

Geographic variability of sardine dynamics in the Iberian Biscay region

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The spatio-temporal variability in the distribution, demographic structure, recruitment, and mortality of sardine within the Iberian Biscay region is described using area-disaggregated data collected during acoustic surveys and at ports since the mid-1980s. Multiple regression models were used to describe log numbers-at-age obtained annually in ten areas covered by three surveys to test the existence of geographic differences in selectivity-at-age, recruitment strength, and mortality and to infer plausible migration routes. Within Iberian waters, sardine biomass was mainly concentrated off western Portugal and the Gulf of Cadiz. In the Bay of Biscay, biomass levels were comparable with those off western Portugal. Recruitment was localized in a few areas (northern Portugal and the Gulf of Cadiz and Bay of Biscay), intermingling with areas dominated by older fish. Recruitment was generally asynchronous among areas, although some recruitment peaks were noticeable across wider regions. Spatial patterns related to strong and weak year classes and year-class slopes were also noted. Clearly distinct dynamics were not evidenced within the Atlanto–Iberian sardine stock area, but the validity of the northern limit was questioned by the connection between sardine dynamics in the Bay of Biscay and the Cantabrian Sea. The results provided some evidence consistent with the hypothesis of sardine movement from recruiting grounds to areas farther along the coast as they grow.

Keywords: Iberian Peninsula, population dynamics, small pelagic fish, stock structure.

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Introduction

The sardine (*Sardina pilchardus*) is a small clupeoid distributed in the Northeast Atlantic from the southern Celtic Sea and North Sea to Mauritania and Senegal, and also across the western and northern Mediterranean Sea (Parrish *et al.*, 1989). Within European Atlantic waters, sardine is mainly fished in the coastal waters of the Iberian Peninsula by Spanish and Portuguese purse-seiners, although small-scale fisheries traditionally operate in the Bay of Biscay (purse-seiners and trawlers; ICES, 2007) and the English Channel (driftnets; Culley, 1971). For management purposes, a single stock of sardine has always been considered for European Atlantic waters, although its geographic limits have changed over time. Exploratory sardine assessments began in 1978 using biological and fisheries data from France, Spain, and Portugal (ICES, 1978). At that time, the stock was delimited within ICES Divisions VIII (Bay of Biscay and Cantabrian Sea) and IXa (western and southern Iberia). However, the biological criteria available for stock delimitation were considered inadequate, and emphasis was placed on the need to clarify relationships between populations within the assumed stock area

(ICES, 1978). The northern border of the stock was redefined in 1980 (ICES, 1980), giving rise to what is currently known as the Atlanto–Iberian stock (AIS) of sardine, delimited by the French/Spanish border in the north and the Strait of Gibraltar in the south (ICES Divisions VIIIc and IXa).

Throughout the 1980s, the biological and fisheries data did not raise serious concerns about the area of delimitation or the biological homogeneity of the AIS. In the mid-1990s, scarcity of sardine in northern Spain and particularly off southern Galicia, one of the most productive areas of the Iberian Peninsula, triggered a crisis in the purse-seine fishery and revived the discussion of sardine stock structure in European Atlantic waters (Carrera and Porteiro, 2003). Total catches halved from the mid-1980s to the mid-1990s, mainly through the decline in catches from fisheries off northern Spain. Examination of acoustic and ichthyoplankton survey data confirmed that declines in sardine abundance, distribution, and spawning areas were more pronounced off northern Spain than off Portugal (ICES, 2000; Stratoudakis *et al.*, 2003; Bernal *et al.*, 2007). Moreover, the northern stock limit was questioned by evidence of a continuous

distribution of eggs and adult fish through the inner Biscay shelf and of large sardine abundance in the French Bay of Biscay (ICES, 2005; Bernal *et al.*, 2007). In the south, a recent study simulating particle advection from combined effects of wind and prevailing currents suggested that eggs and larvae may be advected from the Gulf of Cadiz into coastal waters of northern Morocco (Oliveira and Stratoudakis, 2008). However, concerns about the southern stock limit seem comparatively fewer because no major spawning or recruitment areas, which could impact the dynamics of the AIS, are recognized in northern Morocco (FAO, 2006).

Sardine from the Iberian Peninsula and adjacent regions show variable morphological and life-history traits (Anon., 2006; ICES, 2006a). This heterogeneity is not the result of reproductive isolation because both microsatellite DNA and allozymes showed limited differentiation across the entire Northeast Atlantic, apart from peripheral populations off the Atlantic islands and Mauritania (Chlaida *et al.*, 2005; Atarhouch *et al.*, 2006, 2007; Gonzalez and Zardoya, 2007; Laurent *et al.*, 2007). On the other hand, it is consistent with genetic differentiation following a pattern of isolation by distance, i.e. a geographic pattern characterized by positive correlation between genetic differences and geographic distances between populations (Gonzalez and Zardoya, 2007; Laurent *et al.*, 2007). The combination of shallow genotypic differentiation with geographical variability in phenotypic characters suggests that sardine may be structured as a metapopulation, a regional group of local populations with asynchronous internal dynamics, but linked by sufficient gene flow to establish demographic connectivity; in other words, the exchange of fish between populations affects their mutual size, structure, and life-history traits (Kritzer and Sale, 2004).

The metapopulation hypothesis was suggested by Carrera and Porteiro (2003) to explain the collapse of the Galician fishery in the 1990s, whereas other sardine fisheries off the Iberian Peninsula remained healthy. Those authors proposed that sardine from the Cantabrian Sea (northern Spain) and western Portugal formed two local populations linked by northward and westward migration of juveniles to Galician waters. Successive low recruitments in the 1990s may have caused the contraction of local populations to their core distribution areas, where abundance remained stable, but disrupted the migration flux and decreased the availability of fish to the Galician fishery. Although this hypothesis may conceptually explain the distinct regional abundance and catch trends of sardine, connectivity between year classes across the region and with those in adjacent northern (e.g. the Bay of Biscay) or southern areas (Gulf of Cadiz) of the Iberian Peninsula still remains unclear.

Information on the geographic variability of sardine dynamics is, therefore, needed to clarify demographic connectivity between areas and to define stocks in accord with the spatio-temporal complexity of populations. Similar information has been used to support the hypothesis of metapopulation structure (Williams *et al.*, 2003; Holmes *et al.*, 2008) and to assist the definition of stocks in several species (Horn and Hurst, 1999; Botsford and Paulsen, 2000; Begg, 2005). For this study, area-disaggregated data collected during acoustic surveys and at ports since the mid-1980s were used to investigate geographic variation in sardine dynamics across the Iberian Peninsula and adjacent waters of the Bay of Biscay. Sardine biomass and age structure by area were used to explore spatio-temporal distribution, and numbers-at-age were modelled using year-class curves (YCC) by area to test differences in recruitment strength, age structure,

and mortality, and to explore hypotheses of migration. The location of recruitment areas, synchronicity in year-class strength, and plausible migration routes are discussed in relation to the spatial structure of sardine populations and the identity of the AIS.

Material and methods

Data

Total biomass and numbers-at-age were obtained from annual acoustic surveys of the Atlanto-Iberian sardine stock carried out by Spain and Portugal off the Iberian Peninsula between the mid-1980s and 2007 (Table 1, Figure 1). Similar data were obtained for the Bay of Biscay between 2000 and 2007 during French acoustic surveys directed at the assessment of anchovy. Spanish surveys started in 1986 and were carried out each year (with a few gaps) in early spring (March/April) between the French border in the Bay of Biscay and the Portuguese border in northwest Iberia. Portuguese surveys comprise three seasonal series: spring (March/April), summer (July/August), and autumn (November/December), spanning the Portuguese waters and, since 1992, the Spanish waters of the Gulf of Cadiz. All series started in the mid-1980s, but covered varying periods. The spring series became systematic in 1996 (only two surveys in the 1980s) and is currently the only one used in the assessment of the AIS in combination with the Spanish survey (ICES, 2007). The autumn series was interrupted for 10 years in the late 1980s and restarted in 1997 with some regularity, and the summer series was discontinued in the late 1980s. Overall, a generally poorer coverage of Portuguese waters was obtained during the first half of the 1990s. French surveys span the area from the French-Spanish border in the Bay of Biscay to Brittany (48°N) in late spring (May/June). Acoustic surveys are coordinated under the ICES framework (ICES, 1986, 1998, 2006b). Catchability differences are assumed not to invalidate the comparison of sardine abundance biomass and fish abundance between survey areas and over time (see the Discussion later).

Survey data were disaggregated in ten subareas corresponding to the geographic strata used for acoustic estimation of sardine abundance and age structure (ICES, 2006a; Table 1, Figure 1). Throughout this paper, there was a need to refer to broader geographic regions that encompass several subareas. Therefore, northern, western, and southern Iberia refer to the regions encompassing the eastern Cantabrian Sea to northern Galicia, southern Galicia to southwest Portugal, and southern Portugal to the Gulf of Cadiz, respectively. In addition, the term “Spanish waters/areas” refers to subareas covered by the Spanish survey, i.e. eastern Cantabrian Sea to southern Galicia (but not the Gulf of Cadiz), and western Portugal includes northern and southwest Portugal.

Sardine catch biomass and numbers-at-age by ICES Division (roughly corresponding to the geographic strata of the surveys) within the Iberian Biscay region were compiled for the period 1984–2006 from reports of ICES groups assessing the AIS (ICES, 2006a) since 1984.

Models of abundance-at-age

YCC models (Cotter *et al.*, 2007) were fitted to the log abundance-at-age of sardine obtained in French, Spanish, and Portuguese acoustic surveys. Area-disaggregated data from each national survey were modelled separately. Data from the three Portuguese series were pooled after shifting the age group by 0.42

Table 1. Surveys used for the analysis of sardine distribution and year-class dynamics along the Iberian Biscay region, with a summary of the main changes introduced in survey methodology over time.

Survey	Season	Area	Years	Main changes in survey methodology
French	Spring	Bay of Biscay ICES Divisions VIIIa and b	2000–2002, 2004–2007	RV “Thalassa”; Simrad ER 60 echosounder; parallel transects; day surveying; 20-m vertical opening pelagic gear
Spanish	Spring	Northern Spanish waters ICES Divisions VIIIc and IXa (north)	1986, 1988, 1990–1993, 1996–2007	RV “Thalassa”, RV “Cornide Saavedra” before 1997; change from Simrad EK400 to EK500 echosounder in 1991; change from zigzag day–night transects to parallel day transects in 1997; change from 8- to 18-m vertical opening pelagic gear in 1991; additional purse-seiner sampling since 1997, mainly inside Galician Rias
Portuguese	Spring	Portuguese waters	1986, 1988, 1995–2003, 2005–2007	RV “Noruega”; RV “Capricórnio” in summer 1996; change from Simrad EK 38S to EK400 echosounder in 1992 and to EK500 in 1995; change from zigzag day–night transects to parallel day transects in 1997; change from 20- to 10-m vertical opening pelagic gear in 1996
	Summer	(Gulf of Cadiz since 1992) ICES Division IXa	1985–1988, 1996, 2004	
	Autumn		1984–1987, 1992, 1997–2001, 2005, 2006	

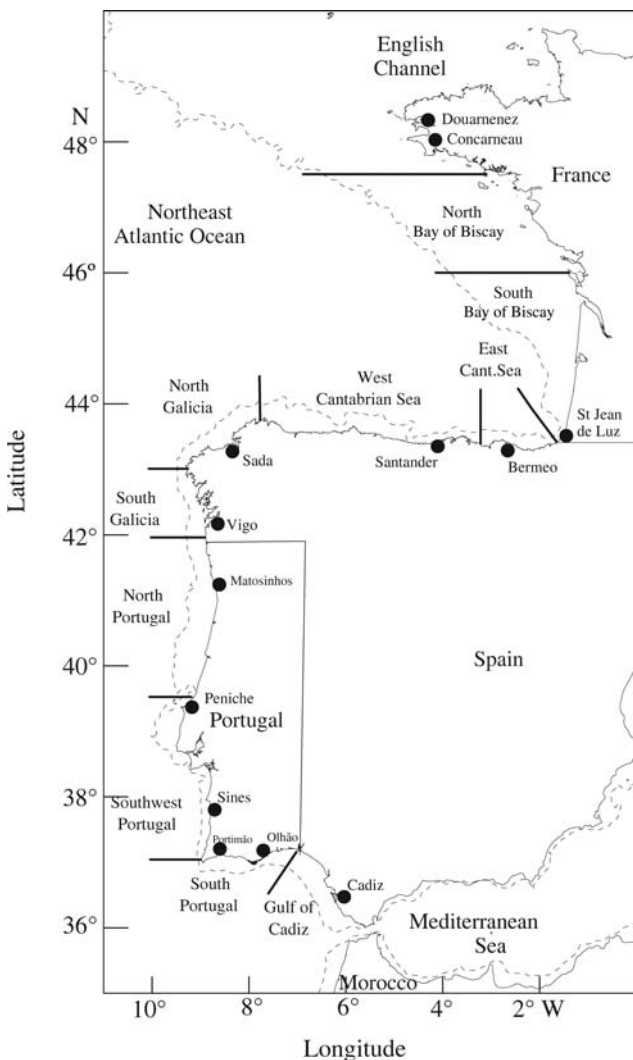


Figure 1. Map of the study region showing the area subdivision (solid lines) considered for acoustic estimation. The main ports for sardine catch sampling are indicated by black dots. The bathymetry shown is 200 m.

and 0.67 years in summer and autumn data, respectively. These values correspond broadly to the time-lag, in decimal years, relative to the spring surveys. The age ranges used in the models were 1–9 years for the Spanish and French surveys and 0.42–6 years for the Portuguese surveys, corresponding to well-represented and fully disaggregated age groups across the study period.

Candidate models were explored based on existing biological information on sardine and plausible hypotheses on year-class dynamics (Table 2). The simplest of candidate models explain year-class abundance-at-age in the entire survey area by their abundance at age 0, the rate of decline in abundance over age, and the distribution. This model has the general form (Model 1, Table 2):

$$\log U_{a,c} = \log U_{0,c} + Z_{age} + V_{area} + e_{a,c}, \quad (1)$$

where $U_{a,c}$ is the abundance of year class c at age a , $U_{0,c}$ the abundance of year class c at age 0, Z the average year-class slope between ages 0 and a , V_{area} a scaling coefficient providing an estimate of the average abundance of year classes in each survey area, and $e_{a,c}$ represents independent, normally distributed errors (Cotter *et al.*, 2007). As surveys provide an index of abundance, the intercept of the YCC ($U_{0,c}$) estimates relative recruitment strength, and the slope (Z) estimates the rate of decline of year-class abundance attributable to the combined effects of mortality (fishing and natural), migration (emigration tends to increase Z and immigration to reduce it), and selectivity/availability of the different age groups to the survey (see below).

Alternative models were used to explore the combination of selectivity (Model 2), geographic differences in total mortality and/or relative recruitment strength (Models 3 and 4), and temporal variation in total mortality (Models 5 and 6). To account for variable selectivity over age (Table 2), the term $\log(\text{age}+1)$ with coefficient S was added to Model 1. A positive estimate of S indicates that younger fish have lower catchability than older fish, i.e. are proportionally less susceptible to capture, whereas a negative estimate indicates the opposite. Selectivity effects increase as the absolute value of S increases.

Comparisons of model estimates of Z among areas are complicated in the presence of selectivity effects and trends in year-class slopes. Therefore, average estimates across the period were calculated from final models using log-index ratios ($U_{a,c} - \log U_{a+\Delta,c}$

Table 2. List of candidate YCC models fitted to log abundance-at-age in acoustic surveys.

Model	Model terms		France	Spain	Portugal	Biological meaning of model
1	$\log U_{a,c} = \log U_{0,c} + Z \text{ age} + V \text{ area} + e_{a,c}$	AICc	393.5	2 233.4	2 394.4	All ages equally selected
		CV	1.5	2.6	1.6	Mortality signal is the same for all areas and year classes
		MSPE	2.9	2.8	2.0	No age-related migrations between areas
		MPB	3.5	1.3	2.1	Year-class signal is the same for all areas
		Δ_i	47.5	190.4	112.8	
2	$\log U_{a,c} = \log U_{0,c} + Z \text{ age} + V \text{ area} + S \log(\text{age} + 1) + e_{a,c}$	AICc	394.2	2 130	2 337.3	Ages selected differently
		CV	1.5	2.2	1.5	Mortality signal is the same for all areas and year classes
		MSPE	3.6	2.8	2.4	No age-related migrations between areas
		MPB	4.8	2.2	2.7	Year-class signal is the same for all areas
		Δ_i	48.2	87	55.7	
3	$\log U_{a,c,r} = \log U_{0,c} + Z_r \text{ age} + V \text{ area} + S \log(\text{age} + 1) + e_{a,c}$	AICc	382.6	2 069.4	2 281.7	All ages equally selected (ages selected differently for Spanish survey)
		CV	1.2	2.0	1.4	Mortality signal varies between areas but is the same for all year classes
		MSPE	2.8	2.8	2	Possible age-related migrations between areas
		MPB	3.3	2.2	2	Year-class signal is the same for all areas
		Δ_i	36.6	26.4	0.1	
4	$\log U_{a,c,r} = \log U_{0,c,r} + Z_r \text{ age} + V \text{ area} + S \log(\text{age} + 1) + e_{a,c}$	AICc	399.4	2 129	2 309	All ages equally selected (ages selected differently for Spanish survey)
		CV	1.8	2.1	1.5	Mortality signal varies between areas but is the same for all year classes
		MSPE	3.4	3.5	2.6	Possible age-related migrations between areas
		MPB	3	2.6	2.3	Year-class signal differs between areas
		Δ_i	53.4	86	27.4	
5	$\log U_{a,c,r} = \log U_{0,c} + Z_r \text{ age} \times \text{year} + V \text{ area} + S \log(\text{age} + 1) + e_{a,c}$	AICc	346	2 043	2 281.6	All ages equally selected (ages selected differently for Spanish survey)
		CV	0.94	1.9	1.4	Mortality signal varies between areas and varies linearly over time
		MSPE	2.7	2.8	1.9	Possible age-related migrations between areas
		MPB	3.1	1.8	1.9	Year-class signal is the same for all areas
		Δ_i	0	0	0	
6	$\log U_{a,c,r} = \log U_{0,c,r} + Z_r \text{ age} \times \text{year} + V \text{ area} + S \log(\text{age} + 1) + e_{a,c}$	AICc	390.7	2 080.2	2 303.4	All ages equally selected (ages selected differently for Spanish survey)
		CV	1.5	2	1.4	Mortality signal varies between areas and varies linearly over time
		MSPE	3.4	3.2	2.4	Possible age-related migrations between areas
		MPB	3.3	1.7	2	Year-class signal differs between areas
		Δ_i	44.7	37.2	21.8	

AIC_c, small-sample AIC. For simplicity, the selectivity term, retained only for the Spanish survey, is enclosed in parenthesis in all subsequent models. Subscripts *a*, *c*, and *r* in model formulae indicate, age, year class, and area, respectively. Shaded areas indicate selected models.

with $\Delta = 0.001$ years) for ages 4–6 years (Z_{4-6}), assumed to be fully selected/available and moderately well represented in all surveys. For final models without selectivity or changes in mortality, $Z_{4-6} = Z$.

Three methods were used to select among candidate models: the Akaike's Information Criterion (AIC), cross-validation (LOOCV), and forward validation (FV). A modified AIC was used, the small-sample AIC (AIC_c) recommended when the number of observations (N) is fewer than $40 \times$ the number of parameters (K ; Burnham and Anderson, 2002). AIC_c is related to the usual AIC as

$$AIC_c = AIC + \frac{2K \times (K + 1)}{N - K - 1}. \quad (2)$$

Values of AIC_c were calculated for all candidate models to identify the best model (lowest AIC_c model) according to this criterion. Differences in AIC_c were calculated for each alternative Model i relative to the best model, $\Delta_i = AIC_{ci} - \text{minimum } AIC_c$. Following Burnham and Anderson (2002), Model i should be selected as the best if $\Delta_i \leq 2$. The other two methods of model selection were used to supplement AIC_c , because this criterion may be invalidated by dependence among observations of log abundance-at-age in YCC models. LOOCV was calculated as the average squared error from leave-one-out cross validation (Hastie *et al.*, 2001). FV was proposed by Cotter *et al.* (2007) as an alternative to LOOCV to estimate prediction error. FV consists of fitting the model to a subset of years from the first in the dataset to year ν , and predicting for year $\nu + 1$. The process is repeated i times (the number of validation steps), including successive years in the fitting, until ν reaches the penultimate year of the dataset. An estimator of the mean square prediction error (MSPE) for each age and area was calculated as

$$MSPE_{a,r} = \sum n_i (\delta_{i+1} \log U_{a,r})^2 \sum n_i, \quad (3)$$

where i indicates the validation step, n_i the number of years of observations fitted for the i th validation step, and $\delta_{i+1} \log U_{a,r}$ is the difference between the predicted and the observed $\log U$ for age a and area r in year $\nu + 1$. An estimate of the mean prediction bias (MPB) was calculated as

$$MPB_{a,r} = \exp\left(\frac{\sum n_i (\delta_{i+1} \log U_{a,r})}{\sum n_i}\right). \quad (4)$$

A FV period of 11 years was used, i.e. in the first validation step ($i = 1$), the model was fitted to data between 1984 (Portuguese surveys) or 1986 (Spanish survey) and $\nu = 1996$, and predictions obtained for $\nu + 1 = 1997$. FV was not used for the French survey because of the limited number of years in the analysis. Estimates of average MSPE and MPB for each area and survey were based on the best sampled age groups in each survey series; ages 2–6 in the Spanish and French surveys, and ages 2–4 in the Portuguese surveys. Finally, residuals by age, year, and year class were inspected for each candidate model and used as additional criteria to decide between models.

Selected YCC models for each survey were used to predict relative recruitment strength (at age 1) by area and for entire survey regions. Recruitment predictions were back-calculated beyond the first year of each survey series using a minimum of four

observations per year class (i.e. for French surveys, recruitment was back-calculated for year class 1995, using data for ages 5–8). Nevertheless, both back-calculated predictions and predictions for very recent year classes with few observations are less reliable than those for year classes with more complete data. Correlations were computed between predicted recruitments in each area from models assuming year-class effects nested within areas (Models 4 and 6; Table 3) using the Pearson correlation coefficient. A significance level of 0.006 was used to account for multiple comparisons (eight for each area) corresponding to the Bonferroni correction needed to maintain an α -familywise of 0.05. Correlations significant at the 1.3% level (corresponding to an α -familywise of 0.1) were considered to be moderate.

All calculations were carried out with R 2.5.0 (R Development Core Team, 2008). Package YCC (Cotter *et al.*, 2007) was used to fit YCC and to estimate forward prediction error and bias, and the package Boot was used to estimate leave-one-out cross validation errors.

Results

Biomass and age structure

Data collected during spring acoustic surveys since 1996 indicate that sardine biomass is, on average, substantially higher and less variable in Portuguese waters and the Gulf of Cadiz (492 000 t, $CV = 0.18$) than in Spanish waters (94 000 t, $CV = 0.54$), and intermediate in the Bay of Biscay (320 000 t, $CV = 0.59$). The northern and the southern parts of Biscay have comparable biomass levels, but distinct temporal variation, with a sharp decline in the north since 2001 and a peak in 2004/2005 in the south (Figure 2). In Spanish waters, average biomass is higher in the western Cantabrian Sea (37 000 t, $CV = 0.61$) and similar between the remaining areas (eastern Cantabrian Sea: 21 000 t, $CV = 1.05$; northern Galicia: 18 000 t, $CV = 0.77$; southern Galicia: 19 000 t, $CV = 0.74$). Biomass fluctuates substantially in all areas and most drastically in the eastern Cantabrian Sea and northern Galicia, where variations of almost two orders of magnitude were observed during a 3–4-year period. Biomass was high in a few years during the late 1980s and early 1990s in northern Galicia and the western Cantabrian Sea, but low during the rest of the 1990s across all Spanish areas (Figure 2). In the Cantabrian Sea, biomass increased to a peak in 2002 and 2003, but declined again to low levels recently, whereas off Galicia (mainly southern), biomass has increased gradually since 2000. In Portuguese waters, mean sardine biomass declined from north to south (north: 203 000 t, $CV = 0.51$; southwest: 112 000 t, $CV = 0.43$; south: 63 000 t, $CV = 0.44$), and increased in the Gulf of Cadiz (114 000 t, $CV = 0.40$; Figure 2). Trends across the study period are difficult to perceive because of gaps in the survey series. Since 1995, biomass has increased in northern Portuguese waters and declined in southern Iberian areas.

Sardine catches in the Iberian Peninsula have exhibited substantial spatio-temporal variation since 1984 (Figure 2). During the late 1980s, half the annual catch, 70 000–120 000 t, was taken off southern Galicia and northern Portugal ($\sim 26\%$ in each area), whereas most of the remaining catch (34%) was taken in the Cantabrian Sea and off southwestern Portugal. The core fishing area moved gradually south during the early 1990s, with 55% of the annual catch, 50 000–70 000 t, landed in western Portugal, and just 16 and 8% in the Cantabrian Sea and southern Galicia, respectively. Catches declined in the northern and western

Table 3. Summary of the best models fitted to abundance-at-age data from acoustic surveys within the Iberian Biscay region.

Survey series	Model	P	Area	V	s.e. _V	Z (year ⁻¹)	s.e. _Z	Z ₄₋₆	Range of Z ₄₋₆	ZY	s.e. _{ZY}	Comments and reservations
French	5	21	NFRA	9.5	2.10	-0.2	0.14	-0.8	[-1.2, -0.3]	-0.12	0.030	Model with lowest AIC _c , CV, MSPE, and MBP; parsimonious
			SFRA	10.0	2.13	-0.4	0.14	-0.7	[-0.9, -0.5]	-0.05	0.030	Short dataseries; strong year effects
Spanish	5	42	ECAN	4.8	0.99	-1.3	0.11	-0.4	[-0.7, -0.2]	-0.02	0.005	Model with the lowest AIC _c and CV, intermediate MSPE and MBE; parsimonious
			WCAN	5.2	1.04	-1.3	0.11	-0.4	[-0.6, -0.1]	-0.02	0.005	Trends in Z' significant in all areas
			NGAL	5.0	1.04	-1.4	0.11	-0.6	[-0.8, -0.3]	-0.03	0.005	Selectivity = 5.9 (0.52)
			SGAL	6.3	1.05	-1.8	0.12	-0.8	[-1.0, -0.7]	-0.01	0.006	Block of positive residuals around 1990 year class off SGAL; strong year effects and trends; trend in MBE by age in WCAN
			ECAN	2.1	1.75	-1.3	0.11	-0.5	[-1.1, 0.2]	-0.04	0.008	Model with low AIC _c , CV, and MBE, intermediate MSPE
Portuguese	3	35	WCAN	3.5	1.75	-1.2	0.11	-0.4	[-0.9, 0.3]	-0.04	0.008	Trends in Z' significant in ECAN and WCAN; selectivity = 5.8 (0.48)
			NGAL	9.6	1.79	-1.5	0.11	-0.5	[-0.7, -0.4]	-0.00	0.009	Improvement in year-class residuals; year effects and trends as in Model 5
			SGAL	6.0	1.95	-1.7	0.12	-0.8	[-1.1, -0.5]	-0.01	0.011	Too many parameters
			NPOR	14.1	0.57	-0.8	0.05	-0.8				Model with low AIC _c , CV, MSPE, and MBE; parsimonious
			SWPOR	13.3	0.51	-0.6	0.05	-0.6				Convex year effect on residuals off CAD
Portuguese	4	107	SPOR	11.6	0.51	-0.3	0.05	-0.3				
			CAD	13.9	0.64	-0.8	0.06	-0.8				
			NPOR	16.3	1.16	-0.8	0.05	-0.8				Model with intermediate AIC _c , CV, MSPE, and MBE
			SWPOR	12.5	0.85	-0.6	0.05	-0.6				Improvement in year-class residuals
			SPOR	11.4	0.84	-0.4	0.05	-0.4				Too many parameters
Portuguese	4	107	CAD	13.3	0.78	-0.8	0.06	-0.8				

Terms are as follows: P, number of model parameters; S, selectivity coefficient; V, area effect coefficient; Z, slope of the YCC; ZY, linear trend of year-class slope; Z₄₋₆, average year-class slope for ages 4-6; s.e., standard error for each parameter; NFRA, northern France; SFRA, southern France; ECAN, eastern Cantabrian Sea; WCAN, western Cantabrian Sea; NGAL, northern Galicia; SGAL, southern Galicia; NPOR, northern Portugal; SWPOR, southwest Portugal; SPOR, southern Portugal; CAD, Gulf of Cadiz. Note that for Models 3 and 4, assuming equal selectivity over ages and constant mortality over time, Z₄₋₆ = Z.

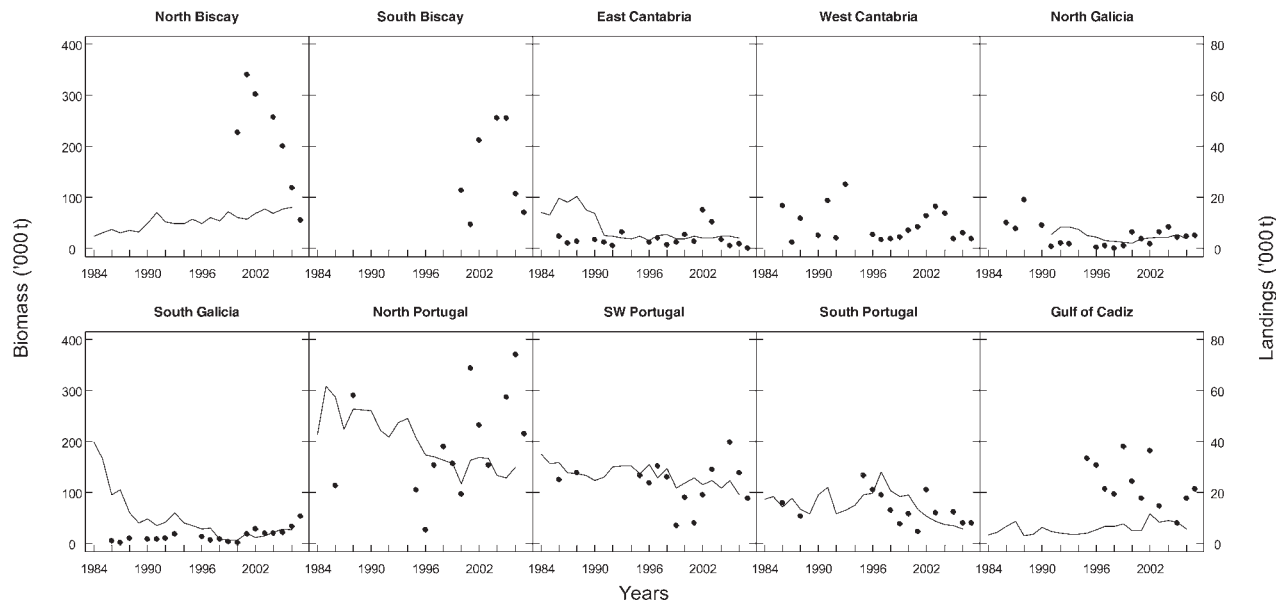


Figure 2. Temporal variation in sardine biomass obtained in spring acoustic surveys (black dots) and commercial catch (lines) by area. Catches are pooled for the northern and the southern Bay of Biscay, for the eastern and the western Cantabrian Sea, and northern Galicia for the years 1984–1990, and only from the eastern and the western Cantabrian Sea for 1991–2006.

Iberian areas from the mid-1980s to the mid-1990s. Apart from the western Cantabrian Sea and northern Galicia, these trends are not consistent with any variation in survey biomass. The decline in catches was more severe and abrupt in Spain during the second half of the 1980s, and particularly in southern Galicia, where a 75% drop (60 000 t) took place within 5 years (Figure 2). Sardine catches in the Bay of Biscay and Gulf of Cadiz are generally low compared with other areas. A gradually increasing trend in catches has been noticeable in the Bay of Biscay (Figure 2).

Boxplots of sardine age distributions by area in spring surveys indicate that young sardine (1 and 2 years old) dominate in the southern Bay of Biscay and the Gulf of Cadiz, and off southern Galicia and western Portugal (Figure 3). In the remaining areas, age distributions are dome-shaped, with peak percentages at age 2 in northern Biscay and southern Portugal and at ages 3–4 in the Cantabrian Sea and northern Galicia. Catch-at-age distributions overall agree with abundance-at-age distributions in corresponding areas, apart from southwestern Portugal.

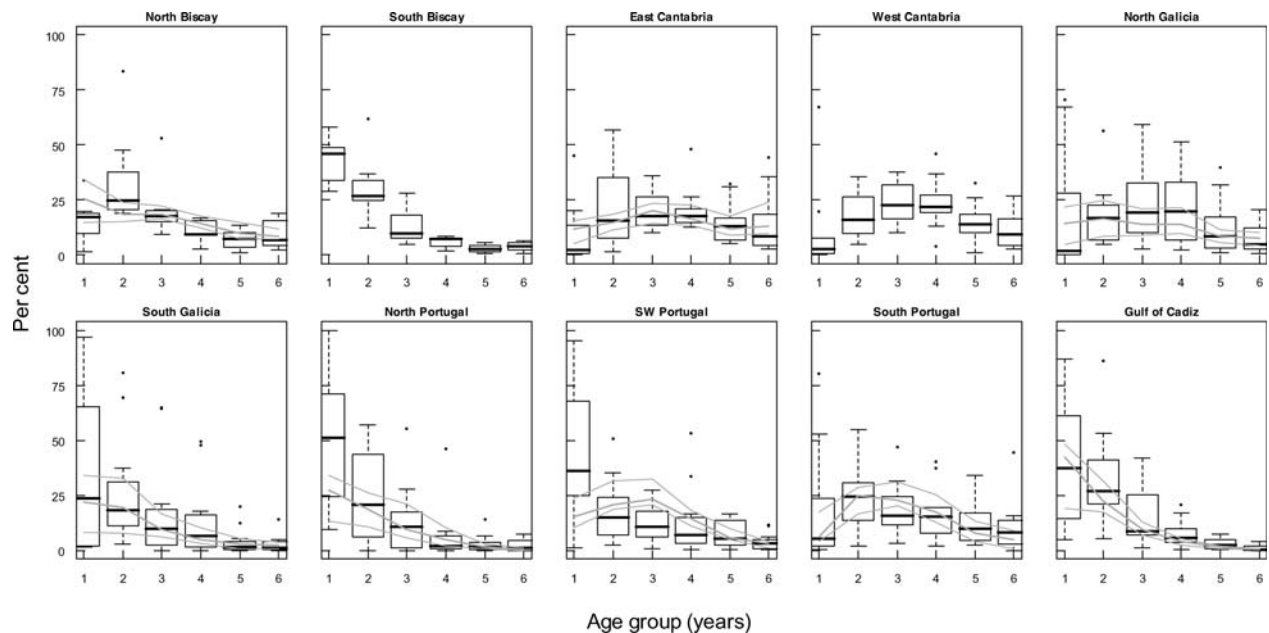


Figure 3. Boxplots of the percentage of sardine abundance by age group and area in spring acoustic surveys during the years 1995–2007. The lines represent the median (thick) and 25 and 75% percentiles of commercial catches in numbers-at-age by area during the years 1991–2006. Catches are pooled for the northern and the southern Bay of Biscay and for the eastern and the western Cantabrian Sea.

Year-class dynamics

Table 2 summarizes the biological meaning and goodness-of-fit of the candidate models fitted to each survey series. The simplest of the candidate models (Model 1, Table 2) was rejected in all survey series, underscoring the need to account for selectivity effects and/or differences in mortality and year-class variation among areas. Model 2, including selectivity, clearly provided a better fit only for the Spanish survey data, with a substantial drop in both AIC_c ($\Delta_i = 103.4$) and LOOCV, and no change in MSPE (although prediction bias did increase, as in all models fitted subsequently to this survey). The positive S coefficient shows that older fish are caught proportionally more than younger individuals in the Spanish survey, reflecting either better selection or more availability of larger, older fish in the area (Table 3). Model 3, assuming variable mortality between the areas covered by the same survey, showed a better fit for all surveys, along with improved predictive ability (apart from the Spanish survey). Addition of a linear trend in mortality within each area (Model 5) caused a further decline in the AIC_c and LOOCV statistics for the French and the Spanish surveys (including selectivity in the latter). For the Spanish survey, Model 5 provided the smallest increase in MPB relative to Model 1. For the Portuguese survey series, Models 3 and 5 showed comparable fitting and predictive performance, making the choice of a best model particularly difficult. Attempts to consider additional parameters, such as non-linear trends in mortality (not shown) or different recruitment variation between areas (Models 4 and 6), deteriorated the goodness-of-fit and predictive statistics for all surveys. However, Models 4 and 6 provided useful information at the level of area, and their results are presented below in more detail. Model 5 was selected as the final model to describe the French and Spanish surveys (Table 3). Model 3, with fewer parameters, was selected as the final model to describe the Portuguese survey data (Table 3). Residuals by year class for the final models are presented in Figure 4.

The average abundance of sardine recruits (at age 1) predicted by the YCC models in the Portuguese survey area (Portuguese waters and Cadiz, 4.3 billion individuals) is ~ 50 times higher than in the Spanish survey area (Galicia and Cantabrian Sea, 81 million fish) for year classes since 1980, and three times higher than in the French Bay of Biscay (1.3 billion fish) for year classes since 1995 (Figure 5). Recruitment variability is substantially different between surveyed regions (Figure 5). The most striking difference is for the early 1990s, when several strong year classes (1991–1993) are noticeable in the Portuguese survey, but are estimated to be among the poorest in Spanish waters. Recruitment strength differs between areas covered by the same survey by a scaling factor, derived from the V_{area} coefficients (Table 3). According to such factors, the average abundance of recruits back-calculated at age 0 (i) is slightly higher in southern than in northern Biscay [by a factor of 1.6, corresponding to $\exp(V_{\text{SFRA}})/\exp(V_{\text{NFRA}})$], (ii) increases from the eastern Cantabrian Sea to southern Galicia by a factor of 4.5, and (iii) declines from northern to southern Portugal by a factor of 12, and increases again in the Gulf of Cadiz by a factor of 10.

The better performance of models with Z nested within areas shows that year-class slopes are significantly different among areas covered by the same survey. Estimates of average year-class slopes for fully selected age groups (Z_{4-6}) are generally higher (in absolute value) in the Bay of Biscay, southern Galicia, northern Portugal, and Cadiz, where young sardine dominate, than in the areas where adults are dominant (Table 3). Slopes became steeper across the period in the Spanish and French areas, particularly in the northern part of the Bay of Biscay. Temporal variation in year-class slopes disrupted this geographic pattern to some extent; slopes became generally more similar for recent year classes, particularly between the Bay of Biscay and Portuguese waters.

The assumption of different recruitment variation by area (Model 6, Table 2) showed substantially higher AIC_c and

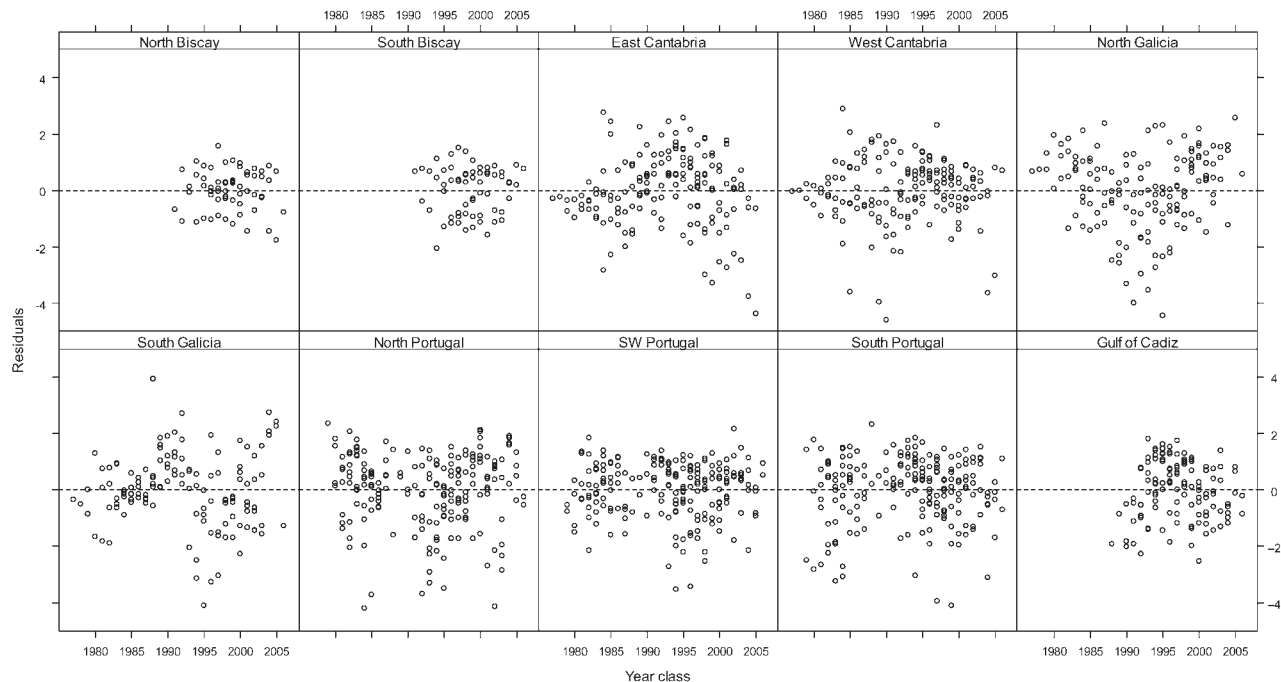


Figure 4. Residuals by year class for final YCC models fitted to French (Model 5), Spanish (Model 5), and Portuguese (Model 3) acoustic surveys.

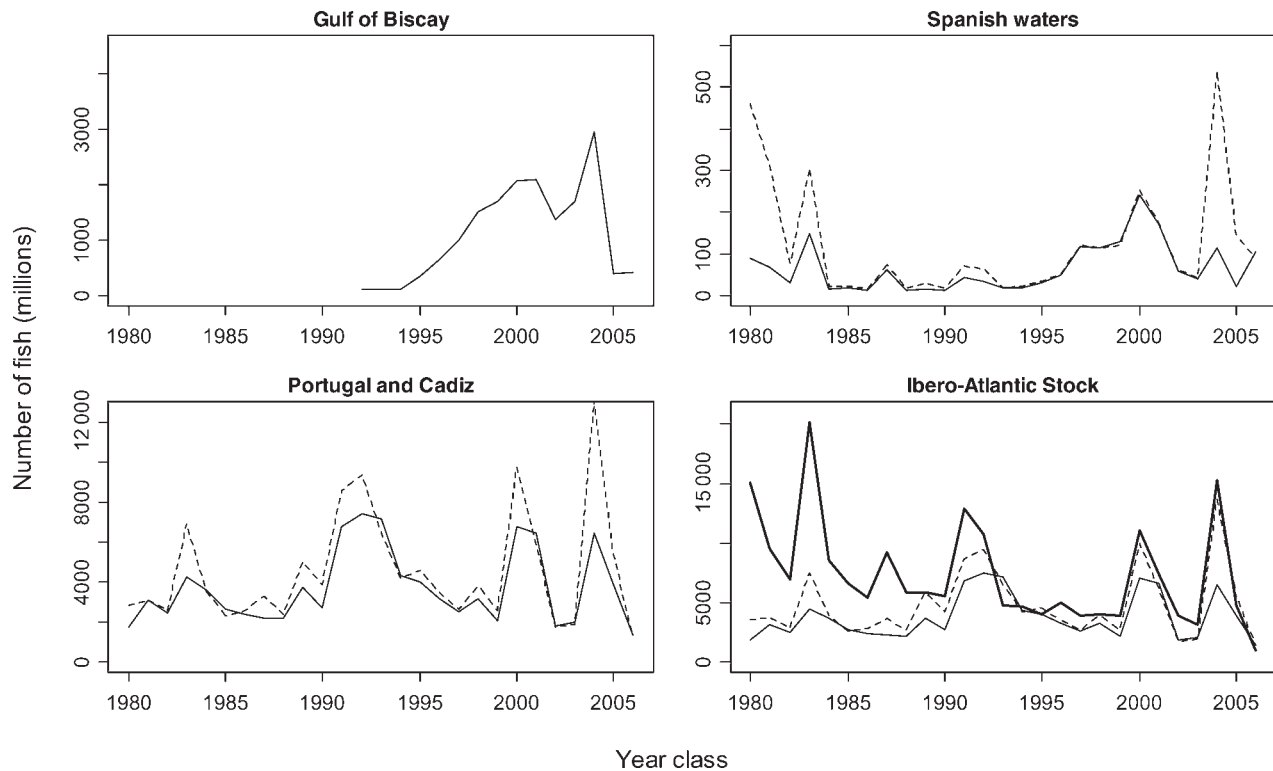


Figure 5. Relative abundance of 1-year-old sardine in French, Spanish, and Portuguese acoustic survey areas predicted by YCC models (top panels and bottom left panel), and a comparison of these predictions (summed across the Spanish and Portuguese survey areas) with recruitment (at age 0) for the AIS obtained in the latest ICES assessment (bottom right panel). Solid lines show predicted values from models assuming the same year-class strength in different areas of the same survey (Models 5 for French and Spanish surveys, Model 3 for Portuguese surveys), dashed lines show predicted (summed across areas) values from models assuming variable year-class strength by area within the same survey (Models 6 and 4 for Spanish and Portuguese surveys, respectively) and the thick solid line shows the ICES assessment estimates. Note the differences in the y-axis scales.

LOOCV than the selected model for the French survey series and provided no obvious difference in recruitment variation between northern and southern Biscay (Figure 6). However, for the Spanish and Portuguese survey series, Models 6 and 4, respectively, reduced temporal trends in residuals in some areas, e.g. southern Galicia and southern Portugal (not shown), and exposed additional geographical variation in sardine recruitment (Figure 6). These models suggest a pronounced discrepancy in recruit abundance among areas, with higher estimates in Galicia than in the Cantabrian Sea, and a higher relative importance of northern Portugal as a recruitment area (see V_{area} coefficients; Table 3). The predicted abundance of recruits (at age 1) was higher and more variable in northern Portugal (mean = 2.2 billion fish, $CV = 100\%$), followed by the Gulf of Cadiz (mean = 1.5 billion fish, $CV = 54\%$), southwestern Portugal (mean = 1.1 billion fish, $CV = 83\%$), southern (mean = 740 million fish, $CV = 65\%$), and northern (mean = 606 million fish, $CV = 57\%$) Bay of Biscay (Figure 6). In Spanish areas, the average abundance of recruits was one order of magnitude lower, ranging from 8 to ~50 million fish from the eastern Cantabrian Sea to Galicia.

Plots of predicted age 1 abundance show that the distribution of some strong year classes was limited to a few survey areas (Figure 6). This was the case for the 1983 year class which was strong off Galicia, particularly in the north, and appeared as the third strongest of the time-series off northern Portugal, but

showed negligible abundance in the Cantabrian Sea and southern Portugal. On the other hand, 1991 and 1992 were the strongest year classes across the area from southwest Portugal to the Gulf of Cadiz and also were conspicuous off the remaining western Iberian coast, but not along northern Iberia. The 2004 year class was outstanding in southern Galicia and the strongest of the time-series in northern Portugal and the Bay of Biscay, whereas the 2005 year class was noticeable in the Gulf of Cadiz. The perspective of sardine recruitment provided by models assuming area-nested year-class effects is not substantially different from that provided by the final YCC models. In the Portuguese survey area, the former model suggests stronger 1983, 2000, and 2004 year classes, and an upward trend in recruitment peaks (Figure 5). In the Spanish survey area, it points to stronger year classes in the early 1980s and an outstanding 2004 year class. This year class was very strong in southern Galicia, but appeared to have been weak off the northern Spanish areas (north Galicia and Cantabrian Sea, Figure 6). Model residuals (not shown) evidence slight underestimation at ages 2–3 in the latter areas, but poor fitting does not fully explain this discrepancy. In fact, observed abundance-at-age for 2- and 3-year-olds is low for the Cantabrian Sea and only moderate for northern Galicia, i.e. half the abundance-at-age observed for the 2000 year class.

Correlations between sardine abundance at age 1 among areas of the Iberian Biscay region are generally weak and mostly positive. Correlation tests indicate that recruitment strength is not

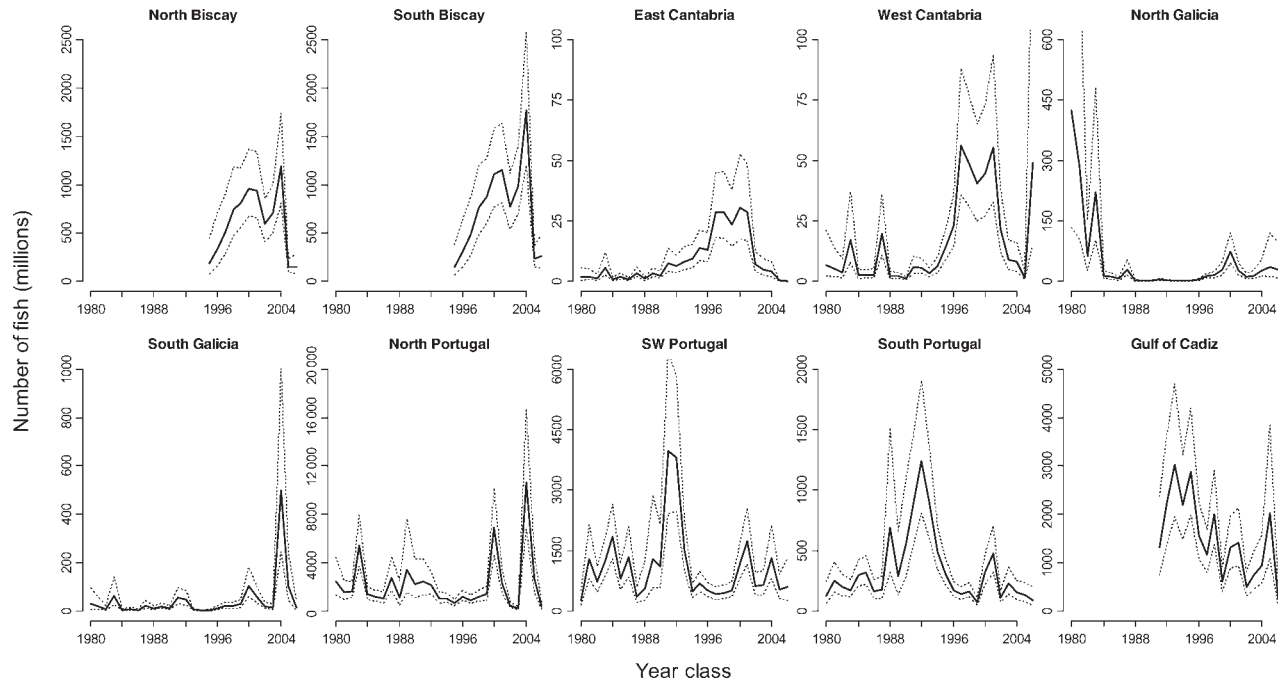


Figure 6. Temporal variation in sardine recruitment (at age 1, solid line) by area in acoustic surveys, predicted (anti-logged) by year-class models assuming the same (French surveys, Model 5) or variable year-class strength by area (Models 4 and 6 for Portuguese and Spanish surveys, respectively). Dotted lines shows predicted values ± 1 s.e. Note the differences in the y-axis scales.

significantly associated between the four main recruitment areas of the Bay of Biscay, northern and southwestern Portugal, and the Gulf of Cadiz, despite some common strong year classes in recent years (Table 4, Figure 6). Year-class variation in the eastern Cantabrian Sea shows a significant positive correlation ($p < 0.006$) with that in the western Cantabrian Sea, and a moderate positive correlation ($p < 0.013$) with year-class variation in northern Biscay, but no obvious relationship with other recruitment areas. Northern Portugal and southern Galicia, two adjacent areas dominated by young sardine, show significantly correlated recruitment ($p < 0.006$), but somewhat surprisingly, recruitment variation in the two western Portuguese areas shows no significant association. Year-class strength off southern Portugal, an area where older sardine dominate, is positively correlated with those in the two adjacent recruitment areas, southwestern Portugal ($p < 0.006$) and the Gulf of Cadiz

($p < 0.013$). Finally, northern Galicia and southern Portugal present opposite year-class variation, as shown by a significantly negative correlation.

Discussion

Data on sardine abundance and age structure analysed here were obtained from separate acoustic surveys (French, Spanish, and Portuguese) over periods of up to 20 years. During the survey periods, methodology changed, and some differences have always been present between national surveys, despite international coordination being established early among participating laboratories (ICES, 1986, 1998, 2006b; Table 1). To compare sardine dynamics in space and time, it was assumed that catchability did not differ substantially within or between survey series. Variation in catchability over time is not a matter of concern in the French surveys, which cover a shorter period,

Table 4. Pearson correlation coefficients between relative recruitment (at age 1) in each area using predicted abundance from models assuming area-based year-class effects (Model 4 for Portuguese surveys, Model 6 for the French and Spanish surveys; see also Tables 2 and 3).

	NFRA	SFRA	ECAN	WCAN	NGAL	SGAL	NPOR	SWPOR	SPOR
SFRA	0.95								
ECAN	<u>0.67</u>	0.43							
WCAN	0.35	0.23	0.53						
NGAL	0.36	0.54	-0.14	0.31					
SGAL	0.49	0.63	0.13	0.25	0.44				
NPOR	0.42	0.42	0.15	-0.11	0.29	0.67			
SWPOR	0.47	0.53	0.05	-0.28	-0.23	0.21	0.32		
SPOR	0.23	0.14	0.18	-0.43	-0.56	-0.15	0.12	0.64	
CAD	-0.06	-0.23	0.39	-0.46	-0.55	-0.20	0.31	0.23	<u>0.64</u>

To account for multiple comparisons between areas, $p = 0.006$ (values emboldened). Values underlined are significant at 1.3% level. ECAN, eastern Cantabrian Sea; WCAN, western Cantabrian Sea; NGAL, northern Galicia; SGAL, southern Galicia; NPOR, northern Portugal; SWPOR, southwest Portugal; SPOR, southern Portugal; and CAD, Gulf of Cadiz.

with no methodological changes. Data obtained from the French and Spanish surveys should also be comparable because the same research vessel, acoustic equipment, and pelagic fishing gear were used. On the other hand, methodological changes were gradually introduced in the Spanish and Portuguese surveys up to the mid-1990s, and their impact on total and age-specific catchability is uncertain (see Table 1 for a summary, and also Marques *et al.*, 2004). Differences between the Spanish and Portuguese surveys are expected to have declined throughout the period because of improved methodological standardization (Marques *et al.*, 2004; ICES, 2006b), but potential differences in selectivity-at-age, the consequence of using different research vessels and fishing gear, are still a matter of concern (ICES, 2006a). The consistency between survey and catch-at-age distributions in corresponding areas suggests that surveys largely reflect the local availability of certain age groups (Figure 3); a conclusion supported by sharp contrasts in age structure obtained with the same research vessel and fishing gear in neighbouring areas of northern Spain and Biscay. Therefore, it seems unlikely that catchability differences between surveys have blurred the major spatio-temporal patterns of sardine dynamics described here, although greater reliability is expected for the past decade.

YCC models provided an opportunity to analyse area-disaggregated data on sardine abundance-at-age. Appealing features of YCC models are the simple statistics and the facility to explore alternative model structures with standard statistical software (Cotter *et al.*, 2004). On the other hand, YCC models have some rigid assumptions (Cotter *et al.*, 2004). For sardine, assumptions of constant or linearly changing year-class mortality are possibly too stringent because, according to the annual stock assessment, fishing mortality may double or halve within 5–6 years (ICES, 2007). The finally selected models provided reasonable fits to each survey series and were generally parsimonious. Models with area-nested year classes had the disadvantage of estimating a large number of parameters, so potentially increasing bias, but exposed interesting small-scale geographic variation in sardine recruitment. The similarity in relative recruitment trends obtained with the two types of model, i.e. models assuming homogeneous and heterogeneous year-class strength among the areas covered by the same survey series (Figure 5), suggests that the overall perspective of recruitment provided by more complex, possibly over-parameterized models was not seriously biased.

Results from YCC models are difficult to compare with those from the ICES assessment of the AIS (ICES, 2007) because of substantial differences in the data, spatial disaggregation, and modeling assumptions and methods. However, the consistency since the early 1990s between recruitment trends obtained with YCC models for the AIS area, i.e. area-based estimates of age 1 abundance summed across the AIS region and estimated in the ICES assessment at age 0 (Figure 5) is worth noting. Counter-intuitively, agreement is better when geographic variations in year-class strength are assumed in YCC models than when the same recruitment variation is assumed for different areas. This agreement is partly understandable because survey data used in assessments (sum of area-disaggregated abundance across the stock region) integrate spatial differences in recruitment to some extent. A broad comparison of mortality signals across the AIS region shows that the average YCC slope (Z_{4-6} by year class = 0.61 year^{-1}) is close to the average annual mortality rate (Z_{4-6} by year = 0.57 year^{-1}) from stock assessments in the same

period. On the other hand, the increasing trend in year-class slopes obtained in the Spanish areas disagrees with the overall decline in fishing mortality indicated in the stock assessment (ICES, 2007), a discrepancy that may reflect decreased age-related migration and/or increased natural mortality across the period.

Area-disaggregated data from Spanish and Portuguese surveys showed that sardine biomass was generally higher off western Portugal (northern and southwest areas) and in the Gulf of Cadiz than in the other Iberian areas. Off northern Spain, average biomass by area was almost one order of magnitude less than that off northern Portugal. Biomass levels were highest in the western Cantabrian Sea, and southern Galicia showed consistently low biomass from the early 1980s in accord with a permanent gap in sardine spawning (Bernal *et al.*, 2007). Surveys carried out in the French Bay of Biscay since 2000 showed that sardine biomass in the area was comparable with that observed off western Portugal (300 000 t). Detailed spatial distributions (ICES, 2005, 2006a) indicate a wide but variable distribution across the whole shelf area, with generally lower concentrations close to the Spanish border.

The distribution of catches provides a distinct perspective on sardine distribution from surveys because of geographic differences in exploitation levels. The ratio of catch to survey biomass is around 5% in the Bay of Biscay and the Gulf of Cadiz, suggesting much lower exploitation rates than in the other areas, where this ratio is ~23%. Low levels of exploitation are consistent with the fact that purse-seine fisheries target anchovy (*Engraulis encrasicolus*) in those areas and take sardine only occasionally or seasonally (Carrera and Porteiro, 2003; ICES, 2006a). In the early 1980s, large catches of sardine off northwestern Iberia created an impression of sardine concentration that contradicted survey data. To explain the discrepancy off southern Galicia, Carrera and Porteiro (2003) suggested that sardine abundance during the spring survey may not reflect the actual abundance available to the Galician fishery (which catches sardine mainly in summer and autumn), and further proposed that catches were of fish migrating north across the area. However, the decline in catches in the 1980s and early 1990s may partly be explained by effort reductions. Off southern Galicia, where the decline was the sharpest, the number of fishing trips per year dropped from 8000 to 3000 between 1982 and 1989 (ICES, 1999). Off the Portuguese coast, numbers of both fishing trips and fishing vessels decreased substantially during the 1990s. Catch limitations implemented since 1997 by Spain and Portugal (ICES, 2007) may also explain uncoupling between abundance and catch trends in recent years. Finally, off southwest Portugal, there is a discrepancy between catch and survey age structure which may be related to low fishing activity off Lisbon, where recruits are abundant.

Data on the age distribution and year-class dynamics by area corroborate earlier indications that sardine of the AIS recruit mainly off northern Portugal and the Gulf of Cadiz and, to a smaller extent, off southwestern Portugal (ICES, 2006a). The present study shows that the Bay of Biscay is an important recruitment area for sardine. Average levels of recruitment (at age 1) in the Gulf of Cadiz, the Bay of Biscay, and southwest Portugal are around 70, 60, and 50%, respectively, of those off northern Portugal. Juveniles are found mainly in the southern part of Biscay and off southern Brittany (ICES, 2006a), in a narrow area off Lisbon (southwest Portugal), over a wide coastal area off northern Portugal, and across a large part of the Gulf of Cadiz shelf (Marques, 2005). These recruitment “hotspots” coincide

with areas of significant river discharge (the Loire in Brittany, the Gironde and the Adour in southern Biscay, the Minho, Douro, Mondego, and Vouga in northern Portugal, the Tagus in Lisbon, and the Guadalquivir in the Gulf of Cadiz) and, therefore, high productivity in winter/spring, when most spawning takes place (Coombs *et al.*, 2006; Stratoudakis *et al.*, 2007). Some of them are important recruitment areas for other fish species, such as off northern Portugal for horse mackerel (*Trachurus trachurus*; Murta *et al.*, 2008), the mouth of the Tagus River for most species, and the Gulf of Cadiz and southern Biscay for anchovy (ICES, 2006a).

Physical processes conditioning the distribution of eggs and larvae may contribute to recruitment success in those areas and explain why sardine recruitment is localized despite widespread spawning across most of the Iberian Biscay region (Bernal *et al.*, 2007). In fact, Santos *et al.* (2004) showed that sardine larvae are retained, along with high concentrations of their prey, inside a recurrent lens of less-saline water fed by the winter discharge of several rivers off the northwest Iberian Peninsula. Along the Moroccan coast, the location of a nursery area for sardine near Dakhla (24°N) has also been associated with topographic and oceanographic characteristics favouring larval retention (Ettahiri *et al.*, 2003), whereas in the northwest Mediterranean, sardine larvae concentrate at the mouth of the Ebro River, an area of high productivity where retention is facilitated by an anticyclonic circulation and the absence of intense currents in winter during the sardine spawning season (Sabatés *et al.*, 2007).

Asynchrony in recruit abundance among the major recruitment areas indicates some level of spatial structure in sardine dynamics which may be associated with environmental variation at a small geographic scale (Cohen *et al.*, 1991). Differences between northern and southwestern Portugal, two adjacent recruitment areas separated by 1.5° of latitude, illustrate this point. Some recruitment peaks are common to several areas, however, despite distinct relative strength, suggesting that region-wide environmental factors may overlay local effects in some years. Therefore, for example, the 1983 recruitment had a more northern distribution (western Iberia) than the 1991 and 1992 recruitments (southwest and southern Iberia), and the 2004 recruitment seems to be strongest in distant areas such as northern Portugal and Biscay. The negative correlation between year-class variation off northern Galicia and southern Portugal seems to reflect these spatio-temporal variations.

This study has also provided some indirect evidence that at least some fish spawned in a given recruitment area emigrate during their life and influence population dynamics in adjacent areas. This type of migration related to fish size is common for small- and medium-sized pelagic fish and has been described for southern African sardine (*Sardinops sagax*) and anchovy (*Engraulis capensis*; Barange *et al.*, 1999, in press), and southern horse mackerel (Murta *et al.*, 2008). For sardine in the Iberian–Biscay region, the existence of preferential recruitment areas intermingling with areas of adult prevalence showing synchronous year-class strength is consistent with size-related migration. Areas with low year-class slopes or strong positive age selectivity, such as off southern Portugal and in the Cantabrian Sea, respectively, are plausible immigration areas. Therefore, sardine distributed off southern Portugal, mostly older fish, may have recruited in either (or both) southwestern Portugal or the Gulf of Cadiz, because there is year-class synchrony for both these recruitment areas. Year-class variation in the Cantabrian Sea shows some

synchrony with recruitment in the Bay of Biscay in the past decade, suggesting that these areas are connected by migration. This is consistent with the results from exploratory area-based assessments showing that immigration of 1-year-old sardine from Biscay to the eastern Cantabrian Sea is a likely hypothesis (ICES, 2006a). Despite weak overall synchrony in year-class variation, the coincidence of some strong year classes (particularly 1983 and 2000) suggests that sardine in the Cantabrian Sea and off northern Galicia are connected to the sardine recruited off western Iberia. Graphic analyses of acoustic survey data showed a northward progression of the 2000 year class up to northern Galicia (Anon., 2006) and of the 2004 year class up to western Cantabria (ICES, 2007). On the other hand, the strong 1991 and 1992 year classes recruited off western Iberia show no signs of northward progression, supporting indications that migration directions may change over time (Anon., 2006).

This study demonstrated that sardine dynamics differ substantially across the Iberian Peninsula and the Bay of Biscay. Recruitment is localized in a few areas and generally asynchronous among areas, although some recruitment peaks are noticeable across wide regions. The results also provided some indirect evidence that year classes recruited in a given area migrate throughout their life and that main migration directions may change over time. Geographic differences in recruitment trends coupled with size-related migrations explain distinct regional trends in abundance. The present findings are consistent with a complex population structure characterized by spatial heterogeneity in phenotypic characters and life-history traits (Andreu, 1969; Silva, 2003; Silva *et al.*, 2006, 2008). Evidence of spatial variability in dynamics does not preclude some fish mixing across the whole region, in agreement with both genetic homogeneity (Kasapidis *et al.*, 2004; Gonzalez and Zardoya, 2007; Laurent *et al.*, 2007) and the similarity in otolith element composition in larger fish (Castro, 2007). Areas of clearly distinct population dynamics, justifying a subdivision of the Atlanto–Iberian sardine stock, were not in evidence. There is, however, evidence of connectivity between sardine dynamics in the Bay of Biscay and the Cantabrian Sea which corroborates previous doubts about the northern stock limit. The combination of shallow genotypic differentiation with variability in phenotypic and vital traits (such as maturity and growth) and the heterogeneous dynamics found here further suggest that sardine from the Iberian Biscay region may be structured as a metapopulation (McQuinn, 1997; Kritzer and Sale, 2004). According to the observed patterns of synchronicity in recruitment and plausible migration routes, as well as phenotypic and vital traits, three populations recruiting in the Bay of Biscay, off northern Portugal, and in the Gulf of Cadiz, respectively, may comprise this metapopulation.

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