Age Truncation and Reproductive Resilience of Red Snapper (*Lutjanus Campechanus*) Along the East Coast of Florida

Susan K. Lowerre-Barbieri, Laura Crabtree, Theodore Switzer, Sarah Walters-Burnsed, and Cameron Guenther

SEDAR41-DW07

Submitted: 21 July 2014
Revised: 25 July 2014
Revised: 7 August 2014
Revised: 3 September 2014

Please cite this document as:

Lowerre-Barbieri, S. K., L. Crabtree, T. Switzer, S. Walters-Bursed, and C. Guenther. 2014. Age Truncation and Reproductive Resilience of Red Snapper (*Lutjanus Campechanus*) Along the East Coast of Florida. SEDAR41-DW07. SEDAR, North Charleston, SC. 37 pp.

Age Truncation and Reproductive Resilience of Red Snapper (*Lutjanus Campechanus*) in Florida East Coast Waters

By

Susan K. Lowerre-Barbieri*[1]

Laura Crabtree[1]

Theodore S.Switzer[1]

Sarah Walters[1]

Cam Guenther[1]

[1]Present address: Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 Eighth Avenue S.E. St. Petersburg, Florida 33701-5020, USA. Susan.Barbieri@myfwc.com; [2] Present address: AECOM, 701 Edgewater Dr., Wakefield, MA 01880. [3]Present address: Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA.

NOT TO BE CITED WITHOUT PRIOR PERMISSION

Abstract: Resilience refers to a system's ability to withstand disturbance while maintaining its essential functionality, structure, and feedback loops. Because reproductive strategies are complex, adaptable systems, which evolved under a given mortality regime, exploitation can cause reproductive "regime shifts" in a stock's reproductive traits which impact long-term productivity and recovery rates. We assessed the age structure of red snapper off the east coast of Florida and demographic trends in reproductive traits which might be impacted by age truncation. The population exhibited age truncation, as the maximum sampled age (21 y) was less than half the expected life span (50+ y) and 84% of the sampled fish were < age 7. Virtually all females sampled (99%, n=696) were mature and although two-year-olds were not fully-recruited, 94% (n= 119) were mature. The population spawning season was from April through September, but the probability of being spawning capable within this time differed significantly by size and age, with June being the only month with predicted probabilities > 90% for all fish. Similarly, spawning fraction peaked in June, although older fish had more temporally distributed spawning activity. Red snapper spawned throughout the day and at multiple sites, with relatively few spawning females collected per site (maximum=13 fish). Batch fecundity increased significantly with size and in more northern zones but was highly variable. Egg dry weight did not differ significantly with size or age. Red snapper reproductive physiology suggests they are resilient and highly adaptive. However, age truncation appears to have restricted the time period over which spawning occurs and potentially has caused earlier maturation. Thus, recovery rates are expected to be affected by environmental conditions in June and if the observed early maturation is due to fisheries-induced evolution.

INTRODUCTION

Fisheries stock assessments traditionally assume an equilibrium state and use spawning stock biomass (SSB) as a proxy for reproductive potential (Murawski et al. 2001) with resilience assessed based on steepness (h) or the slope of the stock-recruitment curve near the origin (Myers et al. 1999, Mangel et al. 2013). However, SSB is an insensitive index of stock reproductive potential (Marshall 2009) and stock resilience is driven by evolutionary ecology and the reproductive biology of a stock. Estimates of h do not integrate these components other than size and age at maturation (Lowerre-Barbieri 2009, Mangel et al. 2013). In addition, there is growing evidence that over-fished stocks are not in equilibrium and that long-term high exploitation rates can change life history parameters, especially maturity schedules (Jørgensen et al. 2007, Heino et al. 2013), as well as truncate age distributions, which can decrease a stock's resilience to climate change and fishing pressure (Hsieh et al. 2008).

A resilience perspective is increasingly being introduced to ecology and conservation (Hughes et al. 2005, Folke 2006, Healey 2009). 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). Reproductive strategies are complex, adaptable systems that have evolved to overcome a given regime of natural mortality (Young et al. 2006, Lowerre-Barbieri 2009, Lowerre-Barbieri et al. 2011a). As such, the system, or reproductive strategy, which leads to the greatest reproductive success can also go through "regime shifts", such as earlier maturation, which can be associated with fisheries-induced evolution or shifts in traits within a species' range of phenotypic plasticity (Heino et al. 2013). With a resilience perspective, the question becomes what is the amount of disturbance a system can sustain before it undergoes a regime shift (Folke 2006)? From a management perspective, the key question is how to assess a stock's reproductive resilience and protect the key traits associated with reproductive success and population stability, such as age structure (Anderson et al. 2008, Hsieh et al. 2010). For many stocks it has been shown that younger, smaller fish exhibit lower reproductive success due to differences in a number of reproductive parameters, including: egg quality (Kamler 2005), spatio-temporal reproductive behavior (Begg and Marteinsdottir 2002; Rowe and Hutchings 2003; Lowerre-Barbieri 2009; Lowerre-Barbieri et al. 2011a), fecundity, and the ability to maintain the energy reserves needed for consequent reproductive cycles (Jørgensen et al. 2006, Rideout & Tomkiewicz 2011). Thus, a first step in assessing reproductive resilience is evaluating demographic trends in these traits.

Red snapper, *Lutjanus campechanus*, support important commercial and recreational fisheries in the Gulf of Mexico and the Southeastern United States, with both the Gulf and South Atlantic (SA) stocks exhibiting highly truncated age distributions (Cowan Jr 2011). The latest benchmark assessment (SEDAR24 2010) indicated the SA red snapper stock was overfished and undergoing overfishing, but also that there had been a sharp increase in abundance due to recent high recruitment in 2006 and 2007. Red snapper are a long-lived (54 y, SEDAR 24 2010), highly fecund species 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), and are acknowledged for their resilience or compensatory reserve and the difficulty in quantifying it (Rose et al. 2001).

In this study, demographic trends in red snapper reproductive behavior are evaluated within the context of age truncation and resilience. The following hypotheses are tested: (1) young fish will recruit to the spawning population (ages one and two); (2) the probability a female is spawning capable within the spawning season does not differ with size or age; (3) spawning activity will be evenly distributed throughout the spawning season and does not differ with size or age; (4)

spawning fish will be concentrated in large numbers at relatively few sites; and (5) batch fecundities and egg dry weight will increase with size and age.

METHODS

Collections of samples. Sampling was conducted off the east coast of Florida (Fig. 1), from roughly 28° 00’ N (Melbourne, FL) to 30° 45’ N latitude, an area considered to be the center of the South Atlantic red snapper population (White & Palmer 2004). Sampling zones corresponded to NMFS statistical zones: 722, 728, and 732. Presumed suitable hard-bottom habitat locations were obtained from participating fishers (commercial and recreational), federal agency partners (i.e., National Marine Fisheries Service, United States Geological Service), and Florida Fish and Wildlife Commission’s historical data. A sampling universe was then built around these locations with primary sampling units delineated as 0.3 nm latitude by 0.1 nm longitude and containing reef habitat. Sampling sites were randomly selected from the universe, and sampling effort was stratified by depth (inshore, inside the 30 m isobath; offshore, between the 30 m and 100 m isobaths). For inshore strata, each month twelve sites were selected per zone. In an effort to preserve the proportionality of sampling to available habitat throughout our sampling universe, twenty sites were selected per zone each month for offshore strata. At each site, date, 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 four-month period (April-July), but poor weather conditions resulted in lower than expected sampling effort in this time period. Thus sampling was extended and the sampling design adjusted to select more stations from the sampling zones and strata that were under sampled during the initial period. 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). For more detail concerning gear descriptions and methodology please reference SEDAR41-DW08.

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 (rough seas, extreme currents, etc.) it was necessary to motor fish sites to maintain the boat over the intended site. For each sampling site, the bottom long line was fished at least 0.1 nm 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 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 two-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 two rigs with the smallest hook combination were used and at offshore sites, two rigs with the largest hook combination were used. We targeted twelve “team drops” per site in the inshore depth strata and ten in offshore strata, as sampling at these sites took longer due to more difficult fishing conditions.

Life history parameters. 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 also measured and somatic weight (SW) calculated as TW-GW. Sex was determined macroscopically, both sagital otoliths removed and stored dry, and ovarian tissue samples taken for histological analysis of reproductive phase. 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).

Reproductive state and parameters. Ovaries were examined histologically. 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). Postovulatory follicles (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).

Histological indicators of spawning activity followed (Lowerre-Barbieri et al. 2009) and (Brown-Peterson et al. 2011). Ovaries with oocytes undergoing OM were assumed to indicate fish that would spawn that evening. Early stages of OM indicated fish that would spawn within 5-14 h (Jackson et al. 2006, Lowerre-Barbieri et al. 2009) and oocytes in this sub-stage exhibited early GVM with little yolk coalescence or hydration. Active spawning was designated by four histological indicators: advanced GVM with well progressed yolk coalescence, germinal vesicle breakdown (GVBD), hydrated oocytes, and newly collapsed POFs. Late OM was characterized by completed GVM or GVBD, yolk coalescence, and sufficient hydration that hydrated oocytes were detectable macroscopically. Ovulation indicated females in the process of actively spawning. Ovulation and newly collapsed POFs are extremely short-lived histological indicators (presumed < 2 h) and were used as the most conservative way to assess spawning time and location. Recent spawning was indicated by degenerating POFs.

The above histological indicators were the basis of a tiered ovarian classification system (Table 1) to evaluate reproduction over different temporal scales: lifetime, annual, intraseasonal (i.e., spawning frequency), and diel (Lowerre-Barbieri et al. 2011b). Maturity occurs at the lifetime scale. The annual reproductive cycle was evaluated based on five reproductive phases: developing, spawning capable, spawning, regressing, and regenerating (Brown-Peterson et al. 2011). These phases were further grouped to indicate reproductive state: (1) non-spawning, (2) spawning-capable, or (3) spawning. Females were assigned as immature if they had thin ovarian walls, well-structured lamellae, and no muscle bundles (Lowerre-Barbieri et al. 2011b). Histological indicators to identify developing and spawning capable phases were slightly modified from (Brown-Peterson et al. 2011), with the most advanced oocyte stage in the developing phase being partially-yolked (i.e., Vtg1). The spawning capable phase indicated females sufficiently developed to spawn within days of receiving the appropriate endocrine signal (i.e., Vtg2 and Vtg3). Spawning/spawners were defined as females with any histological indicator of spawning. Diel and intraseasonal cycles were assessed using the three subphases of spawning: imminent, active, or recent. Active spawning/spawners were defined as females expected to be within 2 h of spawning and were either undergoing late OM or had fresh POFs.

To assess spawning activity at the inter-annual scale we estimated: (1) spawning fraction or the proportion of mature females spawning daily, (2) spawning interval, defined as the number of days between spawning events, and (3) spawning frequency, which refers to the number of spawning events within a spawning season (Lowerre-Barbieri et al. 2011b). Spawning fraction was estimating as the proportion of active spawners (i.e., those which would spawn the night of sampling) or the percent hydrated method; and those which had spawned within 24 h, the percent POF method (Hunter & Macewicz 1985b, Murua et al. 2003). However, due to the wide range of red snapper spawn times (see below) the percent error in assigning day 1 POFs may be higher than in species with short and clear peak in spawn times. 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. To evaluate demographic differences in spawning activity, the proportion of spawning capable females with spawning indicators was by age and TL classes was evaluated (Lowerre-Barbieri et al. 2009).

Batch fecundity was estimated gravimetrically using the hydrated oocyte method (Hunter et al. 1985, Murua et al. 2003). Fresh oocytes were hydraulically separated from each other and from the ovarian membrane and preserved in 2% neutrally buffered formalin (Lowerre-Barbieri & Barbieri 1993). 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 histogical analysis indicated ovulation had begun.

Hydrated oocyte dry weights were measured as a potential indicator of egg quality. Two replicates of 100 hydrated oocytes were selected from the above samples used for batch fecundity, manually separated, and dried for 48h at 68^0 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 across time and demographics.

Otolith analysis. Fish were aged using transverse sections of otoliths. Otoliths were sectioned through the core using a Buehler low-speed Isomet saw. Sections 350-500 μm thick were mounted on glass slides with histomount. The number of annuli and the distance from the edge to the most recent annulus were determined by viewing the sections through a dissecting microscope, using transmitted light. Sections which were difficult to read were also viewed in reflected light. All slides were read twice by two different readers and a third time if there were descrepancies. Ages were assigned to year classes by using a January 1 birthdate (Jearld et al. 1983) to clearly separate fish born in different years.

Data Analysis. Before we could evaluate spatio-temporal patterns in reproductive effort, we needed to assess if 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 demographic effects on reproductive timing at three temporal scales: annual (the spawning season), intra-annual (spawning frequency), and diel (spawn time). Because many physiological processes are driven by size, this was the primary demographic measure we looked at but because some reproductive behaviors may be learned we also assessed age effects. The duration of the population spawning season was based on the first and last occurrence of females with spawning indicators. We then evaluated if the probability of being spawning capable was similar for all months within the spawning season and for fish of different sizes and ages (Lowerre-Barbieri et al. 2009). To ensure adequate sample sizes, fish were grouped into three size categories: small (< 500 mm TL), medium (500 to 700 mm TL) and large (> 700 mm TL) and three age categories: young (< age 4), middle (ages 4 and 5) and older (> age 5). Only months with 30 or more females were used (April through August). The proportion of females in the spawning population was modeled using generalized linear models (PROC GENMOD in SAS), a binomial distribution, and a logit link function. A higher probability of being in the spawning population at time of capture was assumed to be associated with a longer spawning season for that size- or age-class. Females not in the spawning population were categorized as zero and those in the spawning population as one. To evaluate demographic effects on probability of spawning, which should be analogous to the number of breeding opportunities in a year, the proportion of females with spawning indicators in the spawning population was modeled using the same procedure. Spawning-capable females were categorized as zero and spawning-phase females as one (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 if there was a relationship with spawn time and size or age. A bivariate kernel density estimation (KDE) was used to evaluate the location with the highest density (75%) of active spawners and to assess if the spatial distribution of active spawners differed by size or age category.

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

RESULTS

Sampled population. A total of 1,316 red snapper were captured, measured and sexed (583 males and 733 females). All but 11 of these fish were aged and 696 females had ovarian samples taken for histological analysis. Fish < 350 mm TL were not fully-recruited to the sampling gear and location, resulting in only two age one fish being sampled. Fish size exhibited a bimodal pattern of abundance and ranged from 207 to 925 mm TL (Fig. 2). Size did not differ significantly with sex (KS, χ^2 =1.27, P=0.2596), or gear (Kruskal-Wallis, χ^2 =2.252, P=0.2436) but was clearly driven by several strong year-classes. Abundance was dominated by 2-year-olds (16%, 2010 year class), 3-year-olds (25%, 2009 year class), 5-year-olds (29%, 2007 year class) and 6-year-olds (13%, 2006 year class). In contrast, 4-year-olds made up only 5% of the sampled population. This drove the bimodal size distribution, with peaks in the 400-450 mm TL size class and the 650-700 mm TL size class. Few fish (4%) were sampled at depths greater than 60 m (n=58), but all fish sampled at these deeper sites were large (≥ 500 mm TL) and older > age 3. However, larger older fish were also sampled at a wide range of depths and at the 0.9 quantile, size class did not differ significantly with depth of capture (Quantile regression, χ^2=0.0, P=1, n=1,315) nor did age (Quantile regression, χ^2=0.0, P=1.0000, n=1,305).

Reproductive timing. Virtually all of the females sampled in this study (99%) were mature. Immature females (n=8), however, exhibited a wide size range (207-404 mm TL) but were young (age 2, n=7; or age one, n=1) and mostly occurred in April and May (n=7). Maturing age

2 fish overlapped in TL with the immature fish (Fig. 3) and 30 age 2 females ≤ 400 mm TL had indicators of spawning. Immature females exhibited a range of development from: a one-year-old fish which had no primary growth oocytes (Fig. 3A), to fish part-way through the process of recruiting primary growth oocytes (Fig. 3B), as those with a fully-developed population of primary growth oocytes, capable of recruiting to the spawning population within the spawning season (Fig. 3C).

Spawning seasonality was asynchronous, with individual variability in spawning periods. Spawning capable females occurred from April through September (Fig 4A) and spawning females from 4 April to 20 September 2012, corresponding to 170 d in the population spawning season. However, the proportion of spawning capable females differed significantly with month (Binomial regression, n=679, $p < 0.0001$) and size category (Fig. 4B; 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. This same pattern was seen with age categories, with older fish exhibiting a higher probability of being spawning capable in all months (Binomial regression, n=679, $p > 0.0001$).

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 one spawn approximately every 3 days (% hydrated) or once every 5.7 d (POF). The annual spawning frequency thus was higher for the % hydrated method, 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. 5). The proportion of spawning capable females that had indicators of spawning activity differed significantly by month (Binomial regression, n=558, P < 0.001), but not by size (P=0.9801) or age (P=0.5787). All sizes exhibited peak spawning activity in June, with the proportion of spawning capable females with spawning indicators ranging from 0.16 (April) to 0.86 (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.

Red snapper spawned throughout the day. Spawning indicators (OM substages and fresh POFs) differed significantly with hour (Kruskal Wallis, Chi square=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. 6). However, those indicators associated with spawn times (hydrated oocytes and fresh POFs) occurred throughout the day and there was no indication of a size (Kruskal Wallis, χ^2=17.4, P=0.0957, n=115) or age (Kruskal Wallis, χ^2=8.6072, P=0.2821, n=115) effect on spawn time. Females with late OM were collected from 7:11 to 17:01 and four females with newly collapsed POFs were collected from 9:52 to 13:29, indicating at least some spawning occurred throughout the day.

Spatial distribution of spawning activity. Roughly a third of mature females sampled had spawning indicators (219 out of 666) and spawning activity was well distributed throughout the areas sampled (Fig. 7). 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 one active spawner per site (55%, n=92 sample sites). Depth of sampling site did not differ significantly between active spawners and the remaining females

(Kruskal Wallis, χ^2=1.4152, P=0.2342, n=666). Although actively spawning females occurred over a wide range of locations (28.11^0 to 30.58^0 N Latitude to -81.02^0 to -80.05^0 W Longitude), the majority of them (75%) were collected within the area bounded by 28.92 to 29.58^0 N and -80.52 to 80.35^0 W and age categories spawned in similar areas (Fig 7) as did fish in different size categories.

Fecundity and egg dry weight. Larger females produced significantly more eggs per batch than smaller females (Fig. 8). Batch fecundities ranged from roughly 14,000 to 4.2 million eggs per female and significantly increased with TL (BF=-2,273,955 + 5,242.3TL [r^2=0.53, n=44]) and $\log_e$ SW ($\log_e$ BF=1.37+1.46 $\log_e$ SW [r^2=0.63 n=44]). The predictive batch fecundity relationship with SW was improved by including zone (r^2=0.71, P=0.0038), but not age. Relative fecundity (eggs per g 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 per g 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).

DISCUSSION

Reproductive timing. Reproductive timing refers to the temporal scale of reproductive activity (Lowerre-Barbieri et al. 2011b) and over-exploitation and age truncation can affect it at multiple scales. Sexual maturity occurs at the lifetime scale and is a critical component of population dynamics and life history theory (Stearns 1992). Because this study sampled spawning habitat we did not collect representative samples of immature and mature fish and could not estimate traditional size- or age-at-50% mature. However, we were able to show that red snapper recruited to the spawning population (i.e., were spawning capable) at a small size (minimum: 310 mm TL) and young age (minimum: 2-years-old, 94% mature) 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 years or older is unexpected (SEDAR24 2010) but there are no historic maturity estimates for this stock, and thus it is not possible to evaluate how, or if, this parameter has changed over time. However, based on an asymptotic length of 902 mm TL (SEDAR24 2010) and the generality that fish mature at two-thirds their asymptotic length (Jensen 1996), a very rough expectation would be that this stock would mature at approximately 600 mm TL. In our study, fish in this size range (550 to 650 mm TL) had a mean age of 4.8 years (range: 3 to 8 y). Maturation at sizes and ages well below these suggests there may be “fisheries-induced adaptive change” (Heino et al. 2013), as has been seen in other highly-exploited stocks (Jørgensen et al. 2007, Audzijonyte et al. 2013, Marty et al. 2014). These changes can be due to phenotypic plasticity or fisheries-induced evolution and have important implications for fisheries management, as a shift towards earlier maturation will lead to smaller average adult size, and thus lower yields (Kraak 2007) and genetic changes will be difficult and/or slow to reverse (Law 2007). To better assess if either of these caused precocious maturation in SA red snapper, and how this may impact recovery trajectories, it will be important to monitor maturity schedules over time (Enberg et al. 2010).

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 2009a) and spawning frequency (Fitzhugh et al. 2012, Cooper et al. 2013). In this study, the population showed spawning activity from April through September, but the probability of fish being spawning capable differed with size and age. Because of the large number of young, small fish in the

Florida population, predicted probabilities that > 90% of females would be spawning capable did not occur until June. Spawning activity (as indicated by spawning fraction) also peaked in June, although the largest fish distributed their spawning activity more evenly over multiple months. Such changes can decrease the resilience of fish populations to environmental conditions and exploitation (Hsieh et al. 2006, Wright & Trippel 2009b), as the bet hedging strategy which evolved to over-come a variable environment and produce reproductive success has been compromised (Hsieh et al. 2010).

Spatial distribution of spawning activity. Although many reef fish and other snappers aggregate in huge numbers at specific locations to spawn (Claydon 2004, Sadovy de Mitcheson et al. 2013), our study indicated spawning activity is relatively well-distributed and suggested red snapper may not form the large spawning aggregations seen in some other reef fish. However, these relatively low numbers may be due to sampling bias, as all fish were collected with hook and line and the capture of fish at a given site can affect the probability of later catches (i.e., the bite can turn off). There were, however, multiple sampling sites with 100% spawning fraction (Fig. 7), suggesting fish may move to specific sites to spawn. Given the importance of spatio-temporal reproductive behavior to productivity in marine pelagic spawners (Maunder & Deriso 2013), there is a need to better understand spawning site selection and site fidelity (Lowerre-Barbieri et al. 2013, Lowerre-Barbieri et al. 2014). Failing to understand and integrate these elements into our estimates of productivity can lead to extirpation of stock components, which in turn can impact recovery rates (Frank & Brickman 2001, Svedäng et al. 2010).

Little is known about how fishes select their spawning sites, 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), all of which could be impacted by age truncation. Some reef fish use deeper habitat as they age (Collins & McBride 2011), although this pattern was not apparent in our samples. Interestingly, the one description of historic spawning areas based on interviews with fishermen (i.e., bite, schooling, and spawning condition of landed fish), reported spawning activity somewhat closer to shore and further north than what we saw in this study (Moe 1963). The spatial distribution of spawning could shift for multiple reasons, including climate change. However, it cannot be ruled out that this shift is associated with age truncation.

Reproductive resilience. Based on the concept that diversity increases resilience (Hughes et al. 2005), red snapper exhibit several reproductive traits expected to result in reproductive resilience. The most obvious being that they distribute spawning activity over a wide range of sites and do not appear to form large spawning aggregations, defined as “a group of conspecific fish gathered for the purposes of spawning with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive periods” (Domeier & Colin 1997). Fish species differ in the temporal and spatial predictability of aggregation behavior, with population declines most commonly associated with those species which form few aggregations of large numbers over relatively short time periods (Sadovy De Mitcheson et al. 2008). In addition, although many pelagic spawners exhibit diel periodicity and spawn at dusk (Holt et al. 1985), red snapper exhibited a wide range of spawn times in this study (approximately 0700 to 1700). However, this pattern is in contrast to that reported for the Gulf of Mexico, where red snapper spawned from 1330 h to 1830 h with a peak in spawning activity near 1600 h (Jackson et al. 2006). Red snapper also appear to have highly dynamic ovaries, with rapid turnover rates, and low or variable energetic thresholds associated with oocyte recruitment events. Histological ovarian analyses indicated red snapper can produce very large numbers of early primary growth oocytes, not typically seen in other species (Fig. 10). They are also capable of mobilizing very small batches of eggs, although it is not yet clear if individuals can vary their batch size within a spawning season. Similar variability in batch size was reported in a study comparing red snapper reproduction from the east coast of Florida to the Dry Tortugas, mean relative fecundity from the east coast was 235 ± 56 eggs/g versus 27 ± 11 eggs/g from the Dry Tortugas (Brown-Peterson et al. 2009). In this study individual relative fecundity varied from 13 to 602 eggs/g.

Conclusions. 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). Although it appears to be a very resilient species, the SA red snapper stock has undergone extreme age truncation making it difficult to fully assess if reproductive traits such as egg dry weights (used as a proxy for egg quality) spawning fraction, or spawning habitat, in fact have demographic trends when there is a more extended age distribution. However, even in this juvenesced population, we found demographic trends in reproductive timing and fecundity and that age truncation will have lead to a more restricted time associated with peak egg production as well as lower egg production. Thus, recovery rates are expected to be dependent on favorable environmental conditions in June and whether precocious maturation is associated with fisheries induced evolution. To better understand these processes, there is a need for research assessing phenotypic plasticity of maturation in red snapper, spawning site selection, and individual fidelity to spawning sites.

Acknowledgments

We would like to Russ Brodie, Doug Adams, and Justin Solomon for their contributions to field collections. We would also like to thank Jessica Carroll and the age and growth lab personnel for aging these fish. This project was supported by the Cooperative Research Program Contribution XXXX

Table 1. Ovarian classification and terms based on histological analysis.

Reproductive state		Phase	Histological indicators	Signficance
Immature	Nonspawning	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	Nonspawning	Developing	Cortical alveolar and sometimes early yolked oocytes. No evidence of POFs. Some atresia may be present.	Environmental signals have triggered development, but fish are not yet developed enough to spawn.
Mature **Spawning population**	Spawning-capable	Spawning-capable	Yolked oocytes. May be some atresia.	Fish developed enough to spawn.
	Spawning	Spawning	Oocyte maturation, hydration or POFs.	Fish with indicators of spawning activity.
		Subphases:		
		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 +/- 2 h.
		Recent	POFs (12-36 h old)	Spawned within 2 d.
Mature	Nonspawning	Regressing	A high percentage of yolked oocytes undergoing atresia (alpha and beta).	Cessation of spawning.
	Nonspawning	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.

Figure Captions

Fig. 1. (A) Spatial distribution of red snapper, *Lutjanus campechanus*, sampling sites (black) and locations where red snapper were caught (red); (B) the spatial distribution of spawning sites with > 20% spawning fraction and > 10 females sampled per date. The call-out box represents the same sites, with bubble size indicating relative sample size and color the spawning fraction (converted to whole numbers, i.e., 2=20%).

Fig. 2. Top: size and age distribution of sampled red snapper *Lutjanus campechanus.* Sizes classes are baed on 50 mm TL bins (top). Bottom: distribution of age categories (category 1: ages 1-3; category 2: ages 4-5; category 3: ages 6 and older) and size class by depth at capture.

Fig. 3. Micrographs of immature *Lutjanus campechanus* ovaries in varying stages of development (A.-C.) and D. size distribution of immature and mature females.

Fig. 4. *Lutjanus campechanus* (A) predicted probability of being in the spawning population by age category (category 1: ages 1-3; category 2: ages 4-5; category 3: ages 6 and older) and month; (B) predicted probability of being in the spawning population by size category (small (1) < 500 mm TL; medium (2) 500-700 mm TL; and large (3) > 700 mm TL) and month; and (C) monthly proportion of females by reproductive phase: immature, developing, spawning capable, spawning, regressing, and regenerating; sample sizes indicated above each month.

Fig. 5. *Lutjanus campechanus* size-specific spawning fractions by month. Size categories: small (1) < 500 mm TL; medium (2) 500-700 mm TL; and large (3) > 700 mm TL.

Fig. 6. The number of female *Lutjanus campechanus* with spawning indicators by hour sampled. Spawning indicators 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 POFs. Bubble size represents the number of females with that indicator at that time and ranges from 1 to 36.

Fig. 7. Left: Spatial distribution of spawning fraction by sampling site of female red snapper *Lutjanus campechanus*. 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. Right: kernel density estimates of active spawners by age category: A. category 1 ages 2-3, B. category 2: ages 4-5, and C. category 3: ages 6 and older.

Fig. 8. Batch fecundity estimates of *Lutjanus campechanus* increased with size class (100 mm TL increments). Only fish 600 mm TL or larger produced batches greater than a million eggs, but batch size continued to be variable even in these larger fish. Insert: micrograph of an ovary recruiting a very small batch. Arrows indicate the few oocytes undergoing oocyte maturation to be spawned the night of capture.

Fig. 9. Micrographs of regenerating ovaries from red snapper, *Lutjanus campechanus,* compared to other reef fish. Note the large numbers of early primary growth oocytes indicated by the arrow in the red snapper ovary.

Fig. 1

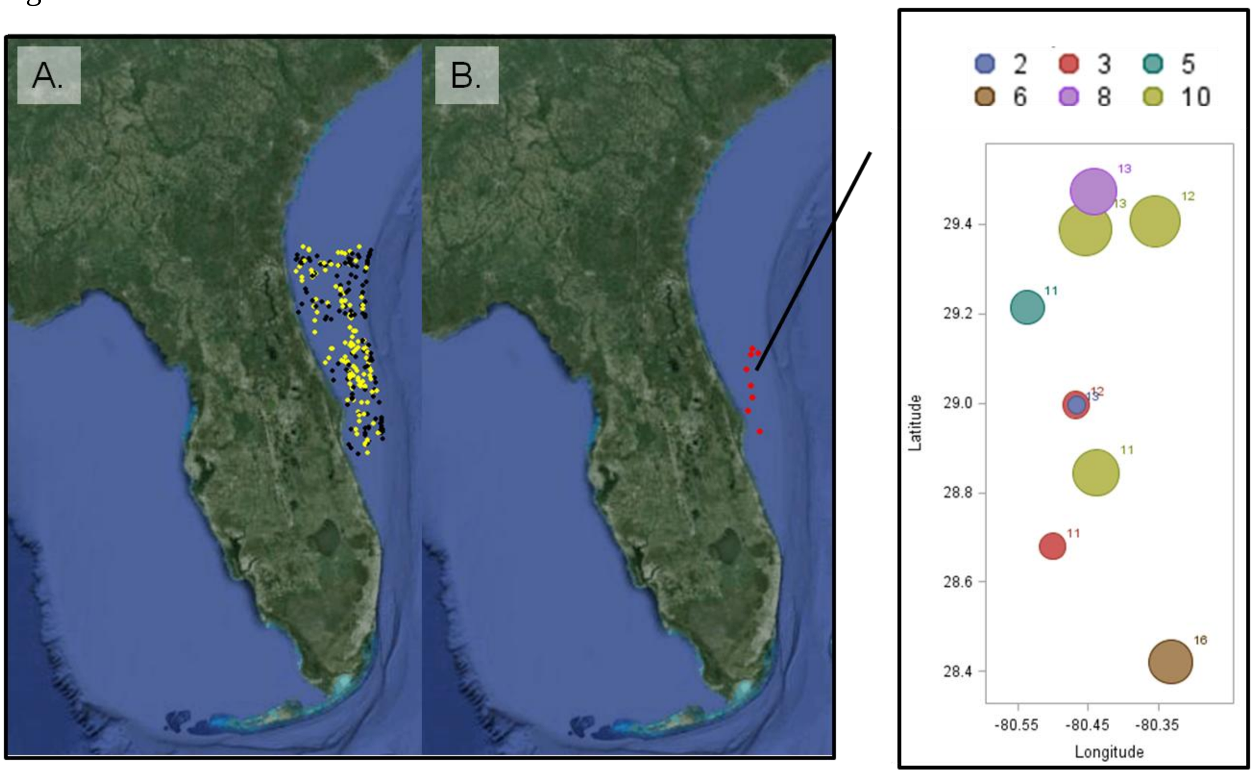

A.
B.
2
3
5
6
8
10
13
13
12
11
12
13
11
11
16
29.4
29.2
29.0
28.8
28.6
28.4
Latitude
-80.55
-80.45
-80.35
Longitude

Fig. 2 Size and age distribution of red snapper (both sexes) and size distribution of females by maturity

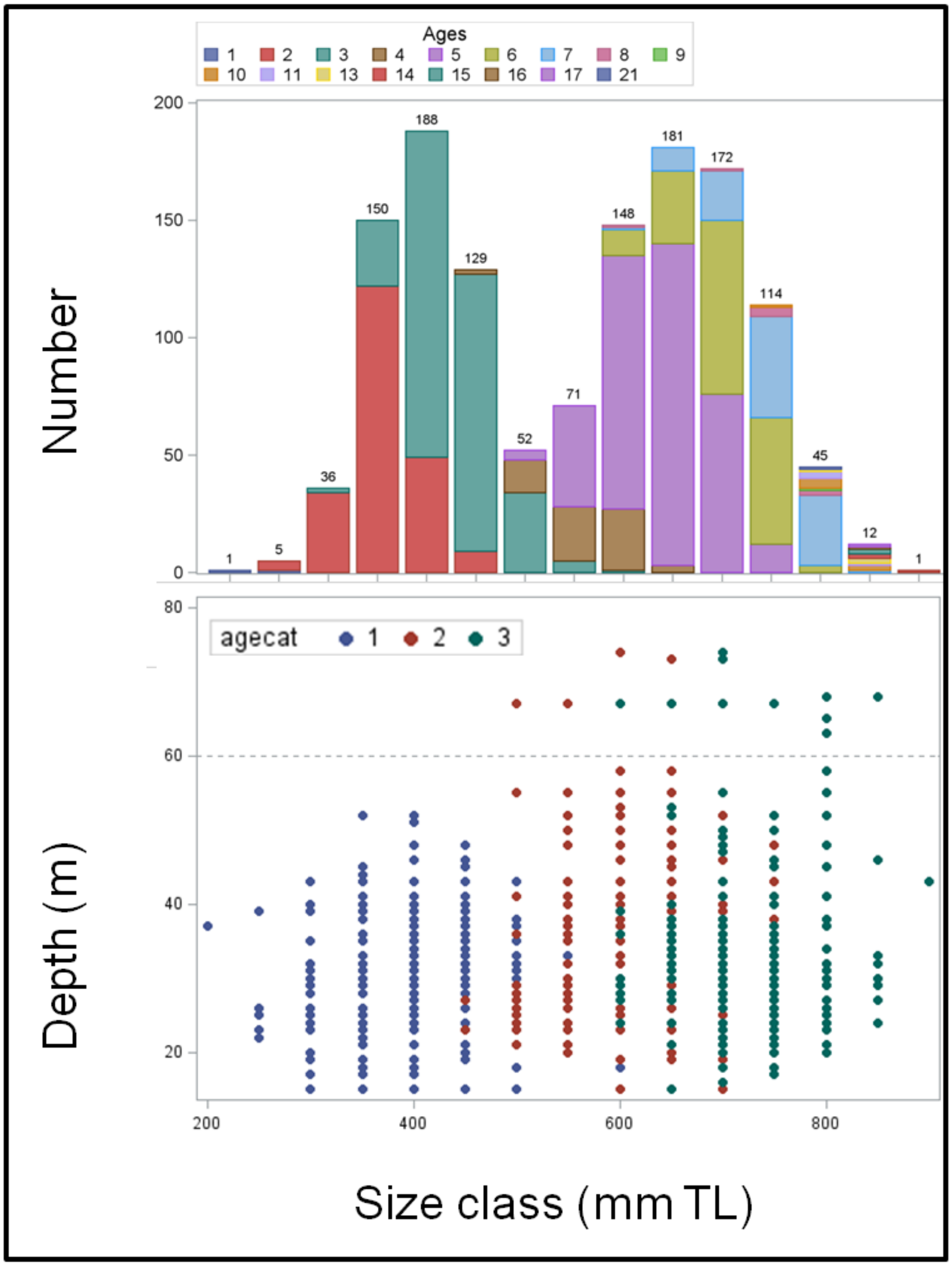


Fig.3.

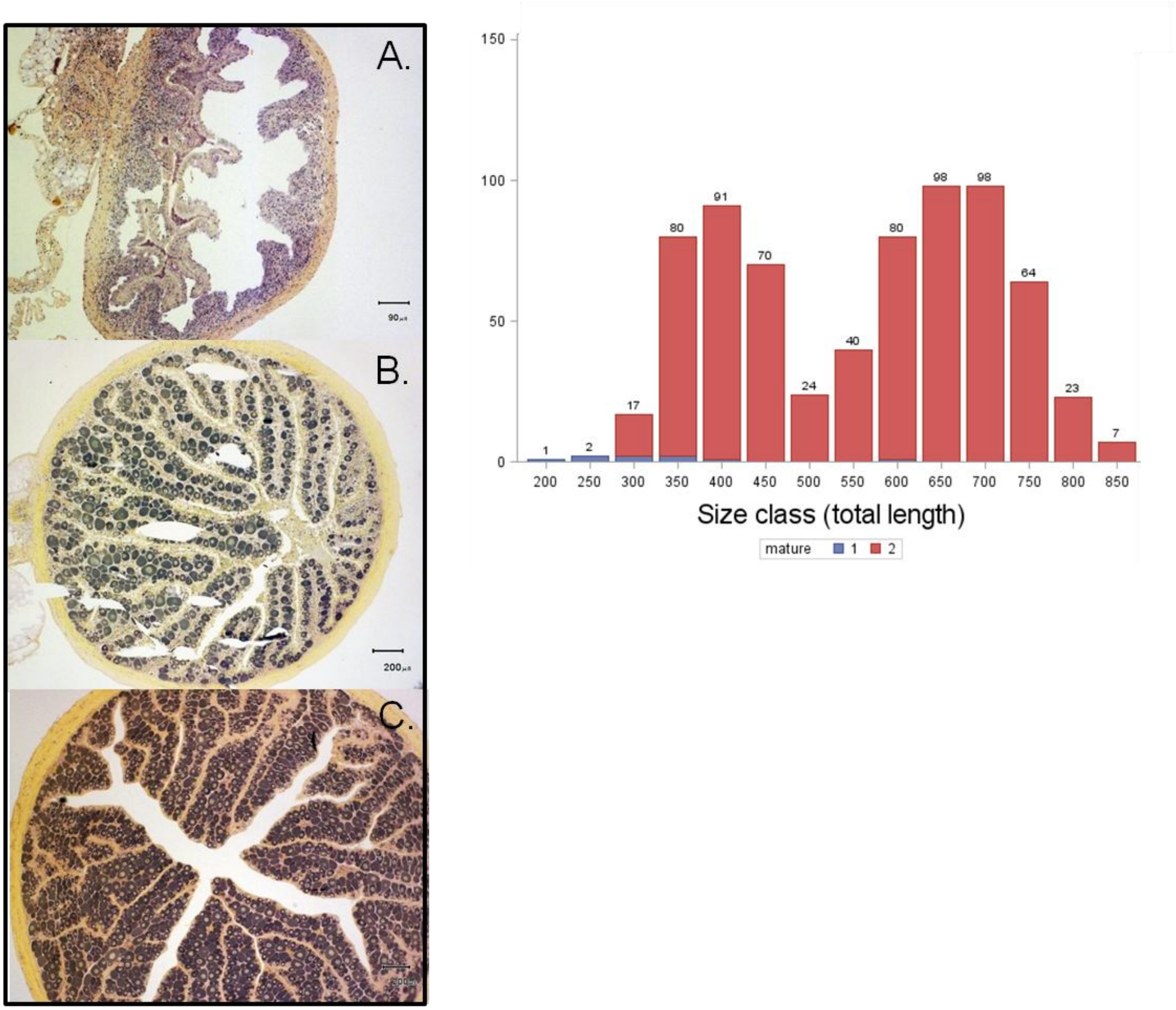

A.
90µm
B.
200µm
C.
200µm
150
100
50
0
1
2
17
80
91
70
24
40
80
98
98
64
23
7
200
250
300
350
400
450
500
550
600
650
700
750
800
850
Size class (total length)
mature 🟦 1 🟥 2

Fig. 4

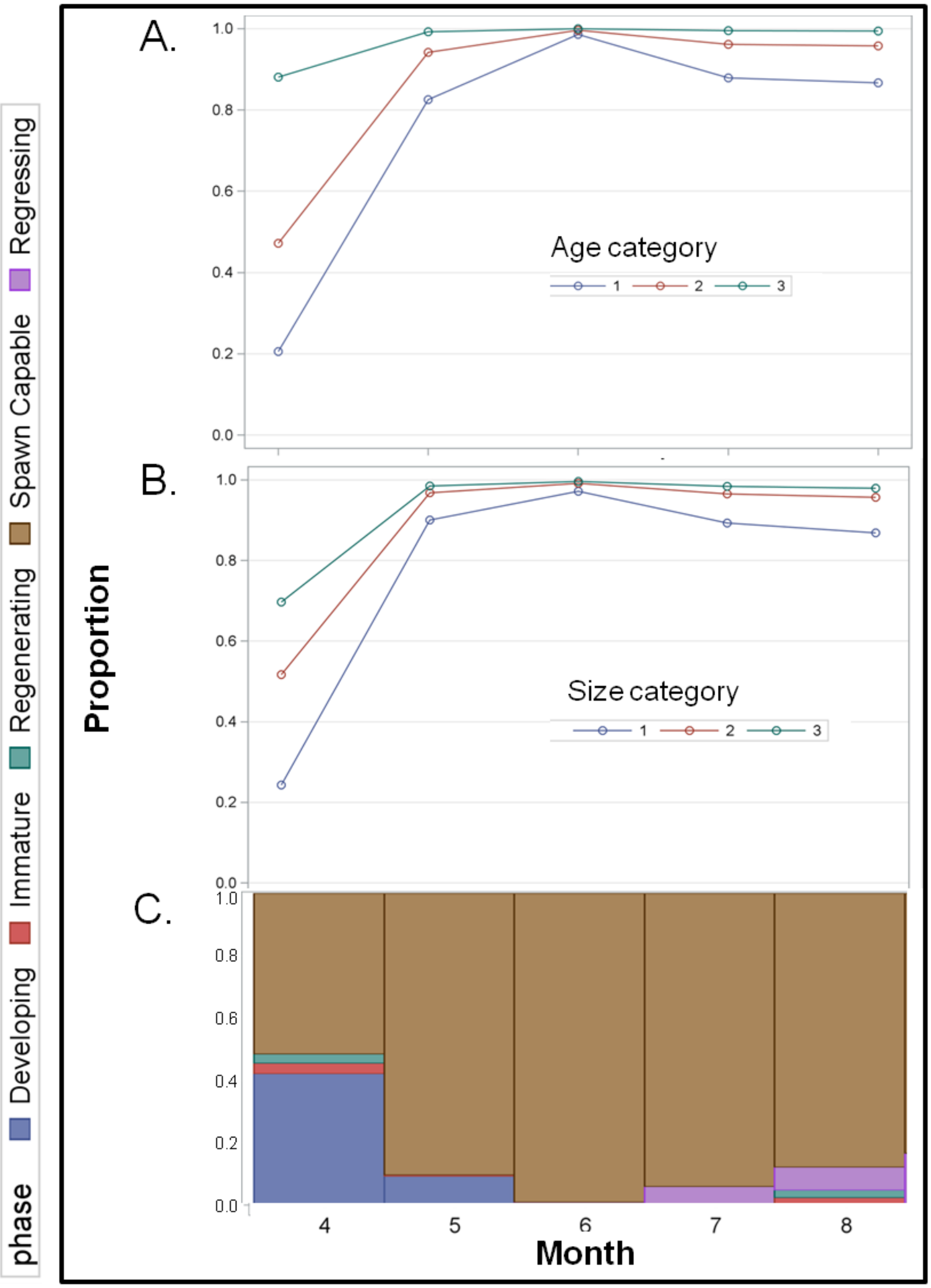

phase
Developing
Immature
Regenerating
Spawn Capable
Regressing
Proportion
A.
1.0
0.8
0.6
0.4
0.2
0.0
Age category
1
2
3
B.
1.0
0.8
0.6
0.4
0.2
0.0
Size category
1
2
3
C.
1.0
0.8
0.6
0.4
0.2
0.0
4
5
6
7
8
Month

Fig. 5.

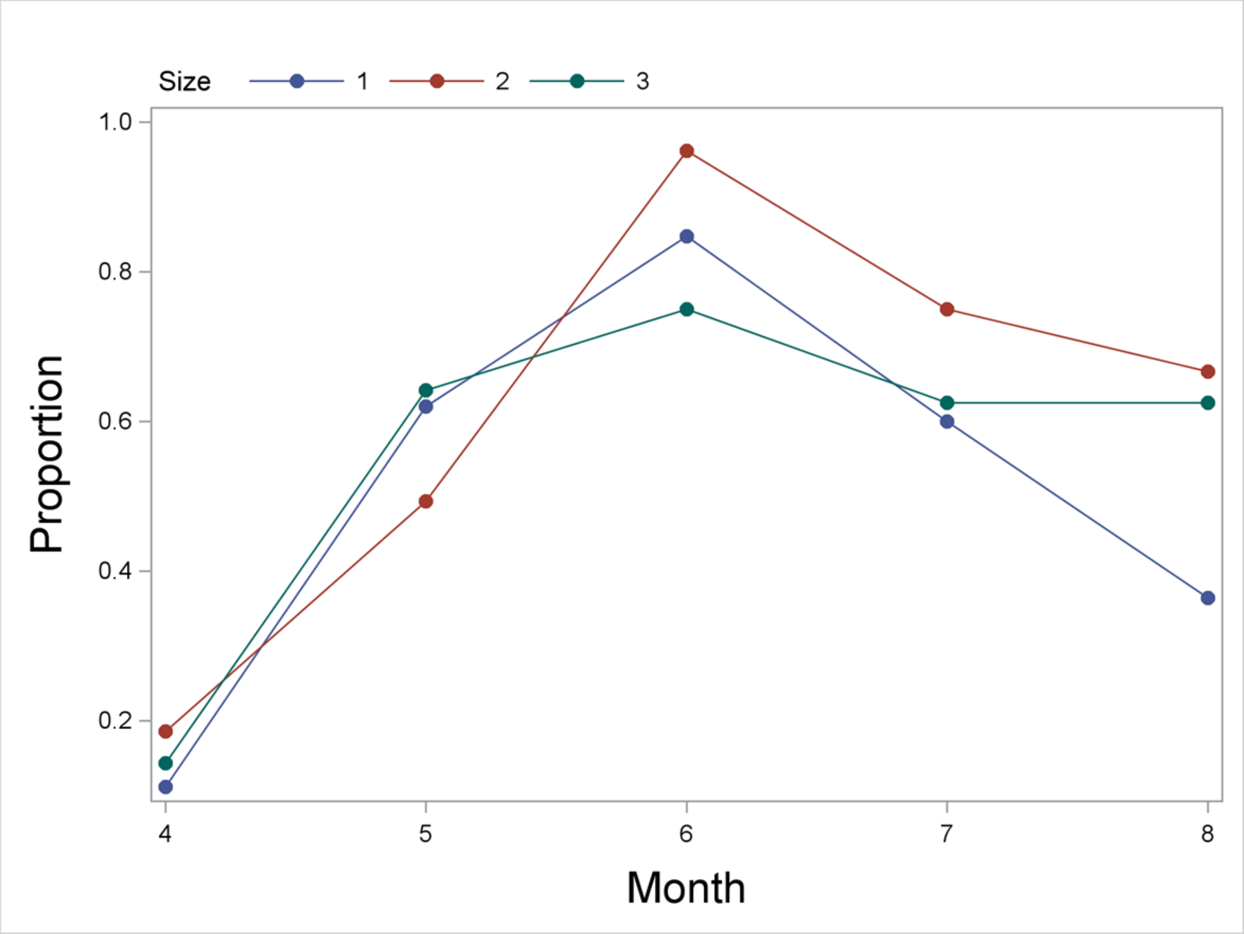


Fig. 6

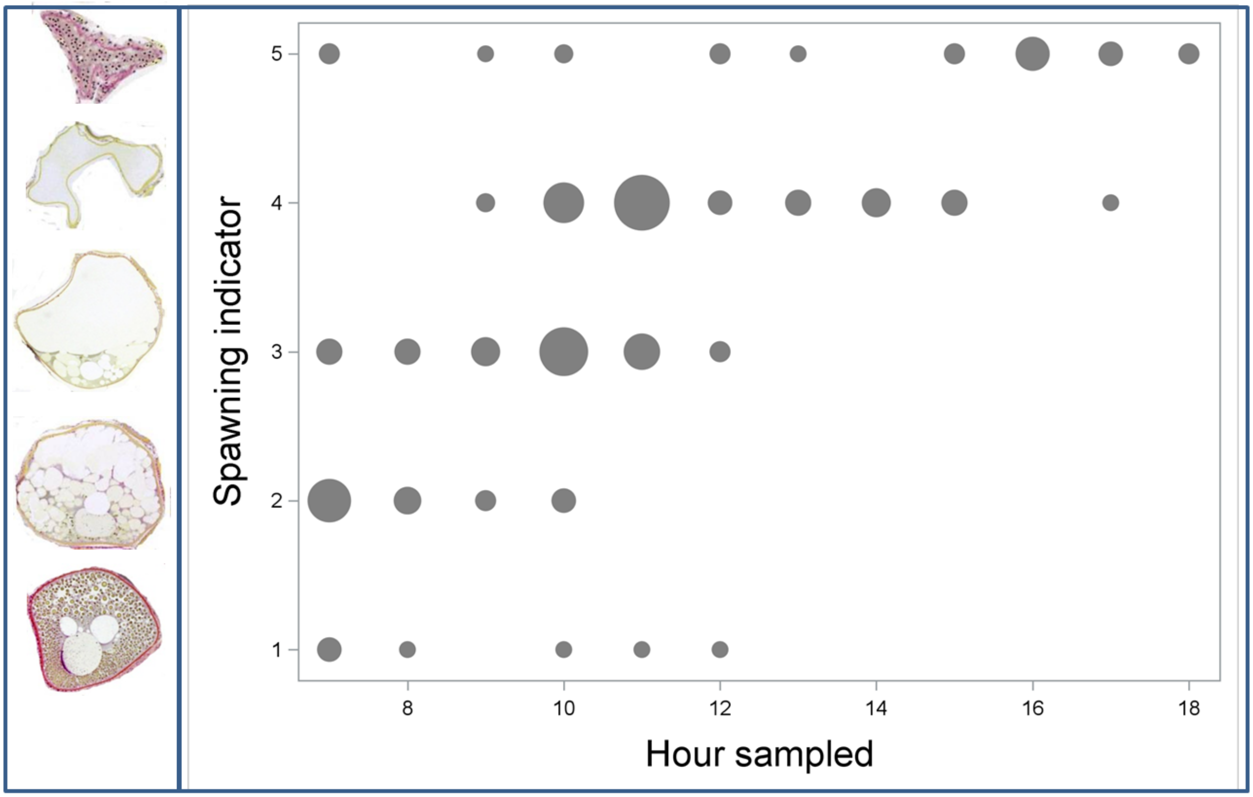


Fig.7

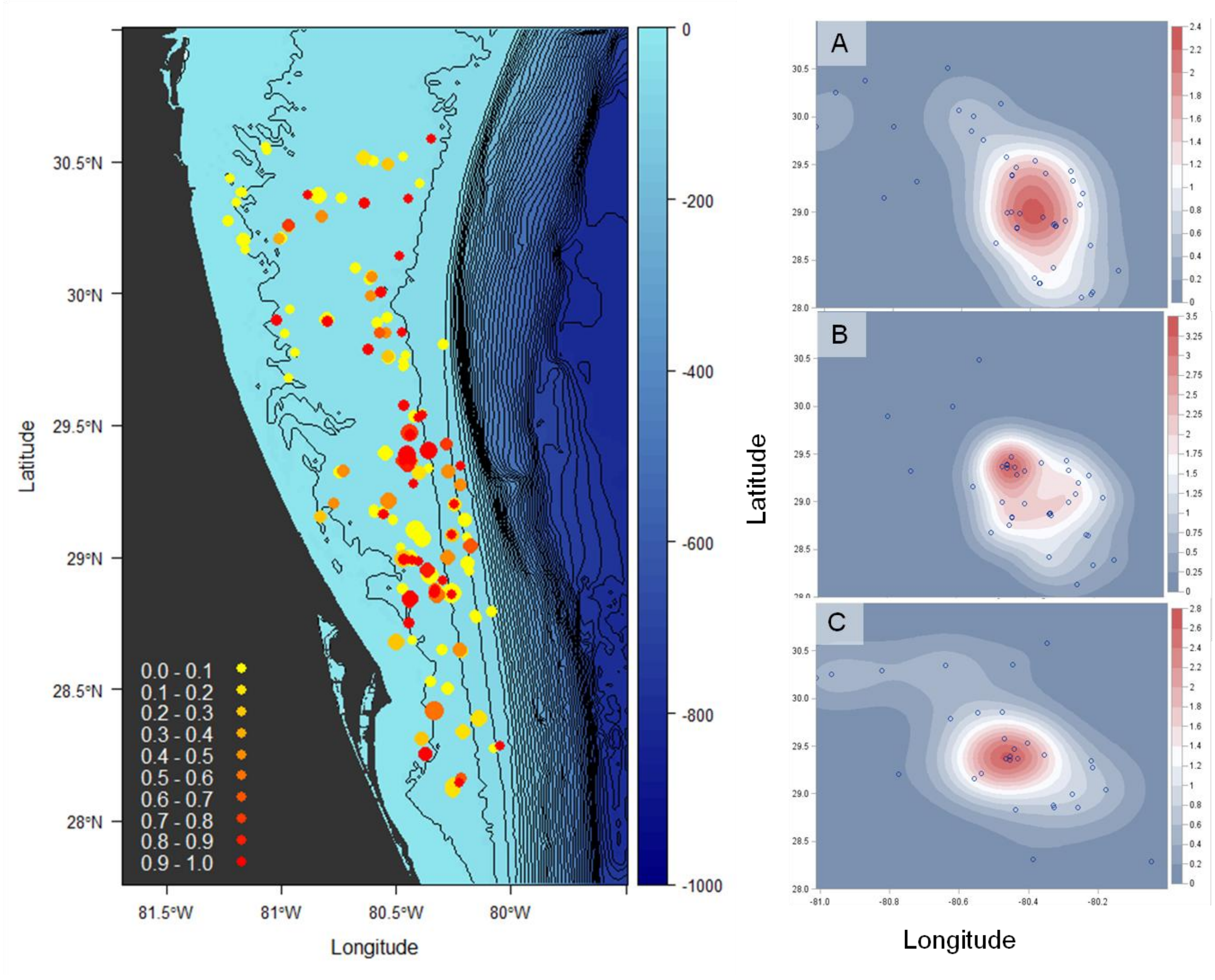

30.5°N
30°N
29.5°N
29°N
28.5°N
28°N
Latitude
81.5°W
81°W
80.5°W
80°W
Longitude
0.0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0
0
-200
-400
-600
-800
-1000
A
B
C
Latitude
Longitude
30.5
30.0
29.5
29.0
28.5
28.0
-81.0
-80.8
-80.6
-80.4
-80.2

Fig. 8.

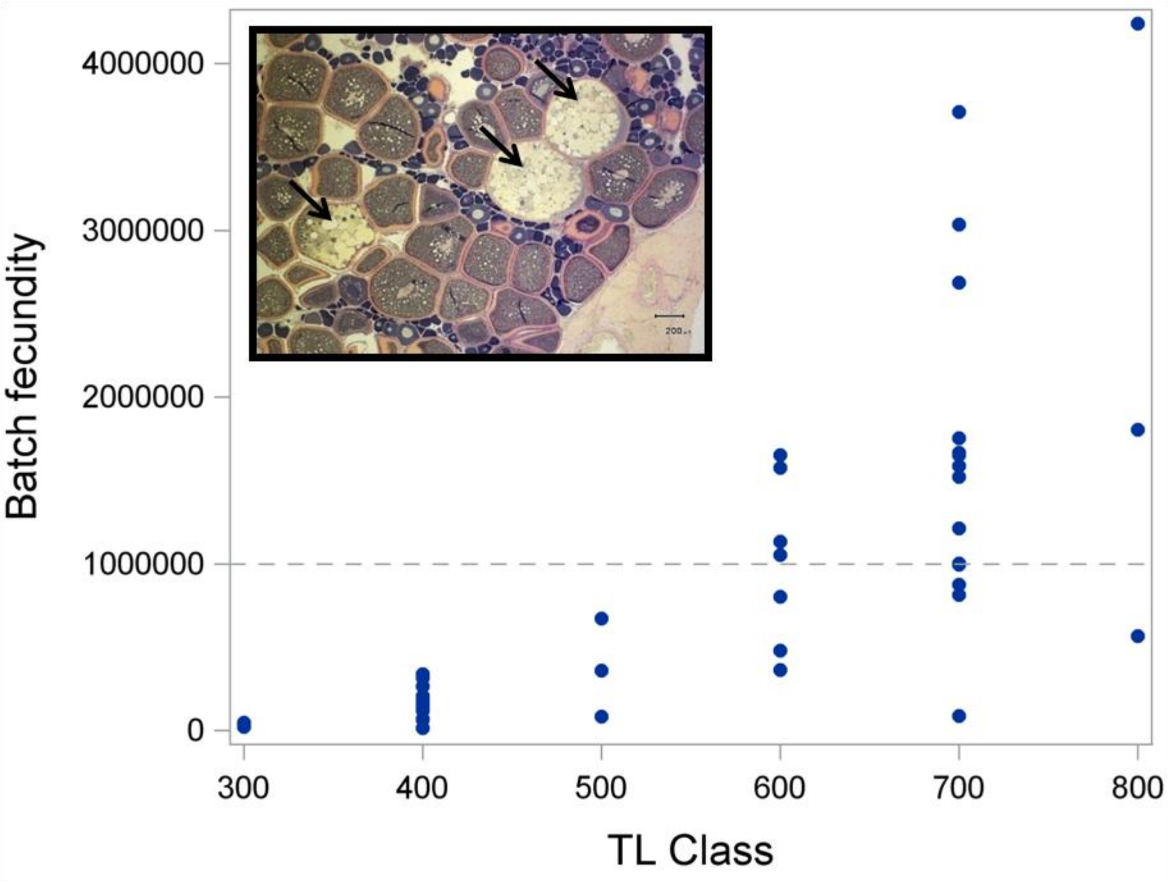
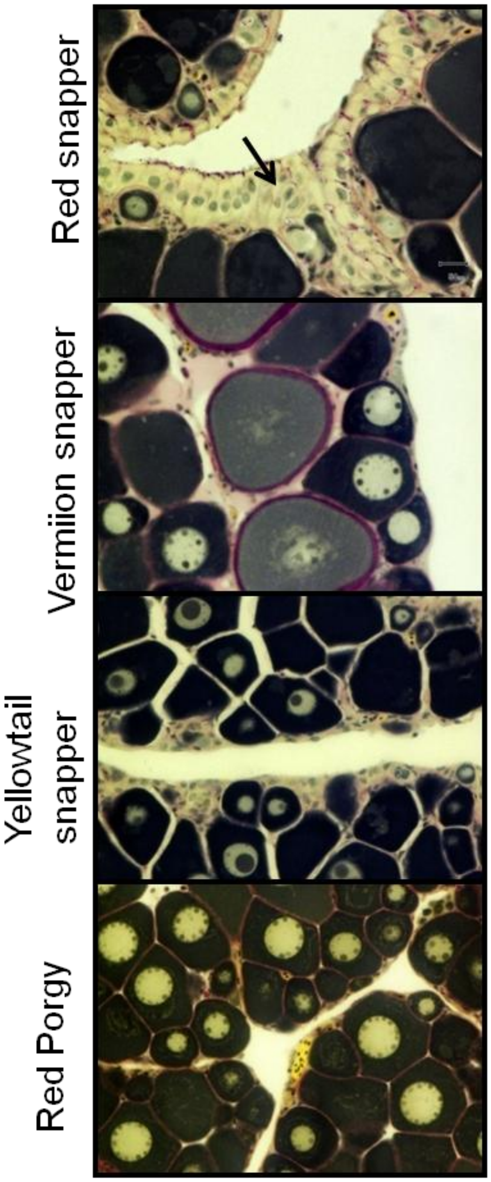

4000000
3000000
2000000
1000000
0
Batch fecundity
300
400
500
600
700
800
TL Class
200

Fig. 9.


Red snapper
Vermiion snapper
Yellowtail snapper
Red Porgy

Bibliography

Anderson CNK, Hsieh C, Sandin SA, Hewiit R, Hollowed A, Beddington J, May RM, Sugihara G (2008) Why fishing magnifies fluctuations in fish abundance. Nature 452:835-839

Audzijonyte A, Kuparinen A, Fulton EA (2013) How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. Evolutionary applications 6:585-595

Brown-Peterson N, Wyanski D, Saborido-Rey F, Macewicz B, Lowerre-Barbieri S (2011) A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science [online serial] 3:52-70

Brown-Peterson NJ, Burns KM, Overstreet RM (2009) Regional differences in Florida red snapper reproduction.

Brulé T, Colás-Marrufo T, Pérez-Díaz E, Sámano-Zapata JC (2010) Red Snapper Reproductive Biology in the Southern Gulf of Mexico. Transactions of the American Fisheries Society 139:957-968

Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. Marine Biology Annual Review 42:265-302

Claydon JAB, McCormick MI, Jones GP (2012) Patterns of migration between feeding and spawning sites in a coral reef surgeonfish. Coral Reefs 31:77-87

Colin PL (1996) Longevity of some coral reef fish spawning aggregations. Copeia 1996:189-192

Collins AB, McBride RS (2011) Demographics by depth: spatially explicit life-history dynamics of a protogynous reef fish. Fishery Bulletin 109:232-242

Collins LA, Johnson AG, Keim CP, Arregu¡n-S nchez F, Munro JL, Balgos MC, Pauly D (1996) Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the Northeastern Gulf of Mexico. ICLARM Conf. Proc. 48

Cooper WT, Barbieri LR, Murphy MD, Lowerre-Barbieri SK (2013) Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing. Fisheries Research 138:31-41

Cowan Jr JH (2011) Red Snapper in the Gulf of Mexico and U.S. South Atlantic Fisheries 36:319-331

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: Defined and reviewed. BullMarSci 60:698-726

Enberg K, Jørgensen C, Mangel M (2010) Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. Canadian Journal of Fisheries and Aquatic Sciences 67:1708-1719

Fitzhugh GR, Shertzer KW, Kellison GT, Wyanski DM (2012) Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. Fishery Bulletin 110:413-425

Folke C (2006) Resilience: The emergence of a perspective for social–ecological systems analyses. Global Environmental Change 16:253-267

Frank KT, Brickman D (2001) Contemporary management issues confronting fisheries science. JSea Res 45:173-187

Haslob H, Rabade-Uberos S, Saborido-Rey F (2013) Seasonal variability of fecundity and spawning dynamics of Baltic sprat. Fisheries Research 138:99-109

Healey MC (2009) Resilient salmon, resilient fisheries for British Columbia, Canada. Ecology and Society 14:2

Heino M, Baulier L, Boukal DS, Ernande B, Johnston FD, Mollet FM, Pardoe H, Therkildsen NO, Uusi-Heikkila S, Vainikka A, Arlinghaus R, Dankel DJ, Dunlop ES, Eikeset AM, Enberg K, Engelhard GH, Jorgensen C, Laugen AT, Matsumura S, Nussle S, Urbach D, Whitlock R, Rijnsdorp AD, Dieckmann U (2013) Can fisheries-induced evolution shift reference points for fisheries management? ICES Journal of Marine Science 70:707-721

Holt GJ, Holt SA, Arnold CR (1985) Die1 periodicity of spawning in sciaenids. Marine Ecology Progress Series 27, 1 7

Hsieh C-h, Reiss CS, Hewitt RP, Sugihara G (2008) Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 65:947-961

Hsieh C-h, Reiss CS, Hunter JR, Beddington JR, May RM, Sugihara G (2006) Fishing elevates variability in the abundance of exploited species. Nature 443:859-862

Hsieh C-h, Yamauchi A, Nakazawa T, Wang W-F (2010) Fishing effects on age and spatial structures undermine population stability of fishes. Aquatic Sciences 72:165-178

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. Trends in ecology & evolution 20:380-386

Hunter JR, Lo NC, Leong RJ, Lasker R (1985) Batch fecundity in multiple spawning fishes. NOAA Tech. Rep. NMFS 36

Hunter JR, Macewicz BJ (1985) Measurement of spawning frequency in multiple spawning fishes. In: Lasker R (ed) An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, Book 36. NOAA Technical Report NMFS

Jackson MW, Nieland DL, Cowan JH (2006) Diel spawning periodicity of red snapper Lutjanus campechanus in the northern Gulf of Mexico. Journal of Fish Biology 68:695-706

Jalabert B (2005) Particularities of reproduction and oogenesis in teleost fish compared to mammals. ReprodNutrDev 45:261-279

Jearld A, Jr., Nielsen LA, Johnson DL (1983) Age Determination. Fisheries Techniques

Jensen AL (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can J Fish Aquat Sci 53:820–822

Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gårdmark A, Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino

M, Rijnsdorp AD (2007) Managing Evolving Fish Stocks. Science 318:1247-1248

Jørgensen C, Ernande B, Fiksen Ø, Dieckmann U (2006) The logic of skipped spawning in fish. Canadian Journal of Fisheries and Aquatic Sciences 63:200-211

Kamler E (2005) Parent-egg-progeny relationships in teleost fishes: an energetics perspective. Rev Fish Biol Fisheries 15:399-421

Kraak SBM (2007) Does the probabilistic maturation reaction norm approach disentangle phenotypic plasticity from genetic change. Mar Ecol Progr Ser 335:295-300

Law R (2007) Fisheries-induced evolution: present status and future directions. Mar Ecol Progr Ser 335:271-277

Lowerre-Barbieri S, Brown-Peterson N, Murua H, Tomkiewicz J, Wyanski D, Saborido-Rey F (2011a) Emerging issues and methodological advances in fisheries reproductive biology. Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science [online serial] 3:32-51

Lowerre-Barbieri S, Ganias K, Saborido-Rey F, Murua H, Hunter J (2011b) Reproductive timing in marine fishes: variability, temporal scales, and methods. Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science [online serial] 3:71-91

Lowerre-Barbieri S, Villegas-Rıos D, Walters S, Bickford J, Cooper W, Muller R (2014) Spawning Site Selection and Contingent Behavior in Common Snook, *Centropomus undecimalis*. PLoS ONE 9: e101809

Lowerre-Barbieri SK (2009) Reproduction in relation to conservation and exploitation of marine fishes. Science Publishers

Lowerre-Barbieri SK, Barbieri LR (1993) A new method of oocyte separation and preservation for fish reproduction studies. FishBull 91:165-170

Lowerre-Barbieri SK, Henderson N, Llopiz J, Walters S, Bickford J, Muller R (2009) Defining a spawning population(Spotted Seatrout *Cynoscion nebulosus*) over temporal, spatial, and demographic scales. Marine Ecology Progress Series 394:231-245

Lowerre-Barbieri SK, Walters S, Bickford J, Cooper W, Muller R (2013) Site fidelity and reproductive timing at a Spotted Seatrout spawning aggregation site: individual versus population scale behavior. Marine Ecology Progress Series 481:181-197

Mangel M, MacCall AD, Brodziak J, Dick EJ, Forrest RE, Pourzand R, Ralston S, Rose K (2013) A perspective on steepness, reference points, and stock assessment. Canadian Journal of Fisheries and Aquatic Sciences 70:930-940

Marshall CT (2009) Implementing information on stock reproductive potential in fisheries management: the motivation, challenges and opportunities. Fish reproductive biology: implications for assessment and management:395-420

Marty L, Rochet MJ, Ernande B (2014) Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. Marine Ecology Progress Series 497:179-197

Maunder MN, Deriso RB (2013) A stock-recruitment model for highly fecund species based on temporal and spatial extent of spawning. Fisheries Research 146:96-101

Moe MA (1963) A survey of offshore fishing in Florida. Florida Department of Natural Resources Marine Research Laboratory

Murawski S, Rago P, Trippel E (2001) Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES Journal of Marine Science: Journal du Conseil 58:1002-1014

Murua H, Kraus G, Saborido-Rey F, Witthames PR, Thorsen A, Junquera S (2003) Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. Journal of Northwest Atlantic Fisheries Science 33:33-54

Myers RA, Bowen KG, Barrowman NJ (1999) Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404-2419

Pecquerie L, Petitgas P, Kooijman S (2009) Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. Journal of Sea Research 62:93-105

Quintero-Hunter I, Grier H, Muscato M (1991) Enhancement of histological detail using metanil yellow as counterstain in periodic acid Schiff's hematoxylin staining of glycol methacrylate tissue sections. Biotechnic & Histochemistry 66:169-172

Rideout RM, Tomkiewicz J (2011) Skipped spawning in fishes: more common than you might think. Marine and Coastal Fisheries 3:176-189

Rose KA, Cowan JH, Winemiller KO, Myers RA, Hilborn R (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2:293-327

Sadovy De Mitcheson Y, Cornish A, Domeier M, Colin PL, Russell M, Lindeman KC (2008) A global baseline for spawning aggregations of reef fishes. Conservation biology : the journal of the Society for Conservation Biology 22:1233-1244

Sadovy de Mitcheson Y, Craig MT, Bertoncini AA, Carpenter KE, Cheung WWL, Choat JH, Cornish AS, Fennessy ST, Ferreira BP, Heemstra PC, Liu M, Myers RF, Pollard DA, Rhodes KL, Rocha LA, Russell BC, Samoilys MA, Sanciangco J (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. Fish and Fisheries 14:119-136

SEDAR24 (2010) Stock Assessment Report South Atlantic Red Snapper. SEDAR. NMFS, 4055 Faber Place Drive, Suite 201 North Charleston, Sc 29405

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York

Svedäng H, André C, Jonsson P, Elfman M, Limburg KE (2010) Migratory behaviour and otolith chemistry suggest finescale sub-population structure within a genetically homogenous Atlantic Cod population. Environmental Biology of Fishes 89:383-397

Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001) Natal homing in a marine fish metapopulation. Science 291:297-299

Vert-pre KA, Amoroso RO, Jensen OP, Hilborn R (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. Proceedings of the National Academy of Sciences of the United States of America 110:1779-1784

Walker B, Holling CS, Carpenter SR, Kinzig A (2004) Resilience, Adaptability and Transformability in Social–ecological Systems. Ecology and Society 9:5

White DB, Palmer SM (2004) Age, growth, and reproduction of the red snapper, *Lutjanus campechanus*, from the Atlantic waters of the southeastern U.S. Bulletin of Marine Science 75:335-360

Woods MK, Fischer AJ, Cowan Jr J, Nieland D Size and age at maturity of female red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Proc Proceedings of the Gulf and Caribbean fisheries institute

Wright PJ, Trippel EA (2009a) Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries 10:283-304

Wright PJ, Trippel EA (2009b) Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries 10:283-304

Young JL, Bornik ZB, Marcotte ML, Charlie KN, Wagner GN, Hinch SG, Cooke SJ (2006) Integrating physiology and life history to improve fisheries management and conservation. Fish and Fisheries 7:262-283