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ARTICLE

Oogenesis and Fecundity Type of Gray Triggerfish in the Gulf of Mexico

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Abstract

The fecundity of Gray Triggerfish *Balistes capriscus* has been difficult to estimate, as few imminently spawning or recently spawned females have been detected. Our study focused on verifying the pattern of oogenesis and fecundity type in Gray Triggerfish. During 1999–2012, females ($n = 1{,}092$) were collected from the eastern Gulf of Mexico, and subsets of these fish were used to calculate condition indices and assess ovarian histology. The gonadosomatic index, hepatosomatic index, and Fulton's condition factor indicated that liver and somatic energy stores increased prior to spawning and were depleted throughout the spawning period, characteristic of a capital pattern of energy storage and allocation to reproduction. Typical of a capital breeding pattern, we also observed (1) a hiatus in oocyte size distribution and (2) group-synchronous oogenesis, which are both traits of a determinate fecundity type. However, evidence that fecundity was not set prior to spawning included the observation of "de novo" vitellogenesis during the spawning season; secondary oocytes increased in number and failed to increase in mean size over time. Thus, Gray Triggerfish exhibit an indeterminate fecundity type with mixed reproductive traits that may characterize species exhibiting female parental care in warmwater environments. Further, we estimated the secondary oocyte growth rate (37 μm/d) based upon the time lag of postovulatory follicle (POF) degeneration. Using oocyte growth rate and the proportion of females bearing POFs, the interspawning interval was estimated to range from 8 to 11 d, indicating that 8–11 batches/female could be produced during the estimated 86-d reproductive period. The hiatus in oocyte size distribution was used to define a minimum size (250 μm) from which to distinguish an advancing batch of secondary growth oocytes. Batch fecundity (BF) ranged from 0.34 to 1.99 million eggs and was significantly related to FL (mm): $BF = 8{,}703.69 \cdot FL - 1{,}776{,}483$ ($r^2 = 0.56$).

The Gray Triggerfish *Balistes capriscus* is an economically important species in recreational and commercial fisheries of the Gulf of Mexico (hereafter, Gulf). Like other Gulf species, measures of reproductive potential for Gray Triggerfish are needed to support assessments of stock status, and reproductive potential estimated from fecundity metrics is most accurate (Paulik 1973; Tomkiewicz et al. 2003; Lambert 2008; McBride et al. 2015). Unfortunately, particular fecundity

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methodologies have been applied to some species without validation, thus necessitating corrections (e.g., Arocha 2002; Gordo et al. 2008; Fitzhugh et al. 2012). An understanding of oogenesis allows for classification of a species' fecundity type and provides insight on spawning frequency (Murua and Saborido-Rey 2003; Witthames et al. 2009).

Although information on Gray Triggerfish reproduction exists in research reports, the pattern of oogenesis and fecundity type in this species have not been validated. In a 2005 Gulf stock assessment, the Gray Triggerfish was assumed to be an asynchronous indeterminate spawner that produces numerous batches (Ingram 2001; SEDAR 09 2006). Previous unpublished studies had difficulties in determining Gray Triggerfish fecundity and/or spawning frequency (Wilson et al. 1995; Hood and Johnson 1997; Ingram 2001; Moore 2001), primarily because females with advanced-stage oocytes (oocyte maturation [OM]) were very rare among the collected samples and because postovulatory follicles (POFs) were detected in few females (Ofori-Danson 1990; Wilson et al. 1995; Hood and Johnson 1997; Ingram 2001; Moore 2001). This has generated uncertainty and a broad range in estimates of spawning frequency.

Part of the difficulty in classifying reproductive traits and fecundity type may lie in the rather unique biology of the Gray Triggerfish. It is a nesting species with a haremic mating system wherein the males and females share short-term parental care (Simmons and Szedlmayer 2012). Considering this mating system, a better understanding of fecundity type for Gray Triggerfish may depend on determining the female reproductive energy strategy utilized from the income–capital breeding typology (Stearns 1992; Jönsson 1997; Jager et al. 2008; McBride et al. 2015). Capital breeders are commonly cold-water species that experience dynamic seasonality. Before the reproductive season begins, energy for reproduction is acquired and stored during periods when food may be abundant (Jager et al. 2008). In income breeders, a rapid transfer of energy to reproduction may occur when ecosystem productivity is high yet the timing of productivity is less predictable in time and space (Santos et al. 2010; McBride et al. 2015). It is also possible for species to exhibit mixed capital and income traits depending on the degree of available surplus energy and demands from activities such as migration and parental care (Jager et al. 2008; McBride et al. 2015). In several fish species, the accessory behaviors of parental care have been associated with high energy demands, which can affect other life history traits (Kuwamura 1997; Donelson et al. 2008; Jager et al. 2008). The objectives of the present study were to (1) verify fecundity type for Gray Triggerfish in the Gulf, (2) classify energy storage in light of the mating system, (3) calculate spawning frequency, and (4) postulate a method to estimate annual fecundity for this species.

METHODS

Sample collection and condition indices.—Hook-and-line sampling of Gray Triggerfish was conducted to observe a time series of reproductive development during May–July 2012 in Gulf waters offshore of Panama City, Florida. All captured specimens were retained, measured for FL to the nearest millimeter, and weighed to the nearest gram. Dorsal spines were extracted for age estimation; livers were excised and weighed; gonads were removed, macroscopically assessed for sex and reproductive state, and weighed; and ovaries were fixed in 10% neutral buffered formalin (<24 h on ice) for further processing in the laboratory (see below). Length, weight, macroscopic sex and reproductive state, and (in some cases) gonad weight, liver weight, and ovary tissue samples were also measured or obtained from specimens collected by trapping, spearing, or hook and line in various fishery-independent and fishery-dependent surveys within the northern Gulf (1999–2012; Table 1). The gonadosomatic index (GSI), hepatosomatic index (HSI), and Fulton's condition factor (*K*; Ricker 1975) based upon weight (g) and FL (cm) were used to examine the relationship between energy storage and reproduction:

TABLE 1. Number of samples obtained for each body index measure (Fulton's condition factor [*K*], gonadosomatic index [GSI], and hepatosomatic index [HSI]) calculated for female Gray Triggerfish from various fisheries-independent and fisheries-dependent sources in the eastern Gulf of Mexico, 1999–2012. Gear types were hook and line (HL; includes bandit reel), trap (TR), and spear (SP).

Source	Sampling gear	*K*	GSI	HSI
Fisheries independent	HL + TR	420	552	204
Fisheries dependent	HL + SP	672	77	34
Total		1,092	629	238

$$\mathrm{GSI} = \left(\frac{\text{Gonad weight}}{\text{Total weight} - \text{Gonad weight}}\right) \times 100,$$

$$\mathrm{HSI} = \left(\frac{\text{Liver weight}}{\text{Total weight} - \text{Liver weight}}\right) \times 100,$$

and

$$K = 100 \times \left(\frac{\text{Total weight}}{\mathrm{FL}^3}\right).$$

Oocyte staging and measurements.—Oocyte stage and oocyte diameter in Gray Triggerfish were used to categorize fecundity type as determinate or indeterminate. The key criteria used to test for determinate fecundity followed Hunter et al. (1992) and Murua and Saborido-Rey (2003). The criteria include (1) a hiatus in the size distribution of developing oocytes, (2) an increase in secondary oocyte diameter through the spawning season, (3) a decrease in the number of secondary growth oocytes through the spawning season, and (4) a

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secondary oocyte growth rate (G) that does not allow for "de novo" vitellogenesis within one spawning period.

Oocyte stage and size data were obtained by examining an approximately 150-mg subsample removed from the posterior region of all available ovaries following the method of Harris et al. (2002). Each subsample was weighed, and the oocytes were disassociated with forceps and plated as a whole mount in a petri dish (150-mm diameter) to be imaged with an EPSON V750 scanner. The top or cover of the scanner rested on the petri dish, parallel with the bottom of the scanner. The scanner's software (EPSON Scan) was set to scan "positive film" at 2,400 dpi in "professional" mode, which allowed for a transmitted light image with high resolution.

The image was then uploaded into ObjectJ, a plug-in for ImageJ (version 1.47 s), to conduct image analysis. Primary growth oocytes were difficult to count and measure in the scans because of their small size (<100 μm) and low degree of clarity (Figure 1). Secondary growth oocytes (including cortical alveolar oocytes and vitellogenic oocytes) from 2012

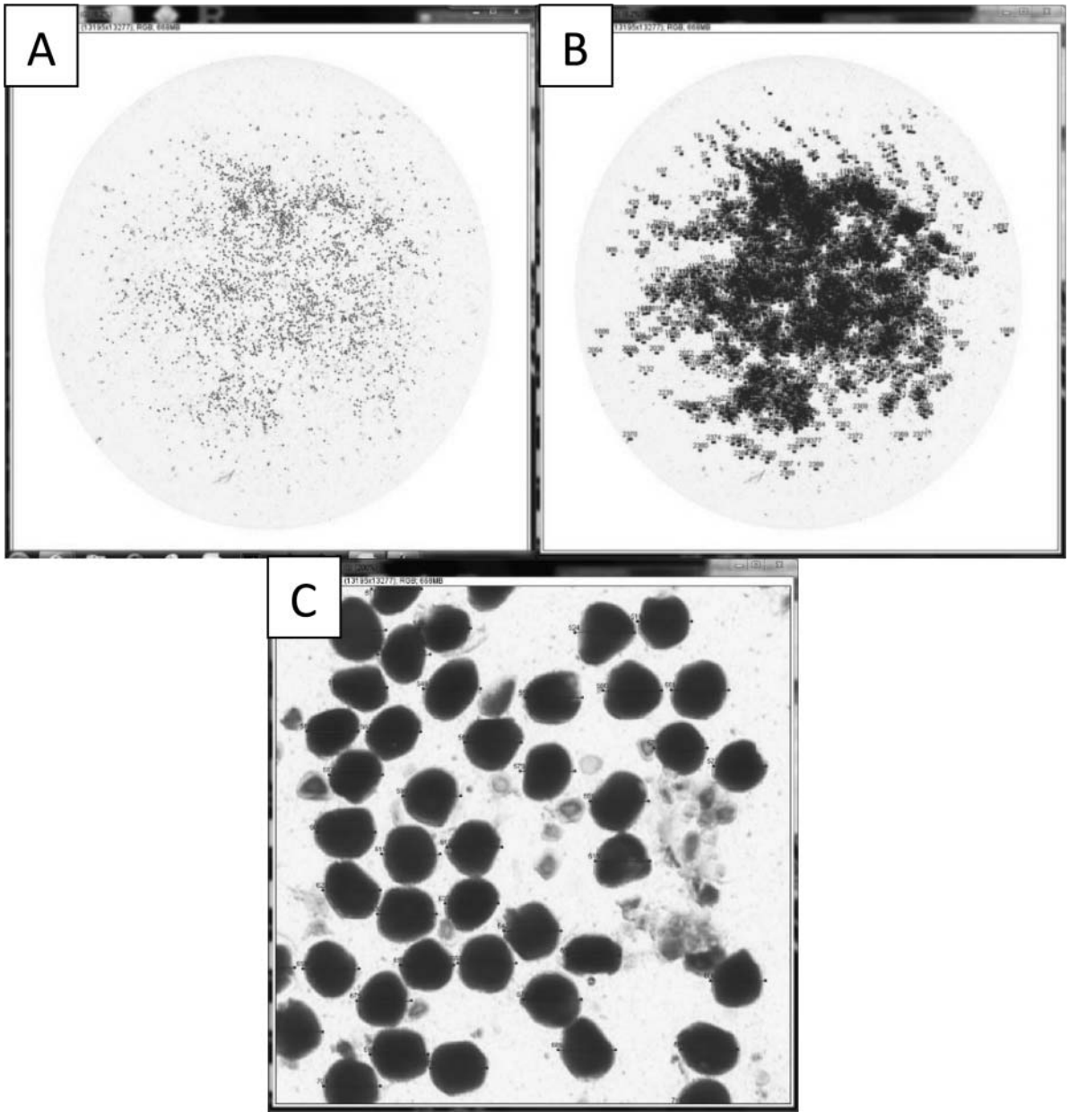


FIGURE 1. Tissue subsamples (~150 mg) were extracted from Gray Triggerfish ovaries, and disassociated oocytes were scanned in a 150-mm Petri dish. Screen captures are shown for **(A)** the lowest scan magnification, **(B)** ObjectJ delineation of secondary growth oocytes, and **(C)** the highest scan magnification at 2,400-dpi resolution. Secondary growth oocytes appear dark against the background using transmitted light.

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samples were automatically counted and measured by using a macro within ObjectJ (Figure 1; //simon.bio.uva.nl/objectj/7a-Examples.html). Counts of secondary oocytes were used to estimate batch fecundity (BF) based upon an oocyte size criterion (see Results) and were expressed as somatic relative fecundity (eggs/g of ovary-free body weight; Kjesbu et al. 1998) and oocyte density (secondary oocyte count/g of ovary weight) for comparison with other studies. Oocyte size frequency histograms were used to assess a hiatus in oocyte development, whereas oocyte enumeration and diameter were regressed against time within the spawning season to resolve determinate fecundity criteria 2 and 3. Three randomly selected females were chosen from each month (May–July; i.e., a total of 9 females) to represent the oocyte size distribution. All regressions were performed using R version 2.13.1.

Postovulatory follicle measurements.—Ovary samples from all years were processed histologically with hematoxylin and eosin stain. Using an ocular microscope camera (MiniVid; 5 MP), photos were taken of each histology slide in which POFs were present. Five random images were chosen from all possible nonrepetitive images of each histology slide with oocytes filling the frame. Each oocyte that represented the leading stage of oogenesis (cortical alveolar or vitellogenic oocytes) and that was sectioned through the germinal vesicle was measured for diameter (Foucher and Beamish 1980). The area of every POF present within the five random images was measured and plotted as a predictor of leading oocyte stage diameter.

Oocyte growth and interspawning interval.—Oocyte growth was determined using methods similar to those of Ganias et al. (2011). The POF area was converted to a percentage of POF duration by using known POF durations from oceanic species with a temperature regime similar to that of Gray Triggerfish (Jackson et al. 2006). Simple linear regression was used to investigate changes in oocyte size, number, and growth over time.

The G of secondary oocytes was calculated using the difference in oocyte size (O_i) after some period of growth (time lag; t_i) and the average size of oocytes from the spawning batch at the beginning of spawning batch development for the whole population (β_o; Ganias et al. 2011). The average oocyte sizes at the beginning of the spawning cycle were observed in fish with the most recent POFs. Because POFs are resorbed relatively quickly in Gulf warmwater fishes, the t_i could be estimated from the percent change in POF area over an expected 24-h duration ($\leq$24 h in 24–28.5°C water; Jackson et al. 2006):

$$G = \frac{O_i - \beta_o}{t_i}.$$

Spawning frequency was calculated using both the interspawning interval (ISI; Ganias et al. 2011) and POF (Parker 1980) methods. The ISI method assumes that the growth of secondary oocytes is group synchronous and that G is constant; thus, the ISI is the difference between the minimum (O_b) and maximum (O_e) observed sizes of secondary oocytes divided by G:

$$\text{ISI} = \frac{O_e - O_b}{G}.$$

The POF method is based upon the proportion of females bearing POFs relative to the total number of mature females sampled during the spawning season. Maturity was designated based upon the presence of vitellogenic oocytes. Because we estimate that POF duration is 24 h, the inverse of the proportion of females bearing POFs yields the expected spawning interval in days (Parker 1980). Due to the often-opportunistic collection of samples during surveys, the sample sizes varied from year to year and were ad hoc with respect to the timing of reproductive development and spawning. Samples were grouped across years to increase the sample size for the POF method. This grouping necessarily assumes that there is no difference in spawning intensity—and, hence, prevalence of POFs—among years.

RESULTS

Field Sampling and Condition Indices

In total, 1,092 female Gray Triggerfish were collected from various fishery-independent and fishery-dependent sources in the northern Gulf during 1999–2012, and 85% of these females were captured from depths of 10–50 m (Table 1). Of the collected females, 629 had gonad weight data for use in calculating GSI; 238 had liver weight data for use in HSI estimation; and 531 were histologically examined for POFs. The HSI peaked in May, 1 month before peak spawning (peak GSI); decreased sharply from May to September; and then began to increase again (Figure 2). Seasonally, K from all 1,092 females decreased after June, consistent with the HSI and GSI evidence that energy stores increased during the spring, were highest at the onset of spawning, and were depleted throughout the spawning period (Figure 3).

Oocyte Size Analysis

Examination of oocyte size frequency distributions suggested a group-synchronous pattern of oocyte development, which is commonly associated with determinate fecundity (Figure 4). The individual oocyte size frequencies for seven of the nine randomly selected females were bimodally distributed, and four of those seven females showed a clear hiatus between the cortical alveolar stage and the vitellogenic oocyte stage. Females that exhibited a unimodal peak in oocyte distribution had smaller oocytes on average, with early vitellogenic oocytes that we expect would have disassociated in size from

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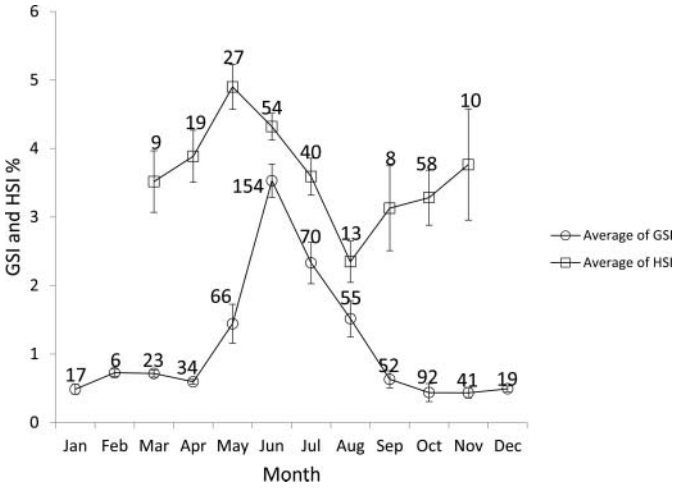


FIGURE 2. Mean (±SE) gonadosomatic index (GSI) and hepatosomatic index (HSI) of female Gray Triggerfish collected from the northern Gulf of Mexico, 1999–2012. Sample sizes are indicated for each month.

the primary growth and cortical alveolar stages over time. However, linear regressions of secondary oocyte diameter ($r^2 = 0.05$, $P = 0.148$; Figure 5) or the number of secondary growth oocytes ($r^2 = 0.01$, $P = 0.491$; Figure 6) versus time during the spawning season were not significant. Secondary growth oocytes did not increase in diameter and did not decrease in number as the spawning season progressed; therefore, contrary to our results on oocyte size frequency distributions, this finding did not support a determinate fecundity type for Gray Triggerfish.

Oocyte Growth and Interspawning Interval

Despite more intensive sampling during the spawning season in some years (e.g., 2012), POFs were rarely found—occurring in only 31 of the 531 females that were sampled for histology. Over 50% of those 31 recently spawned females possessed POFs with a collapsed lumen and thus a smaller POF surface area and a skewed size distribution. However, data on POF surface area for seven recently spawned females collected in 2001 were tested and fulfilled the linear regression assumptions for normality among means (Shapiro–Wilk normality test: $W = 0.8957$, $P = 0.306$). A Shapiro–Wilk normality test also indicated that the diameter of secondary growth oocytes was normally distributed ($W = 0.9288$, $P = 0.541$). Growth of secondary oocytes exhibited an inverse linear trend with POFs: as secondary oocytes grew larger, the surface area of POFs diminished ($r^2 = 0.63$, $P = 0.034$; Figure 7).

By estimating the G of secondary growth oocytes, we calculated the ISI to be 11 d. This computation used the POF duration from oceanic fish species that reside in similar water temperatures (Jackson et al. 2006) and used the POF "clock" to estimate t_i. We found that the maximum POF surface area for a Gray Triggerfish was 12 μm^2. Given that a POF shrinks as it ages and may last about 24 h (1 d), we observed a 74% decrease in POF surface area during an oocyte size regression series from 2001 (Figure 7). Thus, the proportional decrease in POF surface area over time served as the denominator to standardize to 24 h the corresponding growth in secondary oocytes (estimated $G = 37$ μm/d). The resulting ISI of 11 d was rapid enough to allow for de novo vitellogenesis to occur multiple times during the spawning season, which would indicate an indeterminate fecundity type. Therefore, three of the four hypothesis tests supported indeterminate fecundity in Gray Triggerfish.

Using the POF method, we calculated an average ISI of 7.6 d. Females were observed on 43 sampling dates between May 26 and August 19 during 1999–2012. The spawning interval was calculated as the inverse of the proportion of females with POFs ($n = 31$) among the total number of mature females ($n = 236$). Thus, the proportion with POFs (31/236) was 0.131, and the inverse was 7.6. For the 86-d spawning season, estimated as the interval during which POFs were detected, the POF method predicted that a female could produce up to 11 batches/season, and the ISI method predicted up to 8 batches/season.

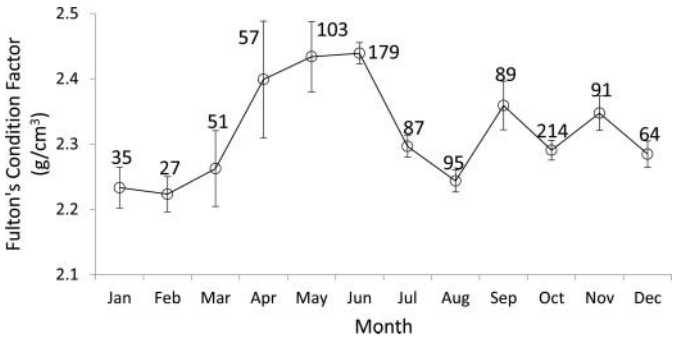


FIGURE 3. Mean (±SE) Fulton's condition factor for female Gray Triggerfish collected from the northern Gulf of Mexico, 1999–2012. Sample sizes are indicated for each month.

Batch Fecundity Estimation

Gray Triggerfish undergoing OM and/or oocyte hydration were rarely collected during routine sampling, thus adding to the challenges in estimating fecundity. Of the 236 maturing females that were collected during the spawning season, only one was a ripe female undergoing OM. Because of the group-synchronous development, the population of advancing vitellogenic oocytes can be considered equivalent to a batch. However, all fish with POFs did possess cortical alveolar oocytes and newly formed vitellogenic oocytes with diameters less than 250 μm (Figure 7). Therefore, to distinguish the oldest batch, only secondary growth oocytes of at least 250 μm in diameter were counted.

Batch fecundity ranged from 0.34 to 1.99 million eggs, and somatic relative fecundity ranged from 590 to 2,686 eggs/g of

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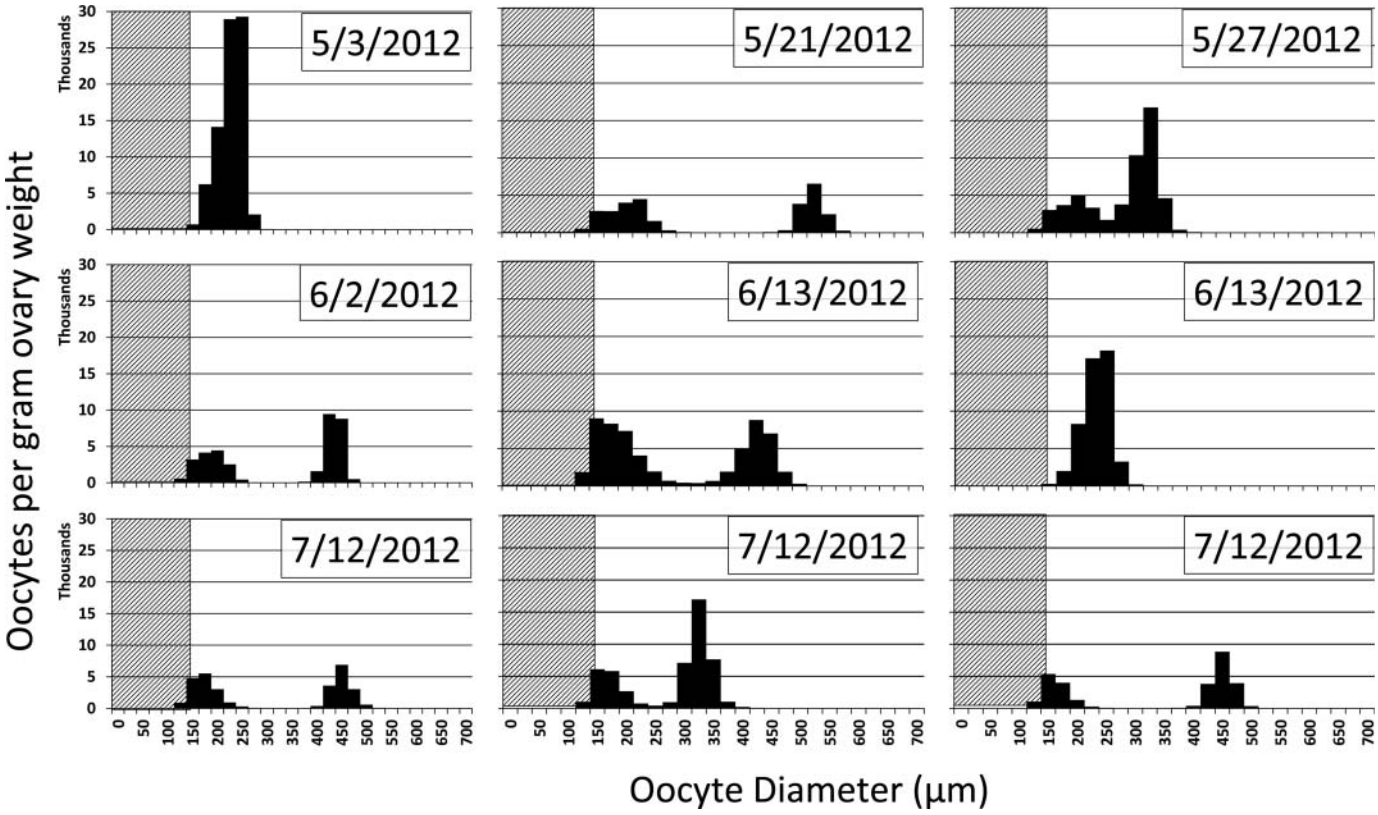


FIGURE 4. Oocyte size frequency (number of oocytes per gram of ovary weight) for nine individual Gray Triggerfish collected from the Gulf of Mexico in May–July 2012 (three randomly selected females per month). The date of capture is displayed for each fish. The hatched bar indicates the diameters of primary growth oocytes.

ovary-free body weight in 266–386-mm FL specimens (Table 2). A portion (56%) of the variance in BF was significantly explained by FL: BF = 8,703.69·FL − 1,776,483 (r^2 = 0.56, $P < 0.0001$; Figure 8).

DISCUSSION

Similar to balistids worldwide, Gray Triggerfish in the Gulf spawn in pairs, are nest builders that establish and defend territories, and guard their eggs (Kuwamura 1997; Kawase 2003; Simmons and Szedlmayer 2012). Perhaps related to this reproductive strategy, Gray Triggerfish exhibit group-synchronous secondary oocyte development, which is unusual for a warmwater species. Wallace and Selman (1981) defined group-synchronous development as the presence of two populations of oocytes that are clearly distinguishable from one another: a larger, more synchronous population; and a smaller, more heterogeneous one. Gray Triggerfish clearly exhibited this pattern, with a distinct size hiatus between cortical alveolar oocytes and vitellogenic oocytes.

A group-synchronous oocyte development pattern is typically associated with determinate fecundity (Murua and Saborido-Rey 2003; McBride et al. 2015), but we found evidence that Gray Triggerfish display indeterminate fecundity. The number of vitellogenic oocytes did not decrease and their diameter did not increase through the spawning season. Both of these results suggested that de novo vitellogenesis was occurring, thus violating the criteria for a determinate fecundity type. Although rare in the literature, other species have exhibited both group-synchronous oocyte development and the potential for de novo vitellogenesis; these include the Spiny Damselfish *Acanthochromis polyacanthus*, Mediterranean Sardine *Sardina pilchardus sardina*, and Blackmouth Angler *Lophiomus setigerus* (Nakazono 1993; Yoneda et al. 1998; Ganias et al. 2004).

Perhaps most diagnostic, we estimated that the *G* of secondary growth oocytes (37 μm/d) was rapid enough to yield multiple batches within an estimated 86-d spawning season. Although there are few published values of secondary oocyte *G*, some comparisons are available from higher-latitude fishes. For two species from the British Isles, reported *G*-values were approximately 3.2 μm/d for Sole *Solea solea* (based upon an increase in mean diameter over 143 d; Witthames and Greer-Walker 1995) and approximately 1.3 μm/d for Atlantic Mackerel *Scomber scombrus* (Greer-Walker et al. 1994). In both cases, secondary oocyte development proceeded slowly enough that de novo vitellogenesis could not occur within the

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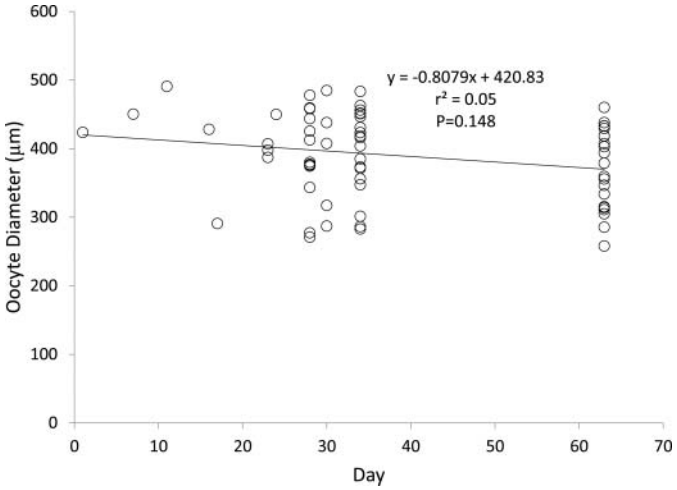


FIGURE 5. Regression of mean secondary oocyte diameter (µm) per individual female Gray Triggerfish against day of collection within the 2012 spawning season (day 1 = May 11).

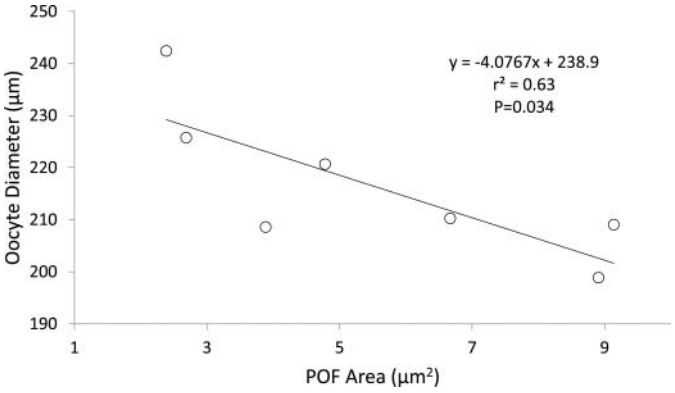


FIGURE 7. Regression of mean secondary oocyte diameter (µm) against mean postovulatory follicle (POF) area (µm^2) in seven female Gray Triggerfish selected from 2001 samples (see text).

spawning season; hence, the fecundity type was considered determinate.

Gray Triggerfish exhibited traits that are common in capital-breeding species. Condition indices (HSI and *K*) peaked just before or close to the onset of spawning, followed by declines throughout the reproductive period, similar to observations in other species with a capital pattern (Alonso-Fernández and Saborido-Rey 2012). The HSI of Gray Triggerfish exceeded the GSI in all months, which emphasizes the importance of the liver for energy storage and mobilization (Htun-Hun 1978; Rinchard and Kestemont 2003). In more extreme capital-breeding species, the seasonal increase in condition indices may occur well outside of the reproductive period (e.g., Htun-Hun 1978; Yoneda et al. 2001; Alonso-Fernández and Saborido-Rey 2012). By contrast, income-breeding species lack seasonal patterns in condition indices or exhibit only weak seasonal patterns (e.g., Domínguez-Petit et al. 2010). Although we postulate that Gray Triggerfish are capital breeders, we cannot reject the possibility that food intake during the spawning season may partially provide the energy needed for egg production. However, the liver in Gray Triggerfish seems to be important for energy mobilization and may help to ensure that oocyte development proceeds even when energy intake is low (e.g., Allen and Wootton 1982; Alonso-Fernández and Saborido-Rey 2012) or when there is a hiatus in feeding during parental care.

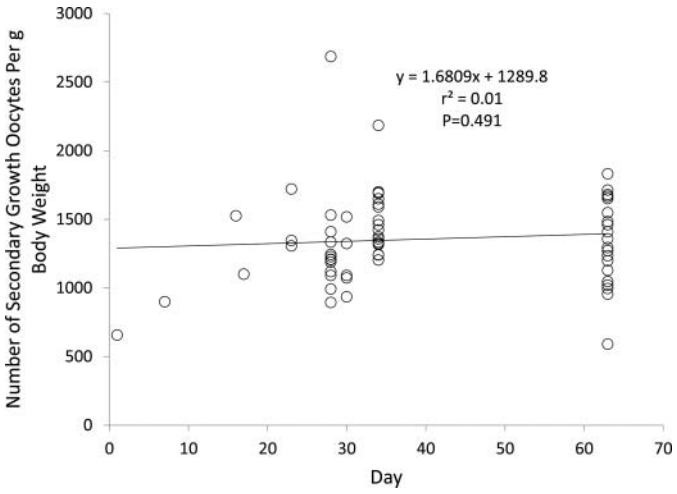


FIGURE 6. Regression of the number of secondary growth oocytes per gram of body weight in female Gray Triggerfish against day of collection within the 2012 spawning season (day 1 = May 11).

We found that Gray Triggerfish in the Gulf show attributes of indeterminate fecundity associated with warmwater environments. However, the species also exhibits group-synchronous oocyte development and a capital breeding pattern associated with territoriality and female parental care—traits that are most often linked with determinate fecundity (McBride et al. 2015). Gray Triggerfish possibly show determinate fecundity elsewhere in their range, which extends from Nova Scotia to Argentina in the western Atlantic (Hoese and Moore 1998). Building on the review by McBride et al. (2015), our findings support a conclusion that such mixed reproductive attributes in fish may be more common than previously thought and may be predicted to occur in lower latitudes for species with energetically demanding accessory reproductive activities, such as female parental care.

Batch Fecundity

Our findings on the reproductive strategy of Gray Triggerfish in the Gulf support use of a fecundity methodology based upon batch size and spawning frequency. Application of an indeterminate fecundity methodology is the cautionary approach when there is uncertainty about a species' fecundity type (Gordo et al. 2008; Lowerre-Barbieri et al. 2011;

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TABLE 2. Fecundity metrics and associated FL information for female Gray Triggerfish used in fecundity analysis (OFBW = ovary-free body weight; batch fecundity = number of secondary growth oocytes ≥ 250 μm in diameter within the ovary).

Statistic	FL (mm)	Somatic relative fecundity (oocytes/g of OFBW)	Oocyte density (oocytes/g of ovary weight)	Batch fecundity	Secondary growth oocyte diameter (μm)
Minimum	266	590	12,653	339,605	250 (limit)
Maximum	386	2,686	47,688	1,990,861	590
Mean ± SE	311.3 ± 3.6	1,356.9 ± 41	24,468.82 ± 1,085.64	932,908.7 ± 41,458.6	370 ± 0.1

Fitzhugh et al. 2012). However, female Gray Triggerfish are rarely sampled in OM or the hydrated oocyte stage, which is typically the basis for identifying a spawning batch. The difficulty of detecting OM in female Gray Triggerfish seems to be a common problem (Wilson et al. 1995; Hood and Johnson 1997; Moore 2001). This could be related to (1) the lack of oocyte hydration during proteolysis or (2) reduced feeding prior to spawning, such that females undergoing OM have a low susceptibility to hook-and-line capture (Wilson et al. 1995; Moore 2001; Simmons and Szedlmayer 2012). MacKichan and Szedlmayer (2007) reported an egg diameter of 620 ± 3 (mean ± SE) μm from Gray Triggerfish nest excavations, which is close to the mean diameter of ova (602 ± 0.72 μm) from the one female we detected as undergoing yolk coalescence and considered to be in spawning condition. In contrast, broadcast spawners with positively buoyant eggs, such as the Red Snapper *Lutjanus campechanus*, have an egg diameter of about 820 μm (Rabalais et al. 1980). A lack of oocyte hydration would result in a much shorter period during which to collect imminently spawning females, which in turn would lead to a low incidence of actively spawning individuals in sample collections. A similar difficulty occurs with the Mediterranean Sardine and is attributed to a relatively long (>10-d) spawning interval (Ganias et al. 2004). Due to the infrequent capture of Gray Triggerfish undergoing OM, we used the spawning batch size separation method (Ganias et al. 2004) to calculate BF. The oocyte size hiatus that develops as the secondary growth oocytes advance provides the basis upon which to define the spawning batch.

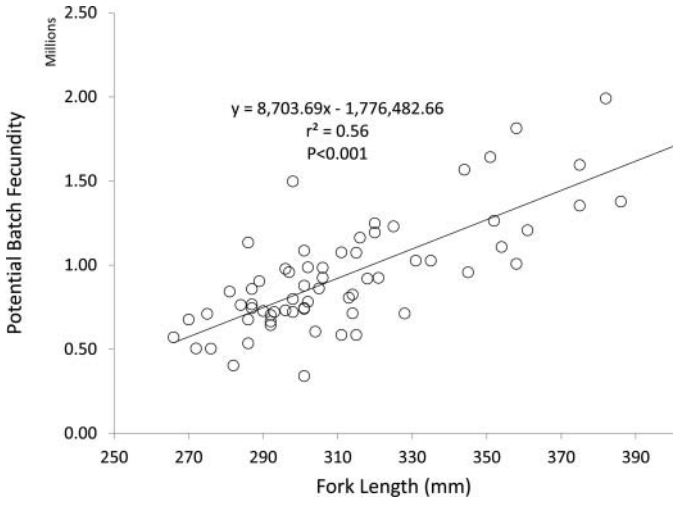


FIGURE 8. Regression of potential batch fecundity against fork length (mm) of female Gray Triggerfish. Batch fecundity was defined as the number of secondary growth oocytes at least 250 μm in diameter within the ovary.

Other investigators of Gray Triggerfish fecundity have applied various criteria based on oocyte size or stage to define the spawning batch. Ingram (2001) reported 400 μm as the diameter that delimited the beginning of a spawning batch based upon the assumption that this size corresponded to the onset of OM. Using this criterion, oocyte density was estimated as 8,015 ± 247 (mean ± SE) oocytes/g of ovary (Ingram 2001, cited in SEDAR 09 2006). However, we found no evidence of OM occurring for oocytes with diameters of 590 μm or less. The only imminently spawning female in our collections had a mean oocyte diameter of 602 ± 0.72 μm for oocytes undergoing OM. Given our finding that secondary oocyte development is group synchronous, the 400-μm criterion would likely identify only a partial batch. Hood and Johnson (1997) indicated that the spawning batch could be identified as the standing stock of vitellogenic oocytes within an ovary—essentially the same conclusion we made. Their results for BF ranged from 0.2 to 1.2 million eggs, with a density of 13,809 ± 6,122 (mean ± SE) oocytes/g of ovary. Our estimated oocyte density was 24,468 ± 1,086 oocytes/g of ovary, which was much higher than the estimates from either Hood and Johnson (1997) or Ingram (2001). The difference between our estimate and that of Ingram (2001) can be readily accounted for by the difference in the minimum oocyte size used to define a spawning batch (250 μm versus 400 μm). The difference between our oocyte density estimate and that calculated by Hood and Johnson (1997) is more difficult to explain, and we can only speculate that factors we did not account for (e.g., year or season effects) were important. Although there are other published estimates of Gray Triggerfish fecundity (Manooch and Raver 1984; Bernardes and Dias 2000), the details provided on methods and oocyte size or stage criteria for fecundity counts were not sufficient for a comparison with our results. The range of our BF estimates

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(0.34–2.0 million eggs) was similar to counts of eggs from nine nests (0.42–1.4 million eggs) examined by MacKichan-Simmons (2008).

Spawning Frequency

As found in many studies, spawning frequency can be difficult to assess due to low sample sizes and uneven sampling through the reproductive season (Stratoudakis et al. 2006; Ganias et al. 2011). Similar to the rarity of female Gray Triggerfish undergoing OM, the occurrence of females exhibiting POFs was comparatively low. This necessitated aggregation of the data across years, which assumes no year effect, such that the proportion of females bearing POFs could be used to calculate the spawning interval (7.6 d via the POF method). However, in one of the study years (2001), samples were evenly distributed over June and July and thus permitted spawning interval estimation via the ISI method (11 d). This estimate depends on two assumptions: (1) that POF degeneration offers a clock by which oocyte growth can be estimated, and the maximum POF surface area we observed (12 μm^2) is representative of a new day-0 POF in Gray Triggerfish; and (2) that the relationship between the rate of POF degeneration and secondary oocyte growth is constant over the spawning season. We think the first assumption is reasonable based on the corresponding observations that cortical alveolar oocytes were the leading gamete stage and that provisioning of yolk for the subsequent batch had not yet begun. Furthermore, the relationship between POF degeneration and secondary oocyte growth was linear for our example from 2001. For the second assumption, there is evidence from the literature that POF degeneration and secondary oocyte growth are both temperature dependent (Kjesbu et al. 1998; Ganias 2012). We also expect that water temperature—and thus rates of POF degeneration and secondary oocyte growth—may change over a several-month-long spawning season. However, a simple assumption may be that any changes in the rate of oocyte growth are proportional to changes in the rate of POF degeneration. Further work is needed to test this assumption. For the purposes of the present paper, the POF and ISI methods were needed to support each other due to the low sample size of individuals that contained POFs. A study of Yellowmargin Triggerfish *Pseudobalistes flavimarginatus* found that spawning grounds were vacated for 10 d between spawns on Australia's Great Barrier Reef (Gladstone 1994). This would be similar to the 11-d spawning interval we calculated for Gray Triggerfish. Earlier estimates of spawning interval for this species vary greatly: from 15 to 37 d in the U.S. South Atlantic (Moore 2001) to 3.7 d in the Gulf (Ingram 2001).

Female Gray Triggerfish in the Gulf exhibited mixed reproductive attributes that were apparently associated with the warmwater environment and with the energetically demanding behaviors required for defense and parental care. Fecundity type in the Gulf should be considered indeterminate, and the hiatus in the size distribution of advancing secondary oocytes can be used to identify a spawning batch. Our estimated scope for the number of batches produced during a spawning season is lower (8–11 d) than that estimated elsewhere in the Gulf (c.f. Ingram 2001), but additional research is needed. In particular, age or size dependency in batch number will be difficult to assess due to the nesting behavior and parental care exhibited by Gray Triggerfish.

Further field collection efforts could improve estimates of Gray Triggerfish fecundity. Due to the nesting and territorial behavior of this species, scuba and spearfishing are necessary to readily identify and collect females that are in spawning condition. A survey could be designed to improve our knowledge of the timing and duration of spawning markers by targeting prespawn and postspawn females in conjunction with (1) visual observations of color phase and the size of females on nests and (2) measurements of environmental variables (perhaps most importantly, water temperature).

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