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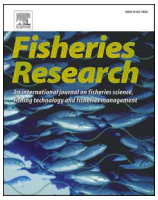

Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the northcentral U.S. Gulf of Mexico

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ABSTRACT

The reproductive biology of yellowfin tuna (*Thunnus albacares)* was investigated from fish collected throughout 2000–2017 in the northcentral U.S. Gulf of Mexico (GOM; n = 1135 females, 776 males), predominately from recreational anglers fishing off the Mississippi River (93 %). Histological evidence, along with mean gonadosomatic index (GSI) values, showed that peak spawning occurred from May to August, with the highest mean GSI value for both sexes observed in May (females, 1.52 %; males, 0.57 %). During the reproductive season, the amount of active spermatogenesis in spawning capable males varied monthly as observed by the progression of germinal epithelium (GE) subphases (i.e., early-GE, mid-GE, late-GE), with the mid-GE subphase observed most frequently throughout the peak spawning season. The upper and lower 95 % confidence intervals among length at 50 % maturity (L_{50}) estimates had the largest degree of separation between the physiological (cortical alveoli, L_{50} =1002 ± 7.18 mm CFL) and functional maturity thresholds (primary or secondary vitellogenesis; L_{50} =1071 ± 4.89 mm CFL), indicating that the physiological maturity threshold should be used with caution as it may underestimate L_{50}. Using the postovulatory follicle (POF) method, the minimum spawning interval was estimated during peak spawning months for all functionally mature females at 2.10 days, with a minimum of 17.30 % daily spawning. Batch fecundity estimates for 24 females was linearly related to size and ranged from 37,956–6.2 million eggs per batch. These data allow for U.S. GOM reproductive parameter estimates to be incorporated, for the first time, into future Atlantic yellowfin tuna stock assessments done by the International Commission for the Conservation of Atlantic Tunas.

1. Introduction

Yellowfin tuna (*Thunnus albacares)* is one of the most exploited species and comprises one of the most profitable fisheries worldwide (Campling, 2012). Estimated global landings of yellowfin tuna were on average 1.25 million metric tons per year in the last decade, making it the second largest tuna fishery worldwide (Pecoraro et al., 2017). In the Atlantic Ocean, yellowfin tuna are caught between 45ºN and 40ºS latitude, primarily by surface gears including purse seine, handline (including rod and reel), and pelagic longline (ICCAT, 2012; Pecoraro et al., 2017). Yellowfin tuna commercial landings in the U.S. Gulf of Mexico (GOM) were highest in the early 1980s, in particular off Louisiana, but have since steadily declined (NOAA[1]). A productive recreational fishery for yellowfin tuna also exists in the northcentral GOM off the coast of Louisiana (Brown-Peterson et al., 2014; Lang et al., 2017), in large part because of the offshore oil platforms that act as fish aggregating devices (Edwards and Sulak, 2006; Snodgrass et al., 2020). The Atlantic stock of yellowfin tuna, which includes yellowfin tuna in the

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[1] NOAA (National Oceanic and Atmospheric Administration) Fisheries Office of Science and Technology, Commercial Landings Query Division. Available from [website, accessed 1 July 2021].

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GOM, is managed by the International Commission of the Conservation of Atlantic Tunas (ICCAT) and a recent assessment stated that the stock was not overfished but cautioned it was near overfishing (ICCAT, 2019b).

Comprehensive knowledge of a species' reproductive biology is necessary for fisheries scientists to provide reliable management advice to ensure sustainability (Morgan, 2008). Specifically, successful fisheries management often aims to conserve the individuals with the highest reproductive potential (Lowerre-Barbieri et al., 2009), which is determined largely by accurate inputs of maturity and fecundity into stock assessment models (Morgan, 2008; Lowerre-Barbieri et al., 2009). Determining spawning season duration, spawning interval (i.e., number of days between consecutive spawns, and fecundity (i.e., number of eggs produced) are important when determining the reproductive potential of an exploited population (Morgan, 2008; Lowerre-Barbieri et al., 2011; Fitzhugh et al., 2012). Recently, the Total Egg Production (TEP) method has been used to estimate reproductive potential in stock assessments (SEDAR, 2018), which requires information on spawning seasonality, batch fecundity, and spawning frequency. Traditionally, determination of spawning stock biomass (SSB) has been used as an estimate of reproductive potential, particularly for tropical tunas; this method relies solely on female maturity estimates (Farley et al., 2014), specifically data on the length and age when a proportion (50% or 95%) of the population reaches maturity (Schaefer, 2001). These data are utilized when determining minimum size limits and related landings regulations to increase the probability that an individual reproduces a minimum of one time before harvest (Caddy and Agnew, 2004; Morgan, 2008; Lowerre-Barbieri et al., 2011).

Female maturity is defined as the size or age when an individual is able to reproduce, thus completing a reproductive cycle through to ovulation (Schaefer, 2001). Determining if a fish is "mature" or "immature" can be investigated using a variety of maturity thresholds, which are assigned based upon a certain stage of ovarian development that is identified by either macroscopic examination of the gonad or microscopic histological review of a gonad tissue sample (Schaefer, 2001; Pecoraro et al., 2017). Detailed criteria used to assign maturity status to individuals often goes unreported in the literature (Lowerre-Barbieri et al., 2011) which poses challenges when comparing yellowfin tuna maturity estimates among studies (Schaefer, 2001; Pecoraro et al., 2017) and recommending scientific advice to stock assessors.

As with other tropical tunas, yellowfin tuna are broadcast batch spawners with indeterminate fecundity (Zudaire et al., 2013; Schaefer and Fuller, 2022). Females have asynchronous oocyte development, expelling batches of hydrated oocytes into the water column multiple times throughout the spawning season (Zudaire et al., 2013; Schaefer and Fuller, 2022). Spawning activity for yellowfin tuna is largely temperature dependent (>24 °C), with females typically spawning overnight and into the early morning hours (Schaefer, 1998; Schaefer and Fuller, 2022). The major spawning ground for Atlantic yellowfin tuna is located in the eastern Atlantic off the Gulf of Guinea with fish spawning from December to April; a smaller proportion of fish spawn off Cape Verde, Africa (ICCAT, 2012). Spawning also occurs in the GOM, primarily from May to August, and in the southeastern Caribbean Sea from July to September (ICCAT, 2012). Based on genetics, stock mixing occurs among the different spawning populations of yellowfin tuna in the Atlantic (Scoles and Graves, 1993; Kitchens et al., 2018). However, the importance of each spawning ground relative to the population as a whole remains unknown, and more research is needed to better understand the overall stock structure of Atlantic yellowfin tuna (Kitchens et al., 2018; ICCAT, 2019a).

The reproductive biology of yellowfin tuna has been investigated throughout the Pacific (McPherson, 1991; Schaefer, 1996, 1998, 2001; Schaefer and Fuller, 2022; Itano, 2000), Indian (Zudaire et al., 2013, 2014), eastern Atlantic (Diaha et al., 2016; Richardson et al., 2018; Pecoraro et al., 2020), and western Atlantic Oceans (including the GOM; Arocha et al., 2001; Brown-Peterson et al., 2014). Currently, ICCAT uses reproductive parameters (i.e., fecundity and maturity estimates) derived from yellowfin tuna landed in the eastern Atlantic (Diaha et al., 2016) since the Gulf of Guinea has been identified as the major spawning ground for the Atlantic stock (ICCAT, 2019b). ICCAT, however, has acknowledged the importance of integrating reproductive data from yellowfin tuna caught in the western Atlantic (ICCAT, 2019a), including the GOM, yet this information is relatively sparse. The goal of this study was to use a comprehensive, long-term dataset, which includes data used in the preliminary findings of Brown-Peterson et al. (2014), to estimate reproductive parameters using histological techniques for yellowfin tuna in the western U.S. Atlantic, in particular the northcentral GOM off of the Louisiana coast. The specific objectives were to estimate female: i) spawning seasonality, ii) length and age at maturity, iii) spawning interval and spawning frequency, and iv) age-and length--specific fecundity. Additionally, we describe the seasonal progression of spermatogenesis histologically within the germinal epithelium (GE; Grier, 2002; Brown-Peterson et al., 2011), which has not been previously documented for yellowfin tuna males.

2. Materials and methods

2.1. Biological sample collection and preparation

Yellowfin tuna were collected throughout the northcentral U.S. GOM (the Florida panhandle west to Venice, Louisiana) from fishery-dependent sources from 2000 to 2017 (Fig. 1). Biological samples were primarily collected from yellowfin tuna landed recreationally ~5–60 nautical miles off the mouth of the Mississippi River (93 %). Recreational samples were obtained opportunistically primarily from charter boat fisheries, private anglers, and to a lesser extent from fishing tournaments throughout the region. Fishery-dependent samples were also collected by at-sea observers from the National Marine Fisheries Service (NMFS) Pelagic Observer Program (POP) aboard commercial vessels off the west Florida shelf in May and June of 2011 and 2012 (7 %). Gear type recorded by the recreational and commercial fisheries were rod and reel (RR) and pelagic longline (PLL), respectively.

Biological information was recorded for each fish sampled in the field including straight fork length (SFL; mm), curved fork length (CFL; mm), sex, and whole weight (W, kg), when possible. When CFL was not recorded, it was converted from SFL using the conversion equation for yellowfin tuna in the western north Atlantic (Scida et al., 2001). Gonads were removed from each fish and weighed to the nearest gram (GW, g). Up to three random subsamples per gonad were immediately preserved in 10 % neutral buffered formalin (NBF). A total of 204 gonads were included from the preliminary analysis (110 ovaries; 94 testes) reported by Brown-Peterson et al. (2014). Beginning in 2011, sagittal otoliths were also collected from each fish in the field when possible following the ICCAT biological sampling protocol (ICCAT, 2006–2016).

Each gonad sample was dehydrated, embedded in paraffin wax, sectioned at 4 μm and stained/counter-stained with hematoxylin/eosin following standard histological procedures. For age determination, each sagittal otolith was embedded in epoxy and cross-sectioned through the core to produce a single 0.5 mm transverse section (Pacicco et al., 2021). Annuli counts were assigned by age readers and fractional ages, whole calendar age, and reader precision were calculated following established protocols for yellowfin tuna (Pacicco et al., 2021).

2.2. Female histological classification

Yellowfin tuna oocyte staging terminology primarily followed Wallace and Selman (1981) and Schaefer (1998), and the most advanced gamete stage (MAGS) was identified in each ovary. Alpha (α) and beta (β) atresia of vitellogenic oocytes were identified following descriptions for yellowfin tuna (Schaefer, 1996). Ovulation was identified by the presence of a postovulatory follicle complex (POF) in the ovary. The

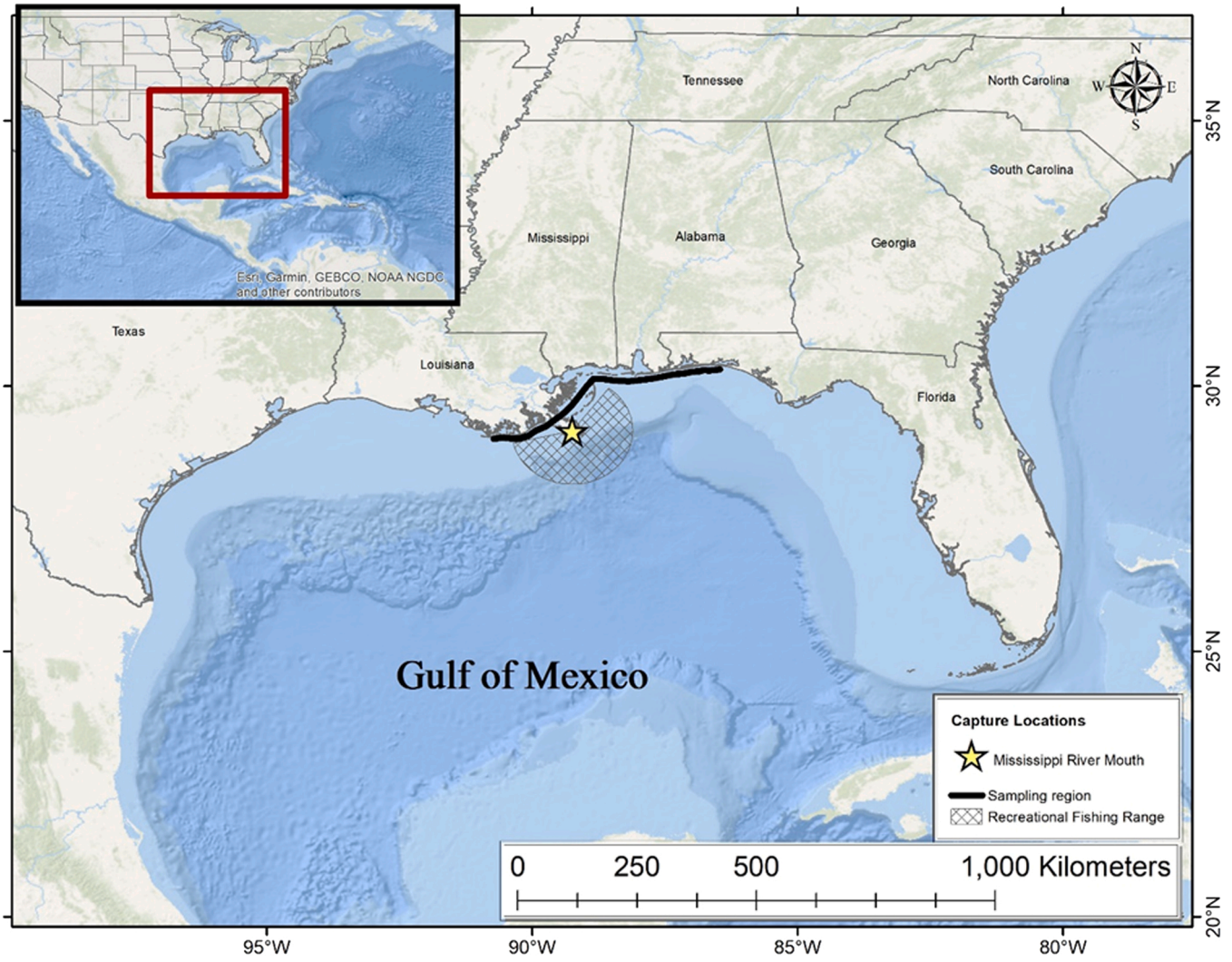

Fig. 1. The general sampling region for yellowfin tuna extended from the west Florida shelf to Venice, Louisiana, within the northcentral Gulf of Mexico, shown by the black line. A majority of recreational sampling occurred between 5 and 60 nautical miles off the Mississippi River (yellow star), denoted by the checkered half-circle.

estimated age of POFs were identified as new POFs (assumed < 6 h after ovulation), old POFs (assumed between 6 and 24 h after ovulation), or absent following the descriptions of Schaefer (1996). Similar to other tropical tunas that spawn in warmer waters (i.e., ≥ 24 °C), POFs were assumed undetectable in ovaries ≥ 24 h (Hunter et al., 1986; Schaefer and Fuller, 2019, 2022).

Ovaries were assigned to a reproductive phase following the standardized terminology of Brown-Peterson et al. (2011) based on histological evaluation of the MAGS, atresia, POFs, and indicators of prior spawning (IPS). Phases included immature, developing (with early developing subphase), spawning capable (with actively spawning subphase), regressing, and regenerating (Table 1). The developing phase (with early developing subphase) includes both developing virgins (i.e., females progressing from the immature phase preparing for a first spawn), as well as repeat spawners (i.e., fish that have spawned previously and are re-entering the reproductive cycle from the regenerating phase). To aid in identifying a reproductively mature female, the presence or absence of IPS were recorded for each ovarian sample. Indicators included the presence of one or more residual hydrated oocytes (Fig. 2, A), ≥ 5 brown-staining phagocytes, extensive atresia of vitellogenic oocytes (Corriero et al., 2003; Brown-Peterson et al., 2011; Farley et al., 2014), pockets of blood vessels/vascularization throughout the ovary, distinct muscle bundles, and loose spacing among oocytes (Brown-Peterson et al., 2011; Lowerre-Barbieri et al., 2011; Fig. 2B). Residual cortical alveolar (CA) oocytes retained in the ovary at the end of the spawning season were identified by a loss of color in the chorion and overall faded appearance of the oocyte (Pacicco, 2020).

2.3. Male histological classification

Testes were assigned a reproductive phase following the standardized terminology of Brown-Peterson et al. (2011) based on spermatogenesis, the appearance of the GE, and presence of spermatozoa (Sz) in the lumens and vas deferens. Males in the spawning capable phase have Sz in the lumens of the lobules and were further classified into three sub-phases (early-GE, mid-GE, late-GE) based on changes within the GE throughout the reproductive season (Grier, 2002; Brown-Peterson et al., 2002, 2011).

2.4. Spawning seasonality

The percent frequency of mature individuals in each reproductive phase was calculated in each month to investigate spawning seasonality for females and males separately. The peak spawning months were defined as > 40 % of females classified in the spawning phases (i.e., spawning capable and actively spawning). The duration of the spawning

Table 1
Female histological classification summary for reproductive phases of yellowfin tuna in the northcentral GOM. Reproductive phase was assigned based on the most advanced gamete stage (MAGS) - PG-primary growth; CA-cortical alveolar; V1, V2, V3- primary, secondary, tertiary vitellogenesis; OM – oocytes undergoing oocyte maturation and in the lipid coalescence, germinal vesicle migration, germinal vesicle breakdown or hydrated stages; the amount of alpha (α) and beta (β) atresia of vitellogenic oocytes in the ovary, the presence or absence of postovulatory follicles (POF), and indicators of prior spawning (IPS).

Reproductive phase	MAGS	Atresia of vitellogenic oocytes	POF	IPS
Immature	PG	Not present	Not present	None or very minimal
Developing	CA, V1, V2	< 50 % α-atresia/ minimal β-atresia	Not present	Present unless developing virgin
Early Developing (subphase)	CA	Not present	Not present	
Spawning Capable	V3	< 50 % α-atresia/ minimal β-atresia	< 24 h may be present	Likely Present
Actively Spawning (subphase)	OM	< 50 % α-atresia/ minimal β-atresia	< 24 h and/or < 6 h may be present	Likely Present
Regressing	CA,V1, V2,V3	≥ 50 % α-atresia and/or extensive β-atresia	< 24 h may be present	Present
Regenerating	PG, CA	minimal β-atresia possible	Not present	Present

season was also determined macroscopically from peak GSI values. The GSI was calculated separately for individual mature females and mature males as:

$$GSI(\%) = GW/(W - GW) \times 100 \quad (1)$$

When a whole weight was not available, it was estimated from the power function:

$$EstimatedwholeWT(kg) = 10^{-8} \times CFL^{3.06} \quad (2)$$

which was derived from observed length-weight data from yellowfin tuna landed in the northcentral GOM as part of this study.

2.5. Estimates of female maturity

Reproductive maturity was investigated using three different maturity thresholds for yellowfin tuna females. Under the first threshold, both developing virgins as well as repeat spawners with CA or more advanced oocyte development as the MAGS were considered mature (physiological maturity; Brown-Peterson et al., 2011; Zudaire et al., 2013). Under the second threshold, repeat spawners and developing virgins with primary (V1) or secondary (V2) vitellogenic oocytes identified as the MAGS were considered mature (functional maturity; McPherson, 1991; Arocha et al., 2001; ICCAT, 2019b). Under the third threshold, a yellowfin tuna female was considered mature when the MAGS was identified as tertiary vitellogenic (V3) or any stage of oocyte undergoing oocyte maturation (OM; Table 1) (spawning maturity; Schaefer, 1996, 1998; Itano, 2001; Schaefer and Fuller, 2022). Repeat spawners in the regressing or regenerating phases with IPS were also identified as reproductively mature under all thresholds.

Length and fractional age at 50 % (L_{50}; A_{50}) and 95 % (L_{95}; A_{95}) maturity of female yellowfin tuna were estimated using the non-linear logistic equation for each maturity threshold

$$P_{mature} = \left[1 + e^{-(\alpha+\beta X)}\right]^{-1} \quad (3)$$

where P_{mature} = the predicted proportion of mature females at length (X; CFL in mm) or age (X; years) and α and β = parameters that represent

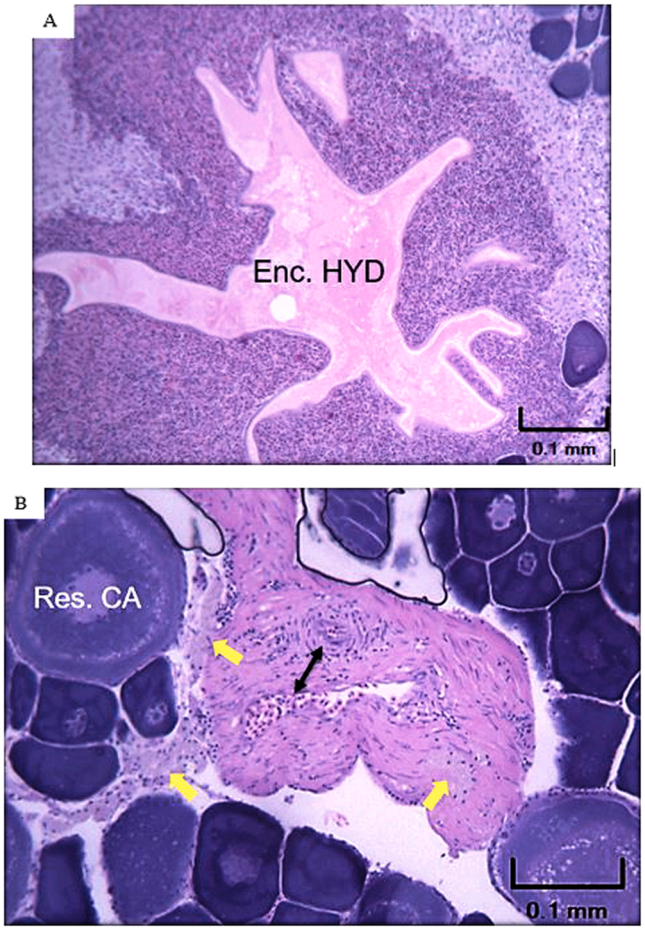

Fig. 2. Indicators of prior spawning in ovaries of reproductively inactive yellowfin tuna (from Pacicco, 2020). A) Encysted hydrated oocyte (Enc. HYD) surrounded by inflammation. B) Blood vessels (black arrows) in muscle bundles, brown-staining phagocytes (yellow arrows), and a residual cortical alveolar oocyte (Res. CA).

the intercept and the slope of the logistic equation, respectively. Predicted maturity ogives and associated analyses were computed using a generalized linear model (GLM) function from a binomial distribution in R vers.3.5.0; (R Core Team, 2021) with additional functions in the add-on packages MASS (vers. 7.3–51.6; Venables and Ripley, 2002), and tidyr (vers. 1.1.2; Wickham, 2020) to assist with the analyses. Standard error was estimated for each parameter assuming a normal distribution of errors around each predicted ogive. To determine the potential significance that maturity threshold has on estimates of maturity for yellowfin tuna, the logistic generalized linear models were run with maturity status (i.e., mature/immature) as a function of the maturity threshold (i.e., physiological/functional/spawning) and either fractional age or CFL as predictors. Specifically, for both fractional age and CFL, we fit a full model (maturity threshold, fractional age or CFL, and their interaction as predictors), a reduced model (the full model with no interaction), and a null model (only fractional age or CFL as predictors) following similar methodology of McBride et al. (2013) and as outlined in McBride (2016).[2]

To determine if the maturity threshold criteria should be considered when evaluating maturity for yellowfin tuna, Akaike's Information Criterion (AIC) and the associated ΔAIC (Akaike, 1973) were used to identify which model had the most relative support given the number of

[2] McBride, R.S., 2016. Maturity schedules: Matching data with models. RPubs by Rstudio. Available from [website; accessed 1 April 2022).

model parameters (K) among the three candidate models. Models with a ΔAIC of 2 or less were considered to have similar support (Burnham and Anderson, 2002). The Akaike weight (AIC wt.) was also calculated for each model and served as the weight of evidence given by each model among the suite of candidate models (Akaike, 1978; Burnham and Anderson, 2002).

Following the above model criteria, the logistic generalized linear models were run where seasonality (peak spawning months: May to August and non-peak spawning months: September to April) replaced the maturity threshold as a predictor of CFL. These models were compared using AIC analysis to determine if it was appropriate to combine all capture months to obtain one estimate of maturity.

2.6. Spawning interval

The spawning fraction (SF), or the proportion of functionally mature females that have spawned within 24 h, was estimated in each capture month using two methods: 1) the POF method (Hunter and Macewicz, 1985; Brown-Peterson et al., 2019), and 2) using all spawning markers in the ovary (i.e., including oocytes undergoing OM in addition to the presence of POF following Porch et al. (2015). The spawning interval (SI, i.e., number of days) between consecutive spawns was calculated as the reciprocal of the SF (Schaefer, 1998; Brown-Peterson et al., 2019). Spawning interval was also estimated by length and calendar age using the POF method when the number of functionally mature females was ≥ 30. The proportion of functionally mature females included females assigned to the developing (V1/V2), spawning capable, actively spawning, regressing, and regenerating phases to estimate the minimum SF of the entire yellowfin tuna spawning population (Lowerre-Barbieri et al., 2011; Porch et al., 2015). When calculating SI using all spawning markers, it was necessary to divide each estimated SI by an adjustment factor of 0.71 to account for the approximate 34-hour time frame in which both oocytes in OM and POFs are visible in the ovary of yellowfin tuna (per Itano, 2000). The minimum percentage of daily spawners in the entire yellowfin tuna population was calculated in each month as the percentage of functionally mature females with ovaries containing POFs and oocytes undergoing OM simultaneously.

To determine how often a spawning capable fish can spawn, SF and SI were calculated using the POF method when the proportion of mature females included only those that were classified as spawning (i.e. those assigned to the spawning capable phase or actively spawning subphase; (Brown-Peterson et al., 2019). To estimate, on an individual fish basis, what percentage of yellowfin tuna in the actively spawning subphase were spawning daily, the percentage of daily spawners was calculated in each month as the percentage of ovaries containing both POF and oocytes undergoing OM.

2.7. Fecundity

Batch fecundity estimates (BFE) were determined for females histologically verified to be in the actively spawning sub-phase with oocytes undergoing OM (Schaefer, 2001; Zudaire et al., 2013; Schaefer and Fuller, 2022). The only fish meeting these criteria were captured from May to June of 2011–2012 and 2014–2015. If the ovary had hydrated oocytes and POFs estimated to be < 6 h old, the sample was not used for BFE because the oocyte counts could be underestimated since some of the batch may have already been released (Hunter et al., 1985).

Estimates of batch fecundity were determined using either a gravimetric or a volumetric method depending on the data provider. All samples of yellowfin tuna landed by commercial PLL ($n = 16$) had BFE calculated using the gravimetric method (Hunter et al., 1985). Three NBF-fixed subsamples (~0.075 g each) were taken from each ovary, weighed, and covered with 33 % glycerin for at least 48 h. Schaefer (1998) determined that oocytes in the germinal vesicle migration (GVM) and hydrated stages were distributed randomly within yellowfin tuna ovaries, and therefore the three locations subsampled for BFE were considered equivalent. The BFE was calculated following the equation from Hunter et al. (1985).

$$\mathrm{BFE} = nGW/w \tag{4}$$

where n = the number of oocytes in OM from all three subsamples; GW = the whole ovary weight (g); and w = total weight (g) of all three gonad subsamples.

Estimates of batch fecundity for ovaries from yellowfin tuna landed recreationally by RR ($n = 8$) were all calculated using the volumetric method (Bagenal and Braum, 1971). A portion of fresh ovarian tissue (1–4 g) was weighed (nearest 0.01 g) and placed in Gilson's solution for a minimum of 3 months to separate the oocytes from ovarian tissue. Oocyte samples from fish histologically confirmed to be in the actively spawning sub-phase were rinsed overnight with running tap water to remove the Gilson's solution. All oocytes were then suspended in 50–200 ml of water and gently stirred until homogeneously mixed. Oocyte size frequency distributions were used to determine that any oocytes > 500 μm were undergoing OM (Franks et al., 2015). Therefore, all oocytes > 500 μm were counted under a dissecting microscope from six 1-ml subsamples with replacement, and the mean of these counts was used to calculate BFE following the equation:

$$\mathrm{BFE} = \mathrm{n} * (\mathrm{V_T}/\mathrm{V_S}) * (\mathrm{GW_T}/\mathrm{GW_S}). \tag{5}$$

where n = number of oocytes counted;

V_T = volume of water used to suspend the entire sample;

V_S = volume of water used for actual oocyte counts; GW_T = weight of the entire ovary; and GW_S = weight of the subsample of ovarian tissue taken for fecundity analysis.

A relative batch fecundity estimate (RBFE, mean number of oocytes per gram of ovary-free body weight) was calculated for each fish following Hunter and Goldberg (1980) as:

$$\mathrm{RBFE} = BFE/(W - GW). \tag{6}$$

Individual BFE and RBFE as a function of female CFL were modeled using a power function and a simple linear regression with AIC analysis was used to explore appropriate fish size relationships. Due to low sample size, BFE and RBFE as a function of female calendar age were not modeled.

3. Results

3.1. Biological sample collection

Overall, yellowfin tuna were collected primarily from May to August (59 %), likely correlated with the timing of peak recreational fishing in the northcentral GOM. Relatively few samples were collected throughout 2000–2009, and no specimens were obtained in 2001 and 2010; sample collection increased beginning in 2011. A total of 1135 ovaries, 776 testes, and 1104 otoliths were sampled from yellowfin tuna landed in the northcentral GOM (Suppl. Table 1), with a total of 1856 gonads sampled sent for histological processing. Whole fish weights were only available for yellowfin tuna landed recreationally ($n = 857$).

The size distribution of females and males ranged from 480 to 1750 and 605–1765 mm CFL, respectively, and represented a relatively normal distribution (Suppl. Fig. 1A). Due to the minimum size limit of 686 mm CFL set for the commercial and recreational sectors, few fish this size or smaller were observed ($n = 6$). Fish captured by RR ranged from 480 to 1765 mm CFL, while individuals caught with PLL were primarily ≥ 1200 mm CFL (Suppl. Fig. 1A). In July and August (the latter portion of the peak spawning season), yellowfin tuna were captured by RR only. Yellowfin tuna calendar ages ranged from 1 to 17 years old, with a majority of the calendar ages ≤ 4 years for both sexes (Suppl. Fig. 1B). Fish captured by RR ranged from 1 to 13 years, while individuals caught with PLL ranged from 3 to 17 years.

3.2. Spawning seasonality

Based on elevated GSI values, yellowfin tuna in the northcentral GOM have a May through August peak spawning season. For both mature males (n = 637) and females (n = 739), mean GSI increased from January to a peak in May (males 0.57 %; females 1.52 %; Fig. 3). For females, a relatively steep decline was observed in July (0.66 %) followed by a marginal increase in August (0.82 %). Males followed a similar trend but the decline in July was less pronounced (0.37 %). Both sexes saw a decline in mean GSI values from August through December.

December was the only month when females showing gonadal recrudescence were not captured (i.e., those in the early developing, developing, spawning capable and actively spawning phases), whereas the highest percentage of spawning females (spawning capable and actively spawning phases) were found from May through August (Table 2). A total of 1110 females were assigned to a reproductive phase based on histological observation of the ovary. A total of 230 females were assigned to the immature reproductive phase (Fig. 4A), ranged from 480 to 1384 mm CFL (mean; 940 ± 8.39 mm CFL, Suppl. Fig. 2), and were not included in percent frequency analysis by month; no other fish were excluded from frequency analysis (i.e. developing virgins were included). When the early developing sub-phase (Fig. 4B) and developing phase (Fig. 4C) were combined, April had the highest percentage of developing fish relative to all months (52 %). Females with ovaries in the early developing-developing phase were first observed at 686 mm CFL (Suppl. Fig. 2).

The highest percentages of ovaries in the spawning capable phase (Fig. 4D) were observed from June to August. Ovaries in the actively spawning subphase (Fig. 4E; F) were observed with the highest percent in May (45 %). A majority of the spawning females ≥ 1300 mm CFL were observed earlier in the peak reproductive season (61 % in May and 68 % in June), while spawning females ≤ 1300 mm CFL were identified primarily in July (63 %) and August (73 %).

Relatively few females in the regressing reproductive phase (Fig. 4G) were observed overall with the highest percentage observed in September (7 %). The highest percentages of regenerating females (Fig. 4H) were seen primarily around the start and end of the reproductive season in the northcentral GOM. Overall, females < 800 mm CFL were not observed in the regenerating phase (Suppl. Fig. 2).

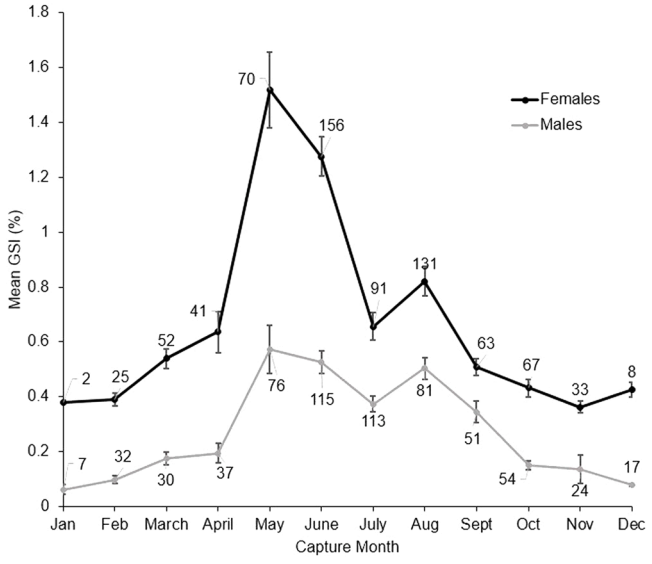

Fig. 3. Mean (± SE) monthly gonadosomatic index (GSI %) for female (n = 739) and male (n = 637) yellowfin tuna captured from 2000 to 2017 in the northcentral Gulf of Mexico. Immature individuals and those not histologically classified are not included. Monthly sample sizes included above (female) or below (male) the mean GSI value.

Table 2
Monthly percentages of mature female yellowfin tuna histologically determined to be in each reproductive phase (excluding immatures) during 2000–2017 rounded to the nearest whole number. Terminology follows Brown-Peterson et al. (2011). n-number of fish in each month; EDEV-early developing; DEV-developing; SC-spawning capable; AS-actively spawning; RGS-regressing; RGN-regenerating. Dashed lines (–) represent 0 % observed.

Month	n	EDEV	DEV	SC	AS	RGS	RGN
Jan.	3	67	–	–	–	–	33
Feb.	37	22	–	–	–	3	76
March	65	37	3	3	3	5	49
April	48	27	25	13	2	–	33
May	83	20	13	13	45	–	8
June	200	16	11	35	33	2	4
July	99	30	10	30	13	4	12
Aug.	159	20	9	36	21	6	8
Sept.	70	9	–	10	9	7	66
Oct.	73	3	1	3	3	3	88
Nov.	33	–	–	3	–	6	91
Dec.	8	–	–	–	–	–	100
Total	878	19	8	21	18	4	30

Spawning capable males were found during all months and ranged in size from 605 to 1765 mm CFL (mean 1203 ± 8.09 mm CFL), although only 11 % of testes were staged as spawning capable in December. The amount of spermatogenesis in spawning capable males varied monthly as observed by GE subphases (Fig. 5). The percentage of spawning capable males in the early-GE sub-phase, indicating the beginning of active spermatogenesis throughout the testis, was highest in January (33 %) and February (23 %). The mid-GE subphase was observed most frequently in all months except February, and September to December. In contrast, the percentage of testis in the late-GE sub-phase, indicating cessation of spermatogenesis, was highest from September (70 %) through December (100 %). Overall, the highest percentages of spawning capable males (≥ 80 %) corresponded with peak GSI values from May through September (Fig. 3).

3.3. Estimates of maturity

Females assigned to the immature reproductive phase (Fig. 4A) ranged from 480 to 1384 mm CFL (940 ± 8.39 mm CFL, Suppl. Fig. 2) but were less commonly identified in fish > 1100 mm CFL, and were found during all months of the year (Suppl. Table 2). There was a clear shift to a larger size at maturity when yellowfin tuna maturity was defined by V1 and V3 oocyte progression compared to CA oocytes alone (Table 3, Fig. 6A). Under the physiological maturity threshold, L_{50} and L_{95} were estimated at 1002 ± 7.18 and 1184 ± 11.75 mm CFL, respectively (Suppl. Fig. 3A; Table 3). Under the functional maturity threshold, L_{50} and L_{95} increased to 1071 ± 4.89 and 1200 ± 9.52 mm CFL, respectively (Suppl. Fig. 3B). Under the spawning maturity threshold, L_{50} and L_{95} increased to 1091 ± 4.80 and 1222 ± 9.71 mm CFL, respectively (Suppl. Fig. 3C).

The logistic generalized linear model that best explained the data was the full model (ΔAIC=0, AIC wt. = 1.00), which accounts for the maturity threshold and interactions. The reduced and null models had ΔAICs > 2 and hence were not supported (Table 4). This suggests that the maturity threshold should be considered as a predictor when estimating maturity. The upper and lower 95 % confidence intervals (CIs) among L_{50} estimates did not overlap under any maturity threshold (Table 3), indicating a significant increase in L_{50} estimates with increasing oocyte development, especially between physiological and functional maturity which had the largest degree of separation. Additionally, upper and lower 95 % CIs among L_{95} estimates did not overlap between physiological and functional maturity.

Female fractional age at maturity did not differ as much under varying thresholds as length at maturity (Table 3). Under the physiological maturity threshold, A_{50} and A_{95} were estimated at 1.85 ± 0.08

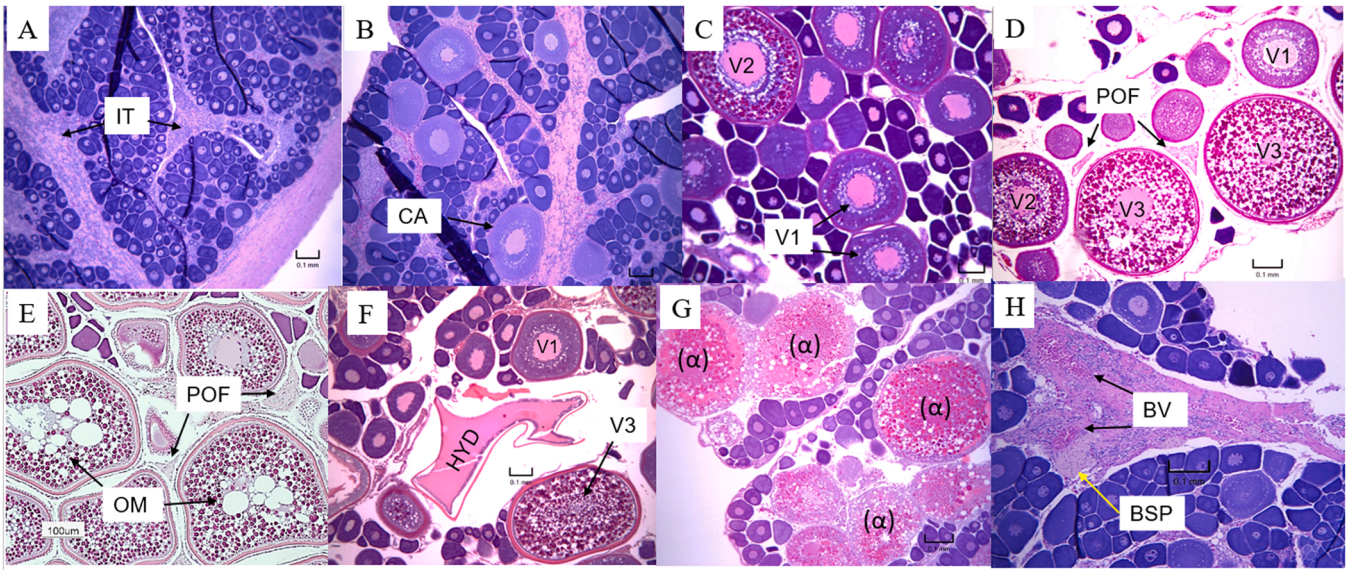

Fig. 4. Phases of yellowfin tuna oocyte development for individuals in the northcentral GOM. Scale bar in all images = 100 μm. A) Immature phase, with primary growth (PG) oocytes tightly packed and abundant interstitial tissue (IT) (black arrows). B) Early developing sub-phase, with cortical alveolar oocytes (CA) where the pink chorion is visible around the circumference of the oocyte (black arrow). C) Developing phase, with primary (V1) (black arrows) and secondary (V2) vitellogenic oocytes. D) Spawning capable phase, showing asynchronous oocyte development with primary (V1), secondary (V2) and tertiary (V3) vitellogenic oocytes, as well as the presence of 24 h post ovulatory follicles (POF, black arrows). E) Actively spawning sub-phase showing oocyte maturation (OM) in the lipid coalescence stage in conjunction with 24 h POFs, indicating daily spawning. F) Actively spawning sub-phase with hydrated oocyte (HYD) and vitellogenic oocytes (V1/V3). G) Regressing phase, with ≥ 50 % alpha (α) atresia of vitellogenic oocytes. H) Regenerating phase, with spacing among PG oocytes and indicators of prior spawning (IPS), including a thick muscle bundle with blood vessels (BV, black arrows) and brown-stained phagocytes (BSP, yellow arrow).

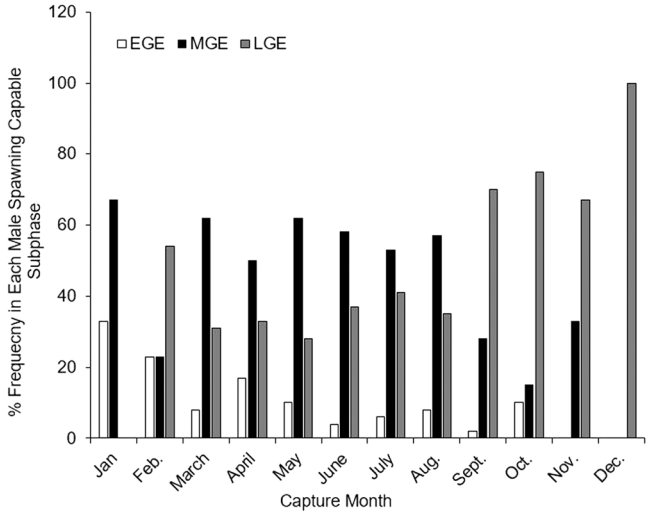

Fig. 5. The percent frequency of yellowfin tuna males observed in each spawning capable subphase in the northcentral Gulf of Mexico from 2000 to 2017. EGE- early germinal epithelium; n = 41, MGE- mid-germinal epithelium.

and 3.55 ± 0.15 years, respectively. Under the functional maturity threshold, A_{50} and A_{95} increased slightly to 2.24 ± 0.06 and 3.97 ± 0.15 years, respectively. Estimates of A_{50} and A_{95} under the spawning maturity threshold were 2.36 ± 0.06 and 4.13 ± 0.16, respectively, similar to functional maturity estimates. Overall, a greater fractional age at maturity was seen when yellowfin tuna maturity was defined when the ovary reached V1 and V3 (functional or spawning) compared to CA (physiological; Fig. 6B). However, results from AIC showed that the reduced model was the best fit to the data and likely has a higher predictive power (ΔAIC=0, AIC Wt. = 0.88), with the full and null models not supported (both ΔAIC >2) (Table 4). Despite the AIC results, the A_{50} under physiological maturity was 0.39 years earlier than spawning

Table 3
Summary of the length (L_{50}/L_{95}) and age (A_{50}/A_{95}) estimates for female yellowfin tuna in the northcentral GOM under each maturity threshold for all months (n = 1099); n- number of mature females in each maturity threshold; corresponding 95 % lower and upper confidence intervals are in italics.

Maturity Threshold	Mature (n) (L_{50}/A_{50})	L_{50} (mm CFL)	L_{95} (mm CFL)	A_{50} (year)	A_{95} (year)
Physiological (CA)	853/484	1002	1184	1.85	3.55
		988-1016	*1207-1161*	1.69-2.01	*3.27–3.83*
Functional (V1/V2)	753/423	1071	1200	2.24	3.97
		1061–1081	*1181–1219*	*2.12–2.36*	*3.67–4.27*
Spawning (V3)	714/403	1091	1222	2.36	4.13
		1082–1100	*1203–1241*	*2.24–2.48*	*4.01–4.25*

maturity (1.85 vs. 2.24 years) and the 95 % CIs do not overlap (Table 3); therefore a potential biological significance likely exists depending on which maturity threshold is used.

Under the functional maturity threshold, L_{50} and L_{95} were 1070 ± 6.10 and 1211 ± 13.27 mm CFL respectively during peak spawning months (n = 436; May to August). During non-peak spawning months (n = 317; September to April) L_{50} and L_{95} were 1077 ± 8.34 and 1182 ± 13.27, respectively (Suppl. Table 3). The AIC analysis showed that the null model, which only considered the effect of length, had the highest predictive power when comparing seasons (ΔAIC=0, AIC Wt. = 0.45), although all models had a ΔAIC < 2 (Suppl. Table 4). Therefore, seasonality does not appear to be a strong predictor when estimating maturity for yellowfin tuna in the northcentral GOM as the 95 % CI overlapped during each seasonality period.

We were unable to estimate male maturity at length due to a lack of immature males. Males in the immature phase (n = 13) ranged in size

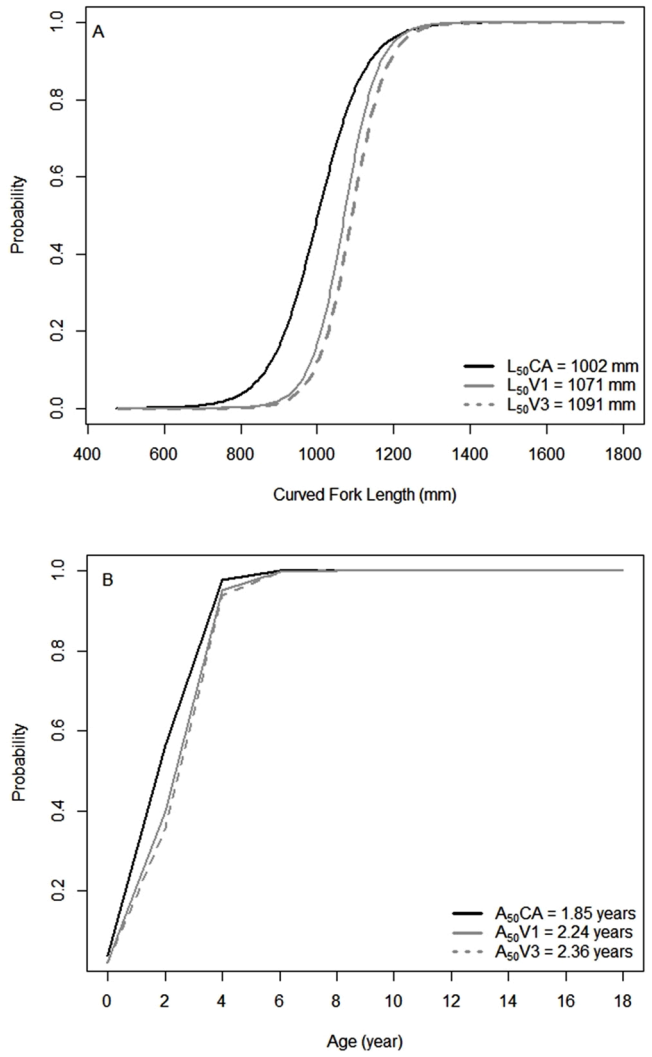

Fig. 6. Female yellowfin tuna maturity ogives calculated using varying maturity thresholds from individuals landed from 2000 to 2017 from the northcentral Gulf of Mexico for all capture months. A) The probability of mature females as a function of curved fork length (mm) (n = 1099). B) The probability of mature females as a function of fractional age (year) (n = 629). The estimates of 50 % maturity from the logistic regressions are located at the bottom right of each graph. CA= cortical alveolar oocytes [physiological maturity], V1 = primary or secondary vitellogenic oocytes [functional maturity], V3 = ovaries containing tertiary vitellogenic oocytes [spawning maturity].

Table 4
Summary of AIC analyses resulting from the series of logistic generalized linear models with maturity as a function of the maturity threshold (Threshold) and either length (L_{mat}) or age (A_{mat}) at 50 % maturity as predictors for female yellowfin tuna in the northcentral GOM. K-the number of parameters in each model, Full- a full model (maturity threshold, CFL or age, and their interaction (*) as predictors), Reduced- a reduced model (the full model with no interaction), and Null- a null model (only CFL or age as predictors).

	Model	K	AIC	ΔAIC	AIC Wt.
L_{mat}	Full: Maturity ~ CFL * Threshold	6	1676.40	0	1
	Reduced: Maturity ~ CFL + Threshold	4	1687.83	11.41	0
	Null: Maturity ~ CFL	2	1798.01	121.59	0
A_{mat}	Reduced: Maturity ~ Age + Threshold	4	1679.08	0	0.88
	Full: Maturity ~ Age * Threshold	6	1683.02	3.93	0.12
	Null: Maturity ~ Age	2	1713.50	34.41	0

between 679 and 950 mm CFL, and the smallest sexually mature male (i.e. the onset of spermatogenesis in the testes) was 740 mm CFL. The calendar age of the youngest mature male was 1 year, however spawning capable males (n = 328) were primarily age-2 (38 %) and age-3 (37 %).

3.4. Spawning interval

The overall SF during all capture months using the POF method was estimated at 0.31, with a SI of 3.28 days for the yellowfin tuna population (i.e., when all functionally mature females were considered) (Table 5). Across peak spawning months, the SF increased to 0.48 with a SI of 2.10 days. The highest SF of 0.52 was observed in both May (0.524) and August (0.522), with corresponding SIs of 1.91 and 1.92 days, respectively.

Spawning interval also changed with fish size and age. When all functionally mature females were considered across all months (n ≥ 30 per month) using the POF method, the SI decreased from 5.56 days for females 980–1080 mm CFL to a low of 2.28 days for females between 1280 and 1380 mm CFL, and then gradually increased as females became larger (3.64 days, 1480–1580 mm CFL). Sample size was too low (≤ 8 females) to accurately assess SI for females > 1580 mm CFL. Similarly, SI decreased from 8.57 days to 2.73 days as females increased in age from 2 to 5 years. There were too few females > 5 years (n ≤ 13 per age) to accurately assess SI for females estimated at 1 year and those estimated between 6 and 17 years.

When all spawning markers in the ovary were included (i.e. oocytes undergoing OM in addition to the presence of POFs), the overall SF during all capture months decreased marginally compared to the POF method (0.36), with a SI of 3.90 days (Table 5). The highest SF was observed in May, at 0.68 with an adjusted SI of 2.06 days. Across peak spawning months, SF increased to 0.57 with an adjusted SI of 2.49 days, but still less frequent than the estimated SI using the POF method (2.10 days; Table 5).

A minimum of 10.5 % of functionally mature females were daily spawners across all months (Table 5) with 84 of the 800 functionally mature female ovaries containing both POF and oocytes undergoing OM simultaneously. However, the overall minimum percentage of daily spawners increased to 17.30 % when considering only peak spawning months, with the greatest percentage (42.86 %) occurring in May (Table 5).

When only spawning capable and actively spawning females were considered rather than all mature fish, the overall SF during all capture months increased to 0.62 with a decreased SI of 1.60 days using the POF method. During peak spawning months, the overall SF increased slightly to 0.65 with a corresponding SI of 1.55 days. Additionally, the percentage of daily spawners was 21.59 % across all months when only considering the 389 spawning capable females. Across peak spawning months, the percentage of daily spawners increased to 23.56 %, with the greatest percentage (57.45 %) occurring in May.

3.5. Fecundity

The BFE of females landed by commercial PLL (n = 16) had a significantly higher mean length (1376 ± 15.38 mm CFL) compared to individuals landed by recreational RR (n = 8, 1261 ± 15.01 mm CFL; ANOVA: $F_{1,22}$ =20.74, P = 0.002). Overall, the relationship between BFE and CFL was best supported using a simple linear model when compared to a power function (ΔAIC 2.68), where,

$$BFE = 0.02(CFL) - 24.83 \quad (7)$$

($r^2 = 0.76$, $P < 0.001$) (Fig. 7A). Batch fecundity estimates ranged from 37,956–6.2 million eggs.

Individuals landed by commercial PPL were generally older with a broader calendar age range (n = 6; 3–9 years) compared to individuals

Table 5
Monthly yellowfin tuna spawning fraction (SF) and spawning interval (SI) in the northcentral Gulf of Mexico from 2000 to 2017 for all functionally mature females estimated two ways: The POF method [SF (POFS); SI (POFS)], and with spawning markers [SF (OM+POFS); SI (OM+POFS)]. % DS= percentage of daily spawners observed each month with ovaries containing both POF and OM. n = the number of functionally mature females, POF=postovulatory follicles, OM=oocytes undergoing final oocyte maturation, dashed lines (–) indicate no POFs or oocytes undergoing OM were observed for calculations. Peak spawning months (Peak) defined as May-August.

Month	Mature (n)	SF (POFS)	SI (POFS)	% DS	SF (OM+POFS)	SI (OM+POFS)
Jan.	3	–	–	–	–	–
Feb.	31	–	–	–	–	–
March	63	0.06	15.75	3.17	0.06	22.18
April	37	–	–	–	0.03	52.11
May	63	0.52	1.91	42.86	0.68	2.06
June	166	0.45	2.21	21.69	0.61	2.31
July	109	0.43	2.32	5.50	0.45	3.13
Aug.	136	0.52	1.92	9.56	0.55	2.55
Sept.	70	0.14	7.00	–	0.16	8.96
Oct.	71	0.04	23.67	–	0.04	33.33
Nov.	42	–	–	–	0.02	59.15
Dec.	9	0.11	9.00	–	0.11	12.68
Overall	800	0.31	3.28	10.5	0.36	3.90
Peak	474	0.48	2.10	17.30	0.57	2.49

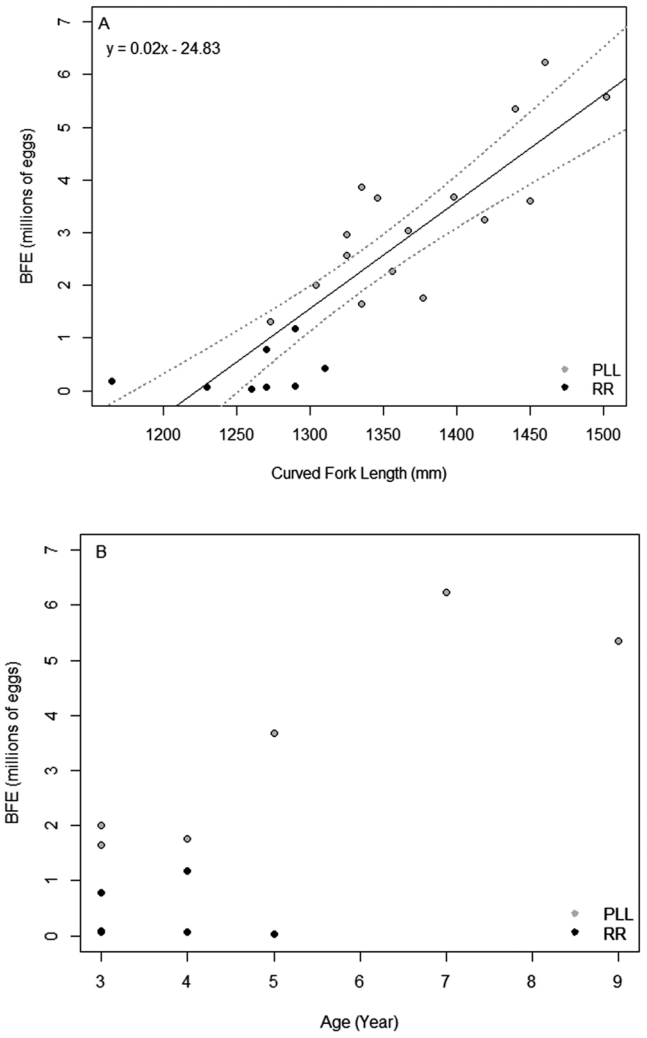

Fig. 7. Batch fecundity estimates (BFE, millions of eggs) of yellowfin tuna captured in the northcentral Gulf of Mexico. Fish separated by capture method; PLL (n = 16) = pelagic longline (gray circles), RR (n = 8) = rod and reel (black circles). A) BFE as a function of curved fork length (mm) represented as a simple linear model for females ranging in size from 1165 to 1502 mm CFL (n = 24; P < 0.001). The gray dashed lines represent the 95 % confidence limits. (B) BFE as a function of age in years (n = 12).

landed by recreational RR (n = 6; 3–5 years). Older females generally had higher BFE; the two oldest females (ages 7 and 9), had the highest BFE of 6.2 and 5.4 million eggs per batch, but individuals caught on PLL had larger BFE regardless of age (Fig. 7B), possibly related to different techniques in estimating BFE between the two capture methods.

The RBFE ranged from 1 to 109 with a mean of 47.25 ± 6.59 oocytes per gram of body weight. The relationship between RBFE and CFL was also best described as a simple linear model compared to a power function (ΔAIC 3.98), where

$$RBFE = 0.33(CFL) - 398.54 \quad (9)$$

(r^2 =0.65; P < 0.001) (Suppl. Fig. 4). The two oldest females had the highest corresponding RBFE of 109 (age-7) and 97 (age-9) oocytes per gram of body weight.

4. Discussion

4.1. Spawning seasonality

Based on both the trend of mean monthly GSI values and the monthly percentages of spawning capable and actively spawning females throughout the year, peak spawning for yellowfin tuna in the north-central GOM was observed from May to August, similar to what has been documented in previous studies in the western north Atlantic (Arocha et al., 2001; ICCAT, 2012). The highest female mean GSI value in our study (May; 1.52 %) was lower than previously reported mean GSI values of other yellowfin tuna studies during the spawning season. In the eastern Atlantic Ocean, female mean GSI values during the peak spawning season (November to April) ranged from 2.08 % to 2.22 % (Diaha et al., 2016). For females in the Indian Ocean, mean monthly GSI values were generally over 2 % for fish > 1000 mm SFL during peak spawning months (Zudaire et al., 2013). In our study, there was a clear reduction in mean monthly GSI in July for both sexes before a marginal increase again in August. This second rise in mean monthly GSI observed later in the spawning season was not reported for yellowfin tuna in the eastern and western Atlantic. However, the dip in GSI corresponds to both a lower percentage of actively spawning females as well as a higher percentage of smaller spawning capable and actively spawning females ≤ 1300 mm CFL prevalent in the latter portion of the peak spawning season (July, 63 %; August, 73 %). It is possible that differences in catchability during sampling, such as gear selectivity and general catch locations, may have contributed to these observations. For instance, in July and August, yellowfin tuna were captured by RR only, while in May and June individuals were captured by both PLL and RR.

Seasonal trends of yellowfin tuna reproduction in the northcentral GOM were best understood by staging gonads through histological techniques, the preferred method for classifying reproductive information of tuna species (Schaefer and Fuller, 2022) due to its increased precision over macroscopic gonad staging (West, 1990). While this region is a known spawning ground for yellowfin tuna, immature fish were also identified in all 12 months, suggesting that both the spawning and non-spawning population inhabit the area. In our study, the mean size of actively spawning females (1256 ± 10.06 mm SFL) was slightly smaller than the size range observed by Arocha et al. (2001) in the GOM (1300–1500 mm SFL) and the range observed by Zudiare et al. (2013) in the Indian Ocean (1280–1380 mm SFL). The time of spawning cessation for females in the northcentral GOM was not easily identified due to the low number of females with regressing ovaries. The small percentage of ovaries in the regressing phase observed in February (2 %) and March (3 %) in the northcentral GOM may represent an early, aborted attempt to spawn early in the year when environmental factors were not favorable (i.e. sub-optimal sea surface temperature, low food availability). These females may potentially just be "skipping a batch" of oocytes and may successfully go on to spawn when and if conditions improve within the same season (Rideout and Tomkiewicz, 2011). A similar phenomenon was observed in GOM cobia *Rachycentron canadum,* a coastal pelagic species that also has a protracted spawning season (Brown-Peterson et al., 2001).

The occurrence of females with regenerating ovaries during peak spawning months was also observed in the Indian Ocean (Zudaire et al., 2013). While misclassification between immature and regenerating females was possible, IPS were observed in regenerating ovaries year-round, supporting accurate staging of mature but non-reproductive females in our study. Spawning markers were also visible in the ovaries year-round in reproductively inactive South Pacific albacore tuna *(Thunnus alalunga*; Farley et al., 2014). Given that yellowfin tuna have a protracted spawning season, it is possible that regenerating females spawned or will spawn outside of the peak season (Zudaire et al., 2013), particularly for smaller individuals. The trade off in energy between somatic growth and reproduction varies with fish size and can contribute to a shorter reproductive season for younger females (Claramunt et al., 2007; Zudaire et al., 2013).

Yellowfin tuna males were observed in the spawning capable phase throughout the year, which is similar to other pelagic species such as GOM cobia (Brown-Peterson et al., 2001) and Atlantic bluefin tuna (*Thunnus thynnus;* Abascal et al., 2004). In Atlantic bluefin tuna, sperm can be found in the vas deferens for long periods of time throughout the reproductive season even if spawning is not imminent (Abascal et al., 2004). Documenting the seasonal progression of spermatogenesis within the GE by assigning spawning capable subphases (i.e., early-GE, mid-GE, and late-GE) aided in determining the start, middle, and end of the male yellowfin tuna spawning season, respectively. However, seasonal analyses of the GE in other scombrids are lacking so comparisons could not be made with similar techniques.

4.2. Estimates of maturity

Physiological maturity, defined by initial appearance of CA oocytes in the ovary, is often defined as "very early maturation" (Brown-Peterson et al., 2011). While physiological maturity indicates that a female may spawn in the current reproductive season (Wright, 2007), this may not always be the case, lending uncertainty to using CA as an indication that the fish will spawn during the current season. In this study, some ovaries with CA development as the MAGS without IPS (i.e., developing virgins) were observed towards the end of the peak spawning season. This suggests those females, although physiologically mature, may not have contributed to the spawning population until the following year. We found that L_{50} was lowest under the physiological maturity threshold (1002/970 mm CFL/SFL) for female yellowfin tuna captured in all months. Length at 50 % physiological maturity from a previous yellowfin tuna investigation in the western Indian Ocean was lower than our estimates, with L_{50} estimated at 750 mm SFL (Zudaire et al., 2013). In the eastern Atlantic Ocean, however, the L_{50} of 992 mm SFL (Diaha et al., 2016) was just outside the range of our upper 95 % confidence interval of 984 mm (Table 6).

Females with the initial appearance of V1/V2 oocytes in the ovary (i.e., functionally mature) are generally closer to a spawning event than those females identified as physiologically mature at the time of capture (Lowerre-Barbieri et al., 2011), and are often assumed to spawn during the current season. For this reason, functional maturity is the recommended threshold used to estimate L_{50} in yellowfin tuna ICCAT assessments (ICCAT, 2019b). In our study, L_{50} was estimated at 1071/1036 CFL/SFL mm, lower than what was observed in the eastern Atlantic Ocean and the value used in ICCAT assessments (1151 mm SFL; Diaha et al., 2016, Table 6). In the Australian Fishing Zone of the north-western Coral Sea, functional L_{50} ranged from 1079 to 1200 mm SFL depending on gear type (handline vs. longline areas; McPherson, 1991), values that are also larger than our 95 % confidence interval of 1026–1056 mm SFL (Table 6).

Ovaries with V3 oocytes (i.e., spawning maturity) are in spawning condition and provide the least amount of uncertainty that the female will contribute to the spawning population in the current reproductive season (Schaefer and Fuller, 2019, 2022). The L_{50} for the yellowfin tuna spawning maturity threshold (V3) marginally increased to 1091/1055 mm CFL/SFL in the present study, although the 95 % CIs overlap those for functional maturity. This suggests that the progression from V1 to V3 oocyte development happens relatively quickly in the warm waters of the U.S. northcentral GOM. In the eastern Atlantic Ocean, L_{50} under the spawning maturity threshold had a broader gap compared to its estimation under a functional maturity threshold (1151 versus 1246 mm SFL; Diaha et al., 2016; Table 6). Yellowfin tuna in the eastern Pacific Ocean generally reached spawning maturity at a smaller size compared to any other geographic location, although multiple areas were included in this investigation (L_{50} =786 mm SFL; Schaefer and Fuller, 2022; Table 6).

For yellowfin tuna, it is crucial to explore maturity under a variety of different maturity thresholds with clearly defined methodology. Results from AIC further indicated that maturity threshold plays a potentially significant role when estimating size at maturity for yellowfin tuna. Based on previous and current studies, potential geographic differences

Table 6
Summary of female yellowfin tuna L_{50} maturity estimates using histological techniques throughout multiple regions and all months under each maturity threshold. Physiological (CA-cortical alveolar oocytes), Functional (V1/V2-primary or secondary vitellogenic oocytes), Spawning (V3-tertiary vitellogenic oocytes). The L_{50} estimate from the present study was converted from CFL to straight fork length (SFL) following Scida et al. (2001) in order to compare to other investigations. The corresponding 95 % lower and upper confidence intervals from the present study in SFL are in italics.

Study	Region	Maturity Threshold (mm SFL)		
		Physiological (CA)	Functional (V1/V2)	Spawning (V3)
Present Study	Northcentral GOM	970 *956–984*	1036 *1026–1056*	1055 *1046–1064*
Diaha et al. (2016)	Eastern Atlantic Ocean	992	1151	1246
Zudiare et al. (2013)	Western Indian Ocean	750		1020
McPherson (1991)	Eastern Australia (varying gear types)		1079–1200	
Schaefer and Fuller (2022)	Eastern Pacific Ocean (combined areas)			786

in maturity likely exist among female yellowfin tuna. Maturity estimates are known to vary both spatially and temporally among regions in South Pacific albacore tuna (Farley et al., 2014), another tropical tuna species. The observed spatial variations in yellowfin tuna may be attributed to regional differences in growth rates or a disproportionate number of mature vs. immature fish collected in a given area causing a bias depending on how sampling was conducted (Farley et al., 2014).

While we acknowledge that females with CA oocytes that are not repeat spawners (i.e. developing virgins) are still considered to be mature, we recommend that a functional maturity threshold be used when estimating maturity for stock assessment purposes. Stock assessments for other tropical tunas, including South Pacific albacore tuna and skipjack tuna (*Katsuwonas pelamis)*, recommend using the spawning maturity threshold as these investigations did not consider females to be reproductively active until the ovary produced V3 oocytes (Farley et al., 2014; Schaefer and Fuller, 2019), even though functional maturity is the method recommended for assessing yellowfin tuna by ICCAT (ICCAT, 2019b). We, along with Schaefer and Fuller (2019), advise against using a physiological maturity threshold for estimating maturity in tropical tuna stock assessments as these estimates could potentially underestimate L_{50} and A_{50}. However, our data indicate little difference in L_{50} between the functional and spawning maturity thresholds, suggesting either can be accurately used for northern GOM yellowfin tuna.

Fractional age at 50 % maturity for yellowfin tuna females ranged from 1.85 (physiological maturity) to 2.36 (spawning maturity) years. We recommend that maturity threshold also be considered when estimating age at maturity between physiological and spawning maturity for yellowfin tuna as the 95 % CIs did not overlap, indicating a potential biological significance. Consideration of differences between the functional and spawning maturity thresholds may not be necessary as the 95 % CIs overlapped and estimates in the present study were similar (2.24 vs 2.36 years). However, we recommend the functional maturity threshold be used for age at maturity to be consistent with length at maturity estimates, especially in regards to stock assessments. The 2019 ICCAT assessment modeled age at maturity as a function of length which was derived from Diaha et al. (2016) to reduce uncertainty regarding ageing methods (ICCAT, 2019b). In contrast, we recommend that fractional age at maturity should use ages derived directly from otoliths since annual ageing methods for yellowfin tuna in the GOM have been validated using bomb radiocarbon (^{14}C) techniques (Andrews et al., 2020). Additionally, length at age has been reported to be highly variable in yellowfin tuna (Shih et al., 2014; Pacicco et al., 2021), which would decrease the accuracy of age estimates based on length.

4.3. Spawning interval

Our estimates of SF and SI using the POF method varied depending on the designation used to classify a mature female (i.e., all mature females or only reproductive actively females). These differences in SI would be significant if using the TEP method to estimate spawning potential for stock assessment purposes, and therefore methodology must be clearly stated regarding how SI was determined. Yellowfin tuna ovaries containing both oocytes in OM and POFs simultaneously occurred in a minimum 10.5 % of functionally mature females across all months, indicating daily spawning of the population occurs in the northcentral GOM. However, when looking at the percentage of daily spawners of spawning capable and actively spawning females, this number increases to 21.59 % overall and 23.56 % during peak months. Daily spawning has also been reported for yellowfin tuna in the eastern Pacific (Schaefer, 1998; Schaefer and Fuller, 2022), and the western tropical Pacific Ocean (Itano, 2000).

Previous yellowfin tuna investigations reported SI estimates slightly more frequent than ours using the POF method for all functionally mature fish, although estimates were more similar when only reproductively active females were considered mature. In the western tropical Pacific Ocean, Itano (2000) reported an estimate of 1.19 days for spawning individuals and a longer SI of 1.99 for all functionally mature females, compared to our estimates of 1.6 and 3.28 days, respectively. In the eastern Pacific Ocean, an SI between 1.18 and 1.79 days was reported depending on reproductive phase classification (Schaefer and Fuller, 2022). In the Coral Sea, SI was estimated at 1.54 days when all functionally mature females were included (McPherson, 1991), a shorter SI than our estimate of 2.10 days during peak spawning months. Arocha et al. (2001) estimated SI in the GOM at 3.18 days, similar to our estimate of 3.28 days for all months, but used the OM method rather than the observation of POFs. Our estimates of SI for yellowfin tuna are slightly longer than mean SI estimates for other actively spawning tropical tuna species such as skipjack tuna (1.18 days; Schaefer and Fuller, 2019) and southern bluefin tuna, *Thunnus maccoyii* (1.10 days; Farley et al., 2015). A potential reason for differing SI estimates between our data and previous studies may be related to the age or length of fish analyzed; we found the lowest SI for females 1280–1380 mm CFL, and that SI decreases as female age increases up to age-5. We suggest that estimating SF and SI may be more appropriate when all spawning markers in the ovary are included (i.e., oocytes undergoing OM in addition to the presence of POFs) compared to the POF method alone, as discussed in Porch et al. (2015). Including all spawning markers for SI estimates eliminates potential spatial bias in capture that may occur when spawning or recently spawned fish may school together. Surprisingly, a marginal decrease in overall SF during all capture months using all spawning markers was observed in yellowfin tuna from this study, suggesting SI estimates based on POF only may be artificially inflated. While we recommend that future studies investigate both methods as larger differences may exist in other species, since all previous SI data for yellowfin tuna rely on the POF method we suggest that our POF-only data be used when including GOM data into estimates of yellowfin tuna reproductive potential.

4.4. Fecundity

Since our study used two different, although acceptable methods of estimating BFE (gravimetric and volumetric), we decided it was best not to report mean values, particularly since preservation of oocytes in Gilson's solution can result in lower batch fecundity estimates (Lowerre-Barbieri and Barbieri, 1993). However, our range of BFE (37, 956–6.2 million eggs per batch) falls in line with similar investigations for yellowfin tuna. In the eastern Pacific Ocean, mean BFE was reported at 2.3 million eggs per batch (Schaefer and Fuller, 2022), while Zudiare et al. (2013) reported a range of 0.32–6.91 million with a mean value of 3.1 million eggs per batch in the western Indian Ocean. In the western central Atlantic, Arocha et al. (2001) reported mean BFE to be 2.16 million but that was based on a small sample size ($n = 6$). In the eastern Atlantic, Diaha et al. (2016) reported a mean BFE of 2.91 million with a range of 0.78–7.56 million eggs per batch and noted high monthly variability. Our study shows that batch fecundity as a function of fish length (1165–1502 mm CFL) was statistically best described using a simple linear model. If our sample size of smaller actively spawning fish (<1300 mm CFL) was higher, the relationship between BFE and CFL would likely have been better represented using a power function. Our data show that fish < 1300 mm CFL generally have lower BFE compared to larger fish regardless of the estimation method used, indicating batch fecundity appears to increase faster in fish of a larger size and follows a nonlinear trend. In theory, the biological relationship between fecundity and fish size in tunas should best represent a nonlinear relationship (Schaefer, 1998; Schaefer and Fuller, 2022). Yellowfin tuna of greater size possess larger ovaries, thus hold more eggs, compared to smaller fish, in part due to their large abdominal cavity (Pecoraro et al., 2020). These larger females also had differing fatty acid profiles compared to smaller females, resulting in offspring having potentially a higher survival rate (Pecoraro et al., 2020).

The significant relationship between RBFE and CFL was unexpected since RBFE adjusts for fish size, especially since the linear equation

generated from our study was only available for a relatively small number of females ranging from 1165 to 1502 mm CFL. No significant relationship was observed between RBFE and length in yellowfin tuna in the Indian (Zudaire et al., 2013) or eastern Atlantic Oceans (Pecoraro et al., 2020), but a significant relationship between RBFE and weight in fish from the eastern Pacific Ocean was documented (Schaefer, 1998; Schaefer and Fuller, 2022). Although Schaefer (1998) suggested that, in general, larger size yellowfin tuna females do not appear to allocate relatively more energy than smaller females to batch fecundity, the relatively large r^2 value (0.65) we see for RBFE vs. CFL suggests this may not be true for GOM females.

A relatively small sample size ($n < 50$) may have limited our fecundity analysis (Hunter et al., 1985). Due to the short time period (a few hours) in which yellowfin tuna ovaries undergo oocyte maturation (Schaefer, 2001; Schaefer and Fuller, 2022), it is often challenging to obtain a sufficient number of fecundity samples. Samples obtained from yellowfin tuna landed commercially are likely the best opportunity to observe females in this state due to the long-range, overnight trips (Schaefer, 2001). Our fecundity analysis was also limited temporally, as samples were only collected in May and June of 2011–2012 and 2014–2015, during the peak of the spawning season. Thus, estimating annual fecundity based on the time of peak spawning may result in inflated estimates. In 2019, the ICCAT working group acknowledged the new fecundity data presented from yellowfin tuna captured in the northcentral GOM and recommended the estimate would be improved with a larger sample size and monthly samples during the spawning season (ICCAT, 2019a). Future reproductive studies should focus on obtaining the complete size range of actively spawning yellowfin tuna to better understand these relationships.

5. Conclusion

The northcentral GOM is home to lucrative yellowfin tuna commercial and recreational fishing industries, which makes them vulnerable to fishing pressure. Thoroughly understanding the reproductive biology of yellowfin tuna will aid in determining the level of exploitation the population can withstand while remaining sustainable (Morgan, 2008). In summary, we found that i) yellowfin tuna peak spawning in the northcentral GOM occurs from May to August, ii) the method used to estimate maturity likely has biological significance, with the early vitellogenic maturity threshold (V1/V2) acceptable for stock assessment purposes but spawning maturity (V3) recommended for the most conservative estimates of 50 % maturity, iii) yellowfin tuna females have the ability to spawn daily especially during peak spawning months, and iv) the relationship between fecundity and CFL was best described using a linear model, although a power function may be more appropriate when larger females are included in the analysis since fecundity likely increases faster in larger females. Data from this study in conjunction with the data from the eastern Atlantic should be used in future ICCAT stock assessments. Future collaborations between scientists from both the eastern and western Atlantic is imperative in continuing to standardize histological reproductive staging techniques and answering remaining uncertainties in yellowfin tuna reproductive biology, in particular those related to age- and length-specific fecundity.

CRediT authorship contribution statement

Ashley E. Pacicco: Investigation, Visualization, Data curation, Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Nancy J. Brown-Peterson:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing, Investigation, Visualization, Data curation, Funding acquisition. **Debra J. Murie:** Conceptualization, Formal analysis, Writing – review & editing. **Robert J. Allman:** Conceptualization, Writing – review & editing, Supervision. **Derke Snodgrass:** Conceptualization, Investigation, Writing – review & editing. **James S. Franks:** Conceptualization, Investigation, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106620.

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