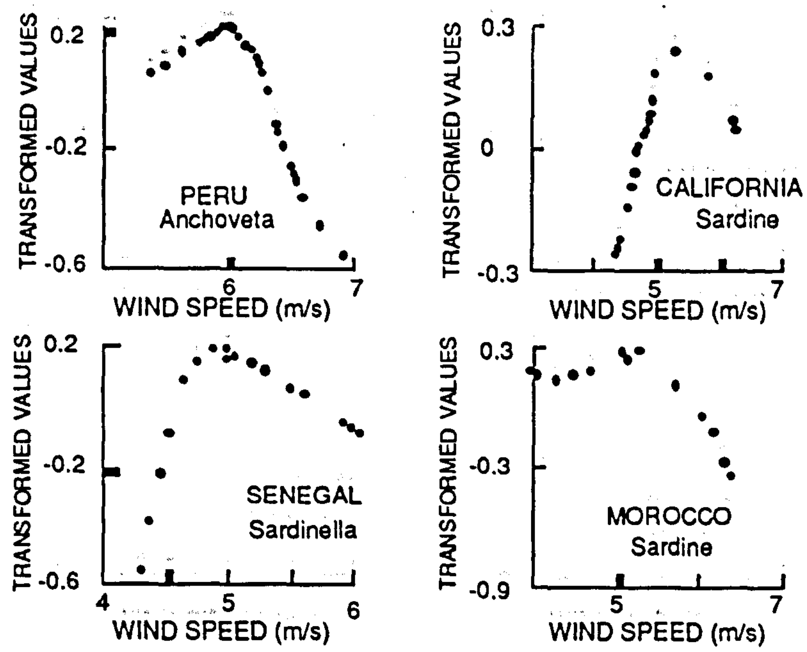


Figure 4 : Optimal transformation obtained using the ACE algorithm (Breiman and Freidman, 1985) for the recruitment of sardine and anchovy in four different upwelling areas (from Cury and Roy, 1989).

## REPRODUCTIVE STRATEGIES

Using a comparative approach as suggested by Parrish *et al.* (1983), Roy *et al.* (1989) investigated the spatial and temporal reproductive dynamics of some coastal pelagic fish off West Africa. The spawning areas are not continuously distributed along the coast and do not always coincide with the location of highly productive areas. Reproduction occurs in places where the continental shelf broadens or in coastal indentations like a bay or downstream of a cap : this strategy allows to minimize the detrimental effects of dispersion on larvae by reproducing where offshore transport is minimum. Similar patterns were also found in other upwelling areas (Parrish *et al.*, 1983). Along the West African coast, contradictory patterns emerged when the timing of spawning is examined simultaneously with the timing of the upwelling. In some areas like Senegal or Ivory Coast, the spawning season coincides with the upwelling season, but in other areas like Sahara and Morocco spawning and upwelling are out of phase (Fig. 5).

The OEW hypothesis was used to account for these contradictory patterns that have emerged (Roy *et al.*; 1992). For the main reproductive areas off West Africa, the mean monthly wind speed is plotted versus the coastal upwelling index (Fig. 5). This allows a comparison to be made between areas of the environmental patterns during and outside the reproductive seasons. For the four different areas, spawning peaks occur at a different value of the upwelling index (between 1 and 3.2 $m^3/s/m$), however high reproductive activity always coincides with time periods of wind speed of about 6 $m.s^{-1}$ (Fig. 5). The following scheme was proposed :

-in areas where wind speed during the upwelling season is close to, or lower than, the threshold value of 6 $m.s^{-1}$, spawning occurs during the upwelling season, thus allowing larvae to benefit from the enhanced food production.

-in areas where wind speed during the upwelling season is higher than the threshold value, spawning occurs outside the upwelling season or when upwelling is minimum. this strategy minimizes the negative effect of strong wind mixing on larval survival.

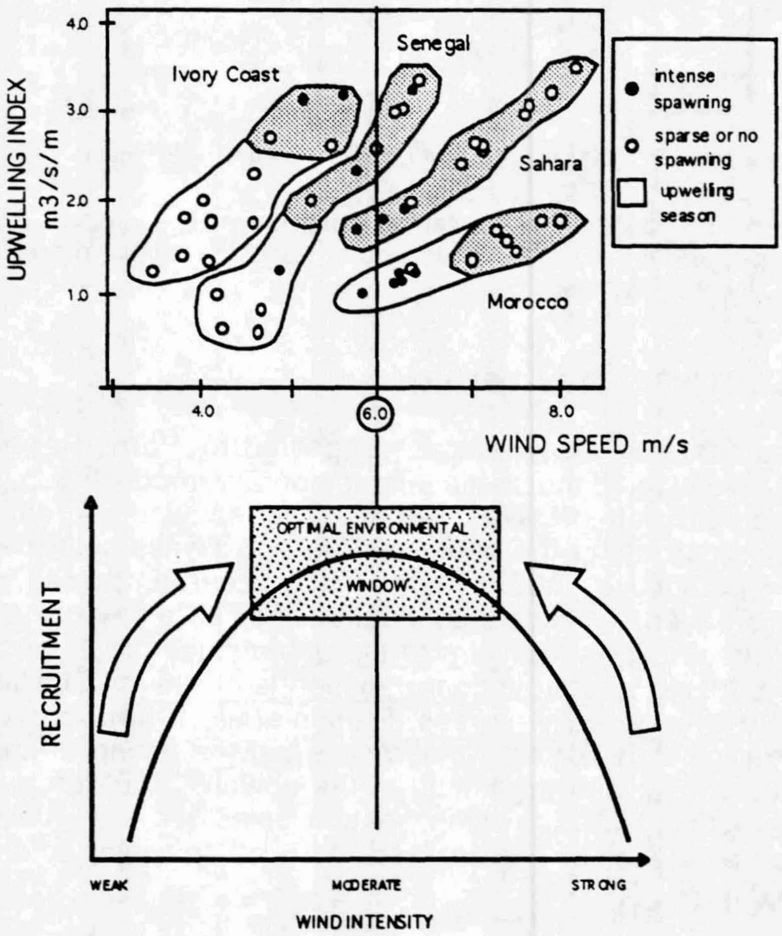


Figure 5. Spawning activities of sardine and sardinella in relation to wind speed and upwelling for four regions off West Africa. Mean monthly upwelling indices are plotted against mean monthly wind speed for each region. The upwelling season are shaded and months with intense spawning are indicated by a black dot. Note that the black dots for all regions are clustered around 6 m/s (upper figure); this value corresponds to the average wind intensity of the OEW (lower figure). (from Roy *et al.*, 1992).

For West African sardine and sardinellas, adequate spawning locations allows to solve the detrimental effect of offshore transport on larvae. Such a spawning habit leaves adjustment of seasonality as an available means for dealing with other factors such as the detrimental effects of turbulence. It appears that the tuning of the spawning season is not related to the seasonal occurrence of the upwelling. Rather, the spawning peaks coincide with the seasonal occurrence of wind speed of 6 $m.s^{-1}$. This reproductive strategy appears to be the result of a compromise between several antagonistic environmental factors. It have evolved in order to invest most of the reproductive effort in the areas where and seasons when the effects of the limiting factors for recruitment success are minimized. From an evolutionary point of view, this pattern can be interpreted as the response of a long term adaptation of reproduction to the environment for maximizing recruitment success.

## THE OEW IN ICES AREAS

The OEW hypothesis assumes that both nutrient enrichment (upwelling intensity), mixing and offshore transport are positively correlated with the magnitude of the wind (Fig. 2). This is the case in tropical or subtropical Ekman-type coastal upwelling areas where trade winds are responsible for the upwelling process. In these regions, the positive correlation between the wind-mixing index, offshore transport and upwelling intensity is the result of the steadiness of the wind regime. The underlying assumption of the OEW hypothesis in this situation are : biological production, offshore transport and mixing are related to wind speed.

In tropical or sub-tropical areas, the seasonallity of the upwelling process is induced by the latitudinal migration of the atmospheric high pressure cells located over the oceans (Acores and Saint Helen Highs in the Atlantic); the duration of upwelling seasons varies from several months (California, Morocco, South-Africa, ...) to almost year-round durations in areas like Cap-Blanc (West-Africa) Baja California or Peru. It is expected that seasonal and interannual fluctuations of the wind create corespondent fluctuations of the ecosystem biological components (Fig. 2).

In temperate regions, biological productivity is highly seasonal and the annual production cycle is dominated by the plankton spring bloom. The initial peak in primary production is attributable to the onset of stratification in waters which were enriched with nutrients earlier in winter by wind mixing. Primary production typically falls during summer due to a pronounced vertical stratification and a shortage of nutrient supply. Mid-latitude production is distinguished from that at lower latitudes by its discontinuities. In temperate areas, temperature, nutrients, light, mixing and grazing are then the expected limiting factors. Tropical or sub-tropical upwelling areas differ from higher latitude ecosystems. The limiting factors controlling biological production are not identical. In temperate areas, the limited duration of the growth season is in total contrast with the almost permanent processes that occur in lower latitude areas (Cushing, 1971; Wyatt, 1980). This suggests that the underlying assumption of the OEW (biological production and mixing are related to wind speed) may not always apply in temperate areas.

## UPWELLING IN ICES AREAS

The ocean dynamics and the biology in the ICES areas may differ from the dynamics of tropical or sub-tropical upwelling areas. However, upwelling locally occurs in temperate areas : coastal trapped waves, tidal energy, eddies, wind curl are known to induce upwelling along the shelf break (Pingree and Mardell, 1981; Bakun and Nelson, 1991; Mazé*et al.*, 1986).

Along the West coast of the Iberian peninsula, northerly winds generates an Ekman type upwelling in spring and summer (Wooster *et al.*, 1976). For the Iberian sardine *(Sardina pilchardus)*, Dickson *et al.* (1988) showed that there is a negative correlation between upwelling indices and catch (Fig. 1); increasing upwelling off the West coast of Portugal and Spain seems to be detrimental to sardine abundance. A recent investigation by Cabanas *et al.* (in prep.) also suggests that recruitment of *S. pilchardus* between 1976-1991 is negatively correlated with the April to September mean of the North-South component of the wind stress off the West coast of Spain (Fig. 6). These results seems to be in agreement with the OEW hypothesis which suggests a negative correlation between wind and recruitment in areas with wind speed greater than 6 m/s. However, *S. pilchardus* reproduction occurs in winter or early spring in the Cantabrian Sea and juveniles later migrate to the upwelling area off the West coast of Spain and Portugal (Garcia *et al.*, 1988; Chesney and Alonso-Noval, 1989). Recruitment variability of the Iberian sardine appears to be correlated with winds occuring after the spawning peak and outside of the spawning area (Robles *et al.*, 1992). Therefore, the effect of wind on larvae could not be invoke to explain the observed relationship between recruitment and upwelling.

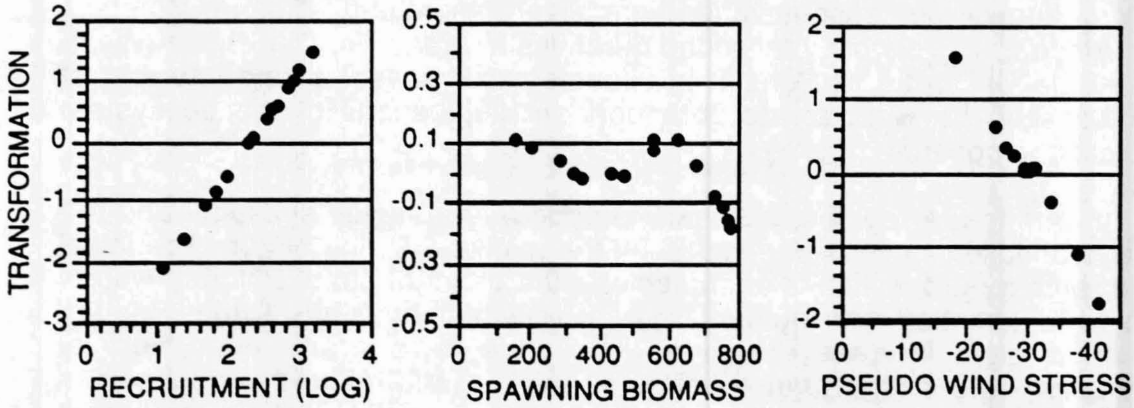


Figure 6 : Optimal transformation obtained using the ACE algorithm (Breiman and Freidman, 1985) for the recruitment of the Iberian sardine using spawning biomass (VPA analysis) and pseudo wind stress off the West coast of the Iberian peninsula (COADS data) as dependant variables (from Cabanas *et al.*, in prep.).

## IDENTIFICATION OF RELEVANT PROCESSES FOR RECRUITMENT SUCCESS.

Time series analysis has shown negative correlations between upwelling intensity and recruitment success of the Iberian sardine population. However, the physical and biological processes involved remain unclear (Chesney and Alonso-Noval, 1989) and it is unlikely that purely empirical approaches will clarify the involved processes. Instead, relevant environmental process for recruitment success of the Iberian sardine can be identified using the approach of Parrish et al. (1983). Since natural selection implies that reproductive strategies reflect responses to the most crucial factors regulating reproductive success, a joint investigation of the early life history of the fish and of the environment is likely to reflect important causal mechanisms. This approach also provides a guide for selection of relevant variables for time-series analysis in a way that makes improved use of the scarce degrees of freedom available (Bakun, 1986).

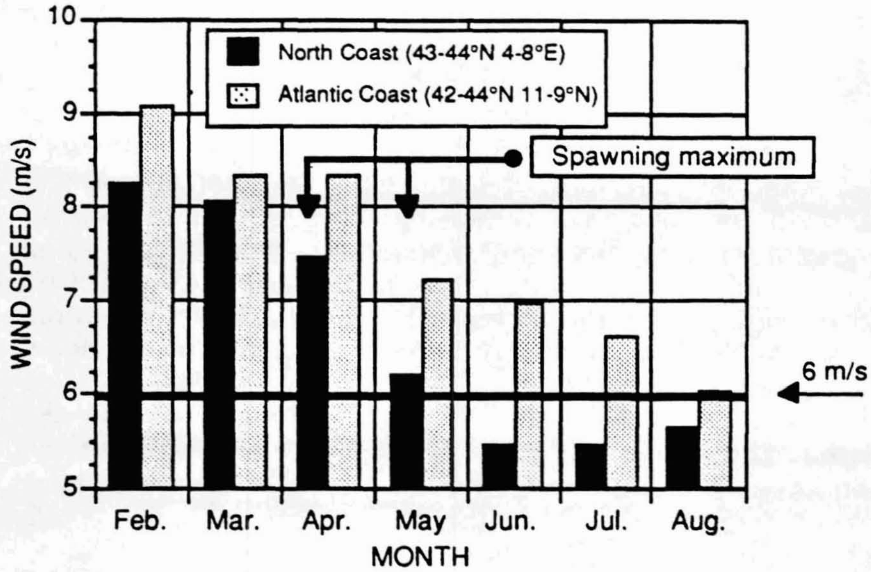


Figure 7 : Monthly mean wind speed off the Atlantic coast and North coast (Cantabrian Sea) of Spain.1960-1990 mean from the COADS database.

Spawning of the Iberian sardine occurs in the Cantabrian sea whyle nursery and feeding grounds are located along the coast of Galicia and off the West Coast of Spain and Portugal (Porteiro *et al.*, 1986; Garcia *et al.*, 1991); migration from the nursery to the feeding and the spawning grounds is observed (Porteiro *et al.*, 1986). Intense spawning occurs during spring in the Cantabrian sea outside the upwelling area (Garcia *et al.*, 1991). Little reproduction occurs during spring or summer in the highly productive upwelling areas off the Spanish West coast. The spawning peak occurs in the Cantabrian Sea between April and May; simultaneously, a sharp decrease of the wind mixing is observed in this area (the value of the wind speed decrease from 8.1 m/s in March to less than 5.5 m/s in June, a value below the thereshold value of the OEW) (Fig. 7). The resulting stabilization of the surface layer appears to set conditions for a phytoplankton bloom and high larvae survival. A similar relaxation occurs along the West coast of Spain but with a smaller amplitude; in that area, wind speed remains greater than 6 m/s during spring and summer. An interpretation of these patterns is that :

-for the Iberian sardine, the detrimental effects of dispersion (offshore transport) are minimized by reproducing outside the upwelling area;

-the timing of the reproductive season is set to take advantage of the annual spring bloom and also to avoid the detrimental effect of strong wind mixing on larvae.

Year to year fluctuations of the timing of the wind relaxation may occur. Larvae survival will be particularly affected by a delay of the wind relaxation or by the occurrence of late storms which will suddenly increase mixing in the surface layers.

## CONCLUSION

Previous studies has shown that strong upwelling is detrimental for the recruitment success of the Iberian sardine population but the environmental process involved remains unclear. An investigation of the reproductive strategies of the Iberian sardine suggests that the sardine has apparently adapted to the environment by reproducing outside the upwelling area along the coast of the Cantabrian Sea in spring and early summer; this is a region where wind speed decreases and reaches the threshold value of the OEW when spawning occurs. This suggests that a time series analysis of recruitment variability should consider the interannual fluctuations of wind off the Cantabrian coast during spring and early summer as a relevant environmental variable. Following the OEW hypothesis, a negative relationship between wind and recruitment would be expected.

The OEW may or may not apply to ICES areas depending on the validity of the underlaying assumptions of the OEW in the area under study. However, OEW hypothesis highlights some important characteristics on the way the environment can affect population dynamics :

-recruitment success does not always depend on a single environmental key factor but rather will be the result of the combination of different factors acting sometimes in opposite ways (i.e. upwelling intensity and wind mixing).

-non-linear relationships are to be expected between the environment and recruitment variability : upwelling can be either beneficial or detrimental, depending on its intensity. A scattergram that reveals no linear relationship does not necessarily mean the absence of a tight link and non-linear statistical techniques are needed to explore the effect of the environment on fish population (Mendelssohn, MS; Cury *et al.*, in press);

-changes through time or between areas may also occur : shift of the wind speed from one side to the other of the threshold value defined by the OEW will change the sign of the relationship between recruitment and the environment.

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## REFERENCES

BAKUN, A. 1986. Definition of environmental variability affecting biological processes in large marine ecosystems. *In*: variability and management of large marine ecosystems. Ed. by K. Sherman and L.M. Alexander. *AAAS selected Symposium* 99:89-108.

BAKUN A. AND C.S. NELSON, 1991. Wind stress curl in subtropical eastern boundary current regions. *J. Phys. Oceanogr.* 21: 1815-1834.

BELVÈZE, H. and K. ERZINI. 1983. The influence of hydroclimatic factors on the availability of the sardine (*Sardina pilchardus*, Walbaum) in the Moroccan Atlantic fishery. *In*: G.D. Sharp and J. Csirke (Ed.) Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, *FAO, Fish. Rep.* 291 (2): 285-327.

BREIMAN, L. and J.H. FRIEDMAN. 1985. Estimating optimal transformations for multiple regression and correlation. *J. Amer. Stat. Assoc.* 80: 580-619.

CABANAS J.M., C. PORTEIRO and C. ROY. In prep. Influence of environmental factors on sardine recruitment in the upwelling area of the Iberian peninsula.

CHESNEY, E.J. and M. ALONSO-NOVAL 1989. Coastal upwelling and the early life history of sardines (Sardina Pilchardus) along the Galician coast of Spain. *Rapp. P.-v. Réun. Cons. Explor. Mer.* 191: 63-69.

CURY P., C. ROY, R. MENDELSSOHNN, A. BAKUN, D. HUSBY and R. PARRISH . In press. Moderate is better : exploring nonlinear climatic effects on the Calofornian anchovy *(Engraulis mordax). Can. J. Fish Aquat. Sci.*

CURY, P. and C. ROY, 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.*, 46 (4): 670-680.

CUSHING, D. 1971. Upwelling and the production of fish. *Adv. Mar. Biol..*, 9:255-334.

DICKSON, R. R., KELLY P. M., COLEBROOK J.M., WOOSTER W.S. and D. H. CUSHING. 1988. North winds and production in the eastern North Atlantic. *J. Plankt. Res.*, 10, 1, 151-169.

GARCIA A., C. FRANCO, A. SOLA, M. ALONZO and J.M. RODIRGUEZ. 1988. Distribution of sardine *(Sardina pilchardus, Walb.)* egg and larval abundances off the Spanish North Atlantic coast (Galician and Cantabrian areas) in April 1987. *ICES CM 1988/H: 21.*

GARCIA A., C. FRANCO A. SOLA and A. LAGO DE LANZOS. 1991. Sardine *(Sardina pilchardus, Walb.)* daily egg production off the Galician, Cantabrian and Bay of Biscay waters in April-May 1990. *ICES C.M. 1991/H: 37.*

LASKER, R. (ed.). 1981. Marine fish larvae. Morphology, ecology, and relation to fisheries. University of Washington Press. Seattle and London. 131p.

MACKENZIE B.R. and W.C. LEGGETT. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. *Mar. Ecol. Prog. Ser.* **73**, 149-160.

MAZÉ R., Y. CAMUS AND J. Y. LE TAREAU. 1986. Formation de gradients thermiques à la surface de l'océan au dessus d'un talus, par interaction entre les ondes et le mélange dû au vent. *J. cons. Int. Explor. Mer.*, 42:221-240.

MENDELSSOHN, R. 1989. Reanalysis of recruitment estimates of the Peruvian anchoveta in relationship to other population parameters and the surrounding environment. In Pauly, D., Muck P., Mendo J. and I. Tsukayama (eds.). 1989. The Peruvian upwelling ecosystem: dynamics and interactions. ICLARM conference Proceedings 18, 438p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH,Eschborn, Federal Republic of Germany and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

MENDELSSOHN, R. MS. If the environment affects fish in a non-linear fashion ... ? To appear in Fish. Bull.

OUDOT, C. et C. ROY. 1991. Les sels nutritifs au voisinage de Dakar : cycle annuel moyen et variabilité interannuelle. In : Variabilité, instabilité et changement dans les pêcheries ouest africaines, Ph. Cury et C. Roy eds. ORSTOM, Paris.

PARRISH, R.H., BAKUN A., HUSBY D.M. and C.S. NELSON. 1983. Comparative climatology of selected environmental processes in relation to Eastern boundary current pelagic fish reproduction. *In* : Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, G.D. Sharp, J.Csirke (eds), *FAO Fish. Rep.*, 291, 3, 731-777.

PETERMAN M.R. and M.J. BRADFORD. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*).*Science* , **235**, 354-356.

PINGREE R.D. and G.T. MARDELL, 1981. Slope turbulence, internal waves and phytoplancton growth at the Celtic Sea shelf break. *Phil Trans. Roy. Soc. lond.* A302:663-682.

PORTEIRO C. , F. ALVAREZ ET N. PEREZ. 1986. Variaciones en el stock de sardina (*Sardina pilchardus, Walb.)* de las costas atlanticas de la Peninsula Iberica. (1976-1985). *Int. Symp. Long Term Changes Mar. Fish. Pop. Vigo*, 1986. 529-541.

ROBLES R., C. PORTEIRO and J.M. CABANAS. 1992. The stock of Atlanto-Iberian sardine, possible causes of variability. *ICES Mar. Sci. Symp.*, 195: 418-423.

ROTHSCHILD B.J. and T.R. OSBORN.1988. The effects of turbulence on planktonic contact rates.*J. Plankton Res.* **10 (3):** 465-474.

ROY C., P. CURY et S. KIFANI, 1992. Pelagic fish recruitment success and reproductive strategy in upwelling areas : environmental compromises. In Benguela Trophic Functioning. Payne, A.I.L., Brink, K.H., Mann, K.H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* , 12 : 135-146.

ROY C., P. CURY, A. FONTANA et H. BELVEZE, 1989. Stratégies spatio-temporelles de la reproduction des clupéidés des zones d'upwelling d'Afrique de l'Ouest. *Aquat. Living Resourc.*, 2:21-29.

ROY, C., CURY P., FONTANA A. et H. BELVÈZE. 1989. Stratégies spatio-temporelles de la reproduction des clupéidés des zones d'upwelling d'Afrique de l'Ouest. *Aquat. Living Resourc.*, 2:21-29.

SAVILLE, A. 1965. Factors controlling dispersal of the pelagic stages of fish and their influence on survival. *Int. Com. for N.W. Atlantic Fisheries*, Special Publication, 6: 335-348.

SHANNON, L.V., CRAWFORD, R.J.M, BRUNDRIT G.B. and L.G. UNDERHILL. 1988. Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. int. Explor. Mer*, 45: 5-12.

SHELTON, P.A., BOYD A.J. and M.J. ARMSTRONG. 1985. The influence of large scale environmental processes on neritic fish populations in the Benguela current system. *CALCOFI, Rep.*, 26: 72-92.

WARE, D.M. and R.E THOMPSON. 1991. What happened to biological productivity in the coastal upwelling domain in the 1920s and 30s ?. *Can. J. Fish. Aquat. Sci.*, 48:12, pp2296-2306.

WOOSTER, W. S., A. BAKUN and D.R. McLAIN. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, 34, 131-141.

WYATT, T. 1980. The growth season in the sea. *J. Plankton Res.* , 2,1.