# Pelagic Fisheries and Environmental Constraints in Upwelling Areas: How much is Possible?

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## Abstract

The relations among fish productivity and five environmental variables are analyzed for eleven upwelling areas of the world. Three 'fish catch productivity' indices, calculated from fish catch statistics, are used as surrogates for fish productivity in the ecosystems. Five environmental parameters are considered in each upwelling areas: coastal upwelling and turbulence indices, sea surface temperature, continental shelf surface and length. On its own, the size of the ecosystem does not explain the observed differences of the pelagic fish productivity indices. Using non-parametric regression methods, it is shown that a combination of several environmental factors is required for high fish productivity. These optimal conditions are a high upwelling index (around 1.3 $m^3/s/m$), a moderate turbulence (around 200-250 $m^3/s^3$), a medium sea surface temperature (15-16°C) and a relatively large continental shelf (around 100 000 $km^2$). The Peruvian ecosystem is the only system which combines all of these environmental conditions. The environmental factors which limit fish productivity are identified in each upwelling zones; they can help to predict changes under future climatic events. The limits of the analysis as well as some possibly circular aspects of the analysis are emphasized.

# Résumé

La productivité halieutique est analysée en relation avec cinq variables environnementales pour onze zones d'upwelling mondiales. Trois indices de productivité sont estimés à partir des statistiques de captures disponibles ; ils sont assimilés à la productivité en poisson d'un écosystème. Cinq variables environnementales sont considérées pour chaque zone d'upwelling : indices d'upwelling côtier et de turbulence, température de surface de la mer, surface et longueur du plateau continental. La taille d'un écosystème en elle-même n'explique pas la disparité observée entre les différentes productivités en poissons pélagiques des zones d'upwelling. Des méthodes régressives non paramétriques révèlent qu'une combinaison de plusieurs facteurs environnementaux est en effet nécessaire pour qu'une forte productivité en poisson soit réalisable. Les conditions optimales sont les suivantes : un fort indice d'upwelling (proche de 1.28 $m^3/s^1/m^1$), une turbulence modérée (proche de 200-250 $m^3/s^3$), une température de surface moyenne (15-16 °C) associés à un plateau continental relativement vaste (d'environ 100 000 $km^2$). L'écosystème péruvien s'avère être le seul qui regroupe l'ensemble des conditions environnementales optimales. Le ou les facteurs environnementaux qui sont supposés limiter la productivité en poisson sont identifiés pour chacune des zones d'upwelling ; ils peuvent aider à prédire les éventuels changements consécutifs aux futurs événements climatiques. Les limites ainsi que les aspects tautologiques de cette analyse sont soulignés.


# Introduction

Approximately one hundred million tonnes of fish and shellfish are extracted every year from the sea and the inland waters since 1989 (Fig. 1). The total marine fish catch represents 75% and around one third of it is composed of pelagic fish (Fig. 1).

Pelagic fisheries are mainly located in the four main upwelling areas which are located in the eastern boundary currents, i.e., the Canary, the Benguela, the California and the Humbolt currents. Two fisheries contribute most to the world pelagic fish catch: the Peruvian and the Chilean fisheries. Annually they land millions of tonnes whereas countries like Morocco, the USA (California) or South Africa contribute hundred thousand of tonnes, while the catches in Côte-d'Ivoire or Ghana remain in the order of a few thousand tonnes. It is natural to think that large upwelling systems are able to produce more than small ones. However is it correct to say that a large upwelling system will always produce as much as a medium one? This is not obvious: the size of an ecosystem is an important factor when considering productivity, however it may not be

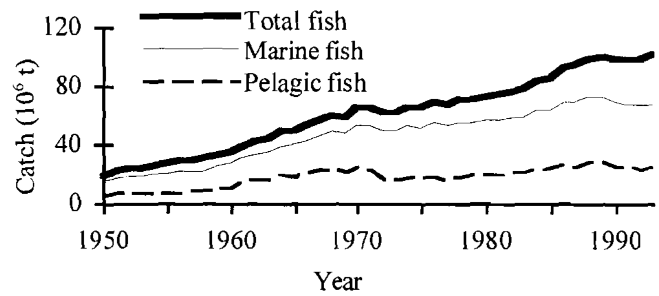



Fig. 1: Marine and pelagic fish contributions to world catches (FAO, 1995).

the only factor affecting pelagic fish productivity. Pelagic fish stocks are known for their instability and numerous authors have examined the causes of catch variations (Sharp and Csirke, 1983; Lluch-Belda *et al.*, 1991; Kawasaki, 1992; Bakun, 1994; Cury *et al.*, 1995). Environmental factors such as turbulence, upwelling intensity, offshore Ekman transport were found to be responsible for recruitment successes or failures. Do environmental factors involved in fish population fluctuations also explain the observed difference in pelagic fish productivity among upwelling systems? The comparative approach constitutes a powerful tool in ecological science as it allows to establish the generality of phenomena (Bakun, 1985). However, as stated by Maynard Smith and Holliday (1979) "we must learn to treat comparative data with the same respect as we would treat experimental results". Whereas it is a currently adopted method in evolutionary biology (Harvey and Pagel, 1991), it is not so frequently used in ecology. A comparative approach could lead to an empirical understanding of the disparity between fish productivity among upwelling systems by identifying the responsible environmental factor(s) which contribute to a low or high productivity. In this paper, the productivity of pelagic fish in eleven upwelling systems is therefore compared and its relationship with the environment examined, using variables such as the area and extent of continental shelves, upwelling intensity, turbulence, and sea surface temperature.

# 1. Is system size enough?

Numerous variables can be used to estimate the biological production of an ecosystem, for example planktonic production, fish biomass, turn-over of living matter, etc. However, such measurements are not available in most upwelling systems, making their comparison impossible. Fish catch statistics are the only data that have been collected in most upwelling systems during long time periods (Table 1). These data are biased for multiple reasons: changes in the availability of fish, in the fishing effort, in the target species, in the markets, etc. However used as a surrogate, fishery data can give an approximate value for biological productivity which can be considered adequate when comparing extreme range of values (from several thousand to millions of tonnes).

'Fish catch productivity' indices can be derived in several ways from catch data (Table 2):

- a 'mean *fish* catch productivity' index can be calculated by averaging the catch data for the period during which the fishery was sustained;
- a 'maximum fish catch productivity' index can be estimated from the observed maximum catch value; and
- a 'maximum fish catch productivity per unit of surface' index can be calculated by dividing the maximum fish catch productivity index by the surface of the continental shelf.

All of these three options were used here.

| Upwelling areas | Pelagic fish species | Time period | Data sources |
|---|---|---|---|
| California | *Sardinops sagax*<br>*Engraulis ringens*<br>*Scomber japonicus* | 1879-1990<br>1928-1991<br>1926-1991 | NMFS<br>(National Marine Fishery Service) |
| Peru | *Sardinops sagax*<br>*Engraulis ringens*<br>*Scomber japonicus* | 1950-1993<br>1950-1993<br>1964-1993 | IMARPE<br>(Instituto del Mar del Perù) |
| Chile | *Sardinops sagax*<br>*Engraulis ringens*<br>*Scomber japonicus* | 1964-1993<br>1952-1993<br>1964-1993 | IFOP<br>(Instituto de Fomento Pesquero) |
| Spain and Portugal | *Sardina pilchardus*<br>*Engraulis encrasicolus* | 1940-1988<br>1968-1988 | FAO (Food and Agriculture<br>Organization of the United Nations) 1995 |
| Morocco | *Sardina pilchardus*<br>*Engraulis encrasicolus*<br>*Scomber japonicus* | 1925-1991<br>1964-1991<br>1964-1991 | FAO (1995)<br>and ISPM<br>(Institut Scientifique des Pêches Maritimes) |
| Senegal | *Sardinella aurita*<br>*Sardinella maderensis* | 1966-1991<br>1966-1991 | CRODT<br>(Centre de Recherches Océanographiques de Dakar-Thiaroye) |
| Côte-d'Ivoire - Ghana | *Sardinella aurita*<br>*Sardinella maderensis*<br>*Scomber japonicus* | 1966-1991<br>1966-1991<br>1966-1993 | CROA (Centre de Recherches Océanologiques d'Abidjan)<br>and FRUB<br>(Fisheries Department Research and Utilisation Branch) |
| Namibia | *Sardinops ocellatus*<br>*Engraulis japonicus* | 1949-1992<br>1964-1992 | Crawford *et al.* (1987) and Crawford (pers. comm.) |
| South Africa | *Sardinops ocellatus*<br>*Scomber japonicus* | 1950-1991<br>1963-1991 | Crawford *et al.* (1987) and Crawford (pers. comm.) |
| Venezuela | *Sardinella aurita* | 1957-1989 | Guzman *et al.* (in press) |
| India | *Sardinella longiceps*<br>*Rasterlliger kanagurta*<br>Anchovy nei | 1896-1989<br>1925-1989<br>1963-1989 | Longhurst and Wooster (1990)<br>and FAO (1995) |

Table 1: Fishery data from eleven upwelling areas and for three main pelagic species (sardine, anchovy and mackerel) collected during different time period.

These productivity indices are calculated for two main pelagic species (sardine and anchovy), and for the pelagic species total (sardine, anchovy and mackerel) (Table 2).

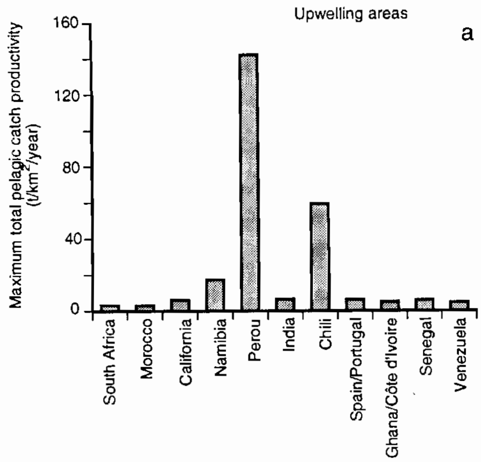
Important differences are observed among pelagic fisheries (Table 2). Three fisheries catch more than one million tonnes: Peru, Chile and Namibia. The Peruvian ecosystem has a maximum total pelagic catch productivity well above that for other systems. Species productivity is also different from one geographic zone to another. For Venezuela maximum catch for sardine is around 80 000 t whereas more than 2 million t are caught in Chile. The anchovy in Morocco never reached more than 19 000 t and more than 12 million t were landed in Peru.

Large ecosystems should a priori be able to produce more fish than small ones. In order to quantify the size of the ecosystems, the length and the surface of the continental shelf were measured. The surfaces of the continental shelves vary from 17 000 $km^2$ for Venezuela to 178 300 $km^2$ for South Africa (Table 3). South Africa, Morocco and California have large continental shelves (higher than 100 000 $km^2$) while Spain-Portugal, Senegal, Côte-d'Ivoire-Ghana or Venezuela have medium to small ones (lower than 60 000 $km^2$).

The Peruvian and Chilean total pelagic catch productivity are the highest among the others whereas their continental shelf surfaces are of medium sizes (Fig. 2a). On the other hand, the South African and the Moroccan ecosystems have a wide continental shelf and a poor fish productivity compared to the others (Fig. 2b). Thus, areas with a large continental shelf

| Upwelling areas | Sardine 'catch productivity' index | | | | Anchovy 'catch productivity' index | | | | Total pelagic 'catch productivity' index | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Time period considered | Mean (t/year) | Maximum (t/year) | Maximum per unit of surface (t/km²/year) | Time period considered | Mean (t/year) | Maximum (t/year) | Maximum per unit of surface (t/km²/year) | Time period considered | Mean (t/year) | Maximum (t/year) | Maximum per unit of surface (t/km²/year) |
| 1 California | 1924-1990 | 130919 | 572661 | 15.6 | 1970-1991 | 141316 | 310811 | 141.9 | 1924-1991 | 200901 | 609979 | 6.0 |
| 2 Peru | 1978-1993 | 2068449 | 3470422 | 43.4 | 1960-1993 | 4486294 | 12277022 | 21.6 | 1958-1993 | 5299183 | 12286264 | 142.0 |
| 3 Chile | 1978-1993 | 1528795 | 2709926 | 15.5 | 1962-1993 | 571572 | 1350626 | 4.2 | 1966-1993 | 1540109 | 3708071 | 59.3 |
| 4 Spain-Portugal | 1927-1988 | 161752 | 241000 | 5.7 | 1968-1988 | 30988 | 66700 | 3.1 | 1937-1989 | 331839 | 368893 | 6.1 |
| 5 Morocco | 1950-1991 | 169858 | 338100 | 3.9 | 1965-1991 | 3552 | 19124 | 1.1 | 1950-1991 | 192885 | 362023 | 3.1 |
| 6 Senegal | 1974-1991 | 101008 | 194693 | 5.9 | — | — | — | — | 1964-1991 | 77234 | 194693 | 5.9 |
| 7 Côte-d'Ivoire - Ghana | 1966-1993 | 74809 | 172977 | 3.2 | 1966-1993 | 52007 | 92988 | 1.7 | 1966-1993 | 7188405 | 270570 | 5.0 |
| 8 Namibia | 1963-1992 | 371720 | 1400100 | 4.0 | 1963-1990 | 161996 | 376000 | 1.1 | 1966-1992 | 507663 | 1561300 | 17.3 |
| 9 South-Africa | 1960-1991 | 113916 | 410200 | 2.9 | 1969-1992 | 234752 | 596000 | 0.2 | 1950-1992 | 274312 | 623200 | 3.5 |
| 10 Venezuela | 1957-1989 | 38032 | 80079 | 4.7 | — | — | — | — | 1957-1989 | 38032 | 80079 | 4.7 |
| 11 India | 1956-1989 | 190523 | 274772 | 2.3 | 1963-1989 | 35529 | 79655 | 3.3 | 1948-1988 | 249382 | 448206 | 6.4 |

Table. 2: Fish catch productivity indices of eleven upwelling ecosystems.



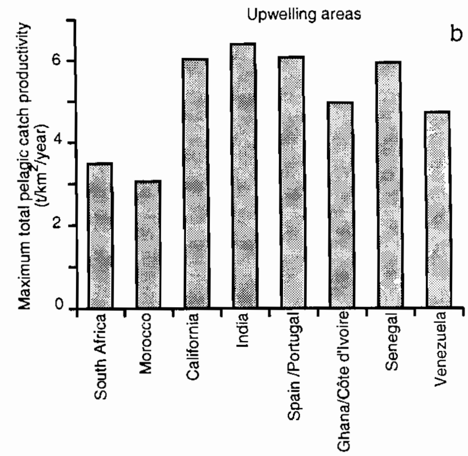




Fig. 2: a) Maximum total pelagic catch productivity per unit of surface (t/km$^2$) for the studied upwelling areas; b) the same as Fig. 2a, but without the Chilean and Peruvian values.

are not necessarily among the most productive. Other environmental variables than surface area undoubtedly play a role in the intrinsic production of upwelling ecosystems.

# 2. How many environmental factors?

Environmental parameters cause fish population fluctuations mainly through their role in the recruitment process (Parrish and MacCall, 1978; Bakun and Parrish, 1982; Cury and Roy, 1989; Lluch-Belda *et al.*, 1989; Cushing, 1990; Cushing, 1995). Five environmental parameters were selected for the analysis: coastal upwelling index (CUI in $m^3/s/m$) using standard assumptions[1], turbulence index ($V^3$ in $m^3/s^3$), sea surface temperature (SST in °C) and continental shelf length or surface (CSl in km and CSs in $km^2$). The turbulence index was calculated by averaging all the cubed wind measurements. The COADS data (Comprehensive Ocean Atmosphere Data Set) collected by merchant ships of opportunity all around the world oceans were used (Roy and Mendelssohn, this vol.). As they are obtained in a similar fashion in all areas, they are strictly comparable and they also provide a data base which is compatible in time with the fishery data. Mean environmental values were calculated for the different upwelling areas (Table 3). Upwelling index varies from 0.36 $m^3/s/m$ for Spain-Portugal to 1.28 $m^3/s/m$ for Namibia. Three areas exhibit strong upwelling indices: Namibia, Peru and Côte-d'Ivoire-Ghana. Turbulence index varies from $10^3$ $m^3/s^3$ for Côte-d'Ivoire-Ghana to 723 $m^3/s^3$ for South Africa. A high

1 *$CUI = rCdV^2 / 2\Omega \sin \phi$ with $V^2$ wind component perpendicular to coast , r air density (0.0012 $g.cm^3$), $\Omega$ angular velocity of earth rotation, $\phi$ latitude, Cd roughness coefficient at interface air/sea.*

| | Upwellings areas | Geographic characteristics: Latitude | Longitude | Continental shelf surface ($km^2$) | Continental shelf length (km) | Environmental parameters (mean from 1946 to 1990): Upw. index ($m^3/s/m$) | Turbulence ($m^3/s^3$) | Sea surface temperature (°C) |
|---|---|---|---|---|---|---|---|---|
| 1 | California | 22°-38°N | — | 101167 | 1778 | 0,54 | 654 | 15,6 |
| 2 | Peru | 5°-18°N | — | 86523 | 1444 | 1,20 | 225 | 19,1 |
| 3 | Chile | 18°N-43°S | — | 62516 | 2778 | 0,93 | 346 | 16,5 |
| 4 | Spain and Portugal | 2°-44°N | 5°-9° | 59864 | 1667 | 0,36 | 628 | 16,3 |
| 5 | Morocco | 21°-36°N | 2°-0° | 118539 | 1667 | 0,66 | 306 | 19,6 |
| 6 | Senegal | 12°-16°N | — | 32887 | 445 | 0,59 | 150 | 23,7 |
| 7 | Côte-d'Ivoire - Ghana | 2°-8°N | 0°-8° | 54647 | 667 | 1,04 | 103 | 27,1 |
| 8 | Namibia | 16°-28°S | — | 90508 | 1334 | 1,28 | 517 | 16,8 |
| 9 | South-Africa | 28°-36°S | — | 178315 | 1778 | 0,65 | 723 | 16,9 |
| 10 | Venezuela | 8°-11°N | 62°-65.5° | 17000 | 389 | — | 332 | 27,1 |
| 11 | India | 8°-15°N | — | 70135 | 778 | 0,40 | 240 | 28.1 |

Table 3: Environmental characteristics of the eleven upwelling areas compared in this study.

upwelling intensity is classically associated with a high turbulence intensity (in Namibia and Chile), but sometimes, it corresponds to a moderate turbulence index (in Peru and Côte d'Ivoire-Ghana). In the same way, moderate upwelling indices may be associated with strong turbulence indices (in California, Spain-Portugal, South-Africa). The mean sea surface temperature ranges between 15.6°C for California and 28.1°C for India.

The relationship between fish catch productivity and environmental factors is explored using non-parametric regressive 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 are a priori unknown. The non-linearity of the relationships as well as the multiplicity of factors can be considered. The ACE (Alternating Conditional Expectation) and the GAIM (Generalized Additive Interactive Modeling) 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,..., p and for n observations, j = 1,...,n, is given by :

$$Y(j) = \Sigma b_i X_i(j) + e(j) \qquad \text{e(j) are independent}$$

The response variable Y and the predictor variables X1.....Xp in the nonparametric model are replaced by functions $T_1(Y)$ and $T_2(X_1)....T_{p-1}(X_p)$ :

$$S(Y(j)) = \Sigma b_i T_i(X_i(j)) + w(j)$$

S(Y) and $T_i(X)$ are unknown and estimated by minimizing: $E((T_1(Y) - \Sigma T_{i+1}(X_i))^2) / var(T_1(Y))$

Several approaches exist to estimate the last equation. ACE includes the $b_i$ in the function $T_i()$, while GAIM estimates the $b_i$'s 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 as they have their own smoothers and convergence criterion (See Cury *et al.*, 1995 for a detailed application).

A regressive analysis is done using the fish catch productivity index as the response variable and five environmental parameters as predictor variables. The transformation shape is found by plotting the transformed values of a variable versus the original values. Results using the ACE algorithm are presented.

## 2.1. Maximum total pelagic catch productivity as a response variable

The relationships between fish catch productivity index and every environmental variable are first explored. Optimal transformations (T1,T2) for the multiple regression were calculated using maximum total pelagic catch productivity index as the response variable and the upwelling index, the turbulence index, sea surface temperature and/or continental shelf surface as the predictor.

T1 (maximum total pelagic catch productivity) = T2 (CUI) $R^2$ : 0.34 (1)

T1 (maximum total pelagic catch productivity) = T2 (V3) $R^2$ : 0.11 (2)

T1 (maximum total pelagic catch productivity) = T2 (SST) $R^2$ : 0.49 (3)

T1 (maximum total pelagic catch productivity) = T2 (CSs) $R^2$ : 0.93 (4)

The transformations for the maximum total pelagic catch productivity are positive and linear in models (1) and (2) (Fig. 3a and 3b) and are close to a log transformation in models (3) and (4) (fig. 3c and 3d). On the whole, the upwelling transformation is linear and positive (fig. 3a). The turbulence is transformed to a nearly dome shaped curve. It first increases to a value around 200 $m^3/s^3$ then decreases strongly (Fig. 3b). The transformation for the sea surface temperature decreases strongly and linearly (Fig. 3c). The estimated transformation of continental shelf surface is close to logarithmic in form, with a breaking point around 100 000 $km^2$ (Fig. 3d). The $R^2$ value for model (4) is very high; however when the response variable is forced to be linear, its value decreases to 0.17.

Multivariate analyses are realized by considering several environmental variables simultaneously in the model. Results which combine three environmental predictors are presented on figures 4 and 5.

Optimal transformations (T1, T2, T3, T4) for multiple regression were calculated using first maximum total pelagic catch productivity index as the response variable and turbulence, sea surface temperature and upwelling index as predictors in model (5) (Fig. 4) or the upwelling index, the turbulence and the continental shelf surface as the predictors in model (6) (Fig. 5). Thus, we have

T1(maximum total pelagic catch productivity) = T2 (V3) + T3 (SST) + T4 (CUI) $R^2$ : 0.59 (5)
T1(maximum total pelagic catch productivity) = T2 (CUI) + T3 (V3) + T4 (CSs) $R^2$ : 0.44 (6)

The response variable transformation is forced to be linear (Fig. 4a). Both transformations of turbulence and of sea surface temperature are linear and negative (Fig. 4b and 4c). On the whole, the upwelling transformation is linear and positive, particularly above a value around 0.7 $m^3/s/m$ (Fig.4d).

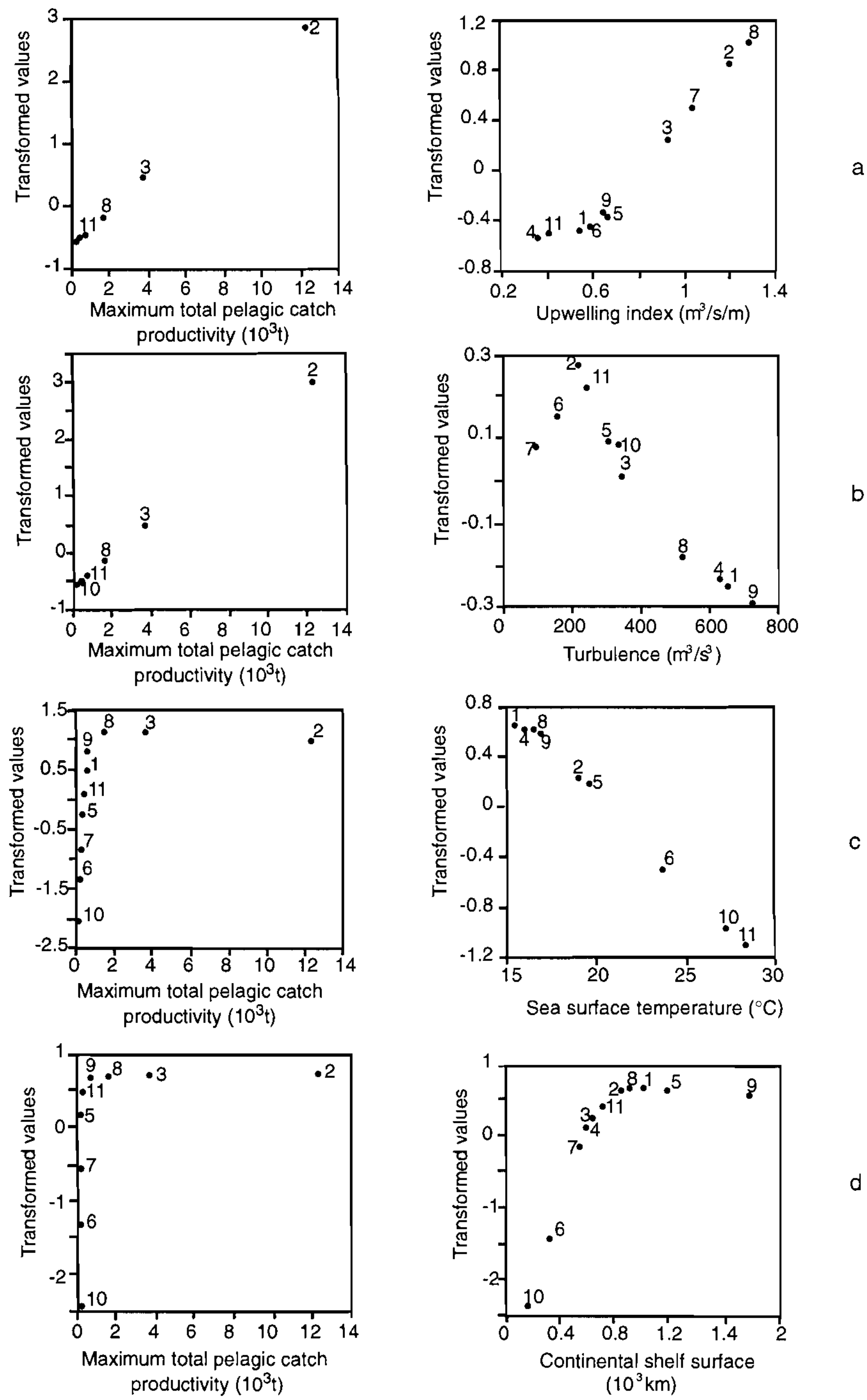



Fig. 3: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence, sea surface temperature and continental shelf surface as the predictor variables. $R^2$ values are for figure a: 0.34; b: 0.11; c: 0.49; and d: 0.93. Numbers identify ecosystems (see Tab. 2 and 3).

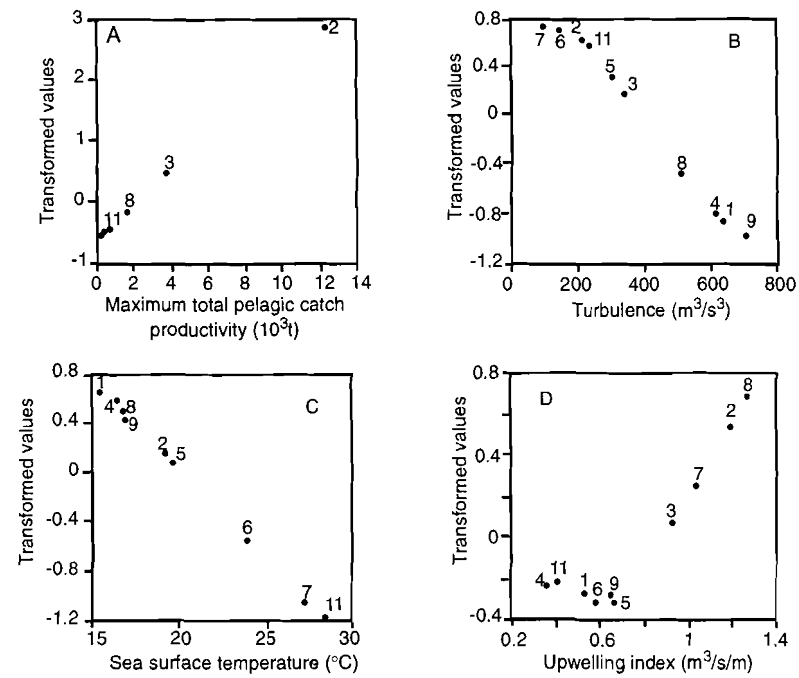



Fig. 4: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and turbulence, upwelling index and sea surface temperature as predictor variables. The transformation of the response variable is forced to be linear. $R^2$= 0.59. Numbers identify ecosystems (see Tab. 2 and 3).

The productivity index transformation can be forced to be linear (Fig. 5a). Generally, a linear and positive relationship appears between upwelling intensity index and the productivity index (Fig. 5b), particulary above a value around 0.7 $m^3/s/m$. The transformation of the turbulence is dome-shaped with a breaking point around 250 $m^3/s^3$ (Fig. 5c). The transformation of the continental shelf surface is close to a log transformation Fig. 5d). It first increases, then stabilizes beyond a value around 100 000 $km^2$.

The transformed value scale gives indication of the relative contributions of the environmental variables to the variance. It indicates a higher contribution either of turbulence and sea surface temperature for model (5) or of upwelling intensity for model (6). The percentage of the observed variance in the total pelagic catch productivity ($R^2$) are: 59% and 44% for models (5) and (6), respectively.

## 2.2. Maximum sardine catch productivity as response variable

Optimal transformations (T1, T2, T3, T4) for multiple regression were calculated using the maximum sardine catch productivity versus upwelling index, turbulence index and sea surface temperature, i.e.,

$$\text{T1 (maximum sardine catch productivity)} = \text{T2 (CUI)} + \text{T3 (V3)} + \text{T4 (SST)} \quad R^2: 0.74 \qquad (7)$$

The estimated transformation of maximum sardine catch productivity as well as the transformation of the upwelling index are linear and positive (Figs. 6a and 6b). The turbulence transformation has a flat top then decreases linearly beyond 200 $m^3/s^3$ (Fig. 6c). The sea surface temperature transformation is strongly negative and linear (Fig. 6d). The resulting model explains 74% of the observed variance of maximum sardine catch productivity.

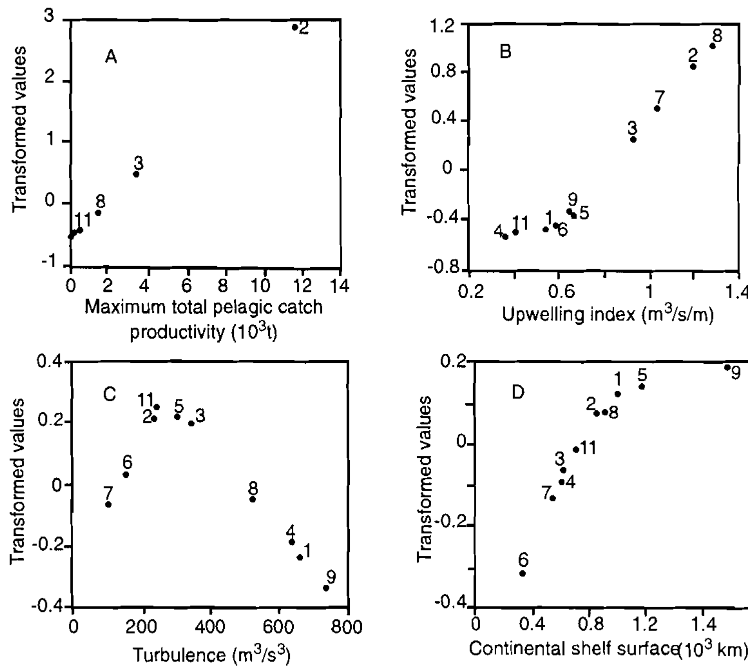



Fig. 5: Optimal empirical transformations from the ACE algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence and continental shelf surface as predictor variables. The transformation of the response variable is forced to be linear. $R^2 = 0.44$. Numbers identify ecosystems (see Tab. 2 and 3).

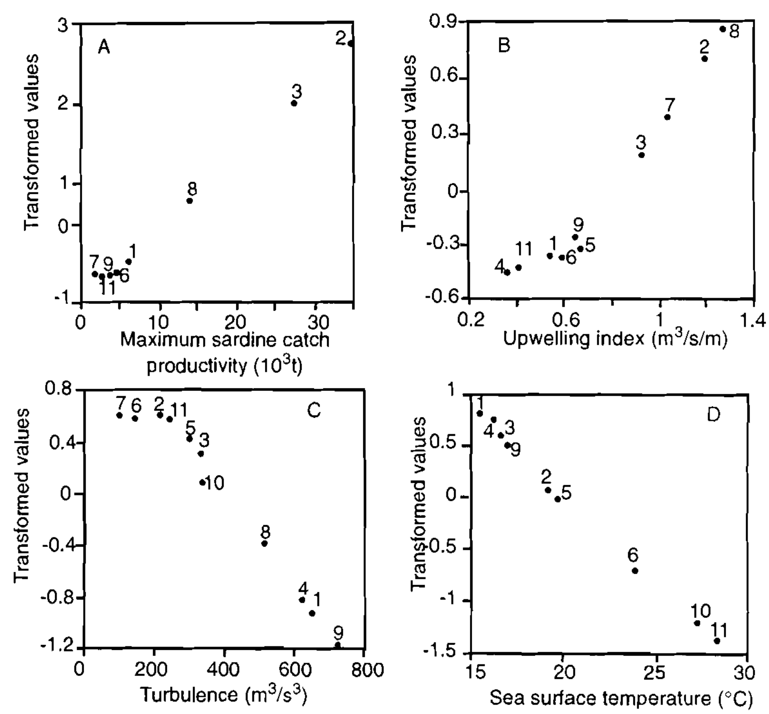



Fig. 6: Optimal empirical transformations from the ACE algorithm using maximum sardine catch productivity as dependent variable and upwelling index, turbulence and sea surface temperature as predictor variables. $R^2 = 0.74$. Numbers identify ecosystems (see Tab. 2 and 3).

## 2.3. Maximum anchovy catch productivity as response variable

Optimal transformations (T1, T2, T3, T4) for the multiple regressive model (8) were calculated using the maximum anchovy catch productivity index versus upwelling index, continental shelf surface and turbulence index, i.e.,

$$\text{T1 (maximum anchovy catch productivity)} = \text{T2 (CUI)} + \text{T3 (CSs)} + \text{T4 (V3)} \quad R^2 : 0.40 \qquad (8)$$

The transformation of maximum anchovy catch productivity is forced to be linear (Fig. 7a). The upwelling index transformation is on the whole linear and positive, particularily beyond a value around 0.7 $m^3/s/m$ (Fig. 7b). Continental shelf surface is transformed to a nearly log shaped curve with a breaking point around 100 000 $km^2$ (Fig. 7c). Turbulence is transformed to a linear and negative transformation (Fig. 7d). The model explains 40% of the observed variance of maximum anchovy catch productivity.

Similar results are found when using continental shelf length instead of its surface. Also, using mean fish catch productivity instead of maximum fish catch productivity indices provide similar results (not shown). Results using the GAIM algorithm instead of the ACE algorithm are similar as well (Fig. 8).

Both monovariate and multivariate analyses suggest similar patterns for the relations among fish catch productivity and environmental variables :
-the transformation of the upwelling index is mostly linear and positive;
-the transformation of the turbulence index is close to be linear and negative particulary after a value around 200-250 $m^3/s^3$;

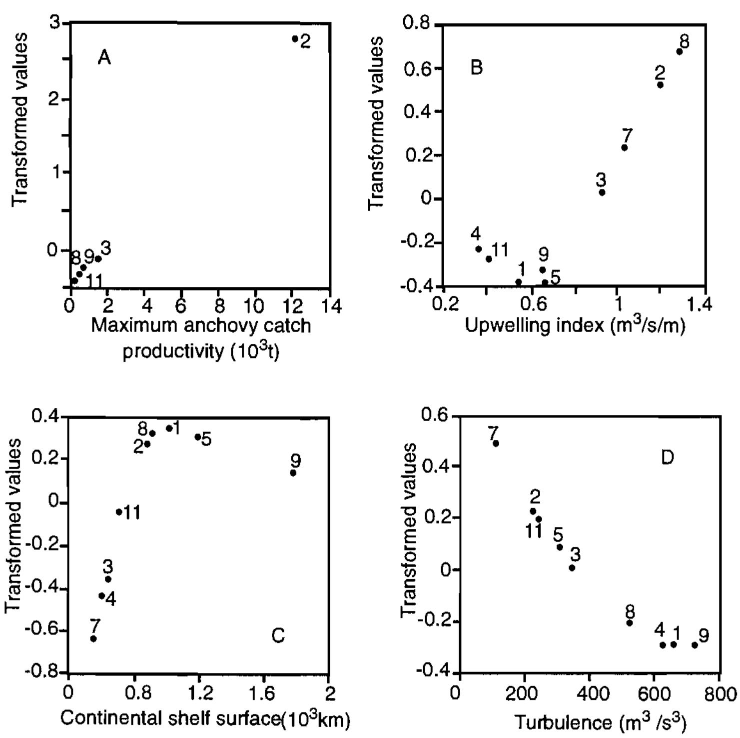



Fig. 7: Optimal empirical transformations from the ACE algorithm using maximum anchovy catch productivity as dependent variable and upwelling index, continental shelf surface and turbulence as predictor variables. The transformation of the response variable is forced to be linear. $R^2$ value is 0.4. Numbers identify ecosystems (see Tab. 2 and 3).

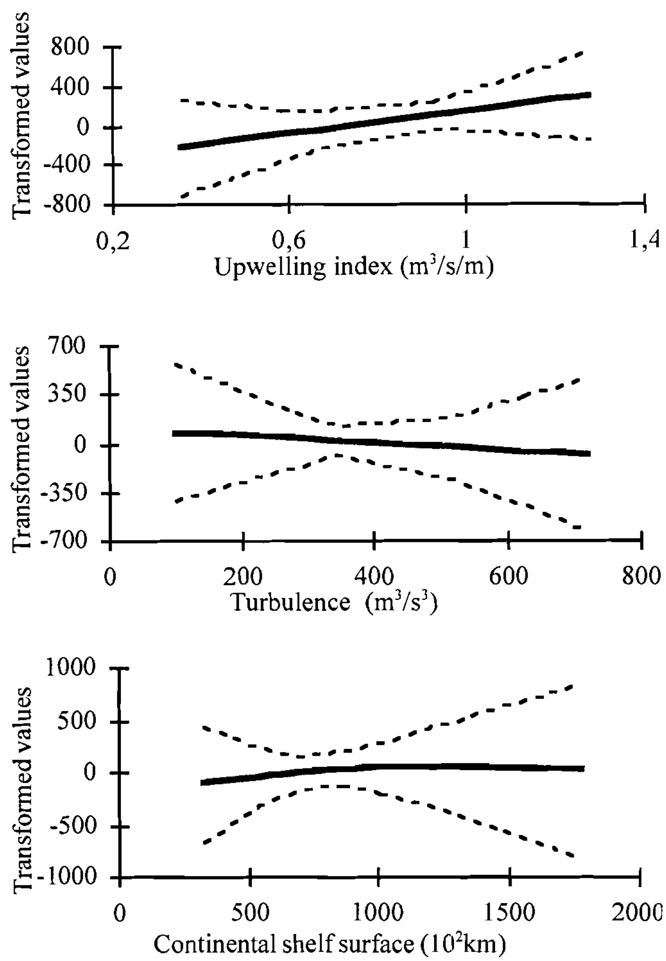



Fig. 8: Optimal empirical transformations from the GAIM algorithm using maximum total pelagic catch productivity as the dependent variable and upwelling index, turbulence and continental shelf surface as the predictor variables. The dashed lines indicates the lower and the upper standard error curves. R2= 0.36.

- the transformation of sea surface temperature is linear and negative; and
- the transformation of continental shelf surface is close to a log transformation with a breaking point around 100 000 km$^2$.

The comparative and exploratory analysis of the relationship among estimates of fish productivity and environmental features of upwelling systems reveals that a combination of several factors is necessary for high productivity:
- a high upwelling intensity (near to 1.28 m$^3$/s/m);
- a moderate turbulence (around 200-250 m$^3$/s$^3$);
- a medium sea surface temperature (15-16°C);
- a relatively large continental shelf (approximately 100 000 km$^2$).

The results of our statistical analysis must be considered with caution, however, as important limitations do exist:
- the comparisons are based on only eleven data points, and consequently, the statistical validity of the results is questionable due to the low number of degrees of freedom;
- one system with extreme values (Peru) plays an important role in all analyses.

This represents important limitation in our comparative analysis. However, it is also true that:

- the number of ecosystems with a documented pelagic fisheries and for which environmental data exist are limited; and
- the number of environmental factors which have been hypothesized impact on productivity is large compared to the number of ecosystems that can be compared.

Nevertheless, the present analysis gives some valuable information and cues. First, it appears that the size of the ecosystem is not the only parameter that influences its fish catches. Upwelling strength, turbulence, and sea surface temperature also play an important role. Only a combination of several environmental factors ensure a high fish productivity. The relationships between fish catch productivity and environmental variables appears to be in agreement with independent ecological knowledge on ecosystem functioning. High upwelling intensities as source of food availability (Wroblewski and Richman, 1987; Cushing, 1990) and small-scale turbulences that increase 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 upwelling intensity and fish catch productivity could be related to these combined effects. In contrast, intense wind-driven turbulent mixing that mixes up patches of larval food appears to be detrimental (Lasker, 1975; Peterman and Bradford, 1987; Cury and Roy, 1989). Bakun (this vol.) identified a 'fundamental triad' of three major processes that combine to yield favorable environmental conditions for fishes: an enrichment process (upwelling, mixing...), a concentration process (water column stability, convergence...) and processes favoring retention within appropriate habitat. In some degree, the environmental parameters we selected may be considered as proxy variables that account for some of the processes involved in such triad. For example, the size of the ecosystem combined with upwelling intensity determines global enrichment of the ecosystem while turbulence is involved in processes that concentrate and retain food and larvae.

A comparison of the environmental values of the upwelling areas with the 'optimal environmental values' is presented on Figure 9 and the limiting factor(s) to productivity are identified (Table 4).

First, it is apparent that the Peruvian ecosystem is the only one which combines all the optimal environmental conditions (Fig. 9). In Chile and Namibia, the upwelling index is favorable; however, it is associated with an excessively high turbulence index. The same high upwelling index is found off Côte d'Ivoire-Ghana, but is associated with low turbulence. In South Africa, Spain and California, the turbulence index is high and associated with a low upwelling intensity, therefore limiting productivity.

In every upwelling areas, except Peru, at least one environmental condition differs from the 'optimal conditions' and consequently tends to limit productivity. But what will happen under changes of one or several environmental factors?

The effect of a gradual or a rapid climatic change on living marine resources is a challenge as numerous parameters are involved. There is no reliable computer-generated climate impact scenario about the next several decade, but generalizations derived from case-to-case assessments of past and present experiences can be used (Glantz, 1992). Such assessments can indeed provide first approximations on how fisheries might respond to environmental changes. Comparative analysis constitutes a good base of information to begin such assessment of possible impacts of environmental changes on fish productivity. Some scenarios for fish productivity under climatic changes derived from previous studies (Fig. 9) can thus be considered for forecast by analogy (Glantz, 1992). How and how much will productivity evolve if one or several environmental parameters change? Let's assume for example two simple scenarios. First, a drastic increase of upwelling intensity that provides more nutrients would probably improve the fish productivity in major ecosystems. The consequences may be stronger in areas where low upwelling intensity is the main limiting factor: Morocco, Senegal and Venezuela (Table 4). Secondly, under a decrease of the intensity of turbulence, a higher fish productivity may be expected in areas where high turbulence is limiting factor: California, Chile, Spain-Portugal, Morocco, Namibia, South-Africa and Venezuela (Table 4).

The reality is obviously more complex as environmental factors change simultaneously. A scenario involving one environmental parameter is thus only a very simplified view of what might occur under climatic changes. However, a qualitative approach allows to predict the increase or the decrease of the fish productivity and can give some preliminary answers.

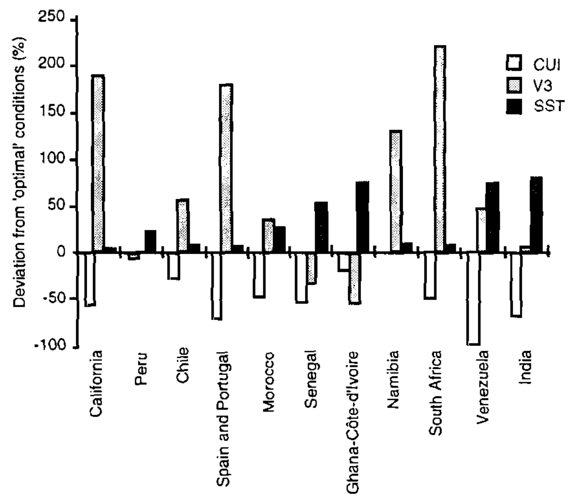



Fig. 9: Relative deviation of the environmental values (%) from the 'optimal environmental values' as defined in the comparative analysis.

Tab. 4: The limiting factor(s) to productivity in upwelling areas. The signs (+ and -) indicate negative or positive deviation from the 'optimal environmental values'. The limiting factors are noted in decreasing order of deviation.

| | Upwelling areas | Limiting factors | | |
|---|---|---|---|---|
| 1 | California | V3 + | CUI - | SST - |
| 2 | Peru | SST + | - | - |
| 3 | Chile | V3 + | CUI - | - |
| 4 | Spain-Portugal | V3 + | CUI - | |
| 5 | Morocco | CUI - | V3 + | SST + |
| 6 | Senegal | CUI - | SST + | V3 - |
| 7 | Côte d'Ivoire - Ghana | SST + | V3 - | CUI - |
| 8 | Namibia | V3 + | CUI + | - |
| 9 | South Africa | V3 + | CUI - | SST + |
| 10 | Venezuela | CUI - | SST + | V3 + |
| 11 | India | SST + | CUI - | V3 + |

# 3. Optimal environmental conditions in the Peruvian ecosystem: reality or tautology?

It is possible to compare environmental variables in a given upwelling area to what appears to be the optimal environmental conditions. These, however, were largely derived from the Peruvian ecosystem's values. Peters (1991) defines a tautology as "purely logical constructs that describe the implication of given premises and never reveal more than those premises contain". As Peru is known to be the most productive upwelling area, it is clear that using our approach it will define the optimal environmental combination of factors. Thus, our results may be regarded as a tautology of poor scientific value. However, our comparative analysis did provide a framework for considering the relative impact of several environmental factors on fish productivity. It emphasized the importance of limiting factors such as turbulence, upwelling intensity or size of the ecosystem. This should promote new insights of how to relate environmental variables to fish productivity in a multivariate context. Paleoecological studies reveal that pelagic fish populations experienced large natural fluctuations which were clearly unrelated to fishing pressure and that past abundances in California or in Peru were sometimes much higher than during the last century (Soutar and Isaacs, 1974; De Vries and Pearcy, 1982; Baumgartner *et al.*, 1992). For California, we identified factors that limit fish productivity but whithout any reference point; this was not possible for Peru. This stresses the limit of our approach as it may be that the Peruvian ecosystem is able to produce even more under other, but still undefined, environmental conditions.

## ACKNOWLEDGMENTS

This work was financed by the Programme National du Déterminisme de Recrutement (PNDR). We thank Claude Roy for providing the environmental data used here.

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