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ARTICLE

Size-Dependent and Temporal Variability in Batch Number and Fecundity of Red Porgy, a Protogynous, Indeterminate Spawner, in the U.S. South Atlantic

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Abstract

Contemporary studies have shown that spawning stock biomass can be a poor estimator of total egg production, with the inclusion of fecundity tending to improve stock–recruit relationships. Since many U.S. fisheries now use spawning potential ratio (SPR) to define overfishing, an understanding of fecundity variation is especially valuable. We studied a commercially important, protogynous sparid, the Red Porgy *Pagrus pagrus*, off the southeast U.S. coast from 2007 to 2010 to estimate annual fecundity (f_a) as a function of batch fecundity (f_b) and batch number (n_b) and to investigate size-based and temporal variation. In total, 1,355 Red Porgy (241–478 mm TL) were collected; subsets of individuals were selected for estimating maturity, n_b, and f_b. Throughout the spawning season, the proportion of females that were capable of spawning increased to 100% on several dates and was generally higher among smaller females than current maturity information would predict. The proportion of females that were actually spawning was also as high as 100% on several dates, suggesting periods of daily spawning. Batch fecundity was positively related to TL, and the relationship varied significantly between years and among months within years. Spawning fraction (and thus n_b) was also size dependent, with relationships varying between years and dependent upon the reproductive indicator used in calculation (i.e., spawning capability, postovulatory follicle presence, or hydrated oocyte presence). Annual fecundity estimates incorporating size-dependent n_b differed from estimates assuming size-independent n_b and varied between years. Through its effect on f_a, the size dependence of n_b ultimately affected perceptions of how fishing mortality rate influenced the SPR. Our findings show the importance of accounting for size-dependent variation in n_b when calculating f_a in indeterminate-spawning species and illustrate the potential implications for stock–recruit relationships and stock exploitation status.

Estimates of spawning stock size are incorporated into both stock–recruit relationships and the calculation of biological reference points, such as the spawning potential ratio (SPR; Table 1; Goodyear 1993; Fitzhugh et al. 2012). The number of eggs produced (population fecundity, f_π) is the best measurement of reproductive potential (Hilborn and Walters 1992); however, since f_π is difficult to estimate, fishery models usually incorporate alternative measures like spawning stock biomass (SSB), which is calculated from total mature biomass or mature female biomass. The use of SSB as a proxy for f_π in stock assessments involves several assumptions, including (1) all mature females spawn, (2) f_π is a linear function of total female biomass, and (3) the relationship between f_π and female biomass does not vary over time (Marshall et al. 2003). These assumptions can be violated for both biological and methodological reasons.

The assumption that all mature females spawn is violated if mature females skip spawning or if some individuals are simply misidentified as mature. Recent evidence indicates that individuals of many species may periodically skip spawning (Rideout

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TABLE 1. Definitions of frequently used symbols and abbreviations.

Abbreviation	Description
d	Spawning season duration
f_a	Fecundity, annual
f_b	Fecundity, batch
f_π	Fecundity, population
HO	Hydrated oocyte
n_b	Batch number
$n_{b,I}$	Batch number, integral method
p	Spawning fraction
POF	Postovulatory follicle of any age
POF_0	Postovulatory follicle(s) less than 1 d after ovulation
SC	Spawning capable
SPR	Spawning potential ratio
SSB	Spawning stock biomass
TL_{50}	Total length at the point of inflection of a logistic function
TW	Total weight

and Tomkiewicz 2011); thus, even fish that have spawned previously may not spawn in all future years. Determining whether an inactive fish is mature can be technically difficult, so the error rate when assigning maturity phases to inactive fish is likely to be high. Even histological techniques, which are widely accepted as the most accurate methods for determining maturity, cannot usually predict skipped spawning in individuals that have been captured outside of the spawning season. This is because reliable indicators of past or future spawning may not be present at times outside of the main reproductive season. The best way to determine the relationship between fish size and involvement in spawning is to assess maturity either immediately prior to or during the active spawning season, when all females that are about to spawn show clear signs of development and when no (or very few) individuals have completed spawning and regressed (Hunter and Macewicz 2003).

When SSB is used as a direct proxy for reproductive output, f_π is assumed to be a linear function of the total weight of all females in the stock. This assumes that a given mass of mature females will always produce the same number of eggs, regardless of the size distribution of individuals. If the true relationship is instead curvilinear, the assumption is violated. If, for example, individual fecundity is a power function of weight, then the use of SSB as a proxy for f_π could simultaneously overestimate and underestimate egg production of the smallest and largest females, respectively (Marshall et al. 2006).

Temporal instability in the relationship between individual fecundity and female body size can also introduce error into the relationship between f_π and SSB, thereby introducing error into the stock–recruit relationship (Marshall et al. 2003). Despite the general paucity of fecundity data, even for many well-studied species in the Northwest Atlantic (Tomkiewicz et al. 2003), extensive studies on Atlantic Cod *Gadus morhua* suggest that temporal variation in fecundity is rather common (Kjesbu et al. 1998; Kraus et al. 2000; McIntyre and Hutchings 2003; Yoneda and Wright 2004; Klibansky 2006). In some instances, variable egg production has been correlated with food availability or water temperature; however, simple environmental correlates have mostly failed to predict observed fluctuations in fecundity (Lambert et al. 2003). Instead, current research has generally been focused on developing simpler methodologies that will allow fecundity–body size relationships to be estimated routinely (Witthames et al. 2009; Armstrong and Witthames 2012).

Estimation of fecundity is often difficult since most fish produce large numbers of small eggs, but it can be particularly challenging to estimate fecundity for species with indeterminate fecundity (hereafter, "indeterminate species"). For such species, fecundity is not fixed prior to the start of spawning, so oocyte counts for individual females do not accurately reflect annual fecundity (f_a). To estimate f_a in indeterminate species, the number of batches (n_b) of eggs produced by a female during the season is multiplied by batch fecundity (f_b), which is the number of oocytes spawned in a single batch (Kjesbu 2009). Typically, n_b is calculated as the product of spawning season duration (d) and the spawning fraction (p), which is estimated as the proportion of mature females that are found to possess reproductive indicators, such as hydrated oocytes (HOs) or postovulatory follicles (POFs), when caught during the spawning season (Murua et al. 2003). As with f_a for determinate species (Duarte and Alcaraz 1989), f_b often scales positively with body size among indeterminate species (Harris et al. 2002; McBride and Thurman 2003; Ganias et al. 2004). Although it is commonly assumed that n_b does not vary with size or age, a recent review showed that most studies (32 of 41) investigating this issue found that spawning frequency, and thus n_b, varied with size or age (Fitzhugh et al. 2012). In some cases, variation in n_b can be the primary cause of variable f_a (Collins et al. 1996; Wootton and Fletcher 2009). Therefore, studies estimating f_a for indeterminate species should determine the extent of variation in n_b as well as f_b.

The Red Porgy *Pagrus pagrus* is a protogynous hermaphrodite (Alekseev 1982) that has been shown to be indeterminate (Daniel 2003). The species is found on reefs along continental shelf margins and is broadly distributed in the Atlantic, with three genetically distinct populations (Ball et al. 2003). In the U.S. South Atlantic Bight (SAB), Red Porgy support an economically important fishery that ranked 11th in total (1985–2008) landings among 73 species included in the snapper–grouper management complex (National Oceanic and Atmospheric Administration [NOAA], fisheries statistics; www.st.nmfs.noaa.gov/st1). The SAB stock is considered overfished, and current landings are an order of magnitude lower than landings observed two decades ago. Macroscopic staging and gonadosomatic index data suggest that the main spawning season for Red Porgy in the SAB occurs from January to March (Manooch 1976). Previous histological staging data revealed a decrease in length at maturity between 1979 and 1994 (Harris

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and McGovern 1997); age at 50% maturity was recently estimated at 1.5 years, and size at 50% maturity was estimated at 289 mm TL (Daniel 2003). A positive relationship between f_b and TL has also been noted previously (Daniel 2003).

To date, the vast majority of data used to determine age- and size-dependent maturity relationships for Red Porgy in the SAB have been collected during periods outside of the spawning season, and this may have compromised accuracy in some cases. Further, no authors have investigated the relationship between n_b and body size or evaluated the level of interannual variation in either f_b or n_b. Because the basic reproductive biology of Red Porgy is very similar to that of many other members of the snapper–grouper complex, an improved understanding of the factors influencing egg production in Red Porgy has the potential to benefit the management of multiple valuable fishery resource species.

METHODS

Field collections.—We sampled the SAB stock of Red Porgy during the spawning season over three consecutive years (2007–2008, 2008–2009, and 2009–2010); however, in 2007–2008, sampling did not begin until midseason. In the latter 2 years (hereafter, "the complete years"), port sampling began in October and occurred regularly until females with spawning-capable (SC) ovaries (i.e., with vitellogenic oocytes that were visible macroscopically) became abundant in the samples, which triggered the start of at-sea sampling. In 2007–2008, all samples were collected through port sampling. In both 2008–2009 and 2009–2010, we conducted at-sea sampling with local commercial hook-and-line fishers throughout the spawning season. When evidence of spawning activity was minimal, at-sea sampling ceased and port sampling resumed for the remainder of the season. Given resource constraints, sampling was designed to maximize temporal resolution within a limited geographic range offshore from Onslow Bay and Long Bay, North Carolina (Figure 1). Since 2000, 84% of SAB Red Porgy commercial landings have been taken off the coasts of South Carolina and North Carolina (NOAA, fisheries statistics; www.st.nmfs.noaa.gov/st1). Therefore, we felt that the spatial extent of our sampling was sufficient to ensure that the implications of our findings would be broadly applicable to the stock, and we chose to focus our efforts on obtaining an improved understanding of temporal variation.

Subsampling and laboratory analysis.—We measured TL for all fish sampled. For a large subset (92%) of fish, sex and maturity were determined macroscopically, and total weight (TW), gutted weight (GW), and gonad weight were each measured before preserving the gonads in a 10% solution of buffered formalin. A group of these fish—from a roughly even distribution of sample dates throughout all seasons—was then selected for histological analysis. Approximately 20 individuals were selected randomly from among all fish caught on each date. For these fish, tissue from the posterior region of the gonad was embedded in paraffin, sectioned, mounted, and stained (Gill's hematoxylin and eosin Y) by staff at the South Carolina Department of Natural Resources (SCDNR). Sex and maturity were determined based on criteria (developed by SCDNR staff) that are used routinely for reproductive analysis of various species as part of the Marine Resources Monitoring, Assessment, and Prediction program. An abbreviated version of this key was presented by Harris and McGovern (1997), whereas a more complete and updated version was provided by Daniel (2003). We note, however, that during our study, traces of atresia could be present but were not necessary for a female to be designated as regenerating (i.e., mature but inactive). Females that exhibited abundant vitellogenic oocytes with less than 50% atresia were deemed to have entered their spawning period and were considered SC. When vitellogenic oocytes were present, they were usually abundant (>200 per histology section) but sometimes were rare (1–10 per histology section); females characterized by the latter were not considered SC. We felt that excluding individuals with only rare vitellogenic oocytes produced a more accurate index of true spawning capability than simple presence/absence of vitellogenic oocytes. Reproductive terminology used here largely follows that presented by Brown-Peterson et al. (2011).

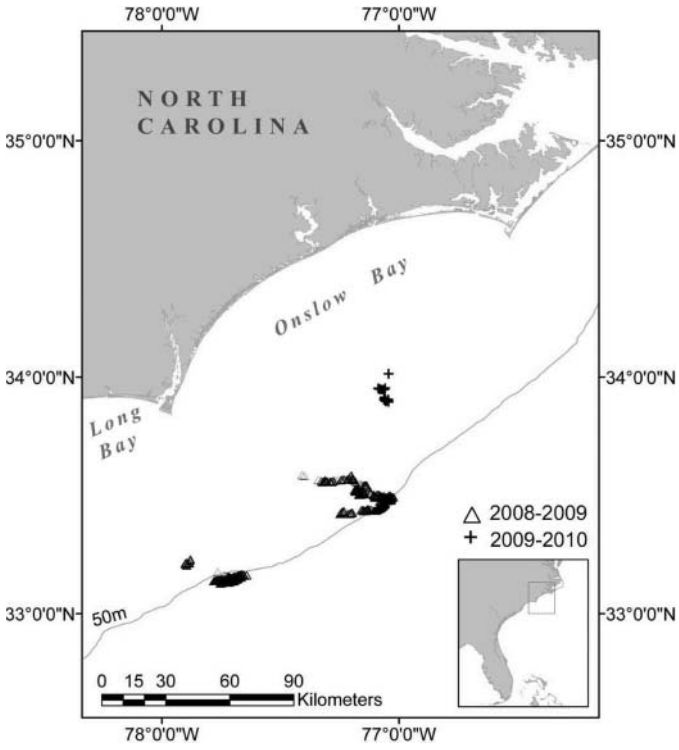


FIGURE 1. Spatial distribution of directed trip sampling locations for Red Porgy during 2008–2009 and 2009–2010. The small rectangle in the inset shows the area covered by the larger map.

Discrimination of postovulatory follicle age.—Although POF degeneration in Red Porgy generally agreed with descriptions provided by Hunter and Macewicz (1985) and although the sea surface temperatures we recorded during the Red Porgy spawning season (14.7–19.0°C) were similar to what

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those authors reported for Pacific Sardine *Sardinops sagax* and Northern Anchovy *Engraulis mordax* (13–19°C), we devised a procedure to help discriminate day-0 POFs (POF_0) that were less than 24 h old from older POFs. Discrimination was possible because many Red Porgy ovaries contained two consecutive daily POF cohorts. First, we identified females collected near the daily spawning peak that contained both a cohort of very recent POFs and a cohort of POFs that appeared similar to published descriptions of 24-h-old POFs (Hunter and Macewicz 1985). We then took images of POFs from both cohorts and used them as reference images to define the morphological endpoints of POF degradation during a 24-h period (Figure 2). In subsequent samples, POFs that were morphologically intermediate between these two endpoints were assigned to the day-0 cohort (POF_0). A similar procedure was not reliable for discriminating 48-h-old POFs, and temporal discrimination was also not possible for HOs; thus, we considered POF_0 to be the most accurate reproductive indicator for Red Porgy.

Estimation of batch fecundity.—For each preserved ovary, we used a syringe to remove subsamples (~0.2 g) of tissue from the anterior and posterior regions and stored them in vials containing 10% buffered formalin. Procedures to count oocytes in the most advanced cohort (including germinal vesicle migration [GVM], germinal vesicle breakdown [GVBD], and/or HOs) generally followed Klibansky and Juanes (2008). Females containing very recent POFs were excluded from f_b analysis. Images were captured with a flatbed scanner (Epson Perfection V500) using predefined settings (8.9 × 8.9 cm; 8-bit gray scale at 2,400 dpi; 8,400 × 8,400 pixels; uncompressed TIFF; 67.2-megabyte file size). The varied size and appearance of GVM, GVBD, and HOs in images resulted in poor automated counts, so we manually counted oocytes by using the Cell Counter plug-in, which took very little time (5–10 min/sample).

Statistical analysis.—We used logistic regression to examine the size dependence of several binary response variables for Red Porgy, including maturity, sex, spawning capability, POF_0 presence, and HO presence. For maturity and sex, we used data from all dates to develop maturation and sex transition ogives. For the latter three variables, we only used data collected within the SC season to calculate size-dependent n_b. To test for interannual differences in these relationships, we first fit a logistic model that included terms for the intercept, slope, year, and the TL × year interaction (β_0, β_1, β_2, and β_3, respectively) to validate the assumption of no interaction. If β_3 was not significant, we then fit the model without β_3 to test the significance of β_2 (Hosmer and Lemeshow 1989; Dalgaard 2008). If either term was significant, we concluded that the models differed between years. For each significant two-parameter model, we calculated the point of inflection (TL_{50}) as $\beta_0/-\beta_1$ (Jennings et al. 2001). We used linear regression to investigate the relationship between f_b, GW, TL, and age. Analysis of covariance (ANCOVA) was used to test for interannual and intermonth differences in f_b when within-group regression slopes were homogeneous. After performing ANCOVA, we calculated relative f_b as $[\log_e(f_b)]/(\text{mm TL})$ to visually compare f_b adjusted for body size among months within 2008–2009 and 2009–2010. All statistical analyses were conducted using the base package of R version 2.14.0.

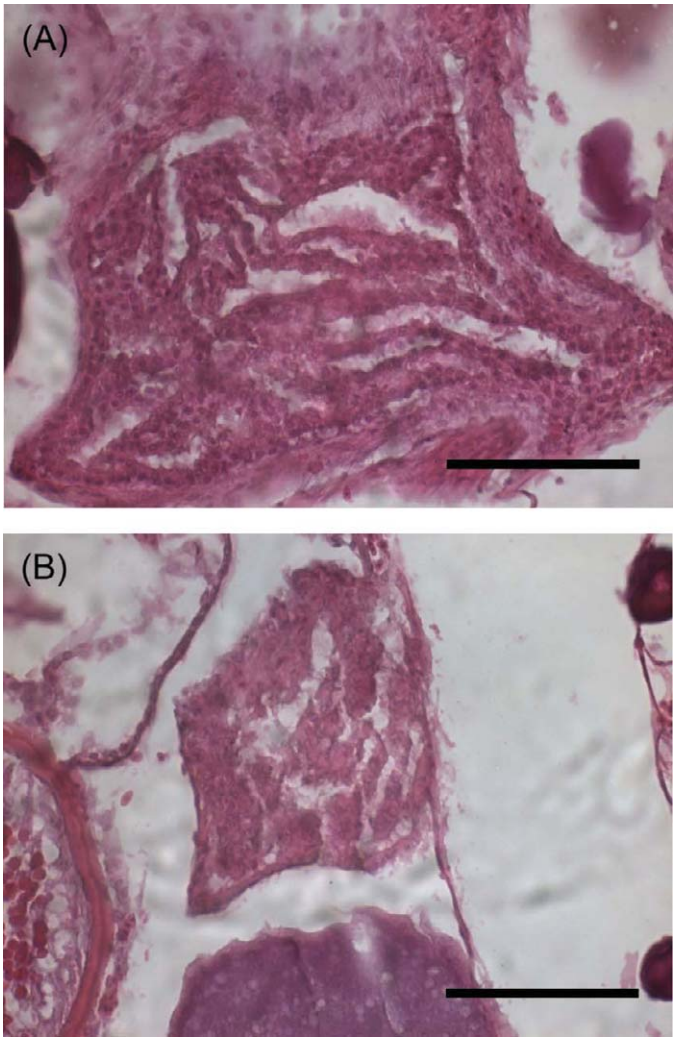


FIGURE 2. Postovulatory follicles (POFs) from two consecutive cohorts in the same female Red Porgy, defining the morphological endpoints of POF degeneration within the first 24 h of ovulation; examples of the largest and newest POFs from **(A)** the POF cohort that just appeared after spawning (0 h old) and **(B)** the previous cohort (24 h old) are shown (scale bar = 100 μm).

Calculations.—Although our calculations largely follow established standards, we provide details below for clarity. We estimated f_b via the method of Hunter et al. (1985) as the number of GVM, GVBD, and HOs per gram of tissue (averaged for two samples) multiplied by the formalin wet weight of both ovaries. We calculated n_b as the product of p and d (Murua et al. 2003). We calculated p as the number of spawning females divided by the number of SC females (Hunter and Goldberg 1980). We estimated p separately by using the presence of either POF_0 or HOs as the reproductive indicator. We present both estimates to enable comparison with other studies, but we considered p based on POF_0 to be more accurate since the stage duration could be

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calibrated to 24 h. We estimated d as the number of days between the first and last sampling dates on which at least one female was detected with a reproductive indicator; three separate estimates of d were obtained using spawning capability, HO presence, or POF_0 presence as the reproductive indicator. The separate estimates of p and d were used to explore how the selection of HOs or POF_0 as the reproductive indicator influenced the calculation of n_b.

Estimates of n_b calculated by using the standard approach ($p \times d$) will only be accurate when the initial date and duration of all spawning periods are the same for all females, thereby producing a distribution of p that is uniform across time. Since a strictly uniform distribution is unlikely, the method of piecewise integration used by Hunter and Leong (1981) should be more accurate. We estimated n_b using the integral method ($n_{b,I}$) as

$$n_{b,I} = \sum_{i=1}^{z-1} \frac{|p_{i+1} - p_i|\,(t_{i+1} - t_i)}{2} + \min(p_{i+1}, p_i)\,(t_{i+1} - t_i), \quad (1)$$

where z is the total number of sampling dates, p_i is the estimate of spawning fraction for the ith sampling date, min() is a function indicating that only the minimum of the set of values in parentheses should be used, and t_i is the ordinal date for the ith sampling date. We completed calculations separately for each year and also for the combined data from the two complete sampling years.

Standard calculations of p essentially fit a horizontal-line model to POF_0 presence or HO presence and TL, leading to a size-independent estimate of n_b. Building on the work of Collins et al. (1998), who calculated n_b for discrete age-groups, and Lowerre-Barbieri et al. (2009), who used logistic regression to test for a relationship between binary reproductive indicators and TL, we calculated three types of size-dependent n_b estimate.

For the first two types, we tested for significant logistic fits between POF_0 or HO presence and TL in females collected during the spawning season based on spawning capability (hereafter, "SC season"). We used significant models to estimate size-dependent p (p_{TL}) and then calculated size-dependent n_b as the product of p_{TL} and d, yielding separate estimates for POF_0 presence and HO presence. For the third type of estimate, we fit the logistic model to spawning capability and TL and used significant relationships to estimate the size-dependent proportion of d for which females were SC ($P[d]_{TL}$). Multiplying $P(d)_{TL}$ by d yields a size-dependent estimate of d (d_{TL}); multiplying d_{TL} by size-independent p (based on POF_0) produced the third type of size-dependent estimate of n_b.

Since Red Porgy are indeterminate, f_a is estimated as the product of f_b and n_b. We estimated the size-dependent f_b by using linear regression as described above; we then multiplied the size-dependent f_b by the size-independent $n_{b,I}$ and each of the three size-dependent estimates of n_b, thus producing a total of four types of f_a calculation. We then converted TL to TW based on a TL–TW relationship (SEDAR 2006) to examine the relationship between f_a and biomass.

To investigate how different calculations of f_a affect the perceived impact of fishing on reproductive potential, we calculated SPR in several ways. Goodyear (1993) defined SPR as potential fecundity per recruit (f/R) in the presence of fishing divided by the f/R in the absence of fishing. We calculated SPR over a range of fishing mortalities by using the four types of f_a to estimate f/R and then separately by using SSB/R based on mature female biomass, a standard proxy for f/R. Calculations of SPR followed the method of Gabriel et al. (1989) and used parameter estimates from this study and from the most recent period (1999–2004) described in the 2006 stock assessment (SEDAR 2006).

RESULTS

Sex and Maturity by Size

In total, 1,355 Red Porgy were returned to the laboratory and examined macroscopically. From these, 823 fish were selected for histological analysis (Table 2). The logistic regression relating sex to TL for the two complete reproductive seasons that we sampled (2008–2009 and 2009–2010) revealed a significant interaction ($P = 0.04$, $n = 636$; Table 3) between size and year effects and thus interannual variation in the size at sex transition. Within each year, sex was significantly related to TL ($P < 0.001$, $n = 341$ for 2008–2009 and 295 for 2009–2010). All of the Red Porgy females that we encountered were mature; thus, TL at 100% maturity was not greater than 241 mm TL—the minimum size of Red Porgy females sampled in our study.

Spawning Capability

Since sampling in 2007–2008 began in the middle of the SC season, d based on spawning capability was not calculated for that year. For the 2008–2009 and 2009–2010 seasons, d based on spawning capability was estimated to be 159 and 165 d, respectively (Table 4), with evidence for a single SC season in each year (Figure 3).

The logistic regression relating spawning capability to TL for the two complete reproductive seasons detected a highly significant interaction ($P < 0.001$, $n = 442$; Table 3) between size and year effects. When examined separately for each year, spawning capability was not related to TL in 2008–2009 ($P = 0.814$, $n = 224$) but was positively related to TL in 2009–2010 ($P < 0.001$, $n = 218$; Table 3; Figure 4).

Spawning Fraction and Batch Number

Several estimates of p, d, and n_b were generated by using the different reproductive indicators (Table 4). In 2007–2008, the presence of POF_0 yielded an estimate of p equal to 0.20 and the presence of HOs yielded a p-estimate of 0.34; however, since sampling began in the middle of the SC season, d and n_b could not be determined (Figure 3). In 2008–2009, POF_0 presence yielded an $n_{b,I}$ estimate of 82, and HO presence yielded an $n_{b,I}$

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TABLE 2. Total number of Red Porgy that were phased macroscopically; the number of fish included in the histologically phased subsample by year, month, and sex; and the TL range for each group. Females are further delineated by the presence of reproductive indicators; individual spawning-capable (SC) females may contain day-0 postovulatory follicles (POF_0), hydrated oocytes (HO), both, or neither.

		Total			Subsample					
Data set	Month	TL (mm)	Males	Females	TL (mm)	Males	Females	SC	POF_0	HO
2007–2008	Dec	361–435	16	11	361–435	12	8	8	2	3
	Feb	292–471	32	49	292–471	23	36	36	7	7
	Mar	303–432	27	12	303–432	27	12	12	2	9
	Apr	326–410	6	9	326–410	6	9	3	0	0
	May	308–370	11	9	308–370	13	7	0	0	0
	Jun	351–441	5	17	351–441	6	14	0	0	0
	All	**292–471**	**97**	**107**	**292–471**	**87**	**86**	**59**	**11**	**19**
2008–2009	Oct	347–437	2	3	347–437	2	3	0	0	0
	Nov	308–431	24	20	308–431	24	19	12	1	4
	Dec	320–443	25	34	320–443	19	24	24	6	20
	Jan	257–454	40	97	257–409	14	73	73	46	13
	Feb	243–455	38	106	274–420	22	56	53	44	12
	Mar	273–415	22	40	273–415	22	40	35	31	20
	Apr	305–393	10	18	305–393	10	17	3	1	1
	All	**243–455**	**161**	**318**	**257–443**	**113**	**232**	**200**	**129**	**70**
2009–2010	Oct	317–417	6	13		0	0	0	0	0
	Nov	284–387	3	30	296–387	2	17	6	0	0
	Dec	308–373	11	16	308–373	8	12	9	0	0
	Jan	241–457	32	227	241–457	18	88	86	81	72
	Feb	245–462	26	72	265–462	10	30	28	26	18
	Mar	252–478	49	105	252–416	23	49	16	13	11
	Apr	282–435	38	43	282–426	16	23	9	2	0
	All	**241–478**	**165**	**506**	**241–462**	**77**	**219**	**154**	**122**	**101**

estimate of 54; in 2009–2010, the $n_{b,I}$ estimates were 98 and 76, respectively.

The logistic regression relating POF_0 presence to TL for the complete years (both years combined) produced a highly significant interaction ($P < 0.001$, $n = 442$) between size and year effects. The response of POF_0 presence to TL differed between years, being significantly negative ($P < 0.001$, $n = 224$) in 2008–2009 and significantly positive ($P < 0.001$,

TABLE 3. Results from logistic models relating binary response variables to Red Porgy TL (mm). Responses are the proportion of all individuals that were male (Male) and the proportion of females that were spawning capable (SC), possessed day-0 postovulatory follicles (POF_0), or possessed hydrated oocytes (HO). Model terms for the intercept (β_0), slope (β_1), year (β_2), and TL × year interaction (β_3) are presented; the interaction (β_3) was only evaluated for the multiyear data set (TL_{50} = TL at the point of inflection, calculated as $\beta_0/-\beta_1$). The *P*-values are for the last parameter listed for each model.

Data set	Response	β_0	β_1	β_2	β_3	TL_{50}	*P*	*n*
2008–2009 and 2009–2010	Male	−9.64	0.0255	−6.07	0.01		0.040	636
	SC	2.73	−0.0016	−12.87	0.03		<0.001	442
	POF_0	3.53	−0.0096	−11.71	0.03		<0.001	442
	HO	−3.17	0.0070	−3.91	0.01		0.044	442
2008–2009	Male	−9.39	0.0248			378	<0.001	341
	SC	2.72	−0.0016				0.814	224
	POF_0	3.29	−0.0088			372	0.026	224
	HO	−2.64	0.0055				0.127	224
2009–2010	Male	−15.71	0.0400			393	<0.001	295
	SC	−10.47	0.0334			313	<0.001	218
	POF_0	−8.26	0.0246			335	<0.001	218
	HO	−7.09	0.0200			355	<0.001	218

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TABLE 4. Red Porgy spawning fraction (p), spawning season duration (d; number of days), and batch number (n_b) estimates for each data set and each reproductive indicator (indicators: SC = spawning capability; POF_0 = presence of day-0 postovulatory follicles; HO = presence of hydrated oocytes). Estimates of n_b calculated by using the integral method ($n_{b,I}$) are also presented.

	p		d			n_b		$n_{b,I}$	
Data set	POF_0	HO	SC	POF_0	HO	POF_0	HO	POF_0	HO
2007–2008	0.20	0.34							
2008–2009	0.72	0.36	159	124	147	89	53	82	54
2009–2010	0.88	0.79	165	106	71	93	56	98	76
2008–2009 and 2009–2010	0.79	0.51	169	134	147	106	75	86	68

$n = 218$) in 2009–2010 (Table 3; Figure 4). The logistic regression relating HO presence to TL for the complete years (combined) also produced a significant interaction ($P = 0.044$, $n = 442$) between size and year effects. The relationship between HO presence and TL was not significant for 2008–2009 ($P = 0.127$, $n = 224$) but was positive and highly significant ($P < 0.001$, $n = 218$) for 2009–2010 (Table 3; Figure 4).

Batch Fecundity

When data were pooled across all three years, TL was a better predictor of f_b ($r^2 = 0.142$) than was GW ($r^2 = 0.112$). Natural log transformation of f_b removed heteroscedasticity and improved both fits ($r^2 = 0.155$ and 0.136, respectively; Table 5). Since TL and $\log_e(f_b)$ had the strongest relationship, we used these variables in further analyses. The ANCOVA revealed a significant effect of year on f_b when all years were included ($P < 0.001$, $n = 285$; Table 6; Figure 5). Year remained a significant factor when only the two complete sampling years were included ($P = 0.002$, $n = 276$; Table 6). Separate ANCOVA models for each year detected significant effects of month within 2008–2009 ($P < 0.001$, $n = 82$) and 2009–2010 ($P < 0.001$, $n = 193$; Table 6). Box plots showed that relative f_b was higher in the middle of the season and lower during earlier and later portions of the season (Figure 6). Variation in TL explained much higher proportions of variation in $\log_e(f_b)$ for several monthly data sets than for the data set that included all years (Table 5). The two highest r^2 values were observed for January 2010 ($r^2 = 0.344$, $n = 140$) and February 2010 ($r^2 = 0.427$, $n = 36$).

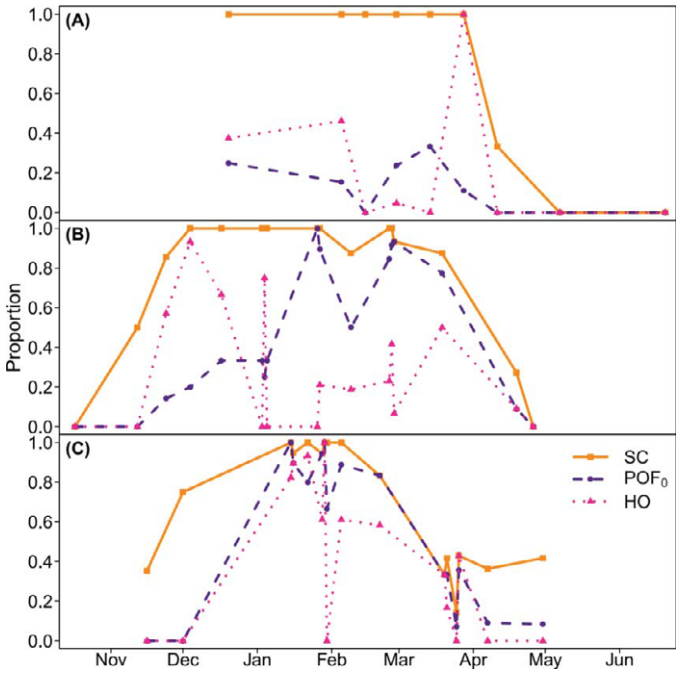


FIGURE 3. Proportion of female Red Porgy on each sampling date that were spawning capable (SC), possessed day-0 postovulatory follicles (POF_0), or possessed hydrated oocytes (HO) during **(A)** 2007–2008, **(B)** 2008–2009, and **(C)** 2009–2010. Tick marks along the x-axis indicate the first day of each month.

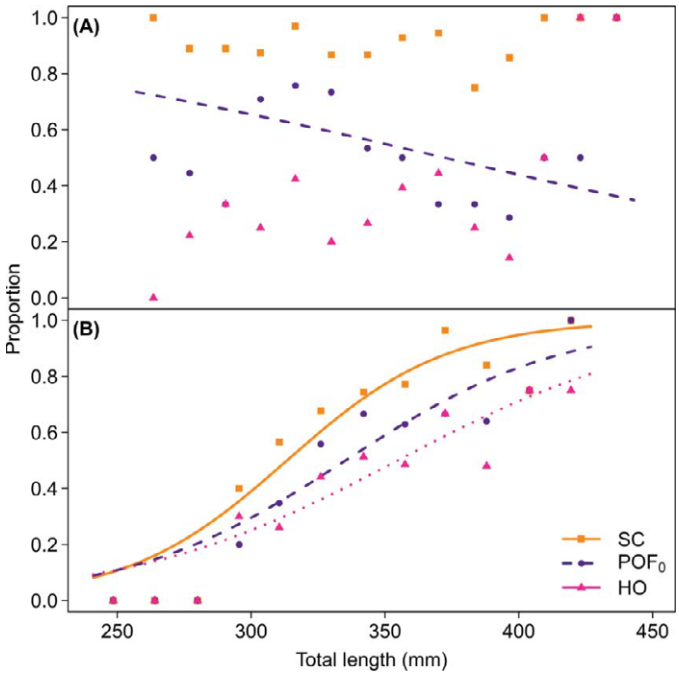


FIGURE 4. Presence or absence of reproductive traits as a function of body size for female Red Porgy sampled in **(A)** 2008–2009 and **(B)** 2009–2010. Lines are fitted logistic functions; points are observed proportions (within size-bins) of spawning-capable females (SC), females that possessed day-0 postovulatory follicles (POF_0), or females that possessed hydrated oocytes (HO).

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TABLE 5. Batch fecundity (f_b) regressions for Red Porgy in each data set. Models estimating $\log_e(f_b)$ are presented in exponential form (GW = gutted weight, g; TL = total length, mm; r^2 = coefficient of determination). The *P*-values are for the regression slope in each model.

Data set	Predictor	Model	β_0	β_1	*P*	r^2	*n*
All years	GW	Linear	−5,100	26.798	<0.001	0.112	275
All years	TL	Linear	−31,869	148.24	<0.001	0.142	285
All years	GW	Exponential	8.83	0.00159	<0.001	0.136	275
All years	TL	Exponential	6.79	0.00835	<0.001	0.155	285
2008–2009 and 2009–2010	TL	Exponential	6.58	0.00891	<0.001	0.172	276
2007–2008[a]	TL	Exponential	6.19	0.01190	0.029	0.518	9
2008–2009	TL	Exponential	6.71	0.00902	<0.001	0.141	83
2009–2010	TL	Exponential	6.14	0.00995	<0.001	0.234	193
Nov 2008	TL	Exponential	11.40	−0.00610	0.458	0.293	4
Dec 2008	TL	Exponential	3.97	0.01570	0.007	0.295	23
Jan 2009	TL	Exponential	8.47	0.00471	0.227	0.232	8
Feb 2009	TL	Exponential	7.64	0.00767	0.012	0.198	31
Mar 2009	TL	Exponential	5.40	0.01140	0.106	0.176	16
Jan 2010	TL	Exponential	5.64	0.01100	<0.001	0.344	140
Feb 2010	TL	Exponential	5.61	0.01290	<0.001	0.427	36
Mar 2010	TL	Exponential	7.58	0.00510	0.576	0.021	17

[a]All observations for this data set are from March 2008.

Annual Fecundity and Spawning Potential Ratio

In 2008–2009, estimated f_a that incorporated the size-dependent n_b based on the negative relationship between POF_0 presence and TL was slightly concave-downward relative to TW. This contrasted with the estimated f_a that incorporated size-independent n_b, which demonstrated an exponential increase with TW and was about 200% higher for the largest females (Figure 7A). The SPR was higher when calculated using the estimated f_a based on a size-dependent n_b than when n_b was assumed to be independent of fish size (Figure 8A).

In 2009–2010, estimates of f_a that incorporated size-dependent n_b based on the positive relationship between SC, POF_0 presence, or HO presence and TL all showed positive exponential relationships with TW. The estimate of f_a that incorporated size-independent n_b was also positively related to TW but was 20–30% lower for the largest females (Figure 7B). The SPR was lower when calculated with f_a estimates based on a size-dependent n_b than when no size dependence of n_b was assumed (Figure 8B).

TABLE 6. Results from ANCOVA modeling of the $\log_e$ (f_b) of Red Porgy as a function of year or month, with TL (mm) as the covariate (P_{Slopes} = *P*-value for the test of slope homogeneity; P_{Group} = *P*-value for the test of adjusted means).

Data set	Group	P_{Slopes}	P_{Group}	*n*
All years	Year	0.915	<0.001	285
2008–2009 and 2009–2010	Year	0.711	0.002	276
2008–2009 (Nov–Mar)	Month	0.445	<0.001	82
2009–2010	Month	0.542	<0.001	193

DISCUSSION

Red Porgy Reproductive Output

This study represents the first investigation in which the size at maturity for the SAB Red Porgy stock was based on large sample sizes collected throughout the spawning season. Our

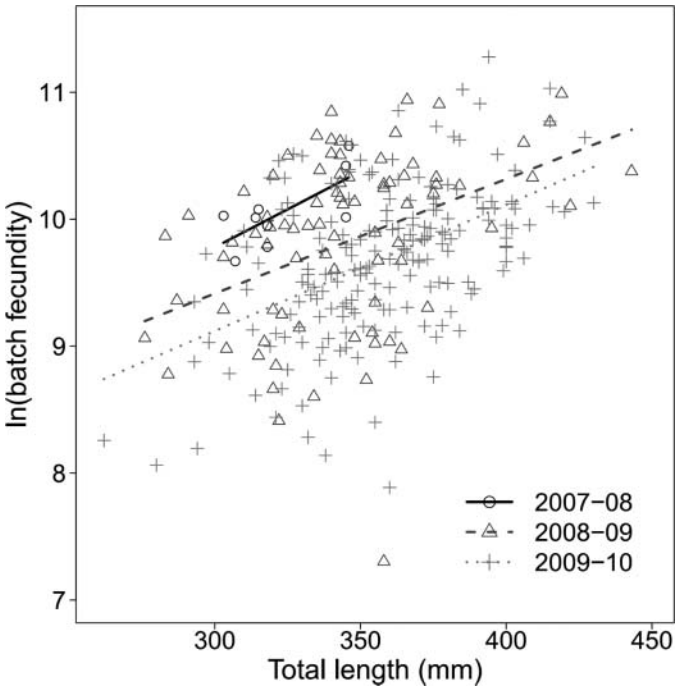


FIGURE 5. Scatter plot of the natural logarithm (ln) of Red Porgy batch fecundity versus TL for each sampling year.

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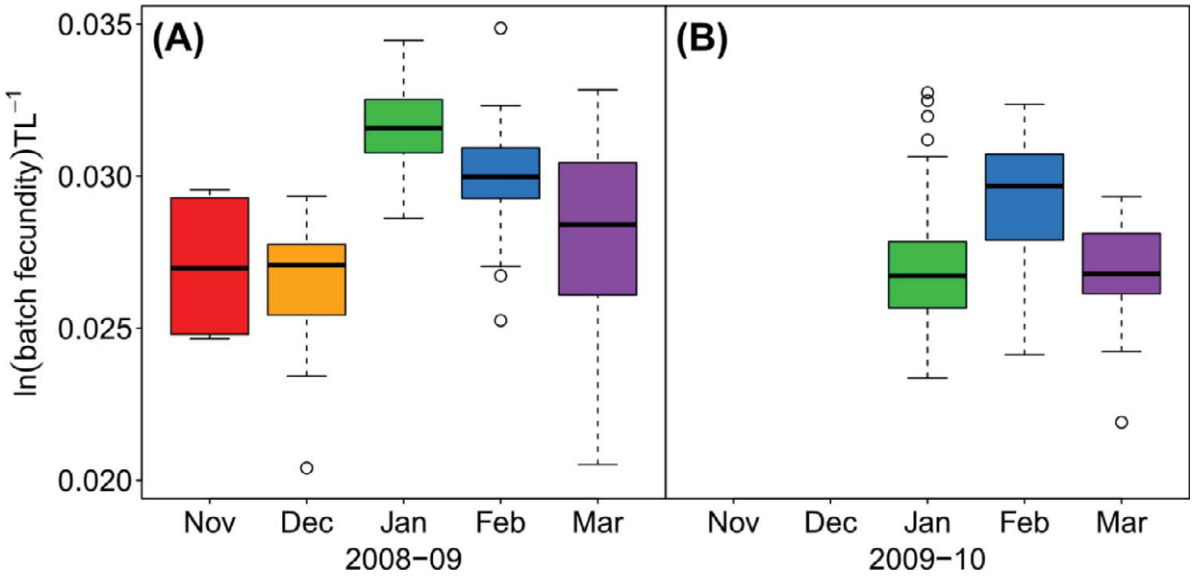


FIGURE 6. Box plots of $\log_e$ (f_b) TL^{-1} for Red Porgy in each sampling month during **(A)** 2008–2009 and **(B)** 2009–2010. Box color corresponds to month. The line within each box represents the median, the lower and upper box ends represent the 1st and 3rd quartiles, and the end of each whisker extends to the most extreme observation within 1.5 times the interquartile range below or above the box. Open circles represent observations outside the whiskers.

findings show that females spawn at smaller body sizes than previous estimates suggest. Prior to this study, the TL_{50} for mature females was estimated separately at 289 mm (Daniel 2003) and 272 mm (SEDAR 2006); however, all of the females that we sampled were mature, including fish as small as 241 mm TL. Since we did not encounter any immature Red Porgy, we could not determine TL_{50} for mature females, but our estimate of TL_{50} for SC females was 255 mm based on both complete years combined. The size when spawning capability is attained should represent an upper estimate of TL_{50} for mature females since some mature fish may not yet have entered their spawning periods. During each year, we also observed a period in which all of the females that we encountered were SC (see Figure 3A–C), suggesting that 100% of females above the minimum TL during those periods spawned. It is important to note that encountering all fish in SC condition also indicates that mature females were unlikely to have skipped spawning.

Since we conducted sampling in and around the spawning season, we were more able to determine maturity than previous studies in which samples were mainly collected after the spawning season, when most mature females were in a regenerating state (Harris and McGovern 1997; Daniel 2003; SEDAR 2006). As was noted by Hunter and Macewicz (2003) in a review of methodologies, even histology cannot always distinguish between regenerating and immature females. In contrast, maturity is often unmistakable during the spawning season, when mature ovaries contain more developed oocytes. Aside from the technical difficulty in distinguishing between regenerating and immature females, the validation of characteristics that are used to make this distinction is strongly lacking. Maturity staging of Red Porgy in this study and other recent studies (Daniel 2003; SEDAR 2006) was largely based on the key developed by Harris and McGovern (1997). However, none of the sources cited in the development of this key actually demonstrated that the characteristics used to distinguish regenerating females from immature females were indicative of maturity. The most relevant of these sources provided a description of gonads from known-age Red Seabream *Pagrus major* (Matsuyama et al. 1988b), but that study neither demonstrated nor suggested that characteristics observed among inactive females indicated maturity. Given this, we suggest that the accuracy of the immature versus regenerating distinction remains in question; furthermore, considering that our data are based primarily on active females, past studies may have overestimated the size at maturity and thus underestimated female spawning stock size.

In our study, female Red Porgy were often found to contain cohorts of both HOs and POF_0. In addition, all females within a sample often contained a cohort of the same reproductive indicator (HOs or POF_0). Together, these observations indicate that Red Porgy were spawning frequently, sometimes daily, with p estimated to be as high as 0.88, yielding one batch every 1.13 d during the spawning season. Published estimates of p exist for nine other snapper–grouper species in the SAB (Collins et al. 1996, 1998; Cuellar et al. 1996; Harris et al. 2002, 2004, 2007; Daniel 2003; Burgos et al. 2007; Danson 2009), with a median p of 0.24 for both POF_0 and HO reproductive indicators. Our findings imply that p in Red Porgy may be much higher than estimates reported for other members of the SAB snapper–grouper complex. Previously, p in Red Porgy has been estimated at 0.37 and 0.40 based on POFs and HOs, respectively (Daniel 2003), although uncertainty in POF

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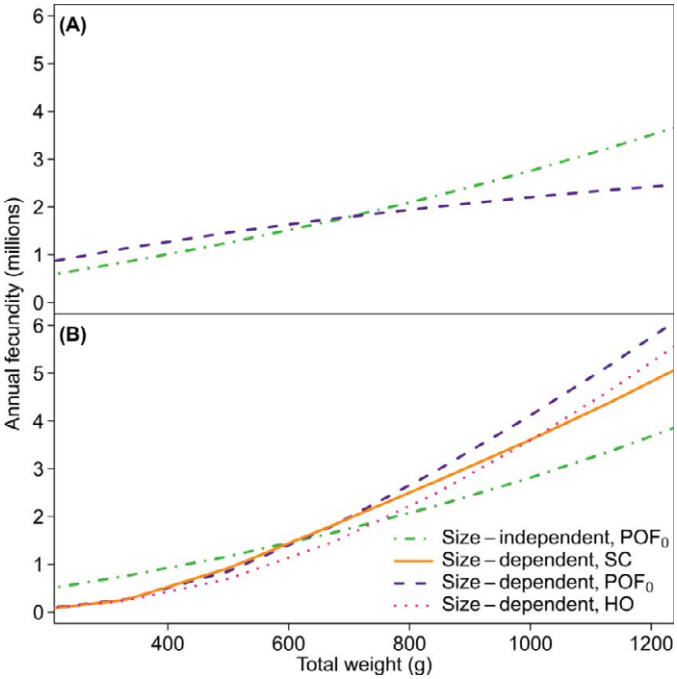


FIGURE 7. Predicted annual fecundity (f_a) versus total weight (g) for Red Porgy sampled during **(A)** 2008–2009 and **(B)** 2009–2010. The f_a was calculated by using a size-independent batch number or by incorporating observed size-dependent relationships based on the proportion of spawning-capable (SC) females, females with day-0 postovulatory follicles (POF_0), or females with hydrated oocytes (HO). During 2008–2009, only POF_0 presence demonstrated a significant relationship with body size.

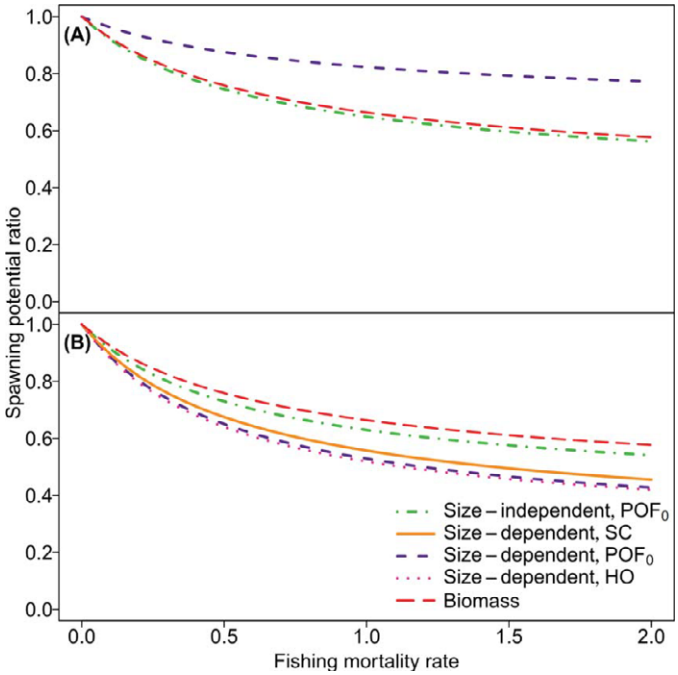


FIGURE 8. Spawning potential ratio (SPR) at different levels of fishing mortality for Red Porgy in **(A)** 2008–2009 and **(B)** 2009–2010. The SPR was calculated from annual fecundity estimated using a size-independent batch number or by incorporating observed size-dependent relationships based on the proportion of spawning-capable (SC) females, females with day-0 postovulatory follicles (POF_0), or females with hydrated oocytes (HO); the SPR calculated using only the biomass of mature females is shown for reference.

duration could have caused a negative bias. Other sparids that exhibit daily spawning include the Bluespotted Seabream *Pagrus caeruleostictus* (Stepkina 1973), Gilthead Bream *Sparus auratus* (Zohar and Gordin 1979), Red Seabream (Matsuyama et al. 1988a), Squirefish *Chrysophrys auratus* (Scott et al. 1993), and Yellow Seabream *Dentex hypselosomus* (Yoda and Yoneda 2009); however, none of these studies explicitly reported estimates of p.

We found that f_b–size relationships were generally weak when data were pooled across all time periods, whereas interannual and intra-annual relationships were often stronger. Higher levels of f_b were observed in 2008–2009 than in 2009–2010, but size-independent n_b was higher in 2009–2010, leading to similar levels of size-dependent f_a for each year (see Figure 7A, B). These findings confirm that n_b and f_b can vary separately and possibly independently, meaning that temporal differences in f_b do not necessarily imply that differences in f_a will be of similar magnitude. In addition, fluctuations in f_a may be driven solely by year-to-year changes in n_b. For example, f_b of Red Snapper *Lutjanus campechanus* did not vary among three years, but n_b ranged from 20 to 35 (Collins et al. 1996). Life history theory recognizes eggs per batch and the number of batches as two separate traits, which have been found to be negatively correlated for marine and freshwater fish species within several orders (Winemiller 1989; Winemiller and Rose 1992). Our findings provide additional evidence that f_b and n_b probably also vary separately among years within a given species; thus, in many cases it may be inappropriate to assume that n_b is temporally constant or varies in a manner similar to f_b.

During each of our study years, f_b was significantly different among months, being lower both early and late in the spawning season. A similar trend was observed by Daniel (2003) but was not statistically significant. Black Sea Bass *Centropristis striata* have also demonstrated higher f_b earlier in the spawning season (Danson 2009), although no appreciable intra-annual variation has been noted for several other SAB snapper–grouper species, including the Vermilion Snapper *Rhomboplites aurorubens* (Cuellar et al. 1996), Scamp *Mycteroperca phenax* (Harris et al. 2002), and Blueline Tilefish *Caulolatilus microps* (Harris et al. 2004). Within the snapper–grouper complex, f_b appears to exhibit three general intra-annual relationships that were previously described by Conover (1985) as concave-down, decreasing, or constant. Conover (1985) posited that the concave-down relationship, as observed for Red Porgy in this study, should maximize reproductive success when environmental conditions vary predictably and are optimal in the middle of the season. Sea surface temperature profiles in our study area are reliably concave-up when Red Porgy are reproductively active (November–April; NOAA National Data Buoy Center,

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stations 41035 and 41036; www.ndbc.noaa.gov), so perhaps egg survival is highest at colder water temperatures. In a study of the Dwarf Perch *Micrometrus minimus*, a viviparous temperate marine species, Schultz (1993) found that females born in the middle of the spawning season experienced the highest survival to first reproduction. Female Dwarf Perch that were born in early spring suffered high mortality immediately after birth, whereas females that were born very late suffered high overwinter mortality, probably related to small body size (Schultz 1993). If recently spawned Red Porgy also experience variable seasonal mortality, then increasing egg production in the middle of the season may lead to higher offspring survival rates on average.

Size Dependence of Batch Number

Significant relationships between the presence of reproductive indicators and Red Porgy body size demonstrated that n_b varied with body size and that these relationships differed between years. In 2008–2009, p based on spawning capability or HO presence did not vary with TL, but p based on POF_0 decreased with TL. Since HOs precede POFs during oocyte development, p based on HOs should also have decreased with TL; however, we may have failed to detect HOs because they last less than 24 h and are not always detected. In 2009–2010, p increased with TL for all reproductive indicators (SC, POF_0 presence, and HO presence), although p was less dependent on TL when using HOs than when using POF_0 (see Figure 4B). Our observations for Red Porgy during year two are aligned with a common pattern among batch-spawning species. Studies of the Yellowfin Tuna *Thunnus albacares* (Schaefer 1998), Baltic Sprat *Sprattus sprattus balticus* (Kraus and Köster 2004), Southern Blue Whiting *Micromesistius australis* (Macchi et al. 2005), and Spotted Seatrout *Cynoscion nebulosus* (Lowerre-Barbieri et al. 2009) each observed an increase in p with TL, while studies of the Gag *Mycteroperca microlepis* (Collins et al. 1998) and Ballyhoo *Hemiramphus brasiliensis* (McBride and Thurman 2003) found that p increased with age. Temporal variation in this pattern, as was observed in our study, may also be common given that (1) Gags only showed a p–TL relationship during one of three study years (Collins et al. 1998) and (2) the pattern was evident for Baltic Sprat during 3 of 4 months (Kraus and Köster 2004). Furthermore, p and d may only sometimes have the same relationship with body size. For the Ballyhoo and Spotted Seatrout, d also increased with age and TL, respectively (McBride and Thurman 2003; Lowerre-Barbieri et al. 2009); however, for Queenfish *Seriphus politus*, d increased with TL, whereas p did not (DeMartini and Fountain 1981). In a laboratory study of Atlantic Cod (Trippel 1998), d and n_b were each higher among second-time spawners than among first-time spawners, although p was not different.

Life history theory suggests that reproductive effort should generally increase with fish age (Roff 1984), and empirical work has shown that across fish species, both potential f_a and reproductive investment (i.e., the product of potential f_a and egg weight) increase with fish length (Duarte and Alcaraz 1989). Most of the research on batch spawners has found that f_b also increases with fish size and that if n_b is constant or increasing, then f_a will also increase. A decrease in n_b with size, as we observed during 2008–2009 for Red Porgy, is somewhat unexpected since it will tend to cause f_a to decrease. One possible explanation for a decrease in n_b with increasing size would be if larger females are more likely to skip spawning individual batches while small females skip less often because they are less likely to survive until the next batch (Peterson and Wroblewski 1984). Jonsson et al. (1991) found that the proportion of females that skipped a year between spawning periods increased with body size for Atlantic Salmon *Salmo salar*. Rideout and Tomkiewicz (2011) suggested that for indeterminate batch spawners, batch skipping is probably a more common tactic than skipping entire years. If local environmental conditions are unfavorable for offspring survival on a particular date, a female with a high probability of survival should benefit from postponing a batch until conditions improve. Because females must provision a limited supply of yolk among their eggs (Lloyd and Gosselin 2007) and because initial offspring size can affect growth rate and survival (Marteinsdottir and Steinarsson 1998), skipping a current batch may also allow for the production of a future batch of larger, more successful offspring. By the end of the spawning season, fewer batches may have been spawned, but higher success per offspring and energy retained for future spawning seasons may increase lifetime reproductive success (Stearns 1992).

Among protogynous species, large females may have another incentive to divert surplus energy from egg production to growth. According to Warner's model (Warner 1984; Munday et al. 2006), the reproductive value of a protogynous fish increases dramatically when it reaches a large body size and can transition to a dominant male; this idea is also supported by empirical research (Warner and Hoffman 1980). Warner's model suggests that as protogynous fish grow, the ratio of female to male reproductive value increases up to a certain size and then decreases, and sex change is predicted to occur when the ratio declines to 1:1. Thus, as females approach the size at which sex transition is favored, the value of investment in eggs should decrease relative to the value of investment in processes (e.g., growth) that would be expected to improve male reproductive success. Sex-specific reproductive values are rarely fixed and tend to be highly variable among individuals based on local demographics (e.g., size distribution, sex ratio, and density) that impact social behavior (Munday et al. 2006). Thus, the reproductive benefit to females of either maximizing egg production or diverting energy to improve future success as a male is likely to be largely dependent on local demographics.

Although the causal mechanisms are not clear, our findings for Red Porgy support the idea that n_b–size relationships vary temporally. Considering that other studies—albeit few in number—have noted similar variation (Collins et al. 1998; Kraus and Köster 2004), temporal variation in the effect of body size on n_b may be common among batch-spawning fishes. The potential for the timing of sex transition to contribute to

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variability in the batch spawning pattern remains speculative but is generally supported by existing theory. Given the potentially large impact of n_b on estimates of f_a, the relationship between n_b and body size deserves further empirical and theoretical study among both gonochoristic and hermaphroditic species.

Effects of Variable Reproductive Indicators on Estimates of Egg Production and Management Reference Points

Incorporating size-based relationships for reproductive indicators into calculations of f_a and SPR produced notable differences compared to models that assumed n_b to be independent of size. The decrease in POF_0 presence at larger body sizes during 2008–2009 resulted in lower f_a in large females, whereas increases in the presence of all reproductive indicators at larger sizes during 2009–2010 resulted in higher f_a for large females (see Figure 7A, B). In turn, size-selective fishing mortality was predicted to have less impact on SPR in 2008–2009 than in 2009–2010. When n_b was assumed to be independent of size, the estimated SPR was generally similar to calculations that were based solely on mature female biomass (see Figure 8A, B).

It is clear that n_b is size dependent, but the relationships can differ depending on the choice of reproductive indicator. We conclude that the presence of POF_0 is the most reliable reproductive indicator and likely produces the most accurate estimates of egg production and SPR. Hydrated oocytes are more readily identifiable when using histological techniques, but their short duration means that they may not be encountered during all times of day. Egg production estimates based on spawning capability are somewhat indirect because they assume that the duration of the SC season is proportional to n_b. However, this is an implicit assumption of standard calculations in which n_b is assumed to be independent of body size. In any regard, spawning capability–size relationships can be useful proxies for n_b–size relationships because (1) spawning capability is easier to assess than POF_0 presence and can be determined macroscopically and (2) vitellogenic oocytes have much longer durations that are not temperature dependent like those of HOs or POF_0 (Fitzhugh and Hettler 1995; Kurita et al. 2011). Thus, for long-term surveys investigating the size dependence of n_b, an assessment of spawning capability may be more feasible than assessing POF_0 or HO presence.

Our results indicate that Red Porgy SPR could be lowered sufficiently (relative to current projections) to impact management if n_b relates positively to body size. If size dependence of p is mostly positive, as is supported by evidence for other species, and if such size dependence is widespread among indeterminate reef fishes, this could have important implications for management of the SAB snapper–grouper complex. The use of nontraditional management strategies (e.g., marine protected areas and maximum size limits) within the offshore fishery has already been discussed or introduced in attempts to protect males from harvest. This is because model simulations have predicted that decreasing fertilization rates due to a loss of male biomass will cause female SSB to be a poor predictor of recruitment in protogynous hermaphrodites (Brooks et al. 2008). Management strategies that are designed to protect larger individuals should also help to prevent the removal of larger females that may be generating a greater number of egg batches each year. Increased biomass of males may also contribute to a reversal in the declining trend in size at sex transition (observed by Harris and McGovern 1997), which could translate to larger female sizes in the stock and thus a potential for greater contrast in the n_b–TL relationship.

Spawning stock biomass is often considered a poor proxy for egg production in determinate-spawning species (Marshall et al. 1998, 2003; Cardinale and Arrhenius 2000), and we have shown that this is also likely true for an indeterminate species. Our work represents one of the more detailed studies of fecundity in an indeterminate protogynous reef fish in terms of the number of reproductively active females that were sampled per year. The level of sampling enabled us to identify size-dependent relationships for both f_b and n_b with sufficient temporal resolution to detect variability between years. Although sampling demands can make it difficult to conduct detailed studies of reproductive dynamics in larger, less-abundant species, the patterns observed for Red Porgy outline a range of potential patterns that may be widespread among similar species. Due to the relatively small body size and accessibility of the Red Porgy, it may prove to be a valuable model species for studying the complex patterns of egg production among indeterminate, batch-spawning, protogynous hermaphrodites.

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