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The Spawning of Skipjack Tuna from Southeastern Brazil as Determined from Histological Examination of Ovaries

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A total of 961 skipjack tuna ovaries from southeastern Brazil was examined to determine their reproductive condition. The Brazilian fish were sampled from November 1981 to July 1982 from the coastal area south of Cabo Frio between 22°S and 28°S latitude. A portion of the population was in near spawning condition in November and this condition continued through March. Ovaries obtained during May–July were mainly regressed. The smallest sexually mature female in our sample was 510 mm. The minimum gonad index of mature fish was 30. Histologically mature ovaries represent a wide range of gonad indexes, including ripening and recently spawned conditions.

Des ovaires de listaos du sud-est brésilien, au nombre de 961, ont été examinés afin d'en déterminer l'état du point de vue de la reproduction. Les poissons brésiliens avaient été échantillonnés entre novembre 1981 et juillet 1982 dans la zone côtière au sud du Cabo Frio, entre 22°S et 28°S de latitude. Une partie de la population s'y trouvait près de frayer, ce qui put être observé jusqu'au mois de mars. Les plupart des ovaires prélevés de mai à juillet étaient en phase de regression. La femelle mature de plus petite taille observée dans l'échantillon mesurait 510 mm. L'indice gonado-somatique minimum des poissons matures était 30. Les ovaires matures du point de vue histiologique représentaient une ample gamme d'indices gonadiques, dont les stades de maturation et d'après-ponte.

Se examinaron un total de 961 ovarios de listado de la costa Sudeste de Brasil para determinar sus condiciones reproductoras. Los peces brasileños fueron muestreados desde Noviembre 1981 a Julio 1982, en la zona costera al sur de Cabo Frio, entre los 22°S y 28°S de latitud. Una parte de la población se encontraba próxima al desove en Noviembre, y esta condición se mantuvo hasta el mes de Marzo. Los ovarios obtenidos durante Mayo–Julio estaban principalmente en fase regresiva. La hembra más pequeña sexualmente madura de la muestra, medía 510 mm. El índice mínimo de gónadas de peces maduros fue de 30. Ovarios histológicamente maduros representaron una amplia gama de indices de gónadas, incluyendo condiciones de madurez y puesta reciente.

1. Introduction

The skipjack tuna *Katsuwonus pelamis* is the most important pelagic resource in many areas throughout the tropical oceans, yet much remains to be learned about its biology, including its reproductive habits. Previous studies on maturation and spawning of skipjack have been conducted on populations from the following areas: Australia (Blackburn and Serventy 1981); western Pacific (Wade 1950; Asano and Tanaka 1971; Hu and Yang 1972; Naganuma 1979); central Pacific (Brock 1954; Marr 1948; Yoshida 1966); eastern Pacific (Schaefer and Orange 1956; Joseph 1963; Blackburn and Williams 1975); and Atlantic Ocean (Simmons 1969; Batts 1972c; Cayré 1981 and included references). The purpose of this paper is to provide information on skipjack reproduction from southeast Brazilian seas. The main objective of the study was to determine the season of spawning by means of histological examination of ovaries.

2. Methods

Gonads were obtained from skipjack taken off southeastern Brazil, south of Cabo Frio along the edge of the continental shelf between 22°S and 28°S (Figure 1). The fish were taken by live-bait boat and were initially frozen or iced.

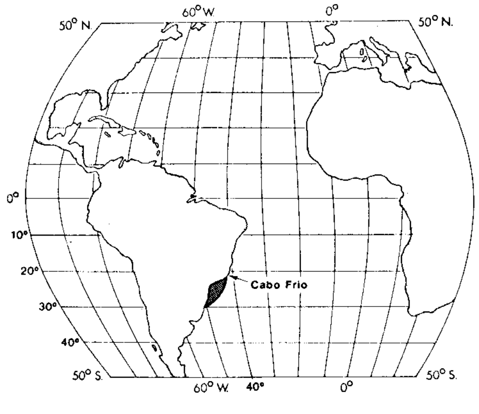

Figure 1. Fishing area (shaded) where Brazil samples were taken.

All gonad samples were fixed in 10% formalin. Some were later stored in isopropyl alcohol. Weights of fish and gonads were taken to the nearest 0.1 g; fork length measurements were taken to the nearest cm.

The ovary specimens were examined externally to determine if they were mature or maturing (enlarging). The smallest fish with mature ovaries in our sample was found to be 510 mm fork length.

A sample of 241 ovaries from fish larger than 510 mm was selected for histological examination of the spawning cycle. One section from the central axis of each ovary was used. Histological examination indicated that the fundamental ovarian structure was similar in all parts of the ovary. Yoshida (1966) similarly found this to be the case for Pacific skipjack.

Tissue was embedded in paraplast, and histological sections were cut at 8μm. Slides were stained with iron hematoxylin. Ovaries' were then classified according to four stages of oocyte development: Regressed, Previtellogenic, Vitellogenic, and Mature (Table 1). Oocyte measurements were taken from the histological slides using an ocular micrometer.

Table 1. Histological classification of skipjack ovaries.

Stage	Condition of Ovary
1. Regressed Ovary	Primary oocytes (< 100 μm diameter) predominate; mode at ca. 50 μm.
2. Previtellogenic Ovary	Vacuolated oocytes (100–300 μm diameter) predominate.
3. Vitellogenic Ovary	Oocytes with yolk deposition in progress (250–400 μm diameter).
4. Mature Ovary	Mature (yolk-filled) oocytes (400 + μm diameter) predominate. Yolk deposition typically progressing in smaller mode (250 μm) of vitellogenic oocytes. Postovulatory follicles may be present.

Because these ovaries had been subjected to freezing earlier in the sampling process, freeze damage was a possibility. We have noted in our results where cold related histological changes may have occurred. Such damage appeared to be minimal.

We did not examine the testes histologically. Histological studies of testes have proven less useful than those of ovaries for describing the spawning schedule of fish (Batts 1972c; Macer 1974).

For fecundity estimates, a small subsample (ca. 0.050 g) was taken from 24 ovaries which histological analysis had verified as being in spawning condition (containing a mode of yolk-filled oocytes). This subsample was weighed and all mature (yolk-filled) oocytes were counted under a dissecting microscope. These subsamples provided between 77 and 369 mature oocytes each. Total fecundity was then estimated by proportion. Relationships between total fecundity and body size, body weight, and ovary weight were determined by regression analysis.

Gonad indexes (G.I.) were calculated using the formula $G.I. = W/L^3 \times 10^8$, where W = weight in grams and L = length in mm, as used by other skipjack investigators (Schaefer and Orange 1956; Yoshida 1966; Batts 1972c). These measurements were taken from 581 fish. A larger sample of 1,905 fish was used to examine the sex ratio. Length frequencies of the fish whose ovaries were examined are shown in Figure 2. The ovaries of some of these fish were also examined histologically and the length-frequencies of these fish are also shown in Figure 2.

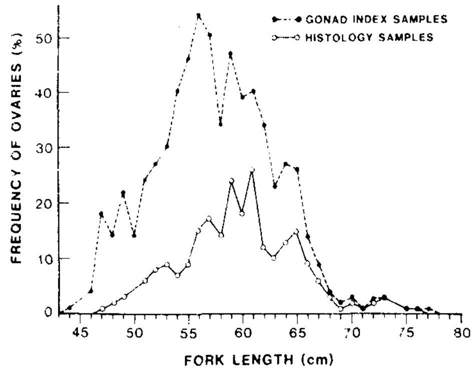

Figure 2. Length frequencies of Brazilian samples and the portions histologically examined.

3. Results

3.1 HISTOLOGY

The ovaries of skipjack tuna are typical of other teleosts in consisting of paired, fusiform organs which are attached to each other at their posterior end by a mesentery. As skipjack can undergo a distinct seasonal spawning cycle, ovary size will vary depending upon the time of sampling. In the sample from Brazil, the ovaries comprised as little as 0.48% of total body weight when the fish were not spawning (July) or up to 4.02% of total body weight when the fish were in spawning condition (January). The ovary was composed of connective tissue septa which were lined with primary oocytes that averaged about 50 μm in diameter. This fundamental structural makeup was most evident when the fish were reproductively inactive, i.e. regressed (Stage 1, Figure 3A), as has previously been described by Batts (1972c). It was less evident when spawning was imminent.

The earliest histological sign of ovarian activity was the appearance of previtellogenic Stage 2 oocytes (Figure 3B). These oocytes were slightly enlarged, up to 300 μm diameter oocytes, and contained several rings of vacuoles situated along the inner periphery.

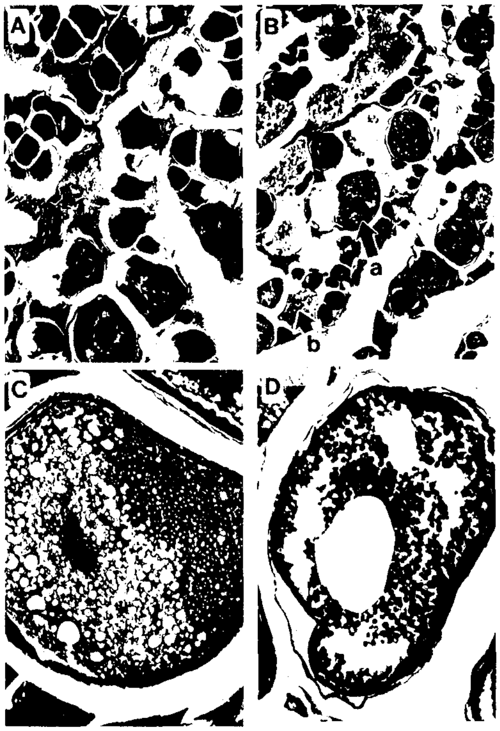

Figure 3. Photomicrographs of histological sections of skipjack ovaries from Brazil. (A) Primary oocytes from inactive ovary, 13 June; 111 X. (B) Secondary oocytes (arrow a), 2 February; atretic oocytes also present (arrow b); 69 X. (C) Vitellogenic oocyte containing dust-like yolk. Larger vacuoles may have contained oil prior to histological clearing; 15 January; 173 X. (D) Mature oocyte; note large vacuole; 15 January; 104 X.

The vacuoles presumably contained lipoidal substances that were removed by the histological clearing agent (xylene) during slide preparation. Previtellogenic oocytes became progressively more numerous in fish at a more advanced stage of the vitellogenic cycle, and eventually became the most abundant type present.

Vitellogenic oocytes with discernible yolk granules appear as the spawning cycle enters stage 3. These granules are very small (Figure 3C) and are "dust-like" in appearance. They clearly differ from the more usual, heavy yolk granules of other vitellogenic teleosts. The oocytes are up to about 400 μm in diameter. Similar appearing oocytes at this stage are shown by Cayré and Farrugio (this volume). However, this condition may be an artifact resulting from freezing of the tissue. Histological examination of freshly fixed, vitellogenic skipjack ovaries will be necessary to clarify this.

Finally, the mature ovary is characterized by the predominance of mature, yolk-filled oocytes of Stage 4. These averaged 498 ± 10.6 μm in diameter (= .50 mm) (n = 29, range 415–616 mm) prior to undergoing hydration which occurs just prior to spawning. Mature skipjack oocytes are similar to those of other teleosts in being surrounded by a granulosa layer and zona radiata. Some of the largest mature oocytes (Figure 3D) commonly contain large vacuoles in their centers. These may have contained oil prior to histological processing. In a few cases, postovulatory follicles were observed (Figure 4A). These showed some distortion from freezing but were otherwise similar in appearance to those seen in the northern anchovy *Engraulis mordax* by Hunter and Goldberg (1980). Also present were what appeared to be hydrated eggs which averaged 0.65 μm in length. These were distorted and may possibly have been mature oocytes that had become swollen and had ruptured during the freezing process. We did not observe running ripe ovaries, which would contain ova approximately 1.0 mm in diameter (Yoshida 1966).

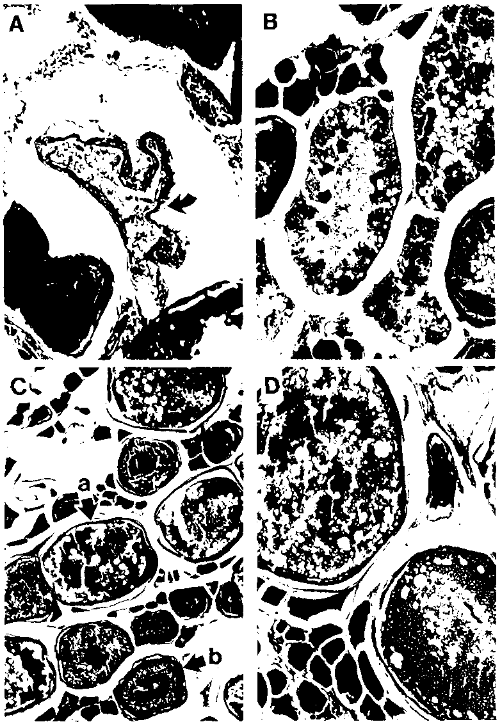

Figure 4. Photomicrographs of histological sections of skipjack ovaries from Brazil. (A) Post-ovulatory follicle (arrow) of uncertain age; some distortion from freezing; 276 X. (B) Atretic oocytes, 14 January; 173 X. (C) Mature (arrow a) and vitellogenic (arrow b) oocytes, 12 January; 173 X. (D) Mature (upper left) and vitellogenic (lower right) oocytes, 12 January; 173 X.

Atresia, or spontaneous degeneration of oocytes (Figure 4B), was observed frequently in fish of certain collections. For example, it was found in 11 of 18 skipjack examined from December 11, 1981. This condition, at the beginning of the spawning season, likely reflects environmental stress. High percentages of atretic oocytes are normally seen late in a spawning cycle, when oocytes that initiate but do not complete yolk deposition degenerate. Also, corpora atretica were commonly noted. These structures, which contain yellow brown granules, represent the last stage in the atretic process (Lambert 1970). Baglin (1982) observed them in the Atlantic bluefin tuna.

3.2 Seasonal Cycle

Histological examination of the ovaries indicated a spawning period from November through March, based upon the occurrence of mature ovaries (Table 2). It was not possible to positively designate when spawning began as no material was available form August to October. Nor were any running ripe ovaries ever seen. The number of spawnings per individual per season are not known, but the presence of a mode of mature oocytes (ripening and spawning imminent) and a vitellogenic mode for a subsequent spawning (Figures 4C, D) indicate that females spawn more than once per season. Brock (1954) and Bunag (1956) reported Pacific skipjack were multiple spawners, and Raju (1964b) claimed the same for Indian Ocean skipjack. Simmons (1969), Batts (1972c), and Cayré (1981) all reported multiple modes of ova diameters in Atlantic skipjack.

Table 2. Percentage monthly distribution of ovary maturity stages in Brazilian skipjack.[1]

		Stage: 1 Re- gressed	2 Previtel- logenic	3 Vitel- logenic	4 Mature
Month	N	%	%	%	%
November 1981	6	16	0	16	67
December 1981	26	15	8	19	58
January 1982	44	4	7	16	73
February 1982	61	5	5	28	62
March 1982	31	10	10	35	42
April 1982	15	60	6	27	6
May 1982	28	89	8	3	0
June 1982	16	100	0	0	0
July 1982	14	100	0	0	0

[1] These were mature sized fish, greater than 510 mm FL.

The frequency of the four histological stages varied according to fish size (Figure 5). The majority of fish fell within the 550–650 mm size class, and most spawning activity probably occurred during December–February, when histological stage 4 predominated. Notice that during this season, larger fish tending to have a high proportion of individuals with mature ovaries entered the sample.

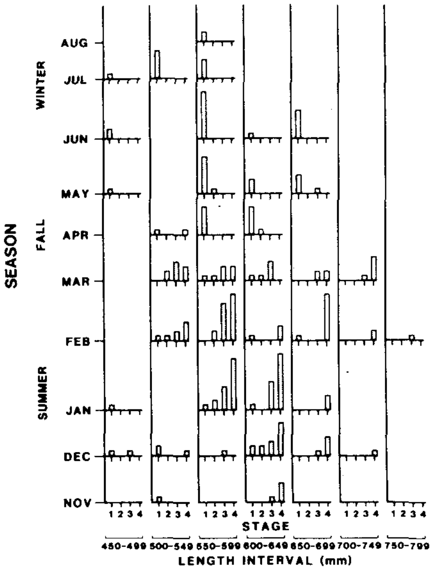

Figure 5. Frequency of occurrence of four histological stages of skipjack ovaries from Brazil, by month and by fork-length interval.

The gonad indexes reflected the same spawning seasonality. They were increased greatly in November–March and then reduced in April–July (Table 3, Figure 6). Some immature fish with small gonad indexes were found in all months, so that monthly distributions of values were highly skewed. The mean index values, which should be normally distributed, are shown with normal 95% confidence intervals.

Table 3. Summary of length, weight, gonad weight, and gonad index data with standard errors for Brazilian skipjack.

		Body Length (mm)		Body Weight (g)		Gonad Weight (g)		Gonad Index	
Month	N	$\bar{x}$	$S_{\bar{x}}$	$\bar{x}$	$S_{\bar{x}}$	$\bar{x}$	$S_{\bar{x}}$	$\bar{x}$	$S_{\bar{x}}$
Nov. 1981	17	610.0	9.0	5229.4	242.9	66.0	7.2	28.0	2.7
Dec. 1981	56	589.4	6.4	4828.6	189.3	72.2	6.9	32.4	2.3
Jan. 1982	87	591.4	3.8	4380.5	103.5	78.0	5.2	35.0	2.0
Feb. 1982	75	600.3	5.9	4565.3	148.1	113.9	6.3	49.1	2.2
March 1982	78	581.9	7.8	4380.8	201.6	66.2	6.0	30.9	2.4
April 1982	86	578.9	3.5	4438.4	85.6	28.3	2.1	14.5	1.0
May 1982	91	600.5	4.5	4949.4	55.7	26.9	1.1	12.2	0.3
June 1982	45	596.1	5.7	4382.2	129.4	21.8	0.9	10.1	0.3
July 1982	46	554.3	4.6	3204.3	111.9	15.7	0.7	9.1	0.3

3.3 Gonad Index and Fork Length at Maturity

There were 94 fish with mature, histological stage 4 ovaries. For these fish, spawning would soon occur or had already occurred. Their average gonad index was 56.70 ± 3.0. Most had indexes between 40 and 80 (Figure 7). Our minimum gonad index recorded for a sexually mature skipjack was 31, from a 620

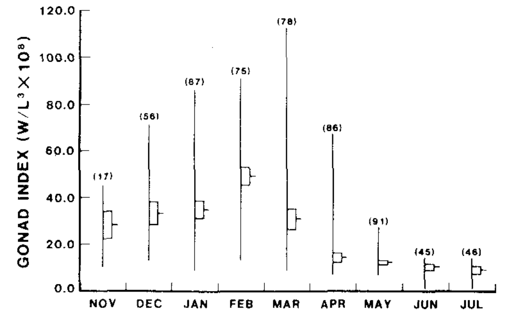

Figure 6. Seasonal gonad indexes for Brazilian skipjack. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval of mean. Sample size above each month.

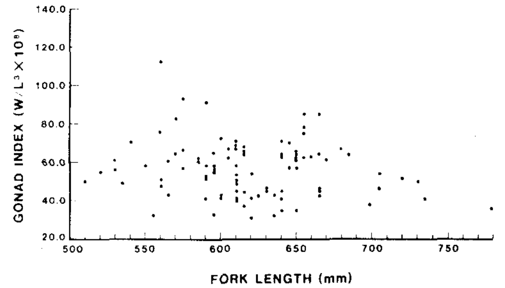

Figure 7. Relationship between gonad index and fish size for mature Brazilian skipjack.

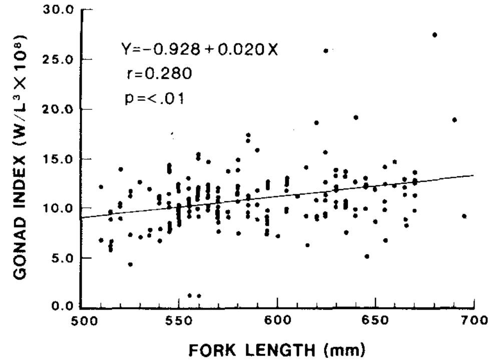

Figure 8. Relationship between gonad index and fish size for reproductively inactive Brazilian skipjack, May–July 1982.

mm fish which contained a mode of yolk filled oocytes. During May–July, when the Brazilian population was reproductively inactive, most indexes fell between 5.0 and 15.0 (Figure 8). Orange (1961) similarly found that only skipjack with indexes over 30 approached maturity.

Yoshida (1966) found that the mean diameter of the most mature mode of oocytes changed little between gonad indexes 35 and 96, and approached an asymptote of about 0.6 mm. Batts (1972c) suggested that gonad indexes for skipjack may exceed 100, and Naganuma (1979) found that skipjack with mature oocytes had indexes of 80 or higher. Evidently skipjack with mature ovaries can obtain a wide range of index values over 30. Furthermore, there is a tendency for gonad indexes to increase with size of fish (Orange 1961). That the relationship of ovary to fish weight may not be linear with increasing fish weight for fish of the same histological stage (i.e. ova diameter) was shown by Hunter and Goldberg (1980) for *Engraulis mordax*.

Our smallest mature or maturing skipjack was 510 mm. There were two such fish. One was vitellogenic (stage 3) with gonad index 45.5; the other was mature (stage 4) with gonad index 50.8. This size is within the range given by Orange (1961), who found that eastern Pacific skipjack from the Revilla Gigedo Islands matured at 550 mm, while those from Cocos Island matured at 400 mm. Miminum size at sexual maturity of skipjack in the Atlantic, Pacific, and Indian Oceans has typically been reported between 400 and 450 mm (Marr 1948; Wade 1950; Brock 1954; Yabe 1954; Postel 1955; Bunag 1956; Schaefer and Orange 1956; Orange 1961; Ronquillo 1963; Raju 1964a; Yoshida 1966; Simmons 1969; Hu and Yang 1972). Chur et al. (1980) reported that skipjack mature in the eastern tropical Atlantic at 390 mm, while Batts (1972c) reported an average of 500 mm for North Carolina fish. Cayré and Farrugio (this volume) determined that 420 mm was the length at which 50% of eastern Atlantic skipjack attain a gonad index of 35 or more. The difference in their value of 420 mm and ours of 510 mm for Brazilian skipjack is due in part to their sampling only from schools in which 50% or more of the females were sexually mature. Furthermore, fish caught off Brazil are larger than those caught in the eastern Atlantic (c.f. Cayré et Farrugio this volume), our smallest specimen being 440 mm.

3.4 FECUNDITY

Our fecundity estimates, based on counts of mature oocytes, varied between 129,807 and 977,566 eggs. The fish were between 510 and 720 mm in length (Table 4). Average fecundity was 385,937 eggs. Values from other skipjack studies are given in Table 5. Our values fall within the range reported in these other investigations, but averaged lower. They are similar to the estimate from the eastern Atlantic of 100,000 to 1,000,000 eggs (Cayré et Farrugio, this volume). Matsumoto et al. (1984) noted the difficulty of the problem of estimating annual egg production, in part because of the large variability among individuals, even of the same size, and because of the uncertainty of the number of multiple spawnings. The oocytes we counted appeared to be from a discrete

Table 4. Length, weight, and fecundity data and regressions for 24 Brazilian skipjack females

Body Length (mm) X_1	Body Weight (g) X_2	Gonad Weight (g) X_3	Fecundity Estimate Y
720	8000	195.3	334263
705	7300	191.5	627868
680	7000	210.9	421800
660	6000	183.3	456583
655	5700	211.3	516930
650	6000	172.2	977566
620	4800	129.8	302080
615	4700	155.2	411460
615	5100	150.6	374963
615	4900	158.7	275479
610	4500	148.0	443816
610	4600	135.0	259411
605	4200	167.4	340200
595	4300	123.2	588000
580	4100	114.6	326731
580	4000	104.9	270642
580	3800	104.6	157925
575	3700	109.2	429354
575	3900	148.2	406327
575	3500	126.0	271551
570	3700	118.6	492447
550	3000	96.5	250245
520	2600	77.3	197039
510	3000	67.4	129807
$\bar{x}$ 607.08	4683.33	141.65	385936.96
S_x 10.60	282.05	8.13	36419.49

Fecundity Regressions:

$Y = 681760.759 + 1758.733\,X_1 \qquad r^2 = .262$

$Y = 87698.857 + 63.681\,X_2 \qquad r^2 = .243$

$Y = 47265.033 + 2390.863\,X_3 \qquad r^2 = .285$

Table 5. Fecundity estimates of skipjack from previous studies

Area	Size range (mm)	Estimate	Worker
Brazil	510-720	129807- 977566	This study
N. Carolina, USA	498-704	141000-1200000	Batts (1972c)
Tropical Atlantic	465-809	262000-1331000	Simmons (1969)
Eastern Pacific	640-710	480000-1000000	Schaefer (1962)
Hawaii	440-870	280000-1900000	Rothschild (1963)
Japan	468-610	110000- 860000	Yabe (1954)
Minicoy, Arabian Sea	418-703	151900-1977900	Raju (1963, 1964b)
Marquesas Islands Pacific Central	430-740	100000-2000000	Yoshida (1966)
Eastern Pacific	614-715	400000-1330000	Joseph (1963)

mode; however, errors are possible if the size modes intergrade or if development is gradual within modes (Hunter and Goldberg 1980).

The relationships between number of mature oocytes and fish length, fish weight, and ovary weight were calculated using linear regression and are given in Table 4. All regressions were positive and significant ($P < .05$). The regression between fecundity and fish length was most similar to that of Batts (1972c) but predicted a lesser fecundity by about 21% for 600 mm fish. Because of the small sample size and the problem of the meaning of ova counts with respect to total fecundity, these relationships should be considered tentative.

3.5 SEX RATIO

The sex ratio in the sample from Brazil was examined, and additionally, a second Brazilian sample (Brazil-2) was examined. The Brazil-2 sample originated from the same fishery as did our primary Brazilian sample, but was sampled in Puerto Rico after transshipment from Brazil. The 1,358 skipjack of our primary Brazilian sample did not depart significantly from a 50:50 ratio of males to females, but the Brazil 2 sample did (Table 6). On five sampling dates of the latter, there were significantly more females than males collected. However, the heterogeneity χ^2 of the Brazil 2 sample was also highly significant, indicating heterogeneity of ratios among the constituent samples taken on different days. The heterogeneity χ^2 of the primary Brazilian sample was not significant, although its probability level was only 9%.

Table 6. Skipjack sex ratios and Chi-square tests.

Sample	N	Males	Females	Tests of Departure from 1:1	d.f.	χ^2	P
Brazil (primary sample)	1358	703	655	Sum, 28 samples	28	39.27	>.05
				Pooled	1	1.70	>.05
				Heterogeneity	27	37.57	>.05
Brazil-2	547	241	306	Sum, 27 samples	27	67.00	<.01
				Pooled	1	7.72	<.01
				Heterogeneity	26	59.28	<.01

Cayré and Farrugio (this volume) examined the sex ratio from a larger Brazilian sample of 2,743 fish (of which our specimens were a subsample). They reported a male:female ratio of 1.10, a significant departure from sexual parity. However, their even larger Atlantic-wide sample showed no such departure. Evidently the deviation from a 50:50 sex ratio in the Brazilian samples increased faster than did the effect of sample size, leading to a statistical change in ratio, where heterogeneity was not balanced out in the pooled sample. We therefore, do not find sufficient reason to reject the hypothesis of a 50:50 sex ratio in the Brazilian skipjack.

4. Discussion

In Table 7 we compare the morphological gonad stages of Batts (1972c) with the corresponding histological stages of this study. In the same table are listed the average gonad indexes corresponding to our histological stages. The average difference in index between vitellogenic and mature ovaries was smaller than the difference between the previtellogenic and vitellogenic stages. This is not unexpected as there was only a slight size increase from vitellogenic oocytes (diameter 0.30–0.40 mm) to mature oocytes (0.50 mm). Notice that our histological mature stage includes Batt's late maturing, ripe, and spawned stages. Though we did not see ovaries that were clearly ripe (i.e. containing a mode of enlarged oocytes up to ca. 1.0 mm in diameter) or ovaries clearly spawned out (i.e. ovaries flabby and regressing), our histological mature stage did contain some postovulatory and atretic follicles. These ovaries were apparently ready to spawn and in some cases this must have already occurred to a limited extent.

Table 7. Comparison of skipjack morphological stages (Batts, 1972) with mean gonad index values (with standard errors of means) and histological stages from this study.

Morphological Stage Batts (1972)	Average Gonad Index (this paper) N	$\bar{x}$	S_x	Histological Stage (this paper)
Stage 1: Immature	181	10.9	0.2	Stage 1: Regressed
Stage 2: Early maturing	9	25.5	2.8	Stage 2: Previtellogenic
Stage 3: Late maturing	32	46.2	2.8	Stage 3: Vitellogenic
Stage 3: Late maturing	94	56.7	1.5	Stage 4: Mature
Stage 4: Ripe	Not directly observed			Stage 4: Mature, but with mode of ripe ova ca. 1.0 mm in diameter.
Stage 5: Spawned	″		″	Stage 4: Mature, but with abundant postovulatory follicles.

Our size for mature oocytes averaged 0.50 mm in diameter and were smaller than the maximum sizes recorded for ripe skipjack ova by Batts (1972c), Yoshida (1966) and Kaya et al. (1982). They worked with fresh material and it is conceivable that some shrinkage occurred in the freezing process of our material. Yoshida (1966) described an advanced stage of oocyte development with well developed oil globules; this class had a mean diameter of 0.49 to 0.74 mm. The mature oocytes we describe could correspond to the lower size limit of this group. Yoshida's description of ova from a running-ripe fish included a mean diameter of 0.96 mm. This likely corresponds to the "ripe fish" described by Batts (1972c). That our collections did not contain fish with running-ripe ovaries is likely the main reason why our maximum ova sizes were smaller.

Running-ripe skipjack are apparently rare in collections. We believe this is because batch spawning (Hunter and Goldberg 1980) occurs and is completed rapidly. Yoshida's (1966) study also suggests that the transition of oocytes to the ripe condition with diameters greater than 0.65 mm is not gradual. Because hydration of ova and subsequent spawning may be rapid, even the hour of sampling can change the gonad stages that are observed (DeMartini and Fountain 1981). Recently Kaya et al. (1982) showed that captured and confined skipjack would ovulate within 8 hours after capture as a response to the stress. These fish were apparently in the unovulated stage at capture, with oocytes of the largest modal size no larger than 0.74 mm average diameter.

As in our study, Cayré and Farrugio (this volume) found very few oocytes larger than 0.50 mm in diameter among mature skipjack from the eastern Atlantic. Since their specimens included mature and post spawned ovaries, this also suggests that batch spawning is a transitory phenomenon.

Table 8 summarizes spawning times reported from different areas of the world's tropical seas. It might at first appear that skipjack are predominantly summer spawners. However, there are reports of year-round spawning, bimodal spawning (two periods of spawning in one year), and one report of winter–spring spawning. Considering the sampling problems, it is likely that skipjack are year-round spawners in the tropics and spring–fall spawners in the subtropics (Matsumoto et al. 1984). The Brazilian area has a subtropical oceanographic climate with seasonal and other periods of upwelling (Mascarenhias et al. 1971). Our data indicate spawning occurs during the southern summer off eastern Brazil, and in this regard is in keeping with the summer spawning times in the majority of previous studies from similar areas. However, inter-year variations in spawning pattern and size classes present can affect the perceived spawning season. Length of spawning season varies with fish size within a given population and larger fish probably travel and spawn over a wider area than do smaller fish. In the eastern Pacific, skipjack from California to Chile appear typically to migrate to the central Pacific to spawn (Orange 1961; Klawe 1963; Rothschild 1965).

The presence of larvae also provides evidence for the spawning season. Matsuura (1982a) reported that on two cruises along the eastern Brazilian coast (June and November–December), skipjack larvae were more abundant in the November–December (spring) cruise. Kikawa and Nishiwaka (1979) summarized plankton samples collected between 1959 and 1971 and reported skipjack larvae occurring off this same coast during both January–March and October–December. These results are consistent with our study which shows the presence of ready-to-spawn skipjack in collections from these same seasons from the nearby area south of Cabo Frio, Brazil.

Table 8. Summary of spawning times for skipjack from different regions.

Area	Spawning Time	Worker
Spring–summer spawners		
Brazil	November–April (southern hemisphere)	This paper
N. Carolina, USA	Late June–early July	Batts (1972c)
Cuba	May, June, July	Suarez-Caabro and Duarte Bello (1961); Gorbunova and Salabarria (1967)
Florida	April–May, July–August	Klawe (1960)
Marshall Islands	July–August	Marr (1948)
Cape Verde Islands	May–September	Postel (1955)
Hawaii	February or April, September	Brock (1954)
Marquesas and Tuamotu Islands	November–April (southern hemisphere)	Yoshida (1966)
Senegal	May–September	Frade et Postel (1955)
Southwest Pacific 0° – 24°S	October–March	Argue et al. (1983), Naganuma (1979)
Year-round Spawners		
Eastern, Western, Tropical Atlantic Ocean	Year-round	Simmons (1969)
Cuba	Year-round	Howell-Rivero y Juarez Fernandez (1954)
Bi-modal Spawners		
Western Pacific	August–September, December–January	Asano and Tanaka (1971)
Indian Ocean	January–April, June–September	Raju (1946a)
Winter–spring Spawners		
Costa Rica	March–April	Schafer and Marr (1948)

The reproductive behavior of skipjack is likely complex. Cayré (1981) reported that skipjack from off Dakar, Sénégal did not appear to have a well-defined spawning period and suggested that the schedule of sexual maturation and spawning could be different for each school, depending upon the conditions that the school had been encountering. Off southern Brazil spawning regimes may be equally complex because of upwelling, the passage of weather fronts, and the interaction of the Brazil Current with the coastal shelf.

Since mature ovaries include a wide range of gonad index values, the index is not a precise indication of maturity stage. Matsumoto et al. (1984) concluded that gonad indexes were not good measures of skipjack maturity (i.e. ova size). However, gonad indexes above 30 do indicate ovaries that are ready for spawning with ripening soon to follow. Our observations of histological stage 4 ovaries with postovulatory follicles present indicate that this stage also includes some fish that had already batch-spawned.

The large variance of the gonad index for maturing and mature ovaries may be due to the following: (1) Ova do not ripen gradually, and the separating mode of ripening eggs (ca. 0.5–1.0 mm) may include a relatively large percentage of the total ova. Alekseyev and Alekseyeva (1981) considered this to be a feature of neritic tunas. (2) Ripening fish probably become increasingly unavailable to the fishery, as indicated by their rareness in samples (Brock 1954; Yoshida 1966; Batts 1972c; Chur et al. 1980). (3) Individuals from the same school tend to be at similar developmental stage, independent of other schools (Yoshida 1966; Cayré 1981) indicating a wide range of origins, ages and conditions of fish in a given area. (4) The physical condition of fish may change rapidly during the ripening, spawning, and post spawning stages.

The above factors do not necessarily indicate that spawning is erratic in time, depending upon the recent histories of individual schools. Rather, in a given spawning area total spawning may be almost continuous, due to the summation of individual spawning activity of numerous, independent schools. Therefore, total egg production may be much less variable than suggested by the observed variance of gonad index.

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