Reproductive biology and fecundity of the Bay of Biscay anchovy population (*Engraulis encrasicolus* L.)

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SUMMARY: This review presents the results of field studies conducted between 1987 and 1992 on the reproductive biology and fecundity of the Bay of Biscay anchovy. Close to 100% of the anchovy population reach maturity during the reproductive season, although the smallest 1-year-old anchovy mature slightly later. At peak spawning, however, the reproductive output (numbers of eggs laid daily per unit body weight) of one year old anchovy is similar to that of older anchovy. Anchovy mainly spawn from 19:00 to 6:00 (GMT) with a peak at 00:00 (GMT). For the females spawning on a given night, the final maturation process of the spawning batch of oocytes starts the night before. The process of nuclear migration proceeds through the night and the first part of the following day. Oocytes start to hydrate early in the afternoon of the day of spawning. Hydration reaches its maximum intensity at dusk and in the early night. Gonads with postovulatory follicles can already be observed before dusk, indicating the start of spawning activities. Anchovy is a batch spawner with indeterminate fecundity. ‘De novo’ vitelogenesis proceeds in immature oocytes during the reproductive season. Annual fecundity is determined by both the number of eggs laid per spawning (batch fecundity) and the number of spawnings per season (frequency of spawning and duration of the spawning season). Batch fecundity presents an increasing pattern as the season advances, from ca. 200 eggs /g in April, to ca. 500 and ca. 650 eggs/g in May and June respectively. The fraction of females spawning per day ranges from 18 to 33%, and increases as the season progresses. This high spawning frequency may be related to the relatively short spawning season. Assuming a two month protracted spawning season, the total reproductive output of Bay of Biscay anchovy can range between ca 9,000 to ca. 11,000 eggs per unit gonad-free body weight (g).

**Key words:** Anchovy, *Engraulis encrasicolus*, spawning, reproductive biology, fecundity, Bay of Biscay.

RESUMEN: BIOLOGÍA REPRODUCTIVA Y FECUNDIDAD DE LA ANCHOA (*ENGRAULIS ENCRASICOLUS* L.) EN EL GOLFO DE VIZCAYA.
– Se presentan los conocimientos adquiridos sobre diversos aspectos de biología reproductiva y fecundidad de la anchoa del golfo de Vizcaya a partir de trabajos de campo llevados a cabo entre 1987 y 1992. Cerca del 100 % de los individuos de la población de anchoa alcanza la madurez durante la estación reproductiva, aunque las anchoas de un año de edad de menor tamaño maduran un poco más tarde. La anchoa pone entre las 19:00 y las 6:00 horas (GMT) con un pico alrededor de la medianoche (00:00 horas GMT). Para las hembras que van a poner una noche dada, la maduración final de la serie de ovocitos que van a ser liberados comienza la noche anterior. El proceso de migración nuclear se extiende desde comienzos de esa noche hasta la primera parte del día siguiente. A comienzos de dicha tarde, los ovocitos comienzan a hidratarse, proceso que alcanza su máximo al anochecer y primeras horas de la noche. Se pueden observar gónadas con foliculos postovulatorios ya al atardecer, indicando el comienzo de las actividades de puesta. La anchoa es un ponedor múltiple con fecundidad indeterminada. Los ovocitos experimentan vitelogenesis “de novo” durante toda la estación de puesta. La fecundidad anual es consecuencia del número de huevos puestos por hembra en cada serie (fecundidad parcial) y el número de puestas por temporada (frecuencia y duración de la puesta). Los valores de fecundidad parcial presentan un claro incremento al avanzar la temporada, desde unos 200 huevos /g en abril, a unos 500 en mayo y 650 en junio. La fracción de hembras en puesta cada día oscila entre 18 y 33 %, y aumenta al avanzar la temporada. Esta alta frecuencia puede ser consecuencia de una temporada de puesta relativamente corta. Suponiendo que la temporada de puesta dure unos 2 meses, se ha estimado una fecundidad anual total de entre 9,000 y 11,000 huevos por g de hembra (sin gónada) para la anchoa del golfo de Vizcaya.

**Palabras clave:** Anchoa, *Engraulis encrasicolus*, puesta, biología reproductiva, fecundidad, Golfo de Vizcaya.

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INTRODUCTION

Wallace and Selman (1981) described the dynamics of development and maturation of oocytes in gonads of teleost fishes. Hunter and Goldberg (1980) and Hunter and Maciewicz (1985) described those processes for the Californian anchovy, *Engraulis mordax*. These authors showed that this species is a multiple spawner with asynchronous development of oocytes: the development of oocytes during the reproductive season is a continuous process with presence of all the oocyte stages and with a new group of oocytes maturing and being released every other week or 10 days in the period of peak spawning (Hunter and Leong, 1981). As a consequence of this, the average Californian anchovy may spawn around 20 times per year, in spite of the fact that in the ovary are presented no more than 3 batches of yolked oocytes. The abundance of oocytes bigger that 0.1 mm diameter at the beginning of the reproductive season could only give place to around 10 spawnings per season. Consequently, in order to reach 20 spawning per year, recruitment of oocytes smaller than 0.1 mm to development and maturation (*de novo* vitellogenesis) must be continuous through the season, meaning that annual fecundity of this species is not fixed at the beginning of the reproductive season.

Andréu (1950) described the gonad structures of the Bay of Biscay anchovy by means of histological techniques. Cort *et al.* (1977) found distinct modes in oocyte size frequency distribution, showing that this species is a partial spawner. Vega *et al.* (1990) described the process of oocyte development and maturation using histological and histochemical criteria and a simplified scale (Hunter and Maciewicz, *op. cit.*). This scale summarise the development of oocytes in 4 classes: unyolked oocytes or oogonia, partially yolked oocytes, yolked oocytes and matured or hydrated oocytes. In addition, phases of atretic oocytes were also described. Motos (1994a) reviewed this classification and validated the criteria for aging anchovy gonadal stages. All these works demonstrated that the Bay of Biscay anchovy is a multiple spawner with asynchronous development of oocytes: *‘De novo’* vitellogenesis is a continuous process during the reproductive season and all oocyte stages are present at the same time in the ovary.

Several authors have pointed out that first maturation in anchovy occurs when they are 1-year old (Furnestin, 1945; Cort *et al.*, 1976; Lucio and Uriarte, 1990). Lucio and Uriarte (*op. cit.*) specified that males with a length of 11.0 cm and females with 11.5 cm already appeared mature. In addition, those authors reported a slightly later maturation of 1-year-old anchovies, less relevant than the delay previously reported in the literature.

Motos (1994b) who studied the gonosomatic index (GSI) evolution during the anchovy spawning season found that small anchovies were in earlier maturity stages than big ones in April, whereas all anchovy sizes sampled during May and June were in fully spawning condition.

A diel spawning cycle is an extended feature among teleosts. Night or dusk spawning has been reported to be a common pattern in Clupeoids (Blaxter and Hunter, 1982). Anchovies show diel spawning cycles with maxima of intensity at dusk or night. Those cycles have already been described for several anchovy species such as Cape anchovy, *Engraulis capensis*, (Shelton y Hutchings, 1981) and Californian anchovy, *Engraulis mordax* (Smith and Hewitt, 1985). In the case of the European anchovy, *Engraulis encrasicolus*, data on diel spawning periodicity has been reported for several Mediterranean populations (Vucetic, 1957; Demir, 1965; Regner, 1985; Palomera, 1989) and for anchovy inhabiting 196

<table>
<thead>
<tr>
<th>Author</th>
<th>Year</th>
<th>Location</th>
<th>Spawning interval</th>
<th>Peak time</th>
<th>Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soviet authors (in Demir, 1965)</td>
<td>1955</td>
<td>Black sea</td>
<td>00:00 a 04:00</td>
<td>02:00</td>
<td>-</td>
</tr>
<tr>
<td>Lisovenko and Andrianov</td>
<td>1995</td>
<td>Black sea</td>
<td>21:00 to 24:00</td>
<td>-</td>
<td>May-August</td>
</tr>
<tr>
<td>Vucetic</td>
<td>1957</td>
<td>Adriatic sea</td>
<td>19:35 a 21:35 (l.h.)</td>
<td>20:35</td>
<td>June</td>
</tr>
<tr>
<td>Varagnolo</td>
<td>1964</td>
<td>Adriatic sea</td>
<td>18:00 a 20:00 (l.h.)</td>
<td>19:00</td>
<td></td>
</tr>
<tr>
<td>Palomera</td>
<td>1989</td>
<td>NW Mediterranean</td>
<td>21:00 a 03:00 (GMT.)</td>
<td>midnight</td>
<td>Summer</td>
</tr>
<tr>
<td>Tsimenides <em>et al.</em></td>
<td>1995</td>
<td>Aegean sea</td>
<td>night</td>
<td>midnight</td>
<td>Summer</td>
</tr>
<tr>
<td>Ré</td>
<td>1984</td>
<td>Atlantic waters - Tejo estuary</td>
<td>18:30 a 23:00 (l.h.)</td>
<td>22:00</td>
<td>April</td>
</tr>
<tr>
<td>Santiago</td>
<td>1988</td>
<td>Bay of Biscay</td>
<td>22:00 a 08:00 (GMT)</td>
<td>-</td>
<td>May-June</td>
</tr>
<tr>
<td>Santiago and Sanz</td>
<td>1992a</td>
<td>Bay of Biscay</td>
<td>22:00 a 02:00 (GMT)</td>
<td>23:00-00:00</td>
<td>May-June</td>
</tr>
<tr>
<td>Motos (unpubl.)</td>
<td>1988</td>
<td>Bay of Biscay</td>
<td>20:00 a 02:00 (GMT)</td>
<td>midnight</td>
<td>June</td>
</tr>
</tbody>
</table>
estuaries along the Portuguese Coast (Ré, 1984). As a rule, they spawn at dusk or at night, with peaks between 18:00 and 4:00 hours (GMT) (Table 1).

This paper reviews the current knowledge on the reproductive biology of the Bay of Biscay anchovy. In addition to an extended literature review, the work is mostly based on the findings achieved during egg and adult surveys conducted from 1987 to 1992 aimed at applying the Daily Egg Production Method (DEPM) for anchovy assessment purposes. In the last few years, several studies were implemented in order to obtain fishery-independent estimates of the size of the Bay of Biscay anchovy population. In 1987, exploratory surveys were conducted to improve the knowledge on anchovy reproductive biology and to check the suitability of this population to be assessed by the DEPM (Parker, 1980) (Santiago and Eltink, 1988; Sanz and Uriarte, 1989).

Consequently, DEPM surveys were carried out from 1988 to 1992 (Santiago and Sanz, 1992a, 1992b; Sanz et al., 1992; Motos and Santiago, 1990; Motos and Uriarte, 1991, 1992, 1993; Motos, 1994a).

**METHODOLOGY**

Adult anchovy samples for fecundity estimation were obtained following two different sampling schemes (Table 2). A series of adult surveys were carried out from 1989 to 1992 to estimate adult reproductive parameters with DEPM stock assessment purposes. The surveys followed a judgement sampling scheme (Picquelle and Stauffer, 1985) with sampling intensity roughly proportional to population biomass. In addition, opportunistic samples were systematically obtained on board commercial fishing vessels during peak spawning in these years.

**TABLE 2. – Summary of sampling strategy for adult anchovy in 1989-1992 DEPM surveys.**

<table>
<thead>
<tr>
<th>SURVEY</th>
<th>VESSELS</th>
<th>DATES</th>
<th>SAMPLES</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOMAN - 8905</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Egg cruise</td>
<td>“IBAIZABAL DOS”</td>
<td>10-21 May</td>
<td>317</td>
</tr>
<tr>
<td>Adult cruise</td>
<td>“SIEMPRE ONGI ETORRI” (commercial purse-seiner)</td>
<td>19-22 May</td>
<td>6</td>
</tr>
<tr>
<td>BIOMAN - 8906</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg cruise</td>
<td>“IBAIZABAL DOS”</td>
<td>14-25 June</td>
<td>437</td>
</tr>
<tr>
<td>Adult cruise</td>
<td>“SIEMPRE ONGI ETORRI” (commercial purse-seiner)</td>
<td>20-23 June</td>
<td>4</td>
</tr>
<tr>
<td>Opportunity sampling</td>
<td>Commercial purse-seine fleet and research vessels</td>
<td>May</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>25</td>
</tr>
<tr>
<td>1990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOMAN - 9005</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg cruise</td>
<td>“IBAIZABAL DOS”</td>
<td>4-15 May</td>
<td>525</td>
</tr>
<tr>
<td>Adult cruise</td>
<td>“DIVINO JESUS DE PRAGA” (commercial purse-seiner)</td>
<td>6-11 May</td>
<td>18</td>
</tr>
<tr>
<td>BIOMAN - 8906</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg cruise</td>
<td>“IBAIZABAL DOS”</td>
<td>29 May-15 June</td>
<td>536</td>
</tr>
<tr>
<td>Adult cruise</td>
<td>“DIVINO JESUS DE PRAGA” (commercial purse-seiner)</td>
<td>31 May-13 June</td>
<td>18</td>
</tr>
<tr>
<td>Opportunity sampling</td>
<td>Commercial purse-seine fleet and research vessels</td>
<td>4 May-15 June</td>
<td>31 (May)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>25 (June)</td>
</tr>
<tr>
<td>1991</td>
<td></td>
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<tr>
<td>BIOMAN - 91</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg cruise</td>
<td>R/V “CORNIDE DE SAAVEDRA”</td>
<td>16 May-7 June</td>
<td>538</td>
</tr>
<tr>
<td>Adult cruise</td>
<td>R/V “CORNIDE DE SAAVEDRA”</td>
<td>16 May-7 June</td>
<td>3</td>
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<tr>
<td></td>
<td>R/V “GWEN DREZ” (commercial purse seiner)</td>
<td>28 May-3 June</td>
<td>8 (North area)</td>
</tr>
<tr>
<td></td>
<td>“DIVINO JESUS DE PRAGA” (Commercial purse seiner)</td>
<td>22-26 May</td>
<td>10 (South area)</td>
</tr>
<tr>
<td>Opportunity sampling</td>
<td>Commercial purse-seine and pelagic trawl fleets</td>
<td>14 May-12 June</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>1992</td>
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<tr>
<td>BIOMAN - 92</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg cruise</td>
<td>R/V “CORNIDE DE SAAVEDRA”</td>
<td>16 May-13 June</td>
<td>617</td>
</tr>
<tr>
<td>Adult cruise</td>
<td>R/V “CORNIDE DE SAAVEDRA”</td>
<td>8 May-13 June</td>
<td>20</td>
</tr>
<tr>
<td>Opportunity sampling</td>
<td>Commercial purse-seine Fleet and Research vessels</td>
<td>14 May-12 June</td>
<td>29</td>
</tr>
</tbody>
</table>
Each adult sample, consisting of at least 1 kg of anchovies (the actual number ranged between 35 and 115 individuals) was randomly collected. Immediately after catching, fish were selected, and, after opening their body cavities, they were introduced into jars with 4% buffered formaldehyde solution for fixation. Non random samples of hydrated females were collected also in stations where this gonadal stage was available.

At the laboratory, total length, total and gonad weight and sex were determined. Correction factors were applied to convert formalin weight to wet weight. Total weight of hydrated females was corrected for the increase of weight due to hydration of ovaries. Data on gonad-free-weight and correspondent total weight of non hydrated females from the specific survey was fitted by a linear regression model. Total weight of hydrated anchovies was then calculated by applying the above regression to their gonad-free-weight (Sanz et al., 1992; Santiago and Sanz, 1992a; Motos and Santiago, 1990; Motos and Uriarte, 1991, 1992, 1993).

Female gonads collected in the night of spawning were categorized into three groups according to the gonadal classification criteria given by Hunter and Macewicz (1985) and described for the Bay of Biscay anchovy by Motos (1994a):

1) females with gonads showing hydrated eggs and no postovulatory follicles (POFs). Those individuals were caught in the hours immediately before spawning (from noon to midnight).

2) females with gonads showing both hydrated oocytes and POFs. Those individuals were caught during the spawning act (19:00 to 5:00 hours GMT).

3) females with gonads exclusively showing brand-new POFs. Those individuals were caught in the hours immediately after spawning. Females with POFs older than 7 hours were classified as day-1. In this way, the category was arbitrarily ended at 7:00 hours GMT.

In addition, in order to further describe the diel cycle of anchovy mature ovaries, gonads with oocytes in the nuclear migration stage were also identified. Early migration corresponds to the beginning of nuclear displacement towards the animal pole. Late migration corresponds to gonads in the stage immediately previous to hydration, showing the nucleus already in the animal pole and with the nuclear membrane still apparent.

Anchovy eggs collected in plankton samples during anchovy DEPM cruises from 1988 to 1992 (Motos et al., 1996) were classified into developmental stages (Moser and Alshtrom, 1985). The incidence of stage I eggs by hourly periods was computed. All the estimations were made with reference to GMT hours.

Spawning frequency (S), i.e. the proportion of females spawning per day, was estimated by the incidence of females with day-1 POF’s, according to the methodology given by Hunter and Macewicz (1985):

- day-0 POF females were those that spawned the night of the capture (0 to 6 hours old),
- day-1 POF were those females that spawned the night before capture (6 to 30 hours old), and
- day-2+ POF were those that spawned 2 or more nights before capture (older than 30 hours).

After weighing and storing in formaline, ovaries were histologically processed. They were embedded in resin and sections were cut at 3 mm and stained with haematoxylin-eosin following standard techniques. These histological slides were screened under the microscope and classified into the above gonadal stage categories following the specific criteria for Bay of Biscay anchovy ovaries developed by Motos (1994a).

For the estimation of batch fecundity, i.e. number of eggs per spawning batch, a set of females with hydrated ovaries was examined. Three pieces of approximately 50-100 mg were removed from different parts of the ovary, weighed with a precision of 0.1 mg and the number of hydrated oocytes counted (Hunter et al., 1985). Previous investigations showed that 3 tissue samples per ovary are adequate to get good precision in the final batch fecundity estimate, and that location of subsamples within the ovary does not affect the estimate (Sanz and Uriarte, 1989). The relationship between batch fecundity and gonad-free female was estimated using linear regression techniques. The fitting lines were compared using ANCOVA (SAS Institut Inc., 1988) to search for spatio-temporal differences in this relationship. In addition, an average figure of relative batch fecundity (number of eggs per spawning batch per unit gonad-free female weight) was calculated for each combination of year and month.

Mean and variance of spawning frequency were estimated following equation (5) of Picquelle and Stauffer (1985). Occasionally a station produced a very small catch resulting in a small subsample size. To reflect the actual size of the station, small samples were given less weight in the estimate. A weighting factor was used, which equalled 1 when the number of mature females in station $i$ ($M_i$) was 25 or greater and equalled $M_i/25$ in other cases. Sta-
tistics (mean and variance) for relative batch fecun-
dity (numbers of eggs laid per female gram per
batch) were calculated from the set of hydrated
oocytes collected in each particular survey.

RESULTS AND DISCUSSION

First maturation.

A total of 5,300 anchovy ovaries were collected
during spring cruises carried out in the period 1987-
1992 and classified by histological maturity stages.
This range is almost identical to the length range of
the international catches of the Bay of Biscay
anchovy during the 2nd quarter (Anon., 1995). The
mean size of 1-year-old anchovies for the spring
period 1987-1994 was 14.3 cm (se=1.4) (Uriarte,
pers.com.). Consequently, 95% of the 1-year-old
anchovy caught by the commercial fleet are within
14.3±2.8 cm, and only 2.5% are smaller than 10.5
cm. Since only 0.2% of the ovaries analysed were
immature (ovaries with exclusively unyolked
oocytes) (Table 3), it can be assumed that nearly 100
% of the female anchovies were mature during the
spawning season. In addition to this, shoals of juve-
nile anchovy are not found in the usual nursery areas
of the Bay of Biscay during May and June (Lucio
and Uriarte, 1990; Motos, 1994b). Consequently, it
can be stated that nearly all the females of the Bay
of Biscay anchovy stock reach maturity in one year.

This fact leads to the conclusion that estimates of
anchovy spawning biomass carried out during May-
June are almost equivalent to the total biomass of
the stock.

Daily dynamics of the spawning ovary

Females with gonads in the hydrated stage (hydrat-
ed oocytes) start to appear at noon (Fig. 1). The inci-
dence of this stage increases towards 17:00 hours
(GMT). Spawning females presenting both hydrated
oocytes and POFs are collected as early as 19:00 hours
(GMT). The incidence increases from this moment,
reaching a peak between 23:00 and 00:00 hours
(GMT) and gradually decreasing afterwards. No
spawning females occur after 6:00 hours (GMT).
Females with gonads exclusively showing brand-new
POFs start to appear at 19:00 (GMT), and reach its
maximum incidence after 00:00 hours (GMT).
Ovaries with oocytes showing early nuclear
migration are more frequently observed from 21:00

<table>
<thead>
<tr>
<th>Unyolked oocytes</th>
<th>Partially yolked</th>
<th>Yolked oocytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage</td>
<td>0.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Number</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td>Range (cm)</td>
<td>11.8-17.4</td>
<td>12.1-17.4</td>
</tr>
</tbody>
</table>

Fig. 1. – Incidence of the appearance of Day-0 gonadal stages during the day. Data was collected in
adult surveys for assessment of the Bay of Biscay anchovy population and correspond to a total of
5,211 gonads processed histologically.
hours of the night prior to spawning and become prevalent during the night (Fig. 2). Late nuclear migration stages are most abundant during the morning and start to diminish afterwards, as the ovary becomes hydrated. The incidence of these stages are minimum during the afternoon, between 15:00 and 20:00 hours (GMT), i.e. the hours of maximum prevalence of hydrated ovaries.

When observing the incidence of newly spawned eggs (stage I) in plankton samples (Fig. 3), maximum values occur from 21:00 to 4:00 hours (GMT) with a peak between 23:00 and 02:00 hours.

The evolution of the incidence of gonadal stages in spawning females allows us to describe the diel dynamics of the ovary (Fig. 4). The final maturation (hydration) process starts the night before for the females going to spawn a given night, and last for approximately 24 hours. At the beginning of the night before spawning, nuclear migration starts in the batch of oocytes to be released. This process extends along the whole night. Nuclear disintegration start at the beginning of the afternoon, and hydration starts shortly after. This process slowly proceeds during the afternoon.

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**Fig. 2.** Incidence of appearance of nuclear migration stages. Early migration corresponds to the beginning of nuclear displacement towards the animal pole. Late migration corresponds to gonads in the stage immediately previous to hydration, showing the nucleus already in the animal pole and still with the nuclear membrane.

**Fig. 3.** Incidence of stage I anchovy eggs (stage previous to the first cellular division) in plankton samples collected in anchovy egg cruises from 1988 to 1992.
but the oocytes eventually swell at the end of the afternoon (21:00 hours GMT). Then, they can be observed brand-new POFs and hydrated oocytes in the gonads, indicating that the individuals presenting them were caught during the spawning act. Spawning activities proceeds up to well into the night but with maximum intensity in the period from 23:00 to 24:00 hours GMT.

A similar pattern is found when the occurrence of newly fertilised egg is analysed. Available information on the duration of the period from fertilisation to first elevage indicates that stage I eggs last less than 1 hour at the temperatures prevalent in these egg cruises (Smith and Hewitt, 1985). Incubation experiments at sea gave evidence that the first cellular cleavages were observed close to 1 hour after fertilisation (Motos, 1994a). Consequently, the spawning peak will take place around 1 hour before what is indicated from the incidence in plankton samples of stage I eggs.

Both data set presented here allow us to conclude that anchovy spawning is centered around midnight (00:00 hours GMT). This is in concordance with previous reports for this same population (Santiago, 1988; Santiago and Sanz, 1992a; Motos and Santiago, 1990) from egg cruises in 1987 and 1988. They also coincide with the spawning pattern found for the anchovy population inhabiting Western Mediterranean waters (Palomera, 1989).

Available information on fish behaviour provides some clues on daily activity patterns of pelagic fishes. In general, adult fishes ascend to surface waters during the night and descend to deeper waters at dawn (Shelton and Hutchings, 1981). For the Bay of Biscay anchovy, ‘in situ’ observations reveal a similar daily activity pattern (Massé, 1996). This pattern also happens during spawning. Different authors have remarked the ecological advantages of nocturnal spawning: Fish shoals spawning at night in surface waters have less risk of being predated by sea birds, fishes, etc. Hubson and Chess (1978), studying reef fish communities, observed egg densities seven times bigger at night than during the day and suggested the possibility of nocturnal spawning to be an adaptation to allow for dispersion of eggs during the beginning of dark hours, when waters are relatively free of predators. In addition, Shelton and Hutchings (op. cit.) added that the behaviour pattern described above can minimize predation on adults as they migrate to deep waters during the day.

**Spawning frequency (S).**

Table 4 shows the estimates of spawning frequency (S) in the Bay of Biscay anchovy population for different months of the reproductive season over the period 1987-1992. An estimate of spawning frequency at the beginning of the reproductive period is...
available from April 1989, showing that the value is lower at the beginning of the reproductive season. In May, S values range from 0.19 to 0.32, indicating that females were spawning every other 3 to 5 days average. These values remained at that level in June (0.23-0.32). Data is scarce after this month. Average spawning frequency of S=0.31 obtained from three samples of small anchovy taken during the 2nd fortnight of July 1988 (Sanz, pers. comm.) also indicates that spawning frequency remains at high values until July, when the reproductive season is well advanced.

As a consequence of this high mean spawning frequency some females should present a very high spawning frequency, i.e., spawning every other day or every two other days. Histological evidence of these were found when more that one reproductive stage occurred in the same ovary, e.g., hydrated oocytes and early migratory nucleus stages, or hydrated oocytes and day-1 POFs, or new POFs and migratory nucleus stages, or migratory nucleus and 2-day-old POFs (Fig. 5). This shows that the final stage of oocyte maturation, i.e., from nuclear migration through hydration onto the release of eggs, can proceed in some females just 24 hours after the preceding one. However, the occurrence of three different reproductive stages in the same ovary is almost nil, showing that daily spawning can last as much as two or exceptionally three days.

The estimates of spawning frequency obtained for the Bay of Biscay anchovy are rather high in comparison to values found for other Engraulididae (Alheit, 1993). It is known that actively spawning anchovy (Day 0 females) are oversampled during the hours of spawning (Santiago and Sanz, 1992a) as it happens in other anchovy populations (Alheit, 1985; Picquelle and Stauffer 1985). Due to this fact, the incidence of exclusively Day-1 females is used to estimate spawning frequency. Alheit (op. cit.) suggested that these high values of spawning frequency may result from an adult sampling scheme based on commercial fishing. In addition to actively spawning anchovies (Day 0), this sampling procedure would also oversample females which spawned the day before (Day 1). However, no major differences were found when comparing spawning fraction values from samples collected by commercial purse-seiners to the values from samples collected by purse-seine in directed cruises in 1990 and 1991. Furthermore, the spawning frequency of females taken by commercial purse seiners and those taken by pelagic trawlers were similar. No significant differences (p<0.05) were found in a one way ANOVA (factor = type of gear) for the different combinations of areas and months of particular years. Estimates of S obtained from the incidence of ‘Day-1’ females are similar regardless of the different sampling type, suggesting that they are not biased and reflect the true fraction of females spawning each night.

The high spawning frequency might be related to the relatively short spawning season in which the species accomplishes its annual reproductive potential (Motos et al., 1996). In addition to this, they might also be a consequence of the relatively high temperature prevalent in the Bay of Biscay during the anchovy spawning season, where sea surface temperature ranges from 15°-18° in May to 20°-24°C in July (Solá et al., 1990; Motos et al., 1996). Alheit (1993) reported that tropical species have a very high spawning fraction in relation to high ambient temperatures.

The variation of spawning frequency throughout the season found for the Bay of Biscay anchovy is similar to that found for other anchovy species (Alheit, 1993), although the reported drop at the end of the reproductive season in other species is not apparent in our data. It seems possible that the Bay of Biscay anchovy keeps high reproductive levels up to the end of the season. The lack of data from this part of the season impedes us from describing how the reproductive process ends.

Concerning atresia, the resorption of oocyte contents in any developmental phase, this phenomenon was not deeply analysed. From the observations made during the study, it seems that atresia is not a

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<tbody>
<tr>
<td>APRIL</td>
<td>0.18 (0.28)</td>
<td>0.29 (0.04)</td>
<td>0.18 (0.28)</td>
<td>0.26 (0.10)</td>
<td>0.28 (0.05)</td>
<td>0.23 (0.17)</td>
</tr>
<tr>
<td>MAY</td>
<td>0.32 (0.18)</td>
<td>0.29 (0.04)</td>
<td>0.26 (0.10)</td>
<td>0.28 (0.05)</td>
<td>0.23 (0.09)</td>
<td>0.32 (0.30)</td>
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significant factor during the period of maximum spawning. Less than 0.5% of the individuals analyzed showed any sign of atretic condition in May-June. The incidence of atresia was more important only in 1991. In that year, winter environmental conditions, i.e. vertical homogeneity and low (13°-14°C) surface temperatures, were still prevalent during the first part of the cruise period (15-20 May) (Motos et al., 1996).

**Fecundity**

Batch fecundity-female weight relationships of Bay of Biscay anchovy were estimated from samples of hydrated females collected from 1989 to 1992. Figure 6 shows the relationships found in April, May and June 1989, reflecting a significant increase of batch fecundity in time (p<0.05). The same pattern was also found in the 1988 DEPM survey when comparing the 1st and 2nd fortnight of May (Santiago and Sanz, 1992a) and in 1990 between May and June surveys (Figs. 7a and b). This increase in batch fecundity is a common feature in Clupeoids (Blaxter and Hunter, 1982) and it might be associated with reduction in egg size, linked to the progressive increase of the temperature in the spawning area as the season goes on (Santiago and Sanz, op. cit.).

Table 5 shows the estimates of specific batch fecundity of females (number of eggs spawned per batch and gram of females) of the Bay of Biscay anchovy in different months of the reproductive season of the period 1987-1992. The figures obtained in these surveys are within the range of the estimates

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<tbody>
<tr>
<td>APRIL</td>
<td>467 (0.31)</td>
<td>498 (0.24)</td>
<td>302 (0.42)</td>
<td>422 (0.28)</td>
<td>427 (0.37)</td>
<td>503 (0.23)</td>
</tr>
<tr>
<td>MAY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>JUNE</td>
<td>646 (0.22)</td>
<td>662 (0.34)</td>
<td>542 (0.35)</td>
<td>542 (0.25)</td>
<td>523 (0.35)</td>
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**Fig. 5.** Anchovy ovary showing day-0 POFs and oocytes in the nuclear migration stage at the same time.
found in other Engraulidae (Alheit, 1993). The within years variability found in specific batch fecundity ranged between 202 (cv=42%) eggs in April to 662 (cv=32%) in June, showing a strong increase of batch fecundity as the season advances. This fact stresses the importance of doing egg and adult cruises concurrently within DEPM surveys. When considering the same month of reference (May), variations among years appear much smaller. Specific batch fecundity ranged between 422 (cv=28%) and 569 (cv=21%) eggs per gram of female (gonad free).

The batch fecundity regression lines obtained in May 1990 and in May 1992 presented negative intercepts significantly different from 0 (p<0.05) (Fig. 7 a and d). Therefore, small anchovies presented a lower relative fecundity than big anchovies in those months/years. This characteristic coincided in both years with a high level of recruitment and consequent high numbers of small 1 year old individual.

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**FIG. 6.** – Comparisons of batch fecundity relationships found in April, May and June 1989.

als at sea (Motos and Uriarte, 1991, 1993). On the contrary, both in 1989 and in 1991, when recruitment and hence small individuals were more scarce (Uriarte and Santiago, 1990; Motos and Uriarte, 1992), the intercepts of the batch fecundity regression lines were not significantly different from 0 (Figs. 6 and 7c). In a similar way, however, in June 1990 the intercept was no longer different from 0. In conclusion, it seems that smaller anchovies may present lower values of relative batch fecundity at the beginning of the spawning peak period (May) when abundance of young individuals is high. This suggests a density-dependent mechanism controlling the onset of first maturity. However, these differences disappear as the spawning season advances.

Motos (1994b) found a similar pattern when studying the evolution of GSI values during the 1991 and 1992 spawning seasons.

Considering the monthly increase in batch fecundity and spawning frequency variations shown before, it is possible to get an approximation of the annual realised fecundity of the Bay of Biscay anchovy. However, the duration of the spawning season remains relatively unknown due to difficulties in adult sampling near the end of it. Anyway, a tentative approach to the annual fecundity figure is showed in Table 6. In this table, it is assumed that the spawning rate does not change with fish size, since our data only shows a fish size effect on batch fecundity at the beginning of the season of years of very high recruitment, which disappear as the season advances. Therefore, assuming a 2.5 month spawning season the annual realised fecundity would range between 110,000 eggs (10 g female) and 350,000 eggs (40 g female). This range is well above of the annual fecundity range of 20,000 to 175,000 eggs, given by Cendrero et al. (1981) after counting the number of oocytes bigger than 250 mm.

Therefore, potential fecundity, calculated as the standing stock of oocytes bigger than a certain egg size, underestimates annual fecundity of Bay of Biscay anchovy. This is a batch spawner with indeterminate fecundity; for this reason, its annual fecundity should be estimated considering both batch fecundity and number of spawnings per year.

The size of the Bay of Biscay anchovy is one of the biggest among the reported size at age of anchovy species. This anchovy grows very fast during the first year of life, reaching a mean length of 14.3 cm (se=1.4) for the 1st birthday (spring of the year next to birth) (Uriarte, pers. com.). This fast growth could explain the lack of size effect on the spawning rate for this species. The gonad maturation process (vitelogenic growth) starts with the beginning of feeding after the winter rest (Lisovenko and Adrianov, 1996), although feeding of the preceding year can provide a portion of the energy necessary for the metabolic processes related to maturation and reproduction (Hunter and Leong, 1981). It seems likely that 1-year-old Bay of Biscay anchovy gets a size enough to be able to catch the sufficient quantity of food to supply energy for reproduction at the same levels as older anchovy. Only the slow growing individuals or those coming from the latest spawnings can not reach, by the first birthday, a size large enough to ensure adequate gonad development. Those individuals would form the portion of small individuals with a later maturation and lower batch fecundity at the beginning of the season recorded in some years (1990, 1992).

### Table 6. Level of annual realised fecundity of the Bay of Biscay anchovy based on actual knowledge of the reproductive biology of the population.

<table>
<thead>
<tr>
<th>Month</th>
<th>S</th>
<th>F</th>
<th>duration</th>
<th># spawnings</th>
<th>Total F</th>
<th>duration</th>
<th># spawnings</th>
<th>Total F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>eggs/g</td>
<td>days</td>
<td></td>
<td>eggs/g</td>
<td>days</td>
<td></td>
<td>eggs/g</td>
</tr>
<tr>
<td>April</td>
<td>18%</td>
<td>200</td>
<td>0</td>
<td>0</td>
<td>15</td>
<td>3</td>
<td>540</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>25%</td>
<td>500</td>
<td>31</td>
<td>8</td>
<td>3,875</td>
<td>31</td>
<td>3</td>
<td>3,875</td>
</tr>
<tr>
<td>June</td>
<td>25%</td>
<td>650</td>
<td>30</td>
<td>8</td>
<td>4,875</td>
<td>30</td>
<td>8</td>
<td>4,875</td>
</tr>
<tr>
<td>July</td>
<td>25%</td>
<td>650</td>
<td>15</td>
<td>4</td>
<td>2,438</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>TOTALS</td>
<td></td>
<td></td>
<td>76</td>
<td>20</td>
<td>11,188</td>
<td>76</td>
<td>19</td>
<td>8,750</td>
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1-1-year-old anchovies up to 140 mm long.

2-Anchovies bigger than 140 mm long or older that 1-year-old.
Hunter and Leong (1981) estimated that northern anchovy, *Engraulis mordax*, could spawn about 20 times per year. Assuming again that the spawning season of Bay of Biscay anchovy may last on average 2.5 months for all age categories and considering the monthly variations in *S*, anchovy could spawn about 19-20 times in a year, which is close to the estimate for northern anchovy (Table 7).

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The DEPM surveys on Bay of Biscay anchovy from 1987 to 1992 have involved a considerable amount of work, in which, in addition to the author, almost the entire staff of the Fisheries Resource Department of AZTI collaborated to some extent. Josu Santiago and Andrés Uriarte worked and discussed with the author many of the issues, their collaboration being fundamental to the work. In addition to them, I would like to express my gratitude to P. Lucio, A. Sanz (scientists); Inma Martin, I. Rico, N. Uriondo and A. Zamakona (technicians), J. Antxustegui and J.P. Santiago (fishermen).

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