SPAWNING FREQUENCY AND BATCH FECUNDITY OF CHUB MACKEREL, *SCOMBER JAPONICUS*, DURING 1985

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ABSTRACT

The average female *Scomber japonicus* collected from April through July of 1985 spawned 8.8 times during the 101-day sampling period. The average interval between spawns was 1.3 days in 32 females with more than one spawning stage in their ovary. The average batch fecundity was 68,400 oocytes, or 168 oocytes per gram female wet weight (without ovary).

RESUMEN

Hembras de *Scomber japonicus* colectadas de Abril a Julio de 1985 desovaron en el periodo de muestreo de 101 días un promedio de 8.8 veces. Treinta y dos hembras tuvieron un intervalo promedio entre los desoves de 1.3 días; los ejemplares poseían más de un estadio de desove en sus ovarios. La fecundidad por cada puesta del grupo promedió 68,400 ovocitos, equivalentes a 168 ovocitos por gramo de hembra (peso húmedo; excluyendo el ovario).

INTRODUCTION

Scomber japonicus, chub mackerel, spawn more than once per season (Knaggs and Parrish 1973; Peña et al. 1986; Asano and Tanaka 1989), but the frequency is unknown. The objective of this study was to determine the frequency of spawning and estimate batch fecundity (number of oocytes per spawn) of *S. japonicus*.

MacGregor (1976) believed that the standing stock of yolked oocytes in the ovary of *S. japonicus* before spawning equalled the potential fecundity for the year, a condition called determinate fecundity (Hunter and Macewicz 1985a). But recent studies of other scombroid fishes indicate that fecundity is not fixed at the beginning of year for black skipjack, *Euthynnus lineatus* (Schaefer 1987); skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986); or yellowfin tuna, *Thunnus albacares* (Schaefer 1988; McPherson 1991). These fishes spawn many times, yielding annual fecundities far greater than the standing stock of yolked oocytes at the beginning of the spawning season. This latter condition is called indeterminate annual fecundity (Hunter et al. 1985). It seems certain that the Atlantic mackerel, *Scomber scombrus* L., spawns more than once per season (Bara 1960; Marídueña 1984), but debate continues about whether the fecundity of *S. scombrus* is determinate or indeterminate (Macer 1976; Johnson 1977; Alheit et al. 1987; Anon 1987; Greer Walker et al. 1987; Watson et al. 1992; Priede and Watson, in press).

To determine whether fecundity of *S. japonicus* is determinate or indeterminate, we compare the production of spawn over our survey period (batch fecundity × daily spawning frequency × survey duration in days) to MacGregor's (1976) estimates of annual fecundity. If *S. japonicus* is determinate, the production of spawn should be lower for our survey period, since we sampled only the peak months of spawning and not the whole season (March to October; Schaefer 1980).

In addition to clarifying the issue of fixed annual fecundity, our estimates of spawning and fecundity rates for *S. japonicus* are of general interest. As a preliminary measure of reproductive effort of the species, they are the baseline data essential for estimating *S. japonicus* biomass from the abundance of eggs or larvae.

METHODS

From April 2 to July 11, 1985, we collected 329 female *S. japonicus* in a series of 30 opportunistic collections taken in the Southern California Bight with hook-and-line or purse seine gear (table 1). All but two of the collections were made during the day, between 0700 and 1510; the two night collections were made between 1955 and 2045 (collection 29) and between 2330 and 0015 (collection 6).

The fish were sexed and measured (fork length), and the females were assigned a maturity stage from the California Department of Fish and Game's (CDFG) standard maturity guide for wetfish (table 2). The guide, based on gross anatomical criteria, is a modified version of the Hjort index (Hjort 1910). Ovaries were removed and preserved in 10% neutral buffered Formalin. The otoliths were removed, and annual growth rings were counted to determine age (year class). Sampling was continued until 20 ran-

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TABLE 1

Number of Female *S. japonicus* per Collection, with Histological Identification

Coll. number	Date		Location		Number of females[1]			
						Mature		
	Mo.	Day	°N	°W	Immature	A[2]	P[3]	Total
1	4	02	33.25	117.38	1	0	0	1
2	4	04	33.43	118.16	2	0	1	3
3	4	05	33.48	118.25	8	3	9	20
4	4	11	33.45	118.09	8	1	11	20
5	4	19	33.44	118.06	3	0	0	3
6	4	21	34.24	119.45	4	0	16	20
7	4	26	33.22	117.36	3	4	3	10
8	5	01	33.45	118.09	3	3	13	19
9	5	05	33.36	117.58	0	5	3	8
10	5	07	33.45	118.09	1	1	3	5
11	5	08	33.24	117.37	0	6	5	11
12	5	09	33.45	118.09	4	0	1	5
13	5	15	33.43	118.16	0	3	17	20
14	5	16	34.27	120.32	0	1	0	1
15	5	17	33.43	118.16	1	5	14	20
16	5	21	33.45	118.09	5	2	7	14
17	5	23	33.43	118.16	0	2	8	10
18	5	30	33.43	118.16	0	0	5	5
19	5	31	33.45	118.09	1	0	7	8
20	6	04	33.45	118.09	1	3	7	11
21	6	05	33.27	117.43	0	7	0	7
22	6	07	33.45	118.09	4	6	10	20
23	6	12	33.27	117.40	0	19	1	20
24	6	21	33.45	118.09	2	3	11	16
25	6	21	33.43	118.14	0	9	1	10
26	6	26	33.27	117.43	5	5	0	10
27	6	30	33.33	117.49	0	8	0	8
28	7	02	33.45	118.09	2	7	11	20
29	7	04	32.47	117.17	0	1	2	3
30	7	11	33.43	118.16	0	1	0	1
All					58	105	166	329

[1]All females were collected off southern California in 1985. Collection 6 was taken by purse seine, the rest by hook and line.
[2]Active: ovaries contain yolked oocytes; if α atresia of yolked oocytes was present, less than 50% of the oocytes were affected.
[3]Postspawning: ovaries with 50% or more of the yolked oocytes in α-stage atresia, or ovaries without yolked oocytes in which β-stage atresia was present.

dom females had been obtained or until no more fish were available in a particular catch.

Ovaries were prepared according to histological techniques described by Hunter and Goldberg (1980) and Hunter and Macewicz (1985a), and the resulting histological slides were analyzed and classified. Rates of absorption of postovulatory follicles were verified from ovaries of 73 females spawned in the laboratory using procedures of Leong (1971). We also used the histological classifications to evaluate the gross anatomical grading scale routinely used by CDFG to assess the reproductive state of *S. japonicus*. Finally, we estimated batch fecundity, using the hydrated oocyte method of Hunter et al. (1985).

TABLE 2

Anatomical Classification Used by California Department of Fish and Game to Identify Mature *S. japonicus*

Stage	Description
[*Immature*]*	
1	Virgin individuals. Very small sexual organs close under vertebral column. Females: often wine-colored, with torpedo-shaped ovaries. Eggs invisible to naked eye. Males: testes very small, knife-shaped, and quite thin. In chub mackerel, testes can be longer than half the ventral cavity.
[*Mature*]*	
2	Maturing virgins or recovering spents. Females: ovaries longer than half the ventral cavity. Eggs may or may not be visible to naked eye. Males: testes easily identifiable, but still thin and knife-shaped.
3	Sexual organs swelling. Eggs definitely visible to naked eye. Ovaries and testes occupying about half the ventral cavity.
4	Ovaries and testes filling nearly ⅔ of ventral cavity. Eggs still opaque. Testes swollen, milt whitish.
5	Ovaries and testes filling ventral cavity. Ovaries often with some large transparent eggs.
6	Roe and milt running. Slight pressure on belly of fish exudes roe or milt.

*Heading not a part of CDFG classification system.

Histological Classification

The oocytes of *S. japonicus* ovaries develop asynchronously; that is, oocytes in many stages of development occur simultaneously in reproductively active ovaries (Wallace and Selman 1981). We used the simplified classification system described by Hunter and Macewicz (1985a, b) to describe the ovaries of *S. japonicus*, instead of the more detailed systems common in teleost literature (see, for example, Andrews[1] or Bara 1960). We categorized the most developed mode of oocytes for each ovary as either unyolked, partially yolked, yolked, or hydrated. We examined the nucleus of the yolked oocytes to see if it had begun to migrate to the animal pole; migration of the nucleus is the precursor to hydration and begins about 24 hours before spawning (Hunter and Macewicz 1985a). After ovulation, the follicles surrounding the hydrated oocytes remain in the ovarian tissue, where they degenerate and are resorbed. All postovulatory follicles were identified and subsequently aged.

The ovarian sections were graded for the presence of alpha (α) atresia of yolked oocytes and grouped into $\alpha < 50\%$ (0 to 49% of the yolked oocytes are in α-stage atresia) or $\alpha \geq 50\%$ (50% or more of the yolked oocytes are in α-stage atresia). Any presence

[1]C. B. Andrews. 1931. Unpublished manuscript: The development of the ova of the California sardine (*Sardina caerulea*). Stanford University, Stanford, Calif. 88 pp.

of beta (β) atresia was also noted. In northern anchovy β atresia follows α-stage atresia of yolked oocytes (Hunter and Macewicz 1985b); we assumed the atretic process was the same in *S. japonicus*. We analysed ovarian atresia (resorption of oocytes) to determine if a female had finished spawning for the season (Hunter and Macewicz 1980, 1985b).

In order to evaluate our histological analyses, it is necessary to define terms for the reproductive status of female *S. japonicus*:

Immature: Females that have never spawned and cannot be expected to do so in the current reproductive season.

Mature: Females that have spawned in the current reproductive season or can be expected to do so.

Active: Mature females capable of spawning at the time of capture or by the end of our sampling period. The ovaries of these females contain yolked oocytes; if α atresia of yolked oocytes is present, less than 50% of the oocytes are affected. Postovulatory follicles may be present.

Postspawning: Mature females incapable of spawning at the time of capture or in the near future but that have spawned previously. Females are considered to be recent postspawning when in their ovaries 50% or more of the yolked oocytes are in the α stage of atresia, and to be late postspawning when there are no yolked oocytes, but β-stage atresia is present in the ovary.

Spawning Frequency

Laboratory calibration. To measure the rate of spawning using postovulatory follicles one must be able to stage the postovulatory follicles according to their age and know how long such stages last. Ovaries from *S. japonicus* induced to spawn in the laboratory were preserved at 0, 6, 12, 18, 24, 48, and 72 hours after spawning, and analyzed. The histological characteristics of *S. japonicus* ovaries are similar to those described for *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985a,b) and *K. pelamis* (Hunter et al. 1986), except that red blood cells are occasionally observed in the lumen of postovulatory follicles. The degeneration and resorption of *S. japonicus* postovulatory follicles are described below as a function of elapsed time after spawning, when fish are held at 20°C.

0–3 hours: Within a few hours after spawning, no degeneration of the follicle is evident. Other characteristics at this time include a convoluted shape with many folds or loops; a lumen containing little granular or particulate material; a definite granulosa cell layer lining the lumen; linearly arranged, cuboidal granulosa cells with prominent healthy nuclei; and a clearly defined thecal connective tissue layer with blood capillaries (figure 1).

6 hours: Similar to a 0–3-hour-old postovulatory follicle, except that degeneration of the postovulatory follicle is evident because a few of the nuclei of the granulosa cells are dense or pycnotic.

12–18 hours: Additional signs of degeneration of the postovulatory follicle are evident. The postovulatory follicle is smaller than it was at 6 hours, and it has fewer convolutions. The granulosa layer still comprises numerous cells, although some cytoplasmic vacuoles or granules are present, and cell membranes are less distinct. More of the granulosa nuclei are pycnotic, and the nuclei are not always linearly arranged. The thecal layer appears slightly thicker than at 6 hours because the follicle has compacted.

24 hours: The postovulatory follicle is about half the size of one at 0–3 hours, and the shape is more angular, with fewer folds. The lumen is smaller and may contain red blood cells. The granulosa layer has degenerated further than at 18 hours; there are fewer cells, some pycnotic nuclei, few intact cell membranes, numerous vacuoles, and no alignment of nuclei. The thecal layer remains a distinct, thick band of cells (figure 1).

48 hours: Very few granulosa nuclei remain in the postovulatory follicle. Although the thecal layer appears thick, the follicle is small, about ⅓ the size at 24 hours, and can be confused with late-stage β atresia (Hunter and Goldberg 1980; Hunter and Macewicz 1985a).

72 hours: The postovulatory follicles are completely resorbed or are indistinguishable from late β atresia.

Analysis of field data. Postovulatory follicles in ovaries of field-caught *S. japonicus* were assigned an age (time after spawning) using the characteristics described above, the time of collection, and the estimated time of peak spawning (about 2200; Schaefer 1980). Twenty-eight collections were taken during the day, when females have oocytes with migratory nuclei, but no oocytes that are fully hydrated. We considered these fish to be capable of spawning on the evening following their capture because we believe that the migratory-nucleus stage persists in the ovary for less than 24 hours, as in Pacific sardine and northern anchovy. We are not able to verify this point because our field samples were taken during the day. But the absence of any fully hydrated oocytes during the day clearly indicates that hydration lasts less than 24 hours.

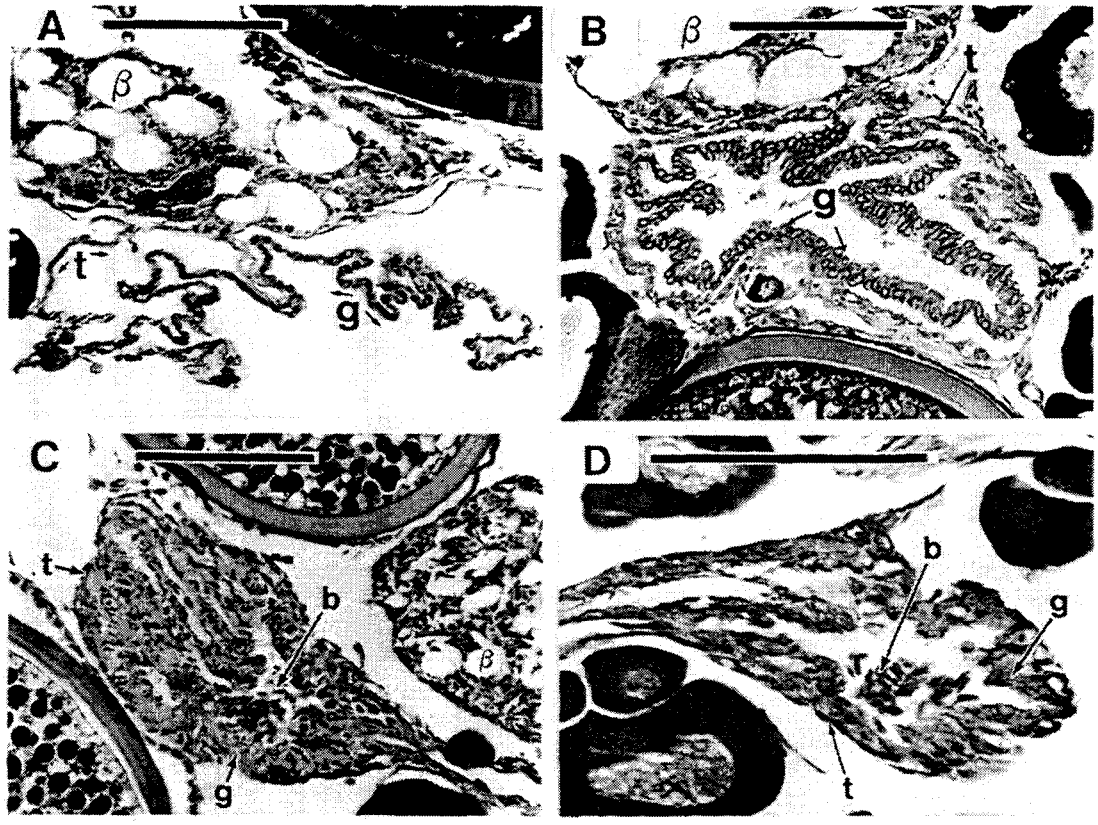

Figure 1. Postovulatory follicles from *S. japonicus* spawned in the laboratory (induced by hormones). No degeneration is evident in *A* (at ovulation) or in *B* (1 hour after spawning). By 24 hours after spawning (*C* and *D*), degeneration is considerable. Bars = 0.1 mm; b = red blood cells; g = granulosa cell layer; t = thecal connective cell layer; β = beta atresia.

To estimate spawning frequency, we identified in each spawning female the presence or absence of the following:

- oocytes with migratory nuclei
- hydrated oocytes within the follicles
- new postovulatory follicles (0–9 hours) and hydrated oocytes
- postovulatory follicles 10–33 hours old
- postovulatory follicles 34 or more hours old

Some of the ovaries contained more than one age of postovulatory follicles (figure 2); others contained oocytes with migratory nuclei as well as postovulatory follicles. All spawning stages were identified, and any combination of these five stages was recorded for each fish.

Batch Fecundity

We estimated the batch fecundity of 13 females. Batch fecundity for each female was the mean of three estimates. Each estimate was calculated by $(N/T_w)O_w$, where N is the number of oocytes in the late migratory-nucleus stage in a weighed tissue sample of the ovary (T_w), and O_w is the ovary weight (Hunter et al. 1985). Tissue could be taken from any location in the ovary, since Peña et al. (1986) showed that with the hydrated oocyte method, location does not affect the estimate of batch fecundity. The migratory-nucleus stage immediately precedes hydration (Hunter and Macewicz 1985a). Oocytes with migratory nuclei can be seen in Formalin-preserved ovaries because they are larger and less opaque than the other yolked but nonhydrated oocytes, and they

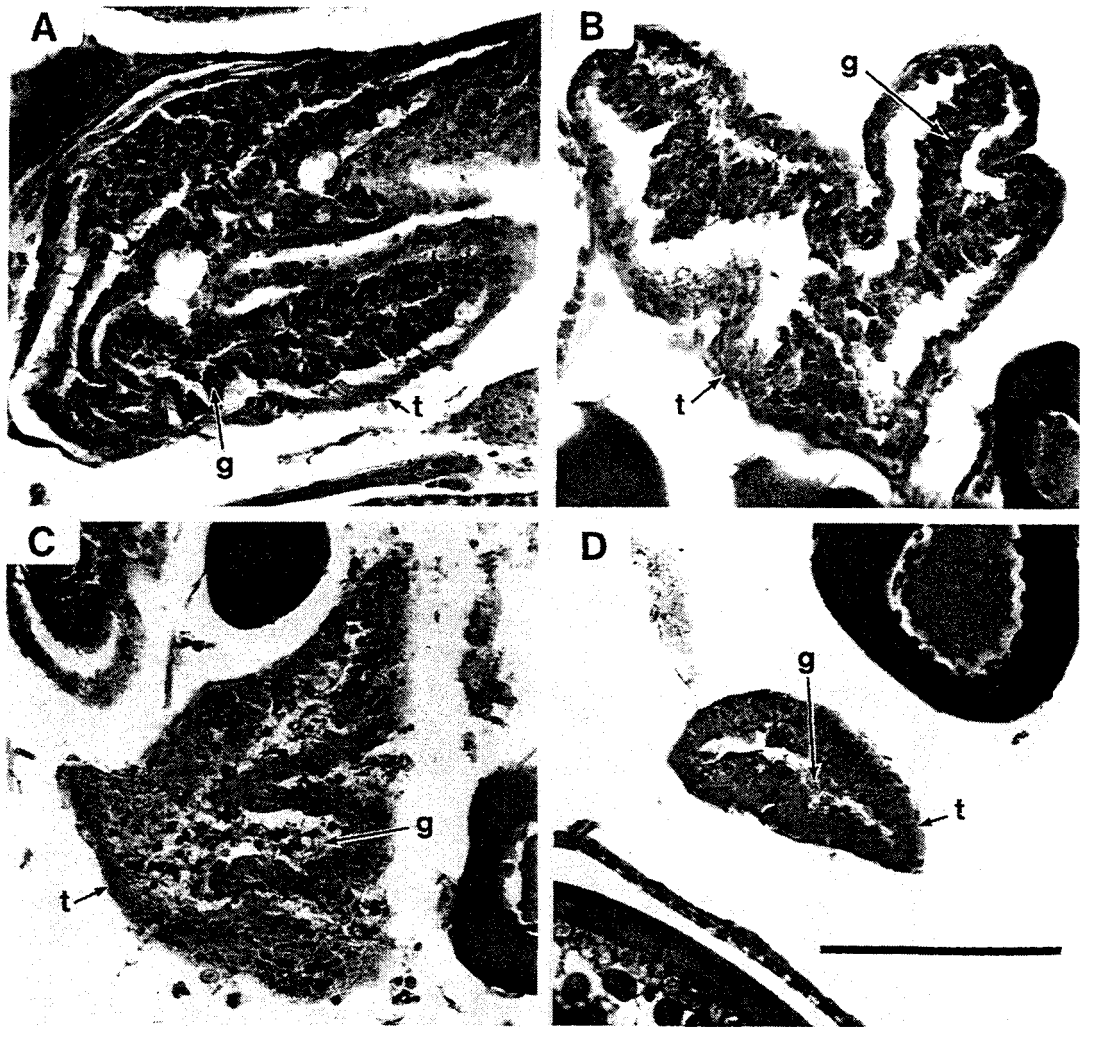

Figure 2. Multiple stages of postovulatory follicles from two *S. japonicus* females collected in the field. Female 9-03 contained postovulatory follicles aged 0–3 hours (*A*) and about 24 hours old (*C*) in her ovary. Female 26-06 contained postovulatory follicles about 12 hours old (*B*) and more than 33 hours old (*D*). Same magnification for *A* to *D*; bar = 0.1 mm; g = granulosa cell layer; t = thecal connective cell layer.

have a clear band on the periphery resulting from the initial fusing of the yolk globules. The more advanced oocytes have a single oil droplet.

RESULTS AND DISCUSSION

Spawning Frequency

Of the 329 female *S. japonicus* analyzed, 271 were mature. Of the mature females, 58 had spawned or would imminently spawn because their ovaries contained postovulatory follicles or oocytes with migratory nuclei (table 3).

The best measures of the percentage of females that spawned per day were the percentage of the mature females having oocytes with migratory nuclei (8.1%), and the percentage of the mature females with postovulatory follicles 10–33 hours old (9.2%). Females with postovulatory follicles older than 34 hours were not used because we were uncertain about their age. Since the oocytes with migratory nuclei and the postovulatory follicles 10–33 hours old indicate different spawning events (figure 3), they can be used as two independent estimates of spawning frequency. The mean of the two estimates

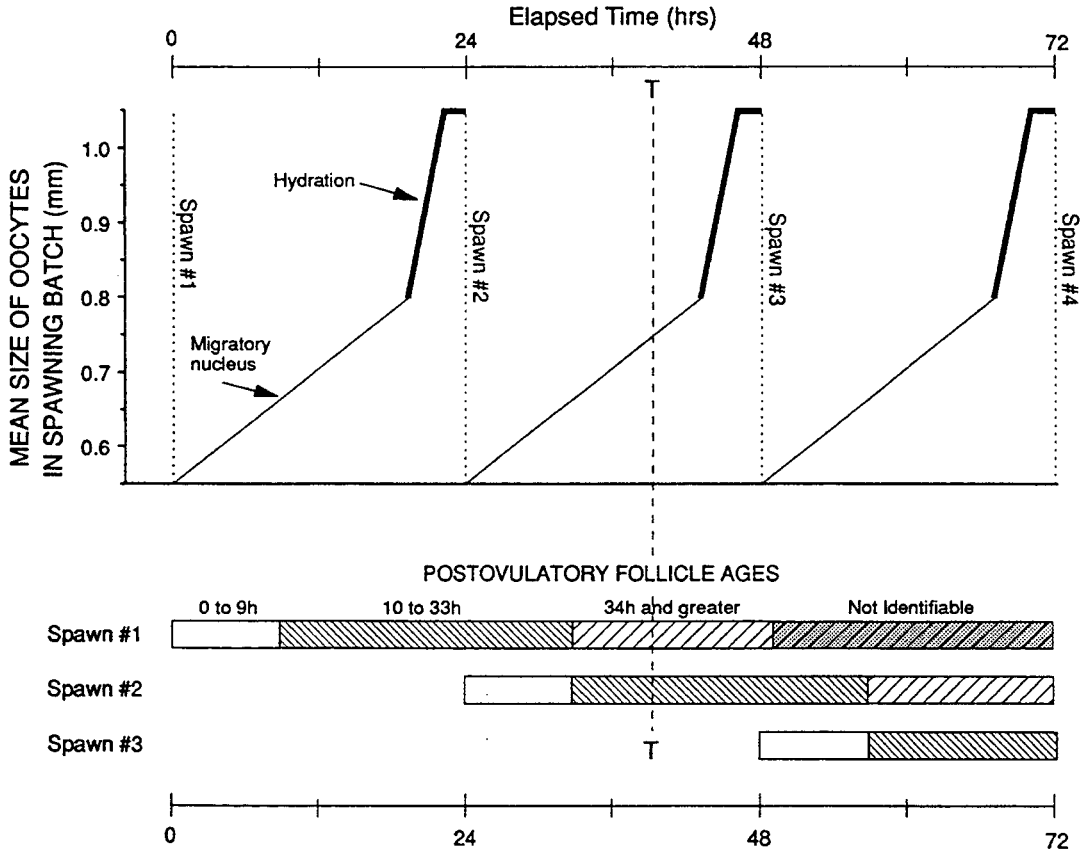

Figure 3. Conceptual diagram showing when various histological stages could be identified in an ovary of an *S. japonicus* female that spawned every day. Stages include migratory nucleus and hydration (0–24 hours before spawning), and postovulatory follicles 0–9 hours old, 10–33 hours old, and 34 hours and older. If a female is collected at time T in the cycle, three spawnings can be identified in the ovary: oocytes with migratory nuclei for spawn #3; 14-hour-old postovulatory follicles from spawn #2; and postovulatory follicles 38 hours old from spawn #1. Stippled area indicates period when postovulatory follicles may be confused with late β atresia.

was 8.7%, indicating that 8.7% of the females spawned per day, or that the average female *S. japonicus* spawned every 12 days. Because the sampling period was 101 days long, this estimate also indicates that the average female spawned 8.8 times during these 101 days.

Most (81%) of the spawning females (those with oocytes with migratory nuclei, or with postovulatory follicles) were collected in June, the month of peak spawning for *S. japonicus* according to the abundance of larvae in CalCOFI plankton collections (Kramer 1960). In June, 20.6% of the females spawned per day, indicating that the average mature female spawned about every five days in June, whereas 2.7% of the mature females spawned per day in May, and 6.8% in July (table 4).

The ovaries of 32 females contained multiple spawning stages. That is, a single ovary contained postovulatory follicles of two different ages, or postovulatory follicles and oocytes with migratory nuclei, or some other combination (table 3). Because we know the approximate age for each of these spawning stages, it is possible to calculate the interval between them. Thus we calculated that the average interval between spawnings for these 32 females was 1.3 days (table 5).

The frequency of spawning tended to increase with female age (table 6). Knaggs and Parrish (1973) concluded that older *S. japonicus* spawn for longer periods than younger ones. In our study none of the mature one-year-old fish were spawning, and only 3.9% of the mature two-year-olds were spawning,

TABLE 3

Spawning Female *S. japonicus* Taken in the Study (N = 58) with Ovaries Indicating Past Spawning (Postovulatory Follicles Present) or Imminent Spawning (Oocytes with Migratory Nuclei)

Coll. number	Fish number	Time PST	Year class	CDFG stage	Migratory nucleus	Postovulatory follicles	
						10–33 hours	33 < age < 72 hrs
7	05	0815	1981	5	+[1]	–	–
9	03[2]	1420	1980	6	+	+	+
13	18	1100	1980	3	+	–	–
13	19	1105	1983	2	+	–	–
15	02	1005	1980	4	+	–	+
15	06	1040	1982	3	–	–	+
15	12	1110	1981	4	–	–	+
16	03	0955	1981	3	+	–	–
21	01	1242	1981	3	–	+	–
21	02	1245	1981	3	+	+	+
21	03	1250	1981	3	+	+	+
21	04	1253	1981	3	+	–	+
21	05	1440	1981	2	–	+	+
21	06	1445	1981	3	–	+	+
21	07	1450	1980	4	+	–	+
22	07	0730	1981	2	+	–	–
23	01	1220	1981	3	–	–	+
23	02	1225	1982	2	–	+	+
23	03	1230	1981	3	–	+	+
23	04	1240	1981	4	+	–	+
23	05	1250	1981	3	–	+	+
23	06	1250	1981	3	–	–	+
23	07	1300	1981	3	+	+	+
23	08	1310	1980	4	–	–	+
23	09	1315	1981	4	–	+	–
23	10	1320	1981	3	–	+	+
23	11	1325	1981	3	–	+	+
23	12	1325	1982	3	–	+	+
23	13	1325	1981	4	+	–	+
23	14	1330	1981	3	+	–	+
23	15	1330	1981	3	–	–	+
23	16	1330	1982	3	–	+	–
23	17	1330	1981	3	+	+	+
23	18	1340	1980	4	+	–	+
23	19	1340	1981	3	+	–	+
23	20	1345	1980	2	–	+	–
24	02	0710	1981	3	–	–	+
25	03	0940	1981	3	–	–	+
25	04	1000	1981	3	–	–	+
25	06	1100	1981	4	–	–	+
25	07	1115	1981	3	–	–	+
25	09	1220	1980	4	–	–	+
26	05	1133	1981	3	–	–	+
26	06	1137	1981	4	–	+	+
26	07	1141	1982	3	+	–	+
26	08	1149	1981	4	+	+	+
26	10	1200	1981	4	–	–	+
27	01	1425	1982	2	–	+	+
27	02	1440	1982	3	–	–	+
27	03	1442	1981	3	–	+	+
27	04	1450	1981	3	–	+	+
27	05	1454	1983	3	–	–	+
27	06	1456	1981	2	–	+	+
27	07	1458	1981	2	–	+	+
27	08	1502	1983	2	–	–	+
28	03	0740	1981	3	+	–	+
28	18	1105	1982	3	+	–	+
29	02	2025	1981	4	–	+	+

[1] + indicates that the state was present.
[2] Ovary had a few hydrated oocytes in the lumen, and new postovulatory follicles, indicating that the female had spawned within the last 0–3 hours, an unusual time of day for *S. japonicus*.

TABLE 4

Percentage of Mature Female *S. japonicus* Classified as Active or Postspawning, and Percentage Spawning per Day

Month	Active[1] %	Postspawning: Recent[2] %	Postspawning: Late[3] %	Number mature females	Spawning per day: MN[4] %	Spawning per day: PO[5] %	Spawning per day: Mean %
April	17	12	71	48	2	0	1.0
May	25	33	41	111	4	1	2.7
June	67	14	19	90	16	26	20.6
July	41	45	14	22	9	4	6.8
All	39	24	37	271	8.1	9.2	8.7

[1]Indicated histologically by presence of yolked oocytes, α atresia <50% of yolked oocytes, and, possibly, postovulatory follicles.
[2]α atresia is present in 50% or more of the yolked oocytes.
[3]There are no yolked oocytes in the ovary, but β atresia is present.
[4]Oocytes with migratory nuclei are present in the ovary; spawning is imminent.
[5]Postovulatory follicles are 10–33 hours old; female spawned the previous night.

TABLE 5

Computation of Mean Interval between Spawnings for *S. japonicus* Females with Combinations of the Following States in the Ovary: Oocytes with Migratory Nuclei (MN); 10–33-Hour-Old Postovulatory Follicles (PO_a); and >33-Hour-Old Postovulatory Follicles (PO_b)

Spawning states present in ovary	Minimal interval between spawnings[1] (i in days)	Number females N	Potential days $i \times N$
MN + PO_b	2	11	22
PO_a + PO_b	1	15	15
MN + PO_a + PO_b	1	6	6
Total		32	43
Average interval between spawnings[2]:	43/32 = 1.34		

[1]The interval between spawnings for females with only a single spawning state in the ovary is ≥3 days, since 72 hours is the maximum period during which postovulatory follicles can be detected.
[2]25 females had a single spawning state. If these females were included, the average interval would be 118/57, or 2.07 days.

TABLE 6

Frequency of Spawning of Mature *S. japonicus* Females by Age and Year Class

Age (years)	Year class	Immature N	Mature N	Spawning per day mean percentage[1]
1	1984	11	3	0
2	1983	2	13	3.9
3	1982	10	44	6.8
4	1981	29	166	9.9
5	1980	5	43	8.1
6+	1978 & 1979	1	2	0

[1]Calculated from the number of mature females having oocytes with migratory nuclei in their ovaries, and from the number of mature females with postovulatory follicles 10–33 hours old in their ovaries; original data in table 3.

compared to 8.7% for the mature females as a whole. These data support the conclusion of Knaggs and Parrish, but more histological data, sampled over the whole spawning season, are needed to determine spawning by age.

The foregoing analysis indicated that the average female *S. japonicus* may spawn 8.8 times in 101 days, but it is clear that individual females do not spawn at regular intervals over this period. Rather, many of the spawnings must occur in rapid succession at daily or every-other-day intervals. It is interesting to speculate on the possible length of the spawning period for an individual female. If a female spawned 8.8 times at an interval of 1.3 days, the period would be 11.4 days long. If the average interval were 2 days, the period would be 18 days long. The latter period fits the data better because the percentage of spawning females with only one spawning stage (44%) would be too high if the spawning cycle were only 11 days long.

Fecundity

The average batch fecundity for the 13 females having oocytes with migratory nuclei was 68,400 oocytes, or 168 oocytes per gram of female wet weight, without ovary (table 7). By multiplying the mean batch fecundity by the number of spawns (8.8) we find that a female averaging 444 g would spawn about 602,000 oocytes during the 101-day survey period. This estimate is nearly five times higher than MacGregor's estimate of 126,000 oocytes for the annual fecundity of a 444-g female. Clearly, the standing stock of advanced oocytes does not indicate potential annual fecundity; consequently, we consider the annual fecundity of *S. japonicus* to be indeterminate.

The average Peruvian *S. japonicus* (281 g, without ovary) was estimated to have a mean relative batch fecundity of 278 oocytes per gram (Peña et al. 1986). This is somewhat higher than our estimate of 168 oocytes per gram for a 444-g female. Owing to high variability and few observations, it is uncertain if these differences reflect actual differences between stocks.

TABLE 7
Batch Fecundity (Number of Oocytes to Be Spawned in the Batch) of Thirteen *S. japonicus* Females with Oocytes in the Late Migratory-Nucleus Stage

Coll. & fish number	Time of day collected	Fork length (mm)	Body weight without ovary (g)	Ovary weight (g)	Batch fecundity	
					Per female	Per g body wt
7-05	0815	324	416.79	34.77	85,566	205.3
15-02	1005	319	382.64	46.56	120,537	315.0
26-08	1149	326	424.29	36.44	92,405	217.8
23-04	1240	310	355.32	35.59	69,930	196.8
21-03	1250	340	496.01	32.54	74,723	150.6
21-04	1253	315	380.92	30.95	57,247	150.3
23-07	1300	320	407.68	25.93	47,801	117.3
23-13	1325	301	320.83	34.22	72,338	225.5
23-14	1330	320	409.68	23.32	36,510	89.1
23-17	1330	300	328.45	22.76	35,807	109.0
23-18	1340	340	494.53	34.01	80,807	205.3
23-19	1340	326	438.70	22.03	23,280	53.1
21-07	1450	340	481.64	46.90	91,680	190.4
				Mean	68,356	168.0

Our batch fecundity of *S. japonicus* (168 oocytes per gram body weight, without ovary) is about three times that estimated for *S. scombrus*, which ranges from 28 to 55 oocytes/g body weight (Alheit et al. 1987; Watson et al. 1992). This difference between species may be partly due to differences in egg size. The *S. japonicus* egg is about 1.0 mm in diameter (Kramer 1960; Fritzsche 1978); the *S. scombrus* egg is about 1.2 mm (Russel 1976; Fritzsche 1978). The ratio of the diameter cubed for the two species is 1:1.7, indicating that the egg mass of *S. scombrus* may be nearly twice that of *S. japonicus*. Thus the differences in batch fecundity may be explainable in part by differences in egg size, assuming that the energy investment per batch was about the same in the two species. Although this is a plausible explanation, it is certainly speculative, because we have no true mean egg size for either population at present. Egg size of both species varies considerably between localities and seasons, making accurate comparisons difficult.

Atresia

Alpha atresia of the advanced yolked oocytes was common throughout the spawning season. Even early in the season (April) 12% of the females were classed as recent postspawning because of the high levels of α-stage atresia (table 4). Anchovy usually do not spawn when their ovaries are in this advanced state of atresia (Hunter and Macewicz 1985b), and we presume this is also the case for *S. japonicus*. In addition, the atretic condition that follows this state, late postspawning (table 4), was common in *S. japonicus* throughout the spawning season.

Hunter and Macewicz (1985b) believe that highly atretic ovaries are a normal occurrence in the annual reproductive cycle in fishes with indeterminate fecundity. They conclude that highly atretic ovaries indicate fish that have ended their reproductive season, and should be considered as synonymous with "spent," or postspawning, ovary classes. High levels of atresia might be induced by abnormal events such as an epidemic or environmental stress rather than by the normal cessation of spawning, but we believe that the normal cessation of spawning is much more likely. It is also possible that during a single spawning season *S. japonicus* may pass through more than one cycle of oocyte maturation, spawning, and atresia.

The most striking feature of our data on atresia was that females with highly atretic ovaries were common early in the spawning season. In anchovy, this condition is prevalent only near the end of the season, when spawning is declining for the stock as a whole. The prevalence of atresia indicates that the spawning cycles of *S. japonicus*, unlike those of the anchovy, are not synchronized for the stock as a whole but rather seem to vary from sample to sample. Spawning may be synchronized at some lower level of organization than the stock, such as the school or school group (Smith 1975). Alternately, schools may segregate according to behavioral traits, with spawning schools occupying different areas from postspawning schools.

Regardless of the mechanisms involved, the patchiness of spawning individuals indicates that obtaining representative samples of an *S. japonicus* stock may be very difficult. Considering the patch-

iness of spawning and postspawning females and the fact that our sampling was opportunistic, our samples may not accurately represent spawning rate of the stock over the 101 days. Since many females spawned at intervals of every 1.3 days, and in June the average female spawned every 5 days, we believe that our estimate of 8.8 spawns per year for the average female may be low.

Evaluation of Anatomical Classification of Ovaries

To determine the value of classifying ovaries by means of gross anatomical criteria, we used the Hjort maturity index modified by CDFG (table 2) as well as histological criteria to classify the *S. japonicus* ovaries (table 8). CDFG considered only stage 1, in table 2, as immature, and stages 2–6 as mature. Histological analysis indicated that the mature females occurred in all stages (table 8). On the basis of the histological evidence, the misclassified immature females in stage 1 were considered to be in postspawning condition, because they were resorbing their ovaries. Surprisingly, the percentage of all females classed as mature was similar regardless of the method used to classify them. When anatomical criteria were used, 90% of all females were estimated to be mature; when histological criteria were used, 82% were mature. The failure to detect postspawning females using anatomical criteria was counterbalanced by histological identification of immature females in CDFG stages 2 and 3.

Spawning females occurred in every anatomical stage except stage 1 (tables 3 and 8). But according to CDFG criteria, spawning females occur only in stages 5 and 6 (table 2). Clearly, the CDFG anatomical criteria do not identify all the spawning females.

Although anatomical staging is useful when studying a population (e.g., the duration of spawning seasons), it is inaccurate when considering individual fish. Our findings agree with those of Asano and Tanaka (1989), who studied reproduction of the Japanese stock of *S. japonicus*. They concluded that females with active ovaries, those actively spawning, and those in postspawning condition cannot be accurately separated if only anatomical criteria are used. Similarly, West (1990) states in his review that macroscopic staging may result in unacceptably high errors when used to examine the ovarian development of an individual fish.

Histological methods obviously provide more detailed and accurate assessments of fish maturity and reproduction. There will always be a need for gross anatomical methods because of the speed and ease that they offer. We believe that the six-stage anatomical grading system of CDFG needs revision. With the unaided eye, only three characteristics actually can be detected: (1) yolked oocytes not present, (2) yolked oocytes visible, and (3) hydrated oocytes visible. The rest of the characteristics used are unreliable or imply knowledge of maturity and spawning that the observer does not have; thus, we recommend a three-stage system.

CONCLUSIONS

Our estimate of spawning rate for the population of *S. japonicus* is lower than one would expect from information available about other scombroid fishes. We estimated that 8.7% of *S. japonicus* females spawned per day, whereas estimates for most other scombroid fishes indicate that they spawn at much higher rates. For example, 85% of female skipjack tuna spawn per day (Hunter et al. 1986); 18%–47% of black skipjack spawn per day (Schaefer 1987); 80% of yellowfin tuna spawn per day (Schaefer 1988); and 18%–62% of *S. scombrus* spawn per day (Priede and Watson, in press). We suspect that the actual rate of spawning of *S. japonicus* females may

TABLE 8

Comparison of California Department of Fish and Game Anatomical Maturity Classification and Histological Classification of the Ovaries of *S. japonicus* Collected in 1985

Number of females	Anatomical classification[1]		Histological classification			
	Stage number	Fish maturity	Immature %	Mature		
				Postspawn %	Nonspawn %	Spawn %
34	1	Immature	44	56	0	0
174	2	Mature	23	68	3	5
91	3	Mature	3	29	32	36
26	4	Mature		4	42	54
2	5	Mature		0	50	50
1	6	Mature		0	0	100
Fraction mature:	294/328 = .90			270/328 = .82		

[1]See table 2 for description of stages.

have been much higher for four reasons: (1) our opportunistic sampling may have biased our estimate; (2) females with multiple stages in the ovary spawned every 1.3 days; (3) our studies of atresia indicated that the distributions of postspawning and spawning females may have been highly contagious; and (4) our samples did not adequately cover the entire spawning season.

We believe that our estimates of a spawning rate of 8.7% of the female population per day and 8.8 spawnings per year for the average female are low. We hope this paper will encourage others to carry out a thorough study with a formal sampling design that takes into account age and size patterns in spawning rate, batch fecundity, and duration of the spawning season.

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