REPRODUCTIVE CYCLE AND BATCH FECUNDITY OF THE BAY OF BISCAY ANCHOVY (*ENGRAULIS ENCRASICHOLUS*) IN 1987

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ABSTRACT

In the 1980s, the anchovy fishery of the Bay of Biscay suffered a deep decline, with landings reaching historical low levels. A revision of the stock management is needed. Understanding the reproductive biology of the anchovy is essential for the rational management of the fishery. This study examines the reproductive cycle and the batch fecundity of this species.

The spawning season for the Bay of Biscay anchovy was found to be from April to July, with a peak spawning period in May and June. The estimate of mean relative batch fecundity, 517 eggs per body gram, is within the range of estimates reported for the Peruvian anchovy and the northern anchovy.

RESUMEN

En la década del 80, la pesquería de la anchoveta del Golfo de Vizcaya ha experimentado un pronunciado declive, alcanzando sus capturas valores mínimos históricos. Por ello, resulta necesario una revisión del manejo del stock.

Para lograr una ordenación piscícola racional es esencial comprender la biología reproductora de la anchoveta. Este estudio examina el ciclo reproductor y la fecundidad parcial de esta especie.

La temporada de desove para la anchoveta del Golfo de Vizcaya se extiende desde abril a julio, alcanzando un máximo en los meses de mayo y junio. La fecundidad relativa media por desove parcial, 517 huevos por gramo de hembra, se halla dentro del rango de valores publicados para la anchoveta del Perú y la anchoa del norte de California.

INTRODUCTION

An important anchovy fishery has traditionally existed in the Bay of Biscay. This fishery is accessible during the reproductive period, when the anchovy migrate from the northern cold waters of the bay to the south and southwest, coinciding with the water's spring warming. The anchovy spawn in an area south of 47°30'N and east of 4°W (figure 1), all along the Spanish and French continental shelf, as well as in oceanic waters.

Landing levels reached a maximum of 85,000 MT in the 1960s. The value of this fishery is due to the high price that anchovy brings in the market, since it is a popular food.

For the last several years the anchovy fishery has been suffering a serious crisis, with a deep decline in catches (figure 2). From 1981 to 1987, the mean annual landing was 14,000 MT. This enormous decline since the 1960s has been accompanied by a gradual decrease of the fishing fleet. Nevertheless, a substantial fleet remains, and suffers economically from the diminished anchovy resource. In 1987, 269 Spanish purse seines dedicated half of their annual fishing activity to the capture of this species. From the French side there were 9 purse seines and 42 pelagic trawls.

In 1988, for the first time, the Bay of Biscay anchovy was included among the species that are sub-

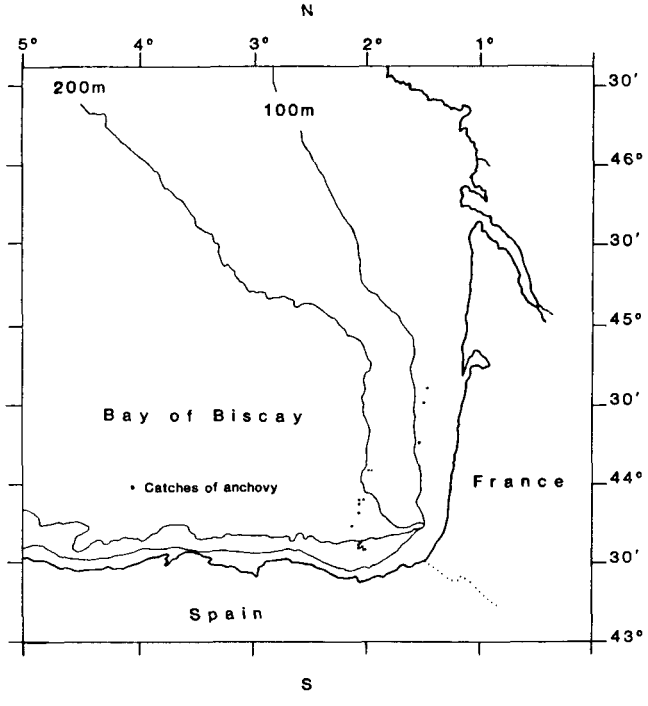

Figure 1. Anchovy spawning area in the Bay of Biscay, and location of anchovy catches for this study.

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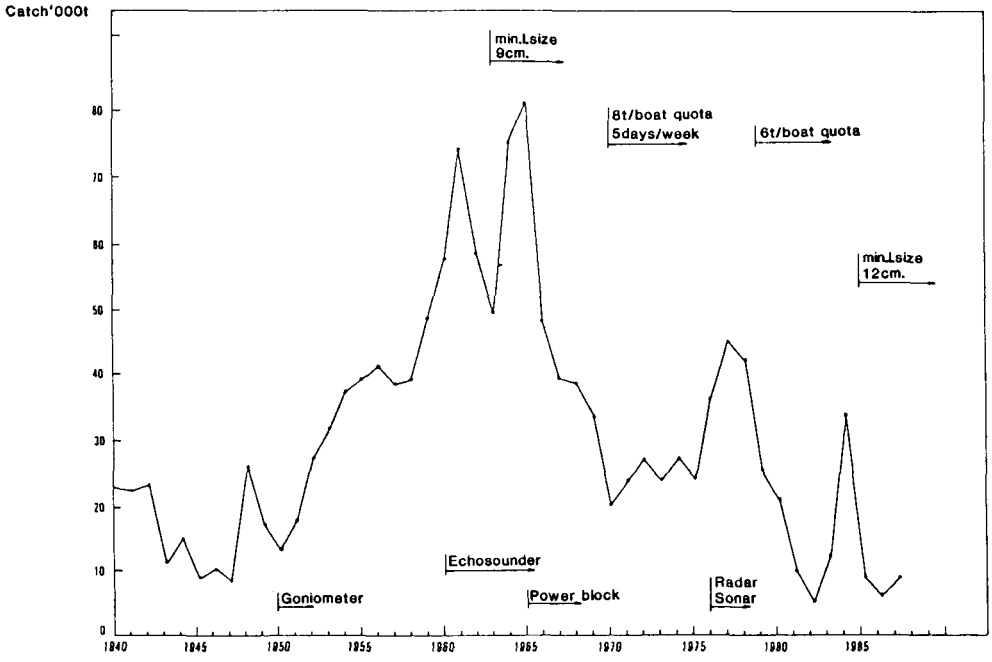

Figure 2. Historical evolution of anchovy fishery management (from Uriarte and Astudillo 1987).

ject to assessment by the International Council for the Exploration of the Sea (ICES). The state of the fishery was discussed, and there was concern that the stock may have collapsed (Anon. 1988), because biomass and recruitment levels are very low (Uriarte and Astudillo 1987). But there are great uncertainties because of the lack of precision in current stock estimates. The Council acknowledged the urgent need for more precise estimates.

Taking into account the studies made in other anchovy species from the same genus (Alheit et al. 1983), and similar studies on small pelagic species from European waters (Alheit 1987), it is now accepted that the Bay of Biscay anchovy has indeterminate fecundity (Anon. 1988).

The egg production method (EPM) of Parker (1980) is currently the best method for assessing stock size in indeterminate spawning fishes like the anchovy. This method is used to calculate the spawning biomass with a daily estimate of production and fraction spawning (Hunter et al. 1985).

It is the goal of the Oceanographic Investigation Service of the Basque Government to apply this method to the Bay of Biscay anchovy in the near future. During the 1987 fishing season, one of our objectives was to develop the necessary techniques (sampling, histology, etc.) to obtain estimates of the different EPM parameters, and to determine some of them, such as batch fecundity.

It is preferable to apply the EPM during the peak of spawning activity. To determine the peak spawning period, it is necessary to examine the gonadal maturity cycle. The first part of this paper describes this subject; in the second part we test several assumptions of ovary subsampling and provide preliminary data on the batch fecundity of this species.

METHODS

Gonad Maturity Cycle

During the 1987 fishing season, we studied the maturity cycle to determine the spawning season and the peak spawning period. Fifty-one samples averaging 44 anchovies were collected from the landings. After the main spawning and catching season, in spring, the number of samples obtained drops considerably (table 1).

TABLE 1
Sampling Summary for the Gonad Maturity Cycle

Month	March		April		May		June		July		October		November	
Day of month	1–15	16–30	1–15	16–30	1–15	16–30	1–15	16–30	1–15	16–30	1–15	16–30	1–15	16–30
Number of samples	1	4	7	9	4	8	5	5	0	3	0	2	3	0
Mean number of anchovies per sample	13	49	49	36	42	48	40	50		26		63	52	

Specimens were measured, total length (1 mm), and weighed (0.1 g). Both ovaries were excised, weighed (0.01 g), and classified according to a modified Holden and Raitt (1974) maturity index with seven stages: immature, virgin, early maturity, mature, spawning, partial postspawning, and final postspawning.

To simplify the analysis, these seven stages were grouped into three categories that included immature and virgin fish (stages 1 and 2); early maturity fish (stage 3); and mature, spawning, and postspawning fish (stages 4 to 7). Monthly percentages of the specimens in each group were calculated, for both males and females, to provide a preliminary estimate of size and endurance. The maturity cycle was also followed by the gonadosomatic index(GSI = gonad weight/gonad-free weight), males and females together.

Batch Fecundity

Twenty opportunistic collections of anchovy were taken at night from mid-April to late May 1987 (table 2 and figure 1), aboard several commercial purse seines of the Basque Country fleet.

After each set, hydrated females, which were identified by a swollen body cavity, were saved whenever encountered, according to a length-stratified sampling scheme that included females from 13 to 19 cm. We tried to include at least 10 specimens per cm increment in the total number of samples, so that the maximum number of different weights was covered.

The body cavity of freshly collected hydrated females was slit open along the side, and fish were preserved in buffered 4% Formalin. We preserved 3 adult anchovies per half-liter of Formalin (Hunter 1985).

TABLE 2
Summary of the Tows

Number	Date	Hour	Position	
			Lat. N	Long. W
1	29–4–87	01.00	44°07′	2°00′
2	29–4–87	02.00	44°07′	2°05′
3	6–5–87	02.30	44°18′	1°58′
4	6–5–87	05.30	44°31′	1°48′
5	7–5–87	01.00	44°38′	1°46′
6	18–5–87	20.30	43°45′	2°19′
7	19–5–87	20.30	43°50′	2°11′
8	19–5–87	08.15	43°54′	2°10′
9	20–5–87	23.30	43°34′	2°03′
10	21–5–87	01.30	43°36′	2°05′
11	21–5–87	03.45	43°34′	2°03′
12	21–5–87	06.30	43°40′	2°08′
13	25–5–87	22.00	43°53′	2°10′
14	26–5–87	03.00	43°49′	2°11′
15	26–5–87	01.45	43°49′	2°11′
16	26–5–87	04.00	43°49′	2°11′
17	26–5–87	05.00	43°53′	2°04′
18	26–5–87	24.00	43°37′	2°08′
19	27–5–87	02.00	43°35′	2°05′
20	27–5–87	04.15	43°35′	2°05′

At the laboratory, the hydrated females were blotted dry, measured to the nearest mm (total length), and weighed to the nearest 0.1 g. Then the ovaries were removed, blotted dry, weighed to the nearest 0.01 g, and placed in the Formalin solution.

Female weights and lengths were corrected for the effects of preservation during the two months of storage; 4% was subtracted from the weight value, and 3% was added to the length value (Hunter 1985).

All the ovaries were analyzed histologically to check for the presence of postovulatory follicles. Hydrated females with postovulatory follicles were rejected.

We have estimated the batch fecundity for the Bay of Biscay anchovy by the hydrated oocytes method (Hunter and Goldberg 1980; Hunter et al. 1985). One subsample each was sectioned from the anterior, middle, and posterior thirds of the biggest ovary. Samples were weighed (0.1 mg) and vialed for microscopic examination. Hydrated oocytes were identified and counted for each subsample.

Batch fecundity was determined from the mean number of hydrated oocytes per unit weight of the sample and the ovary weight.

Statistical Analysis. The hydrated oocytes method for estimating batch fecundity assumes that the oocytes are equally distributed along the ovary (Alheit et al. 1983). Before applying this method, we verified this assumption for the Bay of Biscay anchovy.

Therefore, we tested the effects that position of the ovary subsample and lobe of the ovary might have on the batch fecundity estimate. We estimated the ovarian density of hydrated oocytes (number of hydrated oocytes per gram ovarian tissue) in six subsamples (three from different locations in each ovary) in 25 females. A mixed trifactorial ANOVA was used, with two fixed factors — ovary (right and left) and position of the ovary subsample (anterior, middle, and posterior) — and one random factor — specimens (Sokal and Rohlf 1981).

The effect of position of the ovary subsamples inside the ovary was analyzed for 49 females. A mixed bifactorial ANOVA was used.

The optimum number of subsamples was determined according to the methods developed by Hunter et al. (1985), in which the optimum number of subsamples is the one that yields the better estimate of the variance (σ_A^2) associated with the model that relates batch fecundity (F) and body weight

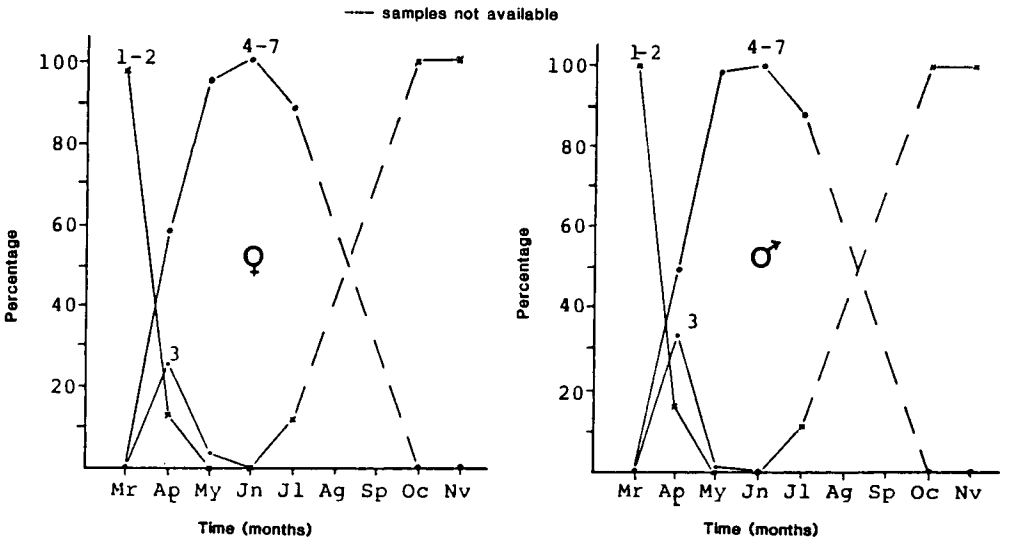

Figure 3. Monthly percentages of female and male grouped maturity stages during 1987 (1–2, immature; 3, maturing; 4–7, mature).

(W) when all eggs are counted. For a linear model (which fit the data, table 8):

$$F = f(W) + a$$

the error term (a) has a mean equal to 0, and a variance equal to σ_A^2. When the number of hydrated eggs in a batch (F) is not counted, $f(W)$ are fitted to the estimated batch fecundities ($\hat{F}$) calculated from m ovarian subsamples:

$$\hat{F} = f(W) + a_i + e_i$$
$$= f(W) + \xi_i$$

the variance around the regression line (σ_ξ^2) based upon data set ($\hat{F}$, W_i) comprises two variance components: σ_A^2 and σ_e^2, the within-ovary variance. The principal statistical parameter to determine the optimum number of subsamples is $\theta = \sigma_e^2/\sigma_A^2$ (Lo et al. 1986), the ratio of the two error sources that determine the final error of the regression line. θ is a measure of the relative variability within tissue samples. The ratio of σ_ξ^2 (the real variance observed) and σ_a^2, i.e., $K = \sigma_\xi^2/\sigma_A^2$ evaluates the adequacy of the sample size, as compared to estimating batch fecundity by counting all eggs in a batch (Hunter et al. 1985).

In the EPM, batch fecundity must be expressed as a function of female weight. An appropriate model must be selected to describe the relationship between batch fecundity (F) and gonad-free weight (W). Four models were fit to our data: $F = a + bW + e$; $F = a\,W^b + e$; $F = a\,e^{bW} + e$; and $F = a + b\ln(W) + e$ (e = error).

In addition, batch fecundity must be expressed in terms of total weight to estimate the reproductive biomass. Gonad-free weight was converted to total weight in the selected model, by the relation between the two weights for nonhydrated females (Hunter and Macewicz 1980).

RESULTS

Gonad Maturity Cycle

In figure 3 we have the gonad maturity cycle per month for males and females. The cycle was similar for both sexes.

In March, when the fishing season began, the anchovies were immature (figure 3), corresponding with minimum values of the GSI (figure 4). As can be seen in figure 3, the first increasing signs of ovarian activity were present from April onwards, with a certain proportion of fish maturing and mature. At the same time we can see an enlargement of the GSI (figure 4).

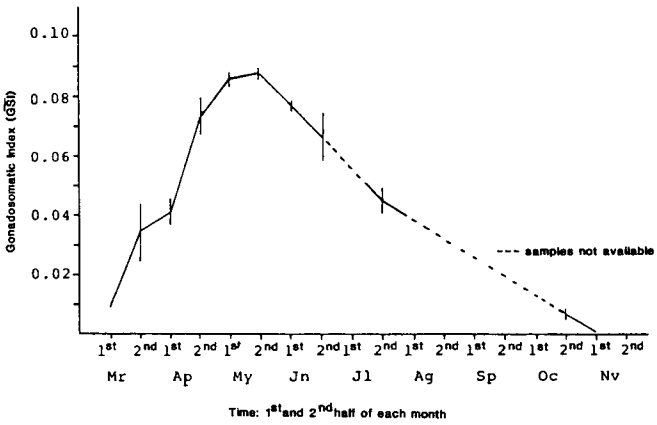

Figure 4. Evolution and standard error of the gonadosomatic index during 1987.

TABLE 3

ANOVA of the Hydrated Oocytes per Ovarian Gram, Obtained from the Right or Left Ovary, and as the Subsamples Are Located Inside the Ovary : in the Distal (I), Central (II), or Apical (III) Part (Fixed Factors), for 25 Anchovies (Aleatory Factor)

Source of variation	DF	SS	MS	*F*	sig. $\alpha = 0.05$
O ovary (right,left)	1	73084	73084	0.636	ns
P position (I,II,III)	2	329278	164639	2.665	ns($P < 10\%$)
A among anchovies	24	8742486	364270	3.14	***
O × P	2	89459	44729	0.385	ns
O × A	24	2758578	114940		
P × A	48	2965280	61776		
O × P × A	48	5571519	116073		

Almost all the fish sampled during May and June were mature, with maximum GSI values in May. From July on, the percentage of mature anchovies declined, and GSI values decreased. Mature fish were absent in the samples taken in October and November, and GSI values descended to 0.

Batch Fecundity

From the 20 opportunistic collections, 79 hydrated females were obtained; 17 of them were rejected because of the presence of postovulatory follicles. So we counted 62 hydrated females for our study.

The statistical analysis to test the effects of the subsampling position indicated that there were no differences between the density of hydrated oocytes from the two sides of the ovary in the 25 hydrated females sampled (table 3). The differences in density of hydrated oocytes from the three subsample positions were not significant at $\alpha = 0.05$, but they were significant at $\alpha = 0.10$ (the observed P was smaller than 10%). To be certain that the subsample position had no effects, 24 hydrated females were added to the 25 females sampled, and a bifactorial ANOVA was applied to the total of 49 females (table 4). This analysis indicated that no significant difference existed between the three subsample positions at either α levels ($\alpha = 0.05$ and $\alpha = 0.10$).

Based on the analysis, we conclude that the density of hydrated oocytes in the ovary was homogeneous between ovaries of the same individual. All the ovarian sections of the anchovy were equally hydrated.

For the Bay of Biscay anchovy, the variance coefficient value (θ) was 0.41 (table 5). According to Hunter et al. (1985) and Lo et al. (1986), if $\theta < 0.5$, the optimum resource distribution is obtained by estimating the batch fecundity of each hydrated female from two ovarian tissue samples, assigning the rest of the effort (economic and work) to sample a larger number of hydrated females. With two subsamples per ovary $K = 1.21$; i.e., the variance around the regression is increased 21% in relation to the one that would be obtained if we were counting the total number of hydrated oocytes in the total number of hydrated females (table 6).

Because the cost of the processing time for a new section is not too high and the increase in variance

TABLE 4

Variance Analysis of Two Factors to Verify the Effect of Subsample Position on the Number of Hydrated Oocytes per Ovary Gram

Bifactorial Variance Analysis: Effects of Inside-Ovary Position (Mixed Model)

Source of error	DF	SS	MS	*F*	sig. $\alpha = 0.05$
Inside-ovary position	2	261944	130972	2.140	ns
Between anchovies	48	9276640	193263	3.158	***
Residual error	96	5874742	61195		
Total	146	15413326			

Mean Number of Oocites per Ovary Gram

	Positions (n = 49 females)			
	I (distal)	II (central)	III (apical)	Total
Mean	2418	2320	2399	2379
SD	355	335	378	325

TABLE 5

Estimate of the Parameter $\theta = s_\epsilon^2/s_A^2$ Used to Determine the Optimal Number of Ovarian Subsamples

Source of error	Formula	Estimation
Within-ovary ($S^2_{\epsilon_{ij}}$)	$S^2_{\epsilon_{ij}} = \frac{\sum_i^n \sum_j^m (F_{ij} - F_i)^2}{n(m-1)}$	2.7984×10^6
Residual value of $\hat{F} = f(W) + \xi : S_\xi^2$	$S_\xi^2 = \frac{\sum_i^n [F_i - f(W)]^2}{n-2}$	7.7928×10^6
Residual value of $F = f(W) + a : S_A^2$	$S_A^2 = S^2 - \frac{S^2_{\epsilon ij}}{m}$	6.8600×10^6
Variance coefficient (θ)	$\theta = S^2_{\epsilon ij}/S_A^2$	0.41

F_{ij} = estimated total number hydrated eggs in the ovary from the j^{th} tissue sample; F_i = estimated total number of hydrated eggs in the ovary; m = number of tissue samples from an ovary; n = number of anchovies.

TABLE 6

Effect of Number of Samples per Ovary (m) on the Ratio K for the Linear Model

m	1	2	3	4	5
K	1.41	1.21	1.14	1.10	1.08

TABLE 7
Batch Fecundity of Bay of Biscay Anchovy

Number	Gonad-free weight (g)	Ovary weight (g)	Batch fecundity	Relative fecundity
0	19.07	3.86	10105	530
2	27.01	5.19	10769	399
3	31.18	6.51	16073	515
4	30.89	6.06	13550	439
5	34.54	7.01	16669	483
6	31.86	8.25	17325	544
7	40.52	8.52	23702	584
8	38.52	7.32	14662	381
9	37.51	9.75	22990	613
10	38.72	6.84	16006	413
11	38.69	9.99	24945	645
12	44.28	7.95	18126	409
14	23.25	4.75	12583	541
15	39.10	8.30	19206	491
16	31.94	6.21	18177	569
24	30.24	6.41	13160	431
25	27.02	3.84	9170	339
26	38.34	7.39	21690	566
27	35.86	7.84	17969	501
29	38.81	9.48	20676	533
30	40.14	6.79	17335	432
34	32.29	5.14	12577	389
35	31.91	6.54	15807	495
39	31.82	6.20	16957	533
40	24.67	4.88	10916	442
41	29.59	8.31	19811	669
42	23.85	4.97	12226	513
54	17.72	3.09	6050	341
55	15.53	2.76	7433	479
56	21.17	3.95	9579	452
57	16.55	3.60	7913	478
59	28.03	7.83	17398	620
60	24.55	6.44	10497	427
61	26.54	4.92	14341	539
62	30.26	7.10	15961	527
63	28.26	5.24	13571	470
64	23.37	4.68	10460	447
65	24.57	4.62	10714	436
66	29.61	7.08	18245	616
67	28.32	6.14	13974	493
68	28.34	7.19	14358	507
69	29.10	7.14	17307	595
70	33.52	8.40	18774	560
72	32.88	7.10	15229	463
77	33.00	7.53	19488	590
80	34.73	6.53	17520	504
82	41.07	10.78	23684	577
83	38.44	11.95	28453	740
86	39.66	10.74	22694	572
88	36.11	8.18	17014	471
89	42.54	12.91	24903	585
90	46.63	11.53	26311	564
91	48.00	11.20	21941	457
93	48.70	14.03	32629	670
104	27.20	6.52	16737	615
105	36.55	8.76	19254	527
117	30.70	7.39	18800	612
119	40.45	9.11	20743	513
121	30.36	6.54	15094	497
194	31.09	8.23	21028	676
239	24.24	6.05	13606	561
255	32.89	6.23	15002	456
		Mean	16772	517
		SD	5252	84
		CV	16.3%	31%

TABLE 8
Relation between Anchovy Batch Fecundity (F) and Gonad-Free Weight (W), Based on 62 Females with Three Subsamples

Model	Parameters a	b	MSE($\times 10^{-6}$)	r^2
$F = a + bW + e$	−2447.64	597.830	7.7928	0.722
$F = a + b \ln W + e$	−43695.10	17578.200	8.5241	0.696
$F = a W^b + e$	290.32	1.164	9.8323	
$F = a e^{bW} + e$	4643.92	0.038	8.5273	

about the regression is increased 14% ($K = 1.14$), taking three tissue samples per ovary would be an easy and inexpensive way to increase precision in the estimation. There is no reason to increase the number of tissue samples beyond three because the reduction in K becomes negligible at a larger sample size (table 6).

Our value of θ was within the range of the estimates for other species of small pelagic fish: for example, *E. mordax*, 0.5 or 0.6 (Hunter et al. 1985); and *Sardinops sagax*, 0.35 (Lo et al. 1986).

We used a data set of 62 hydrated females with no postovulatory follicles, in which three samples were taken from the right ovary to estimate batch fecundity. The different values for the 62 anchovies are listed in table 7. The mean value was 16,772 eggs per female. The relative fecundity, expressed as the number of hydrated oocytes per gram of ovary-free weight, ranged from 436 to 740, with a mean of 517.

Four regression models were evaluated to relate batch fecundity to ovary-free weight (table 8). Mean square error (MSE) was computed for all models and was used to select the most appropriate one. There was hardly any difference between the four MSE values; as Hunter et al. (1985) stated, the simple lineal model is preferable because the regression coefficient has a biological meaning, and batch fecundity for the females in the middle size range is better explained (figure 5).

$$F = -2447.64 + 597.83W^{\star} \qquad (1)$$

The conversion of gonad-free weight ($W^{\star}$) to a weight that included the active but not hydrated ovary (W) was done through the relationship:

$$W = 0.025 + 1.086\, W^{\star}$$

If we reestimate equation 1 in terms of total biomass we obtain:

$$F = -2462.58 + 550.48\, W$$

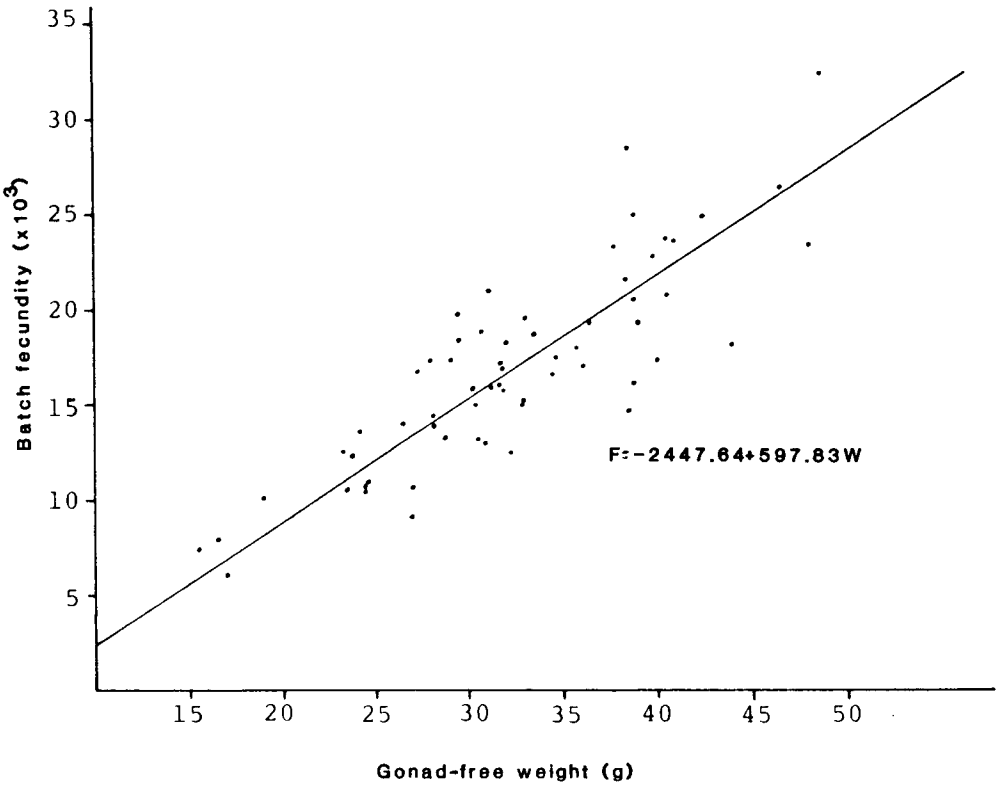

Figure 5. Point diagram of batch fecundity and female gonad-free weight, and the best model for our data set ($F = a + bW$).

DISCUSSION

Judging from the occurrence of grouped gonad stages and the pattern in GSI, it may be concluded that the spawning season for the Bay of Biscay anchovy in 1987 began in April and ended in July. These results confirm what was observed from egg and larval surveys (Arbault and Lacroix 1969, 1971, 1973; Suau and Vives 1979; Dicenta 1984; Santiago and Eltink 1988) and other studies of gonad maturity (Furnestin 1945; Andreu 1950; Cort et al. 1976, 1977, 1979). These studies have shown that the gonad maturity cycle parallels the warming process in spring, when the water goes from 12°C at the end of winter to 20°C at the beginning of summer.

The gonad maturity cycle was characterized by fast gonad development at the beginning of the reproductive period and slow absorption at the end of it. The peak spawning period is the most suitable time to obtain the adult reproductive parameters for the EPM. From the results obtained from the two maturity indices that were used (macroscopic and GSI), May appears to be the best time to conduct an EPM survey.

To determine batch fecundity, the subsamples can be taken from either of the two ovaries, because no significant difference was detected between the hydrated oocyte densities of the right and left ovaries. Also, no differences were seen between the three subsampling positions in the ovary. The location of subsamples has no effect on the batch fecundity estimation for the Bay of Biscay anchovy. Hunter et al. (1985) found the same results for the northern anchovy. Hunter et al., like we did, sampled the anchovy during the night, when the females that were going to spawn were completely hydrated. But, as stated by Hunter et al., if females are captured during the day, position effects may be likely, because hydration does not proceed at a uniform rate throughout the ovary.

The optimum number of ovarian tissue sections is two, but we take three as suggested by Lo et al. (1986) when the cost of the processing time for a new section is not too high. This reduces the increase of variance around the regression to 14%, in relation to the regression based on counting all the hydrated oocytes in the ovary.

The mean batch fecundity was 16,772 eggs per female. The mean relative fecundity value (517 eggs per body g) was within the range of the estimates reported for other closely related species, such as the Peruvian anchovy and the northern anchovy (table 9).

Our data suggest that batch fecundity is linearly related to ovary-free body weight. As an example, we can consider that with a mean batch fecundity of 16,772 eggs, if the spawning frequency is between 3

TABLE 9
Relative Fecundity and Regression between Batch Fecundity and Gonad-Free Weight of Different Anchovy Species

Species	Sub-population	Year	Month	Sample size	Weight range	Relative fecundity Mean	SD	r	Slope
**E.ringens*	north + cent.	1981	Ag/Sp	437	15–18	580	139	0.806	981
**E.ringens*	central	1981	Ag/Sp	254	15–38	637	134	0.769	1213
**E.ringens*	north	1981	Ag/Sp	183	15–38	502	103	0.883	824
**E.mordax*	central	1978		23	9–31	389	141	0.511	528
**E.mordax*	central	1979		44	9–28	438	150	0.784	881
**E.mordax*	central	1980		33	†17.11	444	80	0.903	624
**E.mordax*	central	1981		127	†14.75	601	180	0.873	872
**E.mordax*	central	1981		109	†16.54	606	151	0.724	852
**E.carpensi*		1977		14	†17.24	‡644	153	0.451	1542
E.encrasicholus		1987	Ap/My	62	15–48	517	84	0.839	597

*Data from Alheit et al. (1983)
†Mean weight
‡Parameter not calculated by the hydrated oocytes method

and 7 days, with a spawning period of approximately 90 days per anchovy, the total annual number of spawns per year would be between 12 and 30. These values turn out to be close to those given by Smith (1985) for *E.mordax*, according to different ages. This gives us an annual production range of 201,000–503,000 eggs. This approach is comparatively superior to the range of 23,000–173,000 eggs per spawning period given by Cendrero et al. (1981), who counted the total number of oocytes >250 μ in the ovary.

As we can see, the use of standing-stock oocytes underestimates the annual fecundity. For indeterminate spawners like the anchovy, annual fecundity must be calculated by both the batch fecundity and the number of spawnings per year (Hunter and Macewicz 1985).

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