AGE AND GROWTH OF RED SNAPPER, *LUTJANUS CAMPECHANUS*, FROM THE SOUTHEASTERN UNITED STATES

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ABSTRACT

This study investigated length and age relationships for a sample of red snapper, *Lutjanus campechanus*, from the South Atlantic between the years 1977 – 2006, a period of time that included 3 different management schemes for this species. Total lengths ranged from 197 to1,001 mm with a mean total length of 573 mm. Fractional ages of these fish ranged from 0.5 to 53.67 years with corresponding calendar ages ranging from 1 to 54 years. Von Bertalanffy models were derived using both observed lengths with fractional age and back-calculated lengths to the last annulus. There was no biological difference in theoretical growth between observed and back-calculated lengths. When back-calculating lengths from otolith radius taken along the transverse plane compared to along the sulcal groove, there was no difference in estimates between measurement axes. Mean length, mean age, mean length-at-age, and von Bertalanffy curves were used to test for differences in growth between geographical area, fishery type, and regulatory period. Regulatory periods consisted of the no regulation period (1977 – 1982), the FMP period (1983 – 1991) where a minimum size limit of 305 mm total length was instituted for red snapper, and the Amendment 4 period (1992 – 2006), where the minimum size limit was raised to 508 mm total length. No differences in growth were found between fish caught in the Carolinas (NC/SC/GA) and those caught in Florida or between fish caught in the recreational fishery as opposed to the commercial fishery. However, red snapper 2 – 5 years old were significantly larger at age in the Amendment 4 period than in the other two periods. This shows evidence for a size selective fishery due to the increase in size limits. Von Bertalanffy models, corrected for size limit effects, showed there was no

difference in the growth pattern between areas, fisheries, or regulatory periods, therefore, one corrected von Bertalanffy model ($L_t = 896 * (1 – e^{-0.25 (t + 0.16)})$) was used to represent growth for the entire South Atlantic red snapper population from 1977 to 2006.

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INTRODUCTION

Commercial and recreational fisheries in the United States are an important part of many people's lives, from providing a source of income to opportunities for family vacation. Managing this nation's fisheries resources is necessary to ensure that they will be available to future generations. Assessment of fish populations, according to Jennings et al. (2001), "includes several mathematical approaches that are used to predict how a fished species will respond to different management actions." There are many different models used to assess fish populations such as surplus production models, virtual population analysis (VPA) models, and forward projecting models. Surplus production models are among the simpler models that use landing trends (the number of fish caught), represented by a catch per unit effort (CPUE) time series, to evaluate the potential response of the stock to different management restrictions such as minimum size limits, bag limits, and trip quotas (Quinn and Deriso 1999). VPA models, which are backward and/or forward projecting models, each fall under the broader category of age-structured assessment models. These models require catch at age data, as well as landings data, to enable estimates of recruitment and year class abundance (Quinn and Deriso 1999). Aging fish not only allows age-specific recruitment and year class abundance to be estimated, but also growth rate, mortality rate, age at maturity, and longevity. This information provides an improved understanding of species life history strategy and can be used to provide a foundation for management decisions. Age-specific demographic rates can then, in turn, be used to assess the effects of any management restrictions after they have had time to take effect. For instance, the use of age-specific growth and mortality rates can be used to estimate maximum sustainable yields and the possible effects of catch regulations. Therefore, the most sophisticated stock assessment models require catch at age data (Carlander 1974; Campana 2001).

Age and Growth Analysis

Age and growth determinations of fish can be achieved using several methods. These methods include length-frequency analysis, observations of growth in fishes of known age through laboratory rearing or mark/recapture approaches, and the analysis of regularly formed marks on calcified bony structures (Lux 1971, Manooch 1987). Length-frequency analysis determines age by plotting length-frequency distributions from the population to reveal peaks assumed to represent average lengths for each separate age class. This method is best used for fish that are fast growing with short spawning periods and short life spans. Using length-frequency data to age fish is relatively simple and inexpensive, however, the life history traits (fast growth and short spawning seasons) needed for accurate analysis are not typical of many species, for example, tropical reef fishes such as snappers and groupers (Manooch 1987).

Mark/recapture approaches have been used to estimate growth, movement, and population size for many fishes. Fish are marked externally by fin clipping or through the attachment of a visible tag. Internal tags can be used as well. Assumptions are made with any tagging study that tags will not cause changes in growth, feeding, reproduction, movement, or survival of the fish and that all tags will remain attached to the fish. Directly observing growth of laboratory reared fishes can also be used to assign growth rates to fish of known ages. Although accurate, these two methods of observing growth can become expensive, time consuming, and labor intensive, especially with fish that are extremely sensitive to changes in habitat such as reef fishes (Manooch 1987).

Most fish are poikilotherms; therefore processes such as growth are influenced by the temperature of the surrounding water. Growth is rapid during warm seasons and slows during cold weather. Changes in growth rate are visible on growing bony structures as zones or bands of calcified material of different widths (Lux 1971). These growth zones can be useful for determining daily and/or annual ages. Most bony structures contain a core area representing the initial growth of the structure, and then growth zones that develop throughout the fishes' life are laid down in concentric rings at periodic intervals. One year of growth is represented by one opaque zone and one translucent zone. Translucent zones represent periods of fast growth typically formed in warmer months. In contrast, periods of slow growth, where increments are laid down close together, are distinguished as opaque zones (Lux 1971; Williams and Bedford 1974; Manooch and Potts 1997). Some calcified structures analyzed for aging include scales, otoliths, vertebrae, fin rays and spines, operculur bones, and cleithra. These hard parts, either whole or sectioned, can show periodic marks representing daily or annual increments. The type of structure used depends on the species as well as the method that has been found to be the most accurate for that species. The collection of most hard parts requires sacrifice of the fish for collection, with the exception of scales and fin rays (Lux 1971; Manooch 1982).

Since scales are located just under the epidermal layer of the fish and are easily regenerated if lost, they are the easiest calcified structure to collect. Scale growth is reflected in circuli that form rings on the scale surface. Each complete circulus is considered to be a year-mark or annulus (Lux 1971). Scales are not the most accurate hard part used for aging because scale regeneration can cause loss of circuli and the appearance of circuli disconformities (Pafford et al. 1990). In addition, during later years of life, scales can be resorbed for calcium causing formation of incomplete circuli (Chilton and Beamish 1982). Otoliths or “ear stones” are the most frequently used hard part, as well as the most accurate (Manooch 1982). Similar to other hard parts located internally, such as vertebrae, fin rays and spines, operculur bones, and cleithra, otolith removal requires the fish to be sacrificed (Lux 1971). These other structures are typically used to age pelagic fish, which tend to have brittle otoliths that are difficult to remove and store (Foreman 1996; Uchiyama et al. 1998). Structures other than otoliths have also been used for some reef fishes such as gray triggerfish, *Balistes capriscus*, which have oddly shaped otoliths, which are difficult to remove and section (Manooch 1987; Wilson et al. 1995). Otoliths, however, remain the standard structure used to age most teleost fishes.

Otoliths can be read whole or sectioned; however, whole otoliths may only be useful in young fish when the otolith is translucent enough to enumerate increments. Most otoliths require sectioning for full view of all growth zones. Once sectioned by cutting transversely across the width of the otolith, and viewed under reflected light on a black background, translucent zones are visible as black bands and opaque zones as white bands. Together, one opaque zone and one translucent zone make up one year of growth; however, only opaque zones are typically termed annuli and enumerated in aging (Williams and Bedford 1974). The number of annuli is normally consistent with the number of years the fish has been alive depending on when the first annulus was laid down, the birthdate of the fish, and month of capture (Beckman et al. 1989).

In addition to annuli, representing full years of growth, “false annuli” may appear in otolith sections, sometimes making it difficult to distinguish “true” annuli from “false” ones. These “false” annuli can occur during spawning periods or periods of rapid temperature change. The theory behind growth zones on otoliths is based on differences in somatic growth rates due to distinct changes in water temperature. Fishes living in temperate climates, where seasons are distinct, have clear opaque and translucent zones. These zones are easily distinguished from spawning checks or other “false” annuli. Tropical and subtropical reef fishes, like the red snapper, live in areas of consistent or semi-consistent temperatures causing growth zones to be difficult to interpret. Opaque and translucent zones are still present on otoliths from these species but zones are not as distinct, making age determination of these species difficult (Pannella 1974).

Measuring the distance from the otolith core to each annulus and relating that distance to the size of the fish can provide a growth history for that individual throughout its life (Francis 1990). This method, known as back-calculation, increases the amount of length-at-age data available for an individual. This is especially important for species that are rarely caught in the fishery or that may show low or declining stock levels and cannot afford to be sacrificed in large numbers for aging (Francis 1990). Back-calculation models are extremely valuable to fishery resource managers because they can provide growth data for fish populations from a single sampling trip. Therefore, the use of this technique has become widespread. Using back-calculated growth histories, potential fast and slow growth between years can be established along with estimates of mortality rate and growth parameters for the population by providing estimates of length-at-age for fish not landed by the fishery (Smith 1983; Klumb et al. 2001).

Otolith back-calculation requires a strong relationship between the size of the fish (length) and the size of its otolith (otolith radius). Before a relationship between length and otolith radius is developed, it must be determined if the growth of the fish and the growth of the otolith are correlated. The disadvantage to this method remains that back-calculating growth from otolith increments assumes that the relationship between otolith growth and fish growth is linear. The assumption often holds true at young ages, but somatic and otolith growth rates can be uncoupled at older ages because growth of the fish slows and eventually reaches an asymptote while the otolith continues to grow (Campana 1990; Thorrold and Hare 2002). This may not allow otolith length to be an accurate predictor of size at some ages (Pilling et al. 2003). Continuous accretion of otolith material causes older individuals to have larger back-calculated lengths-at-age then observed (Reznick et al. 1989; Campana 1990). In addition, annual increments during later years start to lay down very close together. This increment "bunching" can make it difficult to age fish at older ages and cause an under- or overestimation of previous lengths at age during back-calculation. Back-calculation is also confounded by "Lee's Phenomenon", which is described as slower estimated growth of older fish when they were at young ages (Lee 1912). This phenomenon is demonstrated during back-calculation where old, slow growing fish tend to have smaller back-calculated lengths at younger ages than observed lengths at those same ages (Reznick et al. 1989; Campana 1990). To improve estimates of previous lengths at age, a proportionality constant must be incorporated into the back-calculation model derived from analysis of individual observed lengths compared to theoretical lengths (Francis 1990). In some species such as red snapper, as the fish becomes older, the otolith changes growth axes. Initially, otoliths accumulate material in a transverse direction along the dorso-ventral axis, yet at older ages, otolith material begins to stack vertically on the proximal surface instead of transversely (Beamish and McFarlane 2000; MIFSS 2005) causing difficulty when back-calculating using otolith radius measurements. Comparing otolith weight to fish length as a method of back-calculation may also improve length-at-age estimates (Pawson 1990). For the sky emperor, *Lethrinus mahsena* (Pilling et al. 2003), ages estimated from otolith weight were not significantly different from ages estimated from increment counts.

Because of the variety of useful information that can be calculated by aging fish, it is important to continue to use age structure when assessing fish stocks. It is also important to preserve age structure. Berkeley et al. (2004a) proposed that age structure of a stock, along with the spatial distribution of recruitment, can be as important as spawning stock biomass in maintaining sustainable population levels of some fished stocks. In addition, it has been hypothesized that it is mostly the larger, older female fish that are producing the offspring most likely to recruit to the population. By removing the largest, and likely oldest, individuals from the population through fishing, age truncation may occur, resulting in a narrow spectrum of age classes. Older fish also tend to spawn earlier in the season; therefore, the spawning season may be shortened by removing older fish as well. Restricting the spawning season can force fish to reproduce during only a small range of environmental conditions (Berkeley et al. 2004a; Berkeley et al. 2004b).

Otolith Form and Function

Otoliths are calcified structures that serve as sound transducers and sources of balance for teleost fishes. Otolith shape is species-specific and changes with function based on species life history, frequency sensitivity, and directional hearing (Gauldie 1988). A fish has 3 pairs of otoliths, all located in the otic bulla within the head. Each pair, the sagittae, lapilli, and asteriscii lay within their corresponding otolithic organ, the sacculus, utriculus, and lagena, respectively (Carlstrom 1963; Popper and Coombs 1982). Every otolith is made up of a calcium carbonate matrix, and depending on the pair of otoliths being formed, the calcium carbonate will crystallize into either an aragonite or vaterite polymorph. Sagittae and lapilli are most commonly made of aragonite and the asteriscii are typically composed of the vaterite polymorph (Campana 1999).

Occasionally, for reasons unknown, aragonite otoliths form regions of vaterite, causing transparency in otolith appearance and/or a build up of crystalline material on and within the otolith. These otoliths are termed “aberrant” and cannot be used for aging because alternating opaque and translucent growth zones are not recognizable (Mugiya 1972; Campana 1999).

Otoliths are acellular and metabolically inert, therefore, resorption, that can provide sources of extra calcium for a fish when needed, is not known to occur. This makes them the best permanent record of fish growth and the most accurate hard part used for age determination (Gauldie 1988; Campana 1999). Sagittal otoliths are the biggest of the three pairs, and are therefore commonly chosen for age analysis (Lux 1971; Gauldie 1988).

Red Snapper Ecology and Life History

Red snapper, *Lutjanus campechanus*, is a large member of the family, Lutjanidae, which includes a number of snapper species. Red snappers are distributed in marine waters throughout the Gulf of Mexico and in United States Atlantic waters north to North Carolina. Rare occurrences of fish as far north as Massachusetts have been reported (Rogers 1999). Commonly, red snappers reside in federal waters, within the US Exclusive Economic Zone (3-200 nautical miles from shore). Adult red snapper aggregate towards structured habitats such as coral reefs, sunken ships, gas and oil platforms, and rocky outcroppings. Juveniles prefer sandy, open bottoms, where small debris becomes covered in silt (Gallaway et al. 1999).

Early life history of red snapper consists of free-drifting planktonic stages, eggs and larvae, and a settled juvenile stage. The egg stage lasts up to 24 hours before eggs hatch into larvae. The larvae then spend about 26 days in the plankton until settling to smooth benthic habitats (Gallaway et al. 1999; Szedlmayer and Conti 1999). Juveniles range from 100 to 320 mm total length, which remains below the currently established minimum size limit of 508 mm total length for the South Atlantic. After reaching about 200 mm total length, juveniles begin to emigrate from the open substrate and recruit to reef systems, which are thought to provide protection from predators and an increase in food resources (Gallaway et al. 1999, Szedlmayer and Lee 2004). As juveniles, they feed mainly on invertebrates such as polychaetes, amphipods, and copepods, but begin to include more fish in their diet as they increase in size. Adult red snapper have been described as piscivorous, opportunistic bottom feeders, consuming mainly fish species.

Squid and crustaceans, such as crabs and shrimp, are also an important part of adult red snapper diet (Bradley and Bryan 1975; Rogers 1999; Szedlmayer and Lee 2004).

Red snapper can reach sexual maturity at two years of age, usually when individuals attain about 300 mm total length. In the Gulf of Mexico, individuals matured between approximately 250 and 500 mm total length or around 2 to 5 years of age. In most cases, 100% of red snapper in the Gulf of Mexico are mature by age 6 (Woods et al. 2003). White and Palmer (2004) reported that for Atlantic red snapper, size at maturity ranged from 287 to 435 mm total length for females and from 200 to 378 mm total length for males. Under current size regulations, all red snapper in the Atlantic should be able to spawn 1 to 3 times before being caught by the fishery (White and Palmer 2004). Spawning occurs in open water away from structured habitats between May and October in the Gulf of Mexico (Bradley and Bryan 1975; Collins et al. 1996), and from April through September in the South Atlantic (Manooch et al. 1998). Spawning peaks generally occur between June and August for all locations. Red snappers exhibit indeterminate, protracted batch spawning, with fecundity being a function of age and length, similar to most fishes. Average fecundity in small red snapper can be fewer than 500 eggs per batch compared to over 1.5 million eggs per batch in larger, older fish. The maximum mean fecundity at age for red snapper is estimated to occur at age 10 (Collins et al. 1996; Ortiz 1998). This relationship between fecundity and size-at-age make large individuals the most important contributors to the population (Collins et al. 1996). Fishery selectivity for the bigger fish because of minimum size limits may have adverse effects on the population's reproductive potential (Berkeley et al. 2004a; Berkeley et al. 2004b).

Red snappers grow rapidly throughout their first 10 years of life, growing approximately 100 mm per year during the first 6 years. Growth slows considerably at older ages, approaching an asymptote by age 10 (Moran 1988). Maximum length in red snappers can reach 1,039 mm total length and individuals can weigh up to 23 kg (Wilson et al. 2001).

Red Snapper Aging

Red snapper ages are most accurately determined by removing and sectioning one of the sagittal otoliths (Baker et al. 2001; Wilson and Nieland 2001; Wilson et al. 2001). Increments form alternating translucent and opaque zones on the otolith, which are enumerated. Each opaque zone is considered an annual mark or annulus; therefore, the number of annuli is equal to the number of years the fish has been alive. This pattern of annuli deposition has been validated for red snapper using radiometric analysis (Baker et al. 2001), however, the precise location of the first annulus has not yet been validated making age determination in this species difficult (Wilson and Nieland 2001; Wilson et al. 2001; Allman et al. 2005). Allman et al. (2005) attempted to improve accuracy in assigning the first annulus in Gulf of Mexico red snapper, by describing its nature, shape, and appearance. The first annulus has been described as a diffuse “triangular-shaped” opaque zone. It has also been found that in most cases, a small translucent area will be present between the core and the first annulus giving the appearance of an extra annulus, further increasing the difficulty in aging this species (Allman et al. 2005). Due to its protracted spawning season, distances from the core to the first annulus can vary considerably and the size of the core can also complicate locating the first annulus

(Mareska 2004). Fish spawned in the fall tend to have a first annulus close to the core compared to fish spawned in early summer, which have a first annulus that is a sufficient distance away from the core. The maximum age for red snapper does appear to differ by region. The maximum age from opaque zone counts recorded for Gulf of Mexico red snapper is 57 years old (Allman et al. 2002), compared to a maximum age recorded for Atlantic red snapper of 45 years old (White and Palmer 2004).

The red snapper fishery is severely overfished in the Gulf of Mexico with high juvenile mortality contributing to the decline in stock size. Snapper nursery grounds overlap with shrimp trawling areas causing juveniles to get caught as bycatch. Extensive aging has been completed for red snapper in the Gulf of Mexico to aid in management strategies because the stocks are easily susceptible to overfishing. Bradley and Bryan (1975) attempted to assign ages to red snapper using length frequency analysis. However, this approach was found to be unreliable because the long duration of the spawning period leads to continuous recruitment of young fish into the population and an overlap in lengths at age. Using length as a predictor of age can also be difficult for older fish because maximum length is reached early and remains fairly constant as the fish continues to age (Moran 1988). After Bradley and Bryan (1975) attempted length frequency analysis, others chose to use scales (Wade 1981; Nelson and Manooch 1982) and otoliths (Nelson and Manooch 1982; Patterson et al. 2001; Wilson and Nieland 2001) to age red snapper in the Gulf of Mexico. Red snapper aged with otoliths were found to be considerably older than those aged with scales, some as old as 57 years (Patterson et al 2001; Wilson and Nieland 2001; Allman et al. 2002).

Since red snappers are not considered overfished in the Atlantic, age studies are sparse in this region. Nelson and Manooch (1982) aged fish from east Florida and the Carolinas and found fish as old as 16 years using scales and sectioned otoliths. Manooch and Potts (1997) aged red snapper from the southeast Atlantic up to 25 years old using sectioned otoliths. Most recently, White and Palmer (2004) found red snapper as old as 45 years off the southern United States by aging with sectioned otoliths. Maximum age of red snapper may differ between Atlantic and Gulf of Mexico regions since Atlantic red snapper aging studies have consistently observed younger maximum ages than in the Gulf.

The purpose of this study was to age Atlantic red snapper from North Carolina to Florida using a larger sample size from the population than has been used previously. The data set included fish collected across three decades. This study also compares size, age, and growth between recreational and commercial fisheries as well as studies the effects of fisheries management on growth, which has not been previously investigated for red snapper in the U. S. South Atlantic.

Differences in size-at-age can exist between areas, fisheries, and years. Bergmann's rule states that "the smaller-sized geographic races of a species are found in the warmer parts of the range, the larger-sized races in the cooler districts" (Mayr 1942; Ray 1960). Therefore, a difference in size-at-age may exist between the Carolinas and Florida. The size-at-age of the catch between fisheries may differ because of differences in selectivity and catchability. Commercial fishermen tend to select for the largest fish to yield the highest economic return, whereas recreational fishermen may not be selective among fish over the minimum size limit. Catchability increases with experience and commercial fishermen are typically more experienced than recreational anglers. There may also be a difference in size-at-age between years due to fishing pressure, selectivity, and the establishment of a minimum size limit of 12 inches (305 mm) total length in 1983, which increased to 20 inches (508 mm) total length in 1992 (SAFMC 1991). Several previous studies have observed differences in size-at-age of reef fishes between time periods due to fishing selectivity, and some have suggested changes in size-at-age within 5 years time (Harris and McGovern 1997; Zhao et al. 1997; Harris et al. 2001). The research objectives for this study were:

1. Determine age-length relationships for red snapper (*Lutjanus campechanus*) in the Atlantic Ocean from North Carolina to Florida for the years 1977-2006.
2. Determine if temporal shifts in red snapper age structure exist.
3. Determine if there are spatial differences in red snapper size and age structure.
4. Determine if there are differences in sizes and ages of red snapper caught between commercial and recreational fisheries.
5. Identify strong year classes that may have existed between 1977 and 2006.
6. Compare theoretical growth curves derived from back calculated lengths to the last annulus vs. those derived from observed length and fractional age.

METHODS

Red snapper were collected from commercial and recreational fisheries through several state and federal programs including the National Oceanic and Atmospheric Administration (NOAA) Southeast Headboat Survey, the NOAA Marine Recreational Fishery Statistics Survey (MRFSS), the NOAA Trip Interview Program (TIP), and the

Florida Fish and Wildlife Conservation Commission (FFWCC). Fish were caught in Atlantic waters off the coast of the United States from North Carolina to Florida between the years 1977 and 2006.

The archived collection that forms the basis of this study is comprised of two sets of otoliths. Set 1 was sectioned by the primary investigator. The other otoliths (Set 2) were previously processed and analyzed by Manooch and Potts (1997). Otolith sectioning and other processing methods for Set 1 are presented in the text below. Methods used for otoliths in Set 2 are presented in their original manuscript and do not differ from those used in the current study (Manooch and Potts 1997).

Otolith Processing

Red snapper otoliths were not sufficiently transparent to age whole, so sectioning was required to view growth zones and estimate age. A previous study has shown there was no difference in opaque zone counts between left and right red snapper sagittal otoliths (Nelson and Manooch 1982); therefore, the left sagittal otolith was chosen for aging purposes to be consistent with previous studies (Nelson and Manooch 1982; Manooch and Potts 1997; White and Palmer 2004). Otoliths were stored dry in coin envelopes. If the left otolith could not be sectioned due to damage or breakage, the right otolith was used instead. Before sectioning, all otoliths were weighed to the nearest 0.01 gram using a microbalance. Each otolith was individually sectioned using a low-speed saw or using a high-speed precision grinder (Cowan et al. 1995).

When using the low-speed saw, whole otoliths were first mounted to clear glass microscope slides using a thermal plastic. The slide was then positioned on the saw and three 0.50 mm transverse sections were generated by making four consecutive cuts with a diamond wafering blade. The cuts were positioned as close as possible to the core (area of initial otolith growth estimated visually before sectioning) to ensure that one of the three sections would contain the core. The sections were then mounted on another clear glass slide with thermal plastic and covered with a mounting medium to reduce the appearance of scratches on the sections made by the blade; thereby enhancing clarity during reading. When using the high-speed grinder, two otoliths could be sectioned at one time but the process results in only one section per otolith. Each otolith was first ground flat from the posterior end along the anterior-posterior plane to the approximate location of the core using the grinding wheel, and then mounted flat side down on a clear slide with ultraviolet (UV) curing glue. Once cured, the otolith halves were cut down to a transverse section using a diamond edged blade and then finally ground to a thin 0.50 mm section using the grinding wheel once again. These sections were also covered with a mounting medium for clarity while viewing the section.

Sectioned otoliths were viewed under reflected light on a black background using a dissecting scope equipped with a camera and image analysis system. Annual growth zones were identified as alternating translucent zones (periods of active growth) which appeared dark, and opaque zones (periods of slow growth) which appeared white. Opaque zones were considered annuli and enumerated from the core to the proximal edge of the section along the dorsal margin of the sulcus acousticus (Figure 1).

Radial measurements were taken from the core to the dorsal edge of the section along the transverse plane using the image analysis system. For comparison of measurement axes, a subsample of additional radial measurements was taken from the

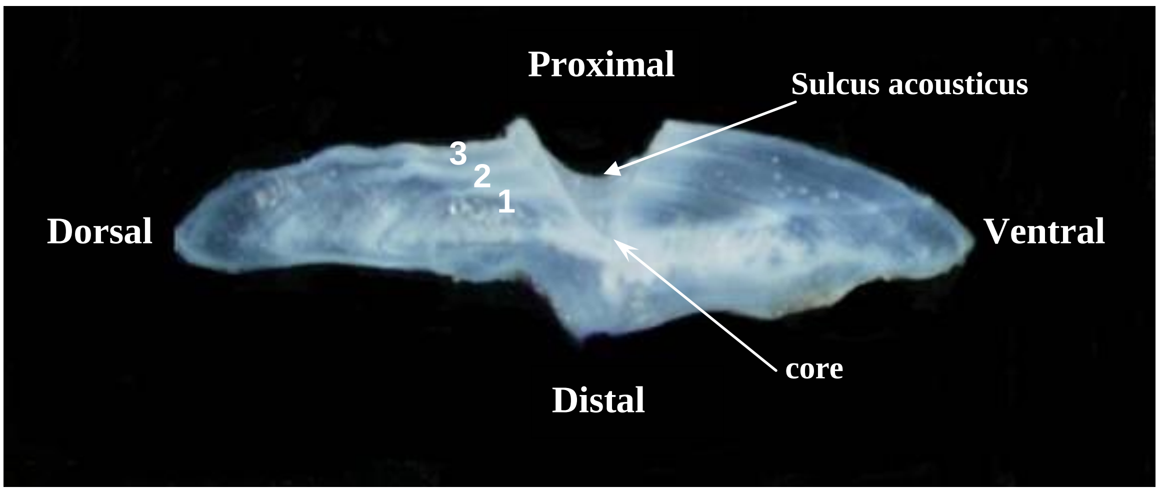

Figure 1. Section of a red snapper otolith with 3 opaque zones (white zones) labeled along the dorsal margin.

core to the proximal edge of the section along the dorsal margin of the sulcus acousticus (sulcal groove). Measurements from the core to each annulus in both radial planes were also taken. If sections were too far away from the core, measurements were not taken to reduce error. All annuli counts were done without prior knowledge of fish length or time of capture. All otolith measurements were taken to the nearest 0.01 mm.

To determine the periodicity of zone formation, two methods were used. First, the section edge (margin) type was denoted as translucent (T) or opaque (O). Then marginal increment (MI) analysis was used to validate the opaque zones as annuli. The MI equals the distance from the last annulus to the section edge; for example, if the final opaque zone is on the section edge, marginal increment equals zero. If measurements were not taken, a numerical code was used to index the amount of margin existing on the edge, relative to the width of the previous increment (Table 1). Percent occurrence of opaque margins along with mean marginal increment, were then plotted by month and timing of annulus formation was determined.

Aging Consistency

To ensure that the reading of annuli counts from this study was consistent with those of other investigators, communication between the primary investigator in this study and another aging biologist with expertise in aging red snapper was established (Pers. Comm. Robert Allman, National Marine Fisheries Service (NMFS) Panama City Laboratory, 3500 Delwood Beach Rd. Panama City, FL 32408).

Due to the lack of direct validation, it can be difficult to determine the location of the first annulus. Confusion of this kind can lead to inconsistency in opaque zone counts

Table 1. Numerical codes used to assign relative edge widths to otolith sections (Pers. Comm. Marcel Reichert, South Carolina Department of Natural Resources, 217 Fort Johnson Rd. Charleston, SC 29422).

Code	Description	Translucent Width
1	Opaque zone on the edge	None
2	Narrow translucent zone on the edge	Less than 30% of previous increment
3	Medium translucent zone on the edge	30 - 60% of previous increment
4	Wide translucent zone on the edge	More than 60% of previous increment

between multiple readers. To increase consistency when aging red snapper, Allman et al. (2005) described the first annulus as a diffuse, “triangular-shaped” opaque zone that, in many fish, contained a small translucent area between the core and the edge of the first annulus (Figure 2). This description was used to identify the first annulus when counting opaque zones in the present study and it helped increase consistency when assigning annuli counts within this study, as well as between researchers from other laboratories.

Increased consistency between annuli counts was also attempted through the use of a reference collection provided by Robert Allman (NMFS Panama City Laboratory, 3500 Delwood Beach Rd. Panama City, FL 32408). The reference collection contained 100 red snapper otoliths along with assigned ages that were agreed upon by multiple readers within the Panama City Laboratory. The principal investigator studied this collection extensively before any red snapper samples from the present study were aged.

To test, statistically, the aging consistency within samples processed by the primary investigator and between labs, a random subsample of 100 otoliths from this study was read twice by the primary investigator and then sent to Panama City to be read. After the subsample was aged, annuli counts were converted to calendar age, using the methods described in the following section, and an average percent error (APE) was calculated to assess within reader as well as between reader variability (Beamish and Fournier 1981).

Age Determination

The age of each fish was calculated based on the number of opaque zones, the species’ assumed birthdate, and then adjusted for month of capture. The assumed

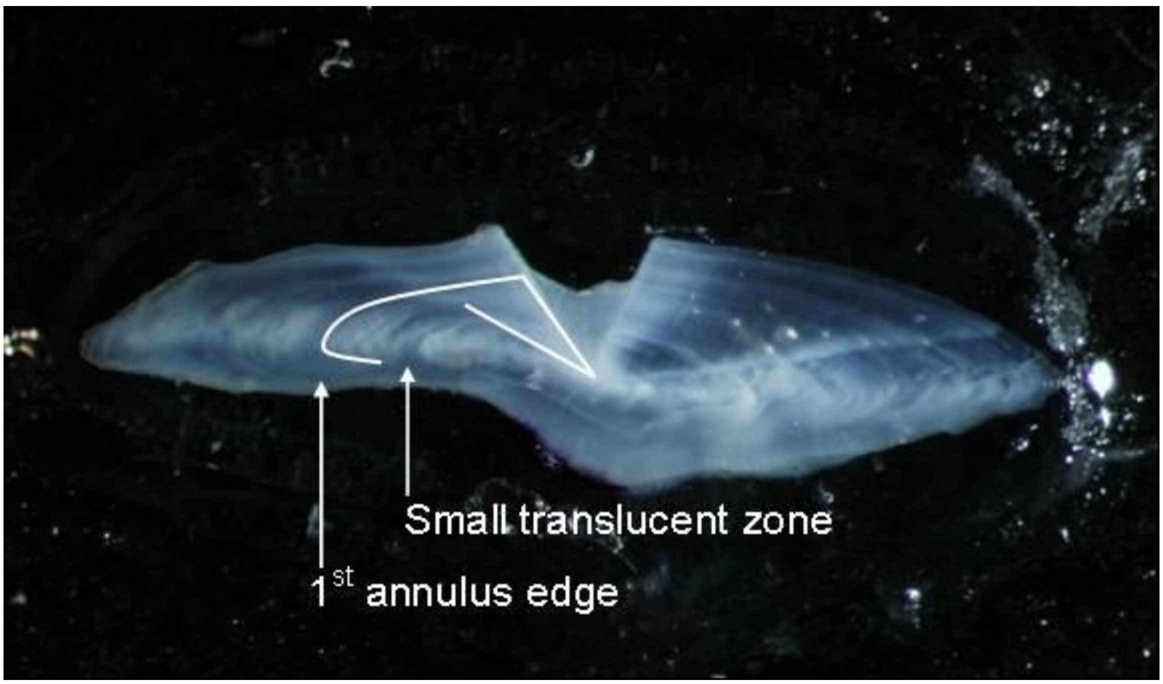

Figure 2. Red snapper otolith section showing shape and location of 1st annulus.

birthdate for red snapper was July 1, since peak spawning generally occurs between June and August in both the Gulf of Mexico and the Atlantic (Bradley and Bryan 1975; Collins et al. 1996; Manooch et al. 1998).

Calendar age was calculated by using the following criteria. If the otolith section had an opaque edge, regardless of when the fish was caught, the calendar age equaled the number of annuli counted on the section. If the section had a translucent edge and was caught in or after May, the calendar age also equaled the number of annuli counted. However, if the section edge was translucent but the fish was caught before May, the marginal increment (MI) or an edge code was needed to determine the calendar age. For these fish, if the MI was greater than or equal to half of the MI range ((max MI – min MI)/2) for that age or the edge code was equal to a 3 or 4, then the calendar age was equal to the number of annuli plus one. Although, if the MI was less than half the MI range or the edge code was recorded as a 1 or 2, then calendar age was only equal to the number of annuli.

Fractional age was calculated by adding or subtracting fractions of a year, corresponding to the month of capture, from the calendar age. The fractions were centered on July since red snapper were assumed to have a July 1 birthdate. For example, if the calendar age was 2 and the fish was caught in October, the fractional age would be 2.25 years.

Data Analysis

To explore spatial and temporal patterns of size and age, the data were subdivided based on geographical area, fishery type, and regulation period. Area was separated into two categories: Florida caught fish and all fish caught in North Carolina, South Carolina, and Georgia. Georgia sample sizes (n=9) were very small and thus, were included with the Carolina samples. North Carolina, South Carolina, and Georgia will be described under a common term, "the Carolinas", for all further analyses. Fishery type was either recreational or commercial. Regulation period was separated into three groups of years based on minimum size limits. In 1983, the Snapper-Grouper Fishery Management Plan (FMP) for the South Atlantic Region was developed that instituted a minimum size limit of 305 mm (12 inches) total length for red snapper. In 1992, Amendment 4 to the FMP raised the size limit to 508 mm (20 inches) total length (SAFMC 1991). Before 1983, no regulation existed for red snapper. Therefore, the period including 1977 – 1982 was labeled as the "no regulation" time period, 1983 – 1991 was labeled as the "FMP" time period, and 1992 - 2006 was labeled as the "Amendment 4" time period.

Analysis of variance (ANOVA) was used to test for differences between mean lengths by sex using the general linear model procedure (PROC GLM) in SAS (SAS Institute 1999). Differences in mean length and age between geographical area, fishery type, and regulatory period were also tested using ANOVA. Mean length-at-age was then compared among groups to determine whether growth differed. If differences in mean length-at-age were detected among groups, growth models were fit and compared.

There are several different growth models that can be parameterized using length and age information from sampled fish. Weight and length measurements from a fish can give insight on how the weight of the fish changes as the fish grows in size. The allometric relationship between fish weight and length was estimated using least squares regression after both variables were natural log transformed. Regression coefficient estimates were then used to parameterize the following equation:

$$W = aL^{b},$$

where W = whole weight (g) and L = total length (mm).

Age and length information can be combined to construct a von Bertalanffy growth model that shows how the length of the fish changes as the fish gets older. Theoretical growth was described by fitting a von Bertalanffy growth model to the observed length and fractional age. The model was expressed as:

$$L_t = L_\infty(1 - e^{-k(t - t_0)}),$$

where L_∞ = theoretical asymptotic total length, k = growth coefficient, and t_0 = hypothetical age at length zero. Model parameters were estimated using a nonlinear, iterative, least-squares approach implemented using the SAS nonlinear regression procedure (PROC NLIN) with the Marquardt option. Marquardt (1963) describes the method used to regress the residuals of the model with respect to the parameters until estimates converge (SAS Institute 1999). The model was also inverse weighted to give equal leverage to samples from age classes that were limited (i.e., older than 10 years) and age classes that were abundant (i.e., younger than 10 years). This kept the age groups with the most samples from overpowering the age groups with fewer samples.

To avoid size-selective fishing effects on the von Bertalanffy length-at-age estimates caused by changes in minimum size limit regulations across the 20 year time span, another technique that adjusts for changes in the minimum size limit on the von Bertalanffy curve was used (Diaz et al. 2004). This model was fit using Microsoft

EXCEL with an iterative approach to minimize weighted fit criteria that incorporated any possible minimum size limits. Hereafter, the Diaz et al. (2004) model is referred to as the “corrected” model and the term “uncorrected” refers to the original von Bertalanffy model fitted using SAS. Models were plotted together and compared to determine how the corrected model affected theoretical mean length-at-age for red snapper. If differences were found in size-at-age between geographical area, fishery type, or regulatory period, corrected von Bertalanffy models (Diaz et al. 2004) were constructed and then compared among groups.

The relationship between total length (L_t) and otolith radius (O_R) was used to back-calculate lengths at age. To validate this relationship, the correlation between the growth of the fish and the growth of the otolith was tested by regressing length on age as well as otolith radius on age and then determining if the residuals from the two regressions were positively correlated using PROC CORR (SAS Institute 1999). If the residuals are positively correlated, it can be assumed that somatic and otolith growth rates are positively correlated (i.e., a fish that is large for its age will have an otolith that is also large for its age). A positive correlation between fish growth and otolith growth is required for back-calculation using the L_t -O_R relationship to provide appropriate length-at-age estimates. The L_t -O_R relationship was established using measurements to the dorsal edge of the otolith section in the transverse plane. A von Bertalanffy model was fitted to the back-calculated data as well to estimate theoretical growth and then was compared to a von Bertalanffy curve developed from corresponding observed data. Back-calculated data in the growth model consisted of only back-calculations to the last annulus to avoid repeated measures (Vaughan and Burton 1994).

The presence of Lee's Phenomenon was tested for in this study by regressing the mean distance between the core and the 1st annulus against calendar age, as well as the mean distance between the 2nd annulus and the 1st annulus against calendar age. If the slope was significantly different across ages for either of these relationships then it was assumed that Lee's Phenomenon is present.

Since many red snapper aging studies (Patterson et al. 2001; Wilson and Nieland 2001; White and Palmer 2004), including this one, have counted annuli along the sulcal groove to the proximal edge of the otolith, this measurement axis could be assumed to be the best for use in back-calculation as well. A previous study on Atlantic red snapper did measure annuli along the sulcal groove (White and Palmer 2004). In this study, the measurements were taken in the transverse plane as opposed to the sulcal groove because more otolith growth is exhibited in the transverse plane, which should result in a better relationship between fish size and otolith size. If the L_t - O_R relationship fits differently based on the measurement axis used, differences in back-calculated growth may occur. Therefore, a subsample containing measurements in both axes was used to compare L_t - O_R regressions between axes, where it might be determined if differences in methodology affect the consistency of length-at-age estimates. To test these differences, von Bertalanffy models were then constructed using back-calculated data from each measurement axis and plotted together for comparison.

As another test for differences in growth among groups (i.e., geographical area, fishery type, and regulatory period), the distance from the core to the first annulus for red snapper ages 2 – 5 years was compared using ANOVA. Because the distance to the first annulus can depend on the time of year the fish is spawned, as well as how fast the fish grows, results using only the first annulus measurements for this test may be hard to interpret or may provide misleading results. Therefore, the distance between the first and the second annuli for ages 2 – 5 was also compared with ANOVA.

RESULTS

A total of 6553 sagittal otoliths taken from Atlantic red snapper were archived between 1977 and 2006. Two sets of otoliths contributed to the collection of samples explored in this analysis. Set 1 (n = 6031) contained samples that spanned the entire collection period between 1977 and 2006. Set 2 (n = 522) was comprised of a subsample taken from 1988 to 1996. Lengths and ages from Set 2 were included in this study in order to provide a more complete analysis of red snapper in the Atlantic by filling in data gaps in Set 1 (Table 2).

Age Validation

Since annuli have not been directly validated for red snapper otoliths, indirect validation was required to ensure that opaque zones were forming once a year and could be counted as annuli. A total of 4263 samples (70.7% of set 1) was measured and used to determine the timing of annulus formation.

As fish age, marginal increments (MI) decrease in size and can be harder to measure. To ensure pattern consistency of mean MI across months, separate analyses were done for ages 2 – 4 and then plotted together (Figure 3). The lowest MI occurred in the month of April and then steadily increased. This pattern was the same for all three

Table 2. Number of red snapper samples collected by year, fishery and area for this study. Number in parentheses represents the count of the total coming from Manooch and Potts (1997) for each category. "C" refers to Commercial, "R" refers to Recreational, and "Unknown" refers to those samples where a fishery was not defined. "FL" refers to Florida and "NC/SC/GA" refers to North Carolina, South Carolina, and Georgia.

Area	FL			Total FL	NC/SC/GA			Total NC/SC/GA	Grand Total
Year/Fishery	C	R	Unknown		C	R	Unknown		
1977		62		62		12		12	74
1978		276		276		7		7	283
1979		46		46		1		1	47
1980		90		90		8		8	98
1981		424		424		3		3	427
1982		133		133		3		3	136
1983		766		766		8		8	774
1984		609		609		30		30	639
1985		527		527		13		13	540
1986		187		187		11		11	198
1987		100		100		1		1	101
1988		19		19	33(33)	4		37	56
1989		26		26	5(5)	34		39	65
1990		22(15)	62	84	28(28)	15(15)	1	44	128
1991		21(21)	4	25	19(19)	7(6)		26	51
1992	16	4(4)		20	33(33)	9(9)		42	62
1993	7	9(7)		16	30(30)	11(9)	1	42	58
1994	1	19(3)		20	44(44)	6(2)		50	70
1995	16(3)	15(3)		31	8(8)	4(3)		12	43
1996	131(103)	33(10)		164		92(40)	1	93	257
1997	64	16		80					80
1998	57	8		65					65
1999	13			13					13
2000	47	5		52					52
2001	146	79		225					225
2002	37	412		449		4		4	453
2003	49	412		461	2	2		4	465
2004	66	342		408	39	3		42	450
2005	47	273		320	95	6		101	421
2006	48	14		62	148	12		160	222
Grand Total	745	4949	66	5760	484	306	3	793	6553

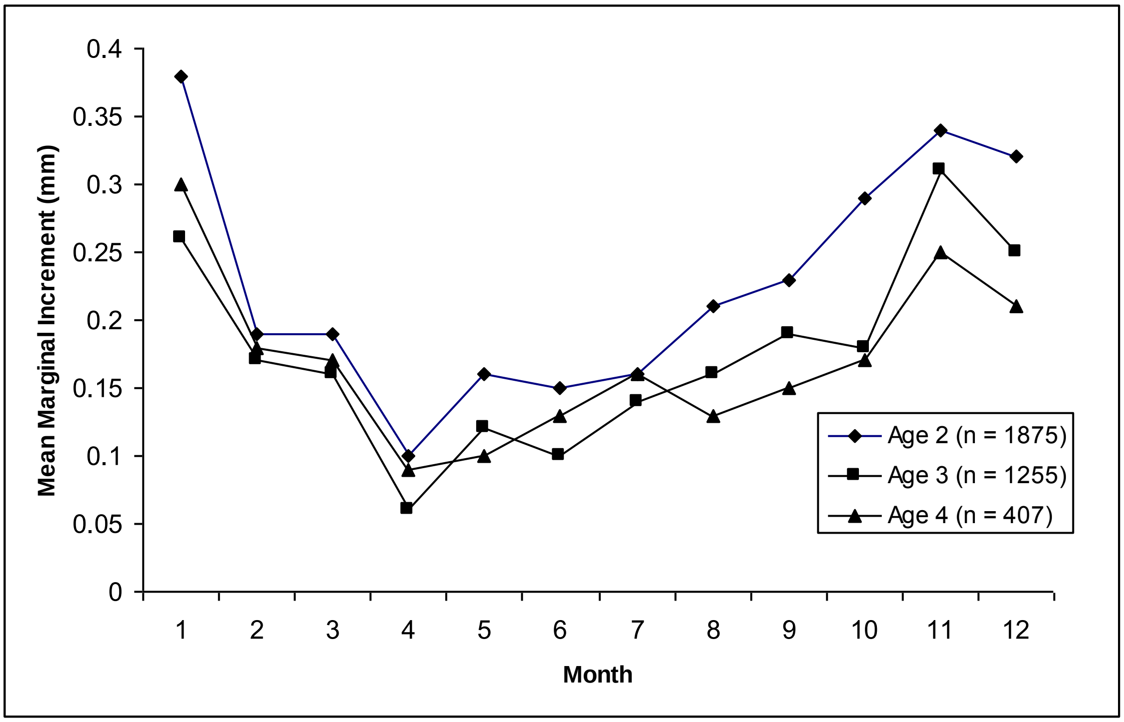

Figure 3. Mean marginal increment plotted against month for red snapper ages 2-4 years.

ages. When the percentage of opaque edges was plotted against month (Figure 4), April was also the month with the highest number of otoliths containing opaque edges. Thus, it was determined that opaque zones were forming in the late winter/early spring and most were formed completely by the month of April.

Aging Consistency

Aspects other than the first annulus can cause difficulty in aging red snapper. On some otoliths, opaque zones were so diffuse in the transverse plane that double annuli appeared along the sulcal groove (Figure 5). This could generate differences in opaque zone counts depending on the reader's choice of counting axis. For this study, opaque zones were only counted if they were separated by a clear translucent zone and could be followed out from the sulcal groove to the transverse plane. In some cases, striations were visible on the otolith section due to variations in the growth of the crystalline matrix that makes up the otolith (Figure 6) or if the otolith was only partially formed or completely aberrant (Figure 7). Both irregularities would cause the otolith to be extremely difficult to read or entirely unreadable. When an opaque zone count could not be detected for an otolith, it was removed and was not used in any age analyses. Of the 6553 samples in this study, 6378 (97.3%) were readable.

The average percent error, or APE, for calendar ages within samples by the primary investigator was 2.01 % and for calendar ages between readers, it was 4.65 %. An APE of less than 5 % is considered acceptable (Beamish and Fournier 1981), therefore, consistency within and between readers was accomplished.

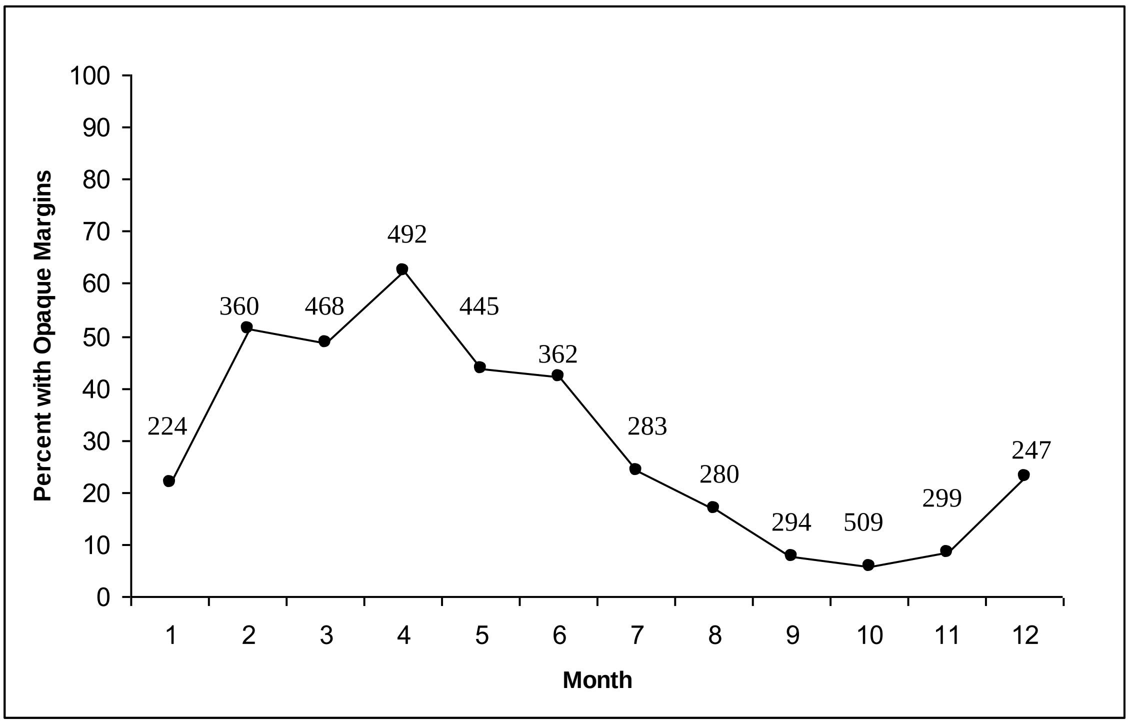

Figure 4. Percent of red snapper otolith sections with opaque margins by month. Numbers above data points represent sample size for each month.

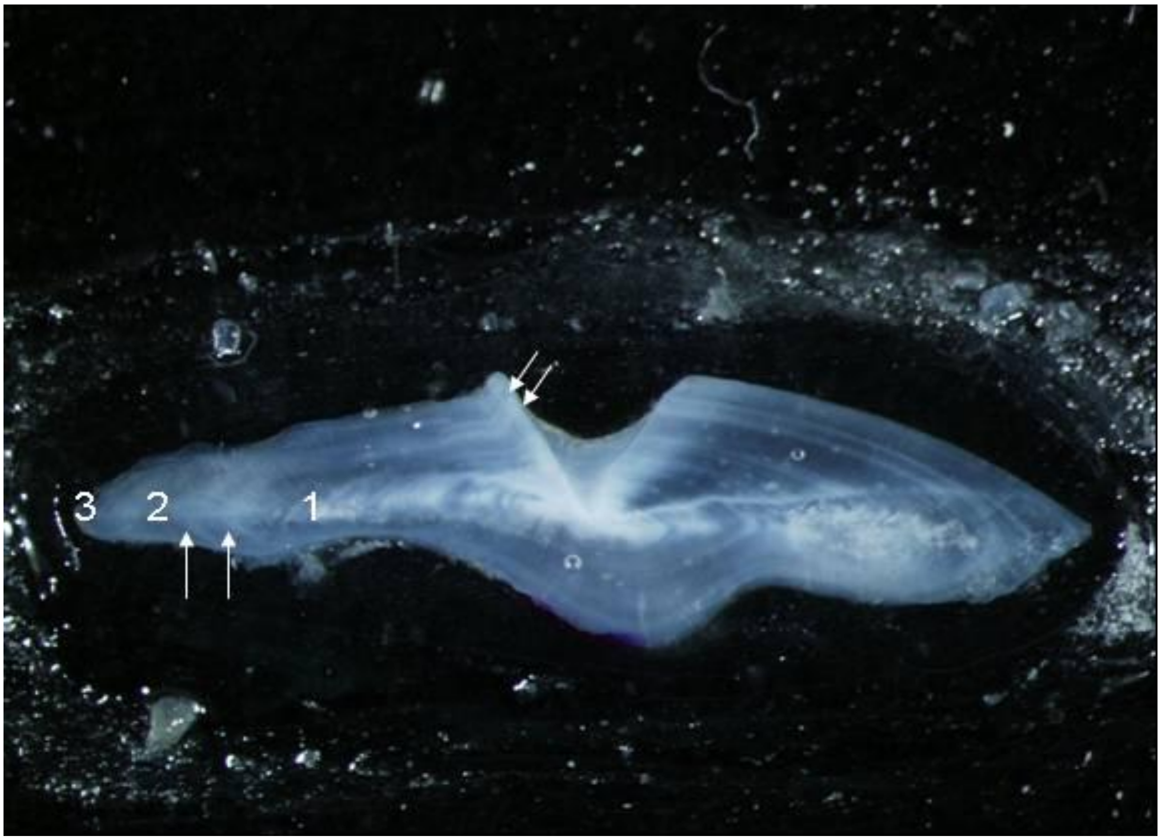

Figure 5. Red snapper otolith section with arrows indicating possible double annuli on the sulcal groove and in the transverse plane around the 2nd annulus.

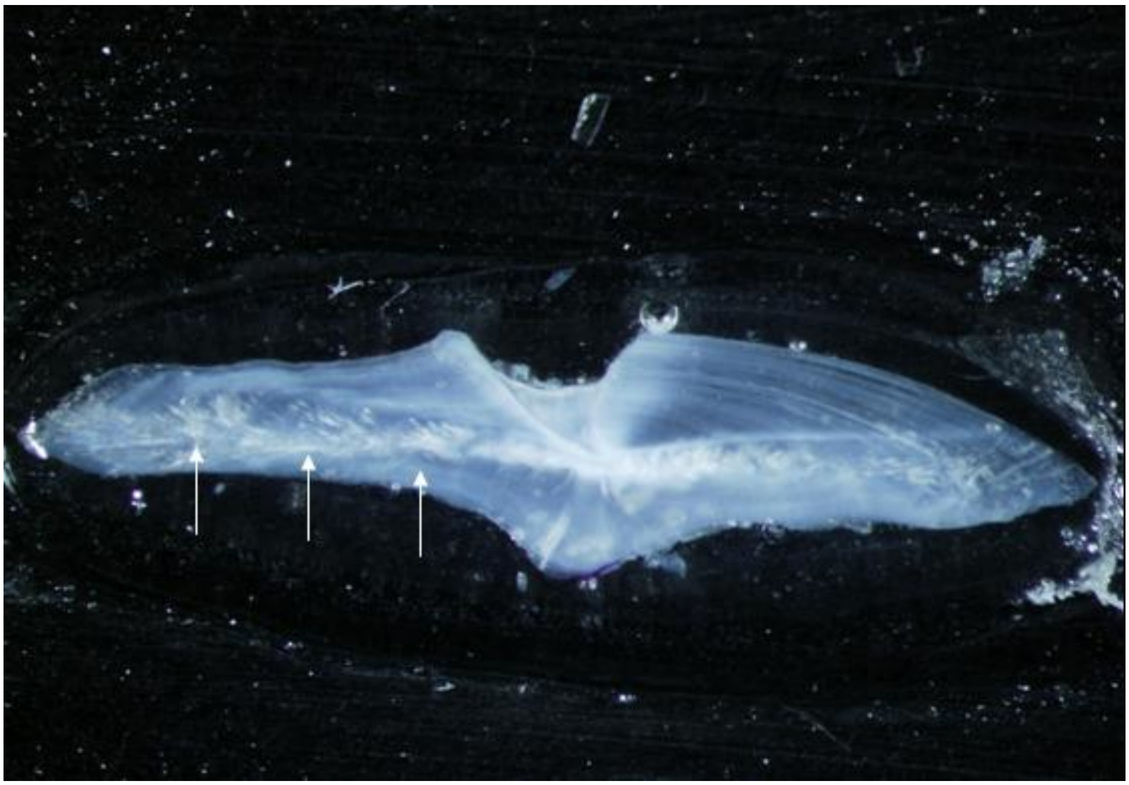

Figure 6. Red snapper otolith section with arrows indicating striations in the crystalline matrix.

Figure 7. Aberrant red snapper otolith section.

Length Analysis

Red snapper in this study ranged from 197 to 1001 mm total length with a mean total length of 573 mm. Females (n = 793) ranged from 258 – 956 mm total length and males (n = 838) ranged from 280 – 955 mm total length. When mean length over all samples was compared between sexes, there was no significant difference found between male (mean total length = 577 mm) and female (mean total length = 571 mm) red snapper (P = 0.46). Therefore, males and females were combined in all further analyses.

ANOVA was used to test for significant differences in mean total length among geographical area, fishery type, and regulatory period. When testing between areas, only fish caught by the commercial fishery between 2003 and 2006 were used. This subsample was chosen to balance sample size between areas and to remove the potential effects of different regulatory periods and fishery type. When lengths between fisheries were tested, only fish caught in Florida between 2001 and 2006 were used. This subsample was also chosen to balance sample size between fisheries and to remove potential effects of different regulatory periods and areas. All fish were used in the test between regulatory periods.

The ANOVA revealed a significant difference in mean length between areas (P = 0.01). Within this subsample, fish caught in the Carolinas were significantly larger than those caught in Florida (Table 3). The subsample test between fisheries showed there was no significant difference (P = 0.34) in mean length of fish caught by the commercial fishery and those caught by the recreational fishery (Table 3). The mean total length for all fish was 430mm, 399mm, and 616mm during the no regulation period, the FMP period, and the Amendment 4 period, respectively (Table 3). Mean total length of the fish from the

Table 3. Mean, standard error, and range of total length for red snapper subsampled for comparison by regulatory period (a), geographical area (b), and fishery type (c). Comparisons by regulatory period include all sampled red snapper. Subsample for area comparison includes only commercially caught fish from 2003 – 2006. Subsample for fishery comparison includes only Florida caught fish from 2001 – 2006.

a)

Regulatory Period	n	Mean (mm)	se	Range (mm)
No regulation (1977-1982)	1065	430	117.19	220 - 905
FMP (1983-1991)	2552	399	99.93	197 - 979
Amendment 4 (1992-2006)	2936	616	113.77	220 - 1001
Total	**6553**			

b)

Area	n	Mean (mm)	se	Range (mm)
FL	210	633	109.15	429 - 967
NC/SC/GA	284	705	103.19	470 - 960
Total	**494**			

c)

Fishery	n	Mean (mm)	se	Range (mm)
Commercial	393	636	109.79	429 - 967
Recreational	1532	591	98.77	430 - 956
Total	**1925**			

Amendment 4 period was much larger than fish from the other two periods.

When fish lengths between regulatory periods were compared, there was a significant interaction between calendar age and regulatory period ($P < 0.0001$). Therefore, simple effects from the ANOVA model were studied in more detail. The simple effects associated with the interaction term were analyzed to reveal that for age 2 and age 3 red snapper, mean total lengths during the no regulation and the FMP periods were significantly smaller than lengths of fish caught during the Amendment 4 period ($P < 0.0001$) (Table 4). For age 4 and 5 red snapper, mean total length during the FMP period was significantly smaller than during the no regulation and Amendment 4 periods ($P < 0.0001$) (Table 4). The subsamples used to test for differences in mean length were also used to test for differences in mean age and mean length-at-age between area, fishery, and regulatory period.

Age Structure

Calendar ages for Atlantic red snapper ranged from 1 to 54 years and fractional ages ranged from 0.5 to 53.67 years. A significant difference in mean age was found within the subsamples between geographical areas, fishery types, and regulatory periods ($P < 0.0001$). Red snapper from Florida were significantly younger than fish caught from the Carolinas, with a mean age of 4.5 years from Florida and a mean age of 6.4 years from North Carolina, South Carolina, and Georgia (Figure 8).

The commercial fishery selected for older fish with a mean age of 4.7 years, whereas, red snapper from the recreational fishery averaged around 3.8 years (Figure 9). When regulatory periods were tested, the Amendment 4 period (mean age = 4.7) included

Table 4. Mean total length in mm for all sampled red snapper, ages 2 – 5 years, by regulatory period.

Age	No regulation	FMP	Amendment 4
2	384	378	513
3	435	432	543
4	580	473	614
5	679	574	672

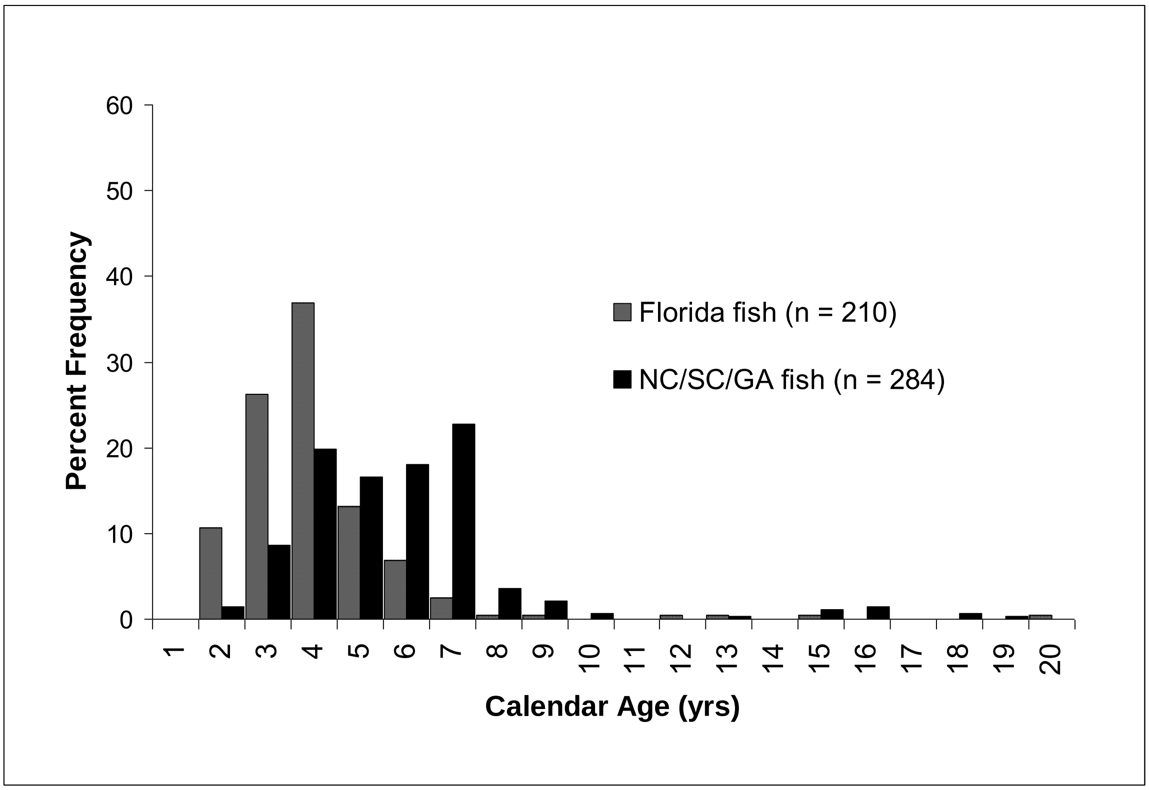

Figure 8. Relative frequency of calendar age for subsampled red snapper up to age 20 by area. Subsampled red snapper included only commercially caught fish from 2003 – 2006.

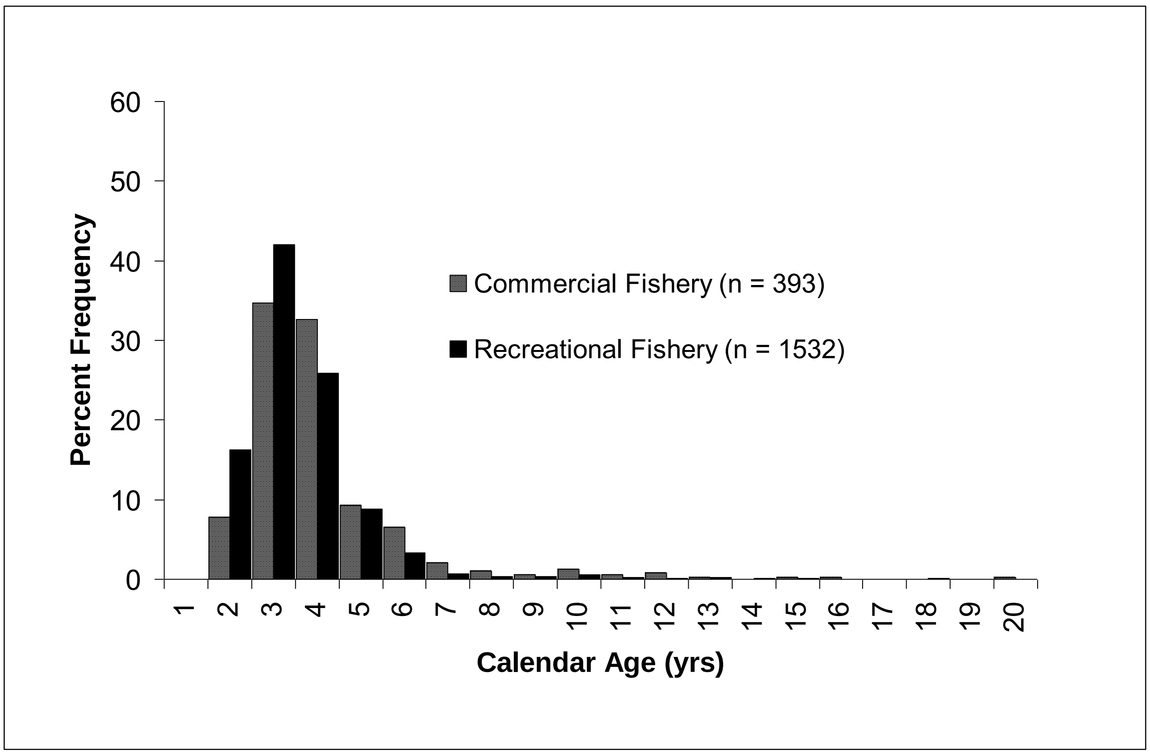

Figure 9. Relative frequency of calendar age for subsampled red snapper up to age 20 by fishery type. Subsampled red snapper included only Florida caught fish from 2001 – 2006.

significantly older fish than either the no regulation (mean age = 2.7 yr) or the FMP (mean age = 2.5 yr) periods (Figure 10). The maximum age between regulatory periods showed to be different with a maximum age of 25, 30, and 54 years in the no regulation, FMP, and Amendment 4 periods respectively, although this difference was not tested statistically.

When percent frequency of red snapper calendar ages was plotted for each year from 1977 – 2006, several cohorts could be followed throughout the fishery year after year (Figure 11) that may indicate the presence of strong year classes in the fishery. Frequency plots showing age progressions across years suggest that strong year classes were present in 1983, 1984, 1986 – 1989, 1991 – 1993, 1996, and 1999 – 2001. These cohorts could be followed through the fishery for as long as 5 – 8 years, first appearing most commonly as age 2 and 3 fish. Moderate to strong year classes appeared to occur every 2 – 4 years. Prior to 1983, large pulses of 2 and 3 year old red snapper were entering the fishery indicating possible strong year classes, but these cohorts could not be followed after age 3.

Length-at-age

Length and age were combined to create an age-length key (Table A.1). The key shows the percentage of red snapper at specific ages within 25 mm length classes. The resolution observed in the age-length key indicated that it may be a useful tool for approximating red snapper age when only total length data is available.

Based on the P-values from multiple ANOVAs, there was no significant difference in length-at-age between red snapper caught off Florida and those caught off

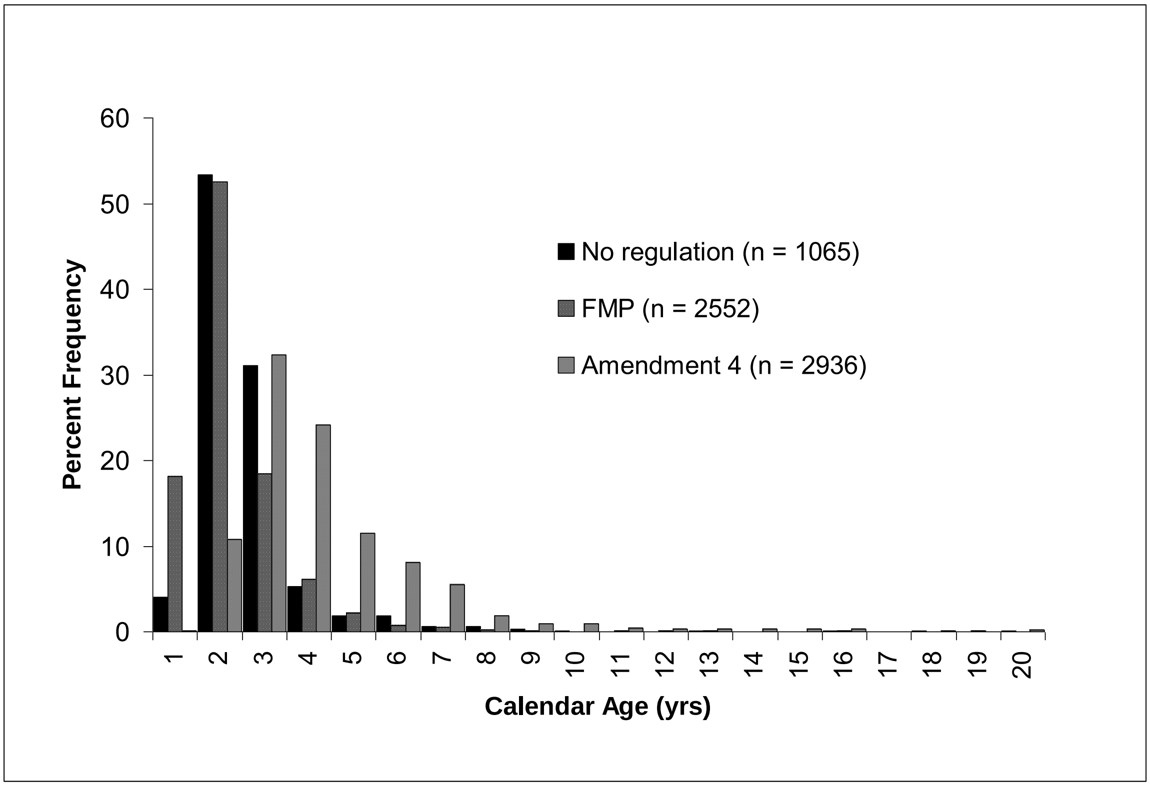

Figure 10. Relative frequency of calendar age for all red snapper up to age 20 by regulatory period.

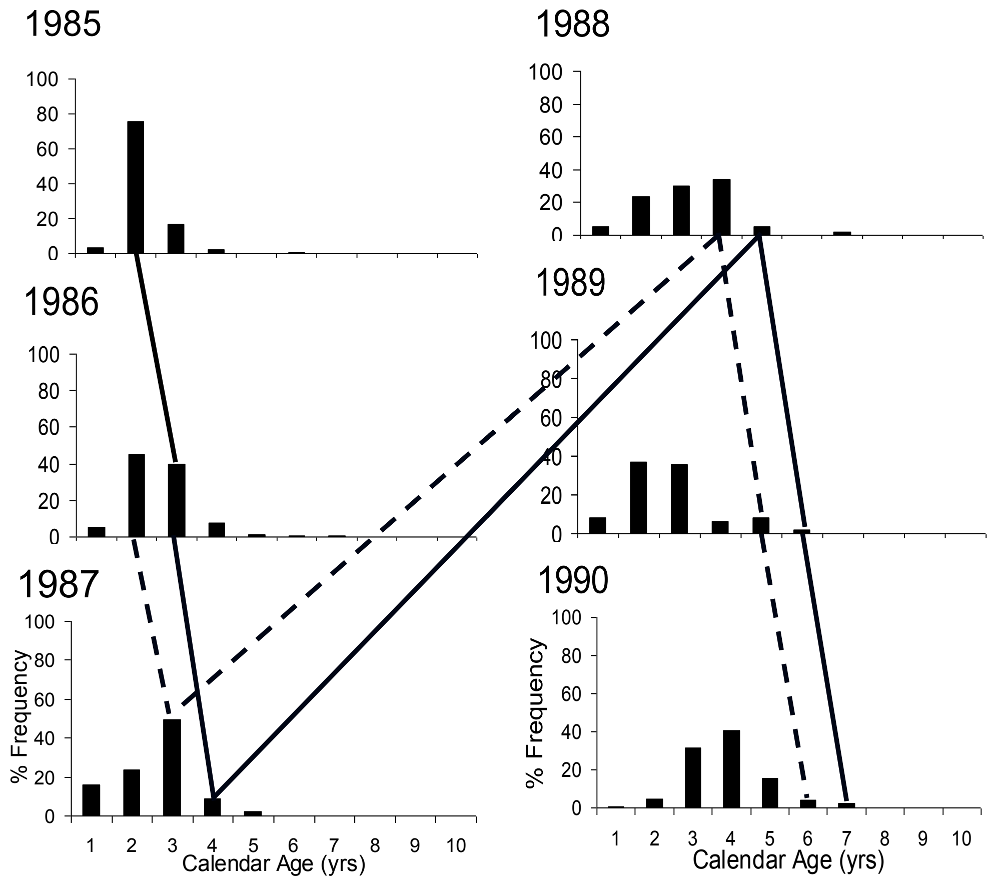

Figure 11. Age frequency plots for red snapper from 1985 to 1990 showing strong year classes in 1983 (solid line) and 1984 (dotted line).

the Carolinas (all P-values > 0.05) (Table 5). Statistical differences in length-at-age were detected for age 2 and 3 red snapper between commercial and recreational fisheries, with the commercial fishery catching larger individuals at these ages than the recreational fishery ($P < 0.05$) (Table 6). However, the statistical difference was likely an artifact of large sample size in the recreational fishery not matched by the commercial fishery, and the modest (25mm) differences between mean length-at-ages 2 and 3 could be interpreted as biologically insignificant.

Length-at-age comparisons between regulatory periods revealed the same results as the test for simple effects in the mean length model (Table 7). Age 2 and 3 red snapper were significantly smaller during the no regulation and FMP periods compared to the Amendment 4 period, and 4 and 5 year old fish were significantly smaller during the FMP period than during the other two periods. Age 1 fish were found to be significantly smaller during the Amendment 4 period as well, but the standard error associated with the mean length at age 1 was extremely high due to the lack of samples for this age in the later time period (Table 7). Therefore, differences in length at age 1 during the Amendment 4 period could not reliably be compared to the other periods.

Collectively, results indicate no difference in growth between geographical areas or fishery types, but highly significantly differences in length-at-age were found between regulatory periods.

Table 5. Comparison of mean total length (TL in mm) at age between areas for subsampled red snapper. Subsample includes only fish caught by the commercial fishery between 2003 and 2006.

	Florida			NC/SC/GA			
Calendar age	n	TL	se	n	TL	se	p-value
2	22	522	5.337	4	523	12.366	0.9418
3	54	561	8.480	24	540	5.485	0.1287
4	76	629	7.840	55	613	8.858	0.1784
5	27	708	14.746	46	698	9.880	0.5325
6	14	767	12.210	50	750	6.331	0.2083
7	5	800	12.944	63	761	6.375	0.0965
8	1	758		10	773	10.134	0.6626
9	1	837		6	793	14.498	0.3031
10				2	833	26.605	
12	1	848					
13	1	917		1	796		
15	1	927		3	815	37.749	0.2772
16				4	852	15.558	
18				2	888	2.500	
19				1	860		
20	1	967					
21				1	950		
24				1	940		
26				1	960		
28				1	925		
31				1	815		
38	1	939					
42				1	925		
44	1	954					

Table 6. Comparison of mean total length (TL in mm) at age between fishery types for subsampled red snapper. Subsample includes only fish caught off Florida between 2001 and 2006. Significant P-values are in bold.

	Commercial			Recreational			
Calendar age	n	TL	se	n	TL	se	p-value
2	30	529	6.186	242	512	2.187	**0.0122**
3	134	565	4.596	627	540	1.880	**<0.0001**
4	126	629	5.683	387	621	3.087	0.2375
5	36	723	12.673	131	714	4.984	0.4591
6	25	755	12.807	50	771	7.828	0.2665
7	8	794	8.727	11	797	15.852	0.8715
8	4	817	19.872	6	745	41.613	0.2253
9	2	790	46.980	6	865	20.152	0.1296
10	5	844	15.641	9	850	15.007	0.7780
11	2	856	15.295	3	845	28.340	0.7890
12	3	886	25.862	2	876	17.820	0.8078
13	1	917		3	895	4.424	0.1311
14				2	860	31.320	
15	1	927		1	910		
16	1	864					
18				1	865		
20	1	967					
22	1	849					
23				1	876		
24				2	917	24.840	
25	1	929					
27	1	931		1	840		
29				1	878		
32				1	865		
33				1	955		
35	1	903					
37	1	935		1	916		
38	1	939		1	956		
40				1	739		
44	1	954					
51				1	907		
54				1	826		

Table 7. Comparison of mean total length (TL in mm) at age between regulatory periods for all red snapper. Significant P-values are in bold.

	No Regulation			FMP			Amendment 4			
Calendar age	n	TL	se	n	TL	se	n	TL	se	p-value
1	42	307	7.350	446	328	2.141	2	290	70.375	**0.0115**
2	556	384	2.226	1296	378	1.330	310	513	2.198	**< 0.0001**
3	324	435	4.091	456	432	3.622	929	543	1.795	**< 0.0001**
4	55	580	10.964	150	473	8.217	692	614	2.762	**< 0.0001**
5	19	679	18.647	54	574	15.089	331	672	5.286	**< 0.0001**
6	19	749	15.406	18	688	22.911	232	706	6.079	0.0939
7	7	771	9.508	12	722	26.649	157	722	6.507	0.2989
8	7	802	16.577	4	803	35.227	54	742	10.450	0.0563
9	3	856	13.860	2	822	16.000	27	800	12.556	0.3354
10	1	858		1	766		28	837	11.390	0.4849
11				3	843	21.942	13	824	13.456	0.5364
12				2	874	2.500	9	864	17.813	0.816
13	1	881		2	857	4.500	9	846	17.741	0.7923
14				1	930		10	859	18.463	0.2742
15							8	872	26.990	
16	1	806		2	848	2.500	8	880	15.528	0.235
17				1	847		1	865		
18	1	905		1	870		3	880	7.602	0.3379
19				2	890	37.500	1	860		0.7262
20	1	804					5	899	19.184	0.114
21	1	850		1	917		2	904	46.500	0.7877
22	1	840		1	885		1	849		
23	1	892					3	889	7.029	0.8498
24				2	877	23.000	4	930	12.791	0.089
25	1	900					3	929	4.909	0.100.
26				1	880		1	960		
27				2	923	56.500	2	885	45.495	0.6607
28				1	905		1	925		
29				2	888	7.500	1	878		0.6003
30				3	892	11.151				
31							2	838	22.500	
32							2	918	52.445	
33							1	955		
34							1	850		
35							2	920	16.740	
37							2	926	9.720	
38							2	947	8.640	
40							1	739		
41							1	913		
42							1	925		
44							4	913	15.730	
47							1	969		
51							1	907		
54							1	826		

Growth Models

Weight-Length Relationship

Only 3209 samples out of the 6553 contained weight data that could be used to estimate a weight-length relationship for red snapper. Weights ranged from 112 to 15,475 g and total length ranged from 197 to 1,001 mm. Since mean lengths were not significantly different by sex, a weight-length relationship was estimated for the sexes combined, and was described as:

$W = 1.20 x 10^{-5} L^{3.05}$ (MSE = 0.01; R^2 = 0.97) (Figure 12).

von Bertalanffy Growth Models

Von Bertalanffy growth models can be used to test for differences in growth between populations and distributions as well as between different methodologies for estimating the von Bertalanffy parameters.

Size limit corrected (Diaz et al. 2004) and uncorrected von Bertalanffy growth curves were very similar; however, the corrected model produced smaller lengths at age than the uncorrected model (Figure 13). In most cases, there was only a slight difference in estimated lengths at age between models, but for ages 1 – 4, the difference was greater. The young ages (ages 2 – 5) are most affected by the 508 mm minimum size limit (Table 8). Since most fish in this age range would have been the faster growers in order to be caught at 508 mm, this would result in larger estimates of length-at-age for these ages than for others. The corrected model accounts for the effects of size-selective fishing and results in lower length-at-age estimates for the ages most affected by the size limit.

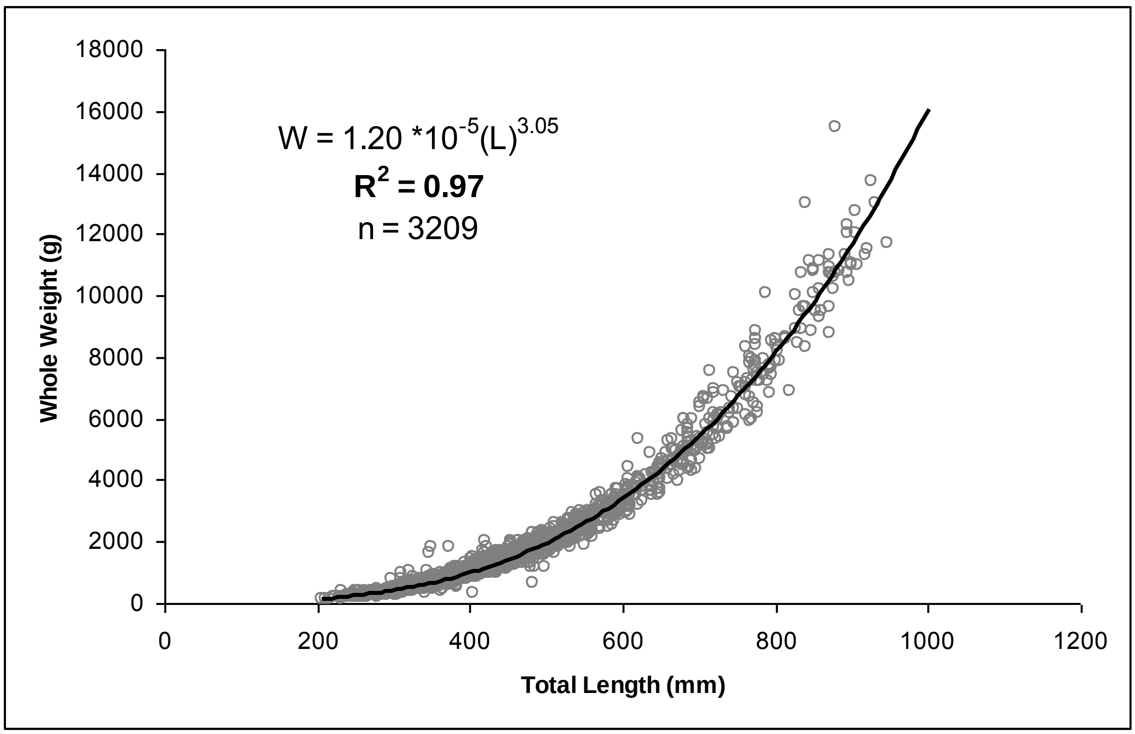

Figure 12. Weight – length relationship for Atlantic red snapper.

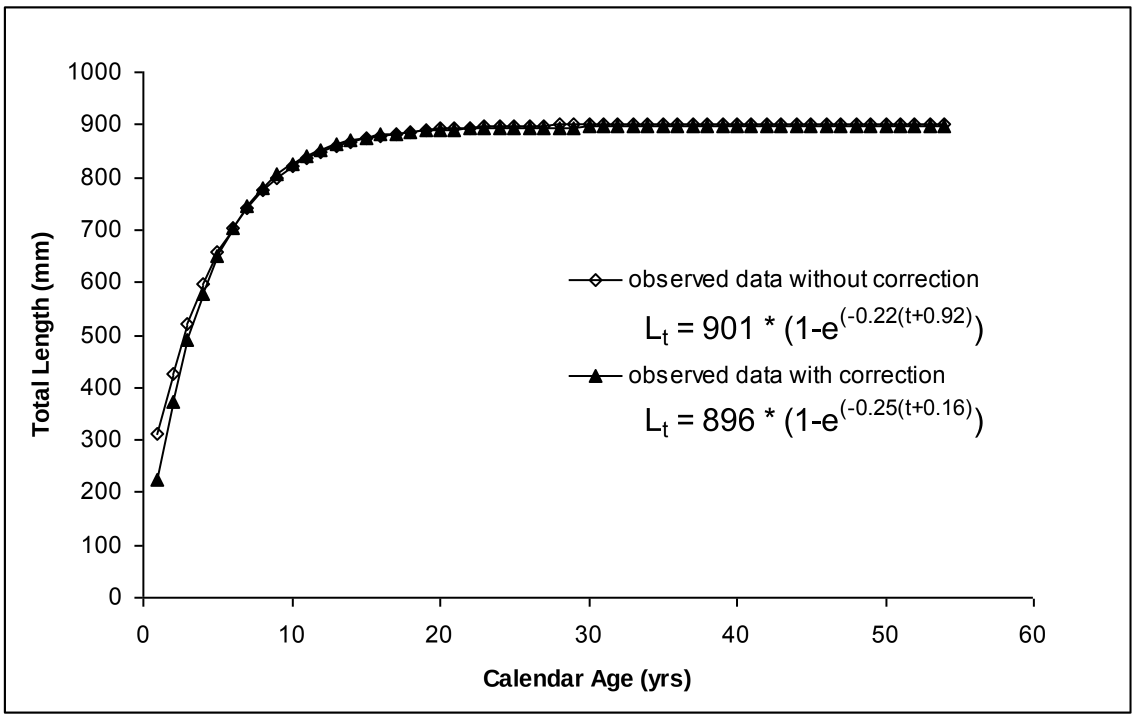

Figure 13. Comparison of von Bertalanffy curves calculated from observed data before and after correcting for size limit changes for red snapper landed in the U. S. South Atlantic.

Table 8. Percentage of red snapper ages 1 – 6 from the "no regulation" period large enough to be selected by a 508 mm total length minimum size limit.

Age	Percentage	n
1	0.00%	42
2	1.62%	556
3	16.98%	324
4	78.18%	55
5	94.74%	19
6	100.00%	19

Total Length – Otolith Radius Relationship

Residuals from otolith radius (O_R) vs. calendar age and total length (L_t) vs. calendar age regressions were plotted against each other to determine if there was a positive correlation between the fish growth and otolith growth. The plot (Figure 14) and a test for correlation (PROC CORR) indicated there was a strong, positive correlation between O_R and L_t ($R = 0.72$; $P < 0.0001$). When total length was regressed on otolith radius, a strong linear relationship was detected ($R^2 = 0.91$) (Figure 15). Therefore, a linear equation was incorporated into the body proportionality hypothesis (Francis 1990) when back-calculating for lengths.

When testing for Lee's Phenomenon, the two regressions, one using mean measurements to the 1st annulus at age and the other using mean measurements between the 2nd and the 1st annulus at age produced different results. The regression using only the 1st annulus reported a significant difference in slope across ages ($P = 0.003$; $R^2 = 0.50$) suggesting the presence of Lee's Phenomenon in the data. However, the regression using the 1st and 2nd annulus revealed no significant difference in slope across ages ($P = 0.62$; $R^2 = 0.02$) possibly indicating that Lee's Phenomenon was not present.

Von Bertalanffy growth curves were developed using back-calculated lengths to the last annulus from fish ranging from 1 – 20 years of age and also from observed data (total length and fractional age) corresponding to those fish used for back-calculation. After twenty years of age, primary otolith growth for this species changes axes from transverse to vertical growth. These two curves were plotted together for comparison to determine if there were differences in the length-at-age estimates from each curve. Back-calculated length-at-age estimates appear slightly lower than the observed estimates for

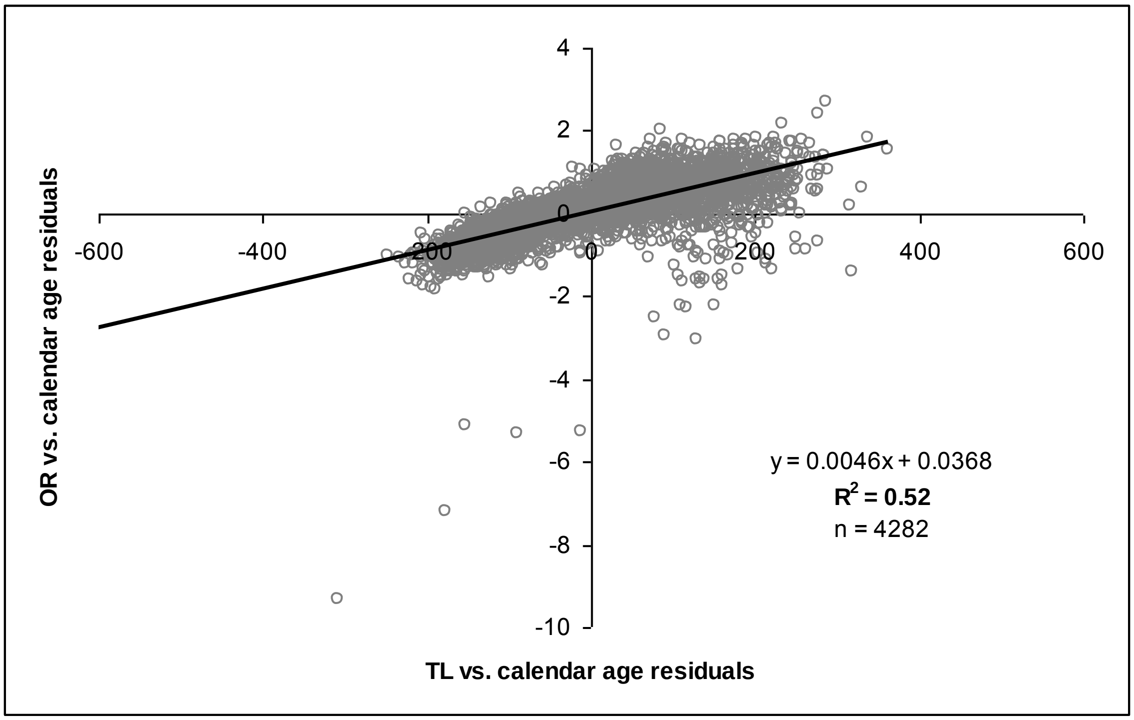

Figure 14. Residuals from otolith radius vs. calendar age regression plotted against residuals from total length vs. calendar age regression for red snapper landed in the U. S. South Atlantic.

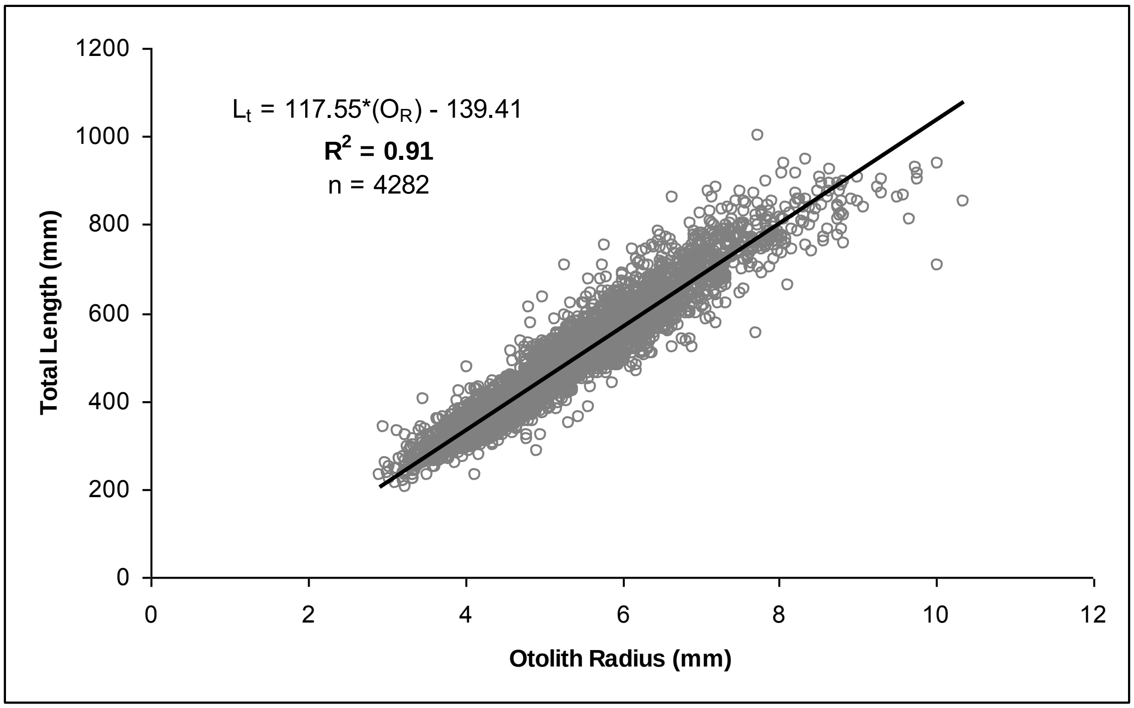

Figure 15. Red snapper total length – otolith radius relationship for all otolith sections measured in the transverse plane.

red snapper 2 – 9 years of age; but at ages over 10 years old, observed estimates are slightly lower than back-calculated lengths at age (Figure 16). Overall, the difference in length-at-age is 40 mm at most, which may not be biologically significant. Therefore, there appears to be no appreciable difference in theoretical growth between the observed data using fractional age and the back-calculated data to the last annulus. A back-calculated table was developed to show mean back-calculated total lengths at the last annulus as well as all previous annuli (Table A.2).

Separate L_t – O_R regressions were fit for each measurement axis for the subsample of otoliths that were measured in both axes. Red snapper in the subsample ranged from 1 – 8 years of age. Both sets of measurements resulted in linear L_t – O_R relationships. The relationship developed using otolith measurements taken along the sulcal groove (R^2 = 0.76) (Figure 17) was more variable compared to the relationship using measurements taken in the transverse plane (R^2 = 0.93) (Figure 18).

Separate von Bertalanffy curves were also developed for each axis using back-calculated lengths at the last annulus resulting from their corresponding L_t – O_R regressions. When these two curves were plotted together, it was apparent that the curves were nearly identical and that there would not likely be any difference in lengths at age estimated from these models (Figure 19).

von Bertalanffy Model Comparison

Significant differences in size-at-age only appeared between regulatory periods; therefore, separate size limit corrected von Bertalanffy growth curves (Diaz et al. 2004) were constructed for each period and plotted together for comparison (Figure 20).

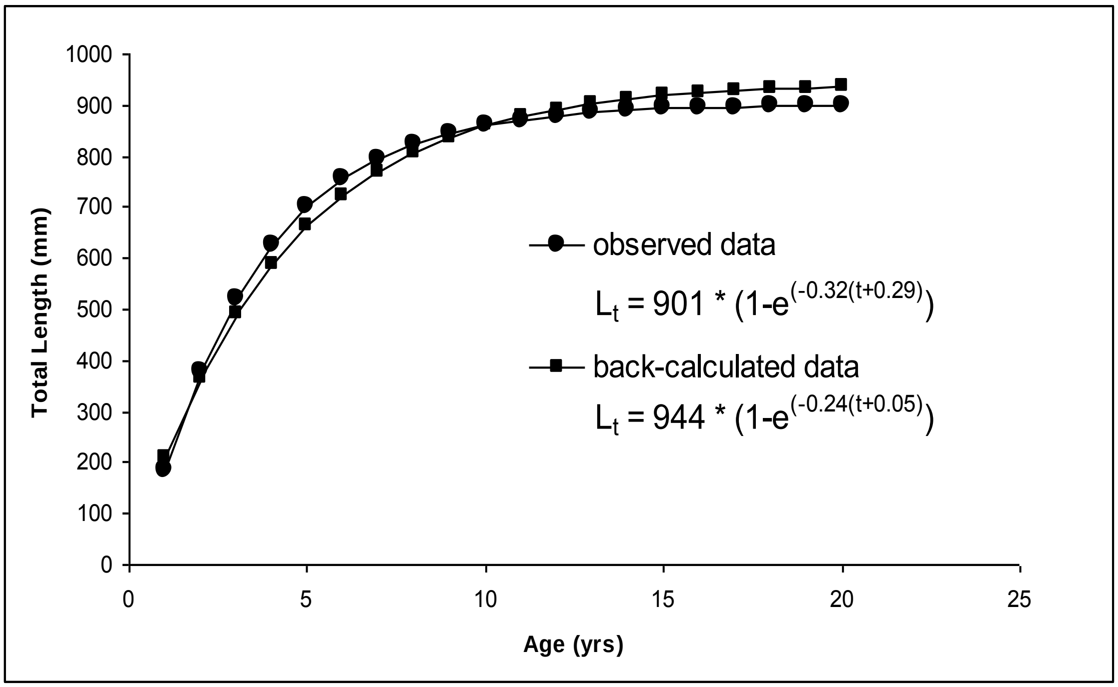

Figure 16. Comparison of von Bertalanffy curves, corrected for size limit effects, modeled on observed lengths and fractional age as well as back-calculated lengths to the last annulus formed for Atlantic red snapper up to age 20.

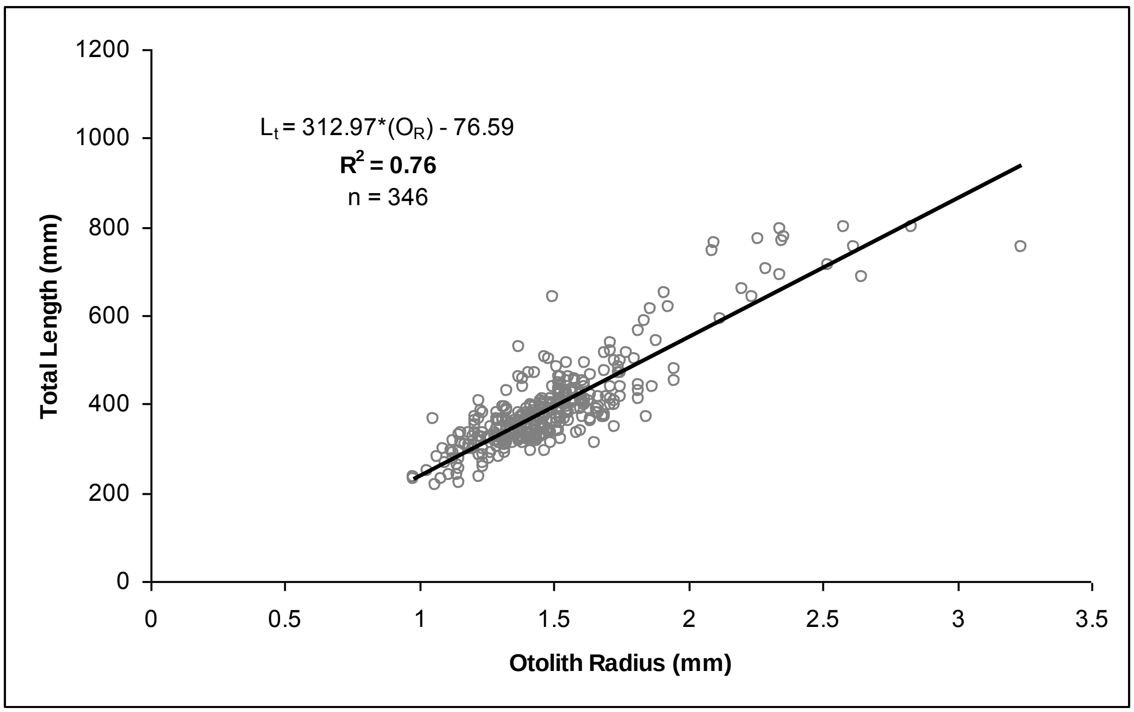

Figure 17. Total length – otolith radius relationship for Atlantic red snapper using measurements taken along the dorsal edge of the sulcal groove.

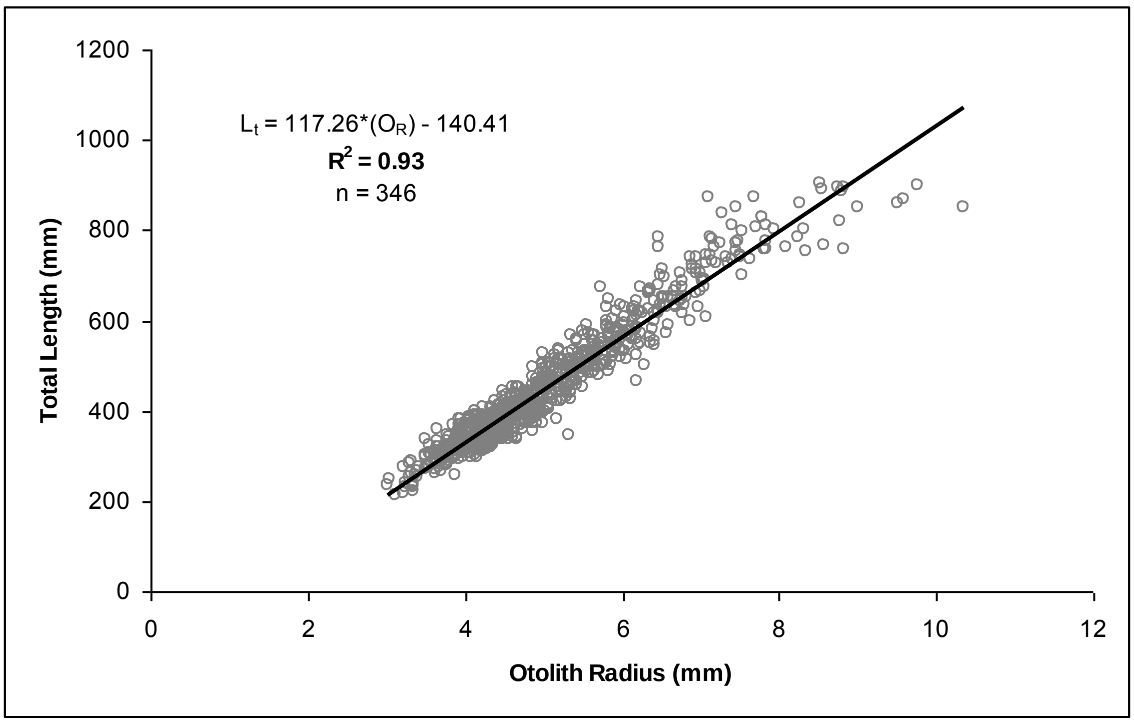

Figure 18. Total length – otolith radius relationship for Atlantic red snapper using measurements taken along the transverse plane.

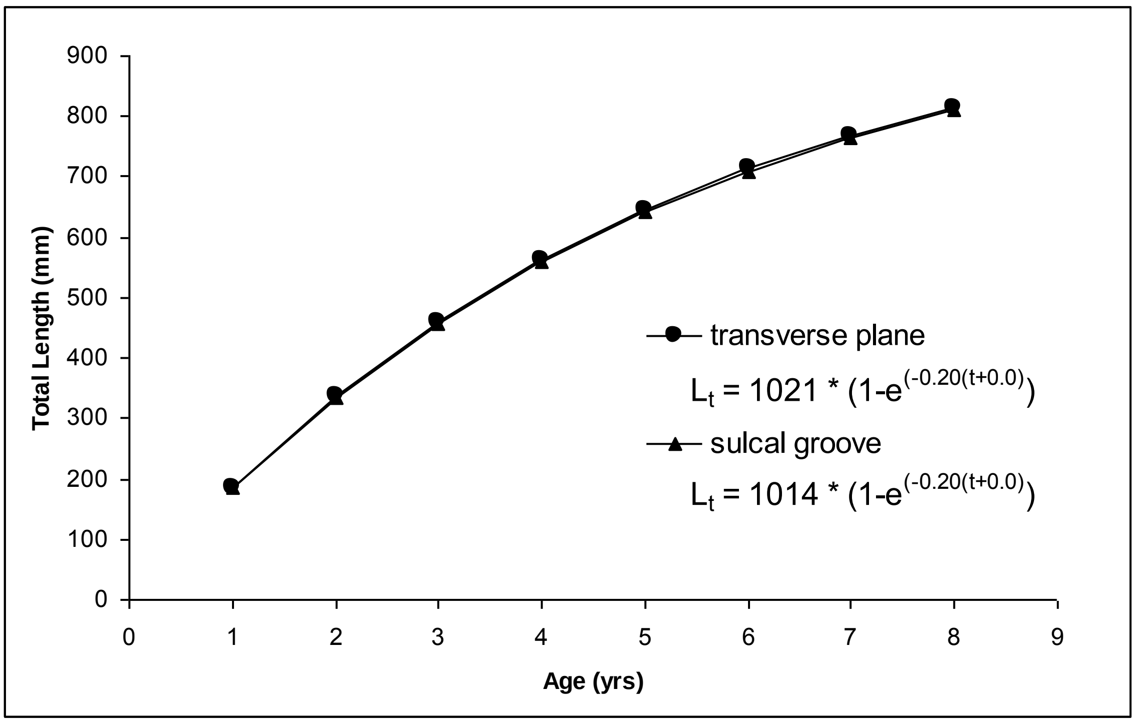

Figure 19. Comparison of von Bertalanffy curves, corrected for size limit effects, for Atlantic red snapper using back-calculated data from measurements taken along the transverse plane and along the sulcal groove.

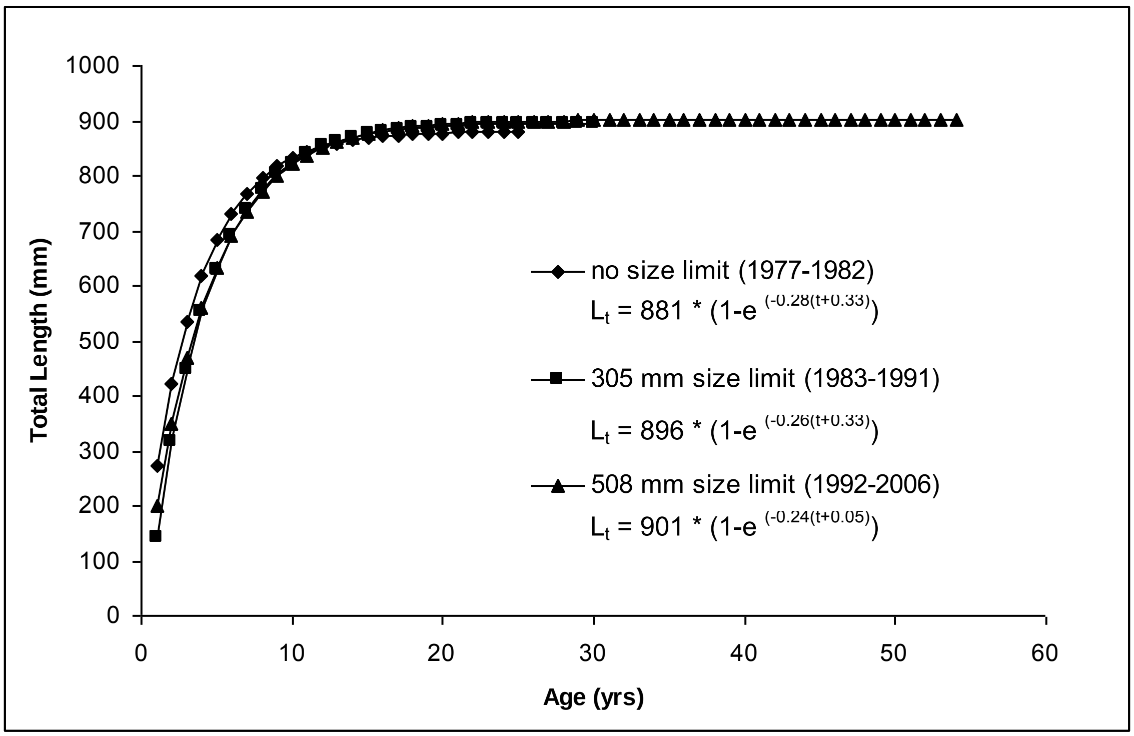

Figure 20. Comparison of von Bertalanffy curves, corrected for size limit effects, across regulatory periods for red snapper in the Atlantic.

When plotted together, the curves showed pattern consistency suggesting that there is no difference in the growth of red snapper between periods. Since there were no noticeable differences in growth between geographical areas, fishery type, or regulatory period, one overall von Bertalanffy growth curve (corrected for size limits) was constructed to represent the entire South Atlantic red snapper population between 1977 and 2006 (Figure 21).

Comparison of 1st Annulus Measurements

When measurements to the first annulus were compared, ANOVA revealed that measurements in the Amendment 4 period were significantly larger than measurements in either the no regulation or the FMP period for red snapper ages 2 – 4 years. There was no difference found for 5-year old red snapper. The comparison of the distance between the first and second annuli showed similar results except that no significant difference was detected for age 4 red snapper as well as age 5.

DISCUSSION

Geographic Variation

This study determined that the mean total length of red snapper off the Carolinas was significantly larger than fish caught off Florida. The initial observation of larger fish off the Carolinas supports Bergmann’s rule that larger individuals of a species exist at higher latitudes (Mayr 1942; Ray 1960). Mean calendar age was also significantly older for fish off the Carolinas than for fish off Florida, indicating that a possible reason for

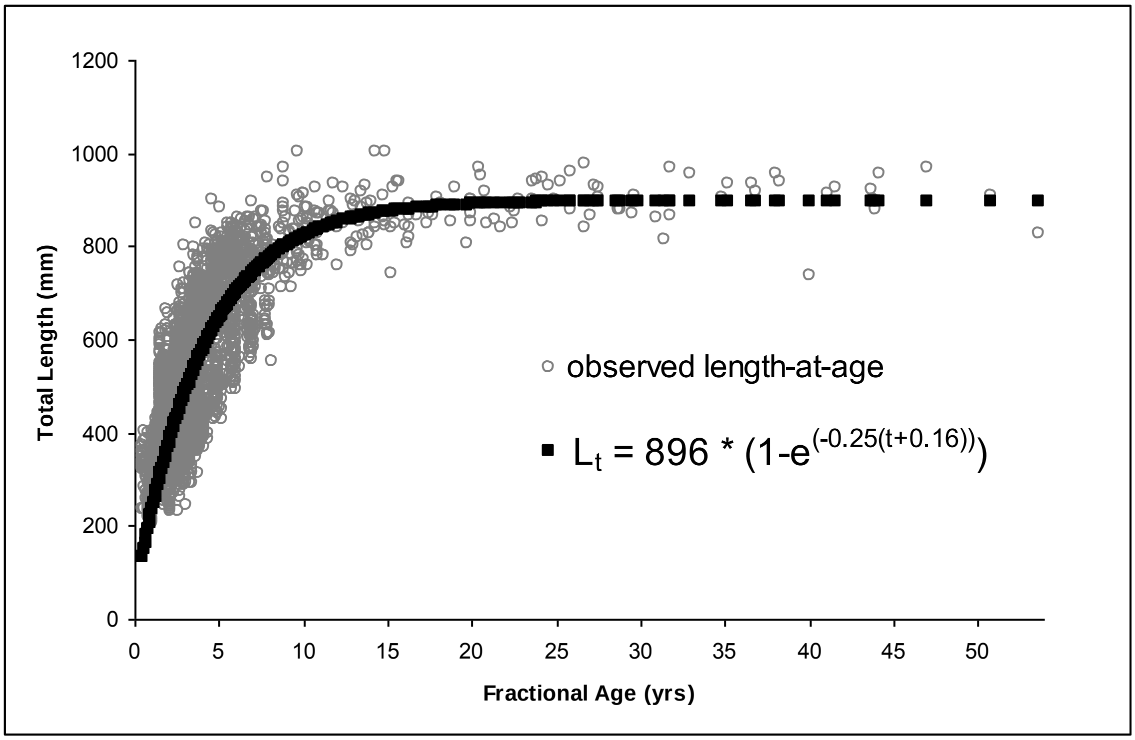

Figure 21. Von Bertalanffy growth curve for all red snapper in South Atlantic from 1977 to 2006.

larger fish is simply the presence of older fish. When lengths at age were compared between geographic areas, there was no significant difference found between fish from the Carolinas and fish from Florida. White and Palmer (2004) also compared lengths at age between latitudes (24.21 N and 34.17 N) corresponding to fish caught in Florida and North Carolina and similarly found no significant difference. Nelson and Manooch (1982) detected statistical differences in red snapper growth between U. S. Atlantic and Gulf of Mexico fish as well as between Florida and North Carolina fish but concluded that differences were small in all comparisons and that data from different areas were similar enough to group together. The results of this study provide further evidence that no considerable differences exist in growth of red snapper among geographic areas.

Fishery Selectivity

Different gear types, depths fished, and fishing experience can often generate variability in the sizes and ages of fish captured by different components of a fishery (Potts et al. 1998; Fitzhugh et al. 2001). White and Palmer (2004) found that on average fishery-dependent fish were significantly larger than fishery-independent fish and only had fishery-dependent data from the commercial fishery so commercial and recreational fisheries could not be compared by the previous study. Other red snapper aging studies from the Atlantic and Gulf of Mexico have not examined differences between fisheries (Nelson and Manooch 1982; Manooch and Potts 1997; Patterson et al. 2001; Wilson et al. 2001). Based on observations in this study, mean lengths were not significantly different between fisheries even though mean ages were different. Comparisons between lengths at age showed that 2 and 3 year old red snapper were significantly larger from the commercial fishery than from the recreational fishery but length differences between the two fisheries (25 mm) at these ages were not likely biologically significant and statistical differences were likely due to a larger sample size in the recreational fishery. However, this significance could suggest that the commercial fishery is selecting for faster growers more intensely than the recreational fishery. Taken as a whole, there were no meaningful differences in red snapper growth between commercial and recreational fisheries in the South Atlantic.

Effects of Management Regulations

The differences in mean length and mean length-at-age detected among regulatory periods for ages 2 through 5, were due to the selectivity brought on by the 508 mm size limit. For ages 2 and 3, the observed differences in mean length could be due to the selection of faster growers after a large increase in the minimum size limit in 1992. The proportions of 2-5 year old fish that are large enough to be selected by the 508 mm size limit in the no regulation period, as well as the comparisons between the distances from the core to the 1st annulus and between the 1st and 2nd annuli suggest this to be true.

Based on length-at-age data collected between 1977 and 1983, when the selectivity of fish was assumed to be equal for all ages, 2% of age 2 and 20% of age 3 red snapper were large enough to be caught if a 508 mm minimum size limit was in effect (Table 8). Based on the fairly small percentages of 2 and 3 year olds, it is likely that the majority of these fish were the faster growers at that age. Significantly larger distances between the otolith core and the 1st annulus suggest that 2 – 4 year old red snapper sampled during the Amendment 4 period were faster growers than fish sampled during the other two periods. Furthermore, distances between the 1st and 2nd annuli were also larger for 2-3 year old red snapper captured between 1992 and 2006 (Amendment 4 period), indicating that these fish were growing faster than fish of the same age during the other two regulatory periods. On the contrary, faster growth seen in the first 2 years of life from annulus measurements could possibly be attributed to more favorable environmental conditions rather than from size limit changes.

At ages 4 and 5, over 75 % of the red snapper at these ages were large enough to be captured with a 508 mm size limit in effect (Table 8). The age 4 and 5 year old fish sampled during this period most likely contain fast, as well as slow, growing fish since the majority of fish at these ages are larger than 508 mm. Thus, differences in length-at-age would to be hard to detect at ages 4 and 5, as well as after age 5, since red snapper in this study were found to be fully selected by age 6 when a 508 mm size limit was in place. It is unknown why age 4 and 5 red snapper displayed smaller mean total lengths during the FMP period than the other two regulatory periods. Smaller mean lengths at ages 4 and 5 could be the result of a density-dependent reduction in growth that may have occurred due to several strong year classes being present during this time period. In contrast, fishing pressure increased in the 1980s due to the development of better technology for locating and catching fish (Huntsman et al. 1993), which could negate large enough densities to result in a size reduction. Future investigation would be required to determine the exact cause of the observed length-at-age pattern for 4 and 5 year old red snapper.

When the selectivity of the fishery with a 508 mm size limit was analyzed for the Amendment 4 period, the percentage of age 2, 3, and 4 year old fish larger than 508 mm increased to 50 %, 76 % and 93 % respectively (Table 9). This further confirms the increased selectivity for faster growing fish due to the 508 mm minimum size limit.

If fisheries in the U. S. South Atlantic have been selectively removing the faster growing red snapper since 1992, in theory, more slow growing fish have been left in the population to reproduce. Growth rate has been shown to have a strong genetic basis (Conover and Munch 2002) and spread of the trait can be dependent on the level of harvest removal each year and the species' generation time. If only slower growing individuals are contributing to the spawning stock and future generations, the size-at-age of fish in the population should decrease over time. A reduction in size-at-age has been observed in several studies of reef fishes, including red porgy, *Pagrus pagrus*, vermilion snapper, *Rhomboplites aurorubens*, and tilefish, *Lopholatilus chamaeleonticeps* (Harris and McGovern 1997; Zhao et al. 1997; Harris et al. 2001). Since the 508 mm minimum size limit in 1992 increased the size selective nature of the fishery for red snapper, a reduction in size-at-age would be expected, not an increase as seen in this study. An increase in length-at-age for red snapper in the south Atlantic was also reported by White and Palmer (2004) between the 1980's and the 1990's.

Different trends in size-at-age for red porgy, vermilion snapper, and tilefish compared to red snapper may be due to several possible reasons. In their study of red porgy, Harris and McGovern (1997) noted a change in gear used to collect this species between early and late time periods in which the majority of the fish in the later time period were caught using chevron traps as opposed to hook and line. The mean size of red porgy caught by hook and line was significantly larger than the mean size of the fish caught in the traps, which likely affected size-at-age patterns, between the time periods.

Table 9. Percentage of red snapper ages 1 – 7 from the "Amendment 4" period large enough to be selected by a 508 mm total length minimum size limit.

Age	Percentage	n
1	50.00%	2
2	50.32%	310
3	76.00%	929
4	93.35%	692
5	90.63%	331
6	98.71%	232
7	100.00%	157

A reduced size-at-age for red porgy from the later time period was also detected when using back-calculation techniques. Mean lengths at age were derived by using back-calculated lengths to the last annulus, as well as to all increments on each otolith section. Lee's Phenomenon can result in a large reduction in mean back-calculated length-at-age if the mean was calculated using lengths at all increments in the presence of many old fish (Campana 1990). Therefore, when a greater number of older fish are present in one time period compared to the other, as in the study by Harris and McGovern (1997), a greater number of small back-calculated lengths are being used to calculate mean length-at-age, causing a reduction during the time period that includes more old fish.

Zhao et al. (1997) used weighted mean back-calculated length from measurements to the last annulus only to compare size-at-age between time periods for vermilion snapper. The investigators claimed to not detect the presence of Lee's Phenomenon in the mean back-calculated lengths at age 1, but by definition Lee's Phenomenon does not refer to smaller sizes only at age 1 (Lee 1912; Campana 1990). Further examination of their data revealed evidence of smaller lengths at other young ages for the oldest individuals. Also, in attempting to show that Lee's Phenomenon was not present, Zhao et al. (1997) reported that measurements from the otolith core to the 1^{st} annulus did not indicate differences in growth during the 1^{st} year of life between young and old fish. However, differences in the distance from the core to the 1^{st} annulus can be confounded by the protracted spawning season exhibited by fishes in the the snapper family. A more appropriate measurement for this comparison might be the difference between the 1^{st} and 2^{nd} annuli.

For tilefish, Harris et al. (2001) found a reduction in mean size-at-age after 10 years of heavy fishing. They also noted that mean age of fish during the later time period was significantly younger than during the earlier time period. A difference in mean age between time periods may affect the interpretation of length-at-age between time periods. Based on size at first reproduction, which is around 500 to 600 mm fork length (Grimes et al. 1988), the reduction in size-at-age observed for tilefish could have been achieved quickly since slower growers are likely capable of reproducing once or possibly more before being captured by the fishery, while faster growers may not have the opportunity to spawn before reaching harvestable size (~ 400 mm) and being removed from the population (Harris et al. 2001). This is not the case for Atlantic red snapper based on recent work on the reproductive biology for this species (White and Palmer 2004). With a 508 mm size limit in effect, almost all fish fast or slow growing, should still have a chance to spawn at least once before recruitment into the fishery. This may be the primary reason that no changes in growth have been detected yet for red snapper.

To detect a noticeable difference in length-at-age in the catch of a species due to genetic changes in growth, time for a full generation, if not several generations, to pass through the fishery are needed, unless extremely heavy exploitation rates were experienced within a short period of time (Harris et al. 2001; Conover and Munch 2002). Since the maximum age of red snapper in the Atlantic is 54 years, the time series available for analysis in this study or from the most recent prior red snapper aging study (White and Palmer 2004) are not sufficiently long enough to detect this change.

If the current pattern of fishing continues to select for faster growers, over time, a reduction in size-at-age of red snapper may become evident in the future. A smaller size-at-age could result in a reduction in the number of red snapper recruiting into the population, most likely due to a smaller size at reproduction. Since fecundity is proportional to size, smaller fish do not produce as many offspring compared to larger fish (Berkeley et al. 2004a). It has also been found that smaller fish produce less viable offspring than larger fish, which results in lowered larval survival. The increased production of smaller, less fit offspring could also be detrimental to a population in the presence of long term unfavorable environmental conditions (Longhurst 2002; Berkeley et al. 2004a; Berkeley et al. 2004b). Over time, the selective nature of the fishery under the 508 mm size limit could result in a population decline for the South Atlantic red snapper stock.

Total length-Otolith Radius Relationship

There was no biological difference found between von Bertalanffy curves derived from the observed data using fractional age and the back-calculated data to the last annulus. Using back-calculated data to the last annulus puts all fish at the same place in time (time of annulus formation) during growth analyses and could be a more accurate way to predict theoretical growth instead of using fractional age, which relies on an assumed birthdate throughout a protracted spawning season.

This study showed no appreciable differences in the growth curve from observed lengths using fractional age and the curves calculated using back-calculated data, therefore, measuring all annuli from every otolith is likely not an efficient undertaking for red snapper. The additional labor and time do not result in more accurate and/or precise growth estimates. If measurements are taken, measurements from either growth axis (transverse plane or sulcal groove) predict equally as well up to age 8 and presumably older. Further investigation will be required to determine whether differences in growth estimates between axes appear at older ages.

Results from the regressions to test for Lee's Phenomenon proved to be inconclusive. The regression relating the mean distance from the otolith core to the 1^{st} annulus to calendar age provided a better model fit than when using the mean distance between the 1^{st} and 2^{nd} annuli, and showed a significant difference in slope whereas the 2^{nd} regression did not. This suggested the presence of Lee's Phenomenon because it appears that the growth of older fish is slower during the first year of life than for young fish; but since red snapper have a protracted spawning season that can last for almost 6 months out of the year, results using only the 1^{st} annulus measurement could be affected by measurement differences for early versus late spawned fish. The distance between the 1^{st} and 2^{nd} annuli should not be affected by spawning time, therefore, might be a better parameter to use in this test. This relationship showed no difference in slope, but much variation was present, making interpretation difficult. The presence of Lee's Phenomenon cannot be ruled out definitively.

von Bertalanffy Growth Models

Comparisons of size limit corrected von Bertalanffy curves showed there were no biological differences in growth pattern between regulatory periods, which suggest that the difference in length-at-age is due to the fishery selection of faster growers. However, when growth curves for each period (Figure 20) were plotted together, there were differences in estimated length at ages 1 – 8 between periods. Several factors could result in length differences between periods. The model for the no regulation period might have been affected by the lack of fish older than 25 years old that were present in the other two time periods, although the maximum age for the FMP period was only 30 years old. The maximum total length in the earlier period was also about 75 to 100 millimeters smaller than maximum length during the FMP and Amendment 4 periods. This most likely depressed the estimate of L_∞ during the no regulation period. However, even with the potential data gaps associated with the no regulation model, the estimated lengths at age for ages 1 – 7 during this time period are all within the range of lengths estimated by back-calculation techniques (Table A.2). The estimated lengths during the other two time periods also fall within the range of back-calculated lengths for ages 2 – 7, but estimated lengths at age 1 were lower than predicted. This may suggest that the models from periods affected by a size limit may have overcorrected for the effects of the size limit, essentially decreasing lengths at age 1 excessively.

The reason that the Amendment 4 regulatory period produced the lowest estimated lengths at age 1 could also be due to extremely low sample size of age 1 fish during this period (n = 2). In addition, during calculation of the von Bertalanffy curve for the Amendment 4 regulatory period, the parameter t_0 had to bound at the low end at -0.05 for Microsoft Excel Solver to successfully estimate the model parameters using the Diaz et al. (2004) fitting criteria. Restricting t_0 in one model and not in the others could generate variability among other parameter estimates between models.

Visual comparison of the corrected and uncorrected von Bertalanffy models using all sampled Atlantic red snapper from this study shows that uncorrected length-at-age estimates are higher for fish ages 1 – 5 (Figure 13). When length-at-age estimates from the corrected and uncorrected models were compared to back-calculated lengths at ages 1 – 5, corrected length-at-age estimates fell in the middle of the range for back-calculated lengths at these ages, whereas, uncorrected estimates were near the maximum length-at-age estimates in the back-calculated range. Lengths at ages 1 – 5 from the corrected model were also very similar to theoretical lengths at these ages reported for Gulf of Mexico red snapper (Nelson and Manooch 1982; Patterson et al. 2001; Wilson and Nieland 2001). The evidence suggests that, overall; the corrected model should be used to predict red snapper lengths at age when size limits are in place.

The von Bertalanffy growth curve has been used to describe growth patterns for several red snapper populations throughout the Atlantic and Gulf of Mexico using observed and back-calculated lengths. Parameters from the von Bertalanffy presented in Table 10 demonstrate only a modest level of variation in growth between Atlantic and Gulf of Mexico red snapper populations, supporting the idea of similar growth for Gulf of Mexico and Atlantic fish. When von Bertalanffy parameters from observed and back-calculated lengths estimated in this study were compared to previous studies, several patterns were seen. L_∞ estimates using back-calculated lengths were higher than those calculated using observed lengths. Parameter estimates from this study compared to previous studies in the Atlantic are very similar for observed and back-calculated lengths. This may suggest consistency in aging methods between studies and laboratories within the Atlantic.

In the Gulf of Mexico, parameter estimates showed little variation between observed and back-calculated lengths and appeared to coincide well with the back-calculated parameter estimates from the Atlantic (Table 10). L_∞ estimates from observed

Table 10. Von Bertalanffy parameters from the present study as well as previously published red snapper growth studies using observed and back-calculated lengths at age.

Location	L∞	k	t_0	Source
Atlantic	Back-calculated lengths			
	975	0.16	0	Nelson and Manooch 1982
	955	0.15	0.18	Manooch and Potts 1997
	944	0.24	-0.05	McInerny (present)
	Observed lengths			
	899	0.22	1.31	White and Palmer (fishery dependent) 2004
	896	0.25	-0.16	McInerny (present)
Gulf of Mexico	Back-calculated lengths			
	941	0.17	0	Nelson and Manooch 1982 (back-calculated)
	Observed lengths			
	941	0.18	-0.55	Wilson et al. 2001
	969	0.19	0.02	Patterson et al. 2001

lengths in the Gulf of Mexico were larger than those in the Atlantic most likely due to larger maximum size of red snapper in the Gulf (Wilson and Nieland 2001). Further investigation into differences between Atlantic and Gulf of Mexico red snapper are needed to more fully understand the factors generating differences between von Bertalanffy parameter estimates.

CONCLUSION

This study provides evidence of a highly size selective fishery for red snapper in the U. S. South Atlantic under a 508 mm size limit. Size selection could have effects on growth over time and could eventually result in a population decline. Current management regulations may not be the most adequate for this species and possibly require modification. Results from this study show that under a 305 mm size limit, the population being sampled was still normally distributed as opposed to the truncated distribution created by a larger size limit (508 mm). In addition, there was no evidence for the selection of faster growing individuals between 1983 and 1991 when only a 305 mm size limit was in place. Lowering the current size limit may reduce the effect of size selection on red snapper.

On the other hand, since larger individuals are the most reproductively valuable to the population, perhaps the development of a slot limit may be a better management recommendation. However, red snapper typically reside in deep waters close to structure such as reefs. Their survival from a catch and release event is extremely dependent on the depth of capture (Burns and Wilson 2004). Since larger individuals usually live in deeper waters, the estimated survival of a red snapper over the slot limit after release is slim to none.

Further investigation would be required to determine the best possible choice of regulations for managing red snapper in the Atlantic.

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APPENDIX

Table A.1. Age – length (total length, mm) key for South Atlantic red snapper from 1977 – 2006.

											Age											
TL (mm)	**n**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
175	1	1																				
200	10	1																				
225	30	0.67	0.27	0.6																		
250	49	0.74	0.22	0.04																		
275	117	0.5	0.41	0.09																		
300	316	0.361	0.535	0.101	0.003																	
325	430	0.226	0.661	0.111	0.002																	
350	547	0.14	0.65	0.19	0.02																	
375	567	0.09	0.63	0.22	0.06																	
400	464	0.05	0.66	0.21	0.08																	
425	251	0.02	0.62	0.23	0.11	0.3																
450	244		0.44	0.41	0.08	0.07																
475	347		0.369	0.522	0.06	0.043	0.006															
500	498		0.27	0.58	0.07	0.06	0.02															
525	369		0.18	0.6	0.14	0.05	0.03															
550	309		0.045	0.6	0.26	0.04	0.042	0.01	0.003													
575	268		0.02	0.49	0.39	0.03	0.04	0.03														
600	247		0.03	0.23	0.52	0.06	0.1	0.05	0.01													
625	204		0.01	0.15	0.53	0.14	0.05	0.09	0.03													
650	153		0.01	0.12	0.54	0.16	0.08	0.06	0.03													
675	164			0.04	0.47	0.32	0.08	0.08	0.01													
700	141			0.035	0.284	0.39	0.163	0.1	0.014	0.014												
725	134			0.023	0.164	0.299	0.246	0.142	0.075	0.03	0.007					0.007						
750	142			0.007	0.04	0.31	0.303	0.183	0.078	0.036	0.036		0.007									
775	100				0.05	0.21	0.31	0.19	0.08	0.05	0.03	0.06		0.02								
800	79			0.013	0.013	0.114	0.304	0.202	0.114	0.038	0.063	0.025		0.038	0.025		0.025				0.013	
825	59				0.017	0.068	0.22	0.135	0.102	0.102	0.05	0.034	0.051		0.068	0.034	0.034	0.017				
850	48						0.041	0.104	0.041	0.063	0.104	0.104	0.063	0.041	0.021	0.041	0.063	0.021	0.041	0.042	0.042	0.042
875	33					0.061		0.061	0.03	0.061	0.091		0.061	0.091	0.061		0.061		0.06			
900	23							0.044			0.173			0.085		0.044			0.044		0.085	0.044
925	21								0.048	0.048		0.048	0.094		0.048	0.048	0.094			0.048		
950	9											0.111									0.111	0.111
975	1																					
1000	3										0.333				0.333	0.334						
Total	**6378**																					

Table A.1 cont. Age – length (total length, mm) key for South Atlantic red snapper from 1977 – 2006.

Age																						
22	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**37**	**38**	**40**	**41**	**42**	**44**	**47**	**51**	**54**
																0.007						
									0.013													
0.034					0.017																	0.017
		0.021			0.021			0.021	0.021	0.021		0.021										
0.03	0.091	0.03		0.03			0.091	0.03											0.06			
	0.044	0.044	0.085			0.044		0.044					0.044	0.044			0.044		0.044		0.044	
		0.142	0.094		0.048	0.048							0.048	0.048	0.048			0.048				
				0.111						0.111	0.111				0.111				0.111	0.112		
					1																	

Table A.2. Mean back-calculated total lengths in mm (± 1 SE) for red snapper from the South Atlantic. (Lengths are estimated for time of completion of annulus formation occurring around April.)

		Annulus (Rings)																			
No. Rings	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	398	250±1.8																			
2	1875	237±1.0	381±1.3																		
3	1255	236±1.6	387±2.1	488±2.3																	
4	407	252±2.5	413±2.7	529±2.9	616±3.1																
5	158	252±3.6	413±4.1	531±4.3	628±4.6	700±4.8															
6	90	235±5.1	386±5.5	502±5.6	598±5.7	679±5.9	739±6.0														
7	27	236±8.4	388±9.6	504±11.0	600±11.0	682±10.2	743±9.2	786±9.6													
8	19	233±14.9	370±18.2	479±19.9	570±19.6	649±18.6	710±17.6	756±18.2	791±18.3												
9	8	229±25.7	380±20.7	497±16.2	593±13.8	662±16.0	722±18.6	768±18.3	808±16.0	840±15.3											
10	17	256±12.3	408±11.9	521±11.9	606±10.7	673±10.8	722±11.9	763±12.1	799±12.5	829±13.1	854±13.2										
11	2	283±56.7	438±57.8	539±43.9	617±22.6	671±4.8	720±1.2	761±1.0	791±2.5	815±2.2	840±3.8	866±4.8									
12	2	213±21.5	366±21.5	444±47.0	541±49.8	632±46.3	701±41.8	750±35.9	785±28.6	820±25.7	850±22.4	874±20.7	898±22.8								
13	4	221±17.2	345±18.4	445±17.9	536±19.5	606±22.7	655±18.3	697±14.1	731±15.8	761±13.3	795±12.1	827±15.3	854±14.3	883±14.9							
20	1	127	245	380	482	525	571	602	627	650	675	702	718	740	755	772	787	804	818	834	845
Total N/ Weighted Mean TL	4263	240	388	501	613	685	730	764	788	817	837	832	847	855	755	772	787	804	818	834	845