

Egg and larval distributions of seven fish species in north-east Atlantic waters

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ABSTRACT

The distribution of egg and larvae of mackerel, horse mackerel, sardine, hake, megrim, blue whiting and anchovy along the European Atlantic waters (south Portugal to Scotland) during 1998 is described. Time of the year, sea surface temperature and bottom depth are used to define the spawning habitat of the different species. Mackerel, horse mackerel, and sardine eggs and larvae presented the widest distribution, whereas megrim and anchovy showed a limited distribution, restricted to the Celtic Sea and the Bay of Biscay respectively. Correspondingly mackerel, horse

mackerel and sardine showed the highest aggregation indices. Blue whiting larvae were found at the lowest temperatures, whereas anchovy eggs and larvae were found in the warmest waters. The analysis is a basis for evaluation of ongoing changes in the pelagic ecosystem of the north-east Atlantic.

Key words: aggregation index, *Engraulis encrasicolus*, ichthyoplankton distribution, *Lepidorhombus whiffiagonis*, *Merluccius merluccius*, *Micromesistius poutassou*, north-east Atlantic, *Sardina pilchardus*, *Scomber scombrus*, spawning habitat characterization, *Trachurus trachurus*

INTRODUCTION

In a scenario of climate change a better understanding of spawning habitat characteristics is necessary to be able to predict the impact on different fish species. Furthermore, this needs to be considered in a multi-species context because it is not always known to what extent different species share spawning habitats or whether conditions that are detrimental for one species can be favourable for another one.

The shelf and shelf break area of the European Atlantic waters is an area where major climatic factors are reflected in general circulation patterns, such as position of the Gulf Stream Wall (Taylor *et al.*, 1992; Taylor, 1995) or changes in transport in the shelf break area (Holliday and Reid, 2001; Holliday, 2003). Equally, throughout the area climatic variability can have a direct effect on local conditions, e.g. upwelling, river runoff or shelf break fronts (Pingree and Mardell, 1981; Pingree *et al.*, 1983, 1986; Borja *et al.*, 1998; Lazare and Jegou, 1998). These regional and local changes may also have an effect on the recruitment of fish species (e.g. Borja *et al.*, 1998, 2002; Allain *et al.*, 2001; Reid, 2001; Petitgas *et al.*, 2002; Bartsch *et al.*, 2004).

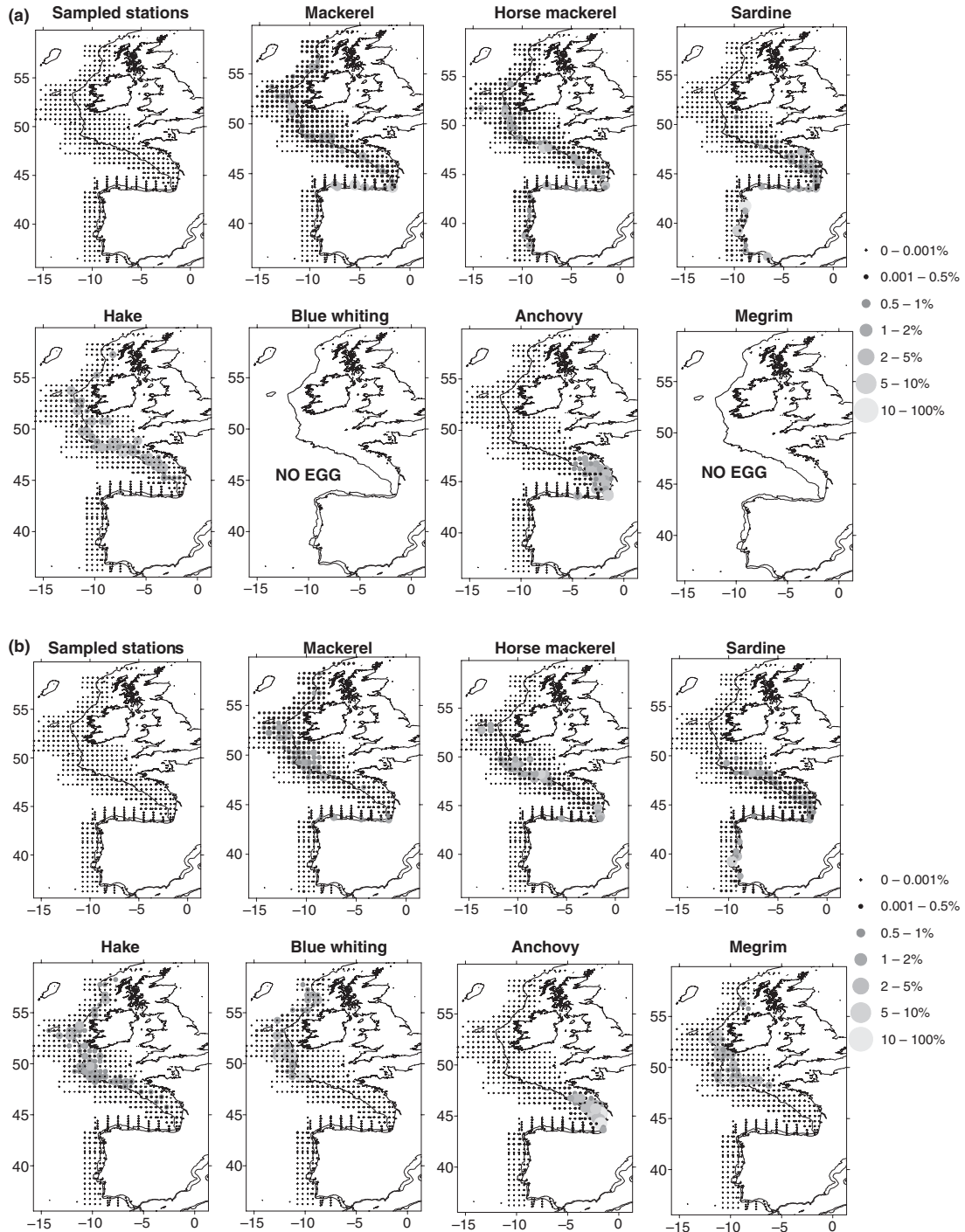
Unfortunately the spatial and temporal spawning distributions of many fish species are out of the coverage capability of most research cruises, which limits the understanding of the factors controlling spawning. Even the limits of factors as basic as temperature are difficult to determine if the cruise coverage does not

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Figure 1. (a) Sampled stations and egg distribution (in percentage of eggs over the total) for each of the species. (b) Sampled stations and larvae distribution (in percentage of larvae over the total) for each of the species.



expand over the whole spawning area and farther. One exception to this limitation is the ICES triennial mackerel and horse mackerel egg survey. This ichthyoplankton survey has an exceptional spatial and temporal coverage, from south Portugal to north of

Scotland and from January to July (Lockwood *et al.*, 1981; Beare and Reid, 2002; ICES, 2004). While the primary analysis is dedicated to mackerel and horse mackerel eggs, the survey also provides samples of eggs and larvae for a range of other species. However, these

Table 1. Samples collected in the ICES 1998 international survey.

Dates	Vessel	Sampler type	Number of samples	Latitude	Longitude
17 January–31 January	Noruega	Bongo	71	36°07′–42°45′N	06°30′–10°45′W
8 February–2 March	Noruega	Bongo	51	37°45′–42°45′N	08°45′–10°45′W
	Noruega	Bongo	41	36°07′–42°45′N	7°30′–10°45′W
	Walter Herwing	Gulf III	175	44°15′–53°15′N	01°45′–12°45′W
14 March–2 April	Cornide Saavedra	Bongo	76	43°15′–45°45′N	01°15′–10°45′W
	Cornide Saavedra	Bongo	51	42°15′–44°45′N	01°15′–10°45′W
13 April–18 May	Tridens	Gulf III	139	42°15′–48°45′N	01°45′–13°15′W
	Scotia II	Gulf III	144	48°45′–58°15′N	08°15′–14°45′W
	Investigador	Bongo	45	43°15′–46°45′N	01°15′–4°45′W
	Tridens	Gulf III	34	43°45′–47°15′N	02°45′–08°30′W
19 May–13 June	G.O.Sars	Bongo	116	48°45′–53°45′N	06°45′–15°45′W
	Celtic Voyager	Gulf III	42	54°45′–58°15′N	07°45′–11°45′W
	Corystes	Gulf III	29	44°45′–48°15′N	01°15′–11°15′W
	Celtic Voyager	Gulf III	38	50°45′–53°45′N	07°45′–15°45′W
	Corystes	Gulf III	135	42°15′–48°15′N	01°30′–10°45′W
14 June–5 July	Scotia II	Gulf III	147	48°45′–59°15′N	05°15′–15°15′W

are not routinely sorted and counted. Within the framework of an EU programme (INDICES, EU Study 97/017) the samples collected during the 1998 triennial survey were re-analysed to quantify the eggs and larvae of seven fish species: mackerel, *Scomber scombrus*; horse mackerel, *Trachurus trachurus*; sardine, *Sardina pilchardus*; hake, *Merluccius merluccius*; megrim, *Lepidorhombus whiffiagonis*; blue whiting, *Micromesistius poutassou* and anchovy, *Engraulis encrasicolus*. These species were selected for their commercial importance.

Based on these data the objective of this study was to characterize the spawning habitat of these seven species in terms of season, bathymetry and temperature in a spatial scale relevant to the distribution of the species.

MATERIAL AND METHODS

The 1998 triennial mackerel and horse mackerel survey covered the European Atlantic waters from 36°07′N to 59°15′N during the period 17/01/1998–05/07/1998 (Fig. 1a,b; Table 1). For the bulk of the survey, plankton samplers were deployed at the centre of half standard ICES rectangles, 0.5° latitude by 0.5° longitude. In the areas to the north of Spain (Cantabrian Sea) and to the south of Portugal the shelf is very narrow, and these sampling rectangle dimensions were inappropriate. Therefore, sampling rectangles of 0.25° latitude by 1° longitude were used. Samples were generally collected in oblique tows using Gulf III or Bongo samplers equipped with 250 µm mesh. Maximum sampling depth was to within 5 m of the bottom

or restricted to 200 m in deeper water off the shelf edge. In stations with a strong thermocline (more than 2.5°C per 10 m), sampling depth was to 20 m below the thermocline. Plankton samples were fixed with a 4% solution of buffered (pH 7–8) formaldehyde, and fish eggs and larvae of the seven target species were identified following the criteria described by Russell (1976). Eggs and larvae of other species were not counted.

The vertical distribution of blue whiting eggs is generally deeper than 250 m depth (Coombs *et al.*, 1981; Ádlandsvik *et al.*, 2001), and was not fully covered in the sampling of the triennial survey. Moreover, eggs of this species were potentially misidentified, as they have similar diameter range (1.04–1.275 mm) with no distinguishable features from those of several other species: *Trisopterus esmarkii*, *Trisopterus luscus*, *Pollachius virens*, *Pollachius pollachius*, *Glyptocephalus cynoglossus*, *Merlangius merlangus*, *Microstomus kitt*, *Melanogrammus aeglefinus* and *Gadus morhua* (Russell, 1976). In addition, megrim eggs were only found in one station. Thus, for these two species the analysis was restricted to larvae. For the rest of the species, both egg and larval data were examined.

The spawning periods and areas of each of the seven species were characterized in terms of the geographical and environmental covariates recorded during all the cruises (date, position, bottom depth and sea surface temperature) using the quotient analysis technique (Van der Lingen *et al.*, 2001). In this method, the covariate of interest is divided into classes (equally sized bins) and the percentage of stations and

Figure 2. Quotient lines of each species egg abundance with respect to month. The vertical bars indicate the number of samples taken each month.

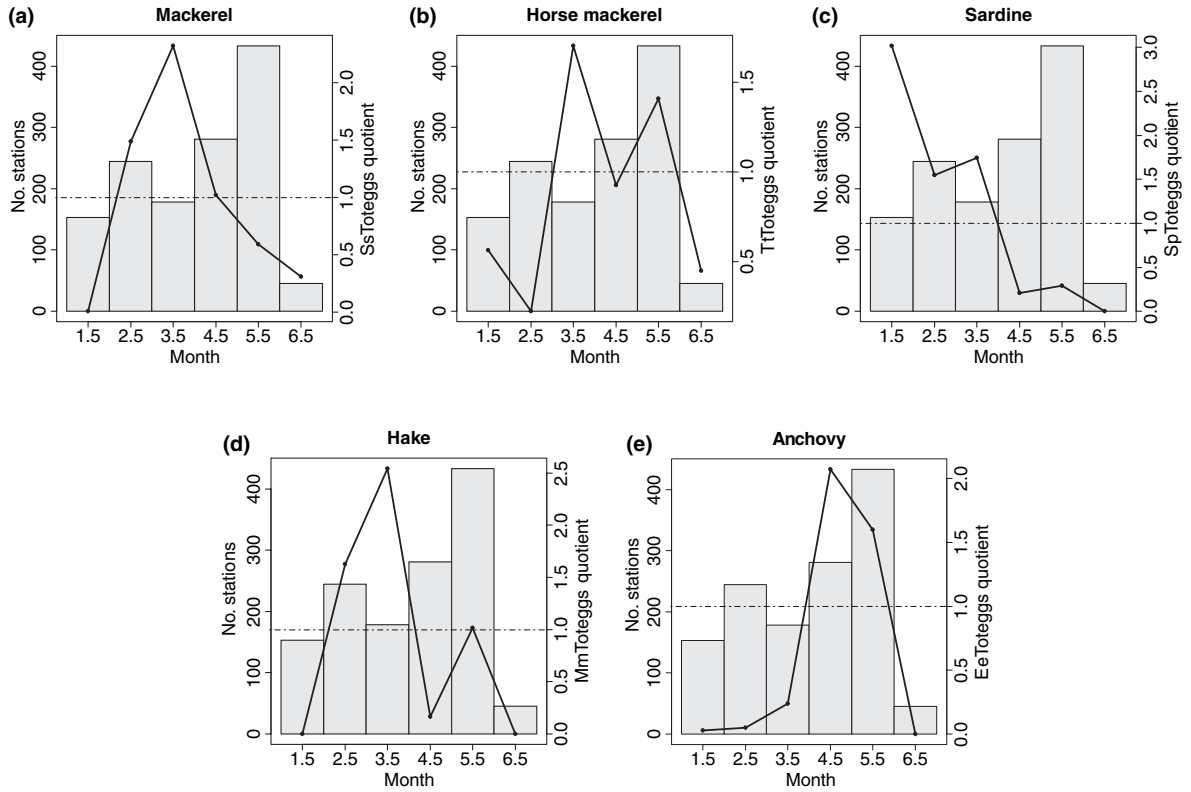
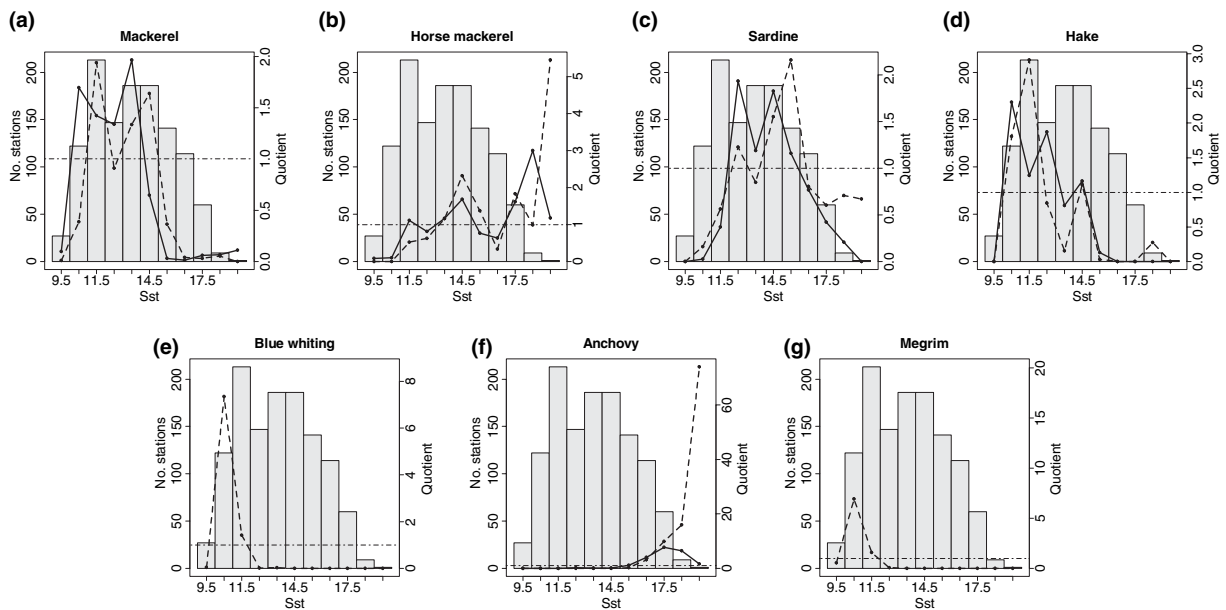


Figure 3. Quotient lines of each species egg and larval abundance with respect to sea surface temperature (solid and dashed line respectively). The vertical bars indicate the number of samples taken in each temperature class.



the percentage of total abundances per class are compared using the quotient:

$$Q_i = \frac{A_i / \sum_i A_i}{N_i / \sum_i N_i}, \quad (1)$$

where N_i and A_i denote, respectively, number of stations and total abundance per class i . Values larger than 1 ($Q_i \geq 1$) indicate an apparent prevalence of the species for particular classes.

In addition, the relationship between temperature and bottom depth and the abundance of eggs and larvae by species were analysed by comparing the distribution of the covariates themselves (all stations equal weight) with the distribution of the same covariates weighted by the egg and larval abundance of each species (Bez and Rivoirard, 2000) using box-plots.

Overlap between species was studied using the Jaccard coefficient (Legendre and Legendre, 1998):

$$I_1 = \frac{C_{11}}{C_{11} + C_{01} + C_{10}}, \quad (2)$$

where C_{01} is the number of samples in which only the second species is present, C_{10} is the number of samples in which only the first species is present and C_{11} is the number of samples in which both species are present. This index is the probability of two species being present given that at least one species is present. Thus, it takes values between 0 and 1. The value 0 corresponds to the case in which the species do not share any distribution areas and 1 to the case in which the distribution areas for both species are identical.

Species diversity was represented by the number of species found at each station and was also analysed in relation to temperature and bottom depth. Sample stations were grouped into classes according to the covariate of interest, and the average number of species in each class, together with the corresponding 95% confidence interval, was computed. However, these statistics depend on the size of the interval defining the classes of the covariate. The dependence of species diversity on interval size was studied by computing the percentage of stations with different numbers of species for a series of groups with increasing intervals.

Finally, a regression model of sea surface temperature on spatial and temporal variables was fitted.

All the analyses were carried out in R (<http://www.r-project.org>) using the library shachar (Spawning HABitat CHARACTERization, M. Bernal, <http://sourceforge.net/projects/ichthyoanalysis/>).

RESULTS

Eggs and larvae of mackerel, horse mackerel and sardine presented the widest distribution, covering much of the time and area of the surveys. Megrim and anchovy showed a more limited distribution, restricted to the Celtic Sea and the Bay of Biscay respectively (Fig. 1a,b).

Quotient analysis applied to the sampling month indicated that the spawning periods of almost all the species were reasonably well represented, except for sardine where the peak of spawning appeared to have finished before sampling began (Fig. 2).

The spawning sequence by species in relation to temperature appeared to be: blue whiting, megrim, hake, mackerel, horse mackerel, sardine and anchovy (Figs 3 and 4) with blue whiting spawning in the coldest waters and anchovy in the warmest. Quotient analysis with respect to temperature showed that for most species, except anchovy and horse mackerel, the

Figure 4. Box-plots of sea surface temperature unweighted and weighted by each species egg (a) and larval (b) abundances.

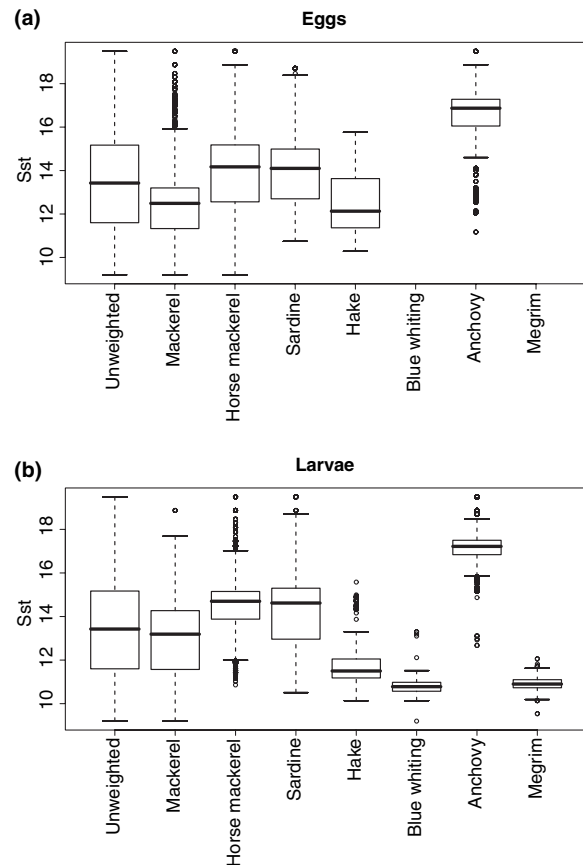
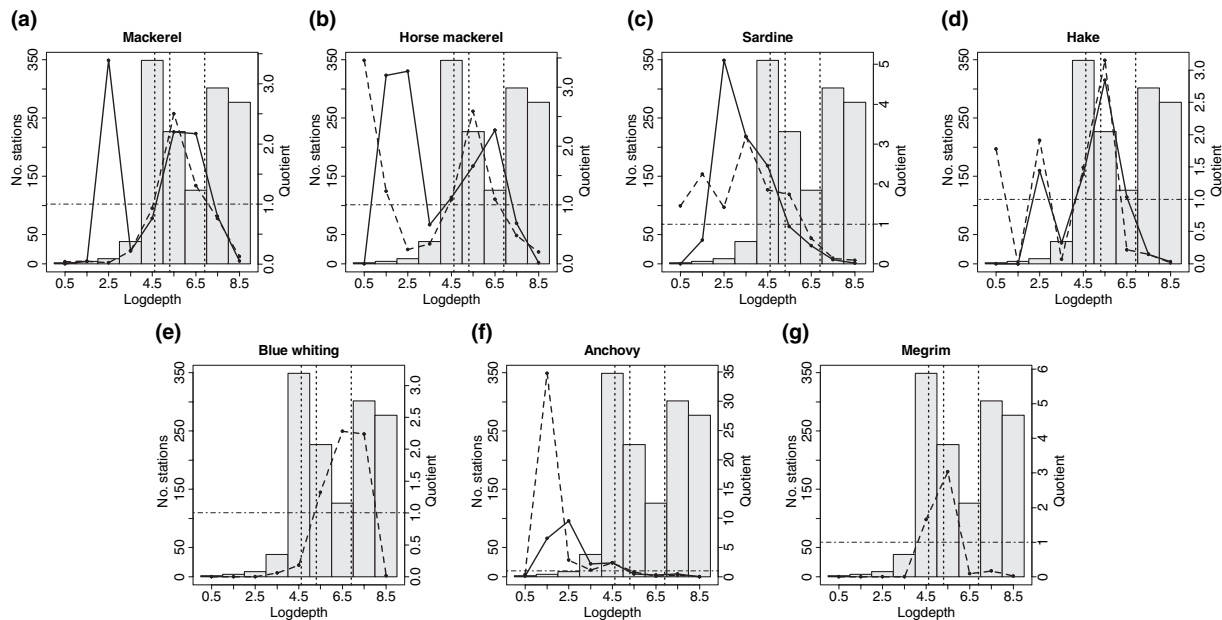


Figure 5. Quotient lines of each species egg and larval abundance with respect to the logarithm of bottom depth (solid and dashed line respectively). Vertical dotted lines represent 100, 200 and 1000 m depths. The vertical bars indicate the number of samples taken in each depth class.



prevalence temperature range was well defined (showing increase, maximum and decline). Anchovy and horse mackerel larvae did not show a decline at higher temperatures (Fig. 3).

The eggs and larvae of most species were found in waters with bottom depth between 100 and 200 m (Figs 5 and 6). Quotient analysis (Fig. 5) showed that anchovy and sardine were mainly distributed in water depths of <100 m, whereas the other species were also found over the shelf break. Blue whiting larvae were only found over the shelf break (Figs 1, 4 and 6).

For all the pairs of species the values of the Jaccard index for eggs and larvae were <0.5 (Table 2), suggesting little overlap over the whole surveyed area. The largest indices were found between mackerel, horse mackerel and sardine. Co-occurrence between these species larvae in relation to blue whiting and megrim was close to 0. Major overlap for anchovy eggs and larvae corresponded to sardine and horse mackerel. Hake eggs did not occur together with any other species, whereas the larvae shared some distribution areas with mackerel and some other species.

Samples with the higher numbers of larvae were generally found in the shelf break area from southern Bay of Biscay up to the Celtic Sea (Fig. 7). The average number of larval species per sample (including only positive samples) increased with temperature (Fig. 8a). The maximum number of larval species

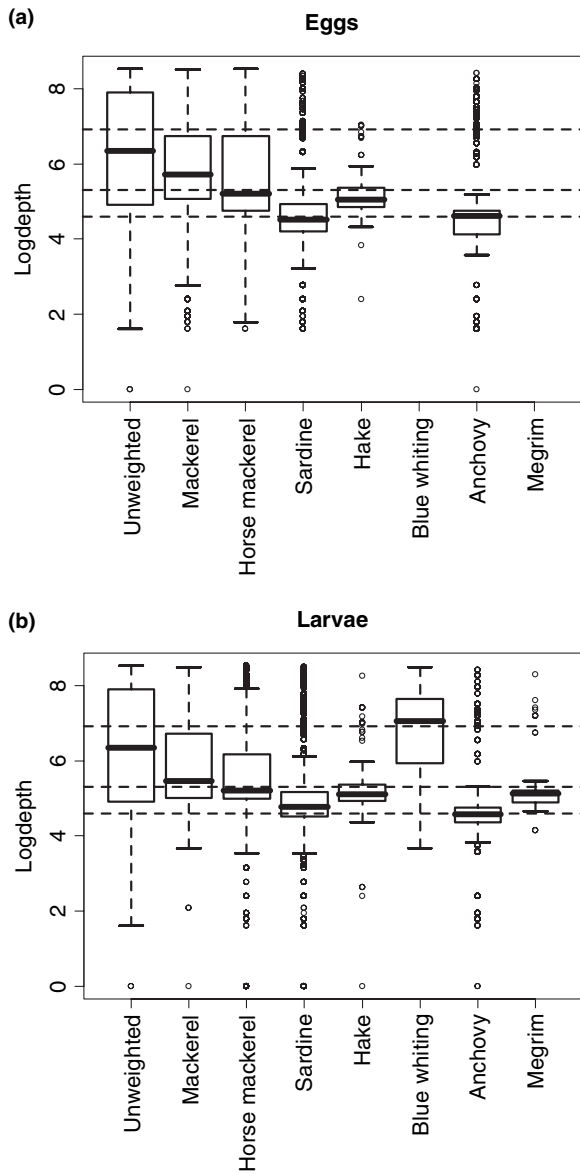
was found between 150 and 250 m depth (Fig. 8b). Figure 9a,b shows the rate at which the number of larval species found increased depending on the temperature and depth class size. Intervals of 2°C result in a 100% probability of finding five species. However, an interval of 4°C is needed to ensure that six species are found (100% probability). In terms of depth, intervals of 200 m depth result in a 100% probability of finding three species. An interval of 1000 m depth is needed to have a 100% probability of finding six species.

The regression model fitted to temperature was $SST (^{\circ}C) = 30.6 - 0.44 \text{ Lat } (^{\circ}) + 0.033 \text{ day of the year}$ (from January to July), $R^2 = 0.74$, $P < 0.01$, $N = 1203$. This means that in case there is a change in temperature of $x^{\circ}C$, the latitude and the day of the year at which certain specific temperature conditions will be found would be incremented by $-x/0.44^{\circ}$ and $x/0.033$ days respectively.

DISCUSSION

The large spatio-temporal scale of the 1998 triennial mackerel and horse mackerel egg survey provides useful information about the spawning distributions and habitat of five other species. Moreover, given the large scale of the survey, the limits of the spatial and environmental spawning conditions of the other species are well covered, resulting in a better characterization

Figure 6. Box-plots of log bottom depth unweighted and weighted by each species egg (a) and larval (b) abundances. Horizontal dashed lines correspond to 100, 200 and 1000 m depths.



of the realized spawning habitat than any regional survey alone. Surveys aimed at local populations or stocks often do not extend beyond the limits of those local populations. The distribution area can be delimited, but not having information about the conditions outside the species distribution area undermines our ability to understand the mechanism. As a consequence, we cannot establish which environmental factors or values set the spatial distribution limits. If longer time series of surveys such as the one presented here were available, favourable environmental conditions for spawning could be inferred from the succession of observed distributions. The areas presenting the determined favourable conditions will form the potential spawning habitat. The relation between the potential spawning habitat and the actually occupied area could be used to assess the stock health. The observation of recruitment success in relation to the relative occupation of the potential spawning habitat may allow further advances in understanding the stock-recruitment relationships.

The weighted approach used in this study was effective in defining habitats. In the present study, environmental parameters have been weighted by eggs and larval densities. Results are then driven by the most abundant stages of eggs and larvae, respectively, i.e. the newly spawned eggs and the newly hatched larvae. As a result of natural mortality, mostly predation, the number of eggs actually available for sampling will reduce with elapsed time from spawning. The same would be true for larvae. As a result, their densities would be expected to decline over the period of development. For example, the box-plots in Figs 4 and 6 are generally narrower for larvae than eggs suggesting higher survival or transport of survivors to such areas.

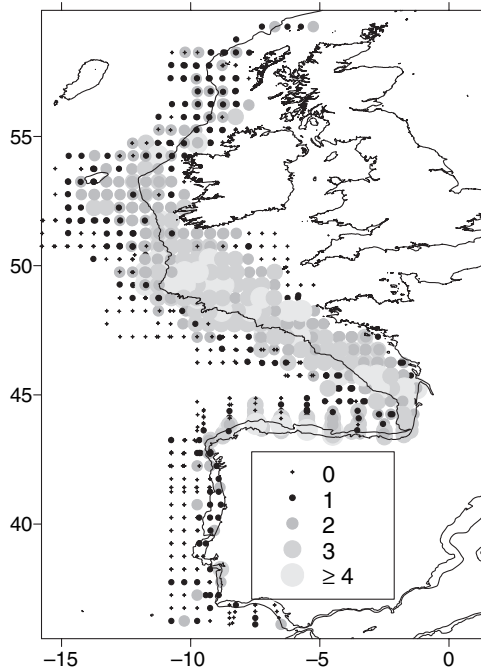
The results indicate clear distribution trends in relation to temperature and bathymetry. However, it should be noted that a single survey does not provide a synoptic overview of the temperature in the area, and cannot follow the evolution of temperatures over the survey period. It is therefore difficult to ascertain

Table 2. Jaccard index for eggs and larvae of each pair of species.

	Mackerel	Horse mackerel	Sardine	Hake	Blue whiting	Anchovy	Megrim
Mackerel	–	0.487	0.227	0.074	–	0.100	–
Horse mackerel	0.386	–	0.313	0.088	–	0.169	–
Sardine	0.261	0.466	–	0.121	–	0.282	–
Hake	0.209	0.157	0.106	–	–	0.027	–
Blue whiting	0.070	0.015	0.019	0.113	–	0.058	–
Anchovy	0.029	0.137	0.164	0.009	0.000	–	–
Megrim	0.046	0.017	0.009	0.148	0.218	0.000	–

Cells in light grey (above the main diagonal) correspond to eggs and cells in dark grey (below the main diagonal) to larvae.

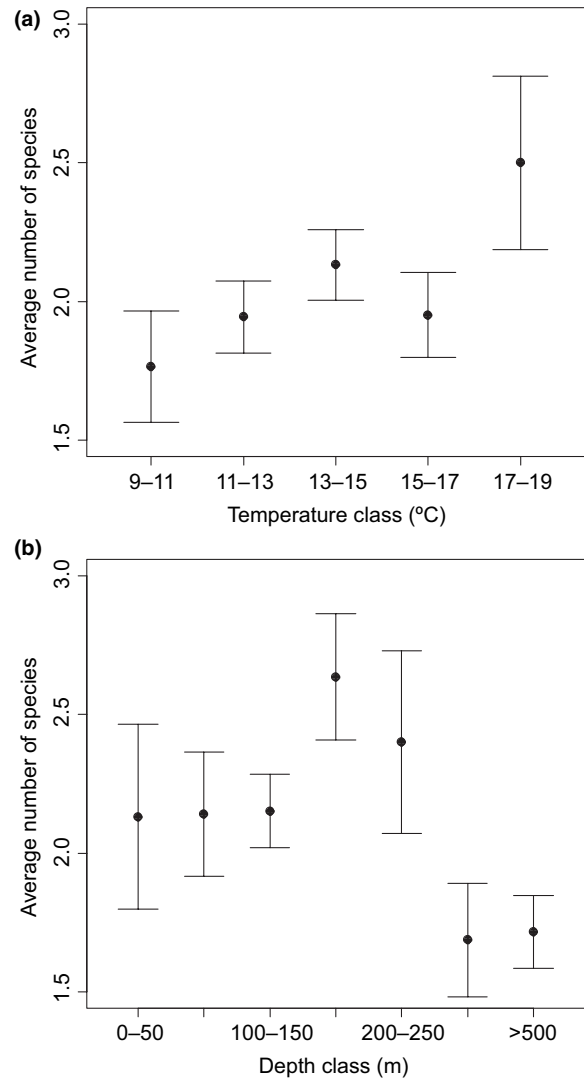
Figure 7. Distribution of the number of larval species per sample.



whether one species occupies one area because of a temperature preference or is present in that area regardless of the temperature conditions, the distribution being related to other factors (productivity, retention areas, return to birth area, etc.). An example of this effect could be in the double peak found in the temperature quotient analysis for sardine (Fig. 3). It is likely that on such a large geographical scale suitable spawning areas in terms of productivity or retention could be found in many locations where the adult fish are present. At this spatial scale, if temperature did not play a primary role and was a proxy of local conditions, the quotient analysis could result in a succession of peaks all along the temperature gradient.

The largest number of the seven investigated species was found over the shelf break area. In the shelf break primary production is enhanced by fronts and internal waves (Pingree and Mardell, 1981; Joint *et al.*, 2001, 2002). Hence, the relationship between spawning distribution and the shelf break might be a proxy of the importance of primary (and associated secondary) productivity. The emerging picture is not only that of spawning within a temperature window, but also related to geographical features likely to enhance primary production (shelf break and river plumes). This would explain the relation of most of the species on the shelf break and the distribution of

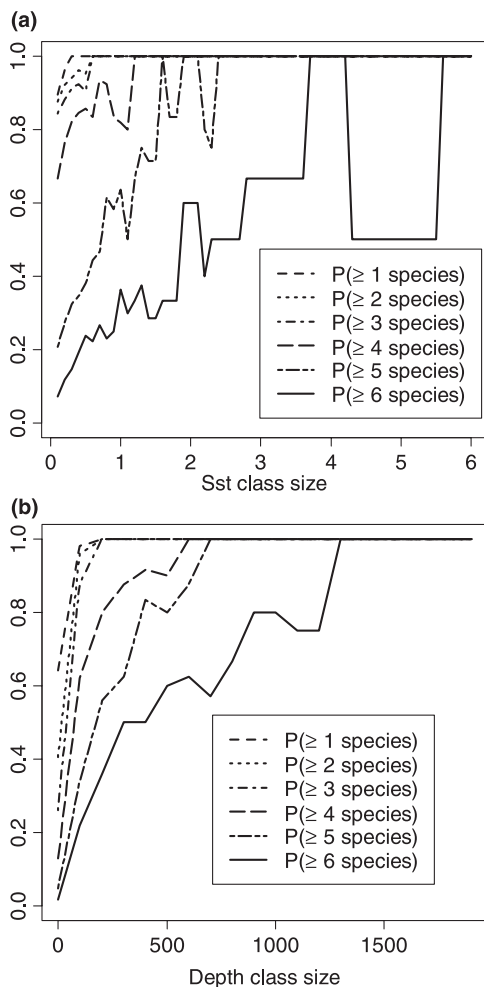
Figure 8. Average number of larval species and the correspondent 95% confidence interval at each temperature (on the left) and bottom depth (on the right) class. Only positive samples (at least one species) were considered for this analysis.



anchovy and sardine into the shelf waters of the Bay of Biscay where high productivity is found in the plume of the large rivers. This extension of the spawning area has already been described for mackerel (Uriarte *et al.*, 2001; Beare and Reid, 2002), but our results suggest that could be applied to some of the other species.

This study was based on the survey of a single year, and discrimination of the factors defining the spawning habitat (e.g. productivity versus temperature) would require further cruises. However, the results show that a large-scale survey, such as the triennial mackerel and horse mackerel egg survey, is potentially

Figure 9. Probability of finding different number of larval species according to the size of temperature (a) and bottom depth (b) classes.



a very useful tool to investigate factors defining spawning habitat. The surveys have been conducted since 1977 and in most cases the plankton samples and associated metadata have been preserved. It would be very useful to carry out a similar analysis on these samples. The present study has clearly indicated the potentially high added value of these surveys, and the rationale for continuing and extending this type of analysis.

The spatio-temporal distribution of spawning by different species is likely to change under a climate change scenario. This study contributes to establishing the large-scale baseline distribution required to evaluate these potential changes. Intergovernmental Panel on Climate Change (IPCC; <http://www.ipcc.ch>) predicts a sea surface temperature increase of 0.2–0.4°C per decade. Based on the regression model fitted

to sea surface temperature, this would result in a northern expansion or southern retreat of the spawning distribution limits of about 0.5–1° of latitude per decade and a change in the spawning timing of about 10–20 days per decade. Obviously, this prediction is based on a very simplified assumption and does not include the influence of other environmental factors or the adult behaviour. Spawning core areas are likely to remain unaffected for longer periods because they are probably located in the middle part of the temperature tolerance range. However, a shift in the northern and southern limits of the distribution is more likely, as has been observed for plankton (Beaugrand *et al.*, 2002; Edwards and Richardson, 2004; Richardson and Schoeman, 2004) and for several species of fish in the North Sea (Beare *et al.*, 2004a,b). If the spawning habitat was controlled by temperature alone, we would expect that the temperature window (even if narrower) would remain accessible despite global warming. However, if the spawning habitat is defined by a number of parameters, e.g. temperature, depth and plankton production, then there is more risk that the preferences or tolerances for these variables will fail to coincide. This may be particularly important for those species with a restricted spawning habitat, such as anchovy and megrim, which may, therefore, be more at risk from climate change.

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