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## Original Article

# Effects of age and size on spawning and egg production in gag and scamp grouper off the southeastern United States

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Stock assessments historically have used age- and size-independent methods to estimate reproductive output in marine fishes. Recent assessments have used total egg production (TEP), often assuming an invariant spawning frequency (SF) for all females. However, spawning parameters vary with age and size, which invalidates this assumption. This study investigated the age- and size-dependence of female spawning fraction, duration, and frequency in two economically valuable species, gag (*Mycteroperca microlepis*) and scamp (*Mycteroperca phenax*), in Atlantic waters off the southeastern United States, with the ultimate objective of quantifying the effect of these dependencies on TEP estimates. Spawning parameters had moderate-to-strong dome-shaped relationships with age and size ($r^2 = 0.63$–$0.94$), peaking at intermediate ages and sizes. As larger, older females approach sexual transition, they may increase their lifetime reproductive success by shifting energy resources away from female reproductive investment (i.e. eggs) towards investment that will promote future male reproductive success (i.e. gonad transformation). The estimate of TEP based on age-dependent SF was 38% lower for gag and 41% lower for scamp than the estimate based on age-independent (AI) SF; therefore, the AI method overestimates stock productivity. Incorporating age- and size-based reproductive data into assessments can lead to more reliable stock productivity estimates and potentially improved management.

**Keywords:** fecundity, hermaphrodite, reproduction, spawning duration, spawning frequency, stock productivity

## Introduction

The federal management of many valuable fisheries off the southeastern United States depends largely on age-structured stock assessments currently conducted through the Southeast Data, Assessment, and Review (SEDAR) process. These assessments aim to estimate biological reference points, determine stock status, and make projections used in the development of management plans and regulations. Calculating reproductive output, or the productivity of the stock, is crucial for determining stock status and making reasonable projections. However, some marine fishes exhibit complex reproductive strategies, which has historically made it difficult to quantify reproductive output and to incorporate the reproductive biology of each species into assessments (Lowerre-Barbieri *et al.*, 2011a, b). This has created the need for generalized assumptions and led to the use of age- and size-independent methods to estimate stock productivity (Lowerre-Barbieri, 2009). However, there is increasing evidence that such methods do not accurately represent the reproductive potential of a fish stock (Rothschild and Fogarty, 1989; Marshall *et al.*, 2003; Klibansky and Scharf, 2013). Age- and size-dependent variation in spawning parameters that affect reproductive output, such as spawning fraction (the proportion of mature females that are actively spawning, PS), spawning duration (SD), and spawning frequency (the number of batches spawned per female in a spawning season, SF) is common in batch-spawning species with indeterminate fecundity (Trippel *et al.*, 1997; McBride and Thurman, 2003; Alonso-Fernández and Saborido-Rey, 2011; Fitzhugh *et al.*, 2012). Thus, it is important to investigate these potential sources of variation in each species to accurately characterize the age-dependent (AD) reproductive contributions in a fish stock.

Recent assessments have begun to quantify reproductive output by estimating total egg production (TEP), the total number of eggs spawned by the stock per spawning season. When age-based data are not available, age-invariant parameters have been used for this calculation (see SEDAR, 2011, 2017). The use of such age-invariant parameters can lead to over- or underestimation of stock productivity, depending on the size/age demographics of the population, and potentially lead to ineffective management (Marshall *et al.*, 2003; Klibansky and Scharf, 2013). Thus, incorporation of age- and size-dependent data will yield more accurate TEP estimates (Marteinsdottir and Thorarinsson, 1998; Murawski *et al.*, 2001; He *et al.*, 2015), and improve stock assessments to better advance management goals.

Gag (*Mycteroperca microlepis*) and scamp (*Mycteroperca phenax*) are large, batch-spawning, protogynous hermaphrodites that occur in the western Atlantic and throughout the Gulf of Mexico (Collins *et al.*, 1987, 1998; Harris *et al.*, 2002). These species support economically important fisheries in the southeastern United States, and because of their slow growth and reproductive strategy, overfishing is of great concern (Harris and Collins, 2000; Harris *et al.*, 2002). Because scamp has not undergone a stock assessment in the Atlantic waters off the southeastern United States since the late 1990s (Manooch *et al.*, 1998), its current stock status is unknown. The most recent gag assessment in this region determined that the stock was not overfished, but was undergoing overfishing (SEDAR, 2014). Thus, improvement in management strategies for these species is likely needed, and more accurate stock productivity estimates could be essential.

This study investigated the influence of age and size on PS and SD in gag and scamp and used those values to characterize the age- and size-dependence of SF for each species, with the ultimate objective of quantifying the effect of these dependencies on TEP estimates. Estimates of TEP using age-independent (AI) vs. AD values of SF were compared. We aimed to highlight the importance of incorporating age- and size-based reproductive data into assessments, which can produce more reliable estimates of stock productivity and lead to improved management.

## Methods

### Sample collection

Samples were collected via fishery-dependent and -independent methods during 1979–2016. Fishery-dependent samples were collected via port sampling primarily from hook and line fisheries, mainly during 1994–1995 and 2004–2005, as described in McGovern *et al.* (1998) and Reichert and Wyanski (2005). Fishery-independent samples were collected annually from April through October during offshore research cruises, primarily using baited chevron traps, as described in Smart *et al.* (2015). Fishery-independent sampling during 1979–2009 was conducted solely by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program, and during 2010–2016 by the Southeast Reef Fish Survey (SERFS). Established in 2010, SERFS consists of a collaborative effort among three groups: the MARMAP program, the Southeast Area Monitoring and Assessment Program-South Atlantic, and the Southeast Fishery independent Survey. SERFS monitors fishes on natural reefs in Atlantic waters off the southeastern United States, with sampling occurring at stations with hard-bottom habitat located on the continental shelf and upper slope from Cape Hatteras, NC (35.3°N) to Port St. Lucie, FL (27.3°N).

### Sample processing

Individual specimens were measured, weighed, and processed following standard MARMAP and SERFS protocols (Smart *et al.*, 2015). Sagittal otoliths were removed for ageing and stored dry. Otolith processing and age determination followed standard MARMAP protocols described in Harris *et al.* (2002), Reichert and Wyanski (2005), and Smart *et al.* (2015). Gag otoliths were examined whole in water, but were sectioned if they were difficult to read or had more than seven increments; all scamp otoliths were sectioned. Transverse sections containing the otolith core were examined using a dissecting microscope, and the number of increments was counted.

Sex and reproductive phase of each fish were determined by histological examination of fixed gonad tissue processed following standard MARMAP protocols (McGovern *et al.*, 1998; Harris *et al.*, 2002; Smart *et al.*, 2015). Gonad sections were examined with a compound microscope, and reproductive phase was assessed using criteria developed by the MARMAP program, with slight modifications to follow terminology in Brown-Peterson *et al.* (2011). Females were categorized as immature or mature, with mature females further categorized as early developing, developing, actively spawning, regressing, or regenerating. Females were deemed actively spawning if there were indicators of imminent or recent spawning. Oocyte maturation (germinal vesicle migration and hydration; Grier *et al.*, 2009) indicated an imminent spawn, and the duration was estimated as 12 h before a spawn based on water temperatures in the region (Jackson *et al.*, 2006; Lowerre-Barbieri *et al.*, 2011a, b). The presence of postovulatory follicle complexes (POC; Grier *et al.*, 2009) in ovaries indicated a recent spawn, and the duration was estimated as 36 and 48 h after a spawn for scamp and gag, respectively, based on documented spawning temperatures and POC resorption studies (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985; Fitzhugh and Hettler, 1995; Sedberry *et al.*, 2006). Consequently, the total duration of spawning indicators was assumed to be 48 h for scamp and 60 h for gag. To ensure correct assignment of females to the immature and regenerating phases, a quality control analysis was conducted, as described in Harris *et al.* (2002). When reproductive phase could not be assessed with confidence, samples were omitted from analyses.

### Data analysis

*Spawning parameter analyses*

Data were restricted to encompass only mature females from the spawning season months for each species: December–May for gag (McGovern *et al.*, 1998) and February–July for scamp (Harris *et al.*, 2002), and calendar ages were calculated as described in Reichert and Wyanski (2005) and Harris *et al.* (2002). Females were grouped into 1-year age and 50-mm total length (TL) size classes; all length measurements henceforth will refer to TL. Due to low sample sizes in the classes representing the larger and older specimens, data for female gag $\geq$12 years old as well as females $\geq$1150 mm were pooled. For scamp, females $\geq$13 years old and females $\geq$750 mm were pooled.

Spawning parameters were calculated for each species for the overall dataset and each age and size class. The number of females actively spawning was divided by the number of mature females to yield the PS (Lowerre-Barbieri *et al.*, 2011b). Based on the total duration of spawning indicators in each species, the PS was then reduced proportionally to a 24-h period (see Priede and Watson, 1993). The SD was estimated as the number of days from the first day to the last day that spawning indicators were observed. The SF was calculated as SF=PS×SD. Lastly, the spawning parameters were related to calendar age and TL via polynomial regression, adding orders to the polynomial in a step-wise process. When adding a higher order was not significant ($p \geq 0.05$), the model was not considered further, and the best fitting model was chosen with Akaike's Information Criterion (AIC; Akaike, 1978).

### *Egg-production analyses*

Stock assessment models for our study species are age-based; therefore, the effect of the age-dependence of SF on TEP was investigated. TEP is calculated as follows:

$$\mathrm{TEP} = \sum_{a=1}^{\max a} n_a \times \mathrm{PF}_a \times \mathrm{PM}_a \times \mathrm{BF}_a \times \mathrm{SF}, \quad (1)$$

where $n_a$ is the number of individuals at age, $\mathrm{PF}_a$ is the proportion of females at age, $\mathrm{PM}_a$ is the proportion of mature females at age, $\mathrm{BF}_a$ is the batch fecundity at age, and SF is the spawning frequency. TEP was calculated using two methods: (i) an AI method using the overall population ($\overline{\mathrm{SF}}=\mathrm{n_{spawners}}/\mathrm{n_{mature}} \times \mathrm{overall\ SD}$) as historically done in stock assessments, and (ii) an AD method using the SF at age $a$ ($\mathrm{SF}_a$).

For gag, terminal year (2012) estimates of $n_a$, $\mathrm{PF}_a$, and $\mathrm{PM}_a$ were obtained from the most recent stock assessment report (SEDAR, 2014). Linear and power regressions were fit to BF and TL data collected by MARMAP during 1996–1997 and 2001–2005, with the best-fit being the power model. The resulting equation ($\mathrm{BF} = 0.00876 \times \mathrm{TL}^{2.62895}$) and the mean length-at-age ($L_a$) in SEDAR (2014) were used to calculate $\mathrm{BF}_a$.

For scamp, the only stock assessment available (Manooch *et al.*, 1998) lacked the population structure parameters needed for a full TEP estimate. Thus, a theoretical population structure was developed using our data and results from Harris *et al.* (2002) and Manooch *et al.* (1998). Scamp $L_a$ was calculated from the 1990 to 1997 von Bertalanffy equation in Harris *et al.* (2002), with a corrected value of $t_0 = -2.57$: $L_a = 897 \times [1 - e^{-0.13(a + 2.57)}]$. Linear and power regressions were fit to BF and TL data from 1996 to 1998 utilized by Harris *et al.* (2002), with the best-fit being the power model. The resulting equation ($\mathrm{BF} = 0.000068 \times \mathrm{TL}^{3.365498}$) and the $L_a$ were used to calculate $\mathrm{BF}_a$.

Scamp $n_a$ were approximated with a modified catch-curve analysis developed by Thorson and Prager (2011), which estimates fishing mortality ($F$) and selectivity-at-age ($S_a$) and calculates $n_a = n_{a-1}\mathrm{e}^{[-(F \times S_{a-1} + M_{a-1})]}$. Inputs to this analysis included a vector of ages (0–22 years), natural mortality-at-age ($M_a$), starting values for estimated parameters, and a vector of catch-at-age data from the terminal year (1996) in Manooch *et al.* (1998). The equation in Charnov *et al.* (2013) was used to calculate $M_a$ $[M_a = K \times (L_a/L_\infty)^{-1.5}]$, using $K$ and $L_\infty$ from the von Bertalanffy equation above. To be consistent with regional assessment methodologies, $M_a$ was scaled so that cumulative survival over fully selected ages (here, ages 5+) under age-variant $M_a$ was equal to the analogous estimate assuming age-invariant $M$. Age-invariant $M$ was calculated using the equation in Hoenig (1983; $M = 4.30596 \times t_{\max}{}^{-1.01}$) and the maximum age in our data ($t_{\max} = 29$).

Scamp $\mathrm{PF}_a$ and $\mathrm{PM}_a$ were calculated using a subset of our data from 2010 to 2016 ($n = 384$). Data were subset to ensure they were taken from a similar time-period as the gag $\mathrm{PF}_a$ and $\mathrm{PM}_a$ (2012), and included all years since the establishment of SERFS to optimize sample size and regional spread. Maturity and sexual transition ogives were developed, classifying fish according to whether they were immature or mature (0 or 1), and female or male, respectively. Generalized linear models were fit to the binary data, assuming a binomial error distribution, with the logit, probit, clog-log, and cauchit links. AIC values were used to assess goodness of fit and to choose the best-fitting link for the model. For both ogives, the best-fit was the model with a probit link. Thus, predicted values of $\mathrm{PM}_a$ and $\mathrm{PF}_a$ were computed from the maturity ($b_0 = -1.0516$, $b_1 = 0.7655$, $a_{50} = 1.37$, $p < 0.001$) and sexual transition ($b_0 = -2.6026$, $b_1 = 0.1978$, $a_{50} = 13.15$, $p < 0.001$) ogives.

The overall age-based $-\overline{\mathrm{SF}}$ from our spawning parameter analyses was used to calculate the AI TEP, and predicted values of $\mathrm{SF}_a$ from our SF vs. age models were used for the AD TEP. When predicted $\mathrm{SF}_a$ values were negative, observed values were used instead. The proportion that each age class contributed to TEP was calculated for both methods as $\mathrm{EP}_a$ / TEP. Per cent difference between methods was calculated for each age class and for population TEP as $[(\mathrm{AD} - \mathrm{AI})/\mathrm{AI}] \times 100$. Lastly, the relative percentage that each age class contributed to the overall per cent difference was calculated as $[(\mathrm{AI_a} - \mathrm{AD_a})/(\mathrm{AI_{Total}} - \mathrm{AD_{Total}})] \times 100$.

## Results

### Sample collection

Reproductive samples from 5601 gag ranging 517–1275 mm and 2–18 years, and 3082 scamp ranging 313–875 mm and 1–22 years, were examined histologically. Of these, 4485 gag and 2351 scamp were classified as mature females and used in further analyses. Sample sizes were reduced further due to lack of age or TL data (Table 1).

### Spawning parameter analyses

For both species, spawning activity was generally highest in females of intermediate age and size, with second- or third-order polynomials as the best-fit models (Table 2). The PS, SD, and SF of both species exhibited strong dome-shaped relationships with TL, with third-order polynomials as the best-fit models for gag, and second-order polynomials for scamp (Tables 2 and 3). All gag spawning parameters increased with TL to distinct peaks around 850–1050 mm and decreased sharply at larger sizes (Figure 1). Scamp spawning parameters exhibited a slightly wider, more flattened dome than in gag, with an earlier peak at 450–650 mm (Figure 2).

For gag, all spawning parameters also had strong, dome-shaped relationships with age (Table 2). Gag PS increased to a peak at ages 8–10 years, with a third-order polynomial as the best-fit model; whereas SD and SF increased sharply to distinct peaks at ages 6–9 years, with second-order polynomials as the best-fit models (Figure 3; Tables 2 and 3). Conversely, the PS of scamp remained generally constant and thus exhibited no significant relationship with age (Figure 4a; Table 3). Nonetheless, both the SD and SF of scamp had significant dome-shaped relationships with age, increasing sharply to a peak at ages 5–8 years, with second-order polynomials as the best-fit models (Figure 4; Tables 2 and 3). For both species, most estimates of SF-at-TL and

SF-at-age, including some peak values, were below the overall SF calculated for the whole population (gag = 29.4 batches, scamp = 22.3 batches; Figures 1–4).

## Egg-production analyses

For both species, the AD method yielded lower egg production estimates than the AI method (Figure 5) both overall and at-age.

**Table 1.** Sample sizes by sex and female maturity classifications for all fish samples examined histologically.

| Group | Gag | Scamp |
|---|---|---|
| Male | 284 | 483 |
| Transitional | 59 | 76 |
| Unknown sex and maturity | 80 | 36 |
| Female, uncertain maturity | 301 | 59 |
| Immature female | 392 | 77 |
| Mature female | 4 485 | 2 351 |
| Total | 5 601 | 3 082 |
| Mature female with TL | 4 442 | 2 344 |
| Mature female with age | 2 125 | 2 117 |

TL, total length.

For gag, the AD population TEP estimate was 38% lower than the AI estimate, with the youngest females showing the largest differences between methods (74–87%), followed by the oldest females (65%; Table 4). The smallest differences between methods (5–10%) were observed at age classes 7–9, during which gag had peak $SF_a$; these differences constituted only 1% of the overall percentage difference between methods in TEP (Table 4). Conversely, age classes 4–6 had the highest egg production estimates (Figure 5a), and the absolute decrease in egg production of these three age classes constituted the largest percentage (82%) of the overall difference between methods in TEP (Table 4). Furthermore, despite peak $SF_a$ in age classes 7–9, their summed egg production estimates constituted only a small proportion of the overall population TEP (6%/10%; AI method/AD method); whereas age classes 4–6 constituted the largest proportion (85%/86%) of population TEP (Figure 6a).

For scamp, the AD population TEP estimate was 41% lower than the AI estimate, with the oldest females showing the largest differences between methods (83–99.7%), followed by the youngest females (83%; Table 5). The smallest differences between methods (22–26%) were observed in the scamp females with peak $SF_a$, age classes 5–8; these differences constituted only 20% of the overall per cent difference between methods in TEP (Table 5).

**Table 2.** Results from stepwise selection process to determine best-fitting models among first-, second-, and third-order polynomial regressions relating gag and scamp spawning parameters to TL and age classes.

| | | Gag | | | | | | Scamp | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1st | | 2nd | | 3rd | | 1st | | 2nd | | 3rd |
| Order | | *p* | AIC | *p* | AIC | *p* | AIC | *p* | AIC | *p* | AIC | *p* |
| **TL** | PS | <0.001 | −38.5 | 0.004 | −47.5 | 0.003 | −58.1 | 0.18 | −30.5 | <0.001 | −46.0 | 0.37 |
| | SD | 0.14 | 152.7 | <0.001 | 125.3 | <0.001 | 122.8 | 0.17 | 108.2 | <0.001 | 84.6 | 0.05 |
| | SF | 0.04 | 113.0 | 0.002 | 102.2 | <0.001 | 84.1 | 0.28 | 73.0 | <0.001 | 51.1 | 0.89 |
| **Age** | PS | 0.002 | −33.4 | 0.03 | −38.0 | 0.004 | −50.0 | 0.53 | −35.6 | 0.04 | −39.6 | 0.89 |
| | SD | 0.95 | 114.8 | <0.001 | 97.6 | 0.67 | | 0.38 | 145.3 | <0.001 | 130.0 | 0.06 |
| | SF | 0.25 | 87.2 | 0.001 | 74.0 | 0.12 | | 0.43 | 92.8 | 0.001 | 80.2 | 0.09 |

When adding a higher order was not significant ($p \geq 0.05$), the model was not considered further. Models chosen based on AIC, are highlighted in grey.
PS, proportion spawning; SD, spawning duration; SF, spawning frequency.

**Table 3.** Results from best-fitting polynomial regressions relating gag and scamp spawning parameters to TL and age classes.

| | | | | | Model parameters | | | |
|---|---|---|---|---|---|---|---|---|
| Species | Predictor | Spawning parameter | $r^2$ | *p* | $b_0$ | $b_1$ | $b_2$ | $b_3$ |
| Gag | TL | PS | 0.94 | <0.001 | 1.22 | −0.006 | $9.17 \times 10^{-6}$ | $-4.11 \times 10^{9}$ |
| | | SD | 0.90 | <0.001 | −94.27 | −0.56 | 0.002 | $-1.33 \times 10^{6}$ |
| | | SF | 0.92 | <0.001 | 324 | −1.49 | 0.002 | $-9.77 \times 10^{7}$ |
| | Age | PS | 0.93 | <0.001 | 0.19 | −0.08 | 0.02 | −0.001 |
| | | SD | 0.78 | <0.001 | −54.07 | 49.23 | −3.50 | |
| | | SF | 0.73 | 0.002 | −27.53 | 14.54 | −0.95 | |
| Scamp | TL | PS | 0.82 | <0.001 | −0.46 | 0.002 | $-1.95 \times 10^{-6}$ | |
| | | SD | 0.92 | <0.001 | −509.4 | 2.38 | 0.002 | |
| | | SF | 0.90 | <0.001 | −88.05 | 0.40 | $-3.62 \times 10^{4}$ | |
| | Age | PS | 0.25 | 0.09 | | | | |
| | | SD | 0.70 | <0.001 | −16.29 | 45.85 | −3.54 | |
| | | SF | 0.63 | 0.003 | −1.59 | 5.85 | −0.45 | |

Values given for scamp PS vs. age are for a second-order polynomial. Model equation: $y = b_0 + b_1x + b_2x^2 + b_3x^3$.
PS, proportion spawning; SD, spawning duration; SF, spawning frequency.

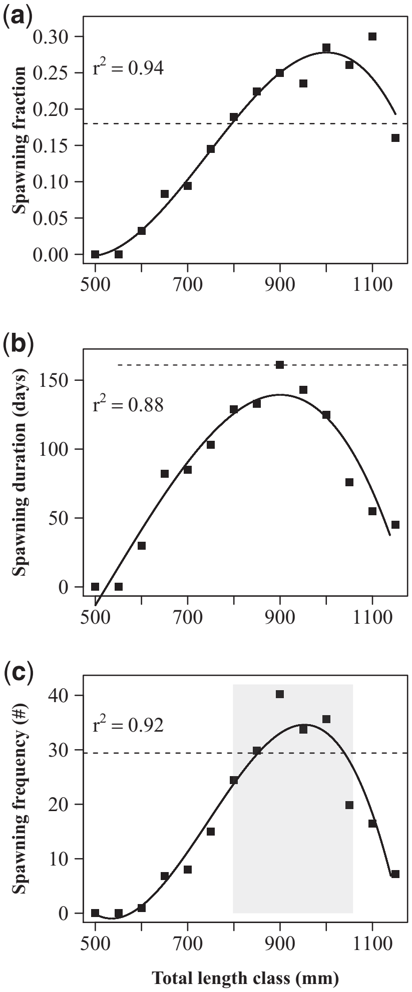

**Figure 1.** Observed (filled squares) PS (a); SD (b); and SF (c) as a function of TL class in gag. Third-order polynomial models fitted to the data (solid lines). Dashed lines represent overall PS (0.18), SD (161), and SF (29.4) for all mature females. Shaded region represents peak range of size at sexual transition (McGovern *et al.*, 1998).

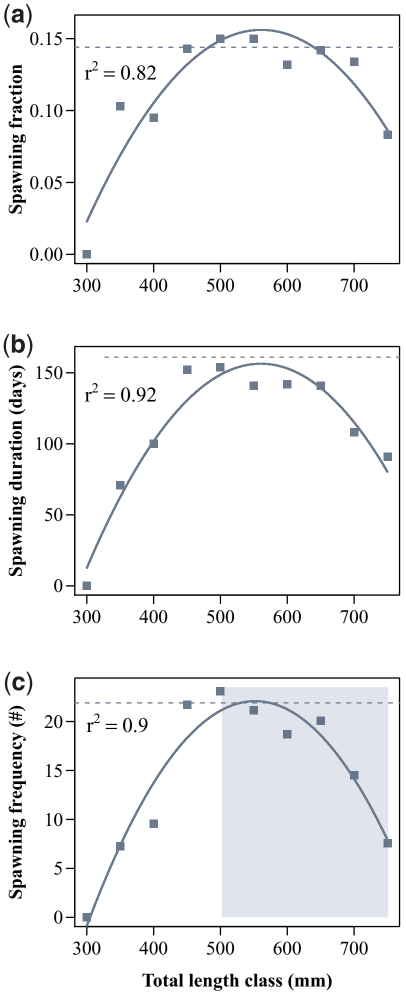

**Figure 2.** Observed (filled squares) PS (a); SD (b); and SF (c) as a function of TL class in scamp. Second-order polynomial models fitted to the data (solid lines). Dashed lines represent overall PS (0.14), SD (161), and SF (22.3) for all mature females. Shaded region represents peak range of size at sexual transition (Harris *et al.*, 2002).

Conversely, the absolute decrease in egg production of age classes 2–5 constituted a larger percentage (77%) of the overall per cent difference between methods in TEP (Table 5). Furthermore, the summed proportion of population TEP contributed by younger females (age classes 2–5) was greater (77%/78%; AI method/AD method) than the contribution from the females with peak $SF_a$ (age classes 5–8, 33%/43%; Figure 6b).

## Discussion

### Spawning parameters

This study presents the first evidence of spawning parameters having dome-shaped relationships with age in marine fishes, and with size in groupers. We hypothesize that for gag and scamp, female spawning activity increases with age and size until reaching a peak, after which it may be more advantageous to divert reproductive energy towards spawning as a male. Spawning parameters increased with age and size until peaking and then decreasing near the known ranges of peak age- and size-at-transition for each species. For gag, all spawning parameters began to decrease near ages 9–11 and near 1000–1100 mm, aligning well with the age (8–11 years; Collins *et al.*, 1987; Hood and Schlieder, 1992; Reichert and Wyanski, 2005) and size (800–1050 mm; McGovern *et al.*, 1998) ranges of peak sexual transition (Figures 1 and 3). Similarly, scamp spawning began to decrease at ages 8–9 and near 650–700 mm, which also encompasses peak sexual transition for this species (5–9 years, 500–750 mm; Harris *et al.*, 2002; Figures 2 and 4). Therefore, it is possible that the major driver of the decrease in spawning we observed in larger, older females is the upcoming sexual transition.

In a Gulf of Mexico study, Collins *et al.* (1998) found that gag SF varied significantly with age and exhibited a slight increasing trend towards peak frequencies at ages 7–9. However, they did not calculate SF for ages ≥10, which prevents us from comparing trends for the oldest ages. It is important to note that we also observed peak SF in gag (34–36 batches) at ages 7–9, a very similar result to the previously reported SF in the southeastern United States (38 batches; Reichert and Wyanski, 2005). In addition, for both species, most age- and size-based estimates of SF were lower than the overall population SF (gag = 29.4 batches, scamp =

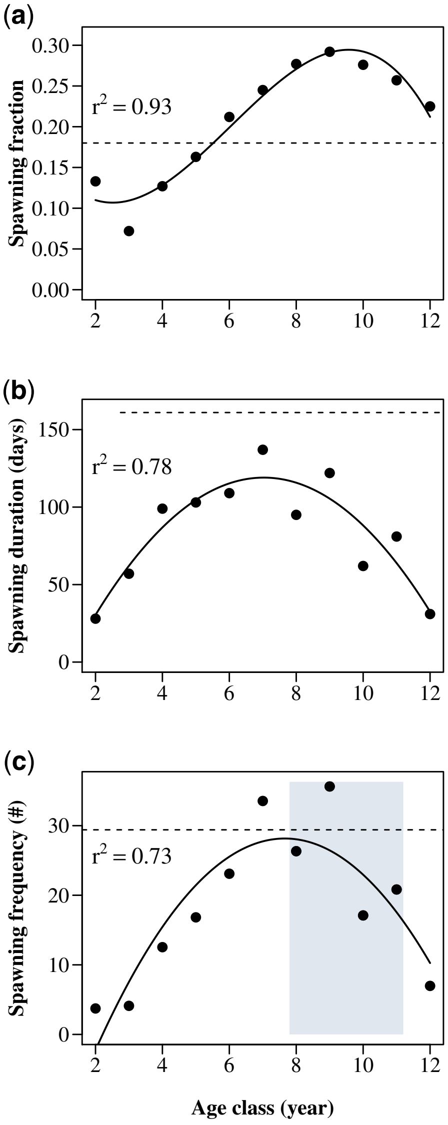

**Figure 3.** Observed (filled circles) PS (a); SD (b); and SF (c) as a function of age class in gag. Third-order (a) and second-order (b and c) polynomial models fitted to the data (solid lines). Dashed lines represent overall PS (0.18), SD (161), and SF (29.4) for all mature females. Shaded region shows peak range of age at sexual transition (Collins *et al.*, 1987; Hood and Schlieder, 1992; Reichert and Wyanski, 2005).

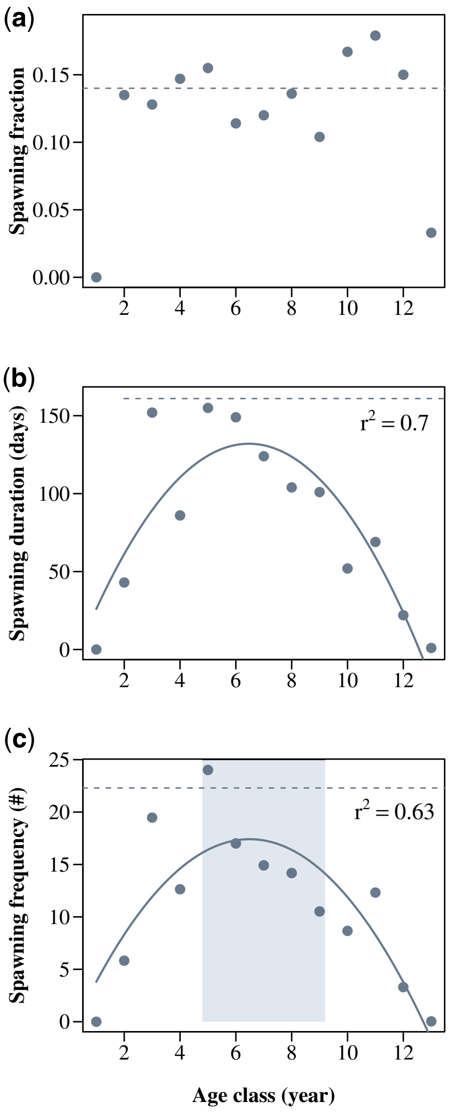

**Figure 4.** Observed (filled circles) PS (a); SD (b); and SF (c) as a function of age class in scamp. Second-order polynomial models fitted to the data and plotted when significant (solid lines). Dashed lines represent overall PS (0.14), SD (161), and SF (22.3) for all mature females. Shaded region shows peak range of age at sexual transition (Harris *et al.*, 2002).

22.3) and below previously reported estimates (gag = 38 batches; scamp = 42); these earlier estimates actually represent the maximum SF, independent of size or age, because females that were regressing or regenerating during the spawning season were excluded from analyses (see Harris *et al.*, 2002; Reichert and Wyanski, 2005). Furthermore, spawning parameters such as PS, SD, and SF have been documented to be both age- and size-dependent in multiple marine, batch-spawning fishes (Trippel *et al.*, 1997; Collins *et al.*, 2001; Fitzhugh *et al.*, 2012; Porch *et al.*, 2015).

Klibansky and Scharf (2018) found the PS and SF of another protogynous hermaphrodite (black sea bass, *Centropristis striata*) to have dome-shaped relationships with size. They proposed that these patterns might be explained by the protogynous reproductive strategy of the species. To maximize lifetime fitness, fishes may adjust their reproductive investment throughout their lifespan (McBride *et al.*, 2015); therefore, protogynous hermaphrodites may trade-off reproductive effort between current female success and future male success. Gilmore and Jones (1992) observed that large gag and scamp, likely males, engage in aggressive displays towards smaller individuals as a form of establishing dominance, suggesting that large males have increased reproductive success. Thus, the largest females, which have already reached a peak in their female reproduction, may shift the energy invested in egg production towards male reproductive effort (e.g. gonadal transformation, energy for displays) to increase their lifetime reproductive success.

In addition, the spawning parameter relationships in our data were species-specific, perhaps reflecting the characteristic ranges of age- and size-at-transition for each species. This suggests that the nature of the sexual transition might be an important driver of the shape of these relationships. The more restricted ranges of age- and size-at-transition in gag could be leading to stronger spawning parameter relationships for this species, with sharper, more defined peaks at later ages and sizes. Because few gag are transitioning at younger ages and smaller sizes, the PS increases with age and TL and does not decrease until reaching the ages and sizes at which sexual transition occurs. In contrast, the wider ranges of age- (2–16 years) and size-at-transition (400–850 mm) in scamp (Harris *et al.*, 2002) could be reflected in the earlier, wider peaks and weaker relationships we observed for this species. Understanding these species-specific patterns is paramount because a species with stronger relationships could be more susceptible to changes in stock composition that can result from size-selective fisheries.

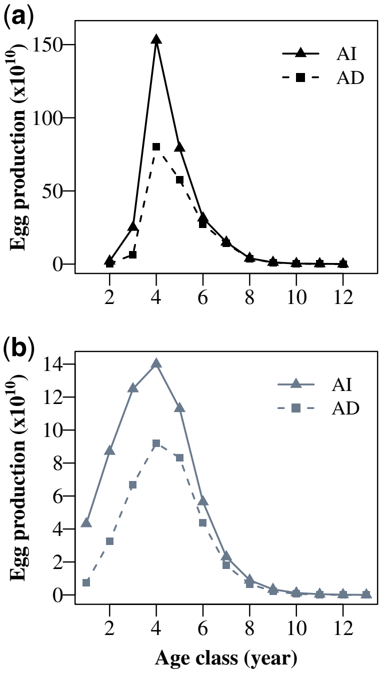

**Figure 5.** Egg production-at-age for gag (a) and scamp (b), based on AI and AD spawning frequencies.

This study provides support for the hypothesis that sexual transition may be an important driver of the age- and size-dependence of spawning in protogynous fishes. However, Klibansky and Scharf (2013) described the SF and PS of red porgy (*Pagrus pagrus*), a batch-spawning protogynous hermaphrodite, as size-dependent, but not dome-shaped. Red porgy is in the family Sparidae, whereas the species with reported dome-shaped relationships (gag, scamp, and black sea bass) are in the family Serranidae. Further investigation should be conducted to understand whether these dome-shaped relationships can be found in other protogynous hermaphrodites.

## Egg production

Improving our understanding of spawning dynamics is paramount due to their influence on the reproductive potential of the stock. We found for both species that AD estimates of egg production, by age class and overall, were consistently lower than AI estimates, with the differences between methods being greatest for the youngest and oldest females. When accounting for age-based variation in spawning activity, we saw that females are not producing as many eggs as would be assumed when using an AI SF. Similarly, the age- and size-dependence of spawning has been shown to influence egg production and fecundity of other marine fishes (Kjesbu *et al.*, 1996; Roumillat and Brouwer, 2004; Klibansky and Scharf, 2018).

Our egg production estimates also reflected how the demographic structure of the population can have a considerable influence on TEP. Removing differences in scale and comparing proportions of TEP at age, the AD method showed that the youngest and oldest females have a much lower relative contribution to the stock than previously thought. It also revealed that TEP in gag is concentrated within fewer age classes than in scamp. Furthermore, for both species, the proportion of population TEP and the percentage of the overall difference in TEP (between methods) were highest from young females that had not yet reached peak spawning activity, but were more abundant in the population. Protection of the younger females, therefore, could have a disproportionate impact on population TEP. However, younger females are thought to have a reduced reproductive

**Table 4.** Egg production-at-age and TEP for gag, based on AI and AD estimates of SF.

| Age (years) | BF ($\times10^3$) | $N$ ($\times10^3$) | PF | PM | SF | AI egg production ($\times10^9$) | AD egg production ($\times10^9$) | %D | Percentage of total %D |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 161.3 | 61.21 | 1.00 | 0.07 | 3.7 | 20.32 | 2.58 | −87.3 | 1.5 |
| 3 | 242.0 | 73.48 | 1.00 | 0.48 | 7.5 | 250.69 | 64.36 | −74.3 | 15.6 |
| 4 | 311.2 | 183.83 | 0.99 | 0.92 | 15.4 | 1525.93 | 801.56 | −47.5 | 60.5 |
| 5 | 366.5 | 79.91 | 0.93 | 0.99 | 21.4 | 791.98 | 577.57 | −27.1 | 17.9 |
| 6 | 408.7 | 32.45 | 0.81 | 1.00 | 25.5 | 315.03 | 273.66 | −13.1 | 3.5 |
| 7 | 439.9 | 17.98 | 0.64 | 1.00 | 27.7 | 149.54 | 141.09 | −5.6 | 0.7 |
| 8 | 462.9 | 6.17 | 0.47 | 1.00 | 28.0 | 39.80 | 37.96 | −4.6 | 0.2 |
| 9 | 479.4 | 2.56 | 0.33 | 1.00 | 26.4 | 11.91 | 10.71 | −10.1 | 0.1 |
| 10 | 491.1 | 1.17 | 0.22 | 1.00 | 22.9 | 3.73 | 2.91 | −21.9 | 0.07 |
| 11 | 499.4 | 0.97 | 0.14 | 1.00 | 17.6 | 2.05 | 1.22 | −40.3 | 0.07 |
| 12+ | 511.6 | 1.00 | 0.05 | 1.00 | 10.3 | 0.68 | 0.24 | −65.1 | 0.04 |
| Total | | | | | 29.4 | 3 111.65 | 1 913.87 | −38.49 | 100 |

Total SF represents the overall SF for all mature females, which was used for the AI estimates. Age class 12+ represents gag aged 12–18 years. %D = per cent difference = [(AD − AI)/AI] ×100. Percentage of total %D = [($AI_a$ − $AD_a$) / ($AI_{Total}$ − $AD_{Total}$)] × 100.
BF, batch fecundity; *N*, number in population; PF, proportion female; PM, proportion mature.

**Table 5.** Egg production-at-age and TEP for scamp, based on AI and AD estimates of SF.

| Age (years) | BF ($\times 10^3$) | *N* ($\times 10^3$) | PF | PM | SF | AI egg production ($\times 10^9$) | AD egg production ($\times 10^9$) | %D | Percentage of total %D |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 20.99 | 238.36 | 0.99 | 0.39 | 3.81 | 43.17 | 7.38 | −82.9 | 14.3 |
| 2 | 39.47 | 147.49 | 0.99 | 0.68 | 8.31 | 87.05 | 32.45 | −62.7 | 21.9 |
| 3 | 63.23 | 102.19 | 0.98 | 0.89 | 11.91 | 125.41 | 66.98 | −46.6 | 23.4 |
| 4 | 91.12 | 73.10 | 0.97 | 0.98 | 14.61 | 140.47 | 92.02 | −34.5 | 19.4 |
| 5 | 121.90 | 43.95 | 0.95 | 1.00 | 16.40 | 113.15 | 83.23 | −26.4 | 12.0 |
| 6 | 154.41 | 17.78 | 0.92 | 1.00 | 17.30 | 56.43 | 43.78 | −22.4 | 5.1 |
| 7 | 187.60 | 6.22 | 0.89 | 1.00 | 17.30 | 23.10 | 17.92 | −22.4 | 2.1 |
| 8 | 220.63 | 2.16 | 0.85 | 1.00 | 16.39 | 8.98 | 6.60 | −26.5 | 1.0 |
| 9 | 252.82 | 0.75 | 0.79 | 1.00 | 14.59 | 3.38 | 2.21 | −34.6 | 0.5 |
| 10 | 283.69 | 0.27 | 0.73 | 1.00 | 11.88 | 1.24 | 0.66 | −46.7 | 0.2 |
| 11 | 312.91 | 0.09 | 0.67 | 1.00 | 8.27 | 0.44 | 0.16 | −62.9 | 0.1 |
| 12 | 340.26 | 0.03 | 0.59 | 1.00 | 3.77 | 0.15 | 0.03 | −83.1 | 0.05 |
| 13+ | 448.54 | 0.02 | 0.23 | 1.00 | 0.06 | 0.04 | 0.0001 | −99.7 | 0.02 |
| Total | | | | | 22.30 | 603.02 | 353.42 | −41.4 | 100 |

Total SF represents the overall SF for all mature females, which was used for the AI estimates. Age class 13+ represents scamp aged 13–22 years. %D = per cent difference = [(AD − AI)/AI] ×100. Percentage of total %D = $[(\mathrm{AI}_a - \mathrm{AD}_a) / (\mathrm{AI}_{\mathrm{Total}} - \mathrm{AD}_{\mathrm{Total}})] \times 100$.
BF, batch fecundity; *N*, number in population; PF, proportion female; PM, proportion mature.

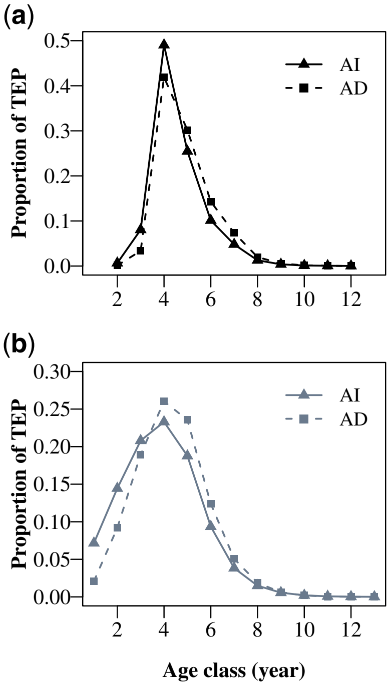

**Figure 6.** Proportion of TEP at age for gag (a) and scamp (b), based on AI and AD spawning frequencies.

value, having lower BF, SD, and SF (Trippel *et al.*, 1997; Wright and Trippel, 2009; Fitzhugh *et al.*, 2012). In a size-truncated stock, the productivity of smaller, younger females alone may not be high enough to replenish the population (Trippel, 1995; Trippel *et al.*, 1997); therefore, it is important to ensure the stock demographic structure is maintained rather than enabling size-selectivity.

Our results support the growing body of evidence that not all mature individuals contribute equally to reproductive output (Lowerre-Barbieri, 2009; Fitzhugh *et al.*, 2012) and highlight the importance of maintaining demographic structure by protecting spawners of all ages and sizes (Berkeley *et al.*, 2004; Hixon *et al.*, 2014). Assuming that all females, regardless of age or size, have the same reproductive value can lead to inaccurate estimates of stock productivity. Using age-based reproductive parameters in future calculations should strengthen stock–recruit models (He *et al.*, 2015) and yield productivity estimates that represent the biology and population dynamics of the stock more accurately. Improved productivity estimates could lead to more successful rebuilding strategies, thus ensuring the sustainability of these stocks. Furthermore, these improved methodologies could be incorporated into assessments to better inform management of other sex-changing, batch-spawning fishes worldwide.

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