Assessing reproductive resilience: an example with South Atlantic red snapper *Lutjanus campechanus*

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ABSTRACT: We developed a conceptual model of reproductive resilience based on spatio-temporal diversity in spawning activity and the 'big old fat fecund female fish' effect, i.e., trends in reproductive traits with size and age. We chose red snapper *Lutjanus campechanus* as our case study, as this species is highly fecund, currently overfished, and long-lived (50+ yr). The intrinsic reproductive resilience of red snapper was assessed in terms of spawning site distribution, variability in time of spawning, and potential reproductive lifespan. To assess how age truncation might erode reproductive resilience, we evaluated the strength of the relationship between size and age and the following traits: spawning habitat, reproductive timing, batch fecundity, and egg quality. Few fish were older than 7 yr. Although younger fish occurred in a more restricted range of depths, there was no trend between size or age and depth. Spawning activity was well distributed over space and time, with actively spawning females collected at 92 of 195 sampling sites over an extended spawning season. Larger, older females exhibited longer spawning periods and higher batch fecundities, but neither greater spawning frequency nor egg dry weight. The ratio of the effective to predicted reproductive lifespan at maximum sustainable yield was 31%. Many parameters estimated in this study are common to fish reproductive studies, but we hope that integrating them into a reproductive resilience framework will help focus the need for research on the underlying relationships between reproductive traits and stock productivity.

KEY WORDS: Spawning · BOFFFF · Fisheries management · Spatio-temporal diversity · Age truncation · Maturation · Maternal effects · Spawner-recruit relationship · Reproductive success

INTRODUCTION

Resilience is defined as 'the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedback loops' (Walker et al. 2004, p. 2). This definition of resilience is being increasingly integrated into ecology, conservation, and ecosystem-based management (Hughes et al. 2005, Folke 2006, Healey 2009). However, in marine fish stock assessments, resilience is measured as the steepness (*h*) or the slope of the stock-recruitment curve near the origin (Myers et al. 1999, Mangel et al.

2013). Although this is a useful measure, it measures only 1 component of a reproductive strategy, i.e. the correlation between abundance (typically measured by spawning stock biomass, SSB) or reproductive output (measured by egg production) and survival of that output. Most exploited marine fishes are highly fecund (Murua & Saborido-Rey 2003) and can produce large year classes even at reduced levels of SSB; thus they will have relatively high steepness and would be considered 'resilient' by this measure. However, highly fecund marine fish can be overfished and are not immune to extinction risk (Sadovy 2001, Sadovy de Mitcheson et al. 2013), suggesting a

need to integrate additional information on a stock's reproductive potential into our stock assessments (Mangel et al. 2013).

Reproductive strategies are complex, adaptable systems that evolved under a given regime of natural mortality (Young et al. 2006, Lowerre-Barbieri et al. 2011a). Highly fecund marine species differ in a range of reproductive traits, including maturity and longevity, gender and mating systems, spatial attributes (e.g. spawning migrations, spawning site selection, and fidelity), and the temporal pattern of reproduction over a lifetime or reproductive timing (Lowerre-Barbieri et al. 2011b). Adaptations to offset natural mortality have led to the selection of these traits; that is, regardless of extremely high fecundity and low larval survival rates, certain adult traits have resulted in greater reproductive success in a given habitat. A species' reproductive compensatory ability depends on the selection pressures under which it evolved (Garrod & Horwood 1984); thus, developing the means to quantify reproductive resilience to fishing and other stressors will improve our predictions of marine fish population growth.

Canale et al. (2012, p. 1) defined reproductive resilience as 'the ability to maintain a constant reproductive output despite unexpected environmental disturbances'. Here, we expand upon this definition (which was applied to small primates) to encompass elements specific to marine fish reproductive strategies. Specifically, we define reproductive resilience as the reproductive capacity of a population to maintain the level of reproductive success needed to result in long-term population stability despite disturbances such as environmental perturbations and fishing. Reproductive success refers to the probability that offspring will survive to reproductive age, and it will be impacted by both reproductive output and factors affecting the survival rate of that output (Lowerre-Barbieri 2009). Our conceptual model assumes that reproductive resilience in marine fishes increases with increased diversity in spatio-temporal spawning behavior, given the importance of these factors to reproductive success (Begg & Marteinsdottir 2002, Rowe & Hutchings 2003). Further, it assumes that reproductive resilience, especially to fishing, is affected by the relationship between size and/or age and a range of reproductive traits (Fig. 1). This is based on the increased recognition of the value of big old fat fecund female fish (BOFFFFs) to stock productivity (Hixon et al. 2014) in terms of increased annual fecundity (Fitzhugh et al. 2012, Cooper et al. 2013), spatio-temporal reproductive behavior (Scott et al. 2006, Anderson et al. 2008), energy reserves (Jør-
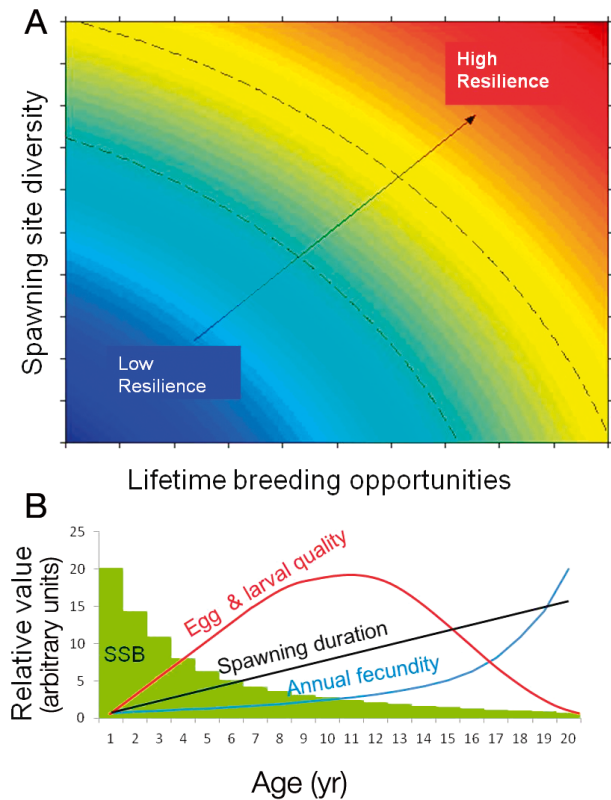

Fig. 1. (A) Conceptual model of reproductive resilience based on spatio-temporal diversity. Dashed curves show how a given resilience level can be met through tradeoffs between spatial and temporal diversity. (B) Potential relationships with age of reproductive traits impacting reproductive success: spawning stock biomass (SSB; a proxy for abundance), annual fecundity (blue), spawning duration as a proxy for the distribution of spawning events within a spawning season (black), and the maternal effects on egg and larval quality (red)

gensen et al. 2006, Rideout & Tomkiewicz 2011), and their impact on both the number of spawning events and how they are distributed over the spawning season (Wright & Trippel 2009), as well as egg and larval quality (Kamler 2005). In addition, reproductive lifespan is an important component of reproductive resilience, as it determines the number of years over which an individual fish potentially can spawn and thus the ability for older, larger fish to outlive periods of poor recruitment. However, we propose that the BOFFFF effect can apply to any reproductive trait which results in a relationship between reproductive success and fish age or size, regardless of sex.

We chose red snapper *Lutjanus campechanus* as our case study given that this species is highly fecund, is currently considered overfished, and is recognized for having high compensatory reserve, i.e. resilience (Rose et al. 2001). Red snapper support important commercial and recreational fisheries in

the Gulf of Mexico and the southeastern USA, with both the Gulf and South Atlantic (SA) stocks exhibiting highly truncated age distributions (Cowan 2011). The latest benchmark assessment (SEDAR24 2010) indicated that the SA red snapper stock was both overfished and undergoing overfishing, but also documented a sharp increase in abundance due to recent high recruitment in 2006 and 2007. Red snapper are long-lived, with a maximum reported age of 54 yr (SEDAR24 2010), and are highly fecund, with indeterminate fecundity and an extended spawning season (Collins et al. 1996, Woods et al. 2003, Brown-Peterson et al. 2009, Brulé et al. 2010).

In this study, we evaluated the reproductive resilience of the SA red snapper stock at the species scale (i.e. the underlying reproductive strategy) and in the current overfished stock. Red snapper reproductive resilience was assessed in terms of potential reproductive lifespan (i.e. that expected in a virgin stock) and within-population diversity in spatio-temporal reproductive behavior. To assess how age truncation might erode reproductive capacity, we evaluated the strength of the relationship between reproductive behavior and demographics, or the BOFFF effect, for the following reproductive traits: spawning habitat, reproductive timing, batch fecundity, and egg dry weight. To quantify the extent of age truncation, we calculated the ratio of current to potential reproductive lifespan as well as the effective reproductive lifespan based on the 90th percentile of the sampled age distribution and that expected for the stock at maximum sustainable yield (MSY). The following specific hypotheses were tested within the above context: (1)

spawning fish would aggregate in large numbers at relatively few spawning sites; (2) the time of spawning events would exhibit diel periodicity; (3) females would mature younger and smaller than predicted based on growth dynamics; (4) spawning seasonality and activity would differ with size and/or age; and (5) batch fecundity and egg quality, as measured by egg dry weight, would exhibit a significant increase with both size and age.

MATERIALS AND METHODS

Sample collections

The sampling area corresponded to the center of the SA red snapper population, off the east coast of Florida (Fig. 2), from roughly 28° 00′ N (Melbourne, Florida) to 30° 45′ N (White & Palmer 2004). The sample area was subdivided every 1° of latitude to create sampling zones which corresponded to National Marine Fisheries Service (NMFS) statistical reporting zones: 722, 728, and 732. Presumed suitable hard-bottom habitat locations were obtained from participating fishers (commercial and recreational), federal agency partners (i.e. NMFS, US Geological Service), and Florida Fish and Wildlife Commission's historical data. A sampling universe was built around these locations, with primary sampling units delineated as 0.3 nautical miles (n miles) latitude by 0.1 n miles longitude grids containing reef habitat. Sampling sites were randomly selected from the universe, and sampling effort was stratified by sampling zone and depth
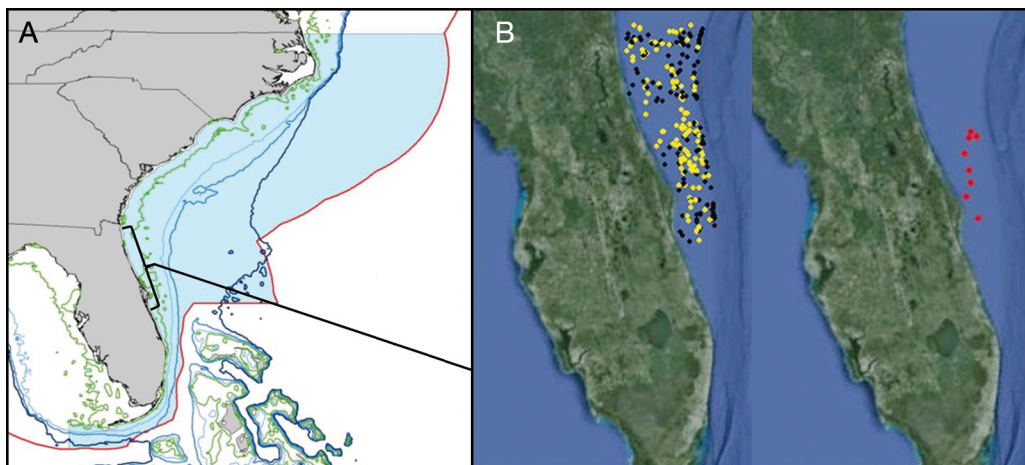

Fig. 2. (A) Spatial distribution of the management zone for South Atlantic red snapper *Lutjanus campechanus* (area filled in blue), and depth contours: 20 m (green) 200 m (light blue), 500 m (medium blue), 1000 m (dark blue), and the US exclusive economic zone (red). (B) left panel: the study site with red snapper sampling sites (black dots) and locations where red snapper were caught (yellow dots); right panel: spatial distribution of key spawning sites with >20% spawning fraction and >10 females sampled per date (red dots)

(inshore, inside the 30 m isobath; offshore, between the 30 and 100 m isobaths). For inshore strata, 12 sites were selected per zone each month. In an effort to preserve the proportionality of sampling to available habitat throughout the sampling universe, 20 sites were selected per zone each month for offshore strata. At each site, date, time (Eastern Standard Time), depth, and latitude and longitude were recorded.

Monthly hooked-gear surveys were conducted from April through October. The study was initially designed to occur over a 4 mo period (April to July), but poor weather conditions resulted in lower than expected sampling effort in this time period. Sampling was extended through October, and the sampling design was adjusted to select more stations from the sampling zones and strata that were undersampled during the initial period (Table 1). From April through August, there was an average of 13 sampling dates per month (range: 10–14), with less effort in September and October (4 and 3 sampling dates, respectively).

Fishing methods and effort were standardized at all sampling sites. Three sampling techniques were used (passively fished vertical and horizontal bottom long lines and an actively fished repetitive timed drop method using Elec-tra-mate© gear), but 88% of the samples (n = 1157) came from the active repetitive timed drop method. All hooks were baited with Atlantic mackerel *Scomber scombrus* cut proportional to hook size. In certain conditions (e.g. rough seas, extreme currents), it was necessary to use the motor to maintain the boat over the intended site. For each sampling site, the bottom long line was fished at least 0.1 n miles away from the other gears. If there was not enough suitable habitat at a site to sample all gears, priority was given to the active fishing and vertical long line gears. Neither long line was deployed if the current exceeded 2 knots, due to gear drift.

Because hook-and-line sampling can be biased due to angler experience or hook size, efforts were made to minimize these effects. Four anglers participated in active fishing, each assigned to a different rig type, with assignments rotated at each sampling site. Each rig consisted of a 2-hook combination (top hook listed first): 8/0 and 11/0, 8/0 and 15/0, or 11/0 and 15/0 size hooks. At inshore sites, 2 rigs with the smallest hook combination were used, and at offshore sites, 2 rigs with the largest hook combination were used. We targeted 12 'team drops' per site in the inshore depth strata and 10 in offshore strata, as sampling at these sites took longer due to more difficult fishing conditions.

Sample processing

Fish were kept on ice until processed in the laboratory, generally within 24 h of capture. Each fish was measured for maximum total length (TL, ±1 mm) and total weight (TW, ±1 g). For hydrated females, used to assess batch fecundity, gonad weight (GW) was measured and somatic weight (SW) calculated as TW – GW. Sex was determined macroscopically, both sagittal otoliths were removed and stored dry, and ovarian tissue samples were taken for histological analysis. A section of ovarian tissue was processed for histological analysis as follows: fixed in 10% neutrally buffered formalin for a minimum of 24 h, soaked in water for 1–2 h, and stored in 70% ethanol. Samples were embedded in glycol methacrylate, sectioned to 3–5 mm thickness, stained with periodic acid–Schiff's hematoxylin, and then counterstained with metanil yellow (Quintero-Hunter et al. 1991).

Samples for gravimetric estimation of batch fecundity using the hydrated oocyte method (Hunter et al. 1985, Murua et al. 2003) were processed following Lowerre-Barbieri & Barbieri (1993). Fresh oocytes were hydraulically separated from each other and from the ovarian membrane and preserved in 2% neutrally buffered formalin. Settling bias was reduced by stirring the samples, and then 2 subsamples (~0.1 g) were removed and the number of hydrated oocytes counted. Estimates of batch fecundity were not used if histological

Table 1. Summary of sites selected (with number of sites sampled in parentheses) for red snapper *Lutjanus campechanus*, according to National Marine Fisheries Service statistical zone and depth stratum (shallow: <30 m, deep: >30 m)

Zone	Depth stratum	April	May	June	July	August	Sept./Oct.
722	Shallow	12 (10)	12 (11)	12 (11)	12 (8)	6 (3)	10 (6)
	Deep	20 (16)	20 (11)	20 (5)	20 (17)	24 (12)	16 (11)
728	Shallow	12 (12)	12 (12)	12 (6)	12 (12)	6 (5)	10 (4)
	Deep	20 (16)	20 (19)	20 (8)	20 (20)	20 (9)	8 (0)
732	Shallow	12 (2)	12 (11)	12 (8)	12 (10)	18 (15)	10 (6)
	Deep	20 (20)	20 (12)	20 (4)	20 (14)	25 (9)	16 (9)
	Total	96 (76)	96 (76)	96 (42)	96 (81)	99 (53)	70 (36)

analysis indicated that ovulation had begun (i.e. fresh postovulatory follicles [POFs] were present).

Hydrated oocyte dry weights were measured as a potential indicator of egg quality. Two replicates of 100 hydrated oocytes were selected from the samples used for batch fecundity, manually separated, and dried for 48 h at 68°C. We recognize that formalin-preserved samples are not ideal (Haslob et al. 2013), but because all samples were preserved over a similar time period, we considered it adequate for our objective of comparing differences with size and age.

Gonadal analysis

Histological indicators used to assess reproductive state and phase (Table 2) followed Lowerre-Barbieri et al. (2009) and Brown-Peterson et al. (2011), with the slight modification that the most advanced oocyte stage in the developing phase was early vitellogenic (i.e. Vtg1). Five oocyte developmental stages were identified: primary growth (PG), cortical alveoli (CA), early vitellogenic (Vtg1), late vitellogenic (Vtg2 and Vtg3), and oocyte maturation (OM). The following characteristics of OM were noted: germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD), yolk coalescence or clarification, and oocyte hydration (Jalabert 2005). Early OM oocytes had only slightly displaced germinal vesicles and little yolk coalescence or hydration, and these fish were expected to spawn within 5 to 14 h (Jackson et al. 2006). Late OM was characterized by completed GVM or GVBD, yolk coalescence, and hydrated oocytes detectable by macroscopic inspection, i.e. the increase in size and clarity due to hydration made them easily distinguished from yolked oocytes (Lowerre-Barbieri et al. 2009). POFs were classified as (1) fresh (i.e. newly collapsed, recognizable by the size and appearance of the granulosa cells' nuclei), (2) less than 24 h, or (3) older than 24 h based on POF size and organization and time of capture (Hunter & Macewicz 1985). The spawning-capable phase indicated

Table 2. Ovarian classification and terms based on histological analysis of red snapper *Lutjanus campechanus*. POF: postovulatory follicle, OM: oocyte maturation, GVM: germinal vesicle migration, GVBD: germinal vesicle breakdown

Reproductive state	Phase	Histological indicators	Significance
Immature			
Non-spawning	Immature	Only oogonia and primary growth oocytes, including chromatin nucleolar and perinucleolar oocytes. Usually no atresia.	Virgin that has not yet recruited to the spawning population.
Mature			
Non-spawning	Developing	Cortical alveolar and early vitellogenic oocytes (Vtg1). No evidence of POFs. Some atresia may be present.	Environmental signals have triggered development, but fish are not yet developed enough to spawn.
Spawning population			
Spawning-capable	Spawning-capable	Late vitellogenic oocytes (Vtg2 & 3). May be atresia.	Fish developed enough to spawn.
	Subphase spawning	Oocyte maturation, hydration, or POFs.	Fish with indicators of spawning activity.
	Imminent	Early OM (GVM with little yolk coalescence)	Will spawn in 14 h.
	Active	(1) Advanced GVM (2) GVBD (3) Hydrated or undergoing ovulation (4) Newly-collapsed POFs	Spawning in ±2 h.
	Recent	POFs (12–36 h old)	Spawned within 2 d.
Mature			
Non-spawning	Regressing	A high percentage of yolked oocytes undergoing atresia (alpha and beta).	Cessation of spawning.
Non-spawning	Regenerating	Only primary growth oocytes present, including chromatin nucleolar and perinucleolar. Muscle bundles, enlarged blood vessels, thick and/or convoluted ovarian wall, and gamma or delta atresia may be present.	Sexually mature, reproductively inactive. Most common outside of the spawning season.

females sufficiently developed to spawn within days of receiving the appropriate endocrine signal (i.e. Vtg2 and Vtg3). Spawning females were those with either OM oocytes or POFs and actively spawning females were those with late OM, or fresh POFs.

Mature females were distinguished from immature females based on the following criteria: size of the ovarian cross section, ovarian wall thickness, lamellar structure and organization, and presence of muscle bundles (Lowerre-Barbieri et al. 2011b). In addition, immature females were assessed in terms of the development of their primary growth oocyte population, to determine whether they were capable of recruiting to the spawning population within the spawning season being sampled. Because there are no historical estimates of sexual maturity in SA red snapper, it was not possible to assess whether over-exploitation had impacted maturity schedules (Jørgensen et al. 2007, Heino et al. 2013). As a proxy for maturation in a virgin stock, we used 2 measures, (1) the Beverton-Holt life history invariant approach suggesting fish species mature at two-thirds their asymptotic length (Jensen 1996); and (2) and the mean maturation to asymptotic length ratio (52%) reported for the subfamily Lutjaninae based on a literature review (Martinez-Andrade 2003). We used the asymptotic length of 902 mm TL (SEDAR24 2010).

Spawning activity was assessed at the annual scale to estimate the population spawning season and at the intraseasonal scale to estimate spawning fraction, interval, and frequency. The population spawning season was based on the first and last occurrence of spawning females. We used the definitions in Lowerre-Barbieri et al. (2011b) for spawning fraction, interval, and frequency. Spawning fraction was estimated both using the percent hydrated method and the POF method (Hunter & Macewicz 1985, Murua et al. 2003). At the population scale, spawning interval was estimated as the reciprocal of the spawning fraction, and spawning frequency was estimated by dividing the number of days in the spawning season by spawning interval (Hunter & Macewicz 1985, Murua et al. 2003). To assess demographic differences in spawning activity, the proportion of spawning-capable females with spawning indicators (both OM and POFs) was evaluated by age and TL classes.

Otolith analysis

Fish were aged using transverse sections of the sagittal otolith. Otoliths were sectioned through the core using a Buehler low-speed Isomet saw. Sections

350 to 500 µm thick were mounted on glass slides with histomount. Sections which were difficult to read were also viewed in reflected light. All slides were read twice by 2 different readers and a third time if there were discrepancies. Percent agreement between all first and second reads was 95.2%. Of the 63 discrepancies, 98.4% differed by a year, and the final age for these fish was determined based on a third read and consensus between the 2 readers. Ages were assigned to year classes by using a 1 January birthdate (Jearld 1983) to clearly separate fish born in different years.

Age truncation

Age truncation was assessed based on potential, observed, and predicted reproductive lifespan at MSY. Reproductive lifespan is the number of years an animal could be reproductively active (Stearns 1992). Changes in this parameter can be used to assess the effects of age truncation on reproductive capacity. Potential reproductive lifespan was used to refer to that expected in an unfished stock, and current reproductive lifespan refers to that observed in the sampled population. If senescence has not been indicated for the species being studied, reproductive lifespan is calculated as the maximum age minus age at maturity. The maximum age reported in the most recent stock assessment, 54 yr (SEDAR24 2010), was used to estimate potential reproductive lifespan. However, given the relationship between maximum age and sample size (Hoenig 1983), we also estimated the effective reproductive lifespan based on the maximum observed age at the 90th percentile and compared this to the maximum age at the 90th percentile estimated for the stock at MSY (SEDAR24 2010).

Data analysis

Before we could evaluate spatio-temporal patterns in reproductive effort, we needed to assess whether sex or gear type affected the size of fish sampled. Because size and age distributions did not meet the assumption of normality, we used nonparametric methods to compare size frequency distributions by sex (Kolmogorov-Smirnov, K-S test) and gear type (Kruskal-Wallis). We used quantile regression to assess overall range of ages sampled versus ranges sampled in each zone.

We evaluated the relationship between fish size and age and reproductive timing. To assess whether

the probability of being spawning capable differed with size or age, we selected data from months with similar sampling effort (April through August) and grouped fish into 3 size categories: small (<500 mm TL), medium (500 to 700 mm TL), and large (>700 mm TL) and 3 age categories: young ($<$ age 4), middle (ages 4 and 5), and older ($>$ age 5). The proportion of females in the spawning population was modeled using a generalized linear model (PROC GENMOD in SAS), a binomial distribution, and a logit link function. A higher probability of being in the spawning population on the date of capture was assumed to be associated with a longer spawning period for fish in that size- or age-class (Lowerre-Barbieri et al. 2009). Females not in the spawning population were categorized as 0 and those in the spawning population as 1. We used the same approach to evaluate demographic effects on the probability of spawning; however, in this analysis, we assessed the proportion of spawning females within the spawning population (Lowerre-Barbieri et al. 2009). Diel periodicity was evaluated by assessing hour of capture with histological indicators of imminent or active spawning. A non-parametric Kruskal-Wallis test was used to assess whether there was a relationship between spawn time and size or age. A bivariate kernel density estimation was used to evaluate the location with the highest density (75%) of active spawners and to assess whether the spatial distribution of active spawners differed by size or age category.

Linear regression was used to model the basic relationship between batch fecundity and 2 measures of size (TL and SW). To linearize the parameters in the batch fecundity to SW and TL relationships, parameters were $\log_e$-transformed. To assess whether zone or age significantly affected batch fecundity, stepwise linear regression was used to model the relationship between batch fecundity and the following main effects: TL, zone, and age. The significance level for variable inclusion was 0.5. All statistical analyses were performed using SAS version 9.13 and an alpha level of 0.05.

RESULTS

Sampled population

A total of 1307 red snapper were aged, 1305 were sexed (722 females and 583 males), and ovarian samples were taken from 696 females for histological analysis. Similar numbers of red snapper were captured in the 2 most southern zones (Zones 732, n =

550; Zone 728, n = 524), with fewer captured in the northernmost zone (Zone 722, n = 233), although the oldest fish was sampled in this zone. Mean size was similar in the 2 northernmost zones (603 and 619 mm TL, respectively), but smaller in the southernmost zone (527.8 mm TL). Fish <350 mm TL were not fully recruited to any of the sampling sites, resulting in only 2 age-1 fish being sampled. Fish size exhibited a bimodal pattern of abundance and ranged from 207 to 925 mm TL (Fig. 3). Size did not differ significantly with sex (K-S, $\chi^2 = 1.27$, p = 0.2596), or gear (Kruskal-Wallis, $\chi^2 = 2.252$, p = 0.2436) but was clearly driven by several strong year-classes. Abundance was dominated by 2 yr olds (16%, 2010 year-class), 3 yr olds (25%, 2009 year-class), 5 yr olds (29%, 2007 year-class), and 6 yr olds (13%, 2006 year-class). In contrast, 4 yr olds made up only 5% of the sampled population. This drove the bimodal size distribution, with peaks in the 400–450 mm and the 650–700 mm TL size classes.

Older, larger fish occurred in a wider range of depths but did not exhibit a significant trend with depth. Few fish (4%) were sampled at depths greater than 60 m (n = 58), but all fish sampled at these deeper sites were ≥500 mm TL and older than age 3 (Fig. 3). However, larger, older fish also occurred in samples over a wide range of depths, and at the 0.9 quantile, size class did not differ significantly with depth of capture (quantile regression, $\chi^2 = 0.0$, p = 1.0, n = 1315), nor did age (quantile regression, $\chi^2 = 0.0$, p = 1.0, n = 1305).

Spatio-temporal diversity in spawning

Red snapper spawned throughout most of the study area, rather than concentrating spawning at a few highly populated sites (Fig. 4). The number of females collected at any given sample site (combination of date and location) exhibited a wide range (0–19), as did the number of active spawners (0–13). Although there were sites where multiple active spawners were sampled, the most common pattern was to collect only 1 active spawner per site (55%, n = 92 sampling sites). Depth of sampling site did not differ significantly between active spawners and the remaining females (Kruskal Wallis, $\chi^2 = 1.4152$, p = 0.2342, n = 666), with active spawners collected over a wide range of depths (15–73 m). Active spawners were sampled from 92 of the 195 unique sampling sites, and the sites with spawning females were distributed over a wide geographic range (28.11°–30.58° N to 81.02°–80.05° W), an area equal to 25 502 km^2.
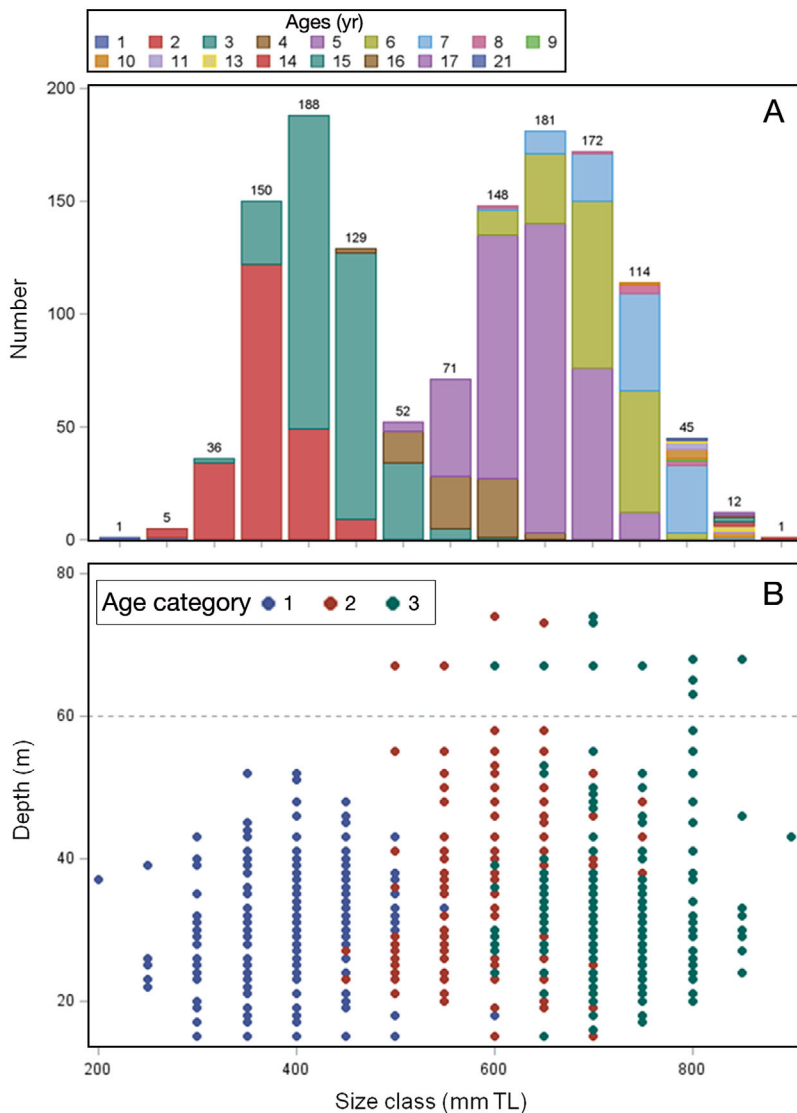
Fig. 3. (A) Size and age distribution of sampled red snapper *Lutjanus campechanus.* Size classes are based on 50 mm total length bins. (B) Distribution of age categories (1: 1–3 yr; 2: 4–5 yr; 3: ≥6 yr) and size class by depth at capture

(hydrated oocytes and fresh POFs) occurred throughout the day, and there was no indication of a size (Kruskal Wallis, $\chi^2 = 17.4$, p = 0.0957, n = 115) or age (Kruskal Wallis, $\chi^2 = 8.6072$, p = 0.2821, n = 115) effect on spawn time. Females with late OM were collected from 07:00 to 17:00 h and 4 females with newly collapsed POFs were collected from 09:00 to 13:00 h, indicating that at least some spawning occurred throughout the day.

Maturity

Virtually all of the females sampled in this study (99%) were mature. Immature females (n = 8), exhibited a wide size range (207–404 mm TL) but were young (age 2, n = 7; or age 1, n = 1) and mostly occurred in April and May (n = 7). Immature females exhibited a range of development from a 1 yr old fish with no primary growth oocytes (Fig. 6A) to fish in the process of recruiting primary growth oocytes (Fig. 6B) and, further, to those with a fully-developed population of primary growth oocytes, capable of recruiting to the spawning population within the spawning season (Fig. 6C) similar to mature regenerating females (Fig. 6D). Based on Beverton-Holt life history invariants, the optimal size at maturation was predicted to be ca. 600 mm TL. Females in this size range (550 to 650 mm TL, n = 221) had a mean age of 4.8 yr (range: 3 to 8 yr). In contrast, the predicted length at maturation based on the size at maturation to size at asymptotic length relationship for the subfamily Lutjaninae was 469 mm TL. Females in this size range (400 to 500 mm TL) had a mean age of 2.82 yr (range: 2 to 4 yr, n = 319). Maturation and spawning capability at sizes and ages less than predicted was confirmed based on the prevalence of small mature femals (Fig. 6E) and on 30 age-2 females ≤400 mm TL with histological indicators of spawning.

Demographic trends in reproductive timing

Spawning seasonality was asynchronous, with individual variability in spawning periods. Spawning-capable females occurred from April through September, and spawning females from 4 April to 20 September 2012, corresponding to 170 d in the popu-

However, 75% of active spawners occurred within a much smaller area (1183 km^2) bounded by 28.92° to 29.58° N and 80.52° to 80.35° W. All age categories spawned in similar areas (Fig. 4), as did fish in different size categories.

Although red snapper spawning exhibited diel periodicity, some fish spawned throughout the day. Spawning indicators (OM substages and fresh POFs) differed significantly with hour (Kruskal Wallis, $\chi^2 = 119.44$, p < 0.0001, n = 224), and exhibited a general trend of later time associated with the expected progression in OM and ovulation (Fig. 5). However, those indicators associated with spawn times
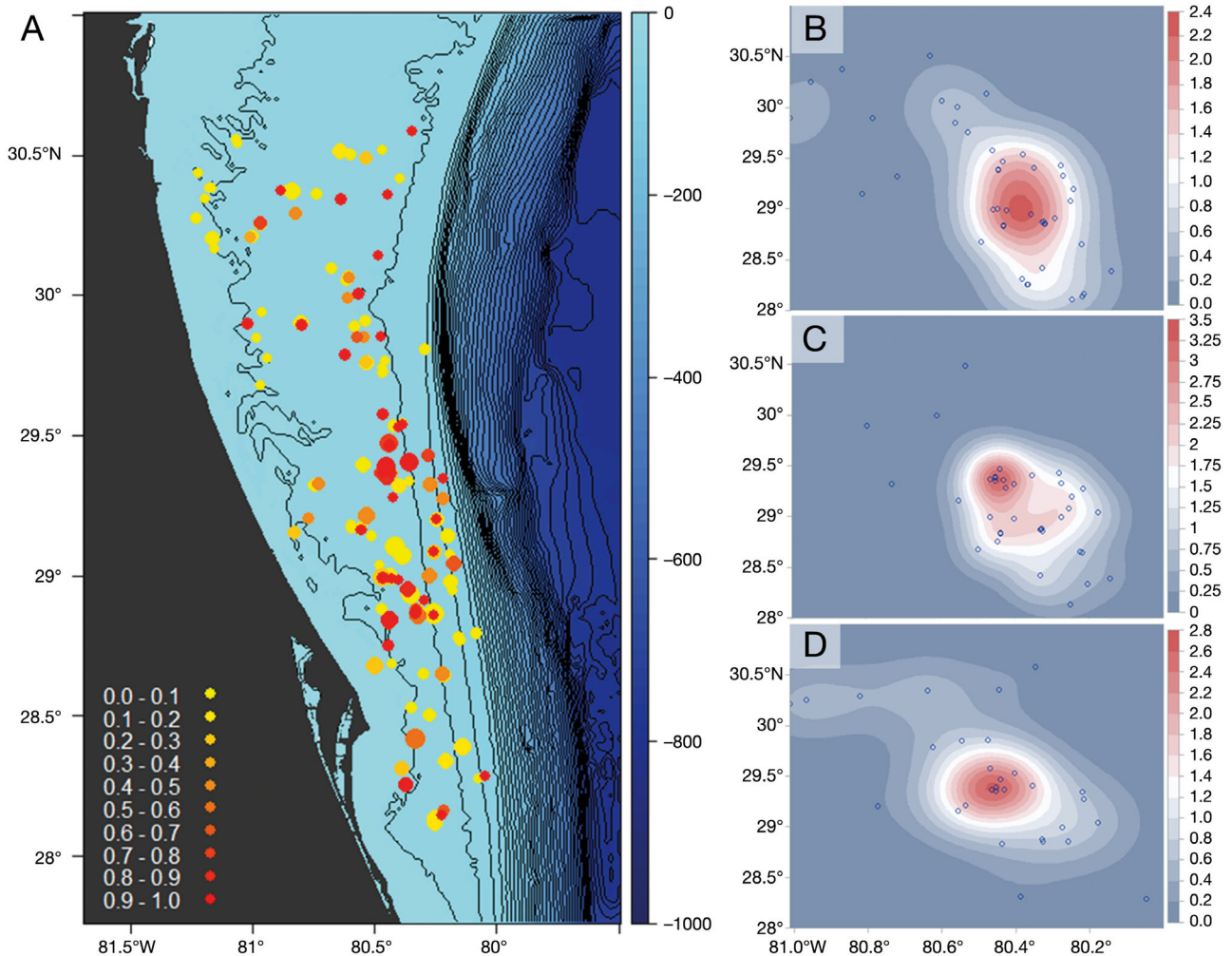
Fig. 4. (A) All sites where female red snapper *Lutjanus campechanus* were sampled. Bubble size represents the number of female red snapper caught (range 1 to 19) and color represents spawning fraction, with yellow representing the lowest spawning fraction and red the highest. Water depth is indicated by the color bar to the right. Also shown are kernel density estimates of active spawners by age category for ages (B) 2–3 yr, (C) 4–5 yr, and (D) >5 yr. Relative densities of spawning females are indicated by the color bar to the right, with red indicating the areas with the highest densities

lation spawning season. However, the proportion of spawning-capable females differed significantly with month (binomial regression, n = 679, p < 0.0001) and age (binomial regression, n = 679, p < 0.0001), with older fish exhibiting a higher probability of being spawning capable in all months (Fig. 7A). A similar pattern was seen with size category (Fig 7B), with the proportion of spawning-capable females differing significantly with month (binomial regression, n = 679, p < 0.0001) and size category (Fig. 7B; binomial regression, n = 679, p < 0.0001). In April, only 24% of small fish (<500 mm TL) were spawning capable, compared to 76% of the large fish (>700 mm TL). Similarly, large fish continued to have a higher proportion of spawning-capable females in July and August than small fish.

Red snapper exhibited high spawning activity, with an overall spawning fraction of 32.7% for the hydrated method and 17.6% for Day 1 POFs. Using traditional methods to assess spawning interval, these percentages correspond to 1 spawn approximately every 3 d (% hydrated) or once every 5.7 d (POF). The annual spawning frequency thus was higher for the percent hydrated method, viz. 57 spawns, compared to approximately 30 based on the POF method. However, spawning activity was not evenly distributed throughout the spawning season, exhibiting a clear maximum in June (Fig. 8). The proportion of spawning-capable females that had spawning indicators differed significantly by month (binomial regression, n = 558, p < 0.001), but not by size (p = 0.9801) or age (p = 0.5787), ranging from
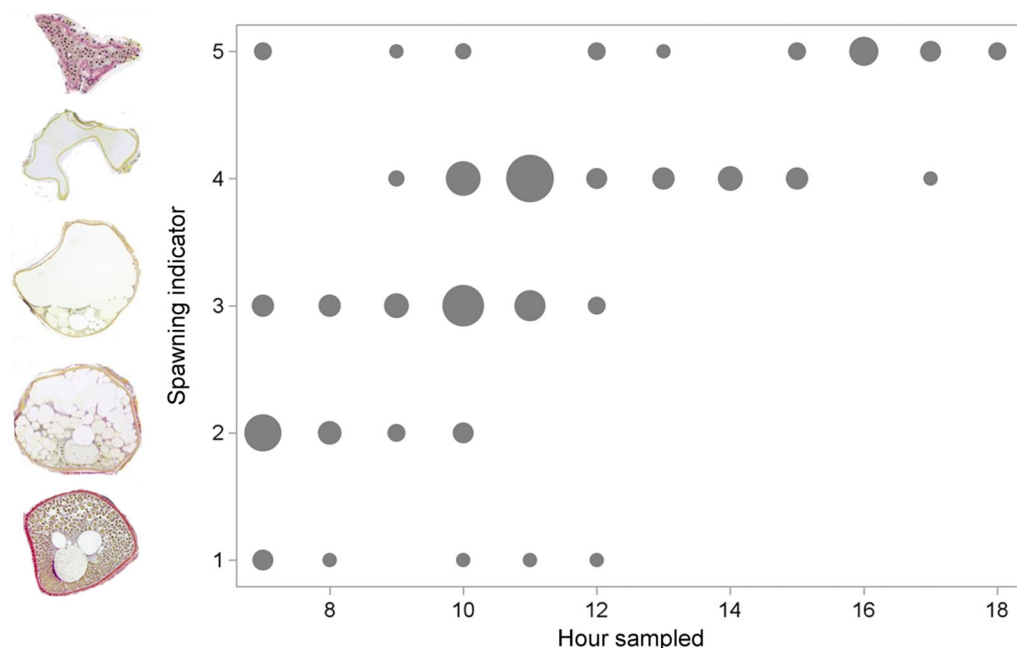
Fig. 5. Number of female red snapper *Lutjanus campechanus* with spawning indicators by hour sampled. Spawning indicators have representative images (left) and are as follows: (1) early germinal vesicle migration (GVM) with little yolk coalescence; (2) advanced GVM; (3) germinal vesicle breakdown; (4) hydrated or undergoing ovulation; and (5) newly-collapsed post-ovulatory follicles. Bubble size represents the number of females: the smallest bubble represents 1 fish and the largest bubble represents 36 fish with that indicator at that time

0.16 in April to a peak of 0.86 in June. In July, the proportion decreased to 0.65, and by August it was 0.47. Although the temporal pattern of spawning activity with size was not statistically significant, large fish (>700 mm TL) demonstrated a more even distribution of spawning activity over the months of May (0.64), June (0.75), and July (0.63) than smaller fish.

Fecundity and egg dry weight

Larger females produced significantly more eggs per batch than smaller females (Fig. 9). Batch fecundities ranged from roughly 14 000 to 4.2 million eggs female^{-1} and significantly increased with log$_e$-transformed TL (log$_e$ batch fecundity = −17.4 + 4.8 log$_e$ TL; r^2 = 0.68, n = 44) and log$_e$-transformed SW (log$_e$ batch fecundity = 1.37 + 1.46 log$_e$ SW; r^2 = 0.63 n = 44). The predictive batch fecundity relationship with log$_e$-transformed TL was improved by including sampling zone (r^2 = 0.75, p = 0.0019), but not age. Relative fecundity (eggs g^{-1} SW) also significantly increased with size (Kruskal Wallis, χ^2 = 9.0651, p = 0.0108, n = 44). However, relative fecundity was highly variable (13 to 602 eggs g^{-1} SW), with some females producing extremely small batches. Egg dry weight did not differ significantly with TL class (2-way ANOVA,

$F_{1,25}$ = 0.77, p = 0.6013) nor age (2-way ANOVA, $F_{1,25}$ = 0.40, p = 0.8750).

Age truncation

SA red snapper exhibit an extended potential reproductive lifespan of 49 yr. The maximum observed age of red snapper in this study was 21 yr, corresponding to a reproductive lifespan of 20 yr or 43 % of that estimated for a virgin stock. The maximum age at the 90 % quantile at MSY was age 16, compared to 6 yr old in this study, resulting in a current effective reproductive lifespan of 5 yr, which is only a third of that at MSY.

DISCUSSION

Spatio-temporal spawning diversity

Red snapper exhibited spawning activity over a wide range of sites, with a low proportion of active spawners and low number of females sampled per site. Although 75 % of active spawners sampled in this study came from a relatively small area, additional spawning activity was observed over a much
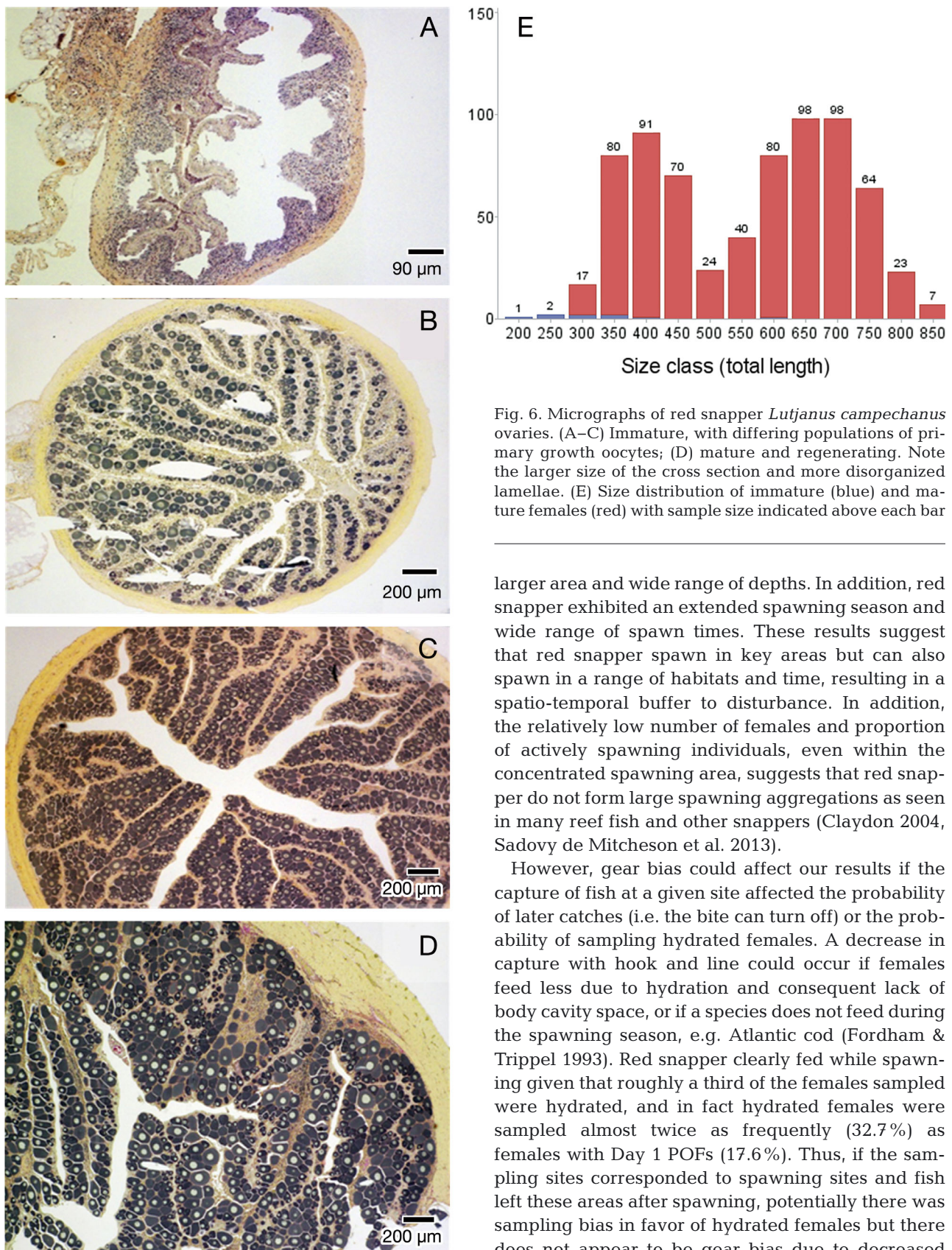
Fig. 6. Micrographs of red snapper *Lutjanus campechanus* ovaries. (A−C) Immature, with differing populations of primary growth oocytes; (D) mature and regenerating. Note the larger size of the cross section and more disorganized lamellae. (E) Size distribution of immature (blue) and mature females (red) with sample size indicated above each bar

larger area and wide range of depths. In addition, red snapper exhibited an extended spawning season and wide range of spawn times. These results suggest that red snapper spawn in key areas but can also spawn in a range of habitats and time, resulting in a spatio-temporal buffer to disturbance. In addition, the relatively low number of females and proportion of actively spawning individuals, even within the concentrated spawning area, suggests that red snapper do not form large spawning aggregations as seen in many reef fish and other snappers (Claydon 2004, Sadovy de Mitcheson et al. 2013).

However, gear bias could affect our results if the capture of fish at a given site affected the probability of later catches (i.e. the bite can turn off) or the probability of sampling hydrated females. A decrease in capture with hook and line could occur if females feed less due to hydration and consequent lack of body cavity space, or if a species does not feed during the spawning season, e.g. Atlantic cod (Fordham & Trippel 1993). Red snapper clearly fed while spawning given that roughly a third of the females sampled were hydrated, and in fact hydrated females were sampled almost twice as frequently (32.7%) as females with Day 1 POFs (17.6%). Thus, if the sampling sites corresponded to spawning sites and fish left these areas after spawning, potentially there was sampling bias in favor of hydrated females but there does not appear to be gear bias due to decreased
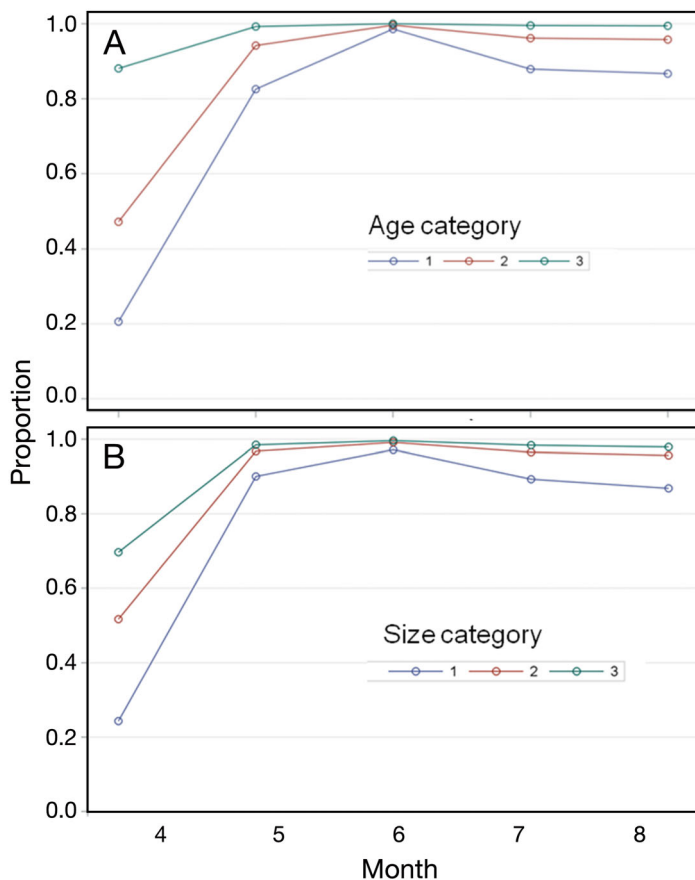
Fig. 7. Proportion of female red snapper *Lutjanus campe-chanus* in the spawning population by month and (A) by age category, where 1 = young (<4 yr), 2 = middle (4 and 5 yr), and 3 = older (>5 yr); and (B) by size category, where 1 = small (<500 mm total length, TL), 2 = medium (500–700 mm TL), and 3 = large (>700 mm TL)
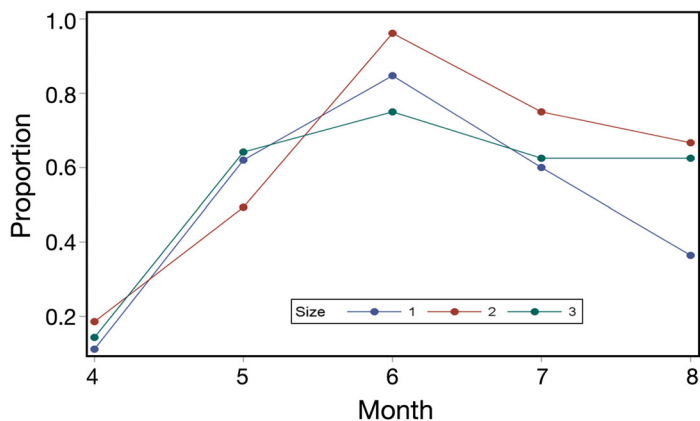

Fig. 8. Size-specific spawning fractions of red snapper *Lut-janus campechanus* by month. Size classes are 1 = small (<500 mm total length, TL), 2 = medium (500–700 mm TL), and 3 = large (>700 mm TL)
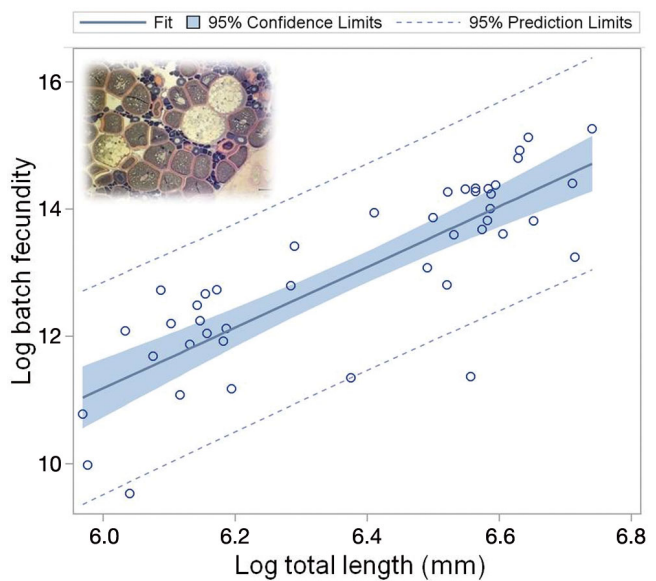

Fig. 9. Distribution of red snapper *Lutjanus campechanus* batch fecundity estimates by size class (based on total length in 100 mm increments). Although batch fecundities were highly variable, there was a significant relationship with size. Fish were capable of recruiting very small batches as can be seen by the isolated hydrating oocytes (light gray) in this micrograph. No fish smaller than 600 mm total length had batch fecundities greater than 1 million

feeding. However, it was not possible to assess how well our sampling indicated spawning site density, and there is a need for further research integrating other methods to assess this (Saul et al. 2013). In addition, the lower sampling effort in September and October could have affected results, if fish shifted their distribution during these months.

Fish species differ in the temporal and spatial pre-dictability of aggregation behavior, with population declines most commonly associated with those spe-cies which form few aggregations of large numbers over relatively short time periods (Sadovy De Mitch-eson et al. 2008). The decreased reproductive resili-ence associated with this reproductive strategy is due to both ecological and fishery factors. As an ecologi-cal example, climate change can cause a disconnect between the timing and location associated with reproductive success, decreasing productivity (Rijns-dorp et al. 2009), whereas from a fisheries perspec-tive, reproductive behavior can impact catchability (Villegas-Ríos et al. 2014), with species forming large spawning aggregations at predictable locations and times being more vulnerable to overfishing (Erisman et al. 2012).

Little is known about the cues used for spawning site selection, but the following hypotheses have

been suggested: natal homing, learned behavior through 'spawning groups' formed at first maturity, or following the behavior of older fish (Colin 1996, Thorrold et al. 2001, Claydon et al. 2012). Some reef fish use deeper habitat as they age (Collins & McBride 2011). However, for the ages we were able to assess, this pattern was not apparent for SA red snapper. The occurrence of some sites with 100% actively spawning females in this study, however, suggests that even if spawning groups are small, red snapper may move to some sites specifically to spawn, but further research is needed to confirm this. An additional factor in understanding how spatial diversity affects reproductive resilience is spawning site fidelity (Adams et al. 2009, Bijoux et al. 2013) and the role it may play in potential site-specific differences in productivity (Lowerre-Barbieri et al. 2013, 2014). Although red snapper have been reported to exhibit high site fidelity in the Gulf of Mexico at artificial reefs (Szedlmayer & Schroepfer 2005), there is no published data on spawning site fidelity or movements associated with spawning.

Maturity

Sexual maturity occurs at the lifetime scale and is a critical component of population dynamics and life history theory (Stearns 1992). In this study, we were unable to collect representative samples of immature and mature fish and could not estimate traditional size- or age-at-50% maturity. However, we were able to show that red snapper recruited to the spawning population at a small size (minimum: 310 mm TL) and young age (94% of 2 yr olds were mature). These results of early maturation are similar to past results (White & Palmer 2004) and for red snapper in the Gulf of Mexico (Woods et al. 2003). Such early maturation in a species which lives to 50 yr or older is unexpected (SEDAR24 2010). Other species of reef fish inhabiting the southeastern region of the US exhibit either lower longevity or higher age at maturity. For example, the vermilion snapper *Rhomboplites aurorubens* matures at age 1 (Hood & Johnson 1999) but has a maximum observed age of 26 yr (Allman 2007). The red grouper *Epinephelus morio* matures at age 2 and lives to approximately 20 yr (SEDAR19 2010) and the mutton snapper *Lutjanis analis*, which matures at approximately 4 yr old, lives to age 40 yr (SEDAR15A 2008). Red snapper in our study matured earlier than the mean reported age at maturity for lutjanids of 3.5 yr and exhibited a much longer potential reproductive lifespan (45 to 49 yr) compared to the mean for lutjanids of 11.7 yr (Martinez-Andrade 2003).

However, due to a lack of historic maturity estimates for this stock, it cannot be confirmed whether the early maturation is a result of overfishing, as has been seen in other species (Jørgensen et al. 2007, Audzijonyte et al. 2013, Marty et al. 2014), or simply a very resilient reproductive strategy. If this early maturation is due to 'fisheries-induced adaptive change' (Heino et al. 2013), it could have important implications for fisheries management. The concern in terms of productivity with a shift towards earlier maturation is that this would lead to slower growth due either to the principle of allocation (i.e. energy allocated earlier to reproduction would mean less energy left over for growth; Stearns 1992) or associated selection for slower growth. If slower growth is selected for, this change in productivity would not be easily reversed (Law & Grey 1989, Kraak 2007, Thorpe 2007).

Demographic trends in reproductive timing

Reproductive timing can be affected by over-exploitation and age truncation at multiple temporal scales. At the annual and interannual scales, age truncation can affect the duration of the spawning season (Anderson et al. 2008, Pecquerie et al. 2009, Wright & Trippel 2009) and spawning frequency (Fitzhugh et al. 2012, Cooper et al. 2013). In this study, although some individual spawning was identified from April through September, recruitment to the spawning population and spawning activity peaked in June. Larger fish, however, distributed their spawning activity more evenly over multiple months. In piscivorous species with an income breeder/batch spawning reproductive strategy, larger individuals are expected to exhibit this pattern because of their increased foraging ability within the spawning season. Restricted spawning seasonality can result in decreased resilience of fish populations to environmental conditions and exploitation (Hsieh et al. 2008, Wright & Trippel 2009), as the bet-hedging strategy which evolved to overcome a variable environment and produce reproductive success has been compromised (Hsieh et al. 2010).

Fecundity and egg quality

Red snapper, similar to other pelagic spawners, exhibited a significant relationship between batch

fecundity and size, but the relationship was not improved by the inclusion of age as an explanatory variable. It did, however, improve with the inclusion of sampling zone, reflecting the smaller size distribution of fish sampled in the most southern zone. Although this is not commonly done, the batch fecundity to size relationship can be used as a metric to understand the importance of the BOFFFF effect. For example, comparing the $\log_e$-transformed batch fecundity to SW relationship of red snapper in this study to another batch spawner with indeterminate fecundity, the spotted seatrout *Cynoscion nebulosus* (Lowerre-Barbieri et al. 2009), it can be seen that the steepness of the slope for red snapper (1.46) is greater than that for spotted seatrout (1.23) but the fit is weaker ($r^2 = 0.63$ compared to $r^2 = 0.72$). The relatively poor fit with red snapper reflects the wide range of batch sizes and this species' capability of mobilizing very small batches of eggs. Similar variability in red snapper batch fecundity has been previously reported, with relative fecundity ranging from 235 ± 56 eggs per gram SW off the east coast of Florida to 27 ± 11 eggs per gram SW from the Dry Tortugas (Brown-Peterson et al. 2009). The ability of red snapper to mobilize small batches may allow them to spawn even when they have relatively low energy reserves.

Reproductive resilience

There is growing awareness that stock productivity can change over time for reasons not associated with abundance or SSB (Vert-pre et al. 2013). The SA red snapper stock has exhibited highly variable recruitment, as well as strong year classes being produced in years with low SSB (SEDAR24 2010), indicating resilience based on the traditional measure of steepness. However, the SA red snapper stock has also undergone fairly extensive age truncation (SEDAR24 2010), and the effects of size and age on reproductive potential are increasingly recognized as important to stock productivity (Berkeley et al. 2004, Hsieh et al. 2010, Hixon et al. 2014). We estimated the potential reproductive lifespan of red snapper to be 49 yr. However, it is difficult to estimate life history parameters in a heavily fished stock and apply them to a virgin stock, and estimates of maximum age, of course, depend on sample size (Hoenig 1983). Thus, if maturation has decreased due to overfishing, a more realistic estimate of potential reproductive lifespan would be 45 to 46 yr. Given that very few fish over the age of 20 yr have been observed in this stock throughout its

range (SEDAR24 2010), we feel that using the maximum age observed in our study, 21 yr, was appropriate to estimate the observed reproductive lifespan and indicated an approximate 50% loss in reproductive life span. However, using the maximum age at the 90% quantile removes the problem of defining reproductive lifespan on extremely rare events (i.e. the capture of old fish in an over-exploited stock). Using this metric, the current effective reproductive lifespan was only a third of that predicted at MSY, suggesting a high degree of age truncation. Because age truncation can lead to regime shifts and reduced productivity (Anderson et al. 2008, Heino et al. 2013), we feel this is concerning. It also makes it difficult to fully assess the BOFFFF effect, as reproductive traits such as egg dry weights (used as a proxy for egg quality), spawning fraction, or spawning habitat, in fact could have demographic trends in a population with a more extended age distribution.

CONCLUSIONS

Our understanding of how fishing impacts populations is changing, as evidenced by a paradigm shift from single-species to ecosystem-based approaches (Walters & Martell 2004, Francis et al. 2007), a concurrent shift from an equilibrium perspective to a resilience perspective (Hughes et al. 2005), and increased research on population productivity and persistence in the face of climate change (Rijnsdorp et al. 2009). Reproductive resilience is emerging as a new conceptual model to assess the impacts of climate change on productivity in diverse species, such as arctic birds (Martin & Wiebe 2004), lemurs (Canale et al. 2012), and palm trees (Montúfar et al. 2011). In this study, we have integrated emerging understanding of reproductive processes, both in terms of spatio-temporal reproductive behavior and demographic effects (or the BOFFFF effect) with this concept to help quantify expected reproductive resilience to fishing. Many of the parameters estimated in this study are common to reproductive studies, but are not always quantified in a way that can be used to compare reproductive components over space, time, or between species. Thus, we have drawn from life history theory, population dynamics, and current stock assessments to present ways to quantify spatio-temporal reproductive diversity, reproductive lifespan erosion, and demographic effects in reproductive output. However, the metrics we present and reproductive traits evaluated are by no means comprehensive, and we hope that future studies will improve upon them.

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