SPAWNING FREQUENCY AND BATCH FECUNDITY OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, OFF CALIFORNIA DURING 1991

BEVERLY J. MACEWICZ AND J. ROE HUNTER
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

In southern California waters, during March–April 1991, the average mature female jack mackerel, *Trachurus symmetricus*, spawned every 5 days, and eight percent of the females spawned at 1–3 day intervals. The average relative batch fecundity was 112 oocytes per gram female weight (without ovary). Batch fecundity was lower for females that had spawned within the last 3 days than for females in which no evidence existed for a previous spawning.

RESUMEN

En aguas de California sur, durante Marzo–Abril de 1991, los especímenes maduros promedio del charrito (*Trachurus symmetricus*) desovaron cada 5 días; ocho porciento de las hembras desovó en intervalos de 1–3 días. La fecundidad relativa promedio por cada puesta fué de 112 ovocitos por gramo (peso corporal de hembra libre de ovarios). La fecundidad por cada puesta en las hembras que habían desovado en los últimos 3 días fué menor que en las hembras en las que no se observó evidencia de desove previo.

INTRODUCTION

Jack mackerel, *Trachurus symmetricus* (Ayres, 1855), range from Baja California to the Gulf of Alaska and from coastal waters up to 1000 miles offshore (MacCall and Stauffer 1983). The southern California fishery usually takes fish 10–30 cm (FL, fork length). No fishery presently exists for larger fish (FL >40 cm), which occur predominantly offshore and to the north (MacCall et al. 1980; MacCall and Stauffer 1983; Mason 1991). The potential value of an offshore trawl fishery for *T. symmetricus* has attracted some interest lately, and if such a fishery were to develop, estimates of *T. symmetricus* biomass from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data would be a valuable management tool.

MacCall and Stauffer (1983) used CalCOFI data and reproductive information on *T. symmetricus* to estimate the average biomass off western North America. Their chief barrier for estimating a time series of *T. symmetricus* biomass from CalCOFI data was the lack of information on daily rates of spawning (spawning frequency) and numbers of oocytes released per spawn (batch fecundity). The object of this paper is to provide new estimates of these two reproductive parameters for *T. symmetricus*.

Relatively little is known about the reproductive biology of *T. symmetricus* from the California Current. Gonad development and sexual maturity were studied by Wine and Knaggs (1975), and some preliminary fecundity estimates are available in MacGregor (1976). Lisovenko and Andrianov (1991) estimated the spawning frequency of *Trachurus murphyi* from Peruvian waters. Other works related to reproduction of *Trachurus* include various analyses of CalCOFI ichthyoplankton data to estimate the seasonality of reproduction, diel time of spawning, and distribution of eggs and larvae (Ahlstrom and Ball 1954; Farris 1961; Kramer and Smith 1970; Moser et al. 1993). Temperature-specific egg incubation rates are also known for *T. symmetricus* (Zweifel and Lasker 1976).

METHODS

Jack mackerel, *Trachurus symmetricus*, were collected about 200 nautical miles off the southern California coast (figure 1) from March 23 to April 9, 1991, during a cooperative cruise on the R/V *Novodrutsk* (from Vladivostok, Russia). A large, nearly square, pelagic trawl with a vertical and horizontal opening of 75–80 meters was towed at 4.2 to 5.5 knots to collect the fish. Most of the 36 trawls were made at night; they lasted from 50 minutes to 8 hours and 40 minutes (Macewicz and Abramenkoff 1993). Surface water temperature ranged from 13.5°C to 14.7°C.

T. symmetricus were randomly sampled from the catch. Up to 100 fish from each haul were sexed, and measured (FL) to the nearest millimeter; their gonads were also classified (Macewicz and Abramenkoff 1993). From each trawl, 5 to 22 females were selected, not on the basis of maturity, but at random. The females were individually weighed (to the nearest gram) and their ovaries were removed and pre-

[Manuscript received February 1, 1993.]

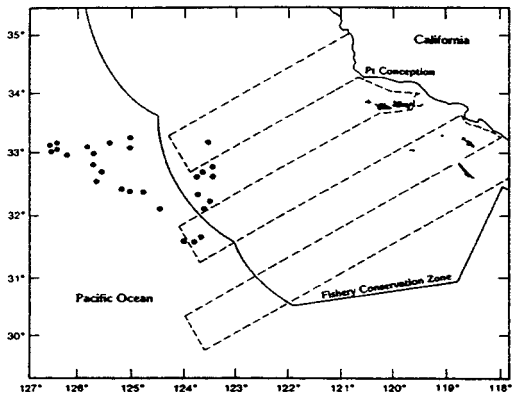

Figure 1. Location of the jack mackerel survey during March 23–April 9, 1991. *Circles* = trawls in which *Trachurus symmetricus* were taken; *dotted line* = the CalCOFI survey pattern.

served in 10% neutral buffered Formalin. Analysis of the preserved ovaries of these female *T. symmetricus* is the subject of this paper.

Histological Classification

The preserved ovaries were weighed to the nearest milligram in the laboratory. A piece of each ovary was removed, dehydrated, and embedded in Paraplast. Histological sections were later cut at 5–6 μm and stained with Harris hematoxylin followed by eosin counterstain (H&E).

Each ovary was classified histologically in the manner developed for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a,b) with a few modifications for the ovarian structure of *T. symmetricus*. Oocytes in *T. symmetricus* ovaries develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). In each ovary we recorded the presence or absence of the following characters: oocytes that had not begun vitellogenesis; oocytes in early vitellogenic stages (0.28–0.54 mm in diameter); advanced yolked oocytes (smallest about 0.42 mm in diameter) in which any stages of nucleus migration (precursor to hydration) or hydration (>0.95 mm in diameter) were noted; and postovulatory follicles.

Unlike the developing oocytes of northern anchovy, those of *T. symmetricus* contain lipid droplets. The lipid first appears in oocytes about 0.19 mm in diameter (before vitellogenesis starts) and then eventually surrounds the nucleus and begins to fuse. Just before the nucleus migrates, partially fused lipid droplets begin moving to the side of the nucleus opposite the direction of migration. This location of the oil droplets on one side of the nucleus is a unique character that signals the onset of the migratory-nucleus stage. For this reason, oocytes in the migratory-nucleus stage can be detected much earlier in *T. symmetricus* than in species lacking an oil droplet, such as the northern anchovy.

Ovarian atresia in most teleosts seems to follow a similar sequence of stages (α, β, γ, and δ), as defined by Bretschneider and Duyvene de Wit 1947; Lambert 1970; and Hunter and Macewicz 1985b. We examined the ovarian sections for the presence of alpha (α) atresia of yolked oocytes and grouped them as follows: none, $\alpha < 50\%$ (1 oocyte to 49% of the yolked oocytes were in α atresia), or $\alpha \geq 50\%$ (50% or more of the yolked oocytes were in α atresia). The presence of beta (β) atresia was also noted. Alpha atresia of *T. symmetricus* was essentially similar to that described and illustrated for northern anchovy by Hunter and Macewicz (1985b); however, β atresia in *T. symmetricus* differed from northern anchovy because numerous vacuoles were scattered between the follicle cells. The vacuoles are probably remnants of the lipid droplets, which take longer than yolk to resorb, and in H&E slides appear empty. Ovarian atresia may indicate that the end of a spawning season is approaching (Hunter and Macewicz 1980, 1985b).

Spawning Frequency

To measure spawning rate from postovulatory follicles, one must be able to estimate the age of the postovulatory follicles on the basis of their deterioration (Hunter and Goldberg 1980; Hunter and Macewicz 1985b). The best way to develop criteria for estimating the age of postovulatory follicles is to spawn fish in the laboratory and sample at known times after spawning. Alheit et al. (1984) were able to estimate age of postovulatory follicles for *Engraulis ringens* by sampling fish at sea through the day and night. They then reconstructed the degeneration rate of the postovulatory follicles by analyzing the time series. This alternative method requires a diel rhythm of spawning so that the elapsed time from spawning to capture can be used to assign ages to postovulatory follicles. Farris (1961) demonstrated that *T. symmetricus* spawn only at night, with a peak around midnight, which indicates that the method of Alheit et al. is possible.

It was not practical for us to spawn *T. symmetricus* females in the laboratory, so we used the method of Alheit et al. (1984). We used the time of day of the

trawls (table 1) to estimate the age of *T. symmetricus* postovulatory follicles. Although some gaps existed in the time series (0600–1200 and 1500–2000), we were able to discriminate between postovulatory follicles 0–6 h old, 12–30 h old, 36–54 h old, and older than 60 h. Because degeneration and resorption of postovulatory follicles is a continuous process, we estimated ages based on the extent of changes in the following: the size and apparent shape of the follicle (from large and convoluted to V-shaped and 1/10 of the original size); appearance of the granulosa cells (from many healthy cells with nuclei linearly arranged, to a few cells containing pycnotic nuclei, cytoplasmic vacuoles, and granules); appearance of the lumen; and the size of the thecal layer. The histological characteristics are very similar to those described for *Scomber japonicus* (Dickerson et al. 1992) and northern anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1985a).

Batch Fecundity

Batch fecundity (F, number of oocytes per spawn) was considered to be the number of oocytes in the ovary that either contained migratory nuclei or were hydrated. We used the gravimetric method (Hunter et al. 1985, 1992) to estimate the mean number of such oocytes that each ovary contained. Dioses et al. (1989) showed that location of tissue samples does not affect estimates of batch fecundity in *T. murphyi*, which indicates that such oocytes are dispersed randomly throughout the ovary. We teased apart oocytes in a few drops of 50% glycerin and then identified, counted, and measured them, using a digitizer linked by a video camera system to a dissection microscope. Hydrated ovaries containing new postovulatory follicles were not used to estimate batch fecundity.

TABLE 1

Number of Mature Female Jack Mackerel, *Trachurus symmetricus*, from Trawl Samples Taken off Southern California in 1991

Trawl number	Date		Trawling midpoint hour	Mature females		
	Mo	Day		Total	Non-spawn	Spawn*
1	03	23	1500	11	5	6
2	03	23	2000	20	12	8
3	03	24	2400	18	10	8
6	03	25	2000	20	5	15
7	03	25	2400	20	6	14
8	03	26	1400	21	3	18
9	03	26	2100	10	2	8
10	03	27	0300	10	0	10
11	03	27	2200	20	2	18
13	03	28	2100	21	6	15
15	03	29	2100	20	5	15
17	03	30	2000	19	4	15
18	03	31	2400	21	3	18
19	03	31	2000	20	2	18
20	04	01	0100	10	0	10
22	04	01	2000	20	4	16
23	04	02	0300	5	0	5
24	04	02	2000	5	0	5
26	04	03	0600	10	3	7
27	04	03	2200	22	12	10
28	04	05	2200	21	8	13
29	04	06	1200	6	5	1
31	04	07	0200	5	5	0
32	04	07	2100	18	10	8
33	04	08	0400	10	5	5
34	04	08	2100	20	12	8
36	04	09	2400	10	8	2
All			*N*	413	137	276
			%		33	67

*Sum of the females identified as having spawned in the last 54 hours or as able to do so within 24 hours.

In Formalin-preserved material, migratory-nucleus-stage and hydrated oocytes are easily identified. Hydrated oocytes are very large and translucent, with faint segmentations resulting from the fusing of yolk globules into "large plates." Oocytes with late-stage migratory nuclei are larger and less opaque than the other yolked oocytes and have a wide, clearish band on the periphery resulting from fusing of some yolk globules. In addition, a reflective oil drop (or several if lipid droplets are still fusing) is prominent in the migratory-nucleus and hydrated-oocyte stages. Oocytes at the migratory-nucleus stage are detectable in whole oocyte material only after most of the lipid droplets have come together and begun to fuse. Early stages of the movement and fusion of lipid droplets in migratory-nucleus oocytes can be accurately identified in histological sections, but in whole oocytes the early stages are difficult to see. Our examination of the ovaries of 42 females (33 in which the migratory-nucleus stage was distinct, and 9 in which it was difficult to see) indicated that the stage could be consistently detected when the mean diameter of the migratory-nucleus-stage oocytes was 0.69 mm or larger. This detection criterion may, however, be different for other microscope imaging systems. Only when the migratory-nucleus-stage oocytes averaged 0.69 mm or larger did we use them to estimate batch fecundity.

To compare the number and size of oocytes in the spawning batch to the other oocytes in the ovary, we measured oocyte size-frequency distributions in three females. We measured about 200 oocytes, and identified them by four developmental stages:

1. unyolked but with lipid droplets
2. early yolking
3. advanced yolked
4. about to be spawned—hydrated or with migrating nuclei

We counted the rest of the oocytes in the weighed subsample by stage. For ovaries with oocytes in stages 3 and 4, we measured 30–50 oocytes in each stage, and counted the remaining in each stage.

We estimated the batch fecundity of 33 females: 6 on the basis of counts of hydrated oocytes, and the rest on counts of migratory-nucleus-stage oocytes. In all, 40 females with ovaries containing hydrated oocytes were collected, but 34 of these had ovaries containing new postovulatory follicles, which indicated that they had just begun to spawn and thus were not suitable to be used for estimating batch fecundity.

RESULTS

Spawning Frequency

Of the 415 female jack mackerel ovaries collected and preserved, 413 were histologically classed as mature because they had ovaries containing yolked oocytes or beta atresia. Two females (one from trawl 11 and one from trawl 36) were classed as immature because their ovaries contained no yolked oocytes and no stages of atresia. The ovaries of 67% of the mature females contained postovulatory follicles (≤54 hours old), or hydrated oocytes, or migratory-nucleus-stage oocytes, indicating that these females had spawned within the last 54 hours or would do so within the next 0–24 hours (table 1).

Spawning frequency was calculated on the basis of histological evidence of three different nights:

Spawned on night of capture: late migratory-nucleus-stage oocytes, hydrated oocytes, or new postovulatory follicles in the ovary

Spawned the night before capture: postovulatory follicles 12 to 30 hours old in the ovary

Spawned two nights before capture: postovulatory follicles 36 to 54 hours old in the ovary.

Some histological stages were not used to estimate spawning frequency because we were not confident that their incidence could be consistently determined. We did not use oocytes in the early migratory-nucleus stage, because we were not confident of the time of day when females became fully recruited into this stage. We show the data, however (spawning night A, table 2). It is interesting that the migratory-nucleus stage was first detected at 2000 hours, about 24 hours before the batch would be expected to spawn. We also did not use postovulatory follicles considered to be older than 55 hours, because they can be confused with very late stages of β atresia.

The percentage of mature females spawning per day is estimated from daily spawning rates computed for three different spawning nights: spawning night B, determined on the basis of females with ovaries containing hydrated oocytes or postovulatory follicles, and spawning nights C and D, based on females with ovaries containing postovulatory follicles of different ages. The percentages of mature females spawning on nights B, C, and D were 20.1%, 23.5%, and 16.9% (table 2). The mean of the three estimates was 20.2%, indicating that the average female *T. symmetricus* spawned every 5 days during the 18-day sampling period.

The ovaries of 8% of the mature females contained histological evidence of two spawnings: that is, a single ovary contained postovulatory follicles of two different ages; or postovulatory follicles and hydrated or migratory-nucleus-stage oocytes; or some other combination. Because we knew the approximate age for each of these characters, we were able to calculate the interval between spawnings. The data indicated that 8% of the population spawned at intervals of one to three days (table 3).

Batch Fecundity

The relation between female weight (W, without ovary) and batch fecundity (F) for 33 females with batch fecundity estimates (table 4) was determined by linear regression analysis. In the resulting equation, $F = -11436 + 126W$ with $r^2 = 0.48$, the intercept for the regression of F on W did not differ from zero ($t = -0.62$, df = 32, $P = 0.541$). Therefore, the regression line was forced through 0, yielding the relation $F = 112W$, where W ranged from 586 to 1,262 g (figure 2).

Covariance analysis indicated that the relation between batch fecundity and female weight was different when the ovary contained postovulatory follicles >11 hours old ($F_{1, 30}$ 20.94, $P < 0.001$), and the r^2 improved to 0.68 in the multiple regression equation with the presence of past spawning as a variable. Thus females that had spawned within the last 12–54 hours had lower batch fecundity than those in which no evidence of past spawning was detected. The mean adjusted fecundity for the average (791 g, without ovary) female in our fecundity data set was 73,655 oocytes (SE = 1,116) when evidence existed for past spawning, and 103,797 oocytes (SE = 1,181) when no such evidence existed.

T. symmetricus ovaries usually contained substantially more advanced yolked oocytes than are released in a single spawning batch. This is in sharp contrast to the northern anchovy, in which most of the advanced-yolked oocytes become hydrated and

TABLE 2

Spawning Frequency of *T. symmetricus* on Four Nights (A–D) and the Presence of Histological Characters Indicating Spawning

		Spawning nights						
		A	B			C	D	
Midpoint hour	Trawl ID number	Early migratory-nucleus-stage oocytes	Hydrated oocytes	Hydrated oocytes & new postovulatory follicles	Postovulatory follicles 0–6 hours old	Postovulatory follicles 12–30 hours old	Postovulatory follicles 36–54 hours old	Total number mature females
1200	29	0	0	0	0	1	0	6
1400	8	0	4	9	0	4	2	21
1500	1	0	1	1	0	3	1	11
2000	17	2	0	2	5	7	2	19
	6	3	0	4	1	2	6	20
	22	1	0	2	3	9	2	20
	24	1	0	0	0	2	3	5
	2	4	0	0	2	1	1	20
	19	3	0	5	1	7	5	20
2100	13	1	1	2	0	7	4	21
	15	4	0	1	1	4	6	20
	32	5	0	0	0	2	2	18
	9	3	0	1	3	0	2	10
	34	3	0	1	1	2	1	20
2200	11	2	3	0	4	5	6	20
	28	5	0	0	1	4	5	21
	27	2	0	0	0	5	5	22
24/0	36	0	0	0	0	1	1	10
	7	3	0	0	4	4	5	20
	3	5	0	1	0	1	2	18
	18	4	1	0	7	7	3	21
0100	20	3	0	0	2	3	3	10
0200	31	0	0	0	0	0	0	5
0300	10	1	0	1	4	4	2	10
	23	1	0	0	1	4	0	5
0400	33	0	0	0	1	3	1	10
0600	26	3	0	0	2	5	0	10
All	N	59	10	30	43	97	70	413
Females spawning per night	%	14.3		20.1		23.5	16.9	
	SE	1.8		3.5		2.6	1.9	

Some females have more than one histological character, but no female is counted more than once per given spawning night.

are spawned as a single batch. In the 33 females used to estimate batch fecundity, we also measured the size and estimated the number of the remaining advanced-yolked oocytes (not included in the spawning batch). We determined that the ratio of the number of oocytes in the fecundity batch to the remaining advanced-yolked oocytes was 1.01 (SD = 0.41) and that the average mean diameter of the remaining advanced-yolked oocytes was 0.55 mm (SD = 0.026). Thus, just before spawning, there existed the equivalent of about two batches of advanced-yolked oocytes, one of which would definitely be spawned. Under some circumstances (such as higher water temperature, reduced food availability, or the last spawn) all the advanced oocytes may be hydrated and spawned at once, thus doubling the batch fecundity. Our results also indicated that size modes of oocytes, or an oocyte size threshold should not be used as an alternative to counts of oocytes in the hydrated or migratory-nucleus stages, because they may yield inaccurate estimates of batch fecundity in *T. symmetricus*.

To estimate how many batches of yolked oocytes an ovary contained, we counted all the oocytes larger than 0.25 mm in the ovaries of the three females (A, B, and C) illustrated in figure 3. Histological criteria indicate that 0.25 mm is about the diameter of an oocyte at the onset of vitellogenesis. By dividing the total number of oocytes larger than 0.25 mm by their batch fecundity, we obtained estimates of 6, 4, and 7 batches for females A–C, respectively. Thus *T. symmetricus* ovaries may contain

TABLE 3
Occurrence (+) of Histological Criteria in the Ovaries of 33 Spawning *T. symmetricus* Females Indicating Different Spawning Events

Trawl #	Fish number[a]	Migratory-nucleus oocytes	Postovulatory follicles			Elapsed time between spawnings (day)
			≤6 hours old[b]	12–30 hours old	36–54 hours old	
11	1604	–	+	+	–	1
17	1633	–	+	+	–	1
3	1617	+	–	+	–	2
7	1610	+	–	+	–	2
17	1601	+	–	+	–	2
18	1608	+	–	+	–	2
18	1620	+	–	+	–	2
19	1647	+	–	+	–	2
19	1649	+	–	+	–	2
23	1628	+	–	+	–	2
26	1603	+	–	+	–	2
26	1605	+	–	+	–	2
26	1607	+	–	+	–	2
27	1613	+	–	+	–	2
28	1617	+	–	+	–	2
32	1618	+	–	+	–	2
8	1619	–	+	–	+	2
10	1607	–	+	–	+	2
18	1617	–	+	–	+	2
22	1611	–	+	–	+	2
6	1618	+	–	–	+	3
7	1605	+	–	–	+	3
9	1610	+	–	–	+	3
10	1604	+	–	–	+	3
11	1602	+	–	–	+	3
15	1612	+	–	–	+	3
17	1625	+	–	–	+	3
18	1628	+	–	–	+	3
19	1608	+	–	–	+	3
20	1618	+	–	–	+	3
24	1699	+	–	–	+	3
27	1620	+	–	–	+	3
28	1602	+	–	–	+	3

[a]Females are listed in order of time elapsed between spawnings.
[b]Ovary may also contain hydrated oocytes; ovaries of two females (11–1604 and 18–1617) contained only hydrated oocytes. Because spawning was imminent, they are included in this group.

the equivalent of 4–7 spawning batches of yolked oocytes, if one includes oocytes in the earliest vitellogenic stages.

Annual Spawning Cycle and Ovarian Atresia

The atretic state of *T. symmetricus* ovaries taken in this study is best considered within the context of the annual spawning cycle. According to monthly averages of the standing stock of jack mackerel larvae in the California Current from 1951 to 1984 (Moser et al. 1993), about 27% of the season's production had been completed by the end of the cruise. During the cruise period, about 10% of the average number of larvae produced in a year were spawned (shaded area in figure 4).

Our analysis of ovarian atresia indicates that about 5% of the *T. symmetricus* in the collection area had ended or were close to ending spawning for the year. The ovaries of 3 (0.7%) of the 413 mature females were classified as inactive and were judged not able to spawn at the time of capture or in the near future because they contained beta atresia but no yolked oocytes. The presence of beta atresia in these ovaries indicated that the ovaries may have been active during the current season (Hunter and Macewicz 1985b). An additional sign of season completion, for 4% of the females, was the presence in their ovaries of the alpha stage of atresia in 50% or more of the yolked oocytes (Hunter and Macewicz 1980, 1985b). This lends credence to our assumption that this highly atretic condition is related to the end of spawning for female *T. symmetricus*. Finally, the small loss (4.7%) of females to the spawning population seems reasonable, since only about a fourth of the production for the spawning season had been completed.

TABLE 4

Batch Fecundity (Number of Oocytes to Be Spawned in the Batch) of 33 *T. symmetricus* Females Taken March 23–April 9, 1991, and 2 Females Taken May 27, 1970

Year	Fork length (mm)	Weight without ovary (g)	Ovary weight (g)	Batch fecundity	Postovulatory follicles*
1991					
	383	586.4	24.612	51,987	+
	393	598.2	44.786	52,965	+
	395	605.5	21.508	52,147	–
	415	632.9	31.102	63,997	+
	398	637.7	26.343	52,736	+
	382	638.5	47.462	75,915	–
	396	643.8	41.250	56,395	–
	400	654.6	62.410	82,476	+
	394	659.3	31.707	73,392	+
	406	665.0	47.000	109,593	–
	412	668.8	25.230	61,628	+
	403	671.4	22.568	31,752	+
	406	697.6	29.357	72,269	–
	417	706.2	27.754	86,400	–
	413	722.5	25.455	48,360	+
	405	735.8	33.952	70,205	+
	423	739.9	32.126	59,946	+
	422	744.8	29.226	91,661	–
	429	755.5	42.482	129,838	–
	417	756.7	35.283	100,267	–
	423	761.7	99.310	115,847	–
	422	775.4	32.637	81,073	+
	432	776.7	40.255	123,961	–
	421	793.5	35.530	85,795	–
	435	826.8	54.153	120,063	–
	454	902.3	39.669	72,685	+
	445	904.3	64.735	112,648	–
	440	945.8	63.191	134,716	–
	485	1105.9	46.083	94,654	+
	493	1160.8	64.237	164,711	+
	492	1162.8	58.214	116,788	+
	504	1194.3	58.669	94,543	+
	488	1262.4	123.550	171,466	–
1970					
	543	1576.2	141.8	192,000	*
	540	1602.0	120.0	159,000	*

*+ = presence of postovulatory follicles 12 to 54 hours old, indicating these females had spawned recently.
* = unknown if postovulatory follicles were present, data are from MacGregor 1976.

About a third of the females had ovaries containing minor levels of alpha-stage atresia (less than 50% of yolked oocytes affected). This condition seemed surprisingly common (35% of the mature females), since only a fourth of the season's production had been completed. In comparison, during the peak months of the northern anchovy spawning season, females classed in this state—i.e., containing minor levels of alpha atresia—constitute only about a twentieth of the population (Hunter and Macewicz 1985b).

DISCUSSION

This study indicates that jack mackerel, *Trachurus symmetricus*, females spawn many times during the year. The average *T. symmetricus* female spawned 3.6 times during the 18-day sampling period. Over the same period about 10% of the annual crop of *T. symmetricus* larvae were produced (figure 4), according to the annual larval production curve from Moser et al. (1993). Thus the average female may spawn 36 times per year according to these data.

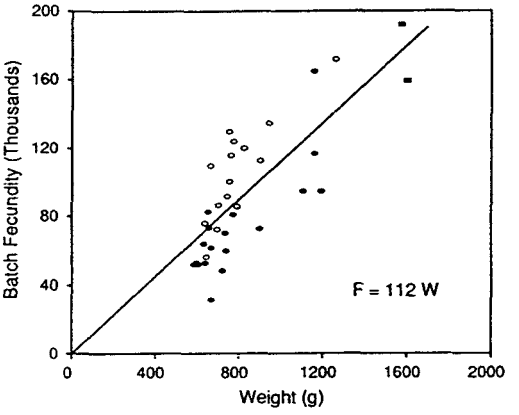

Figure 2. Batch fecundity (F) of *Trachurus symmetricus* as a function of female weight (W, without the ovary); the batch was estimated from numbers of migratory-nucleus-stage oocytes or hydrated oocytes; regression line was forced through zero. *Closed circles* = females that had spawned 12 to 54 hours before capture; *open circles* = females with no histological evidence of a past spawning; *Squares* = females with unknown spawning history, from MacGregor 1976.

Data from two other studies indicate high spawning rates in *T. symmetricus*. The frequency of *T. symmetricus* females with ovaries containing hydrated oocytes ranged from 0 to 24% in monthly sets of samples compiled over several years by Wine and Knaggs (1975) from southern California data. Wine and Knaggs did not intend for their data to be used to estimate spawning frequency, and biases could exist because of sampling during inappropriate times of day (DeMartini and Fountain 1981; Schaefer 1987). Lisovenko and Andrianov (1991) used the hydrated-oocyte method to estimate spawning frequency for *Trachurus murphyi* taken off Peru in 1980–85. Our interpretation of their data indicate that the average *T. murphyi* female may spawn about 15 times per year. Wine and Knaggs's data indicate about 21 spawnings for *T. symmetricus*, whereas our initial guess for *T. symmetricus*, based on our point estimate and the average larval production curve, was about 36 spawnings. All data considered, 25 spawnings per year seems a reasonable guess of the annual number of spawnings for the average female *Trachurus*. This means that the average *T. symmetricus* female may spawn about 2,800 oocytes per gram

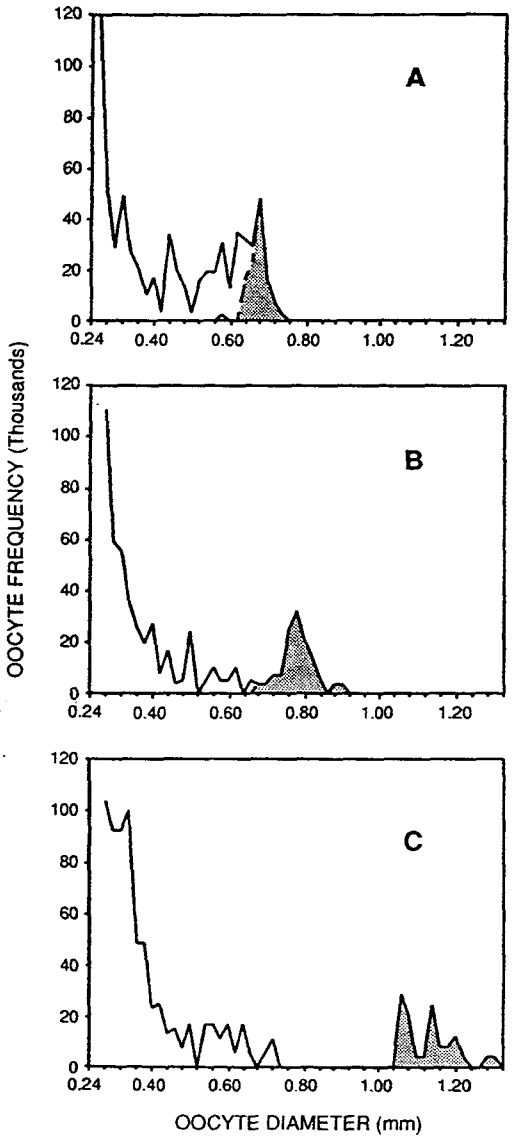

Figure 3. Oocyte size-frequency distributions of three *Trachurus symmetricus* females showing progressive maturation of a spawning batch from female A to female C. *Shaded area* = batches about to be spawned: in *A*, early migratory-nucleus-stage oocytes (mean diameter = 0.67 mm); in *B*, well-advanced migratory-nucleus-stage oocytes (mean diameter = 0.78 mm); and in C, hydrated oocytes (mean diameter = 1.13 mm).

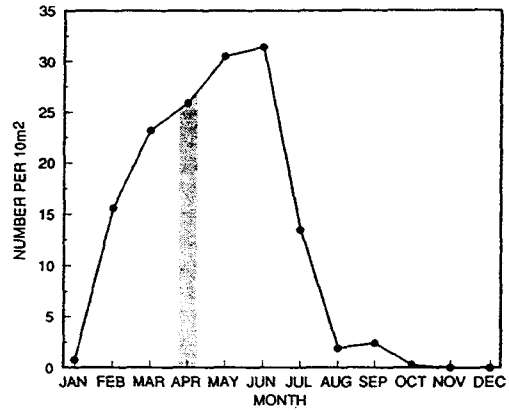

Figure 4. Annual spawning season as indicated by the average number of *Trachurus symmetricus* larvae per 10 m² taken in the CalCOFI surveys 1958–84, from Moser et al. 1993. *Shaded area* indicates portion of spawning season considered in this paper.

body weight per year (25 × 112). More accurate data, particularly age-specific data, would be highly desirable.

The potential annual fecundity of various *Trachurus* species has been estimated over the years (Chigirinskiy 1970; Kaiser 1973; Macer 1974; Andrianov 1985; Arruda 1986), but we suspect these data are a loss. Owing to the high spawning rates of *Trachurus* indicated by this study and the two cited above, and the limited number of batches of yolked oocytes in the ovary, it seems unlikely that the standing stock of yolked oocytes in the ovary at the beginning of the spawning season is an accurate measure of annual fecundity in any *Trachurus* species. In other words, it is probably preferable to consider annual fecundity as being indeterminate in *Trachurus*. Thus the only accurate way to measure annual fecundity is to measure spawning frequency and batch fecundity throughout the spawning season.

Only a few studies of batch fecundity exist for *Trachurus*, and most of these are not particularly useful for making comparisons. We believe that only the two determinations based on hydrated oocytes are useful in MacGregor's (1976) preliminary study of *T. symmetricus*; for the other 28 of his specimens, MacGregor may have used inaccurate criteria (all dense-yolked oocytes) to identify the oocytes composing the batch in *T. symmetricus*. Paschenko[1] identified the spawning batch as all oocytes above 0.50 mm (as shown in MacGregor 1976, figure 2) so his fecundities are probably overestimated. It is obvious

[1]Paschenko, V. M. Distribution, biology and biomass assessment of the jack mackerel *Trachurus symmetricus* (Ayres). Presented to the 1979 U.S.–U.S.S.R. Bilateral Meeting on Fisheries Assessment in the North Pacific, Seattle, June 5–8, 1979.

from our few oocyte size-frequency distributions that all the dense-yolked oocytes are not spawned at once, because only about half of them undergo final maturation synchronously. Chigirinskiy (1970) also used an inaccurate oocyte criterion for identifying the spawning batch of *T. japonicus* (yolked oocytes >0.38-mm diameter). Although Lisovenko and Andrianov (1991) used hydrated oocytes to identify the oocytes composing the spawning batch in *T. murphyi*, they do not give the weight or length of the females; consequently, comparison to their study is difficult. The most useful study is that of Dioses et al. (1989), who used hydrated oocytes to estimate batch fecundity of *T. murphyi* off Peru. The relative batch fecundity of *T. murphyi* in his study—about 235 oocytes per gram female weight—is about twice that of *T. symmetricus* in this study (112 oocytes per gram).

Batch fecundity may change seasonally in *T. symmetricus*, as it does in a number of other fishes (Conover 1985; Alheit 1987; Kjesbu 1989). Two kinds of indirect evidence suggest a possible seasonal change in batch fecundity. First, females with low levels of ovarian atresia were more prevalent than expected, considering that only 27% of the year's spawnings had been completed. These females appeared to continue spawning at undiminished rates, but atretic losses may have reduced the batch size. Second, batch fecundity was lower in females with evidence of past spawning, indicating that there may be a link between batch fecundity and spawning rate.

ACKNOWLEDGMENTS

D. Abramenkoff collected the samples on shipboard. M. Stepanenko, Y. Yermakov, and all the other scientists and the crew of the Russian ship *Novodrutsk* contributed greatly to the success of the cruise. M. Wilkins coordinated the cooperative Russian–U.S. cruise. N. C. H. Lo gave considerable statistical advice. The suggestions of L. Jacobson and the two anonymous reviewers greatly improved the manuscript, and R. Allen improved the illustrations.

LITERATURE CITED

Ahlstrom, E. H., and O. P. Ball. 1954. Description of eggs and larvae of the jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish. Wildl. Serv. Fish. Bull. 97(56):209–245.

Alheit, J. 1987. Variation of batch fecundity of sprat, *Sprattus sprattus*, during spawning season. ICES CM 1987/H:44, 9 pp.

Alheit, J., V. H. Alarcon, and B. J. Macewicz. 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25:43–52.

Andrianov, D. P. 1985. Study on the reproduction of Peruvian scad, *Trachurus murphyi* (Carangidae), of the Peruvian shelf. J. Ichthyol. 25(2):32–40.

Arruda, L. M. 1986. Fecundity of horse mackerel *Trachurus trachurus* (L. 1758) off the Portuguese coast. Inv. Pesq. 50(4):565–570.

Bretschneider, L. H., and J. J. Duyvene de Wit. 1947. Sexual endocrinology of non-mammalian vertebrates. Monogr. Prog. Res., vol. II. N.Y.: Elsevier.

Chigirinskiy, A. I. 1970. The nature of oogenesis and fecundity in the Japanese horse makcerel [*Trachurus japonicus* (Temminck et Schlegel)]. J. Ichthyol. 10(6):755–760.

Conover, D. O. 1985. Field and laboratory assessment of pattern in fecundity of a multiple spawning fish: the Atlantic silverside, *Menidia menidia*. Fish. Bull., U.S. 83:331–341.

DeMartini, E. E., and R. K. Fountain. 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547–560.

Dickerson, T. L., B. J. Macewicz, and J. R. Hunter. 1992. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Calif. Coop. Oceanic Fish. Invest. Rep. 33:130–140.

Dioses, T., V. H. Alarcon, M. H. Nakama, and A. Echevarria. 1989. Desarrollo ovocitario, fecundidad parcial y distribucion vertical de los cardumenes en desove del jurel *Trachurus murphyi* (N). Pacifico Sur (Numero Especial) 1989:287–294.

Farris, D. A. 1961. Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). U.S. Fish. Wildl. Serv. Fish. Bull. 61(187):247–279.

Hunter, J. R., and S. R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

Hunter, J. R., and B. J. Macewicz. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.

———. 1985a. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 79–94.

———. 1985b. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:119–136.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*), R. Lasker, ed. NOAA Tech. Rep. NMFS 36, pp. 67–77.

Hunter, J. R., B. J. Macewicz, N. C. H. Lo, and C. A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull., U.S. 90:101–128.

Kaiser, C. E. 1973. Gonadal maturation and fecundity of horse mackerel *Trachurus murphyi* (Nichols) off the coast of Chile. Trans. Amer. Fish. Soc. 102(1):101–108.

Kjesbu, O. S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish. Biol. 34:195–206.

Kramer, D., and P. Smith. 1970. Seasonal and geographic characteristics of fishery resources. Calif. Current Region–I. Jack mackerel. Commer. Fish. Rev. 32(5):27–31.

Lambert, J. G. D. 1970. The ovary of the guppy, *Poecilia reticulata*. The atretic follicle, a *corpus atreticum* or a *corpus luteum praeovulationis*. Z. Zellforsh 107:54–67.

Lisovenko, L. A., and D. P. Andrianov. 1991. Determination of absolute fecundity of intermittently spawning fishes. J. Ichthyol. 31(9): 143–155.

MacCall, A. D., and G. D. Stauffer. 1983. Biology and fishery potential of jack mackerel (*Trachurus symmetricus*). Calif. Coop. Oceanic Fish. Invest. Rep. 24:46–56.

MacCall, A. D., H. W. Frey, D. D. Huppert, J. A. McMillan, and G. D. Stauffer. 1980. Biology and economics of the fishery for jack mackerel in the northeastern Pacific. NOAA Tech. Memo. NMFS 4.

Macer, C. T. 1974. The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. J. Fish Biol. 6:415–438.

Macewicz, B. J., and D. N. Abramenkoff. 1993. Collection of jack mackerel, *Trachurus symmetricus*, off southern California during 1991

cooperative U.S.–U.S.S.R. cruise. SWFSC Admin. Rep., La Jolla, LJ-93-07, 13 pp.

MacGregor, J. S. 1976. Ovarian development and fecundity of five species of California Current fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 18:181–188.

Mason, J. E. 1991. Variations in the catch of jack mackerel in the southern California purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 32:143–151.

Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. 1993. Distributional atlas of fish larvae and eggs in the California Current region: taxa with 1000 or more total larvae, 1951 through 1984. Calif. Coop. Oceanic Fish. Invest. Atlas 31.

Schaefer, K. M. 1987. Reproductive biology of the black skipjack, *Euthynnus lineatus*, an eastern Pacific tuna. Inter-Amer. Trop. Tuna Comm. Bull. 19(2):169–260.

Wallace, R. A., and K. Selman. 1981. Cellular and dynamic aspects of the oocyte growth in teleosts. Am. Zool. 21:325–343.

Wine, V. L., and E. H. Knaggs. 1975. Maturation and growth of jack mackerel, *Trachurus symmetricus*. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 21:1–26.

Zweifel, J. R., and R. Lasker. 1976. Prehatch and posthatch growth of fishes – a general model. Fish. Bull., U.S. 74:609–621.