Aspects of the Life History of Red Grouper, *Epinephelus morio*, Along the Southeastern United States

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Project Final Report

Report Title: Aspects of the Life History of Red Grouper, *Epinephelus morio*, Along the Southeastern United States

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II. Abstract: Red grouper collected from NC/SC were 315 to 851 mm TL and 2 to 20 years old. Red grouper collected from eastern FL were 240 to 840 mm TL and 1 to 14 years old. Marginal increment analysis indicated that increment formation occurred during July and August of each year. Histological interpretation of reproductive tissue from 2,068 fish caught off NC/SC revealed that 87% were female, 6% were transitional and 7% were male. For fish captured off FL, 75% were female, 12% male and 13% transitional. Off NC/SC, age at 50% maturity was 2.4 years and size at 50% maturity was 487 mm TL. Off FL, age at 50% maturity was 2.1 years and the size at 50% maturity was 529 mm TL. Red grouper are protogynous and females dominated fish between the ages of 2 to 6 and less than 680 mm TL. Females were in spawning condition from February through June off NC and January through May off FL. Spawning occurred every 2-3 days or approximately 42 times during the spawning season. Red grouper in spawning condition were collected at depths of 33 to 90 m, however, spawning activity tended to occur in waters deeper than 40 m. Age at 50% transition was 7.2 years and 690 mm TL off NC/SC and 8.2 years and 687 mm TL off FL. Catch curve analysis of NC fishery-dependent data provided a total mortality of 0.75 and indicated that red grouper are fully recruited at age 4. Off FL, a catch curve analysis of fishery-dependent data provided a total mortality of 0.64 and fish were fully recruited to gear at age 5.

III. Executive Summary:

- The red grouper is a protogynous serranid that occurs in the western Atlantic from Massachusetts to Rio de Janeiro, Brazil, the Gulf of Mexico and Brazil. There is a disjunct distribution of red grouper off the Atlantic coast. Red grouper are commonly caught off NC, northern SC and southern FL but are rare from southern SC to northern FL.
- Red grouper were obtained from three different sources for this study: NC/SC commercial fishermen (n = 1,928), NC/SC fishery-independent samples (n = 218), and eastern FL commercial fishermen (n = 436).
- There were significant differences in the mean size of fish collected as well as the mean depth fish were captured for the three data sources: NC/SC commercial fishermen (527 mm TL; 38 m); NC/SC fishery-independent (529 mm TL; 35 m); and FL fishery dependent (605 mm TL; 45 m). More red grouper are available to fishermen off NC/SC in shallower water than off FL due to a broader continental shelf. Shelf edge habitat is close to shore off FL.
- Differences in aspects of the life history of red grouper from NC/SC and eastern FL can be attributed to differences in the depth of capture.
- Ages of red grouper ranged from 2 to 20 years for fish collected off NC/SC and 1-14 years for fish off FL. For the three data sources, there was a significant difference in the size at age of fish between the ages of 2-5. Smaller younger fish were more available to fishery-independent gear and were more commonly captured by fishermen off NC than off FL.
- Histological interpretation of reproductive tissue from 2,068 fish caught off NC revealed that 87% were female, 6% were transitional and 7% were male. For fish captured off FL, 75% were female, 12% male and 13% transitional.
- Off NC, age at 50% maturity was 2.4 years and size at 50% maturity was 487 mm TL. Off FL, age at 50% maturity was 2.1 years and the size at 50% maturity was 529 mm TL.
- Females were in spawning condition from February through June off NC and January through May off FL. Spawning occurred every 2-3 days or approximately 42 times during the spawning season. Red grouper in spawning condition were collected at depths of 33 to 90 m, however, spawning activity tended to occur in waters deeper than 40 m.
- Age at 50% transition was 7.2 years and 690 mm TL off NC and 8.2 years and 687 mm TL off FL. For both NC/SC and FL, the percentage of individuals undergoing sexual transition was at a minimum during the spawning season. Percent transition gradually increased after the spawning season reaching a maximum during the summer when there was no spawning activity.
- Catch curve analysis of North Carolina fishery-dependent data provided a total mortality of 0.75 and indicated that red grouper are fully recruited at age 4. Off FL, a catch curve analysis of fishery-dependent data provided a total mortality of 0.64 and fish were fully recruited to gear at age 5.
- Assuming that red grouper do not compensate for the loss of larger males, the SPR of females is ~0.27. If red grouper do compensate form the loss of males by becoming males at smaller sizes then the SPR of females is 0.18.

- Assuming that there was no release mortality and no sex ratio compensation then the SPR for females off NC/SC at an age of entry of 4 and F = 0.55, female SPR is 0.3 and male SPR is 0.1. For females off FL at an age of entry of 5 and F = 0.44, female SPR was 0.49 and male SPR was 0.2.
- If it is assumed that there is release mortality and red grouper are able to compensate for the loss of males by becoming males at smaller sizes then the females SPR off NC/SC is 0.18 and male SPR is 0.22. For FL caught fish, SPR was 0.28 for females and 0.31 for males.

IV. Purpose:

A. Detailed description of problem or impediment of fishing industry that was addressed.

The red grouper, *Epinephelus morio*, is a protogynous serranid that is associated with reef habitat throughout the Western Atlantic from Massachusetts through the Gulf of Mexico and into Brazil (Brule and Deniel 1996; Johnson et al. 1998). Red grouper are reported to occur at depths of 24-120 m (Johnson et al. 1998) and are usually associated with reef habitat as adults (Moe 1969, Johnson and Collins 1994, Johnson et al. 1998).

From 1983 through the 1995, landings (NC to eastern FL) of grouper increased reaching a peak of 207,000 lbs (Figure 1). Eastern Florida landings dominated the catch through the middle 1980's (Figure 2) when a decline occurred, concurrent with a tremendous increase in North Carolina red grouper landings. During 1986-1995, 45% of the red grouper from the southeastern United States were landed in east Florida and 53% were landed in North Carolina. Red grouper are rarely landed in Georgia or South Carolina (Figure 2). This disjunct distribution prompted Chapman, Sedberry and McGovern to seek funding from MARFIN to use genetic techniques to determine if red grouper from North Carolina and eastern Florida are separate stocks. This study was funded in 1998. We intend to complement that study by comparing aspects of the age, growth, reproduction, and fecundity of red grouper from eastern Florida and North Carolina.

Despite the commercial importance of red grouper, studies of the life history of red grouper along the east coast of the United States are few and dated. The only study that examined aspects of the age and growth of red grouper along the southeastern United States was conducted by Stiles and Burton (1994), however, this study was based on few data that were collected during 1977-1988. Although Stiles and Burton (1994) examined data from North Carolina to Key West Florida there was no comparison of aspects of the age and growth of red grouper caught off of North Carolina and eastern Florida. Recent data are needed to determine if fishing pressure has caused a change in the size at age of red grouper. In the Gulf of Mexico, Johnson and Collins (1994) found that there was a larger size at age of red grouper collected in 1991-1992 than in 1979-1981. An increase in the size at age has been noted for other groupers including gag in the Gulf of Mexico (Johnson et al. 1993), gag off the southeastern United States (Harris and Collins, 2000) and snowy grouper off the southeastern states (Wyanski et al., 2000). Sustained heavy fishing also has been implicated as a cause of a change in the size at age of vermilion snapper (Zhao et al. 1997) and red porgy (Harris and McGovern 1997) along the southeastern Atlantic states as well as the Gulf of Mexico[1].

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[1] Peter Hood, personal communication. Florida Department of Environmental Protection.

There have been no studies published on the reproductive biology of red grouper along the southeast Atlantic. Coleman et al. (1996) provided information on the seasonal and spatial aspects of spawning of red grouper from the northwestern Gulf of Mexico. Red grouper females were in spawning condition from late fall to late spring with peak spawning occurring during April.

There are few data on which to base a management plan for red grouper, and basic life history data off the southeastern U.S. are needed. The disjunct distribution of red grouper suggests that there may be differences in aspects of the life history of red grouper off of North Carolina and Florida and that different management regulations may be required for the two regions. White grunt, *Haemulon aurolineatum*, which have a similar distribution to red grouper, grow slower and achieve larger sizes off North Carolina than white grunt off of southeast Florida (Padgett 1997). Currently, life history data from red grouper collected in the Gulf of Mexico are being used for assessment purposes and to make management decisions on red grouper off the southeastern United States.

B. Objectives of the project

The goal of the proposed research was to estimate the age structure and provide life history and population data needed to refine fishery management plans for red grouper, *Epinephlus morio,* off the southeast US coast. Specific objectives included:

1. Randomly sample red grouper from the southeastern U.S. (proportional to historical landings for each region) for a life history study.
2. Generate age-length keys and to determine sex ratio, size and age of maturity, and maturity schedules for fish caught in eastern Florida and North Carolina.
3. Estimate population various population parameters for red grouper caught off of Eastern Florida and North Carolina.
4. Provide these data in a timely fashion to the NMFS, and the South Atlantic Fishery Management Council.

V. Approach

Sampling

Fishery-dependent red grouper samples were obtained from commercial fish houses in Wrightsville Beach NC, Southport NC, Calabash, NC, Murrells Inlet, SC, Mt. Pleasant SC, Key West FL, Ft. Pierce, FL, Miami FL, and Jacksonville, FL. The whole catch was sampled in most cases, although random samples were taken when the catch was large. Commercial fishing trips usually lasted less than six days, and fish were caught using snapper reels (Wyanski et al., 2000). When possible, the approximate location and depth of the catch was obtained from the fishermen.

Fishery-independent samples were obtained primarily off of NC and SC during the Marine Resources Monitoring Assessment and Prediction Program (MARMAP) cruises on the *R/V Palmetto*. MARMAP samples reef fishes at randomly selected areas of hard bottom habitat off the southeastern United States between Cape Hatteras, NC and Fort Pierce, FL. Fishes were captured with chevron traps (Collins, 1990) baited with clupeids and soaked for approximately 90 minutes. Some samples were obtained using longline and hook and line. All fish were captured during daylight hours, and the location and depth of the sampling sites were recorded.

Total length (TL, to the nearest mm) and gutted fish weight (± 0.01 lb and converted to kg) were measured in each fish sampled from the commercial fishery. Gutted fish weight (GFW) was converted to whole fish weight (FW) using the relationship FW (kg) = 1.053 GFW (kg)– 0.3647, modified from Goodyear and Schirripa (1993). For all fish collected by MARMAP, TL, fork length (FL) and standard length (SL) were measured to the nearest mm. Whole weight in small groupers (less than 2.5 kg) was measured to the nearest g with a triple beam balance. Larger groupers were weighed to the nearest 50 g using an electronic scale.

Red grouper collected with various fishing gear during MARMAP cruises between 1991 and 1996 were used to analyze the relationship between depth and size, age, sex and reproductive stage. These specimens were not included in other analyses.
The area sampled by MARMAP was divided in three regions: north of 32^{o}N, between 32^{o}N and 30^{o}N, and south of 30^{o}N. For each region, catch per unit effort (CPUE), estimated for the period 1991-2000 was expressed as number of red grouper caught per trap.

Sagittal toliths were extracted by accessing the base of the cranium through the operculum and scraping the otic bulla with a chisel until the otic chamber was exposed. In most specimens from the commercial fishery, only the left otolith was obtained, whereas both otoliths were obtained for fishery-independent caught fish. Otoliths were rinsed in water and stored dry in paper envelopes. Gonads of specimens from the commercial fishery were extracted, wrapped in cheesecloth, and preserved in 10% seawater formalin. Preserved gonads were weighed to the nearest g, and a sample from the posterior area of the gonad was obtained for histological analysis to determine sex and reproductive stage. The gonads from 18 specimens were weighed both before and after preservation to establish a relationship between fresh and preserved gonad weights, and preserved gonad weights were converted to fresh gonad weights. Gonads obtained from MARMAP sampling were preserved for histological analysis immediately after extraction.

Age and growth

Otoliths were embedded in epoxy resin and sectioned (0.8 mm thick) through the core along a dorso-ventral plane with a low-speed saw equipped with a high-concentration diamond wheel. Sections were mounted on glass slides. Increments (one opaque and one translucent zone) were counted independently by two readers with no reference to fish length or date of capture. Otolith sections were examined with a dissecting microscope (30x) using transmitted light. If the readers disagreed on the number of increments of any specimen, the primary reader analyzed the section several months later, with no reference to previous readings. If two of the three readings coincided, that age was assigned to the specimen; otherwise, the specimen was eliminated from analyses.

Otolith radius and increment radii were measured only on sections cut through the core and on which the readers agreed on the increment count. An image of the section was obtained with a video camera connected to the microscope and a frame digitizer. Images were analyzed on a computer monitor and measurements were made with digital image processing software. Otolith radius was measured from the core to the edge of the section, on the ventral edge of the sulcus acousticus (Figure 3). The distance from the core to the center of each increment was measured along the same axis. To detect possible bias, the size distribution of fish from which otolith radius and increment radii were measured was compared to the size distribution of all samples using a Kolmogorov-Smirnov two sample test (KS) (Sokal and Rholf, 1981).
For each fish, the marginal increment was calculated as

$$MI = \frac{OR - I_L}{I_L - I_{L-1}}$$

where OR is the otolith radius, I_L is the distance between the otolith core and the last increment and I_{L-1} is the distance between the otolith core and the next to last increment. Mean marginal increment was plotted as a function of the month of capture. If the increments were deposited annually, the monthly mean marginal increment should demonstrate a minimum value. The first day of the month with lowest mean marginal increment was assigned as birth date for all specimens aged.

Length frequency distributions from fishery-dependent and fishery-independent samples were compared using a Kolmogorov-Smirnov two-sample test. Age-length keys from fishery-dependent and fishery-independent samples were obtained by creating a matrix containing the number of samples by age within 20 mm TL intervals (Ricker, 1975). Age-length keys from commercial and MARMAP samples were compared using Fisher´s exact test, following the procedure outlined by Hayes (1993). A comparison was made for each 20-mm length interval between 440 and 700 mm TL. To maintain the power of the test, comparisons were limited to length intervals with a sample size greater than six in both age length keys. The following adjusted significance level was used to compensate for the high number of tests required to compare age length keys:

$$\alpha^{*} = 1 - e^{(\ln(1-\alpha)/n)}$$

where α^* is the significance level for n individual tests and α is the desired experimentwise error (Hayes, 1993).

A geometric mean regression was fitted to the total length and otolith radius (OR) data, following the procedure described by Ricker (1992). Back-calculated lengths at age for individual fish were obtained using the body proportional hypothesis (Francis, 1990):

$$TL_i = \left[(c + dS_i)/(c + dS_c)\right]TL_c$$

where TL_i is the total length at time of formation of the *i*th increment, c and d are the intercept and slope of the TL-OR geometric mean regression, S_i is the distance from the otolith core to the *i*th increment, S_c is the otolith radius at time of capture, and TL_c is the total length of fish at time of capture. To avoid biases, otolith sections that presented some degree of inclination from the dorso-ventral plane, thus increasing the apparent otolith radius, were not used either to calculate the geometric mean regression, although back-calculated lengths at age were obtained from them. To detect the presence of Lee's phenomenon (Ricker, 1975), linear regression analysis was used to detect trends in mean length at age back-calculated from fish of increasing age.

The parameters of the von Bertalanffy growth curve (Ricker, 1975) were estimated by fitting a mixed model design (Lindstrom and Bates, 1990) to all back-calculated lengths at age. This model was selected because of the lack of independence between back-calculated ages in each fish. The NLMIX macro for the SAS software (Littel et al., 1996) was used following the procedure established by Jones (2000).
To facilitate comparison with previous studies, a second von Bertalanffy growth equation was fitted to the observed age and total length data using the NLIN procedure and Marquardt´s algorithm (SAS, 1990). To reduce the effect of the differences in the sample size in each age class, fish length was weighted by the inverse of the number of fish in each class. Observed and back-calculated mean lengths at age were compared using one-way analysis of variance (ANOVA).

Reproduction

A portion of the posterior area of each gonad was preserved in 10% seawater formalin for 14 d, and then transferred to 50% isopropanol for the same period. Samples were vacuum infiltrated, blocked in paraffin and sectioned with a rotary microtome. Three transverse sections 6 to 8 μm thick were mounted on glass slides, stained with double-strength Gill haematoxylin, and counter-stained with eosin-y.

The sex and reproductive stage of each specimen was assessed independently by two readers using histological criteria (Table 1). In case of disagreement, both readers analyzed the section simultaneously. If agreement could not be reached, the sample was eliminated from analyses. Females in the developing, spawning, spent or resting stages were considered mature. Individuals undergoing sex transition were considered active males when there was sperm present in the collecting ducts and sinuses. Females with migratory nucleus oocytes, hydrated oocytes or postovulatory follicles were considered in spawning condition.

To verify that immature females and resting females were clearly distinguished, the size distributions of specimens assigned to these two categories were compared with the size distribution of active females. Mature females in the developing, running ripe and spent states were considered active. An overlap in the size distributions of resting and active females indicated that the criteria used were appropriate (Wyanski et al., 2000).

Age at 50% maturity (A_{50}) and length at 50% maturity (L_{50}) were estimated using the PROBIT procedure (SAS, 1990). The model that best fit the maturity data (gompit, logit or probit models) was selected with the LOGISTIC procedure (SAS, 1990). Age at 50% sexual transition and length at 50% sexual transition were estimated in the same manner.

Spawning season was defined as the number of days between the dates of capture of the first and last specimens with hydrated oocytes, migratory nucleus oocytes, or post-ovulatory follicles (Collins et al. 1998). The duration of the spawning season was verified by examining the monthly trend of the gonadosomatic index (GSI), defined as

$$GSI = \frac{FGW}{FW - FGW} * 100$$

where FGW is the fresh gonad weight, and FW is the total weight of the fish. The number of days between each spawning event was estimated by dividing the total number of active females by the number of females observed with recent (< 24 h) post-ovulatory follicles (Hunter and Macewicz, 1985). To detect possible biases, the number of days between spawning events was also estimated using the number of females with hydrated oocytes and the number of females with hydrated oocytes or migratory nucleus oocytes. Spawning frequency was estimated by dividing the duration of the spawning season by the number of days between each spawning event.

Population dynamics

Total mortality (Z) was estimated using catch curve analysis on fishery-dependent samples. A linear regression was fitted to the descending limb of the natural logarithm of the frequency of samples on each year class (Ricker, 1975). The following relationships between natural mortality and life history parameters were used to obtain a series of estimates of natural mortality:

$\text{Log}(M) = 0.0066 - 0.279 * \log(L_{\infty}) + 0.6543(K) + 0.4634 * \log(T^{o}C)$ (Pauly, 1980)
$\text{Ln}(Z) = 1.44 - 0.982 * \text{Ln}(t_{max})$ (Hoenig, 1983)
$M = 0.0189 + 2.06 * K$ (Ralston, 1987)
$M = 1.63 * K$ (Jensen, 1996)

where M is natural mortality, Z is total mortality, L_{inf} and K are parameters from the von Bertalanffy growth equation, $T^{o}C$ is the average water temperature, and t_{max} is the maximum age observed. An average bottom water temperature of 17.6^{o} C in winter and 24.4^{o} C in summer, reported by Mathews and Pashuk (1986) for Onslow Bay (NC), was used with Pauly´s (1980) equation. Because Hoenig's (1983) equation relates total mortality rates to the maximum age observed in the population, using the maximum age observed in an unfished population would provide an estimation of natural mortality. In all cases, von Bertalanffy parameters estimated from back-calculated lengths at age were used. Fishing mortality (F) on completely recruited cohorts was estimated by subtracting natural mortality from total mortality.

A model to estimate YPR and SPR was constructed, following Ricker´s (1975) approach and using the algorithm presented by Gabriel et al. (1989). The model followed a theoretical cohort of fish from age 1 to age 15 under different combinations of age at entry and fishing mortality and estimated the total yield in g per recruit (YPR) and the spawning biomass per recruit (SBPR) produced by the cohort during its lifetime. Under equilibrium conditions (constant natural and fishing mortality) these values are equivalent to the YPR and SBPR produced by the population each year.

Fishery managers control the size at entry to the fishery, rather than the age at entry. To incorporate variability in length at age, fish larger than the theoretical length at age of entry were considered fully recruited to the fishery and were allowed to be captured regardless of age. For each age at entry to the fishery considered (tc) and each age (t), the fraction of each of the cohort available to the fishery p(tc,t), was estimated by comparing fishery-dependent and fishery-independent age-length keys. It was assumed that fishermen kept the legal sized fish, and released all undersized fish. Yield calculations were based on the number of fish captured and retained.

Age-specific survival rates of released fish were also built into the model. Release survival rates were estimated from depth-specific release survival rates and from the distribution of fish by age and depth from fishery-independent data. Release survival rates observed by Wilson and Burns (1996) for red grouper were used: 95% in water shallower than 45 m, and zero when depth >65 m. Between 45 and 65 m, an intermediate value of 45% was assumed. The CPUE of red grouper by MARMAP was used to provide an age- and depth-specific index of abundance. Age-specific release survival rates were estimated as

$$s_a = \sum_d a_{ad} s_d$$

where s_a is the release survival rate at age *a*, a_{ad} is the abundance index of fish of age *a* at depth strata *d*, and s_d is the observed survival rate at depth strata *d*.

Fishing mortality, release mortality and natural mortality were assumed constant throughout the year for each model run. Each cohort was assumed to enter the fishing grounds on the birth date at age 1. To estimate the fraction of total mortality that occurs at time of spawning (Gabriel et al., 1989), it was assumed that all the spawning activity occurred on the first day of the month that had the highest frequency of spawning individuals.

The number of fish remaining at the end of each year (N_{t+1}) was estimated as

$$N_{t+1} = Nl + Nrs + Ns$$
$$Nl = N_t \cdot p(tc,t) \cdot e^{-M-F}$$
$$Nrs = \left[N_t \cdot (1 - p(tc,t)) \cdot e^{-M} - N_t \cdot (1 - p(tc,t)) \cdot e^{-M-F}\right] \cdot ps(t)$$
$$Ns = N_t \cdot (1 - p(tc,t)) \cdot e^{-M}$$

where Nl is the number of legal fish not captured by the fishery, Nrs is the number of surviving sublegal fish that were captured and released, Ns is the number of sublegal fish not captured by the fishery, Nt is the number of fish at the beginning of the year, p(tc,t) is the proportion of fish at age *t* larger than the theoretical minimum legal length at age of entry tc, ps(t) is the release survival at age *t*, M is natural mortality rate and F is fishing mortality.

The model recorded the numbers of males and females and estimated spawning biomass for each sex. Based on observations by Coleman et al. (1996), it was assumed that red grouper compensate for the loss of males by initiating sex transition at younger ages and thus keeping a constant sex ratio. To include sex ratio compensation in the model, the percentage of males by age class was approximated to a linear form, following the approach for number-compensated protogyny with fixed maturation described by Huntsman and Schaaf (1994). The slope of the linear regression at each combination of fishing mortality and age at entry was adjusted to keep sex ratio at the observed value of 6.6 females per male. Age at maturity of female red grouper was considered constant because of the lack of historical maturity data. For comparative purposes, the model was run assuming no release mortality and no sex ratio compensation. YPR and SPR estimations were obtained for F values ranging from 0 to 1, and for age at entry to the fishery from 1 to 10 years old. For each value of tc, I estimated the fishing mortality that maximizes YPR (F_{max}) and the fishing mortality where the slope of the yield curve is 10% of the initial value ($F_{0.1}$). Sex-specific spawning stock biomass per recruit was calculated by estimating the number of mature individuals of each sex alive at time of spawning. SPRs were expressed as ratios between observed SBPR and the SBPR calculated when F = 0.

The sensitivity of the model to changes in the values of natural mortality and von Bertalanffy growth rate was tested in nine different scenarios combining three values of F (0.2, 0.4 and 0.6) and three ages at entry to the fishery (3, 5 and 7 years old). In each scenario, yield per recruit, female SPR and male SPR were calculated with M values of 0.1 and 0.3 and k values 10% higher and 10% lower than the estimated k from back-calculated data. These estimations were compared to YPR and SPR calculated using the estimated value of k and a value of M=0.2.

A. Detailed description of the work that was performed.

Sampling

Fishery-dependent samples were obtained from 1,928 red grouper that were landed off NC and SC. Red grouper from NC/SC ranged in length from 384 to 851 mm TL ($\bar{x}$ = 562.6, SD = 66.70). Many of the fish sampled (21.9%) were smaller than the minimum legal size of 508 mm TL (20 inches). Commercial fishermen captured red grouper between 32°30'N and 33°57'N, and between 76°56'W and 79°19'W, with depth ranging between 27 and 76 m ($\bar{x}$ = 34.3, SD = 6.59). An approximate location and depth of capture was reported for 34% of the samples (Figure 4).

Off eastern FL, samples from 436 red grouper were obtained from commercial fishermen. These fish ranged in length from 240 to 840 mm TL ($\bar{x}$ = 604.9, SD = 87.85). Off FL, Commercial fishermen captured red grouper between 23°46'N and 31°57'N, and between 79°56'W and 79°19'W, with depth ranging between 27 and 76 m ($\bar{x}$ = 44.7, SD = 19.24). A location and depth of capture was reported for 83% of the samples (Figure 4).

During the cruises conducted by MARMAP, 218 red grouper were captured north of 32°00'during May 1996 to June 2000 with specimens ranging in length from 315 to 779 mm TL ($\bar{x}$ = 547.0, SD = 102.93). Red grouper were captured at depths from 25 to 95 m ($\bar{x}$ = 38.5, SD = 16.1), and between 32° 08´N and 34° 19´N, and between 76°07´W and 79°18'W (Figure 5). Only 20 red grouper were caught south of 32°00' during 1996-2000.

From 1991 to 2000, red grouper CPUE north of 32°N was 9.1 x 10^{-2} specimens per trap. During the same period, CPUE between 32°N and 30°N was 0.2 x 10^{-2} specimens per trap, whereas south of 30°N was 10.7 x 10^{-2} specimens per trap. Catch per unit effort was significantly lower in the region between 32°N and 30°N than in the other two regions (G test, $P<0.05$).

Analysis of Variance and the Scheffe multiple range test indicated that the mean length of fish caught off southern FL (604.9 mm TL) was significantly greater than fish caught with either fishery dependent gear off NC/SC (562.6 mm TL) or fishery independent gear off NC/SC (528.6 mm TL). Furthermore, the mean size of fish caught with fishery dependent gear off NC/SC was significantly larger than the mean size of fish caught with fishery independent gear in the same region. The length frequency distribution of fishes (Figure 6) showed that smaller fishes were caught off NC/SC than off FL and that fishery independent caught a greater number of smaller fishes than fishery dependent gear.

The mean size of fish caught was related to the mean depth sampled. The mean depth that red grouper were caught by commercial fishermen off FL (44.7 m) was significantly greater than the mean depth of red grouper caught with fishery dependent off NC/SC (38.3 m) or with fishery independent gear off NC/SC (35.4 m).

The relationships between length measurements (mm) and fish weight (g) of fish caught off NC/SC from both sources were:
FL = 0.95 (TL) + 8.72 (n = 452, r^2 = 0.99)
SL = 0.83 (TL) – 3.59 (n = 450, r^2 = 0.97)
SL = 0.86 (FL) – 13.30 (n = 354, r^2 = 0.98)
$W= 5.94*10^{-6}(TL)^{3.1568}$ (n = 1911, r^2 =0.94).
For fish caught off eastern FL, the relationships between length measurements (mm) of fish caught off eastern FL by commercial fishermen were:
FL = 0.94 (TL) + 13.55 (n = 430, r^2 = 0.99)
SL = 0.82 (TL) – 6.49 (n = 430, r^2 = 0.98)
SL = 0.88 (FL) – 17.64 (n = 430, r^2 = 0.98). Weights were not recorded for fish landed off eastern FL.

<u>Age and growth</u>

Otoliths were obtained from 2,110 specimens that were caught with fishery dependent and fishery independent gear off NC/SC and 436 fish that were landed off eastern FL. Otolith radius and increment radius were measured for 1,030 otoliths from NC/SC and 344 from FL. Length distribution of fish selected for measurement did not differ significantly from the length distribution of all samples (KS, P>0.05). Marginal increment analysis showed that annual increments were deposited between July and August (Figure 7), therefore the age assigned to each specimen was equivalent to the number of increments observed. The assigned birth date for red grouper was July 1.

Initially the two readers agreed on the age of 54% of the red grouper sampled from NC/SC. An additional 38.6% of the counts differed only by one year. After an additional count by the primary reader, an age was assigned to 2,030 specimens (95% of the samples). Agreement between readers was much better for samples from FL (94%). A random sample of 100 otoliths was sent to Panama City NMFS. Agreement between readers at the Panama City Lab and SCDNR was 95%.

The relationship between otolith radius and fish length for NC/SC caught fish was approximately linear and was described by the following geometric mean regression:
TL = 226.076 * OR + 271.637 (n = 770, r = 0.73). The plane of the section in 289 otoliths presented some degree of inclination away from the dorso-ventral plane. These otoliths were not included in the TL-OR regression. Increments in

otoliths of fish 13 years and older were closely spaced and difficult to measure, and thus back-calculated lengths were obtained for ages 1-12 (Tables 2, 3).

Ages of fish caught off NC/SC from the commercial fishery ranged from 2 to 20 years, although no fish from 13 to 19 years old were collected. Fish sampled by MARMAP ranged in age between 2 and 10 years old (Figure 8). Red grouper caught off FL ranged in age from 1 to 14 years. The size at age was significantly smaller for fish caught with fishery independent gear between the ages of 2-4. Age 4 and 5 red grouper caught by commercial fishermen off NC/SC had a significantly smaller size at age than fish caught by commercial fishermen off FL. There was not a significant difference in the size at age for fish older than 5. Age length keys for fishery-independent and fishery-independent sources collected off NC/SC as well as FL fishery dependent samples are presented in Tables 5, 6 and 7.

The von Bertalanffy growth parameters for fish caught off NC/SC (fishery-dependent and fishery independent combined) estimated from back-calculated length with the mixed model design at age were L_∞ = 836.1 mm TL (SE = 7.08), K = 0.170 yr^{-1} (SE = 0.003), t_o = -1.278 (SE = 0.018), while the parameters obtained from observed length at age were L_∞ = 853.2 mm TL (SE = 3.81), K = 0.209 yr^{-1} (SE = 0.004), t_o = -0.812 (SE = 0.069).

The NLIN procedure and Marquardt's algorithm weighted by the inverse number of fish in each size class provided the following growth parameters for observed size at age:
NC/SC Fishery independent and fishery dependent combined
L_∞ = 859.8 mm TL (SE = 14.18), K = 0.207 yr^{-1} (SE = 0.027), t_o = -1.669 (SE = 0.611)

NC/SC Fishery independent only
L_∞ = 727.9 mm TL (SE = 19.94), K = 0.517 yr^{-1} (SE = 0.243), t_o = -1.109 (SE = 0.534)

NC/SC Fishery dependent only
L_∞ = 859.8 mm TL (SE = 15.25), K = 0.214 yr^{-1} (SE = 0.028), t_o = -1.549 (SE = 0.408)

FL Fishery dependent
L_∞ = 730.1 mm TL (SE = 22.37), K = 0.273 yr^{-1} (SE = 0.049), t_o = -1.415 (SE = 0.606)

Lee´s phenomenon, a decreasing trend in the mean length at age back-calculated from specimens of increasing age, was not observed (linear regression, $P > 0.05$). In addition, except for age 4, no significant differences were observed when comparing mean back-calculated length using all increments against mean back-calculated lengths using only the last increment for NC/SC caught fish. This indicates that the differences between mean observed and mean back-calculated lengths using all increments (Table 4) are explained by additional growth since the formation of the last increment.

Reproduction

Sex and developmental states were assigned to 2,068 specimens that were caught off NC/SC. Of these, 1,796 (86.8%) were classified as females, 121 (5.9%) as transitionals, and 151 (7.3 %) as males. Females ranged from 315 to 739 mm TL and 1 to 10 years old. Transitional individuals ranged from 455 to 744 mm TL and from 3 to 10 years old. Males were 509 to 851 mm TL and 3 to 20 years old. The mean length for females (546.5 mm TL, SD = 60.3) was significantly smaller than that for males (640.8 mm TL, SD = 77.2; KS P <0.001).

For fish caught off eastern FL, sex and maturity were determined for 418 fish. Females made up 75.1%, males 11.7% and transitionals 13.2%. Females ranged from 240 to 780 mmTL and 1 to 13 years old. Transitional individuals were 425 to 810 mm TL and 2 to 12 years old. Males were 600 to 840 mm TL and 3 to 14 years old. The mean size of females (580.5 mm TL; SD = 73.2) was significantly smaller than males (710.9 mm TL; SD = 61.2).

The sex ratio differed significantly from 1:1 in favor of females at ages 2 to 6 for all fish collected. In addition, throughout the southeast coast, females were significantly more abundant than males when TL<680 mm (Figure 9). Between ages 4 and 7, the mean length of males was significantly higher than the mean length of females for fish caught off NC/SC (Figure 10). Off eastern FL, males were significantly larger at ages 4 through 8.

For fish collected off NC/SC, age at 50% maturity was estimated as 2.36 years (probit analysis with normal link function, 95% CI = 1.77 - 2.74), and length at 50% maturity as 487.2 mm TL (probit analysis with normal link function, 95% CI = 481.9 -491.7). Off eastern FL, age at 50% maturity was 2.08 years (probit analysis with normal link function, 95% CI = -0.97 – 3.29), and length at 50% maturity as 529.22 mm TL (probit analysis with normal link function, 95% CI = 512.0 – 542.9).

The overlap in the length distributions of individuals classified as resting females and active females as well as the lack of overlap with immature fish indicated that the criteria used to differentiate resting females from immature females were adequate (Fig. 11). A number of inactive females mostly between 3 and 5 years old (n = 372) presented characteristics intermediate between immature and resting females, and their maturity could not be assessed.

Female individuals with hydrated oocytes, migratory nucleus oocytes or postovulatory follicles indicated that red grouper have a protracted spawning season, approximately 115 days long, from mid February to mid June for fish caught off NC/SC. There was a peak of spawning activity in April (Figure 12).

Postovulatory follicles were observed in females captured during March and June. Atretic oocytes were more common toward the end of the spawning period (May through July), although females with atretic oocytes were observed during most of the year. The distribution of GSI values also indicated that female red grouper spawn during the spring and early summer. Female GSI ranged from 0.03 to 8.20 (Figure 13), while male GSI ranged from 0.04 to 1.25 (Figure 13).

A greater percentage of females were in spawning condition off eastern FL than NC/SC. The spawning season for females was similar off NC/SC and FL. A much greater percentage of individuals were in late developing condition off FL than NC/SC and these individuals were collected for a longer period of time. The distribution of the GSI for female red grouper collected off eastern FL was similar to NC/SC (Figure 13).

Similar estimations of spawning frequency for fish caught off NC/SC (8.8 days, equivalent to 13 spawning events per season) were obtained if hydrated oocytes or postovulatory follicles were used as evidence of imminent or recent spawning (Table 9). Combining the frequencies of hydrated oocytes and migratory nucleus oocytes produced a higher spawning frequency (2.8 days, equivalent to 41 spawning events per season). Spawning frequency was not determined for fish caught off eastern FL due to small sample size. Red grouper in spawning condition were collected at depths of 33 to 90 m, however, spawning activity tended to occur in waters deeper than 40 m (Figure 14), where most of the active females, transitional individuals and males were found. In shallower water, most of the individuals captured were immature females, resting females, or inactive females of uncertain maturity. Spawning individuals of both sexes were captured along the North Carolina and South Carolina coast, and off the Florida Keys (Figure 15). Male red grouper have a longer season of reproductive activity than females (November to August).

Fish undergoing sex transition were found throughout the year with similar trends occurring for fish captured off NC/SC and eastern FL (Figure 16). The percentage of individuals was at a minimum during peak spawning in April-May. The number of fish undergoing sex transition gradually increased reaching a maximum during the summer when red grouper were not spawning. As fish starting developing in the fall, the percentage of transitional fish declined.

Fifty percent of the females caught off NC/SC changed sex at 7.24 years old (probit analysis with logistic link function, 95% CI = 6.92-7.66) and at 690.4 mm TL (probit analysis with logistic link function, 95% CI = 678.8-704.1). For fish caught off FL, fifty percent of the females changed sex at 8.26 years old (probit analysis with logistic link function, 95% CI = 7.3-10.09) and at 686.8 mm TL (probit analysis with logistic link function, 95% CI = 661.5-724.5). No immature females undergoing transition were observed.

Population dynamics

The catch curve on NC/SC fishery-dependent data obtained in 1998 (Figure 17) indicated that red grouper were not fully recruited to the fishery until age 4. For ages 4 and older, Z was 0.75. Red grouper caught off eastern FL were fully recruited to the gear at age 5. For ages 5 and older, Z was 0.64. Estimations of natural mortality using Pauly's (1980) equation ranged between 0.18 and 0.21. Using Ralston's (1987) equation, the estimated value of M was 0.37, while Jensen´s (1996) equation yielded an estimation of 0.28. If 20 years old is the maximum age of the stock off the Carolinas, the estimated value of M obtained with Hoenig´s (1983) equation is 0.22. For yield per recruit and spawning potential ratio analysis, an intermediate value of 0.2 was used.

Catch per unit effort indicated that older fish tended to be more abundant in deeper waters. Estimated age-specific release survival rates decreased with age (Table 10). One year old fish were only found in water shallower than 45 m, therefore release survival rate at this age was considered to be 95%.

If release mortality was considered negligible for NC/SC red grouper caught with fishery-dependent and fishery-independent gear, YPR was maximized by delaying harvest until 5 years old and applying a relatively high fishing mortality (Figure 18). Alternatively, if release mortality was included in the model for NC/SC red grouper caught with fishery-dependent and fishery-independent gear, red grouper yield per recruit was maximized if age at entry to the fishery (tc) was 4 years old, equivalent to a minimum legal size of 535 mm TL and fishing mortality rate was 0.4 (Figure 19). In addition, F_{max} and $F_{0.1}$ were maximized if harvest is delayed until red grouper are 4 year old (Table 11). Yield per recruit was also determined for individual data sets (NC/SC fishery-independent, NC/SC fishery-dependent, and FL fishery dependent) assuming that there was no release mortality (Figure 20).

Assuming that there was no release mortality and no sex ratio compensation then the SPR for females off NC/SC at an age of entry of 4 and F = 0.55, female SPR is 0.3 and male SPR is 0.1 (Figure 21). Under these same conditions, the SPR for fish caught off FL at an age at entry of 5 and F = 0.44, female SPR is 0.5 and male SPR is 0.2. When release mortality and sex ratio compensation were not included in the model, male spawning biomass decreased more rapidly than female spawning biomass for any combination of F and tc. If release mortality was included, both male and female spawning biomass decreased more rapidly (Figure 22). Under these conditions, male spawning biomass was particularly vulnerable to fishing mortality. Male and female SPR isopleths bent upward indicating that even at low F and tc there is a loss of spawning biomass due to release mortality. When release mortality and sex ratio compensation were included, male spawning biomass was more resilient to exploitation that female spawning biomass for any combination of F and tc (Figure 23), as individuals changed sex at smaller lengths translating any loss of male spawning biomass into a decrease in female spawning biomass.

The model with release mortality and sex ratio compensation behaved predictably to changes in M and k (Table 12). A lower value of natural mortality (M = 0.1) produced higher values of YPR and higher values of female and male spawning biomass per recruit. Female SPR and male SPR tended to decrease rapidly with increasing F and tc, indicating that the stock is more sensitive to exploitation at lower values of M. A higher value of natural mortality (M = 0.3) had the opposite effect, decreasing YPR and sex specific spawning biomass per recruit while female and male SPR tended to be higher. Increasing or decreasing the value of k by 10% produced similar results.

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Table 1. Histological criteria to assess sex and reproductive state in red grouper, *Epinephelus morio*, based in Moe (1969), McGovern et al. (1998) and Wyanski et al. (2000).

Reproductive state	Male	Female
Uncertain maturity	Inactive testes; unable to assess maturity.	Inactive ovaries with primary growth oocytes only; unable to assess maturity.
Immature	No immature males observed.	Primary growth oocytes only, no evidence of atresia. In comparison to resting females, most primary growth oocytes < 80 um, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, oogonia abundant along margin of lamellae, ovary wall is thinner.
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spematozoa in lobular lumina and ducts.	Predominance of oocytes with cortical alveoli formation through late vitellogenesis.
Developing, previous spawn		Developing stage as described above plus postovulatory follicles.
Running ripe	Predominance of spermatozoa; little or no occurrence of spematogenesis.	Completion of yolk coalescence and hydration in most advanced oocytes; zona radiata becomes thinner.
Spent	No spermatogenesis; some residual spermatozoa in lobules and ducts.	More than 50% of vitellogenic oocytes with alpha or beta atresia.

Table 2. (Continued)

Resting	Little or no spermatocyte development; empty lobules and sinuses.	Primary growth oocytes only; traces of atresia. In comparison with immature females, most primary growth oocytes >80 um, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongated and convoluted, oogonia less abundant along margin of lamellae, ovarian wall is thicker, melanomacrophage centers and/or foci of inflammatory cells may be present.
Transitional	Protogyny: testicular proliferation (mitotic spermatogonial development and possibly limited spermatogenesis) within lamellae of spent or resting ovaries and development of peripheral sinuses in musculature of ovarian wall.	
Mature specimen, state unknown.	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive state.	Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive stage.
Unknown	Postmortem histolysis or inadequate quantity of tissue prevent assessment of reproductive state.	Postmortem histolysis or inadequate quantity of tissue prevent assessment of reproductive state.

Table 2. Mean back-calculated total lengths (mm) at age for red grouper caught off NC/SC.

		Mean back calculated lengths at successive increments											
Age	N	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
2	2	226.1	310.3										
3	71	268.8	359.6	423.4									
4	471	266.4	360.0	425.7	485.8								
5	364	268.2	365.0	436.6	493.6	551.4							
6	68	279.4	370.9	443.0	503.0	563.8	616.1						
7	49	272.4	364.6	430.4	491.2	552.4	606.4	652.1					
8	15	272.0	355.8	418.9	477.5	541.2	593.2	639.6	686.0				
9	8	272.1	359.0	428.9	496.5	550.9	607.6	659.4	691.4	725.0			
10	5	236.5	316.0	379.6	437.0	503.9	545.3	580.7	618.1	656.9	681.9		
11	0												
12	3	219.5	320.5	391.7	469.1	527.2	567.1	611.2	645.3	679.9	707.3	732.4	765.8
n		1056	1054	983	983	512	148	80	31	16	13	3	3
Average		268.0	362.1	430.3	489.8	552.2	606.7	644.5	672.5	695.2	691.4	732.4	765.8

Table 3. Mean back-calculated total lengths (mm) at age for red grouper caught off eastern FL.

		Mean back calculated lengths at successive increments											
Age	N	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
2	5	385.4	449.9										
3	55	379.5	436.0	477.6									
4	58	405.4	458.1	504.6	544.3								
5	80	411.7	463.1	504.7	542.2	575.4							
6	59	418.7	472.8	513.6	550.9	584.0	613.8						
7	37	422.2	472.9	511.8	546.4	580.3	611.4	638.2					
8	29	410.2	458.8	491.9	523.4	552.4	579.8	606.8	630.6				
9	8	399.1	445.7	481.2	515.6	544.9	574.1	600.5	625.0	646.5			
10	6	421.4	474.1	508.6	541.4	571.0	600.9	631.4	659.1	688.2	711.0		
11	2	394.4	443.8	479.4	503.4	531.5	561.4	585.7	612.9	637.1	658.6	681.1	
12	1	443.3	498.7	548.2	596.1	636.3	667.1	688.4	711.8	738.7	761.4	780.0	795.4
n		342	340	335	280	222	142	83	46	17	9	3	1
Average		406.0	459.8	501.0	542.2	574.1	603.1	622.4	634.3	666.5	704.9	714.1	765.4

Table 3. Mean length at age. Comparison between back calculated lengths using all increments vs. using last increment for samples collected off NC/SC. ANOVA one way. Standard error uses a pooled estimate of error variance. * = P < 0.05.

Age	Back-calculated using all increments (standard error)		n	Back-calculated using last increment (standard error)		n	P
3	430.3	(1.00)	1054	423.4	(3.71)	71	0.0747
4	489.8	(1.21)	983	485.8	(1.54)	471	0.0333 *
5	552.2	(1.80)	512	551.4	(1.95)	364	0.7484
6	606.8	(3.66)	148	616.1	(5.47)	68	0.1570
7	644.5	(5.35)	80	652.1	(6.78)	49	0.3777
8	672.5	(8.62)	31	686.0	(12.06)	15	0.3635
9	695.2	(13.99)	16	725.0	(20.89)	8	0.2577
10	691.4	(34.27)	8	681.9	(45.19)	5	0.8719

Table 4. Mean length at age. Comparison between back-calculated lengths using all increments vs. observed lengths for samples collected off NC/SC. One way ANOVA. Standard error uses a pooled estimate of error variance. * = P< 0.05.

Age	Back-calculated using all increments (SE)		n	Observed (SE)		n	P	
3	430.3	(1.00)	1054	490.2	(2.19)	221	<0.0001	*
4	489.8	(1.21)	983	531.0	(1.26)	930	<0.0001	*
5	552.2	(1.80)	512	579.4	(1.67)	598	<0.0001	*
6	606.8	(3.66)	148	663.4	(3.65)	149	<0.0001	*
7	644.5	(5.35)	80	680.8	(5.72)	70	<0.0001	*
8	672.5	(8.62)	31	711.2	(9.60)	25	0.0040	*
9	695.2	(13.99)	16	751.6	(16.87)	11	0.0164	*
10	691.4	(34.27)	8	734.1	(34.27)	8	0.3932	

Table 5. Age length keys for red grouper from fishery-independent samples collected off NC/SC (1996-2000). Age 12+ is a combination of ages 12-20.

		Age (years)										
Length class (mm TL)	Number	2	3	4	5	6	7	8	9	10	11	12+
301-320	3	0.33	0.67	0	0	0	0	0	0	0	0	0
321-340	1	1	0	0	0	0	0	0	0	0	0	0
341-360	5	0.4	0.6	0	0	0	0	0	0	0	0	0
361-380	2	0.5	0.5	0	0	0	0	0	0	0	0	0
381-400	4	0	1	0	0	0	0	0	0	0	0	0
401-420	6	0	0.67	0.33	0	0	0	0	0	0	0	0
421-440	8	0.13	0.13	0.75	0	0	0	0	0	0	0	0
441-460	12	0	0.08	0.92	0	0	0	0	0	0	0	0
461-480	20	0	0.10	0.90	0	0	0	0	0	0	0	0
481-500	16	0	0.06	0.94	0	0	0	0	0	0	0	0
501-520	17	0	0	0.65	0.35	0	0	0	0	0	0	0
521-540	10	0	0	0.70	0.30	0	0	0	0	0	0	0
541-560	14	0	0	0.21	0.79	0	0	0	0	0	0	0
561-580	11	0	0	0	0.91	0.09	0	0	0	0	0	0
581-600	10	0	0	0.20	0.70	0.10	0	0	0	0	0	0
601-620	5	0	0	0	0.40	0.60	0	0	0	0	0	0
621-640	12	0	0	0.17	0.33	0.17	0.33	0	0	0	0	0
641-660	13	0	0	0	0.62	0.38	0	0	0	0	0	0
661-680	12	0	0	0	0.42	0.42	0.17	0	0	0	0	0
681-700	10	0	0	0	0.30	0.20	0.30	0.20	0	0	0	0
701-720	9	0	0	0	0.22	0.22	0.56	0	0	0	0	0
721-740	2	0	0	0	0	0.50	0	0.50	0	0	0	0
741-760	3	0	0	0	0	0	0.33	0.33	0	0.33	0	0
761-780	1	0	0	0	0	0	0	1	0	0	0	0
Total	206											

Table 6. Age length keys for red grouper from fishery-dependent samples (1996-2000). Age 12+ is a combination of ages 12-20.

		Age (years)										
Length class (mm TL)	Number	2	3	4	5	6	7	8	9	10	11	12+
301-320	0	0	0	0	0	0	0	0	0	0	0	0
321-340	0	0	0	0	0	0	0	0	0	0	0	0
341-360	0	0	0	0	0	0	0	0	0	0	0	0
361-380	0	0	0	0	0	0	0	0	0	0	0	0
381-400	1	0	0	1	0	0	0	0	0	0	0	0
401-420	0	0	0	0	0	0	0	0	0	0	0	0
421-440	0	0	0	0	0	0	0	0	0	0	0	0
441-460	7	0.14	0.29	0.57	0	0	0	0	0	0	0	0
461-480	85	0	0.45	0.53	0.02	0	0	0	0	0	0	0
481-500	230	0	0.38	0.55	0.05	0	0	0	0	0	0	0
501-520	243	0	0.19	0.67	0.13	0	0	0	0	0	0	0
521-540	241	0	0.05	0.69	0.25	0	0	0	0	0	0	0
541-560	232	0	0.05	0.59	0.35	0	0	0	0	0	0	0
561-580	190	0	0.01	0.50	0.48	0.01	0	0	0	0	0	0
581-600	174	0	0.02	0.39	0.57	0.02	0	0.01	0	0	0	0
601-620	132	0	0	0.24	0.69	0.05	0.02	0	0	0	0	0
621-640	55	0	0	0.07	0.65	0.18	0.07	0.02	0	0	0	0
641-660	49	0	0	0.04	0.37	0.43	0.16	0	0	0	0	0
661-680	52	0	0	0.06	0.15	0.52	0.25	0.02	0	0	0	0
681-700	43	0	0	0.07	0.05	0.6	0.19	0.09	0	0	0	0
701-720	37	0	0	0.03	0	0.57	0.24	0.14	0.03	0	0	0
721-740	18	0	0	0	0.11	0.22	0.28	0.22	0.11	0.06	0	0
741-760	15	0	0	0.07	0.07	0.07	0.07	0.20	0.33	0.20	0	0
761-780	5	0	0	0	0	0	0.60	0.20	0.20	0	0	0
781-800	5	0	0	0	0	0	0	0	0.40	0.20	0	0.4
801-820	3	0	0	0	0	0	0	0	0	0	0.33	0.67
821-840	2	0	0	0	0	0	0	0	0	0.50	0	0.50
841-860	1	0	0	0	0	0	0	0	0	0	0	1
Total	1828											

Table 8. Age length keys for red grouper from FL fishery-dependent samples. Age 12+ is a combination of ages 12-14.

		Age (years)										
Length class (mm TL)	Number	2	3	4	5	6	7	8	9	10	11	12+
301-320	0	0	0	0	0	0	0	0	0	0	0	0
321-340	0	0	0	0	0	0	0	0	0	0	0	0
341-360	0	0	0	0	0	0	0	0	0	0	0	0
361-380	0	0	0	0	0	0	0	0	0	0	0	0
381-400	0	0	0	0	0	0	0	0	0	0	0	0
401-420	0	0	0	0	0	0	0	0	0	0	0	0
421-440	4	0.25	0.75	0	0	0	0	0	0	0	0	0
441-460	9	0.22	0.78	0	0	0	0	0	0	0	0	0
461-480	6	0	1.0	0	0	0	0	0	0	0	0	0
481-500	20	0	0.55	0.30	0.15	0	0	0	0	0	0	0
501-520	35	0.06	0.23	0.29	0.31	0.03	0	0.09	0	0	0	0
521-540	36	0.03	0.19	0.25	0.31	0.17	0	0.03	0.03	0	0	0
541-560	21	0	0.14	0.29	0.19	0.14	0.24	0	0	0	0	0
561-580	34	0	0.12	0.29	0.32	0.12	0.09	0.06	0	0	0	0
581-600	32	0	0.06	0.28	0.31	0.22	0.06	0.03	0	0	0.03	0
601-620	32	0	0	0.13	0.28	0.31	0.13	0.13	0.03	0	0	0
621-640	36	0	0.03	0.08	0.44	0.25	0.08	0.08	0.03	0	0	0
641-660	24	0	0	0.13	0.21	0.29	0.04	0.13	0.21	0	0	0
661-680	43	0	0.02	0.07	0.26	0.16	0.07	0.16	0.21	0.02	0	0.02
681-700	24	0	0	0.04	0.21	0.17	0.29	0.25	0	0.04	0	0
701-720	19	0	0	0	0.16	0.26	0.26	0.16	0.05	0.11	0	0
721-740	8	0	0	0	0.13	0.25	0.38	0.13	0.13	0	0	0
741-760	10	0	0	0	0	0.40	0.40	0	0.10	0.10	0	0
761-780	7	0	0	0	0	0.14	0.29	0.14	0.14	0.29	0	0
781-800	4	0	0	0.25	0	0.25	0	0	0	0.25	0.25	0
801-820	4	0	0	0	0	0	0.25	0.25	0.25	0	0	0.25
821-840	2	0	0	0	0	0	0	0.50	0	0	0	0.50
Total	410											

Table 9. Spawning frequency estimations. Active females include late development, spawning and spent females. The number of spawning events per season was calculated assuming that females spawn continuously during a 115 day long spawning season.

Month	Active females	HO	MNO	HO+MNO	<24 h old POF
Feb	9	0	2	2	0
Mar	6	1	3	4	1
Apr	17	4	8	12	1
May	19	2	0	2	3
Jun	37	3	9	12	5
Total	88	10	22	32	10
Spawning frequency		8.80		2.75	8.80
Number of spawning events per season		10.6		41.8	10.6

Table 10. Estimation of age-specific release survival rates. Relative catch per unit effort (CPUE) is the fraction of the age-specific CPUE in each depth range. Depth- and age-specific survival rates are obtained multiplying age-specific CPUE by the depth-specific survival rates.

	Depth range (m)		
	<45	45-65	>65
	Effort (number of traps)		
	1986	907	112

Age	Catch in number		
2	10	0	0
3	27	1	0
4	97	1	2
5	54	11	7
6	14	3	5
7+	12	3	6

Age	Relative CPUE		
2	1.00	0.00	0.00
3	0.92	0.08	0.00
4	0.72	0.02	0.26
5	0.27	0.12	0.61
6	0.13	0.06	0.81
7+	0.10	0.05	0.85

	Depth specific release survival rate			Age-specific survival rate
Age	0.95	0.45	0	
2	0.95	0.00	0.00	0.95
3	0.88	0.03	0.00	0.91
4	0.68	0.01	0.00	0.69
5	0.25	0.05	0.00	0.31
6	0.12	0.03	0.00	0.15
7+	0.09	0.02	0.00	0.11

Table 11. Yield per recruit based reference points. F_{max} = fishing mortality that maximizes yield per recruit at age of entry (tc). $F_{0.1}$ = fishing mortality where the slope of the yield curve is 0.1 of the original value.

tc	Release mortality		No release mortality	
	F_{max}	$F_{0.1}$	F_{max}	$F_{0.1}$
1	0.23	0.15	0.23	0.16
2	0.27	0.17	0.28	0.18
3	0.35	0.20	0.39	0.21
4	0.40	0.22	0.67	0.25
5	0.33	0.21	1.00	0.31
6	0.26	0.18	1.00	0.35
7	0.21	0.16	1.00	0.40
8	0.18	0.14	1.00	0.46
9	0.16	0.13	1.00	0.53
10	0.14	0.12	1.00	0.62

Table 12. Sensitivity analysis of the yield per recruit (YPR) and spawning potential ratio (SPR) model. Values indicate percent change on the output values as compared with YPR, sex-specific spawning biomass per recruit (SBPR) and SPR calculated with M=0.2 and k=0.1697

Percent change on the output values

M=0.1

F	tc	YPR	Female SBPR	Male SBPR	Female SPR	Male SPR
0	0		118.54	192.96		
0.2	3	89.76	111.90	73.92	-3.04	-40.63
0.2	5	118.20	113.10	73.96	-2.49	-40.62
0.2	7	152.48	114.45	75.52	-1.87	-40.09
0.4	3	65.46	79.70	56.02	-17.77	-46.74
0.4	5	95.24	83.38	58.02	-16.09	-46.06
0.4	7	130.64	86.71	59.19	-14.57	-45.66
0.6	3	52.78	62.26	45.19	-25.75	-50.44
0.6	5	81.99	71.21	44.19	-21.66	-50.78
0.6	7	116.20	74.72	46.23	-20.05	-50.09

M=0.3

F	tc	YPR	Female SBPR	Male SBPR	Female SPR	Male SPR
0	0		-58.72	-44.28		
0.2	3	-42.85	-48.99	-38.31	23.57	10.71
0.2	5	-51.16	-49.16	-38.81	23.14	9.82
0.2	7	-58.37	-49.75	-38.79	21.73	9.85
0.4	3	-36.48	-41.09	-32.96	42.69	20.30
0.4	5	-46.60	-43.44	-32.49	37.01	21.16
0.4	7	-55.03	-44.53	-32.83	34.37	20.54
0.6	3	-32.43	-37.27	-27.54	51.94	30.03
0.6	5	-43.52	-39.41	-29.17	46.76	27.11
0.6	7	-52.52	-40.86	-29.62	43.25	26.30

Table 12. Continued.

Percent change on the output values

k increased 10%

F	tc	YPR	Female SBPR	Male SBPR	Female SPR	Male SPR
0	0		14.11	9.62		
0.2	3	15.60	17.40	12.74	2.89	2.85
0.2	5	12.99	16.96	12.45	2.50	2.59
0.2	7	10.73	16.78	12.32	2.34	2.46
0.4	3	17.57	19.09	15.61	4.37	5.46
0.4	5	14.39	18.37	14.94	3.73	4.86
0.4	7	11.74	18.11	14.65	3.51	4.60
0.6	3	18.81	19.98	17.66	5.15	7.34
0.6	5	15.32	19.16	16.62	4.42	6.39
0.6	7	12.50	18.86	16.21	4.16	6.02

k decreased 10%

F	tc	YPR	Female SBPR	Male SBPR	Female SPR	Male SPR
0	0		-14.49	-10.73		
0.2	3	-15.68	-17.12	-13.39	-3.08	-2.98
0.2	5	-13.65	-16.79	-13.16	-2.69	-2.73
0.2	7	-11.78	-16.64	-13.05	-2.52	-2.60
0.4	3	-17.23	-18.40	-15.72	-4.57	-5.59
0.4	5	-14.83	-17.86	-15.21	-3.95	-5.02
0.4	7	-12.68	-17.67	-14.98	-3.72	-4.77
0.6	3	-18.17	-19.05	-17.31	-5.34	-7.37
0.6	5	-15.59	-18.45	-16.54	-4.64	-6.51
0.6	7	-13.33	-18.23	-16.23	-4.38	-6.16

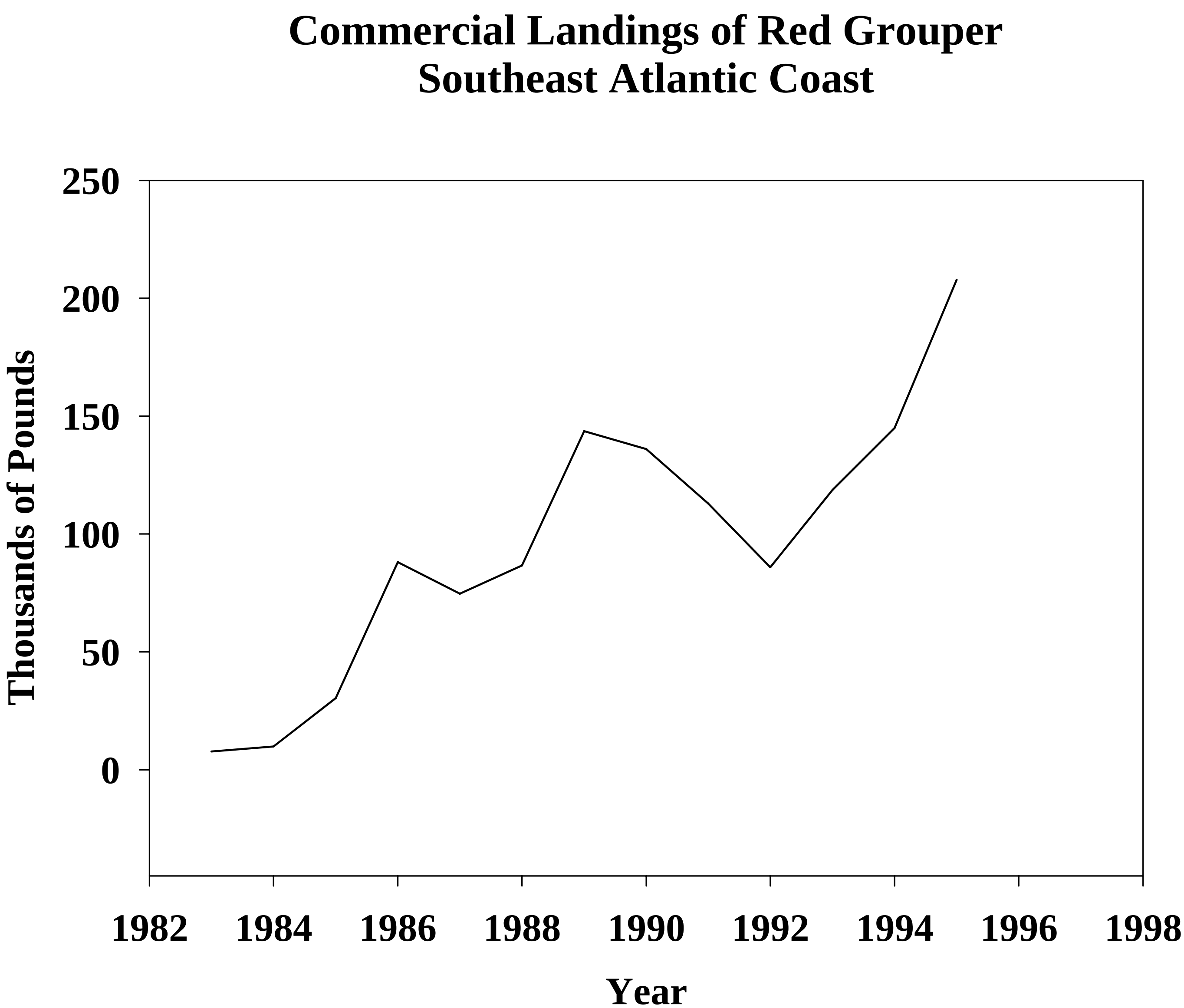

Commercial Landings of Red Grouper
Southeast Atlantic Coast
Thousands of Pounds
250
200
150
100
50
0
1982
1984
1986
1988
1990
1992
1994
1996
1998
Year

Figure 1

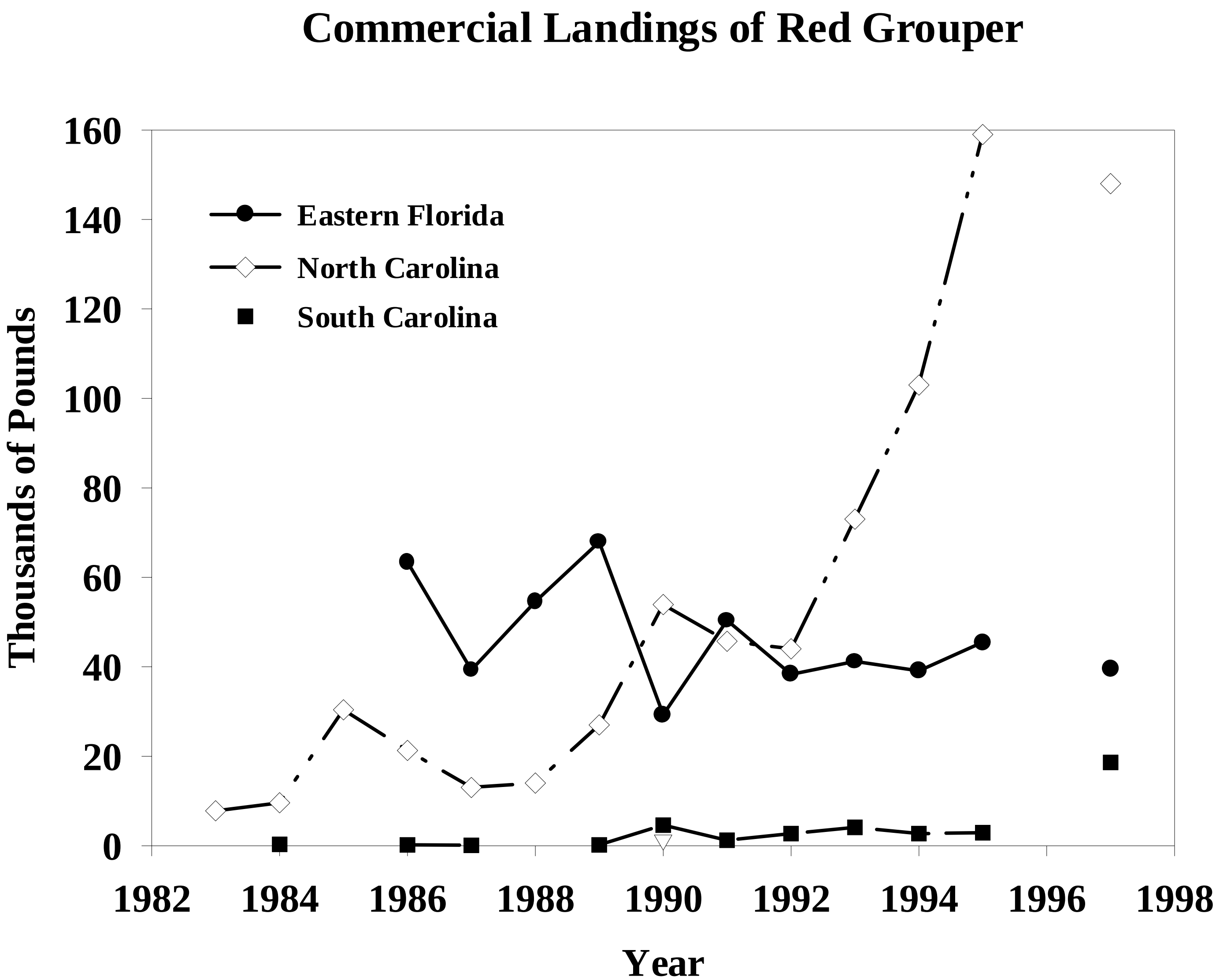
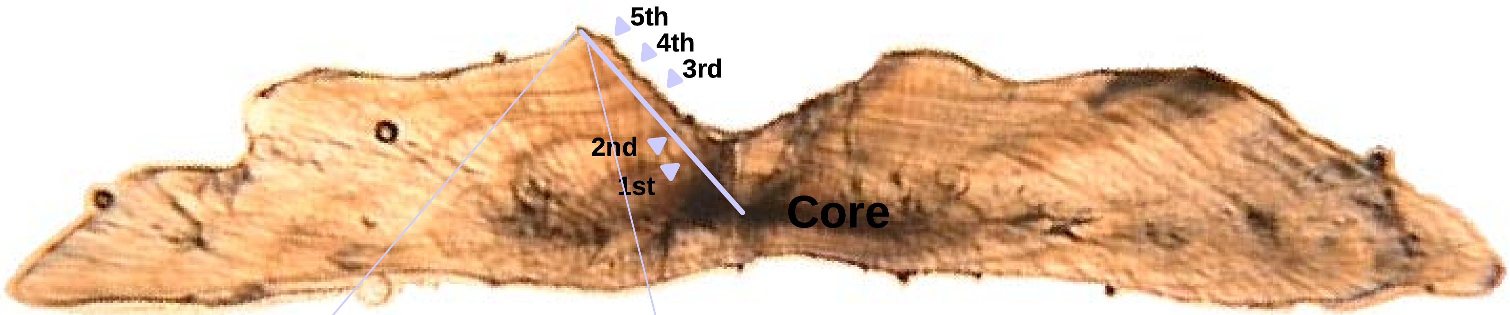
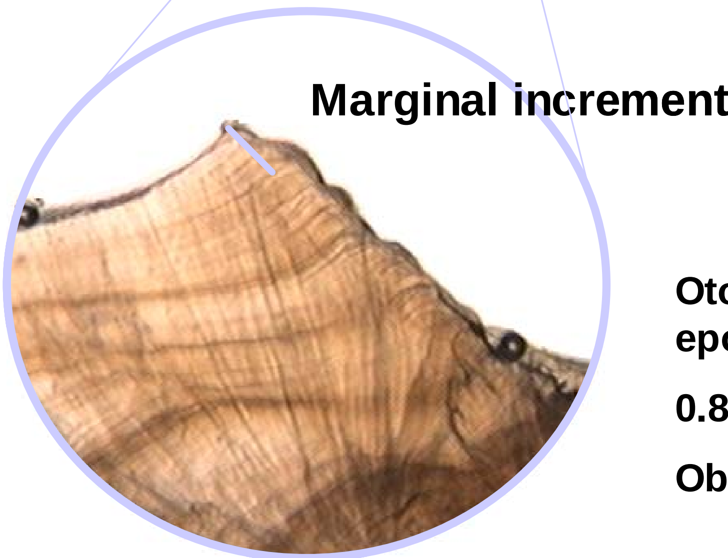

Commercial Landings of Red Grouper
Eastern Florida
North Carolina
South Carolina
Thousands of Pounds
0
20
40
60
80
100
120
140
160
1982
1984
1986
1988
1990
1992
1994
1996
1998
Year

Figure 2

Red grouper otolith





Otoliths embedded in transparent epoxi resin.

0.8 mm sections through the core

Observed under transmited light

Figure 3

Fishery Dependent Collection Sites

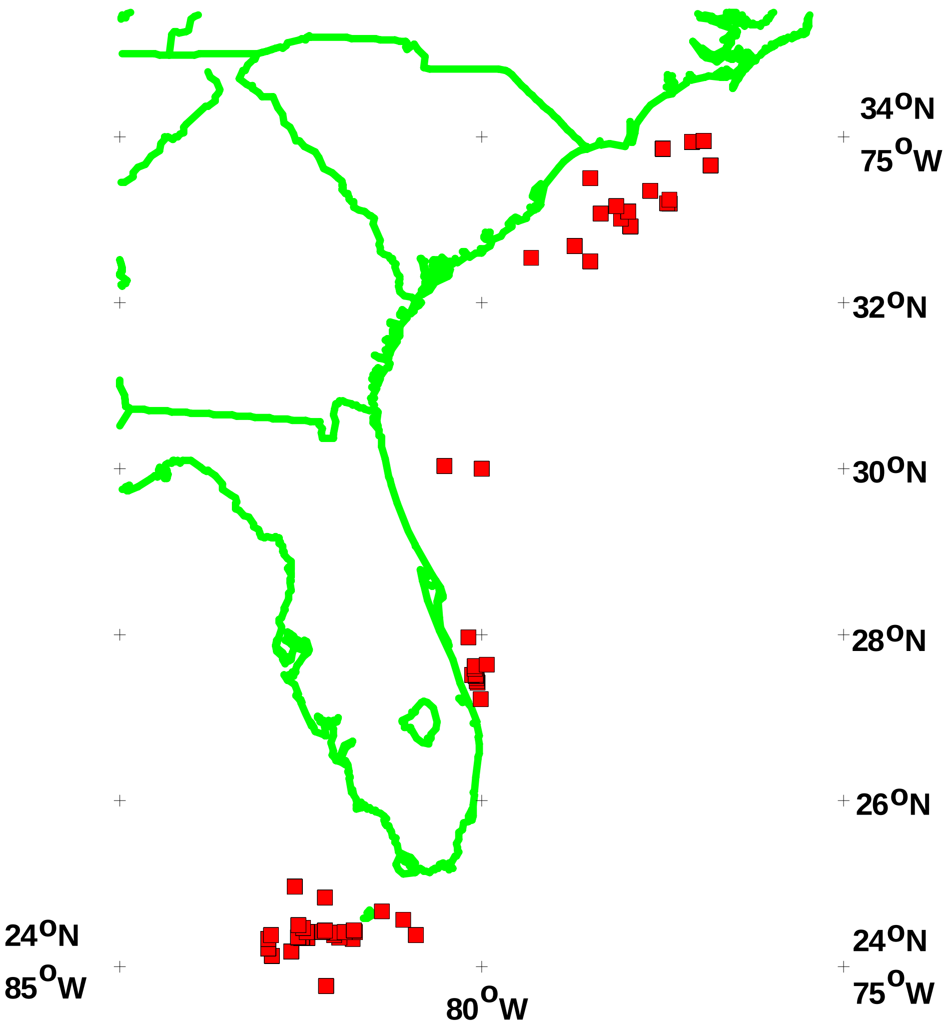


Figure 4

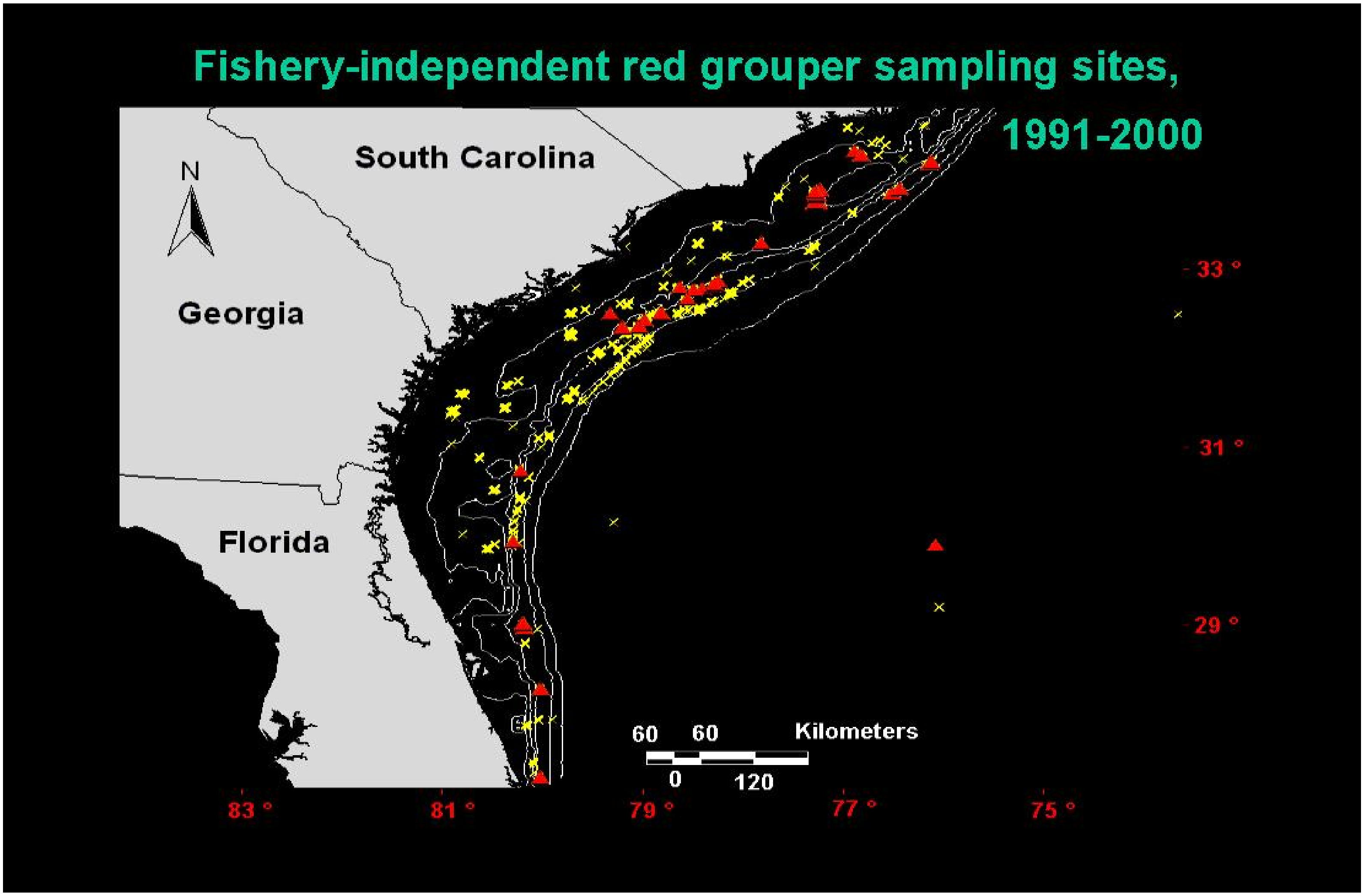

Fishery-independent red grouper sampling sites,
1991-2000
South Carolina
N
Georgia
Florida
33 °
31 °
29 °
60 60 Kilometers
0 120
83 °
81 °
79 °
77 °
75 °

Figure 5

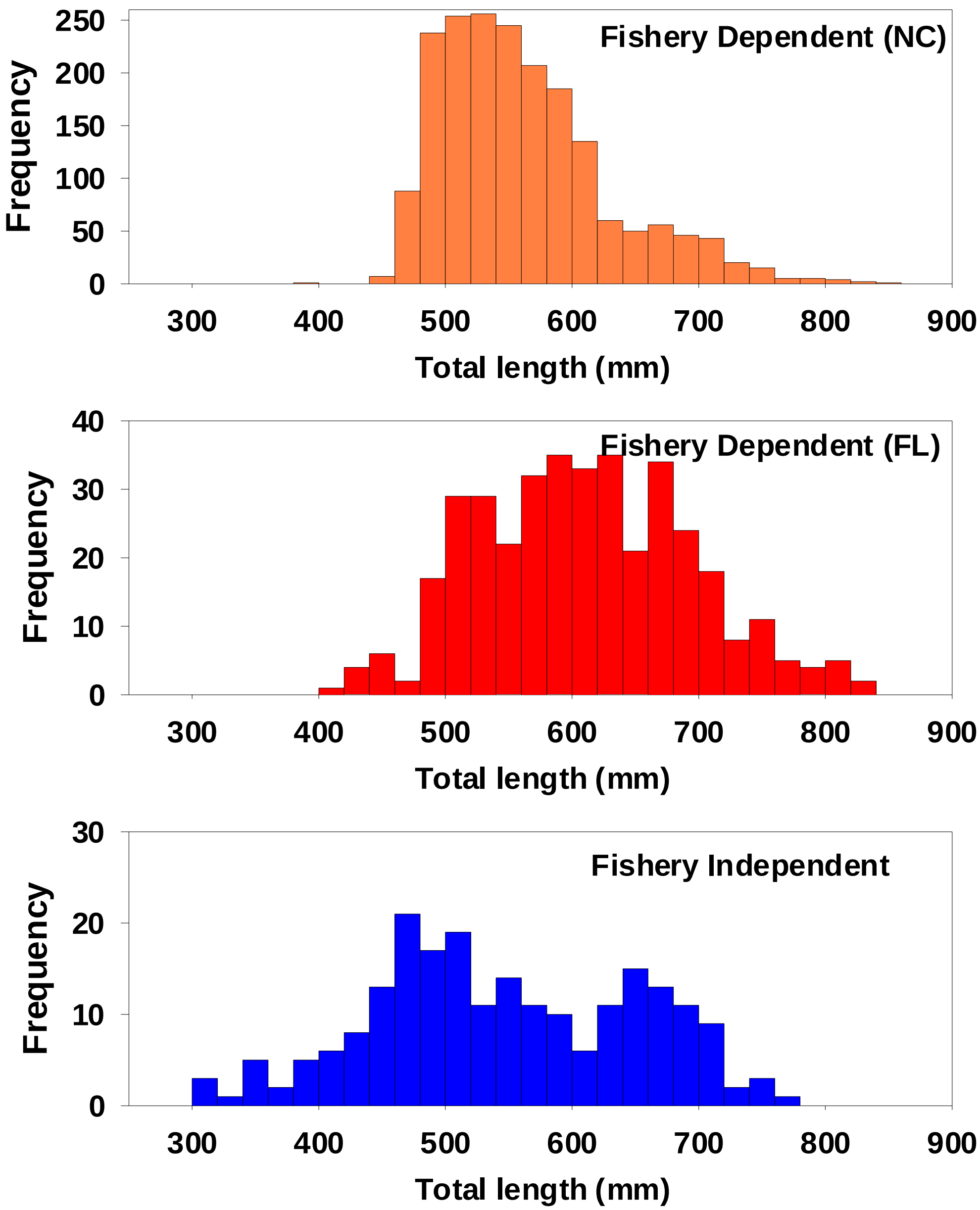

Fishery Dependent (NC)
Frequency
250
200
150
100
50
0
300
400
500
600
700
800
900
Total length (mm)
Fishery Dependent (FL)
Frequency
40
30
20
10
0
300
400
500
600
700
800
900
Total length (mm)
Fishery Independent
Frequency
30
20
10
0
300
400
500
600
700
800
900
Total length (mm)

Figure 6

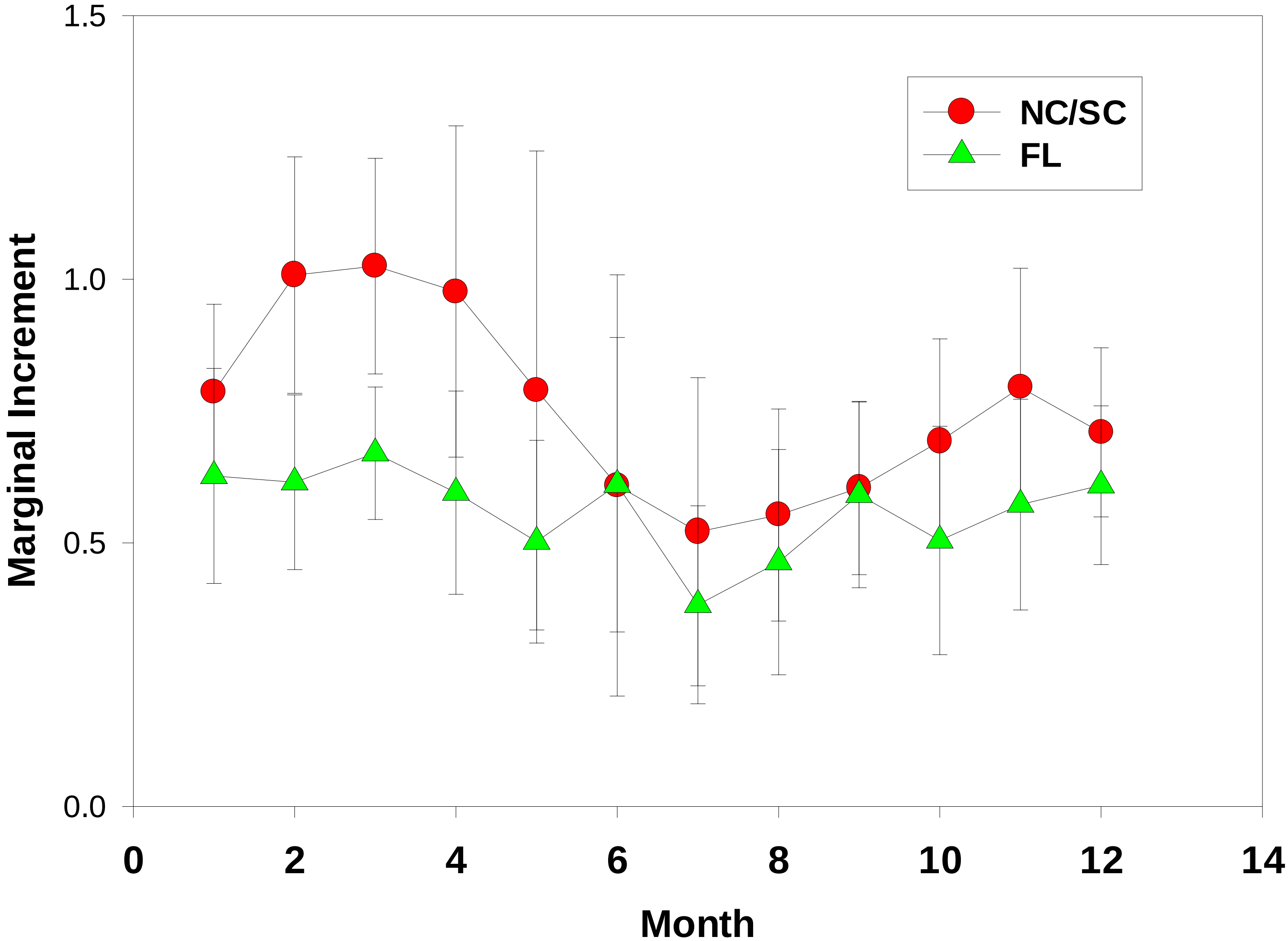


Figure 7

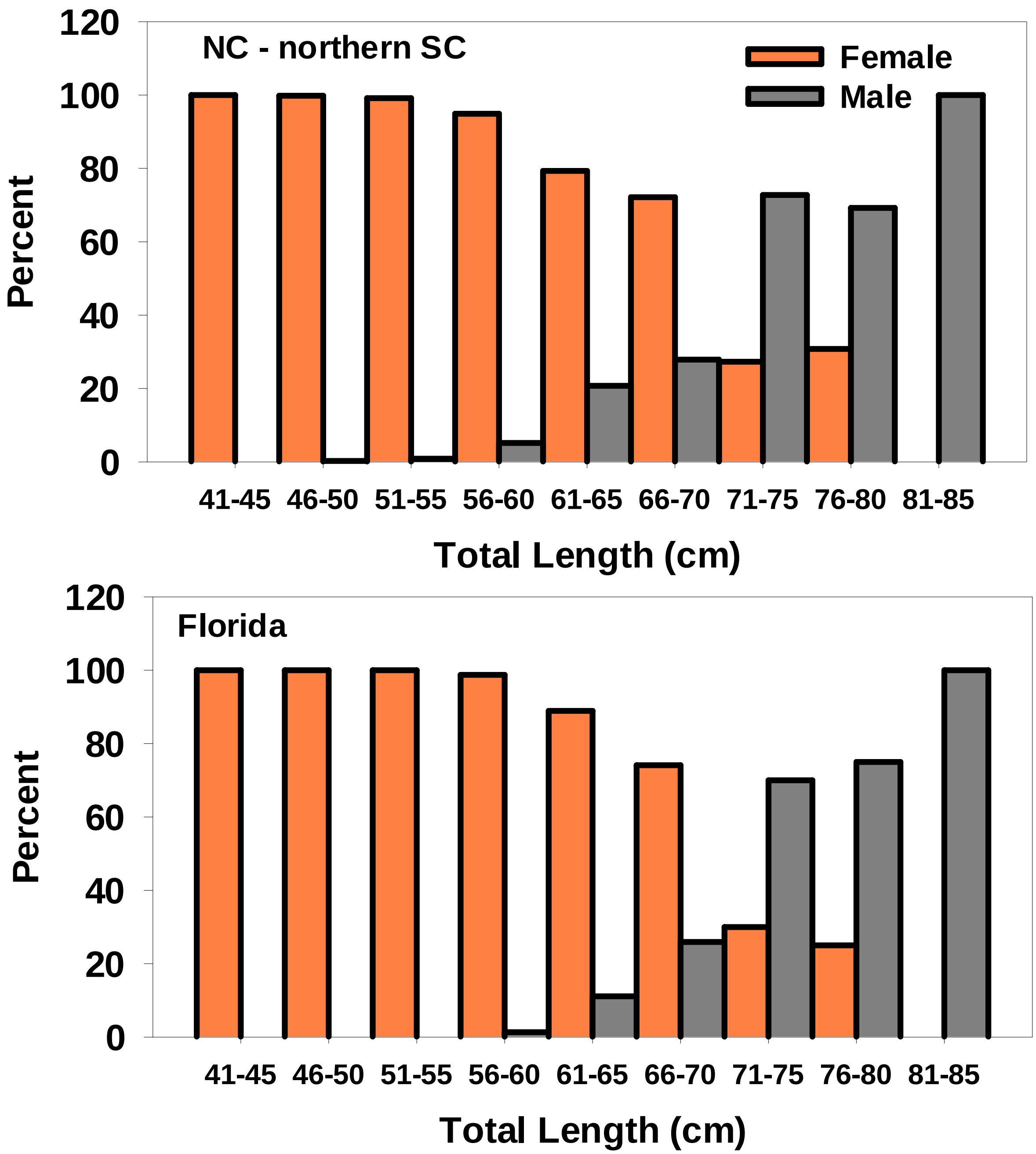
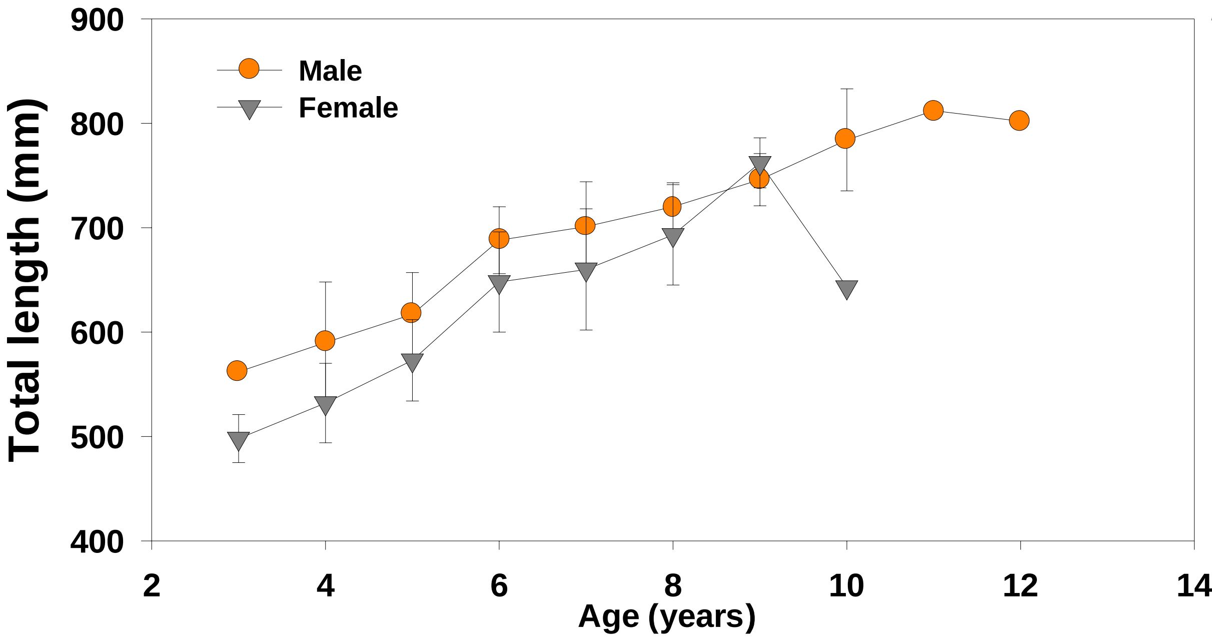

NC - northern SC
Female
Male
Percent
120
100
80
60
40
20
0
41-45 46-50 51-55 56-60 61-65 66-70 71-75 76-80 81-85
Total Length (cm)
Florida
Percent
120
100
80
60
40
20
0
41-45 46-50 51-55 56-60 61-65 66-70 71-75 76-80 81-85
Total Length (cm)

Figure 9


900
800
700
600
500
400
Total length (mm)
Male
Female
2
4
6
8
10
12
14
Age (years)

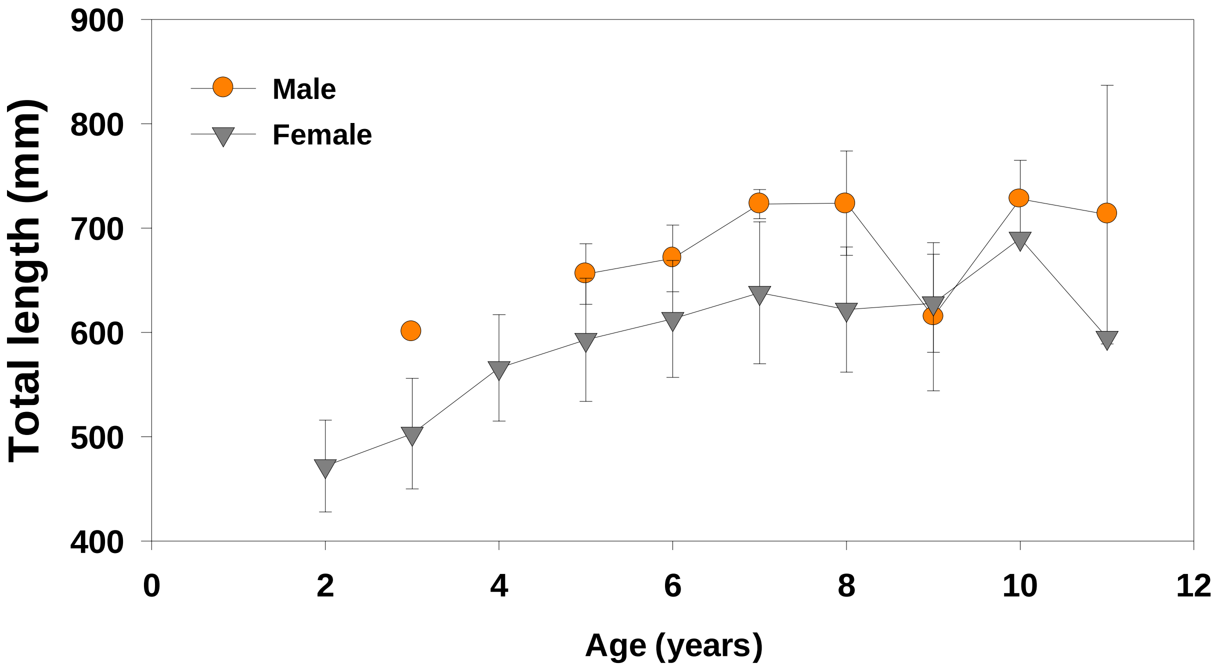

900
800
700
600
500
400
Total length (mm)
Male
Female
0
2
4
6
8
10
12
Age (years)

Figure 10

Frequency of Immature, Resting and Active

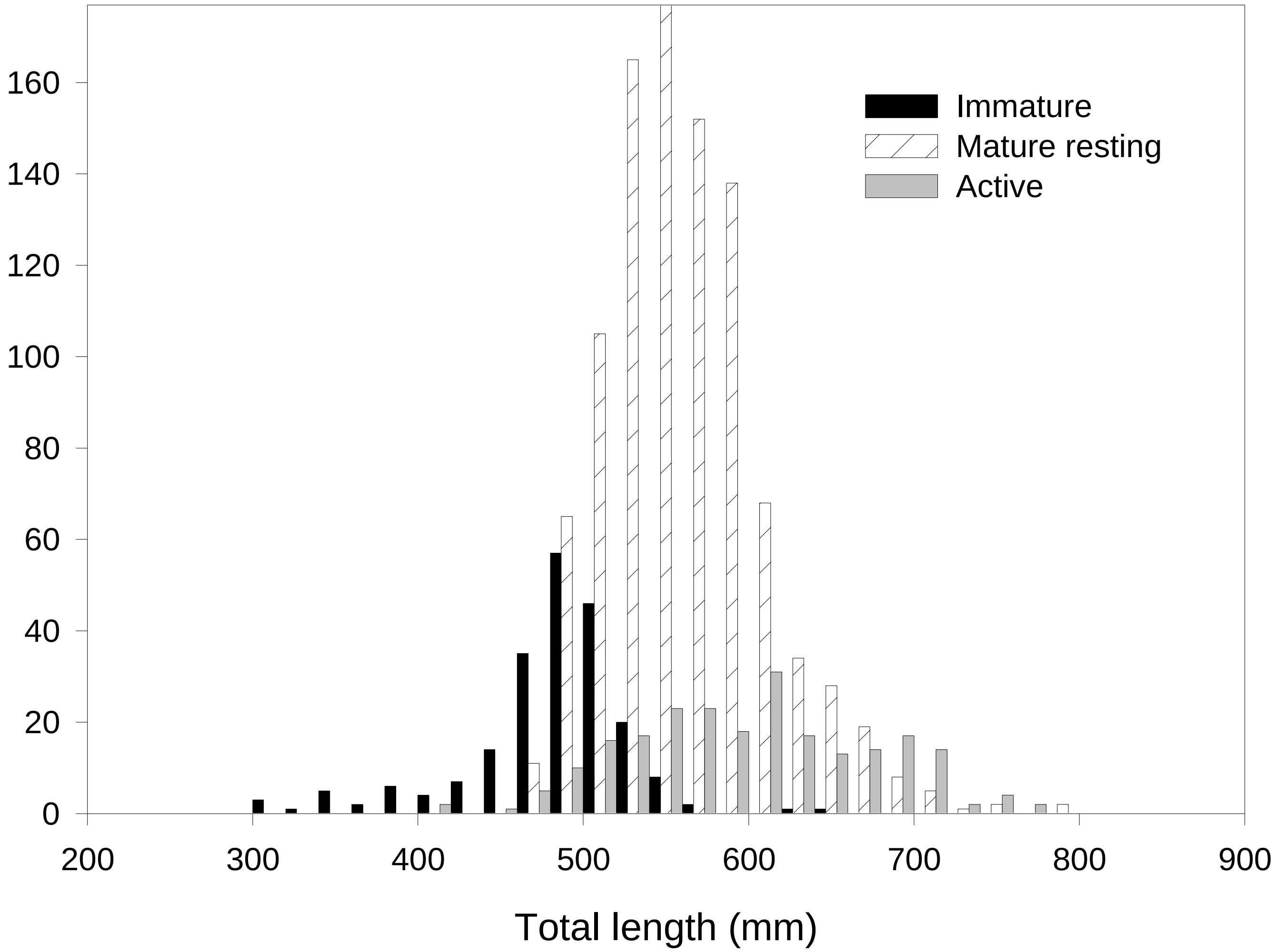
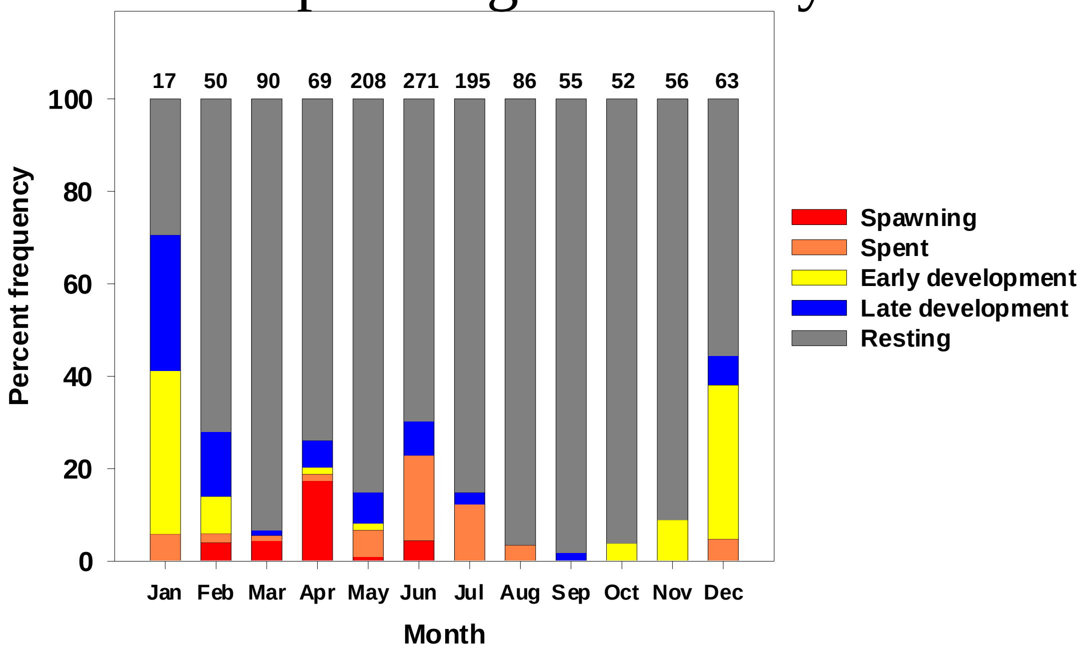


Figure 11

Female Spawning Seasonality

NC/SC



FL

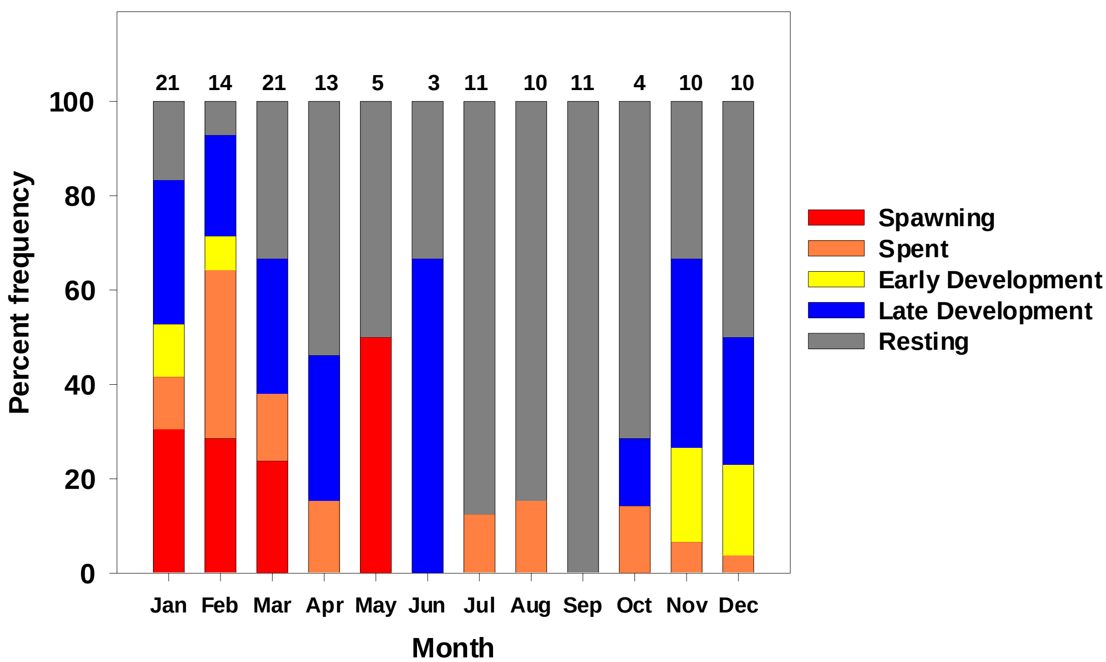
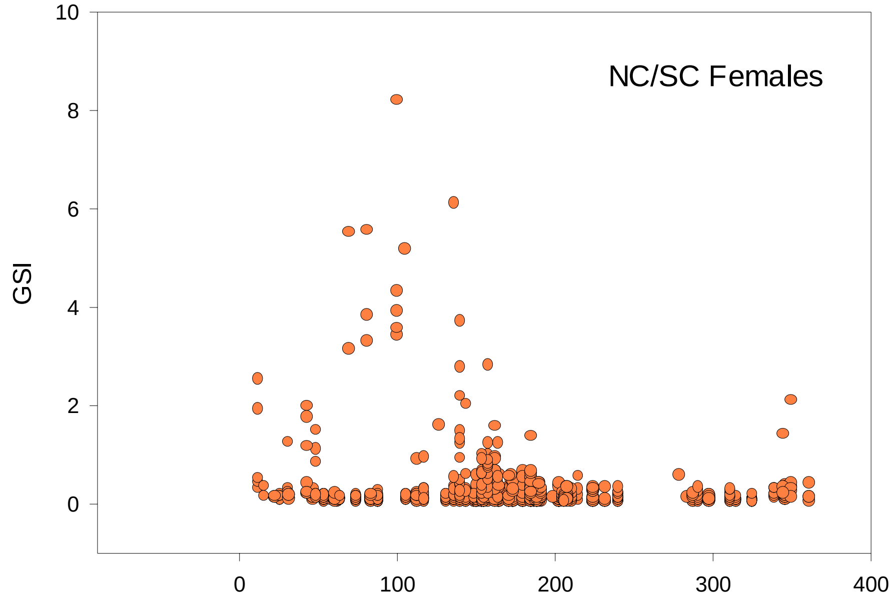


Figure 12

Gonadosomatic Index for Females



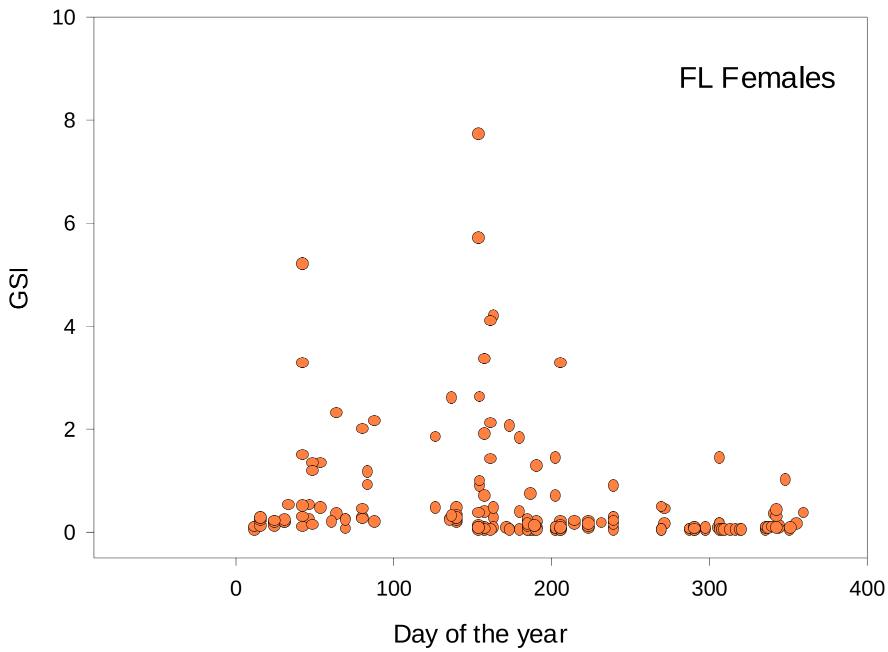


Figure 13

Distribution of Sex and Maturity Stages with Depth for Red Grouper Caught with Fishery-Independent Gear off NC/SC

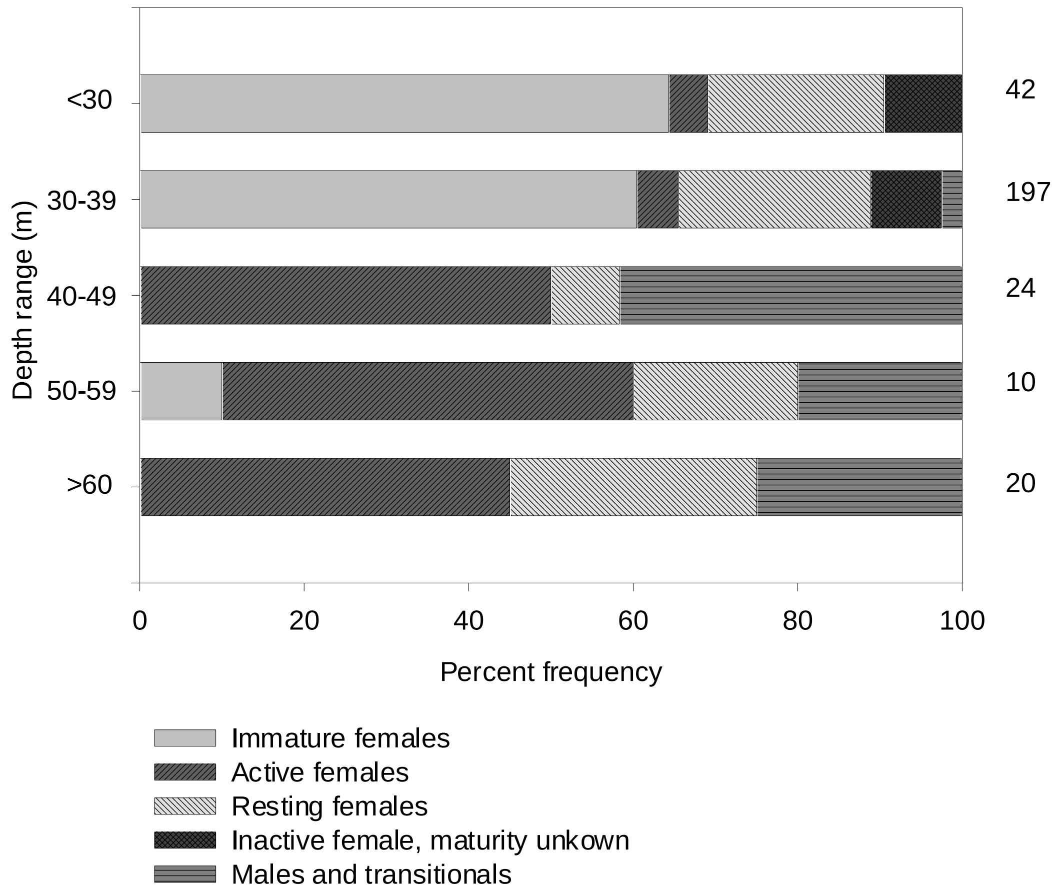


Figure 14

Spawning Locations of Red Grouper

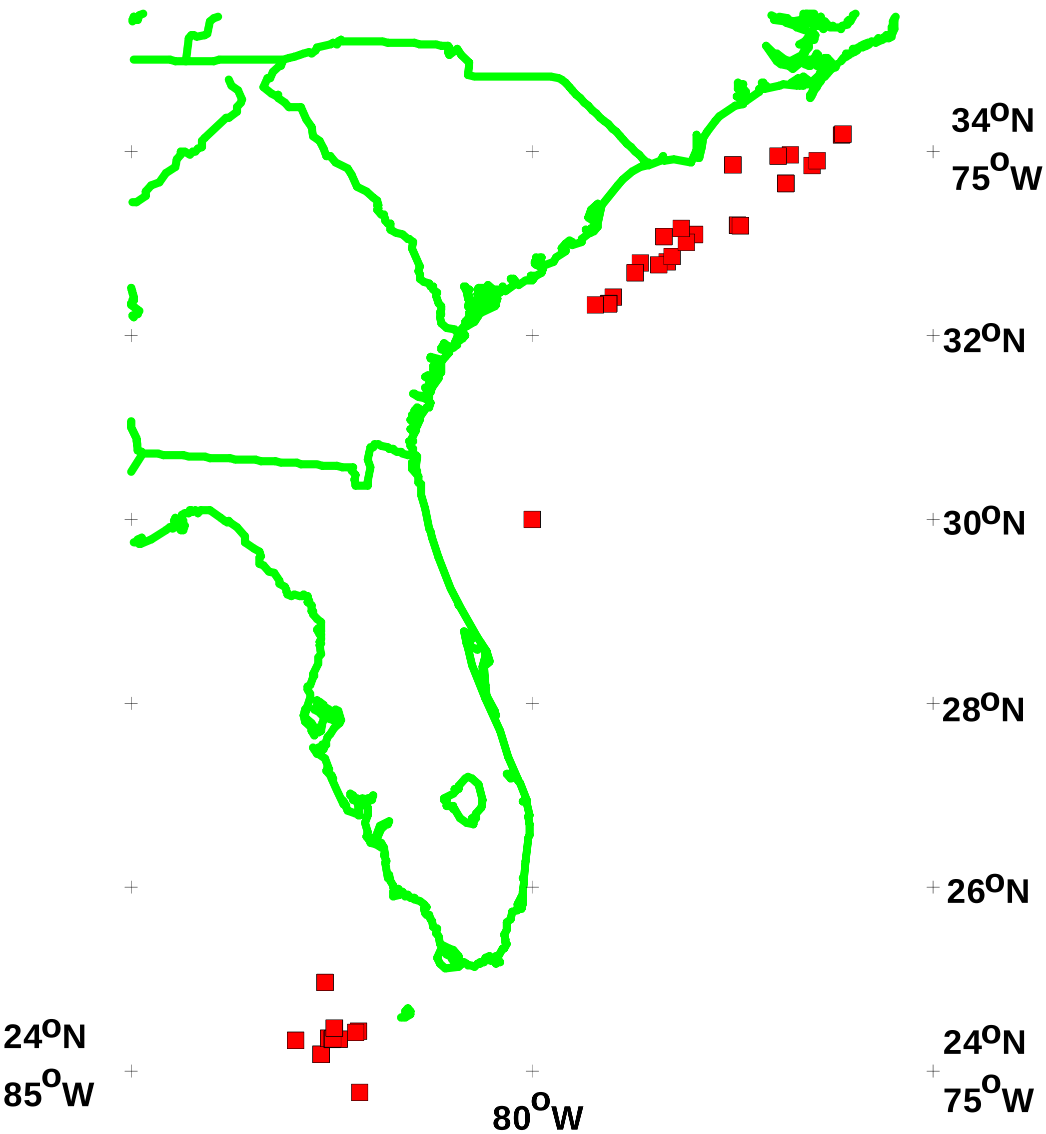


Figure 15

Monthly Distribution of Fish Undergoing Transition

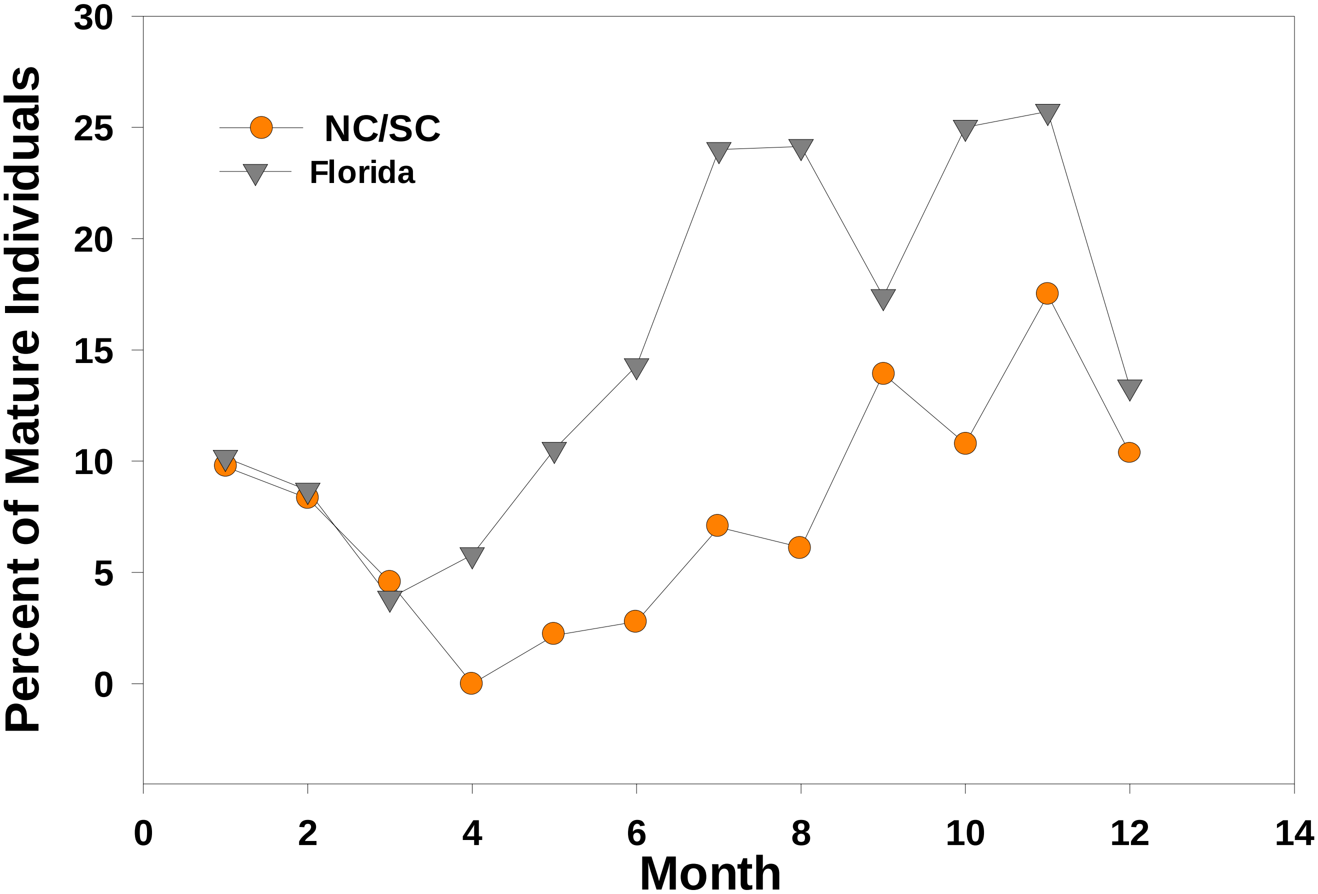
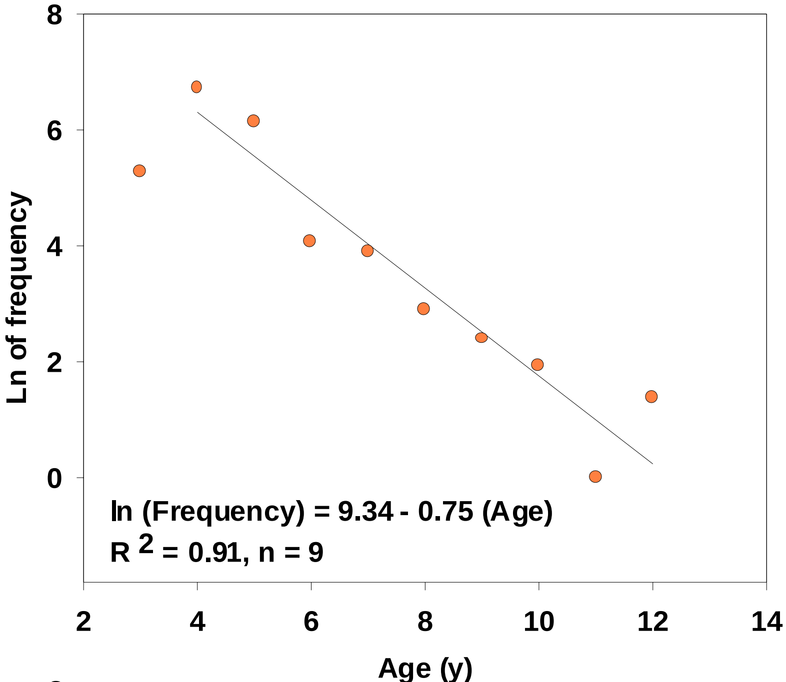


Figure 16

Catch Curve Analysis for Red Grouper Caught off NC/SC and FL

C.



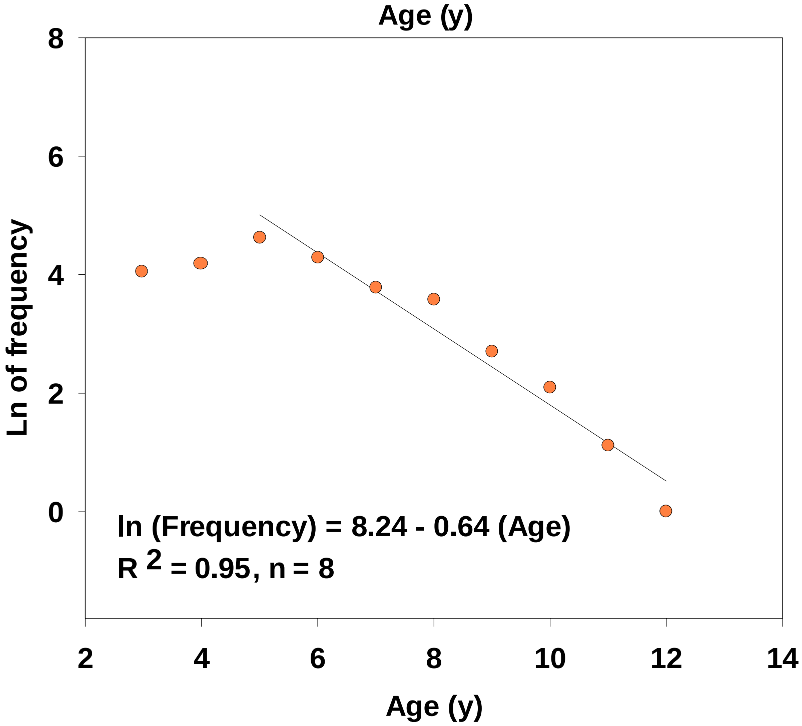


Figure 17

YPR for NC/SC Assuming no Release Mortality

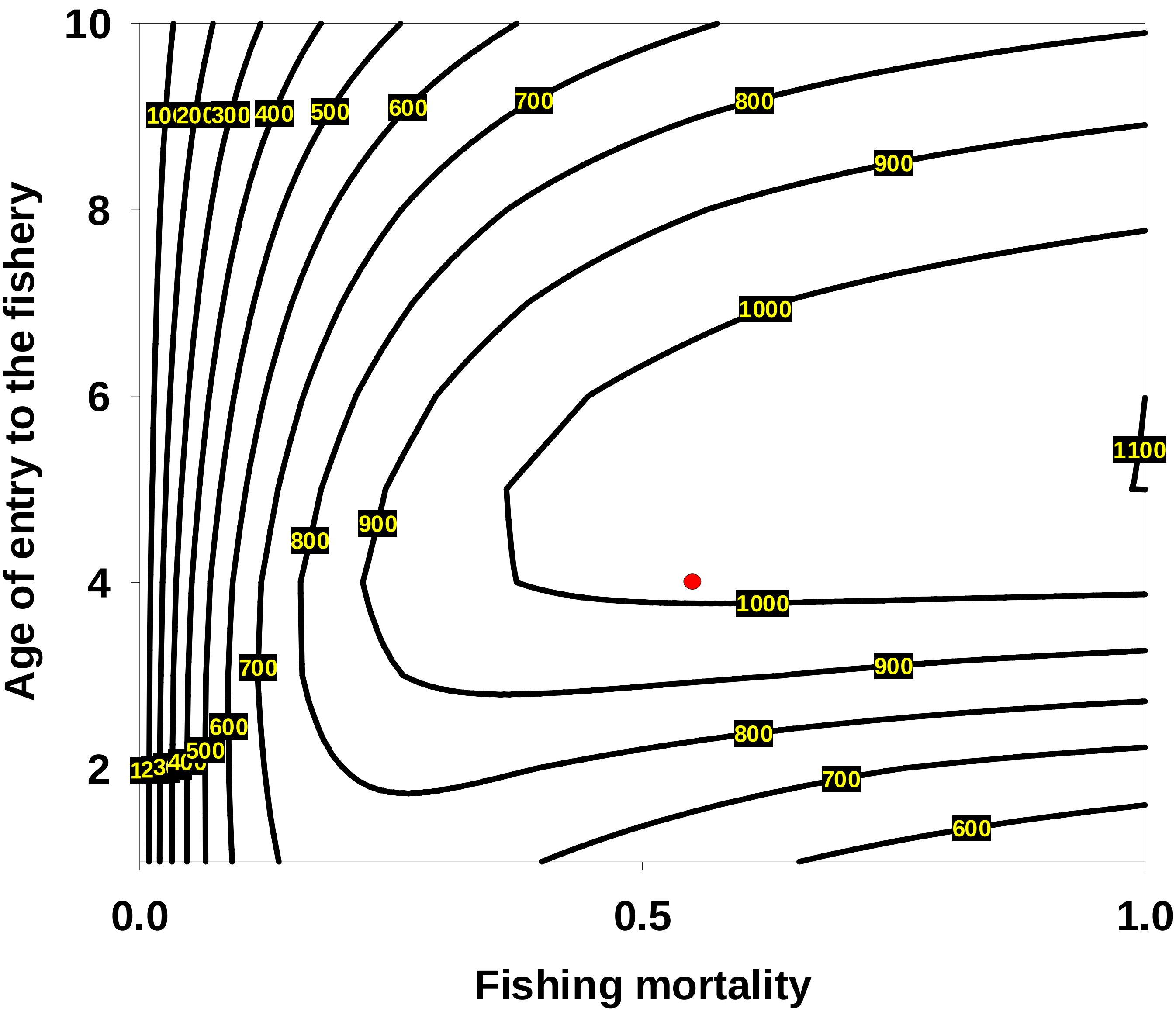


Figure 18

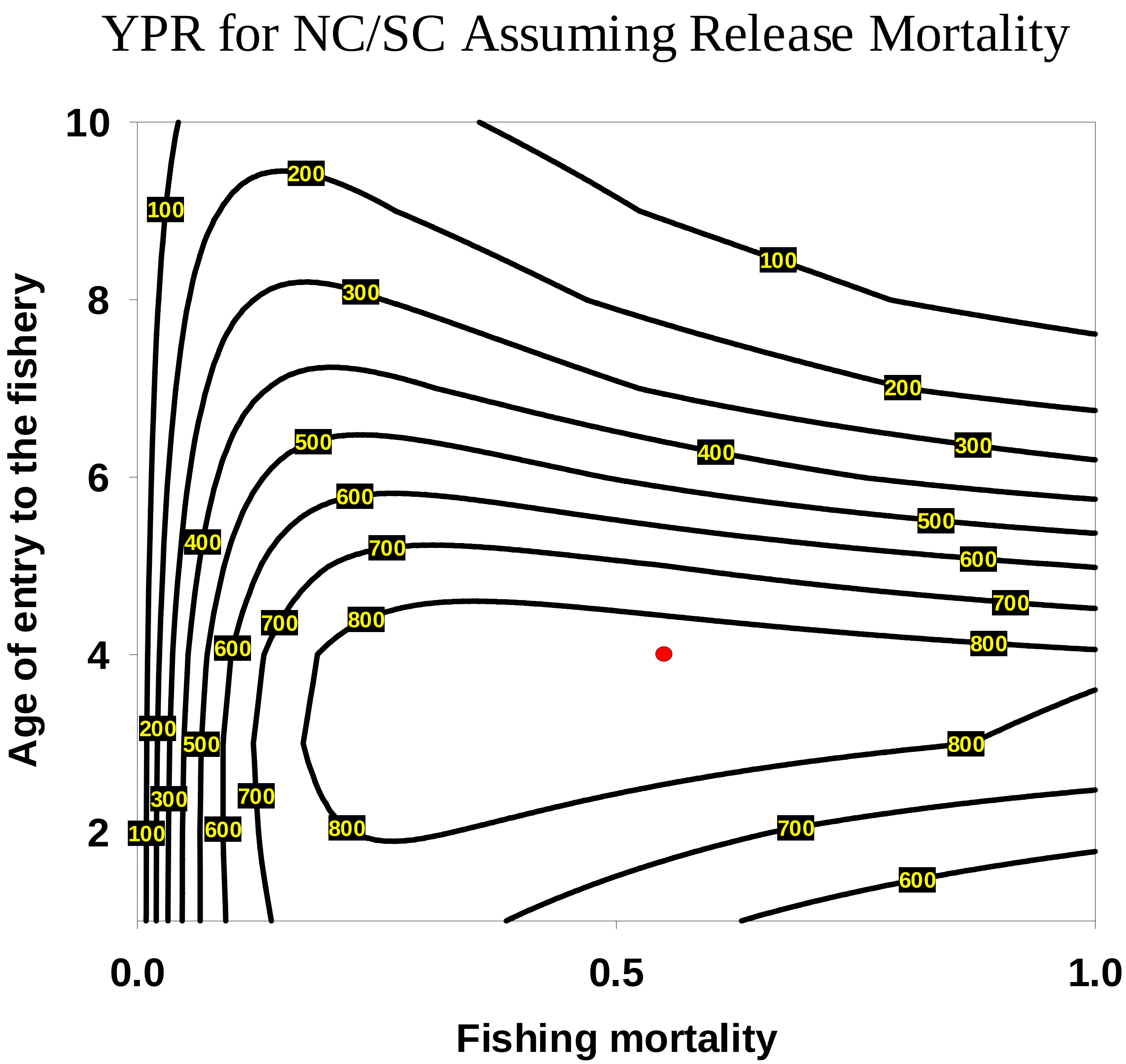

YPR for NC/SC Assuming Release Mortality
10
8
6
4
2
0.0
0.5
1.0
Age of entry to the fishery
Fishing mortality
100
200
300
400
500
600
700
800

Figure 19

YPR Assuming no Release Mortality for Each Data Source

NC/SC Fishery Ind

NC/SC Fishery Dep

FL Fishery Dep

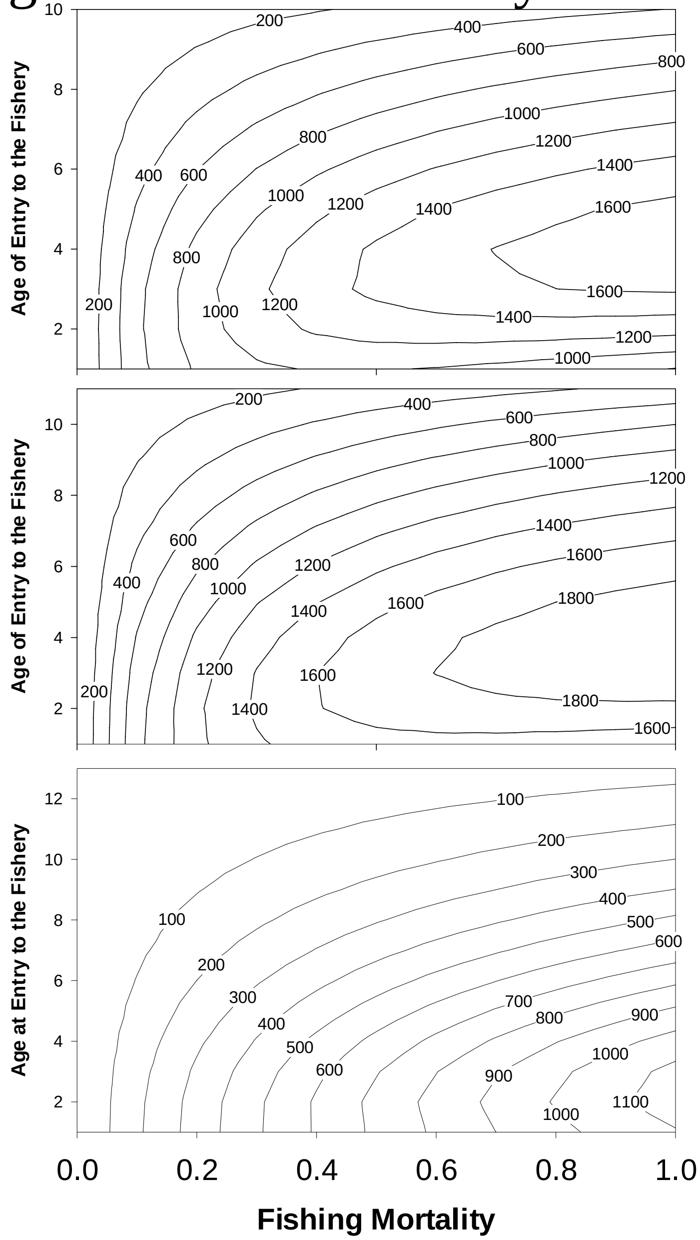


Figure 20

Red Grouper with no Release Mortality and no Sex Ratio Compensation

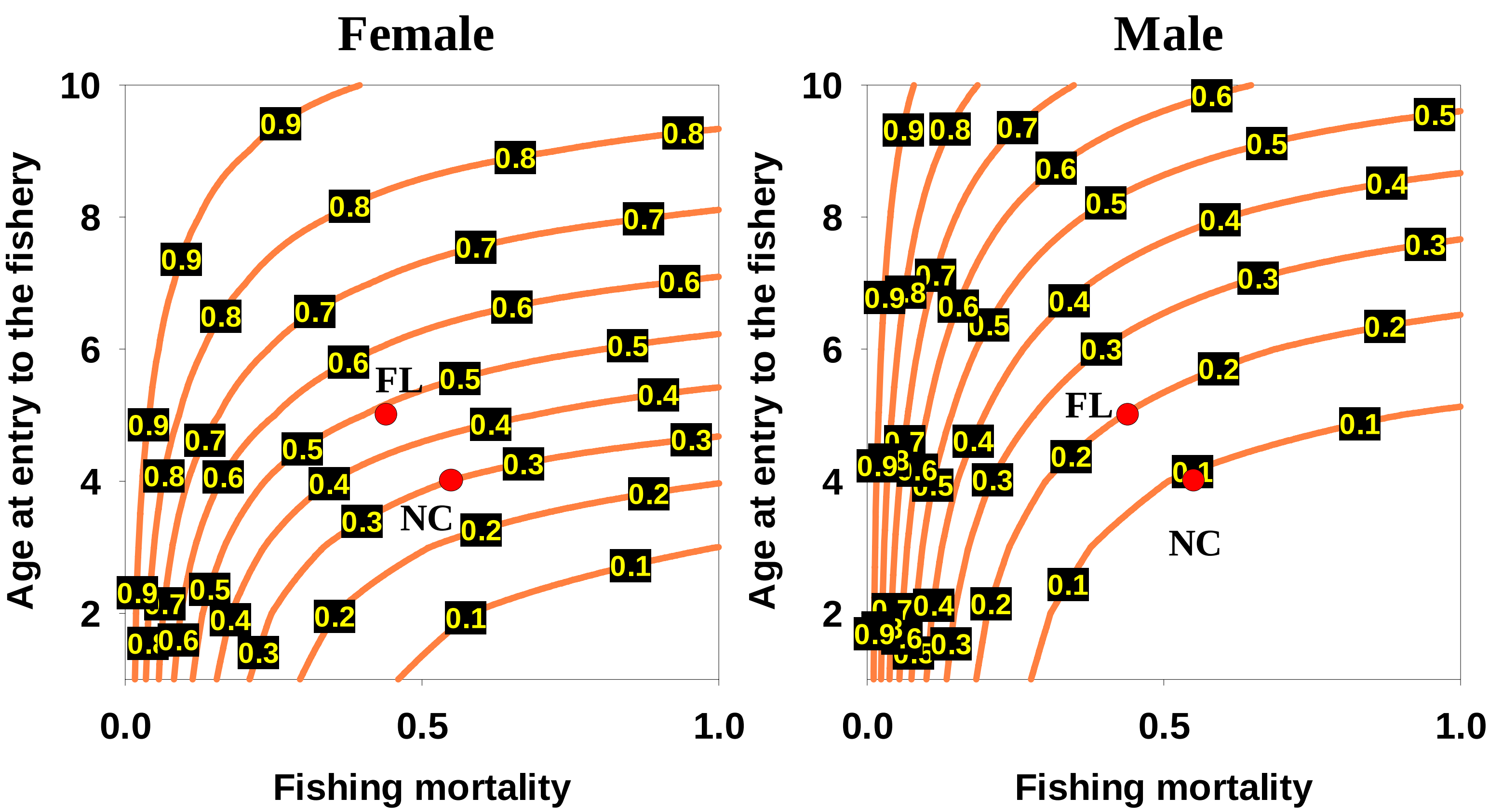


Figure 21

Red Grouper with Release Mortality and no Sex Ratio Compensation

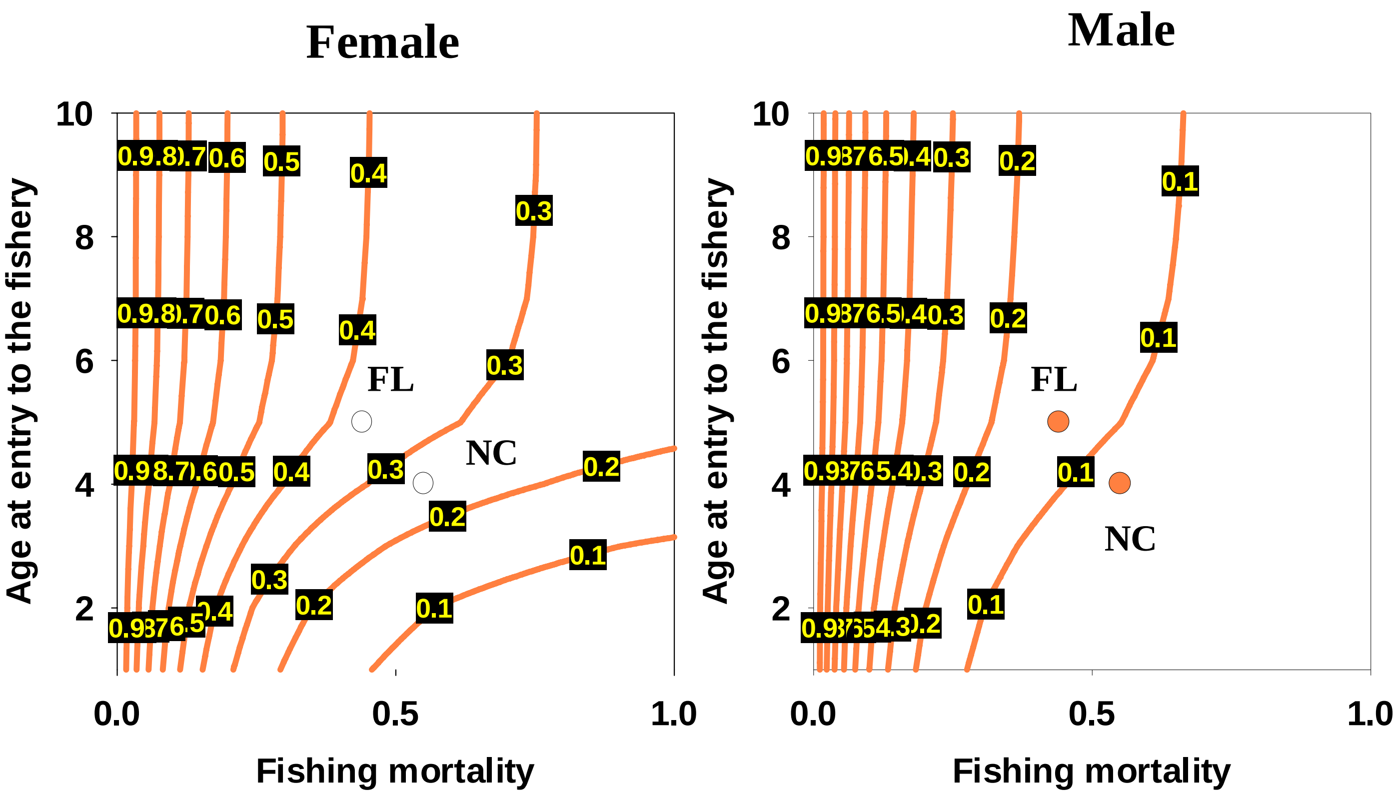


Figure 22

Red Grouper with Release Mortality and Sex Ratio Compensation

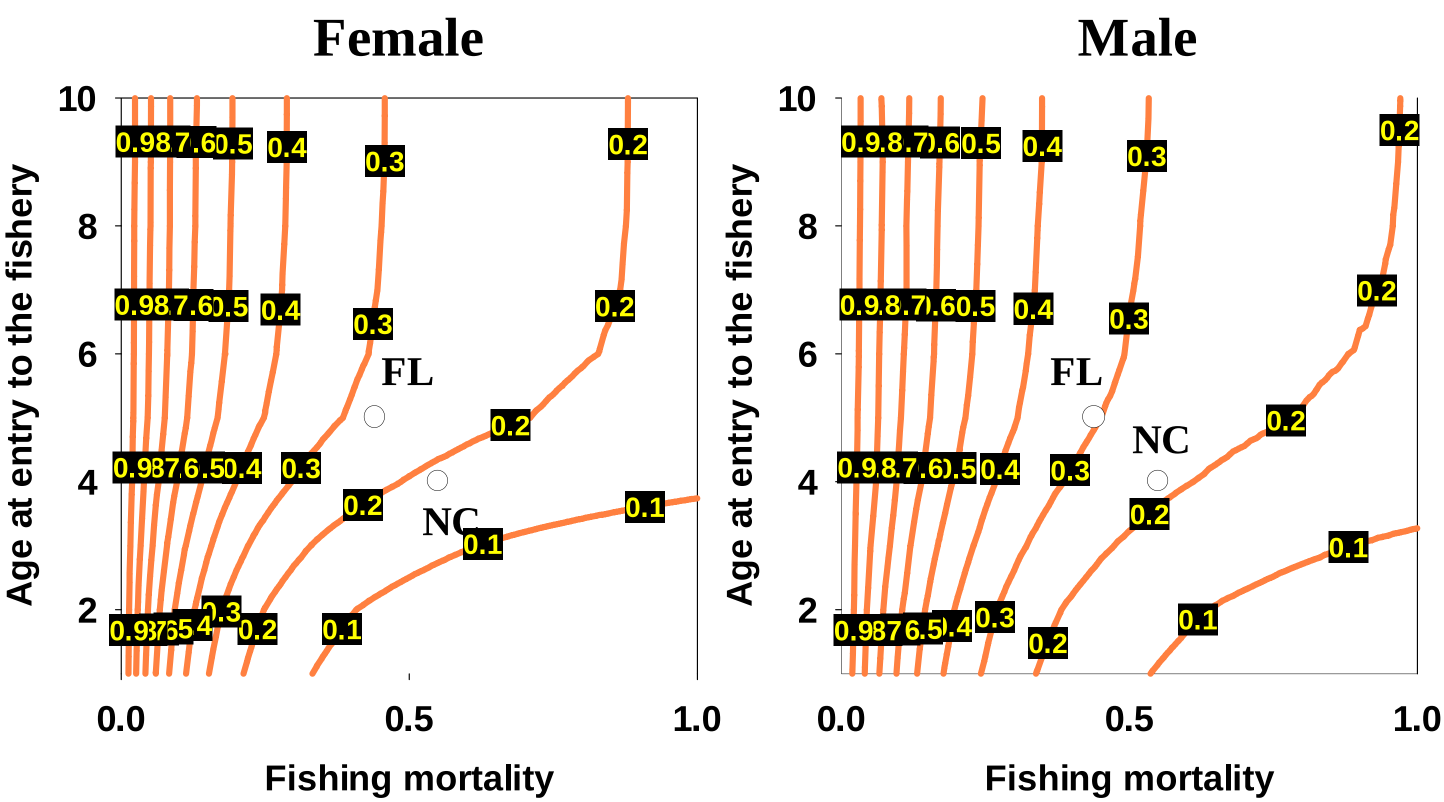


Figure 23

B. If significant problems development which resulted in less than satisfactory or negative results, they should be discussed.

There were no significant problems encountered during the project.

D. Description of need, if any, for additional work.

VI. Evaluation

1. Were the goals and objectives attained? How? If not, why?

The goal of the proposed research was to estimate the age structure and provide life history and population data needed to refine fishery management plans for red grouper, *Epinephlus morio*, off the southeast US coast. Specific objectives included:

1. Randomly sample red grouper from the southeastern U.S. (proportional to historical landings for each region) for a life history study.
2. Generate age-length keys and to determine sex ratio, size and age of maturity, and maturity schedules for fish caught in eastern Florida and North Carolina.
3. Estimate population various population parameters for red grouper caught off of Eastern Florida and North Carolina.
4. Provide these data in a timely fashion to the NMFS, and the South Atlantic Fishery Management Council.

All of the goals and objectives listed above were attained. Details of how these goals and objectives were met are provided in Findings, Section V.

2. Were modifications made to the goals and objectives? If so, explain.

We had proposed to use VPA to estimate population parameters. However, there were problems with the NC landings data that prohibited us from using VPA. Therefore, population parameters of red grouper off NC/SC and FL were estimated using catch curve analysis, yield per recruit and spawning potential ratio.

B. Dissemination of project results:

Much of the data that were collected from NC/SC were incorporated into a Masters Thesis that was conducted by Julian M. Burgos under the direction of George Sedberry, Pat Harris and Jack McGovern who were the principal investigators of this project. Mr. Burgos successfully completed defended his thesis in 2001.

Burgos, Julian M. 2001. Life history of the red grouper (*Epinephelus morio*) off the North Carolina and South Carolina coast. Masters Thesis. University of Charleston. 90 pp.

There have been several talks at scientific meetings that have resulted from work including one that is scheduled for the AFS meeting in Baltimore, MD in August 2002.

Burgos, J. 2000. Life history of red grouper (*Epinephelus morio*) off the North Carolina and South Carolina coast. AFS Meeting, Savannah, GA.

Burgos, J. 2000. Life history of red grouper (*Epinephelus morio*) off the North and South Carolina coast. University of Charleston, Student Colloquium.

McGovern, J.C. J. Burgos, G.R. Sedberry and P.J. Harris. 2002. Aspects of the Life History of Red Grouper (*Epinephelus morio*), Along the Southeastern United States. Thirteenth Annual MARFIN Conference, Tampa, FL.

Lombardi, L.L., J. C. McGovern, L. A. Collins, J. M. Burgos, J.K. Loefer, and J. Mikulus. 2002. Aspects of the Life History of Red Grouper (*Epinephelus morio*) from the northeast Gulf of Mexico and southeastern Atlantic. American Fisheries Society Meeting, Baltimore, MD.

We expect that at least two papers will be published in scientific journals as a result of this project. One paper is currently in preparation on the life history of red grouper off the Carolinas. A second paper will produced in the near future that will compare aspects of the life history of red grouper off the Carolinas to fish landed off eastern FL.