

Sardine spawning off the European Atlantic coast: Characterization of and spatio-temporal variability in spawning habitat

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Abstract

Data on the occurrence of sardine (*Sardina pilchardus*) eggs from 42 national ichthyoplankton surveys along the European Atlantic coast were collated in order to describe the spawning habitat and spawning distribution of sardine in recent decades (1985–2005). A modification of existing spawning habitat characterisation techniques and a newly developed method to compare the probability of egg presence across surveys carried out with different sampling gears were used. Results showed that sardine spawning off the Atlantic European coast is mainly restricted to the shelf area, with the main geographical range being between the Strait of Gibraltar (the southern limit of data available for this analysis) and the middle part of the Armorican shelf (latitude around 47.5° North), and along a temperature range of 12–17 °C. Spawning grounds within these limits show a nearly continuous geographical distribution, covering a large proportion of the shelf of the Iberian peninsula and adjacent waters, except for: (1) a persistent gap at the north west corner of the Iberian peninsula, (2) a small secondary break at the Spanish–French border in the inner part of the Bay of Biscay and (3) at the south west corner of the peninsula where there is a narrowing of the shelf width. These discontinuities were used to separate spawning into four nuclei and to describe the changes in spawning distribution in the time series. The relative importance of each nucleus and the degree of separation between adjacent nuclei varies between years, with the exception of the permanent gap at the northwest corner of the Iberian peninsula, which is persistent throughout the time series. Year to year changes in the proportion of the potential spawning habitat in which spawning actually occurred, changing from around 60% before the mid 1990s to around 40% thereafter, and

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did not show any relationship with spawning stock biomass. Evolution of potential habitat occupation over the Armorican shelf shows larger variability than that observed in the Iberian peninsula, with percentages of occupation ranging from around 30% up to nearly 80% of the shelf in recent years (within the limitations of the relatively sparse data for this region).

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1. Introduction

Spawning areas of fish species with a pelagic egg phase have been traditionally delimited and monitored using ichthyoplankton data from dedicated surveys (e.g. from egg production surveys). Spawning area distribution has been used as additional information to investigate species distribution and can help to identify boundaries between different populations and/or fisheries stocks (see a review in Cadrin et al., 2005). Changes in spawning area extension have also been used to assess stock health, by relating the area occupied by eggs with spawning stock biomass (SSB) (Zenitani and Yamada, 2000; Stratoudakis et al., 2003; Gaughan et al., 2004) or by analysing the variability in spawning area coverage between decades (Stratoudakis et al., 2003; Bellier et al., 2007). Estimates of spawning area have also been used to set cost-effective sampling objectives according to stock state and management needs (Mangel and Smith, 1990; Smith, 1990) or to use spawning area as an index of abundance in assessment models (Deriso et al., 1996). Nevertheless, relationships between spawning area, egg production and spawning stock biomass are unclear, and previous attempts to relate these parameters for different species or areas have produced variable results (Stratoudakis et al., 2006). However, the significance and shape of the relationship between spawning area and stock biomass can provide indications on the mode of utilisation of the spawning habitat and can be used to link spawning strategies with ecosystem productivity (Somarakis et al., 2004).

Sardine (*Sardina pilchardus*, Walb.) is widely and continuously distributed along the North East Atlantic (NEA) shelf from Mauritania to the English Channel (Parrish et al., 1989), with occasional occurrences to Senegal in the south (Freon and Stequert, 1979) and the coast of Scotland in the north (Beare et al., 2004). Within this broad area, there is no comprehensive information on the spawning grounds, since time series of wide scale ichthyoplankton surveys at sardine spawning time are not available. However, within Atlantic European waters various sources of ichthyoplankton data have been collected in the past two decades, which can, in principle, be used to describe sardine spawning grounds and their evolution over time. Data from these sources are diverse in terms of survey plans, sampling methods, and spatio-temporal coverage, requiring special attention for compilation and analysis (see Table 1).

The aim of this paper is to integrate, for the first time, data from all available and suitable ichthyoplankton surveys that sample sardine eggs in Atlantic European waters, and to use these data in a common framework in order to draw a general picture of the main sardine spawning areas and variability in time. Although there are previous attempts to model egg probability of presence (Borchers et al., 1997; Mangel and Smith, 1990; Stratoudakis et al., 2003), no appropriate statistical method to compare egg probability of presence obtained from different ichthyoplankton survey gears, and thus derived estimates of area occupied by eggs, was available for the analysis of the data presented in this paper. Therefore, a new modelling methodology was developed to allow the analysis of spawning areas from different ichthyoplankton surveys and methods. The main focus of the paper is to use the large amount of data to show the general patterns in spawning distribution at the North Atlantic European scale, and to derive simple indices that could be applied through the entire area and across all the database to describe spawning habitat. Three main questions are to be tested from the analysis of the data: (1) are there discontinuities in the NEA sardine spawning grounds that may support some degree of isolation between different sardine populations? (2) Where are these discontinuities located and are these fixed over time? (3) Is there any relation between the extension of spawning areas and the health of the Atlanto-Iberian stock?

Table 1
List of available national surveys

| Survey | Latitude range | | Longitude range | | N. stat | Maximum dens | Mean dens |
|----------------------------------|----------------|-------|-----------------|------|---------|--------------|-----------|
| ring1185.ipimar | 36,65 | 41,83 | 10,23 | 7,42 | 72 | 627 | 16 |
| ring0186.ipimar | 36,65 | 41,83 | 10,35 | 7,42 | 112 | 613 | 31 |
| ring0386.ipimar | 36,65 | 41,83 | 10,35 | 7,42 | 113 | 7714 | 131 |
| sareggs0388.ipimar | 36,68 | 41,82 | 10,15 | 7,51 | 309 | 1680 | 81 |
| sareggs0488.iew | 41,92 | 44,32 | 9,72 | 1,97 | 516 | 2758 | 140 |
| sareggs0490.iew | 41,92 | 44,72 | 9,58 | 2,33 | 475 | 2063 | 62 |
| bongos1090.ipimar ^a | 36,38 | 41,83 | 9,95 | 7,42 | 86 | 401 | 15 |
| calvet0591.iew | 43,32 | 46,62 | 5,12 | 1,28 | 538 | 2295 | 106 |
| bongos1091.ipimar | 36,67 | 41,83 | 10,2 | 7,42 | 84 | 1105 | 29 |
| bongos0392.ipimar | 36,67 | 41,83 | 10,2 | 7,42 | 86 | 308 | 47 |
| calvet0492.iew | 41,87 | 44,47 | 9,9 | 3,92 | 437 | 2451 | 119 |
| bongos1092.ipimar ^{a,b} | 36,67 | 41,17 | 10,2 | 8,42 | 45 | 753 | 62 |
| bongos0393.ipimar ^{a,b} | 36,38 | 41,83 | 10,08 | 7,42 | 92 | 1515 | 107 |
| bongos0493.iew | 41,98 | 44,17 | 9,67 | 1,9 | 43 | 956 | 38 |
| bongos0394.iew ^b | 42 | 47,76 | 9,72 | 1,75 | 113 | 148 | 6 |
| bongos0395.ipimar | 36,12 | 42,75 | 10,75 | 6,75 | 69 | 3713 | 122 |
| bongos0395.iew | 39,25 | 44,88 | 10,76 | 1,75 | 112 | 96 | 8 |
| bongos0595.iew | 43,38 | 46,88 | 8,75 | 1,74 | 121 | 834 | 14 |
| sareggs0397.ipimar | 35,97 | 41,83 | 10,17 | 5,77 | 373 | 5569 | 77 |
| sareggs0397.iew | 41,97 | 44,32 | 9,83 | 1,88 | 515 | 5381 | 57 |
| sareggs0199.ipimar | 36 | 41,9 | 10,29 | 5,77 | 417 | 13,431 | 228 |
| sareggs0399.iew | 41,89 | 44,08 | 9,6 | 1,96 | 398 | 3616 | 116 |
| sareggs0599.azti | 43,32 | 46,13 | 4,61 | 1,22 | 344 | 62 | 2 |
| calvet1199.ipimar | 36,12 | 41,86 | 10 | 6,15 | 127 | 3220 | 108 |
| calvet0300.azti | 43,67 | 47,87 | 5,43 | 1,26 | 133 | 2820 | 213 |
| calvet0300.ipimar | 36,44 | 41,86 | 10 | 6,38 | 121 | 6360 | 165 |
| calvet0300.iew ^a | 41,95 | 50,18 | 9,67 | 1,73 | 112 | 460 | 22 |
| bongos0400.iew | 42,25 | 44,63 | 9,9 | 1,75 | 103 | 1321 | 44 |
| bongos0500.iew | 42,25 | 44,62 | 9,9 | 1,75 | 130 | 370 | 23 |
| sareggs0500.azti | 43,33 | 46,88 | 4,53 | 1,22 | 442 | 949 | 100 |
| bongos0301.iew | 42,25 | 45,75 | 10,25 | 1,32 | 95 | 5592 | 120 |
| calvet0301.ipimar | 36,12 | 41,86 | 10 | 6,15 | 117 | 2184 | 48 |
| bongos0401.iew | 42,24 | 45,75 | 10,25 | 1,32 | 123 | 976 | 82 |
| calvet0501.azti | 43,66 | 50,02 | 7,24 | 1,26 | 106 | 1019 | 66 |
| sareggs0501.azti | 43,32 | 47,38 | 5,62 | 1,22 | 614 | 1691 | 41 |
| sareggs0102.ipimar | 35,97 | 41,8 | 10,34 | 6,33 | 484 | 4640 | 105 |
| sareggs0302.iew | 42,06 | 44,28 | 9,52 | 2 | 313 | 1896 | 102 |
| sareggs0502.azti | 43,33 | 46,63 | 4,24 | 1,29 | 376 | 1808 | 137 |
| bongos0303.iew | 41,98 | 44,05 | 9,55 | 1,75 | 40 | 2246 | 209 |
| sareggs0205.ipimar | 35,92 | 41,8 | 10,08 | 6 | 408 | 8020 | 179 |
| sareggs0405.iew | 41,93 | 44,14 | 9,68 | 1,45 | 375 | 3231 | 169 |
| sareggs0505.azti | 43,33 | 46,88 | 4,82 | 1,22 | 415 | 1610 | 193 |

Latitude is Latitude North, in degrees decimals, Longitude is Longitude West, in degrees decimals. N. stat is number of stations. Prefix identify the kind of survey: *sareggs* refers to DEPM surveys, *ring* to oblique ring net surveys, *bongos* to oblique bongo surveys, and *calvet* to vertical CalVet surveys. The prefix for each survey is followed by the survey date in month–year format (mmyy), and a suffix to indicate the different national institutes that performed the survey.

^a Effective surface area fixed, not estimated.

^b Temperature not available.

2. Materials and methods

2.1. Survey data

Available ichthyoplankton data from all broad scale national surveys carried out within the sardine distribution area in Atlantic European waters during the sardine spawning season were compiled within the framework of the EU project SARDYN (Table 1). All surveys include the following covariates: station position,

date and time, surface water temperature, total sardine egg number and concentration per unit sea surface area (estimated as the volume of water filtered by the net divided by maximum sampling depth, and referred as *effective surface area* in the rest of the paper). In some of the surveys, some temperature observations were missing, and in others the effective surface area was not directly measured, but estimated from trigonometry. Sardine egg concentration in eggs per m² was estimated as the total number of sardine eggs found, divided by the effective surface area in square meters.

Two main differences are noted within the available surveys; those surveys whose main objective was to obtain sardine/anchovy Daily Egg Production (DEPM) estimates of Spawning Stock Biomass (SSB) and surveys with other main objectives. Surveys dedicated to obtain DEPM estimates of sardine or anchovy SSB have been coordinated through different ICES Working Groups (see for example ICES, 2006b) and have a similar survey plan and use the same net sampler (California Vertical Tow net: CalVET) with a dense grid of stations. These surveys are noted by the “sareggs” prefix in Table 1, and are the most suitable for performing spatial modelling of sardine egg densities. Surveys where the main objective was other than DEPM estimates are identified depending on the main ichthyoplankton net sampler used; “ring” for vertical towed ring nets, “calvet” for vertical CalVET surveys, and “bongos” for Bongo oblique tow surveys (see review in Sameoto et al., 2000). Surveys in 1995 and 1998 were carried out within a coordinated sampling plan for the Annual Egg Production Method estimation of mackerel and horse mackerel SSB, which includes other countries apart from Spain and Portugal, although sardine eggs are only routinely sorted and counted within these surveys in Spain and Portugal. Nevertheless, the 1998 survey was subsequently reviewed within the EU project INDICES to sort and quantify eggs of all fish species, and provides the largest coverage survey for sardine within the EU waters (for a review of INDICES result see Ibaibarriaga et al., 2007a). The 1998 survey is thus included directly in the broad scale surveys within Table 2, as explained.

Of the 42 surveys considered in Table 1 (and used for habitat characterisation), 24 surveys from 9 years, together with the coordinated 1998 INDICES survey, were considered for modelling spawning areas in Atlantic European waters (Table 2). Table 2 shows the coverage and number of stations of these combined surveys. Combined surveys contain only national surveys with similar survey characteristics, except for the case of the 1992 survey, in which the Portuguese survey was carried out with bongos and the Spanish survey was carried out with CalVET nets. In most cases, adjacent surveys were carried out synchronously or in consecutive months, with the exception of 1999, 2002 and 2005 in which surveys covering the Portuguese and southern Spanish coast were carried out in January and surveys covering the North Spanish and South Bay of Biscay areas were carried out consecutively from March to April until May to June. This survey timing is in agreement with the assumed spawning peak in the different regions (see Coombs et al., 2006) and with the established survey timing for DEPM based assessment of sardine SSB (ICES, 2000). Survey names are as in Table 1,

Table 2
List of combined surveys

| Survey | Latitude range | | Longitude range | | N. stat | Maximum dens | Mean dens |
|---------------------|----------------|-------|-----------------|------|---------|--------------|-----------|
| sareggs88.iberia | 36,68 | 44,32 | 10,15 | 1,97 | 825 | 2758 | 118 |
| calbon92.iberia | 36,67 | 44,57 | 10,2 | 1,45 | 667 | 2451 | 90 |
| bongos93.iberia | 36,38 | 44,17 | 10,08 | 1,9 | 135 | 1515 | 73 |
| bongos95.iberia | 36,12 | 46,88 | 10,76 | 1,74 | 302 | 3713 | 37 |
| sareggs97.iberia | 35,97 | 44,32 | 10,17 | 1,88 | 888 | 5569 | 65 |
| bongos98.bigiberia | 36,12 | 59,25 | 15,78 | 1,25 | 1334 | 16911 | 123 |
| sareggs99.bigiberia | 36 | 46,13 | 10,29 | 1,22 | 1159 | 13431 | 123 |
| calvet00.bigiberia | 36,44 | 50,18 | 10 | 1,26 | 365 | 6360 | 139 |
| sareggs02.bigiberia | 35,97 | 46,63 | 10,34 | 1,29 | 1173 | 4640 | 114 |
| sareggs05.bigiberia | 35,92 | 46,88 | 10,08 | 1,22 | 1198 | 8020 | 181 |

Latitude is Latitude North, in degrees decimals, Longitude is Longitude West, in degrees decimals. N. stat is number of stations. Prefix identify the kind of survey: *sareggs* refers to DEPM surveys, *ring* to oblique ring net surveys, *bongos* to oblique bongo surveys, and *calvet* to vertical CalVet surveys. The prefix for each survey is followed by the survey date in month–year format (mmyy), and a suffix to indicate the different national institutes that performed the survey.

but only including the year, with the exception of 1992 which is identified with the suffix “calbon”, to indicate that it is a mixture of CalVET and bongo national surveys.

Fig. 1 shows observed sardine egg distribution for all years that combined surveys were used in the analysis, with egg concentrations represented as different colours in the same scale across surveys and years. Six of the ten available surveys covered the southern and central Armorican shelf, off the French coast, while the other four surveys covered only the Iberian peninsula. Surveys up to 1995 do not cover the Gulf of Cádiz (south Iberian peninsula), while the rest of the time series do. Fig. 2 summarises visually the ichthyoplankton coverage in terms of number of combined surveys which had sampled a given area. Also, the ICES limits of the Atlanto-Iberian stock of sardine (shelf within the Iberian peninsula, white dashed line in Fig. 2) and the part of the Armorican shelf that was covered at least 4 times (black dashed line in Fig. 2) are highlighted.

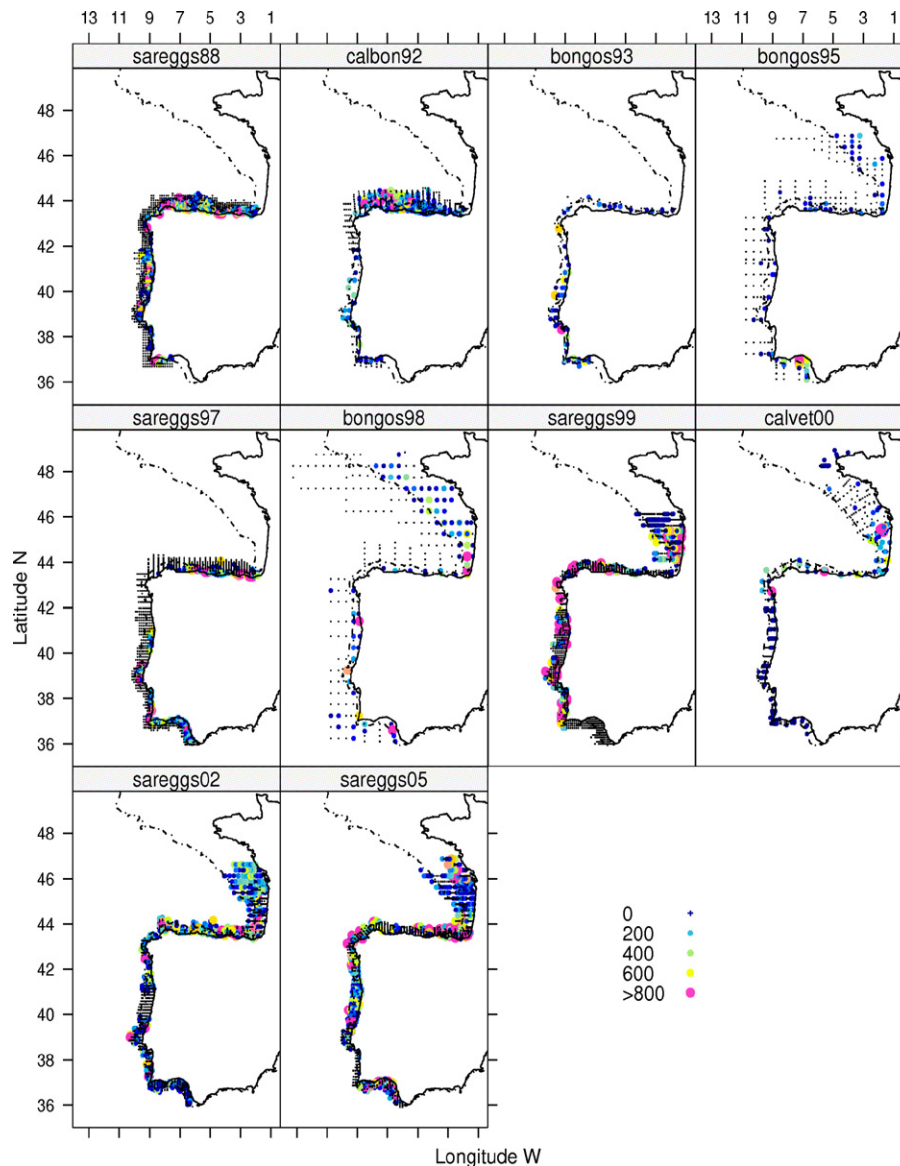


Fig. 1. Sampling coverage and egg concentrations (number of eggs/m²) observed in the combined sardine surveys. Legend on egg concentration on the right.

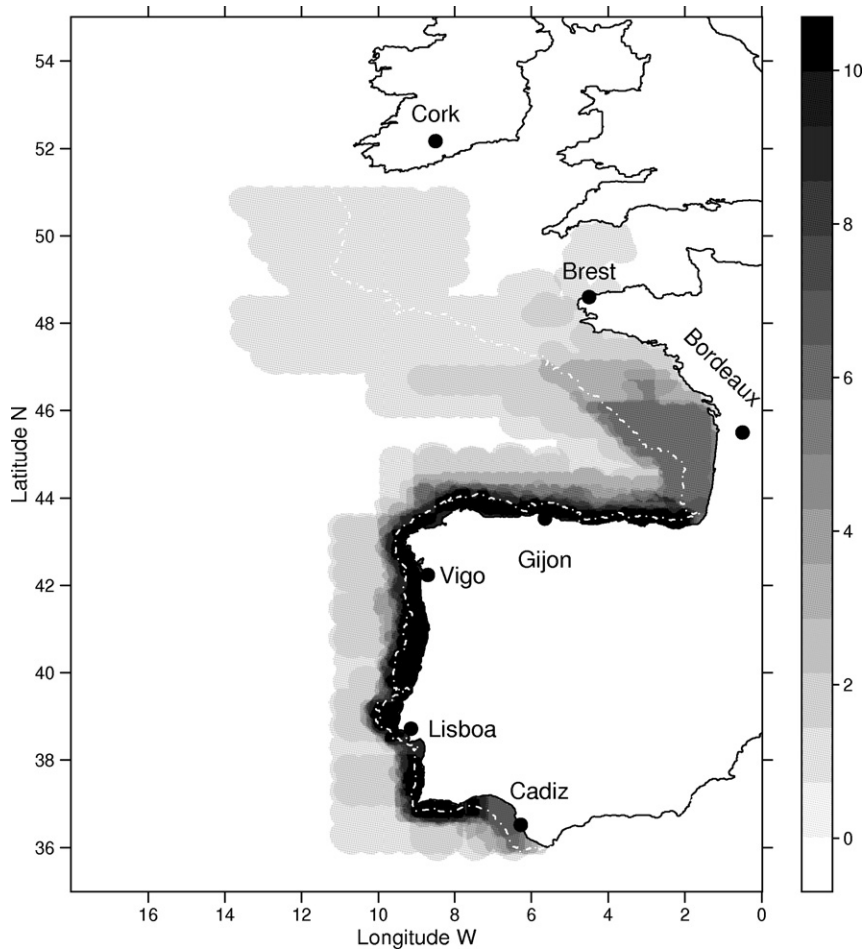


Fig. 2. Sampling coverage (in gray scale on the right) of the different areas through the North East Atlantic (NEA), and limits of the shelf within the ICES sardine stock area (white dashed line) and the portion of the Armorican shelf that was sampled at least four times (black dashed line).

2.2. Characterisation of spawning habitat

In order to establish the characteristics of the spawning areas in relation to simple geographical covariates and to water temperature, a variation of common spawning areas characterisation techniques were used. Single parameter quotient analysis (SPQ) is commonly used to investigate areas of spawning preference/avoidance, by comparing a null hypothesis of an even distribution of eggs with the observed egg distribution in relation to any covariate of interest (van der Lingen et al., 2005; Ibaibarriaga et al., 2007a). This method has been specifically used in comparative studies of sardine and anchovies spawning habitat in different parts of the world (Lluch-Belda et al., 1991; van der Lingen et al., 2001; Twatwa et al., 2005). Here, a modified version of this method is used to assess spawning preferences in relation to depth, location in the north–south axis, and temperature. First, survey egg concentrations are corrected by total duration of the egg phase (from fertilisation to hatching), in order to avoid bias due to differences in egg phase duration. Duration of the egg phase is dependent on sea water temperature (Pepin, 1991), and thus local temperature variations lead to variations in egg phase duration. Other local effects on egg availability to the net, such as variable egg mortality, are ignored in this paper. Differences in egg phase duration influences the availability of eggs to the sampling gear, and thus may cause bias when comparing local egg densities between sites with different temperatures (see for example correction in duration of Stage I in AEPM procedures, Lockwood et al., 1981). Total duration of the egg phase is estimated from egg incubation experiments using multinomial models (Ibaibarriaga

et al., 2007b) and observed surface temperatures at each sampling location. Note that as the estimates of egg-phase duration come from an incubation experiment independent from the survey, the correction does not require that the eggs obtained from the survey are staged.

Once egg concentrations were corrected for local egg phase duration, corrected egg densities are analysed using SPQ. Confidence intervals of the null hypothesis of even distribution are computed by a resampling procedure in order to test for the significance of quotient values larger or smaller than one. In short, corrected egg concentrations for each station (with its original explanatory variables – depth, temperature, etc.) are randomly selected from the vector of original corrected egg concentrations, with replacement. Once a new pseudo-survey with the randomly selected egg concentrations is created, the SPQ analysis is performed and the quotient value for each bin of the explanatory variable is stored. The procedure is repeated a large number of times (999 for this analysis) and the 0.025 and 0.975 percentiles of the observed quotient values within each bin are used as the confidence intervals for the null hypothesis in that bin. As the values of the explanatory variable are not changed through the procedure, the number of stations within each bin will remain constant (although their egg concentration values will not). Preference values are defined as values of the covariate in which the corrected egg concentration quotient is significantly larger than the null hypothesis (i.e., significantly larger than 1, or above the upper confidence interval). Avoidance values are those values of the covariate for which the corrected egg concentration quotient is significantly lower than one (i.e., below the lower confidence interval). Tolerance range is defined as the range of non-significant avoidance, while preference range is the range of significant preference.

2.3. Comparative estimation of spawning areas

In order to compare the different surveys, irrespective of sampling methods and/or spatial survey coverage, the following methodology was used:

1. *Spatial modelling*: Models of egg concentration (standardised to variable egg phase duration as explained in the previous section) for each year are fitted, using quasi-Poisson GAMs (see specific section below).
2. *Model predictions*: Once the concentration models are fitted, surfaces of probability of presence of eggs on a dense regular grid within the limits of each year survey are estimated. Probabilities of egg presence are derived following the method described in Stratoudakis et al. (2003). In short, the local predicted egg concentration at each grid point is used to derive the probability of observing an egg for a given sampler under the assumed Poisson distribution.
3. *Identification of main spawning areas*: Mean probability of egg presence across all years for areas sampled at least four times is estimated as the average of the predicted probabilities for the different sampled years in each point of the predictive grid.
4. *Delimitation of basic potential spawning area*: Based on the basic results from the spawning habitat characterisation (Section 2.2), the area in which spawning can occur is delimited using simple indexes (i.e., latitudinal range and depth range of spawning areas).
5. *Sampled potential spawning area*: The section of the potential spawning area, defined as above, covered within any given survey is identified.
6. *Estimation of spawning area*: The spawning area in any given year is estimated as the product of egg presence at each point of the predictive grid, and the area represented by the point, integrated over the limits establish in point 5 above.
7. *Area standardisation*: Estimated spawning area is then compared with the total surveyed potential spawning area in any given year, to obtain an index of percentage occupancy.
8. *Comparisons with spawning biomass*: In order to compare the index of occupancy with the available SSB estimates, the index is computed both only within the assumed limits of the stock, and in the surrounding areas. SSB estimates are obtained from the ICES assessment of sardine, and compared with a series of percentage coverage of the sampled potential spawning area, both within the ICES limits of the Iberian sardine stock and in the covered Armorican shelf (see Fig. 2).

With this procedure, derived probabilities of presence across years, even with different sampling gears, are directly comparable, and the use of an index of percentage occupancy of the sampled shelf reduces the bias due

to variable year to year sampling coverage. For illustrative purposes in relation to the precision of the estimates, approximate bootstrap estimates of percentage occupancy for each year are obtained using a parametric bootstrap re-sampling procedure (Efron and Tibshirani, 1994) on the egg concentration models, and then estimating area coverage and percentage occupancy for each bootstrap iteration within each year.

2.4. Spatial modelling

Models of egg concentration are obtained using quasi-Poisson GAMs with egg abundance as the response variable, an offset to account for the effective surface area (Borchers et al., 1997) and two bivariate smoothers, the first to account for the position of the sampled station (x – y coordinates in Mercator projection) and the second a combination of temperature and bottom depth. Both temperature and bottom depth are derived variables from previous models, in order to be able to predict its value in any given point of a dense grid over the potential spawning area. Temperature models are obtained by fitting bivariate position GAMs (x – y coordinates in Mercator projection) with normal error distribution. A large amount of maximum degrees of freedom is provided to the model (150 df) in all cases but for the 1993 survey, in which only a few temperature observations were available, the maximum degrees of freedom were set to 10. A published bottom depth model (NOAA bathymetry model, web page: <http://ingrid.ldgo.columbia.edu/SOURCES/.WORLDBATH/>) was used for this variable as the most suitable best broad coverage model available for the area. Once the temperature model for a given year is fitted, temperature observations for the year are substituted by fitted temperatures at the sampling locations, and similarly for bottom depth observations.

Both for the temperature and the egg concentration models, variables within each smoother are standardised against the other accompanying variable (i.e., x against y for temperature and concentration models, and fitted temperature against fitted bottom depth for the concentration models) in order to fit isotropic bivariate smoothers (Wood, 2006). Maximum available degrees of freedom for each concentration model are fixed at a fifth of the total number of observations, with each bivariate smoother taking up a maximum of a tenth of the number of observations. Error distribution is assumed as quasi-Poisson, to allow for any residual over-dispersion of the data.

Final df used in the model, both for the temperature and egg concentration models, are selected using General Cross Validation techniques (Wood, 2006), in order to obtain the best compromise between precision and possible bias.

2.5. Software

All methods developed for this paper, as well as some tutorials and examples and other methods described in Stratoudakis et al. (2006), have been included in a series of R packages (R is an open source statistical language and software available at <http://www.r-project.org/>; see a review in R Development Core Team, 2005) and are publicly available on an open source software web page: <http://sourceforge.net/projects/ichthyoanalysis>.

3. Results

Fig. 3 shows the sardine spawning habitat characterisation in relation to temperature, logarithm of bottom depth, and distance along the 100 m contour line. Temperature tolerance (non-significant avoidance) range is between 12 and 17 °C, while the temperature preference range is between 13.5 and 15 °C. Bottom depth tolerance is between the coastline and a depth of 200 m, near the shelf edge. Bottom depth preferences are found between depths around 10 m to depths around 150 m. Due to the very low number of observations below 10 m and to the use of a logarithmic scale, the bottom depth preference and tolerance range can both be set to cover approximately the shelf area. Preferences using distance along the 100 m depth contour, show a general northern limit around 1600 km north from the reference point at the north Portuguese–Spanish coastal border. This distance is equivalent to a latitude around 47.5°N. Nevertheless, a small number of observations are available from this limit northwards. At the southern limit, no evidence of a decline in the quotient is observed, indicating that the southern limit of the spawning area is not well defined by the available data (as expected since

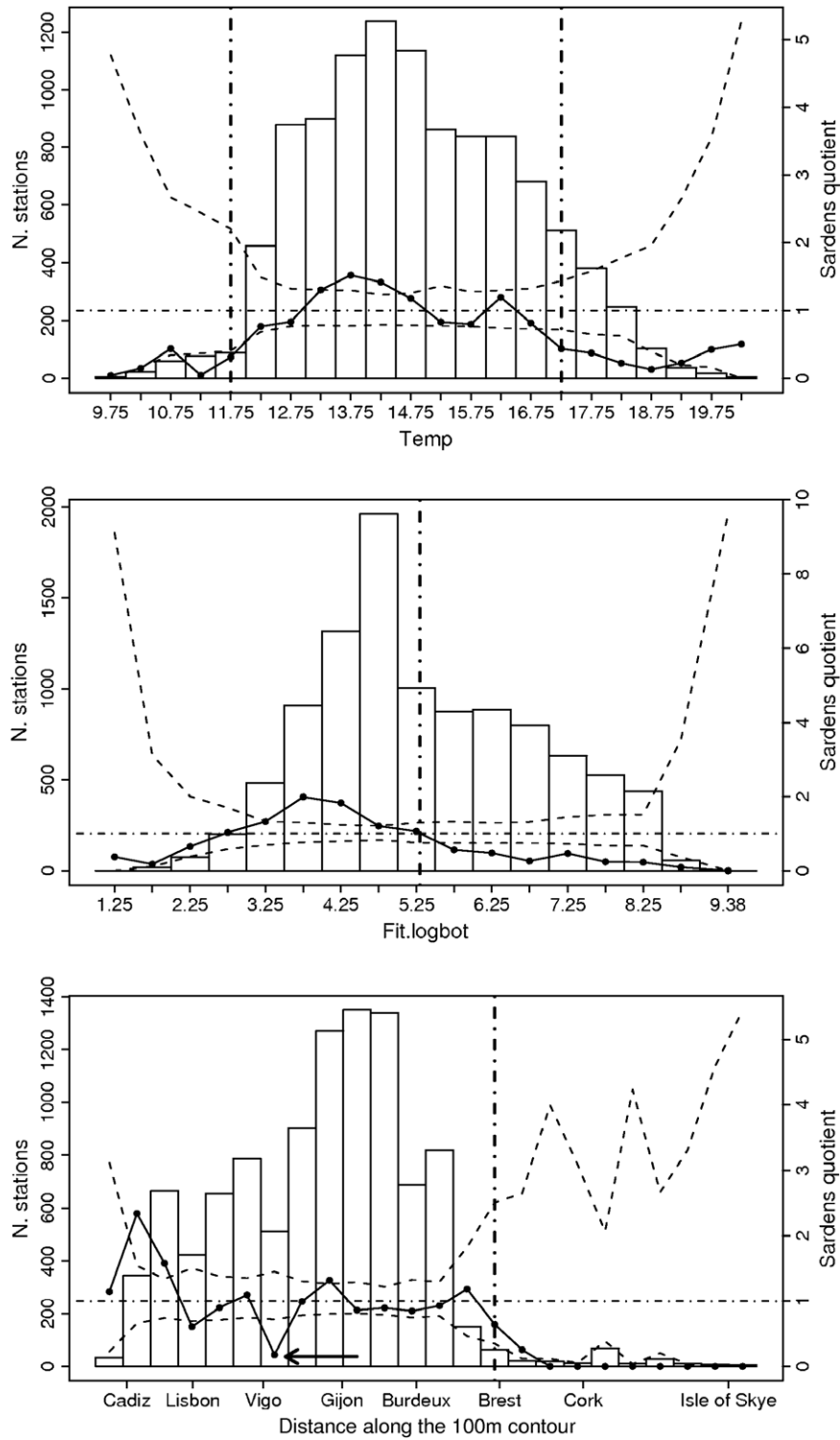


Fig. 3. Spawning area characterisation in relation to temperature (top), logarithm of bottom depth (middle) and distance along the 100 m depth contour line. Histograms represent the number of observations within each bin of the covariate, the continuous line represents the egg concentration quotient value. The horizontal dashed line represents the null hypothesis of evenly distributed eggs, and the thin dashed lines represent its upper and lower confidence intervals. Vertical dashed lines mark the limits of the tolerance area (see text). The arrow in the bottom panel shows the discontinuity in the spawning area.

spawning is known to continue down the coast of north-west Africa). An intermediate gap of spawning avoidance is also observed in the area of the southern Galician Rias (northwest corner of the Iberian peninsula). Areas of significant spawning preference are found in the south Portugal–Gulf of Cádiz region, and in the central Cantabric area; this later preference region appears due to the high concentration of eggs found in the coastal stations of this area. Using these results, a simple definition of the potential spawning habitat as the shelf between the Strait of Gibraltar and a northern limit at latitude 48°N was used.

Table 3 shows a summary of the temperature models fitted to the observed temperatures. All models explain around 90% or more of the deviance, except for the 1993 model which explains around 77% of the variance. Due to the large number of degrees of freedom (df) used, the models nearly act as interpolation models. The total number of observations, and thus the maximum available df, is very low for the years with bongo surveys (1993, 1995 and 1997, see also Tables 1 and 2).

Table 4 shows a summary of the egg concentration models. Percentage of deviance explained varies between 32% (1993) up to 95% (1995 and 1997), with most models explaining more than 60% of the deviance. Two of the three bongo surveys (1993 and 1998) show the lower explained % deviance, probably due to the lower number of observations in relation to the egg distribution pattern. Fig. 4 shows the predicted probability of egg presence for a sampled area equivalent to a CalVET net (0.05 m²) for the years with at least Iberian coverage. A gap in the spawning grounds is shown in the northwest corner of the Iberian peninsula in all but the 1993 survey, in agreement with the results from the spawning characterisation results (see Fig. 3). The 1993 survey has the lower number of stations, even less than the rest of the bongo-based surveys, and shelf occupation is most of the times based on one or two stations only within each transect. Raw survey data for the 1998 survey show a strange offshore distribution of eggs in the Gulf of Cádiz (see Fig. 1), in agreement with the modelled results.

Two small secondary gaps in the distribution of eggs can be observed in some of the years of the time series; (1) a gap between the Armorican shelf and the north east Iberian shelf (Fig. 4, years 1995 and 2002), near the

Table 3
Summary of the temperature models

| Model | Initial df | Chosen smoother | % Deviance |
|-------------------|------------|----------------------------|------------|
| sareggs88.tempgam | 150 | s(Stand. $x, y, k = 107$) | 91.82 |
| calbon92.tempgam | 150 | s(Stand. $x, y, k = 80$) | 89.54 |
| bongos93.tempgam | 10 | s(Stand. $x, y, k = 7$) | 77.31 |
| bongos95.tempgam | 150 | s(Stand. $x, y, k = 87$) | 94.48 |
| sareggs97.tempgam | 150 | s(Stand. $x, y, k = 126$) | 94.96 |
| bongos98.tempgam | 150 | s(Stand. $x, y, k = 82$) | 98.7 |
| sareggs99.tempgam | 150 | s(Stand. $x, y, k = 137$) | 98.65 |
| calvet00.tempgam | 150 | s(Stand. $x, y, k = 76$) | 94.93 |
| sareggs02.tempgam | 150 | s(Stand. $x, y, k = 129$) | 91.94 |
| sareggs05.tempgam | 150 | s(Stand. $x, y, k = 121$) | 89.61 |

Table 4
Summary of the density models

| Model | Initial df | Chosen smoother | % Deviance |
|---------------|------------|----------------------------|------------|
| sareggs88.gam | 163 | s(Stand. $x, y, k = 77$) | 78.34 |
| calbon92.gam | 131 | s(Stand. $x, y, k = 63$) | 80.16 |
| bongos93.gam | 25 | s(Stand. $x, y, k = 5$) | 31.9 |
| bongos95.gam | 45 | s(Stand. $x, y, k = 18$) | 95.29 |
| sareggs97.gam | 175 | s(Stand. $x, y, k = 87$) | 95.07 |
| bongos98.gam | 55 | s(Stand. $x, y, k = 27$) | 83.8 |
| sareggs99.gam | 209 | s(Stand. $x, y, k = 104$) | 87.86 |
| calvet00.gam | 71 | s(Stand. $x, y, k = 35$) | 65.61 |
| sareggs02.gam | 233 | s(Stand. $x, y, k = 116$) | 66.92 |
| sareggs05.gam | 233 | s(Stand. $x, y, k = 116$) | 72.88 |

border between Spain and France, and (2) a gap between south of Lisbon and the Algarve, in the south west corner of the Iberian peninsula (Fig. 4, years 1988 and 2002). Both gaps are related to narrow shelf areas, the first one associated with the Cape Breton Canyon and the second to a narrow shelf section between Cape Sagres and Cape Espichel.

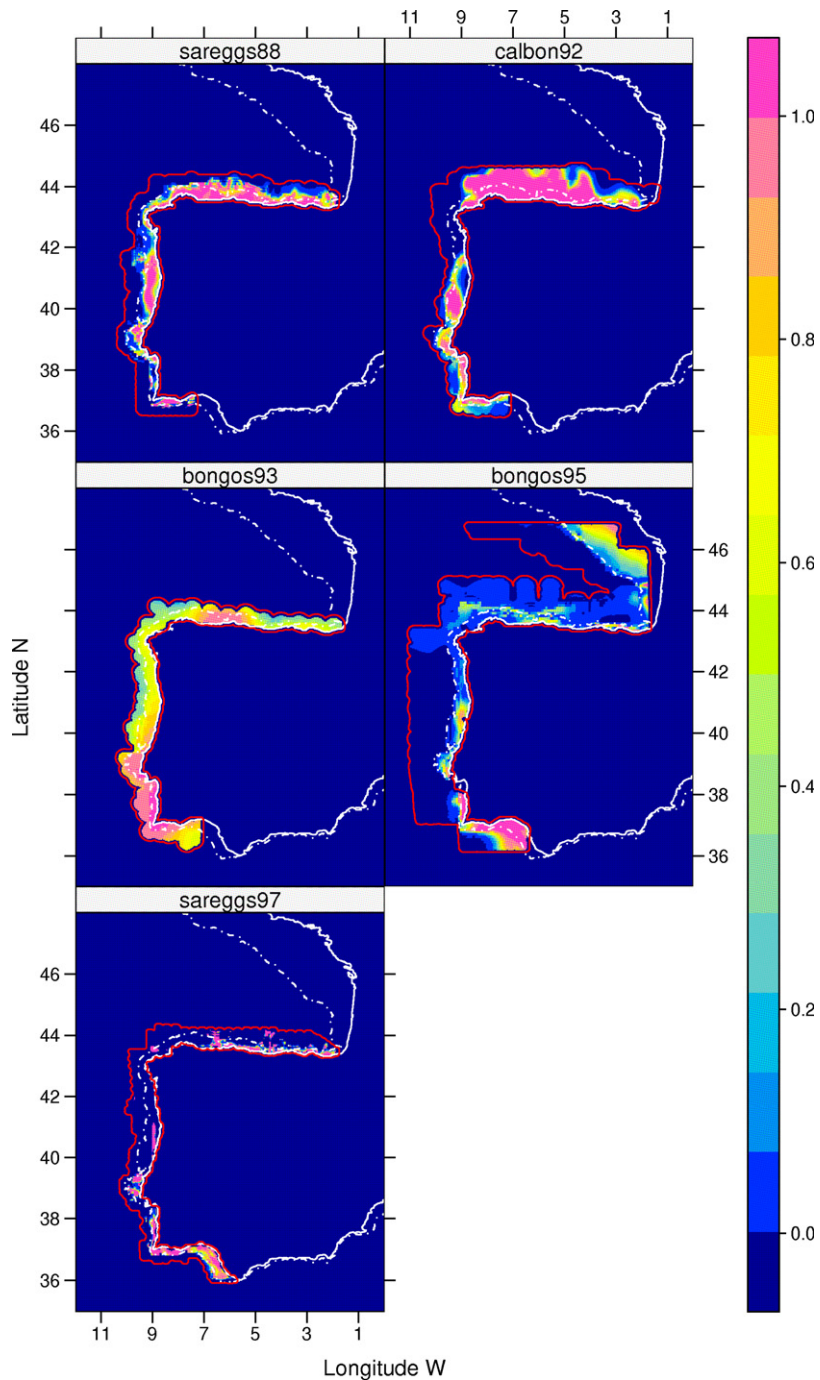


Fig. 4. Derived probability of egg presence (from 0 to 1) from the egg concentration models. Colour scale on the right side of the figure. Red lines in the figure represent sampled area for each year.

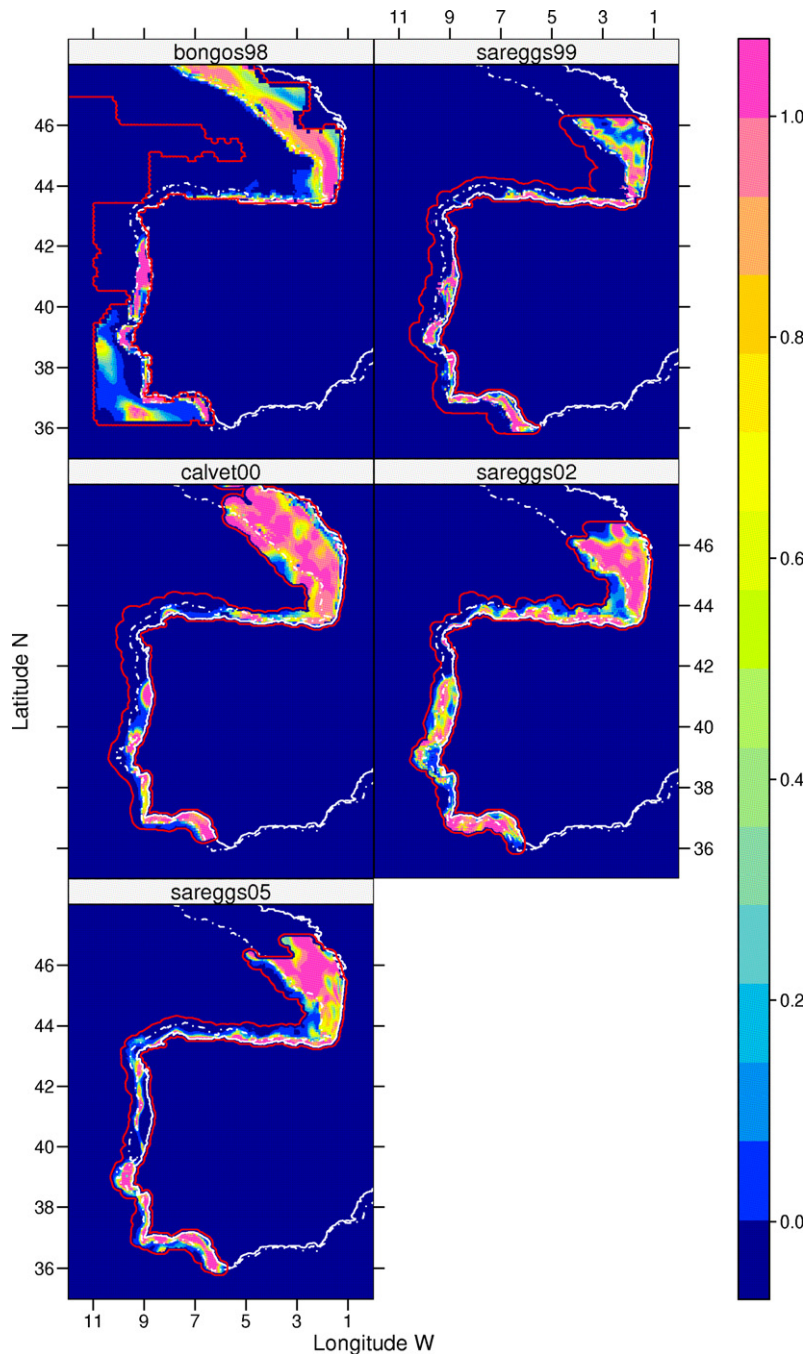


Fig. 4. (continued)

Spawning grounds in the early years of the time series (1988, 1992 and 1993) cover most of the shelf off the north and northwest Spanish coast, while spawning in this area nearly disappears in following years. The 1992 results show the most offshore distribution of spawning off the northwest Iberian peninsula, this result being also corroborated by the 1990 survey off northern Spain (sareggs0390.ieo, results not shown). Spawning off the north Portuguese coast shows variable intensity through the time series, while spawning in the Gulf of Cádiz (south Iberian peninsula) is intense through all years that cover this area. Spawning over the Armorican shelf is generally intense, covering most of the shelf.

Mean probability of egg appearance in the areas surveyed at least 4 times is shown in Fig. 5. This figure summarises most of the above mentioned characteristics of spawning distribution. Persistent spawning areas are located in the southwest and western regions of the Iberian peninsula, in the northern part of the peninsula and over the French Armorican shelf. In all cases the bulk of spawning is restricted to shelf areas, with generally low or very low probability of egg presence outside the shelf. The only area in which spawning through all the shelf shows a low probability of presence (below 0.3) is the north west corner of the Iberian peninsula, north of the border between Spain and Portugal. This gap is also accompanied in recent years with spawning restricted to a thin coastal section of the shelf from the Spanish–Portuguese border to the western Cantabric area, where the shelf is significantly reduced.

A comparison between the SSB levels, the percentage of the shelf occupied within the stock area and the percentage of shelf occupied off the French coast (within the limits established in Fig. 2) is shown in Fig. 6. Results from the bongo surveys are shown with a different symbol, as the number of stations within the shelf is low and thus the estimates of area occupied are expected to have lower precision. This is corroborated by the bootstrap based confidence intervals of percentage occupancy (vertical lines in Fig. 6), which show larger bounds for the bongo-based surveys. Confidence intervals for the 1997 and 1999 survey were not estimated, due to problems in the convergence of the models fitted to generated data. The pattern of shelf occupancy within the stock limits (circles in the figure) shows a clear shift around the mid 1990s, with nearly 60% of

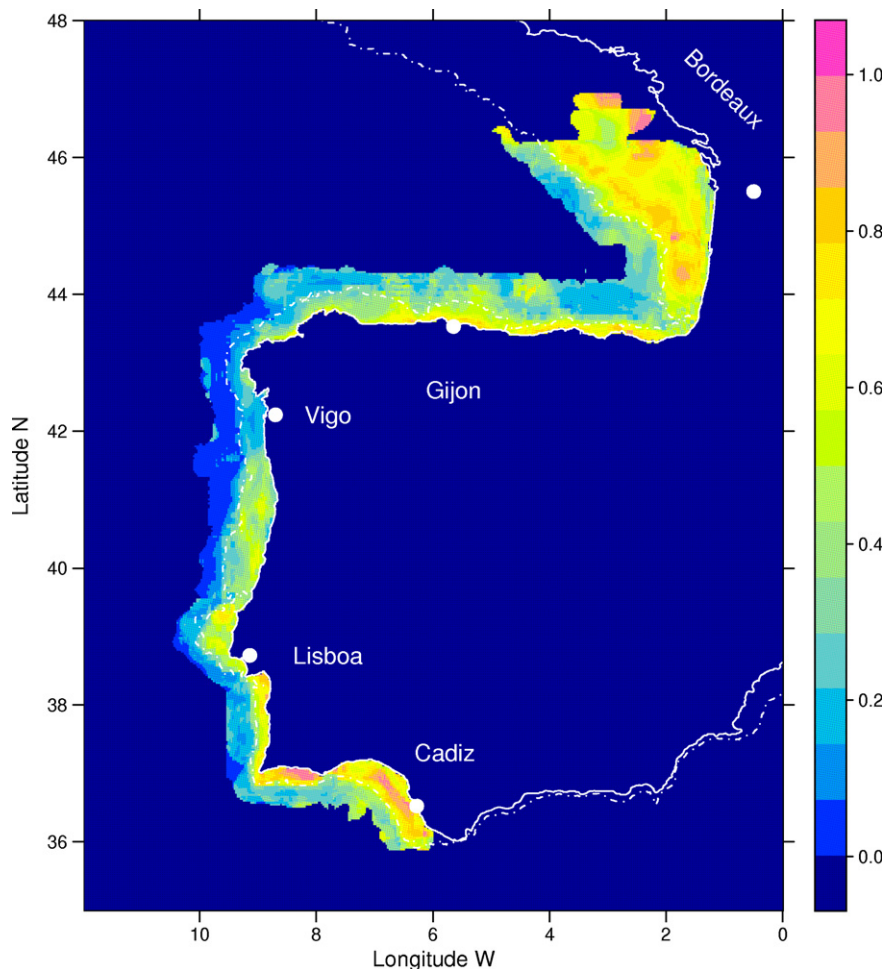


Fig. 5. Mean probability of egg presence (from 0 to 1) within the areas surveyed at least 4 times. Colour scale (as in Fig. 4) shown on the right side of the figure.

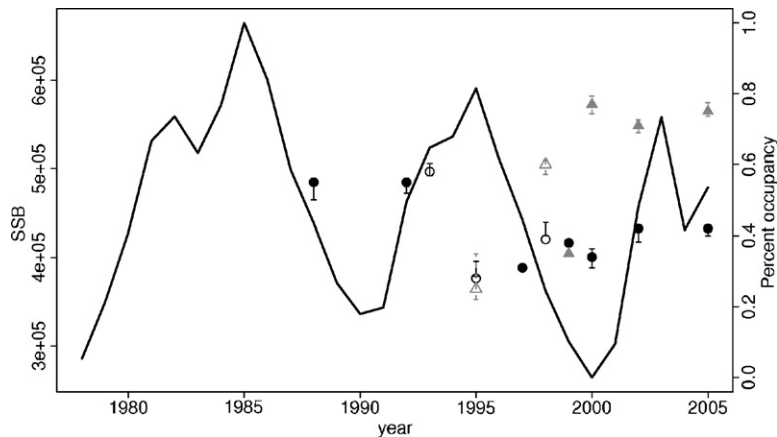


Fig. 6. Comparison between the time series of sardine SSB within the ICES stock unit (solid continuous line, scale on the left in tonnes), the percentage of shelf occupied by eggs within the same limits (circles, scale on the right), and the degree of shelf occupied with eggs in the Armorican shelf (triangles, scale on the right). Solid symbols indicate “non-bongo” based surveys, while open symbols indicate bongo-based survey.

the shelf around the Iberian peninsula occupied in the early surveys (1988, 1992 and 1993) and less, or around 40% of the shelf, occupied in the remainder of the time series. This change in occupancy is mainly due to changes in the occupancy of the west and central North Iberian Shelf (Fig. 4). Results for the Armorican shelf are only available since the middle 1990's, and based on a lower number of observations. Percentages of occupation in the Armorican shelf show an early variable period (1995, 1998 and 1999) with variable percentage occupation below 60% and three later values (2000, 2002 and 2005) with percentages of occupation of around 80%.

4. Discussion

Sardine spawning habitat in European Atlantic waters shows clear limits both in terms of temperature and bottom depth, with spawning restricted to the shelf, and to temperatures between 12 and 17 °C. Survey coverage between those limits is good in the ichthyoplankton database used in this paper. This temperature range coincides with that described using a similar dataset by Coombs et al. (2005); spawning restricted to the shelf has also been described by Furnestin and Furnestin (1959) and Ibaibarriaga et al. (2007a).

In terms of the distribution from the southern to the northern limit of the studied area, sardine shows a wide distribution throughout European Atlantic waters, as described by other authors (Stratoudakis et al., 2004), although survey coverage and definition of the northern and (especially) southern limits are far from good. Data compiled for this paper provide the most comprehensive dataset to describe sardine spawning areas in the NEA, but the northern distribution limit is only clearly surpassed by a single international coordinated survey in the database (the INDICES survey in 1998) and the southern limit is set at the Strait of Gibraltar due to lack of data availability further south. These problems are common for other ichthyoplankton survey analyses, in which the distribution area is, in the best cases, covered only until the limits of the main spawning areas, and residual spawning continues outside the survey limits (see a discussion of problems related to this issue in Castro et al., 2005). Other fragmented data apart from that used in this paper can in principle be gathered to complement the coverage, especially beyond the limits of the Atlanto-Iberian stock of sardine; net-based ichthyoplankton surveys not included in the database (e.g. Ettahiri et al., 2003), or Continuous Underway Fish Egg Sampler (CUFES, Checkley et al., 1997) based surveys (e.g. Planque et al., 2007).

Distribution of spawning grounds within the North-South limits shows, both in the characterisation analysis and in the mean probability of egg presence, a nearly continuous pattern, confined by the local characteristics of the shelf and only interrupted persistently in the region to the north of the border between Spanish and Portuguese waters, at the northwest corner of the Iberian peninsula. A small secondary break in the distribution also appears in the mean probability plots in the region of the Cap Breton Canyon (from

Cap Breton to the North), at the Spanish–French border, where the continuity of the shelf is severely disrupted and is in some years devoid of eggs. Another area with a narrow shelf is at the southwest corner of the Iberian peninsula (Cape St Vicente to the south of Lisbon), but in this case only in certain years can a small associated gap in spawning distribution be observed, and not in the mean probability of presence distribution (Fig. 5).

Using both the geographically imposed constraints on the distribution (i.e. places where the narrow shelf reduces the potential spawning habitat) and the observed gap in the Spanish–Portuguese northern border, four main spawning nuclei can be defined; (1) Southern – to the south of Iberian peninsula (Gulf of Cádiz, Algarve and northwards up to the coastal surroundings of Lisbon), (2) Western – the western Iberian peninsula (surroundings of Lisbon to the Portuguese–Spanish northern border), (3) Northern – the north Iberian peninsula (Cape Estaca de Bares to Cape Breton Canyon) and (4) the Armorican Shelf. Spawning in each of the four nuclei is always present, but depending on the year, variable levels of spawning in adjacent areas make the limits between the different nuclei more or less conspicuous. Also, the relative importance of each of the four nuclei in terms of occupied spawning area varies between years. In the early years of the time series (especially in 1988 and 1992), spawning areas of all nuclei, except for the Armorican Shelf (not sampled in this period), are widely occupied, and only a reduced gap between the western and northern nuclei remains obvious. Subsequently in the time series (since 1995), spawning areas in the western and northern Iberian nuclei are reduced and confined to a narrow coastal strip (in the northern nucleus) or to restricted areas (in the western nucleus, see clear example in the 1995 and 2000 surveys, Fig. 4), with spawning not spreading throughout all the available habitat and a clear gap in sardine egg distribution emerging at the northwestern corner of the Iberian Peninsula. The gaps between the southern and western, and the western and northern nuclei are more conspicuous in this period of the time series (1995–2005). Spawning areas over the Armorican shelf are only sampled in this later period (1995–2005) and show two different situations: an early situation in 1995 and 1999 in which spawning is patchy and some areas devoid of eggs within the shelf, and a later situation in 2000, 2002 and 2005 in which spawning spreads through much of the shelf.

Globally, the time series of shelf occupation within the Iberian peninsula shows two well characterised periods, before and after 1995. Within each period, nearly constant percentages of occupation of the shelf (around 60% and 40%, respectively) are observed, which do not follow the inter-annual variation in estimated spawning biomass for the Atlanto-Iberian stock of sardine. The change in percentage occupation of the continental shelf, as well as the yearly variations in spawning intensity described in the paragraph above, does not match with the perception of the evolution of the sardine stock according to ICES. Although in both periods (before and after 1995) different pulses of SSB levels have taken place, the levels of spawning occupancy within each period are quite stable, indicating that biomass levels within the Iberian peninsula have no direct effect on the occupied area for spawning. In contrast to the situation in the Iberian peninsula, spawning on the Armorican shelf seems to show an increase in percentage occupation, although somewhat later in the time series (from 2000 onwards). Nevertheless, variability in this area seems to be larger, in agreement with previous acoustic observations of more variable percentage of the population occupying this area (ICES, 2006b). In any case, a limited dataset exist in this area, and SSB estimates for the sardine population in the Armorican shelf are only available since 2000, preventing a full analysis of the evolution of both the SSB values and the spawning habitat in the Armorican Shelf. Apart from the comparison between spawning area extension and SSB, other information on spawning (e.g., spawning intensity, distribution of adult parameters, see a review in Stratoudakis et al., 2006; ICES, 2006a,b) should be used in order to further investigate sardine spawning behaviour in the NEA and to test different existing hypothesis on small pelagic stock size and spawning areas relationships (e.g., Carrera and Porteiro, 2003; Wyatt and Porteiro, 2002; Bakun and Broad, 2003).

Methodologically, this paper contains some modification of currently available spawning characterisation methods and a newly developed method for the estimation and comparison of spawning areas. SPQ analysis (van der Lingen et al., 2005) has been extended to include confident intervals of the null hypothesis and egg concentrations have been corrected to avoid sampling bias due to the effect of temperature on egg phase duration. Overestimation of egg concentration due to variable egg-phase duration can be large, as the duration can vary from 2 to 4 days at the temperatures observed off the Iberian peninsula. For example, assuming a constant hourly mortality rate of 3% (ICES, 2006b) and using those extreme durations, overestimation of egg abundance in the site with longer duration can reach around 23%. Egg probability of presence, and afterwards

estimates of occupied area, are obtained from GAM based egg abundance models, allowing comparison between different sampling gears. Other spatial modelling techniques can also be used instead (for example see a review in Guisan and Zimmerman, 2000), although using environmental explanatory variables can be difficult.

Both the application of the modified SPQ analysis and the estimation of egg probability of presence through this paper rely on some simplifications/assumptions: (1) estimated confidence intervals of the SPQ null hypothesis are based on independency assumptions, and thus may be underestimated, (2) the characterisation of the spawning habitat using SPQ analysis is performed with a few variables, in order to be able to include as many surveys as possible, (3) a simplistic potential habitat definition is used, based on depth and latitudinal distribution alone, and (4) a Poisson distribution is assumed to derive probabilities of presence from abundance models. The first simplification on the SPQ null hypothesis may lead to underestimation of its real confidence intervals, and therefore affect the limits of the tolerance (enlarging it) and preference (reducing it) range. Although small changes in the definition of the potential spawning area are not expected to affect the analysis presented in this paper, other ways of constructing the confidence intervals for the null hypothesis of the SPQ can also be investigated, like changing the re-sampling unit to transects or even whole surveys. The next two simplifications (2 and 3) are imposed by the characteristics of the data, but are not expected to affect the results at a global scale (for more complex characterisation exercises see for example Planque et al., 2007). The third assumption (Poisson distribution of eggs) is quite restrictive, but given the flexibility allowed to the models used in this paper, most of the spatial variability is explained by the models and the residual distribution approaches a dispersion parameter similar to the Poisson one (variance equal to the mean, results not shown). All the methodological developments presented in this paper are applicable to other species and/or habitats and provide a standardised framework to analyse ichthyoplankton data in order to characterise and describe changes in spawning habitats.

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