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ENVIRONMENTAL CONSTRAINTS AND PELAGIC FISHERIES IN UPWELLING AREAS: THE PERUVIAN PUZZLE

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Pelagic fish catch statistics are used as surrogates to evaluate the potential fish productivity in upwelling ecosystems. A comparison between 10 upwelling areas of the world shows that the Peruvian ecosystem is three- to ten-fold more productive than the others. The size of the ecosystem, estimated by the surface of the continental shelf, does not by itself explain the observed disparity. Upwelling systems are characterized by different combinations of two different environmental variables: the upwelling intensity and the mixing generated by the wind. Using generalized additive models, an exploratory analysis is performed in order to identify the environmental conditions that maximize the total pelagic fish catch productivity (mainly sardine, sardinella and anchovy). The analyses consider fish catch as the dependent variable and the two environmental factors as the independent variables. Optimal environmental conditions appear to be a combination of: a high upwelling index (~ 1.2 $m^3 \cdot s^{-1} \cdot m^{-1}$) and moderate wind-mixing (~250 $m^3 \cdot s^{-3}$). The Peruvian ecosystem is the only upwelling system that has these characteristics, making it unique and singularly productive. These empirical results stress the importance of considering a combination of environmental factors when explaining pelagic fish productivity in upwelling systems.

Approximately 100 million tons of fish and shellfish have been extracted annually from the sea and inland waters since 1989 (F.A.O. 1997). The total marine fish catch represents 75% of that amount and approximately one-third is pelagic fish. The most important pelagic fisheries are located in the upwelling areas of eastern boundary currents, i.e. the Canary, the Benguela, the California and the Humboldt Current systems. Two fisheries contribute most to the world pelagic fish catch: the Peruvian and the Chilean fisheries. Annually, the landings off Peru and Chile reach millions of tons, whereas such countries as Morocco, California, South Africa and Ivory Coast-Ghana can contribute several hundred thousand tons. The size of an ecosystem is an important factor when considering productivity, but this may not be the only factor affecting pelagic fish productivity. It may be believed that large upwelling systems are able to sustain large fisheries. However, will a medium-size upwelling system produce as much as a large one? Pelagic fish stocks are well known for their instability, and numerous authors have examined the causes of recruitment and catch fluctuations (Sharp and Csirke 1983, Pauly and Tsukayama 1987, Pauly *et al.* 1989, Cury and Roy 1991, Kawasaki 1992, Lluch-Belda *et al.* 1992, Cury *et al.* 1995, Bakun 1996). Environmental factors such as wind-mixing, offshore transport and upwelling intensity play an important role in recruitment success or failure. Do environmental factors involved in fish population fluctuations also cause the observed difference in pelagic fish productivity among upwelling systems?

The comparative approach is a powerful tool in ecological science, because it makes it possible to establish the generality of phenomena (Bakun 1985, 1996) and, as mentioned by Maynard Smith and Holliday (1979 p. 7) "we must learn to treat comparative data with the same respect as we would treat experimental results". However, whereas the comparative approach is a method currently adopted in evolutionary biology (Harvey and Pagel 1991), the method is seldom used in ecology. A comparative method can lead to an empirical understanding of the disparity in fish productivity among upwelling systems by identifying the responsible environmental factor(s) that contribute to low or high productivity. In this paper, pelagic fish productivity in 10 upwelling systems is compared and the relationships with the environment are examined using variables such as the size of the continental shelf, the upwelling intensity and wind-mixing.

IS BIGGER BETTER FOR ECOSYSTEM SIZE?

Biological productivity of an ecosystem can be estimated in many ways, through planktonic production,

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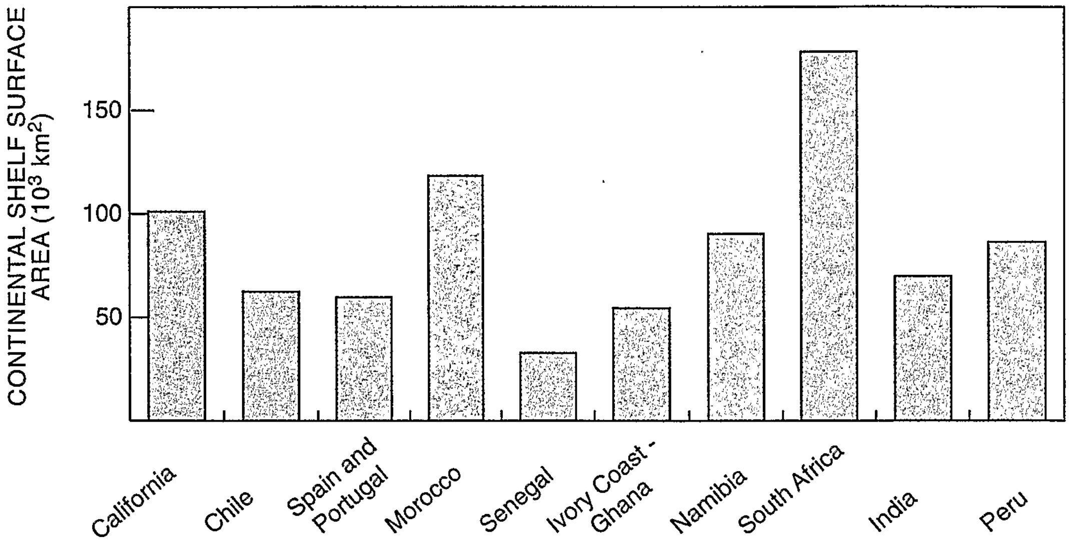

Fig. 1: Size of the continental shelf for each of the 10 upwelling areas

living matter turnover, energy transfer, fish biomass, etc. However, long time-series of such indices are not available in most upwelling systems and extended comparisons are difficult to perform. Fish catch statistics are the only data that have been collected in most upwelling systems over long periods (most of them from the beginning of the fisheries). These data are biased for a multiple of reasons: changes in the availability of fish, in the fishing effort, in the target species, in the markets, etc. However, when used as a surrogate, fishery data can provide a rough estimate of biological productivity. Therefore, these values can be considered adequate, because they give an order of magnitude estimate of "what it is possible to fish" in an ecosystem, ranging from several thousand tons to millions of tons.

A maximum pelagic fish catch "productivity index" is used here, by considering the maximum catch value observed during the whole time period of a fishery. This value is used to track the carrying capacity of pelagic fish in the ecosystem. This productivity index is calculated for the main pelagic species (i.e. sardine, sardinella and anchovy). Important catch-level differences are observed between pelagic fisheries (Table I). The Peruvian ecosystem clearly distinguishes itself, with a maximum catch of

Table I: Maximum pelagic fish catch, surface area of the shelf and maximum pelagic fish catch per unit of surface area for 10 upwelling areas and for three main pelagic species (sardine, sardinella and anchovy)

Upwelling areas	Latitude	Longitude	Period considered	Maximum pelagic fish catch (10^3 tons)	Surface area of the shelf (10^3 km^2)	Maximum productivity per unit of surface area (tons·km^2)
California	22–38°N	–	1924–1991	609	101	6.0
Chile	18°N–43°S	–	1966–1993	3 708	62	59.3
Spain and Portugal	32–44°N	5–9°E	1937–1989	368	59	6.2
Morocco	21–36°N	2–0°E	1950–1991	362	118	3.1
Senegal	12–16°N	–	1964–1991	194	32	5.9
Ivory Coast-Ghana	2–8°N	0–8°W	1966–1993	270	54	5.0
Namibia	16–28°S	–	1966–1992	1 561	90	17.3
South Africa	28–36°S	18–26°E	1950–1992	623	178	3.5
India	8–15°N	–	1948–1988	448	70	6.4
Peru	5–18°N	–	1958–1993	12 286	86	142.0

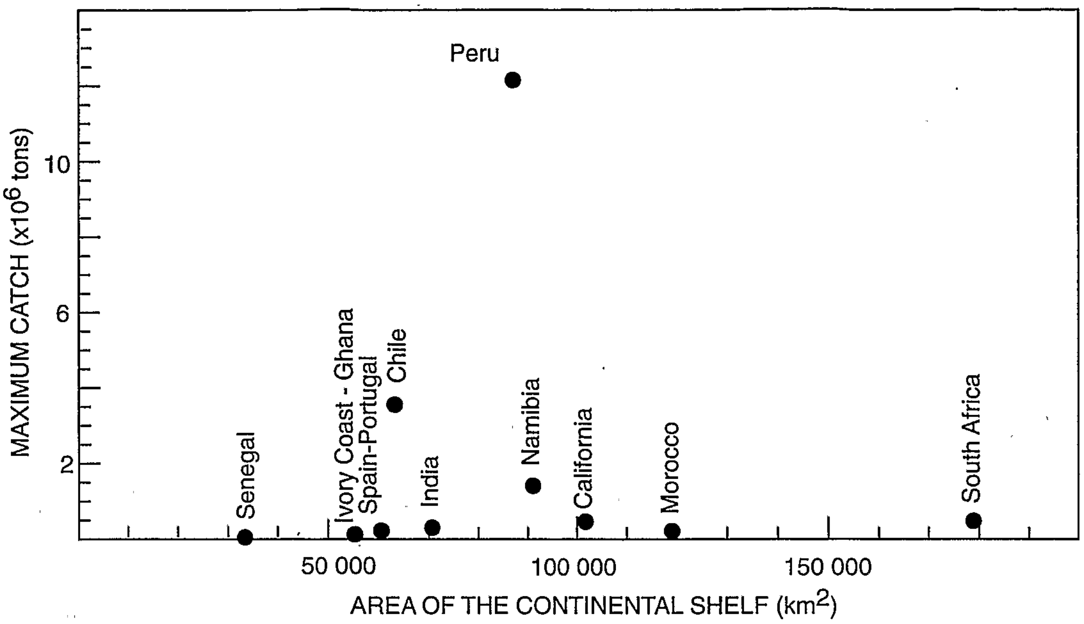

Fig. 2: Maximum pelagic fish catch productivity indices (tons) v. the area of the continental shelf (km^2) for the 10 upwelling areas

12 millions tons, and only two other fisheries have been able to catch more than one million tons within a year: Chile and Namibia. The other areas have never fished more than 623 thousand tons.

In order to quantify the size of the ecosystems, the surface area of the continental shelf was estimated (Fig. 1, Table I). The sizes of the continental shelves vary from 32 887 km^2 for Senegal to 178 315 km^2 for South Africa. South Africa, Morocco and California have large continental shelves ($>100\ 000\ km^2$) whereas Spain-Portugal, Senegal and Ivory Coast-Ghana have medium-sized to small ones ($<60\ 000\ km^2$).

The Peruvian and Chilean productivity indices are the largest among the 10 estimated, whereas the continental shelf surface areas of these countries are medium in size (Figs 1, 2). Conversely, the South African and the Moroccan ecosystems have a wide continental shelf and a poor fish productivity per unit shelf area compared with the others (Figs 1, 2). Even when the productivity index is divided by the size of the shelf, there is no clear relationship between the productivity per unit area of the ecosystems and their size (Fig. 3). Therefore, ecosystems with a large continental shelf are not necessarily among the most productive. Other environmental variables undoubtedly play a role in the intrinsic pelagic fish production of the upwelling ecosystems.

ENVIRONMENTAL CONSTRAINTS AND FISH PRODUCTIVITY

Environmental factors cause fish population fluctuations, because they are recognized to play a major role in recruitment success (Parrish and MacCall 1978, Bakun and Parrish 1982, Cury and Roy 1989, Lluch-Belda *et al.* 1989, Cushing 1990, 1995, Lluch-Belda *et al.* 1992). Two environmental variables were selected for the analysis: a Coastal Upwelling Index (*CUI*, $m^3{\cdot}s^{-1}{\cdot}m^{-1}$), which is the offshore component of the wind-induced Ekman transport (Bakun 1973), and a wind-mixing index (V^3, $m^3{\cdot}s^{-3}$) calculated as the cube of the wind speed. A CD-Rom-based version of the COADS data (Comprehensive Ocean Atmosphere Data Set), collected by merchant ships all around the world oceans (Woodruff *et al.* 1987) was used to build monthly time-series of wind data (Mendelssohn and Roy 1996) and to calculate the *CUI* and V^3 indices. Mean values of the two indices from 1946 to 1990 were then calculated for these indices for the different upwelling areas (Table II).

Upwelling indices vary from 0.31 $m^3{\cdot}s^{-1}{\cdot}m^{-1}$ for South Africa to 1.28 $m^3{\cdot}s^{-1}{\cdot}m^{-1}$ for Namibia. Three areas exhibit strong upwelling indices: Namibia, Peru and Ivory Coast-Ghana. The wind-mixing index varies

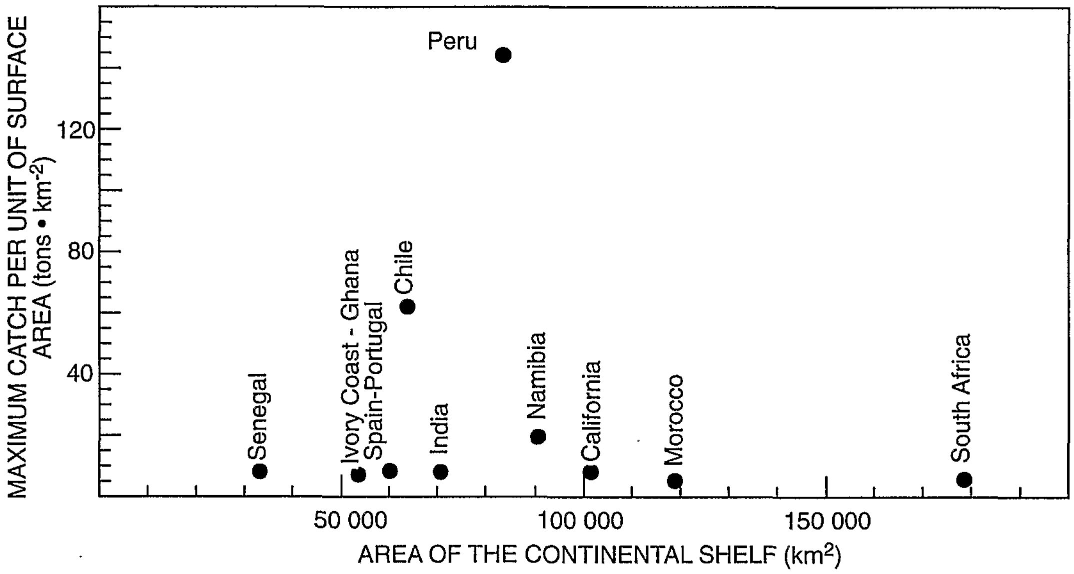

Fig. 3: Maximum pelagic fish catch per unit area (tons·km^2) for the 10 upwelling areas

from 103 $m^3 \cdot s^{-3}$ for Ivory Coast-Ghana to 770 $m^3 \cdot s^{-3}$ for South Africa. Classically, a high upwelling intensity is associated with a high wind-mixing intensity (in Namibia and Chile), but in low-latitude ecosystems, moderate wind-forcing can generate rather intense upwelling because of the latitude-dependency of the *CUI*. This is the case off Peru and Ivory Coast-Ghana, which are characterized by a moderate wind-mixing intensity but a fairly strong upwelling index. In the same way, moderate upwelling indices can be associated with strong wind-mixing in mid-latitude ecosystems such as California, Spain-Portugal and South Africa.

Table II: Environmental characteristics (coastal upwelling and wind-mixing indices) calculated from COADS (mean from the period 1946–1990) of the 10 upwelling areas (latitude and longitude as in Table I)

Upwelling areas	Coastal upwelling index ($m^3 \cdot s^{-1} \cdot m^{-1}$)	Wind-mixing index ($m^3 \cdot s^{-3}$)
California	0.36	654
Chile	0.93	345
Spain and Portugal	0.36	627
Morocco	0.66	305
Senegal	0.59	150
Ivory Coast-Ghana	1.04	103
Namibia	1.28	517
South Africa	0.31	770
India	0.44	239
Peru	1.20	224

The relationship between the productivity indices and the two environmental factors is explored using non-parametric regression models. Iterative algorithms that extend linear multiple regression analysis to generalized additive models provide a method to explore the relationship between the response and the predictor variables when the form of these relationships is unknown. The non-linearity of the relationships as well as the multiplicity of factors can be considered. The Alternating Conditional Expectation (ACE) and the Generalized Additive Interactive Modeling (GAIM) statistical methods estimate optimal transformations for multiple regressions (Hastie and Tibshirani 1990). The usual linear multiple regression model for predicting a response variable Y from p predictor variables X_i, $i = 1, \ldots, p$ and for n observations, $j = 1, \ldots, n$, is given by:

$$Y(j) = \Sigma\, b_i X_i(j) + e(j) \quad , \qquad (1)$$

where $b_i s$ are coefficients estimated by the model and $e(j)$s are error terms and are independent.

In the non-parametric model, the response variable Y and the predictor variables $X_1 \ldots\ldots X_p$ are replaced by functions $T_1(Y)$ and $T_2(X_1) \ldots\ldots T_{p-1}(X_p)$:

$$T_1(Y(j)) = \Sigma\, b_i\, T_{i+1}(X_i(j)) + w(j) \quad , \qquad (2)$$

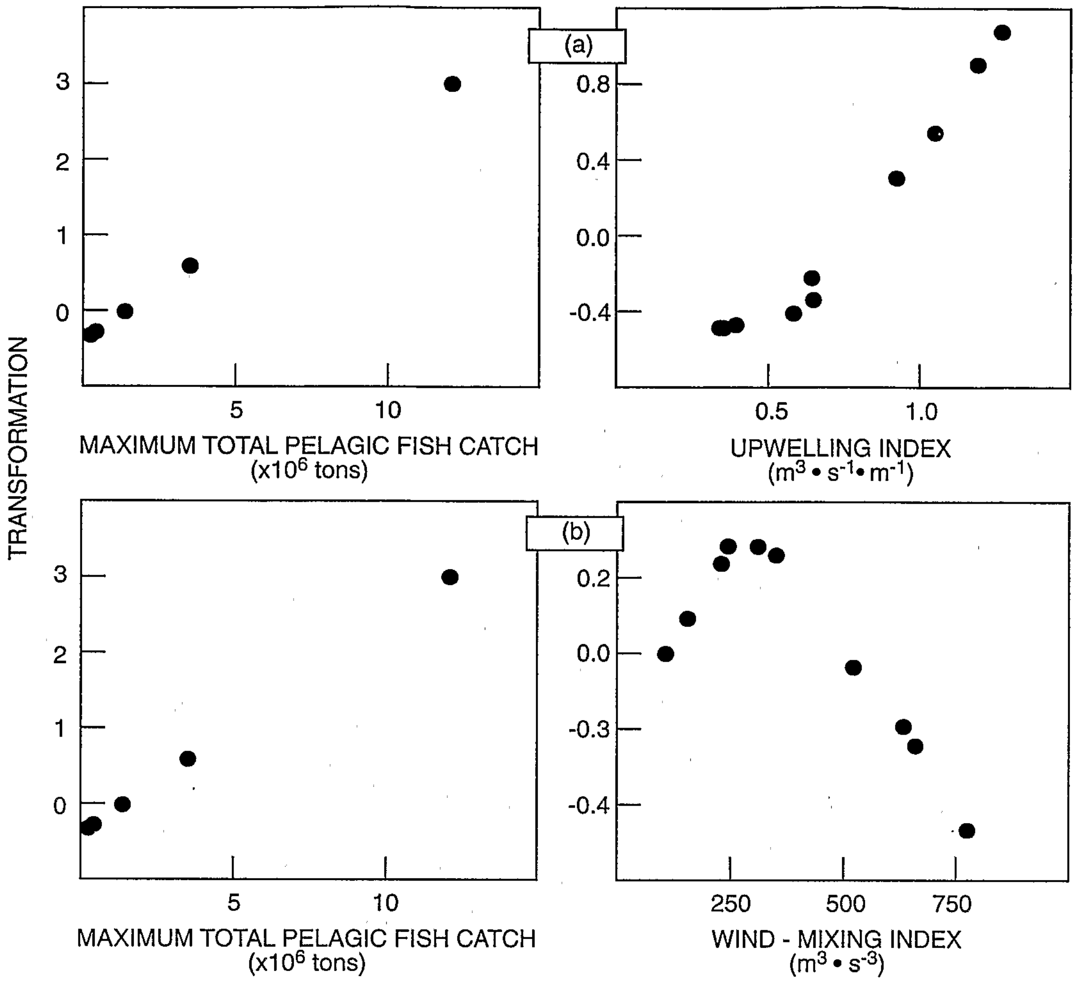

Fig. 4: Optimal empirical transformations from the ACE algorithm using (a) the maximum total pelagic fish catch (productivity index) as the dependent variable and the upwelling index as the independent variable ($r^2 = 0.35$), (b) the maximum pelagic fish catch productivity index as the dependent variable and the wind-mixing index as the independent variable ($r^2 = 0.12$)

where $w(j)$ is an error term and $T_1(Y)$ and $T_i(X)$ are unknown and estimated by minimizing:

$$E((T_1(Y) - \Sigma\, b_i\, T_{i+1}\,(X_i))^2) \,/\, \mathrm{var}\,(T_1(Y)) \quad . \quad (3)$$

Several approaches exist to estimate Equation 3. ACE includes the b_i in the function $T_i()$, whereas GAIM estimates b_i in order to perform analysis of deviance tests on the parameters. GAIM produces an analysis of deviance as well as coordinates for plotting the function estimates and their standard errors. The algorithms converge to optimal solutions for a given criterion because they have their own smoothers and convergence criteria (see Cury *et al.* 1995 for a detailed application to fishery data).

A regression analysis is done using the productivity index as the response variable and the environmental factors as the predictor variables. The shape of the transformation is found by plotting the transformed values of a variable versus the original values. Results given by the ACE algorithm are presented below.

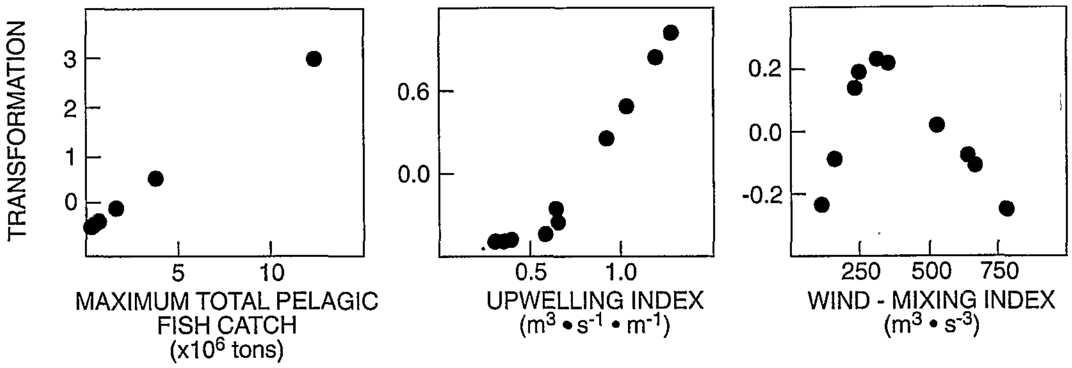

Fig. 5: Optimal empirical transformations from the ACE algorithm using the maximum total pelagic fish catch (productivity index) as the dependent variable and the upwelling index and the wind-mixing index as the independent variable (r^2 = 0.43). Data are used from all 10 ecosystems

The relationships between the productivity index and each individual environmental variable are first explored. Optimal transformations ($T1$, $T2$) for the multiple regression are calculated:

$$T1\text{ (Productivity index)} = T2\,(CUI) \qquad r^2 = 0.35 \quad (4)$$

$$T1\text{ (Productivity index)} = T2\,(V^3) \qquad r^2 = 0.12 \quad . (5)$$

Although the methodologies produce non-linear transformations for both dependent and independent variables, in order to produce a readily-interpretable result, the transformation was forced for the productivity index ($T1$) to be linear. The transformation produced for the upwelling index is linear and positive (Fig. 4a). The wind-mixing index is transformed to a nearly dome-shaped curve with a breaking point around 250 $m^3 \cdot s^{-3}$ (Fig. 4b).

Multivariate analyses are carried out by considering simultaneously the two environmental variables in the model. The optimal transformations ($T1$, $T2$, $T3$) for the multiple regression are calculated using the productivity index as the response variable and wind-mixing and the upwelling index as the predictors in Model 6 (Fig. 5).

$$T1\text{(Productivity index)} = T2\,(CUI) + T3\,(V^3)$$
$$r^2 = 0.43 \quad . \qquad (6)$$

The transformation of the response variable is again forced to be linear (Fig. 5). The transformations for wind-mixing and the upwelling index are similar to those given by the univariate analysis: the upwelling transformation is linear and positive and the transformation for wind-mixing is dome-shaped with a breaking point around 250 $m^3 \cdot s^{-3}$ (Fig. 5). The scale of the transformed value gives an indication of the relative contributions of the environmental variables to the variance. It indicates a greater contribution by upwelling intensity than by wind-mixing. Both univariate and multivariate analyses suggest similar patterns that relate fish catch productivity to environmental variables.

This comparative and exploratory analysis of the relationship between estimates of fish productivity and environmental characteristics in upwelling systems reveals that a combination of several factors is necessary to promote a high fish productivity (Faure and Cury 1998). These "optimal environmental conditions" that appear to maximize the pelagic fish catches in upwelling areas are:

(i) a high upwelling intensity (the maximum observed is 1.28 $m^3 \cdot s^{-1} \cdot s^{-1}$);
(ii) a moderate wind-mixing (around 250 $m^3 \cdot m^{-3}$).

DISCUSSION

The Peruvian puzzle

The results of the statistical analysis must be considered with caution, because important limitations arise from using a comparative approach based on only 10 data points. Consequently, the statistical validity of the results is questionable as a result of few degrees of freedom, particularly for the multivariate analyses. This is unavoidable because:

(i) the number of ecosystems with documented pelagic fisheries and for which environmental

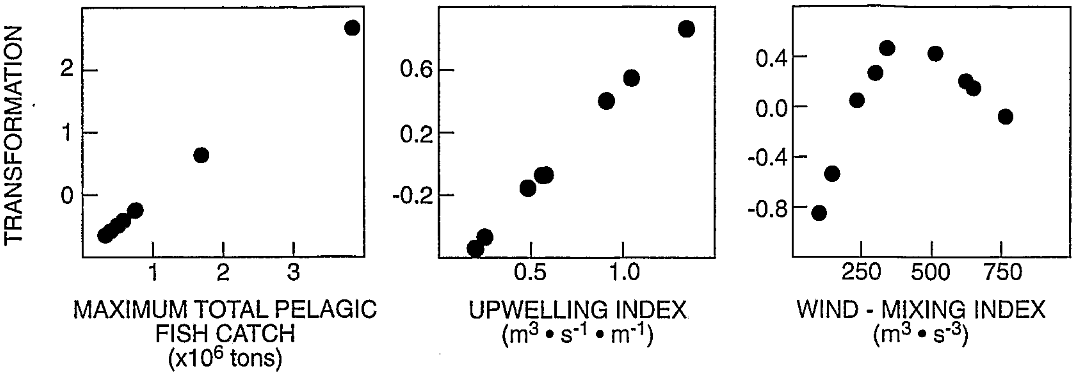

Fig. 6: Optimal empirical transformations from the ACE algorithm using the maximum pelagic fish catch (productivity index) as the dependent variable and the upwelling index and the wind-mixing index as the independent variable ($r^2 = 0.53$). Data from the Peruvian ecosystem are excluded

data exist is limited;

(ii) the number of environmental factors that are hypothesized to play a role in productivity is large compared with the number of ecosystems considered.

Nevertheless, the relationships between the fish productivity and the environmental variables appear to be in agreement with independent ecological knowledge on ecosystem functioning. High upwelling intensity as a source of food availability (Wroblewski and Richman 1987, Cushing 1990) and small-scale turbulence that increases the encounter rate between food particles and larvae (Rothschild and Osborn 1988, Mackenzie and Leggett 1991) are thought to be beneficial to larval survival. The positive relationship between the upwelling intensity and the pelagic fish catch could be related to these combined effects. In contrast, intense wind-driven turbulent mixing that disperses patches of larval food appears to be detrimental (Lasker 1975, Peterman and Bradford 1987, Cury and Roy 1989). Bakun (1996) identified a "fundamental triad" of three major processes that combine to yield favourable environmental conditions for successful fish reproduction: an enrichment process (e.g. upwelling, mixing), a concentration process (e.g. water column stability, convergence) and processes favouring retention within the appropriate habitat. To some degree, the environmental factors that have been selected here could be considered as proxy variables that account for some of the processes involved in the "triad". For example, the upwelling intensity determines the global enrichment of the ecosystem and wind-mixing is involved in the processes that concentrate food for larvae.

From this analysis, it appears that the size of the ecosystem does not strongly influence the productivity index. In upwelling areas, the maximum pelagic fish productivity depends on a combination of environmental factors with values within specific ranges. The values should be maximum for the upwelling index (1.28 $m^3 \cdot s^{-1} \cdot m^{-1}$) and moderate for the wind-mixing index (250 $m^3 \cdot s^{-3}$). These optimal values are very close to those observed off Peru (1.2 $m^3 \cdot s^{-1} \cdot m^{-1}$ and 224 $m^3 \cdot s^{-3}$ respectively), which is the most productive upwelling ecosystem and the only one that combines these optimal environmental conditions. Can it be that these "optimal conditions" are responsible for the very high productivity of the Peruvian ecosystem?

The Peruvian data were included in the analysis described above. As a consequence, it could be tautological to explain the high productivity in that area using data from it. In other words, it must be questioned whether the results are essentially derived from the Peruvian values or not. To avoid circularity in the study, a similar analysis was performed without the Peruvian data, giving almost identical results (Fig. 6); the transformation of the upwelling index is linear and positive and the transformation of the wind-mixing index is dome-shaped, but with a breaking point around 400 $m^3 \cdot s^{-3}$ ($r^2 = 0.53$). Removing the Peruvian data point had little effect on the shape of the transformation, but a difference is observed when considering the absolute value of the breaking point of the wind-mixing transformation. This result supports the previous consideration: the high productivity of the Peruvian upwelling ecosystem results from a unique combination of intense upwelling and moderate wind-mixing. In Chile and Namibia, the upwelling index is favourable, but is associated with a negative effect of too strong wind-mixing. The same high upwelling index is found off Ivory Coast-Ghana, but it is associated with a low mixing index. Off South Africa, Spain and California, the wind-mixing index is high and associated with a low upwelling intensity, so limiting productivity. In each upwelling area, except Peru, at least one environmental condition differs from that of the "optimal conditions" and consequently tends to limit productivity. The Peruvian ecosystem appears to be the only one that combines the optimal environmental conditions.

CONCLUSION

Optimal environmental conditions that maximize the pelagic fish catch in upwelling ecosystems have been identified using a comparative approach with fishery and environmental data from 10 upwelling areas in the Atlantic, Indian and Pacific oceans. This comparative analysis provides a framework for considering the relative impact of several environmental factors on fish productivity. It emphasized the relative importance of limiting factors such as wind-mixing, upwelling intensity or the size of the ecosystem, but many others can play a major role in the recruitment process (see Hutchings *et al.* 1998 for a review). The present results should promote new insights of how to relate environmental variables to fish productivity in a multivariate context. Palaeoecological studies reveal that pelagic fish populations have experienced large natural fluctuations that were clearly unrelated to fishing pressure, and that past abundance was sometimes much higher than that during the last century in California or in Peru (Soutar and Isaacs 1974, De Vries and Pearcy 1982, Baumgartner *et al.* 1992). For California, factors are identified that limit fish productivity (low coastal upwelling intensity and high wind-mixing), but this was impossible for Peru. This stresses the limit of the approach presented here, because it is clear that the Peruvian ecosystem might be able to produce even more under other, but still unknown, environmental conditions. Upwelling regions of the world have short foodwebs, with only one or two steps between phytoplankton, and are a major source of food for man, whereas there are up to six substantial trophic levels in ecosystems such as coral reefs (Birkeland 1997). Productivity is not limiting in upwelling systems, but the efficiency with which the foodweb is coupled is important. Many upwelling systems appear to have large, organic-rich deposits, which is suggestive of inefficient use of primary productivity. A fundamental factor to consider appears to be how to enhance the efficiency of the foodwebs.

To predict the effect of climate change on living marine resources is a challenge for the scientific community. At present, there is no reliable computer-generated, climate-impact scenario for the next several decades, but generalizations derived from case-by-case assessments of past and present experiences can be used (Glantz 1992). Such assessments can provide first approximations of how fisheries might respond to environmental changes. The comparative analysis constitutes a good base of information to begin an assessment of the possible impacts of environmental changes on fish productivity (Faure and Cury 1998). Some scenarios for fish productivity under climatic changes derived from previous study can therefore be used to forecast by analogy (Glantz 1992). How and how much will the productivity evolve if one or several environmental variables change in upwelling areas? The present comparative analysis provides a framework for considering the relative impact of several environmental factors on fish productivity. Assume, for example, two simple scenarios. First, a marked increase in the upwelling intensity, providing more available nutrients, would probably improve fish productivity in many ecosystems. The consequences could certainly be stronger in areas where low upwelling intensity is the main limiting factor, i. e. Morocco or Senegal. Second, with a decrease in the wind-mixing intensity, a greater fish productivity would be expected in areas where high mixing appears to be an important limiting factor, i.e. California, Chile, Spain-Portugal, Morocco, Namibia and South Africa. The reality is more complex because environmental factors change simultaneously. A scenario involving one environmental variable is a very simplified view of what might occur under climatic changes. However, a qualitative approach allows one to predict the increase or decrease of fish productivity and can give some preliminary answers.

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