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SEXUAL MATURITY, BATCH FECUNDITY, SPAWNING FREQUENCY, AND TEMPORAL PATTERN OF SPAWNING FOR THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, DURING THE 1979 SPAWNING SEASON

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ABSTRACT

Fifty percent of anchovy females reach sexual maturity by 96 mm standard length (95% confidence level 94-97 mm). Spawning batch fecundity, estimated from counts of hydrated eggs, was an exponential function of female weight. ($\ln Y = 4.2886 + 1.6281 \ln X$, where Y = number of hydrated eggs and X = female weight less ovary weight in grams). In the Los Angeles Bight the proportion of the population spawning/day (incidence of day-old post-ovulatory follicles) declined from 13.4% of the females in January-February to 10.0% in March-April and fell to 3.4% by June. Incidence of atresia in ovaries increased as the frequency of spawning declined. The percentage of females classed as post-spawning on the basis of the atretic condition of the ovary was 0.3% in January-February and 12% in March-April. Spawning of anchovy in Monterey Bay had nearly ended in March, and 71.9% of the females were classed as post-spawning.

The incidence of females with new post-ovulatory follicles and with hydrated eggs indicated that by sunset eggs were completely hydrated and spawning began; spawning reached a maximum between 2200-2300 hours and ended by 0200 hours. At 0600 hours females destined to spawn the next night began to hydrate eggs.

RESUMEN

El 50% de las anchovetas hembras alcanzan la madurez sexual al llegar a los 96 mm de longitud normal (nivel de confianza de 95%, 94-97 mm). La fecundidad del grupo desovante, calculado mediante recuento de óvulos hidratados, fue una función exponencial del peso de la hembra ($\ln Y = 4.2886 + 1.16281 \ln X$, donde Y = el número de óvulos hidratados y X = el peso de la hembra menos el peso del ovario en gramos). En la Bahía de Los Angeles la proporción de la población desovante diaria (incidencia de folículos post-ovulatorios de un día) disminuyó del 13.4% de las hembras durante enero-febrero al 10.0% en marzo-abril, y bajó al 3.4% en junio. La ocurrencia de atresia en los ovarios aumentó mientras que la frecuencia del desove disminuía. El porcentaje de hembras clasificadas como post-desovantes, a base de la condición atrética del ovario, fue 0.3% en enero-febrero y 12% en marzo-abril. El desove de anchoveta en la Bahía de Monterey casi había terminado en marzo, y 71.9% de las hembras fueron clasificadas como post-desovantes.

La presencia de hembras con nuevos folículos post-ovulatorios y con óvulos hidratados indicaba que, a la hora de la puesta del sol, los óvulos estaban completamente hidratados y se iniciaba el desove. El desove alcanzó un máximo entre las 2200-2300 horas y terminó a las 0200 horas. A las 0600 horas las hembras destinadas a desovar la siguiente noche empezaron a hidratar óvulos.

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INTRODUCTION

To assess anchovy spawning biomass using the gonad-egg model of Parker (1980), spawning frequency and batch frequency must be estimated. This paper provides data on spawning frequencies and fecundity for the 1979 spawning season of the northern anchovy, *Engraulis mordax*. We also estimate the probability of sexual maturity of females as a function of length, examine the atretic state of the ovary using histological criteria, and reexamine the relation between the reproductive state of females and time of day. We combine our data with those of Hunter and Goldberg (1980) to establish general relationships between batch fecundity and weight and between time of day and spawning.

METHODS

Female anchovy were collected during two major survey periods in the Los Angeles Bight: January 26-February 16, 1979 (61 collections, total females = 619) and March 22-April 14, 1979 (48 collections, total females = 601). An additional set of three collections was taken June 9-19 in the Los Angeles Bight (33 females), and a set of five collections (150 females) was taken in Monterey Bay during March 20-22, 1979. Most of the fish were taken at night using a midwater trawl, but in January-February, 15 collections were from lampara nets set by commercial fishing vessels, and all the Monterey samples were from commercial vessels.

Our plan was to measure and sex a minimum of 25 fish per sample, weigh and preserve the first 10 mature females for histological examination, and all immature specimens until the quota of 10 mature females was obtained. In practice, the number of fish sexed remained constant, but the number of mature females preserved varied. In some cases, we increased the sample size of females to compensate for fewer samples, and in others a high incidence of immature females and a highly biased sex ratio reduced the number of mature females to less than 10. In April 1979, we sampled a single area throughout one night to determine the consistency of spawning frequency within a single aggregation of schools. In this case we set the quota at 20 mature females/sample to increase the precision of the estimate. The variation in sample size of females has produced some statistical problems that have not been resolved. For this reason, error terms are not provided for spawning frequency estimates.

Batch fecundity was estimated for 32 females taken in January-February and 12 females taken in March-April by counting the number of hydrated eggs in a weighed sample of the gonad (Hunter and Goldberg 1980). The females used showed no evidence of recent spawning (no post-ovulatory follicles).

Many of the smaller females taken in January-February 1979 had small ovaries. Small females that had spawned within 24 hours could be confused with immature females if a judgement were made on the basis of ovary size alone. To avoid a histological examination of every immature ovary, we examined a subset of 160 females ≤ 12 g (body weight less ovary weight) to establish a weight criterion for immaturity. For these females we calculated the ratio of ovary weight/(body weight less ovary weight), grouped the data into eight ratio classes ($N = 20$ females per class), and calculated the percent of females in each class that were mature on the basis of histological criteria. Probit analysis (Finney 1952) was used to fit a line to the regression of maturity probability on $\log_{10}$ of the ratio of body weight/ovary weight (Figure 1). This analysis indicated that for females of 12 g or less, the probability of maturity was less than 5% when the gonad weight/body weight ratio ≤ 0.01. Henceforth, all females ≤ 12 g were considered immature if the ratio was 0.01 or less; all other females were examined histologically.

HISTOLOGICAL CLASSIFICATION

Spawning Frequency

For estimation of spawning frequency, females were examined histologically and classified into the five classes defined by Hunter and Goldberg (1980).

Hydrated. Ovaries with many hydrated eggs (eggs enlarged by fluid uptake just prior to ovulation) and no post-ovulatory follicles. Spawning considered to be imminent.

Age 0 day. New post-ovulatory follicles, showing no sign of degeneration. Hydrated eggs may occasionally be present. Elapsed time from spawning less than 24 hours.

Age 1 day. Regressing post-ovulatory follicles showing degeneration as described by Hunter and Goldberg (1980). Elapsed time from spawning equal to or greater than 24 hours but less than 48 hours.

Non-spawning (mature). Ovaries with many yolked oocytes; may contain post-ovulatory follicles in advanced

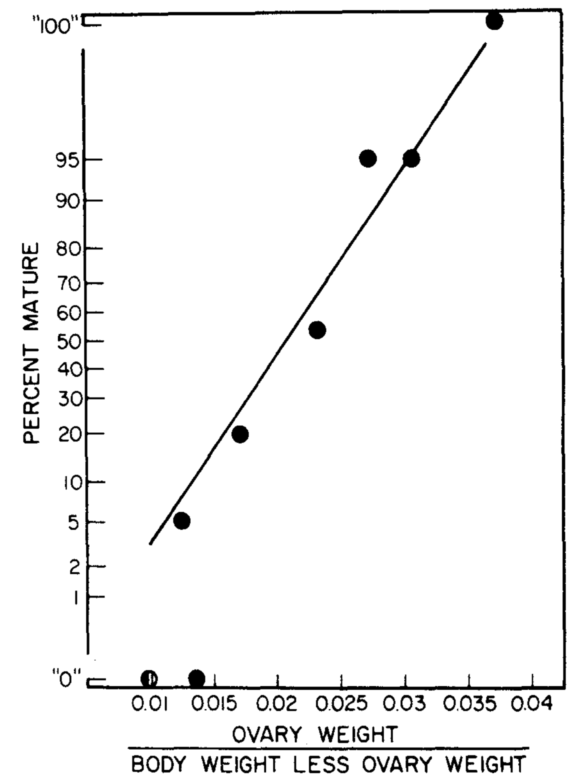

Figure 1. Percent of mature females (body weight ≤ 12 g) in eight classes of the ratio, ovary weight/(body weight less ovary weight);($N = 2$ females/class): percentage plotted at the mean ratio within each class. Females taken in January-February 1979 in the Los Angeles Bight. Line fit using probit analysis; equation for line is $Y = 21.52 + 9.837\,X$, where Y = % maturity in probits (Finney 1952) and $X = \log_{10}$ of the ratio.

stages of degeneration which cannot be readily distinguished from other atretic structures. May include females with highly atretic ovaries. Elapsed time from spawning 48 or more hours.

Immature. Few or no yolked oocytes. No atresia present in ovary other than late-stage corpora atretica. (A weight criterion was used to classify immaturity in some females ≤ 12 g; see methods section.)

We also determined the atretic condition of the ovaries of all mature female anchovy taken in 1979 including those with post-ovulatory follicles and hydrated eggs. This analysis provided an additional measure of the spawning potential of the population because rates of ovarian atresia would be expected to increase in ovaries as the end of spawning approaches and all yolked oocytes are resorbed. During the initial phase of the atretic process, the oocyte is resorbed and yolk globules are broken down and resorbed by hypertrophying granulosa cells of the follicle (the α stage of Bretschneider and Duyvené de Wit 1941; Lambert 1970). In the next stage (ß stage), all the yolk is gone, there remains a rather compact structure with one or more cavities (corpora atretica); the tissue is composed of granulosa and theca cells with penetrating blood vessels. The degeneration of the granulosa and theca cells begins in this stage. In the third and fourth stages (stages γ and δ of Lambert 1970), regression of theca and granulosa cells continues thereby reducing the size of the follicle, and a yellow-brown pigment appears. This pigmented condition is characteristic of late-stage corpora atretica.

The incidence and extent of the above atretic oocyte stages in the ovary and the presence of yolked eggs were used as criteria for five classes of atretic ovarian condition (Table 1). All ovaries were assigned to one of the classes on the basis of the criteria given in the table. The presence of late corpora atretica was not used as a criterion because they may persist in the ovary for a long time and occur in ovaries regardless of the incidence of other atretic stages. The earliest atretic stage (α) was the most useful character because the size of the oocyte is still apparent.

We also include in the table the percentage of all mature females taken in 1979 that had post-ovulatory follicles (ages 0-1 day) combined with those with hydrated eggs. This percentage, defined as total spawning activity, decreased with an increase in atretic condition, indicating, as expected, that atretic condition of the ovary and spawning activity are correlated.

SEXUAL MATURITY

All females collected in February 1978 were mature (Hunter and Goldberg 1980); whereas only 64% of the females taken in January-February 1979 were mature, and 91% were mature in March-April 1979. Data for 1979 were grouped by 5-mm standard length (SL) classes, percent maturity calculated for each class (Table 2), and the probability of maturity regressed on the $\log_{10}$ of the mean length of females in each class using probit analysis (Finney 1952). The estimated length at 50% maturity was the same for January-February, 96 mm (95% CI 94-97 mm) as for March-April, 96 mm (95% CI 94-98 mm). A good fit was obtained between probability of maturity and length in both sets (Figure 2).

The maturity lines for the two surveys in 1979 had different slopes because females 105-119 mm had a higher probability of maturity in March-April than they did in

TABLE 2

Percent Maturity of Female Northern Anchovy in the Los Angeles Bight by Length Class for February 1978, January-February 1979, and March-April 1979.

Length class (mm)	February 1978		January-February 1979		March-April 1979	
	N	% mature	*N*	% mature	*N*	% mature
71- 75	2	100	4	0		
76- 80	5	100	19	5		
81- 85	1	100	56	11		
86- 90	4	100	69	29	2	50
91- 95	3	100	80	48	7	86
96-100	6	100	70	56	46	67
101-105	8	100	58	76	120	80
106-110	17	100	39	82	134	94
111-115	47	100	46	87	117	96
116-120	53	100	33	94	59	100
121-125	36	100	31	94	48	100
126-130	24	100	50	100	40	100
131-135	35	100	44	100	19	100
136-140	25	100	13	100	15	100
141-145	18	100	5	100	3	100
146-150	9	100	1	100		
151-155	2	100	1	100		100
156-160					1	
Σ	295		619		611	

TABLE 1

Characters Used to Classify the Atretic Condition of Ovaries of Northern Anchovy[1] and the Total Spawning Activity within Atretic Ovary Classes.

Atretic ovary class	Total spawning activity[2]	Yolked oocytes present	Incidence of α stage[4] atresis in: Unyolked oocytes	Yoked oocytes[3] Small	Large	Incidence of ß stage atresia[4]	Other diagnostic characters
No atresia	0.36	+	0	0	0	0	
Minor atresia	0.21	+	•	•	0	+	
Early post-spawning	0.10	+	•	+	+	•	Less than 50% all yolked oocytes are in α stage atresia
Post-spawning	0	+	•	+	+	•	Greater than 50% all yolked oocytes are in α stage atresia.
Late post-spawning	0	0	•	0	0	+	

[1] + = present; 0 = absent; and • = may occur.

[2]Proportion of all mature females within each class having hydrated eggs or post-ovulatory follicles (ages 0 and 1). Combined data for January-February 1979 and March-April 1979 in Los Angeles Bight and March 1979 in Monterey Bay. Number of females in each of the five classes were: 592 (no atresia), 323, 92, 46, and 49 (late post-spawning).

[3]Distinction between atretic large and small yolked oocytes can be made only early in α stage of atresia when size differences are apparent, but yolked oocytes can be separated from unyolked throughout the α stage because of staining differences in hematoxylin and eosin preparations.

[4]α and ß stages of atresia are defined in text.

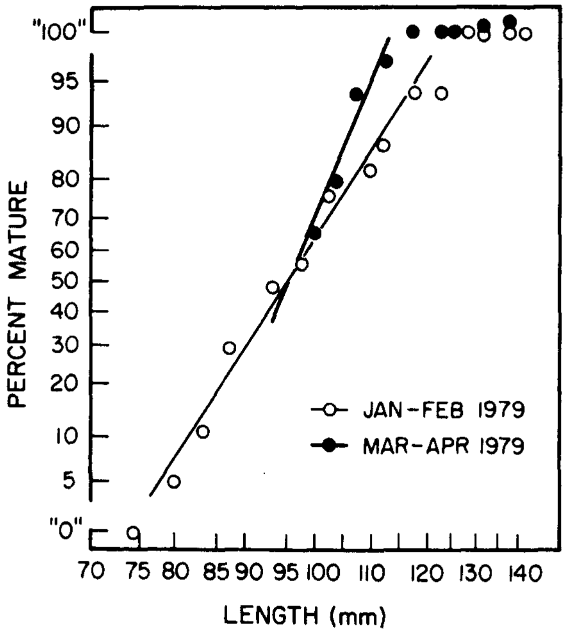

Figure 2. Percent maturity of female anchovy taken in Los Angeles Bight in January-February 1979 (open circles) and March-April 1979 (solid circles) as a function of standard length. Points are percent of females that were mature in each 5-mm class of length and are plotted at mean length within class. Equations for lines are: January-February, $Y = -29.793 + 17.572\ X$ and March-April, $Y = -48.30 + 26.899 X$; where Y = % maturity in probits (Finney 1952) and $X = \log_{10}$ standard length.

January-February 1979, whereas the probability of maturity for smaller females remained the same. The change in slope of the maturity line during 1979 and the difference in maturity between 1978 and 1979 could be caused by differences in sampling or statistical uncertainties. It could also be a measure of a real difference in the maturity-length relation as the spawning season progressed.

FECUNDITY

The spawning batch fecundity of female anchovy, on a unit weight basis, varied from 389 hydrated eggs/g female weight less ovary weight to 444 eggs/g, and the mean for all fecundity estimates was 421 ± 36 eggs/g (Table 3). MacGregor (1968) and Hunter and Goldberg (1980) concluded that for assessment work, the mean number of eggs per unit weight (relative fecundity) was sufficient and presented their data in that form. The existence of a larger data set (Table 4), based on hydrated eggs, permitted a reexamination of the fecundity weight relation. We regressed the number of hydrated eggs per female on female weight less ovary weight, using the combined data for 1978 and 1979. The geometric mean regression (Ricker 1973) yielded the equation $\ln Y = 4.183 + 1.620 \ln X$, where Y = number hydrated eggs, X = female weight less ovary weight, $r^2 = 0.51$ and $s^2_{y \cdot x} = 0.1295$ (the 99% confidence intervals for the slope did not include 1; Figure 3, upper). The form of this relation was similar to the one between gonad weight and female weight for mature nonspawning females with eggs of 0.65 mm (major axis) in the most advanced mode (Hunter and Goldberg 1980). To compare the two equations, we estimated ovary weight using their equation, $\ln G = -4.213 + 1.069 \ln W + .555\ D \ln W$ (G = ovary weight, W = female weight, and D = major egg axis [.65 mm]) and multiplied the estimated ovary weight by the mean number of advanced eggs per gram of ovary (8,630 ± 921); Hunter and Goldberg 1980). The two equations give similar results although based on different females and methods of calculation (Figure 3, lower). The regression equation appears to be a reliable method of estimating batch fecundity for females of the central subpopulation of northern anchovy and is more accurate than expressing fecundity on a unit weight basis. The error in using relative fecundity becomes substantial for females larger than 25 g (Figure 3, lower).

TABLE 3

Relative Batch Fecundity (Eggs per Unit Weight) for Females with Hydrated Eggs Taken in Each Survey and Calculated from Regression Equation for Batch Fecundity where X = Mean Weight of All Females Taken in Survey.

	Weight of all mature females (less ovary)		Relative batch fecundity			
			Mean for females with hydrated eggs		From regression equation, where X = mean weight of all females[3]	
Survey period	N	X±2SE[2] g	N	X±2SE[2] eggs/g (without ovary)	weight less ovary eggs/g	weight with ovary eggs/g
February 1978[1]	328	17.29±0.74	23	389±59	409	389
January-February 1979	394	16.40±0.67	32	444±57	396	376
March-April 1979	558	15.50±0.39	12	423±67	383	364
All data	952	15.87±0.30	67	421±36	388	369

[1]From Hunter and Goldberg (1980).
[2]±2 times standard error of mean.
[3]$\ln Y = 4.183 + 1.620 \ln X$, where X = female weight less ovary and $\ln Y = 4.100 + 1.620 \ln X$, where X = female weight with ovary. Estimate of total egg ($\ln Y$) increased by factor ½ $s^2_{y \cdot x} = 0.0647$ to correct for bias in taking antilog (Beauchamp and Olson 1973).

TABLE 4
Batch Fecundity of Northern Anchovy from Counts of Hydrated Eggs: Data for Three Surveys in the Los Angeles Bight.

Female weight less ovary (g)	Ovary weight (g)	Total hydrated eggs	Survey[1]	Female weight less ovary (g)	Ovary weight (g)	Total hydrated eggs	Survey[1]
9.3	1.171	3822	1	18.1	3.092	8978	3
9.3	1.406	2874	2	18.5	2.819	6420	2
9.8	1.202	3538	1	20.1	3.296	9447	1
10.8	1.190	2894	2	20.2	5.298	9595	2
10.8	2.109	6178	2	20.3	2.798	7714	2
11.7	1.485	3604	2	20.4	3.017	6181	1
11.9	1.202	5950	1	20.6	3.996	13266	1
11.9	1.704	4201	2	21.3	4.539	9159	2
12.5	1.038	4625	2	21.4	2.910	6292	2
12.7	1.697	4001	3	21.9	4.253	12461	1
12.9	2.155	6386	1	22.8	5.479	11902	2
13.1	1.995	4742	2	22.9	3.988	9366	1
13.1	1.586	4585	3	22.9	1.990	2794	2
13.4	1.888	4556	3	23.0	4.047	12742	2
13.7	1.575	6288	1	23.4	4.159	8354	2
14.2	3.083	8818	3	23.5	4.812	16662	1
14.6	1.287	3270	1	23.7	6.366	14196	2
14.7	1.352	3822	3	23.7	6.031	15310	2
14.9	1.523	4455	3	24.3	4.131	12515	2
15.2	2.473	5852	3	24.4	1.906	5392	1
15.3	2.114	5279	2	24.5	3.556	10217	2
15.4	0.835	3234	1	24.7	3.793	10621	2
16.0	2.210	4336	1	24.8	5.561	14037	3
16.0	1.235	4592	1	25.5	5.686	11577	1
16.0	2.586	7040	3	25.7	5.648	13955	2
16.1	2.058	4862	2	26.3	4.228	8548	2
16.4	2.750	8922	3	26.8	8.049	20797	2
16.6	2.622	5677	2	26.9	2.956	5972	1
16.6	5.624	13363	2	28.0	9.645	23044	2
17.2	3.275	7895	2	28.1	6.388	14668	2
17.2	2.148	7258	1	30.4	1.967	6292	1
17.3	2.473	5744	2	31.2	4.793	10577	1
17.3	3.883	7958	3	31.9	3.796	9251	1
17.9	2.369	8216	1				

[1]1 = February 1978, $N = 23$;
2 = January-February 1979, $N = 32$;
3 = March-April 1979, $N = 12$.

We used counts of hydrated eggs to estimate spawning batch fecundity because it was a more rapid and more accurate method than counting the number of eggs in the most advanced mode (Hunter and Goldberg 1980). This method requires that fecundity be calculated in terms of female body weight, less gonad weight, because hydration of the ovary significantly alters the total weight of the female. On the other hand, to assess spawning biomass, fecundity must be expressed in terms of total weight. Our fecundity measurements can be converted to a total weight basis using the ratio of the two body weights for females without hydrated eggs (w/W, Table 5). This ratio was 0.95, and it varied little between seasons, regions, or years. The fecundity equation was re-estimated from the data in Table 4 using total female weight (female weight less ovary weight/0.95) as the independent variable. The geometric mean regression (Ricker 1973) of numbers of hydrated eggs (Y) on total female weight (female weight less ovary/0.95; X) was $\ln Y = 4.100 + 1.620 \ln X$, where $r^2 = 0.51$, and $s^2_{y.x} = 0.1295$.

We believe it is preferable to use the regression equation to estimate batch fecundity for assessment of spawning biomass rather than the average relative fecundity. In Table 3, we use the equation to estimate the relative batch fecundity for the mean of the weight of all mature females taken in each survey, and we compare these values to means calculated on a unit weight basis. Regression estimates of relative fecundity using the mean weight of females taken in a survey differ by 5-11% from the average relative fecundity for the same survey because of differences in the weights of hydrated females within the samples used for the unit weight averages.

FREQUENCY OF SPAWNING

Spawning frequency is best estimated from the incidence of day-old post-ovulatory follicles (day 1), because incidence of females with hydrated eggs or new post-ovulatory follicles are affected by the time of capture and sexual composition of the school (Hunter and Goldberg 1980). The ovaries of 13.4% of the mature females taken in January-February 1979 (Table 6) and 10.0% of those taken in March-April 1979 (Table 7) had day-old post-ovulatory follicles. Thus, on the average, female anchovy in the Los Angeles Bight spawned every 7-10 days during the three peak months of spawning in 1979. Only 3.5% of the 29 females taken in June 1979 in the Los Angeles Bight has post-ovulatory follicles. Although the sample size is small, these data indicate that the frequency of spawning had declined by June.

Incidence of day-old post-ovulatory follicles reported by Hunter and Goldberg (1980) were 15% for February 1978 and 14.2% for a small sample taken in March 1977. Thus, data for the peak spawning months in 1979 was in keeping with past results. As in the past study, no relation existed between incidence of day-old post-ovulatory follicles and size of the mature females, time of day, or locality within the Los Angeles Bight.

Ovaries of females taken in Monterey Bay in March 1979 were distinctly different: none contained day-old post-ovulatory follicles, and only two (1.3%) had new post-ovulatory follicles (day 0; Table 8). Thus, spawning had nearly ended in Monterey Bay by March, whereas it continued at a high level to the south in the Los Angeles Bight. Abundance of anchovy larvæ and eggs taken in the 1979 CalCOFI survey also indicated that spawning ended in Monterey by March but continued in the Los Angeles Bight and south along the Mexican coast (Stauffer and Parker 1980).

In a recent study Laroche and Richardson (in press) point out that the northern subpopulation of the northern anchovy off Oregon and Washington probably spawn fewer times than the central subpopulation we studied. They noted degeneration of oocytes in ovaries of females

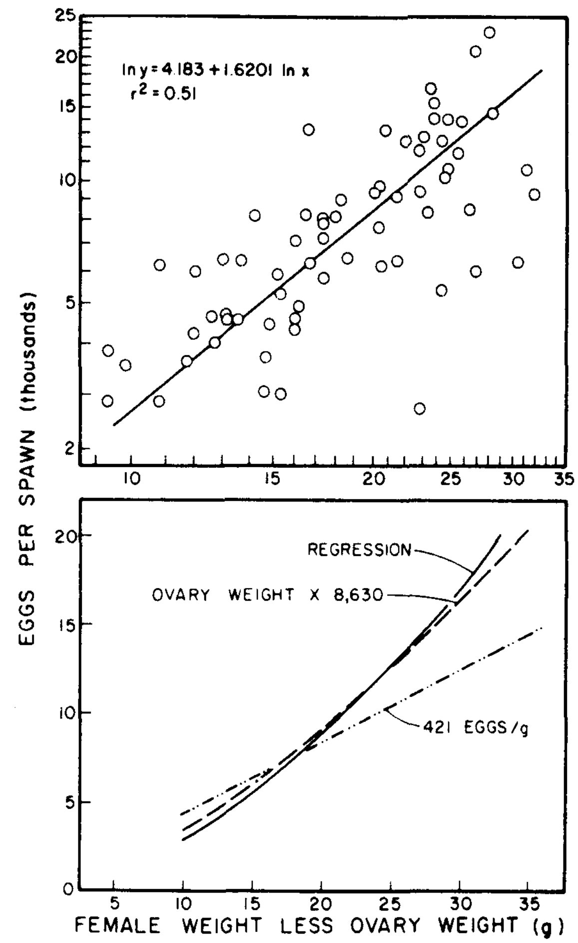

Figure 3. Batch fecundity of northern anchovy taken in the Los Angeles Bight, 1978-79. Upper panel: regression of ln total number hydrated eggs on ln female weight (less ovary weight). Lower panel: three methods of estimating batch fecundity are compared: solid line from regression in upper panel; dashed line, ovary weight (G) times mean number eggs (non-hydrated) in advanced mode (8630 ± 921) where $1nG$ = $-4.213 + 1.069\ 1nW + D\ (0.555\ 1nW)$. W = female weight (less ovary) and D = size of eggs (0.65 mm: from Hunter and Goldberg 1980), and dash-dot line is mean relative fecundity for 1978-79. 421 eggs/g female weight (less ovary).

TABLE 5

Mean Body Weight of Females[1] with (W) and without (w) the Ovary Included and Regression of W on w for Various Survey Periods and Regions.

	Total body weight (W) in g			Body weight less ovary (w) in g			$W = -a + bw$ where:		
Survey and region	N	X	s	X	s	w/W	a	b	r^2
February 1978 (Los Angeles Bight)	69[2]	20.2	8.05	19.2	7.45	0.950	.514	1.078	0.997
January-February 1979 (Los Angeles Bight)	355	17.1	7.15	16.2	6.64	0.947	.409	1.077	0.998
March-April 1979 (Los Angeles Bight)	536	16.2	5.10	15.5	4.70	0.957	.520	1.081	0.995
March 1979 (Monterey)	145	19.3	6.64	18.5	6.18	0.959	.516	1.073	0.997
All data combined	1099	17.2	6.36	16.4	5.90	0.954	.450	1.076	0.997

[1]Only sexually mature females included: females with hydrated eggs excluded.
[2]Gonad weight not available for all females examined.

TABLE 6
Reproductive State of Female Northern Anchovy Collected in the Los Angeles Bight in January-February 1979.

			Number of females in various reproductive states				Total females	
				Post-ovulatory follicles		Mature		
Collection number[1]	Month and day	Time of day (hours)	Hydrated eggs	*0 day*[2]	*1 day*	no evidence *of spawning*	Mature	Immature
3040	2 10	18.03	–	2	1	5	8	3
3034	2 09	18.08	4	–	4	2	10	0
3025	2 07	18.12	3	–	3	4	10	0
3006	1 27	18.23	–	1	1	3	5	6
3017	2 03	18.27	1	–	1	8	10	0
3019	2 04	18.27	7	–	–	3	10	0
3000	1 26	18.37	–	–	–	1	1	12
3020	2 06	18.73	1	–	1	8	10	0
3012	1 29	18.88	–	–	–	2	2	5
3007	1 27	19.12	–	–	1	3	4	7
3046	2 13	19.17	–	–	1	7	8	1
3041	2 10	19.32	2	–	–	7	9	10
3018	2 03	19.48	5	–	1	4	10	0
3026	2 07	19.70	–	–	–	10	10	0
3001	1 26	20.05	–	–	–	2	2	8
3013	1 29	20.18	1	2	–	–	3	2
3035	2 09	20.27	2	1	–	6	9	0
3021	2 06	20.38	2	2	3	2	9	0
3042	2 10	20.63	3	–	–	6	9	3
3029	2 08	20.67	2	1	5	2	10	0
3008	1 27	20.93	–	–	1	2	3	12
3002	1 26	21.30	–	–	–	–	0	10
3036	2 09	21.62	2	–	2	6	10	0
3014	1 29	21.67	–	–	2	3	5	1
3022	2 06	21.82	–	5	1	4	10	0
3043	2 10	21.85	–	1	–	9	10	0
3030	2 08	22.27	1	1	–	8	10	0
3003	1 26	22.33	–	–	–	–	0	11
3009	1 27	22.45	–	–	–	1	1	16
3027	2 07	22.72	–	–	3	7	10	0
3037	2 09	23.02	–	–	–	3	3	0
3044	2 10	23.30	–	–	–	5	5	1
3015	1 29	23.55	–	3	–	7	10	0
3023	2 06	23.70	–	3	–	–	3	0
3010	1 27	23.75	–	–	–	6	6	7
3031	2 09	00.05	–	–	2	8	10	0
3028	2 08	00.12	–	1	3	6	10	0
3038	2 10	00.52	–	1	1	8	10	0
3004	1 27	00.72	–	–	–	–	0	14
3011	1 28	00.78	–	–	–	7	7	8
3045	2 11	00.95	–	2	–	–	2	0
3024	2 07	01.12	–	3	–	2	5	0
3032	2 09	01.63	–	1	4	5	10	0
3039	2 10	02.03	–	1	3	6	10	0
3016	1 30	02.90	–	1	–	1	2	2
3033	2 09	03.00	–	4	1	5	10	0
2006	2 05	03.42	–	1	1	8	10	0
2001	1 27	03.50	–	2	–	1	3	7
2005	2 02	04.00	–	–	–	7	7	3
2002	1 27	04.17	–	–	1	4	5	8
2004	1 30	04.50	1	–	1	3	5	5
2007	2 07	04.50	–	–	–	5	5	5
2010	2 16	04.50	–	–	–	9	9	1
2003	1 27	05.00	–	–	–	2	2	11
2008	2 07	05.00	1	1	4	4	10	0
1002	2 08	05.00	–	–	–	2	2	9
2009	2 16	05.33	1	1	1	7	10	0
1004	2 12	05.50	–	1	–	7	8	2
1001	2 07	05.50	–	2	–	1	3	14
1003	2 08	06.00	–	–	–	3	3	11
1005	2 15	06.00	–	–	–	1	1	10
S			39	44	53	258	394	225
%			9.9	11.2	13.4	65.5	63.6	36.4

[1]Collection numbers in 1000 and 2000 series were commercial lampara sets; 3000 and 4000 were midwater trawl.
[2]Females with hydrated eggs and day 0 post-ovulatory follicles included in this class.

TABLE 7
Reproductive State of Female Northern Anchovy Collected in the Los Angeles Bight in March-April 1979.

Collection number[1]	Month and day	Time of day (hours)	Number of females in various reproductive states: Hydrated eggs	Post-ovulatory follicles: 0 day[2]	Post-ovulatory follicles: 1 day	Mature no evidence of spawning	Total females: Mature	Total females: Immature
3064[3]	4 07	18.80	2	1	4	13	20	0
3054	4 03	18.92	1	–	1	8	10	0
3079	4 12	18.92	2	1	–	7	10	11
3082	4 13	18.92	–	–	4	6	10	–
4008	3 24	19.15	–	1	2	11	14	1
4001	3 22	19.25	–	–	–	11	11	0
3050	4 02	19.33	–	1	3	6	10	0
4004	3 23	19.57	3	1	1	9	14	1
3071	4 08	20.25	1	–	–	9	10	0
3055	4 03	20.35	–	–	3	7	10	0
3083	4 13	20.35	2	–	–	8	10	1
3058	4 05	20.43	–	–	2	8	10	0
3073	4 09	20.50	–	–	–	10	10	0
3065[3]	4 07	20.57	1	2	1	16	20	0
3047	4 01	20.60	–	–	3	7	10	0
3060	4 06	20.72	2	–	1	7	10	0
4009	3 24	21.30	5	8	–	1	14	1
3074	4 09	21.75	–	–	1	9	10	0
3072	4 08	21.78	–	1	–	9	10	0
3059	4 05	22.00	–	2	2	6	10	0
4005	3 23	22.05	5	3	2	5	15	0
3048	4 01	22.12	–	–	2	4	6	0
3066[3]	4 07	22.30	1	7	2	9	19	0
3061	4 06	22.50	1	2	1	6	10	0
4002	3 22	22.67	–	2	2	11	15	0
3057	4 04	22.83	–	1	–	7	8	2
3077	4 11	22.87	–	–	–	11	11	1
4010	3 24	23.42	–	2	2	10	14	1
3075	4 09	23.50	–	1	–	9	10	0
3067[3]	4 08	00.02	–	7	1	12	20	0
3062	4 07	00.03	–	1	1	8	10	0
4006	3 24	00.38	–	2	1	7	10	0
3051	4 03	00.48	–	–	3	7	10	0
3076	4 10	00.90	–	2	–	8	10	0
3080	4 13	01.10	–	–	1	4	5	18
3049	4 02	01.13	–	–	2	8	10	0
3078	4 12	01.57	–	–	–	10	10	0
3063	4 07	01.58	–	1	1	9	11	0
3068[3]	4 08	01.67	–	5	1	14	20	0
3084	4 14	02.98	–	4	–	5	9	1
4007	3 24	03.08	–	–	1	12	13	2
3069[3]	4 08	03.33	–	5	1	13	19	0
3081	4 13	03.42	–	–	1	9	10	0
3052	4 03	03.62	–	3	–	7	10	0
4003	3 23	03.65	–	1	1	9	11	2
3070[3]	4 08	04.92	–	4	2	13	18	1
2026	3 23	05.00	–	–	–	–	–	10
3053	4 03	05.05	–	–	–	10	10	0
Σ			26	71	56	405	558	53
%			4.7	12.7	10.0	72.6	91.3	8.7

[1]Collection numbers in 1000 and 2000 series were commercial lampara sets, 3000 and 4000 were midwater trawl.
[2]Female with hydrated eggs and day 0 post-ovulatory follicles included in this class.
[3]Collection is part of a 7-collection series taken in same locality on same night.

TABLE 8
Reproductive State of Female Northern Anchovy Collected in Monterey Bay, California, in March 1979.

Collection number	Month and day	Time of day (hours)	Number females in various reproductive states: Hydrated eggs	Post-ovulatory follicles: 0 day	Post-ovulatory follicles: 1 day	Mature no evidence of spawning	Total mature females[1]
2014	3 21	02.30	–	1	–	29	30
2020	3 22	03.15	–	–	–	30	30
2017	3 21	03.45	–	–	–	30	30
2023	3 22	04.15	–	1	–	29	30
2011	3 20	05.00	–	–	–	30	30
Σ			0	2	0	148	150
%				1.3		98.7	100

[1]All females judged sexually mature, but many ovaries in post-spawning condition (see Table 9).

taken in the peak month of July and spawning in the northern subpopulation occurs only from mid-June to mid-August. We examined a small sample of 25 females taken in four research trawl catches taken off Oregon July 18-21, 1977. Ovaries of ten of these females (40%) had new post-ovulatory follicles and four (16%) had day-old post-ovulatory follicles. Twenty-three of the ovaries from these females (92%) exhibited no or only minor atresia, but the ovary from one female was in the early post-spawning condition and that from another in the late post-spawning condition. The latter female had clearly completed spawning for the season. On the basis of this evidence we suggest that the spawning frequency during peak periods of spawning is about the same for the northern as for the central sotck (about once a week), but the northern stock may be limited to about four spawnings per year because of the short duration of the spawning season.

INCIDENCE OF ATRESIA

In January-February 1979, when the frequency of spawning was the highest (13.4%), only 0.3% of the mature females were classed as post-spawning on the basis of ovarian atresia, whereas in March-April 1979, when spawning frequency had declined to 10.0%, 14% of the mature females were classed in one of the three post-spawning stages and 5% clearly were incapable of further spawning (Table 9). In Monterey during March, little spawning occurred, and 71.9% of the females were classed in one of the three post-spawning stages. Thus the incidence of ovarian atresia was inversely correlated with the frequency of spawning, and this indicates that the decrease in the frequency of spawning during the season may be caused by a cessation of spawning. In other words, the interval between spawning may be a biological rhythm having a period of about a week, and the change in the observed spawning frequency may be caused by cessation of spawning by some females in the population rather than changes in the interval between spawning in individual females.

TABLE 9
Incidence of Atretic Classes of Ovaries in Mature Female Northern Anchovy Taken in the Los Angeles Bight and Monterey Bay in 1979.

Region and month	N^1	Percentage of Females[2]: No atresia	Minor atresia	Early post-spawning	Post-spawning	Late post spawning
Los Angeles Bight January-February	394	64.4	35.3	0.3	0	0
Los Angeles Bight March-April	558	57.7	28.3	9.0	1.4	3.6
Monterey Bay March	149	10.8	17.3	27.3	25.3	19.3

[1]All mature females.
[2]Stages of atresia defined in methods.

TEMPORAL PATTERN OF SPAWNING

The seven trawl samples taken during a single night in the same locality (March-April 1979, Table 6) provide an illustration of the temporal pattern of spawning within a single group of schools. The percent of females with hydrated eggs decreased from 10% at sunset to zero by midnight, whereas the number of females with new post-ovulatory follicles increased sharply at 2100 hours and varied between 25 and 35% throughout the rest of the night (Figure 4, upper). The incidence of new post-ovulatory follicles in this series was consistently higher than the mean of all collections taken in March-April 1979 (13%, Table 6). Thus, on this particular night, more spawning may have occurred in this group of schools than was typical for all schools in the Los Angeles Bight in March-April. The frequency of day-old post-ovulatory follicles ranged from 5 to 20% but did not vary with time of day; the mean was 9%, close to the average (10%) for the March-April survey period as a whole.

The temporal pattern of spawning for all surveys combined (February 1978, January-February 1979, and March-April 1979) was similar to the one for a single night. Percent of females with hydrated eggs declined

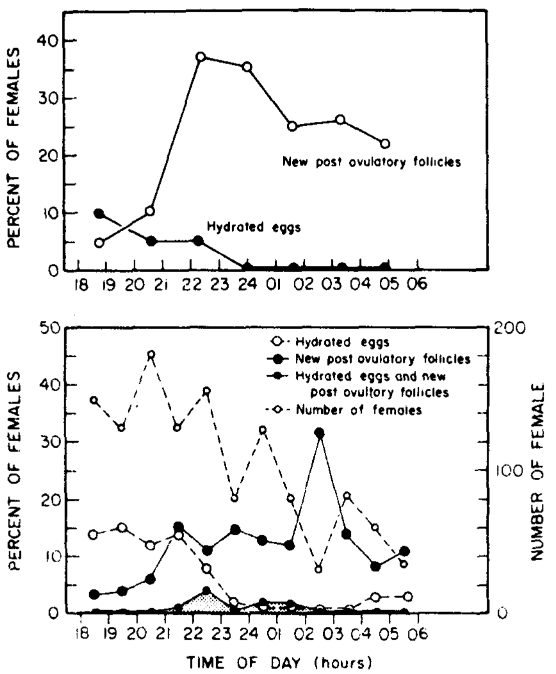

Figure 4. Percent of females in various reproductive stages as a function of time of day. Upper panel: percent of females with only hydrated eggs and females with new post-ovulatory follicles. Samples of 18-20 females taken over a single night at the same locality in the Los Angeles Bight in April 1979. Lower panel: percent of females with only hydrated eggs, only new post-ovulatory follicles, and with both hydrated eggs and new post-ovulatory follicles (shaded area), as a function of time of day. Data are from surveys in the Los Angeles Bight (1978-79). Number of females in each hour class (upper dashed lines) ranged from 35-183.

from about 14% at sunset to 0 at 0100 hours. The occurrence of females with new post-ovulatory follicles increased sharply at 2100 hours and varied between 10-15% throughout the rest of the night (Figure 4, lower). These combined data reveal two additional patterns not resolved in smaller sample sizes: a reappearance of females with hydrated eggs around 0500-0600 hours and the occurrence of females with both hydrated eggs and new post-ovulatory follicles. The reappearance of females with hydrated eggs indicates that hydration for the next night of spawning began in the early morning. The process probably continued throughout the day, resulting in females being ready to spawn at sunset. This view is supported by the fact that our histological examination of hydrated ovaries collected between 0500-0600 hours indicated that they were in the early stages of hydration (characterized by the disappearance of the nuclear membrane, diffused nuclear elements lying in one pole of the eggs, and only partial fusion of yolk globules into the large plate-like bodies).

The best indicator of the time of spawning may be the occurrence of females with both hydrated eggs and new post-ovulatory follicles, because these females were caught while spawning. Their low frequency in the collections indicates that spawning was completed rapidly, and the time of occurrence indicates that the period of maximum spawning occurred between 2100 and 0200 hours, with a peak between 2200 and 2300 hours (Figure 4, lower, shaded area).

On the basis of these results, nightly pattern of spawning in anchovy can be divided into three periods: early spawning period (1800 to 2100 hours), some spawning occurs but the ovaries of most reproductively active females are in the hydrated state; maximum spawning (2100-0200 hours), most females spawn (females with hydrated eggs decline to 0 and females with new post-ovulatory follicles reach the maximum number for the night); and post-spawning (0200-0600 hours), little or no spawning occurs and females destined to spawn the next night begin hydration.

DISCUSSION

This study provided the first quantitative estimate of the size threshold for sexual maturity in female northern anchovy. Clark and Phillips (1952) reported that only a few females mature at 90-100 mm SL, about 30% mature at 100-200 mm, and 50% at 130 mm, whereas Brewer (1978) and Hunter and Goldberg (1980) found significant numbers of mature females less than 90 mm. The present study provided functions from which the probability of maturity can be estimated for any length. The slope of maturity line changed somewhat over the spawning season, but the length at 50% probability of maturity remained the same.

Data collected on the occurrence of female anchovy with hydrated eggs and post-ovulatory follicles in the Los Angeles Bight were similar to those presented by Hunter and Goldberg (1980) for February 1978. The mean interval between spawnings was about 7 days in their study, and it ranged from 7-10 days during the peak spawning months in the present study. The larger number of observations in the present study, combined with past data of Hunter and Goldberg (1980) allowed us to calculate a weight function for batch fecundity and enabled us to describe in greater detail the temporal pattern of spawning behavior.

This paper has provided the reproductive data needed for biomass assessment using the model of Parker (1980). It also indicates needed refinements for future surveys and alternate sampling procedures. That the spawning frequency in Monterey Bay was distinctly different from that of the Los Angeles Bight emphasizes the importance of obtaining samples representative of the entire central subpopulation. Error terms need to be developed for spawning frequency estimates when sample sizes are highly variable. In addition to the incidence of day-old post-ovulatory follicles, the incidence of females with new post-ovulatory follicles or hydrated eggs could be used as a measure of spawning frequency, if appropriate weights were developed for the time of sampling. If anchovy could be sampled during the day, it might be possible to use females with hydrated eggs alone as the measure of spawning frequency. This is an attractive alternative to use of post-ovulatory follicles because it would cost less, as histological examination would not be required.

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