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LIFE HISTORY OF SWORDFISH, *XIPHIAS GLADIUS*, CAUGHT IN THE NORTHERN GULF OF MEXICO§

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ABSTRACT: The current study examined 93 Swordfish, *Xiphias gladius,* (64 females, 27 males, 2 unknown) ranging in size from 77.6–246.3 cm lower jaw fork length (LJFL) from the northern Gulf of Mexico (GOM). Samples were collected between March and August in 2005–2007, 2017–2019 and 2021. Age estimates of 51 Swordfish resulted in a maximum observed age of 11 years (205.0 cm LJFL) and 7 years (190.4 cm LJFL) for females and males, respectively. Observed and back—calculated length—at—age data were fitted to 4 growth models (2— and 3—parameter von Bertalanffy, Gompertz, and logistic). The 2—parameter von Bertalanffy was the model that best fit the data (L_{inf} = 210.2 cm LJFL, k = 0.25). Histological examination of gonadal tissue from 91 fish indicated that females reached 50% and 95% physiological maturity at 116 ± 6 cm LJFL and 143 ± 8 cm LJFL, respectively, corresponding to ages 2—3 years. All males >82 cm LJFL were physiologically sexually mature. Only 10% of females were reproductively active, with spawning capable females captured in June. Reproductively active females exhibited asynchronous oocyte development indicating batch spawning. Most males (96%) were spawning capable from April–August. *Philometra* sp. infection was found in all ovaries examined (n = 16) but with low abundance (2.25 ± 0.42); male philometrids were more prevalent than females (91.7% and 66.7%, respectively). Swordfish in the northern GOM appear to achieve sexual maturity at a younger age, grow faster, and have shorter theoretical longevity than previous reports from other regions world—wide.

KEY WORDS: Highly Migratory Species, billfish, age—growth, reproduction, parasites

INTRODUCTION

Swordfish, *Xiphias gladius*, is a highly migratory pelagic species found circumglobally in tropical, subtropical, and temperate waters between 45°N and 45°S. They are a monotypic species of Xiphiidae, characterized by an elongated, flattened rostrum and a sister group to Istiophoridae which include marlins and spearfishes (Palko et al. 1981). Swordfish are categorized into 3 genetically distinct stocks in the Atlantic Ocean (Alvarado Bremer et al. 2005), but the International Commission for the Conservation of Atlantic Tunas (ICCAT) uses geographic boundaries to separate these stocks (North Atlantic, South Atlantic, and Mediterranean; ICCAT 2019). Within the North Atlantic Stock, management regulations of the US Atlantic Ocean, US Gulf of Mexico (GOM), and US Caribbean territories are governed by the Atlantic Highly Migratory Species Management division of NOAA Fisheries under the Consolidated Atlantic Highly Migratory Species Fishery Management Plan (FMP). The FMP for Swordfish was created in 1985 in response to the Atlantic Swordfish stock becoming overfished while also experiencing overfishing (Federal Register 1985). The intent of the FMP was to reduce the harvest of smaller Swordfish (<22.7 kg dressed weight), create a monitoring program, and limit bycatch from foreign longline fisheries. These measures, coupled with amendments to the FMP as well as the biology of the species that contributes to its resilience (Neilson et al. 2013), allowed the North Atlantic stock to rebound and it is currently considered to be fully recovered, not overfished, and not experiencing overfishing (ICCAT 2019).

The bulk of life history information for Swordfish comes from the Atlantic Ocean and its adjacent seas; however, the data are still largely region—specific. Therefore, a sampling program was initiated in 2018 to gather information on age, growth, and reproduction of Swordfish from the three Atlantic stocks (Gillespie et al. 2021). Previous age and growth studies have been conducted on Swordfish from the South Atlantic (Quelle et al. 2014), the Mediterranean and Aegean seas (e.g., Tsimendies and Tserpes 1989, Tserpes and Tsimendes 1995, Tserpes et al 2001, Valerias et al. 2008, Akyol and Ceyhan 2013), and the western North Atlantic including the Straits of Florida (Berkeley and Houde 1983, Ehrhardt 1992, Arocha et al 2003). Studies detailing the reproductive biology are more scarce and include those from the Mediterranean and Aegean seas (Macias et al. 2005), the western North Atlantic, including the Straits of Florida (Taylor and Murphy 1992, Arocha 2002, Arocha 2007), and the Indian Ocean (Poisson and Fauvel 2009a,b). The GOM has previously been suggested as a nursery habitat for Swordfish (Arata 1954, Arnold 1955); however, life history data of Swordfish (age, growth, and reproductive biology) are limited in the GOM (Gillespie et al. 2021). Govoni

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§This article is based on a presentation given in November 2019 at the 72nd meeting of the Gulf and Caribbean Fisheries Institute, Puta Cana, Dominican Republic.

et al. (2003) and Rooker et al. (2012) confirmed the presence of larval Swordfish in the GOM. Govoni et al. (2003) noted that based on back calculation of spawning dates that year—round spawning occurs in the north—central GOM whereas spring spawning occurs in the western GOM. However, the exact location and timing of spawning remains unknown.

Parasites, especially those that parasitize tissues, are capable of influencing host growth and vital rates (Wood et al. 2015); however, parasitological data are often ignored in fish ecology (Timit and Poulin 2020). Histological examination of the gonads is necessary to confirm spawning and seasonality of GOM Swordfish reproduction, but these sections are also useful in the detection of certain parasite taxa that frequent fish ovaries (e.g., nematodes of Philometridae). Gonad—dwelling philometrids can have potentially deleterious effects on their fish hosts (Moravec and de Buron 2013), yet their prevalence in many fishery—important species is underreported (Bakenhaster et al. 2014). Parasites have been used as biological tags for Swordfish stock delineation (Iles 1971, Castro—Pampillón et al. 2002, Garcia et al. 2011, Mattiucci et al. 2014), but none of those studies reported any philometrid infections in the hosts they examined. Therefore, any data on Swordfish philometrids from fish near their spawning grounds could provide insight on if this parasite is reducing host fecundity, as has been observed for other fish species (Moravec and de Buron 2013).

Swordfish support a commercial fishery in the GOM (NOAA 2019), and are also a prized sport fish in the region. Recreational fishing effort for Swordfish in the northern GOM has historically occurred but has been limited, although recently interest has been growing at a fast rate. In Louisiana, a new recreational fishery for Swordfish has developed with an increase in recreational landings of more than 3,000% between 2014–2020 (LDWF 2021). This increased interest provided the opportunity to conduct life history assessments of Swordfish in the northern GOM. This paper provides the first assessment of age, growth, reproduction, and gonadal parasitism of Swordfish from the northern GOM. The results of this study will inform future stock assessments and support effective management of Swordfish populations in the region.

Materials and Methods

Specimen Collection

Swordfish were opportunistically sampled from fishery—independent and fishery—dependent surveys in March—May and August 2005–2007 (n = 27), from March–July 2017–2019 (n = 51) and June 2021 (n = 15) in the northern GOM (n = 93; Figure 1). For the fishery—independent samples (n = 19), Swordfish were captured via pelagic longline gear during a NOAA fisheries survey in March and April of 2005 and during a Bluefin Tuna sampling cruise by the NMFS Southeast Fisheries Science Center in April and May of 2007. For both sampling cruises, fish were measured for lower jaw fork length (LJFL, cm, defined as the straight measurement from the anterior tip of the lower jaw to the fork of the tail), weighed (W, kg), and sexed. The gonads were extracted and frozen at sea for histological examination upon return. For fishery—dependent samples (n = 74), fish were captured offshore where anglers employed either daytime deep drop methods with various bait types to target a depth range of 300 m and deeper or nighttime shallow drop methods targeting 30–90 m. All fish were measured for LJFL and weighed. Whole anal fins were removed and placed on ice until frozen in the laboratory. Sex was determined initially by macroscopic inspection of gonads and then a thin mid—section was excised and placed in 10% neutral buffered formalin for histological processing. The remaining gonad was placed on ice, transported to the laboratory, and frozen until grossly examined for parasites.

Age and Growth

The relationship between the observed weight and length of the fish for combined sexes was modeled using $W=aL^b$ where W is weight, L is length, and a and b are constants (Ogle 2013). In order to use this model, length and weight data were transformed to a logarithmic scale following the methods outlined by Ogle (2013).

Only fishery—dependent Swordfish were used for age determinations (n = 51). The second anal spine was selected for ageing based on the methods of Berkeley and Houde (1983) because it possesses the largest diameter and smallest matrix. Prior to processing, the anal fins were thawed, and the second spine was removed. We followed the spine processing method outlined by Sun et al. (2002). Briefly, the spine was cleaned of

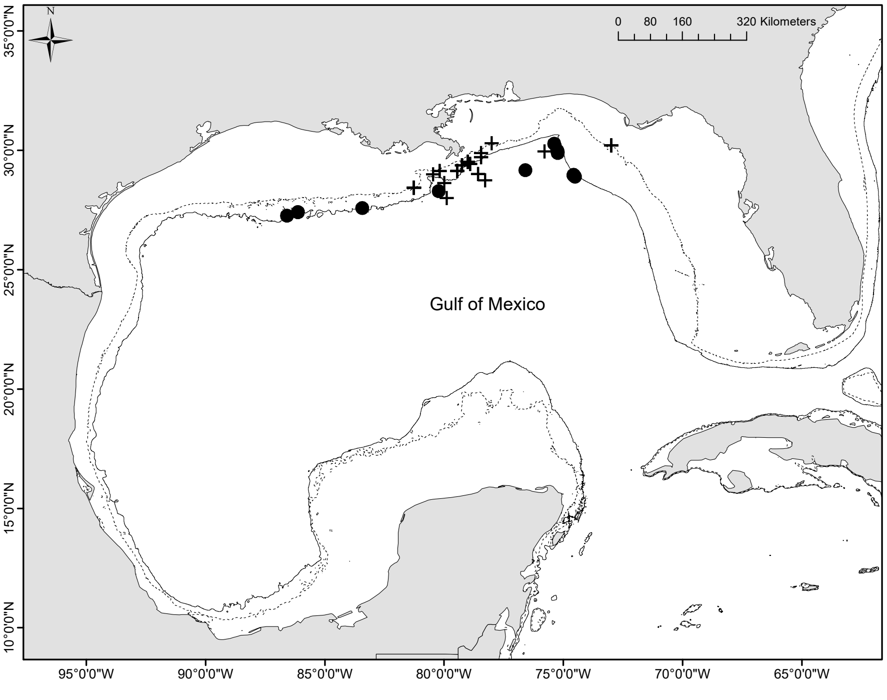

FIGURE 1. *Fishery independent (●) and fishery dependent (+) collection locations of Swordfish from the northern Gulf of Mexico from 2005–2021. Depth contours shown at 200 m and 2000 m.*

excess tissue, the width of the condyle base measured, and the spine was marked for sectioning at a distance equal to ~½ the condyle width. Three to 5 transverse cross sections (0.45 mm thick) were cut with an Isomet low speed saw (Buehler; Lake Bluff, IL), beginning at the marked location and moving towards the posterior end of the spine. Cross sections were allowed to dry 24 h and then mounted on glass microscope slides with Cytoseal 60 (Fisher Scientific, Pittsburgh, PA).

Digital images of each spine were taken using an image capturing dissecting microscope (Leica Microsystems, Wetzlar, Germany, Model EZ4HD). On each image, annuli were digitally marked and counted. Based on prior studies (e.g., Berkely and Houde 1983, Tserpes and Tsimendies 1995), the annuli of each spine were defined as a translucent band that is continuous around the circumference beginning at the focus. Two independent readers enumerated the translucent bands on each spine without prior knowledge of sex, size, or previous counts. In cases where readers recorded different ages, spine sections were re—read by both readers until an agreement was reached. If there were still disagreements or if the section was of poor quality, the specimen was discarded and not considered for subsequent analysis. The index of average percent error (APE; Beamish and Fournier 1981) was used to estimate error between readers for their initial counts.

We were unable to collect spines from Swordfish < 127.0 cm LJFL due to recreational size limits; therefore, we used a back calculation based upon the relationship of spine radius and LJFL for combined sexes to generate length—at—age to fill in the missing size classes for growth modeling. The focus to the distal margin of each annulus and the focus to the distal margin of the entire cross section radius were measured and used to back calculate lengths at previous age using the Dahl—Lea method (Lea 1910). Observed and back calculated lengths—at—age for combined sexes were used to model growth. Four growth models were fitted to the combined data: the 3—parameter von—Bertalanffy growth function (VBGF) (von Bertalanffy 1938), the 2—parameter VBGF (Fabens 1965), the Gompertz (Gompertz 1825), and the logistic (Ricker 1975):

3—parameter VBGF: $L_t = L_{inf}(1-e^{-k[t-t_0]})$, Equation 1

2—parameter VBGF: $L_t = L_{inf} - (L_{inf} - L_0)e$, Equation 2

Gompertz: $L_t = L_{inf}(e^{-k[t-t_0]})$, and Equation 3

logistic: $L_t = L_{inf}/(1-e^{-k[t-t_0]})$, Equation 4

where L_t is the predicted length at age t, L_{inf} is the asymptotic average length, L_0 is size at birth, k is the growth rate coefficient, and t_0 is theoretical length at age zero. Models were compared using the Akaike Information Criterion (AIC, Akaike 1974), calculated as AIC= 2LL + p where LL is the negative log—likelihood and p is the number of parameters in the model. The model with the lowest AIC was considered the best fit of the models compared. To determine the quality of fit of each model ΔAIC was calculated; ΔAIC values <2 were considered to be a good fit and values >2 were considered to be of poor fit. Parameters from the model of best fit were used to calculated theoretical longevity following the methods of Fabens (1965) where the estimated age at 95% of the maximum size is reached using the calculation LJFL=[5(ln2)]/k.

Reproductive Biology

A total of 91 Swordfish (64 females, 27 males) were analyzed histologically. The overall sex ratio was calculated and a post—hoc Chi Square analysis was conducted to determine if the ratio differed from 1:1.

Gonadal tissue was weighed (GW, 0.01g) in the laboratory and the Gonadosomatic Index (GSI) was calculated for each fish as

GSI = [GW/(W—GW)] x 100. Equation 5

In cases where gonadal tissue was frozen prior to fixation, a small piece of the tissue was thawed in 10% neutral buffered formalin at 4°C and allowed to fix for a minimum of 7 days. Fixed gonadal tissue was rinsed overnight in running tap water, dehydrated, embedded in paraffin, sectioned at 4 µm, and stained with hematoxylin and eosin following standard histological procedures. Stained tissue was histologically classified into one of 6 reproductive phases following the terminology of Brown—Peterson et al. (2011): immature, early developing, developing, spawning capable, regenerating, or regressing, and the most advanced gamete stage (MAGS) was determined for each individual. Indicators of prior spawning (IPS, i.e., oocyte atresia, muscle bundles, abundant blood vessels) were used to differentiate immature females from those in the regenerating phase as well as developing virgins from repeat spawners in the early developing phase. Residual spermatozoa in the lumens of the lobules was considered an IPS for males. Spawning capable males were further divided into 3 subphases (early GE, mid GE, late GE) based on spermatogenic activity (Brown—Peterson et al. 2011). Mean (± se) length and age were compared between reproductive phases using a Student's t—test.

Sexual maturity was defined in 2 ways. Physiological maturity, following Brown—Peterson et al. (2011) and Lowerre—Barbieri et al. (2011), was determined when the MAGS included cortical alveolar (CA) oocytes in females and primary spermatocytes (Sc1) for males, representing the early developing, developing, spawning capable, regressing and regenerating phases. Functional maturity, following Saber et al. (2020), was assigned if the MAGS included primary vitellogenic (Vtg1) oocytes or secondary spermatocytes (Sc2), representing fish in the developing, spawning capable, regressing and regenerating phases as well as males and females with IPS in the early developing phase. Size at physiological and functional maturity for Swordfish was estimated using a logistic regression, with 0 indicating immature and 1 indicating sexually mature (R Core Team).

Parasitological Examination

Only gonad samples from 2019 (n = 16; 12 female and 4 male) were macroscopically examined for philometrid nematodes. Gonads were defrosted in a refrigerator overnight, opened lengthwise beginning at the distal end of the gonad, and then examined for nematodes under a dissecting microscope. Nematodes were removed (generally whole worms for males and broken sections of worm bundle for females) and placed in physiological saline before being enumerated (for worm bundles, an anterior and posterior end must be present to count as one individual). Nematodes were then placed in 70% ethanol and later cleared in glycerol for morphological examination. We follow Bush et al. (1997) for parasite ecology terms: prevalence is the percentage of fish parasitized (with 95% CI) and abundance is the number per host whether infected or not (mean ± se). In some cases (n = 4), we were unable to examine both lobes of the ovary because only one lobe was provided from the recreational fisherman; therefore, we calculate an ovarian lobe abundance, defined as the number of philometrids per lobe regardless if the individual is parasitized or not, with the average abundance presented for those individuals that had both lobes examined. We only used "live" individuals when calculating abundance (i.e., no dead or melanized worm bundles were included). We only examined frozen material, so the complete removal of intact worm bundles was very difficult and resulted in many worms breaking during removal. Therefore, our abundance values likely represent an underestimate of true abundance as our counts are conservative. Parasite abundance data is often right—skewed; however, our lobe abundances were normally distributed. We used a Student's t—test ($a = 0.05$) to compare lobe abundance of females in different reproductive phases and Pearson's correlation analysis to determine if lobe abundance was correlated with host features (LJFL, W, GW).

RESULTS

A total of 93 Swordfish were collected and analyzed for this study. Females (n = 64) weighed 3.9–140.0 kg and measured 77.6–246.3 cm LJFL. Males (n = 27) weighed 4.8–80.7 kg and measured 82.0–198.1 cm LJFL. Sex was not confirmed for 2 individuals that weighed 12.5 and 99.6 kg and measured 102.0 and 205.0 cm LJFL, respectively. Swordfish < 118 cm LJFL were only captured with fishery independent sampling. The LJFL and W morphometric conversion for combined sexes is $W=0.000003L^{3.25}$.

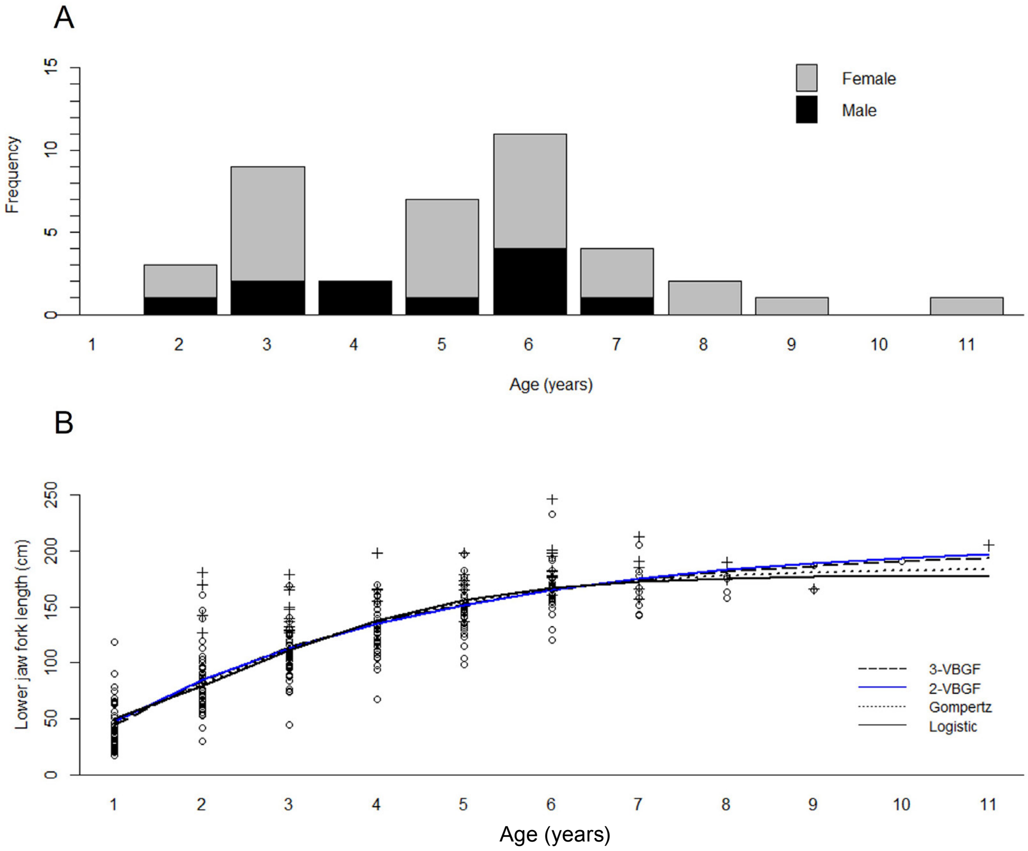

FIGURE 3. *Ages of Swordfish caught in the northern Gulf of Mexico 2017–2019. A. Observed age distribution of females (grey; n = 40) and males (black; n = 11). B. Observed (+) and back calculated (O) lengths—at—age for combined sexes. The 2—parameter von Bertalanffy growth function (2—VBGF) was the best fit model, followed by the 3—parameter von Bertalanffy growth function (3—VBGF), Gompertz, and logistic models.*

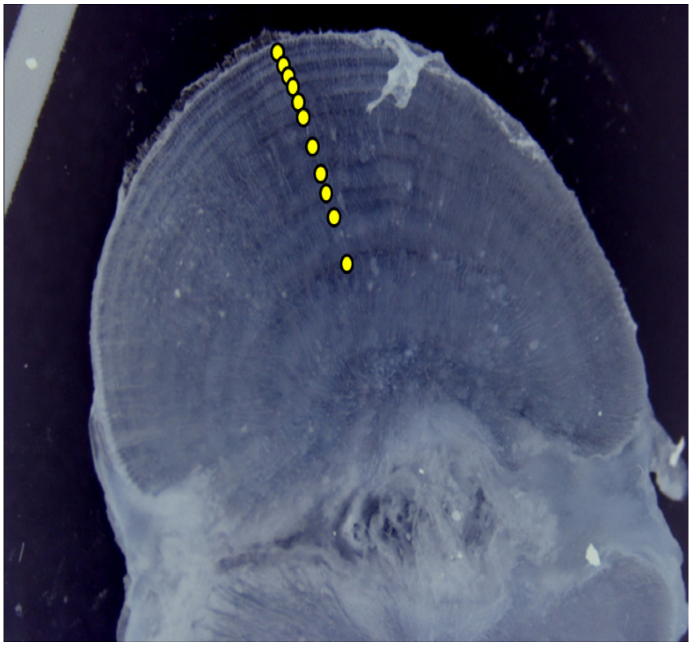

FIGURE 2. *Cross section of the second anal spine of an 11—year—old female Swordfish measuring 205.0 cm lower—jaw—fork length. Each yellow mark indicates an annulus (translucent band).*

Age and Growth

A total of 51 anal spines (40 female, 11 male) were retained for age and growth analyses. In most cases, annular bands were easily distinguished (Figure 2). Consensus age estimates were reached for all spines, with an APE of 6.41%. Observed ages (Figure 3A) ranged from 2–11 years for females (127.0–246.3

TABLE 1. *Observed, back calculated, and model predicted mean (± se) lower jaw fork lengths (LJFL, cm) at age for Swordfish captured in the northern GOM. Sexes combined. N–number of observed fish at each age; VBGF–2, 2–parameter von Bertalanffy; VGBF–3, 3–parameter von Bertalanffy.*

Age	N	Observed LJFL	Back Calculated LJFL	Predicted VBGF—2 LJFL	Predicted VBGF—3 LJFL	Predicted Gompertz LJFL	Predicted Logistic LJFL
1			44.0 ± 2.8	46.4	45.1	47.9	50.6
2	4	154.7 ± 12.2	79.9 ± 3.4	82.7	84.8	81.0	79.6
3	11	145.6 ± 5.3	106.6 ± 3.0	110.9	114.5	111.8	110.9
4	4	170.9 ± 9.3	127.0 ± 3.7	132.8	136.7	136.2	137.4
5	8	170.9 ± 9.3	146.6 ± 3.9	149.9	153.3	153.6	155.8
6	15	186.7 ± 5.4	163.6 ± 4.8	163.2	165.7	165.4	166.7
7	5	182.2 ± 9.8	165.5 ± 6.7	173.6	175.0	173.1	172.7
8	2	182.0 ± 8.0	168.4 ± 4.4	181.7	182.0	178.0	175.8
9	1	166.0	176.0 ± 10.9	188.0	187.2	181.0	177.3
10			190.6	192.9	191.1	182.9	178.1
11	1	205.0		196.7	194.0	184.1	178.5

cm LJFL) and 2–7 years for males (142.2– 98.1 cm LJFL). Due to low sample numbers, males and females were combined for all subsequent analyses and Dahl—Lee back calculation was conducted. Linear regression based on back calculated data for combined sexes resulted in: $LJFL = 0.6801(S) + 14.0642$ ($r^2 = 0.82$; $p < 0.01$); where S = anal fin spine radius (mm). Back calculated and observed LJFL at age are summarized in Table 1.

Of the models examined, the 2—parameter von Bertalanffy (L_{inf} = 210.2 cm LJFL, k = 0.25) had the lowest AIC value and as such was the best fit to the combined observed and back calculated data (Figure 3B, Table 2). Additionally, the 3—parameter von Bertalanffy was considered a good fit to the data, whereas both the Gompertz and the logistic models were considered poor fits (Table 2). Theoretical longevity and 95% confidence intervals (CI) were calculated for all 4 growth models and estimated to be 14 (CI 12-17), 12 (CI 10-17), 7 (CI 6-9), and 5 (CI 4-6) years for the 2—parameter von Bertalanffy, 3—parameter von Bertalanffy, Gompertz, and logistic models, respectively.

Reproductive Biology

Of the 93 Swordfish sampled, histological samples of gonadal tissue were obtained for 64 females and 27 males, with a significantly female—dominated sex ratio (2.37:1 female:male; $x^2 = 37.56$, $p < 0.001$). Most fish were determined to be physiologically (90.3%) or functionally (86.0%) mature. The largest immature female was 128.3 cm LJFL, and the smallest physiologically mature female was a 129.5 cm LJFL fish in the regenerating phase captured in March prior to the beginning of the reproductive season. In contrast, the smallest reproductively active, functionally mature female was a 150.3 cm LJFL fish in the developing phase captured in June. All females >128 cm LJFL were physiologically mature, whereas all females undergoing ovarian recrudescence (i.e., developing and spawning capable phases) or with IPS that were classified as functionally mature were >147 cm LJFL. The only immature male was 82.0 cm LJFL, and the smallest mature male was a spawning capable individual 96.0 cm LJFL captured in April. However, a 117.5 cm LJFL male in the early developing phase captured in March was physiologically but not functionally mature. Due to the lack of immature male fish, size— and age—at—maturity could not be calculated. A physiological maturity ogive was calculated for females, but the model for the functional maturity ogive would not converge. We calculated 50% and 95% physiological maturity for females to be

TABLE 2. *Comparison of 4 growth models of observed and back calculated lengths at age for Swordfish captured in the northern GOM. Sexes combined for model calculations. Confidence intervals are represented by the values within parenthesis. VBGF–2, 2–parameter von Bertalanffy; VGBF–3, 3–parameter von Bertalanffy; L_{inf}–asymptotic average length; k–growth coefficient; T_0–theoretical length at age zero; AIC–Akaike Information Criteria.*

Model	L_{inf} (cm)	k	T_0	AIC	ΔAIC	Theoretical Longevity (years)
VBGF–2	210.2 (195.0 – 228.9)	0.25 (0.21 – 0.29)	–––	2871.47	0	14
VBGF–3	202.7 (185.9 – 226.9)	0.29 (0.21 – 0.36)	0.13	2872.44	0.96	12
Gompertz	186.0 (174.8 – 200.5)	0.49 (0.40 – 0.59)	1.62	2875.22	3.75	7
Logistic	178.9 (169.6 – 190.3)	0.71 (0.59 – 0.84)	2.31	2880.72	9.25	5

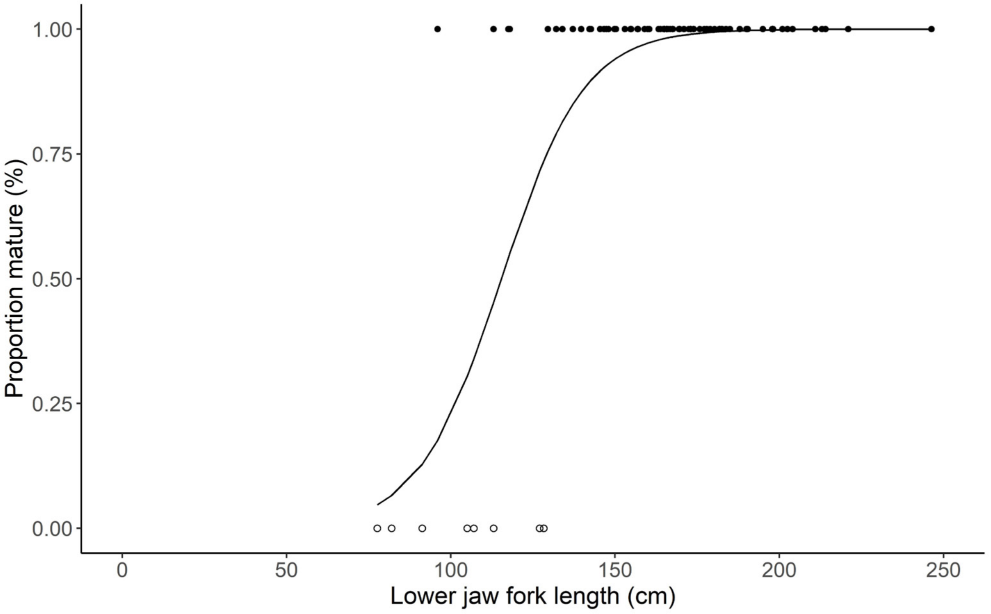

FIGURE 4. *Physiological maturity ogive for female Swordfish captured in the northern Gulf of Mexico, 2005–2021.* L_{50} *is 115.38 cm LJFL (± 6.02 cm LJFL, se),* L_{95} *is 143.47 LJFL (± 7.88 cm LJFL, se).*

115.38 ± 6.02 cm LJFL, and 143.47 ± 7.88 cm LJFL, respectively (Figure 4). Lack of ages for immature females precluded calculating age—at—maturity ogives.

When combining data from all years, Swordfish were collected from March—August, although no females were collected in July. Additionally, male gonad weight was not recorded for the March 2005 samples. Although GSI values were very low for both sexes, female GSI increased beginning in April, peaked in June, and then declined in August (Figure 5). The mean GSI of the 2 spawning capable females captured in June was 0.84 ± 0.15, while that of developing females in June was 0.54 ± 0.02, both higher than the June mean GSI for all females (0.52 ± 0.02) that included many fish in the early developing and regenerating phases. Male mean GSI values peaked in May and were lower from June-August (Figure 5). The GSI values suggest a May-June spawning season in the northern GOM.

Histological analysis confirmed a summer spawning season in GOM Swordfish. Whereas female Swordfish in the early developing sub—phase (mean LJFL 179.3 ± 4.0, n = 27, mean age 5.78 ± 0.35, n = 19) were found during all months of sampling and were the most common phase observed in June and August, reproductively active females (i.e., developing and spawning capable phases) were only seen in June and August (Table 3). Developing females were both smaller (173.5 ± 6.1 cm LJFL, n = 7) and younger (4.2 ± 0.73 years, n = 5) than spawning capable females (183.5 ± 17.5 cm LJFL, 7.5 ± 1.5 years, n = 2). Spawning capable females were only captured in June and had a larger mean LJFL and older mean age than females in any reproductive phase except for regressing females (185.8 ± 18.3 cm LJFL, n = 2). The asynchronous oocyte development seen in spawning capable females (Figure 6) indicates batch spawning. Females in the regressing phase were captured in June and August (Table 3), confirming spawning had just ceased. Females in the regenerating phase (age range 3—6 years) were captured during all months of sampling, dominated the collections from March—May, but were not as frequent during the spawning months of June and August (Table 3). The mean LJFL of regenerating females (162.4 ± 6.6 cm, n = 18) was significantly greater than that of females in the immature phase (109.5 ± 6.5 cm, n = 8; $t_{20.1}$ = –5.725, p <0.001), although there was not a significant difference in age between regenerating and immature females (4.0 ± 0.44 and 2.67 ± 0.33 years, respectively; t_{10} = –1.651, p = 0.103).

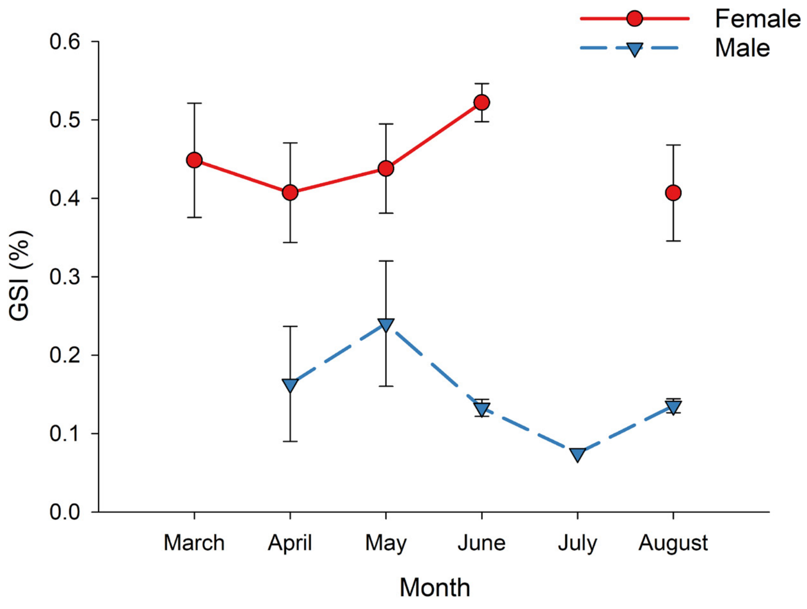

FIGURE 5. *Mean (± se) monthly Gonadosomatic Index (GSI) of mature female (red) and mature male (blue) Swordfish captured from the northern Gulf of Mexico, 2005–2021.*

Histological analysis showed that the majority of male Swordfish captured (96%) were in the spawning capable phase from April through August (Table 3), in contrast to females that were only reproductively active in June and August. Testicular recrudescence appeared to begin in March with the appearance of a male in the early developing sub—phase. Although males were spawning capable from April-August, spermatogenesis decreased as the season progressed; this

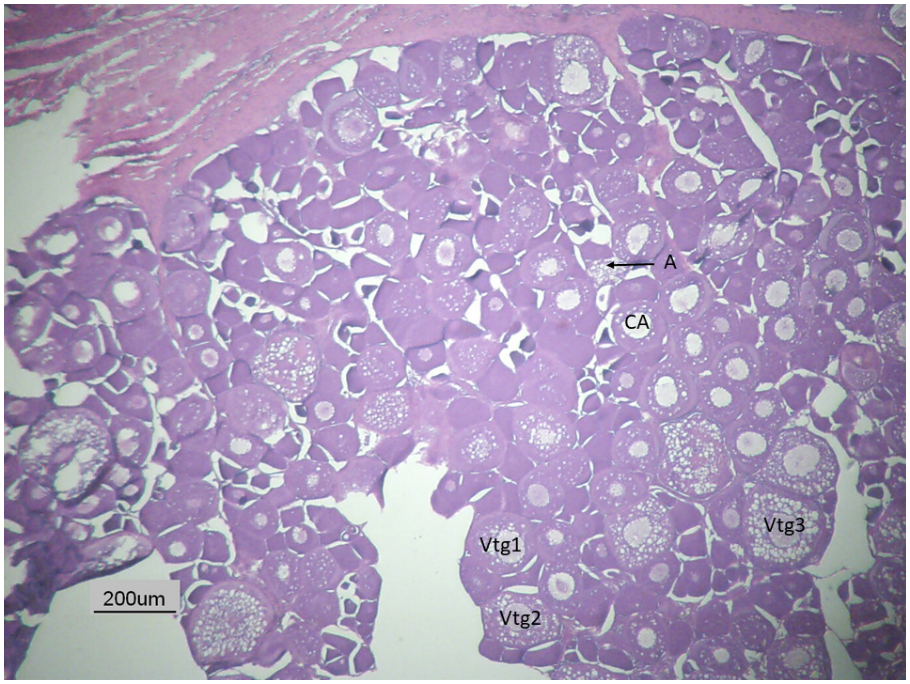

FIGURE 6. *Female Swordfish in the spawning capable reproductive phase, captured in the northern Gulf of Mexico in June 2017, showing asynchronous oocyte development indicative of batch spawning. A—atresia, CA—cortical alveolar, Vtg1—primary vitellogenic, Vtg2—secondary vitellogenic, Vtg3—tertiary vitellogenic.*

is reflected in the lower GSI values after May (Figure 5). No males in the regressing or regenerating phases were captured (Table 3).

Parasitological Analysis

Philometrids were only found in ovaries (prevalence = 91.7%, 59.8–99.6%), and all ovaries examined had evidence of philometrid infection (granulomatous encapsulations around dead worms). Mean ovarian lobe abundance was relatively low (2.25 ± 0.42) and did not differ by reproductive phase (Figure 7A; t_{33} = 0.55, p = 0.62). Ovarian lobe abundance was also not correlated with LJFL (r = 0.46, p = 0.13), weight (r = 0.43, p = 0.15), or gonad weight (r = 0.39, p = 0.21).

Male philometrids (Figure 7B) were more prevalent (91.7%, 59.8–99.6%) than females (66.7%, 35.4–88.7%). No ovigerous or larvigerous females were found in any ovarian lobe nor observed in any histological section. In general, female philometrids infecting fish in the regenerating phase were found most commonly near large melanomacrophage/granulomatous aggregates within the ovary (Figure 7C). Male philometrids were found more haphazardly throughout the ovarian lobes. Melanomacrophage centers occurred immediately adjacent to the philometrid worm bundles and leukocytic infiltrates were generally observed within close proximity, but healthy ovarian tissue was observed adjacent to bundles in both the regenerating (n = 9, Figure 7D) and early developing (n = 3, Figure 7E) phases.

Female nematodes were generally thin and difficult to extract entirely; therefore, limited morphological data is available in helping to determine the species. However, we identified the nematode as a species of *Philometra* based on the lack of cuticular ornamentations, the caudal morphology, and the oral aperture without a sclerotized ring. Males most closely resemble those of *Philometra katsuwoni* from the Skipjack Tuna, *Katsuwonus pelamis*, in that they have 2 large lateral lobes at the level of the cloaca each bearing 2 papillae (Figure 7B), have unequal spicules, and possess alae near the distal end of the dextral spicule. The posterior lateral lobes of this species of *Philometra* are 74–126 µm.

DISCUSSION

This study is the first to investigate aspects of the life history of Swordfish caught in the GOM. Furthermore, our study occurred almost 20 years after a major biological study on western north Atlantic Swordfish and therefore provides an opportunity to show changes during this time period. Despite a relatively small sample size, we report reproductively active Swordfish in the northern GOM during the summer, which corresponds with the timing of previous collections of larval fish in the region (Rooker et al. 2012) and confirms that Swordfish are spawning in the GOM. We also demonstrate the efficacy of increasing sample size by using back—calculated data for the generation of growth

TABLE 3. *Monthly percentages of the reproductive phases of female and male Swordfish captured from the northern Gulf of Mexico. Imm—immature, EDev—early developing, Dev—developing, SC—spawning capable, Rgs—regressing, Rgn—regenerating.*

Month	N	Imm	EDev	Dev	SC	Rgs	Rgn
Female							
March	7	42.80	14.3	0	0	0	42.8
April	8	37.5	12.5	0	0	0	50.0
May	7	28.6	14.3	0	0	0	57.1
June	35	0	60.0	17.1	5.7	2.8	14.3
August	7	0	42.8	14.3	0	14.3	28.6
Male							
March	2	50	50	0	0	0	0
April	3	0	0	0	100	0	0
May	4	0	0	0	100	0	0
June	14	0	0	7	93	0	0
July	1	0	0	0	100	0	0
August	3	0	0	0	100	0	0

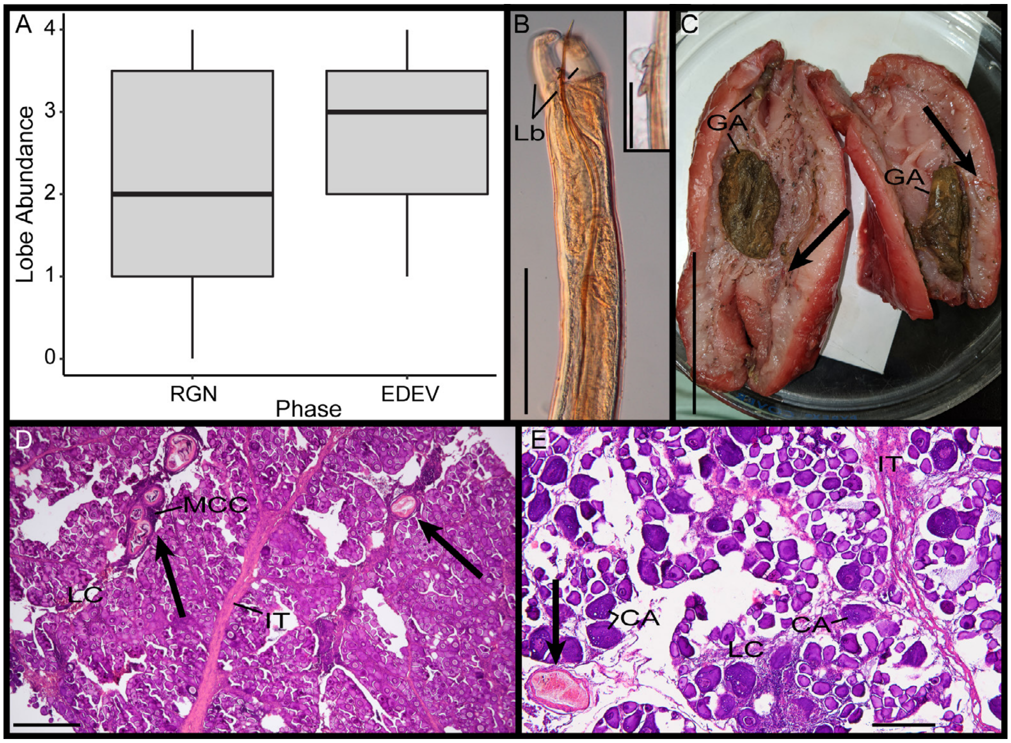

FIGURE 7. *Evidence of an unidentified species of* Philometra *infecting the ovary of Swordfish from the north-central Gulf of Mexico. A. Ovarian lobe abundance of* Philometra *in Swordfish in the regenerating (RGN) and early developing (EDEV) phases. Grey boxes are the interquartile range, the thick black line is the median, and the whiskers represent the range. B. Posterior end of a male demonstrating the 2 large lateral lobes (Lb) and the serration associated with the shorter, sinistral spicule (insert; Scale bar 25 μm). Scale bar 200 μm. C. Both lobes of the ovary opened lengthwise showing large granulomatous aggregates (GA) and immature female worm bundles (arrows). Scale bar 5 cm. D. Sectioned ovarian tissue of a female Swordfish in regenerating phase with a philometrid infection; worm bundles (arrows) are surrounded by melanomacrophage centers (MCC) and leucocytic infiltrates (LC) near healthy ovarian tissue. IT—interstitial tissue. Scale bar 500 μm. E. Sectioned ovarian tissue of a female Swordfish in early developing phase. Note presence of worm (arrow) directly adjacent to cortical alveolar oocytes (CA) and presence of leucocytic infiltrates (LC). IT—interstitial tissue. Scale bar 200 μm.*

models. Previous studies have shown this is an effective technique for providing realistic estimates of L_{inf} and growth rate in data—limited species such as istiophorid billfishes (Cerna 2009, Sun et al. 2015, Hoolihan et al. 2019). Finally, this is the first report of a species of *Philometra* parasitizing Swordfish, despite members of this genus commonly found in other pelagic species (Moravec and de Buron 2013).

Fishery dependent studies often are confounded by a lack of smaller sized fish being sampled, largely due to fishing regulations that dictate a minimum size for retention. This leads to an underrepresentation of all size classes which in turn impacts the accuracy of growth model parameters (e.g., Goodyear 2019). The current study was subjected to these limitations as current regulations in the GOM do not allow retention of Swordfish $<$ 119.3 cm LJFL. One means to remedy the missing size classes is to conduct back—calculation methods (e.g., Cerna 2009, Sun et al. 2015, Hoolihan et al. 2019), as we present in this paper. However, future research could also benefit from working with a small group of vessels and applying for a NOAA Exempted Fishing Permit to collect a limited number of sub—legal fish. The addition of these sub—legal Swordfish would help strengthen the estimated parameters from the growth models.

Overall, age and growth parameters vary throughout the regions where Swordfish life history has been examined. Swordfish in the Mediterranean Sea (e.g., Tsimendes and Tserpes 1989, Tserpes and Tsimendes 1995), western North Atlantic Ocean (e.g., Berkeley and Houde 1983, Ehrhardt 1992, Arocha et al. 2003), and western North Pacific Ocean (e.g., Sun et al. 2002) grow at a faster rate but to a smaller size than Swordfish collected from Hawaii and the eastern South Pacific Ocean (DeMartini et al 2007, Cerna 2009). Results from the current study follow this same trend of disparities among geographic regions. Age and growth studies in the Atlantic Ocean did not all utilize the same suite of growth models, despite the Chapman model being the preferred ICCAT method; however, the current study and those from the North Atlantic, South Atlantic, and Mediterranean Sea that were compared (e.g., Tserpes and Tsimenides 1995, Arocha et al. 2003, Aykol and Ceyhan 2013, Quelle et al. 2014) all conducted the 3—parameter von Bertalanffy model. As such, comparisons between managed ICCAT regions of the Atlantic Ocean are made based on this model to ensure consistency. Output from the 3—paramerter von Bertalanffy model from the current study indicate that GOM Swordfish grow to a smaller size at a faster rate and have a shorter theoretical longevity than other Atlantic Ocean stocks managed by ICCAT (i.e., North Atlantic, South Atlantic, Mediterranean; Table 4). Although the maximum observed size included in our models is similar to the size range of Swordfish from the Mediterranean Sea and North Atlantic Ocean (e.g., Tserpes and Tsimenides 1995, Arocha et al. 2003, Aykol and Ceyhan 2013), our data predicts an L_{inf} value lower than the other studies. It should be noted that the study by Arocha et al. (2003), in the western North Atlantic Ocean, did not conduct a combined sex investigation using the 3—parameter von Bertalanffy and only did so using Chapman's generalized model. However, the results from Arocha et al. (2003) likely indicate that Swordfish from the western North Atlantic Ocean, excluding the GOM, also exhibit larger combined L_{inf} values as both sexes had high-

TABLE 4. *Comparison of Swordfish growth parameters among studies in the Atlantic Ocean using the 3—parameter von Bertalanffy growth function on combined sexes when available. Sex specific parameters listed for Arocha et al. (2003) as female = * and male = #. Values in parentheses represent 95% confidence intervals (CI). Theoretical longevity was calculated from reported k values. LJFL—lower jaw fork length; L_{inf}–asymptotic average length; k–growth coefficient.*

Size Range (LJFL, cm)	L_{inf} (cm) ± CI	k ± CI	Theoretical Longevity	Location Reference
127 – 246	202 (185 – 226)	0.29 (0.21 – 0.36)	12	Gulf of Mexico Current Study
62 – 210	238	0.19	18	Mediterranean Sea Tserpes and Tsimenides 1995
51 – 242	283	0.15	23	Mediterranean (Aegean) Sea Aykol and Ceyhan 2013
66 – 309	358	0.09	37	South Atlantic Quelle et al. 2014
63 – 246*	312.2*	0.09*	38*	North Atlantic
74 – 284#	223.1#	0.15#	23#	Arocha et al. 2003

er values than the combined sex data from the current study. Similarly, estimates of theoretical longevity for combined sexes were found to be lower within the GOM, with a mean of 12 years and a range of 9—16 years based on confidence intervals of k compared to other studies which ranged between 18 and 37 years (Table 4), which is consistent with other growth model parameters as theoretical longevity is directly inferred from *k*. Not all prior studies within the Atlantic Ocean reported confidence intervals for k (i.e., Tserpes and Tsimenides 1995, Arocha et al. 2003, Quelle et al. 2014) and those that did (i.e., Aykol and Ceyhan 2013) still indicate that values from other regions did not likely overlap the GOM values. However, the lowest calculated longevity from Akyl and Ceyhan (2013; 17.3 years) was found to be similar to the highest calculated longevity from the current study (16.5 years). This disparity in L_{inf} and theoretical longevity values may be due to geographical variability, a smaller overall sample size in this study, fitting the model to back—calculated ages, or differences in resource availability between the distinct localities. Additionally, many of the prior studies did not present confidence intervals for their values and as such we cannot infer if L_{inf} are statistically different among regions. Continued research is necessary to fully determine why there is an apparent difference in age and growth parameters between the current study and the larger Atlantic Ocean. It could be possible that larger, older swordfish only occur outside of the GOM or that the larger fish caught in the US South Atlantic may be migrants from the GOM, but without DNA or tagging studies we can only speculate on these apparent differences in maximum size among regions.

Similar to other populations of Swordfish, the GOM sex ratio is significantly skewed towards females, and females tend to be larger than males. Potential explanations for the observed female—dominated populations, particularly during the reproductive season, include an inherent spatial zonation between sexes (Gillespie et al. 2021), larger numbers of smaller males classified as "unknown" when macroscopically sexed (Gillespie et al. 2021), greater physiological tolerance of larger females for lower temperatures (Poisson and Favel 2009a), and greater fishing selectivity of larger females (Neilson et al. 2013). Furthermore, the spatial migration of females covers a broader geographic area to sustain higher energy requirements required for egg production (Neilson et al. 2013), and thus females are more likely to be captured in the fishery, producing a skewed sex ratio.

Our data suggest that GOM Swordfish are reproductively active at a smaller size then reports from most other regions. The range of immature females we captured was 77.6 – 128.3 cm LJFL, in contrast to the range of immature females from the northern Atlantic (92 – 180 cm LJFL, Saber et al. 2020). Importantly, the range of sizes for immature fish corresponds to the minimum size for retention of < 119.3 cm LJFL in the GOM. The smallest sexually mature female from the GOM was a 129.5 cm LJFL fish in the regenerating phase captured in March; while histologically this fish appeared to have spawned during the previous year, there were few IPS, so this fish was considered physiologically, but not functionally, mature. Our estimates of L_{50} and L_{95} for physiological maturity of females (116 and 143 cm LJFL, respectively) are smaller than the calculated L_{50} for female Swordfish from Florida (182 cm LJFL, 5.5 years; Taylor and Murphy 1992), the north Atlantic (168 cm LJFL, 95% confidence intervals 165–171 cm, Saber et al. 2020), the northwest Atlantic, an area that includes the GOM (179 cm LJFL, Arocha and Lee 1996), or the Indian Ocean (170.4 cm LJFL, Poisson and Fauvel 2009a). Typically, functional maturity is used for Swordfish maturity estimates (Taylor and Murphy 1992, de Serna et al. 1996, Young et al. 2003, Poisson and Favel 2009a, Saber et al. 2020), and functional maturity estimates are usually larger than physiological estimates (Lowerre—Barbieri et al. 2022). Furthermore, macroscopic, rather than histological, criteria are often used to determine maturity, resulting in larger L_{50} values due to misclassification of early developing females as immature. For instance, macroscopic physiological L_{50} for the North Atlantic population was estimated to be 127 cm LJFL, similar to our estimate, while functional L_{50} using a macroscopic metric was 203 cm LJFL (Saber et al. 2020). Although we were unable to calculate 50% functional maturity for direct comparisons, GOM Swordfish appear to mature at a smaller size than other north Atlantic populations based on all GOM Swordfish > 148 cm LJFL being functionally mature, similar to the size of 95% physiological maturity (143 cm LJFL). For instance, the smallest reported mature female from Florida waters (~170.0 cm LJFL, age 4;

Taylor and Murphy 1992), and reproductively active females in the north Atlantic (145—245 cm LJFL, Saber et al. 2020) are generally larger than our smallest reproductively active female of 150.3 cm LJFL. In contrast, female Swordfish from the Mediterranean appear to have L_{50} values more similar to the GOM (114 cm LJFL for macroscopic physiological maturity, and 134 cm LJFL for histological functional maturity, Saber et al. 2020; 140 cm LJFL (functional), Macias et al. 2005; 142 cm LJFL (functional), de la Serna et al. 1996). The apparent similarity in size at maturity for the GOM and Mediterranean populations should be considered in stock assessments, as it appears that these groups can reproductively contribute to the stock earlier in life than Swordfish from other North Atlantic areas. Additionally, the smallest functionally mature females from our study ($\geq$ 143 cm LJFL) are similar in size to previous reports of functional maturity from Pacific waters (eastern Australia, 136.0 cm LJFL, converted from orbital—fork length in Young et al. 2003 using Uchiyama et al. 1999; Hawaiian waters, 151.4 LJFL, converted from eye—fork length in Demartini et al. 2000 using Uchiyama et al. 1999). Since GOM Swordfish appear to grow faster, yet have lower longevity than other stocks, it is not surprising that they achieve sexual maturity at a relatively small size, such that they have multiple opportunities to reproduce during their lifetime. As maturity data continue to accrue from various Swordfish populations, a better understanding of reproductive dynamics will emerge and the apparent differences in maturity for the north Atlantic areas can be incorporated into future ICCAT assessments.

Both GSI and histological data suggest a summer spawning season for Swordfish in the GOM. Limited data prevents defining the length of the spawning season, but reproductively active females were seen in the summer in June and August, and spawning capable males were captured from April through August. In contrast, Arocha (2007) suggested GOM Swordfish likely spawn from December through March, as only a single spawning female was captured in the region in June. Inference of spawning time by back—calculating larval Swordfish ages suggested spawning during all seasons in the north—central GOM with a peak in spring, and spawning is likely focused in the northern portion of the Gulf Loop Current (Govoni et al. 2003). Rooker et al. (2012) also found Swordfish larvae year—round in the GOM just south of our collection area, with a peak in larval abundance in July near the Loop Current. Our capture of spawning capable females in June, despite the small sample size, corresponds to the timing of the Rooker et al. (2012) larval collections. A summer spawning season has been reported for Swordfish from Florida (peak spawning April through July; Taylor and Murphy 1992), the northern Atlantic (Saber et al. 2020, although samples did not include the GOM or Caribbean), eastern Australia (Young et al. 2003), the Mediterranean Sea (Tserpes et al. 2001, Macias et al. 2005, Corriero et al. 2014), the Indian Ocean (Poisson and Fauvel 2009a), and Hawaiian waters (DeMartini et al. 2000). Interestingly, Saber et al. (2020) reported few reproductively active female Swordfish in the North Atlantic from June through October, similar to our findings, despite a larger sample size. In general, the Atlantic Ocean Swordfish spawning season is related to the 24°C isotherm, with a more extended season in tropical areas compared with a shorter season in warm—temperate areas such as the Mediterranean Sea (Arocha 2007), the GOM, and the western North Atlantic north of Cape Hatteras. Indeed, female Swordfish captured off warm waters of south Florida (Cape Canaveral to the Florida Keys) were found to be in spawning condition 11 months of the year, although peak spawning occurred from April through July in spring—summer months (Taylor and Murphy 1992). Histological evidence from developing and spawning capable GOM females suggests Swordfish have asynchronous oocyte development, are batch spawners, and have indeterminate fecundity as also reported by Arocha (2002), Macias et al. (2005) and Poisson and Fauvel (2009a). This is in contrast to a previous, earlier report by Taylor and Murphy (1992) that Swordfish exhibit group synchronous oocyte development. Thus, the occurrence of Swordfish larvae during most months of the year (Govoni et al. 2003, Rooker et al. 2012) is not surprising given the ability of Swordfish to produce multiple batches of oocytes.

We report low mean GSI values (<1%) for female Swordfish during the spawning season, likely because we captured no actual spawning females. Other studies have also shown low Swordfish GSI values during the spawning season (Tserpes et al. 2001, Young et al. 2003, Vega et al. 2009, Poisson and Fauvel 2009a), although mean GSI values during the peak spawning months ranged from 1—2% in those studies. In contrast, GSI values during peak spawning times are typically >7 in the Mediterranean (de la Serna 1996, Tserpes et al. 2001, Corriero et al. 2004; Macias et al. 2005). The predominance (>75%) of reproductively inactive females (i.e., early developing, regressing and regenerating phases) in the GOM during the spawning months of June and August likely contributed to the low mean female GSI values we observed. However, the spawning capable females we captured in June also had low GSI values, but these were fish just entering into the spawning capable phase without large numbers of late vitellogenic oocytes (see Figure 6). It is likely that these fish were not captured in the main GOM Swordfish spawning area; newly spawned Swordfish larvae were captured further south in the GOM than our sampling areas (Rooker et al. 2012). Blue Marlin (*Makaira nigricans*), another migratory large pelagic species, also has low mean GSI values (<1%) during the spawning season (Shimose et al. 2009, Sun et al. 2009), suggesting this may be a common strategy for highly migratory species. The high percentage of females in the early developing sub—phase during the likely spawning months of June and August could be explained by delayed ovarian development of smaller, younger fish, since mean LJFL and age of the early developing fish were less than those of the spawning capable females. The occurrence of regenerating females with little to no atretic oocytes larger than the size at 50% maturity during the spawning months may indicate that Swordfish exhibit skip spawning. The prevalence of skip spawning is becoming better understood (Rideout and

Tomkiewicz 2011) and has been suggested to occur in other pelagic species (Secor 2007, Brown—Peterson et al. 2008) but has not previously been hypothesized for Swordfish.

As far as we are aware, this is the first report of a philometrid infecting Swordfish. Previous parasitological examinations have largely focused on external parasites and those associated with the gastrointestinal tract (e.g., Iles 1971, Hogans et al. 1983, Castro—Pampillón et al. 2002, Garcia et al. 2011, Mattiucci et al. 2014). The lifecycle for philometrid nematodes is poorly understood, but presumably uses a crustacean intermediate host and one or more paratenic hosts to reach its final host (Moravec and de Buron 2013). Male and female nematodes eventually recruit to the ovaries (or other tissues for some species) of their final host, mate, and first stage larvae are released once a larvigerous female ruptures when in contact with water (Moravec and de Buron 2013). This reproductive strategy seems to align with the reproductive cycle of its host as has been suggested for *Philometra saltatrix* and its host the Bluefish, *Pomatomus saltatrix* (Clarke et al. 2006) and *P. floridensis* and its host the Red Drum, *Sciaenops ocellatus* (Bakenhaster et al. 2014). Our data generally support this hypothesis (a mirroring of host—parasite reproductive cycles) in that we observed no ovigerous nor larvigerous females in any of our examined Swordfish. Evidence of previous philometrid infection (dead worms) were present in all Swordfish examined, further supporting the hypothesis and supporting batch spawning in GOM Swordfish. We further observed no differences in the abundance of philometrids based on reproductive phase, nor any correlation between host metrics suggesting that Swordfish are not necessarily accumulating a more intense infection over time. Philometrids have been reported to have varying impacts to the reproductive output of marine teleosts (Clarke et al. 2006, Moravec and de Buron 2013, Bakenhaster et al. 2014), but we did not observe any large pathogenic effects from philometrids in the fish we examined; however, we only examined fish in 2 reproductive phases and have a limited sample size. Future research should seek to examine Swordfish in other reproductive phases (and potentially associated with different spawning grounds) to determine what impact this parasite may have on host fecundity.

The species of *Philometra* we found parasitizing Swordfish likely represents an undescribed species based on the morphological features of the male. The species most closely resembles *P. katsuwoni* which also found in a pelagic host, the Skipjack Tuna. However, enough morphological evidence of the males is present to suggest these are distinct species, based on the large (74-126 μm) posterial lateral lobes in comparison to lobes < 75 μm in *P. katsuwoni* [from line drawings in Petter and Baudin—Laurencin (1986) and Cárdenas et al. (2009)]. Previous researchers have described species of *Philometra* based strictly on material only from one sex (Moravec 2006, Moravec and de Buron 2013, Moravec et al. 2016); however, we believe that doing so in this instance is not warranted. All material we examined was from frozen ovaries, which likely distorted some morphological features and made the females even more fragile. Additional specimens from fresh, non—frozen Swordfish are required to accurately determine if this truly is an undescribed species. If this philometrid species is only found in the ovaries of Swordfish from the GOM then perhaps it can be considered as a biological tag for GOM Swordfish, as other parasite species have been suggested for the Mediterranean Sea and South Atlantic (Iles 1971, Garcia et al. 2011, Mattiucci et al. 2014).

Understanding life history parameters, specifically growth rates and spawning characteristics, is essential to creating successful management plans. The current study provided an opportunistic assessment of age, growth, and reproduction of GOM Swordfish that previously represented a large data gap for this species. Furthermore, this study provided insights on parasites associated with Swordfish gonads. Although more samples are needed to adequately inform management for stock assessments, this study shows that GOM Swordfish are growing to a smaller size at a faster rate and are reproductively active at a younger age and size than conspecifics collected in the Florida Straits and north Atlantic Basin. Further studies on GOM Swordfish should be undertaken to better understand the life history and population dynamics of this prized fish that supports commercial and recreational fisheries.

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