Hydrobiologia (2008) 612:185–199
DOI 10.1007/s10750-008-9482-1

FISH HABITAT MAPPING

European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005

Paloma Martín · Nixon Bahamon · Ana Sabatés · Francesc Maynou · Pilar Sánchez · Montserrat Demestre

Abstract Generalized additive models are proposed for a better understanding of the underlying mechanisms for anchovy variations in abundance. Environmental variables derived from satellite imagery (surface chlorophyll, sea surface temperature and wind-mixing index), river discharge (Rhône River and Ebre River) and anchovy landings (landings per unit of effort) as proxy for abundance were used, and three fishing zones were defined along the Catalan Coast. A time shift among wind index mixing, sea surface temperature and chlorophyll was observed for these variables to be significantly correlated with anchovy. Results pointed out to processes that appear to greatly influence species abundance and affect different life stages of anchovy (conditions preceding reproduction, larvae growth and survival and recruits growth). A high proportion of anchovy LPUE variability could be explained by environmental variables. Thus, some univariate models explained deviance are more than 50%, even up to around 70% of anchovy variability. In several cases the deviance explained by a given variable was even higher at the longer time-lags. Among all univariate and bivariate models fitted, the model that best explained anchovy LPUE variability, 79% of total deviance, was a model proposed for the central zone, based on the additive effect of surface chlorophyll and Rhône River discharge, considering time lags of 15 and 18 months, respectively, for each variable.

Keywords *Engraulis encrasicolus* · NW Mediterranean · Environmental conditions · Anchovy landings · GAM

Guest editor: V. D. Valavanis
Essential Fish Habitat Mapping in the Mediterranean

P. Martín (✉) · N. Bahamon · A. Sabatés · F. Maynou · P. Sánchez · M. Demestre
Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas, P. Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain
e-mail: paloma@icm.csic.es

Introduction

The European anchovy (*Engraulis encrasicolus* L. 1758) is widely distributed in the whole Mediterranean Sea and constitutes one of the main fishing resources. In the western basin, anchovy landings show a decreasing trend since the early 1990s. This is not, though, a common trend for the anchovy landings around the Mediterranean (for example, anchovy landings in the Italian coast, the bulk of which is captured in the Adriatic Sea, started an increasing trend since early 1990s; FAO Fish Stat Dataset).

Life history traits of small pelagic fishes (high mobility, plankton based food chains and short life span) make them particularly sensitive to environmental forcing. Populations of small pelagic fishes, such as sardine and anchovy, show evidence of important natural fluctuations in their abundance (Lluch-Belda et al., 1989). These fluctuations seem to be related, among other factors, to climate variability (e.g. Beamish, 1995; Bakun, 1996; Alheit & Hagen, 1997; Sabatés et al., 2006). The timing of seasonal spawning peak and the location of the anchovy spawning grounds are generally associated with months/areas of high productivity, and specifically with conditions favouring adult feeding (Somarakis et al., 2004). Although overfishing has played a role in many of the major declines of small pelagic stocks, environmental variability is also thought to be a key contributor to this extreme population variability (e.g. Bakun, 1996; Cury et al., 2000; Boyer et al., 2001). Research effort has been oriented to demonstrate the importance of environmental factors on recruitment variability (e.g. Bakun & Parrish, 1991; Borja et al., 1996; Cole & McGlade, 1998; Alheit & Hagen, 1997; Bakun & Broad, 2003).

Previous studies conducted in the Mediterranean have focussed on anchovy biology and yield variability, and their link with environmental conditions, which may affect different life stages. Thus, habitat conditions have been related with anchovy growth, reproduction, abundance, recruitment and landings (see, among others, Lloret et al., 2001, 2004; Basilone et al., 2004, 2006; Patti et al., 2004; García Lafuente et al., 2005; Santojanni et al., 2006).

The main spawning areas of anchovy in the northwestern Mediterranean are located in the vicinity of the mouths of the two largest rivers in the region, the Rhône and the Ebre (Palomera & Sabatés, 1990; Palomera, 1992; García & Palomera, 1996). Larvae have been found strongly associated with the presence of less saline water (Palomera, 1992; Sabatés et al., 2001; Coombs et al., 2003). Anchovy displays different spawning duration, which can be related to differential latitudinal sea surface temperature (Sabatés et al., 2007a; Zarrad et al., 2006). Along the Catalan coast, spawning starts earlier in the southern part, where lasts for several months from April to October (peak in May–June), gradually spreading northwards (peak June–July) (Palomera, 1992). Trophic studies of adult anchovy and larvae have shown that this species feeds on small zooplankton. The main prey of adults are copepods, and to a lesser extent, molluscs, cladocerans, other crustaceans and appendicularians (Tudela & Palomera, 1995, 1997; Plounevez & Champalbert, 2000), while stomach contents of larvae consist mostly of copepod eggs, nauplii and copepodites (Tudela et al., 2002).

In 2005, anchovy annual landings in the Catalan Coast were around 3,800 ton and the purse seining fleet consisted of 112 vessels (DGPAM fishing statistics and fleet census, the General Direction of Fishing and Maritime Affairs of the Catalan Government). The number of vessels operating in summer during the anchovy season can be higher, given that the fleet from southern ports beyond the study area moves northwards as the anchovy season advances, operating also into the Gulf of Lions.

Anchovy landings, as in other Mediterranean areas, depend on recruitment success and fish growth (Pertierra & Lleonart, 1996; Patti et al., 2004; Santojanni et al., 2006). Therefore, changes in environmental conditions at different life stages are likely to be reflected in the short term in the landings.

The present study addressed the definition of the conditions characterizing the anchovy essential fish habitat (EFH) in the Catalan coast, using environmental variables derived from satellite imagery, river discharge data, and landings (landings per unit of effort) as proxy for abundance. The aim is to elucidate to what extent anchovy landings variation can be explained by environmental conditions.

Materials and methods

Study area

The Catalan coast is located in the NW Mediterranean Sea, south of the Gulf of Lions (Fig. 1). The northern sector, which is more directly influenced by strong northerly winds, is generally colder than the central and southern parts and a surface thermal front roughly coincides with the limit of frequent northerly winds (López García et al., 1994). The Catalan coast is characterized by a continental shelf, which is, in general, quite narrow. It widens clearly in the southernmost part, in the vicinity of the Ebre River Delta, and in the north between the main submarine canyons, south of the Gulf of Lions. Input of continental water plays an important role in this region. The southern shelf receives a significant river outflow from the Ebre River, while the northern areas are affected by the outflow of the Rhône River, the

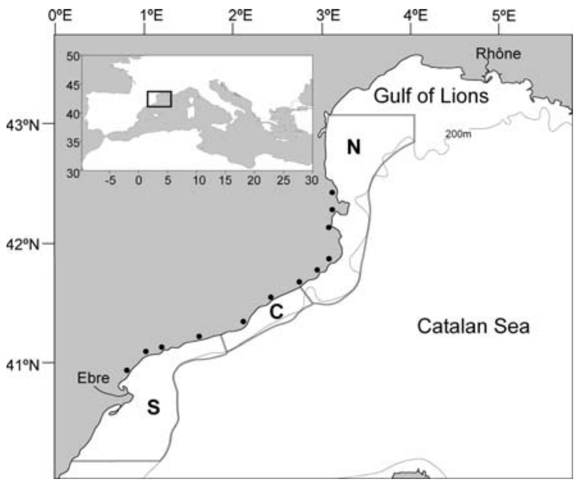


Fig. 1 Study areas showing the three defined zones along the Catalan Coast, North (N), Centre (C) and South (S). The dots indicate the fishing ports located in each zone

largest river in the Western Mediterranean basin, which outflows into the Gulf of Lions.

Considering the physical features along the Catalan coast and the daily displacements of the purse-seining fleet, three zones, limited by the 200 m depth isobath, are defined in the study area (North, Centre and South). This is due to the fact that, although the landings data are obtained daily by port, fleets travel to fishing grounds which are shared by different ports, thus the geographical origin of the landings cannot be ascertained with precision.

Data

We have considered the following as the main environmental variables determining anchovy abundance: chlorophyll (as an indicator of primary production, given that anchovy is a plankton feeder species); sea surface temperature (temperature is known to determine the species distribution, trigger maturation and enhance growth of larvae); wind (wind is known to play a major role in the processes of water mixing and local fertilization); and Rhône and Ebre Rivers flow rates (as anchovy is known to be associated with river plume during spawning and waters rich in nutrients and low salinities).

Data on mean monthly values of surface chlorophyll-a (CHL; mg m^{-3}), sea surface temperature (SST; °C), and wind speed (m s^{-1}), in each of the three zones considered were extracted from the environmental database developed in the frame of the EnviEFH project, through an ad hoc protocol designed in ArcGIS 9.2 environment. The cube of the wind speed (WI) was used as an index of wind-induced turbulent mixing that is independent of the wind direction, and has been used in a number of ecological studies (Ueyama & Monger, 2005; Lloret et al., 2004). Average monthly flow rates (m^3 s^{-1}) at the mouth of Rhône River (RR) and Ebre River (ER), 2000–2005, were obtained from Compagnie Nationale du Rhône—Station Beaucaire and Confederación Hidrográfica del Ebre—Station Tortosa.

Daily anchovy landings, per vessel and port, along the Catalan Coast, during 2000–2005 (75181 records on anchovy daily landings in total), were obtained from the DGPAM fishery statistics. During this period fishing effort has not displayed any marked inter-annual variations (around 12500 ± 1500 fishing days per year with records of anchovy landings; DGPAM fishing statistics). As anchovy is caught during spring/summer, when most of the individuals are 1-year old (Pertierra & Lleonart, 1996), landings of anchovy can be considered as a proxy for annual recruitment strength. Anchovy is a high valued species, and discards are considered to be negligible, hence landing per unit of effort (LPUE; kg per day and vessel) is assumed to be a proxy of the species abundance. Data on daily landings from ports included in each zone were merged and monthly LPUE were estimated by zone.

Statistical analyses

The decomposition of the monthly anchovy LPUE time series by zone is based on loess smoothing (Cleveland et al., 1990), allowing the identification of the seasonal pattern and trend during 2000–2005.

For each zone, time-lagged cross-correlations were performed between anchovy LPUE and CHL, SST and WI; RR was cross-correlated with anchovy LPUE from north and central zones; and ER was cross-correlated with anchovy LPUE from the southern zone. The partial correlation coefficient was estimated by fitting autoregressive models of successively higher orders up to 24-month lag. The lags showing the highest significant correlations between LPUE and individual variables were chosen for further hypothesis validation using generalized additive models (GAMs).

The influence of the environmental variables on the anchovy LPUE was modelled using a log-Gaussian link function in generalized additive models (Hastie & Tibshirani, 1990). GAMs extend the generalized linear model (GLM) by replacing the linear predictors by the sum of non-parametric smoothing spline functions of the covariates (environmental variables) plus a conventional parametric component of the linear predictor. The non-parametric curves are estimated iteratively, cycling through the predictors until the optimal multivariate fit is reached using back-fitting algorithms. The GAMs used in the analysis has the form:

$$y = \beta_0 + \sum_{j=1}^{p} f_j(X_j) + \varepsilon$$

where β_0 is the intercept; the covariates (X_j) can be just one variable (univariate model) or a number of them (p) (multivariate model) and the function f_j is the cubic spline (specific for each covariate) representing the nonparametric term of the equation. The cubic spline function makes the difference with the linear models; ε is the error term. The link function is the log of the response variable. The candidate predictors are the environmental variables: mean monthly values of CHL, SST and WI, as well as Rhône River discharges for models in the north and central zones, and Ebre River discharges for models in the south zone.

In order to ensure that the overall level of smoothing is optimal, and to guard against trapping by local minima, a highly efficient global minimization with respect to an overall smoothing parameter is made at each iteration, based on mgcv algorithm (Wood, 2000).

Model predictors were tested for statistical significance ($P \leq 0.05$). The model deviance explained by individual predictors (e.g. time-lagged CHL) was compared against the deviance of models with combined predictors (e.g. time-lagged CHL + time-lagged SST). Step-wise selection was applied to select the best models. The best model combination was that representing the largest (total) amount of deviance, having all terms in the equation below a significant level ($P \leq 0.05$) of deviance reduction. The total deviance compares the fit of the saturated model to the null model, thus, expresses the total variability around a fitted line which can be decomposed to explained and unexplained (error) variability. Other criteria (used in package mgcv in R, www.R-project.org) were also taken into account to select the best model: the smaller the gradients at convergence, the better; model residual closer to normal distribution the better; and definite positive Hessian that if not positive then some of covariates could be highly collinear or show very high variance.

Results

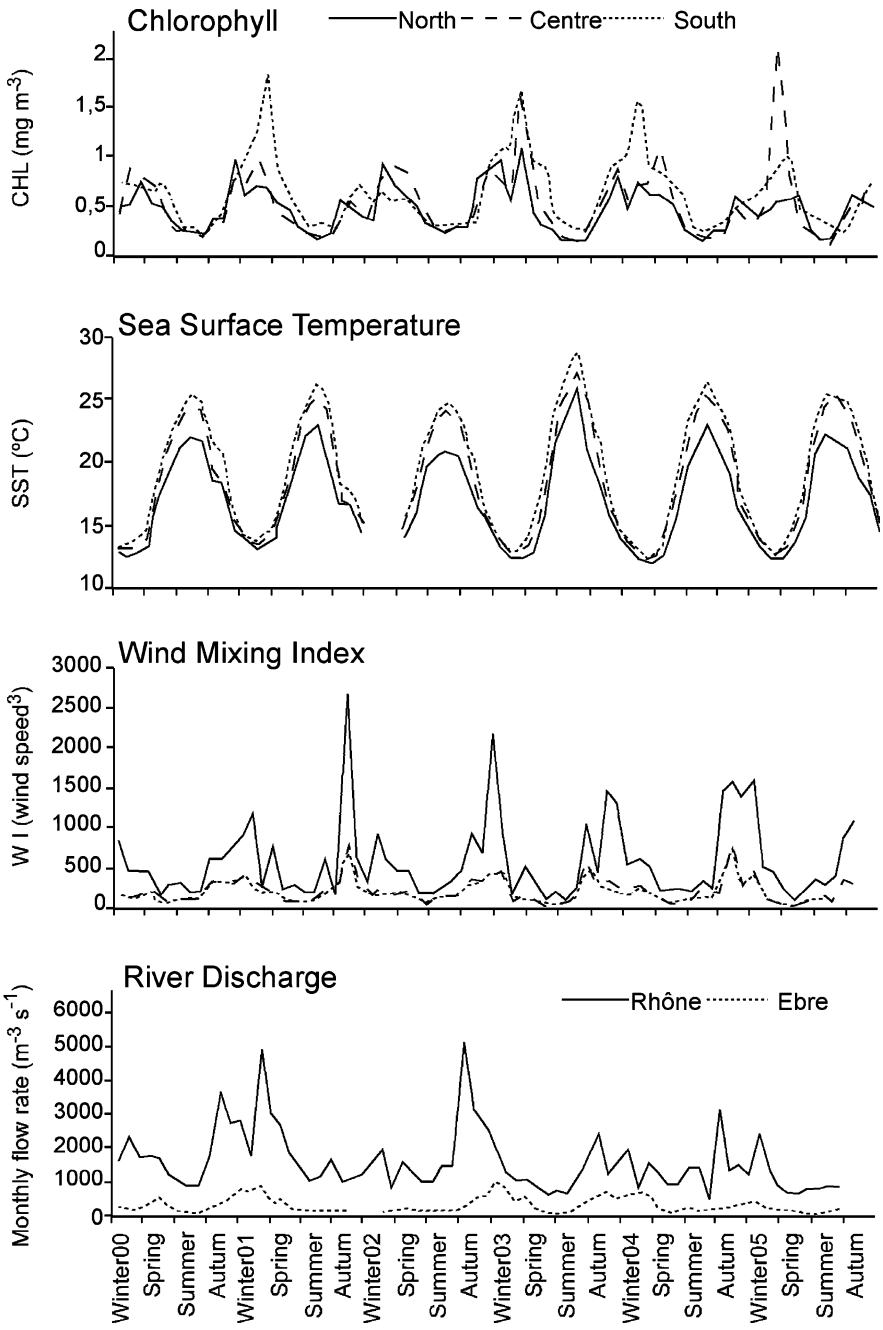
Environmental conditions along the Catalan Coast

Figure 2 shows the data used in the analyses, by variable, quarter and zone. Chlorophyll peaked in winter, and a secondary peak was also observed in autumn. The southern zone appeared to be the most productive, although highest values were attained in the central zone in March 2005. Sea surface temperature exhibited a clear seasonal pattern, with peaks in summer. Latitudinal differences were also observed: while in the colder months (winter) SST was similar in the three zones considered, in summer maximum values were lower in the northern zone and highest in the south. Wind-mixing index was clearly highest in the northern zone, with peaks in winter and autumn (secondary); the central and south zones exhibited the same pattern and values. As for Rhône and Ebre River's monthly flow, the reservoirs constructed in the river basins have modified their natural pattern, diminishing seasonal variations. Rhône River discharge is much larger than that of Ebre, and peaks were observed in autumn and winter, but also in spring, whereas Ebre flow peaks were observed mainly in winter.

Anchovy LPUE seasonal pattern

Overall landings during 2000–2005 were higher in the northern zone. The decomposition of anchovy LPUE data series allowed the identification of the seasonal pattern, which differed among zones (Fig. 3). Thus, highest LPUE during the year was reached first in the southern zone (peak in May–June), gradually expanding northwards (peak in July in central zone and in June–September in north zone). Moreover, it was in the southern zone that the anchovy LPUE seasonal pattern was more distinct

Fig. 2 Monthly means of surface chlorophyll concentration, sea surface temperature, wind-mixing index, and Rhône and Ebre Rivers discharge, by quarter and zone, during 2000–2005



(lowest remainder of the decomposition of LPUE data series). Trends of LPUE during 2000–2005 in the central and south zones were similar, with maximum values attained in summer 2002. The north zone showed high landings over the whole period, especially between 2001 and 2003.

Time-lagged cross-correlations

Time-lagged cross-correlations between anchovy LPUE and environmental variables provided a first approach to potential optimal conditions for anchovy abundance. A seasonal pattern prevailed for most

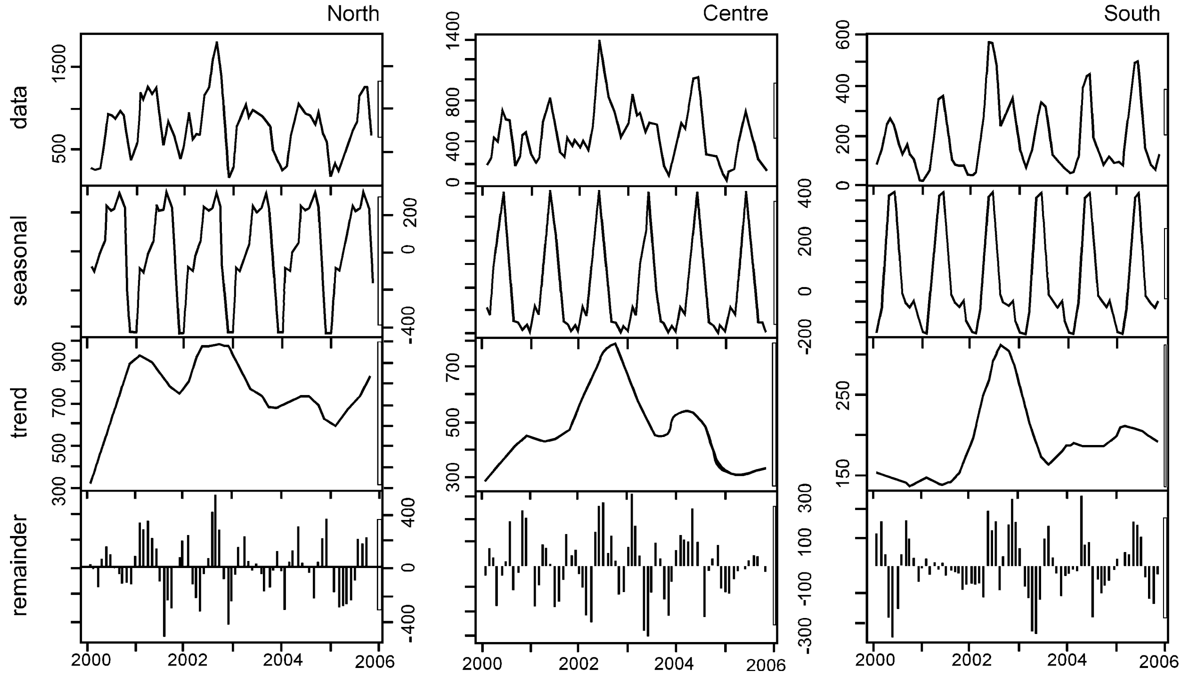


Fig. 3 Decomposition of the monthly anchovy landings time series (2000–2005), in zones North, Centre and South: data, seasonal pattern, trend and remainder

paired cross-correlations (Table 1, results related with Tables 2 and 3). Maximum positive and negative correlations generally alternated every 6 months. Furthermore, the correlations in the months preceding and following the month with highest correlation (the time-lags mentioned below) were also significant, thereby pointing not only to a given month, but to a 2–3-months period when the correlation between anchovy and a given variable was significant. CHL in the northern zone showed the highest positive correlations with time lags of 5 and 18 months, and negative correlations with 0 and 12 months lag. In the central and southern zones, the pattern was similar, the highest positive correlations were estimated at 3 and 15-months lag, whereas the highest negative correlations were observed at 8–9 months lag. SST showed the highest correlations in northern zone at 0, 5, 12 and 18 months-lag; 3, 10 and 15 months lag in central zone; and 4, 10 and 16 months in southern zone. As for WI, the time lag for the variable to be significantly correlated with anchovy was longer than in the case of CHL, and of the same sign. In the north, Rhône River discharges showed the highest (positive) correlation at 18-month lag; the same correlation pattern was observed in the central zone. In the south, the Ebre River discharges showed the highest (positive) correlation with anchovy at 14-month lag.

Modelling approach using GAMs

The different time response of anchovy LPUE to the environmental conditions by zone was validated by fitting univariate and multivariate GAMs (Tables 2 and 3). The time lags of the environmental variables showing the highest correlations with anchovy LPUE were used to GAM development.

In the univariate models, i.e. anchovy LPUE fitted against single environmental variables, the deviance explained by the models was generally higher in the south zone than in the central and north zones indicating a stronger association of the environmental conditions and anchovy landings (Table 2). The models with non-lagged environmental conditions explained very low deviance of the anchovy LPUE series, and in some cases the environmental variable was not significant (not shown here).

Some univariate models explained a large amount of the model deviance (more than 50%, even up to around 70%). In several cases the deviance explained by a given variable was even higher at the longer

Table 1 Lagged cross-correlations between monthly anchovy LPUE and chlorophyll (CHL), sea surface temperature (SST), and wind-mixing index (WI), in zones North (1), Central (2) and South (3), as defined in Fig. 1

	Lag (months)																				
	−20	−19	−18	−17	−16	−15	−14	−13	−12	−11	−10	−9	−8	−7	−6	−5	−4	−3	−2	−1	0
CHL1	0.22	**0.36**	**0.44**	**0.37**	0.26	−0.01	−0.20	**−0.37**	**−0.40**	**−0.37**	**−0.35**	−0.22	−0.03	**0.25**	**0.44**	**0.51**	**0.47**	**0.24**	−0.07	**−0.33**	**−0.43**
CHL2	−0.23	−0.12	0.04	0.17	**0.32**	**0.34**	0.26	0.04	−0.15	**−0.27**	**−0.35**	**−0.36**	**−0.37**	−0.22	−0.02	0.19	**0.42**	**0.54**	**0.43**	0.16	−0.15
CHL3	−0.21	−0.04	0.17	**0.39**	**0.57**	**0.62**	**0.45**	0.17	−0.16	**−0.40**	**−0.57**	**−0.57**	**−0.46**	−0.23	0.04	**0.27**	**0.44**	**0.47**	**0.33**	0.04	**−0.25**
SST1	−0.15	**−0.36**	**−0.48**	**−0.48**	**−0.33**	−0.08	0.16	**0.33**	**0.42**	**0.43**	**0.37**	0.21	−0.04	**−0.31**	**−0.51**	**−0.56**	**−0.44**	−0.18	0.11	**0.36**	**0.52**
SST2	**0.28**	0.08	−0.13	**−0.32**	**−0.46**	**−0.48**	**−0.39**	−0.14	0.17	**0.45**	**0.56**	**0.49**	**0.29**	0.06	−0.18	**−0.39**	**−0.56**	**−0.57**	**−0.44**	−0.14	0.20
SST3	**0.28**	0.01	−0.23	**−0.42**	**−0.52**	**−0.51**	**−0.38**	−0.12	0.23	**0.54**	**0.69**	**0.59**	**0.32**	−0.03	**−0.34**	**−0.55**	**−0.64**	**−0.59**	**−0.41**	−0.10	**0.28**
WI1	**0.27**	**0.29**	0.23	0.17	0.03	−0.16	**−0.32**	**−0.44**	**−0.31**	−0.10	0.11	0.22	**0.29**	**0.33**	0.21	0.17	−0.02	−0.10	**−0.32**	**−0.46**	**−0.40**
WI2	0.11	0.22	**0.28**	**0.34**	**0.27**	0.14	−0.07	−0.22	**−0.30**	**−0.38**	**−0.29**	−0.13	0.19	**0.40**	**0.43**	**0.29**	0.19	0.06	−0.07	**−0.27**	**−0.39**
WI3	0.20	**0.38**	**0.40**	**0.33**	0.18	0.02	−0.11	−0.23	**−0.31**	**−0.37**	**−0.33**	−0.18	0.16	**0.45**	**0.62**	**0.49**	**0.24**	0.00	−0.22	**−0.34**	**−0.40**
RR1	0.20	**0.33**	**0.38**	**0.36**	0.25	0.08	−0.15	−0.23	−0.24	−0.19	−0.16	−0.14	0.00	0.10	0.22	**0.26**	**0.24**	0.13	−0.11	**−0.26**	−0.21
RR2	0.16	**0.41**	**0.52**	**0.47**	**0.44**	**0.40**	0.25	0.05	−0.16	**−0.29**	**−0.38**	**−0.28**	−0.16	0.00	0.07	0.14	0.17	0.22	0.17	0.07	−0.11
ER3	−0.23	−0.11	0.10	0.26	**0.45**	**0.52**	**0.54**	**0.38**	0.11	−0.21	**−0.43**	**−0.53**	**−0.47**	**−0.31**	−0.07	0.15	**0.26**	**0.25**	0.13	−0.02	−0.21
d.f.	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70

In addition, Rhône River discharge (RR) was cross-correlated with anchovy LPUE in zones North (1) and Central (2), and Ebre River discharge (ER) was cross-correlated with anchovy LPUE in zone South (3) (n = 72 months; in bold, significant $P < 0.05$)

Table 2 Model deviance (%) of monthly anchovy LPUE explained by univariate GAMs

Zone	Environmental variable											
	CHL			SST			WI			River discharge		
	Time Lag		Model deviance	Time Lag		Model deviance	Time Lag		Model deviance	Time Lag		Model deviance
North	5	(+)	37.8	5	(−)	36.9	7	(+)	17.6	5	(+)	16.9 RR
	12	(−)	21.4	12	(+)	23.9	13	(−)	29.3			
	18	(+)	40.5	18	(−)	41.1	19	(+)	25.4	18	(+)	22.9RR
Central	3	(+)	44.9	3	(−)	34.8	6	(+)	19.0			
	8	(−)	15.2	10	(+)	44.1	11	(−)	35.6			
	15	(+)	20.6	15	(−)	34.6	18	(+)	41.3	18	(+)	51.4RR
South	3	(+)	22.5	4	(−)	56.9	6	(+)	42.7	4	(+)	15.3ER
	9	(−)	58.0	10	(+)	69.7	11	(−)	49.2			
	15	(+)	48.3	16	(−)	56.7	18	(+)	64.2	14	(+)	18.9ER

The time lags (month) for the environmental variables are those showing the highest significant *P*-values in the cross-correlation analysis. The sign of the correlation (+ and −) between the environmental variable and anchovy LPUE is indicated

CHL = Chlorophyll (mg/m^3); SST = Sea Surface Temperature (°C); WI = Cubed wind speed (m^3/s^3); RR = Rhône River discharge (m^3/s); ER = Ebre River discharge (m^3/s)

time-lags. It is remarkable that the Rhône River discharge explained 51% (18 months lag) of the total deviance of the model in the central zone. The models proposed for the southern zone, with CHL, SST and WI as predictor variables, at time-lags of 15, 16 and 18 months, respectively, were selected to illustrate our results on univariate GAMs (Figs. 4 and 5). When the response was positive, anchovy LPUE showed a linear relationship with CHL (positive) and SST (negative). In the case of WI, though, the situation was different: linear relationship could be assumed within a certain WI range (aprox. 250–400), beyond which higher WI did not result in increasing LPUE. The model based on WI was the best among these three, explaining better the evolution of anchovy LPUE, including both the maximum LPUE observed in summer 2002 and the secondary LPUE peak in autumn 2002 (64.2% model deviance). The model based on CHL explained well the LPUE peaks, but failed to reproduce 2003 (56.7% model deviance), while the model based in SST explained the seasonality, but showed a lack of fit for LPUE in 2002.

Multivariate GAMs suggested that the maximum number of significant covariates to explain the anchovy LPUE was two. The bivariate models presented here are those combining chlorophyll with another environmental variable (SST, WI and river discharge). Some bivariate models slightly improved the univariate model fitting (Table 3). It is worth mentioning the model proposed for the central zone, where the predictions based on the additive effect of CHL and Rhône River discharge, lagged 15 and 18 months, respectively, explained 79.2% of LPUE deviance (Figs. 6 and 7). GAMs suggested a major role of river discharge as environmental variable explaining anchovy LPUE variance.

Potential optimal environmental ranges defining anchovy EFH

Results evidenced the different timing of the response of anchovy LPUE to environmental conditions and thus, models were proposed for each zone separately. The significant time-lags in northern zone appeared to be longer as compared to those identified in the central and southern zones (Tables 2 and 3). These different time-lags are in fact pointing to the same time of the year. Thus, for example, when considering the time of the year with higher LPUE as starting point to go backwards, 5 months-lag in the northern zone, and 3-months lag in the central and south zones, would point to environmental conditions in winter the same year. Likewise, time lags of 18 months (north zone) and 15 months (central and south zones) would be related with winter the preceding year, and time-

Table 3 Model deviance (%) of monthly anchovy LPUE explained by bivariate GAMs

Zone	Time Lag		Model covariates	Total deviance	Time lag		Model covariates	Total deviance	Time lag		Model covariates	Total deviance
North	(+)	5	CHL	38.1	(−)	12	CHL*		(+)	18	CHL*	44.0
	(−)	5	SST*		(+)	12	SST*		(−)	18	SST	
	(+)	5	CHL*	38.3	(−)	12	CHL*	34.4	(+)	18	CHL	42.1
	(+)	7	WI		(−)	13	WI		(+)	19	WI*	
										18	CHL	43.9
										18	RR	
Central	(+)	3	CHL	45.0	(−)	8	CHL*	45.9	(+)	15	CHL*	37.5
	(−)	3	SST*		(+)	10	SST		(−)	15	SST	
	(+)	3	CHL	58.3	(−)	8	CHL*	39.8	(+)	15	CHL	40.5
	(+)	6	WI		(−)	11	WI		(+)	18	WI	
										15	CHL	79.2
										18	RR	
South	(+)	3	CHL*	58.4	(−)	9	CHL	72.4	(+)	15	CHL	70.2
	(−)	4	SST		(+)	10	SST		(−)	16	SST	
	(+)	3	CHL	43.8	(−)	9	CHL	60.3	(+)	15	CHL	59.0
	(+)	6	WI		(−)	11	WI*		(+)	18	WI	
										15	CHL	48.4
										15	ER	

The time lags (month) for the environmental variables are those showing the highest significant *P*-values in the cross-correlation analysis. The sign of the correlation (+ and −) between the environmental variable and anchovy LPUE is indicated

CHL = Chlorophyll (mg/m^3); SST = Sea Surface Temperature (°C); WI = Cubed wind speed (m^3/s^3); RR = Rhône River discharge (m^3/s); ER = Ebre River discharge (m^3/s)

*Non-significant model covariates ($P > 0.05$)

lags of 10 months in central and south zones and 12 months in the northern zone point to summer the previous year. Our results indicated that high CHL and low SST in winter, preceded by high WI, are conditions favouring anchovy abundance, as well as high river discharge and extended summer conditions. The potential optimal environmental ranges defining anchovy essential fish habitat in the Catalan coast (those matching anchovy LPUE values above the average from best-fitting univariate GAMs) were practically coincidental with the observed monthly values during the season concerned (Table 2 and Figs. 2, 4 and 6). Thus, for example, SST optimal environmental ranges as deduced from best-fitting univariate GAMs were the following, for southern zone: winter-early spring, 12.5–17°C, and summer, 20.5–29.3°C. These ranges reflect the seasonal pattern shown in the time-lagged cross-correlations, maximum positive and negative correlations alternating every 6 months.

Discussion

Anchovy LPUE seasonality

During the time period considered in this study, 2000–2005, anchovy landings displayed certain stability and fishing effort remained at similar level, which facilitates the detection of landings seasonality and the effect of environmental variables on anchovy abundance.

Anchovy LPUE along the year showed a seasonal pattern, characteristic of the species in the Mediterranean. The anchovy fishing season can last for several months (late spring–autumn), but the bulk of the landings concentrate in a shorter period, which can be of only 1–2 months, in spring–summer; landings in winter are lowest. Since anchovy spawns and is caught during spring/summer, when most of the individuals are 1-year old (Pertierra & Lleonart, 1996), the peak of landings corresponds to anchovy

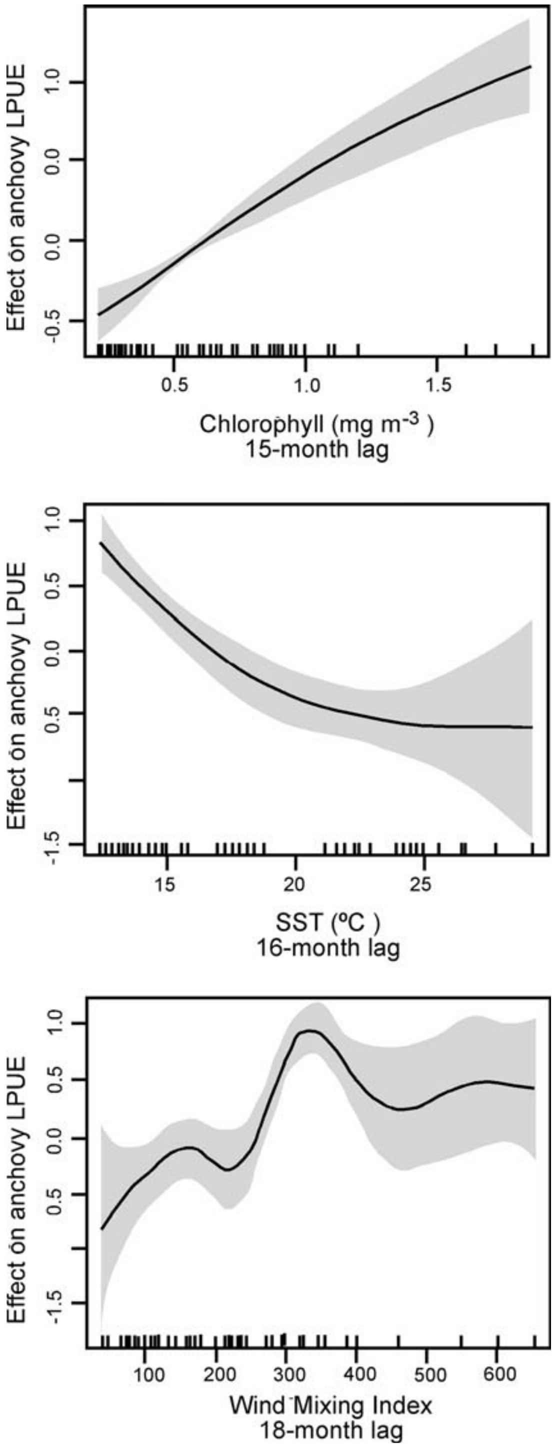


Fig. 4 Univariate GAMs proposed for the southern zone. Effect of surface chlorophyll, sea surface temperature, and wind-mixing index on anchovy LPUE, considering time lags of 15, 16 and 18 months respectively, for each variable (95% confidence intervals shown)

recruitment to the fishery. Landings peak occurs first in the southern zone, later shifting northwards. This pattern would be related with the species reproductive cycle in relation with the sea temperature evolution. Thus, spawning starts in the southern zone, where surface temperature increases earlier than in the north, and extends progressively northwards (Palomera, 1992; Sabatés et al., 2007a). Anchovy reproduction in the Gulf of Lions has been reported to take place in summer (SAC-GFCM, 2007).

Anchovy LPUE and winter conditions in the previous and same years

Our results suggest that windy and colder winters which increase primary production by the end of winter and beginning of spring, before anchovy spawning, would result in higher anchovy landings the following year. The observed shift among WI, SST and CHL for their corresponding time-lags to be significantly cross-correlated with anchovy (WI significant time-lags were advanced with regard to those of SST and CHL) suggests that these variables would be involved in different phases of a same process. From our results, the relationship between anchovy LPUE and WI was positive at 18–19 months-lag (winter preceding spawning the year before the observed landings peak); was negative with SST at 16–18 months-lag; and positive with CHL within 15–18 months-lag (Table 2). Thus, periods with strong winds which favour vertical mixing, correspond with a certain time shift to low temperature and increased primary production. In the western Mediterranean, Estrada (1985) reported that cold years tended to be more productive, partly because winter mixing may reach greater depth, and in part because the formation of deep water (enrichment mechanism of superficial waters) in the Gulf of Lions may occur over a larger area. This enhanced production during cold winters and spring also gives rise to an increase in zooplankton production (Fernández de Puelles et al., 2007). Positive correlations between reproductive investment and prior phytoplankton and zooplankton abundance (food concentration) have been reported in clupeoid species in different geographic areas (e.g. Hay & Brett, 1988; Luo & Musick, 1991; Regner, 1996; Lapolla, 2001; Peebles, 2002). It has been argued that the high productivity may afford adequate

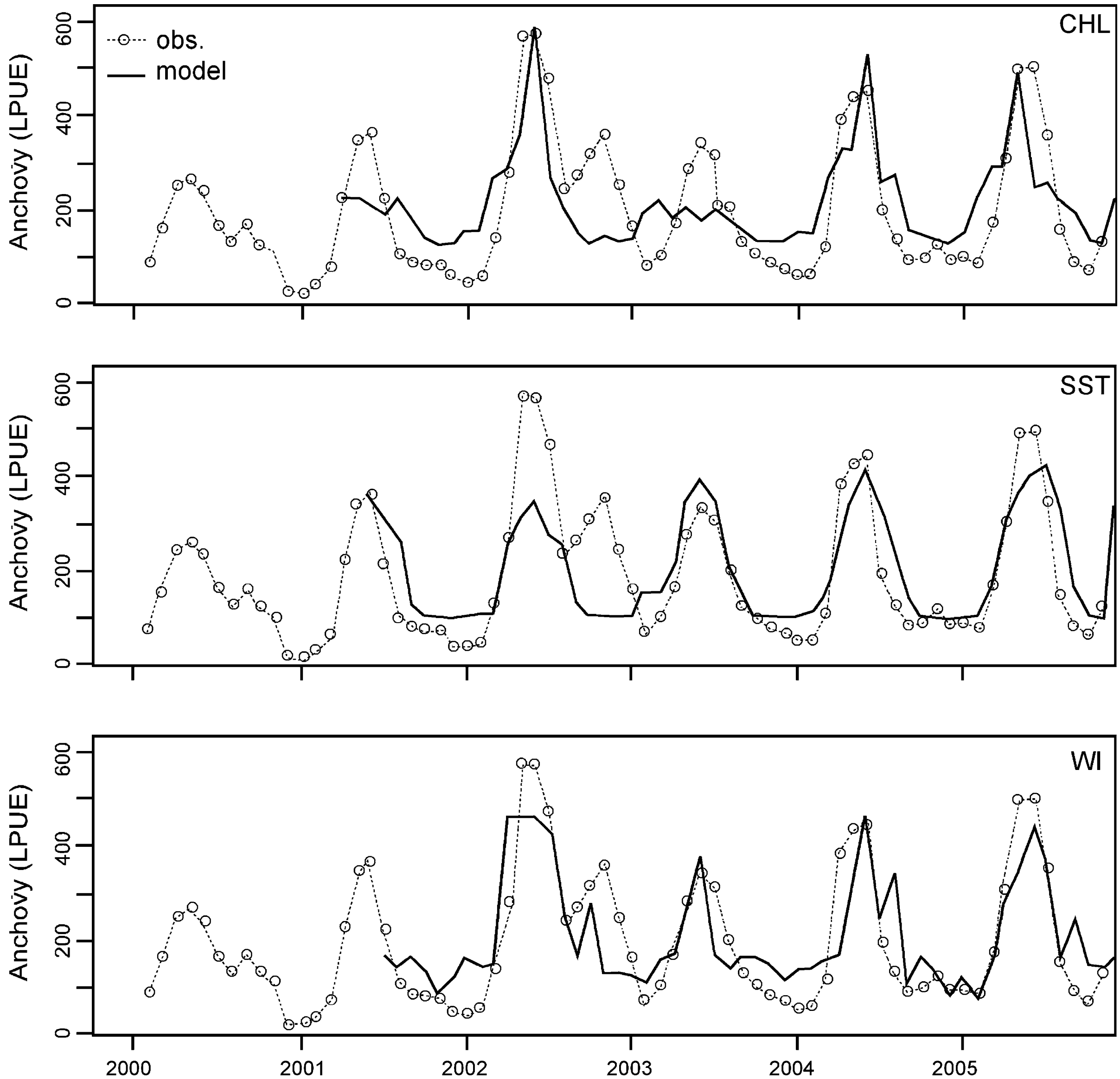


Fig. 5 Univariate GAMs proposed for the southern zone. Model predictions and observed monthly anchovy LPUE, based on surface chlorophyll, sea surface temperature, and wind-mixing index, considering time lags of 15, 16 and 18 months, respectively, for each variable

adult feeding (Blaxter & Hunter, 1982), thereby increasing spawning intensity and affording a suitable habitat for larval development and survival (Castro & Cowen, 1991; Peebles et al., 1996). Within the Mediterranean, Somarakis (2005), in his study conducted in the northern Aegean Sea, emphasized the importance of adult prey availability in determining anchovy egg production. In the Adriatic Sea, Basilone et al. (2006) reported that inter-annual variations of gonadosomatic index of anchovy were mainly governed by changes in the amount of chlorophyll in the period preceding spawning, suggesting that the intensity and seasonality of spawning were governed by oceanographic processes in the months prior to spawning. These processes would be probably associated with prey availability, increase in anchovy energy reserves and gonadal development.

Anchovy abundance and production in the Catalan Coast depends on recruits' growth, as these are the main component of the landings. It has been reported

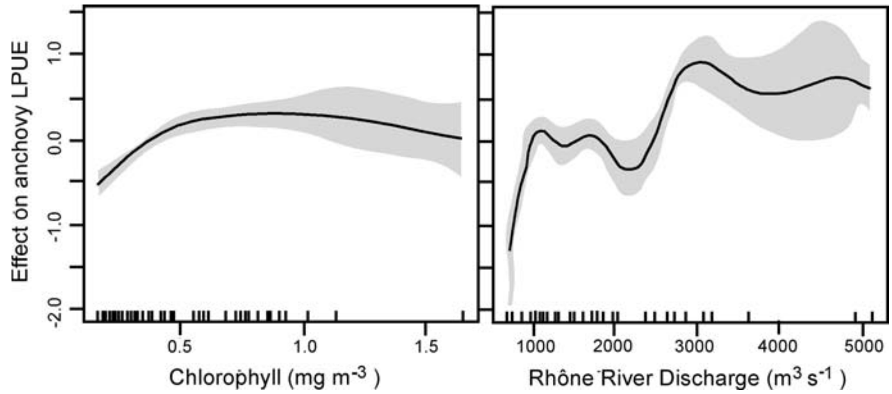


Fig. 6 Bivariate GAM proposed for the central zone. Effect of surface chlorophyll and Rhône River discharge on anchovy LPUE considering time lags of 15 and 18 months respectively, for each variable (95% confidence intervals shown)

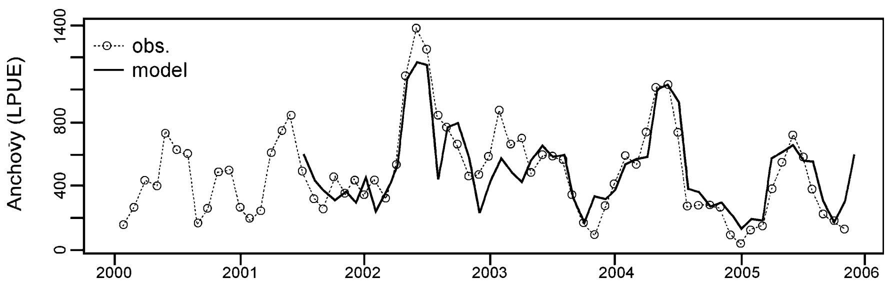


Fig. 7 Bivariate GAM proposed for the central zone. Model predictions and observed monthly anchovy LPUE, based on the additive effect of surface chlorophyll and Rhône River discharge, considering time lags of 15 and 18 months respectively, for each variable

that sea surface estimates of chlorophyll concentrations are good indicators of food availability for anchovy (Basilone et al., 2004). These authors, in line with our results, showed in their studies conducted in the Strait of Sicily a good correspondence between anchovy growth and chlorophyll concentration.

Anchovy LPUE and summer conditions in the previous year

The observed relationships of sea surface temperature, wind mixing index and chlorophyll, with anchovy LPUE at time lags pointing to conditions by the end of summer were of opposite sign to those linked to winter conditions (positive for SST and negative for WI and CHL). In summer, when larvae are in the plankton, high temperature and low wind intensity, which favours the stability of the water column, would allow maintaining larval food patches, associated during the summer period with the deep chlorophyll maximum, located at depths of 40–80 m (Sabatés et al., 2007a). This would favour larvae survival, in line with the water column stability hypothesis proposed by Lasker (1981). Similar to our results, Basilone et al. (2006) indicated that anchovy in the Strait of Sicily have evolved to spawn when seasonal wind speeds are lowest. Temperature would also enhance faster larval growth rate (Palomera et al., 2007), the period when larvae are more vulnerable to mortality by predation being reduced (Bailey & Houde, 1989). In any case, this positive relationship with SST by the end of summer might point to a longer spawning period. Thus, the deviance explained by the univariate models (Table 2, SST) was much higher in the southern zone, and decreased in central and north zones, especially in this last one. This variability would be in line with the observations by Palomera (1992), indicating a longer reproduction period for anchovy in the southern Catalan Coast than in the north.

The above discussed summer conditions, low WI and high SST, are related with low CHL, and, hence, a negative relationship between CHL and anchovy, lacking any significance regarding the species biology, was observed. In fact, in summer chlorophyll at surface is barely detectable, which is a feature of the oligotrophic character of the study area temperate latitude (Estrada, 1985).

Anchovy LPUE and river discharge

This study has shown a positive relationship between anchovy and river discharge for central and north zones with Rhône River, and for the southern zone with Ebre River.

The relationship between river runoff and small pelagic fish production is well established for a number of species in different estuarine areas of the world, e.g. the Mississippi (Grimes, 2001), Black Sea (Daskalov, 1999), and Mediterranean (Lloret et al., 2001, 2004; Santojanni et al., 2006). Waters under the influence of continental run-off are more productive and have higher nutrient, and phytoplankton and zooplankton concentrations than adjacent oceanic waters (Cruzado & Velásquez, 1990; Razouls & Kouwenberg, 1993). Santojanni et al. (2006) indicated that seasonal peaks of phytoplankton production in the northern Adriatic tend to coincide with maximum Po River flow rates in autumn. These authors also found a link between anchovy recruitment and Po River discharge the preceding year. Since anchovy larvae feed mainly on juvenile copepod stages (Tudela et al., 2002) and in the initial developmental stages may also feed on phytoplankton (Lasker, 1975), conditions in the waters under the influence of river discharge would be favourable to anchovy larval development.

Results in the southern zone agree with those by Lloret et al. (2004). These authors pointed out the importance of Ebre River discharges for anchovy production and hypothesized that river runoff influences spawning and the survival rate of the anchovy early stages and, hence, recruitment. Likewise, Lloret et al. (2001) also found anchovy catch and catch per unit of effort in the Gulf of Lions to be significantly correlated with Rhône River flow during the reproductive season, at a time-lag of 13 months. In our study, though, anchovy LPUE in zone north was best explained considering a time-lag of 18 months. An explanation for this difference in the significant time-lags could be that Lloret et al. (2001) considered the river discharge only during the reproduction period. Nevertheless, the relationship between anchovy and river discharge was much more evident in the case of Rhône River flow and the central Catalan Coast (Table 2). This relationship, related with the Rhône River run-off with a 18-months time-lag, corresponds to the winter–spring discharge the preceding year, before the species reproduction in the Gulf of Lions. Thus, higher Rhône discharge in the Gulf of Lions would result in higher landings in fishing grounds located southwards Gulf of Lions. Although this relationship might seem surprising, it has to be taken into account that the Gulf of Lions is one of the main anchovy spawning areas in the NW Mediterranean (García & Palomera, 1996), and, moreover, environmental conditions increasing primary production, as river discharge, would favour adult feeding thereby increasing spawning intensity (Blaxter & Hunter, 1982; Castro & Cowen, 1991; Peebles et al., 1996). Furthermore, recent studies have demonstrated that larvae from the spawning grounds of the Gulf of Lions were transported towards the Catalan coast by the shelf-slope current along the continental slope towards nursery areas (Sabatés et al., 2001; 2007b). Sabatés et al. (2007b) pointed out that the dependence of anchovy population of the Catalan coast on this transport mechanism still has to be determined. Our results suggest that this dependence might be strong and further studies are required to understand the underlying mechanisms driving this relationship.

Conclusions

A high proportion of anchovy LPUE variability could be explained by environmental variables. Results in the three fishing zones in the Catalan Coast pointed to the same processes having a great influence on anchovy abundance, which would affect different life stages of anchovy. These are the following: environmental conditions in winter (period preceding reproduction) and by the end of summer the previous year (larvae growth and survival), and winter conditions some months before the landings peak the same year (recruits growth).

A close link between Rhône River discharge in the Gulf of Lions and anchovy landings in the central fishing zone of the Catalan Coast has been highlighted, thereby supporting previous findings on anchovy larvae advection from the Gulf of Lions.

Acknowledgements We acknowledge the DGPAM, the General Direction of Fishing and Maritime Affairs of the Catalan Government, for providing the data on the anchovy fishery. This study was funded by the EC EnviEFH project (SSP8 Contract Number 022466).

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