Spawning of anchovy *Engraulis encrasicolus* in the Northwestern Mediterranean relative to hydrographic features in the region

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ABSTRACT: The present study furnishes conclusive evidence for the existence of latitudinal differences in the duration of anchovy spawning related to temperature cycle and hydrographic features; 2 main spawning areas were found, one off northern and another off southern Catalonia (NW Mediterranean, NE Spain). Total egg production was similar in the 2 spawning areas and even somewhat higher in the northern area, where the spawning cycle was shorter (ca 2 mo). The areas of highest egg abundance were located relatively far offshore, between 10 and 30 miles from the coast, spanning a very broad range of bottom depths, from 50 to 1000 m. The presence of a shelf-slope front of variable intensity running along the entire coast (Font et al. 1988) suggests that anchovy take advantage of the productivity associated with the front for reproductive purposes, particularly since the front is the most important enrichment phenomenon in the region during summer, the time of maximum spawning (Estrada & Margalef 1988). In addition, the distribution of spawning activity brings to light its association with the zones of influence of the outflows of 2 large rivers, the Rhône and the Ebro. On the whole, the reproductive behaviour of *Engraulis encrasicolus* in the Northwestern Mediterranean takes advantage of the most favourable conditions to ensure the success of early life stages in a region in which enrichment phenomena are more limited than those described for other clupeoid species.

INTRODUCTION

The most abundant clupeoids off the coast of Catalonia (NW Mediterranean, NE Spain) are sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus*, which are the basis for the pelagic fishery in the region. These 2 species account for 60 % of commercial catches, and although sardine makes up the larger share, fishing pressure is heavier on anchovy because of the higher prices brought by this species. The proportion of anchovy in the catches rose from 1965 (Larrañeta 1981) as catches of both species increased. Beginning in 1980, however, catches underwent a significant decline, especially those of anchovy, which yielded 15 776 t in 1980 but only 5066 t in 1985, although the stock is presently in a recovery phase.

*Engraulis encrasicolus* is widely distributed in the Northeast Atlantic and Mediterranean and adjacent seas (Reid 1967), and the species inhabits areas with very different environmental features, i.e. areas with high productivity (e.g. the Canary Current region), areas with warm waters and moderately high productivity, and areas with low productivity and extreme conditions (e.g. the Black Sea). Its distribution range includes bays, lagoons, and estuaries. Nevertheless, there have not been many studies on the species, as pointed out in the review by Blaxter & Hunter (1982). In the past 10 yr there have been important contributions on anchovy eggs and larvae by Regner (1985) for the Adriatic and Ré (1987) for the Mira estuary in Portugal. Recently some studies designed to apply the Egg Production Method in the Bay of Biscay have been made (Motos & Santiago 1990).

The spawning behaviour of anchovy in the Western Mediterranean was described by Fage (1935), who suggested that adults came inshore to spawn. Andreu & Rodríguez Roda (1951) and Bas & Morales (1954) confirmed these findings off Catalonia and posulated the existence of 2 spawning stocks, one consisting of age 2+ individuals at the start and height of the spawning season and the other consisting of younger mature 1-yr-olds at the end of the spawning season.
Conversely, Suau (1979) suggested that anchovy migrated towards deeper waters during the spawning season.

In view of the limited and sometimes contradictory information on the spawning ecology of *Engraulis encrasicholus* in the Western Mediterranean and the importance of anchovy in the fishery off Catalonia, the object of this study was to investigate the spatio-temporal distribution of spawning in relation to the environmental features in the region.

**STUDY AREA**

The topography of the continental shelf off Catalonia is highly variable. The northern part of the region is characterized by 3 submarine canyons that approach the coast to within a few miles; between the canyons the shelf is 40 km wide. In the central part of the region the shelf narrows to the Sant Jordi Gulf, after which it broadens out to 60 km opposite the Ebro River delta in the southern part of the region (Fig. 1). The inflow from the Rhône River (north of Cape Creus; Fig. 1) over the shelf in the Golfe du Lion is one of the most important sources of inland waters off the coast of Catalonia (Castellón et al. 1986, Font 1987, La Violette et al. 1990) and plays a major role in determining the circulation pattern in the northern part of the region, occasionally altering the hydrodynamic conditions prevailing there. The most important influx of freshwater run-off in the south comes from the Ebro River. Current flow in the region is southwesterly along the edge of the continental shelf. Associated with this current is a typical shelf-slope front separating less saline inshore waters from the waters of the open sea (Font et al. 1988), though the front may exhibit considerable spatio-temporal instability (Wang et al. 1988). Font et al. (1990) described the intrusion of water from the slope onto the shelf caused by the sudden broadening of the shelf north of the Ebro River delta, which is a source of permanent upwelling in that area. The formation of instabilities in the shelf-slope front may be related to shelf structure and plays an important role in shelf-slope water exchange (Tintoré et al. 1990).

**MATERIAL AND METHODS**

**Sampling area.** A total of 11 anchovy egg and larval cruises were carried out off Catalonia between latitudes 40° 12' N and 42° 24' N (Cape Creus - Ebro River delta) between 1983 and 1985. Table 1 presents a summary of the sampling cruises carried out during these 3 yr.

Sampling was performed using a grid of stations used throughout over the 3 yr sampling period. The grid basically comprised 39 stations, though on certain surveys this number was increased (Fig. 1). Stations were arranged along 17 transects perpendicular to the

![Fig. 1. Study area and sampling stations. (+) Stations sampled during all 3 yr of the study period; (*) new stations sampled when the basic station grid was extended](image-url)
Table 1. *Engraulis encrasicolus*. Summary of anchovy egg abundance cruises carried out off the Catalonian coast between 1983 and 1985. Positive stations = eggs present

<table>
<thead>
<tr>
<th>Cruise dates</th>
<th>Cruise area (km²)</th>
<th>No. of stations</th>
<th>No. of positive stations</th>
<th>Mean abundance (no. 10 m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>14−26 Apr 1983</td>
<td>12,246</td>
<td>45</td>
<td>12</td>
<td>561</td>
</tr>
<tr>
<td>14−20 May 1983</td>
<td>12,246</td>
<td>45</td>
<td>36</td>
<td>815.6</td>
</tr>
<tr>
<td>8−12 Jun 1983</td>
<td>12,246</td>
<td>45</td>
<td>42</td>
<td>2135.4</td>
</tr>
<tr>
<td>19−25 Jul 1983</td>
<td>12,246</td>
<td>45</td>
<td>36</td>
<td>951.1</td>
</tr>
<tr>
<td>7−14 Sep 1983</td>
<td>12,246</td>
<td>45</td>
<td>16</td>
<td>29.4</td>
</tr>
<tr>
<td>4−10 Oct 1983</td>
<td>12,246</td>
<td>45</td>
<td>7</td>
<td>3.8</td>
</tr>
<tr>
<td>27 Apr−3 May 1984</td>
<td>11,814</td>
<td>39</td>
<td>15</td>
<td>53.4</td>
</tr>
<tr>
<td>16−21 Jun 1984</td>
<td>10,487</td>
<td>35</td>
<td>32</td>
<td>755.8</td>
</tr>
<tr>
<td>17−22 Aug 1984</td>
<td>12,831</td>
<td>42</td>
<td>24</td>
<td>125.4</td>
</tr>
<tr>
<td>30 Sep−5 Oct 1984</td>
<td>12,175</td>
<td>40</td>
<td>5</td>
<td>3.2</td>
</tr>
<tr>
<td>12−20 Jun 1985</td>
<td>17,118</td>
<td>54</td>
<td>40</td>
<td>420.9</td>
</tr>
</tbody>
</table>

Results on the vertical distribution of anchovy eggs have indicated a distribution confined to above the thermocline (Palomera 1991), and these results were taken into account in designing the analysis of the temperature at which spawning took place. Mean temperature was calculated at the different sampling intervals in the upper 50 m during months of vertical mixing (April to May) and above the thermocline in those months in which a thermocline was present (June to October).

**RESULTS**

**Spatio-temporal distribution**

Anchovy eggs were present on all the cruises, that is, from April to October, and were most abundant from May to July (Table 1). Figs. 2 to 4 indicate the distribution of anchovy eggs in the different months.

Spawning commenced in the second half of April off the Ebro River delta as only anchovy eggs, but no larvae, (Palomera & Sabatés 1990) were found during surveys carried out in late April 1983 and 1984. In the rest of the region, however, neither eggs nor larvae appeared until May. This agrees with the findings of Palomera & Rubies (1979) for an annual sampling cycle conducted off Barcelona, in which anchovy larvae appeared in May onwards. This agrees with the findings of Palomera & Rubies (1979) for an annual sampling cycle conducted off Barcelona, in which anchovy larvae were recorded only from May onwards. Spawning duration also varied from north to south: off the Ebro River delta, though the presence of eggs was sporadic and egg abundance was low, eggs were collected until October in both 1983 and 1984, whereas in the rest of the region eggs were collected on the October cruise only at a single station in 1983. Larval abundance in October was also very low, a further indication that spawning was drawing to an end (Palomera & Sabatés 1990).
Fig. 5 depicts the spatio-temporal distribution of eggs along the coast over the 6 mo sampling period carried out in 1983. Mean abundance values along the 6 northernmost transects indicated a short spawning season (May to July-August?), with a peak in June and July that accounted for 98% of total spawning. Spawning was also short in the area covered by the central transects, abundance was considerably lower, and spawning was concentrated in May (45%) and June-July (55%). In the southern region, in the vicinity of the Sant Jordi Gulf and the Ebro River delta, spawning peaked in May and June; these months accounted for 86% of spawning, though, as already pointed out above, spawning went on until October.

Mean abundance on the 11 surveys ranged from 3.2 to 2135.4 anchovy eggs per 10 m² of sea surface (Table 1). The highest values of all surveys, more than 10 000 eggs per 10 m² of sea surface, were recorded at 3 stations near the shelf edge in the northern part of the region in June and July 1983 (Fig. 2). There were clear differences in abundance between 1983 and 1984 (Table 1, Figs. 2 & 3), when spawning was poorer and values higher than 1000 eggs per 10 m² of sea surface were recorded at only a few stations. The study area was extended in June 1985 (Fig. 1), when peak spawning had been recorded in the previous 2 yr, in an effort to determine the full offshore extent of spawning. No eggs were collected at 66% of the extra stations added, and eggs were present only at some of the new stations located over the narrow portion of the shelf, where spawning occurred in all 3 sampling years, though abundance values were very low (12 to 28 eggs 10 m⁻²).

The main spawning areas in the northern and southern parts of the region also exhibited differences. The surveys were designed to cover the continental shelf, which is wider in the southern part of the region. Peak spawning in the south was located mainly between 20 and 30 miles offshore. In the northern part of the region, however, high spawning abundance values were concentrated between 10 and 20 miles offshore, even on the June 1985 survey, on which sampling was extended further offshore (Figs. 2, 3, & 4). The difference in the distance from the coast in these
2 areas was thus clearly related to the location of the shelf break and the slope. This suggests that the largest aggregations of spawning adults form near the edge of the shelf.

**Egg production**

Table 2 presents monthly estimates of anchovy egg abundance for the entire spawning period in 1983. The estimates were calculated more as a means of comparing production in the 2 spawning areas than as an assessment of annual spawning. The 2 different areas considered in the region are separated in Fig. 1 by a line drawn perpendicular to the coast off Barcelona; the northern part of the region represented an area 5627 km², the southern part of the region 6184 km².

Egg production off Catalonia during the spawning season attained the highest values in the northern part of the region in June and July. The highest value in the southern part of the region was recorded in June; though close, this value was nonetheless lower than the values in the north. The lowest production rates were recorded in the south in October.
Table 2. *Engraulis encrasicolus*. Monthly and total egg production in the northern and southern study areas in 1983. $D_i$ = duration of Cruise $i$ in days.

<table>
<thead>
<tr>
<th>Month</th>
<th>Northern area</th>
<th>Southern area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$D_i$</td>
<td>Egg abundance ($\times 10^3$)</td>
</tr>
<tr>
<td>April</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td>May</td>
<td>28</td>
<td>25.5</td>
</tr>
<tr>
<td>June</td>
<td>32</td>
<td>1351.6</td>
</tr>
<tr>
<td>July</td>
<td>47</td>
<td>970.3</td>
</tr>
<tr>
<td>September</td>
<td>38</td>
<td>0</td>
</tr>
<tr>
<td>October</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>Annual total ($P_a$)</td>
<td></td>
<td>44667.7</td>
</tr>
</tbody>
</table>

Relationship between spawning and the environment

Studies carried out to date have indicated that temperature is the main factor regulating the onset of spawning in anchovy (Furnestin & Furnestin 1959) and that the minimum temperature is approximately 13 °C (Fage 1920), with spawning intensifying as the temperature rises. In the Mediterranean, Aldebert & Tournier (1971) found that spawning commenced in the Golfe du Lion when the water temperature reached 14 to 15 °C, and Regner (1985) found anchovy eggs in the Adriatic from 13 to 15 °C.

For the study area as a whole, the water temperature at which anchovy eggs were collected ranged from 13.0 to 25.5 °C (Fig. 6). The temperature range in the north was the same as in the rest of the region, with eggs present in May from 13.5 °C, and 73% of positive stations recorded at temperatures between 15.0 and 20.0 °C. In the south, eggs appeared in April at temperatures between 13 and 13.5 °C on various occasions, but, unlike in the northern part of the region, the range of temperatures over which eggs were collected was wider, with 70% of positive stations recorded at temperatures between 14.0 and 22.0 °C. The difference in the duration of spawning between the 2 areas would seem to be related to a decrease in temperature. In September 1983 the surface temperature in the northern area had fallen to about 2 °C below the temperature recorded in July (Fig. 7), coinciding with the end of spawning in the area; this temperature was sustained through the month of October. In contrast, in the southern area, the temperature decrease was not as great (1 °C in September), and the temperature was still higher than the temperature in the north in July; spawning went on, though egg abundance was lower.

Turning to the relationship between spawning and salinity, anchovy is a species that is able to tolerate a broad range of salinities (Reid 1967), and eggs have been found at salinity levels between 17 and 40%.
(Demir 1968). Thus, the salinity range recorded in the study area, 29.1 to 38.2‰ (Masó & Duarte 1989), would not act as a factor limiting the spawning of this species. Nevertheless, in June 1983 a plume of fresh water (salinities of 29 to 31‰) from the Rhône River was detected at the surface in the northern part of the study area (Castellón et al. 1986), and it was associated with a large spawning area in which the highest values of anchovy egg abundance were recorded at the time. This might indicate a preference of anchovy for lower salinities, although the author believes that it is more closely related to a shift in the area of anchovy distribution southward from the Golfe du Lion in order to spawn. Adults were thus probably taking advantage of the optimum feeding conditions associated with the plume of fresh water, since phytoplankton production was higher there, as evidenced by high chlorophyll values (Masó & Duarte 1989).

**DISCUSSION**

Earlier studies of the spawning season of anchovy in the Western Mediterranean (D'Ancona 1931, Fage 1935, Demir 1965) and more specifically off the coast of Spain (Andreu & Rodríguez Roda 1951, Planas & Vives 1951, Palomera & Rubiès 1979) agreed that the species basically spawns from April to September. The results of the present study provide conclusive evidence of latitudinal differences in the duration of the spawning period off the coast of Catalonia associated with local temperature fluctuations.

Despite the difference in the duration of the spawning period, total egg production (Table 2) was similar in both spawning areas and in fact even somewhat higher in the northern area where the cycle was shorter. Since the spawning period was mainly limited to 2 mo, this means that spawning intensity was considerably higher. In the northern part of the region, anchovy seemed to spawn at the time of year when water temperature was high and the outflow from the Rhône River was still substantial (Tintoré et al. 1990), creating, in terms of stability and productivity, an environment favourable to spawning. Richardson (1981) reported similar spawning behaviour for the northern subpopulation of *Engraulis mordax* (40 to 50°N), which spawns during June and July, while the central subpopulation (30 to 40°N) spawns practically all year long. Coinciding with our observations, Parrish et al. (1983) suggested that the northern anchovy subpopulation spawning is related to the combination of greater stability in weather conditions and enrichment phenomena, in this case the influx of inland waters. Hence it appears that individual stocks have adapted their spawning strategy to a short spawning period to ensure greater egg and larval survival. The findings on larval mortality published by Palomera & Lleonart (1989), who reported lower mortality of anchovy larvae in the northern part of the region, would seem to bear this out. Furthermore, Alheit et al. (1983) for *E. ringens* and Laroche & Richardson (1980) for *E. mordax* pointed out that relative fecundity appeared to vary with latitude, and they concluded that anchovies at higher latitudes may attain higher fecundity levels. Such variability might be the cause underlying the differences in egg production observed for *E. encrasicolus* in our region, although the hypothesis of higher batch fecundity in the northern part of the region requires further substantiation.

Based on the peak spawning (i.e. egg abundance) recorded, previous studies have suggested that adults of *Engraulis encrasicolus* spawned over a specific range of bottom depths. Off the Atlantic coast of Morocco, Furnestin & Furnestin (1959) reported that peak spawning of anchovy occurred over bottom depths ranging between 25 and 100 m, with a maximum at 50 m, though never close inshore, while during the rest of the year shoals of adult anchovy were located over deeper depths (200 m) at the edge of the continental shelf. Aldebert & Tournier (1971) recorded peak spawning in the Golfe du Lion between the 60 and 120 m isobaths, contrasting with very low abundance levels inshore. Off Catalonia the depth range would thus seem to be much broader and less well-defined than in the previous cases, though here again spawning did not take place inshore. The egg distribution charts, particularly for the periods of peak spawning, clearly show the most important spawning areas where abundance values were highest to be located relatively far from shore.

Considering bottom topography in the region, with large variations in shelf width, spawning peaks did not seem to be related to an attempt by adults to seek a particular range of bottom depths for spawning. The highest abundance levels (>1000 eggs 10 m⁻²) were generally recorded from 10 to 30 miles offshore, which in this region spans a very broad range of bottom depths, from 50 to 1000 m. The presence of the shelf-slope front, which, subject to certain fluctuations in intensity, runs along the entire shelf (Font et al. 1988), suggests that anchovy may take advantage of the productivity associated with the front, particularly bearing in mind the substantial enrichment associated with the front during the peak spawning period (summer) (Estrada & Margalef 1988). Sabatés (1990a) pointed out the important role of this frontal zone in the spawning and aggregation of larvae of a number of fish species.

Spawning was clearly associated with 2 areas under the influence of the inflows of 2 large rivers, i.e. the Rhône and the Ebro Rivers. A similar association has
also been reported for anchovy in the Bay of Biscay in the vicinity of the mouth of the Loire River (Arbault & Lacroix 1977). The importance of the influx of inland waters from the Golfe du Lion became apparent in June 1983, when the highest levels of anchovy eggs and larvae were recorded in the zone covered by the surface plume of fresh water in the northern part of the region, whereas the larvae of most other fish species were located at the outer edges of this plume (Sabatés 1990b). Moreover, in the vicinity of the Ebro River delta the highest concentrations of anchovy eggs were recorded in the permanent upwelling zone described by Font et al. (1990), caused by the intrusion of slope waters onto the continental shelf.

The association of spawning by pelagic species with regions of high production, such as eastern boundary currents (Peru; California; Canary; Benguela) has been widely documented in recent years. The areas of maximum spawning by certain pelagic species, like anchovy and sardine in the North Pacific and anchovy off Namibia, are located near thermal fronts (O'Toole 1977, Lasker et al. 1981). Parrish et al. (1983) described some common environmental patterns that influence the spawning strategies of anchovys and sardine in these regions. However, no evidence of this type of behaviour had previously been reported for Engraulis encrasicolus, especially in the Mediterranean, where the hydrographic processes that underlie enrichment phenomena are smaller in scale than those active in other areas where similar linkages between spawning and environment take place.

Acknowledgements. I thank all participants on the sampling cruises for their collaboration in samples collection. I particularly thank Ms B. Moli, L. Recasens, S. Verón and Dr A. Sabatés for their assistance in sorting the material examined. Drs P. Olivari, A. Sabatés, Messers. P. Rubiés and J. Salat made valuable comments on the original manuscript. Mr R. Sacks prepared the English version. The study was supported by a grant from the Fundación Ramón Areces.

LITERATURE CITED


This article was submitted to the editor

Manuscript first received: April 30, 1991
Revised version accepted: December 16, 1991