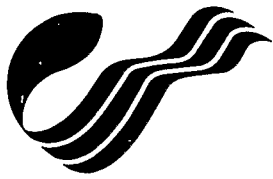


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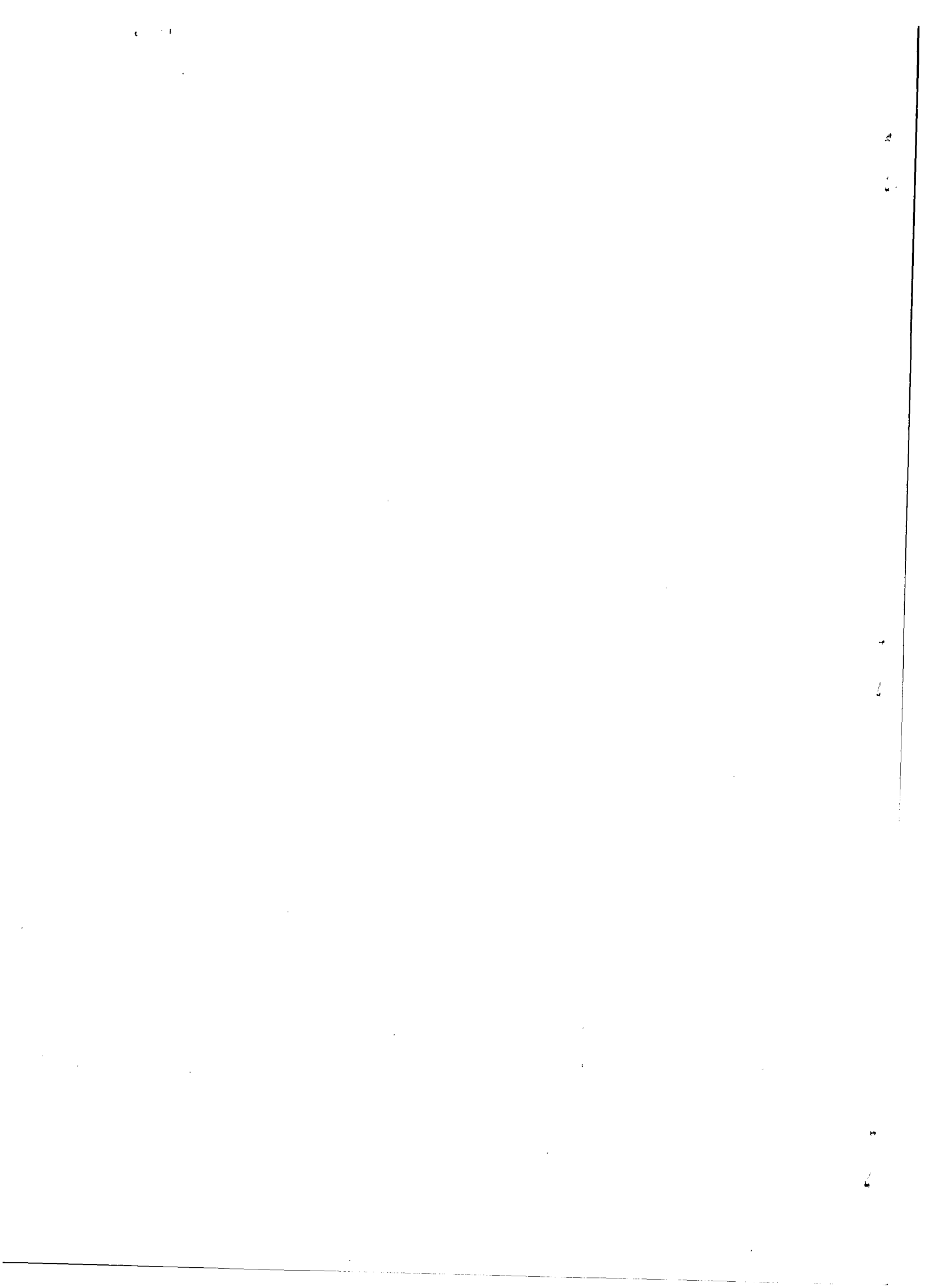


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Optimal Environmental Window and Pelagic Fish Recruitment Success in Upwelling Areas¹

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Food availability and physical constraints such as turbulence are now considered as important factors that affect larval survival and pelagic fish recruitment. In Ekman-type upwelling, vertical advection, new inputs of nutrients and turbulence are linked to wind speed. According to the literature, food availability for larvae is related to biological dynamics (primary production) up to a point where the biological processes are disturbed by physical processes (turbulence generated by wind mixing). This limitation does not exist for non Ekman-type upwelling where upwelling intensity is not correlated with wind speed. We hypothesize that relations between annual recruitments and upwelling intensity are dome shaped in Ekman-type upwellings and linear for non Ekman-type upwellings. A statistical method is used to analyse the form of the relationships between recruitments and upwelling indices or wind mixing. The recruitment of the Peruvian anchoveta (*Engraulis ringens*), of the Pacific sardine (*Sardinops sagax caerulea*) and of the West African sardines and sardinellas are thereby examined. Results show that for Ekman-type upwelling the annual recruitment increases with upwelling intensity until wind speed reaches a value of roughly $5-6 \text{ m}\cdot\text{s}^{-1}$ and decreases for higher values. For a non Ekman-type upwelling the relationship between recruitment and upwelling intensity is linear. These results confirm the existence of an optimal environmental window for recruitment.

La disponibilité en nourriture et des contraintes physiques comme la turbulence sont des facteurs importants pour la survie des larves et le recrutement des espèces pélagiques. Dans un upwelling d'Ekman, les mouvements verticaux, les apports en sels minéraux et la turbulence sont liés à la vitesse du vent. D'après la littérature, la disponibilité en nourriture pour les larves est associée à des processus biologiques (production primaire) qui peuvent être perturbés par des processus physiques (turbulence). Ce facteur limitant disparaît quand l'intensité de l'upwelling est indépendante du vent local. Nous proposons une relation en forme de dôme entre le recrutement et l'intensité de l'upwelling pour un upwelling d'Ekman et linéaire pour les autres types d'upwellings. Une méthode statistique est utilisée pour analyser la forme des relations entre recrutement, les indices d'upwelling ou la turbulence. Le recrutement de l'anchois du Pérou (*Engraulis ringens*) de la sardine du Pacifique (*Sardinops sagax caerulea*) et des sardines et sardinelles ouest-africaines est étudié. Les résultats montrent que, dans les upwellings d'Ekman, le recrutement annuel s'accroît avec l'intensité des upwellings jusqu'à ce que le vent atteigne une vitesse proche de $5-6 \text{ m}\cdot\text{s}^{-1}$ et décroît ensuite pour des vitesses plus élevées. Quand l'intensité des upwellings est indépendante des vents locaux et que la turbulence est faible, la relation entre recrutement et upwelling est linéaire. Ces résultats confirment l'existence d'une fenêtre environnementale optimale pour le recrutement.

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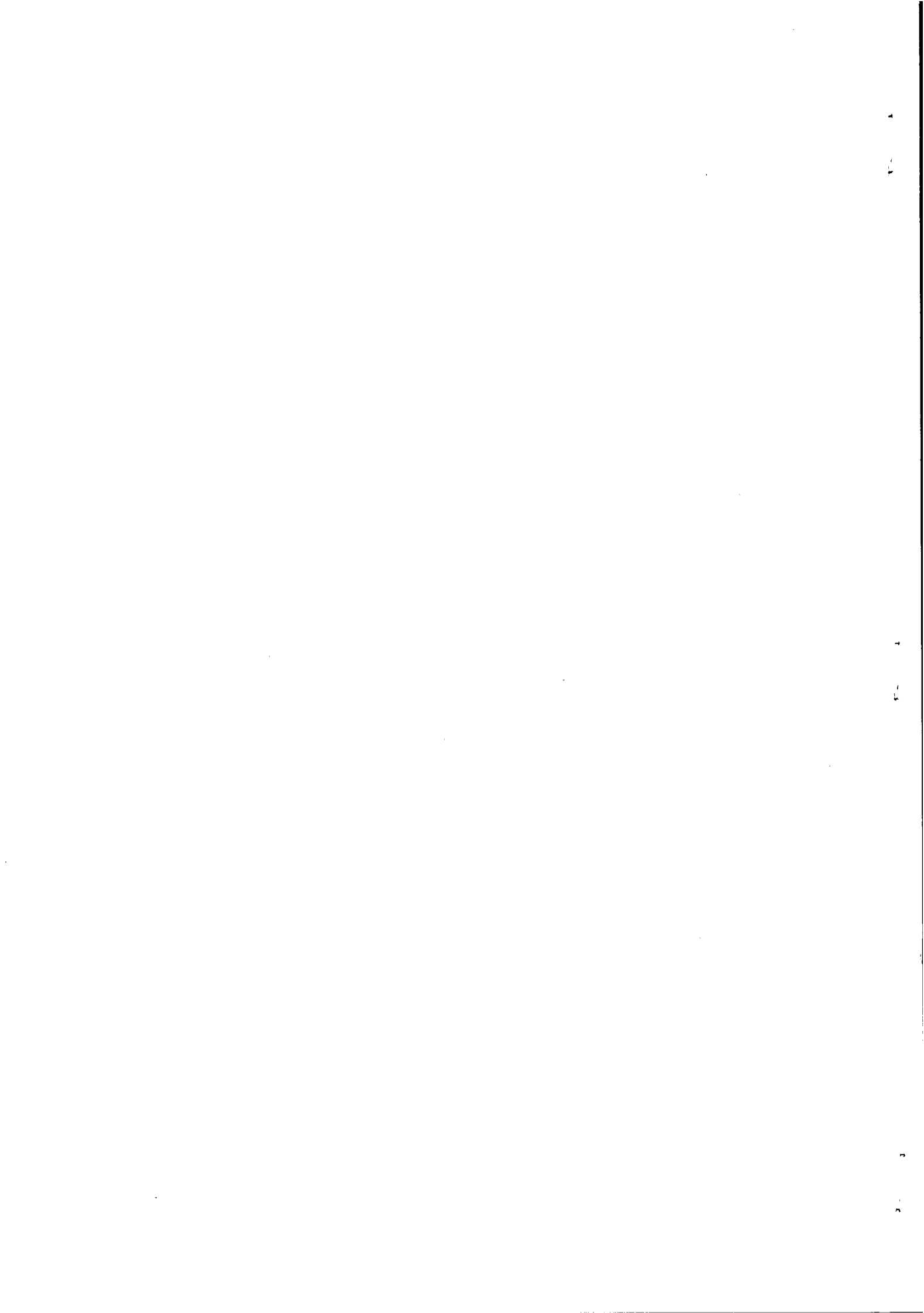
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Large variability in pelagic fish recruitment is frequent and may have an important effect on fisheries (Smith 1985). Larvae survival is especially variable and the role of different sources of mortality at the prerecruit stage has been intensively studied. The main causes of larval mortality appear to be starvation and predation (Blaxter and Hunter 1982) and several environmental factors have a determinant effect on recruitment (Shepherd et al. 1984). Currently two theories have emerged to explain recruitment success in relation to environment. With the match-mismatch hypothesis, Cushing (1975) emphasizes that the annual production of fish larvae is matched or mismatched to the production of their food. In other words, a stock releases its larvae into the annual production cycle at the best time to secure good survival on average. The impor-

tance of food availability for larvae is the core of this energetic approach. The second hypothesis is based on Hjort's (1914, 1926) suggestion; early first feeding for larvae is the most vulnerable stage in the life history of fish. Some authors (Lasker 1975, 1981a, 1985; Peterman and Bradford 1987) provide evidence that turbulence in the euphotic layer increases larval mortality during "critical periods" (May 1974). A stable environment is usually needed to allow aggregations of food organisms to be formed and maintained. This stability hypothesis (Lasker 1981b) takes into account dynamic physical processes even though food availability is again the crucial factor for larval survival.

The time and space scales used for these studies are mostly microscales (Lasker 1978; Methot 1983; Peterman and Bradford 1987). It is interesting to try to reconcile the ideas which have been developed within a fine scale using a broader scale. In this paper we analyze the relationships that may exist between

¹This work is dedicated to Dr. Reuben Lasker, a generous man and a pioneer in recruitment studies.



annual recruitment indices and upwelling intensity or wind mixing for some pelagic fish stocks in upwelling areas. The comparison between areas where upwelling intensity and wind mixing are closely related and areas where they are independent will illustrate the potential effect of turbulence on recruitment.

Analysis of the Relationships between Recruitment and Upwelling

Upwelling and Turbulence in Pelagic Fish Habitats.

The main coastal upwelling areas are located on the eastern boundaries of the oceans where the equatorward trade winds induce offshore Ekman transport. Cold, nutrient rich subsurface waters are brought to the euphotic layers enhancing primary production. Weak winds reduce primary productivity because they disrupt the upwelling process and the renewal of nutrients in the surface layers (Huntsman and Barber 1977). In the classical Ekman scheme the magnitude of the offshore transport in the upper layer is considered to be an indication of the amount of water upwelled along the coast into the surface layers (Bakun 1973). Higher wind induces higher offshore transport and increases upwelling. Therefore upwelling intensity and nutrient input into the euphotic layers could be estimated using offshore Ekman transport calculated from the wind component parallel to the coast. Ekman-type upwellings are found off Peru, California, Morocco, and Senegal.

Off Ivory Coast and Ghana, trade winds are weak and the strong cooling of the sea surface temperature during the boreal summer cannot be interpreted as classical Ekman-type upwelling (Bakun 1978; Picaut 1983). All attempts to correlate the intensity and duration of this upwelling with local winds have failed (Houghton 1976). Many mechanisms have been proposed as explanations of this upwelling among which are internal waves generated in the western part of the Atlantic (O'Brien et al. 1978), upward thermocline slope at the coast due to the intensification of the eastward Guinea Current (Inghan 1979), or local cooling downstream of a cape (Marchal and Picaut 1977). Since local winds are not the driving force of this non-Ekman type upwelling, Cury and Roy (1987) used interannual anomalies of coastal sea surface temperature to estimate its intensity. The sign of anomalies was changed in their presentation so that a positive value was associated with a strong upwelling intensity.

The energy transferred through the water column by the wind creates turbulence in the surface layers. The rate at which turbulent kinetic energy of the wind is added to the surface layer is roughly proportional to the cube of the wind speed (Niiler and Kraus 1977; Elsbery and Garwood 1978). Therefore a wind mixing index that estimates turbulence in the upper layer is usually given by wind speed cubed (Bakun and Parrish 1980; Husby and Nelson 1982). Wind mixing indices, when available, were used (Peru, Morocco); otherwise wind speed (Senegal) or upwelling indices (proportional to wind speed squared) were used (California).

In Ekman-type upwelling, high wind speed enhances upward water movement and also generates turbulence in the surface layers. Therefore, off Peru, Morocco, and Senegal annual wind mixing index and upwelling intensity are positively correlated (Fig. 1). In non Ekman-type upwelling off Ivory Coast, Ghana where wind is not the driving force, annual wind mixing and upwelling intensity are independent variables (Fig. 2).

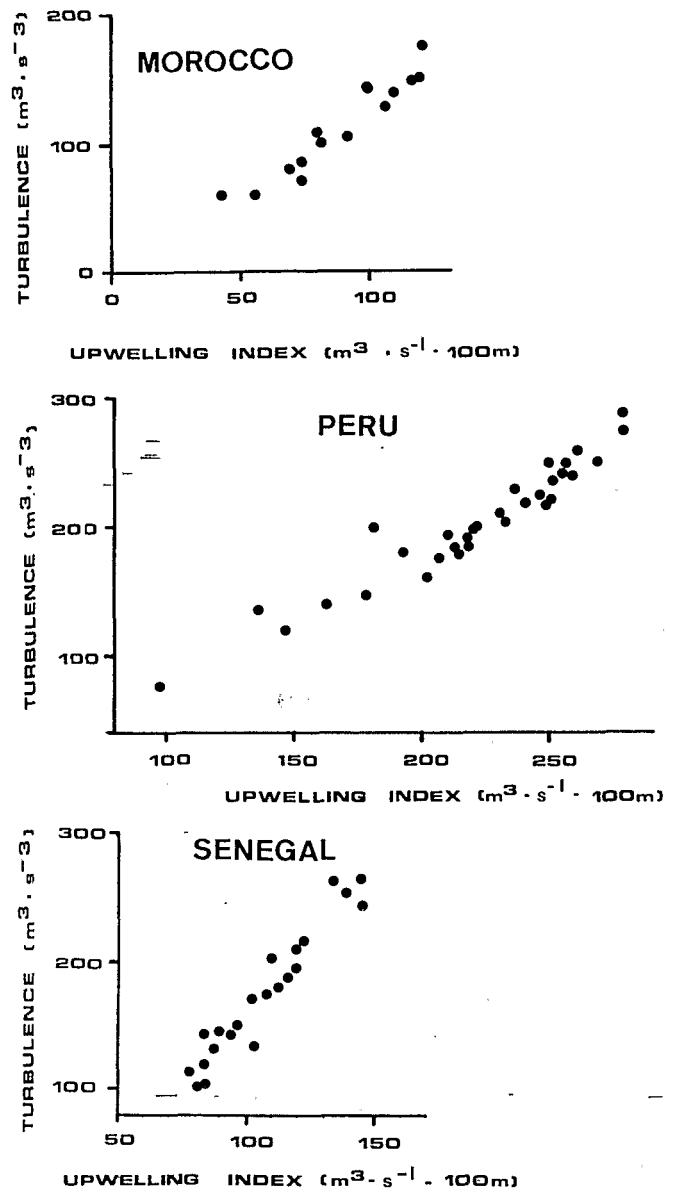


FIG. 1. Relationship between annual upwelling ($m^3 \cdot s^{-1} \cdot 100 m^{-1}$ coastline) and turbulence ($m^3 \cdot s^{-3}$) indices for Ekman-type upwellings in Peru from 1953 to 1985 (Mendo et al. 1987), in Morocco from 1968 to 1981 (Belvèze 1984) and Senegal from 1964 to 1986 (C. Roy, unpubl. data).

Theoretical Approach

Acceptable food concentrations associated with stable ocean conditions must be present in the larvae's environment for survival (Lasker 1981a). Strong turbulence generated by high wind speed has a negative effect on larval survival by desegregating food and larvae patches (Saville 1965; Peterman and Bradford 1987) and on the recruitment (Lasker 1981a; Mais 1981). In an Ekman-type upwelling, vertical advection, new inputs of nutrients and turbulence (wind mixing) are linked with wind speed. Therefore in an Ekman-type upwelling, increasing upwelling intensity from weak to moderate should have a positive effect on recruitment since increased primary production would enhance food availability, wind mixing remaining low. Strong upwelling should have a negative effect on recruitment because wind mixing is high even if the primary production increases. This limitation should not exist in the case where the

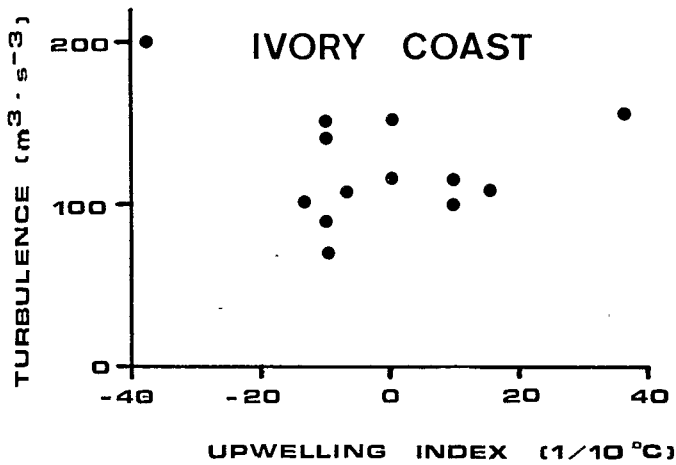


FIG. 2. Relationship between annual upwelling ($1/10^{\circ}\text{C}$) and turbulence ($\text{m}^3\cdot\text{s}^{-3}$) indices for a non Ekman-type upwelling in Ivory Coast, from 1966 to 1981 (1971 and 1972 are missing, Cury and Roy (1987) and ship of opportunity data).

strength of the upwelling is not correlated with wind intensity. We hypothesize that the relationships between recruitment variability and annual upwelling indices are dome shaped in Ekman-type upwellings (Fig. 3) and linear for non Ekman-type upwellings.

There are two limiting factors that explain the nonlinearity of the curve for Ekman-type upwelling. On the left side of the curve wind mixing is weak and the limiting factor is the production of food due to the low intensity of the upwelling; on the right side of the curve, the upwelling is strong and turbulence is then the limiting factor. There is therefore an "optimal environmental window" for moderate upwellings where the effects of the limiting factors are minimized (Fig. 3).

Statistical Method

In analyzing the relationship between recruitment and environmental factors most of the statistical methods are linear or an a priori transformation is used (essentially a logarithmic

transformation) (Parrish and MacCall 1978; Anthony and Fogarty 1985; Stocker et al. 1985; Crecco et al. 1986). We applied a statistical technique developed by Breiman and Friedman (1985) that empirically estimates optimal transformations for multiple regressions. The response variable Y and the predictor variables X_1, \dots, X_p are replaced by functions $T_1(Y)$ and $T_2(X_1), \dots, T_{p+1}(X_p)$. A procedure estimates these functions T_i by minimizing

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

An iterative algorithm (ACE: Alternating Conditional Expectation) permits the calculation of these transformation functions which do not belong to a particular parameterized family and which are even not monotone. It also differs from other empirical statistical methods usually used in that the transformations are unambiguously defined and estimated without use of ad hoc heuristics, restrictive distributional assumptions, or restriction of the transformation to a particular parametric family. If we fix the values of all but one variable and solve the problem of what new transformation will minimize the normalized residual sum of squares, then the solution is a conditional expectation that can be estimated empirically using a smoothing algorithm. 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 of the variables. 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. This procedure, previously used in fishery studies by Mendelsohn and Cury (1987) and Mendelsohn and Mendo (1987) thus also provides a method for estimating maximum correlation, and gives new insights into the relationship between the response and predictor variables (i.e. it allows the identification of discontinuities in the relationship).

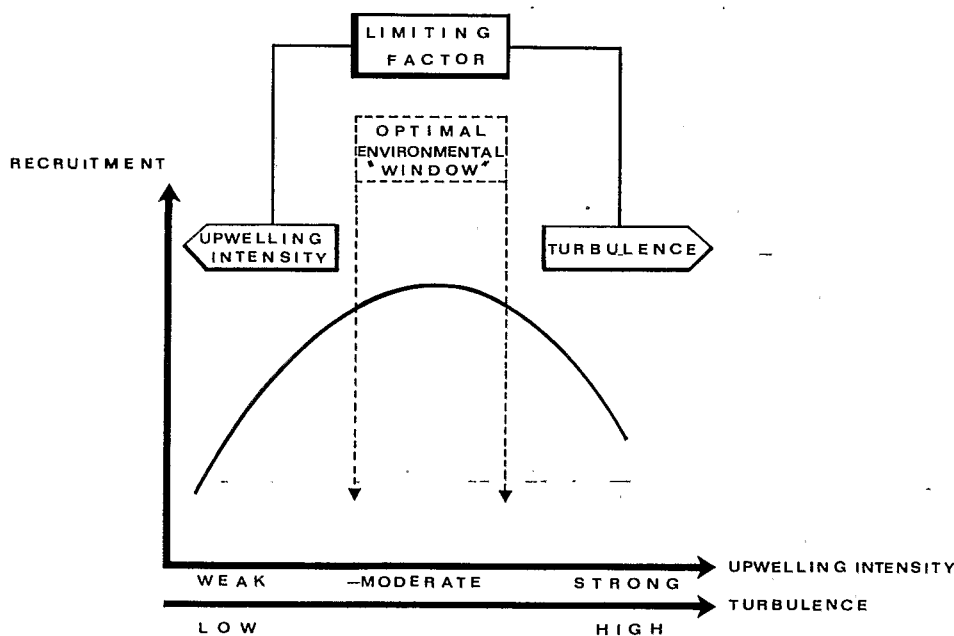


FIG. 3. Theoretical relationship between recruitment and environmental factors in upwelling areas.

TABLE 1. Recruitment (number of 3-mo-old fish) and mean annual parent stock (adult biomass of 3-mo or older fish) of the Peruvian anchoveta (Pauly et al. 1987). Annual turbulence and upwelling indices off Trujillo (Mendo et al. 1987).

Year	No. Recruits ($\times 10^9$)	Adult biomass (tons $\times 10^6$)	Turbulence index ($m^3 \cdot s^{-3}$)	Upwelling index ($m^3 \cdot s^{-1} \cdot 100 m^{-1}$ coastline)
1953	260	5.965	179	192
1954	252	9.378	229	236
1955	156	8.195	251	256
1956	106	5.017	259	261
1957	141	2.828	291	277
1985	172	3.661	221	239
1959	487	7.163	212	233
1960	573	11.618	199	220
1961	554	16.428	195	219
1962	394	14.688	188	217
1963	651	12.945	185	212
1964	364	14.183	185	217
1965	721	12.902	180	214
1966	635	15.175	221	250
1967	484	18.739	218	248
1968	352	12.859	273	278
1969	609	13.265	225	245
1970	568	14.428	250	268
1971	73	13.708	206	233
1972	105	3.106	239	254
1973	42	3.122	243	258
1974	22	3.446	148	177
1975	115	2.761	252	251
1976	90	4.420	238	250
1977	188	1.155	190	216
1978	209	3.878	163	202
1979	66	1.421	178	207
1980	392	2.504	201	181
1981	331	9.003	138	136

Review of some Pelagic Fish Stocks of Upwelling Areas

Peruvian Anchoveta

The idea that strong winds and turbulence in the upper layer can be detrimental to the survival of the Peruvian anchoveta (*Engraulis ringens*) was presented by Walsh et al. (1980). Using monthly anchoveta recruitment estimates, Mendelssohn and Mendo (1987) reinforced the idea of an effect of turbulence on short-term recruitment fluctuations. However, anchoveta recruitment also depends on the adult biomass level (Csirke 1980) and the dome shaped stock-recruitment relationship suggests a strong effect of parental cannibalism on anchoveta egg standing stocks (Santander 1987). The recruitment depends both on the parent stock and on environmental fluctuations.

We used the data updated in a recent synthesis on the Peruvian anchoveta stock (Pauly and Tsukayama 1987). These authors estimated a recruitment index (number of 3-mo-old fish) and adult biomass using virtual population analysis from 1953 to 1982 (Table 1). An annual turbulence index was calculated for one of the major anchoveta spawning areas located off Trujillo using monthly turbulence indices (wind speed cubed) of Mendo et al. (1987) (Table 1). Upwelling indices were not included in the calculation as they are strongly correlated with the turbulence indices (see Fig. 1) and do not improve fit.

Optimal empirical transformations (T1, T2, T3) for the multiple regression were calculated using the method previously described.

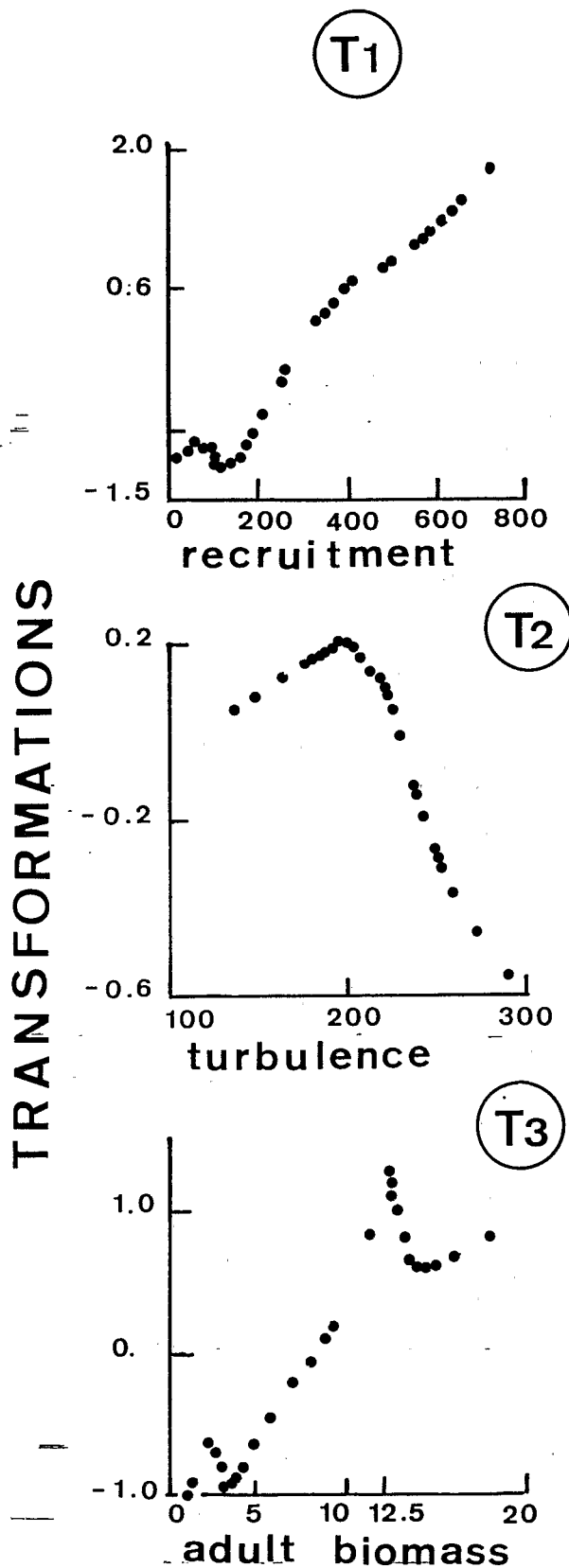


FIG. 4. Optimal empirical transformations for recruitment (No. of recruits $\times 10^9$) (T1), turbulence index ($m^3 \cdot s^{-3}$) (T2) and adult biomass ($t \times 10^6$) (T3) for the Peruvian anchoveta.

$$(1) \quad T1 (\text{Recruitment}) = T2 (\text{turbulence}) + T3 (\text{adult biomass}).$$

TABLE 2. Recruitment (number of year class at age 2) and parent stock (adult biomass of 2-yr-old fish) of the Pacific sardine (MacCall 1979). Annual upwelling index off Monterey (Bakun 1973).

Year	No. Recruits ($\times 10^9$)	Adult biomass (tons $\cdot 10^3$)	Upwelling Index ($m^3 \cdot s^{-1} \cdot 100 m^{-1}$) coastline
1946	1.625	566	92.8
1947	1.667	405	84.8
1948	3.875	740	78.1
1949	4.261	793	68.8
1950	3.690	780	70.1
1951	0.290	277	77.4
1952	0.397	136	68.7
1953	0.972	202	90.8
1954	1.197	239	81.3
1955	0.382	170	160.5
1956	0.264	108	139.8
1957	0.588	90	113.4
1958	1.586	177	97.1
1959	0.905	122	162.3
1960	0.288	88	91.6
1961	0.111	54	88.8
1962	0.074	27	94.8
1963	0.056	21	76.4
1964	0.011	11	152.8
1965		3	

The plot of the transformed values of the data against the original values are shown in Fig. 4. The estimated transformation of the recruitment is almost linear (Fig. 4, T1). Turbulence is transformed to a nearly dome shaped curve (Fig. 4; T2). It first increases to a value around $200 m^3 \cdot s^{-3}$ (which corresponds to a wind speed between 5 and $6 m \cdot s^{-1}$) and then decreases strongly. The transformation of parent stock is almost linear in shape with a small decrease for high values of adult biomass (higher than $12.5 \cdot 10^6 t$) (Fig. 4, T3). The resulting transformed model (1) explains 70% of the observed variance in the recruitment data. Recruitment is positively correlated with stock biomass; however, the relationship between recruitment and turbulence is non-linear. It suggests that the upwelling is beneficial for the recruitment until the wind speed reaches values of $5-6 m \cdot s^{-1}$ and that for higher wind speed, turbulence has a negative effect on recruitment.

These transformations suggest that both high turbulence and low adult biomass may have played an important role in the collapse of the Peruvian anchoveta. In 1972 and 1973 the parent stock was low (Table 1) and produced few recruits which had difficulties surviving in an environment where turbulence was higher than $200 m^3 \cdot s^{-3}$ (Table 1; Fig. 4, T2). Consequently, overfishing was apparently not the only factor preventing a recovery of the stock.

Pacific Sardine

The Pacific sardine (*Sardinops sagax caerulea*) fishery like the Peruvian anchoveta fishery is well documented. Analyses of the sardine stock-recruitment relationship (Clark and Marr 1955; Radovitch 1962; Murphy 1967) showed density dependence, often by assuming a Ricker functional relationship. Following Cushing (1971), who concluded that clupeoid stocks tend not to have strong density dependent regulatory mechanisms, MacCall (1979) showed that the stock-recruitment relationship presented no curvature (density-dependent regulation of the recruitment). We used new population esti-

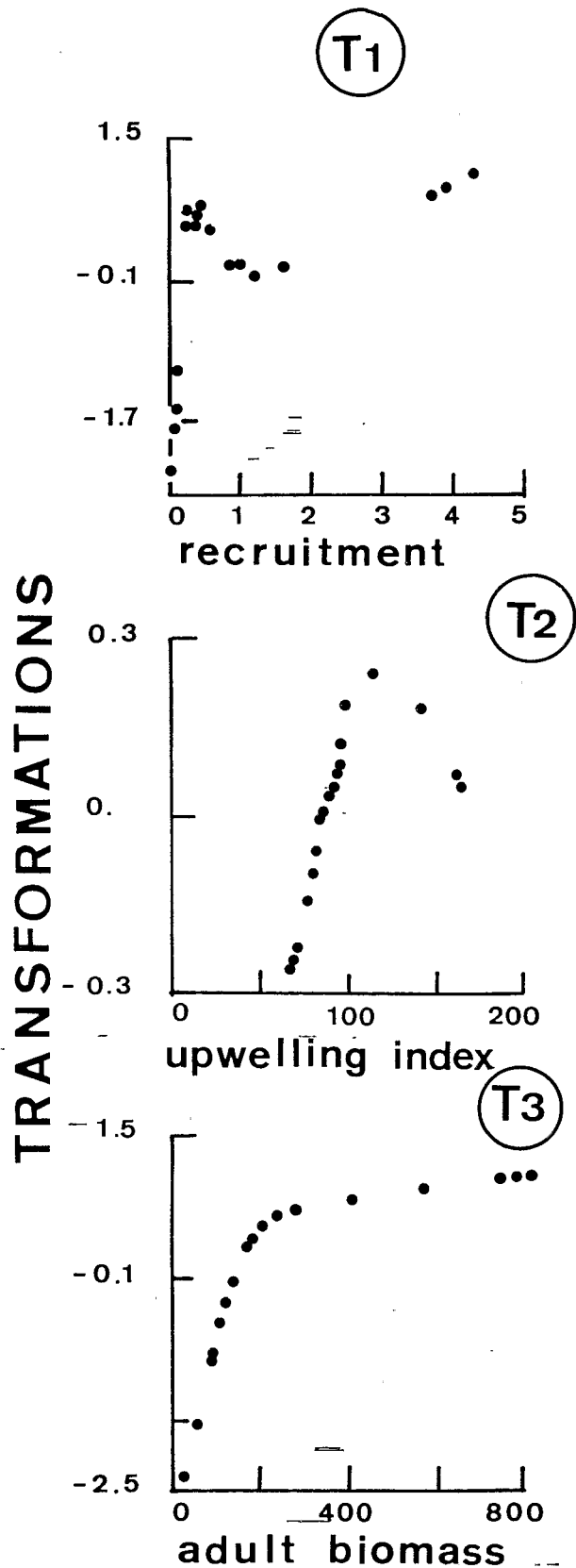


FIG. 5. Optimal empirical transformations for recruitment (No. of recruits $\times 10^9$) (T1), upwelling index ($m^3 \cdot s^{-1} \cdot 100 m^{-1}$ coastline) (T2) and adult biomass ($t \times 10^3$) (T3) for the Pacific sardine.

TABLE 3. Recruitment (CPUE of age 0 group) of the Moroccan sardine (Belvèze 1984). Seasonal turbulence and upwelling indices off Tantan during the reproductive period (Belvèze 1984).

Year	CPUE (tons·d ⁻¹)	Upwelling index (m ³ ·s ⁻¹ ·100 m ⁻¹) coastline	Turbulence index (m ³ ·s ⁻³)
1968	2.08	81.7	103.5
1969	2.15	42.1	61.0
1970	5.80	81.4	111.3
1971	1.38	56.1	60.2
1972	1.78	73.6	87.6
1973	0.89	73.6	71.1
1974	0.64	92.1	105.5
1975	0.96	120.3	155.8
1976	0.55	121.0	178.0
1977	0.46	116.6	152.9
1978	2.25	99.1	146.3
1979	0.63	69.1	79.1
1980	2.74	108.6	140.7
1981	0.78	105.6	128.7

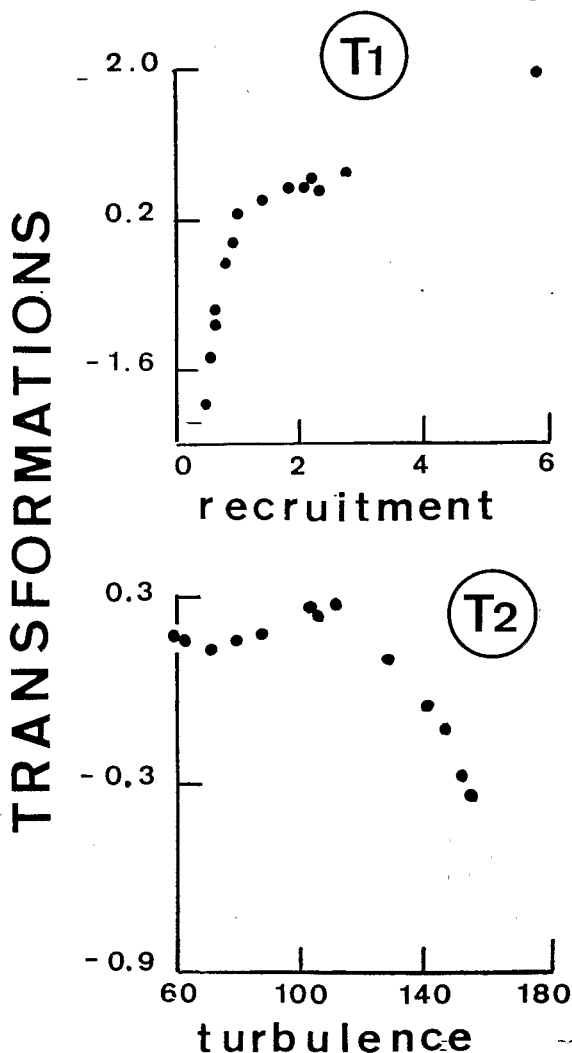


FIG. 6. Optimal empirical transformations for recruitment (t·d⁻¹) (T1) and turbulence index (m³·s⁻³) (T2) for the Moroccan sardine.

mates of the recruitments and Pacific sardine biomass calculated by MacCall (1979) (Table 2). The annual recruitment (year class at age 2) was estimated using a cohort analysis of aged

landings data from 1945 to 1964. The adult biomass was calculated as all fish of age 2 or older. The only environmental data available were monthly upwelling indices off Monterey (36°N, 122°W) from Bakun (1973) that were averaged over the whole year (Table 2).

Optimal transformations (T1, T2, T3) for the multiple regression were calculated using the current year upwelling index and adult biomass, and year class at age 2 for recruitment 2 yr later. For example recruitment index in 1948 is associated with annual upwelling index and adult biomass calculated in 1946

$$(2) \quad T1 (\text{recruitment}) = T2 (\text{upwelling index}) + T3 (\text{adult biomass}).$$

The transformation for the recruitment index presents a sharp increase for low values (under $0.5 \cdot 10^9$ fish), it decreases for values between 0.5 and $1.0 \cdot 10^9$ and increases slowly for higher values (Fig. 5, T1). The upwelling index transformation is dome shaped with a breaking point around a value of $100\text{--}120 \text{ m}^3 \cdot \text{s}^{-1}$ per 100 m of coastline (this value corresponds roughly to an alongshore wind speed of $5 \text{ m} \cdot \text{s}^{-1}$) (Fig. 5, T2). The transformation of adult biomass is typically a Beverton and Holt stock–recruitment relationship (Fig. 5, T3); it shows a curvature for sardine biomass of $200 \cdot 10^3$ metric tons. Model (2) explains 87% of the recruitment variance.

These relationships provide some complementary information on the waning years of the Pacific sardine fishery. After 1954, the adult biomass was under $200 \cdot 10^3$ metric tons (Table 2) and the recruitment–adult biomass relationship was on a slope where a minor stock produced a minor recruitment. After 1954, the upwelling intensity was higher than in the past (Table 2), and may have had a negative effect on recruitment. MacCall (1983) suggested that the rate of decline was sustained because the fishery consistently exceeded sustainable yields. The transformations of the Ekman index and the adult biomass suggest that this was not the only factor producing the collapse. It may have been due to a conjunction of several depressive factors on recruitment; excessive upwelling, or-too depressed biomass associated with a high exploitation rate.

West African Sardines and Sardinellas

Morocco

For Morocco, a recruitment index for sardine (*Sardina pilchardus*) may be obtained by using CPUE (Catch Per Unit of Effort) of age 0 and age 1 of the following year (Belvèze and Erzini 1983; Belvèze 1984) (Table 3). Monthly turbulence indices at 28°N, 13°W from October to April (Belvèze 1984) were used to calculate an annual wind mixing index during the reproductive and larval growth periods.

Optimal transformations (T1, T2) are estimated for the simple regression between recruitment and turbulence.

$$(3) \quad T1 (\text{recruitment}) = T2 (\text{turbulence}).$$

The model explains only 21% of the observed variance in recruitment. An estimation of stock size is not available and it would certainly contribute to an explanation of a much greater part of the variance if included in the model. However, the transformation of recruitment (Fig. 6, T1) is very close to a log transformation. The transformation of the turbulence appears to increase very slowly to a value of $120 \text{ m}^3 \cdot \text{s}^{-3}$ (which corresponds to a wind speed close to $5 \text{ m} \cdot \text{s}^{-1}$); for higher values of wind speed it decreases strongly (Fig. 6, T2).

TABLE 4. CPUE, fishing effort for the Senegalese round sardinella fishery (Fréon, 1983). Seasonal wind speed, turbulence, and upwelling indices off Yoff (Fréon 1983; C Roy, unpubl. data).

Year	CPUE (tons·10 h ⁻¹)	Effort 10 h·10 ³	Wind speed (m·s ⁻¹)	Turbulence index (m ³ ·s ⁻³)	Upwelling index (m ³ ·s ⁻¹ ·100 m ⁻¹)
1964				152	97
1965				178	113
1966	13.54	0.607	4.90	145	90
1967	11.62	0.673	4.66	144	84
1968	12.70	0.880	4.46	105	85
1969	9.86	1.325	4.37	120	83
1970	7.56	1.469	4.29	133	87
1971	10.68	1.262	5.01	176	109
1972	16.32	1.455	6.00	255	137
1973	11.38	2.590	5.30	211	117
1974	9.78	3.509	5.99	241	144
1975	7.22	4.062	5.50	218	122
1976	8.06	4.820	5.93	261	134
1977	8.61	5.157	5.61	202	111
1978	9.15	4.913	5.01	172	103
1979	6.68	5.996	4.53	115	78
1980	7.01	6.203	5.21	186	115
1981	6.09	7.773	5.03	135	103
1982	2.30	10.206	4.77	142	93
1983	2.00	10.841	4.51	106	82
1984				135	104
1985				265	144
1986				194	119

TABLE 5. CPUE, fishing effort for the Ivoiro-ghanian sardinellas fishery (Cury and Roy 1987, unpubl. data). Annual turbulence (C. Roy, unpubl. data) and upwelling index off Abidjan (Cury and Roy 1987).

Year	CPUE (tons·d ⁻¹)	Effort (d·10 ³)	Turbulence index (m ³ ·s ⁻³)	Upwelling index (1/10°C)
1965				29.7
1966	7.33	3.420	91	-9.3
1967	8.51	3.746	111	15.8
1968	7.35	4.073	70	-10.6
1969	5.30	3.616		-18.3
1970	3.81	5.716	117	7.5
1971	4.64	5.484		7.8
1972	6.47	3.930		4.5
1973	3.29	2.483	200	-37.8
1974	4.87	2.024	113	-6.8
1975	7.96	1.768	155	0.8
1976	10.64	1.824	158	36.1
1977	12.23	2.003	120	1.2
1978	9.26	2.200	103	9.4
1979	6.53	2.681	105	-13.2
1980	5.75	2.409	142	-10.7
1981	9.52	2.207	151	-9.9

Senegal and Ivory Coast-Ghana

In Senegal and Ivory Coast-Ghana, recruitment indices are not available for Sardinellas (*Sardinella aurita* and *Sardinella maderensis*). Fréon (1983) and Cury and Roy (1987) studied pelagic fish stocks in these upwelling areas and showed that annual CPUE is a function of fishing effort and of the upwelling intensity during the fishing year and 1 yr before. The upwelling intensity 1 yr before the fishing year appears to have an important effect on recruitment (sardinellas are recruited to the fishery after 1 yr). In Senegal, the upwelling is an Ekman-type upwelling and wind speed is used as an upwelling index (Fréon 1983). The monthly averages of the wind speed over the upwell-

ing season (November to May) were used to estimate interannual upwelling intensity and wind mixing. In Ivory Coast-Ghana, the upwelling is not caused by the local wind and sea surface temperature anomalies (deviation from a mean cycle during the upwelling seasons) were used as an upwelling index (Cury and Roy 1987). CPUE, fishing effort, upwelling or turbulence indices are presented in Table 4 for Senegal and Table 5 for Ivory Coast-Ghana.

Optimal transformations (T1, T2, T3, T4) for the multiple regression between CPUE and fishing effort, environmental indices during the fishing year and 1 yr before are calculated

$$(4) \quad T1(CPUE_i) = T2(\text{fishing effort}_i) + T3(\text{ind}_i) + T4(\text{ind}_{i-1})$$

where i = year index, ind. = upwelling index (Ivory Coast-Ghana) or wind speed (Senegal).

For Senegal and Ivory Coast-Ghana the models explain respectively 97 and 94% of the observed variance in CPUE. Empirical transformations of CPUE for Senegal and Ivory Coast-Ghana are curved and suggest that a log transformation is suitable (Fig. 7, T1 and Fig. 8, T1). The transformations of effort are nearly linear and have a negative slope. The relationship between CPUE and effort is negative and can be approximated with a linear model (Fig. 7, T2 and Fig. 8, T2). The transformation of upwelling index or wind speed during the fishing year increases for Ivory Coast and Senegal and shows a platform for Senegal (Fig. 7, T3 and Fig. 8, T3). The contribution of this index to the explication of the CPUE variance was interpreted as the effect of availability of the fish; fish seem less available during strong upwelling. The models used by Fréon (1983) and by Cury and Roy (1987) to analyze CPUE in Senegal and in Ivory Coast empirically integrate the upwelling index 1 yr before fishing to evaluate recruitment. Therefore analyzing the form of the transformation of this parameter that maximizes the correlation in the model allows us to identify

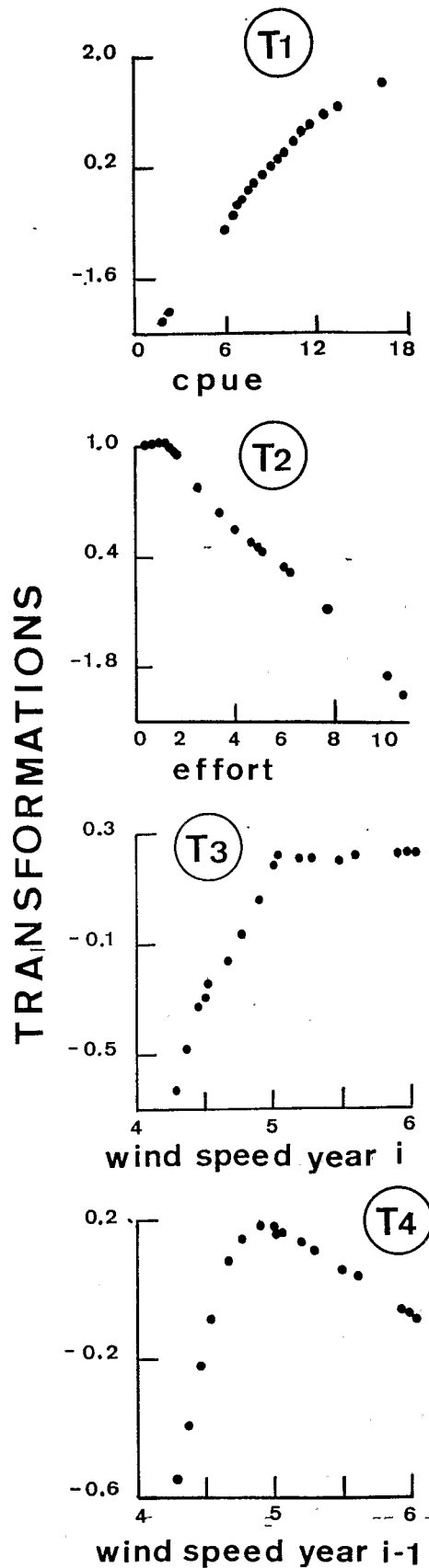


FIG. 7. Optimal empirical transformations for CPUE ($t \cdot d^{-1}$) (T1), fishing effort ($10 h \times 10^3$) (T2), wind speed ($m \cdot s^{-1}$) during the fishing year (T3) and wind speed during the previous year (T4) for the Senegalese round sardinella.

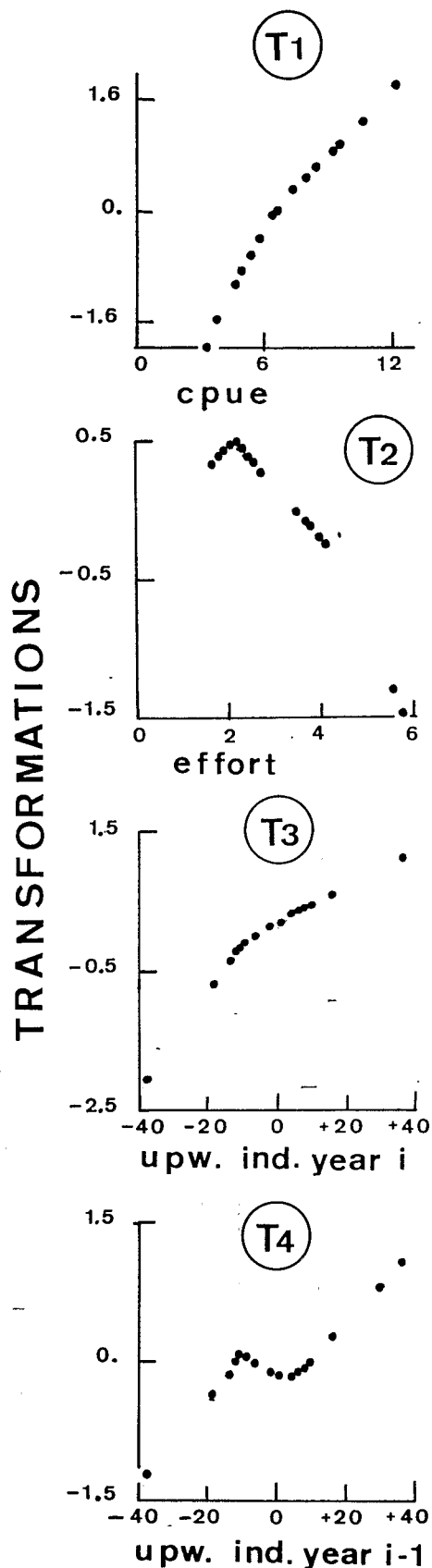


FIG. 8. Optimal empirical transformations for CPUE ($t \cdot d^{-1}$) (T1), fishing effort ($d \cdot 10^3$) (T2), upwelling index ($1/10^\circ C$) during the fishing year (T3) and upwelling index during the previous year (T4) for the Ivoirian sardinellas.

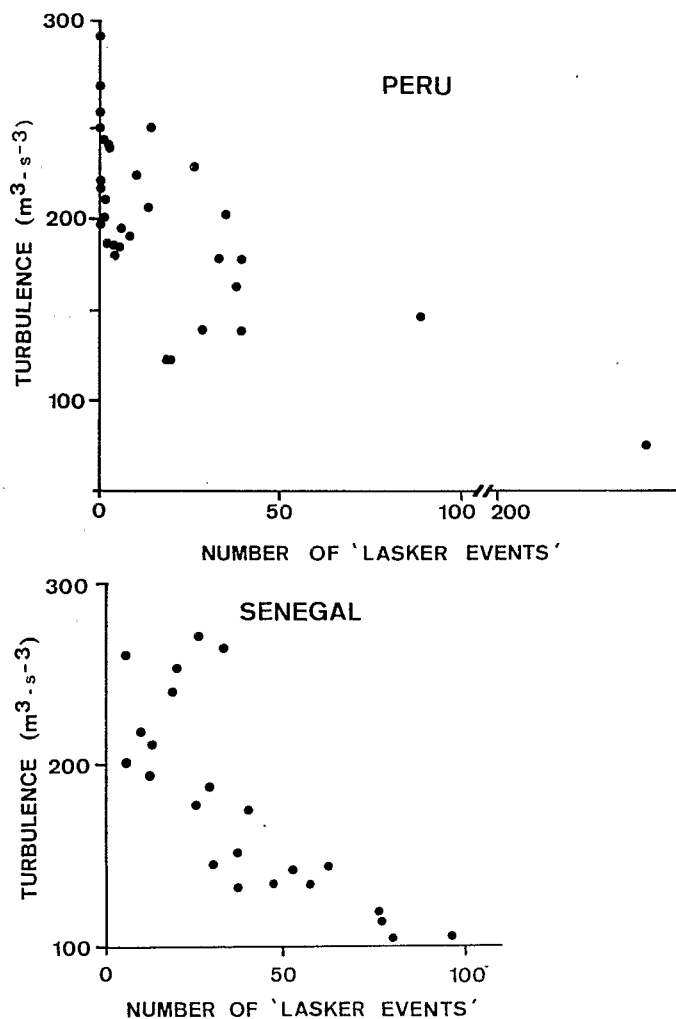


FIG. 9. Relationship between annual turbulence indices ($\text{m}^3 \cdot \text{s}^{-3}$) and occurrence of "Lasker events" in Peru and Senegal (from Mendelssohn and Mendo (1987) and C. Roy, unpubl. data). The number of "Lasker events" measures the number of 4-d periods during which the wind speed did not exceed $5 \text{ m} \cdot \text{s}^{-1}$ (see Peterman and Bradford (1987) for details about the calculation).

the relationship between the environmental parameter and recruitment. For Senegal, the transformation of wind speed 1 yr before the fishing year is dome shaped with a breaking point centered at $5 \text{ m} \cdot \text{s}^{-1}$ (Fig. 7, T4). For the Ivory Coast-Ghana the transformation of the upwelling index is nearly linear with just a platform for values around zero (Fig. 8, Table 4). This suggests that recruitment and upwelling are positively correlated in Ivory Coast-Ghana.

The transformations of the indices that evaluate upwelling intensity in Senegal and in Ivory Coast-Ghana are consistent with our hypothesis that a linear relationship exists between recruitment and upwelling in a non Ekman-type upwelling and that a dome shaped relationship exists in an Ekman-type upwelling.

Discussion: "5–6 $\text{m} \cdot \text{s}^{-1}$ Wind Speed" as an "Optimal Environmental Window"

"Lasker Events" and Average Seasonal Wind Speeds

Peterman and Bradford (1987) and Mendelssohn and Mendo (1987) used an index reflecting Lasker's hypothesis (1978),

called the "Lasker event". It measured the number of 4-d periods during which the wind speed did not exceed $5 \text{ m} \cdot \text{s}^{-1}$. While arrived at from different time scale studies, our results are also consistent with these previous studies which present evidence of the importance of this criterion and its impact on larvae survival.

Husby and Nelson (1982) noted that ... "the average intensity of turbulent wind mixing over a spawning season is not likely to be well correlated with interannual variability in recruitment. Rather, the existence of sufficient time-space windows within which turbulence does not exceed critical values may be the relevant factors." The validity of this assumption based on Lasker's (1978) hypothesis is confirmed by the result of Peterman and Bradford (1987); these authors show that it is the succession of calm periods more than the mean wind speed that is correlated with daily larval mortality rates. Our results are in agreement with these observations; Fig. 9 shows that the number of Lasker events during an upwelling season is negatively correlated with the average wind speed cubed for Peru and Senegal (data not available for the other areas). Therefore, wind speed on average over a spawning season could be used as a rough index of the number of low turbulence events during the spawning season.

Physical and Biological Significance of $5\text{--}6 \text{ m} \cdot \text{s}^{-1}$

What is the significance of the $5\text{--}6 \text{ m} \cdot \text{s}^{-1}$ value considering oceanographic features and enrichment processes? From a physical point of view, the threshold wind speed of $5 \text{ m} \cdot \text{s}^{-1}$ is a value at which wind stress begins to exert a measurable mixing effect on the surface layer in near-shore waters (Kullenberg 1971, 1972, 1974, 1976, and 1978). Also, when the wind speed is greater than about $7 \text{ m} \cdot \text{s}^{-1}$, wave breaking becomes obvious (Pond and Pickard 1978) and generates strong turbulence. From a biological point of view, wind speed of approximately $5 \text{ m} \cdot \text{s}^{-1}$ has been found to be a "threshold" value above which wind mixing tends to desegregate phytoplankton patchiness (Therriault and Platt 1981; Demers et al. 1987). These authors demonstrate that if the winds are strong enough to surpass this threshold for surface layer mixing, wind mixing dominates all other potential sources of variance of the phytoplankton patchiness; below this threshold the phytoplankton patchiness can be ascribed to biological causes. The threshold effect on recruitment success is consistent with this observed dynamic of phytoplankton.

Dispersion might not be the only factor affected by strong wind mixing. Huntsman and Barber (1977) showed that primary production and zooplankton biomass in the Northwest African upwelling is also affected by strong wind mixing. They show that strong winds produce a strong mixed layer and a light limited phytoplankton population. Therefore larval survival in the case of strong wind mixing could also be affected by the reduction of primary production.

Increased offshore transport of eggs and larvae with increased upwelling intensity is often cited as a cause of larval mortality (Bakun and Parrish 1980; Parrish et al. 1983). At this stage of this analysis it is impossible to know the relative importance of this detrimental factor. Since reproductively active fish avoid areas with strong offshore Ekman transport (Parrish et al. 1983; Husby and Nelson 1982; Roy et al. 1989), we think that turbulence in a reproductive area is perhaps a dominant factor.

Validity of the Theory

Review of information on some of the most important and well studied pelagic fish stocks of upwelling areas indicates that

the facts are consistent with the theory. When calculating the transformations of the different variables, taken one by one, like recruitment with parent stock or recruitment with upwelling (plots not presented here), it appears that each variable explains a significant percentage of recruitment variance and also that the transformations are similar to those obtained when simultaneously analysing recruitment, parent stock, and upwelling. Stock–recruitment and recruitment–upwelling relationships are both important for recruitment success. For an Ekman-type upwelling, the optimal transformations of turbulence (or upwelling index) in the Peruvian, Californian, Moroccan, and Senegalese ecosystems are very close to those predicted by theory. A dome shaped relationship exists between recruitment and upwelling intensity estimated from wind data. The non-linearity always appears for values of wind speed around $5\text{--}6\text{ m}\cdot\text{s}^{-1}$. This value is common for all the transformations and suggests that for different Ekman-type upwelling ecosystems there is a common and optimum wind mixing level in the stable layers of the upper ocean.

The validity of the theory is reinforced by the results obtained in Ivory Coast-Ghana. In this ecosystem local trade winds are weak and not correlated with upwelling intensity. Our theory suggests that strong wind mixing becomes a limiting factor even if upwelling intensity enhances primary production, but that if this limiting factor is not present, primary production and availability of food is the only limiting factor and recruitment should increase with upwelling intensity. The transformations, obtained with Ivory Coast-Ghana data, clearly illustrate that recruitment and upwelling intensity are almost linear and positively correlated.

Conclusion

Upwelling intensity differs from one area to another. In a given upwelling area, pelagic fish reproductive strategy tends to reach the optimal environmental window (as defined by our theory) by locally optimizing physical constraints. For example, in a weak upwelling area fish tend to reproduce in the most productive time–space areas. In the case of a moderate upwelling, fish reproductive strategies have to compromise between high productivity and strong turbulence. In the case of a strong upwelling, the turbulence is the only limiting factor for recruitment. Thus, local optimal environmental parameters may differ from one area to another and recruitment can be sometimes positively or sometimes negatively correlated with upwelling intensity. In upwelling areas the “match-mismatch” or “stability hypothesis” theories should both be valid considering our general relationship between recruitment success and environmental limiting factors.

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