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# Reproductive biology of the swordfish *Xiphias gladius* in the Straits of Florida and adjacent waters

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The swordfish *Xiphias gladius* Linnaeus inhabits all tropical, subtropical, and temperate oceans of the world, including the Mediterranean Sea and the Gulf of Mexico. In the western Atlantic, it is found from Newfoundland to Argentina (Palko et al. 1981, Nakamura 1985). Swordfish occur in the Florida Straits at all times of the year. Prior to 1970, swordfish were pursued primarily by recreational fishermen. During the 1970s, the fishery in Florida attracted displaced Cuban-Americans and New England longline fishermen, and by 1980 commercial landings from the east coast of Florida had reached nearly 1500 mt (Berkeley and Irby 1982).

Little is known about the reproductive biology of swordfish in the western Atlantic. Ovchinnikov (1970) and Berkeley and Houde (1980) reported contradictory findings on male and female sizes-at-maturity. Wilson (1984) reported that males mature at younger ages than do females in the U.S. south Atlantic. Descriptions of swordfish spawning season and spawning grounds have been based on the temporal and areal distribution of infrequently-collected larvae and juveniles (Arata 1954, Tibbo and Lauzier 1969, Markle 1974, Grall et al. 1983). Our research objectives were to determine the size- and age-at-maturity, spawning season, and approximate spawning grounds of swordfish in the Straits of Florida and adjacent waters. Data were collected as part

of a joint Florida Marine Research Institute and University of Miami investigation of the fishery and biology of the swordfish. Samples gathered during this research have been used to develop a method to determine the ages of swordfish and to describe their growth (Berkeley and Houde 1984).

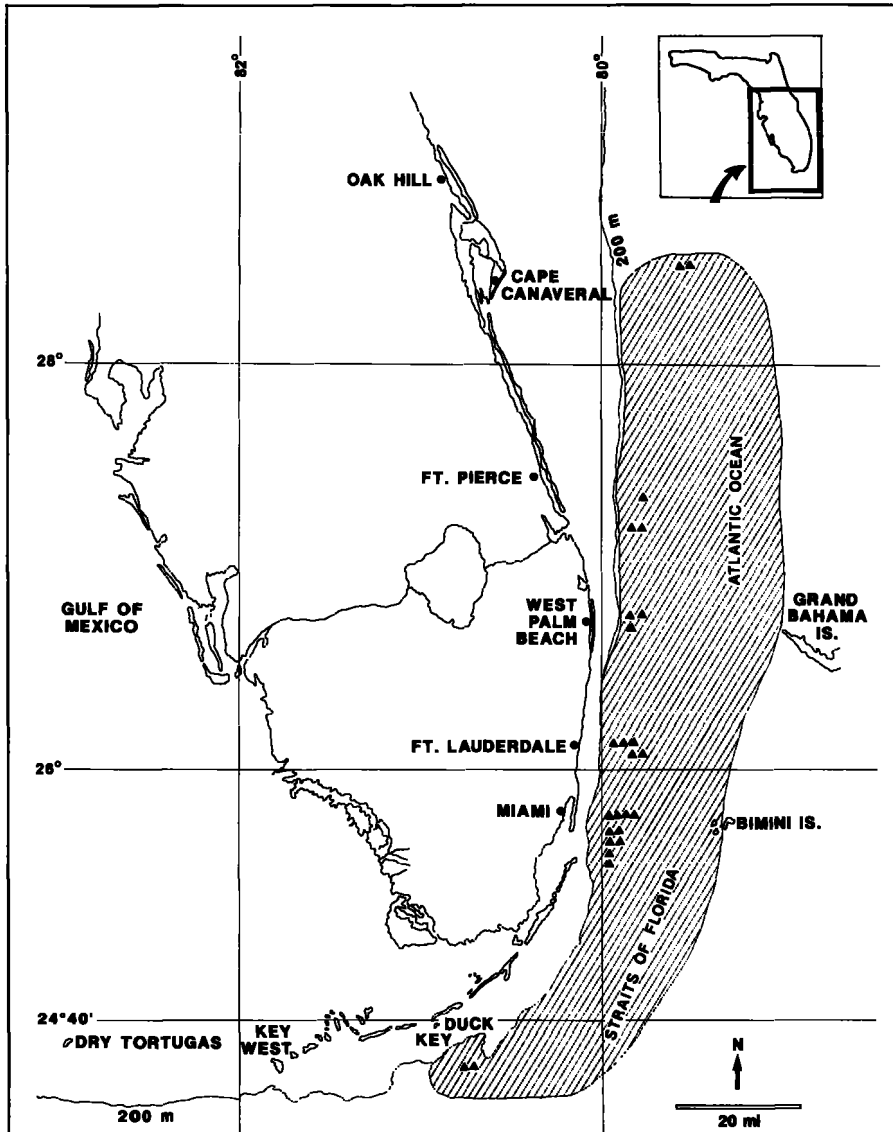
## Methods and materials

Swordfish were sampled from recreational and commercial catches made off southeast Florida (Fig. 1) from June 1977 through November 1980. Each year most of the collections were made April through September. Samples were taken at least once each month over the 2.5 yr sampling period, except in December when no samples were taken either year. Because of the varied conditions of landed swordfish, a variety of length measurements (to the nearest cm) were taken: total length (TL), distance from the tip of the bill to the midpoint of the line connecting the distal edges of the caudal-fin lobes; fork length (FL), from the tip of the bill to the distal end of the central ray of the caudal fin; lower jaw to fork length (LJFL), from the tip of the lower jaw to the distal end of the central ray of the caudal fin; eye to fork length (EFL), from the posterior margin of the eye's bony orbit to the distal end of the central ray of the caudal fin; and trunk length (TRNKL), from the posterior mar-

gin of the gill cavity to the point of least circumference of the caudal peduncle. Lower jaw to fork length is used throughout this paper unless otherwise noted. For fish measured only for TL, FL, EFL, or TRNKL, LJFL was estimated using the appropriate regression equation (Table 1). Whole weight (W) was determined to the nearest pound and converted to kilograms for our analyses. Portions of ovaries and testes were collected and preserved in Davidson's fixative (Humason 1972). Whole gonads, macroscopically judged ripe or mature based on the presence of transparent eggs, were preserved and then weighed to the nearest gram.

Swordfish maturity was described using histological features to define gonadal development. Subsamples of preserved gonads were embedded in paraffin, sectioned at 6 $\mu$ m, stained with Mayer's haematoxylin and eosin, and mounted for microscopic examination. Swordfish were assigned to one of eight developmental classes following Murphy and Taylor (1990) and based on the appearance of histological features described by Grier (1981) for males and Wallace and Selman (1981) for females. These developmental classes and the mean observed oocyte diameters are (1) Immature, <20 $\mu$ m; (2) Developing, 71 $\mu$ m; (3) Maturing, 160 $\mu$ m; (4) Mature, 434 $\mu$ m; (5) Gravid, 723 $\mu$ m; (6) Spawning/Partially Spent, 823 $\mu$ m; and (7) Spent, 181 $\mu$ m. The relationship between swordfish maturity and length was described for each sex using maturity data for fish grouped into 10 cm size-classes. A logistic distribution function was fit to the percentages of mature fish ( $\geq$  Class 4) and the midpoints of their size-classes (Saila et al. 1988) in order to predict a maturity schedule. A similar distribution function was generated for maturity against age.

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**Figure 1**

Areal extent of sampling locations (shaded area) off southeast Florida during June 1977–November 1980. Triangles indicate where female swordfish *Xiphias gladius* were found with histological evidence for recent (postovulatory follicles) or imminent (hydrated oocytes) spawning (see "Methods and materials").

**Table 1**

Linear regressions of lower jaw to fork length (LJFL) on total length (TL), fork length (FL), eye to fork length (EFL), or trunk length (TRNKL); and nonlinear regressions of whole weight (W) on lower jaw to fork length and LJFL on W, for swordfish *Xiphias gladius* off southeast Florida (regression analysis, SAS 1982).

Equation	N	Range	r <sup>2</sup>
LJFL = -6.03 + 0.662(TL)	401	32–432 cm TL	0.982
LJFL = -5.51 + 0.714(FL)	100	30–396 cm FL	0.983
LJFL = 8.89 + 1.076(EFL)	316	68–249 cm EFL	0.995
LJFL = 15.71 + 1.402(TRNKL)	324	18–189 cm TRNKL	0.987
W = 1.050 × 10 <sup>-5</sup> LJFL <sup>3.088</sup>	127	27–281 cm LJFL	0.973
LJFL = 48.58W <sup>0.306</sup>	127	0.090–168.0 kg W	0.980

Ages for the swordfish that comprise this data set were determined by Berkeley and Houde (1984), who counted unvalidated age marks found on thin-sections of the second anal-fin spine.

Temporal differences in mean oocyte diameters were used to define spawning season. To determine mean oocyte diameter for each individual, 100 oocytes in a common lamella were measured with an ocular micrometer. Mean oocyte diameters were calculated for all collections in a given month and plotted to examine monthly changes. The distribution of oocyte diameters was also examined within individuals to determine whether swordfish undergo multiple spawns or a single spawn each year.

We used the distribution of swordfish captured in near-term spawning condition to delimit their spawning grounds off southeast Florida. Histological features indicative of recent or imminent spawning included post-ovulatory follicles and hydrated oocytes (DeMartini and Fountain 1981, Hunter and Macewicz 1985). For a variety of fishes, it has been found that oocytes hydrate during the late-afternoon or evening just prior to spawning (*Serrius politus*, DeMartini and Fountain 1981; *Engraulis mordax*, Hunter and Macewicz 1985; *Cynoscion nebulosus*, Brown-Peterson et al. 1988; *Sciaenops ocellatus*, Fitzhugh et al. 1988). Postovulatory follicles are identifiable only for a short time. Following spawning, they are rapidly absorbed (within 6 h for *Callionymus enneactis*, Takita et al. 1983) and quickly become indistinguishable from other atretic structures (within 2 d in *Engraulis mordax*, Hunter and Macewicz 1985).

Batch fecundity was estimated gravimetrically from counts of ova >750 μm diameter in a 2–3 g portion from the midsection of each preserved ovary (n = 7).

## Results

Sex and length data were collected from 554 swordfish: 211 females 72–281 cm, and 343 males 82–235 cm. Gonads were avail-

**Table 2**

Observed and predicted percentages of mature ( $\geq$  Class 4, see "Methods and materials") swordfish *Xiphias gladius* in 10 cm LJFL length intervals. Predicted percentages were calculated from logistic distribution functions fit to observed maturity data (see "Results"). Numbers in parentheses are numbers of fish examined.

Lower jaw to fork length interval midpoint (cm)	Male		Female	
	Observed %(N)	Predicted %	Observed %(N)	Predicted %
80			0(1)	0
90	0(3)	11	0(2)	0
100	33(3)	24	0(7)	0
110	46(11)	45	0(17)	0
120	64(11)	69	0(19)	1
130	90(10)	85	0(14)	3
140	96(24)	94	0(8)	5
150	93(14)	98	0(2)	10
160	100(11)	99	0(3)	18
170	100(14)	100	50(4)	30
180	100(11)	100	60(10)	47
190	100(8)	100	56(16)	64
200	100(6)	100	71(14)	78
210	100(5)	100	75(16)	87
220	100(1)	100	100(10)	93
230	100(1)	100	100(6)	97
240			100(3)	98
250			100(5)	99
260			100(2)	100
270				
280			100(3)	100

**Table 3**

Observed and predicted percentages of mature ( $\geq$  Class 4, see "Methods and materials") swordfish *Xiphias gladius* by assigned age group (ages from Berkeley and Houde 1984). Predicted percentages were calculated from logistic distribution functions fit to observed maturity data (see "Results"). Numbers in parentheses are numbers of fish examined.

Age (years)	Male		Female	
	Observed %(N)	Predicted %	Observed %(N)	Predicted %
0	0(1)	4		
1	30(10)	29	0(13)	0
2	80(10)	79	0(18)	1
3	93(14)	97	0(6)	5
4	92(12)	100	18(11)	14
5	100(12)	100	38(8)	37
6	100(8)	100	60(10)	66
7			100(3)	87
8	100(2)	100	83(6)	96
9			100(4)	99
10			100(1)	100

able for histological processing from 295 fish (133 males and 162 females), of which 149 were ascribed ages.

Male swordfish mature at a smaller size and younger age than do females. Males begin to mature at  $\sim$ 100 cm at age 1 (Tables 2, 3). The proportion of mature males in our samples increased rapidly thereafter, and all males were mature by 160 cm or age 5. In contrast, the smallest mature females were  $\sim$ 170 cm or age 4, and all females were mature by 220 cm or age 9. The predicted length at 50% maturity, based on the fit of logistic distribution functions to the percentage mature within size-classes, was significantly less (approximate *t*-test, Sokal and Rohlf 1981;  $t' = 36.5$ , *df* 33,  $P < 0.001$ ) for males (112 cm) than for females (182 cm). Likewise, age at 50% maturity was significantly younger for males (1.4 yr) than for females (5.5 yr;  $t' = 17.7$ , *df* 16,  $P < 0.001$ ). The logistic distribution functions for maturity by size-class and age fit observed data well (Tables 2, 3) and are as follows:

Males:

$$\% \text{ Mature} = 1 / (1 + e^{(-0.0976(\text{LJFL} - 112)})$$

( $n = 15$ ,  $r^2 = 0.980$ )

$$\% \text{ Mature} = 1 / (1 + e^{(-2.223(\text{AGE} - 1.40)})$$

( $n = 8$ ,  $r^2 = 0.990$ )

Females:

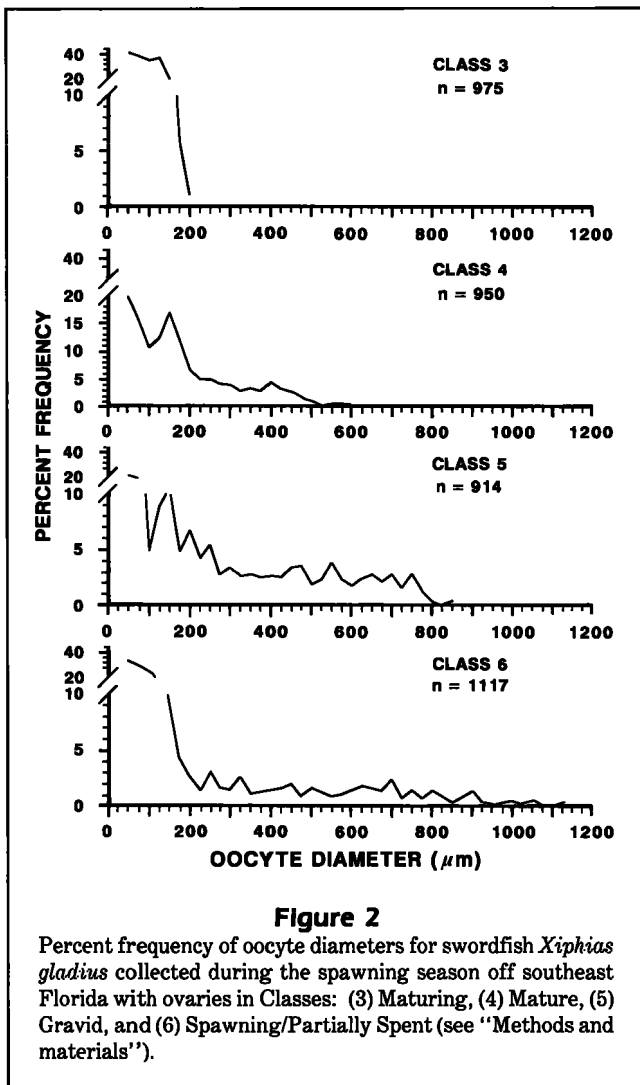
$$\% \text{ Mature} = 1 / (1 + e^{(-0.0690(\text{LJFL} - 182)})$$

( $n = 20$ ,  $r^2 = 0.966$ )

$$\% \text{ Mature} = 1 / (1 + e^{(-1.234(\text{AGE} - 5.45)})$$

( $n = 10$ ,  $r^2 = 0.976$ )

Swordfish from southeast Florida waters demonstrate group-synchronous oocyte maturation (*sensu* Wallace and Selman 1981). This pattern of oocyte development is characterized by the presence of at least two distinct groups of dissimilar-sized oocytes during the spawning season. Ovaries from all swordfish in our samples contained a dominant group of oocytes  $< 200 \mu\text{m}$  diameter (Fig. 2). All oocytes within Maturing ovaries (Class 3) were  $< 200 \mu\text{m}$ , although lipid deposition suggests preparation for active vitellogenesis. Mature ovaries (Class 4) contained an additional distinct group of vitellogenic oocytes at 200–600  $\mu\text{m}$ . A third group of oocytes, 600–1100  $\mu\text{m}$ , were present only in Gravid and Spawning/Partially Spent fish (Classes 5 and 6). This largest



group of oocytes proceeds through final maturation and represents the clutch (Wallace and Selman 1981) to be shed during the next spawning event.

The reproductive season for swordfish is protracted. Mature or actively spawning females were found during each month sampled, except January. Gravid or actively spawning males were found during all months sampled (Fig. 3). The greater numbers of spawning fish taken from late-spring to midsummer suggests increased spawning activity then. In addition, mature swordfish show a sharp increase in their maximum oocyte diameters to  $>800\mu\text{m}$  beginning in April and extending through July, indicating peak spawning activity then (Fig. 4).

Histological features (postovulatory follicles and hydrated oocytes) provide evidence for active swordfish spawning off the Atlantic coast of Florida from about  $24^{\circ}40'N$  in the Straits of Florida southwest of

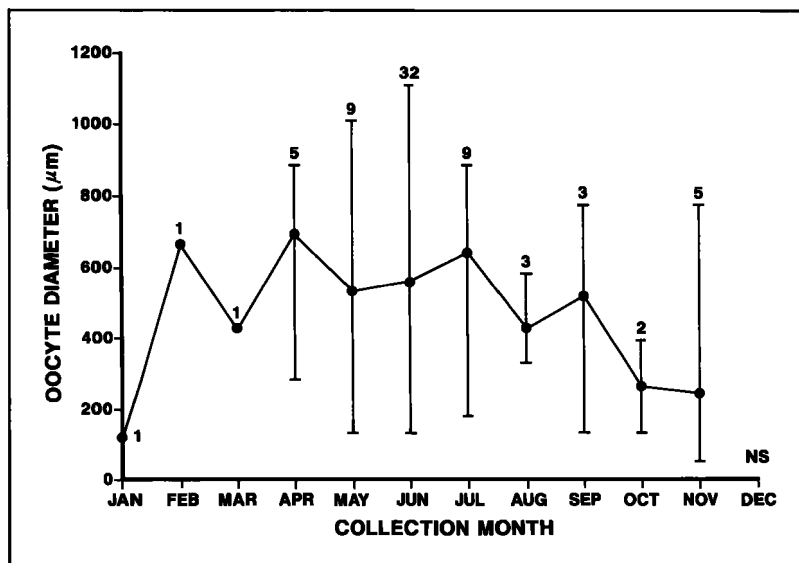
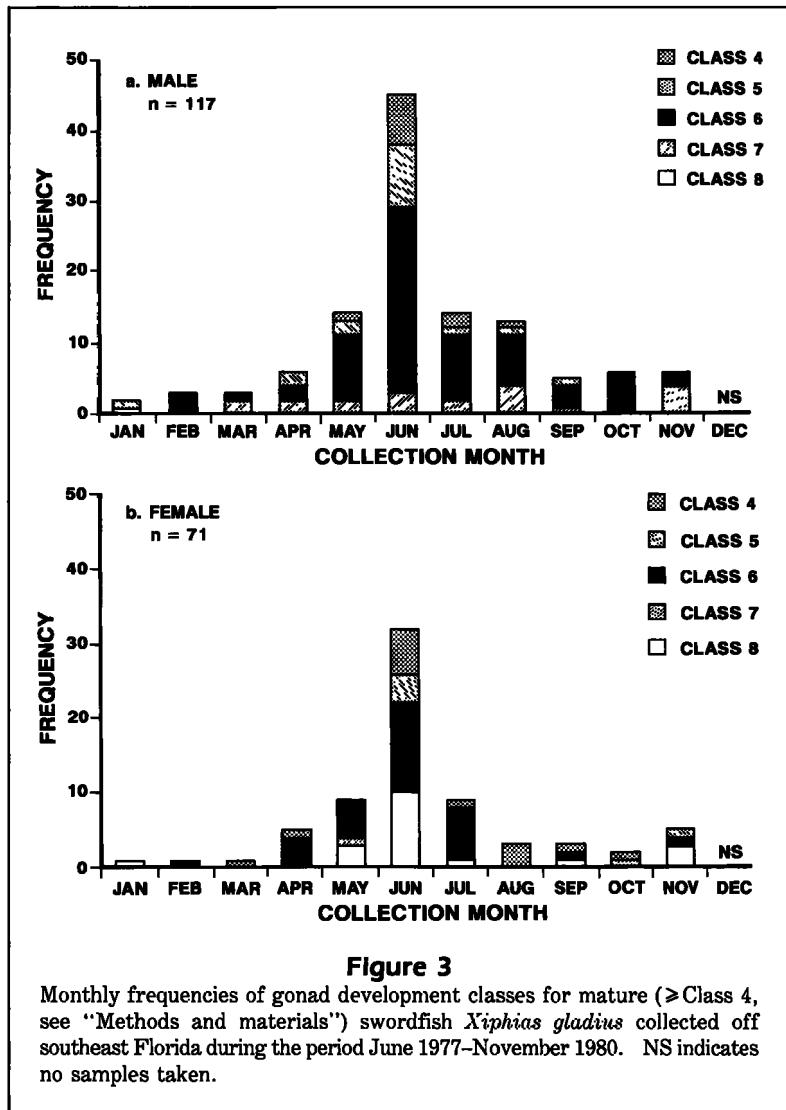
Duck Key to about  $28^{\circ}25'N$  just west of Cape Canaveral (Fig. 1). The easternmost location where fish in spawning condition were collected was 16km east of Grand Bahama Island at 480m depth. About 25% of the fish collected at the westward extent of our sampling area (about the 200m contour) exhibited evidence of recent or imminent spawning.

There was a preponderance of smaller males in our spring and summer samples. Overall, males significantly dominated the catch (345 M:216 F;  $\chi^2$  29.7, df 1,  $P < 0.001$ ); although at sizes  $>200\text{cm}$ , females significantly outnumbered males (22 M:67 F;  $\chi^2$  22.8, df 1,  $P < 0.001$ ). There was no histological indication of hermaphroditism throughout the 72–281cm length range. During spring and summer, males were dominant (266 M:152 F;  $\chi^2$  31.1, df 1,  $P < 0.001$ ); but during the fall and winter there was no significant difference in abundances of sexes (79 M:64 F;  $\chi^2$  1.6, df 1,  $P > 0.05$ ).

The batch fecundity of the seven swordfish sampled was 1.4–4.2 million eggs for swordfish 177–281cm and 69–268kg (Table 4). There was no obvious relationship between our estimates of batch fecundity and length or weight. The correlation coefficients between batch fecundity and length ( $r$  0.21) and between batch fecundity and weight ( $r$  0.64) were not significantly different from zero (table of critical values for correlation coefficients, df 5,  $P > 0.05$ , Rohlf and Sokal 1981).

## Discussion

Sizes-at-maturity have been reported for swordfish in the Atlantic and Pacific Oceans and Mediterranean Sea (Ovchinnikov 1970, Berkeley and Houde 1984, DeMetrio et al. 1989). However, in these reports maturity was determined by visual inspection of gonads, and no explanations were given as to whether the sizes reported were for first maturity or for 50% maturity. Berkeley and Houde (1984) reported that western Atlantic male and female swordfish mature at  $\sim 21\text{kg}$  and  $74\text{kg}$ , respectively. This corresponds closely to the lengths-at-50%-maturity we present for swordfish off southeast Florida. Using equations in Table 1, we determined 50% maturity of males at 18kg (112cm LJFL converted to whole weight) and 50% maturity of females at 77kg (182cm). Ovchinnikov (1970) reported that male swordfish "reach maturity" in the Atlantic at about 100cm (type of measure unknown). However, he reported a smaller size-at-maturity for females (70cm). DeMetrio et al. (1989) reported that male swordfish in the eastern Mediterranean Sea first begin to mature at 82–105cm LJFL and that nearly all are mature when  $>135\text{cm}$ . Females



in the Mediterranean first reach maturity at 106–135 cm LJFL, and about 50% of the females  $>$ 135 cm are mature. This is in contrast to our findings that the smallest mature females off Florida were  $\sim$ 170 cm LJFL and that 50% of females reached maturity when  $\sim$ 180 cm.

Female swordfish from the Pacific Ocean mature at sizes comparable to or somewhat smaller than those in the western Atlantic. From 1949 to 1958, Yabe et al. (1959) examined 372 female swordfish taken by a Japanese longline fleet in the North Pacific. They found only five mature females and suggested that females in the North Pacific begin to mature at 150–170 cm EFL (170–192 LJFL). Kume and Joseph (1969) concluded that female swordfish off California begin to mature at slightly smaller sizes, 139 cm EFL (158 cm LJFL), and are regularly found in ripe condition at  $>$ 170 cm (192 cm LJFL).

The ages-at-maturity we estimated for male (1.4 yr) and female (5.5 yr) swordfish off southeast Florida are somewhat younger and older, respectively, than those determined for male and female swordfish collected farther north in the U.S. South Atlantic. From a relatively small sample collected off North Carolina and South Carolina, Wilson (1984) determined that males mature between ages 2 and 3 (15 mature males of 24 examined). Females mature between ages 4 and 5 (2 mature females of 18 examined). Although Wilson (1984) relied on a different technique (thin-sectioned otoliths) than did our study (thin-sectioned spines) to determine swordfish ages, he compared the two aging techniques and found they provided similar swordfish ages through at least age 5.

Female swordfish mature at a younger age in the eastern Mediterranean Sea than in the western Atlantic or Pacific Oceans. In the eastern Mediterranean,

**Table 4**

Estimates of batch fecundity for seven swordfish *Xiphias gladius* sampled off southeast Florida, including lower jaw to fork length, age (Berkeley and Houde 1984), whole weight, gonad development class, and oocyte diameters.

Batch fecundity (millions)	Lower jaw to fork length (mm)	Age (yr)	Whole weight (kg)	Gonad class	Hydrated oocyte size		
					N	$\bar{x}$	range
1.398	256	6	107	6	1754	0.98	0.83-1.16
2.814	252	9	223	6	1288	1.04	0.75-1.14
2.836	207	8	116	6	1656	1.56	1.30-1.77
3.071	177	—	69	6	2036	1.55	1.33-1.73
3.125	233	—	170	6	2121	1.35	1.17-1.57
4.220	281	—	268	6	2912	1.54	1.34-1.68
4.220	256	9	210	6	1232	1.11	0.96-1.23

DeMetrio et al. (1989) found mature female swordfish as young as age 2, with most mature by age 3. However, Yabe et al. (1959) suggested that female swordfish in the North Pacific mature at age 5 or 6. This is in agreement with our age-at-50%-maturity for females (5.5 years). Although we found no information on maturation of male swordfish from the Pacific, most male swordfish in the eastern Mediterranean reach maturity by age 2 (DeMetrio et al. 1989), again similar to our findings off southeast Florida.

The observed protracted spawning of swordfish off southeast Florida, with peak activity during April through July, agrees with reported spawning seasons determined from temporal changes in the abundance of larvae and juveniles. Taning (1955) reported that spawning off Florida and elsewhere in the North Atlantic occurs throughout the year, with peak larval abundances during February through April. The temporal distribution of larval abundance in the western North Atlantic suggests that swordfish spawn during December through September, with a peak in April (Arata 1954, Markle 1974, Grall et al. 1983). Off the coast of southern California, gonads of female swordfish are inactive from late-August through mid-November (Weber and Goldberg 1986). This period of inactivity coincides with low mean oocyte diameters of swordfish in the western Atlantic (Fig. 4), suggesting that swordfish in the eastern Pacific and western Atlantic may have similar annual spawning seasons.

Two histological features present in ovarian tissue—hydrated oocytes and postovulatory follicles—provided evidence that female swordfish spawn off the coast of southeast Florida between the Florida Keys and Cape Canaveral. The presence of hydrated oocytes indicates an imminent spawn, certainly within 12h. Young postovulatory follicles found in many female swordfish provide evidence that spawning occurred within 24h of

capture. Further, short-term studies of the movement of swordfish, using acoustic tags, have shown that fish that were likely mature (70–140kg) remained in the same general area (<90km from tagging) for up to 5d during the peak of the spawning season (April) off Baja California (Carey and Robison 1981). More extensive movement occurred for a 70kg swordfish tracked for 2.5d in November in the vicinity of Cape Hatteras, North Carolina. This fish traveled 240km in 67h, heading from cold continental shelf waters off Cape Hatteras to warmer Sargasso Sea waters.

The combination of this information on net random movement of swordfish with our observed histological evidence for recent or imminent spawning suggests that spawning occurs in our sampling area. Additionally, Grall et al. (1983) found major concentrations of swordfish larvae and juveniles in the western Atlantic in the waters near the Lesser Antilles, in the Yucatan Straits, and in the Florida Straits, implying the presence of a large spawning population in these areas.

Changes in sex ratios as swordfish increase in size apparently result from differences in growth between the sexes and possibly from seasonal differences in their distribution. Swordfish larger than ~230cm are female because males have shorter life spans and slower growth rates (Berkeley and Houde 1984, Wilson 1984). The dominance of males in our summer collections may be explained by seasonal differences in the distribution of the sexes. Guitart-Manday (1964) found a similar preponderance of males (72%) in samples from the mainly summertime commercial fishery off Cuba. Beckett (1974) reported that few males were taken in the northern swordfish fisheries in waters <18°C, whereas in more tropical latitudes, males account for 67–100% of the catch. Off southeast Florida, surface-water temperatures remain >18°C throughout the year, ranging from ~22°C in February to 29°C in August (Atkinson et al. 1983). Our observed seasonal changes in sex ratios of swordfish collected off southeast Florida imply that whereas some males and females are year-round inhabitants of these waters, more females than males move north during the summer, which results in a dichotomous distribution that becomes more acute the farther north the fish migrate. At the northern extent of the range in the western North Atlantic, off New England and the Canadian maritimes, most, if not all, fish captured are females (Lee 1942, Tibbo et al. 1961).

Our estimates of batch fecundity (1.4–4.2 million ova) are comparable to the estimate of Yabe et al. (1959) and to estimates for smaller swordfish by Uchiyama and Shomura (1974). Our estimates are somewhat less than those made for larger fish collected by the latter authors. Yabe et al. (1959) estimated the fecundity of a swordfish 186 cm TRNKL (276 cm LJFL from Table 1) to be 3–4 million ova (1.2–1.6 mm in diameter). Uchiyama and Shomura (1974) estimated the fecundity of an 80 kg swordfish (185 cm LJFL from Table 1) to be 3.0 million ova, which closely agrees with our determinations. However, they estimated that a 200 kg swordfish (244 cm LJFL from Table 1) would have a fecundity of ~6 million ova, which is more than our estimates for swordfish over 200 kg.

Our estimates of fecundity and maturity schedules can be used in analyzing the effect of fishing on the spawning-stock biomass or spawning potential of swordfish in the U.S. South Atlantic (e.g., spawning-stock biomass per recruit analysis, Gabriel et al. 1989). Recent assessments of the status of swordfish in the Atlantic have utilized several techniques, including dynamic pool models (“yield per recruit”), to determine the effects that fishing and age at entry to the fishery have on yield (ICCAT 1991). Our quantitative estimates of the female maturation process and fecundity can be used in further analyzing the effect of fishing on the abundance of mature swordfish (and by implication the production of new recruits).

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