National Research Council Canada
Conseil national de recherches Canada

NRC·CNRC

Reprinted from
Canadian Special Publication of Fisheries and Aquatic Sciences 121

Climate Change and Northern Fish Populations

Edited by Richard J. Beamish

Moderate is better: exploring nonlinear climatic effects on the California northern anchovy (*Engraulis mordax*)

By P. Cury, C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby, and R.H. Parrish
Pages 417-424

Canada

Moderate is better: exploring nonlinear climatic effects on the Californian northern anchovy (*Engraulis mordax*)

Philippe Cury, Claude Roy, Roy Mendelssohn, Andrew Bakun, David M. Husby, and Richard H. Parrish

Cury, P., C. Roy, R. Mendelssohn, A. Bakun, D.M. Husby, and R.H. Parrish 1995. Moderate is better: exploring nonlinear climatic effects on the Californian northern anchovy (*Engraulis mordax*), p. 417–424. *In* R.J. Beamish [ed.] Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121.

Abstract: The effect of environmental variability on marine population dynamics remains a challenging problem for fisheries science. The impact of four decades of environmental change on larval abundance of the northern anchovy (*Engraulis mordax*) off California is analyzed using recently developed nonlinear statistical techniques that extend linear multiple regression analysis. The three techniques used are: alternating conditional expectation, additivity and variance stabilization, and generalized additive interactive modelling. The dependencies of larval abundance on upwelling intensity and total anchovy biomass are nonlinear and account for 84% of the interannual variability; a linear regression analysis explained 37% of the variance. The higher larval abundances are produced with medium to large adult biomasses coupled with moderate upwelling intensity. These empirical results suggest that marine populations will respond to climatic trends, but will do so in a nonlinear manner. These nonlinear satistical algorithms, which are not yet widely used in ecology, provide a promising method for exploring the form of the relationships between environmental changes and populations responses.

Résumé : L'effet de la variabilité environnementale sur la dynamique des populations marines demeure un problème non résolu pour la science des pêches. Les conséquences de quatre décennies de changements environnementaux sur l'abondance des larves de l'anchois du Pacifique (*Engraulis mordax*) au large de la Californie sont analysées au moyen de méthodes statistiques non linéaires récemment mises au point qui complètent l'analyse de régression multiple linéaire. Les trois techniques utilisées sont : alternance des espérances mathématiques conditionnelles, additivité et stabilisation de la variance, et modélisation additive interactive généralisée. La dépendance de l'abondance des larves à l'égard de l'intensité des remontées d'eau et de la biomasse totale d'anchois est non linéaire et représente 84 % de la variabilité interannuelle. Une analyse de régression linéaire explique 37 % de la variance. Les abondances plus élevées de larves sont produites par des biomasses adultes moyennes à grandes jumelées à une intensité modérée des remontées d'eau. Les résultats empiriques portent à croire que les populations marines réagissent aux tendances climatiques mais de façon non linéaire. Ces algorithmes statistiques non linéaires, qui ne sont pas encore largement utilisés en écologie, représentent une méthode prometteuse d'analyse des formes de relations entre les changements environnementaux et les réactions des populations animales.

P. Cury and **C. Roy**. ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération), Département Terre–Océan–Atmosphère, 213 Rue La Fayette 75480 Paris Cedex 10, France.

R. Mendelssohn, A. Bakun, D.M. Husby, and **R.H. Parrish**. Pacific Fisheries Environmental Group, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942, USA.

Introduction

Precipitous declines or sudden recoveries have been observed in the world's largest fisheries of clupeoids. These boom and bust phenomena are found in the sardine and anchovy fisheries of the Benguela, the California, the Canary, and the Peru Current ecosystems (Sharp and Csirke 1983; Pauly and Tsukayama 1987). This instability appears to be due to changes in recruitment success (i.e., the addition of young fishes to the fishable population). Significant variations in recruitment are likely to arise both from excessive biomass depletion due to intensive fishing pressure and from alteration in the mortality rates of the embryonic and larval stages due to particular sensitivity to environmental change (Lasker 1981, 1985; Smith 1985; Beverton 1990). However, recent studies suggest that the final recruitment success is not necessarily linked to early larval abundance (Peterman et al. 1988) and that predation plays a major role in prerecruit mortality (Sissenwine 1984).

Environmental and ecological time series are now available for several decades. If some strong relationships do exist between environmental fluctuations and fish population dynamics, ecologists are now in a good position to identify emergent patterns. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) data represent one of the most impressive marine data sets available, covering a multidecadal time period for the entire southern California ecosystem (Smith and Moser 1988). Since 1951, larvae from the central population of the northern anchovy (*Engraulis mordax*) have been sampled over the entire range of its distribution. Environmental data have been collected independently and during the sampling cruises.

Analysis of the relationships between two or more fundamental variables have most commonly employed linear statistical methods (Tyler 1992) or used an a priori transformation, such as a logarithmic transformation (Parrish and MacCall 1978; Crecco et al. 1986). However, a scattergram that reveals no linear relationship does not necessarily mean the absence of a tight link (Kareiva 1990; R. Mendelssohn, unpublished data). While nonlinearities are not new to ecologists, rigourous statistical methods to deal with them are. Recently developed nonlinear statistical methods provide useful tools to explore the relationship between different sets of variables (Breiman and Friedman 1985; Buja et al. 1989; Hastie and Tibshirani 1990; Gifi 1990). In this paper, we apply these nonlinear statistical techniques to the California Current anchovy and attempt to reconcile the empirical results to previous theoretical and field studies.

Data

Annual mean abundance of northern anchovy larvae in the principal reproductive area (32–34°N, 117.5–119°W) was calculated by averaging all sampled stations. From 1951 to 1990, 32 years were intensively sampled; a total of 3257 stations are represented. Mean annual larval number per square metre for the period 1951–75 are from Smith and Eppley (1982). P.E. Smith (Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, CA 92038) provided us with the data from 1975 to 1990. Larvae are mostly found during the first two quarters; however, for certain years larvae were abundant during the third or fourth quarter (1954, 1955, 1956, 1966, 1967, 1972, 1989). Moreover, in some years, larvae were more abundant during the third and fourth quarters (1952, 1953). This led us to use annual mean abundance of northern anchovy larvae. No data were collected in 1970, 1971, 1973, and 1976. Poor data are available during 1974, 1977, 1982, and 1983 where only one quarter among four was sampled. For these reasons those 8 years were excluded from the analysis.

Anchovy biomass during this period was variable. By combining available fisheries data, sonar surveys, and egg production information, MacCall and Methot (1983), Methot (1989), and Jacobson and Lo (1991) have produced estimates of total anchovy biomass. We use these estimates in our analysis.

Because of our lack of understanding of the casual mechanisms that may be responsible for the observed variations in larval number, several environmental time series were selected for our analysis. Temperature has a strong effect on larval growth and consequently on larval stage duration (Blaxter and Hunter 1982; Houde 1989). To test for the relevance of low-frequency temperature variability, the temperature collected at each sampling station at 10 m depth was averaged over the year. The consistent presence of massive populations of small pelagic clupeoid fishes in coastal upwelling regions around the world suggests a strong link of the population dynamics of these fishes to the upwelling process. Coastal upwelling is a dominant oceanographic process off the California coast (Reid et al. 1958). Northerly winds cause coastal water to move offshore, and the deficit at the coast is compensated for by an upward flow of cold and nutrient-rich subsurface water. An estimate of the upwelling intensity is given by the offshore component of the Ekman transport (Bakun 1973), which is the wind-driven flow integrated over the ocean layer affected by the wind. The relative constancy in direction of the wind blowing along the California coast leads to a tight relationship between indices of upwelling and those of wind mixing that is roughly proportional to the cube of the wind speed (Elsberry and Garwood 1978). The upwelling index tracks variability in the main features of the upwelling process: the offshore flow of coastal water, the coastal enrichment by the upward nutrient input, and the mixing of the surface layers by the wind.

Variations in the upwelling process in the northern anchovy reproductive area from 1951 to 1990 are represented by an annual upwelling index derived from monthly values at 33°N, 119°W. This index is calculated using geostrophic winds derived from atmospheric pressure fields by the U.S. Navy Fleet Numerical Oceanography Center. Bakun (1973) details the procedure used to derive geostrophic winds from atmospheric pressure analyses and to estimate upwelling indices. As mentioned in Bakun (1973) these indices should be used with caution when considering long-term variability in this region. During the 1950s and 1960s the origin of the pressure fields charts changed (Bakun 1973). The procedure used to produce the pressure fields has also evolved from hand analysis to computer analysis. The bias introduced by these changes remains unknown. Discrepancies between the calculated and measured winds at the latitude of the Southern California Bight have also been noted (Bakun 1973, 1975; Halliwell and Allen 1987) and mean annual deviations range between 0 and 26%.

Methods

Present knowledge of the relationships between the anchovy larval number and relevant population and environmental variables is not sufficient to know a priori their correct form. Therefore, it is desirable to have methods that use the data (i.e., nonparametric) to estimate the appropriate functional form. Iterative algorithms have recently been developed that extend linear multiple regression analysis to generalized additive models (Hastie and Tibshirani 1990). These models are additive in empirically estimated transformations of the data. These procedures, which are not yet widely used in ecology, provide a method for exploring the form of the relationships between the response and the predictor variables when the forms of these relationships are unknown. Empirical, objective identification of possible nonlinear relationships are also made possible.

The usual linear mutiple regression model for predicting a response (or dependent) variable Y from p predictor variables X_i, where $i = 1, ..., p$, and for n observations, where $j = 1, ..., n$, is given by

$$Y(j) = \sum_{i=1}^{p} b_i X_i(j) + e(j)$$

where the $e(j)$ are independent, identically distributed, zero mean random variables, and a mean term is implicitly defined by putting X_p, for example, equal to one. The nonlinear multiple regression model (or generalized additive model is given by

$$S(Y(j)) = \sum_{i=1}^{p} b_i T_i(X_i(j)) + w(j)$$

where the functions $S(Y)$ and $T_i(X)$ are unknown and must be nonparametrically estimated from the data. The $w(j)$ are independent, identically distributed, zero mean random variables, usually assumed to be gaussian but not restricted to that assumption.

There are several approaches to estimating the latter equation under differing assumptions about the optimization criteron and about the transformations, including alternating conditional expectations (ACE) (Breiman and Friedman 1985), additivity and variance stabilization (AVAS) (Tibshirani 1988), and generalized additive interactive modelling (GAIM) (Hastie and Tibshirani 1990). The basic approach of each algorithm is iterative, where at each iteration, given the present estimates of $S()$ and $T_i()$, $i \neq k$ (where $i, k = 1,1 - p$), the partial residual:

$$S(Y(j)) - \sum_{j \neq k}^{p} b_i T_i(X_i(j))$$

is calculated, and the transformation $T_k()$ is calculated as the conditional expectation of the partial residual given X_k. This conditional expectation is estimated from the data using some form of scatterplot smoother. As the b_i are simply scaling factors, ACE and AVAS include the b_i in the function $T_i()$, while GAIM estimates the b_i's to perform analysis of deviance tests on the parameters, similar to the more usual analysis of variance tests in linear regression analysis.

The algorithms converge to optimal solutions for a given criterion (such as the maximum correlation between the transformed dependent variable and the transformed predictor variables in the ACE algorithm). Each algorithm has its own smoother and convergence criterion. There is a fundamental trade-off between bias and variance governed by the smoothing parameter. A very small value of the smoothing parameter produces a nearly exact fit but with high bias. A high value of the smoothing parameter will give a very smooth fit that is unbiased but with a high variance.

There are a number of properties of the ACE procedure that can lead to some anomalies (Breiman and Firedman 1985; Hastie and Tibshirani 1990). For a single predictor, ACE is symmetric in X and Y, whereas one expects a regression procedure to treat Y differently from X. ACE is not equivariant under monotone transformations of the predictors, exhibits strange behaviour in low-correlations settings, and does not reproduce model transformations. Moreover, disjoint clusters are collapsed by ACE, and the crossing of eigenvalues can cause discontinous behaviour.

AVAS is a modification of ACE designed for regression problems and uses an asymptotic variance-stabilizing transformation (the $S(Y(j))$ is assumed to be strictly monotone). While AVAS does not share many of ACE's anomalies, there is much less theoretical support for the technique than there is for ACE. In particular, global convergence of AVAS has not been established. Both algorithms use locally weighted nonlinear smoothers. GAIM uses cubic smoothing splines (which are linear smoothers) in the implementation that is available. GAIM also produces pointwise error bands that give better confidence in the observed nonlinearities that are found, but is restricted to transformations of the X variables only.

Thus, results from any one of these algorithms must be considered with caution. As in using any statistical method, interpretation of the results must consider potential biases due to the assumptions underlying the techniques. One way to deal with the problem is to examine results using the three different techniques for the same data set. When each of the algorithms produces similar results there is more confidence in the findings. Consistency of the results with present ecological knowledge also reinforces confidence in their correctness.

Results

The relationships between larval number and temperature, the upwelling index, and total anchovy biomass were initially explored by plotting the raw data (Fig. 1). No significant linear relationship was found between anchovy larval numbers and the temperature index as the data appear to be randomly scattered (Fig. 1A). When larval numbers are plotted versus the upwelling index (Fig. 1B), low larval numbers are observed for both weak and strong upwelling intensities. High larval numbers are to be found for moderate upwelling index values: about 1.5 $m^3 \cdot s^{-1}$ per metre of coastline. Larval number and the total anchovy biomass appear to be positively correlated; however, the data appear scattered for high biomass values (Fig. 1C).

A linear regression analysis using biomass and upwelling as predictor variables explained 37% of the variance in larval number, and the effect of upwelling on larval number was not

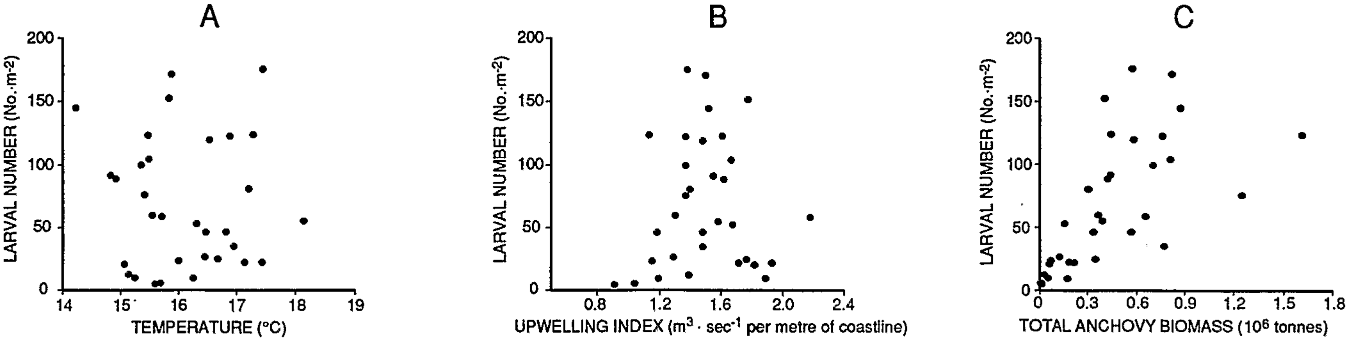

Fig. 1. Mean annual northern anchovy larval number for 1951–90 versus: (A) mean temperature at 10 m depth; (B) mean annual upwelling index; and (C) total anchovy biomass.

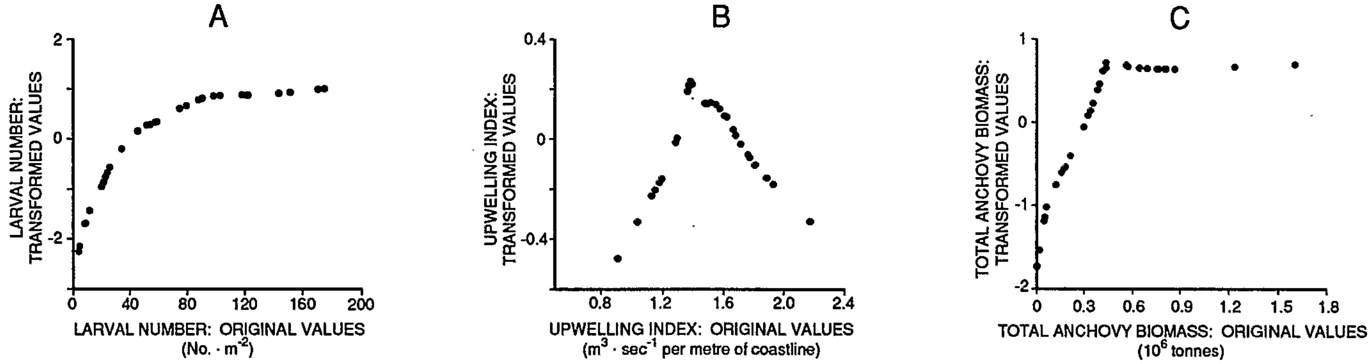

Fig. 2. Optimal empirical transformations from the ACE algorithm using larval number as the dependent variable and upwelling index and total anchovy biomass as the predictor variables. The shapes of the transformations are found by plotting the empirically transformed values of a variable versus their original values. The plots are for 1951–90. (A) Mean annual anchovy larval number (this variable is standardized in the ACE algorithm). (B) Mean annual upwelling index. (C) Total anchovy biomass.

significant. Using the ACE algorithm for the same variables explained 84% of the variability in larval number. The shape of the optimal empirical transformations of both the dependent and the predictor variables from this model are presented in Fig. 2. As the transformations $S()$ and $T_i()$ are conditional expectations empirically estimated by scatterplot smoothers, the iterative algorithms upon convergence return a new, transformed value for each observed value of Y or X_i. The form of the transformation is obtained by plotting the new, transformed value of Y or X_i versus the original, observed value. The estimated transformation of larval number is close to logarithmic in shape (Fig. 2A). The upwelling transformation is nearly dome-shaped with a maximum value around 1.5 $m^3 \cdot s^{-1}$ per metre of coastline (Fig. 2B). The transformation of the total biomass is approximately linear up to a value of about 0.5 Mt, but no real increase occurs above this value (Fig. 2C). When either the upwelling or the total anchovy biomass is separately considered in the analysis, each explains, respectively, 24% and 61% of the larval number variance. In each case, the shape of the transformations (figures not presented) is similar to that obtained when both variables are incorporated into the analysis. In the same way, considering separately biomass below and above 0.5 Mt gives similar transformations for the upwelling index. Identical results were obtained using AVAS (the plots are not presented here because they are similar in shape and the amount of explained variance is the same). Figure 3 presents the optimal empirical transformations from the GAIM algorithm using the logarithm of larval number as the response variable to make the results compatible with the previous results obtained with ACE (the GAIM algorithm only transforms the X variables). The r^2 is equal to 74%. The estimated fit for the transformed anchovy biomass values (Fig. 3A) is close to the transformation obtained using the ACE algorithm (Fig. 2C). The GAIM algorithm produces a smoother dome-shaped relationship for upwelling, in part due to the degrees of freedom used in the smoothing algorithm (Fig. 3B).

Estimating a generalized additive model for anchovy larval number, adult biomass, and upwelling can be viewed as an attempt, under additive restrictions, to empirically transform the three-dimensional surface formed from these observations so that the relationships between them become nearly linear. An interpolated estimate of the three-dimensional surface of the original data, using distance-weighted least squares

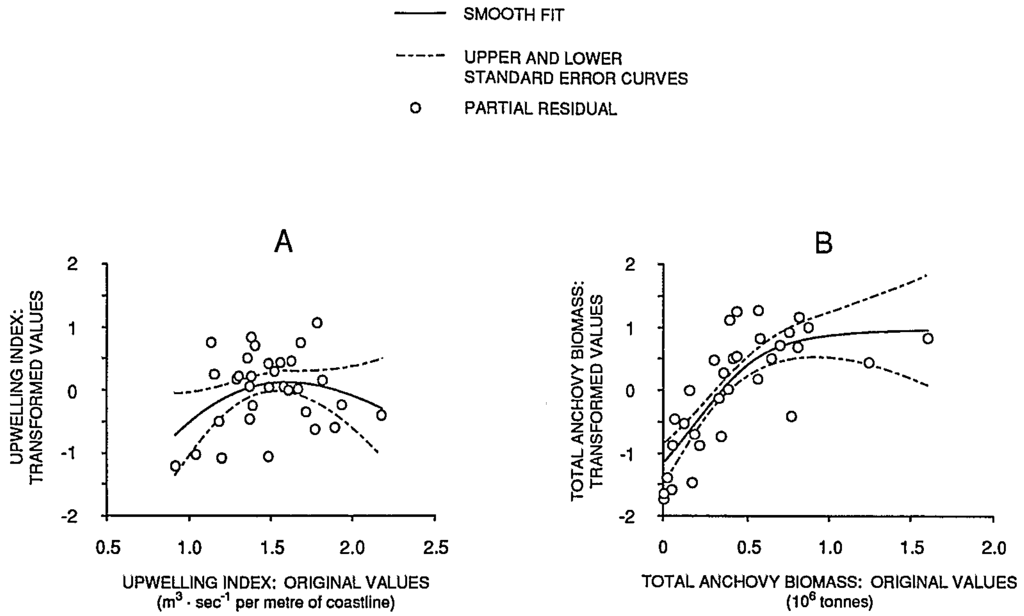

Fig. 3. Smooth fit, pointwise 2× standard error curves and partial residuals for the upwelling index and the total anchovy biomass using the GAIM algorithm. The logarithm of larval number was used as the dependent variable. The shapes of the transformations are found by plotting the empirically transformed values of a variable versus their original values. The plots are for 1951–90. (A) Mean annual upwelling index. (B) Total anchovy biomass.

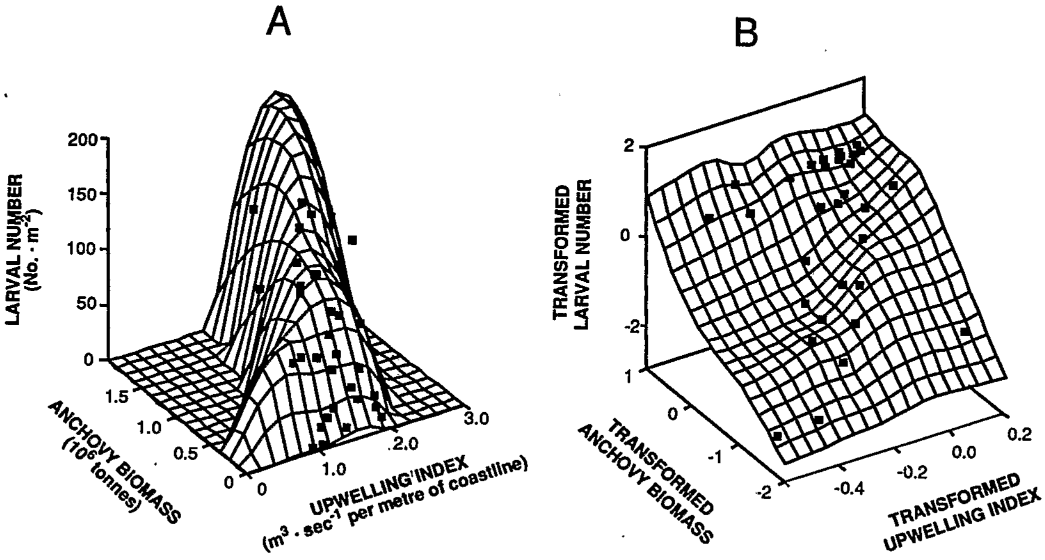

Fig. 4. Interpolated three-dimensional surfaces (using distance-weighted least squares) and the location of the actual values (squares). (A) Original data (larval number versus upwelling index and total anchovy biomass). This interpolated three dimensional surface shows similar nonlinear relationships between larval number and upwelling index, and also larval number and anchovy biomass as obtained from the ACE algorithm. (B) Empirically transformed data obtained from the ACE algorithm. The algorithm has successfully transformed the three variables so that the relationships between them is nearly linear.

(Fig. 4A), shows the dome-like relationship between larval number and upwelling, as well as the asymptotic relationship between larval number and adult biomass. The interpolated estimate of the three-dimensional surface for the transformed valules of the observations is nearly linear in all directions, which shows that the data have been successfully transformed so that the relationships are linear (Fig. 4B).

Discussion

Our results suggest that the larval anchovy number in the California Current has a dome-shaped relationship with upwelling and an asymptotic relationship with total biomass. Recent theories and hypotheses provide an interpretation of these results. In the present case, the abundance of larvae appears to be more related to the physical processes associated with upwelling than to direct effects of temperature. Indeed, this apparent absence of a relationship between larval number and temperature conforms to recent suggestions that variations in surface temperature are likely to have minor net effects on early life history survival (Pepin 1991). The graphical results suggest that larval number should be modeled on a log scale, indicating that the effects of the predictor variables are on a proportional rather than on an absolute basis. Density dependence, often invoked in fish population dynamics, appears to be nonlinear with a strong asymptotic effect on larval abundance at high biomass levels.

Various studies have identified both negative and positive effects of environmental factors on production and survival of larvae. Food production (Cushing 1990; Wroblewski and Richman 1987) 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. Food production may also benefit adult nutrition and therefore larval production (Smith and Eppley 1982). In contrast, intense wind-driven turbulent mixing that disaggregates patches of larval food appears to be detrimental (Lasker 1975; Peterman and Bradford 1987). It is also possible that destruction of food patches may alter adult nutrition. In addition, offshore transport that displaces larvae from favorable coastal areas appears to be a detrimental factor (Parrish et al. 1981).

For the northern anchovy, the relationship between larval number and upwelling intensity is dome shaped, suggesting that upwelling can be either beneficial or detrimental, depending on its intensity. Abundance of surviving larvae increases from low to moderate upwelling intensity, possibly because of the beneficial effect of increased food production and contact rates. It decreases for strong upwelling, possibly due to offshore transport and wind-driven turbulent mixing. Optimal conditions for a high number of surviving larvae correspond therefore to moderate upwelling intensity. These results are in striking conformity to other studies that have indicated that larval survival and recruitment success are regulated by a combination of different factors, each of which may depend in some way on upwelling intensity, rather than a single key factor (Therriault and Platt 1981; Husby and Nelson 1982; Wroblewski et al. 1989; Cury and Roy 1989; Roy et al. 1992).

To maintain, over decades, the homogeneity of environmental and ecological time series is clearly a difficult task. Analytical and methodological changes have certainly affected the consistency of the time series we use in the present analysis. As noted in the introduction, changes in the procedure used to produce the pressure fields have occurred since 1946: three different techniques have been used to estimate the total biomass of the northern anchovy and the sampliing frequency of the larval number has also changed through time. How it may affect our present analysis remains an open question.

Drastic fish population changes that take place within decades in many ecosystems are a social and economic challenge for fisheries (Glantz and Thompson 1981; Cury and Roy 1991) and of crucial interest for fish population modeling (Steele and Henderson 1984). Through modern electronic computation, new statistical methods permit exploration of nonlinear relationships between environmental changes and population responses. In ecology, these recently developed tools (Efron and Tibshirani 1991) are providing new insights and are refreshing our views of population dynamics (Mendelssohn and Cury 1987; Cury and Roy 1989; Swartzman et al. 1992). However, detecting nonlinear environmental effects on population dynamics remains a challenge for several reasons:

1) Several decades of data are sometimes available at different time scales but usually summarized to annual values, thereby only giving a few data points for the analysis. This is an important limitation because much more data are needed when exploring nonlinear relationships.
2) Collecting environmental and ecological data in an ecosystem during several decades is a long and exacting task. Regular financial support is difficult to find for these long-term projects.
3) The homogeneity of the time series over several decades is often questionable; analytical and methodological changes may affect their quality.
4) Our lack of understanding of causal mechanisms leads to an empirical choice between several variables; this choice may or may not be relevant to the population dynamics.
5) Low rather than high correlations are expected between climate variability and fish population responses, making definite relationships hard to establish.

Thus, caution should be added to optimism when exploring nonlinearities in fish population dynamics.

Over the past several decades, the stable global marine fish catch may have tended to mask the fact that the clupeoid contribution, which previously represented about one half of the marine fish catch in the upwelling areas, has now declined to only one third (Smith 1985). Recently it was suggested that the major coastal upwelling systems of the world have been increasing in upwelling intensity as greenhouse gases have accumulated in the earth's atmosphere (Bakun 1990). Our results suggest that the future of pelagic fish stocks will depend both on exploitation rates by fisheries and on climatic changes. Population fluctuations are not related in a linear manner to the density dependent and independent factors. Moderate upwelling intensity is better for larval survival. Thus, even if climatic changes are gradual and monotonic, the response of marine resource populations should not be expected to have the same well-behaved character. In that case, trend extrapolation may yield misleading predictions.

Acknowledgements

This is contribution No. 6 to the Climate and Eastern Ocean Systems (CEOS) project, a NOAA–ORSTOM–ICLARM cooperative project supported by the NOAA Climate and Global Change Marine Ecosystem Response Project and by the Terre–Océan–Atmosphère Department of ORSTOM. We thank P.E. Smith, who gave data and advice, and D.H. Cushing, L. Hutchings, L. Legendre, A. MacCall, B.R. MacKenzie, B. Peterson, R.M. Peterman, and F. Schwing, who provided valuable comments. A. Nichols drew the figures.

References

Bakun, A. 1973. Coastal upwelling indices, west coast of North America 1946–71. NOAA Tech. Rep. NMFS SSRF-671: 103 p.

Bakun, A. 1975. Daily and weekly upwelling indices, west coast of North America 1967–73. NOAA Tech. Rep. NMFS SSRF-693: 114 p.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science (Wash., D.C.) 247: 198–201.

Beverton, R.J.H. 1990. Small marine pelagic fish and the threat of fishing: are they endangered? J. Fish Biol. 37: 5–16.

Blaxter, J.H.S., and J.R. Hunter. 1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 1–223.

Breiman, L., and J.H. Friedman. 1985. Estimating optimal transformations for mutiple regression and correlation. J. Am. Stat. Assoc. 80(391): 580–619.

Buja, A., T. Hastie, and R. Tibshirani. 1989. Linear smoothers and additive models (with discussion) Ann. Stat. 17: 453–555.

Crecco, V., T. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: a predictive approach. Can. J. Fish. Aquat. Sci. 43: 457–463.

Cury, P., and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can J. Fish. Aquat. Sci. 46: 670–680.

Cury, P., and C. Roy [ed.]. 1991. Pêcheries ouest-africaines: variabilité, instabilité et changement. ORSTOM, Paris, France. 525 p.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26: 249–293.

Efron, B., and R. Tibshirani. 1991. Statistical data analysis in the computer age. Science (Wash. D.C.) 253: 390–395.

Elsberry, R.L., and R.W. Garwood. 1978. Sea surface temperature anomaly generation in relation to atmospheric storms. Bull. Am. Meteorol. Soc. 59(7): 786–789.

Gifi, A. 1990. Nonlinear multivariate analysis. John Wiley & Sons, Chichester, UK. 579 p.

Glantz, M.H., and J.D. Thompson [ed.]. 1981. Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. Wiley-Interscience, London, UK. Publ. 11: 491 p.

Halliwell, G.R., Jr., and J.S. Allen. 1987. The large-scale coastal wind field along the west coast of North America 1981–1982. J. Geophys. Res. 92: 1861–1884.

Hastie, T., and R. Tibshirani. 1990. Generalized additive models. Chapman & Hall, London. 335 p.

House, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. U.S. 87: 471–496.

Husby, D.M., and C.S. Nelson. 1982. Turbulence and vertical stability in the California current. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 113–129.

Jacobson, L.D., and N.C. Lo. 1991. Spawning biomass of the northern anchovy in 1991. NMFS, SWFC Admin. Rep. LJ 91-19. 53 p.

Kareiva, P.M. 1990. Stability from variability. Nature (Lond.) 344: 111–112.

Lasker R. 1975. Field criteria for survival of anchovy larvae: the relation between onshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. 73: 453–462

Lasker, R. [ed.]. 1981. Marine fish larvae. Morphology, ecology, and relation to fisheries. University of Washington Press, Seattle, WA. 131 p.

Lasker, R. 1985. What limits clupeoid production? Can. J. Fish. Aquat. Sci. 42: 31–38.

MacCall, A.D., and R.D. Methot. 1983. The historical spawning biomass estimates and population model in the 1983 anchovy fishery management plan. NMFS, SWFC Admin. Rep. LJ 83-17. 53 p.

MacKenzie, B.R., and W.C. Leggett. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar. Ecol. Prog. Ser. 73: 149–160.

Mendelssohn, R., and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. Can. J. Fish. Aquat. Sci. 44: 408–428.

Methot, R.D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. Am. Fish. Soc. Symp. 6: 66–82.

Parrish, R.H., C.S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1(2): 175–203.

Parrish, R.H., and A.D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Fish. Bull. U.S. 167: 1–110.

Pauly, D., and I. Tsukayama. 1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Stud. Rev. 15: 351 p.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. FIsh. Aquat. Sci. 48: 503–518.

Peterman, M.R., and M.J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science (Wash., D.C.) 235: 354–356.

Peterman, M.R., M.J. Bradford, N.C. Lo, and R.D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchoby (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45: 8–16.

Reid, J.L., Jr., G.I. Roden, and J.G. Wyllie. 1958. Studies of the California current system. Calif. Coop. Oceanic Fish. Invest. Prog. Rep. 23: 219–226.

Rothschild, B.J., and T.R. Osborn. 1988. The effects of turbulence on planktonic contact rates. J. Plankton Res. 10(3): 465–474.

Roy, C., P. Cury, and S. Kifani. 1992. Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. *In* A.I.L. Payne, K.H. Brink, K.H. Mann, and R. Hilborn [ed.] Benguela trophic functioning. S. Afr. J. Mar. Sci. 12: 135–146.

Sharp, G.D., and J. Csirke [ed.]. 1983. Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. FAO Fish. Rep. 291: 1224 p.

Sissenwine, M.P. 1984. Why do fish populations vary?, p. 59–94. *In* R.M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen. Springer-Verlag, Berlin, Germany. Life Sci. Res. Rep. 32.

Smith, P.E. 1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42: 69–82.

Smith, P.E., and R.W. Eppley. 1982. Primary production and the anchovy population in the southern California Bight: comparison of time series. Limnol. Oceanogr. 27(1): 1–17.

Smith, P.E., and H.B. Moser. 1988. CalCOFI time series: an overview of fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 29: 66–78.

Steele, J.H., and E.W. Henderson. 1984. Modeling long-term fluctuation in fish stocks. Science (Wash., D.C.) 224: 985–987.

Swartzman, G., C. Huang, and S. Kaluzny. 1992. Spatial analysis of bering sea groundfish survey data using generalized additive models. Can. J. Fish. Aquat. Sci. 49: 1366–1378.

Therriault, J.C., and T. Platt. 1981. Environmental control of phytoplankton patchiness. Can. J. Fish. Aquat. Sci. 38: 638–641.

Tibshirani, R. 1988. Estimating transformations for regression via additivity and variance stabilization. J. Am. Stat. Assoc. 83(402): 394–405.

Tyler, A.V. 1992. A context for recruitment correlations: why marine fisheries biologists should still look for them. Fish. Oceanogr. 1(1): 97–107.

Wroblewski, J.S., J.G. Richman, and G.L. Mellor. 1989. Optimal wind conditions for the survival of larval northern anchovy, *Engraulis mordax*: a modeling investigation. Fish. Bull. U.S. 87: 387–398.

Wroblewski, J.S., and J.G. Richman. 1987. The non-linear response of plankton to wind mixing events—implications for survy of larval northern anchovy. J. Plankton Res. 9(1): 103–123.