SWORDFISH REPRODUCTION IN THE ATLANTIC OCEAN: AN OVERVIEW

Freddy Arocha

Instituto Oceanográfico de Venezuela, Universidad de Oriente, Apartado de Correos No. 204, Cumaná-6101, VENEZUELA, E-mail farocha@sucre.udo.edu.ve; farochap@gmail.com

ABSTRACT There are 3 unit stocks of Atlantic swordfish, *Xiphias gladius*, separated into Mediterranean, North and South Atlantic with no precise delimitation between them, and each contains its spawning grounds far from stock boundary areas. This overview characterizes the reproductive information for each stock unit and describes reproductive metrics in detail. Spawning in the western North Atlantic consists of 2 spawning groups: one in open ocean waters and the other in waters close to land masses and fast current systems. Spawning occurs from December to June within the subtropical area (13°N–35°N). Within the Mediterranean, spawning takes place between June and August, and appears to be restricted between 35°N and 40°N. The information for the South Atlantic is limited, but spawning concentrations are present in April–June on the western side off Brazil and the equatorial area, and from October to March in the central-eastern equatorial area. In the western North Atlantic, females are observed to mature at larger sizes ($M_{f50} = 178.7$ cm) and older ages (age 5.03) than in the South Atlantic ($M_{f50} = 156$ cm) and Mediterranean Sea ($M_{f50} = 142.2$ cm). Estimates of batch fecundities in swordfish in the Atlantic Ocean appear to be similar, and can reach up to 8–9.9 million eggs per spawn.

RESUMEN En el Océano Atlántico existen 3 unidades de stock de pez espada, *Xiphias gladius*, conformadas por la del Mediterráneo, la del Atlántico Norte y la del Atlántico Sur, no contentan con una delimitación precisa entre ellas, y cada una contiene sus áreas de reproducción y desove alejadas de las zonas límites de las unidades de stock. Esta visión general caracteriza la información reproductiva en cada unidad de stock y describe la reproducción en detalle. La reproducción del pez espada en el Atlántico nor-occidental está compuesta por dos grupos reproductivos: uno en aguas oceánicas y otro en aguas cercanas a las costas y de fuertes corrientes. La reproducción ocurre de diciembre a junio en el área subtropical (13°N–35°N). En el Mediterráneo, la reproducción ocurre entre junio y agosto, done parece estar restringida entre los 35°N y 40°N. La información para el Atlántico Sur es limitada, pero concentraciones para la reproducción están presentes de abril a junio en el lado occidental cercano al Brasil y en el área ecuatorial, y de octubre a marzo en el área ecuatorial centro-oriental. En el Atlántico nor-occidental, las hembras maduran a tallas mayores ($M_{f50} = 178.7$ cm) y a edades mayores (edad 5.03) que en el Atlántico Sur ($M_{f50} = 156$ cm) y el Mar Mediterráneo ($M_{f50} = 42.2$ cm). Los estimados de fecundidad por tanda en el pez espada del Océano Atlántico parecen ser similares, y pueden alcanzar hasta 8.0–9.9 millones de huevos en cada desove.

INTRODUCTION

Swordfish (*Xiphias gladius*) are highly migratory meso-pelagic fishes widely distributed throughout tropical and temperate waters between 45°N and 45°S, and in large enclosed basins such as the Gulf of Mexico (GOM), the Caribbean Sea, and Mediterranean seas (Palko et al. 1981, Nakamura 1985). The Atlantic population structure has at least three genetically distinct units: Mediterranean, western North Atlantic, and South Atlantic (Kotulas et al. 1995, Chow et al. 1997, Alvarado-Bremer et al. 2005). For fishery management purposes, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recognizes a North and South Atlantic stocks separated by an imaginary boundary located at 5°N and a Mediterranean stock separated by the Strait of Gibraltar (ICCAT 2006). Although, the possibility for a northeast Atlantic unit is not excluded, the admixture with Mediterranean swordfish may confound analyses (Chow and Takeyama 2000, Kotulas et al. 2006).

The information on swordfish reproduction in the Atlantic is fragmented and limited. The temporal and spatial spawning patterns have been inferred from the abundance of larvae (Sella 1911, Tåning 1955, Gorbunova 1969, Grall et al. 1983, Govoni et al. 2000), gonad assessment by means of a gonad index (de la Serna et al. 1992, Arocha and Lee 1995, Mejuto and García 1997), and by microscopic examination of developmental stages of oocytes (Taylor and Murphy 1992, Arocha 1997, Correiro et al. 2004). Most authors have inferred swordfish spawning patterns in the Atlantic Ocean using a single method, although some studies have attempted to integrate several methods with more than one technique (Arocha 1997, Govoni et al. 2003, Correiro et al. 2004).

In recent years there has been an increasing need for reproductive population parameters in marine fishes, which are essential to obtain accurate estimates of the effect of fishing on the reproductive potential of the stock (Mace 1993, Murawski et al. 2001). Size-and-age-at-maturity and specific fecundity are basic parameters to estimate
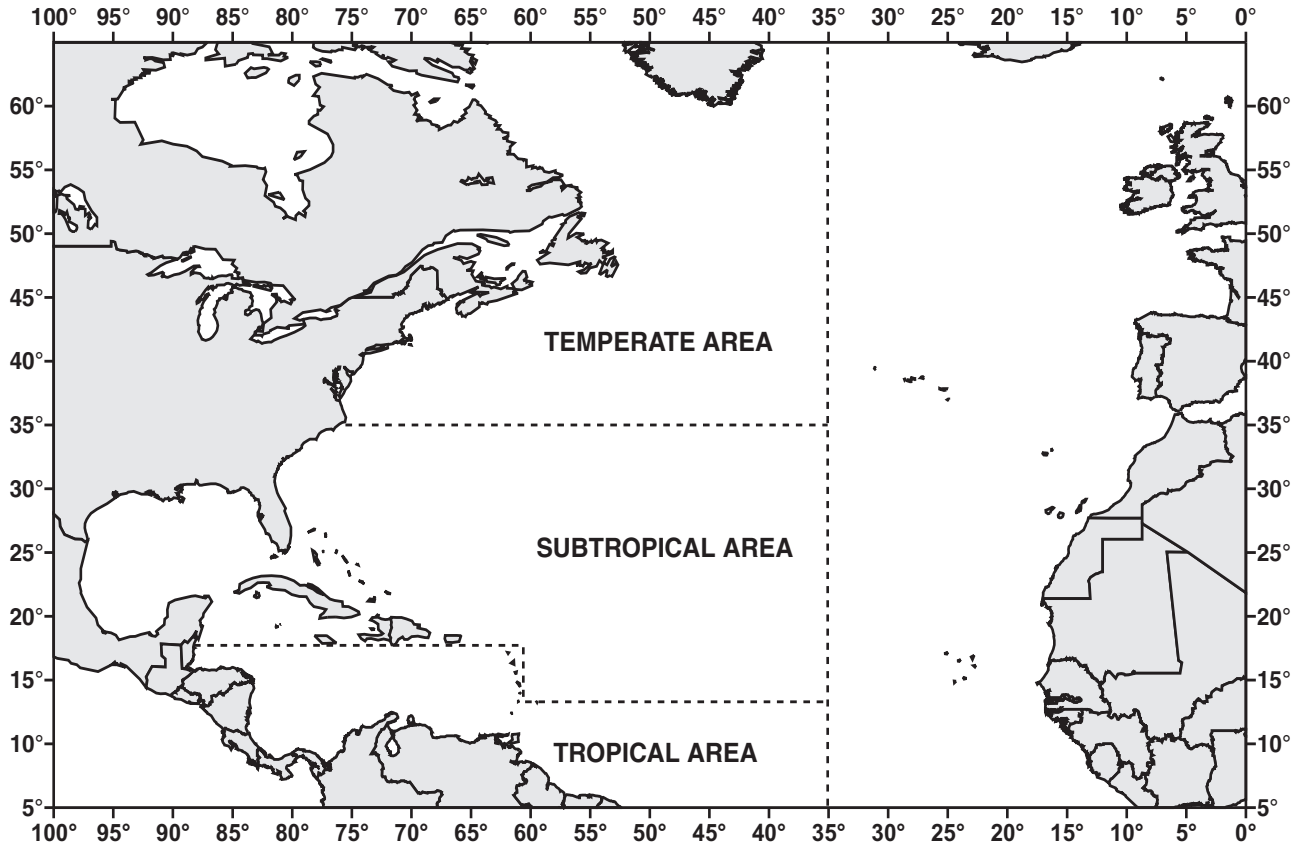
Figure 1. Map of the North Atlantic Ocean showing the boundaries of the 3 areas (i.e., temperate, subtropical, tropical) into which the study on swordfish reproduction in the western North Atlantic was divided (Arocha 1997).

spawning potential ratio (SPR) in fishery stock assessments (Goodyear 1993) and spawner-recruit relationships. Swordfish reproductive population parameters have been estimated for the three recognized stock units in the Atlantic (de la Serna et al. 1996, Arocha 1997, Hazin et al. 2001), but assumptions and techniques differ between studies.

The present paper is an overview of the temporal and spatial spawning patterns currently known for swordfish throughout its Atlantic Ocean distribution. Reproductive population parameters (maturity-at-size and batch fecundity) will be reviewed and contrasted by stock structure. This paper provides an integrated view of the spawning of swordfish in the Atlantic Ocean as is currently known.

MATERIALS AND METHODS

Selection of data

The data selected for the description of temporal and spatial spawning patterns were obtained from the most recent and comprehensive studies available for the Atlantic Ocean, these include: Arocha (1997) and Govoni et al. (2003) for the western North Atlantic; Mejuto and García

(1997), and Ueyanagui et al. (1970) for the South Atlantic; Cavallaro et al. (1991), de la Serna et al. (1996), Tserpes et al. (2001), Correiro et al. (2004), and Macias et al. (2005) for the Mediterranean Sea.

The data selected for the review on reproductive population parameters come from the studies of de la Serna et al. (1996) for the Mediterranean stock, Arocha (1997) for the North Atlantic stock, and Hazin et al. (2001, 2002) for the South Atlantic stock.

Data for spawning indication and location

North Atlantic stock. The region was divided into the 3 areas used in the study of Arocha (1997) for the western North Atlantic. The areas were defined as: tropical (5°–13°N in the Atlantic side and 5°–18°N in the Caribbean side), subtropical (13°–35°N in the Atlantic side and 18°–35°N in the Caribbean side), and temperate (35°–55°N) (Figure 1). The subtropical area was further subdivided into the Atlantic subarea (ATL) which included specimens caught in the Atlantic Ocean outside the Antillean Island chain; the GOM and Windward Passage subarea (GOMWP) which included specimens caught in the
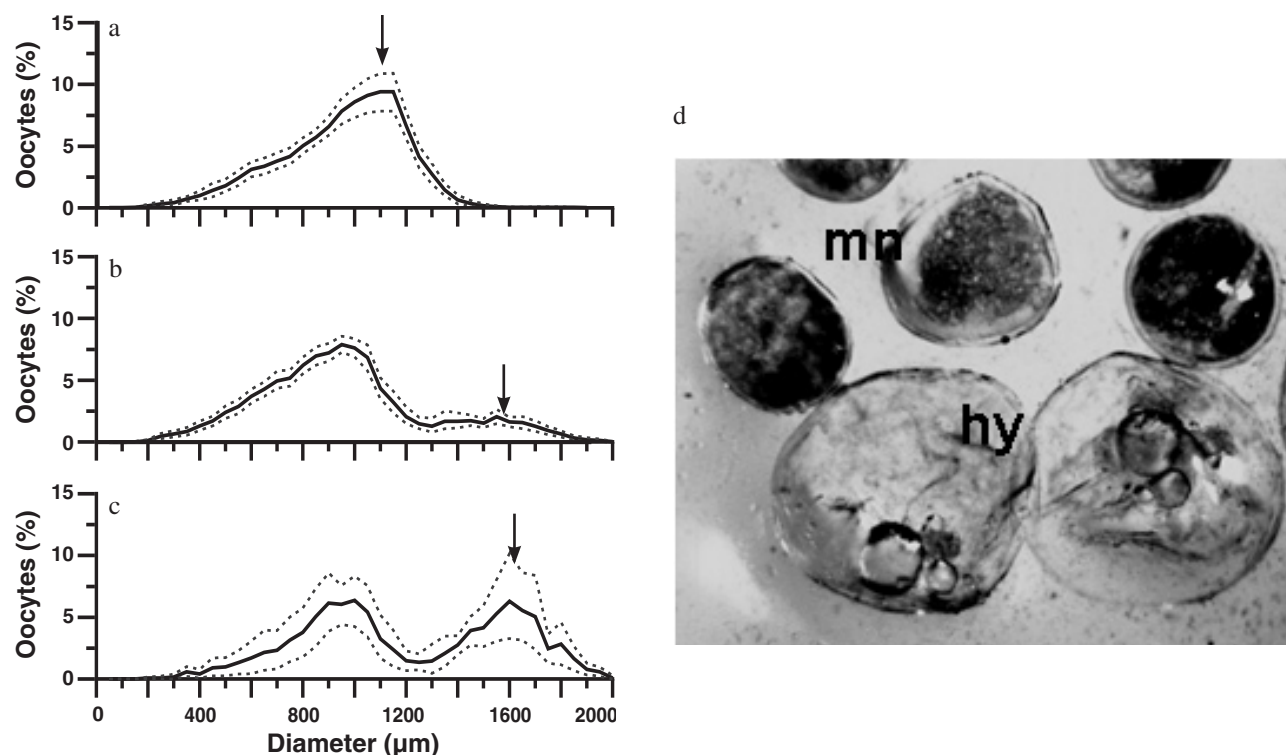
Figure 2. Typified size frequency distributions of fresh whole oocytes in spawning females in the western North Atlantic (after Arocha 2002). a) Bootstrapped frequency distribution of migratory nucleus oocytes (arrow) as the most advanced group of oocytes; b) Bootstrapped frequency distribution of oocytes with unovulated hydrated oocytes (arrow) as the most advanced group of oocytes; c) Bootstrapped frequency distribution of oocytes with ovulated hydrated oocytes (arrow) as the most advanced group of oocytes, dashed lines depict 95% confidence limits; d) Image of whole hydrated (hy) and migratory nucleus (mn) oocytes.

Windward Passage, Yucatan Channel, and the GOM; the Straits of Florida and southeastern US subarea (SOFSE) which included specimens east of 82°W in the Straits of Florida to 35°N, along the southeastern US coast.

Spawning was inferred from a combination of techniques. Classification of sexually mature females (>150 cm lower jaw-fork length, LJFL) in spawning condition was based on the relative gonad index (RGI) (Erickson et al. 1985). This index was adjusted to the mean oocyte diameter of 10 of the largest and most advanced group of oocytes (MAGO) in the ovary such that the RGI value would ensure that females were at an advanced maturity stage (Arocha 1997). The resulting RGI value of the RGI vs mean MAGO diameter was estimated by an iterative search method to obtain the best fit of 2 straight lines (Somerton 1978, Cayré and Laloë 1986, Arocha 1997). The point of intercept of the 2 lines would be the RGI value at which oocytes would be considered to complete vitellogenesis. The estimated RGI value (27.64), termed $_{spawn}$RGI, was utilized to indicate that spawning was about to happen or occurring. Spawning females were defined as those presumed to spawn within 24–48 h based on the

presence of migratory-nucleus phase or hydrated oocytes as the most advanced stage of development in the gonad or those that had spawned in the last 12–24 h and contained post-ovulatory follicles (POF) in the gonad of recently spawned females. Spawning females were identified using typified size frequency distributions of fresh oocyte diameters (Figure 2) as defined by Arocha (2002). Once spawning females were defined and identified, the combined information of the seasonal distribution of spawning females, the seasonal distribution of young larvae (<10 days from fertilization [DFF], from Govoni et al. 2003), and the seasonal distribution of females with mean maximum RGI (maxRGI, RGI >27.64) were used to describe the seasonal shift in time and location of imminent spawning in the western North Atlantic.

South Atlantic Stock. The classification of sexually mature females in spawning condition was based on the gonad index traditionally used by European scientists working on swordfish (e.g., Kume and Joseph 1969), combined with examination and measurement of oocytes in histological sections from the studies of Hazin et al. (2001, 2002). The temporal and spatial distribution of spawning

TABLE 1

Monthly mean oocyte diameter of the most advanced group of oocytes ($\overline{MAGO}$), standard error ($S_{\overline{x}}$), oocyte diameter range (µm), and sample size of fish (*n*) of sexually active female swordfish ($\overline{MAGO} > 1000$ µm) in the western North Atlantic.

	$\overline{MAGO}$	$S_{\overline{x}}$	range (µm)	*n*
January	1423	46.8	1108–1818	27
February	1336	30.8	1048–1825	48
March	1289	99.0	1012–1777	8
April	1487	121.6	1060–1883	8
May	1655	64.8	1142–2078	19
June	1305	121.9	1080–1611	4
July	–	–	–	–
August	1110	47.9	1062–1158	2
September	1145	–	–	1
October	1097	–	–	1
November	–	–	–	–
December	1365	56.2	1096–1709	12

swordfish in the South Atlantic was inferred from gonad indices (GI) estimated from female fish caught by Spanish longline vessels during 1986–1996 (Mejuto and García 1997). The authors considered that female fish with a GI > 3.0 'to be spawning or with ripe egg', and calculated GI values for 2 size groups of fish, small (<165 cm LJFL) and large (>165 cm LJFL). Additionally, an overall mean GI value and an overall mean GI maximum (GImax) value for each size group were then calculated and grouped into

spatial areas of 5X5 degrees squares. However, in the absence of detailed gonad assessment data for the South Atlantic and with the knowledge that length based GI values (e.g., Kume and Joseph 1969) for near spawning fish are > 5.0 (Arocha and Lee 1993, Corriero et al., 2004), only data from the large fish group (>165 cm LJFL) and overall mean GI maximum (GImax) value grouped into 5X5 degrees squares were used to describe seasonal and spatial changes in the present work.

Mediterranean stock. The classification of sexually mature females in spawning condition was based on the length based gonad index (GI) of Kume and Joseph (1969), combined with examination and measurement of sectioned oocytes in histological stains of intraovarian inclusions from the studies of Correiro et al. (2004) and Macías et al. (2005). The time and location of imminent spawning was inferred from the combination of females with maximum gonad indices, the presence of hydrated oocytes in their ovaries, and the seasonal distribution of eggs and young larvae (age = 5 d, from Cavallaro et al. 1991).

Data for reproductive population parameters

North Atlantic Stock. Estimates for the maturity fraction included only specimens caught during the spawning period. For the age maturity fraction, direct age was determined from anal fin rays sections (Ehrhardt et al. 1996). Estimates of batch fecundity were estimated as the number of fresh unovulated and fully hydrated whole oocytes (Figure 2b) from the mean of three sub samples taken from both ovaries and raised to the ovary tissue weight. In the

TABLE 2

Monthly relative gonad index of female swordfish (>150 cm lower-jaw-fork-length) in the 3 areas of the western North Atlantic, with mean relative gonad index ($\overline{RGI}$), standard error ($S_{\overline{x}}$), and sample size of fish (*n*).

	Temperate area			Subtropical area			Tropical area		
	$\overline{RGI}$	$S_{\overline{x}}$	*n*	$\overline{RGI}$	$S_{\overline{x}}$	*n*	$\overline{RGI}$	$S_{\overline{x}}$	*n*
January	7.3	0.64	8	29.2	4.18	96	6.9	0.38	5
February	6.9	0.28	19	41.0	3.36	114	7.1	0.57	47
March	6.7	0.65	9	21.9	4.70	44	7.8	0.80	13
April	6.3	0.29	26	18.2	4.79	29	–	–	–
May	6.2	0.63	113	38.2	7.72	26	5.2	0.30	39
June	5.9	0.19	129	30.7	9.89	19	9.4	1.51	15
July	6.4	0.15	269	4.3	–	1	5.8	0.88	12
August	6.7	0.42	86	37.5	12.33	15	5.8	0.77	8
September	5.3	0.17	117	25.6	12.14	10	7.3	0.97	16
October	5.8	0.38	41	24.8	8.56	12	10.1	2.46	15
November	5.8	0.45	16	7.9	0.70	49	25.0	10.74	11
December	–	–	–	21.3	4.32	52	10.4	1.96	40

fish length relationship, a re-scaling factor was used to set the origin at 150 cm LJFL, as no mature individuals were found below that size. F_0 in the model used in Arocha (1997) was defined as the minimum initial fecundity that is present when the fish starts hydrating oocytes. Age was determined directly from anal fin rays sections.

South Atlantic stock. Estimates for the maturity fraction included specimens caught throughout the year. Estimates of batch fecundity were estimated from counts of fixed whole oocytes >800 μm (from Hazin et al. 2001).

Mediterranean stock. Estimates for the maturity fraction included only specimens caught during the spawning period. Estimates of batch fecundity were estimated from counts of fixed whole oocytes >650 μm (from de la Serna et al. 1996).

RESULTS

Spawning season and location

North Atlantic Stock. The main spawning season was defined from December to June, based on the presence of fish with mean MAGO above migratory nucleus stage of development (>1200 μm) (Table 1). Some mature fish had vitellogenic oocytes in August, indicating a possible late summer spawning. During other times of the year mean MAGO remained below 1000 μm.

The mean relative gonad index (RGI) in females did not indicate spawning activity in the temperate area (Table 2). Mean RGI for females remained below spawning threshold (27.64) and showed no significant differences between months (ANOVA $F = 1.494$, df $= 10$, 822, $P > 0.05$). In the tropical area (Table 2), significant differences in mean RGI between months were observed for females (ANOVA $F = 3.748$, df $= 10$, 210, $P < 0.05$). The differences found were caused by the high mean RGI observed in November and December from a couple of females with mean MAGO <1200 μm (November). These fish were caught near the limits between the tropical and subtropical areas in the Caribbean side, and a single female with hydrated oocytes (December). In general, mean RGI did not reach the spawning threshold indicating the absence of regular spawning activity throughout the year in the temperate and tropical areas.

In the subtropical area (Table 2), the mean RGI surpassed the spawning threshold (27.64) in January, February, May, June, and August. The mean RGI was high in December, peaked in February, returned to high levels in March and April, and peaked again in May and June. There was another peak in August, and mean RGI remained high in September and October. These observations suggest an almost year round spawning with peak seasons, but in different locations.

The spatial distribution of spawning in the subtropical area was investigated for 3 subareas. In the ATL subareas, mean maxRGI was high during all months when fishing activity was high, except March when only one spawning female fish was caught (Table 3). Spawning females occurred from December to February (Table 4), in the area northeast of the Antillean Island chain between 18° and 25°N (Figure 3). Spawning females were also encountered in April and May, but far east of the Antillean Island chain between 13° and 15°N. Larvae distribution in the vicinity of the area was restricted to the Antillean Island chain where most larvae were 15–35 DFF from January to March. No data were available for the rest of the season due to the few fishing vessels operating in the area from June to November, but observers on board commercial longliners fishing close to the Anegada Passage during the summer have indicated that ovaries from swordfish gave no indication of being mature or spawned (D. Lee, pers. comm., NOAA-NMFS-SEFSC, Miami, FL).

In the GOMWP, the mean maxRGI was variably high from December to May, and again in October (Table 3). In June, when mean maxRGI was at its lowest value, only one spawning female fish was collected. The rest of the months, all female fish had values below the spawning threshold. Spawning females occurred in the Windward Passage and in the Yucatan Channel from December to March (Table 4). No spawning females were found in the GOMWP during the rest of the year. Larvae distribution was mostly associated with the GOM. In the western GOM larvae were present in the spring/summer (most likely between March and June), but were 20–25 DFF. In the north-central GOM, larvae of <10 DFF were present in all seasons, although the largest concentration of larvae was found during the spring/summer period.

The mean maxRGI for the SOFSE area was variably high in May, June, August, and September (Table 3). The rest of the year, mean maxRGI was below the spawning threshold, except in February and April, when only few spawning female fish were collected. Spawning females were encountered in the SOFSE in February and in May–June (Table 4) and the one spawning female collected in February with migratory-nucleus phase oocytes was found in the SOF. The rest of the spawning females were found in the southeastern waters of the US between 25° and 35°N (Figure 4). Larvae of <10 DFF were only found in the waters of the southeast US during the spring/summer and in summer/fall (likely from July–November) period. Although larvae were found throughout the area in all seasons, most were 15–30 DFF.

TABLE 3

Monthly maximum relative gonad index of female swordfish (>150 cm lower jaw-fork length) in the subtropical area of the western North Atlantic, with mean maxRGI (max$\overline{RGI}$), standard error ($S_{\overline{x}}$), and sample size of fish (_n_) of female swordfish in the Atlantic subarea (ATL), the Gulf of Mexico and the Windward Passage subarea (GOMWP), and the Straits of Florida and southeastern US subarea (SOFSE).

	ATL subarea			GOMWP subarea			SOFSE subarea		
	max$\overline{RGI}$	$S_{\overline{x}}$	_n_	max$\overline{RGI}$	$S_{\overline{x}}$	_n_	max$\overline{RGI}$	$S_{\overline{x}}$	_n_
January	95.7	8.05	21	78.4	27.58	2	–	–	–
February	69.6	3.87	45	71.9	9.00	13	40.5	0.02	2
March	30.9	–	1	82.8	8.95	8	–	–	–
April	102.2	–	1	60.8	8.95	4	30.7	–	1
May	89.4	4.65	3	60.4	–	1	80.5	8.22	7
June	–	–	–	32.4	–	1	105.4	18.58	4
July	–	–	–	–	–	–	–	–	–
August	–	–	–	–	–	–	95.2	18.19	5
September	–	–	–		–	–	98.1	4.10	2
October	–	–	–	61.3	26.14	3	–	–	–
November	–	–	–	–	–	–	–	–	–
December	73.5	16.20	7	60.4	12.99	5	–	–	–

South Atlantic Stock. The temporal and spatial distribution of mean GImax show female fish spawning year round along the equatorial Atlantic, although, the number of females with GImax was highest in April-June, and in October–December (Figure 4). The number of females with GImax during October–December were only concentrated in the east equatorial Atlantic. In contrast, during April–June fishes with GImax were mostly concentrated from the central towards the western side of the equatorial Atlantic. Another area of fish with GImax at spawning levels was located east of Trinidade and Martin Vaz Islands (~29°20'W–20°30'S) off the Brazilian coast for the same time period (Figure 4). In January–March, female fish with GImax were located around the Rio Grande Rise (~35°W–32°S), around Trinidade and Martin Vaz Islands, and in the western-central equatorial Atlantic (Figure 4). Fish with GImax at spawning levels were also observed in the center of the equatorial Atlantic in July–September (Figure 4).

Larvae collections obtained from Japanese longliners in the 1960s, indicated potential spawning off Fortaleza and Recife (Brazil) and around Trininade and Martin Vaz Islands in November–April, and in the central Atlantic from May–October. Larvae were collected over warm waters with sea surface temperatures of 26°C (Ueyanagi et al. 1970).

Mediterranean Stock. Swordfish spawning (based on fish with hydrated oocytes, GI >7.0, and the distribution of eggs and larvae) was localized in the western Mediterranean, east of the Strait of Gibraltar up to the Baleares Islands, in the southern Tyrrhenian Sea (off Sicily) and the Strait of Messina, inside the Gulf of Taranto in the Ionian Sea, and in the Levantine Sea (eastern Mediterranean) southeast of the Island of Rhodes-Greece (Figure 5). Imminent spawning takes place between June and August throughout the Mediterranean Sea. In the western Mediterranean, maturing fish (with vitellogenic

TABLE 4

Total number of female fish (_n_; >150 cm lower jaw-fork length) and number of spawning females (SF) during the spawning season in the Atlantic subarea (ATL), the Gulf of Mexico and Windward Passage subarea (GOMWP), and the Straits of Florida and southeastern US subarea (SOFSE) of the western North Atlantic.

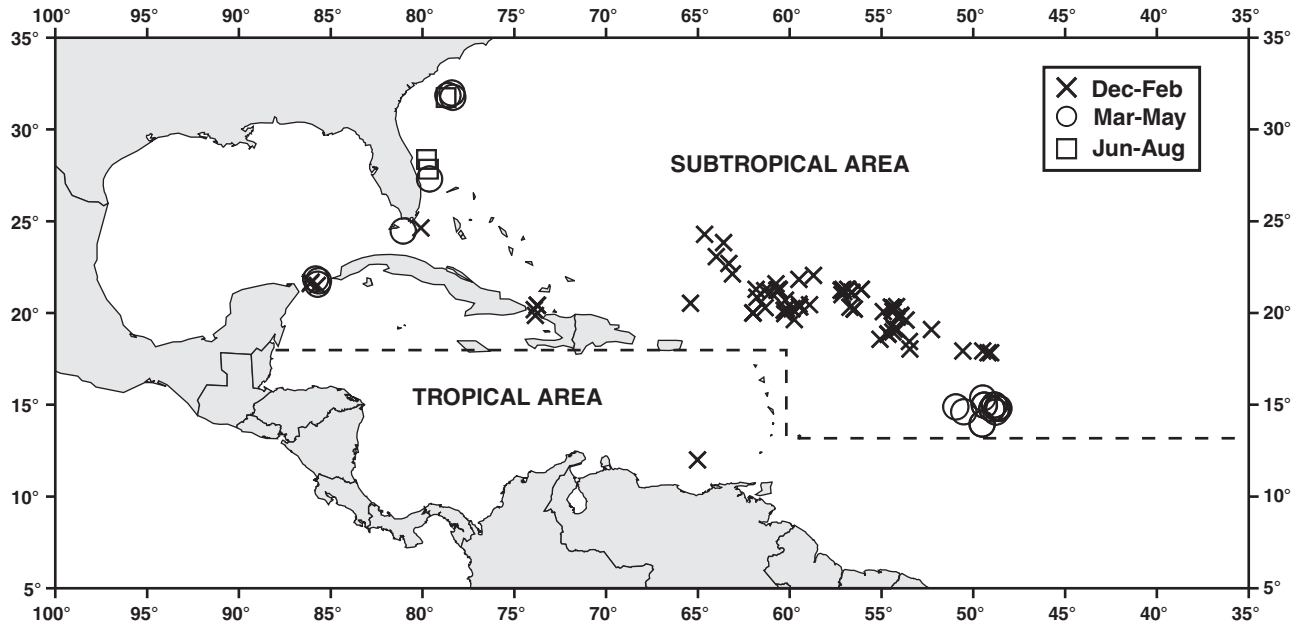|	ATL		GOMWP		SOFSE	
	_n_	SF	_n_	SF	_n_	SF
December	46	9	12	1	1	–
January	120	32	11	1	1	–
February	74	30	36	5	9	1
March	9	–	33	3	8	–
April	13	4	5	–	29	–
May	42	13	10	–	17	5
June	–	–	1	–	19	3

Figure 3. Temporal and spatial distribution of spawning female swordfish by month in the western North Atlantic.
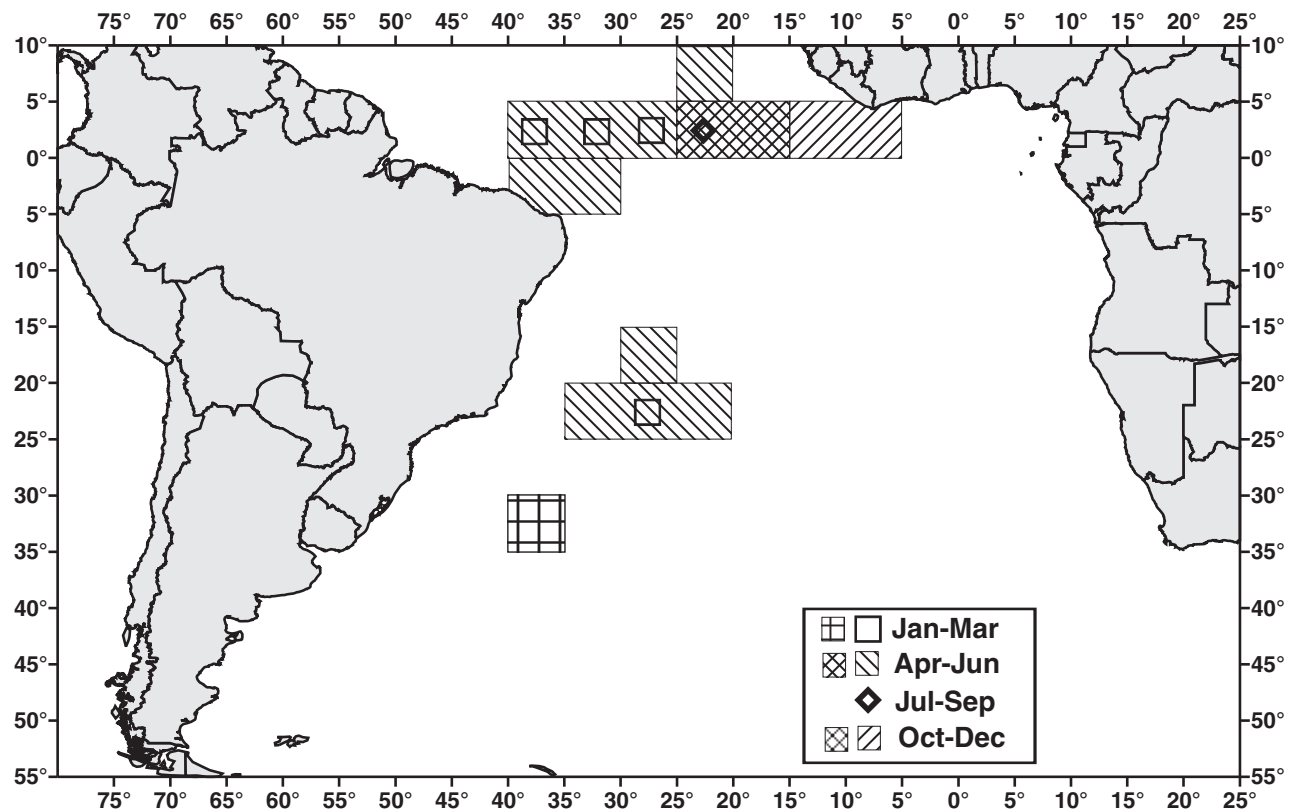

Figure 4. Temporal and spatial distribution of spawning female swordfish by month in the South Atlantic (after Mejuto and García 1997).

oocytes) first appear between April and June, and peak spawning (females with hydrated oocytes and POFs) takes place in July and August. It appears that fish >150 cm LJFL start spawning (GI>7.0) in June, in July all spawning fish are between 120 cm and 230 cm LJFL, and at the end of the season only fish of 130–170 cm LJFL were spawning (Figure 6).

In southern Italy (Tyrrhenian and Ionian Sea, and the Strait of Messina) and around Malta, maturing females (with vitellogenic oocytes) appear between April and early June, and spawning females (with hydrated oocytes and POFs, and GI>9.0) occur from late June through July in the Gulf of Taranto (Ionian Sea), and from July to August in the Strait of Messina and southern Tyrrhenian Sea. Swordfish eggs and larvae were only found in July in the Strait of Messina, the southern Tyrrhenian Sea, and the Ionian Sea. Post-spawning swordfish were located around Malta in July–August. In the eastern Mediterranean, spawning swordfish (GI>7.0) were found only in July, and by August most fish had spawned.

Reproductive population parameters

Maturity fraction. The mean size or age at which 50% of the females are mature (M_{f50}) for each recognized stock were estimated by the various authors using different assumptions and estimation techniques (Table 5). Estimates for maturity fraction of female fish from the North Atlantic stock only included specimens that had been caught during the 6 month (December–June) spawning period when reproductively active females were present. Maximum likelihood estimates of M_{f50} were 178.7 cm LJFL and 5.03 yr old Females attained full maturity at 209.3 cm LJFL and age 8.7. The smallest observed reproductively active female was 150 cm LJFL and age 4. For the South Atlantic stock, estimate of M_{f50} included gonad samples from fish collected off northern Brazil. Swordfish in Brazilian waters mature at an estimated M_{f50} of 156 cm LJFL based on the logistic regression model (Table 5). Females begin to mature at about 125 cm LJFL and attain full maturity by about 195 cm LJFL. In the Mediterranean, least squares estimate of M_{f50} was 142.2 cm LJFL for female fish caught during the three month (June–August) spawning period when reproductively active females were present. They begin to mature at about 110 cm LJFL and attain full maturity at 200 cm LJFL.

Batch Fecundity. In the western North Atlantic, the relation between fish length (LJFL)/age and batch fecundity (B_F) was best explained by a three parameter model that incorporated an additive term to the power model (Table 6). In both batch fecundity relationships (length and age), the minimum initial batch fecundity (F_0) is nearly

the same. Both relationships suggest a steady level of batch fecundity up to the size and age when full maturity is reached (200 cm LJFL / Age 8). After full maturity is attained, batch fecundity increases markedly suggesting that batch fecundity in swordfish is relatively low before females reach full maturity. In the South Atlantic, the relation between fish length (LJFL) and batch fecundity (B_F) was expressed by a linear model (Table 6). For the Mediterranean swordfish, the relation between the fish length (LJFL) and batch fecundity (B_F) of 16 fish was best described by a power function (Table 6).

The mean batch fecundity at length for 29 female swordfish in the western North Atlantic was 3.91×10^6 oocytes (Table 6). These values ranged from 0.99×10^6 hydrated oocytes for a 166 cm LJFL female to 9.00×10^6 hydrated oocytes for a 245 cm LJFL female, thus indicating a wide range in batch fecundity in relation to body size. The mean batch fecundity was 3.84×10^6 oocytes based on age, and it ranged from 2.53×10^6 to 9.00×10^6 oocytes for an age 4 and age 12 female fish. In the South Atlantic, batch fecundity at length for 10 female swordfish ranged from 2.0×10^6 to 8.6×10^6 oocytes for a length range of 160 cm to 194 cm LJFL. Mean batch fecundity was 5.1×10^6 oocytes. For Mediterranean swordfish, mean batch fecundity was 5.90×10^6 oocytes, and it ranged from 2.14×10^6 to 9.91×10^6 oocytes for a length range of 150 cm to 193 cm LJFL.

DISCUSSION

Spawning season and location

Spawning seasonality and location of North Atlantic and Mediterranean swordfish was better defined than for the South Atlantic stock. In the North Atlantic and Mediterranean Sea, spawning was defined and identified by a combination of methods that included ratios that standardize gonad mass to body size, like the GI and RGI (de la Serna et al. 1996, Arocha 1997), microscopic examination and measurement of whole oocytes and oocyte cytology (Arocha 2002, Correiro et al. 2004, Macías et al. 2005), and the distribution of eggs and aged young larvae (Cavallaro et al. 1991, Potoschi et al. 1994, Govoni et al. 2003). Spawning in the western North Atlantic consists of 2 spawning groups proposed by Arocha (1997) and later confirmed by Govoni et al. (2003). The first is in open ocean waters south of the Sargasso Sea and east of the Lesser Antilles, and the second in waters relatively close to land masses and fast current systems like the Windward Passage, Yucatan Channel/Loop Current, Straits of Florida/ Gulf Stream. Spawning in open ocean waters begins in December through May, although the data collected in
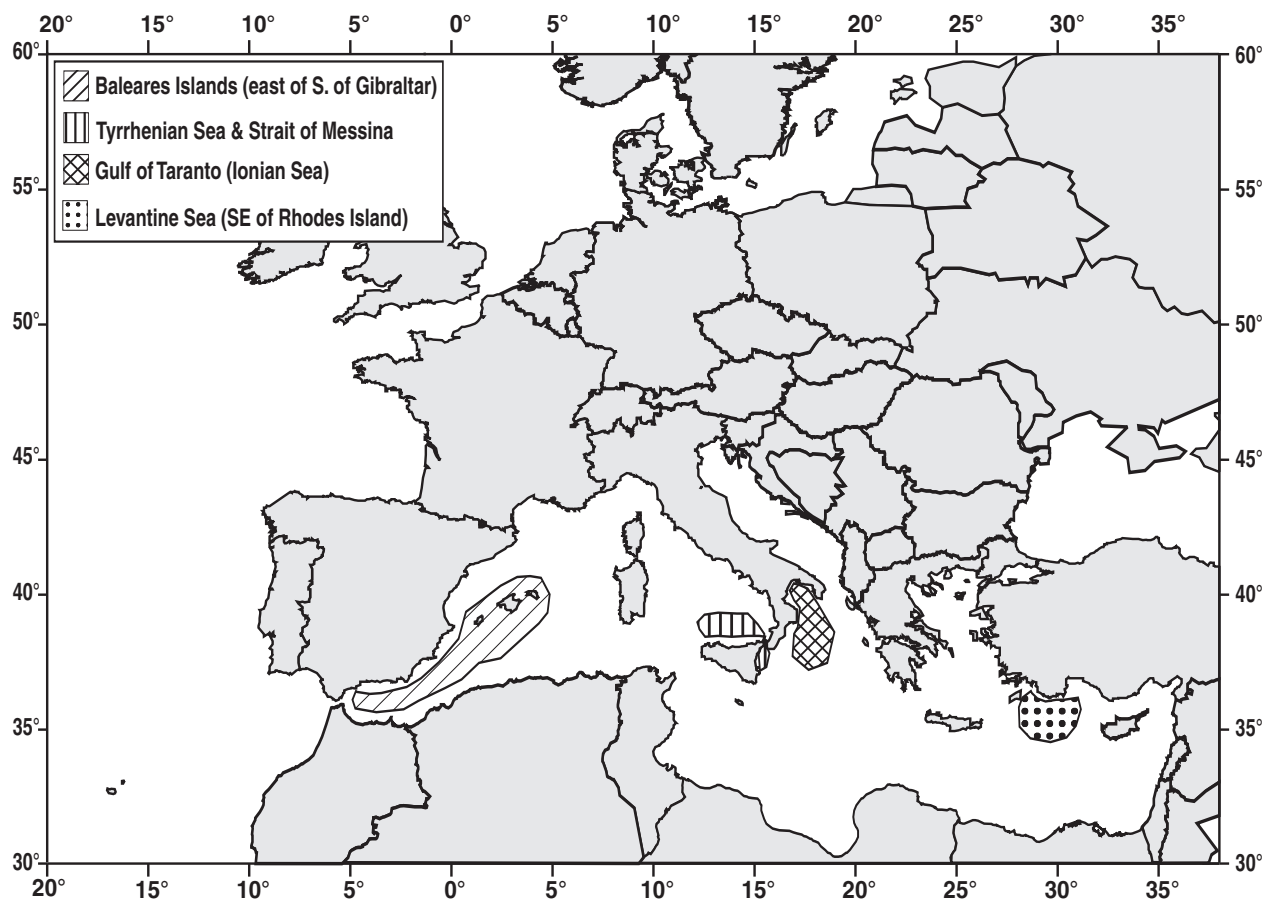
Figure 5. Spatial distribution of spawning female swordfish in the Mediterranean Sea. June–August spawning occurs in the area east of Gibraltar to the Balearic Islands, in the southern Tyrrhenian Sea and the Strait of Messina. Spawning in June–July takes place in the Gulf of Taranto (Ionian Sea), and in the Levantine Sea spawning is in July.

March was low. Larvae (<20 mm) from south of the Sargasso Sea peak from February to April (Tåning 1955) and transit to the Lesser Antilles and into the Caribbean during the first half of the year (Grall et al. 1983, Govoni et al. 2003). The abundance of larvae in the Lesser Antilles (Tibbo and Lauzier 1969, Markle 1974) and the large numbers of juveniles caught by the Venezuelan longline fishery during the second half of the year (Arocha 1997) indicate the southeastern Caribbean as a nursery area. The group spawning close to land masses and strong currents spawn progressively in an east to west and northwest direction as the season progresses. Spawning begins in December through March in the Windward Passage and Yucatan Channel, young larvae from this spawning group concentrate in the GOM during the spring/summer season (Govoni et al. 2003). Additionally, the large number of juveniles discarded by the US longline fishery (Cramer 1996) denote the GOM as a nursery area. Later in the season, the group spawns in the Straits of Florida up to 35°N from May to June, coinciding with spawning dates

and abundances of young larvae in late spring and summer (Govoni et al. 2003). Similarly, juvenile discards from the longline fishery (Cramer 1996) and the larval abundance in the Charleston Bump area (Govoni et al. 2000) also indicate that the waters of the southeastern US serve as a nursery area.

The presence of spawning females in the subtropical area of the western North Atlantic appears to be associated to movements between feeding grounds and spawning grounds. Adult swordfish seem to move between spawning grounds and energy-rich feeding areas of higher latitudes (temperate area) as inferred from the information on selected tagged recaptured specimens obtained from historical data (Brown 1995, Jones et al. 1996). Smaller females and most males which reside at lower latitudes (south of 35°N) show limited movements conditioned by the seasonal displacement in latitude of warm isotherms (24–25°C) (Arocha 1997, Weidner et al. 1999, Weidner et al. 2001), most likely because of their restricted movement ability and reduced capacity to compensate their body
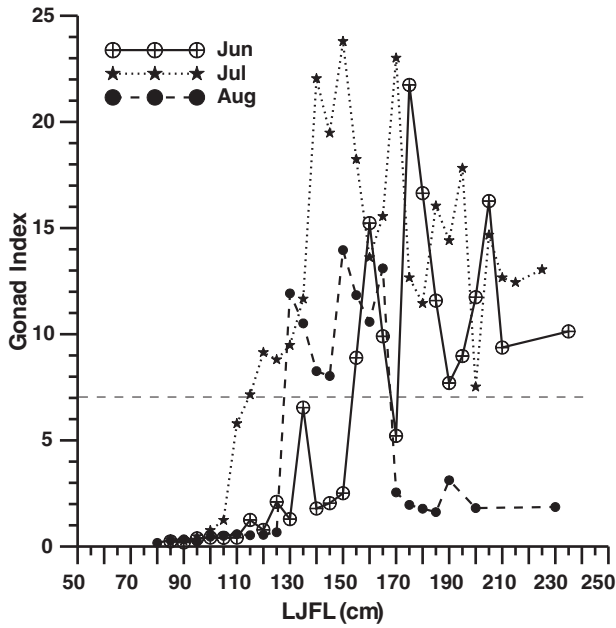
Figure 6. Western Mediterranean swordfish female monthly gonad index by size (lower jaw-fork length, LJFL) during the spawning season. Dashed line represents the spawnGI value of 7.0 (after de la Serna et al. 1996).

temperature requirements favourable to their physiological demand. Therefore, during the boreal winter their bioenergetics requirements may be fulfilled in the Caribbean island passages and the shelf breaks of Venezuela, GOM and along the US southeast coast due to substantial concentrations of squid resources and meso-pelagic prey species in these areas (Boyle 1987, Stromme and Saetersdal 1989, Hopkins et al. 1996, Flanning et al. 2006). In addition, spawning females seem to prefer waters with temperatures of 24° C and 25° C at depths between 0 and 150 m

(Arocha 1997). Conversely, historical collections of larvae presumed to be a month old collected in the subtropical area were associated to similar depths and temperatures (Tåning 1955, Markle 1974, Govoni et al. 2000) as those of the spawning females. Consequently, the absence of spawning females in the temperate area is most likely due to unsuitable conditions for swordfish larvae to survive the cooled waters of the Gulf Stream as it moves north of 35°N (Gaylord and Gaines 2000). In contrast, in the tropical area where some spawning activity was observed, it appears to be a nursery area downstream from the open water spawning group of the western North Atlantic.

Swordfish in the Mediterranean Sea have a distinct spawning season. They begin to spawn in June and by the end of August most fish have spawned. Peak spawning occurred from late June to July throughout the Mediterranean spawning grounds on the basis of seasonal changes in gonad development (de la Serna et al. 1996, Corriero et al. 2004) and spawning dates obtained from aged juvenile fish (Megalofonou et al. 1995). Additionally, abundant eggs and larvae are only present in July (Cavallaro et al. 1991, Potoschi et al. 1994) and juvenile fish are common in commercial catches from September to February (Di Natale et al. 2002). All spawning took place within the Mediterranean Sea and seemed to be restricted to the area between 35° and 40°N. There was no indication that swordfish spawned west of Gibraltar, in the Adriatic or the Black Sea. In the waters off Tunisia and south of Malta, all fish caught during the spawning season were immature or spawned out (Macías et al. 2005).

Spawning in the Mediterranean seems to be associated to movements between winter-feeding grounds in Morrocan Atlantic waters and the waters west of the Strait of Gibraltar (out to 15°W) in the eastern North Atlantic

TABLE 5

Maturity fraction models, parameter estimates at size (lower jaw-fork length) and age in years (only for western North Atlantic), estimates of first maturity, 50% maturity (M_{f50}), full maturity, and sample size of fish (n) for each swordfish stock in the Atlantic Ocean. [1]Arocha 1997, [2]Hazin et al. 2002, [3]de la Serna et al. 1996.

Unit Stock	Model	Parameters	First maturity	M_{f50}	Full maturity	n
[1]North Atlantic	$M_f = \dfrac{1}{1+e^{-a(X_i-b)}}$	Size: $a=0.151$; $b=178.73$ Age: $a=1.236$; $b=5.03$	Size: 150.0 cm Age: 4.0	Size: 178.7 cm Age: 5.03	Size: 209.3 cm Age: 8.7	Size: 470 Age: 184
[2]South Atlantic	$M_f = \dfrac{1}{1+e^{(a+b\cdot Length)}}$	$a=11.724$; $b=-0.075$	125.0 cm	156.0 cm	195.0 cm	127
[3]Mediterranean	$M_f = \dfrac{1}{1+e^{-a(Length-b)}}$	$a=0.073$; $b=142.2$	110.0 cm	142.2 cm	200.0 cm	223

TABLE 6

Batch fecundity models, parameter estimates at size (lower jaw-fork length), and age in years (only for western North Atlantic), sample size of fish (n), mean batch fecundity ($\bar{B}_f$), batch fecundity range, and fish size and age range for each swordfish stock in the Atlantic Ocean, F_0 = minimum initial fecundity that is present when first start hydrating oocytes, and r^2 = coefficient of determination. [1]Arocha 1997, [2]Hazin et al. 2001, [3]de la Serna et al. 1996.

Unit Stock	Model	Parameters	r^2	n	$\bar{B}_f$	$\bar{B}_f$ range	Size/Age range
[1]North Atlantic	$B_f = F_0 + a \cdot Length^b$ $B_f = F_0 + a \cdot Age^b$	Size: $F_0 = 1757430;$ $a = 11.5748;$ $b = 2.8814$ Age: $F_0 = 1846990;$ $a = 77.407;$ $b = 4.637$	Size: 0.725 Age: 0.781	Size: 29 Age: 19	Size: $3.91 \cdot 10^6$ Age: $3.84 \cdot 10^6$	Size: $0.99–9.00 \cdot 10^6$	Size: 155–251 cm Age: 4–12
[2]South Atlantic	$B_f = a \cdot Length - b$	$a = 29.811;$ $b = 0.2003$	0.978	10	$5.10 \cdot 10^6$	$2.00–8.60 \cdot 10^6$	160–194 cm
[3]Mediterranean	$B_f = a \cdot Length^b$	$a = 7.013 \cdot 10^{-3};$ $b = 3.994$	0.557	16	$5.90 \cdot 10^6$	$2.14–9.91 \cdot 10^6$	150–193 cm

and spawning grounds in the Mediterranean Sea (de la Serna and Alot 1990, Pujolar et al. 2002). Mediterranean swordfish may remain in eastern North Atlantic feeding grounds until late spring when the northward displacement of the 18° C surface isotherm can cause the return into warmer Mediterranean waters (Mejuto and Hoey 1991), and fish spawn when surface waters temperatures reach 24°–26°C (Palko et al. 1981, Cavallaro et al. 1991, Corriero et al. 2004).

In contrast, the available information on the seasonality and spawning location of South Atlantic swordfish was limited to a gonad index value that was not accompanied by biologically comprehensive analyses (West 1990). Early research on swordfish reproduction off southern Brazil (20°–28°S) suggested spawning during the first trimester of the year based on histological examination of sectioned portions of the ovary (Amorim and Arfelli 1980). However, a recent study using histological techniques (Hazin et al. 2002), observed no spawning in the southwestern equatorial Atlantic (0°–10°S), but suggested that spawning occurred further north in the area where Mejuto and García (1997) observed high incidence of females with maximum gonad indices. Larval abundance and distribution was very limited and biased due to the unsystematic and broadly spaced collections in the area (Gorbunova 1969, Ueyanagi et al. 1970, Grall et al. 1983). Nonetheless, the spatial distribution was within proximity of known spawning grounds in the western South Atlantic.

Spawning swordfish in the South Atlantic appear to be concentrated around the Equator (5°N–5°S) throughout the year when temperatures in the area remain >24° C (Carton et al. 1996, Conkright et al. 1998), suitable for spawning and survival of larvae. Similar to the western North Atlantic, movements between feeding grounds and spawning grounds seem to be associated to the southward seasonal displacement in latitude of the warm isotherms (24°–25° C). This may allow smaller and larger fish to take advantage of the southern feeding grounds in the temperate waters off Uruguay and southern Brazil during the austral summer inferred from net displacement of conventional tag-recapture information in the southwestern South Atlantic (ICCAT 2006).

Swordfish in the Atlantic Ocean have an extended spawning season over a broad area in both hemispheres, but a relatively short one and in a relatively localized area in the Mediterranean. These differences appear to be attributed to displacement of the 24°C isotherm in the northern and southern hemisphere, and its seasonal appearance in the Mediterranean. In the western Atlantic, the 24° C isotherm has an ample distribution with a spread of about 50 degrees latitude that contracts and expands seasonally in each hemisphere giving swordfish the opportunity to spawn progressively in the season and enhance survival of the larvae. In contrast, spawning swordfish in the Mediterranean have a small seasonal window of opportunity when the

24° C isotherm appears in the Mediterranean between late spring and late summer when all spawning takes place. It becomes evident that each stock in the Atlantic has developed its own reproductive strategies that have not been addressed in the present work and should be addressed in future studies.

Maturity fraction and batch fecundity

Maturity estimates for swordfish caught in the Atlantic and Mediterranean differ between unit stocks. In the western North Atlantic, females were observed to mature at larger sizes and older ages than in the South Atlantic and Mediterranean Sea.

In the western North Atlantic, Taylor and Murphy (1992) estimated a length at 50% maturity of 182 cm LJFL for females from the Straits of Florida for the period of 1977–980, and preliminary estimate of 50% maturity from Arocha et al. (1994) was 189 cm LJFL for females spawning in the western North Atlantic in the period of 1990–1993. Arocha (1997) using maximum likelihood estimation procedure obtained an estimated length at 50% maturity of 185.4 cm LJFL for the females from the Straits of Florida used in the study of Taylor and Murphy (1992). Similarly, estimates of female age-at-maturity was 5.45 yr using least squares (Taylor and Murphy 1992), while maximum likelihood estimates for the same data set and re-estimated by Arocha (1997) were 5.6 years.

Variation in size/age-at-maturity of females from western North Atlantic for the period 1990–1995 (Arocha 1997) with respect to earlier estimates mentioned above can probably be attributed to restricted location of the sampling population, estimates based on fish caught throughout the year or during the spawning season, and different parameter estimation techniques. Thus, as a result of expanding the sampling population and considering fish from the spawning period, the estimated M_{f50} was lower in Arocha (1997) than in the earlier study (Arocha et al. 1994). Accordingly, using different parameter estimation techniques, maximum likelihood estimates of M_{f50} at size and age were higher than least squares estimates for the same data set (Taylor and Murphy 1992, Arocha 1997).

The size-at-maturity of Mediterranean swordfish is the smallest of those observed for any other breeding unit in the world. Estimated M_{f50} in the Mediterranean was 142.2 cm LJFL compared to 178.7 cm LJFL in the western North Atlantic (Arocha 1997), 156 cm LJFL in the South Atlantic (Hazin et al. 2002), 162.2 cm LJFL in the central North Pacific (DeMartini et al. 2000), 175.1 cm LJFL in the western South Pacific (Young et al. 2000), and 170 cm LJFL in the western Indian Ocean (Poisson et al. 2001). The low M_{f50} observed in the Mediterranean Sea may be a consequence of prolonged exploitation of swordfish in the area, that dates back to more than a thousand years when subsistent harpoon and gillnet near shore fisheries started around 1000–177 B.C. and expanded in the beginning of the 19th century when fishing became more sophisticated by the introduction of motor boats and modified harpoons (Ward et al. 2000). This fishing practice involved targeting large swordfish females basking at surface waters (Sella 1911, Di Natale 1991). Consequently, the numbers of older specimens were substantially reduced as observed by the low mean size of the catches for the past 30 yr, and now the fishery relies on 2 or 3, most likely immature age classes (ICCAT-GFCM 1993, De Metrio et al. 1999). Another contributing factor may be the low genetic diversity and degree of mixing of the Mediterranean population with those of the Atlantic, that would limit gene flow with populations that are comparatively less exploited (Magoulas et al. 1993, Ward et al. 2000, Cimmaruta et al. 2006).

Female swordfish in the South Atlantic appear to mature at a size smaller than any other swordfish breeding units in the world oceans, except the Mediterranean. However, the M_{f50} estimate should be considered preliminary because samples from which the estimate was derived were limited to a localized area in the western equatorial South Atlantic where numbers of mature fish were low and the geographical location was not considered a spawning area (Hazin et al. 2002).

Estimates of batch fecundity in Atlantic swordfish appeared to be similar; all estimates approach 8–9.9 million eggs per spawn. Other studies reported lower batch fecundity estimates in the Straits of Florida and in the western Indian Ocean off Reunion Island with batch fecundity estimates of 0.9–4 million eggs (Taylor and Murphy 1992, Poisson et al. 2001), and in the western South Pacific off Australia was 1–2.5 million eggs per spawn (Young et al. 2003). These differences between batch fecundity estimates may be methodological.

Batch fecundity estimates for the different Atlantic swordfish breeding units were derived using different techniques that may have resulted in potentially biased estimations. In multiple spawning fish like swordfish, with asynchronous oocyte development and indeterminate fecundity (Arocha 2002), batch fecundity can be estimated as the number of migratory-nucleus and hydrated oocytes that have not ovulated (Hunter et al. 1985). Consequently, counts of oocytes which have not entered the final stages of maturation and/or counts from ovarian samples which had been placed in fixation liquids that cause significant shrinkage will create potential bias in batch fecundity estimates (Hunter et al. 1985). Batch fecundity estimates from the South Atlantic were based on counts that had

been placed in Gilson's fluid (Hazin et al. 2001) which causes significant shrinkage and compression of oocyte size distribution which make difficult the separation of maturing oocytes from the ones that had entered the maturation phase (Schaefer 2001). Estimated batch fecundity in Mediterranean swordfish was based on counts of oocytes > 650 μm which most likely included oocytes which had not entered the maturation phase. In Corriero et al. (2004), histological sections of oocytes with late vitellogenesis from Mediterranean swordfish averaged about 600 μm, and post vitellogenesis oocytes (which included migratory-nucleus and early hydration oocytes) averaged about 850 μm. In western North Atlantic swordfish histological sections of oocytes in late vitellogenesis can measure up to 900 μm (Arocha 2002). Batch fecundity estimates from the western North Atlantic in the Straits of Florida (Taylor and Murphy 1992, Arocha 1997) were based on counts of oocytes >750 μm, but the authors offered metrics on hydrated oocytes which included 750 μm oocytes. The Arocha (1997) study used only counts of fresh unovulated hydrated oocytes, but did not include migratory-nucleus oocytes to avoid potential bias in the estimates because the duration of the migratory-nucleus phase is unknown in swordfish. In tropical tuna species where the duration of migratory-nucleus phase is known, counts of migratory-nucleus and hydrated oocytes have been used to estimate batch fecundity because the migratory-nucleus phase and hydration occurs over a short period of time (Schaefer 1998, 2001).

Batch fecundity increases with size and age, but there are few studies with size/age relationships. Linear relationships were estimated when a low number of samples were available (Hazin et al. 2001, Poisson et al. 2001, Young et al. 2003), but when the number of samples increased the relationship was nonlinear (Arocha 1997, de la Serna et al. 1996). Most swordfish batch fecundity estimates were based on studies over a relatively localized area during 2–3 yr of sampling. In contrast, batch fecundity estimates for the western North Atlantic were from a broad area over a period of 5 yr (Arocha 1997). Thus, it is probable that estimates of batch fecundity from several spawning periods may result in potential biased estimates. Schaefer (1998) found significant interanual variability in batch fecundity of *Thunnus albacares* of similar size and from the same geographical location. Similar results have been found in fish species whose reproductive biology has been investigated intensively such as *Engraulis mordax* (Hunter et al. 1985).

The combined use of gonad indices and maximum size oocytes calibrated with histological information proves to be an efficient method to define temporal and spatial spawning patterns in non-schooling large pelagic fish like swordfish. Estimating the fraction of the population that matures assumes that specimens can be accurately classified as immature or mature. It is critical that the techniques to classify a female as sexually mature, with the use of ovary weight and/or egg size, be precise and validated, and to reduce the chance of misclassifying mature females it is recommended to limit the analysis to data collected during the spawning period. Further, the use of statistical estimation procedures that take into consideration the binomial nature of the maturity data should be considered. The estimates of batch fecundity in non-schooling large pelagic fish are complicated by the inadequate gonad sample size that can be resolved with scientific observers or trained fishers to collect samples during the spawning season. The variation in batch fecundity estimates due to estimation techniques can be resolved by using counts of unovulated hydrated oocytes.

The variation observed in the reproductive estimates, gonad indices and population parameters were mostly attributed to methodological techniques that can be corrected in future studies. The seasonality and spawning location in swordfish can be efficiently accomplished by sampling of ovarian tissues from adult specimens from commercial and recreational fisheries to map the temporal and spatial spawning distribution of swordfish. Additionally, larval surveys targeting swordfish in selected locations and specific times can provide fine-scale information on spawning. However, this technique is inefficient for large-scale spawning estimations.

The reproductive information for Atlantic swordfish presented illustrates the limited knowledge on the species, regardless of the available information for the western North Atlantic swordfish. All recent studies have been produced using data collected in the 1990s. Thus, considering there are no new comprehensive studies on reproductive dynamics, the temporal and spatial spawning patterns as well as the reproductive population parameter estimates are likely outdated. Consequently, there is a need to re-estimate and expand them, particularly for the South Atlantic stock. Future estimates should consider large-scale temporal and spatial spawning variability that would enhance the estimation of reproductive population parameters for all swordfish stocks in the Atlantic Ocean.

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Literature Cited

Alvarado Bremer, J.R., J. Mejuto, J. Gómez-Márquez, F. Boán, P. Carpintero, J.M. Rodríguez, J. Viñas, T.J. Greig, and B. Ely. 2005. Hierarchical analyses of genetic variation of samples from breeding and feeding grounds confirm genetic partitioning of northwest Atlantic and South Atlantic populations of swordfish (*Xiphias gladius* L.). Journal of Experimental Marine Biology and Ecology 327:167–182.

Amorin, A. and C. Arfelli. 1980. Reproducción de pez espada (*Xiphias gladius*, L.) (1758) en el sudeste y sur de Brasil. ICCAT, Collective Volume of Scientific Papers 9:624–626.

Arocha, F. 1997. The reproductive dynamics of swordfish *Xiphias gladius* L. and management implications in the northwestern Atlantic. PhD thesis. University of Miami, Miami, FL, USA, 383 p.

Arocha, F. 2002. Oocyte development and maturity classification of swordfish from the north-western Atlantic. Journal of Fish Biology 60:13–27.

Arocha, F. and D. Lee. 1993. Preliminary observations on sex ratio and maturity stages of the swordfish, *Xiphias gladius*, in the northwest Atlantic. ICCAT, Collective Volume of Scientific Papers 40:425–432.

Arocha, F. and D. Lee. 1995. The spawning of swordfish in the Northwest Atlantic. ICCAT, Collective Volume of Scientific Papers 44:179–186.

Arocha, F., D. Lee, and J. Grubich. 1994. Observations on sex ratios, maturity stages, and fecundity of swordfish, *Xiphias gladius*, in the Northwest Atlantic Ocean. ICCAT, Collective Volume of Scientific Papers 42:309–318.

Boyle, P.R. 1987. Cephalopod Life Cycles. Vol. 2: Comparative reviews. Academic Press Inc., London, UK, 441 p.

Brown, C. 1995. Preliminary examination of size and location data for U.S. tagged and recaptured swordfish. ICCAT, Collective Volume of Scientific Papers 44:217–224.

Carton, J.A., X. Cao, B.S.Giese, and A.M. Da Silva 1996. Decadal and interannual SST variability in the tropical Atlantic Ocean. Journal of Physical Oceanography 26:1165–1175.

Cavallaro, G., A. Potoschi, and A. Cefali. 1991. Fertility, gonadsomatic index and catches of eggs and larvae of *Xiphias gladius* L. 1758 in the southern Tyrrhenian Sea. ICCAT, Collective Volume of Scientific Papers 35:502–507.

Cayré, P., and F. Laloë. 1986. Review of the gonad index (GI) and the introduction to the concept of 'critical value': application to the skipjack tuna, *Katsuwonus pelamis*, in the Atlantic Ocean. Marine Biology 90:345–351.

Chow, S. and H. Takeyama. 2000. Nuclear and mitochondrial DNA analyses reveal four genetically separated breeding units of the swordfish. Journal of Fish Biology 56:1087–1098.

Chow, S., H. Okamoto, Y. Uozumi, Y. Takeuchi, and H. Takeyama. 1997. Genetic stock structure of the swordfish (*Xiphias gladius*) inferred by PCR-RFLP analysis of the mitochondrial DNA control region. Marine Biology 127:359–367.

Cimmaruta, R., M. Paoletti, P. Bondanelli, M.N. Santos, A. Garcia, and G. Nascetti. 2006. Genetic structure of Mediterranean and Atlantic swordfish investigated using allozymes and RFLPs. International Commission for the Conservation of Atlantic Tunas, Working Document SCRS/2006/040, Madrid, Spain.

Conkright, M., S. Levitus, T. O'Brien, T. Boyer, J.Antonov, and C. Stephens. 1998. World Ocean Atlas 1998 CD-ROM Data Set Documentation. Technical Report 15, NODC Internal Report, Silver Spring, MD, USA, 16 p.

Corriero, A., F. Acone, S. Desantis, D. Zubani, M. Deflorio, C. R. Bridges, M. Labate, G. Palmieri, B. G. McAllister, D. E. Kime, and G. De Metrio. 2004. Histological and immunohistochemical investigation on ovarian development and plasma estradiol levels in the swordfish (*Xiphias gladius* L.). European Journal of Histochemistry 48:413–422.

Cramer, J. 1996. Recent trends in the catch of undersized swordfish by the U.S. pelagic longline fishery. Marine Fisheries Review 58:24–32.

DeMartini, E.E., J.H.Uchiyama, and H.A.Williams, 2000. Sexual maturity, sex ratio, and size composition of swordfish, *Xiphias gladius*, caught by the Hawaii-based pelagic longline fishery. Fishery Bulletin 98:489–506.

DeMetrio, G., M. Cacucci, P. Megalofonou, N. Santamaría, and L. Sion. 1999. Trends of swordfish fishery in a northern Ionian Port in the years beteween 1978 and 1997. ICCAT, Collective Volume of Scientific Papers 49:94–99.

de la Serna, J.M. and E. Alot. 1990. Consideraciones relativas a los desplazamientos efectuados por el pez espada (*Xiphias gladius*) en el área del estrecho de Gibraltar y otras observaciones relacionadas con la biología de la reproducción. ICCAT, Collective Volume of Scientific Papers 33:353–359.

de la Serna, J.M., E. Alot, and M.D. Godoy. 1992. Análisis preliminar de la madurez sexual del pez espada (*Xiphias gladius*) en el área Atlántica próxima al estrecho de Gibraltar. ICCAT, Collective Volume of Scientific Papers 39:522–537.

de la Serna, J.M., J.M. Ortiz, and D. Macías. 1996. Observations on sex-ratio, maturity and fecundity by length-class for swordfish (*Xiphias gladius*) captured with surface longline in the western Mediterranean. ICCAT, Collective Volume of Scientific Papers 45:115–140.

Di Natale, A. 1991. Interaction between marine mammals and Scombridae fishery activities: the Mediterranean case. In: Report of the GFCM/ICCAT Expert Consultation on Evaluation of Stocks of Large Pelagic Fishes in the Mediterranean Area. Bari, Italy. June 21–27, 1990. FAO Report No. 449. Food and Agriculture Organization of the United Nations, Rome, Italy. 140–142 p.

Di Natale, A., J.M. de la Serna, G. DeMetrio, V. Restrepo, A. Srour, and G. Tserpes. 2002. On the reduction of juvenile swordfish catches in the Mediterranean. ICCAT, Collective Volume of Scientific Papers 54:1529–1533.

Ehrhardt, N., R. Robbins, and F. Arocha. 1996. Age validation and growth of swordfish, *Xiphias gladius*, in the northwestern Atlantic. ICCAT, Collective Volumes of Scientific Papers 45:358–367.

Erickson, D., J. Hightower, and G. Grossman, 1985. The relative gonadal index: an alternative index for quantification of reproductive condition. Comparative Biochemical Physiology 81A:117–20.

Flannig, P., G. Melvin, C. O'Donnell, and M. Dahl. 2006. Spatial and diel distribution of pelagic forage species throughout the Lesser Antilles from an acoustic and mid-trawl survey. 59th Annual Gulf and Caribbean Fisheries Institute Conference, November 6–11, Belize City, Belize (ABSTRACT).

Gaylord, B. and S.D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. American Naturalist 155:769–789.

Goodyear, C.P. 2003. Spawning stock biomass per recruit in fisheries management: foundation and current use. Canadian Special Publication of Fisheries and Aquatic Sciences 120:67–81.

Gorbunova, N.N. 1969. Breeding grounds and food of the larvae of the swordfish *Xiphias gladius* Linneus (Pisces, Xiphiidae). Problems in Ichthyology 9:375–387.

Govoni, J.J., B.W. Stender, and O. Pashuk. 2000. Distribution of larval swordfish, *Xiphias gladius*, and probable spawning off the southeastern United States. Fishery Bulletin 98:64–74.

Govoni, J.J., E. Laban, and J. Hare. 2003. The early life history of swordfish (*Xiphias gladius*) in the western North Atlantic. Fishery Bulletin 101: 778–789.

Grall, C., D. de Sylva, and E. Houde. 1983. Distribution, relative abundance, and seasonality of swordfish larvae. Transactions of the American Fisheries Society 112: 235–246.

Hazin, F., H. Hazin, C. Boeckmann, and P. Travassos. 2001. La reproduction de l'espadon (*Xiphias gladius*) dans l'Atlantique sud-ouest equatorial: La ponte et la fecondité. ICCAT, Collective Volume of Scientific Papers 52:1233–1240.

Hazin, F., H. Hazin, C. Boeckmann, and P. Travassos. 2002. Preliminary study on the reproductive biology of swordfish, *Xiphias gladius* (Linnaeus, 1758), in the southwestern equatorial Atlantic Ocean. ICCAT, Collective Volume of Scientific Papers 54:1560–1569.

Hopkins, T., T. Sutton, and T. Lancraft. 1996. The trophic structure and predation impact of a low midwater fish assemblage. Progress in Oceanography 38:205–239.

Hunter, J.R., N. Lo, and R. Leong. 1985. Batch fecundity in multiple spawning fishes. National Oceanographic and Atmospheric Administration, Technical Report NMFS 36:79–94.

International Commission for the Conservation of Atlantic Tunas (ICCAT). 1993. Report of the Second GFCM/ICCAT Expert Consultation on Stocks of Large Pelagic Fishes in the Mediterranean Sea. Iraklion. Crete, Greece, September 17–23, 1992. ICCAT, Collective Volume of Scientific Papers 40:11–111.

International Commission for the Conservation of Atlantic Tunas (ICCAT). 2006. Report of the 2006 ICCAT swordfish stock structure workshop. International Commission for the Conservation of Atlantic Tunas, SCRS/2006/010 Working Document, Madrid, Spain.

Jones, C., D. Rosenthal, T. Jackson, M. Judge, and E. Prince. 1996. Cooperative Tagging Center Annual Newsletter: 1996. National Oceanographic and Atmospheric Administration Technical Memorandum NMFS-SEFSC 391. 22 p.

Kotulas, G., A. Magoulas, N. Tsimenides, and E. Zorros. 1995. Marked mitochondrial-DNA differences between Mediterranean and Atlantic populations of the swordfish, *Xiphias gladius*. Molecular Ecology 4:473–481.

Kotulas, G., J. Mejuto, P. Kasapidis, G. Tserpes, A. Antoniou, B. Garcia-Cortes, P. Peristeraki, K. Oikonomaki, and A. Magoulas. 2006. Genetic structure of the swordfish *Xiphias gladius* stocks in the Atlantic using microsatellite DNA analysis. ICCAT, SCRS/2006/035 Working Document, Madrid, Spain.

Kume, S., and P.J. Josheph.1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130°W. Bulletin of the Far Seas Fisheries Research Laboratory 2:115–162.

Mace, P.M. 1993. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Canadian Journal of Fisheries and Aquatic Science 51:110–122.

Macías, D., A. Hattour, J.M. de la Serna, M.J. Gómez-Vives, and D. Godoy. 2005. Reproductive characteristics of swordfish (*Xiphias gladius*) caught in the southwestern Mediterranean during 2003. ICCAT, Collective Volume of Scientific Papers 58:454–469.

Magoulas, A., G. Kotoulas, J. de la Serna, G. DeMetrio, N. Tsimenides, and E. Zouras. 1993. Genetic structure of swordfish (*Xiphias gladius*) populations of the Mediterranean and the eastern coast of the Atlantic: analysis of mitochondrial DNA markers. ICCAT, Collective Volume of Scientific Papers 40:126–136.

Markle, G. 1974. Distribution of larval swordfish in the Northwest Atlantic. National Oceanographic and Atmospheric Administration, Technical Report NMFS SSRF 675:252–260.

Megalofonou, P., J. Dean, G. DeMetrio, C. Wilson, and S. Berkeley. 1985. Age and growth of juvenile swordfish, *Xiphias gladius* Linnaeus, from the Mediterranean Sea. Journal Experimental Marine Biology and Ecology 188:79–88.

Mejuto, J. and B. Garcia. 1997. A preliminary analysis of gonadal indices of the swordfish (*Xiphias gladius*) in the Atlantic Ocean. ICCAT, Collective Volume of Scientific Papers 46:336–344.

Mejuto, J. and J.J Hoey. 1991. An approach to a stock hypothesis for the swordfish (*Xiphias gladius*) of the Atlantic Ocean. ICCAT, Collective Volume of Scientific Papers 35:482–501.

Murawski, S.A., P.J. Rago, and E.A. Trippel. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES Journal of Marine Science 58:1002–1014.

Nakamura, I. 1985. Billfishes of the world. Fisheries Synopsis No.125 (5), Food and Agriculture Organization of the United Nations, Rome, Italy, 58 p.

Palko, B.J., G. Beardsley, and W.J. Richards. 1981. Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus. National Oceanographic and Atmospheric Administration, Technical Report, National Marine Fisheries Service Circular 441, 21 p.

Poisson, F., C. Marjolet, and C. Fauvel. 2001. Biologie de la reproduction de l'espadon (*Xiphias gladius*). In: F. Poisson and M. Taquet, eds. L'espadon: de la recherche a l'exploitation durable. IFREMER Programe Palangre Réunionnais, Rapport final, St. Denis, Reunion Island, France, p. 170–211.

Potoschi, A. G. Cavallaro, P. Sturiale, and G. Lo Duca. 1994. Eggs and larvae of swordfish, tuna and albacore caught in the Ionian Sea. Biologia Marina Mediterranea 1:119–124.

Pujolar, J.M., M.I. Roldán, and C. Pla. 2002. A genetic assessment of the population structure of swordfish (*Xiphias gladius*) in the Mediterranean Sea. Journal of Experimental Marine Biology and Ecology 276:19–29.

Schaefer, K. 1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Inter-American Tuna Tropical Commission, Bulletin 21:201–272.

Schaefer, K. 2001. Reproductive biology of tunas. In: B. Block and E.D. Stevens, eds. Tuna physiology, ecology, and evolution. Vol. 19 Fish Physiology. Academic Press, New York, NY, USA, p. 225–270.

Sella, M. 1911. Contributo alla conoscenza della riproduzione e dello sviluppo del pesce-spada (*Xiphias gladius* L.). R. Comitato Talassografico Italiano 442 Memoria II:5-20.

Somerton, D. 1978. HIATT, a program for fitting a pair of strait lines to crustacean growth increment data. NORFISH, NC14. Washington Sea Grant, National Marine Fisheries Service, 8 p.

Stromme, T. and G. Saetersdal. 1989. Final report. Surveys of the fish resources in the shelf areas between Suriname and Colombia 1988. Reports on Surveys with R/V Dr. Fridtjof Nansen. Institute of Marine Research NORAD/UNDP/FAO Programme, Bergen, Norway, 135 p.

Tåning, Å.V. 1955. On the breeding areas of the swordfish (*Xiphias*). Papers in Marine Biology and Oceanography, Deep Sea Research Supplement 3:438–450.

Taylor, R. G. and M. Murphy. 1992. Reproductive biology of the swordfish *Xiphias gladius* in the Straits of Florida and adjacent waters. Fishery Bulletin 90:809–816.

Tibbo, S. and L. Lauzier. 1969. Larval swordfish (*Xiphias gladius*) from three localities in the western Atlantic. Journal of the Fisheries Research Board of Canada 26:3248–3251.

Tserpes, G., P. Peristeraki, and S. Somarakis. 2001. On the reproduction of swordfish (*Xiphias gladius*) in the eastern Mediterranean Sea. ICCAT, Collective Volume of Scientific Papers 52:740–744.

Ueyanagi, S., S. Kikawa, M. Uto, and Y. Nishikawa. 1970. Distribution, spawning, and relative abundance of billfishes in the Atlantic Ocean. Bulletin of the Far Seas Fisheries Research Laboratory 3:15–45.

Ward, J., J. Porter, and Elscot. 2000. Broadbill swordfish: Status of established fisheries and lessons for developing fisheries. Fish and Fisheries 1:317–336.

Weidner, D., F. Arocha, F. Fontes, W. Folsom, and J. Serrano. 1999. Latin America. South America. Atlantic. Venezuela, Guyana, Suriname, and French Guiana. In: World Swordfish Fisheries: An Analysis of Swordfish Fisheries, Market Trends, and Trade Patterns, Past-Present-Future. Vol. IV. National Oceanographic and Atmospheric Administration, Technical Memorandum NMFS-F/SPO 34, 235 p.

Weidner, D., G. Laya, W. Folsom, and J. Serrano. 2001. Latin America. Caribbean. Anguilla to the British Islands. In: World Swordfish Fisheries: An Analysis of Swordfish Fisheries, Market Trends, and Trade Patterns, Past-Present-Future. Vol. IV. National Oceanographic and Atmospheric Administration, Technical Memorandum NMFS-F/SPO 50, 387 p.

West, G. 1990. Methods of assessing ovarian development in fishes: A review. Australian Journal of Marine and Freshwater Research 41:199–222.

Young, J., A. Drake, T. Carter, and J. Farley. 2000. Reproductive dynamics of broadbill swordfish (*Xiphias gladius*) in the eastern Australian AFZ: preliminary results. 13th meeting of the standing committee on tuna and billfish, Noumea, New Caledonia, 5–12 July 2000, p. 1–12 .

Young, J., A. Drake, M. Brickhill, J. Farley, and T.Carter. 2003. Reproductive dynamics of broadbill swordfish, *Xiphias gladius*, in the domestic longline fishery off eastern Australia. Marine and Freshwater Research 54:315–332.