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RELATIONSHIPS BETWEEN ANCHOVY (*Engraulis encrasicholus*) RECRUITMENT AND THE UPWELLING IN THE BAY OF BISCAY DURING THE PERIOD 1967-1994

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ABSTRACT

Oceanographical conditions in Spring and Summer, caused by Northerly-Easterly winds of medium and low intensity, in the Bay of Biscay induce good levels of recruitment to the anchovy population. This wind regime produces upwelling conditions with, generally, low degrees of turbulence. Indices of these two environmental variables, upwelling and turbulence, were built by the authors, showing which were significantly correlated with an index of annual recruitment of anchovy ($p<0.0001$) for the period 1967-1989. In this paper the authors present new data for the period 1967-1994, with three different sources of recuitment data. The upwelling index could be responsible of about 70% of the variance in the index of recruitment of the Bay of Biscay anchovy, being the turbulence less important in the recruitment. The likely explanations to this relationship are outlined and discussed in the frame of current hypothesis about the processes determining recruitment of marine populations. Enhancement of the productivity and increased availability of food to the early life history stages of anchovy seem to be the main consequence of the prevalence of weak upwelling conditions in this area during Spring.

KEY WORDS: anchovy, *Engraulis encrasicholus*, recruitment, environment, upwelling, turbulence, Bay of Biscay

INTRODUCTION

Understanding the mechanisms involved in determination of recruitment in marine fish populations is a major challenge in fisheries' research. In the last years, the relevance of meso-scale ocean processes, and the climatic conditions driving them, in setting recruitment levels has become increasingly apparent (BAKUN & PARRISH, 1982; BAKUN et al., 1991). Natural selection implies that reproductive strategies are the reply to the most crucial environmental factors regulating reproductive success (BAKUN, 1995). Consequently, fish populations set their spawning periods and areas so that survival through early life history stages is enhanced and recruitment levels are increased under weakly climatic conditions.

Some different hypothesis have been put forward trying to explain the main mechanisms leading to recruitment variability (see review in HEATH, 1992). Namely, physical and biological (food and predation) processes are the bases of the different hypothesis. HJORT (1914) suggested that first feeding was a critical period and that coincidence of high prey abundance during this life period was a necessary condition for survival and recruitment success ("critical period" hypothesis). CUSHING (1975), noted that the timing of both peak spawning activity of fish and the Spring phytoplankton bloom could be a major determinant of interannual survival variability (known under the "match-mismatch" theory).

SINCLAIR (1988) argued against predominance of food-chain processes in determining spawning strategies. Some authors (ILES & SINCLAIR, 1982; SINCLAIR, op.cit.) postulate that physics predominates over food chain processes in the control of population biology ("member/vagrant" hypothesis). Maintenance of the spatial integrity of any marine population is regarded as the most important factor, and spawning times are adapted to the physical dispersive characteristics of an area rather than to biological production characteristics. Retention of early life history stages by a favourable oceanographic condition is fundamental for survival. However, there is evidence in the literature of both dispersal and food chain processes having influence in year-class survival (HEATH, op.cit.).

Lasker's "ocean stable" hypothesis accounts for physical processes affecting food chain characteristics of the environment (LASKER, 1978). Long periods of stable oceanic conditions lead to fine scale particle aggregations enhancing food availability and survival of larval stages. PETERMAN & BRADFORD (1987) found that mortality of larval anchovy, *Engraulis ringens*, was inversely related to the number of calm periods during the spawning season. BAKUN (1985) found that the spawning peak of pelagic fishes in upwelling areas coincides with a seasonal minimum in offshore Ekman transport. CURY & ROY (1989) have shown that recruitment seem to be maximized at the "optimal environmental window" for moderate winds in upwelling systems and with detrimental effects on lower and higher values.

SEPHERD et al. (1984), claim that the problem arising when correlating climatic and fisheries variables (recruitment principally), owes to the fact that there is no limit in the amount of correlations to carry out and in many cases it is difficult to establish which correlations are simply a matter of luck.

The reason for this lays in the fact that the parameters affecting the success of a fishery, can follow one another or overlap in time, and even interact against each other. Thus, for example, temperature works better as a predictor in species living close to the limits of their ranks, whilst wind velocity and direction are important in as much as they affect the currents and are critical during the drifting period of the larvae (BAKUN et al.,1991).

The fishery for anchovy in the Bay of Biscay has changed dramatically during this century. JUNQUERA (1986, 1988) relates the increase (1920-1960) and drop (1967-1986) of catches of anchovy, as well as other biological events in the Bay of Biscay, to general oceanographic changes in the Northern hemisphere. The rising period of the fishery was concurrent with a regime of sea surface temperature warming, while the decreasing period coincided with a cooling trend of surface temperatures and a lowering of salinity.

VALENCIA, *et al.* (in press), studying time series (over 40 years), of sea surface temperature, wind and irradiance, have demonstrated that some environmental phenomena developed in the SE Bay of Biscay, e.g. low sea surface temperature (0.5 °C under the mean) in the 70's, are a local response to great scale oceanographic and meteorological events in the NE Atlantic.These authors have shown a relationship between these environmental phenomena with the dominance of northerly winds, which produce upwelling that cooled down the surface waters in the southern area of the Bay of Biscay.

Anchovy is a short living species for which recruitment plays a major role in setting the level of the stock. Spawning of anchovy in the Bay of Biscay occurs each year during Spring (FURNESTÍN, 1945;

ARBAULT & LACROIX-BOUTIN, 1977; CORT el al.,1986; LUCIO & URIARTE, 1990; MOTOS et al., in press), and the population spawns mainly in areas where increased biological production potentially occurs (MOTOS et al., in press): river plumes, shelf and shelf break fronts and oceanic gyres (SWODDIES)(Figure 1). In general, spawning is limited to the French and Spanish coasts (South of 46°30'N and East of 5°W).

Anchovy spawners continuously produce eggs from April to July, although there is some marginal spawning in March and in August-September. Spawning activities are triggered by the Spring warming up of sea surface waters and the major part of the reproductive effort coincides with its maximum warming rate, which normally occurs in May-June (CORT et al., 1979; MOTOS et al. in press). Therefore, most eggs are produced at peak spawning, during May and June.

The time span for development of eggs and larvae depends on temperature (BLAXTER & HUNTER, 1982). At the prevalent temperature in the area during peak spawning, egg development lasts for three days (MOTOS, 1994) and larval development takes as much as 60 to 90 days (SMITH, 1985; PALOMERA et al., 1988). Data from the tuna live-bait fleet indicate that early juvenile stages start schooling as early as August and they occur during Summer and Autumn in SE Bay of Biscay (CORT et al., 1976; MARTIN & LUCIO, 1988; MARTIN, 1989; URIARTE & MOTOS, 1991). Consequently, anchovy eggs and larvae develop from March-April to July. After metamorphosis, anchovy juveniles occur from August up to next Winter when they disperse in the area. Oceanographical events happening in concurrent periods and areas should play a primordial role in the dynamics of this early life history stages and in the subsequent recuitment strength.

BORJA et al. (in press) have shown, for the period 1967-1989, that oceanographical conditions caused by Northerly-Easterly winds of medium and low intensity in Spring-Summer in the Bay of Biscay seem to induce good levels of recruitment to the anchovy population. This wind regime produces weak upwelling conditions with generally low degrees of turbulence. Indices of these two environmental variables, upwelling and turbulence, were shown to be significantly correlated with an index of annual recruitment of the anchovy ($p<0.0001$) for that period. Both physical parameters explained about 70% of the variance in the index of recruitment of the Bay of Biscay anchovy.

In the forementioned paper the authors stated that the relationship between recruitment of anchovy in the Bay of Biscay and oceanographical conditions (upwelling and turbulence) needed to be checked with the most recent years of data in order to exclude espureous correlations. The possible confirmation of this relationship would largely enhance the comprehension of the dynamics of this resource in the Bay of Biscay, with potential use for the future management.

The current paper completes the series of data up to 1994 and review the consistency of the relationships between the environment and the anchovy recruitment.

MATERIAL AND METHODS

Recruitment variability of the Bay of Biscay anchovy population was studied by means of a recruitment index (IR), calculated by URIARTE (1993) for the period 1965-1994. It derives from the matrix of Spanish purse seine catches of anchovy (in numbers at age) for the first half of each year. The index of the level of the recruitment produced from the spawning of each year is calculated by summing up all catches (corrected by effort) obtained from the cohort born in each year (BORJA et al., in press), and expressed as number of individuals (in thousands) per cohort per vessel.

Anchovy spawning occurs in Spring and first catches included in the recruitment index happen in February-March of the following year, once anchovies are one year old. Spanish catches from the first half of each year account for about 95% of the total annual catch.

In this paper, for the most recent period 1986-1994, two new measures of recruitment were studied: the DEPM population estimates in numbers of one year old anchovies and the 1996 ICA Assessment estimates of anchovies of 1 group (ANON., in press). The one year old anchovies of 1993 were not measured by any DEPM or acoustic survey, but for the purposes of this analysis it has been assumed that the number of this anchovies were the same than those detected by the DEPM in 1992. This is based on the fact that the cumulative catches of the year classes of 1991 and 1992 (YCC) were approximately equal (table 10.10 of ANON., 1996) and the recruitment at age 1 estimated by the ICA assessment performed in 1995 (ANON., 1996) were equal for the 1991 and 1992 year classes.

The upwelling and turbulence were calculated from the time series of wind stress and direction in the Bay of Biscay, between 1967 and 1989 (SMITH & BAKUN, 1989) . This series is a spatial mean of the geostrophical pressure field derived from satellite data, in a 3°x3° rectangle centered in 45°N and 2°W, therefore, located in the inner part of the Bay of Biscay which is the main spawning area for anchovy (MOTOS et al., in press). The wind index gives direction and intensity averaged over six hours for the area of reference. The data for the period 1990-1994, for the same area, has been provided by the Data Manager Head Services from PEFG of the NMFS (USA).

Turbulence was calculated as the cube of wind stress (BAKUN & PARRISH, 1982), from May (spawning season) to January of the next year; the period which showed for the turbulence index the highest correlation with the index of recruitment for 1967-1989 (BORJA et al., in press). This provides information on wind induced turbulent mixing, giving an idea of vertical stability of the sea.

Upwelling is related to surface transport generated by wind. The SE region of the Bay of Biscay presents a striking change in the coast orientation. The French coast shows a N-S orientation, while the Spanish coast has an E-W orientation, being the Basque Country a transitional region (Figure 1). Northern winds produce upwelling on the French coast, whereas Eastern winds produce it on the Spanish coast.

Upwelling values for every 6-hour-observation were calculated by means of the algorithms provided by BAKUN (1973), being expressed as $m^3.s^{-1}.km^{-1}$ of coast. Monthly upwelling was calculated as the mean of available daily data.

BORJA et al. (in press) established that the expected time period where environmental conditions are critical for survival of early life stages is from March to July because it contains the peak spawning and most of the developmental period of anchovy eggs and larvae up to late larvae or even early juvenile stages.

Assuming that upwelling conditions could in general favour the recruitment of anchovy, the synthetic upwelling index created by BORJA et al.(in press) for a given year is based on the addition of the upwelling values of the months showing on average positive upwelling events between March and July. For the same reason, given that the spawning area of anchovy extends along the French and Spanish coasts of the Southeastern bay of Biscay, the authors decided to add up the upwelling values found in both coasts.

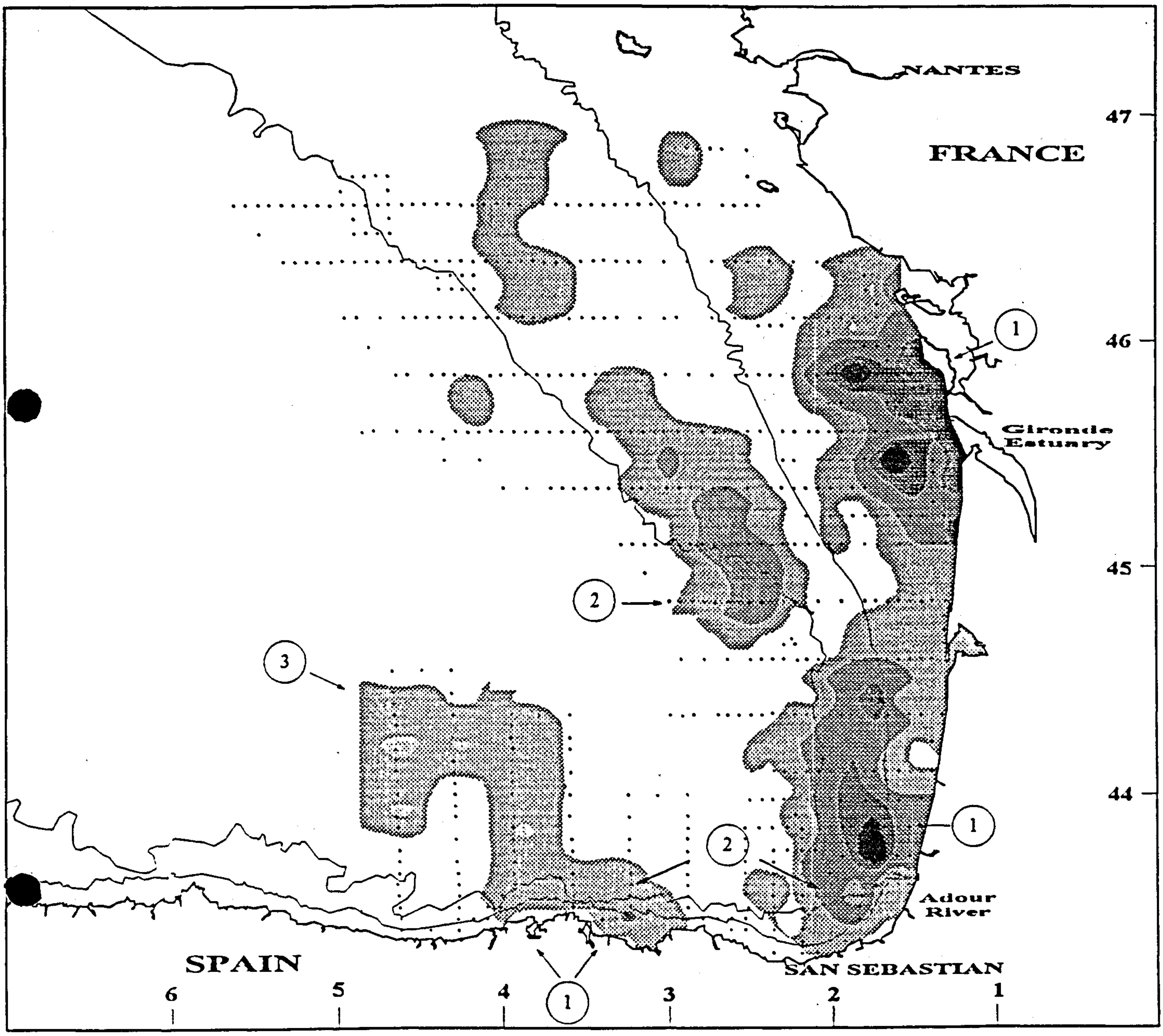

Figure 1: Bay of Biscay map showing the major spawning areas of anchovy (example corresponding to the survey of 1992 made from 16 May to 13 June) (MOTOS et al.,1995

1-Coastal spawning associated with the areas influenced by river plumes.
2-Shelf edge spawning areas associated with the shelf break fronts.
3-Offshore spawning areas associated with oceanic eddies

RESULTS

Figure 2 plots the interannual variability in the recruitment and upwelling indexes from 1967 to 1995. Upwelling values over 800-900 $m^3.s^{-1}.km^{-1}$, between March and July, favour good recruitments (>2000 thous.indiv. captured per cohort and vessel).

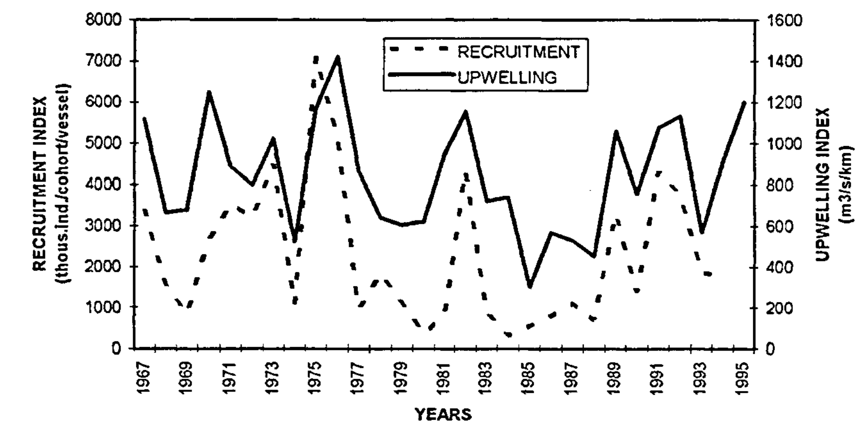

FIGURE 2: Plot of the interannual variability of recruitment and upwelling indexes

The parallelism of both series holds for the most recent years of data as well as for the whole period. The extension of the data series with 5 new years up to 1994 confirm the previously found relationship between the recruitment and upwelling indexes (Table 1), with a slightly increase of the correlation coefficient.

Table 1: Comparison between the results obtained by BORJA et al (in press) for the period 1967-1989 and the results obtained in this paper for the period 1967-1994. The results refer to the correlation between upwelling and recruitment and upwelling+turbulence with the recruitment (n:number of data, df: degrees of freedom, R^2 : explained variance).

	BORJA et al. (in press)			**This Paper**		
Years	**1967-1989**			**1967-1994**		
	n	**df**	**R^2**	**n**	**df**	**R^2**
Upwelling (U)	23	22	60.42%	28	27	61.15%
U + Turbulence	23	21	67%	28	26	64.72%

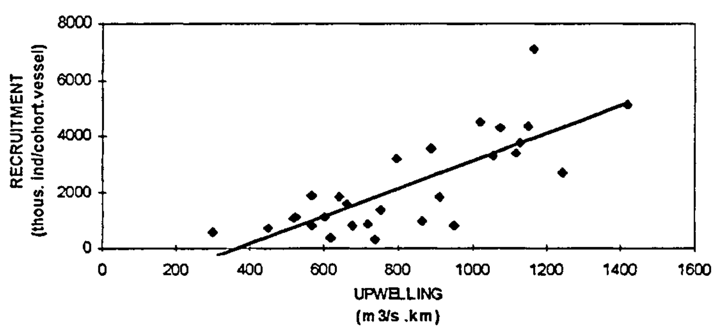

FIGURE 3: Linear regression model between recruitment and upwelling indexes for the 1967-1994 period.

On the other hand, 1994 year has not a definitive value of this variable, because of the lack of 2 years old data corresponding to 1996.

Table 2 shows the results of fitting a lineal regression model of upwelling on the index of recruitment to the complete 1967-1994 data set, whilst Figure 3 shows the fitted model.

Table 2: Linear model of a regression analysis between recruitment (dependent variable) and upwelling (independent variable), with 27 degrees of freedom. The correlation coefficient was 0.78 and the R^2=61.15%.

Regression analysis				
PARAMETER	ESTIMATE	STANDARD ERROR	T- statistic	P- value
Intercept	-1820.65	670.15	-2.717	0.0116
Slope	4.93	0.77	6.397	0
Analysis of Variance				
SOURCE	SUM OF SQ.	MEAN SQ.	F- Ratio	P- Value
Model	$4.95.e^7$	$4.95.e^7$	40.92	0
Residual	$3.14.e^7$	$1.21.e^6$		
Total (Corr.)	$8.09.e^7$			

On the other hand Table 3 shows the regression analysis for both upwelling and turbulence. With the complete set of data the inclusion of turbulence in the analysis does not seem to reduce significantly the residual error of the regression model.

Therefore the role of the turbulence on determining the recruitment is not significant statistically, suggesting a minor role in the determination of the recruitment compared with the upwelling index. Here, as in BORJA et al. (in press) it is found that turbulence could affect negatively the index of recruitment.

Table 3:Multiple regression analysis between recruitment (dependent variable), upwelling and turbulence (independent variables), with 27 degrees of freedom. The correlation coefficient was 0.80 and the R^2=64.72%.

Regression analysis				
PARAMETER	ESTIMATE	STANDARD ERROR	T- statistic	P- value
Constant	74.99	1358.17	0.055	0.956
Upwelling	4.89	0.75	6.525	0
Turbulence	-14.67	9.22	-1.59	0.124
Analysis of Variance				
SOURCE	SUM OF SQ.	MEAN SQ.	F- Ratio	P- Value
Model	$5.24.e^7$	$2.62.e^7$	22.93	0
Residual	$2.86.e^7$	$1.14.e^6$		
Total (Corr.)	$8.09.e^7$			

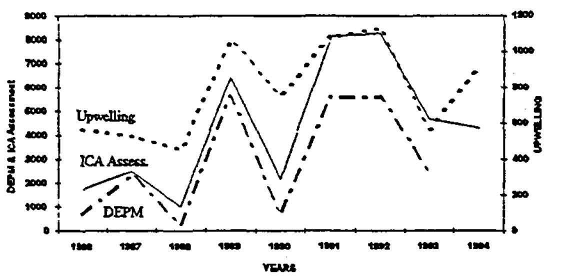

FIGURE 4: Plot of DEPM, ICA assessment and upwelling between 1986 and 1994

The comparison between the DEPM estimates of one year old anchovies and the upwelling index of the year before (period 1986-1993) is represented in the Figure 4 and the regression model and Anova test are shown in Table 4. Figure 4 shows also the comparison between the recruitment estimates at age 0 provided by ICA assessment and the upwelling index of the same year (period 1987-1994). The respective regression model and Anova test are shown in Table 5.

Table 4: Linear model of a regression analysis between DEPM (dependent variable) and upwelling (independent variable), with 7 degrees of freedom. The correlation coefficient was 0.89 and the R^2=78.93%.

Regression analysis				
PARAMETER	ESTIMATE	STANDARD ERROR	T- statistic	P- value
Intercept	-2876.66	1285.27	-2.238	0.0665
Slope	7.53	1.59	4.741	0.0032
Analysis of Variance				
SOURCE	SUM OF SQ.	MEAN SQ.	F- Ratio	P- Value
Model	$3.09.e^7$	$3.09.e^7$	22.48	0.0032
Residual	$8.25.e^6$	$1.37.e^6$		
Total (Corr.)	$3.92.e^7$			

Table 5: Linear model of a regression analysis between ICA assessment at age 1 (dependent variable) and upwelling (independent variable), with 8 degrees of freedom. The correlation coefficient was 0.88 and the R^2=78.4%.

Regression analysis				
PARAMETER	ESTIMATE	STANDARD ERROR	T- statistic	P- value
Intercept	-2798.6	1490.8	-1.88	0.1026
Slope	9.14	1.81	5.03	0.0015
Analysis of Variance				
SOURCE	SUM OF SQ.	MEAN SQ.	F- Ratio	P- Value
Model	$4.71.e^7$	$4.71.e^7$	25.34	0.0015
Residual	$1.3.e^7$	$1.86.e^6$		
Total (Corr.)	$6.01.e^7$			

DISCUSSION

The addition of new data of recruitment and upwelling indexes to the series of BORJA et al (in press) has confirmed that this two variables are positively correlated. On average, about 61% of the historical variability of the recruitment index is explained by the upwelling index. The role of the turbulence is of less relevance in the determination of the recruitment, but it could be important to explain some years with unexpected recruitments. Here, as in BORJA et al. (in press), it could have a negative influence.

Spring upwelling conditions and the recruitment of anchovy in the Bay of Biscay.

The highest correlation between the recuitment and the upwelling indexes was found when the whole period from March to July was considered. This time span coincides with the development period of anchovy eggs and larvae. Therefore, this correlation says that Northern and Eastern winds producing upwelling conditions in Spring favour anchovy recruitment.

In the Bay of Biscay offshore transport of surface waters and upwelling events result when Northerly and Easterly winds blow along the French and Spanish coast, respectively. According to VALENCIA et al. (in press), during the Spring-Summer transition, wind speed and direction are quite variable in the SE region of the Bay of Biscay. During this period, Northerly and Easterly winds are prevalent instead of Southerly and Westerly winds, which prevail in the Autumn-Winter period. Whilst the mean wind speed show maximum values in Winter, it decreases in Spring and even drops significantly down from Spring to Summer.

The rather variable direction of the wind, and reduced wind speed, together with the dramatic change in the orientation of the French and Spanish coasts, clearly differentiates this region from typical upwelling areas such as California, Peru or, in a local comparison, from the western Iberian coast. In regions of intense upwelling, turbulence are considered low if they stay under 400 $m^3.s^{-3}$ (HUSBY & NELSON, 1982) or 200 $m^3.s^{-3}$ (CURY & ROY, 1989), depending on the areas. In the bay of Biscay, Spring values of turbulence over 155 $m^3.s^{-3}$ are considered high by BORJA et al. (in press), because turbulence over 200 $m^3.s^{-3}$ are only found in Winter and Autumn. Values over 400 $m^3.s^{-3}$ are very scarce in this area.

The low intensity of the winds producing upwelling conditions in the bay of Biscay does seldom imply a breakdown of surface water layers by colder and richer deep waters. The upwelling effect can be restricted to pushing up the thermocline close to the surface (VALENCIA, et al., in press), making light more accessibly to the plankton concentrations at this fringe and increasing the subsurface chlorophyll maximum. In this way, productivity can be enhanced around the thermocline without cold subsurface waters being detectable at the surface. For instance, in May upwelling conditions are generated by a mean wind velocity of 4,5 $m.s^{-1}$, which causes low turbulence ($90 m^3.s^{-3}$). Therefore the Northern and Eastern regimes of wind in Spring will produce weak upwelling processes, associated with stability and shallow but pronounced stratification of surface waters.

The offshore horizontal transport of coastal waters produced by the Northern and Eastern regime of winds may play by it self another relevant role in the enhancement of the productivity in the bay. The influence of the low salinity plumes of several rivers in the Bay of Biscay (Gironde, Adour, and many smaller Spanish rivers) are apparent in surface water layers along important shelf areas. Those areas are known as spawning grounds for anchovy (MOTOS *et al.*, in press), probably due to the enrichment produced by the outflow of those rivers. When the offshore advection of coastal waters under upwelling conditions are relevant in the Spring, there is a spreading out of the influence of the river plumes over wider areas than normal, and the effect of enrichment of sea surface waters is expanded. Eggs moving in those waters will remain in a rather stable, nutrient rich environment.

Therefore, two factors of enrichment of global productivity in the Bay of Biscay may be linked to prevalent Northeastern wind conditions: Weak upwelling conditions and extension of the area influenced by the river outflows. Both factors, together with low turbulence and stability, may act to enhance the probability of anchovy early life history survival by means of increasing food availability.

These Spring upwelling conditions are, in general, coincident with the suitable environment described for the small pelagic recruitment in the literature: The weak upwelling conditions, the relative stability and expected enhancement of food availability matches well with the "Ocean stable" hypothesis of LASKER (1978). This hypothesis states that food quality is also improved as dinoflagelates are better food for anchovy larvae than diatoms. The latter are produced in the presence of intense upwelling, whilst dinoflagelates appear in calm and stable conditions (LASKER, 1981)

The low wind speed and turbulences associated to the upwelling conditions during the spawning of anchovy in the bay are in agreement with the BAKUN & PARRISH (1982) statement about the pelagic fishes in upwelling regions which are deemed to choose for spawning areas of lowest turbulence and mixing. MENDELSSHON & MENDO (1987) and CURY & ROY (1989) suggest 5 $m.s^{-1}$ as the wind speed for environmental windows leading to maximum recruitment of small pelagicfishes. VALENCIA et al. (in press) find that the upwelling conditions in the bay take place close to this threshold velocity.

CURY & ROY (1989) indicate that nonlinear statistic methods should be used to cope with the expected dome shape relationship between recruitment and upwelling in Ekman-type upwelling systems. Otherwise, the relationship could be masked. In the Bay of Biscay we have shown that a linear model can sufficiently explain the relationship between both variables. This may be due to the fact that the maximum upwelling indices found during the spawning period of anchovy in this area (between 1200 and 1400 $m^3.s^{-1}.km^{-1}$) are about the range suggested by those authors for the optimal environmental windows. Therefore in the Bay of Biscay, the weak upwelling conditions limits the study to the left side of the dome shape curve (the increasing branch of the curve), where the curve can be approach by a linear relationship.

Advection from the spawning centres under the North and Eastern regime of winds.

Transport from spawning centres will vary depending on the wind direction that induces upwelling. Thus, a northerly wind will make that waters close to the Gironde estuary move towards Cap-Ferret, and those close to the Adour towards the Spanish self edge and coasts (Figure 1). On the other side, Easterly winds blowing in the Northern areas will cause a Northeastward displacement over the continental shelf, which will eventually move towards the shelf edge on its northern side, while in the Adour and Cantabrian coast the transport will be towards shelf edges of those areas.

Emerging 3 mm larvae can only swim at speeds of 0,1 to 0,2 $cm.s^{-1}$, depending on water temperature, and they are not capable of overcoming typical surface currents of this weak upwelling conditions, of the order of 10-15 $cm.s^{-1}$. Therefore, the larvae will need food close to them to survive. Fortunately, under those regimes of wind, eggs and larvae will be transported in a "nourishing environment" which facilitate food availability to them. During this transport towards the outer shelf or, in cases, further beyond it, eggs and larvae will be dispersed. This dispersion may imply a reduction of larval competition and cannibalism by adults since they will continuously be moved out of the spawning centres.

SINCLAIR (1988) states that retention of early life history stages by a favourable oceanographic system is fundamental for survival. The advection and dispersion of eggs and larvae towards offshore and along the Cantabrian sea, under the Northerly-Easterly wind regime, do they imply an increase of mortality of the anchovy larvae? There are no direct studies of this subject available by the time being. However, some authors reported that anchovy juveniles can be detected occurring both in offshore and inshore areas (CORT *et al.* 1976, URIARTE & MOTOS, 1991) at the end of Summer and Autumn in years of good recruitment, indicating that good survival was general in all areas. Taking into account the weak strength of the Northerly-Easterly regimes of wind in this region and the limited geographical area of the SE corner of the Bay of Biscay, it is not clear that Ekman transport towards offshore areas will imply any detrimental for the survival of larvae. Enhanced biological production resulting from prevalent oceanographical conditions could assure good survival rates over most of the area. In addition, the vertical environment of anchovy early life history stages - layers above the thermocline - would be more stable, reducing the risk of vertical dispersive processes and related losses towards the bottom.

Downwelling conditions in the Bay of Biscay in Spring

In the Bay of Biscay, the usual speeds of Western and Southern winds are in general stronger than those coming from the North or East. In general the former predominate in the Autumn and Winter seasons producing relative high turbulence and downwelling along the Spanish and French coasts (BORJA et al., in press). Years with those winds prevailing in Spring and early Summer show downwelling conditions and coincide in general with low recruitment levels of anchovy. The most relevant example of downwelling conditions in both coasts in Spring happened in 1983, which resulted in subsequent bad recruitment.

The consequences of the downwelling conditions and relative high turbulence are: low stability and stratification, and less intense and deeper thermoclines than under weak upwelling conditions. Plankton will be transported and dispersed with the eggs and larvae within a wide column of water. In that sense food availability will be reduced to the larvae. In addition the areas of influence of the river plume will be diminished due to the advection of waters towards the coast. All these features would probably imply a general drop of productivity in the SE Bay of Biscay during the periods of prevalence of that regime of wind and a reduction of the suitable environment for the success of the early life history stages of anchovy.

Balance between Downwelling and Upwelling conditions in the Bay of Biscay in Spring

Upwelling events are usual in the French Coast during Spring, while those events are less frequent along the Spanish coast in that period. By the end of Spring and in Summer weak upwelling conditions become also frequent along the Cantabrian coasts. The major spawning grounds of anchovy are known to expand between May, June and July (CORT *et al.*, 1976; MOTOS *et al.* in press), extending from the French shelf towards the West along the Spanish shelf and towards the North. That expansion has been related to migration of successive size classes of adults triggered by temperatures (CENDRERO ed., 1994). In the years of best recruitments, like in 1975, 1976, 1982, it is observed that upwelling conditions along the Cantabrian coast were already prevalent during the Spring (BORJA et al., in press). These observations emphasize the idea that recruitment of anchovy in the Bay of Biscay is enhanced by the opening of spatial and temporal windows of weak upwelling conditions. The traditional spawning centres close to the major rivers and along the continental shelf edge will always assure a minimum level of recruitment for the population, but the major variations of recruitment will depend on the conditions induced by the regimes of wind during the early life history stages.

It is a common feature in the bay of Biscay that Winter downwelling conditions last until April followed by weak upwelling conditions afterwards. Anchovy takes profit of this change for spawning. In general, spawning activities of anchovy in March and at the beginning of April are low. However we have found that the inclusion of March in the computation of the upwelling index improved the correlation with the recruitment index. This improvement is principally due to the influence of years 1970 and 1973. Both years produce good recruitment, in which more than 50% of the Spanish annual captures occurred between March and April (BORJA et al., in press). This phenomenon can be interpretated to be linked to an earlier onset of the Spring season (URIARTE 1988), which might indicate an early spawning in those years. Therefore, upwelling conditions at the beginning of the Spring may induce early spawning. Alternatively, it may happen that earlier upwelling conditions play a role in setting the condition factor of spawners during the incoming spawning season, with potentially important implications in the future survival of the offspring (BLAXTER & HUNTER, 1982).

Influence of turbulence on the recruitment of anchovy.

Another factor affecting recruitment is the turbulence set up from May to January. It includes the developmental time of most egg and larvae and all the juvenile phases up to Winter dispersion. Turbulent mixing may disrupt food aggregations at the subsurface chlorophyll maximum and may affect the vertical distribution of eggs, larvae and juveniles, leading to higher rates of mortality (or losses towards the bottom).

The addition of the turbulence index between May and October to the regression of upwelling index on the recruitment index did not imply an increase of the explained variance of the regression model. This may be partly due to the fact that, in general during the Spring and Summer seasons turbulence is always low and the interannual variation is minima compared to the Autumn and Winter seasons or to the recruitment index. During Spring and most of the Summer the early life history stages of anchovy are unable to beat and overcome the currents, so that they are transported by them approximately until they reach 80 mm (THEILACKER & DORSEY, 1980). Juveniles of the Bay of Biscay anchovy reach those lengths about the end of August and September when schools of juveniles of that length are observed and caught for live bait purposes in the tuna fishery (MARTÍN, 1989).

The inclusion of Autumn and Winter months in the index of turbulence improved the fitting of the recruitment index by the regression model. In these periods the pelagic schools of juveniles approach the French and Spanish coasts for overwintering (CORT et al. 1976, URIARTE & MOTOS, 1991, PROUZET & LURO, 1991). The above results suggest that during Autumn and Winter, turbulence may affect the survival of juveniles. This may be due to a disruption of particle food aggregations around the thermocline, or to disturbing the normal spatial migration pattern of juveniles.

JUNQUERA (1986, 1988) suggested that environment may have driven the major changes in the fishery and the population of the Bay of Biscay anchovy during the current century. Our study provides a link between the environment and the population since 1967: The positive relationship between the level of anchovy recruitment and an index of upwelling induced by the prevalence of the Northerly and Easterly winds in the Bay of Biscay during Spring and early Summer. Low turbulence up to the next Spring seems to help the success of recruitment too. Oceanographic processes linked to this regime of wind seem to enhance stability and general productivity in the Bay of Biscay and therefore increase the availability of larvae and juveniles to food, increasing their survival expectations. Several direct oceanographic and ecological mechanisms have been discussed in order to explain this finding (weak upwelling conditions, widening of the influence of river outflows, stability and stratification of the water profile, etc.). These mechanisms fits well with the ideas of BAKUN & PARRISH (1982) and ROY (1993) about the physical factors driving recruitment and with the LASKER's ideas (1978) about mortality variability of early life history stages by food chains. However these or other underlying mechanisms should be further identified and studied in future field research.

The obtained results suggest the potential use of this upwelling index to forecast the recruitment of the Bay of Biscay anchovy, calculated either by direct (DEPM) or indirect methods (from captures).

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