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Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean

A. Silva, M. B. Santos, B. Caneco, G. Pestana, C. Porteiro, P. Carrera, and Y. Stratoudakis

We investigate spatial and temporal variations in sardine maturation patterns and discuss the implications for stock structure, using recent samples collected opportunistically across the species range and data collected regularly for the assessment of the Atlanto-Iberian stock. Maturity ogives were fitted to maturity-at-length data using Generalized Linear Models, and maturation patterns are summarized by length at first maturity (L_{50}). Sardine attain sexual maturity at a total length of 10.9—16.8 cm. The percentage of mature small sardine increases from north to south across the Northeast Atlantic. L_{50} is low in the Mediterranean and Moroccan waters, but maturation is delayed towards the limits of the species' range. Sardine mature smaller in the Gulf of Cadiz than in other areas of the Atlanto-Iberian stock, although there is no indication of a different maturation pattern north of the stock boundary. These results are not sufficient to review the stock structure of sardine, but question the hypothesis of homogeneous biological properties of sardine populations within the stock area. Sardine maturation length reduced and the spawning period extended in western Iberia during the past two decades. Associated increases in fish condition and fat reserves during the summer feeding season suggest that variations in reproductive traits may have been caused by environmentally driven changes in food availability.

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Introduction

Spatial and temporal trends in maturation have been documented for many fish species. On wide geographic scales, maturation tends to co-vary with growth in such a manner that the ratios between length/age at first maturity and maximum length at age remain approximately stable across the distribution range of species (Beverton, 1992). Populations inhabiting colder habitats generally grow more slowly, live longer, and delay maturation when compared with those from warmer areas of the distribution, the differences reflecting the ability of the species to adapt to large-scale patterns in environmental conditions (Beverton, 1992). As is the case for other life history traits, maturation expresses the interaction between the genetic background and environmental influences, and provides evidence of geographic and/or reproductive isolation of fish populations (Begg, 2005). Therefore, differences in maturation have been taken as evidence for population discreteness within holistic approaches for the identification of fish stocks (Begg and Waldman, 1999; Begg et al., 1999; Berg and Albert, 2003). Apart from their value in stock identification, spatial variations in maturation within the boundaries of a stock should be taken into account in stock assessment if they are associated with large spatial differences in population abundance (Hilborn and Walters, 1992).

Temporal trends in fish maturation have often been interpreted as compensatory density-dependent effects that regulate population growth (Rose et al., 2001).

Density-dependent changes in maturation arise from food limitation attributable to increased intraspecific competition. The length or the age of maturation may be directly affected through changes in the quantity of energy reserves available for gonad development (Morgan, 2004), or indirectly via changes in growth which in turn influence the triggering of maturation (Engelhard and Heino, 2004). Density-dependent effects may explain the decrease in length/age at first maturity in many fish populations that have shown extensive declines in biomass (Armstrong, *et al.*, 1989; Nash *et al.*, 2000; Engelhard and Heino, 2004). As most of these populations belong to heavily exploited fish stocks, fishing mortality has been suggested as the selective pressure inducing a rapid evolution of maturation characteristics (Barot *et al.*, 2005). However, it has often proved difficult to disentangle the direct influence of population density from that of long-term environmental trends, and this is further confounded by the effects of environmental conditions on population abundance, which in turn can trigger density-dependent maturation (Rose *et al.*, 2001).

The sardine (*Sardina pilchardus*) is a commercially important clupeoid distributed in the northeastern Atlantic from the North Sea to Senegal and throughout most of the Mediterranean Sea (Parrish *et al.*, 1989). Its largest populations and the more productive sardine fisheries are situated off Morocco (stock biomass 1—5 million tonnes; catches around 600 000 t in recent years; FAO, 2003), whereas abundance and fishing intensity are low in the Mediterranean (http://www.faocopemed.org). Within Atlantic European waters, the sardine is considered to belong to a single stock for assessment purposes, the Atlanto-Iberian stock, with biomass around 500 000 t and catches around 100 000 t in recent years (ICES, 2005).

The Atlanto-Iberian sardine stock is delimited by the French/Spanish border in the north, and by the Strait of Gibraltar in the south (ICES Divisions VIIIc and IXa). It is exploited mainly by the purse-seine fleets of Spain and Portugal, and it has been assessed since the early 1980s assuming that it consists essentially of self-reproducing populations that share homogeneous life history properties. However, recent studies provide evidence of geographic differences in morphometric characters, age structure, and population dynamics within the stock area, which challenge the assumption of a single management unit (ICES, 2000; Carrera and Porteiro, 2003; Silva, 2003). The stock boundaries have also been questioned on the basis of evidence of a continuous distribution of sardine eggs and adults extending into French waters and of possible mixing among populations across the southern border of the stock (ICES, 2000; Stratoudakis *et al.*, 2003). Uncertainty regarding the definition of the stock unit has affected the level of confidence in stock estimates and knowledge of long-term trends in abundance, and has highlighted the need for biological information that can both assist in defining management units and provide data to pursue stock assessment at finer spatial scales (ICES, 2005).

The main goal of this manuscript is to study the spatial and temporal variability of sardine maturation patterns and to discuss their contribution to the definition of stock structure. Data collected recently across most of the area of distribution of the species are used to describe large-scale geographic variability in life history traits such as longevity, maximum length, and maturity at length. Despite the narrow temporal scale and the limited sampling intensity, the samples provide an opportunity to compare sardine maturation over a wide geographic area, using data collected and analysed with similar methodology. Data on length, weight, sex, maturity, fat content, and age routinely collected by Spain and Portugal since the early 1980s for the assessment of the Atlanto-Iberian sardine stock are used to compare sardine maturation patterns among stock areas, and to assess the temporal stability of such patterns by following interannual changes in the length at first maturity (L_{50}). Data on population abundance (from landings and estimated biomass) of the Atlanto-Iberian sardine stock are used to explore the existence of potential relationships with size at maturity (positive if both parameters represent a response to environmental conditions; negative if there is density-dependent competition). Finally, fish condition (weight and fat content at length) is used to explore the relationship between the accumulation of energy reserves during summer feeding and the size at first maturity.

Material and methods

Sardine samples collected within the remit of various international projects during the period 1999—2004, mainly for studying stock structure, are used to describe broad geographical patterns in sardine maturation. Overall, 51 samples of sardine (generally 100 fish) collected from the north (English Channel to southern France), south (northern Morocco to Mauritania), east (Azores and Madeira), and west (western Mediterranean) of the distribution of the Atlanto-Iberian stock were used (Figure 1). All samples were collected within the spawning season, either in the ports (five samples) or during research surveys, but the final distribution of samples among areas and years is very unbalanced (e.g. 28 samples in south France and only one sample in Mauritanian waters). Samples were transferred frozen to the laboratory of IPIMAR, where fish were thawed and processed following routine biological sampling (see below).

Biological samples from sardine commercial landings and acoustic surveys have been regularly collected from the area since the early 1980s, and are used to describe temporal trends and small-scale spatial variation in the maturation pattern of the stock. Samples from landings by purse-seiners were collected once or twice a month between 1981 and 2003 at the main ports of the Iberian Peninsula (Figure 1). Sampling started more recently and has been
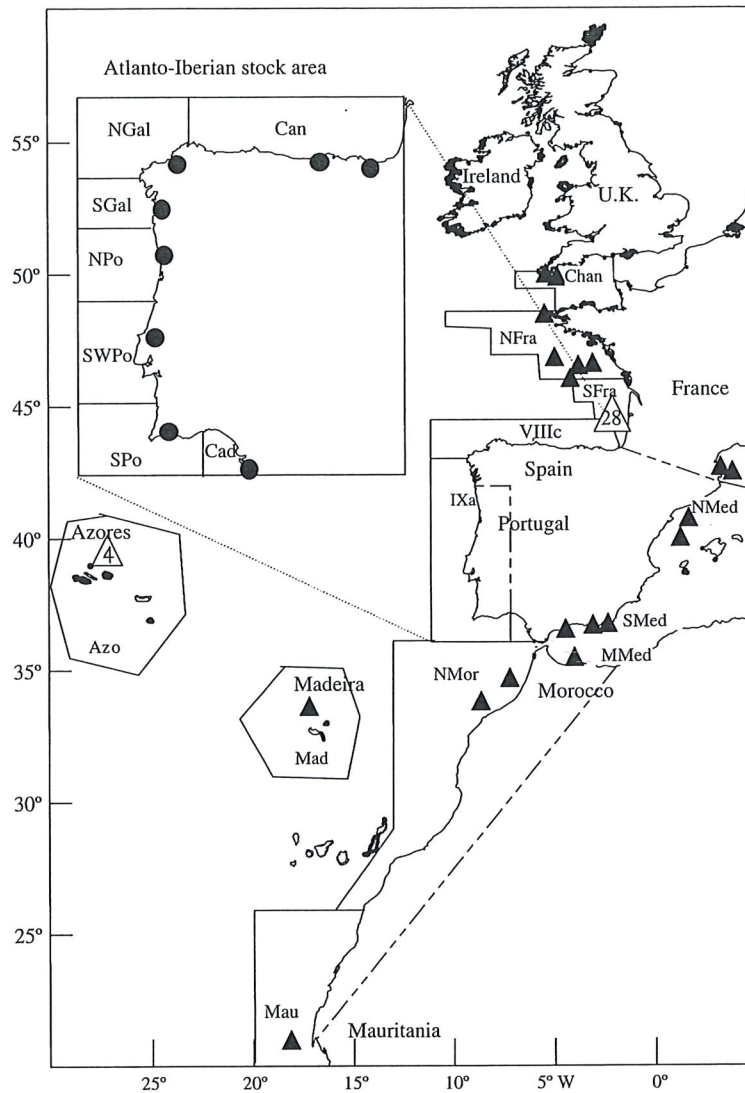
Figure 1. Map of the study area showing boundaries of ICES Divisions and FAO Divisions. The location of samples collected for broad spatial-scale analyses is indicated by the black triangles; larger symbols show the number of samples collected from close locations. The area of the Atlanto-Iberian sardine stock with the corresponding ICES Subdivisions is enlarged on the top left of the map. Ports where samples for small-scale spatial analyses were collected are represented by black circles.

less regular in the Cantabrian Sea, North Galicia (1993), and Cadiz (2000), providing around 800 fish by port and year. Ports located in southern Galicia and in northern, southwestern, and southern Portugal account on average for 80% of the total landings of the stock. Sampling regularity in these ports was generally good, with an average of 1200 fish collected per port per year, except during periods of low sardine abundance or seasonal closures of the fishery. Each sample consists of six fish per half-centimetre class (Spanish ports) or a random collection of 100 fish (Portuguese ports). Samples from acoustic surveys have been collected irregularly since 1984 in spring

(Spanish and Portuguese waters) and autumn (Portuguese waters). During such surveys, random collections of 40 fish (Spanish survey) or length-stratified samples of 10—15 fish per half-centimetre length class (Portuguese surveys) were taken from each fishing haul.

Total length (cm), macroscopic maturity, and visceral fat stage were recorded for all fish. Total weight (g) was recorded for all market samples, but gutted weight (Wgut) and gonad weight (Wgon) are only available since the mid-1980s in sardine samples collected at Portuguese ports. Age data from survey samples collected within the stock area and from opportunistic samples collected

outside this area are used to summarize the age structure of sardine populations across the study area. Macroscopic maturity stage was determined by visual examination of the gonads using a six-stage key: 1, immature; 2, developing; 3, pre-spawning; 4, spawning; 5, spawning/recovering; 6, post-spawning (Pinto, 1957; Pinto and Andreu, 1957). Fish at maturity stage 2 and above were considered to be mature (here used as a synonym for "adults", i.e. potentially part of the spawning population) and those in stages 3–5 were assumed to be showing spawning activity. The classification of the fat stage (1, no fat visible; 2, thin thread of fat surrounding part of the gut; 3, thicker layer of fat partially surrounding the gut; 4, thick layer of fat surrounding the gut) was based on the key proposed by Furnestin (1943).

Length-based maturity ogives were obtained from samples grouped into areas roughly according to ICES or FAO Divisions. For a broad geographic comparison of maturity, ogives were obtained from interannually pooled samples from the areas outside the stock and from pooled survey data (separately for the 1980s and the 1990s–2000s) for areas within the stock region. To explore temporal trends in maturity within the stock area, maturity ogives were estimated from market samples pooled for each spawning season (October–January, spanning the first part of the spawning season up to the peak). The sampling period used to estimate maturity ogives was based on an analysis of sardine spawning seasonality as a function of fish length in the 1980s and 1990s. The probability of spawning (sp) was modelled as an anisotropic bi-variate function ($f(.)$) of fish length class (l) 12–18 cm and month (mo) (September–August, coded with numbers 1–12) within each area and period using Generalized Additive Models with a binomial error distribution and a logit link (Wood, 2000). The general form of the models is

$$\text{logit}(E[\text{sp}]) = f(l, \text{mo}).$$

Eight models were fitted to data for each combination of area/period providing an explained deviance of 30–62%, with sample size ranging from 7130 to 21 205 observations. These models were used to predict the probability of spawning of fish 14 cm (mean L_{50}), 15.5 cm (mean L_{75}), and 18 cm long throughout the year. The last length class was assumed to represent the spawning seasonality of larger fish.

Generalized Linear Models (GLMs; McCullagh and Nelder, 1989) with a binomial error distribution and a logit link were fitted to the proportion of fish mature (m) by length class (l). The model has the general form

$$\text{logit}(E[m]) = a + bl.$$

where a and b are the intercept and slope of the ogive, respectively. Estimates of the length at 50% maturity (L_{50}) and of the slope of the ogive at L_{50} (slope) were derived from the model parameters as

$$L_{50} = -a/b,$$

$$\text{Slope} = b/4.$$

The standard error of L_{50} was estimated using the formula for the approximate variance of a ratio of two random variables (Mood *et al.*, 1974):

$$\text{s.e.}_{L_{50}} = (a/b)^2 \left[\text{var}(a)/a^2 + \text{var}(b)/b^2 - 2\text{cov}(a,b)/ab \right],$$

and the s.e. of the slope at L_{50} is

$$\text{s.e.}_{sl} = \text{s.e.}_{b}/4.$$

Standard errors of the parameters were corrected to account for the inflation of variance (relative to the nominal binomial variance) attributable to the combination of data from different samples (see below). This correction was carried out by multiplying the parameter standard errors by the square-root of the replication estimate of overdispersion (McCullagh and Nelder, 1989; Millar *et al.*, 2004). Asymptotic confidence intervals were calculated using the *t*-statistic. Geographical differences and temporal trends in L_{50} within western Iberian waters were tested for the period 1985–2003 by linear regression analysis. The effects of area (factor variable), year (continuous variable), and their interaction were tested by *F*-test using a forward procedure (McCullagh and Nelder, 1989). The inverse standard errors of L_{50} were used as weighting factors. The northern and southern Iberian areas were not included in this analysis owing to a lack of data. All calculations were carried out with R 1.9.1 (The R Development Core Team, 2004).

Results

Large-scale spatial variation in life history parameters

Sardine total length in all samples used in this study ranged between 7.0 and 29.5 cm, corresponding to ages of 0–13 years (Table 1). Length and age range decreased from north to south in the northeastern Atlantic and were generally smaller in the Mediterranean Sea. Cape Finisterre at the northwestern corner of the Iberian Peninsula seems to form a boundary in the length and age distribution of samples from the Atlantic, with higher median lengths and ages in areas to the north ($\approx$20 cm and 3 years) than to the south ($\approx$17 cm and 1 year old). The sample from Mauritania was an exception to this trend, showing a similar length distribution to northern areas but a reduced age range. Samples from the western Mediterranean and from the Atlantic islands of the Azores and Madeira had smaller length and age ranges than those from southern Iberia.

Table 2 summarizes information on sardine maturation by area. Point estimates of L_{50} varied between 10.9 and 16.8 cm (mean 14.3 cm, CV 10%), and slopes in L_{50} ranged

Table 1. Data used to summarize sardine maturation patterns by area within northeastern Atlantic and western Mediterranean waters. Information on sardine length and age in samples and mean landings and abundance by area is also provided. Area codes: Chan, English Channel; NFr, North France; SFr, South France; CanE, East Cantabrian Sea; NGal, North Galicia; SGal, South Galicia; NPo, North Portugal; SWPo, Southwest Portugal; SPo, South Portugal; Cad, Gulf of Caduz; SMed, Southwest Mediterranean; Nmed, Northwest Mediterranean; Mmed, Moroccan Mediterranean; Nmor, North Morocco; Mau, Mauritania; Azo, Azores; Mad, Madeira.

Area	ICES FAO Area	Period	Month	n	Median length range (cm)	Median age range (years)	Landings ('000 t)	Abundance ('000 t)
Chan	VIIe	2003	Jan, Nov	180	23.5 (18.0–27.0)	6 (2–12)	12.6	—
NFr	VIIIa	2000–2003	Mar–Jun	387	19.0 (11.5–24.5)	3 (1–8)	11.2	281
SFr	VIIIb	1997–2001	Mar–Jun	2050	19.0 (11.5–26.0)	2 (1–10)		
Can	VIIIc-E	1986–1989	Mar–Apr	979	22.0 (11.5–27.0)	4 (1–11)	33*	61
		1990–2003	Jan–May	6800	21.5 (11.5–29.0)	4 (1–13)	8.5	60
NGal	IXa-N	1986–1989	Mar, Apr	598	21.5 (11.0–25.5)	5 (1–10)	33*	57
		1990–2003	Mar–May	2279	21.0 (11.0–26.0)	3 (1–12)	12.0	8
SGal	IXa-N	1986–1989	Feb–Apr	633	18.5 (12.0–25.5)	3 (1–10)	51.8	11
		1990–2003	Mar, Apr	3284	17.5 (12.0–29.5)	2 (1–12)	13.4	10
NPo	IXa-CN	1984–1988	Nov, Mar	4707	17.0 (9.5–25.5)	1 (0–8)	50.3	197
		1996–2003	Nov, Mar	15808	15.0 (7.0–24.0)	1 (0–10)	40.9	149
SWPo	IXa-CS	1984–1988	Nov, Mar	2804	17.0 (8.0–23.0)	2 (0–8)	31.8	118
		1996–2003	Nov, Mar	13183	17.5 (12.0–22.0)	1 (0–9)	27.7	115
SPo	IXa-AS	1984–1988	Nov, Mar	2262	17.5 (12.0–22.5)	1 (0–8)	16.3	74
		1996–2003	Nov, Mar	9495	18.5 (9.5–25.0)	2 (0–9)	18.0	83
Cad	IXa-SC	1996–2003	Nov, Mar	9491	16.5 (9.5–25.0)	2 (0–9)	5.3	139
SMed	37.1.1	1999	Dec	106	14.5 (13.0–20.5)	1 (1–3)	4.7	37
MMed	37.1.1	2004	Oct	46	13.5 (12.5–16.0)	0 (0–1)	14.0	—
NMed	37.1.1/2	1999	Dec	60	15.0 (13.5–19.0)	1 (1–3)	11.0	76
NMor	34.1.11	2000–2003	Jan	139	17.0 (12.0–19.0)	2 (1–4)	14.6	22
Mau	34.3	2003	Feb–Apr	89	23.0 (13.5–19.0)	1 (1–3)	11.0	76
NMor	34.1.11	2000–2003	Jan	139	17.0 (12.0–19.0)	2 (1–4)	14.6	22
Mau	34.3	2003	Feb–Apr	89	23.0 (13.5–26.5)	3 (0–6)	11.5–37.5	670
Azo	Xa	2000–2004	Jun, Nov	324	16.5 (11.5–18.5)	0 (0–2)	<1	—
Mad	XIa	2003	Mar	64	17.0 (16.0–19.5)	1 (1–4)	<1	—

*Total CanE and CanW landings.

from 0.13 to 0.53 cm^{-1} (mean 0.30 cm^{-1}, CV 42%). There is some evidence of an overall increase in the percentage of small sardines mature from northern France to the Gulf of Cadiz but, unlike for length and age distributions, there is no clear boundary at Cape Finisterre. Instead, L_{50} is considerably higher in northern France (16.8 cm) but comparable among areas to the south of this region. At the southern extent of the Iberian Peninsula (Gulf of Cadiz), L_{50} was 2.4 cm lower than the overall mean, and transition to maturity is clearly steeper than in more northerly areas (slope in L_{50} 0.52 cm^{-1}) in recent years. The area of transition from a higher L_{50} in the west to a lower L_{50} near Cadiz is not clear because maturity parameters from southern Portugal were closer to those from Cadiz in recent years but similar to the western Iberian areas during the 1980s. Therefore, the most evident discontinuity in the maturation pattern of sardine within the Atlanto-Iberian stock area occurred in the Gulf of Cadiz.

Maturity ogives could not be estimated for the western Channel, the Mediterranean, or North Moroccan areas, because immature fish were either absent or present in only small numbers within the samples. This would be expected for the Channel where the minimum length of fish sampled was 18 cm. Conversely, the small fish (12–13.5 cm) in the Mediterranean and Moroccan samples were mostly adults, providing some indication that L_{50} values in those areas would be at least as low as those in northwestern Iberian areas. The samples from Mauritania (L_{50} 16.2 cm) and Azores (L_{50} 15.7 cm) suggest that sardine length at first maturity may increase towards the southern and the western limits of distribution of the species.

Spatio-temporal variation in maturity at length along the Iberian Peninsula

Annual maturity ogives are seldom defined for the northern stock areas (Cantabria and north Galicia) because samples are dominated by large fish (median length ≈21 cm, median age ≈4 years; Table 1). Pooled survey data provided estimates of L_{50} between 13.3 and 15.6 cm, within the range of variation of L_{50} in the more southerly areas (Table 2). Similarly, most of the sardine sampled in the

Table 2. Maturation parameters of sardine summarized by area and period within the northeastern Atlantic and western Mediterranean. Crude estimates of the mean length at age 1 and of the growth during the second year of life are also provided. Area codes: NFr, North France; SFr, South France; CanE, East Cantabrain Sea; NGal, North Galicia; SGal, South Galicia; NPo, North Portugal; SWPo, Southwest Portugal; SPo, South Portugal; Cad, Gulf of Cadiz; SMed, Southwest Mediterranean; Nmed, Northwest Mediterranean; Mmed, Moroccan Mediterranean; Nmor, North Morocco; Mau, Mauritania; Azo, Azores; Mad, Madeira.

Area	Period	Month	L_{50} [CI] (cm)	Slope in L_{50} [CI] (cm^{-1})	Minimum length at maturity (cm)	Mean length $\pm$ s.d. at age 1 (cm)
NFr	2000–2003	Mar–Jun	16.8 [16.4, 17.2]	0.21 [0.16, 0.25]	14.5	15.1 ± 1.63
SFr	1997–2001	Mar–Jun	14.0 [13.7, 14.4]	0.23 [0.19, 0.28]	12.5	15.8 ± 1.44
Can	1986–1989	Mar, Apr	14.6 [13.9, 15.3]	0.25 [0.13, 0.37]	13.5	15.6 ± 1.18
	1990–2003	Jan–May	13.8 [13.5, 14.0]	0.29 [0.26, 0.33]	11.5*	15.3 ± 2.21
NGal	1986–1989	Mar, Apr	15.6 [15.1–16.1]	0.34 [0.23–0.46]	13.5	13.8 ± 1.89
	1990–2003	Mar–May	13.3 [12.2–14.3]	0.18 [0.12–0.23]	12.0	16.4 ± 1.58
SGal	1986–1989	Feb–Apr	13.4 [12.8, 14.0]	0.53 [0.32, 0.74]	13.0	15.6 ± 3.95
	1990–2003	Mar, Apr	13.9 [13.5, 14.4]	0.23 [0.19, 0.28]	12.0*	17.0 ± 4.12
NPo	1984–1988	Nov, Mar	14.6 [14.4, 14.8]	0.25 [0.22, 0.28]	12.0	15.5 ± 3.93
	1996–2003	Nov, Mar	14.3 [14.1, 14.4]	0.23 [0.21, 0.26]	11.0	15.0 ± 3.87
SWPo	1984–1988	Nov, Mar	14.7 [14.3, 15.1]	0.17 [0.14, 0.20]	10.5	15.9 ± 3.98
	1996–2003	Nov, Mar	14.3 [14.1, 14.6]	0.20 [0.18, 0.22]	11.5	14.2 ± 3.77
SPo	1984–1988	Nov, Mar	13.9 [13.6, 14.3]	0.25 [0.20, 0.30]	12.5	16.4 ± 4.05
	1996–2003	Nov, Mar	12.4 [12.0, 12.9]	0.24 [0.20, 0.27]	11.0	16.3 ± 4.03
Cad	1996–2003	Nov, Mar	10.9 [9.7, 12.1]	0.52 [0.07, 1.03]	10.0	15.5 ± 3.93
SMed	1999	Dec	—	—	13.0*	15.6 ± 1.00
MMed	2004	Oct	—	—	12.5*	15.2 ± 1.4
NMed	1999	Dec	—	—	13.5*	14.6 ± 0.83
NMor	2000–2003	Jan	—	—	12.0*	14.9 ± 1.79
Mau	2003	Feb–Apr	16.2 [14.7, 17.7]	0.13 [0.06, 0.20]	13.5*	17.8 ± 1.15
Azo	2000–2004	Jun, Nov	15.7 [14.9, 16.5]	0.21 [0.07, 0.36]	14.5	16.5 ± 1.82
Mad	2003	Mar	—	—	16.0*	17.8 ± 0.66

*Minimum, length in samples.

Gulf of Cadiz were mature, in both survey (Table 2) and market samples. However, unlike in northern Spanish waters, small sardine were found in the area during all spawning seasons. Four maturity ogives were defined based on survey data from the Gulf of Cadiz, providing the lowest pooled estimate of L_{50} within the stock area (see above).

Off western and southern Iberia, maturity-at-length data covered both juvenile and adult fish, defining clear maturity ogives in most spawning seasons. Patterns of spawning seasonality suggested no major differences among size classes, areas, or periods that could hamper the comparison of maturity ogives (Figure 2). In general, spawning activity extended from late autumn to late spring, with a peak between December and March. Smaller fish have shorter spawning seasons, but maximum activity of the different size classes was synchronized. In addition, there was a pronounced increase in the duration of the season and in the intensity of peak spawning in all areas from the 1980s to the 1990s, particularly for smaller fish. Acoustic survey data (not shown) support the above changes in spawning seasonality between decades. Although the spawning season expanded between decades, neither the peak nor the overall pattern of activity showed marked temporal shifts.

The above results confirm that samples used to construct maturity ogives generally cover the progress of the spawning season up to the peak of spawning (January) of fish of different size in each area and period. In two cases (south Galicia and south Portugal during the 1980s), the spawning season shifted slightly towards spring, possibly introducing a positive bias in L_{50}.

Figure 3 shows annual estimates of L_{50} based on GLM parameters for the spawning seasons 1981–2003 off western and southern Iberia (from south Galicia to south Portugal). L_{50} was not significantly different among the three western areas ($p = 0.18$). Overall maturation patterns were comparable in the four areas, as indicated by the similarity among the lengths of 25% (≈ 12.0 cm), 50% (≈ 14 cm), and 75% (≈ 15 cm) maturity, based on data pooled for the study period. Figure 3 also suggests that L_{50} decreased in the four areas; this is corroborated by decadal survey data (Table 2). In fact, when the period from 1985 is considered, there is a significant linear decline in L_{50} ($p < 0.001$), and differences in this trend are not significant among the three western areas ($p = 0.85$). Downward shifts of L_{50} were observed also for the northern areas of the stock (Cantabrian Sea and north Galicia), resulting in a
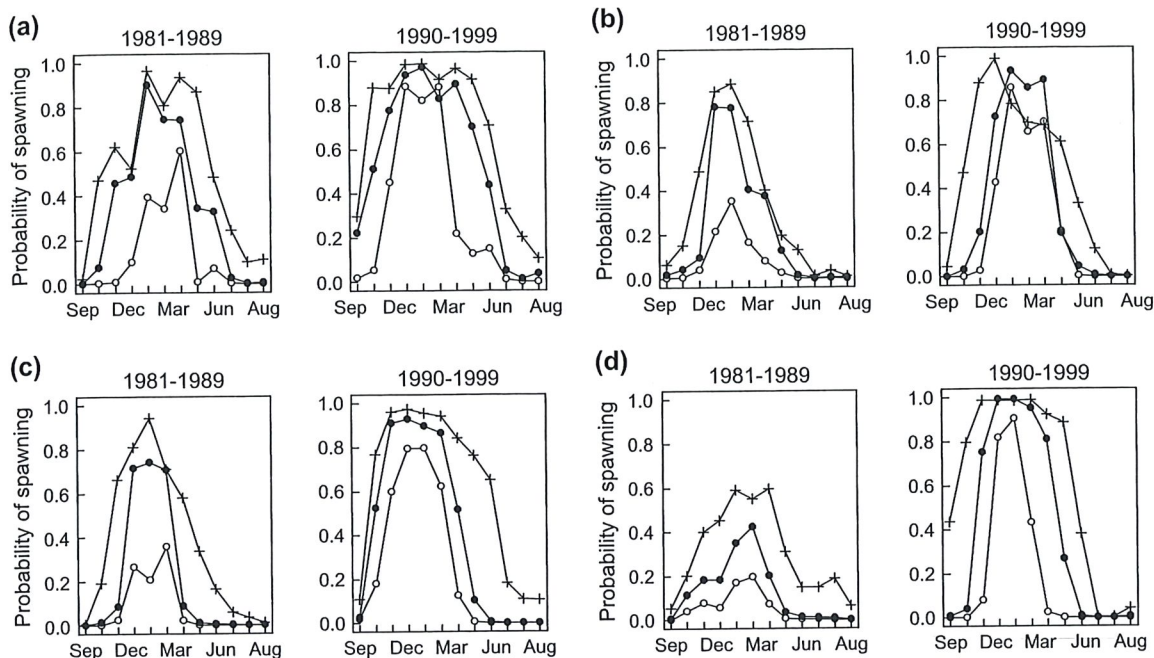
Figure 2. Probability of spawning of 14 (○), 15.5 (●), and 18 cm (+) sardine in the 1980s and 1990s off (a) southern Galicia, (b) northern, (c) southwestern, and (d) southern Portugal.

decline in the average length at first maturity for the Atlanto-Iberian stock of sardine, from 14.5 cm in the 1980s to 13.3 cm in the 1990s.

Annual changes are similar in southern Galicia and northern Portugal, where L_{50} rose from the early to the mid-1980s and decreased towards the late 1990s. Off southern Galicia, there was an associated increase in the slope of the maturity ogives (not shown). Off southwestern Portugal, L_{50} declined after a period of high values during the mid-1980s. The series of L_{50} for southern Portugal has large temporal gaps owing to the lack of small immature fish in samples during most of the 1990s, precluding analysis of temporal trends. For the early 1980s, L_{50}s are within the range of variation of values for the other stock areas.
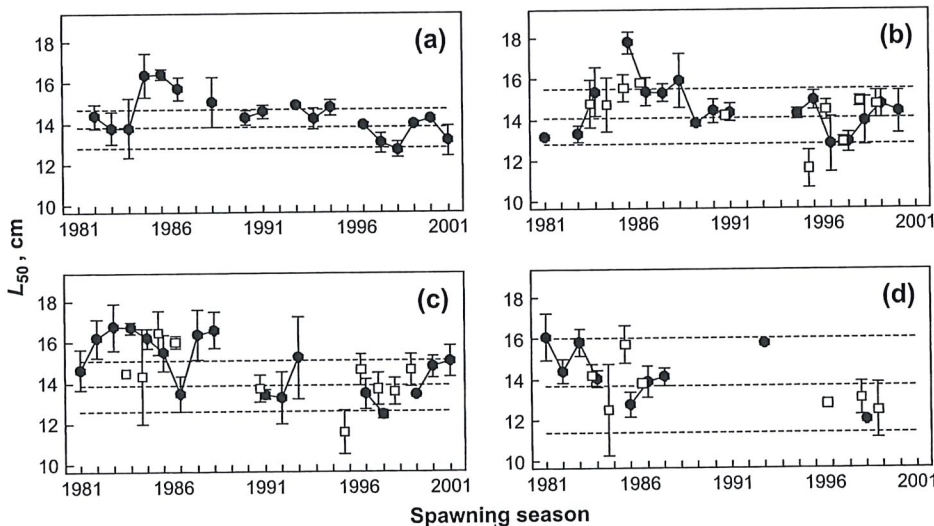

Figure 3. Variations in L_{50} in the spawning seasons of 1981–2003 by area. (a) IXa-N, (b) IXa-CN, (c) IXa-CS, (d) IXa-SA. Circles, data from market samples; squares, data from autumn acoustic surveys. Bars represent 95% confidence limits. Dashed lines show L_{25}, L_{50}, and L_{75} based on data pooled for the study period.

However, there is indication mainly from survey data that L_{50} was significantly lower in the late 1990s (Table 2). Data on gonad weight provide some support to maturity data, given the significant negative correlation between L_{50} and the gonadosomatic index of maturing fish (in the range $L_{25}-L_{75}$) in western Portuguese areas (Figure 4).

Relationship between L_{50}, condition, and abundance

The influence of fish body condition on maturation was explored using data from the western Iberian areas on the mean total weight and the percentage of fish with medium/high visceral fat (fat stage >2; % fat) in summer (July and August). This is when plankton production and sardine body condition peak. Therefore, fish weight and fat reserves in summer are a reliable index of the energy made available for reproduction in the current spawning season (Koops *et al.*, 2004), and possibly also for the spawning season of the following year (Hunter and Leong, 1981). As the mean weight and the % fat showed similar temporal variations in the different length classes, 18-cm fish (the best sampled length class during the study period) were used, assuming to be representative of the average condition of the whole population. The two variables showed an increasing trend through the period in all areas: pooled data for 1982−1985 and 2000−2003 showed increases of 8−11% in mean weight and of 26−58% in the percentage of fish with fat. L_{50} was significantly negatively related to the mean weight-at-length (Spearman rho = −0.35, $p = 0.01$) and to the percentage of fish with fat (Spearman rho = −0.47, $p = 0.005$) in the current summer season. However, the correlation improved when L_{50}

Figure 4. Relationship between L_{50} and the mean gonadosomatic index (GSI) of maturing fish (12−15.9 cm) in corresponding spawning seasons for 1987−2003 off northern (○) and southwestern (●) Portugal. A linear regression line is superimposed on the data to illustrate the trend.

was related to fish weight (Spearman rho = −0.51, $p = 0.0003$) and % fat (Spearman rho = −0.61, $p = 0.0003$) in the previous summer, indicating that condition has a prolonged effect on the length at first maturity (Figure 5).

The influence of population abundance on the length at first maturity was also studied, using data on sardine landings and biomass (from acoustic surveys) off western Iberia. The long-term trends in maturation do not show an association with local annual landings or survey abundance indices in Portuguese waters. Such a result was expected considering there were no major changes in sardine abundance within those areas during the study period. However, off southern Galicia L_{50} was significantly correlated with landings ($r = 0.48$, $p = 0.02$; Figure 6). Landings are considered to be representative of the large decrease in sardine abundance in this area (Table 1; Carrera and Porteiro, 2003), so the above relationship provides some evidence of a density-dependent effect on maturation. There is also some indication that population abundance may influence maturation on a shorter time scale, because recent shifts in sardine abundance have been followed by wide variations in L_{50}. In fact, owing to the strong incoming 2000 year class, sardine abundance increased by a full order of magnitude in northern Portugal from 1999 to 2000 (ICES, 2002). Maturation length rose 2.0 cm in the area and increased also in the adjacent areas (south Galicia and southwest Portugal) the following spawning season, to where the cohort spread during its first year of life (Figure 3).

Discussion

All data analysed in this study were collected using the same macroscopic criteria for maturity, so the only concern with data quality relates to the accuracy of macroscopic staging. The reliability of macroscopic maturity data is supported by the significant correlation between L_{50} and the gonadosomatic index of maturing individuals observed since 1987 off western Portugal (Figure 4). GSI data further strengthen the hypothesis of a decline in the length at first maturity in the area. Additional information on the accuracy of maturity staging is limited to a few recent intercalibration exercises, which point to some uncertainties in maturity classification. A recent intercalibration of macroscopic staging of sardine ovaries with histological criteria showed that 24% of stage 1 gonads were misclassified (they were in fact stage 2), and 27−36% of post-spawning fish were wrongly identified as pre-spawning (early spawning season) or spawning/recovering (late spawning season; ICES, 2003). These results indicate that both the proportion of mature fish and the proportion of active individuals may have been slightly underestimated in the past.

The samples analysed across the area of distribution of sardine suggest an increase in the percentage of small sardine that are mature from north to south within the Northeast Atlantic. There is also evidence of earlier maturation in
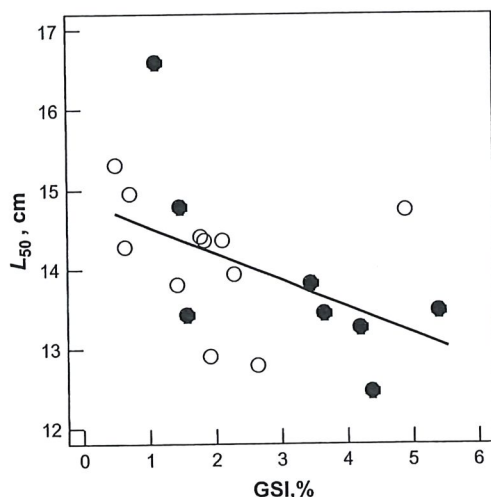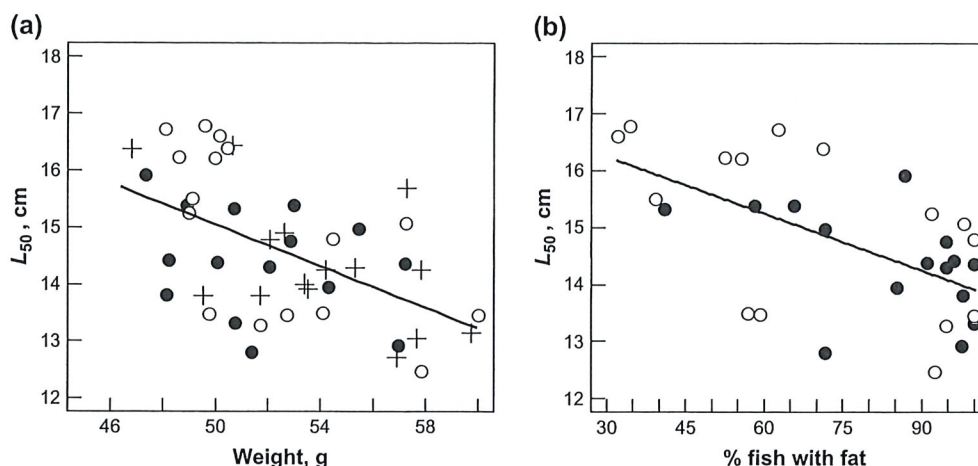
Figure 5. Relationship between L_{50} in a given spawning season (October—January) and (a) the mean weight-at-length, and (b) the % of fish in fat stage >2 in the summer of the preceding year (July and August) off northern Portugal (black circles), southwestern Portugal (open circles), and southern Galicia (plus signs; only weight data available). The mean weight and % fish in fat stage >2 are shown for the best sampled length class in the areas, 18 cm. A linear regression line is superimposed on the pooled data to illustrate the trend.

the Gulf of Cadiz, and in Mediterranean and Moroccan waters and, possibly, delayed maturation towards the northern (north France), southern (Mauritania), and western (Azores) limits of distribution (Table 2). Earlier results on sardine maturation support the broad spatial trends in maturity described here, corroborating the upward shift in L_{50} from southern to northern France, and the low length at first maturity of sardine off Cadiz compared with northwestern Iberian areas (Table 3). Further, they support the increase in maturation length towards the southern (Saharan Morocco) and western (Canary Islands) extent of sardine range. Large-scale spatial variation of sardine length at maturity shows an overall positive relationship with longevity and
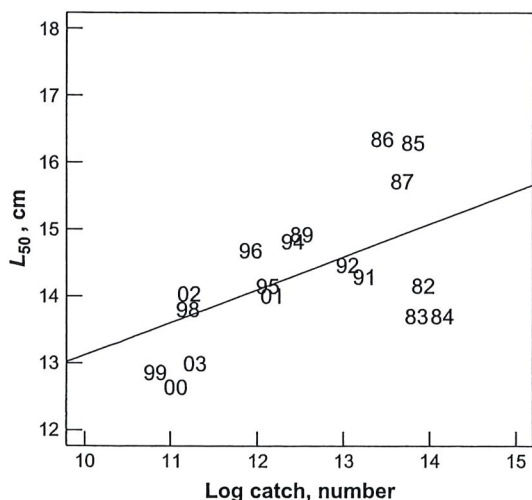

Figure 6. Relationship between L_{50} and landings in southern Galicia in the period 1982–2003. Text numbers show the year. A linear regression line is superimposed on the data to illustrate the trend.

maximum fish size (Tables 1 and 2) and bears some direct association with growth during the first year (Andreu and Fuster de Plaza, 1962; Morales-Nin and Pertierra, 1990; FAO, 2001). A similar geographic pattern of maturation has been reported for horse mackerel (*Trachurus trachurus*) (Abaunza *et al.*, 2003): L_{50} varies from 15 to 23 cm in north African waters and 16 cm in northwestern Mediterranean to 16–19 cm off southern Portugal, and increases gradually to the northern areas, attaining 20–25 cm in the North Sea and English Channel. Length at maturity is also higher in sardine populations with greater maximum size. These broad spatial patterns suggest that maturation has an inverse relationship with the potential growth span of the species across its range, conforming to the general principles of life history strategy (Beverton, 1992; Rose *et al.*, 2001).

In Atlantic waters, the most striking discontinuities in the length at first maturity of sardine are at the southern (south Morocco/Mauritania) and western (Atlantic Islands) limits of distribution, and also between the southern and the northern French waters. At the southern limit of the species, there is some evidence of differences in morphological characters, age structure, spawning areas, growth, and maturation between north/central Morocco and south Morocco/ Mauritania, pointing to the existence of separate sardine populations (FAO, 2001). Additionally, ongoing studies on sardine genetics indicate that sardine from the Azores and Madeira (western) and Mauritania (southern) are distinct from those in the Atlantic between southern Iberia and the English Channel (Kasapidis *et al.*, 2004). By contrast, the abrupt increase in L_{50} between southern and northern French waters is neither explained by genetic differentiation (Kasapidis *et al.*, 2004) nor by major discontinuities in the distribution of sardine between the areas (Bellier *et al.*, 2004; ICES, 2005). The predominance of large mature sardine in northern French waters and in the

Table 3. Literature information on sardine maturation within the northeastern Atlantic and western Mediterranean. Area codes: CMor, Central Morocco; SMor, South Morocco; CanI, Canary Islands; Med, Mediterranean Sea; see also legend of Table 1. Notes: (1) Maturity key from Pinto and Andreu (1957); (2) Maturity stage 2 (initial development) not included in fraction mature; (3) Age readings from scales; (4) Maturity key from Hjort (1910); (5) Maturity key not referred to; (6) Age readings from otoliths; M, male; F, female.

Area	Period	Month	Length range (cm)	Age range (year)	L_{50} (cm)	Minimum length at maturity (cm)	Maturation age (year)	Notes	Reference
Chan	1935–1938	—	18.0–26.0	2–8	~19.0	—	3–5	—	Hickling, 1945.
	—	—	—	—	20.5	—	4	—	Hodgson and Richardson, 1949
NFr	1928–1929	Spawning season	9.0–20.0	0–5	17.0–18.0	—	During the 3rd year	3, 4	Le Gall, 1930
SFra	1941–1943		8.0–20.0	0–4	15.5	—	End 2nd year		Furnestin, 1943
SGal	1951–1954	Jan–Mar	12.0–20.0		14.5	12	0–1	1, 2	Andreu, 1955
	.1981		11.0–23.5	1–8	14.5	13.5	1.3		Pérez et al., 1985
Cad	1958–1964	Spawning season	7.0–20.0	0–3	—	10.5	—	1, 2	Rodriguez-Roda, 1970
SMed	1949–1955		8.0–16.0		11.5	—	1	3, 4	Larrañeta, 1976
	1989–1991	Oct–Jan	8.0–23.0		12.6–13.8	—	—	1, 2	Abad and Giraldéz, 1993
Med	Synopsis		22 (max)	8 (max)	10–14	—	0–2		Larrañeta, 1959
NMor	1959–1964	Oct–May	11.0–21.0	0–3	11.5	11.5	—	1, 2, 3	Rodriguez-Roda, 1971
CMor	1967–1968		12.0–21.0		M: 13.0 F: 15.0	11.8 12	—	5	Sedletskaya, 1973
SMor	1967–1968	Spawning season	12.0–23.0		M: 13.5 F: 16.5	11.8 13.4	—	5	Sedletskaya, 1973
	1974–1975		11.0–24.0	1–6	—	M: 13.0 F: 15.0	—	5, 6	Krzeptowski, 1983
CanI	1995–1996	Nov–Mar	6.0–23.0	—	15	—	—	2	Mata et al., 1997

English Channel (Furnestin, 1943; Hickling, 1945) supports the hypothesis that nursery grounds of these sardine populations are located in the south, possibly in the Bay of Biscay (Furnestin, 1943). The French waters north of the Gironde Estuary (French coast, $45°30'N$) are distinctive oceanographically from those of the Bay of Biscay, with considerably lower temperature attributable to a persistent cold-water mass (Puillat *et al.*, 2004). Colder water conditions also prevail in the northern areas of the English Channel and North Sea, restricting sardine spawning activity to a few months during summer and autumn (Stratoudakis *et al.*, 2004). Such conditions may influence the migration of juveniles to southern areas, and also constrain the reproductive development of the few small fish that remain in the areas.

Atlanto-Iberian sardine stock maturation is comparable among the western areas of distribution, the mean L_{25}, L_{50}, and L_{75} being around 12, 14, and 15 cm, respectively. There is limited information on maturation length in northern Spanish waters (north Galicia and Cantabria), which is dominated by large adults, possibly immigrants from adjacent recruitment areas off northwestern Iberia or the Bay of Biscay (Carrera and Porteiro, 2003). Nevertheless, decadal L_{50}s for these areas are similar to those for western Iberia. The long-term average maturation pattern of sardine off southern Portugal is uncertain because of the scarcity of data, but recent information points to similarity with sardine maturation in the Gulf of Cadiz. In the latter area, sardine mature smaller than the general pattern, which in turn is similar to that observed in the southwestern Mediterranean. A similar spatial pattern was demonstrated for sardine morphometry, the similarity extending also to northern Morocco (Silva, 2003). However, earlier studies on meristic characters distinguished European Atlantic from Northwest African sardine populations (Parrish *et al.*, 1989), whereas Mediterranean and Northwest African sardine have been considered a different subspecies from the European Atlantic sardine (Bauchot and Pras, 1980). The lack of genetic distinction among sardine populations around the Iberian Peninsula (Kasapidis *et al.*, 2004) suggests that maturation differences are mainly driven by environmental conditions common to both Mediterranean and Atlantic waters of southern Iberia, which are themselves distinct from the prevailing conditions off western Iberia. Differences in maturation may be mediated by growth, because lower mean lengths at age have been observed in both the Gulf of Cadiz and Mediterranean waters than off Galicia and central Portugal (Rodríguez-Roda, 1970).

The long-term samples off western Iberia show an increasing trend in the percentage of small sardines maturing each spawning season since the early 1980s, along with associated increases in spawning activity (mainly of smaller fish) and in the duration of the spawning season between the 1980s and the 1990s. These changes suggest an improvement in the overall reproductive potential of sardine, and may be the result of enhanced fish condition during

that period. In fact, for other clupeoid species, most of the energy spent in a specific spawning season comes from fat reserves stored during the current and the previous season (Hunter and Leong, 1981). This hypothesis is supported here by the significant correlation between mean sardine weight and % fat at length with the length at first maturity.

Temporal changes in sardine condition may have been caused by environmentally driven variation in food availability. There is evidence of environmental change off western Iberia during the last two decades (Santos *et al.*, 2001, 2005; Borges *et al.*, 2003; Guisande *et al.*, 2004), and these seem to be part of wider temporal and spatial variations in the hydroclimatic conditions of the whole North Atlantic (Ottersen *et al.*, 2001). Based on satellite-derived sea surface temperature data, Santos *et al.* (2005) document a shift in the upwelling regime off western Iberia, from a weak intensity in the 1980s to stronger in the 1990s, during both winter and summer. This increased upwelling intensity may have enhanced plankton productivity in the area and hence food availability for sardine and other clupeoid populations. Sardine condition and therefore L_{50} may also be partially regulated by density dependence, as observed for other pelagic species (Parrish and Mallicoate, 1995). The fact that the long-term decline in L_{50} was inversely related to abundance off southern Galicia, an area that experienced a great decrease in its sardine population during the last two decades (Carrera and Porteiro, 2003), strengthens this possibility. It is also likely that variations in both sardine condition and abundance were affected by changes in environmental conditions observed in the past two decades off western Iberia.

In spite of the above evidence of environmentally driven changes in the length at first maturity, the hypothesis of an evolutionary trend in sardine maturation is not excluded. In fact, the pronounced changes in the abundance and age structure of sardine populations in mainly the northern areas of the stock (Galician and Cantabrian waters; ICES, 2000) might have provided scope for the selection of early maturing phenotypes. It can be argued that selective changes would not likely take place over such a short time (<20 years), because most experimental studies suggest that 10–20 generations are needed for selection to occur (Swain *et al.*, 2005). However, only four generations were needed for the growth rate of Atlantic silverside (*Menidia menidia*), a short-lived pelagic species (Connover and Munch, 2002), to evolve. Sardine have moderate longevity (7–8 years), but they mature during the first two years of life, as do other short-lived pelagic species. Therefore, the possibility that the maturation of sardine evolved over just two decades warrants further investigation.

Maturation reaction norms (Heino *et al.*, 2002; Barot *et al.*, 2004) are a useful tool in exploring evolutionary trends in maturation, because they allow disentangling the influence of growth and mortality (assumed to reflect environmental variation) on maturation. Estimation of reaction

norms for sardine maturation could complement these analyses, because variation in growth may explain the geographic and temporal changes in maturity at length described. Age data are available from commercial and survey length-stratified samples of sardine covering part of the area and period analysed here, and they can be used in future to pursue such an approach. Nevertheless, the estimation of reaction norms for sardine requires careful consideration in relation to sampling design, consistency of age determinations, and also to whether age and length distributions derived from commercial samples are representative of the whole populations.

Overall, there is clear evidence that sardine may attain sexual maturity at a wide range of lengths across its distribution area, varying from 11 cm to almost 17 cm (mainly age groups 0 and 1), in relation to broad patterns of growth and longevity. Within the Atlanto-Iberian stock, maturation patterns by length are comparable across the western areas (from southern Galicia to southwestern Portugal), and there is no evidence of pronounced differences towards the northern areas (northern Galicia and Cantabria). On the other hand, sardine mature smaller in the Gulf of Cadiz than in the remaining stock areas, and there is no indication of a different maturation pattern north of the stock boundary (southern French waters). As is the case with other life history traits, length at maturity does not provide direct evidence of stock structure, so these results are not sufficient to review the identity of the sardine stock in Atlantic European waters. However, they do assist in delineation of areas with distinct phenotypic groups of sardine, and this information can be utilized along with evidence from other approaches to stock identification for management purposes.

Acknowledgements

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