The Optimal Environmental Window Hypothesis in the ICES Area: The example of the Iberian sardine

C. Roy[1], C. Porteiro[2], and J. Cabanas[2]

[1]Département TOA, ORSTOM, 213 rue La Fayette, 75480 PARIS Cedex 10, France: [2]Centro Oceanografico de Vigo, Instituto Espanol de Oceanografia, Cabo Estay Canido, Apartado de Correos 1552, 36280 Vigo, Spain.

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 an 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 (Figure 1). In a nearby area, Belvèze and Erzini (1983) found a positive relationship between the catch of the Moroccan sardine *(Sardina pilchardus)* and upwelling (Figure 1).

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 (Figure 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.

The Optimal Environmental Window (OEW) hypothesis (Cury and Roy, 1989) assumes that the relation between recruitment and upwelling indices is dome shaped (Figure 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 (Figure 3).

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 (Figure 4). The non-linearity always appears for values of wind speed around 5-6 ms^{-1} (Figure 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 ms^{-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).

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 (Figure 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 (Figure 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 $m^3s^{-1}m^{-1}$), however high reproductive activity always coincides with time periods of wind speed of about 6 ms^{-1} (Figure 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 ms^{-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.

For West African sardine and sardinellas, adequate spawning locations allow 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 ms^{-1}. This reproductive strategy appears to be the result of a compromise between several antagonistic environmental factors. It has 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 hypothesis assumes that both nutrient enrichment (upwelling intensity), mixing and offshore transport are positively correlated with the magnitude of the wind (Figure 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 (Azores 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 coresponding fluctuations of the ecosystem biological components.

The OEW in ICES areas

In mid-latitude or 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. Mid-latitude ecosystems differ from tropical or sub-tropical upwelling areas : temperature, nutrients, light, mixing and grazing are the expected limiting factors of biological production. In temperate areas, the limited duration of the growth season is also 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 may not always apply in temperate areas.

The upwelling off the Iberian Peninsula

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 : 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 (Figure 1); increasing upwelling off the West coast of Portugal and Spain seems to be detrimental to sardine abundance. 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 along the Atlantic coast but also in the Cantabrian sea; moreover, spawning activity is not synchrone along the Iberian peninsula coasts. 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; Sola *et al.*, 1992). Off Portugal, reproduction is maximum in winter with a second peak in early spring (Cunha and Figueiredo, 1988; Ré *et al.*, 1990). Recruitment variability of the Iberian sardine appears to be correlated with winds occuring after the main spawning peak (Portugal) or outside of the spawning area (Cantabrian sea) (Robles *et al.*, 1992). Therefore, it appears to be difficult to invoke the effect of wind on larvae to explain the observed relationship between recruitment and upwelling.

Identification of relevant processes for recruitment success: The Cantabrian Sea spawning area

Time series analysis has shown negative correlations between upwelling intensity and recruitment success of the Iberian sardine population (Dickson *et al.*, 1988). 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 processes 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).

As an example we choose to investigate the reproductive pattern of *S. pilchardus* in the Cantabrian sea. Spawning of the Iberian sardine occurs in the Cantabrian sea while 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). Intense spawning occurs during spring in the Cantabrian sea outside the upwelling area (Garcia *et al.*, 1991). Little reproduction occurs during spring 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 ms^{-1} in March to less than 5.5 ms^{-1} in June, a value below the thereshold value of the OEW) (Figure 6). 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 the reproductive patterns in the Cantabrian sea is that :

- 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.

Conclusion

Previous studies have shown that strong upwelling is detrimental for the recruitment success of the Iberian sardine population but the environmental process involved remains unclear. The coast of the Cantabrian sea is an area where high concentration of eggs and larvae are found; high reproductive activity occurs in spring when the wind speed reaches the threshold value of the OEW. 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. This suggests that a time series analysis of recruitment variability of the Iberian sardine 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. However, the coast of Portugal is also thought to be an important spawning area for sardine; reproductive activity is maximum during winter when wind mixing generated by storms is high. Both areas may contribute to the overall recruitment of the Iberian sardine population.

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, submitted; 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 (Roy *et al.*, 1992).

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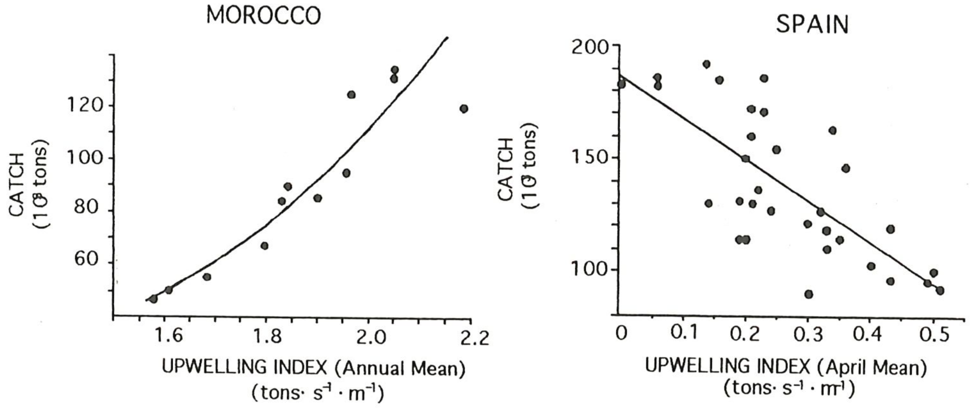

Figure 1 An example of positive and negative correlations between catch and upwelling index obtained for the same species *(Sardina pilchardus)* at two different locations: the sardine off Morocco (from Belvèze and Erzini, 1983) and the sardine off Spain (from Dickson *et al.*, 1988).

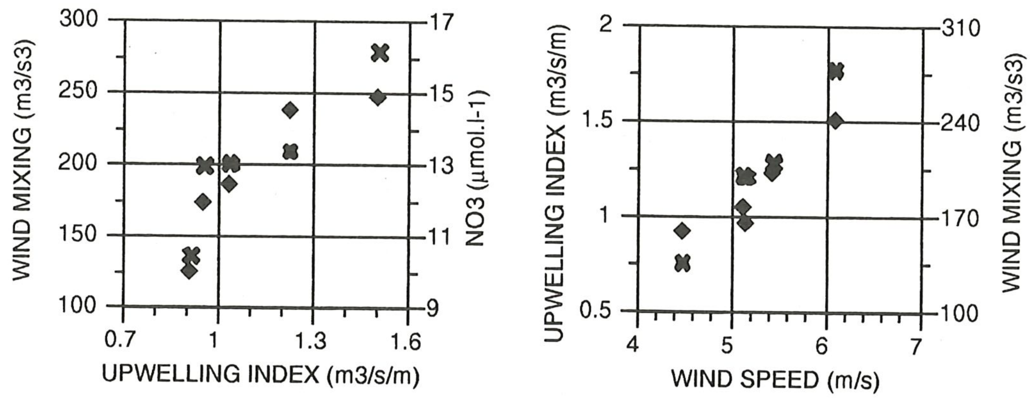

Figure 2 Relation between monthly values of (left) upwelling index and wind mixing or Nitrate concentration; (right) wind speed and upwelling index or wind mixing. Data from 1985 to 1989 at the Cap-Vert coastal stations (Sénégal). Mean calculated during the upwelling season from January through May (See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

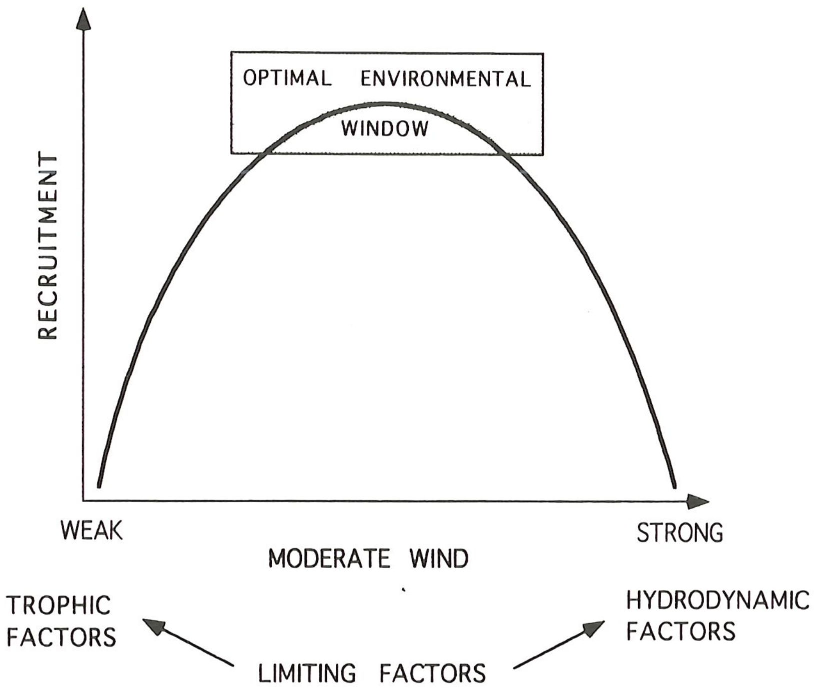

Figure 3 Theoretical relationship between recruitment and environmental factors in upwelling areas (adapted from Cury and Roy, 1989).

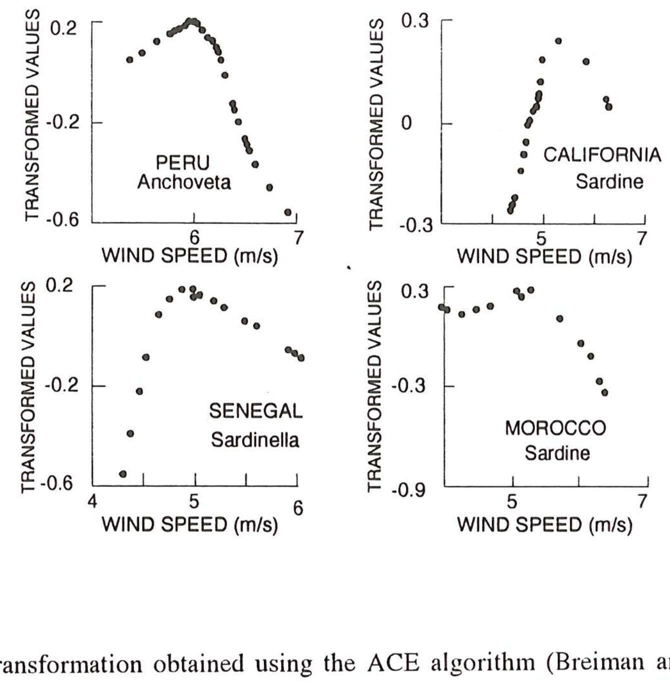

Figure 4 Optimal transformation obtained using the ACE algorithm (Breiman and Freidman, 1985) for the recruitment of sardine and anchovy in four different upwelling areas (from Cury and Roy, 1989).

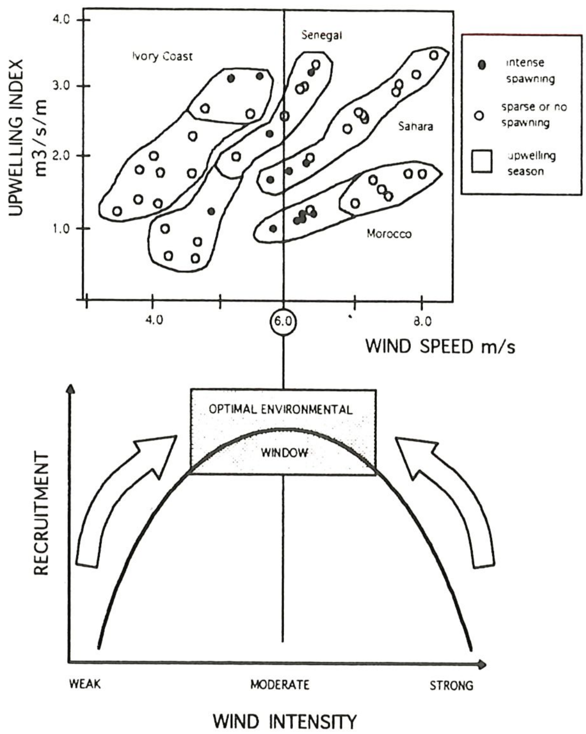

Figure 5 Spawning activities of sardine and sardinella in relation to wind speed and upwelling for four regions off West Africa. Mean monthly upwelling indices are plotted against mean monthly wind speed for each region. The upwelling seasons are shaded and months with intense spawning are indicated 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).

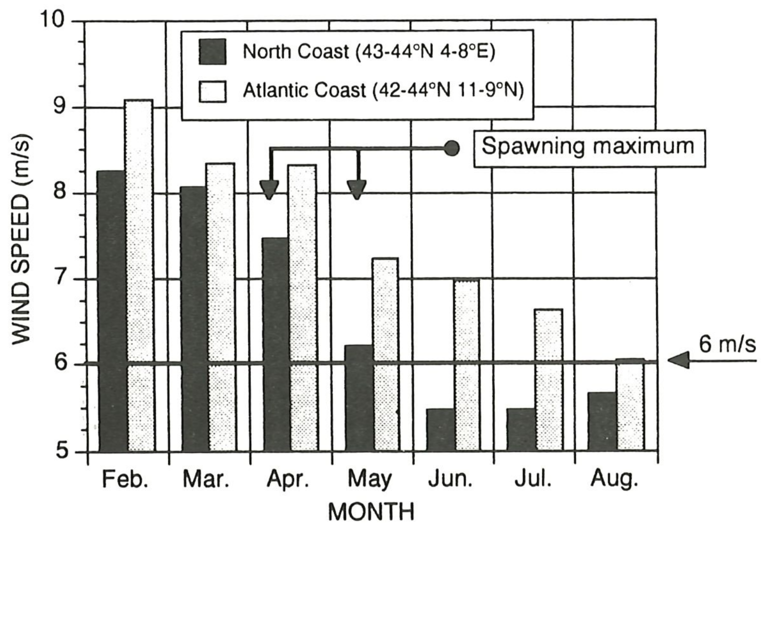

Figure 6 Monthly mean wind speed off the Atlantic coast and North coast (Cantabrian Sea) of Spain. 1960-1990 mean from the COADS database.