

Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean)

J. LLORET,^{1,*} I. PALOMERA,¹ J. SALAT¹
AND I. SOLE²

¹Institut de Ciències del Mar (CMIMA-CSIC), Pg. Marítim de la Barceloneta 37-49, E-08003 Barcelona, Catalonia, Spain

²Universitat Politècnica de Catalunya, Escola Superior d'Enginyers Industrials, Diagonal 647, E-08028 Barcelona, Catalonia, Spain

ABSTRACT

Time series analyses (Box–Jenkins models) were used to study the influence of river runoff and wind mixing index on the productivity of the two most abundant species of small pelagic fish exploited in waters surrounding the Ebre (Ebro) River continental shelf (north-western Mediterranean): anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*). River flow and wind were selected because they are known to enhance fertilization and local planktonic production, thus being crucial for the survival of fish larvae. Time series of the two environmental variables and landings of the two species were analysed to extract the trend and seasonality. All series displayed important seasonal and interannual fluctuations. In the long term, landings of anchovy declined while those of sardine increased. At the seasonal scale, landings of anchovy peaked during spring/summer while those of sardine peaked during spring and autumn. Seasonality in landings of anchovy was stronger than in sardine. Concerning the environmental series, monthly average Ebre runoff showed a progressive decline from 1960 until the late 1980s, and the wind mixing index was highest during 1994–96. Within the annual cycle, the minimum river flow occurs from July to October and the wind mixing peaks in winter (December–April, excluding January). The results of the analyses showed a significant

correlation between monthly landings of anchovy and freshwater input of the Ebre River during the spawning season of this species (April–August), with a time lag of 12 months. In contrast, monthly landings of sardine were significantly positively correlated with the wind mixing index during the spawning season of this species (November–March), with a lag of 18 months. The results provide evidence of the influence of riverine inputs and wind mixing on the productivity of small pelagic fish in the north-western Mediterranean. The time lags obtained in the relationships stress the importance of river runoff and wind mixing for the early stages of anchovy and sardine, respectively, and their impact on recruitment.

Key words: Box–Jenkins transfer function models, Ebre (Ebro), *Engraulis encrasicolus*, Mediterranean, river runoff, *Sardina pilchardus*, wind mixing

INTRODUCTION

Most fishery production worldwide is associated with three nutrient enrichment processes: coastal upwelling, tidal and/or wind mixing, and land-based runoff including major river outflow (Caddy and Bakun, 1994). Terrestrially enriched river discharge favourably influences biological processes (i.e. growth, survival and recruitment) that affect fisheries production (Grimes, 2001). River effects are most noticeable in oligotrophic seas (e.g. Mississippi River in the Gulf of Mexico: Grimes, 2001; Rhône River in the Mediterranean: Lloret *et al.*, 2001) and in semi-enclosed systems such as the Black Sea (Daskalov, 1999). Winds promote nutrient enrichment through mixing or upwelling, thus enhancing the productivity of some exploited species, especially small pelagic fishes (e.g. Bakun and Parrish, 1991).

Although the Mediterranean is considered oligotrophic (Margalef, 1985), some areas are more productive due to bathymetric, hydrographical and

*Correspondence. e-mail: lloret@icm.csic.es

Received 13 September 2002

Revised version accepted 3 February 2003

meteorological conditions, such as the presence of a wide shelf (e.g. Gulf of Lions, Gulf of Gabes and the northern Adriatic: Bombace, 1993; Caddy, 1993), river runoff (e.g. areas close to the Rhône, Po, Nile or Ebre mouths: Caddy, 1993; Lefevre *et al.*, 1997; Solic *et al.*, 1997; Morovic, 2002), and wind mixing (e.g. northern Adriatic and Gulf of Lions: Estrada, 1996; Salat, 1996; Diaz *et al.*, 2000; Morovic, 2002). These areas are important fishery zones because they are potential preferred spawning areas for many fishes (e.g. anchovy: Palomera, 1992; Salat, 1996; Coombs *et al.*, 1997, 2003; Agostini, 2000; Sabatés *et al.*, 2001). Preferred spawning habitats are found around the world in areas where enrichment, concentration and retention processes combine to yield favourable reproductive habitats (Bakun and Parrish, 1991; Bakun, 1998).

The shelf waters surrounding the Ebre River outfall (north-western Mediterranean) are a good example of waters that are productive due to these physical and biological processes, essentially due to the freshwater input from the Ebre River, the strong and predominant north-westerly winds and a relatively wide shelf (Salat *et al.*, 2002). The Ebre River discharges into the north-western Mediterranean Sea after a 928-km-long passage. The catchment area of 85 835 km² includes the mountains bordering the northernmost parts of the Iberian Peninsula, mainly the Pyrenees. The river Ebre flows through areas where agriculture and farming from which nutrient discharges, especially nitrogen, are considerable (Cruzado *et al.*, 2002). It is one of the most important rivers of the Iberian Peninsula because it provides habitat to numerous endemic freshwater fish species and birds, and water for agriculture, human use and industrial activities (Comín, 1999).

The predominant air mass blowing over the north-western Mediterranean basin is a dry, continental wind (Astraldi and Gasparini, 1992). During winter this wind is more frequent, strong, dry, and cold and can persist for several days. The Mistral is a well known wind of this type, blowing from the north-west with great intensity in the Gulf of Lions. In the areas surrounding the Ebre River delta, the equivalent wind, locally called the Mestral, blows from the north-west and behaves as does the Mistral in the Gulf of Lions, inducing intense water mixing on the shelf and bringing nutrients to the surface (Margalef, 1968; Estrada *et al.*, 1985; Estrada, 1996; Salat, 1996). Anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) are heavily exploited by trawlers and purse seiners in the areas surrounding the mouth of the Ebre River. Different studies provide evidence that these are preferred spawning areas for both anchovy and

sardine (Palomera, 1992; Salat, 1996; Olivar *et al.*, 2001).

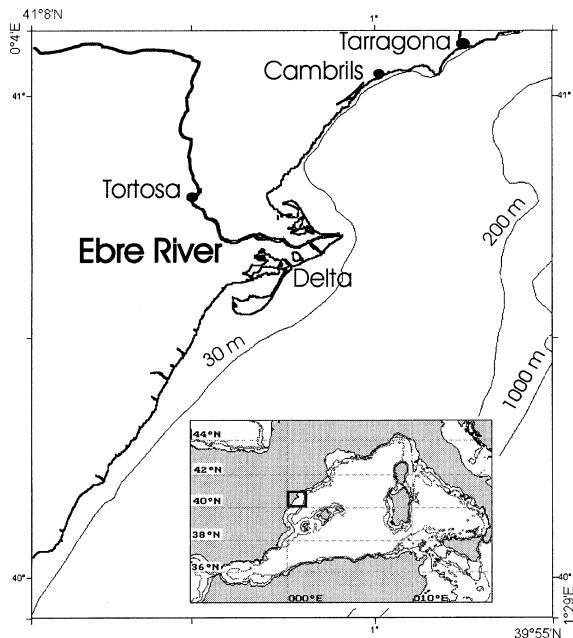
The purpose of this paper is to model the relationships between Ebre River runoff and wind conditions with landings of anchovy and sardine caught from waters surrounding the Ebre River delta, using transfer function models (Box and Jenkins, 1976). Transfer function models are a subclass of the Box-Jenkins autoregressive integrated moving average (ARIMA) models, a group of linear, stochastic-dynamic models that can describe fairly complex behaviour. The Box-Jenkins methodology has also been used to model dynamics of marine species in other areas in relation to climate variability (e.g. Keller, 1987; Fogarty, 1988; Hare and Francis, 1995; Stergiou *et al.*, 1997; Tsai *et al.*, 1997; Downton and Miller, 1998; Lloret *et al.*, 2000, 2001). The basic working hypothesis behind this study is that recruitment of anchovy and sardine in the north-western Mediterranean is influenced by the amount of water discharged from the Ebre River and by local wind conditions during the spawning season, through enhanced fertilization, which favours survival of larvae. This study also intends to characterize the dynamics of river runoff, wind mixing and landings of anchovy and sardine by analysing the trend and seasonality of the time series.

MATERIALS AND METHODS

Data sources

A series of monthly landings of anchovy and sardine at Tarragona harbour was available for the periods January 1990–December 2001 and January 1990–September 2001, respectively. That harbour is the most important in the area in terms of landings and fleet. As these time series span more than 50 months, they are suitable for a time-series analysis (Pankratz, 1991). Landings were from purse seiners, the fleet devoted to these species in the study area. Because fishing effort (number of boats and monthly time at sea) remained nearly stable during the entire study period (around 26 purse seiners fishing at night, from Sunday to Friday, excluding holidays), landings can be considered as a raw measure of catch per unit effort. Wind data (hourly observations of speed and direction, 1990–2001) were obtained from the Cambrils meteorological station (Servei de Meteorologia de Catalunya; Fig. 1). The intensity of input of mechanical energy by the wind, which would then become available for turbulent mixing of the upper ocean, was computed by means of a 'wind mixing index' (Bakun and Parrish, 1991), which is roughly

Figure 1. Location of the study area showing the course of the Ebre River and location of meteorological (Cambrils and Tarragona) and gauging (Tortosa) stations, and the main landing port (Tarragona).



proportional to the cube of the wind speed. Thus, the monthly wind mixing index series was obtained by averaging the cube of the hourly records of wind speed. Wind information recorded at the Tarragona meteorological station (Instituto Nacional de Meteorología), situated near Cambrils station (Fig. 1), was used to fill gaps (for 4 months) in the Cambrils series, through a linear regression between the monthly wind mixing indices calculated at both stations during the entire period. Monthly mean flow data ($\text{m}^3 \text{ s}^{-1}$) of the Ebre River (1952–2001), recorded near its mouth (gauging station of Tortosa; Fig. 1), were obtained from the Confederación Hidrográfica del Ebro.

Description of the time series: analysis of trend and seasonality

We used the decomposition method ‘tramo-seats’ which is included in the software package ForeTESS developed by the Polytechnical University of Catalonia (Prat *et al.*, 2001). This method is an extension of the X-11 decomposition method (Makridakis and Wheelwright, 1989). The ‘tramo-seats’ method uses multiple moving averages to decompose the time series into trend and seasonal components. While the seasonal component shows the spectral peaks at seasonal frequencies (the seasonal value for a given month is the percentage above/below the annual

mean), the trend represents the smoothed evolution of the series.

Transfer function analyses between landings and environmental variables

To determine and quantify the possible relationships between the monthly time series of landings (anchovy and sardine) and the selected environmental variables (river flow and wind mixing index), we constructed four linear transfer function models (Box and Jenkins, 1976), one for each species and environmental variable. As input time series (river flow and wind mixing index) we used only the values for the spawning period of each species, because this is the time interval when larvae are in the water column, and that is postulated as a key determinant of interannual survival variability (Cushing, 1982; Houde, 1987). Reproduction periods considered were April–August for anchovy (Palomera, 1992) and November–March for sardine (Palomera and Olivar, 1996). The values for the remaining months of the input series were replaced by ‘zeros’ that meant ‘no influence on landings’ in our models. Thus, we compared the environmental conditions only during the spawning seasons with the landings obtained afterwards. Transfer function models were built following the Box and Jenkins’ modelling strategy (Box and Jenkins, 1976; Appendix 1) using the software package ForeTESS (Prat *et al.*, 2001). The linear transfer function models were expressed by the following general equation (Pankratz, 1991):

$$Y_t = f(X_t) = v_0 X_t + v_1 X_{t-1} + v_2 X_{t-2} + \dots + N_t. \quad (1)$$

where Y is the landings (anchovy or sardine), X the environmental factor (river runoff or wind mixing), t the unit of time (month) and N is the disturbance (error) term. Coefficient v_0 is a weight that states how Y_t responds to a change in X_t (current month change in X_t); coefficient v_1 states how Y_t responds to a change in X_{t-1} (1 month earlier change in X_t); coefficient v_2 states how Y_t responds to a change in X_{t-2} (2 months earlier change in X_t), and so forth. The v weights can be positive or negative. The larger the absolute value of any weight v_k , the larger the response of Y_t to a change in X_{t-k} . The sum of these weights gives the total gain. Only significant coefficients at a $|T| > 3$ ($P < 0.05$) were considered.

RESULTS

Description of environmental variables and landings: analysis of trend and seasonality

Landings, river runoff and wind mixing displayed noticeable seasonal and interannual fluctuations

(Figs 2–4). Landings of anchovies varied from 0.1 t (for May 2000) to 344 t (for June 1994) and those of sardines varied from 0.1 t (for December 2000 and January 2001) to 1500 t (for October 1995). Over the long term, landings of anchovy declined (Fig. 2a), while those of sardine increased (Fig. 2b). Monthly anchovy landings peaked during spring/summer when, on average, catches were up to 150% above the annual mean landings (Fig. 3a), while those of sardine peaked during spring and autumn, when they were about 30 and 60% above the annual mean landings, respectively (Fig. 3a). Seasonality in landings of anchovy was thus stronger than for sardine. The monthly average Ebre runoff, which varied from $19 \text{ m}^3 \text{ s}^{-1}$ (July 1955) to $2171 \text{ m}^3 \text{ s}^{-1}$ (December 1959), showed a progressive decline from 1960 until the late 1980s (Fig. 4a). Minimum river flows occurred from July to October when seasonal values were down to 60% below the annual mean flow (Fig. 3b). The monthly values of the wind mixing index varied from $2 \text{ m}^3 \text{ s}^{-3}$ (September 1990) to $66 \text{ m}^3 \text{ s}^{-3}$ (April 1994) and were highest during 1994–96 (Fig. 4b). Excluding January, values of wind mixing peaked in winter/spring (December–April), when seasonal values were up to 100% above the annual means (Fig. 3b). The seasonality of the wind mixing index was thus stronger than for the Ebre runoff.

Figure 2. Monthly time series and trend of landings of anchovy (a) and sardine (b), over the period 1990–2001.

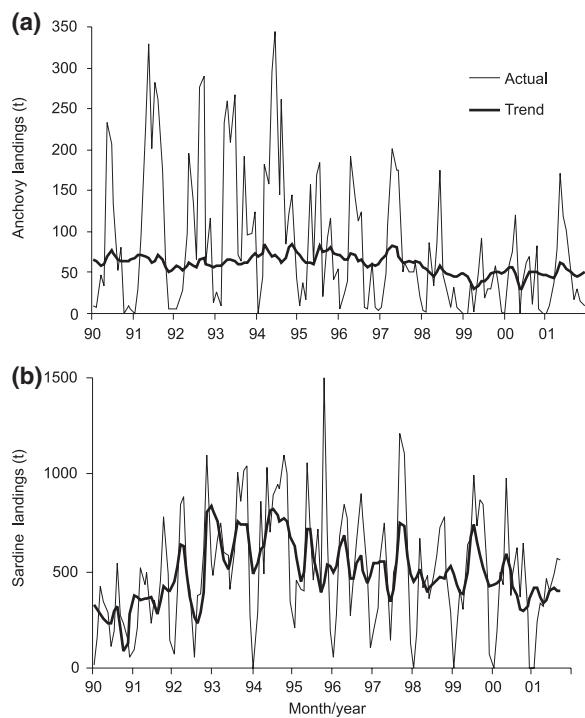


Figure 3. Mean seasonal patterns (% above/below the annual mean) of the full time series of landings of anchovy and sardine (a; 1990–2001) and wind mixing index (b; 1990–2001) and river runoff (b; 1952–2001).

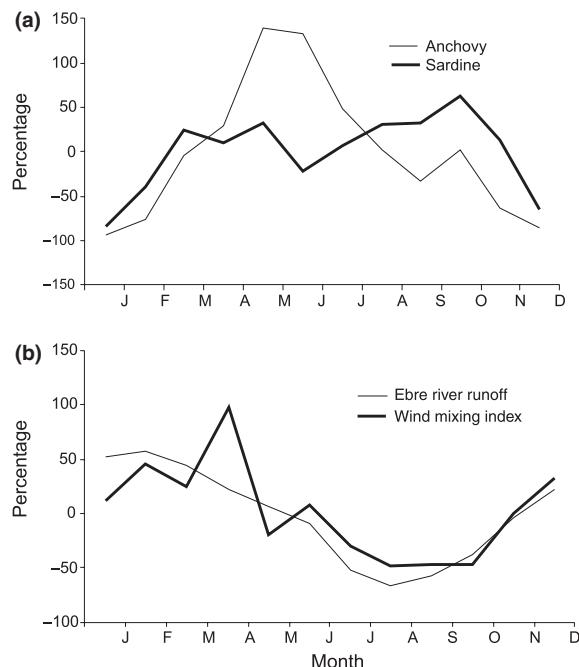
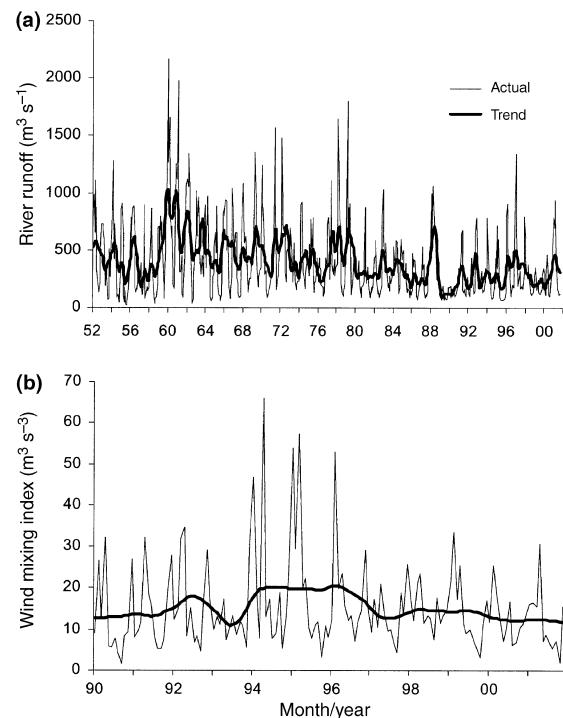


Figure 4. Monthly time series and trend of the Ebre River runoff (a; 1952–2001) and the wind mixing index (b; 1990–2001).



Relationships between landings and environmental variables

Anchovy

The transfer function models between landings and environmental variables showed that anchovy landings were positively correlated with river flow during the reproduction season at a time lag of 12 months. Thus, the transfer function model fit to anchovy landings (Y_t ; output) and Ebre runoff (X_t ; input) is represented by the following equation:

$$Y_t = f(X_t) = 0.189X_{t-12} + N_t \quad (2)$$

The coefficient at $t-12$ (0.189) was the only significant one (T -value = 4.421, $P < 0.05$). The rest of coefficients (e.g. $t-10$, $t-11$, $t-13$, $t-14$, $t-1$ and $t-2$) were not significant ($|T| < 3$, $P > 0.05$). Thus, the model estimated that an additional $1 \text{ m}^3 \text{ s}^{-1}$ of Ebre runoff during the reproduction season of anchovy leads to a 0.189 t of added landings of this species after 12 months. The r^2 -value of the model was 0.24 (residual standard deviation = 45.08 t). This indicated that 24% of the variance of the anchovy landings is explainable by the variance of the Ebre flow at a lag of 12 months. Figure 5a compares model landings (i.e. landings explained by the Ebre's runoff) with actual landings during the study period. However, there was no relationship between landings of anchovy and the wind mixing index: no coefficient of the model was significant ($|T| < 3$, $P > 0.05$).

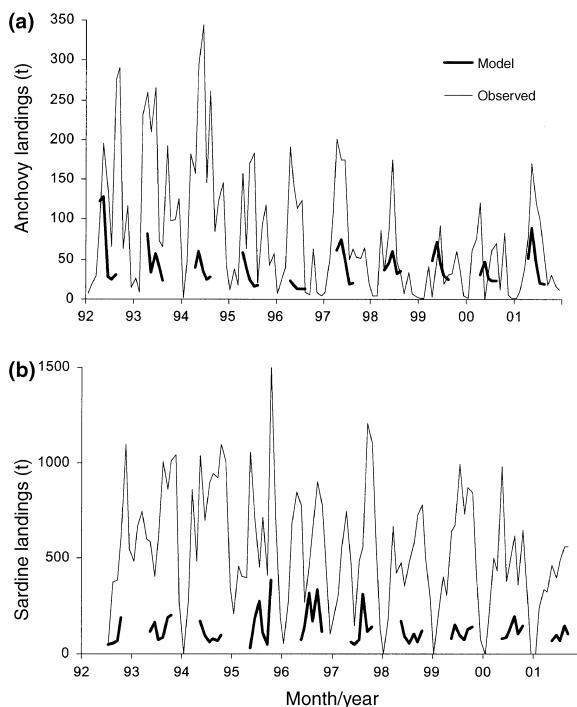
Sardine

Sardine landings were positively correlated at a time lag of 18 months, with the wind mixing index during the reproductive season of this species. The transfer function model fitted to sardine landings (Y_t ; output) and wind mixing index (Z_t ; input) is represented by the following equation:

$$Y_t = f(Z_t) = 5.851Z_{t-18} + N_t \quad (3)$$

The coefficient at $t-18$ (5.851) was the only significant one (T -value = 3.510, $P < 0.05$). Thus, the model estimated that an additional $1 \text{ m}^3 \text{ s}^{-3}$ of the wind mixing index during the sardine's reproductive season leads to a 5.851 t of added landings of sardine after 18 months. The r^2 -value of the model was 0.19 (residual standard deviation = 214.65 t). This indicated that 19% of the variance of the sardine landings was explainable by the variance of the wind mixing index at a lag of 18 months. Figure 5b compares model landings (i.e. landings due to the wind mixing index) with the actual ones during the study period. Landings of sardine were not related to the Ebre's flow during the spawning season: no coefficient of the model was significant ($|T| < 3$, $P > 0.05$).

Figure 5. Comparison between the expected landings from the models and the observed (actual) landings of anchovy (a) and sardine (b), over the period 1992–2001. Model values represent (a) the contribution of the river outflow to the landings of anchovy 12 months after spawning and (b) the contribution of wind mixing to the landings of sardine 18 months after spawning.



DISCUSSION

The coastal zones of the Mediterranean are often oligotrophic, as only small freshwater discharges caused by episodic rain storms flow through otherwise dry rivers and because wind mixing, tides and upwelling are weak or absent. Very often, long stretches of coastline are fertilized by the discharge of nutrient-rich urban and industrial effluents (Cruzado *et al.*, 2002). Exceptions to this rule are estuarine areas receiving the discharges of large rivers (e.g. Po, Rhône and Ebre) collecting the runoff from snow-covered mountain ranges (e.g. Alps and Pyrenees), wastewater from large cities and intensive agricultural and industrial activities, and some relatively wide continental shelves exposed to strong winds. The waters surrounding the Ebre River delta are an example of both types of nutrient enhancement. Direct nutrient inputs from the Ebre outflow may account for 10–25% of the total nutrient content in the water column on the adjacent continental shelf (Salat *et al.*, 2002). These nutrients are introduced at the surface, thus becoming directly available for surface phytoplankton. The

remaining nutrients are only available at the surface through winter mixing induced by the strong winds blowing over the area (Salat, 1996). During the rest of the year, and in the absence of strong winds, phytoplankton production is restricted to the deep chlorophyll maximum, located at 40–80 m (Margalef, 1968; Estrada, 1996).

The application of linear transfer function models between landings and environmental variables during the spawning season of anchovy, showed that the landings of this species were significantly positively correlated with river flow, with a time lag of 12 months, but were not correlated to the wind mixing. Anchovy spawns and is caught mainly during spring/summer (Palomera, 1992), when most of the individuals are 1-yr old (Pertierra and Lleonart, 1996). Therefore, the landings of anchovy can be considered as a proxy of recruitment. Thus, the time lag at which the correlation between runoff during spawning and landings takes place (i.e. 1 yr) corresponds to the age at which anchovy reaches the minimum exploitation size. Accordingly, our results suggest that river runoff influences spawning and the survival rate of the anchovy early stages and, hence, recruitment. This is in agreement with the reproductive behaviour of anchovy. Spawning of anchovy is restricted to the surface and larvae remain above the thermocline until they are able to swim freely (Palomera, 1991; Olivari *et al.*, 2001). Larva survival depends on food availability at the surface which, in turn, depends on the nutrient content of the surface waters. An increase of surface primary productivity in the enriched continental waters enhances zooplankton production, the main food for anchovy larvae (Tudela *et al.*, 2002). Strong runoffs during April and May (when anchovy starts spawning) are followed by a stabilization of water masses due to solar heating and a decrease in wind activity. During this season, the thermocline inhibits vertical mixing and nutrients at the surface become depleted. In such conditions, the only source that may contribute to surface productivity is nutrient input from river outflow (Salat, 1996).

The contribution of freshwater discharge in enhancing recruitment of anchovy has been demonstrated in other areas of the Mediterranean (e.g. Rhône River outflow in the Gulf of Lions: Lloret *et al.*, 2001; Po River outflow in the Adriatic: Levi *et al.*, 1999; runoff of several rivers in the Black Sea: Daskalov, 1999). Moreover, large quantities of anchovy are found in areas influenced by river outflows (Bakun, 1998; Agostini, 2000), and their larvae are associated with the presence of less saline water at the surface of continental influence (Palomera, 1992;

Coombs *et al.*, 1997, 2003; Sabatés *et al.*, 2001). Freshwater discharge is generally known to enhance productivity of marine species in other areas of the world ocean (e.g. cod off the north coast of Norway: Skreslet, 1976; cod in the Gulf of St Lawrence: Bugden *et al.*, 1982; Chouinard and Fréchet, 1994; American lobster and Atlantic halibut in the Gulf of St Lawrence: Sutcliffe, 1973; sprat, whiting and horse mackerel in the Black Sea: Daskalov, 1999; róbalo in central-south Chile: Quiñones and Montes, 2001; anchovy in coastal waters off south-western Taiwan: Tsai *et al.*, 1997; various species in the Gulf of Mexico: CAST, 1999; Grimes, 2001; various species in the Gulf of Lions: Lloret *et al.*, 2001). Strong circumstantial evidence of the relationship between river discharge and fish production is that when flows have been controlled or eliminated, major declines in fisheries have followed (Grimes, 2001). One of the best examples is the decrease of the Nile River flow by 90% during the filling of the Aswan High Dam in 1965–69, which resulted in a decline in the primary production off the Nile delta and in the Egyptian fishery landings in the Mediterranean of about 80%, as well as in a simplification of community structure (Bebars and Lasserre, 1983). In the Ebre delta, the observed relationship of anchovy landings to river discharge and the decreasing trend of the Ebre runoff during at least part of the last 40 yr could have caused a decline of the local anchovy stock. This situation could deteriorate further if, by any anthropogenic or natural factor, river runoff is further reduced.

The transfer function model showed that landings of sardine were positively correlated with the wind mixing index, with a time lag of 18 months, but not correlated with river runoff. Sardine is caught mainly during the spring and autumn, when most individuals are between 1 and 2 yr old. Sardine spawns during wintertime, when the water column is vertically homogeneous and relatively cool (Palomera and Olivari, 1996). At that time, vertical mixing associated with wind storms will affect the entire surface layer, carrying nutrients to the entire euphotic zone. Sardine larvae exhibit greater vertical dispersal than anchovy, with preference levels below 30 m depth (Olivari *et al.*, 2001). Survival of sardine larvae is therefore closely related to vertical mixing and, consequently, to wind stress as a contributing mechanism. Positive relationships between wind activity and recruitment of pelagic species are found in other areas (e.g. anchovy of the south-western Atlantic: Bakun and Parrish, 1991; anchovy and sardine in northern Chile: Yáñez *et al.*, 2001; sprat, anchovy and horse mackerel in the Black Sea: Daskalov, 1999). Yet, very strong wind mixing

can also lead to increased mortality in fish larvae as a result of poor feeding success due to dispersal of food concentrations (Bergeron, 2000).

The particular life history of small pelagic fish (i.e. high mobility, plankton-based food chains and short life span) makes these species particularly sensitive to environmental forcing (Regner, 1996; Agostini, 2000). Because adults (Whitehead, 1985; Tudela and Palomera, 1997) and larvae (e.g. Conway *et al.*, 1991, 1998) of sardine and anchovy feed on plankton, an increase in planktonic production (through increased river runoff or wind mixing) during the spawning period may affect these species rapidly. Their response to climate variations can be quick and dramatic, and the effects can be transported higher up in the food chain, thus affecting other fish populations (Agostini, 2000). The results obtained in this study reveal the importance of Ebre river discharges on anchovy production, and wind mixing on sardine production. As the environmental variables are centred on the spawning period and their impact is on survival at the early stages of these species, we conclude that events in this period have a significant impact on recruitment. However, the models explained only a small amount (<25%) of the variability of landings of sardine and anchovy. This indicates that other variables, such as the parental stock biomass and density dependent processes (e.g. Myers and Cadigan, 1993; Fromentin *et al.*, 1997; Bjørnstad *et al.*, 1999), may also influence year class strength. Although the variability of landings explained by the model was small, the results provide evidence, independent of the studies directly targeted on larvae, that the environmental variables considered play a role in the recruitment success of the species studied. Although we used linear models, because they are relatively easy to build and interpret, it is possible that complex non-linear models might better describe the relationships between landings and environmental variables, especially at extreme values of the environmental factors.

APPENDIX 1. BOX-JENKINS MODELLING STRATEGY

The Box and Jenkins modelling strategy considers three steps: identify the model, estimate the coefficients and verify the model. These procedures apply to stationary series (time series with no systematic change in mean and variance) where the data are normally distributed. First- or second-order differencing (non-seasonal and/or seasonal) remedies a non-stationary mean, and logarithmic transformation

remedies a non-stationary variance and also non-normal distributions of original data. The data analysis tool employed for the identification of transfer function models is the cross-correlation function for the input and output. Estimation of the coefficients of the model was carried out by the maximum likelihood method. Verification of the model was through diagnostic checks of residuals. Thus, the autocorrelation and the partial autocorrelation functions of the residuals (noise or disturbance) and the cross-correlation functions involving input and residuals were examined. In case of evidence of transfer model inadequacy from the behaviour of individual autocorrelations, autoregressive and/or moving average parameters were fitted and the iterative cycle of identification, estimation and diagnostic checking was repeated until a suitable model was found. It is important to note that we are not interested here in forecasting landings using environmental variables but only in assessing the role of the input variables (river runoff and winds) in explaining the behaviour of the output variable (landings).

ACKNOWLEDGEMENTS

Our sincere thanks to Dr Albert Prat, Dr Josep M^a Catot and Daniel Martínez for providing the software, and to the Servei de Meteorologia de Catalunya, the Instituto Nacional de Meteorología and the Confederación Hidrográfica del Ebro for providing data. This research was supported in part by the EU. The authors thank two anonymous referees and Dr S. Coombs for their useful comments.

REFERENCES

- Agostini, V. (2000) Relationships between Small Pelagics and the Environment: Where Have We Been and Where Do We Go from Here? Scientific Advisory Committee GFCM. Working Group on Small Pelagics, p. 11.
- Astraldi, M. and Gasparini, G.P. (1992) The seasonal characteristics of the circulation in the North Mediterranean Basin and their relationship with the atmospheric-climatic conditions. *J. Geophys. Res.* **97**:9531–9540.
- Bakun, A. (1998) Ocean triads and radical interdecadal stock variability: bane and boon for fishery management science. In: *Reinventing Fisheries Management*. T.J. Pitcher, P.J.B. Hart & D. Pauly (eds) London: Chapman & Hall, pp. 331–358.
- Bakun, A. and Parrish, R.H. (1991) Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. *ICES J. Mar. Sci.* **48**:343–361.
- Bebars, M.I. and Lasserre, G. (1983) Analysis of the Egyptian marine and lagoon fisheries from 1962–1976, in relation to the construction of the Aswan Dam (completed in 1969). *Oceanol. Acta* **6**:417–426.

- Bergeron, J.P. (2000) Effect of strong winds on the nutritional condition of anchovy (*Engraulis encrasicolus*) larvae in the Bay of Biscay, Northeast Atlantic, as inferred from an early field application of the DNA/C index. *ICES J. Mar. Sci.* **57**:249–255.
- Bjørnstad, O.N., Fromentin, J.M., Stenseth, N.C., Johannessen, T. and Gjøsaeter, J. (1999) A test for density-dependent survival in juveniles stages of cod. *Ecology* **80**:1278–1288.
- Bombace, G. (1993) Ecological and fishing features of the Adriatic Sea. In: *Large Marine Ecosystems: Stress, Mitigation and Sustainability*. K. Sherman, L.M. Alexander & B.D. Gold (eds) Washington, DC: American Association for the Advancement of Science, pp. 119–136.
- Box, G.E.P. and Jenkins, G.M. (1976) *Time Series Analysis: Forecasting and Control*. New York: Prentice Hall Inc., p. 575.
- Bugden, G.L., Hargrave, B.T., Sinclair, M.M., Tang, C.J., Therriault, J.C. and Yeats, P.A. (1982) Freshwater run-off effects in the marine environment: the Gulf of St Lawrence example. *Can. Tech. Rep. Fish. Aquat. Sci.* **1078**:1–89.
- Caddy, J.F. (1993) Contrast between recent fishery trends and evidence from nutrient enrichment in two large marine ecosystems: the Mediterranean and the Black Seas. In: *Large Marine Ecosystems: Stress, Mitigation and Sustainability*. K. Sherman, L.M. Alexander & B.D. Gold (eds) Washington, DC: American Association for the Advancement of Science, pp. 137–147.
- Caddy, J.F. and Bakun, A. (1994) A tentative classification of coastal marine ecosystems based on dominant processes of nutrient supply. *Ocean Coast. Manage.* **23**:201–211.
- CAST (1999) *Gulf of Mexico Hypoxia: Land and Sea Interactions*. Council for Agricultural Science and Technology, Task Force Report No. 134, p. 44.
- Chouinard, G.A. and Fréchet, A. (1994) Fluctuations in the cod stocks of the Gulf of St Lawrence. *ICES Mar. Sci. Symp.* **198**:121–139.
- Comín, F.A. (1999) Management of the Ebro River Basin: past, present and future. *Water Science and Technology* **40**:161–168.
- Conway, D.V.P., Tranter, P.R.G., Puelles, M.L.F. and Coombs, S.H. (1991) Feeding of larval sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* Walbaum). *ICES CM Biol. Oceanogr. Committee* **76**:7.
- Conway, D.V.P., Coombs, S.H. and Smith, C. (1998) Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. *Mar. Ecol. Prog. Ser.* **175**:35–49.
- Coombs, S.H., Giovanardi, O., Conway, D., Manzueto, L., Halliday, N. and Barrett, C. (1997) The distribution of eggs and larvae of anchovy (*Engraulis encrasicolus*) in relation to hydrography and food availability in the outflow of the river Po. *Acta Adria.* **38**:33–47.
- Coombs, S.H., Giovanardi, O., Halliday, N.C., Franceschini, G., Conway, D.V.P., Manzueto, L., Barrett, C.D. and McFadzen, I.R.B. (2003) Wind mixing, food availability and mortality of anchovy larvae *Engraulis encrasicolus* in the northern Adriatic Sea. *Mar. Ecol. Prog. Ser.* **248**:221–235.
- Cruzado, A., Velásquez, Z., Pérez, M., Bahamón, N., Grimaldo, N.S. and Ridolfi, F. (2002) Nutrient fluxes from the Ebro River and subsequent across-shelf dispersion. *Cont. Shelf Res.* **22**:349–360.
- Cushing, D.H. (1982) *Climate and Fisheries*. New York: Academic Press, p. 373.
- Daskalov, G. (1999) Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. *Fish. Res.* **41**:1–23.
- Diaz, F., Raimbault, P. and Conan, P. (2000) Small-scale study of primary productivity during spring in a Mediterranean coastal area (Gulf of Lions). *Cont. Shelf Res.* **20**:975–996.
- Downton, M.W. and Miller, K.A. (1998) Relationships between Alaskan salmon catch and North Pacific climate on interannual and interdecadal time scales. *Can. J. Fish. Aquat. Sci.* **55**:2255–2265.
- Estrada, M. (1996) Primary production in the northwestern Mediterranean. *Sci. Mar.* **60**(Suppl. 2):55–64.
- Estrada, M., Vives, F. and Alcaraz, M. (1985) Life and the productivity of the open sea. In: *Key Environments: Western Mediterranean*. R. Margalef (ed.) London: Pergamon Press, pp. 148–197.
- Fogarty, M.J. (1988) Time series models of the Maine lobster fishery: the effect of temperature. *Can. J. Fish. Aquat. Sci.* **45**:1145–1153.
- Fromentin, J.M., Stenseth, N.C., Gjøsaeter, J., Bjørnstad, O., Falk, W. and Johannessen, T. (1997) Spatial patterns of the temporal dynamics of three gadoids species along the Norwegian Skagerrak coast. *Mar. Ecol. Prog. Ser.* **155**:209–222.
- Grimes, C.B. (2001) Fishery production and the Mississippi river discharge. *Fisheries* **26**:17–26.
- Hare, S.R. and Francis, R.C. (1995) Climate change and salmon production in the Northeast Pacific Ocean. In: *Climate Change and Northern Fish Populations*. R.J. Beamish (ed.). *Can. Spec. Publ. Fish. Aquat. Sci.* **121**:357–372.
- Houde, E.D. (1987) Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* **2**:17–29.
- Keller, A. (1987) Modeling and forecasting primary production rates using Box-Jenkins transfer function models. *Can. J. Fish. Aquat. Sci.* **44**:1045–1052.
- Lefevre, D., Minas, H.J., Minas, M., Robinson, C., Williams, P.J. and Woodward, E.M.S. (1997) Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions. *Deep-Sea Research II* **44**:801–832.
- Levi, D., Bonanno, A., Patti, B. and Mazzola, S. (1999) A preliminary study of the influence of the river Po (northern Adriatic) in predictions of commercial anchovy (*Engraulis encrasicolus*) catch using Fuzzy logic. In: *III SAP (Sustainable fisheries) Meeting*, Hamburg, 6–10 April 1999 (<http://www.ifm.uib.no/sap>). Last accessed 20 December 2003.
- Lloret, J., Leonart, J. and Solé, I. (2000) Time series modelling of landings in Northwest Mediterranean Sea. *ICES J. Mar. Sci.* **57**:171–184.
- Lloret, J., Leonart, J., Solé, I. and Fromentin, J.M. (2001) Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. *Fish. Oceanogr.* **10**:33–50.
- Makridakis, S. and Wheelwright, S. (1989) *Forecasting Methods for Management*, 5th edn. New York: John Wiley & Sons Inc., p. 320.
- Margalef, R. (1968) Fluctuaciones de varios años de período medio en la producción de fitoplancton en el Mediterráneo occidental. *Collectanea Botanica* **VII**:Fasc. II, No. 41, pp. 117–130.
- Margalef, R. (1985) Introduction to the Mediterranean. In: *Key Environments: Western Mediterranean*. R. Margalef (ed.) London: Pergamon Press, pp. 1–16.

- Morovic, M. (2002) Seasonal and interannual variations in pigments in the Adriatic Sea. *Proc. Indian Acad. Sci. (Earth Planet. Sci.)* **111**:215–225.
- Myers, R.A. and Cadigan, N.G. (1993) Density-dependence juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.* **50**:1576–1590.
- Olivar, M.P., Salat, J. and Palomera, I. (2001) A comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **217**:111–120.
- Palomera, I. (1991) Vertical distribution of eggs and larvae of *Engraulis encrasicolus* in stratified waters of the western Mediterranean. *Mar. Biol.* **111**:37–44.
- Palomera, I. (1992) Spawning of anchovy *Engraulis encrasicolus* in the northwestern Mediterranean relative to hydrographic features in the region. *Mar. Ecol. Prog. Ser.* **79**:215–223.
- Palomera, I. and Olivar, M.P. (1996) Nearshore ichthyoplankton off the Costa Brava (northwest Mediterranean Sea). *Publ. Espec. Inst. Esp. Oceanogr.* **22**:71–75.
- Pankratz, A. (1991) *Forecasting with Dynamic Regression Models*. New York: John Wiley & Sons Inc., p. 386.
- Pertierra, J.P. and Lleonart, J. (1996) NW Mediterranean anchovy fisheries. *Sci. Mar.* **60**:257–267.
- Prat, A., Gómez, V., Solé, I. and Catot, J.M. (2001) *ForeTESS, System for Automatic Seasonal Adjustment and Forecasting of Time Series*. Barcelona: Department of Statistics, High School of Engineering, Polytechnical University of Catalonia.
- Quiñones, R.A. and Montes, R.M. (2001) Relationship between freshwater input to the coastal zone and the historical landings of the benthic/demersal fish *Eleginops maclovinus* in central-south Chile. *Fish. Oceanogr.* **10**:311–328.
- Regner, S. (1996) Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. *Sci. Mar.* **60**:167–177.
- Sabatés, A., Salat, J. and Olivari, M.P. (2001) Advection of continental water as an export mechanism for anchovy (*Engraulis encrasicolus*) larvae. *Sci. Mar.* **65**:15–28.
- Salat, J. (1996) Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Sci. Mar.* **60**(Suppl. 2):21–32.
- Salat, J., Garcia, M.A., Cruzado, A., Palanques, A., Arín, L., Gomis, D., Guillén, J., de León, J., Puigdefàbregas, J., Sospedra, J. and Velásquez, Z.R. (2002) Seasonal changes of water mass structure and shelf-slope exchanges at the Ebro Shelf (NW Mediterranean). *Cont. Shelf Res.* **22**:327–348.
- Skreslet, S. (1976) Influence of freshwater outflow from Norway on recruitment to the stock of Arcto-Norwegian cod. In: *Freshwater on the Sea*. S. Skreslet, R. Leinebo, J.B.L. Mathews & E. Sakshaug (eds) Oslo: The Association of Norwegian Oceanographers, pp. 233–237.
- Solic, M., Krstulovic, N., Marasovic, I., Baranovic, A., Pucher-Petkovic, T. and Vucetic, T. (1997) Analysis of time series of planktonic communities in the Adriatic Sea: distinguishing between natural and man-induced changes. *Oceanologica Acta* **20**:131–143.
- Stergiou, K.I., Christou, E.D. and Petrakis, G. (1997) Modelling and forecasting monthly fisheries catches: comparison of regression, univariate and multivariate time series methods. *Fish. Res.* **29**:55–95.
- Sutcliffe, W.H. (1973) Correlations between seasonal river discharge and local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St Lawrence. *J. Fish. Res. Bd. Can.* **30**:856–859.
- Tsai, C.F., Chen, P.Y., Chen, C.P., Lee, M.A., Shiah, G.Y. and Lee, K.T. (1997) Fluctuation in abundance of larval anchovy and environmental conditions in coastal waters off southwestern Taiwan as associated with the El Niño-Southern Oscillation. *Fish. Oceanogr.* **6**:238–249.
- Tudela, S. and Palomera, I. (1997) Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). *Mar. Ecol. Prog. Ser.* **160**:121–134.
- Tudela, S., Palomera, I. and Quilez, G. (2002) Feeding of anchovy *Engraulis encrasicolus* larvae in the northwest Mediterranean. *J. Mar. Biol. Ass. UK* **82**:349–350.
- Whitehead, P.J.P. (1985) FAO species catalogue. Clupeoid fishes of the world. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1 – Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fish. Synop.* **7**:303.
- Yáñez, E., Barbieri, M.A., Silva, C., Nieto, K. and Espíndola, F. (2001) Climate variability and pelagic fisheries in northern Chile. *Prog. Oceanogr.* **49**:581–596.