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PELAGIC FISH RECRUITMENT SUCCESS AND REPRODUCTIVE STRATEGY IN UPWELLING AREAS: ENVIRONMENTAL COMPROMISES

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Past work has shown that indices of recruitment or abundance of pelagic fish in eastern boundary currents can be both negatively and positively related to upwelling intensity. Such 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" hypothesis. New evidence for such a relationship is presented for the Moroccan sardine *Sardina pilchardus* and the northern anchovy *Engraulis mordax*. Recruitment success increases with upwelling intensity when wind speed is low to moderate. In areas or periods of strong wind, recruitment success decreases with upwelling intensity. Using a comparative approach, the spatial and temporal reproductive dynamics of West African coastal pelagic fish are investigated. In some areas, the spawning season coincides with the upwelling season, but in other areas spawning and upwelling are out of phase. High reproductive activity coincides with the seasonal occurrence of wind speed of about 5–6 $m \cdot s^{-1}$, which is the value defined as the "optimal environmental window". This pattern is hypothesized to be the response, from an evolutionary point of view, of a long-term reproductive adaptation to the environment that maximizes recruitment success.

Vorige werk het getoon dat indekse van rekrutering of talrykheid van pelagiese vis in oosgrensstrome sowel 'n negatiewe as 'n positiewe verband met opwelintensiteit kan hê. Sulke bevindinge bevraagteken die bestaan van 'n gesamentlike teorie wat rekrutering in verband bring met die omgewing in opwelstreke. Positiewe en negatiewe korrelasies kan egter albei geldig wees as die verband tussen rekrutering en opwelintensiteit koepelvormig is soos deur die hipotese van 'n "optimale omgewingsvenster" gesuggereer word. Nuwe bewyse vir so 'n verband word vir die Marokkaanse sardyn *Sardina pilchardus* en die noordelike ansjovis *Engraulis mordax* aangebied. Rekruteringsukses neem toe soos opwelintensiteit toeneem by lae tot matige windsnelheid. In streke of tydperke van sterk wind neem rekruteringsukses af met toenemende opwelintensiteit. Deur gebruik te maak van 'n vergelykende benadering word die voortplantingsdinamika van Wes-Afrikaanse pelagiese kusvis in ruimte en tyd ondersoek. In sommige gebiede val die kuitskiet- en die opwelseisoen saam, maar in ander is hulle uit fase. Hoë voortplantingsbedrywigheid val saam met die seisoensvoorkoms van windsnelheid van sowat 5–6 $m \cdot s^{-1}$, die waarde wat as die "optimale omgewings-venster" gedefinieer is. Die hipotese is dat hierdie patroon die reaksie, uit 'n evolusionêre oogpunt, is van 'n langtermynse voortplantingsaanpassing by die omgewing wat rekruteringsukses maksimaliseer.

Whereas the total world catch of marine fish has been stable over the past few decades, the contribution of clupeoids has declined from one-half to one-third (Smith 1985). This decline is attributable mainly to large fluctuations in the catches of clupeoids in upwelling areas. Recently, Beverton (1990) stressed that fishing and excessive depletion has the potential to cause temporary disappearance of local pelagic stocks and disruption of ecosystems. An abundant and well-documented literature is now available on pelagic fish of the world's upwelling areas (Sharp and Csirke 1983, Pauly and Tsukayama 1987, Payne *et al.* 1987, Crawford *et al.* 1987, Pauly *et al.* 1989, Cury and Roy 1991). The main conclusion drawn from all these studies is that the environment plays an important role in the dynamics of pelagic fish, even if fishing increases their natural instability.

Scientific progress in the problem area of recruitment variability has been made by combining results at different temporal or spatial scales. The physical environment at scales of motion comparable with feeding scales of larvae has shown the negative effects of wind-generated turbulence on larval survival (Lasker 1981, Peterman and Bradford 1987), or more recently a positive effect on planktonic contact rates (Rothschild and Osborn 1988, MacKenzie and Leggett 1991). At a population level, the importance of food availability for larvae led Cushing (1975, 1990) to formulate the "match-mismatch" hypothesis, in which the annual production of fish larvae matches or mismatches the production of their food. For pelagic fish in the California Current, Parrish *et al.* (1981) suggested that wind-induced offshore transport of surface water may have a detrimental effect on recruitment success.

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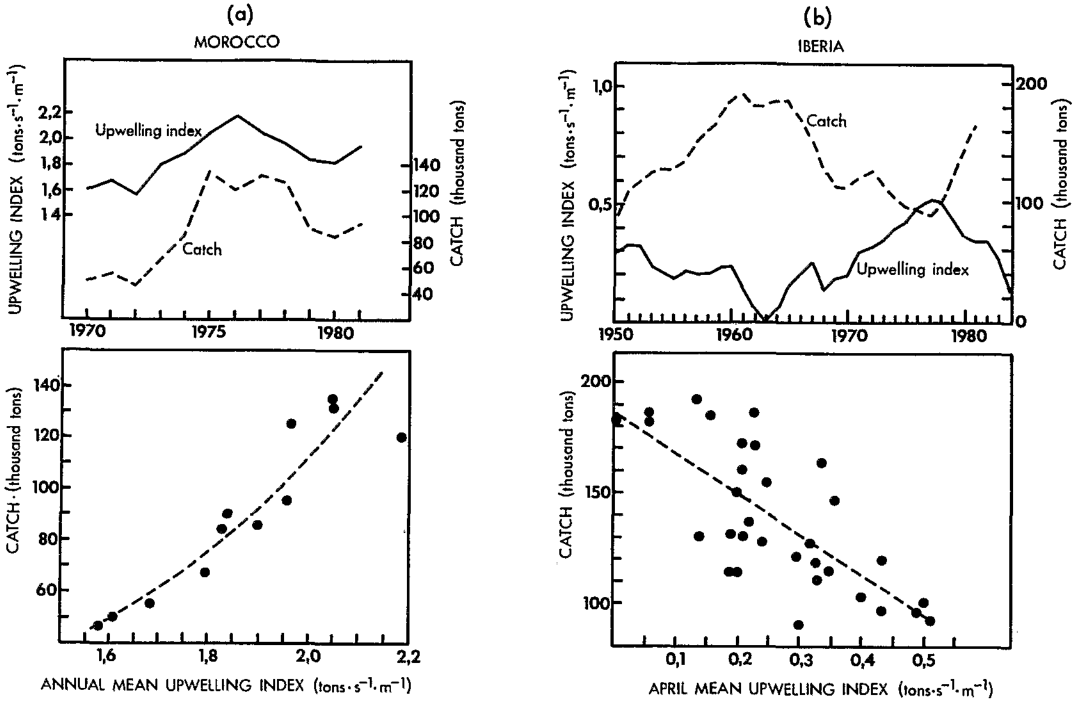

Fig. 1: An example of negative and positive correlations between catch and upwelling index obtained for the same species (*Sardina pilchardus*) at two different locations — (a) a positive correlation between the Moroccan sardine catch in Zone B and the upwelling index for the preceding three years, from 1970 to 1981 (after Belvèze and Erzini 1983); (b) a negative correlation between the Iberian catch of sardine and the upwelling index in April at Porto over the preceding three years, from 1954 to 1984 (after Dickson *et al.* 1988, by permission Oxford University Press)

Although the turbulence mechanism acts to cause larval starvation on a time-scale of a few days, the transport hypothesis acts on much longer time-scales and indirectly may cause mortality of late larvae and juveniles by displacing them from the favourable coastal environment. In some rare cases, longshore transport may have a beneficial effect by transporting eggs and larvae in the direction of the recruitment ground (Shelton and Hutchings 1982). The "transport hypothesis" has been generalized by Sinclair (1988) in a "member/vagrant" theory, in which the importance of spatial scale constraints is developed.

Many attempts have been made to correlate environmental fluctuations to recruitment indices. For the South African pilchard *Sardinops ocellatus*, the relationship between year-class strength and sea-surface temperature is positive in the southern Benguela (Shelton *et al.* 1985) but negative off Namibia (Shannon *et al.* 1988). The potential influence of environmental factors on the recruitment success of anchovy *Engraulis capensis* and pilchard in the pelagic fishery off South Africa appears to be strongly buffered in the pulsing and variable southern Benguela (Hutchings and Nelson 1985). For the Iberian sardine *Sardina pilchardus*, Dickson *et al.* (1988) found a negative correlation between catch and upwelling indices (Fig. 1), in total contrast to the findings of Chesney and Alonso-Noval (1989). In a nearby area, Belvèze and Erzini (1983) found a positive relationship between the catch of Moroccan sardine *Sardina pilchardus* and upwelling (Fig. 1).

In this paper, an attempt is made to reinforce the "Optimal Environmental Window" (OEW) hypothesis presented by Cury and Roy (1989). This hypothesis suggests that, in upwelling areas, a dome-shaped relationship exists between recruitment success and upwelling intensity. By means of a comparative approach, the spatial and temporal reproductive dynamics of coastal pelagic fish in West Africa are investigated in regard to the dome-shaped relationship between recruitment

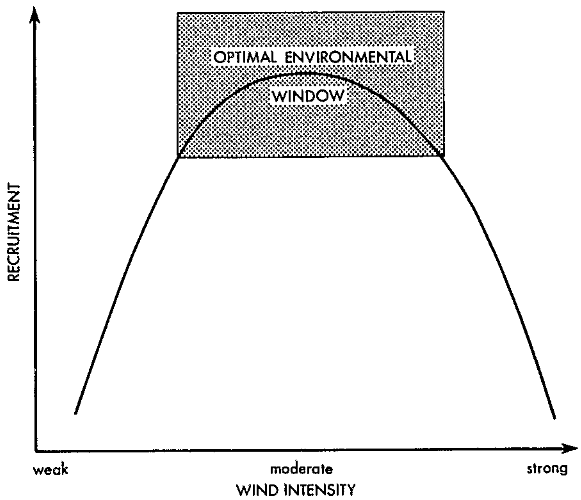

Fig. 2: Theoretical relationship between recruitment and environmental factors in upwelling areas (adapted from Cury and Roy 1989)

and upwelling intensity.

"OPTIMAL ENVIRONMENTAL WINDOW" AND RECRUITMENT SUCCESS

Because many environmentally based models for marine fish recruitment have failed or deteriorated when tested with new data sets, they have sometimes been strongly criticized (Walters and Collie 1988). Does that mean that results obtained previously are spurious and just artefacts? There may be some reasons why the models failed. For instance, the dynamics of the ecosystem may have changed with time and new factors may have come into play. Dominance of other species (Skud 1982, Cury 1988, Shannon *et al.* 1988) or change in environmental key factors (Binet *et al.* 1991) may then be identified. The relationships between the variables may also be nonlinear and the use of linear regressions (or *a priori* transformations) may result in rejection of possible nonlinear links. Attention will be focused on this last point.

Theoretical and statistical approaches

The OEW hypothesis assumes that the relation between recruitment and upwelling indices is dome-shaped (Fig. 2). The nonlinearity of the curve is explained by considering the positive or negative effects of several environmental factors. On the left side of the curve, wind and upwelling intensities are weak to moderate; enhanced food production or increased encounter rate between larvae and food particles as a result of small-scale turbulence may then be beneficial for survival of larvae. On the right side of the curve, upwelling is strong, and wind-mixing and offshore transport are then detrimental factors (Fig. 2).

In analysing the relationship between recruitment and environmental factors, most studies use linear statistical methods or assume an *a priori* transformation (e.g. a log-transformation). A statistical technique developed by Breiman and Friedman (1985) empirically estimates optimal transformations for multiple regressions. The response variable Y and the predictor variables $X_1, \ldots, X_p$ are replaced by functions $T_1(Y)$ and $T_2(X_1), \ldots, T_{p+1}(X_p)$. The algorithm estimates these functions T_i by minimizing

$$e^2 = \frac{E\{(T_1(Y) - \sum_{j=1}^{p} T_{j+1}(X_j))^2\}}{\mathrm{Var}\,[T_1(Y)]} .$$

An iterative algorithm (ACE: Alternating Conditional Expectation) permits the calculation of those transformation functions which do not belong to a particular parameterized family and which are even not monotonic. The algorithm converges to an optimal solution and does not produce a given equation, but rather an empirical smoothed transformation of each of the data points for each variable. The transformation is not expressed in a particular unit (unless a functional transformation can be discerned from the plot) and its shape is found by plotting the transformed values of a variable versus the original values.

Comparative ecological validation

Five pelagic fish stocks from different upwelling areas were analysed using this exploratory statistical method (Cury and Roy 1989). The comparative approach revealed a dome-shaped relationship between recruitment success of pelagic fish and upwelling intensity and an OEW for wind speeds of roughly 5–6 $m \cdot s^{-1}$.

Using new estimates of recruitment for the Peruvian anchoveta, Mendelssohn (1989) obtained similar results. With extended time-series for the Pacific sardine, Ware and Thompson (1991) support the existence of an optimal environmental window, but at a wind speed of around 7–8 $m \cdot s^{-1}$. Using catch per unit of effort

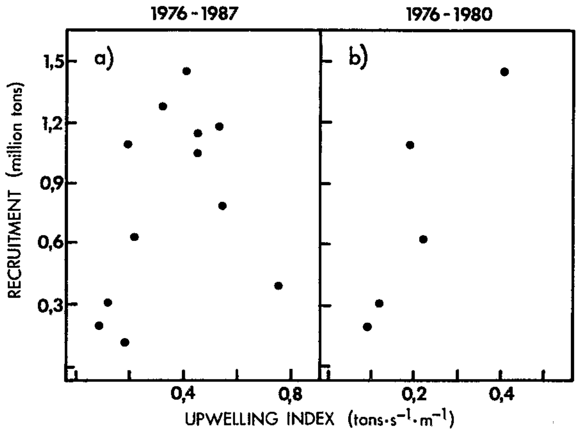

Fig. 3: Relationship between recruitment index of the central stock of the Moroccan sardine *Sardina pilchardus* (estimated as 0-year age-class from cohort analysis — F.A.O. in prep.) and mean upwelling index calculated from wind speed data at Essaouira — (a) 1976–1987, (b) 1976–1980 (to compare with the results obtained by Belvèze and Erzini 1983)

(*cpue*) of the Moroccan sardine as a function of past environmental data, Orbi *et al.* (1991) showed that the relationships between *cpue* and the previous two years' upwelling indices were dome-shaped.

THE MOROCCAN SARDINE *SARDINA PILCHARDUS*

A recruitment index for the central stock of Moroccan sardine was estimated from 1976 to 1987 by means of cohort analysis (F.A.O. in prep.). A mean annual upwelling index in the reproductive area between 27 and 30°N is calculated during the reproductive season (January–March) from coastal wind data collected slightly farther north at Essaouira (31°40'N). The relationship between recruitment and upwelling intensity appears to be dome-shaped: for upwelling indices lower than 0,3 tons·s^{-1}·m^{-1} or higher than 0,5 tons·s^{-1}·m^{-1}, the recruitment decreases. It is at a maximum for an upwelling index of some 0,45 tons·s^{-1}·m^{-1} (Fig. 3a). This corresponds to a wind speed at Essaouira of about 4–5 m·s^{-1}. The optimal transformations for the multiple regression between recruitment index, adult biomass and upwelling index are presented in Figure 4. The transformed variables explain 79 per cent of the recruitment variability. The transformation of the recruitment is linear and the transformation of the adult biomass appears to be decreasing (Fig. 4). The transformation of upwelling index is dome-shaped and similar to a smoothing of the raw data plotted on Figure 3a. The wind speed measured at Essaouira appears to be lower than the wind in the spawning area, as estimated from maritime reports. This would explain the low value of wind speed for the OEW off Morocco given by this analysis.

The dome-shaped relationship between recruitment and upwelling indices appears to be different from the linear positive relation obtained by Belvèze and Erzini (1983). However, when considering the same time period (prior to 1980), results are similar (Fig. 3b). After 1980, upwelling was stronger in that area and apparently had a negative effect on recruitment (Fig. 3a).

THE NORTHERN ANCHOVY *ENGRAULIS MORDAX*

Methot (1989) combined the analyses of catch,

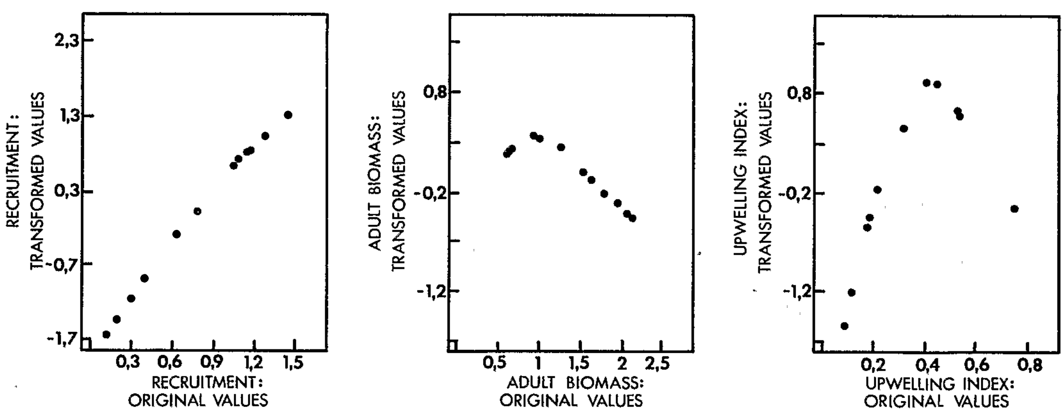

Fig. 4: Optimal empirical transformations for recruitment (million tons), adult biomass (million tons) and upwelling index (tons·s^{-1}·m^{-1}) for the Moroccan sardine from 1976 to 1987 (biological data from F.A.O. in prep.; mean upwelling index calculated from wind speed data at Essaouira)

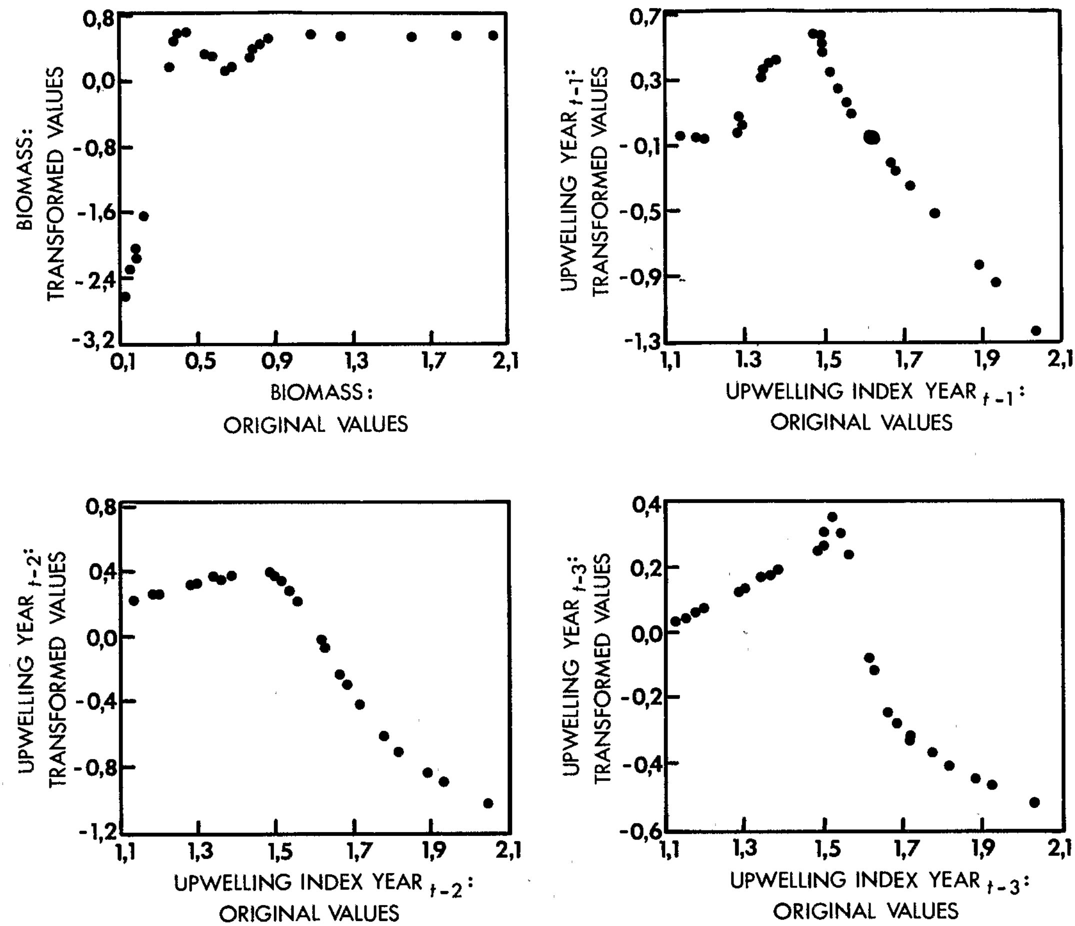

Fig. 5: Optimal empirical transformations for the northern anchovy total biomass (million tons) and the upwelling indices (tons·s^{-1}·m^{-1}) one, two and three years before, from 1954 to 1985 (biological data from Methot 1989, upwelling index at 33°N, 119°W provided by D. M. Husby, Pacific Fisheries Environmental Group)

abundance and age composition data of the central population of northern anchovy into a stock synthesis model and produced estimates of total and spawning biomasses and of recruitment indices. However, the estimates of spawning biomass and total biomass are not independent. The recruitment index is calculated on the basis of certain assumptions as to the anchovy's availability to the Mexican fishery. For an initial analysis of the northern anchovy, and in order to consider independent times-series, the total biomass estimates (Methot op. cit.) and the annual mean of the upwelling index calculated in the spawning area at 33°N, 119°W were used, both for the period 1954–1986.

The time-series of total biomass is assumed to describe the interannual fluctuations in population abundance from 1954 to 1986. It was related to the upwelling index one, two and three years before in order to take into account the environmental effect on fish one, two or three years old. The transformations are presented in Figure 5; they explain 71 per cent of the total variance in biomass. The transformation of the total biomass has an approximately logarithmic shape, with an inflection point at around 0,5 million tons. The shape of the upwelling transformations lagged by one, two and three years are similar and dome-shaped, with an inflection point at an upwelling value of some 1,5 tons·s^{-1}·m^{-1}. At 33°N, this value corresponds to an average wind speed of about 5–6 m·s^{-1}.

From the abundance of anchovy larvae off southern

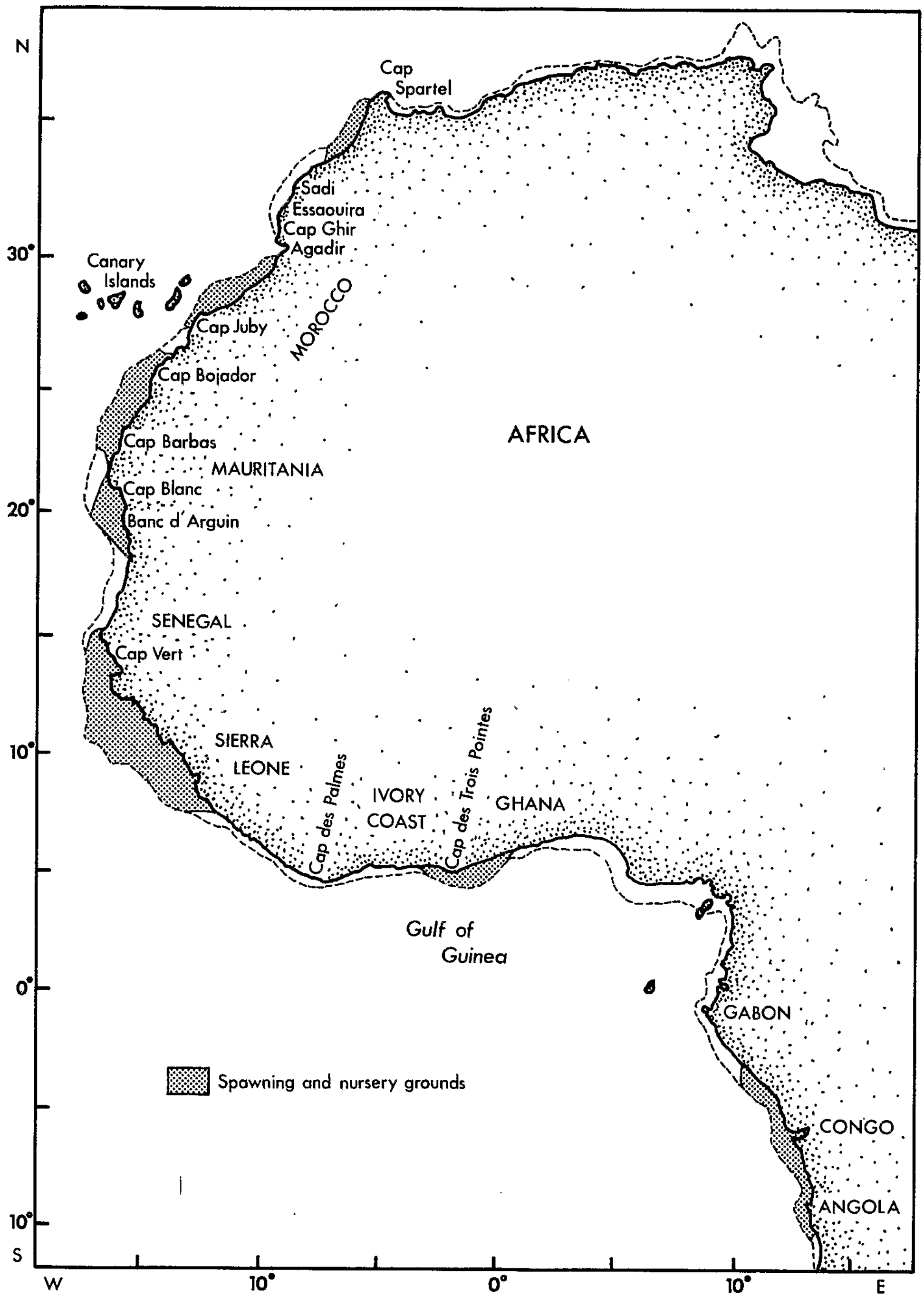

Fig. 6: Spatial distribution of the main spawning and nursery areas of sardine *Sardina pilchardus* and sardinellas *Sardinella aurita* and *S. maderensis* off the West African coast (after Roy *et al.* 1989)

California between 1951 and 1990, Cury *et al.* (in prep.) found that fewer larvae were produced when upwelling intensity was both weak or strong. Smith and Eppley (1982) correlated the abundance of anchovy larvae with primary production and zooplankton standing stock, and concluded that "the intensity of spawning activity of the adult anchovy in part depends on zooplankton abundance three quarters earlier and in part on the productivity of the area in the same season". The destruction of fine-scale food strata and dispersion of anchovy larvae could lead to recruitment failure, particularly if unfavourable conditions persist through the spawning season (Lasker 1978). Peterman and Bradford (1987) gave evidence that high wind speed was associated with high mortality rates of larvae. Husby and Nelson (1982) suggested that "too much stability prior to or during a spawning season might produce equally adverse spawning conditions by severely inhibiting the upward flux of nutrients and reducing primary production". A modelling investigation confirms this hypothesis that there must be optimal conditions of wind speed, duration and frequency of wind events for maximum survival of northern anchovy larvae (Wroblewski and Richman 1987, Wroblewski *et al.* 1989).

PELAGIC FISH REPRODUCTIVE STRATEGY

A key question arises from the previous results. Is there any link between environmental factors for recruitment success and the reproductive strategy of pelagic fish? By means of a comparative approach, the links between the environment and the reproductive dynamics of West African coastal pelagic fish are investigated.

Spatial patterns

Several clupeoid spawning areas can be identified along the West African coast. They are not distributed continuously within the upwelling areas. There are three spawning areas off Morocco (Conand 1975, Domanevsky and Barkova 1976, Belvèze 1991, Fig. 6): south of Cap Spartel (36–32°N), from Cap Ghir to Cap Juby (30–27°N) and from Cap Bojador to Cap Barbas (26–22°N). Off Mauritania and Senegal (Fig. 6), spawning activity is intense on the Arguin Bank south of Cap Blanc (18°30′–21°N) and from the Cap Vert Peninsula to the coast of Sierra Leone (Conand 1977, Boëly *et al.* 1982). Off the Ivory Coast and Ghana, the main spawning area of *Sardinella aurita* is located around Cap des Trois Pointes, between 2°W and 1°E (ORSTOM/FRU 1976).

There are other highly productive regions along the West African coast, but they have not been identified as main spawning areas even though sporadic spawning occurs there. This is the case for the coastline north of the Cap Vert Peninsula, where upwelling takes place during winter, and for the permanent upwelling area between Cap Barbas and Cap Blanc. Migrations from highly to apparently less productive areas have also been observed at the time of spawning along the Moroccan coast (Belvèze 1991).

INTERPRETATION

The spawning areas off West Africa are not continuous along the coast and do not always coincide with the location of highly productive areas. This suggests that biological production is not the only factor controlling the spatial distribution of the spawning areas. However, the major spawning areas share a common topographic feature: they are all located in places where the continental shelf broadens or in coastal indentations such as a bay or downstream of a cape (Roy *et al.* 1989). Offshore flow from the coastal area is minimized in such locations. In certain cases where the continental shelf is wide, phytoplankton biomass is high and productivity is apparently retained over the inner shelf (see Fig. 12 of Roy 1991). This feature suggests that the structure of the circulation over a wide continental shelf may provide an area of retention inshore. Spawning in such areas reduces offshore loss of reproductive products and keeps the larvae in a productive coastal area.

Temporal patterns

The pelagic fish populations off West Africa reproduce throughout the year, but with marked seasonal peaks (Fig. 7). From Cap Spartel to Cap Juby, *Sardina pilchardus* spawns outside the upwelling season, mainly during winter and early spring (Furnestin and Furnestin 1959, Belvèze and Erzini 1983). In the Sahara region, from Cap Bojador to Cap Barbas, the main spawning season coincides with decreasing intensity of upwelling, from October to December, but with a minor spawning peak in April and May (F.A.O. 1985). South of Cap Vert, *Sardinella aurita* and *S. maderensis* reproduce mainly during the upwelling season (boreal winter and spring), with a major peak in May and June (Fréon 1988). At the end of June, the adults migrate northwards to reproduce in the waters surrounding the Arguin Bank from July to August (Boëly *et al.* 1982). Along the Ivory Coast,

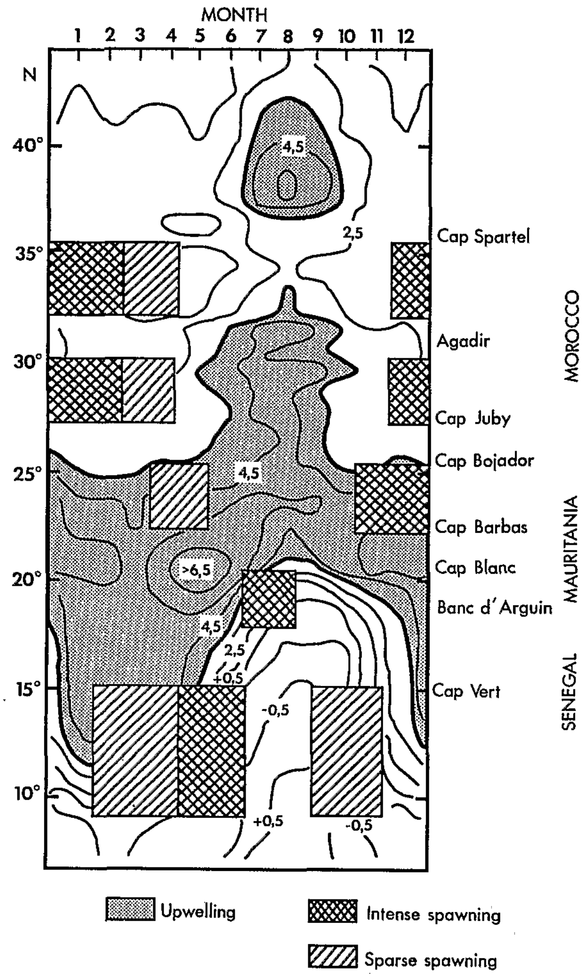

Fig. 7: Spatial and temporal upwelling intensity estimated from the difference between offshore temperature and longshore temperature (after Wooster *et al.* 1976) and the main reproductive areas and seasons of sardine and sardinellas in the eastern tropical Atlantic, 5–45°N (redrawn after Roy *et al.* 1989)

Ghana and Congo, *S. aurita* reproduces mainly during the two upwelling seasons, January/February and July/August (ORSTOM/FRU 1976). In those areas, *S. maderensis* reproduces throughout the year, but activity is greatest during the two upwelling seasons.

From this regional comparison, two different patterns emerge. In mid-latitude areas such as Morocco, fish avoid spawning during the upwelling season; spawning there takes place during winter or early spring. Off the Sahara, where upwelling is permanent, spawning takes place when upwelling is at a minimum. In low latitude areas, the main spawning activity is during the decreasing phase of the upwelling (Senegal) or during the upwelling seasons (Ivory Coast, Ghana, Congo).

INTERPRETATION

Bakun and Parrish (1982) and Parrish *et al.* (1983) showed that the timing of the reproductive season in the four main upwelling ecosystems is set to minimize offshore Ekman transport. Along the coast of West Africa, the Moroccan and the Saharian sardine populations show a similar pattern by spawning outside the upwelling season (Morocco) or when the upwelling is at a minimum (Sahara). However, in low-latitude ecosystems, the pattern is contradictory. Off Senegal and in the Gulf of Guinea, spawning peaks when upwelling weakens or is active, i.e. during a period of strong offshore transport.

Bakun and Parrish (1982) also found a discrepancy in this generalization: the Peruvian anchoveta reproduces in a low-latitude area (Chimbote, 9°S) during the austral winter upwelling, which is the season of strongest offshore Ekman transport. Parrish *et al.* (1983) resolved the discrepancy by examining the depth of the mixed layer; it varies in phase with Ekman transport but with a greater amplitude. The thinner mixed layer of the austral summer is apparently carried offshore nearly four times as fast as the deeper mixed layer in winter. Therefore, spawning of the Peruvian anchoveta appears tuned to minimize the rapidity of offshore loss of eggs and larvae.

Off Senegal, coastal advection is directed offshore only during the upwelling season; during summer, advection from the south-west carries warm tropical surface waters onto the continental shelf (Mittelstaedt 1983). Off the Ivory Coast and Ghana, the summer upwelling season is also the time when the eastward flow of the Guinea Current reaches its maximum (Lemasson and Rébert 1973). Therefore, it is apparently difficult to associate the occurrence of the reproductive season in these two areas with any feature that minimizes offshore transport.

The OEW hypothesis offers a complementary means of examining possible links between spawning and the environment. For the main reproductive areas, it is possible to plot the mean monthly wind speed against the offshore component of the Ekman transport (i.e. the coastal upwelling index defined by Bakun 1973) and then to mark the months when reproduction does occur (Fig. 8). This allows a comparison between areas of the environmental patterns during the reproductive seasons. Off Senegal, the Ivory Coast and Ghana, winds are always weak or moderate. Owing to the effect of latitude, Ekman transport and upwelling index are higher there than off Morocco, where winds are stronger. In the four different areas, spawning peaks at a different value of the upwelling index, but the peaks coincide with wind speeds of about 6 $m \cdot s^{-1}$ (Fig. 8). One could therefore draw the following scheme:

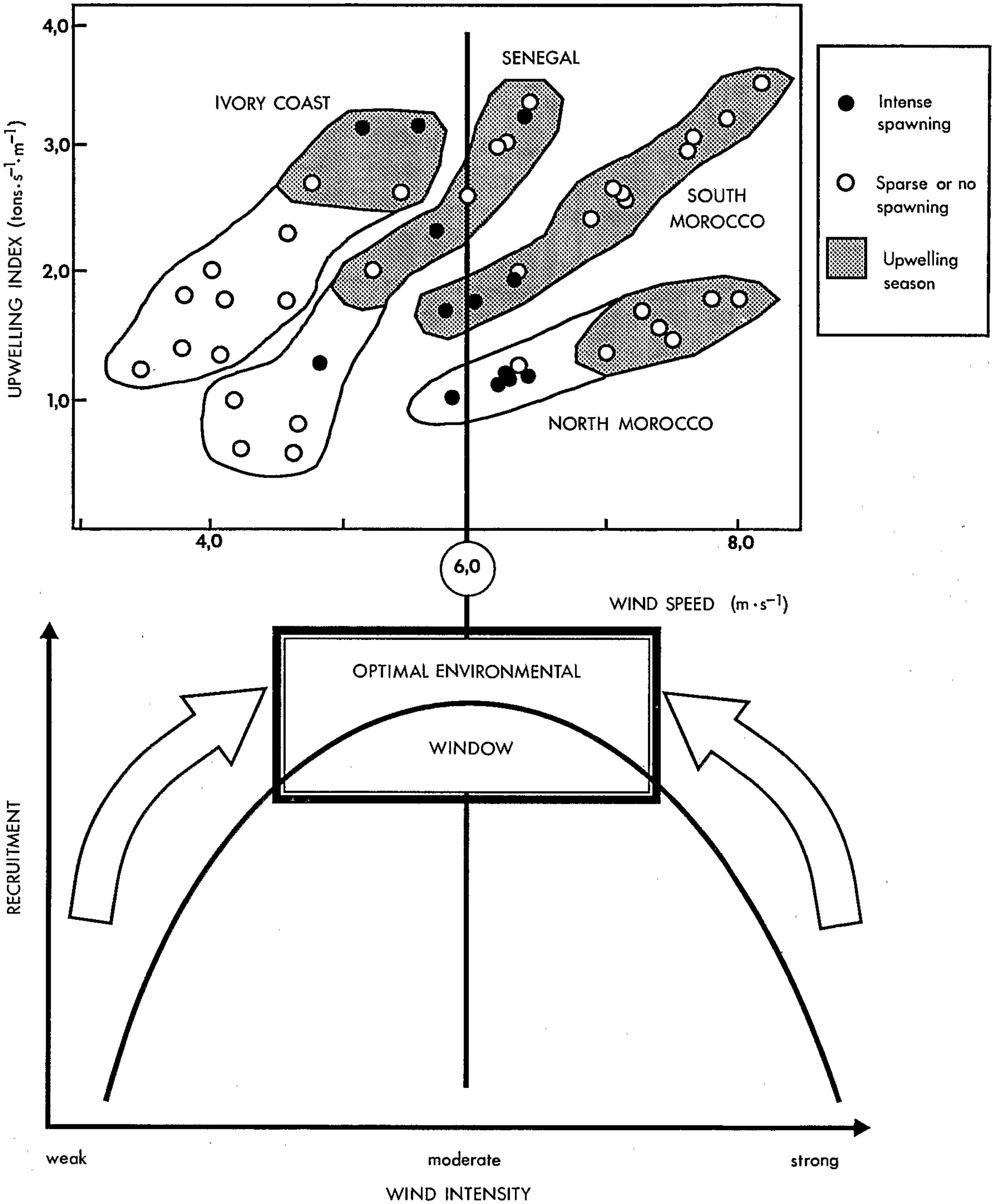

Fig. 8: Spawning activity of sardine and sardinellas in relation to wind speed and upwelling off West Africa, north Morocco (30–27°N), south Morocco (26–22°N), Senegal (15–9°N) and Ivory Coast (5°N, 2°W to 1°E). Mean monthly upwelling indices (tons·s^{-1}·m^{-1}) are plotted against mean monthly wind speed (m·s^{-1}); wind speed and upwelling indices were calculated using data from maritime reports (see Roy 1991 for details). The upwelling seasons are shaded and the months with intense spawning are indicated by a black dot. Note that black dots for all regions are clustered around 6 m·s^{-1} (upper figure); this value corresponds to the average wind intensity of the OEW (lower figure)

- In areas where wind speed during the upwelling season is close to, or lower than, the threshold value of 6 m·s^{-1}, spawning takes place during the upwelling season in order to benefit from 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 at its minimum. This minimizes the negative effect of strong wind-mixing on larval survival.

The interpretation is based on the coincidence of the timing of reproductive activity of pelagic fish off West Africa with the times when wind speed is some 5 or 6 m·s^{-1}. In areas such as off north or south Morocco, these periods also coincide with the times of the year when offshore Ekman transport is at its minimum. For these areas, both the offshore transport hypothesis and the current interpretation offer a coherent scenario to account for the patterns observed. The positive correlation between mixing and offshore Ekman transport, both induced by wind, stands in the way of an ability to separate the contribution of these two processes. However, the apparent consistency among widely separated regions of wind intensity around which spawning peaks occur is intriguing. For a given wind speed, the magnitude of offshore transport is a function of latitude, but wind-mixing is latitudinally independent. The apparent consistency of the wind speed associated with spawning peaks could be interpreted as a result of the dominance of wind mixing over other detrimental factors in the timing of reproduction.

DISCUSSION

Clearly, these new examples of the existence of a dome-shaped relationship between recruitment of small pelagic fish and upwelling support the OEW hypothesis proposed by Cury and Roy (1989). According to the nonlinear relationship between recruitment and upwelling intensity, both positive and negative correlations between fish recruitment or abundance and environmental factors may apply in various areas. Intensification or relaxation of upwelling may also account for changing the sign of the correlation through time.

In fisheries science, nonlinear relationships need to be studied more thoroughly by means of new methods. Statistical techniques are now available to explore nonlinear relationships between environmental and ecological time-series. Therefore, a statistical technique such as "optimal transformations in multiple regression", developed by Breiman and Friedman (1985) and first introduced to fishery science by Mendelssohn and Cury (1987) and Mendelssohn and Mendo (1987) appears to give some new insight into old data sets and sometimes provides new evidence for theories developed in respect of fish population regulation. Validation of the model has been carried out by means of a "comparative ecological approach", an approach that appears to be a powerful method in studies of fish recruitment (Bakun 1989).

An interpretation has been proposed to account for the different reproductive patterns of pelagic fish that have emerged along the West African coast. The spawning season is not related to the seasonal occurrence of the upwelling, but rather to the seasonal occurrence of wind speed of 5–6 m·s^{-1}. Fish seem to have solved the detrimental effect of offshore transport by selecting adequate locations for spawning where the offshore loss of reproductive products is minimized. Such spawning habits may leave the adjustment of seasonality as an available means for dealing with such other factors as the detrimental effects of turbulence. The reproductive strategy appears to be the result of a compromise between several antagonistic environmental factors. For coastal pelagic fish, it may have evolved in order to invest most of the reproductive effort when the effect 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.

This interpretation of pelagic fish reproductive strategy off West Africa gives a complementary explanation to the reproductive habits of the Peruvian anchoveta. In the low-latitude area off Chimbote (9°S), reproduction occurs over a wide continental shelf during periods of strong offshore volume transport, but with wind speed <6 m·s^{-1} (see Fig. 8 of Bakun and Parrish 1982). A wide continental shelf associated with a wind speed lower than the threshold value of the OEW may allow the Peruvian anchoveta to reproduce successfully off Chimbote during a period of strong offshore transport.

ACKNOWLEDGEMENTS

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