

Bioenergetics of small pelagic fishes in upwelling systems: relationship between fish condition, coastal ecosystem dynamics and fisheries

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ABSTRACT: Coastal upwelling ecosystems provide the bulk of the world's fishery yields, but the biochemical ecology of the species that make up these fisheries has, surprisingly, been ignored. Biochemical indicators can provide a mechanistic, ecosystem-based link between population and ecosystem dynamics. Here we investigated long-term, inter-annual changes in the proximate composition and energetic condition of European sardine *Sardina pilchardus* and its relationship with oceanographic conditions in the Western Iberian Upwelling Ecosystem. Energy density (ED) ranged between 4.0 and 14.2 kJ g⁻¹, and the seasonal cycle largely determined temporal variability, explaining >80% of the observed variation. ED variations were also closely linked with water (total R² = 99.0% in whole body; total R² = 95.0% in muscle) and lipid dynamics (total R² = 99.6% in whole body; total R² = 92.5% in muscle). After adjusting for seasonality (rED) and restricting the temporal analysis to the end of the feeding period (August to October), spring/early-summer oceanographic conditions explained 67% of the late-summer energetic peak. Interestingly, the sardine rED peak in year (*t*) explained >54.4% of the variation in the annual catches of year (*t* + 1), indicating that adult energetic condition during spawning is partially translated into the fishery through parental effects in recruitment strength. Our results support earlier findings indicating that sardine population dynamics seem to be controlled by bottom-up effects, but the linkages between population dynamics and patterns in environmental variability via physiological condition seem to have previously been overlooked. We also provide empirical evidence that biochemical assessments during critical periods of the life-cycle of fish are essential in understanding the population dynamics of coastal upwelling ecosystems and in developing a more solid basis for stock management and conservation.

KEY WORDS: *Sardina pilchardus* · Sardines · Proximate composition · Energy density · Western Iberian Upwelling Ecosystem

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INTRODUCTION

Many of the highly productive mid-latitude marine ecosystems, particularly coastal upwelling regions, appear to have a 'wasp-waist' food web, whereby the

bottom and top of the food chain have high species diversity, while the intermediate trophic levels are occupied by only a few small planktotrophic fish species (Cury et al. 2000). Among these species are sardines, epipelagic fishes that form highly dense neritic

shoals and play an important role in the food chain and in the ocean's ecology. They serve as a major prey item for other fish, birds and marine mammals and constitute the major target of pelagic fisheries around the world (Beckley & van der Lingen 1999). Over the last decades, fisheries of small pelagics have experienced dramatic changes in yields and alternating dominance of species (sardine vs. anchovy) around the world (Lluch-Belda et al. 1989). In the Pacific Ocean, these biological regime shifts seem to be associated with multidecadal fluctuations in sea surface temperature, equatorial currents and atmospheric pressure systems (Chavez et al. 2003).

Evidence for the widespread effects of climate variability on fish populations has accumulated in recent years (Attrill & Power 2002, Edwards & Richardson 2004) and, though top-down (consumer-driven) removal of fish biomass can have a strong regulatory effect (e.g. Worm & Myers 2003, Bailey et al. 2006), mid-latitude coastal fisheries appear to be controlled by phytoplankton production (Ware & Thomson 2005, Frank et al. 2006). Yet, the marked variability in the condition of these exploited fish populations appears to be fuelled by current management practices based on abundance, biomass, or landings (Hsieh et al. 2006), but which ignore climate regime shifts and oceanographic variability (Chavez et al. 2003), food supply to adult fishes (Shulman & Love 1999, Shulman et al. 2005) and their energy condition (Dutil & Lambert 2000).

Although biochemical approaches have commonly been used in studies of boreal and polar marine trophic chains (e.g. see review in Dalsgaard et al. 2003), the biochemical ecology of marine food webs from low-latitude temperate zones, where the major pelagic fisheries and upwelling systems are located, has surprisingly been overlooked, and related studies are scarce (Schülein et al. 1995, Paiting et al. 1998). In fact, biochemical indicators can provide major insights into the mechanisms controlling the abundance of small pelagic fishes, since they integrate the impacts of environmental forcing on feeding and are directly linked to fitness, thus offering a powerful complement to traditional indicators (e.g. condition factor).

Here we investigated a more than one decade relationship between the nutritional condition of the European sardine *Sardina pilchardus* and factors of environmental forcing (namely sea surface temperature and Ekman transport) along the western coast of Portugal. Concomitantly, we investigated a potential relationship between inter-annual variations in sardine bioenergetics (based on proximate composition analyses) and reproductive success (recruitment) and catches. The western coastal area of Portugal is situated in the Western Iberian Upwelling Ecosystem

(WIUE), which comprises the northern limit of the Canary Current Upwelling System (1 of the 4 major eastern boundary currents of the world). The main feature of the region is the occurrence of coastal upwelling during spring and summer in response to the intensification of northerly winds (Fiúza et al. 1982). During autumn and winter, southerly and westerly winds prevail, which along with the interaction of a meridional density gradient on the shelf and slope, cause a poleward flow of warm, salty water that constitutes the Iberian Poleward Current (IPC; Relvas et al. 2007). Yet, an increase in the frequency of equatorward winds and upwelling events during winter (Borges et al. 2003) and a steadily weakening of these winds in the main upwelling season (April to September) have also recently been demonstrated (Lemos & Pires 2004).

MATERIALS AND METHODS

Sampling. The present study was performed over a period of 12 yr, beginning in January 1984 and concluding in July 1995. Monthly samples (with few gaps) consisting of 2 groups of 6 to 12 adult sardines *Sardina pilchardus* were taken from a commercial purse seine vessel's catches off the western Portuguese coast, at the fishing port of Peniche (Fig. 1). Since this study was conducted under the framework of a national biotechnological programme that began in 1982 for the 'upgrading of small pelagic fish caught off the Portuguese coast', the size and gender of the specimens analysed were not available. Thus, the bioenergetic models were restricted to relations with the proximate constituents, i.e. without taking fish mass or condition factors into consideration. Nonetheless, acknowledging some of the data-set limitations, the usefulness of long-term data (e.g. oil:meal ratios), collected for industrial/biotechnological purposes, in reconstructing the historical variation in reproductive potential is indisputable (Schülein et al. 1995, Paiting et al. 1998, Marshall et al. 1999). Moreover, although size may influence the chemical characteristics of sardines (Caponio et al. 2004), other studies with small pelagic fish species have revealed no relationship between size (or age) and proximate composition (e.g. Van Pelt et al. 1997, Foy & Paul 1999, Payne et al. 1999, Eder & Lewis 2005). Our most recent findings also show that gender has no effect on lipid dynamics (specifically on total fatty acid accumulation) in adult sardines (Garrido et al. 2008b). During the sampling period, larger sized specimens were always chosen from the monthly catches (M. Pires pers. comm.) and, thus, the 2 monthly groups analysed should adequately characterize the nutritional condition of the non-juvenile sardine popu-

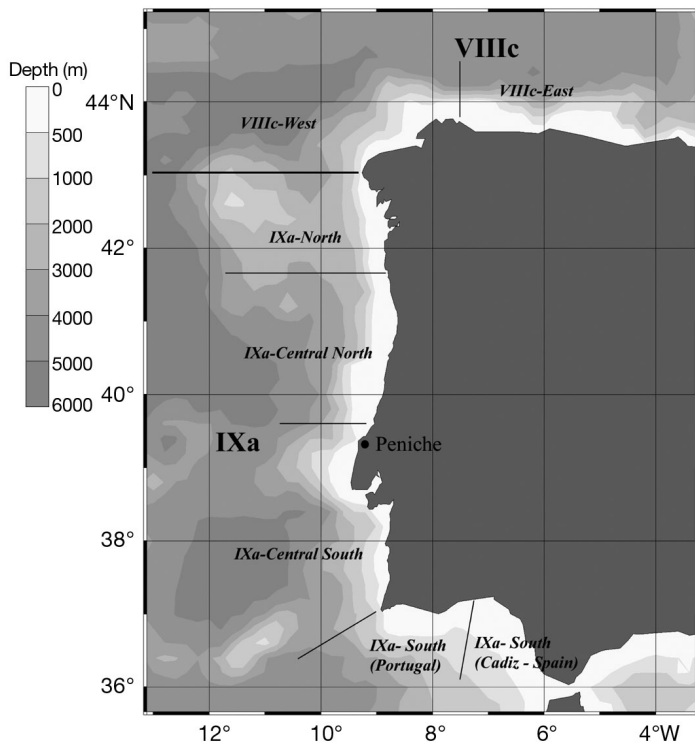


Fig. 1. Sampling location (Peniche) on Portuguese western coast. Subdivisions used by the International Council for the Exploration of the Sea for the Atlanto-Iberian areas are also presented

lation off the western Portuguese coast (sexual maturity occurs mostly between 11 and 17 cm of total length; Silva et al. 2006). To perform biochemical analyses in the muscle, all specimens of 1 group were beheaded and gutted, the bones and skin removed, and the muscle tissues were then pooled and homogenized twice in a common meat grinder. The entire bodies of the specimens in the second group were homogenized. The 2 group samples (designated as muscle and whole body) were stored at -20°C until the biochemical analyses were done (in duplicate for each group every month).

Biochemical analyses. Water, protein, lipid and ash contents were determined according to procedures by the Association of Official Analytical Chemistry (AOAC 1984, 1990). Moisture content was determined by constant-weight drying in an oven at 100°C . Protein levels were ascertained by a modified Kjeldahl method, using the value 6.25 as a conversion factor for total nitrogen content to protein. Fat content was evaluated using the Soxhlet extraction method with ethyl ether, and ash content was determined by incinerating in a muffle furnace at 550°C to constant weight. Since carbohydrate content is generally low in fish and its contribution to the energetic value is negligible (Payne

et al. 1999, Anthony et al. 2000), energy density was estimated by converting proximate constituents based on assumed energy equivalents of 5.65 kcal g^{-1} for proteins and 9.5 kcal g^{-1} for lipids (Winberg 1971). All biochemical values were expressed as means \pm SD.

Environmental data. Monthly values of sea surface temperature (SST) and wind over a $1^{\circ} \times 1^{\circ}$ cell off Peniche (39°N , 10°W), from 1984 to 1995, were provided by the International Comprehensive Ocean Atmosphere Data Set (COADS) (<http://icoads.noaa.gov/products.html>) (Woodruff et al. 1998). The offshore Ekman transport (Q_x), caused by the northern component of the wind stress vector, was computed following Bakun's (1973) formulae:

$$\begin{aligned} Q_x &= -\frac{\tau_y}{\rho_{sw} f} 1000 \\ &= -\frac{\rho_a C_D |v| v}{\rho_{sw} f} 1000 (\text{m}^3 \text{s}^{-1} \text{km}^{-1}) \end{aligned} \quad (1)$$

where ρ_a is the density of air (1.22 kg m^{-3}), C_D is a dimensionless drag coefficient (1.3×10^{-3}), ρ_{sw} is the density of seawater ($\sim 1025 \text{ kg m}^{-3}$), v is the monthly average wind vector with magnitude $|v|$ and f is the Coriolis parameter ($9.175 \times 10^{-5} \text{ s}^{-1}$ for Peniche). The term f was calculated as:

$$f = 2\omega \sin(f_i) \quad (2)$$

where ω is the angular velocity of the earth ($7.29 \times 10^{-5} \text{ s}$) and f_i is the latitudinal position at the place i . Positive values of Q_x indicate upwelling-favourable offshore Ekman transport along the western coast.

Recruitment and landings data. Recruitment (age-0 group; estimated by virtual population analysis) and commercial catch time series data were taken from a publication of the ICES (International Council for the Exploration of the Sea) Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (ICES 2005). It is worth noting that the composition of the commercial catch-at-age of sardines in the study area (western Portugal) shows that juveniles are available to the fishery and, therefore, the yield variability of commercial catches should represent recruitment variability (Borges et al. 2003).

Statistical analyses. Statistical analysis of the data was carried out with SAS (v. 9.2). Data analyzed were monthly (equally spaced), collected over a period of 12 yr (from January 1984 to July 1995), for a total number of 139 mo. The body biochemical variables had 15 missing observations, mainly in 1986 and 1987 (10 out of 15), and the muscle biochemical variables had 11 missing observations, mainly in 1984 (beginning of sampling period) and 1986 (8 out of 11).

Preliminary examination of the data involved the use of techniques such as correlation analysis and regression analysis. To assess seasonality in each of the vari-

ables, indicator variables were created for each of the months and a multiple regression analysis was used, in which the dependent variable was a biochemical variable (energy, water, lipids, ash and proteins) and the independent variables were 11 of the 12 indicator variables (1 month was used as the reference month). Time dependency was not accounted for in this part of the analysis, but it was taken into consideration in subsequent analyses; hence, autoregressive (AR) procedures were used. Generalizations of the Durbin-Watson test were used to test for the presence of higher order autoregressive components.

In the context of the present paper, a simple linear regression model with first-order autoregressive errors [AR(1)] can be defined as:

$$y_t = \beta_0 + \beta_1 x_t + \varepsilon_t \quad (3)$$

$$\varepsilon_t = \rho \varepsilon_{t-1} + a_t \quad (4)$$

where y_t and x_t are the t th observations of the response (energy density for body or for muscle) and regression variables (i.e. water, lipids, ash, or protein), respectively, at time t ; ε_t is the error term in the model at time t , a_t is an NID(0, σ_a^2) random variable, and ρ is the autocorrelation parameter. This model can be easily extended to a multiple regression model with p independent variables and an autoregressive error of order k , [AR(k)], by adding additional terms to the model given above. The AUTOREG procedure in SAS was used when autocorrelation in the residuals was present. In cases where there was no time dependency in the residuals, standard multiple regression analysis was used. The goodness-of-fit statistics reported are total R^2 such that:

$$\text{Total } R^2 = 1 - (\text{SSE}/\text{SSC}) \quad (5)$$

where SSC is defined as the corrected sum of squares of the total response variable and SSE is the final error sum of squares, and Akaike's information criterion (AIC) such that:

$$\text{AIC} = -2\ln(L) + 2k \quad (6)$$

where L is the value of the likelihood function evaluated at the parameter estimates and k is the number of estimated parameters. Restricted maximum likelihood was used to estimate model parameters since observations were missing in the data.

Moreover, in order to seasonally adjust each one of the time series, an adaptation of the X11 Seasonal Adjustment Program (developed by the US Bureau of the Census) was used. The X11 procedure in SAS incorporates sliding spans analysis, and it requires that the series be complete. To this end, estimation using regression was used to replace missing values in the data. That is, the variable with the missing observations was treated as the dependent variable,

while the variable that correlated to the highest degree with the dependent variable was used as the independent variable. If, after this first step, missing observations were still evident in the dependent variable, the strong seasonality present in the series was taken advantage of and was used for prediction purposes, thus completing the gaps in the data. This process is sometimes referred to as regression mean imputation. It is important to note that because correlation with other series and seasonality within each series was part of the estimation of missing values, the monthly/seasonal fluctuations were captured quite well by the process.

The X11 procedure allows additive and multiplicative adjustments, where an additive model is defined as:

$$Y_t = S_t + C_t + I_t \quad (7)$$

Here, Y_t is the original series at time t , S_t is the seasonal component at time t , defined as the intra-year variation that is repeated from year to year, C_t is the trend cycle component at time t that includes variation due to the long-term trend and other long-term cyclical factors and I_t is the irregular component or residual variation at time t . To seasonally adjust a series in an additive model implies subtracting the seasonal factor (S_t) from the original series (Y_t), and consists of only the trend cycle and the irregular component.

RESULTS

Temporal changes in proximate composition

Time series of monthly variation in the biochemical composition of European sardine *Sardina pilchardus* are shown in Fig. 2. Water content ranged between 54.6 (August 1991) and 79.1% of wet weight (WW) (March 1991) in the whole body and between 59.8 (October 1988) and 80.6% WW (February 1991) in the muscle. An inverse scenario was observed for the lipid

Table 1. *Sardina pilchardus*. Correlation analyses to assess the linear association between the proximal chemical constituents in the whole body of European sardines. *significant linear associations between the corresponding variables at the 1% level of significance; ns: non-significant linear associations. Data series used in this analysis contain missing values

	Water	Lipids	Ash	Proteins
Water	1.00			
Lipids	-0.99*	1.00		
Ash	0.52*	-0.54*	1.00	
Proteins	0.40*	-0.49*	0.16 ns	1.00

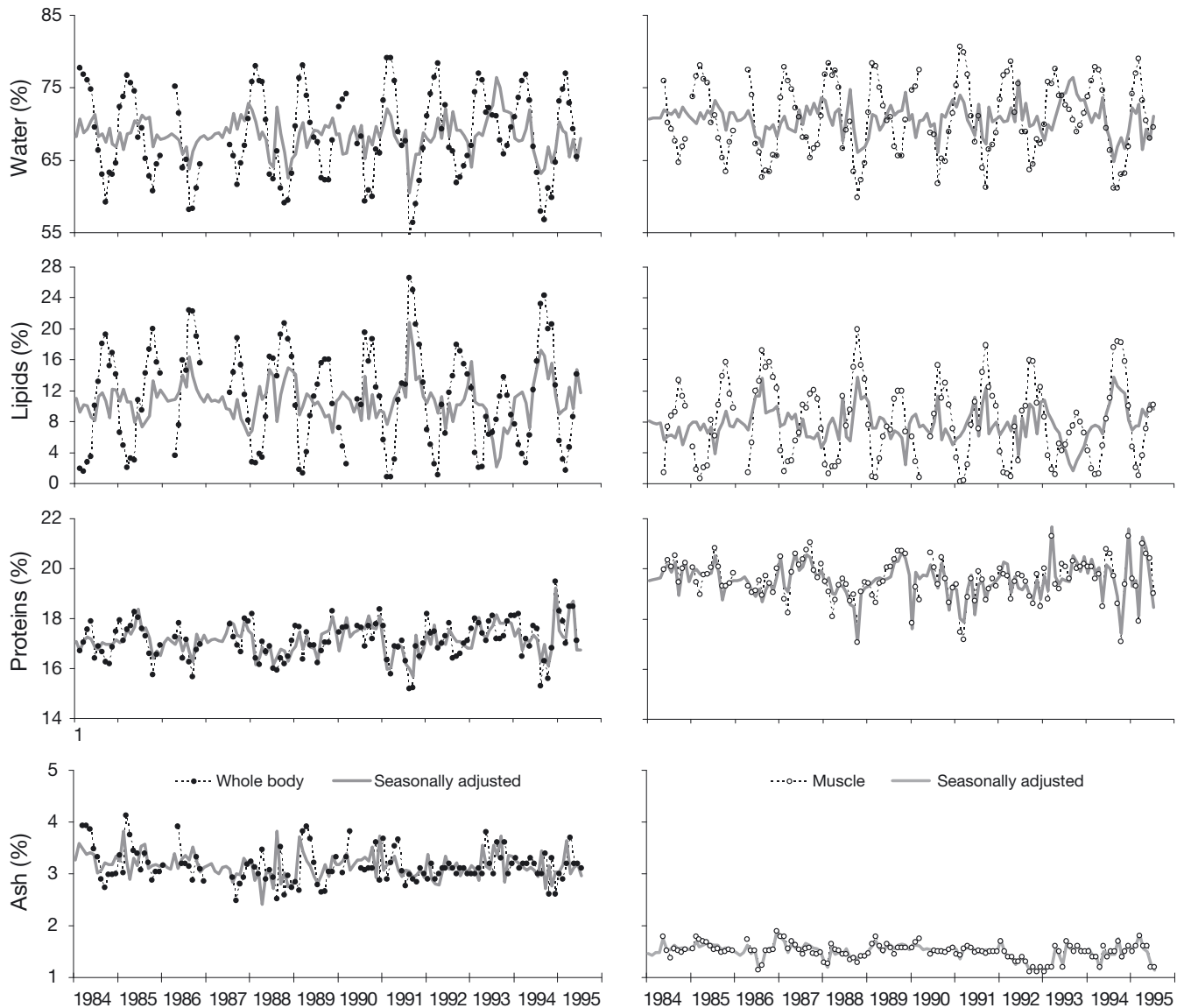


Fig. 2. *Sardina pilchardus*. Long-term temporal variations (1984 to 1995) in the water, lipid, protein, and ash contents (% wet weight of body and muscle mass) of European sardine. Seasonally adjusted time series are represented by the thick grey line

content (Fig. 2), which varied between 0.8 (March 1991) and 26.6% WW (August 1991) for the whole body and between 0.3 (March 1991) and 19.9% WW (October 1988) in the muscle. A significant negative correlation was attained between these 2 biochemical constituents ($p < 0.0001$) (Table 1). Both variables showed a marked seasonal variability that explained a large proportion (around 80%, $p < 0.0001$) of the variation in each time series (Table 2). The data used in these analyses contained missing values. It is noteworthy that the results provided in Tables 1 & 2 assume independence in the data (i.e. the results do not account for the time dependency in the data).

Significant temporal changes in the protein content were also observed (Fig. 2). The lowest levels were attained in August 1991 (15.2% WW), and the highest, in December 1994 (19.5% WW) in the whole body. While positively correlated with water content, proteins were negatively associated with lipid levels (Table 1), i.e. contrary to the lipid trend, the highest protein levels were observed in winter periods, while the lowest were attained in the summer. The ash content varied significantly between 2.5 (August 1987) and 4.1% WW (February 1985) for the whole body and between 1.1 (September 1992) and 1.9% WW (December 1986) in the muscle (Fig. 2).

Table 2. *Sardina pilchardus*. Assessment of seasonality in energy density and biochemical constituent contents in the whole body and muscle of European sardines, performed using regression analysis, with 11 dummy variables representing the 12 mo of the year (1 mo is used as a reference class). R²: percent of total variability in each of the variables explain by seasonality alone (note that no attempt was made to account for time dependency in the data since the interest laid in assessing only the seasonality effect). Data series used in the analyses contain missing observations

Variable	R ² (%)	F	p
Whole body			
Energy	81.23	44.07	<0.0001
Water	81.55	45.00	<0.0001
Lipids	80.06	40.87	<0.0001
Protein	32.68	4.94	<0.0001
Ash	33.81	5.20	<0.0001
Muscle			
Energy	80.15	42.58	<0.0001
Water	80.69	44.05	<0.0001
Lipids	77.78	36.92	<0.0001
Protein	16.71	2.12	0.0243
Ash	9.18	1.07	0.3948

Energy density and empirical bioenergetic models

Energy density (ED, kJ g⁻¹) temporal dynamics (Fig. 3) was closely linked with lipid content (Model 2 [M2]—for whole body, total R² = 99.60%; for muscle, total R² = 92.50%; Table 3) and much of the ED variation in the whole body and muscle was explained by seasonality (>80%; Table 2). ED ranged between 4.0 (March 1991) and 14.2 kJ g⁻¹ WW (August 1991) in the

whole body and between 4.1 (March 1991) and 11.9 kJ g⁻¹ WW (October 1988) in the muscle. A significant negative relationship between ED and water content was obtained (Model 1 [M1]—for whole body, total R² = 98.98%; for muscle, total R² = 94.96%; Table 3). The sardine energetic peak was always attained at the end of summer and beginning of autumn (August to October), and it was more pronounced in the years 1986, 1991 and 1994, with average values of 12.3, 13.3 and 13.2 kJ g⁻¹ wet body mass, respectively (Fig. 3). The lower energetic peak was observed in 1993 with 8.47 kJ g⁻¹ wet body mass. The empirical models of ED based on protein and ash contents for adult sardines are also shown in Table 3 (Models M3 & M4).

Energy density and environmental conditions

Deviations from the seasonal cycle in ED are dynamic indicators of the total energy budget available for the sardines to reproduce and are driven by past feeding conditions, which are determined by environmental forcing. The linkage between sardine energetic condition and environmental variability in the Western Iberian Upwelling Ecosystem was examined by comparing the entire time series of adult sardine ED (whole body) with SST and offshore Ekman transport (Q_x) (Fig. 3). When we examined the temporal structure of the association between seasonally adjusted energy density (rED; thick grey lines in Fig. 3) and the given environmental variables, we found significant lagged associations with SST and Q_x (lags of 2 and 3 mo; see Appendix, Table A1). A multiple regression

Table 3. *Sardina pilchardus*. Empirical models (M1 to M4) of energy density (ED, kJ g⁻¹ wet weight) for adult European sardines based on the proximate constituents of the whole body and muscle (% wet weight). Both estimates contain the correlation structures in the data taken into consideration. Akaike information criteria (AIC) are given, with smaller values indicating a better fit. Restricted maximum-likelihood was used to estimate the parameters in the models, since they were fitted to series containing missing values. Statistical significance at the *5%; **1% level of significance, AR(1): first-order autoregressive models; SE: standard error, in parentheses

Bioenergetic model	Variable	Whole body					Muscle				
		Estimate (SE)	t	p	Total R ² (%)	AIC	Estimate (SE)	t	p	Total R ² (%)	AIC
M1	Intercept	36.24 (0.31)	118.03**	<0.0001	98.98	12.93	40.68 (0.94)	43.42**	<0.0001	94.96	202.88
	Water (%)	-0.41 (0.00)	-91.07**	<0.0001			-0.46 (0.01)	-34.49**	<0.0001		
	AR(1)	0.22 (0.10)	2.34*	0.0209			0.37 (0.09)	4.17**	<0.0001		
M2	Intercept	4.20 (0.04)	109.65**	<0.0001	99.60	-101.32	4.87 (0.15)	32.42**	<0.0001	92.50	250.20
	Lipids (%)	0.38 (0.00)	131.21**	<0.0001			0.45 (0.02)	29.16**	<0.0001		
	AR(1)	0.34 (0.09)	3.93**	0.0001			0.28 (0.09)	3.07**	0.0027		
M3	Intercept	16.42 (2.69)	6.10**	<0.0001	87.29	349.15	7.62 (2.51)	3.04**	0.003	86.02	348.32
	Proteins (%)	-0.41 (0.15)	-2.75**	0.007			0.07 (0.13)	0.57**	0.5726		
	AR(1)	0.46 (0.09)	5.39**	<0.0001			0.54 (0.08)	6.57**	<0.0001		
M4	Intercept	11.61 (1.06)	10.96**	<0.0001	87.26	349.66	9.25 (1.15)	8.01**	<0.0001	85.97	348.61
	Ash (%)	-0.79 (0.31)	-2.53*	0.0128			-0.15 (0.73)	-0.21	0.8319		
	AR(1)	0.50 (0.08)	5.91**	<0.0001			0.52 (0.08)	6.29**	<0.0001		

model that included lag effects of the second and third order for SST and of the third order for Q_x , as well as adjusted for the time dependency in the data, explained about 36% of the total variation left in the rED, the seasonally adjusted series (Model 1, Table 4). Lagged SST was negatively associated with rED, and

lagged Q_x was positively associated with sardine condition (Fig. 4). The combination of environmental conditions that triggered positive anomalies in sardine energy density—colder ocean temperatures associated with positive Ekman transport values—correspond to upwelling conditions favourable for the spring/early summer phyto- and zooplankton blooms. These environmental conditions are critical for adult fish feeding in order to maximize their late summer energy peak before starting into the prolonged winter spawning season. Therefore, restricting rED analysis to the end of the main feeding period (between August and October), we found that the spring/early summer environmental variability (best model included the 3 mo lagged SST and the 2 and 3 mo lagged Q_x) explained 67% of the late summer peak of rED (Model 2, Table 4). The results for testing for individual variables and lags are shown in Appendix Table A1—with full data set; and Table A2—end of the main feeding period, i.e. summer peak.

Energy density, recruitment and landings

Do better feeding conditions and sardine energetic condition translate into enhanced reproductive success and fish production? No significant association between sardine higher rED and recruitment ($t + 1$) was attained (total $R^2 = 24.53\%$, $p = 0.1214$) (Table 5). We also examined the association of landings in year ($t + 1$) on the sardine energetic peak condition (rED) in year (t), by aggregating annual landings from the ICES zones corresponding to the western Portuguese coast (ICES subdivisions IXa center-north and IXa center-south). Adult energetic condition (at the end of the main feeding period) in year (t) explained $>54.4\%$ of the variation in catches in year ($t + 1$) (Table 5). The time correlation in residuals was strong; hence, it was necessary to account for the time dependency in this part of the analysis.

DISCUSSION

Biochemical indicators of sardine condition

The best biochemical predictors for sardine *Sardina pilchardus* condition were the lipid and water contents, which explained $>98\%$ of the variance in ED. Both proteins and ash also proved to be good biochemical indicators by explaining around 80 to 85% of the ED variance. Thus, it was possible to accurately estimate the energetic condition of adult European sardine based on several empirical bioenergetic models (Table 3). Since ED was not modelled as a function of

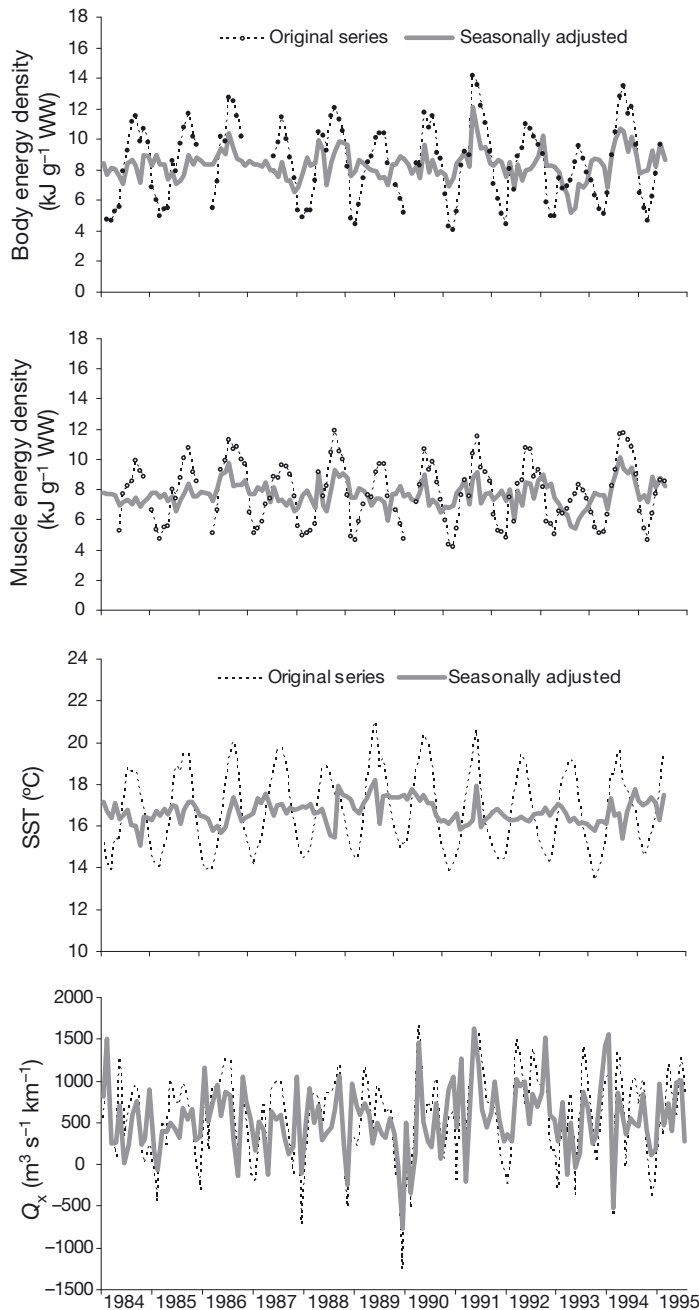


Fig. 3. *Sardina pilchardus*. Long-term temporal variations (1984 to 1995) in the energy density (kJ g^{-1} wet weight) of the whole body and muscle of European sardine, and in the sea surface temperature (SST, $^{\circ}\text{C}$) and Ekman transport (Q_x , $\text{m}^3 \text{s}^{-1} \text{km}^{-1}$, positive values mean offshore transport). Seasonally adjusted time series are represented by the thick grey line

size, the validity of the models for juveniles may be reduced, because sardine juveniles may allocate energy differently than adults (Caponio et al. 2004). However, several other studies with small pelagic fish species have revealed no relationship between size (or

age) and proximate composition (e.g. capelin—Van Pelt et al. 1997, herring—Foy & Paul 1999, capelin—Payne et al. 1999, mackerel—Eder & Lewis 2005). The magnitude and direction of the correlation between ED and size or age differed greatly among studies and

Table 4. *Sardina pilchardus*. Models assessing the importance of sea-surface temperature (SST) and scaled offshore Ekman transport ($Q_x/100$) in predicting the seasonally adjusted body energy density (rED) for the entire monthly time series (from January 1984 to July 1995, Model 1) and restricted to the end of the main feeding period of European sardines (i.e. summer peak, averaged between August and October, Model 2). Akaike information criteria (AIC) are given, with smaller values indicating a better fit. The variables included in the models were the ones that showed significance in the entries in Table A1 (full data set) and Table A2 (end of feeding period) (in Appendix 1). Statistical significance at the *5%, **1% level of significance; AR(1): first-order autoregressive models; SE: standard error, in parentheses

	Without autocorrelation					With autocorrelation				
	Coefficient (SE)	<i>t</i>	<i>p</i>	Total R ² (%)	AIC	Coefficient (SE)	<i>t</i>	<i>p</i>	Total R ² (%)	AIC
Model 1										
SST (Lag 2)	-0.03 (0.19)	-0.16	0.8759	13	349.62	-0.09 (0.16)	-0.53	0.5949	36	314.91
SST (Lag 3)	-0.40 (0.19)	-2.15	0.0332*			-0.25 (0.17)	-1.46	0.146		
Q_x (Lag 3)	0.05 (0.02)	2.31	0.0228*			0.03 (0.02)	1.63	0.1068		
AR (1)						0.52 (0.08)	6.57**	<0.0001		
Model 2										
SST (Lag 3)	-0.27 (0.47)	-0.58	0.5655	32.27	113.16	-0.07 (0.42)	-0.17	0.8665	67.44	99.23
Q_x (Lag 2)	0.09 (0.10)	0.88	0.3842			0.15 (0.07)	2.30*	0.0288		
Q_x (Lag 3)	0.18 (0.08)	2.19*	0.037			0.11 (0.06)	1.88	0.0699		
AR(1)						0.73 (0.12)	6.10**	<0.0001		

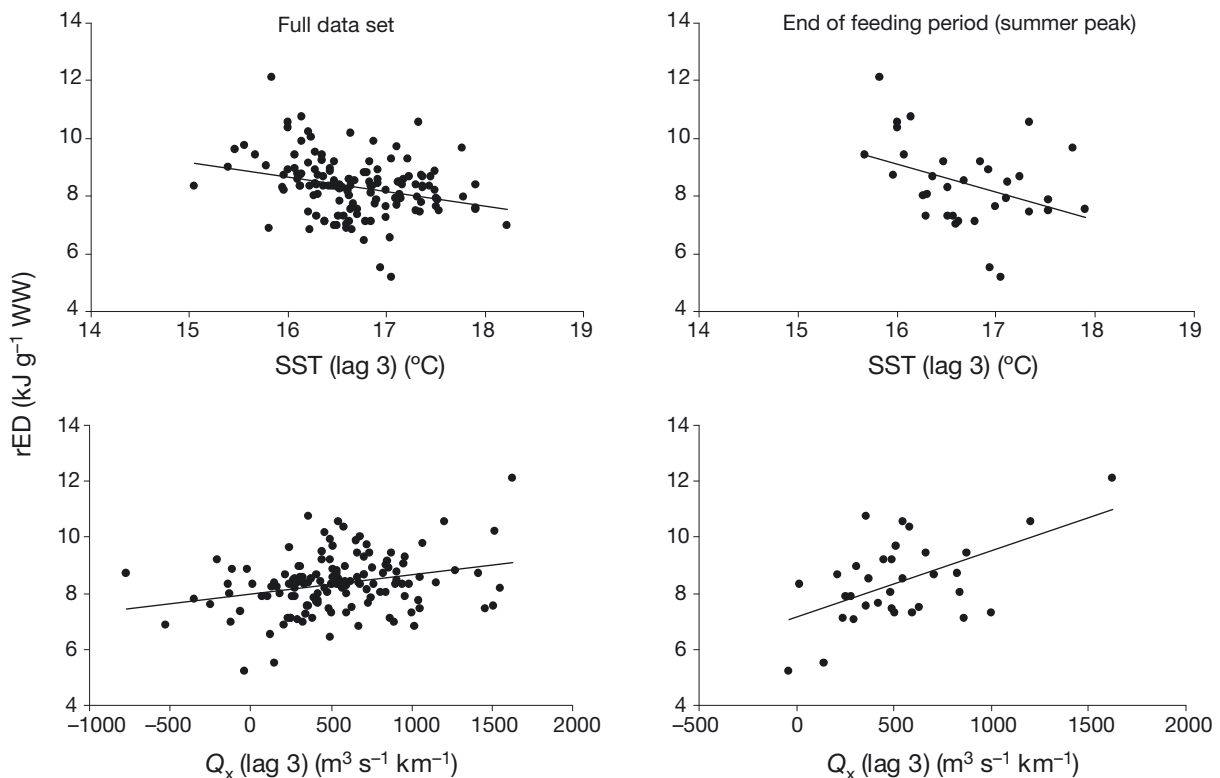


Fig. 4. *Sardina pilchardus*. Relationships between seasonally adjusted sardine energy (rED, kJ g^{-1} wet weight) and earlier oceanographic conditions, namely seasonally adjusted sea surface temperature (SST) and Ekman transport (Q_x) with a 3 mo lag, during the entire studied period (left panels) or restricted to the end of the main feeding period (summer peak; right panels).

Since autocorrelation was not taken into account, these statistics are only used for comparative purposes

Table 5. *Sardina pilchardus*. Relationships between seasonally adjusted energy density (rED) at the end of the main feeding period of European sardines (between August and October) and sardine recruitment (1000s) in the following year ($R0_{(t+1)}$) as well as catches (10^3 tons) in the following year ($t + 1$) and 2 yr thereafter ($t + 2$). Time series of catches corresponds to the total across the ICES subdivisions IXa central-north and IXa central-south (western Portuguese coast), while recruitment estimates are relative to the entire Ibero-Atlantic stock. Akaike information criteria (AIC) are given, with smaller values indicating a better fit. Restricted maximum-likelihood was used to estimate the parameters of each of the models (with or without taking autocorrelation into account). Results without autocorrelation assume independence, whereas those with autocorrelation provide information on models that required adjustments for time dependency. Statistical significance at the *5% level of significance; AR(1): first-order autoregressive models; SE: standard error, in parentheses

Dependent variable	Without autocorrelation					With autocorrelation				
	Coefficient (SE)	<i>t</i>	<i>p</i>	Total R ² (%)	AIC	Coefficient (SE)	<i>t</i>	<i>p</i>	Total R ² (%)	AIC
$R0_{(t+1)}$	1032287 (602933)	1.71	0.1214	24.53	357.25					
Catch ($t + 1$)	-3.08 (1.62)	-1.90	0.0902	28.58	75.11	-2.78 (1.05)	-2.66*	0.0289	54.44	72.89
AR(1)						0.72 (0.25)	2.85*	0.0213		
Catch ($t + 2$)	1.54 (1.61)	0.95	0.3688	10.18	66.13					

fish groups, indicating that using a single relationship between ED and size could potentially bias the outcome of bioenergetic models (Madenjian et al. 2000, Trudel et al. 2005).

It has also been assumed that a condition factor (weight/length³) can be used as an indicator of fish condition; however, it seems that lipids and ED are often poorly correlated with such a condition factor, since it usually only explains <40% of the ED variance (Jonas et al. 1996, Sutton et al. 2000, Trudel et al. 2005). The advantage of using biochemical approaches instead of common morpho-physiological indices as indicators of fish condition has been shown in clupeoids (Shulman & Love 1999). The utilization of lipid reserves can actually result in an increase in body weight due to a consequent increase in the water content, i.e. water replaces lipids while maintaining body shape (Love 1980).

Sardines play an important role in food web dynamics and their high biomasses; the shoaling behaviour and high ED of sardines may explain their importance as prey for numerous marine predators. European sardine condition in summer (ED up to 14.2 kJ g⁻¹ WW) showed higher ED values than other pelagic demersal prey species (Childress et al. 1990, Van Pelt et al. 1997, Lawson et al. 1998, Payne et al. 1999, Anthony et al. 2000, Tierney et al. 2002, Eder & Lewis 2005). These prey quality estimates may be crucial inputs to bioenergetic models of predator consumption in the Atlanto-Iberian coastal ecosystem.

Biochemical energetics, feeding ecology and reproduction

Sardines feed year round and are capable of performing both particle- and filter-feeding depending on

prey size (Garrido et al. 2007a). Their omnivorous diet comprises the major plankton groups in the water column, namely crustacean eggs, copepods, decapods, cirripedes, fish eggs, dinoflagellates and diatoms (Garrido et al. 2008a). Contrarily to phytoplankton, which are particularly important during spring and summer, zooplankton are a more perennial dietary component in the WIUE (Garrido et al. 2008a,b). While zooplankton is the major contributor to the proteins of sardines (Bode et al. 2004), fatty acids of herbivorous origin contribute significantly to the lipidic fraction of this fish, particularly off western Iberia, as a result of higher primary productivity related to upwelling events (Garrido et al. 2007b, 2008a,b).

The seasonal cycle of sardines' metabolic energy depends primarily on the seasonal investment in the spawning season. The accumulation of energy reserves for sardines off western Iberia begins, every year, from energetic exhaustion around March to April (with an average of 5.1 kJ g⁻¹ wet body mass) and reaches a peak at the end of September to October (with an average of 11.2 kJ g⁻¹ wet body mass), i.e. after the occurrence of the spring and summer planktonic blooms. The decreasing period of adult ED values after September to October reflects primarily the beginning of the protracted spawning season, when a large portion of the energy accumulated is invested in gametogenesis, but also lower food availability and quality (discussed below) during that period. Also, the fact that available energy just prior to spawning reflects the spring/early summer upwelling conditions (Model 2, Table 4; more discussion below) agrees with the evidence that feeding intensity for sardines during these periods is significantly higher than that observed during late summer (Garrido et al. 2008a).

One may argue that the energy allocated to sardine reproduction may also come directly from feeding dur-

ing the spawning season. However, the lipid content of sardine muscle reserves that has been accumulated during the entire resting stage of reproduction sharply decreases when sardines start to reproduce, suggesting that most of the energy invested in reproduction comes from these reserves, a result that is in accordance with other studies on small pelagic fish (e.g. Hunter & Leong 1981).

Sardines have a fractional spawning system that depends on the release of multiple egg batches at intervals (Cunha et al. 1992). Being indeterminate spawners, the fecundity of sardines within a given season is not fixed *a priori*; instead, further batches can be produced in years of abundant food availability during the spawning season (Blaxter & Hunter 1982). This strategy extends the season to several months and, therefore, may be considered an exploratory reproductive behaviour in response to the variability and unpredictability of habitat conditions in coastal upwelling ecosystems. The spawning season is also characterized by age-dependent fecundity (larger individuals spawn over a longer time period and start spawning earlier and finish later than the smaller individuals) (Zwolinski et al. 2001). Because the seasonal cycle is so strong, sardines in February to March are always lean irrespective of the amount of energy they were able to accumulate prior to the spawning season. Sardine ED at the end of the spawning season remained fairly constant over the years and was independent of being preceded by a productive or unproductive spring/early summer. Thus, the amount of energy accumulated by the fish seems to be directly translated in more or less energy available for reproduction, and, therefore, the spawning season may end when the available energy decreases below a certain threshold. In the northern anchovy, two-thirds of the energy required for reproduction during a season was provided by the reserves accumulated prior to the reproductive period (Hunter 1981).

Effect of environmental forcing on sardine bioenergetics

Sardine-enhanced energetic fitness in some years (namely 1991 and 1994) could not be corroborated with plankton data, but the occurrence of earlier favourable environmental conditions (high Q_x values) suggests increased food availability off the western Portuguese coast in those years. A similar, but opposite, interpretation can be made for 1993, when the lowest ED values were registered (Fig. 3). These assumptions are supported by the strong inter-annual correlation between the upwelling index and shelf production off north-western Iberia (Joint et al. 2002). Moreover, when we restrict our rED analysis to the end of the feeding

period (between August and October), the spring/early summer conditions explained 67 % of the late summer energetic peak (Model 2, Table 4). The differences in upwelling intensity would influence the diatom-dominated phytoplankton blooms and the mixing of stratification gradients, which are responsible for the phytoplankton assemblage composition and seasonal succession. Fish conditions benefit more from diatom-based food chains (St John & Lund 1996, Pedersen et al. 1999) than from the more heterotrophic food chains occurring in summer (flagellates and ciliates) and early fall (dinoflagellates) (for more details on phytoplankton succession in upwelling systems see Kudela et al. 2005). Since the last are less efficient in the transfer of energy to higher trophic levels (Cushing 1989, Nagata et al. 1996), sardine conditions would primarily be enhanced by grazing on zooplankton that contain the dietary lipids of diatom origin from spring and early summer blooms. In fact, since some zooplankton groups, namely copepods (one of the major contributors to the sardine's dietary carbon; Garrido et al. 2008a), are known to accumulate large lipid stores (mainly wax esters and triacylglycerols) in the hepatopancreas, digestive tract, ovaries and in oil sacs and droplets (Lee et al. 2006), sardine ED variations may be linked to the seasonal lipid dynamics in these groups of prey. Although less relevant for the overall energetic condition of *Sardina pilchardus*, muscle proteins also have a zooplankton origin (Bode et al. 2004). Nonetheless, in other small pelagic species, protein is regarded as an essential source of energy to fuel reproduction (Bradford 1993).

Note that the role of diatoms in marine food webs has recently been questioned, in connection with their teratogenic effect on copepods (Miralto et al. 1999, Ianora et al. 2004). The established concept of energy flow from diatoms to fish by means of copepods is presently being debated by questioning the ecological significance of laboratory experiments on diatom toxicity (Jones & Flynn 2005) and by defending the classical model for a diatom-dominated system based on large-scale field studies (Irigoien et al. 2002). Diatoms may also be an important link between climatic and some ecosystem changes (Irigoien et al. 2000) and may, therefore, be a keystone for the lifehistory success of small pelagic planktotrophic fish such as sardines, the biological features of which are closely linked to the basic characteristics that influence ecosystem productivity.

Sardine bioenergetics, recruitment and landings

The weak relationship between enhanced rED and recruitment success in the following year ($p > 0.05$)

(Table 5) seems, at first glance, to support the deterministic role of environmental factors in the survival of early life-history stages, e.g. the coastal upwelling conditions during winter (discussed above). Yet, these recruitment estimates are relative to the entire Ibero-Atlantic stock (delimited by the French/Spanish border in the north and by the Strait of Gibraltar in the south; ICES Divisions VIIIc and IXa) and are not exclusive to the WIUE, i.e. the recruitment data available have a low spatial resolution. Silva et al. (2006) showed that regional differences in the maturity, age structure and condition factor of sardines are observed; thus, a database that integrates the Cantabrian, western and southern Iberian spawning sites (ICES 2005) is not adequate.

In the WIUE, the main spawning and recruitment areas are located off the NW Portuguese coast, where young fish are mainly caught (Ré et al. 1990, Alvarez & Alemany 1997, Marques et al. 2003). Interestingly, sardine rED (at the end of the main feeding period) in year (t) explained >54.4% of the variation in regional catches (ICES subdivisions IXa central-north and IXa central-south) in year ($t + 1$) (Table 5), indicating that adult energetic condition during spawning is partially translated into the fishery through recruitment strength.

Sardine spawners in better physiological condition have higher reproductive outputs (more batches of eggs per season and more viable eggs per batch) than fish in lower condition, which increase the probability of recruitment success and produce a stronger year-class that, apparently, is influential enough to be reflected in the fisheries of the following year. In fact, the beginning of the sardine spawning season in October (Figueiredo & Santos 1988, Ré et al. 1990) is known to generate a gradual increase in the new recruits to the fishery during the second semester of the following year (e.g. ICES 1982). As a consequence, the catches in the WIUE are generally higher during the second half of the year in comparison to the first semester, reflecting the influx of new recruits (e.g. ICES 2005). Nonetheless, other factors also potentially determine recruitment strength, namely predation, cannibalism, advection of eggs (and larvae) and the density of the parental stock (Beckley & van der Lingen 1999, Coetzee et al. 2008).

CONCLUSIONS

Our results support earlier findings which indicate that sardine population dynamics seem to be controlled by bottom-up effects (Santos et al. 2001, Borges et al. 2003). Although acknowledging the dataset limitations, it was apparent that the variability of sardine

ED related to the environmental forcing during the spring/early summer months is sufficiently important to be reflected in the fisheries. Thus, the condition of spawners, prior to the reproductive season, is a prerequisite to detecting the environmental and ecological effects on recruitment and, therefore, needs to be taken into consideration in stock management. Rapid energy determinations (e.g. indirectly by proximate constituents or directly by calorimetry) offer a low-cost and straightforward tool for fisheries assessments. Besides considerations of variable mortality, the inclusion of ED or other biochemical indicators may provide mechanistic proxies for reproductive investment beyond traditional spawning biomass. Our results provide empirical evidence that energy assessments during critical periods of the fish life-cycle (at the end of the feeding period) are an essential aspect in understanding the population dynamics in small pelagic fishes in coastal upwelling ecosystems and in developing a more solid basis for stock management and conservation.

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Appendix. Relationships between sardine energy density and individual environmental variables (sea surface temperature and offshore Ekman transport) with full data set (Table A1) and restricted to end of feeding season (Table A2)

Table A1. *Sardina pilchardus*. Relationships between seasonally adjusted energy density (rED; full data set) and the seasonally adjusted series of sea-surface temperature (SST) and offshore Ekman transport (Q_x). Akaike information criteria (AIC) are given. Restricted maximum-likelihood was used to estimate the parameters of each of the models (with and without taking autocorrelation into account). Statistical significance at the *5%, **1% level of significance; AR(1): first-order autoregressive models; SE: standard error, in parentheses

Explanatory variable	Without autocorrelation					With autocorrelation				
	Coefficient (SE)	<i>t</i>	<i>p</i>	Total R ² (%)	AIC	Coefficient (SE)	<i>t</i>	<i>p</i>	Total R ² (%)	AIC
Sea-surface temperature										
SST	0.16 (0.17)	0.99	0.3242	0.80	365.64	0.25 (0.15)	1.64	0.1031	34.24	318.47
AR(1)						0.57 (0.08)	7.63**	<0.0001		
Lag 1 (SST)	-0.20 (0.17)	-1.20	0.2320	1.17	365.17	-0.21 (0.16)	-1.30	0.1951	33.70	319.42
AR(1)						0.56 (0.08)	7.35**	<0.0001		
Lag 2 (SST)	-0.38 (0.16)	-2.32*	0.0222	4.25	358.97	-0.14 (0.16)	-0.89	0.3771	33.13	318.48
AR(1)						0.55 (0.08)	7.16**	<0.0001		
Lag 3 (SST)	-0.53 (0.16)	-3.33**	0.0011	8.47	351.54	-0.30 (0.17)	-1.78	0.0783	34.31	314.63
AR(1)						0.53 (0.08)	6.78**	<0.0001		

Table A1 (continued)

Explanatory variable	Without autocorrelation					With autocorrelation				
	Coefficient (SE)	<i>t</i>	p	Total R ² (%)	AIC	Coefficient (SE)	<i>t</i>	p	Total R ² (%)	AIC
Ekman transport (Q_x)										
Q_x	0.00 (0.00)	-0.23	0.8207	0.04	366.58	0.00 (0.00)	-0.13	0.8977	32.75	321.19
AR(1)						0.56 (0.08)	7.45**	<0.0001		
Lag 1 (Q_x)	0.00 (0.00)	-0.12	0.9057	0.01	366.62	0.00 (0.00)	-0.91	0.3642	33.21	320.36
AR(1)						0.57 (0.08)	7.56**	<0.0001		
Lag 2 (Q_x)	0.00 (0.00)	1.46	0.1459	1.74	362.15	0.00 (0.00)	0.28	0.7779	32.78	319.18
AR(1)						0.56 (0.08)	7.33**	<0.0001		
Lag 3 (Q_x)	0.00 (0.00)	3.26**	0.0015	8.12	352.01	0.00 (0.00)	2.12*	0.0363	35.09	313.23
AR(1)						0.54 (0.08)	7.04**	<0.0001		

Table A2. *Sardina pilchardus*. Relationships between seasonally adjusted energy density (rED) at the end of the main feeding period of European sardines (between August and October) and the seasonally adjusted series of sea-surface temperature (SST) and offshore Ekman transport (Q_x). Akaike information criteria (AIC) are given. Restricted maximum-likelihood was used to estimate the parameters (with and without taking autocorrelation into account). Statistical significance at the *5% level of significance; **1% level of significance; AR(1): first-order autoregressive models; SE: standard error, in parentheses

Explanatory variable	Without autocorrelation					With autocorrelation				
	Coefficient (SE)	<i>t</i>	p	Total R ² (%)	AIC	Coefficient (SE)	<i>t</i>	p	Total R ² (%)	AIC
Sea-surface temperature										
SST	0.26 (0.36)	0.70	0.4880	1.56	121.49	0.07 (0.24)	0.29	0.7743	56.60	105.64
AR(1)						0.75 (0.10)	7.53**	<0.0001		
Lag 1 (SST)	-0.27 (0.40)	-0.68	0.4998	1.48	121.52	-0.23 (0.28)	-0.81	0.4241	57.67	105.02
AR(1)						0.76 (0.10)	7.64**	<0.0001		
Lag 2 (SST)	-0.76 (0.43)	-1.77	0.0859	9.22	118.82	-0.65 (0.41)	-1.60	0.1201	60.35	103.03
AR(1)						0.76 (0.10)	7.81**	<0.0001		
Lag 3 (SST)	-0.99 (0.42)	-2.34*	0.0258	15.04	116.64	-0.41 (0.46)	-0.89	0.3811	56.33	104.92
AR(1)						0.73 (0.11)	6.66**	<0.0001		
Ekman transport (Q_x)										
Q_x	0.00 (0.00)	0.33	0.7459	0.34	121.90	0.00 (0.00)	0.56	0.5786	57.44	105.40
AR(1)						0.76 (0.10)	7.98**	<0.0001		
Lag 1 (Q_x)	0.00 (0.00)	-0.33	0.7422	0.35	121.90	0.00 (0.00)	-0.78	0.4409	57.89	105.08
AR(1)						0.76 (0.10)	7.82**	<0.0001		
Lag 2 (Q_x)	0.00 (0.00)	2.25*	0.0315	14.07	117.01	0.00 (0.00)	2.48*	0.0188	63.74	99.52
AR(1)						0.75 (0.10)	7.14**	<0.0001		
Lag 3 (Q_x)	0.00 (0.00)	3.57**	0.0012	29.08	110.68	0.00 (0.00)	2.14*	0.0410	60.20	101.21
AR(1)						0.71 (0.12)	5.95**	<0.0001		