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ARTICLE

Estimating the Dependence of Spawning Frequency on Size and Age in Gulf of Mexico Red Snapper

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Abstract

In 2011, a large multivessel survey was conducted to provide nearly synoptic sampling of Red Snapper *Lutjanus campechanus* throughout their reproductive season in the U.S. Gulf of Mexico. A total of 2,487 Red Snapper were caught with a female : male ratio that was approximately 1:1. The ovaries of 1,002 females were histologically examined. Females ($n = 391$) were found with spawning markers (postovulatory follicles and hydrated oocytes) throughout the study area, but primarily in outer shelf waters. Statistical models were developed to quantify and test the dependence of the proportion of females bearing spawning markers (spawning fraction) on female length and age, time of year, depth, gear type (vertical line or longline), or region (east or west of the Mississippi River). Most of the variance in spawning fraction was explained by the time of year; spawning fractions were generally low in spring, peaked in midsummer, and declined by fall. There was also strong statistical evidence of a positive relationship between spawning fraction and either age or length. The effects of region and gear type were not significant once time of year and size or age were accounted for. These results demonstrate the need to account for differences in the time of year and age structure of the population when the productivity of populations of Red Snapper are compared. For example, productivity has been hypothesized to be greater in the western Gulf than in the eastern Gulf, as evidenced by regional patterns of egg and larval abundance. Our results suggest that this regional difference is not due to any intrinsic difference in the biology of the fish, but simply a consequence of there being more large, old Red Snapper in the western Gulf. Recent stock assessments have indicated that Red Snapper

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are increasing in abundance and there is a need to continue monitoring to detect any possible compensation in reproduction.

Many tropical and subtropical fishes exhibit indeterminate fecundity and spawn multiple times over an extended period that may last much of the year. Several studies have demonstrated that the number of eggs produced during a spawning event (batch fecundity) increases with age or body length at a faster rate than does body weight (Cooper et al. 2013; Hixon et al. 2014; He et al. 2015). Moreover, evidence is emerging that spawning frequency also increases with age and body size (LaPlante and Schultz 2007; Mehault et al. 2010; Fitzhugh et al. 2011; Cooper et al. 2013; Klibansky and Scharf 2013). As a result, egg production in tropical and subtropical species is probably less correlated to mature (spawning) biomass than has been observed for species from higher latitudes (Fitzhugh et al. 2011; Lowerre-Barbieri et al. 2011; Klibansky and Scharf 2013).

Red Snapper *Lutjanus campechanus* are indeterminate spawners that inhabit the tropical and subtropical waters of the southeastern United States and Mexico. They are long lived (>50 years: Wilson and Nieland 2001) and considered to have a periodic life history (Winemiller and Rose 1992), yet maturity can occur at age 2 (SEDAR 2013). Full reproductive potential has been estimated to occur by about 12–15 years of age (Goodyear 1995; Woods 2003; Kulaw 2012). The Red Snapper population in the northern Gulf of Mexico has been harvested commercially since the mid 19th century and currently supports one of the most important recreational fisheries in the world. Perhaps not surprisingly, the assessment and management of this species has been highly controversial (Shipp and Bortone 2009). Even the U.S. Congress has weighed in on the matter, holding congressional hearings and sponsoring several bills specifically addressing Red Snapper (e.g., Senate Bill 157 and Congressional Bill H.R. 3099).

One area of active debate concerns the level of abundance to which the Red Snapper stock must rebuild, which depends partly on the perceived relationship between egg production and age or size, and which is tied directly into fisheries management by law through the Magnuson–Stevens Fishery Conservation and Management Act (MSFCMA). Recent stock assessments (Porch 2004, 2007) modeled Red Snapper egg production in the Gulf of Mexico as the product of batch fecundity and maturity at age. Porch et al. (2007) acknowledged the need to account for age or size dependence in the number of annual spawns. Until recently, however, the available data were insufficient to determine whether such a relationship existed, let alone to quantify it.

In 2011 a congressionally supported supplemental survey, in which Red Snapper was one of the target species, was conducted throughout the northern Gulf of Mexico (Campbell et al. 2012). Nearly 2,500 Red Snapper were sampled from multiple

vessels operating throughout the Red Snapper spawning season (April through October) and across all known spawning areas, resulting in the most spatially and temporally extensive survey of Red Snapper spawning ever conducted. Nevertheless, the survey was not perfectly synoptic in that all areas and depths were not sampled on the same dates. Previous work has suggested that the spawning intensity of Red Snapper and other species varies considerably during the course of the season and in different locations (Woods 2003; Porch et al. 2007; Brown-Peterson et al. 2009; Lowerre-Barbieri et al. 2011). For this reason, the perceived relationship between spawning frequency and age or size is likely to vary depending on when and where reproductive samples are taken (Lowerre-Barbieri et al. 2011). For example, since older Red Snapper tend to be caught in deeper water, sampling deep and shallow waters at different times of the spawning season could alter the apparent relationship between spawning frequency and age.

The objective of this paper was to use the samples obtained from the supplemental survey to develop unbiased estimates of the relationship between spawning frequency and body length or age. The proposed modeling framework attempted to “standardize” these estimates by explicitly accounting for the effects of any factors that may have varied systematically during the sampling.

METHODS

Field survey and laboratory processing.—Red Snapper were caught by hook-and-line gear (vertical line and longline) deployed from Dry Tortugas, Florida, through Brownsville, Texas, and from the inner shelf (9 m) to a depth of about 180 m according to a stratified random design as described in Campbell et al. (2012). The time of day of all catches were recorded as the gear was retrieved. All of the Red Snapper caught were measured for TL and FL (mm), weighed (kg), and dissected to extract otoliths and gonads. Gonads were sexed and macroscopically staged while on the vessel, and ovaries were frozen for further processing in the laboratory.

Red Snapper were aged from sectioned otoliths as described in Allman and Fitzhugh (2007) and Allman et al. (2012). Frozen ovaries were weighed (nearest 0.1 g) and subsamples were taken from the right posterior lobe and placed into 10% neutral buffered formalin (NBF) for histological preparation (hematoxylin and eosin-y stain; Mass Histology Services, Worcester, Massachusetts). Histological examination determined the presence-absence of spawning markers in females (postovulatory follicles and/or hydrated oocytes: Hunter and Macewicz 1985; Murua et al. 2003). During selected cruises, a sample of 50 Red Snapper

TABLE 1. Number of Red Snapper females and fraction bearing histological spawning markers by age-class from the 2011 congressional supplemental survey.

Age-class	Number of females	Fraction with spawning markers
1	2	0.00
2	67	0.16
3	78	0.19
4	174	0.38
5	224	0.34
6	157	0.42
7	137	0.51
8	45	0.42
9	25	0.56
10+	83	0.57

ovaries were weighed and tissue subsamples fixed in fresh formalin at sea prior to freezing the remainder of the ovaries, for the purpose of quality assessment. A comparison test of histology sections from the paired freshly preserved and frozen-preserved ovarian tissue subsamples was conducted to determine whether spawning markers could be readily identified after freezing.

Models of spawning fraction.—We defined spawning fraction as the proportion of females bearing spawning markers. This definition is similar to usage elsewhere (Priede and Watson 1993; Murua et al. 2003; Lowerre-Barbieri et al. 2009; Kurita et al. 2010; Kurita 2012), but differs in that we refer to the proportion of all sampled females in the survey without further distinction of active or mature females. In later calculations (see section below), we address the conversion of spawning fraction to daily probabilities of spawning. This separation of steps recognizes that various factors may govern the duration of spawning markers, which subsequently can affect daily probabilities and the estimated total number of spawns (Priede and Watson 1993; Kurita 2012).

Tabulations of the 2011 survey results appeared to confirm previous findings that the proportion of females with spawning markers (spawning fraction) increases with age or size (Table 1) and varies with the time of year (Table 2). However, the size and age of the Red Snapper in the sample also tended to vary with the time of year, and somewhat older fish on average were sampled near the peak of the spawning season. Accordingly, the apparent relationship between spawning fraction and age (or length) may be confounded to some unknown degree by the relationship between spawning fraction and time of year, and it is therefore necessary to model the effects of age and time of year simultaneously in order to disentangle them. The situation is further complicated by observations of variations in spawning fraction by depth, gear type (vertical line or longline), and region (east or west of the Mississippi River).

Models are often used to help distinguish the response of a measure to an explanatory variable of interest from its response

TABLE 2. Summary of Red Snapper females from the 2011 congressional supplemental survey. Within each approximate 2-week period, the initial date of sampling is listed. The numbers of sampling dates and females and fraction of females bearing histological spawning markers are indicated, along with the mean and range of age. The survey covered a total period of 198 d.

Start date (month/day)	Number of dates	Number of females	Fraction with spawning markers	Mean age (years)	Age range (years)
4/9	9	58	0.02	6	2–14
4/19	9	52	0.00	8	2–31
5/3	8	70	0.21	7	3–14
5/17	9	87	0.28	5	2–14
5/31	12	90	0.63	6	2–29
6/15	6	39	0.62	9	2–34
6/29	1	2	1.00	21	8–34
7/13	8	58	0.79	8	3–28
7/26	10	123	0.67	6	2–22
8/9	10	58	0.62	7	3–21
8/23	7	58	0.66	5	1–15
9/10	7	34	0.29	6	2–24
9/20	9	173	0.23	5	2–25
10/4	12	79	0.10	6	2–22
10/19	4	11	0.09	7	4–9

to other variables of perhaps less interest. This is particularly true where the sampling is unbalanced in the sense that more measurements are made for some levels of the explanatory variables than for others. In the present case we are particularly interested in distinguishing real changes in spawning fraction with age or length from perceived changes that result by sampling different stages under different average conditions as illustrated in Table 3. If the model is approximately correct, then important biophysical relationships should be reflected by parameter estimates that are statistically different from the corresponding null model (where the explanatory variable is assumed to have no effect) and substantially increase the fraction of the variance explained by the model.

The standard approach for modeling dependent variables that can have only two possible outcomes (e.g., success or failure to detect spawning markers) is a binomial regression. The dependent variable is treated as the outcome of a Bernoulli trial such that the total number of successes from a series of like trials is approximately binomially distributed. The maximum likelihood estimate for the probability of observing a success (p) is therefore obtained by minimizing the negative log-likelihood expression:

$$-\ln L = -\sum_i^N o_i \ln(p) + (1 - o_i) \ln(1 - p), \quad (1)$$

where i denotes one of N observations, o is an indicator that takes on a value of 1 for a “success” (spawning markers present) and a

TABLE 3. Plausible biophysical and sampling-related explanations for perceived trends in spawning frequencies of Red Snapper by stage, depth, region, gear, and season. If the model is approximately correct, biophysical causes for changes in spawning frequency should manifest as parameter estimates that are statistically different from the null model.

Independent variable	Biophysical causes	Sampling issues
Stage (age or length)	Body cavity size and/or energy reserves increase with stage.	Older, larger stages sampled under more favorable conditions (depth, region, gear, season).
Depth	Spawning conditions improve with depth.	Stages that spawn more frequently are sampled more often at depth.
Region	Spawning conditions differ between regions (east and west).	Stages that spawn more frequently are disproportionately sampled between regions.
Gear	Spawning behavior makes some fish more vulnerable to one gear than another.	Stages that spawn more frequently are more vulnerable to one gear than another.
Season	Spawning conditions vary consistently through the year.	Stages that spawn more frequently are disproportionately sampled through the year.

value of 0 for a “failure” (spawning markers absent), and p is the probability of observing a spawning marker.

One of the most common forms of binomial regression is the logistic regression, which assumes that the probability p of observing a success (presence of spawning markers) can be well approximated by a logistic function of a linear combination of explanatory variables x :

$$p(x) = 1/(1 + e^{\alpha + \beta \cdot x}). \quad (2)$$

Equation (2) can be linearized by the logit transformation, $\ln[p/(1 - p)]$ and falls into the class of generalized linear models handled by many standard statistical packages. Probit regression is similar except it assumes $p(x)$ follows the cumulative standard normal distribution. The two approaches tend to give similar results, but logistic regressions may be somewhat more robust to outliers inasmuch as the logistic function has thicker tails than the probit.

The logistic model above implies that the probability of observing an event changes monotonically with the value of the explanatory variable x , increasing to a maximum of one if β is negative and decreasing to a minimum of zero otherwise. It seems reasonable to expect a monotonic relationship between the probability of spawning (spawning fraction) and length or age, but even the largest, oldest females may not be in spawning condition at all times. For this reason it is advantageous to incorporate a scale parameter that allows the maximum spawning fraction to be something less than one, in which case the appropriate model would take the form

$$p(x) = \pi/(1 + e^{\alpha + \beta \cdot x}). \quad (3)$$

We allow for the possibility that the relationship between spawning fraction and age or length may vary across regions and gear types by allowing π , α , and β to vary categorically with each of the four combinations of gear and region

(effectively gear–region–stage interaction terms). The relationship between spawning fraction and depth, if present, is assumed to be monotonic. This would be consistent with observations that there is an ontogenetic shift in the distribution of Red Snapper, and older, large fish tend to move to deeper water (Patterson 2007; Mitchell et al. 2014). If the cause of this shift is related to spawning behavior, then one might expect spawning frequency to increase with depth.

Field observations suggest that Red Snapper spawning is seasonal, as has also been demonstrated for Pouting *Trisopterus luscus*, and may be common among other species (Alonso-Fernández and Saborido-Rey 2011; Lowerre-Barbieri et al. 2011). A seasonal pattern would imply that the relationship between spawning fraction and time of year is dome-shaped rather than monotonic. A dome-shaped relationship could be mimicked by the use of categorical variables that represent discrete intervals of time, say 1 month, in which case our model would take the form:

$$p(s, d, r, g, m) = \pi_{grm}/(1 + e^{\alpha_{grm} + \beta_{gr}s + \delta d}), \quad (4)$$

where s is a continuous variable representing the stage of life (here either age or length), d is a continuous variable representing depth, m is a categorical variable representing the month, g is a categorical variable representing gear type (longline or vertical line), r is a categorical variable representing region (east or west of the Mississippi River), π_{grm} is the scaling parameter, which may vary categorically by gear, region, and month (absent a gear or regional effect, $\pi_{grt} = \pi_r$), α_{grt} is the linear intercept parameter, which may vary categorically by gear, region and month (absent a gear or regional effect, $\alpha_{grt} = \alpha_t$), β_{gr} is the slope parameter for age or length, which may vary categorically by gear and region (absent a gear and regional effect, $\beta_{gr} = \beta$), and δ is the slope parameter for depth.

An important drawback of the model described by equation (4) is the large number of parameters associated with the time intervals (months), some of which will be poorly estimated if

few samples are available for that month (as was the case for some months in our Red Snapper example). Alternatively, one can use a functional form to represent the dependence of spawning fraction on time of year. We chose to use the flexible gamma function:

$$p(t|s) = \left(\frac{t}{\mu}\right)^{\mu/(\kappa + \gamma s)} e^{-(\mu - t)/(\kappa + \gamma s)}, \quad (5)$$

where t is the fraction of the year elapsed beginning on January 1, μ is the mode (time of peak spawning) and the expression $\kappa + \gamma s$ represents the dispersion coefficient (which is allowed to increase linearly with age or length to accommodate the possibility of age or size dependence in the duration of the spawning season). Note that this form of the gamma density has been divided by the value at the mode such that the maximum value is always 1.0.

The full model used in this paper is given by the product of equation (4) (without the categorical month effects) and equation (5); i.e.,

$$p(s, d, r, g, t) = \frac{e^{(\mu - t)/(\kappa + \gamma s)}}{1 + e^{\alpha_{gr} + \beta_{gr}s + \delta d}} \left(\frac{t}{\mu}\right)^{\mu/(\kappa + \gamma s)}. \quad (6)$$

This model allows the duration of the spawning season to vary with age or length, but assumes that it is the same across regions, gear types, and depth. For completeness, we note that all of the models posed in equations (1)–(6) treat the explanatory variables s (length or age) and d (depth) as though they are measured without error. In the case of length and depth, the measurements were made by scientific observers and the error is negligible for all practical purposes. The age of the fish is subject to reader error, but Allman et al. (2005) suggested that this error is relatively small and unbiased for Red Snapper.

Statistical estimation and comparisons of alternative models.—Equation (6) does not fall into the class of general linear models owing to the incorporation of the scaling parameters π and the gamma function of t . Nevertheless, the parameters are easily estimated by numerical minimization of the likelihood expression given by equation (1), where p_i is understood to be the probability of observing a spawning marker predicted by equation (6) given the values of the explanatory variables s , t , d , g , and r associated with sample i . In this study the numerical minimization was accomplished using Excel Solver and AD Model Builder.

Statistical comparisons among alternative models were made using Akaike's information criterion (AIC; Akaike 1973):

$$\text{AIC} = -2 \ln L + 2n,$$

where n is the total number of parameters estimated and L is the measure of goodness of fit (e.g., likelihood function) being maximized. The AIC attempts to identify the most parsimonious

explanation of the data by balancing the relative improvement in model fit against the number of parameters required to achieve that fit. The “best” model is considered to be the one with the lowest AIC. A “rule of thumb” is that differences in AIC (ΔAIC) of less than 2 constitute weak evidence that one model is better than another, differences between 3 and 10 are regarded as moderate evidence, and differences greater than 10 are regarded as strong evidence (Burnham and Anderson 2002). A pseudo- R^2 statistic was also computed as the fraction of the variance explained by the regression:

$$R^2 = 1 - \frac{\sum_i^N (o_i - \hat{p}_i)^2}{\sum_i^N (o_i - \bar{o})^2},$$

where \bar{o} is the mean of the observations and \hat{p} is the maximum likelihood estimate of the probability that a fish will have spawning markers.

Conversion to total number of spawns.—The average spawning fraction during the course of a year for age or length s is obtained as

$$\bar{p}(s) = p(s) \int_{t=0}^1 p(t|s) dt. \quad (7)$$

In cases where $p(t|s)$ is estimated to be essentially 0 at $t = 1$,

$$\int_{t=0}^1 p(t|s) dt \cong \int_{t=0}^{\infty} p(t|s) dt = \frac{\Gamma(\mu/(\kappa + \gamma s + 1) \kappa^{\mu/(\kappa + \gamma s) + 1}}{(\mu/e)^{\mu/(\kappa + \gamma s)}}, \quad (8)$$

where the right hand side of equation (8) is simply the inverse of the gamma density evaluated at the mode. In cases where spawning occurs throughout the year so that $p(t|s) > 0$ at $t = 1$, the integral in equation (8) can be evaluated numerically.

The prevalence of hydrated oocytes and postovulatory follicles (histological spawning markers) can be detected over a period of time and may be influenced by temperature and the diel spawning pattern. Following Priede and Watson (1993), the average spawning fraction can be converted to a daily probability of spawning P :

$$\bar{P}(s) = \frac{24}{T_M} \bar{p}(s) \quad (9)$$

where T_M is the duration in hours that spawning markers can be detected. The expected number of spawns during the course of a year is therefore obtained from multiplying equation (9)

by the number of days as follows:

$$N(s) = 365 \frac{24}{T_M} \frac{\Gamma(\mu/(\kappa + \gamma_s + 1) \kappa^{\mu/(\kappa + \gamma_s) + 1}}{(\mu/e)^{\mu/(\kappa + \gamma_s)}} p(s). \quad (10)$$

Final oocyte maturation and hydration have been estimated to begin during morning hours (0830 hours) and remain evident throughout the day (to about 1800 hours, or 10 h duration: Jackson et al. 2006). Field observations and spontaneous spawning in tanks have indicated that ovulation occurs in mid to late afternoon, peaking at about 1600 hours with spawning commonly occurring before sunset around 2000 hours in summer months (Papanikos et al. 2003, 2008; Jackson et al. 2006). While postovulatory follicles have been noted to appear as early as 1100 hours, new postovulatory follicles are not thought to be common until after 1600 hours as ovulation peaks and postovulatory follicle duration is not thought to exceed about 24 h in the Gulf of Mexico during summer (Nieland et al. 2002; Jackson et al. 2006). Together, these findings indicate that T_M is about 34 h.

RESULTS

Survey Summary

The 2011 congressional supplemental survey was conducted over 846 sea-days (April to October) and included 1,171 longline (four vessels) and 1,939 vertical-line (two

vessels) stations (Campbell et al. 2012). Histological analyses were conducted on 1,002 females, of which 992 were aged. Based on comparison of the 50 paired quality control histology sections (freshly fixed versus initially frozen) it was visually apparent that freezing reduced the ability to resolve oocyte details such as germinal vesicles, follicular membranes, lipid vacuoles, and yolk globules. However, spawning markers (hydrated oocytes, postovulatory follicles) could be distinguished in the frozen samples. Comparison of the leading oocyte stage (primary growth, cortical alveolar, vitellogenesis, and oocyte maturation including hydration) yielded 90% agreement and presence-absence of postovulatory follicles yielded 82% agreement.

Females with spawning markers ($n = 391$) were distributed throughout the U.S. Gulf survey area, predominantly along the outer shelf at depths between 15 and 158 m (Figure 1). The distribution of females with or without spawning markers overlapped spatially; females without markers were caught at an average depth of 60 m and females with markers were caught at an average depth of 62 m. These depths center on a discrete depth zone (50–100 m) that encompasses the high-relief paleoreefs found on the outer shelf of the southeastern United States (Koenig et al. 2000).

Modeling the Spawning Fraction

Stepwise model building exercises were developed beginning with the null model ($p = \pi$), which assumed all fish have

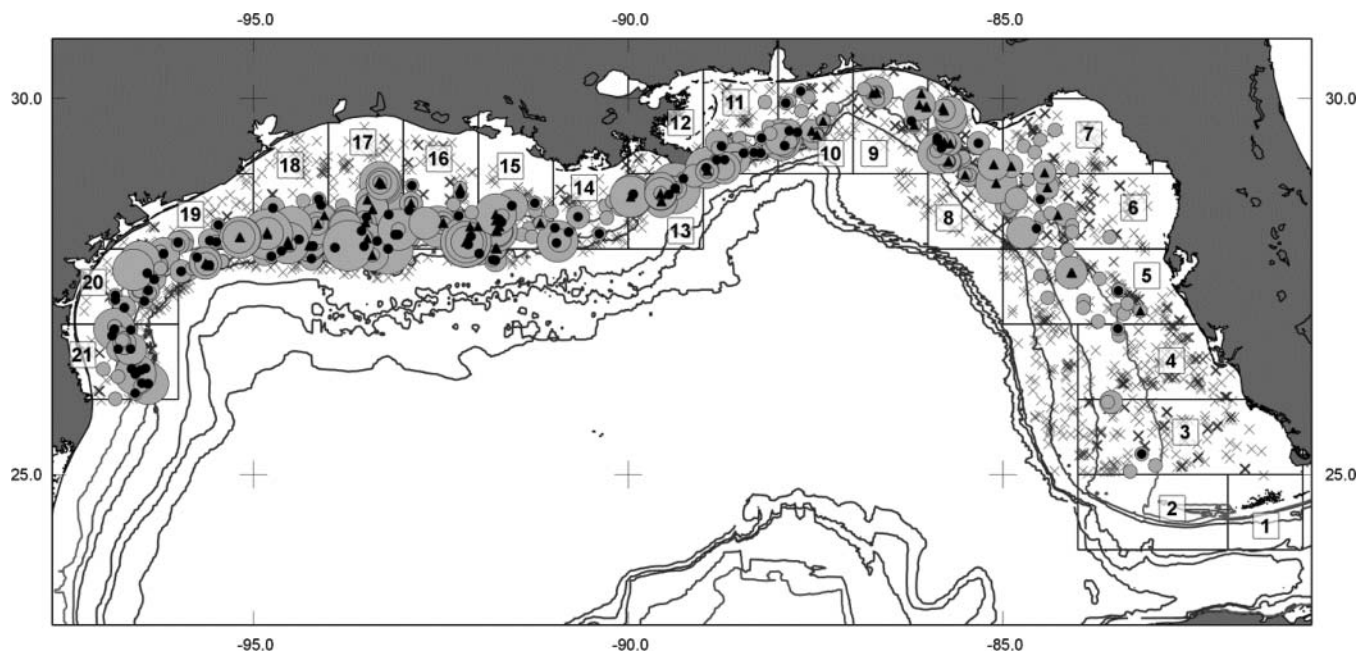


FIGURE 1. Distribution of sampling stations with zero (× symbol) and positive catches of Red Snapper during the 2011 supplemental survey (grey circle; progressively increasing size of circle indicates number landed per set: 1–4, 5–10, 10–13, 14–17, 18+). Solid dark symbols indicate capture locations of females with spawning markers (round symbols: bottom longline gear, triangles: bandit gear). The 50-, 100-, 200-, 1,000-, 1,300-, and 2,000-m isobaths are indicated. Statistical subareas are denoted from 1 to 21 within U.S. Gulf of Mexico waters. Numbers along horizontal and vertical borders of figure are longitude and latitude, respectively. Note that symbols are for graphical illustration and do not reflect scale of area fished per station.

the same probability of being found in spawning condition. In the first step, the logistic age or length effects were added to the null model. The corresponding AIC values were decreased by more than 40 and about 6% of the residual variance was explained (Table 4). Accordingly, the statistical evidence for

both the age and length effects was strong and these terms were retained in all subsequent models.

In the second step, the spawning fraction was allowed to vary with time of year to accommodate the biological dynamics of the spawning season. Initially, the duration of the

TABLE 4. Length-based and age-based models for Red Snapper spawning fractions developed during the stepwise model building procedure (based on the binomial regression of equation 6). The shaded column highlights the final models. The use of t' indicates the model allows the seasonal effect to vary with age or length. Subscripts refer to gear or region (subscripts in parentheses identify the gear–region combination when gear and region effects are estimated simultaneously); l = length, a = age, t = time elapsed, d = depth, g = gear type, r = region (see text for explanation), NA = not applicable.

Statistic	P	$p(l)$	$p(l,t)$	$p(l,t')$	$p(l,t,d)$	$p(l,t,g)$	$p(l,t,r)$	$p(l,t',d,r,g)$
Length-based models								
μ			0.536	0.535	0.537	0.538	0.542	0.541
κ			0.024	0.003	0.025	0.026	0.026	0.015
γ				0.000037				0.00002
δ					0.474			0.671
$\pi_{1(1,1)}$	0.390	0.547	0.866	0.858	0.886	0.775	0.986	0.987
$\alpha_{1(1,1)}$		3.295	9.084	12.762	6.311	9.803	63.044	43.042
$\beta_{1(1,1)}$		−0.008	−0.027	−0.042	−0.025	−0.030	−0.180	−0.130
$\pi_{2(2,1)}$						0.899	0.928	1.000
$\alpha_{2(2,1)}$						150.899	3.451	−6.253
$\beta_{2(2,1)}$						−0.436	−0.009	−0.040
$\pi_{1,2}$								0.822
$\alpha_{1,2}$								6.096
$\beta_{1,2}$								−0.027
$\pi_{2,2}$								0.884
$\alpha_{2,2}$								108.642
$\beta_{2,2}$								−0.334
AIC	1,339	1,283	1,000	992	986	999	989	981
r^2	NA	0.06	0.30	0.31	0.32	0.31	0.32	0.33
Age-based models								
Statistic	p	$p(a)$	$p(a,t)$	$p(a,t')$	$p(a,t,d)$	$p(a,t,g)$	$p(a,t,r)$	$p(a,t',d,r,g)$
μ			0.538	0.535	0.537	0.539	0.542	0.540
κ			0.026	0.012	0.025	0.026	0.025	0.018
γ				0.0020				0.0010
δ					0.330			0.276
$\pi_{1(1,1)}$	0.388	0.563	0.940	0.878	0.920	0.896	1.000	1.000
$\alpha_{1(1,1)}$		1.889	1.696	1.547	1.170	1.653	6.808	6.658
$\beta_{1(1,1)}$		−0.513	−0.650	−0.861	−1.055	−0.636	−2.633	−3.189
$\pi_{2(2,1)}$						0.934	0.952	1.000
$\alpha_{2(2,1)}$						0.222	1.773	1,406.203
$\beta_{2(2,1)}$						−0.491	−0.573	−364.045
$\pi_{1,2}$								0.970
$\alpha_{1,2}$								0.620
$\beta_{1,2}$								−0.704
$\pi_{2,2}$								0.881
$\alpha_{2,2}$								753.651
$\beta_{2,2}$								−202.841
AIC	1,327	1,283	1,008	1,007	995	1,011	995	993
R^2	NA	0.05	0.29	0.29	0.30	0.29	0.31	0.32

spawning season was assumed to be independent of age or length (i.e., $\gamma = 0$). In that case the AIC values were further reduced by over 200 and about 30% of the residual variance was explained. Accordingly, the statistical evidence for a seasonal effect on the spawning fraction was strong and these terms were retained in all subsequent models.

In the third step, the potential variation in the duration of the spawning season with age or length was investigated by estimating the parameter γ . The resulting AIC values suggested little evidence for a variation in season duration with age ($\Delta\text{AIC} < 3$) and only moderate evidence for a variation in season duration with length ($\Delta\text{AIC} < 10$). Moreover, the percentage of variation explained by the model was negligibly improved.

Finally, the effects of incorporating the covariates depth, gear, and region were examined by adding the corresponding parameters to the seasonal model derived from step 2 (one covariate at a time). The model fits suggested little evidence for gear effects ($\Delta\text{AIC} < 3$), but strong evidence for either a regional or depth effect ($\Delta\text{AIC} > 10$). None of these models, however, contributed to explaining a substantial fraction of the variance. Even the full model incorporating all parameters did not substantially improve the explanatory power of the regression (Figure 2). For the length-based analysis, the r^2 for the full model was 33% compared with 30% for the length + season model. For the age-based analysis, the r^2 for the full model was 32% compared with 29% for the age + season model. Accordingly, the final model included only age or length and time of year.

The spawning season was estimated in the final model to occur primarily from early April through late October, with a peak in July (Figure 3). The spawning fraction was estimated to increase rapidly with length or age (Figure 4), starting at very low values for fish under 300 mm (age 1) and beginning to level off around 500 mm (age 6–7). There were no obvious trends in the residuals (difference between model fit and observed data) to suggest that the model was not fitting the oldest (or youngest) age-classes (Figure 2). The asymptotic estimates of the variance of the parameters and associated correlation matrix (obtained from the Hessian via the application in AD Model Builder) are shown in Table 5.

Conversion to Total Number of Spawns

The expected number of spawns per year was computed according to equation (10). The duration of the spawning season did not vary with age or size in the base models (the terms not being significantly different from zero); therefore, the integral of $p(t|s)$ was a constant equal to 0.295 for all ages and equal to 0.288 for all lengths. The value of $p(s)$ for the base model followed the logistic functions specified by the estimates for the parameters π , α , and β in Table 4. The value of T_M , the time during which the prevalence of hydrated oocytes and postovulatory follicles (histological spawning markers) in

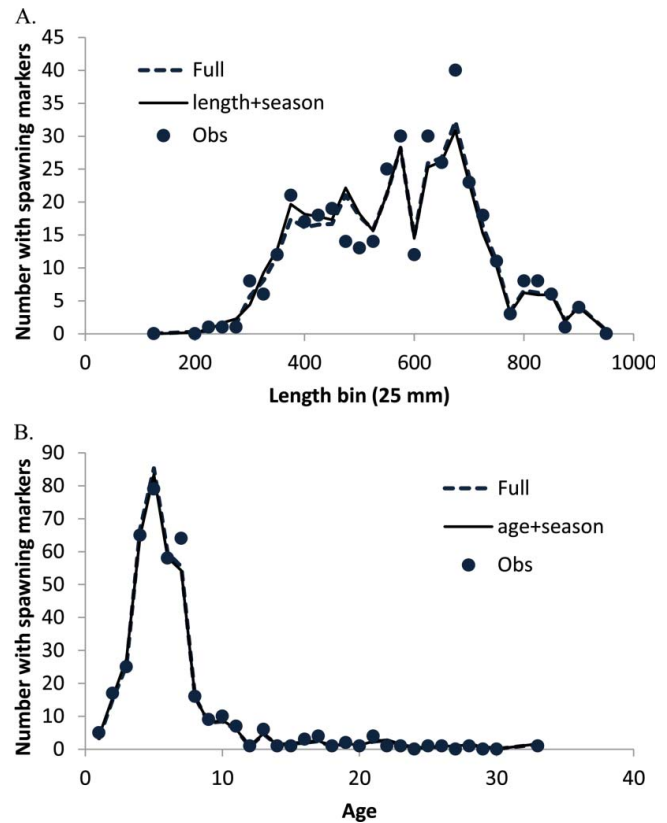


FIGURE 2. Observed number of Red Snapper with spawning markers compared with the corresponding predictions of the final model (length + season, or age + season) and full model (all covariates included). Panels show the results for (A) length and (B) age.

Red Snapper can be detected, was set to 34 h (see discussion below). The resulting ogive indicates that 2-year-old Red Snapper spawn an average of 29 times per year, while the largest, oldest Red Snapper spawn an average of about 71 times per year (Figure 5).

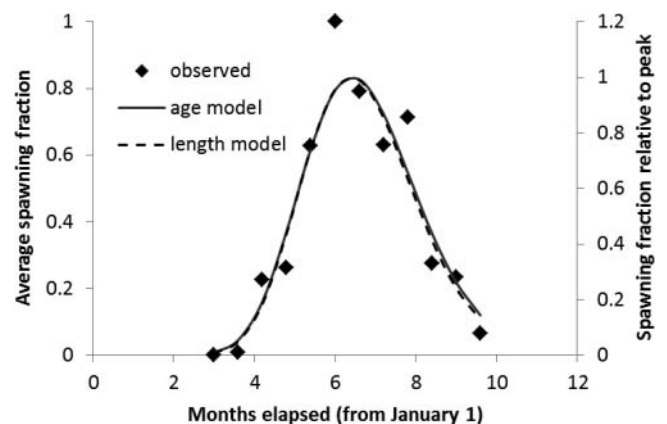


FIGURE 3. Average observed spawning fraction of Red Snapper (primary axis) compared with model predictions of relative proportion of females with spawning markers (secondary axis) by time of year for age-based and length-based models.

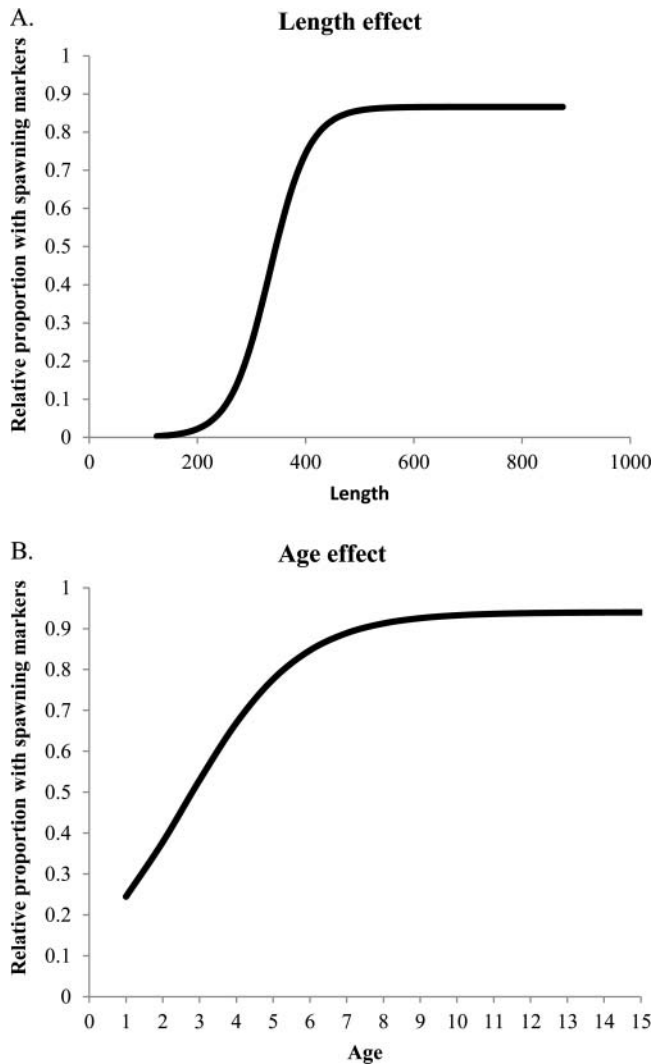


FIGURE 4. Predicted relationships between spawning fraction of Red Snapper (proportion of females with spawning markers) and (A) length (mm) or (B) age (years).

DISCUSSION

Our estimates of spawning frequency and related quantities such as spawning frequency are intended to reflect the population of sampled Red Snapper females regardless of whether they are active or not. Others have expressed these quantities in terms of active females only (Priede and Watson 1993; Stratoudakis et al. 2006; Kurita 2012). The two sets of metrics will lead to equivalent perceptions of the target population as long as the units are consistent. For example, the total number of spawning events in the population can be computed equivalently as either the product of spawning frequency per female and the number of females or the spawning frequency per active female and the number of active females. More importantly, neither set of metrics necessarily represented the average values observed in the population at large owing to the size selection of the gear and spatial variations in the

TABLE 5. Correlation matrix for final models to determine Red Snapper spawning fractions.

Statistic	Estimate	SE	Correlation coefficients					
			π	α	β	μ	κ	
Length-based model								
π	0.8660	0.0315	1.0					
α	-0.2723	0.1086	0.2	1.0				
β	9.0840	3.5484	-0.2	-1.0	1.0			
μ	0.5363	0.0048	-0.3	0.2	-0.2	1.0		
κ	0.0244	0.0019	-0.5	0.2	-0.2	0.2	1.0	
Age-based model								
π	0.9399	0.0409	1.0					
α	-0.6504	0.1740	0.6	1.0				
β	1.6962	0.6135	-0.4	-0.9	1.0			
μ	0.5381	0.0050	0.0	0.1	0.0	1.0		
κ	0.0255	0.0019	-0.1	0.1	0.1	0.1	1.0	

availability of different size- and age-classes of the target species. It is possible in principle to adjust our estimates of spawning fraction to account for variations in selection and availability, but these are not as well understood for Gulf of Mexico Red Snapper as they are for a few other species (see Lowerre-Barbieri et al. 2009). Alternatively, population-level estimates of spawning frequency may be obtained by multiplying the estimated spawning frequency at size or age by independent estimates of the size or age structure of the female population (as might be obtained by a stock assessment). In this sense the procedure is similar to multiplying an age-length key by size composition data to determine the age structure of a population.

The estimates of spawning frequency (number of spawns per year) for Red Snapper from this study increase with age from 29 events per year for 2-year-old fish to about 71 per year for fish age 10 and older, corresponding to interspawning intervals ranging between 6.5 and 2.5 d. Not surprisingly, this range brackets previous estimates of interspawning intervals

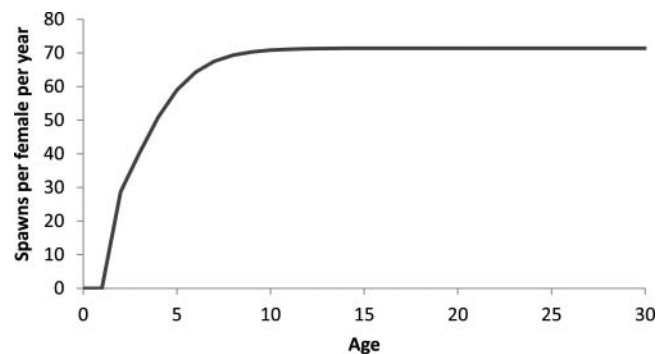


FIGURE 5. Estimated number of Red Snapper spawns at age (years) from the final model, $p(a, t)$, in Table 4.

that were averaged across multiple age-classes (3.97–5.95 d: Collins et al. 1996; 3.4–4.2 d: Woods 2003; 4.3 d: Brown-Peterson et al. 2009) and is consistent with the frequency of spontaneous spawning observed under experimental aquaculture conditions (Papanikos et al. 2008). There was no evidence that spawning frequency decreased for the oldest fish sampled, but even our oldest fish (34 years) was considerably younger than the maximum age of Red Snapper (over 50 years). While it is possible that senescence may occur at some point, it is unlikely to be an important factor to consider in stock assessments as such old fish are very rare in the population.

More importantly, the fact that younger mature Red Snapper do not spawn as often as older mature fish implies that they contribute less to the reproductive potential of the population than might be inferred from their maturity alone (Figure 6; Porch 2004). For this reason, the per-capita fecundity of each age- or size-class of Red Snapper should be modeled as the product of spawns per female per year and batch fecundity rather than as the product of maturity and batch fecundity. The effect of replacing maturity with spawns per female on the perception of the per-capita fecundity of young fish is somewhat mitigated by the rather low batch fecundity of younger Red Snapper (Figure 7a). This is true even when one accounts for the fact that young Red Snapper tend to be much more abundant than larger, older fish. If, for example, the per-capita fecundity at age is multiplied by the equilibrium age structure associated with the maximum sustainable yield (SEDAR 2013), one finds that fish between 2 and 4 years old account for only 3% of the total egg production based on spawning frequency compared with 5% based on maturity (Figure 7b).

The seasonality of spawning was in general agreement with previous studies. Spawning begins in late April or early May, reaches a peak in midsummer, and declines by fall. It is possible that some spawning may occur outside the time period

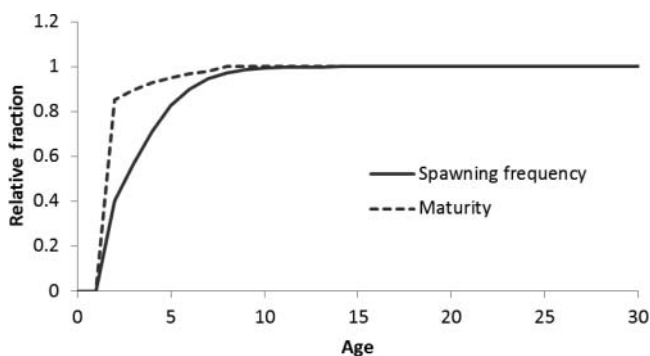


FIGURE 6. Comparison of maturity of Red Snapper and relative spawning frequency at age (years). Female maturity was based upon the presence of vitellogenic or maturing oocytes during the peak reproductive months of June, July, and August. The label on the vertical axis, relative fraction, refers to the value for maturity at age or spawning frequency at age divided by their respective maximum values (to put the two measures on the same scale).

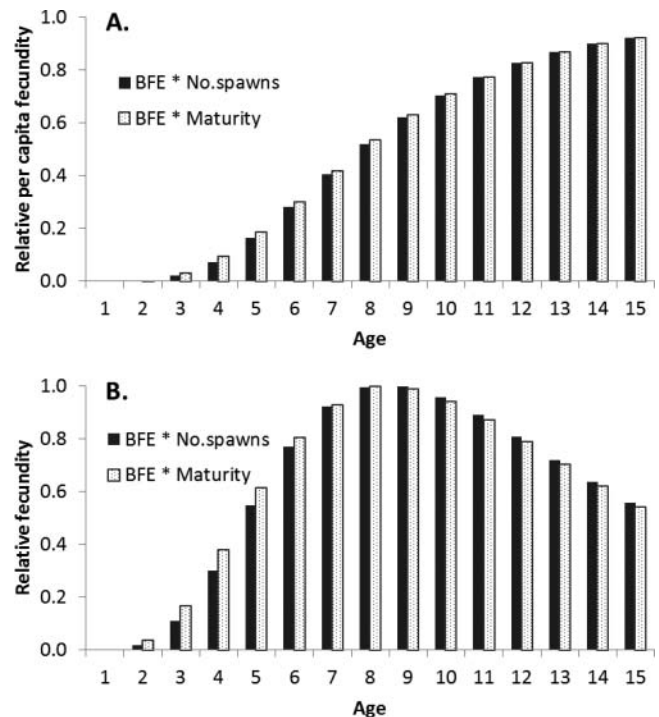


FIGURE 7. Trends in (A) relative per-capita fecundity at age (years) and (B) relative population fecundity at age (combined fecundity of all members in the age-class) in Red Snapper when the calculated number of spawns per female per year is used (solid bars) compared with the trends when spawning frequency is assumed to be proportional to maturity (open bars). The label “BFE * No. Spawns” refers to the calculation where age-specific estimates of batch fecundity are multiplied by age-specific estimates of the number of spawns per year. Similarly, the label “BFE * Maturity” refers to the calculation where age-specific estimates of batch fecundity are multiplied by age-specific estimates of maturity. The relative (population) fecundity is obtained by multiplying the per-capita fecundity at age by the relative abundance of each age-class at the equilibrium level associated with fishing at the maximum sustainable yield.

sampled during this study (April–October) when conditions are favorable; however, this has not been detected during several prior studies spanning decades (Collins et al. 1996; Woods 2003). The data also hint that the spawning season of 2- and 3-year-old Red Snapper is shorter than that of older Red Snapper; no 2- and 3-year-old fish were found in spawning condition before late May and very few after August. The season durations predicted by the models where the parameter γ was estimated are consistent with this observation (Figure 8), but the statistical evidence was not strong and little additional variance was explained. It is possible, therefore, that this apparent trend is spurious. Nevertheless, the matter is of sufficient importance to merit further sampling. As Wright and Trippel (2009) pointed out, an increase in the duration of the spawning season with age has implications beyond merely increasing the total number of annual spawning opportunities. By expanding the duration of the spawning season, older fish may increase their chance of spawning during favorable

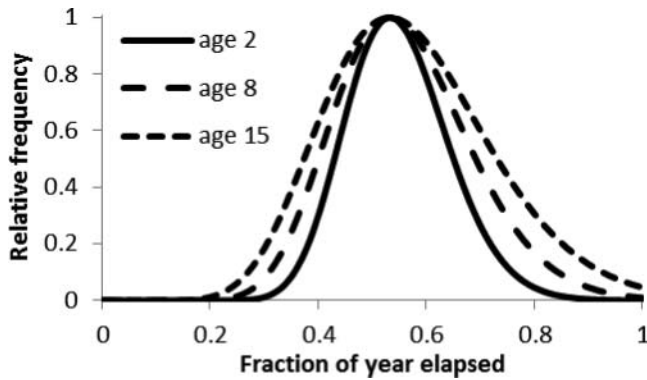


FIGURE 8. Estimated variation in the duration of the Red Snapper spawning season with age (i.e., ages 2, 8, and 15 years) corresponding to the final model, $p(a, t')$, in Table 4.

conditions, thereby reducing the variance and increasing the mean of progeny survival.

Spawning frequency was also estimated to increase with depth and to vary east and west of the Mississippi River. However, while the AIC indicated strong support for including either depth or region in the model, the support for including both simultaneously was weak. This implies that the two effects may be somehow correlated. The average depth sampled in the west (63 m) was slightly deeper than in the east (57 m), so it is possible that perceived regional differences may be partly attributable to differences in average depth. Nevertheless, it is important to point out that depth and region together contributed to explain less than 3% of the total variance and it remains possible that the estimated trends are spurious. This seems particularly likely in the case of the regional model where spawning frequency in the east was estimated to drop to essentially zero for fish below 400 mm largely as a consequence of having very few samples of fish below that size.

The existence of regional differences in the productivity of Red Snapper could have important implications for the management of Red Snapper. The highest spawning frequencies in our samples were exhibited by females caught in areas of the western Gulf associated with outer shelf banks and reef tracts (the western Louisiana shelf and central to the southern Texas shelf) which also happen to be the areas with the greatest concentration of Red Snapper eggs and larvae (Lyczkowski-Shultz and Hanisko 2007). The results of our study indicate that the regional effects were small, implying that the apparently higher spawning frequencies observed in these areas is mostly a reflection of the greater average size of fish and the time of year when the samples are taken, rather than any intrinsic differences in individual fish behavior. It is possible of course that spawning frequency does vary over different spatial and temporal scales owing to differences in ambient conditions. Nevertheless, it is clear that any comparisons must also account for possible differences in local population age structure and the time of year that the collections are made. A population that appears to enjoy a higher per-capita spawning frequency may simply have

a higher proportion of older, larger fish. Similarly, the differences in the apparent spawning frequency of Red Snapper caught on longlines and vertical lines were attributable primarily to the differences in the size and age of fish caught by those gears.

The reproductive tissues used in this study were initially frozen, as opposed to the more common practice of preserving them first in 10% buffered formalin (but see Young et al. 2003). This occurred because the survey utilized commercial vessels working over extended days at sea with contracted samplers and, early in the study design, there were concerns about the routine use of formalin under such conditions. We tested the ability to discern spawning markers from frozen samples by comparing the results from blind reads of paired subsamples (one subsample initially frozen, one subsample initially fixed as fresh tissue) from 50 females. The results indicated 90% agreement for the leading oocyte stage and 82% agreement for presence-absence of postovulatory follicles, suggesting the ability to detect spawning markers may be slightly lower for frozen samples than for those fixed initially in formalin. Young et al. (2003) encountered similar sampling circumstances, but reported no difference between samples that were frozen and those that were fixed in formalin in terms of the classification of oocyte stage, presence or absence of postovulatory follicles, or degree of atresia. In any case, we have no reason to expect that the degree of underestimation we observed would vary in time and space. Therefore, while it is possible that spawning frequency could be somewhat higher than estimated here, the statistical inferences and estimated relative trends in spawning frequency would not be affected.

Previous studies have demonstrated a clear relationship between the batch fecundity of Red Snapper and size or age (Collins et al. 1996; Woods 2003; Porch et al. 2007; Kulaw 2012). The present study has further demonstrated that spawning frequency also increases with size or age and is consistent with the idea that it is important to conserve old ages in the population (Hixon et al. 2014). What remains is to determine how egg quality may vary with age and other factors. For example, egg quality and fertilization success in Red Snapper are known to be related to adult nutrition (Papanikos et al. 2003). Moreover, the abundance of Red Snapper has been increasing rapidly and is expected to continue increasing over the next few years. This raises the possibility that surplus energy for growth and reproduction may be reduced (Goodwin et al. 2006; McBride et al. 2015). Thus, there is a need to continue monitoring Red Snapper reproductive ecology while remaining mindful of important temporal and spatial scales.

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