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On the Growth and Exploitation Pattern Effects on the Recuperation from Overfishing of the Red Snapper, *Lutjanus campechanus*, in the Gulf of Mexico.

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ON THE GROWTH AND EXPLOITATION PATTERN EFFECTS ON THE
RECUPERATION FROM OVERFISHING OF THE RED SNAPPER,
LUTJANUS CAMPECHANUS, IN THE GULF OF MEXICO

By

Vallierre K. W. Deleveaux

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements of
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2012

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on the Recuperation from Overfishing
of the Red Snapper, *Lutjanus campechanus*,
in the Gulf of Mexico.

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The red snapper stock in the Gulf of Mexico has been classified as severely overfished, and overfishing continues, therefore several management actions have been imposed on the Gulf red snapper fishery, including closed seasons, quotas and minimum sizes. For this reason the red snapper is often referred to as one of the most intensively managed stocks in the United States. A recovery plan for red snapper, which includes a reduction of the shrimp bycatch mortality to 50% of the 2001-2003 level, had been established so that a 20% SPR would be attained by the year 2032.

Due to the very long history of high exploitation levels in the red snapper fishery (>130 yrs) there was a need to assess whether the minimum size regulations were serving their intended purpose of protecting the spawning stock, reducing the probability of recruitment failure and increasing the yield from the stock. To meet this objective a good descriptor of red snapper growth was required in order to simulate the existent exploitation pattern of the gears involved in the fisheries. An extensive analysis of red snapper growth was conducted using data supplied by the National Marine Fisheries Service (NMFS) Panama City, Florida Laboratory. The data set (database 1 (DB1)) contained information on otolith

ageing and the annuli measurements made along the dorsal side of the sulcus acousticus as well as total length measurements collected from 370 fish between age 2 and 17. Data for the previous growth studies on red snapper, which were collected from the directed fisheries, indicated an underrepresentation of several age categories of fish. Due to the selectivity of the gears a major portion of the age two fish and even possibly some segment of the age three fish (smaller, slow-growing individuals) were not included in the data collection, therefore it is necessary to ensure that proportionality exists between the otolith and somatic growth. The results of the analysis here indicated that the back-calculated otolith radius-total length measurements were uncoupled for several age classes, meaning that the growth in total length was not proportional to the otolith growth in all age classes. This, therefore, indicated that the data was not suitable for providing a good descriptor of the growth of the red snapper when used in back-calculations of size-at-age. To resolve this issue it was necessary to evaluate the use of the annulus measurements made along the dorsal side of the sulcus acousticus (best for ageing procedures) for growth estimation through back-calculation procedures. It was apparent that otoliths grow asymmetrically and the sulcus acousticus radius is a partial measure along the proximal-distal axis. Following this observation, since otolith growth is at a maximum along the dorso-ventral axis, it was proposed that radius measurements along the dorso-ventral axis and of the area of annuli along the dorso-ventral axis of the otolith would likely be more representative of the total otolith's growth, which was expected to be directly proportional to somatic growth in length. To investigate these propositions

additional data sets and otoliths were requested from the NMFS Panama City Laboratory. Data and otoliths from a total of 519 individual fish between 0 and 8 years old were received (database 2 (DB2)). This database, after adding the measurements made along the dorso-ventral axis showed that there was a stronger relationship between the total length and the dorso-ventral axes measurements than for the proximal-distal axes ($R^2 = 0.9596$ vs $R^2 = 0.8884$). More importantly, the analysis indicated that there was coupling of the total length-otolith radius data in all the represented age classes, which indicated that there was a proportional relationship between the total length and the otolith measurements. Both the dorso-ventral axis and area measurements proved to be more directly proportional to somatic growth than the sulcus acousticus measurements. The area measurements, however, were deemed to be too impractical for widespread use due to the length of time required to determine and accurately measure the area of each annulus within the transverse section of the otolith. The measurements made along the dorso-ventral axis were used for all subsequent analyses.

Several back-calculation models were selected to generate growth function parameters for comparison purposes. These models included several multiple regression models, the age-effects model (Morita & Matsuishi, 2001), a log-power model (Ehrhardt, 1992) and the Modified Fry model (Vigliola & Meekan, 2009). The result of each model was tested by comparing the mean of the observed lengths-at-age to the mean of the back-calculated lengths-at-age. It was found that all of the models used approximated the observed data as there was no significant difference between the observed mean lengths-at-age and the back-calculated

mean-lengths-at-age at the 0.05% level. The von Bertalanffy growth function parameters for a 2-way multiple regression model using the data from DB2 gave values of $L_{\infty} = 1232.913$ mm, $k = 0.114$ yr⁻¹, and $t_0 = -0.353$ yr. The 3-way multiple regression model gave results of $L_{\infty} = 1081.697$ mm, $k = 0.128$ yr⁻¹, and $t_0 = -0.158$ yr. The parameters determined from the age-effects model were $L_{\infty} = 1109.627$ mm, $k = 0.145$ yr⁻¹, and $t_0 = -0.204$ yr. Growth parameter values of $L_{\infty} = 927.558$ mm, $k = 0.179$ yr⁻¹, and $t_0 = 0.156$ yr were generated from the power model while for the Modified Fry model the results were $L_{\infty} = 924.870$ mm, $k = 0.184$ yr⁻¹, and $t_0 = -0.087$ yr.

Next, how well the age structure of the samples represented the stock was investigated. It was found that the age two fish were underrepresented due to the selectivity of the fishing gears. Also, the larger and older fish in the size-at-age distributions were mostly absent, perhaps also due to fishing gear selectivity and the resulting exploitation pattern (Walter & Ingram, 2009). This problem was approached by treating the age two and the older age classes as containing missing data, which would suggest a slower growth rate for smaller fish and perhaps a larger maximum size for older fish. A Monte Carlo approach was used to generate experimental length-at-age data from the Modified-Fry model which would then be used to simulate an unbiased virgin red snapper length-at-age population structure based on the results of the Modified Fry model. The growth parameters that resulted for the unbiased population structure were $L_{\infty} = 1201.40$ mm, $k = 0.124$ yr⁻¹, and $t_0 = -0.177$ yr.

Finally, to evaluate the appropriateness of the use of minimum size in the management framework to recuperate the red snapper stock it was necessary to consider the life history, the fishing mortalities due to the shrimp fishery, to the discards below the minimum size and to the closed season discards, and the temporal distribution of the fish stock. The minimum size limits are responsible for the majority of the discards from the directed fisheries. The release mortality rates for these discards are estimated to range from 71-82% for the commercial fishery and 15-40% for the recreational fishery (NMFS, 2006). Although the commercial fishery has the higher discard mortality rate, the recreational fishery releases a substantially higher number of red snapper each year due to the very large number of participating individuals in that fishery. This is perhaps the primary reason the minimum size limits have not been effective in meeting the desired management goals. A new deterministic size-age equilibrium SPR model was developed that utilizes a transitional mortality schedule matrix to generate a yield per recruit, for the purpose of estimating the effectiveness of the minimum size to control exploitation in the directed fisheries. Several management scenarios, different minimum sizes under different levels of shrimp bycatch, were investigated that estimated the likelihood of red snapper recuperation to the management goal of 20% SPR by 2032. The results indicated that only in the complete absence of any shrimp fishery bycatch would the SPR approach 18.5%, still short of the goal, regardless of any minimum size selected. At the target 50% shrimp bycatch reduction level the SPR is only projected to increase to about 7.2%, regardless of the minimum size

implemented. These results show the minimum size regulations to be ineffective in meeting their intended goal of protecting the spawning stock for red snapper in the Gulf of Mexico.

Dedication

This work is dedicated to Zena, Spencer, Joelle, Edison and Pat.

Thank you!

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Chapter 1. Introduction and Statement of the Problem

1.1 Introduction

The Gulf of Mexico red snapper, *Lutjanus campechanus*, (Poey, 1860) belongs to the family Lutjanidae, which includes several species that are very important and valuable to commercial and recreational fisheries. There are reported to be 17 genera and 105 species in the family which are found in tropical and subtropical regions. The family is primarily marine, but there are a few estuarine species (Allen, 1985; Anderson Jr, 1987; Rocha & Molina, 2008). *L. campechanus* (Figure 1.1) are large-bodied, pink to bright red colored fish with a transition to a lighter shade on the underside. The species has a characteristic red iris and juveniles have a black spot on the upper sides below the soft dorsal rays which fades with growth to larger sizes (Moran, 1988). These are demersal fish, usually ranging from 10 – 130 m in depth with juveniles living in shallower waters on muddy and sandy substrates in association with bottom structures and vertical relief (Allen, 1985; Moran, 1988). Adults are usually found in deeper waters, over limestone or rock bottoms and may not be associated with any relief objects. Juveniles tend to be more social animals while the adults are more solitary in nature. Sexual maturity occurs at about two years in age (Gallaway, Szedlmayer, & Gazey, 2009; Szedlmayer & Shipp, 1994; C. A. Wilson & Nieland, 2001). Spawning in red snappers occurs over an extended period, from May through early October in the northern Gulf of Mexico, with a peak period of June – August (Collins, Johnson, & Keim, 1996; Moran, 1988).

Red snappers are pelagic batch spawners, meaning during this period the fish may simultaneously release eggs and sperm to the water column numerous times, roughly every 4 – 6 days, resulting in about 30 egg batches per season (Moran, 1988) (Collins et al., 1996). Depending on the size of the female, the total eggs spawned per batch may vary from about a thousand for a small fish to over 3.4 million for a large healthy female (Collins et al., 1996; Collins et al., 2001). Spawning occurs away from reef areas over firm sand bottoms. Red snappers produce planktonic eggs which hatch after about 24 hours, and the larvae settle from the water column at about 27 days (Gallaway et al., 2009; Rabalais, Rabalais, & Arnold, 1980)(). Settlement occurs in low relief areas where there is some protection from predation (Gallaway et al., 2009). As juveniles mature they migrate to the offshore high relief reef areas.

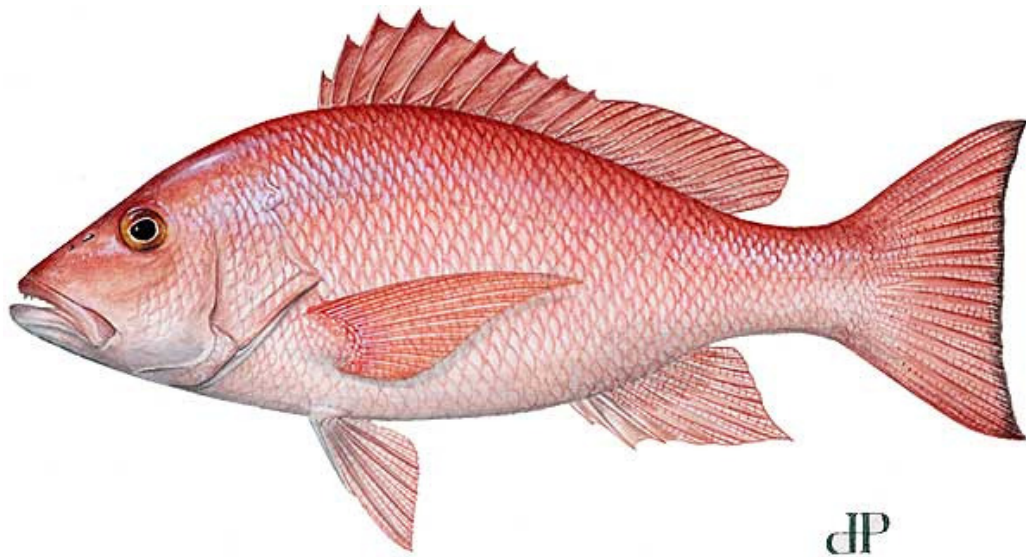


Figure 1.1 Red snapper, *Lutjanus campechanus* (Poey 1860) (© 1992, Diane Rome Peebles.)

The red snapper is long-lived (>50 years), and reaches lengths of 950 mm and weights of over 16 kg (Patterson III, Cowan Jr., Wilson, & Shipp, 2001; C. A.

Wilson & Nieland, 2001). Red snapper have a near linear growth rate to about 710 mm for the first six to eight years of life (which is approximately 75% of the maximum size)(Szedlmayer & Shipp, 1994; C. A. Wilson & Nieland, 2001)(Fischer, Baker Jr., & Wilson, 2004). Growth slows and there is increased variability in the size at age after this period.

The red snapper is a carnivorous species that feeds primarily on fish, but its size influenced the composition of the other varied prey, which include shrimp, crabs, squid and tunicates (McCawley, Cowan Jr., & Shipp, 2006; Ouzts & Szedlmayer, 2003). Ouzts and Szedlmayer (2003) found that red snapper fed throughout the day and in a variety of habitat types. Fish were the dominant prey throughout the day, but the second most important prey group changed with time period: stomatopods for dawn, tunicates for daytime hours, and crabs for dusk and night periods.

The US fishery for red snapper in the Gulf of Mexico (GOM) is valued at about \$20 million (ex-vessel) a year. The fishery occurs on the shelf of the entire Gulf, extending from SW Florida to Mexico. There are three major sectors in the red snapper fishery, two are direct and one indirect. The direct fisheries include the commercial and recreational sectors and the indirect fishery is the result of bycatch in the Gulf shrimp fishery. The commercial fishery is prosecuted by handline and longline fleets and recreational fleet uses handlines. The commercial fleets generally operate in deeper waters, further away from shore. The directed fishery for red snapper has been in existence since before 1850 in the Gulf of Mexico (C. Porch, 2004). Commercial exploitation in the Gulf of

Mexico began along the north-west coast of Florida and expanded westward along the coast and south into Mexican waters, primarily onto the Campeche Bank (Shipp & Bortone, 2009). The highest recorded landings of red snapper occurred in 1965 when 14 million pounds were landed, with approximately half coming from Mexican waters. Landings declined steadily after Mexico closed its Exclusive Economic Zone (EEZ) to foreign fishing in 1975 until management regulations established quotas for the commercial and recreational fisheries in 1984 (Schirripa & Legault, 1999; Shipp & Bortone, 2009).

The direct fisheries are managed under a total allowable catch (TAC) system where the TAC is split between the commercial and recreational fisheries in a 51:49 percent ratio respectively (Hood et al., 2007; SEDAR (Southeast Data, Assessment, and Review), 2005). Management regulations imposed on the commercial fishery include quotas, a minimum size, specific closed seasons and trip catch limits. In 2007, individual fishing quotas (IFQ) were established in the commercial fishery to reduce overcapacity and to mitigate the adverse impact of a derby type fishery (Keithly, 2001; Waters, 2001)(SEDAR (Southeast Data, Assessment, and Review), 2005)(Nieland, Fischer, Baker Jr., & Wilson III, 2007). The gears utilized in the commercial fishery are longlines and hand lines. The recreational fishery is primarily executed by hand lines from private boats, head boats, or from charter vessels for hire. These vessels tend to operate in shallower waters than the commercial fishery vessels, therefore tend to harvest smaller fish. This fishery has its own season, minimum size limit, and also has a per-person bag limit (Assessment, 2009). Juvenile red snapper are caught by the

shrimp trawl fleet operating in the Gulf of Mexico. The juveniles are primarily composed of age 0 and age 1 fish that have not yet recruited to the commercial fisheries (Gallaway & Cole, 1999; Gazey, Gallaway, Cole, & Fournier, 2008; SEDAR (Southeast Data, Assessment, and Review), 2005). The shrimp fishery annually removes roughly 25-45 million fish while the recreational and commercial fisheries combined land roughly 3-4 million red snapper annually (SEDAR (Southeast Data, Assessment, and Review), 2005). Management efforts to reduce the large bycatch from the shrimp trawl fishery have included the mandated use of bycatch reduction devices (BRDs) (Gallaway & Cole, 1999). There is also some red snapper bycatch mortality that results from the fisheries on other snappers (e.g. vermillion) and groupers (e.g. red) in the Gulf of Mexico (SEDAR (Southeast Data, Assessment, and Review), 2005).

The Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) is the law that governs marine fisheries management in the federal waters of the United States. This law was enacted in 1976, amended in 1996 and reauthorized in 2006. National Standards 1 of the reauthorized Act states: “conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery for the United States fishing industry” (Dell’Apa, Schiavinato, & Rulifson, 2012). Management of the red snapper began under the Reef Fish Fishery Management Plan (FMP) which was implemented in 1984 (Hood et al., 2007). The first red snapper stock assessment was made in 1988, which concluded that the stock was significantly overfished (C. Goodyear & Phares, 1990). A reduction

of fishing mortality in the order of 60-70% was recommended to rebuild the spawning stock potential ratio to 20% (C. P. Goodyear, 1988). This initial stock assessment also identified shrimp trawl bycatch as a significant source of mortality of juvenile red snapper (ages 0-1). More recently, the NMFS agreed that there are two separate Gulf of Mexico red snapper stocks, inhabiting areas east and west of the Mississippi River, although the degree of mixing and reproductive isolation is unknown (SEDAR (Southeast Data, Assessment, and Review), 2005). The current management regulations that govern red snapper fishery activities for the commercial sector include: individual fishing quotas (IFQ), a size limit, a vessel licensing requirement, a red snapper access license and trip catch limits. For the recreational sector the regulations include: quotas, a size limit, a season, bag limit and special management zones where more restrictive limits are enforced (Hood et al., 2007).

The MSFCMA requires management to prevent overfishing and to rebuild overfished stocks. Rebuilding the red snapper stock has proven challenging, in part because of the difficulty in reducing one of the major sources of mortality, that due to the shrimp bycatch (Gallaway & Cole, 1999; Gazey et al., 2008; Schirripa, 1999). The GOM Shrimp Fishery is the second most valuable US commercial fishery with a value exceeding \$ 580 million a year in recent years. However, this fishery has a tremendous bycatch associated with it that impacts many other species living in and near the benthos of the Gulf of Mexico (Hendrickson & Griffin, 1993). In the case of the red snapper there is a significant bycatch of age 0 and 1 juveniles by the shrimp trawl gear (Gallaway &

Cole, 1999; Schirripa & Legault, 1999; SEDAR (Southeast Data, Assessment, and Review), 2005). The 1997 Amendment 9 to shrimp fishery FMP requires the use of bycatch reduction devices (BRDs) on all shrimp trawling vessels in the Gulf. The shrimp industry estimates that a loss of about 10% of the shrimp catch occurs due to the BRDs, thereby resulting in ca. \$58 million a year loss to the shrimp fishers. However, the estimates of the reduction in red snapper bycatch ranged from 12 - 27% (SEDAR7, 2005)(Gallaway & Cole, 1999), which was much less than the estimated and targeted 50% rate, which was believed to be necessary to rebuild the red snapper stocks (Schirripa & Legault, 1997).

This dissertation presents a size-structured yield-per-recruit stock assessment model that will analyze the effectiveness of the minimum size management strategy in controlling the fishing mortality in the Gulf of Mexico red snapper fishery for the purpose of recovering the over-exploited fish stocks. This model will also assist in providing a more comprehensive understanding of the consequences for assessment and management of the uneven temporal distributions of the red snapper stock and the fleets that harvest it.

1.2 Statement of the Problem

The Gulf of Mexico red snapper commercial and sport fishery has existed for more than a century. Since 1984, a variety of management measures have been applied to speed up the recovery of the red snapper stock. However, these management actions, such as minimum size, seasons and quotas, have not

been effective according to the results of recent assessment efforts (MSAP, 2005; SEDAR 7).

The shrimp fishery affects the red snapper stock through its bycatch, which consists of almost exclusively of age-0 and age-1 individuals. The commercial fishery operates with both hand lines and longlines and has best harvests primarily in the spring, while the recreational fishery operates, using only hand lines, and achieves its greatest harvests during the summer and early fall. The commercial, recreational and shrimp fisheries exploit different fractions (size structures) of the stock; hence, their effects on the stock are different.

The red snapper stock has been subjected to long and heavy exploitation, such that the current stock has been estimated to be at about 5% of the virgin (unexploited) stock biomass. This low stock level is clearly not solely the result of exploitation by the directed fisheries alone, and significant effects are due to the bycatch from the large shrimp fisheries which decimates the age 0 and age 1 year classes in the Gulf of Mexico (Schirripa & Legault, 1997)(Schirripa, 1999). In spite of the low adult stock levels, the recruitment of juveniles remains high and does not seem to follow the parent stock (Schirripa and Legault, 1999; Porch, 2004). It would appear that recruitment in the red snapper is not dependent on the parent stock beyond a certain point, but may be driven by density dependent factors (SEDAR (Southeast Data, Assessment, and Review), 2005).

The Gulf of Mexico Fishery Management Council (GMFMC) has taken action to rebuild the red snapper stock. In 1990 the restoration benchmark was initially set to 20% SSB by 2000, but subsequently amended to 20% transitional

SPR by 2007 later that year by the Reef Fish Fishery Management Plan (FMP) (SEDAR7 DW40). In 1993 the stock recovery date was again changed to 2009. The stock objectives could not be met so the time frame was extended to 2019 in 1996 because the results from the current assessment models were not consistent with the status of the snapper stock (Hood et al., 2007).

It is known that the directed fisheries exploit different size fractions of the adult stock. Commercial vessels generally fish in deeper waters, catching larger fish while recreational vessels generally fish in shallower waters, capturing smaller fish. During the open season, the minimum size regulations require many undersized fish to be released after being brought to the surface, resulting in a significant depth-related mortality to the released fish (Dorf, 2003)(Baker Jr & Wilson III, 2007), (Rummer, Patterson, Cowan, Fitzhugh, & Nieland, 2007). There is additional mortality during the closed seasons as fisheries for other species continue to catch and release red snapper of all sizes. There is also probably additional mortality due to physical injury of hooked fish that escape capture, opportunistic predation by birds, mammals, sharks on the hooked fish and similar predation on the released fish that may survive the decompression trauma (Dorf, 2003).

There was a general dissatisfaction in the previous stock assessment at the SEDAR 7 stock assessment workshop in Miami during August 2004. The biological parameters used in the stock assessments used by the GMFMC scientists did not yield satisfactory results as the relative abundance indices and stock predictions were inconsistent. The SEDAR 7 assessment workshop

reconvened in December 2004, reviewed their options and considered the adoption of a new spatially-explicit age structured assessment model that considered a longer time series of data. The new model, "Catchem", which was developed by Dr. Clay Porch of NMFS (Southeast Fisheries Science Center - Miami), was accepted for use at the SEDAR 7 Review Panel meeting in April 2005. The GMFMC at that time set the target recovery date for the stock to 2032 based on the estimated time for the stock to recover in the absence of fishing mortality plus the estimated 19.6 years mean generation time (Schirripa & Legault, 1999) for the species (SEDAR (Southeast Data, Assessment, and Review), 2005)(Assessment, 2009). This new stock recovery date replaced the previous recovery date of 2019 which was established during 1996. A stock assessment update using the Catchem model was held during 2009 (Assessment, 2009) and a new assessment (SEDAR 31) is planned for 2012 and 2013.

1.3 Goals and Objectives

The goal of this work is to improve the understanding of the exploitation of the Gulf of Mexico red snapper stocks, with attention to the effectiveness of minimum size strategies. In order to accomplish this goal it will be necessary to thoroughly consider the recruitment dynamics and life history of the red snapper in the Gulf of Mexico. My effort was to show a connection between the trends in recruitment abundance which required establishing linkages among the temporal differences in the size structure of the stock and distribution of fishing effort. This

should improve our understanding of the effectiveness of the minimum size regulations imposed on the red snapper fisheries as a means to control the fishing mortality on the undersized fish.

This work developed a size-structured yield-per-recruit stock assessment simulation model that will analyze the effectiveness of the minimum size management strategy in controlling the fishing mortality in the Gulf of Mexico red snapper fishery for the purpose of recovering the over-exploited fish stocks. This model will also assist in providing a more comprehensive awareness of the stock interactions with temporally selective fishing effort.

My efforts here may lead to a better understanding of the effectiveness of minimum size strategies on the dynamics of subtropical fish populations and facilitate the incorporation of relevant environmental data as important inputs and improvements to stock assessments and fisheries management.

Chapter 2. Growth of the Red Snapper, *Lutjanus campechanus*.

2.1 Background

Individual growth in fish is the net result of anabolic and catabolic processes. However, for an analysis of population growth there is a need to express individual growth in mathematical terms – therefore models are used to relate the size to age. Some models are based on purely empirical relations; others are based on a theoretical basis of differential equations that link the anabolic and catabolic process e.g. von Bertalanffy growth function (Katsanevakis, 2006).

The primary information usually collected for growth studies include age, length at age, weight at age and sex. Age is an important variable as it is used in calculations for growth rates, mortality rates and productivity (Campana, 2001). Stock assessments provide resource managers with the scientific advice needed to determine the effects of fishing on fish populations. This procedure requires the production of quantitative data on the magnitude of a fish population, and estimates of the total removals due to human activities (landings and bycatch), life history data (growth rates, age of first maturity, longevity and age specific mortality) in models to derive estimates of recent, current state and future trends of the fish population numbers or biomass, recruitment levels and fishing mortality rates (Mace et al., 2001). In stock assessments the relationships between age, length and weight of the fish are used to convert numbers of fish to biomass. Therefore, accurate growth information and good estimates of the

numbers of juveniles recruiting to a fishery are important components of any stock assessment. There are several examples of stock declines or collapses which have been contributed to by inaccurate determinations of growth and life history parameters. For example, the case of the orange roughy (*Hoplostethus atlanticus* Collett) where its longevity was underestimated and resulted in the overestimation of growth, productivity and mortality rates. These rates were subsequently used in population models which generated overly optimistic total allowable catches (TACs) and led to the decline of the fishery (Campana, 2001)(Hilborn, Annala, & Holland, 2006).

Among the factors known to affect growth rates are temperature, food availability and competition (Jones, 1986), (Nordwall, Näslund, & Degerman, 2001) (Pörtner et al., 2001). Growth information is especially relevant in studies regarding the timing and magnitude of spawning, maturity, larval duration, juvenile duration, settlement, recruitment and habitat use (Collins et al., 2001), (Drass et al., 2000), (Victor, 1986), (Woods, Fischer, Cowan Jr., & Nieland, 2003). Growth rates have an important impact on survival and predation rates, especially at larval and juvenile stages (Bergenius, Meekan, Robertson, & McCormick, 2002), (Miller, Crowder, Rice, & Marschall, 1988)(Bergenius et al., 2002).

Hard parts are the primary means to age fish. These parts include scales, vertebrae, fin spines, opercular bones and otoliths, among others (Campana, 2001; Green, Mapstone, Carlos, & Begg, 2009). Since most fish are poikilotherms, their metabolic processes are influenced by the temperature of

their environment. This is why growth is fast during warm periods and slow during colder periods. Calcareous material is continually deposited in the hard parts during anabolic processes. This is reflected in the hard parts as wide, translucent, bands being formed during the warm, fast growth periods and narrower, opaque, bands during the colder, slower growth periods. The appearance of these bands as light or dark is dependent on whether the light source used is reflected from or transmitted through the calcareous material. The translucent band appears dark when viewed with reflected light because it allows a higher proportion of the impacting light to pass through it rather than being reflected back to the viewer as compared to the opaque band (Green et al., 2009). These bands have been shown to be deposited on the scales, otoliths and other hard parts of many fishes on a daily and annual basis and shown to be positively correlated to growth (Campana, 2001). We assume that the bands are indicators of growth in fishes.

Sagittal otoliths (fig. 2.1) are the primary ageing structures used in red snappers, as they are reported to be the largest, clearest and most reliable hard parts to interpret (Fischer, Chesney, & Cowan Jr., 2010). During a course of a year usually one opaque and one translucent band are deposited in the hard parts (C. A. Wilson, Stanley, & Nieland, 2001), (Fischer, Patterson III, Cowan Jr., Fitzhugh, & Nieland, 2007). Generally, the opaque bands are considered as the annuli and are counted in the ageing process.

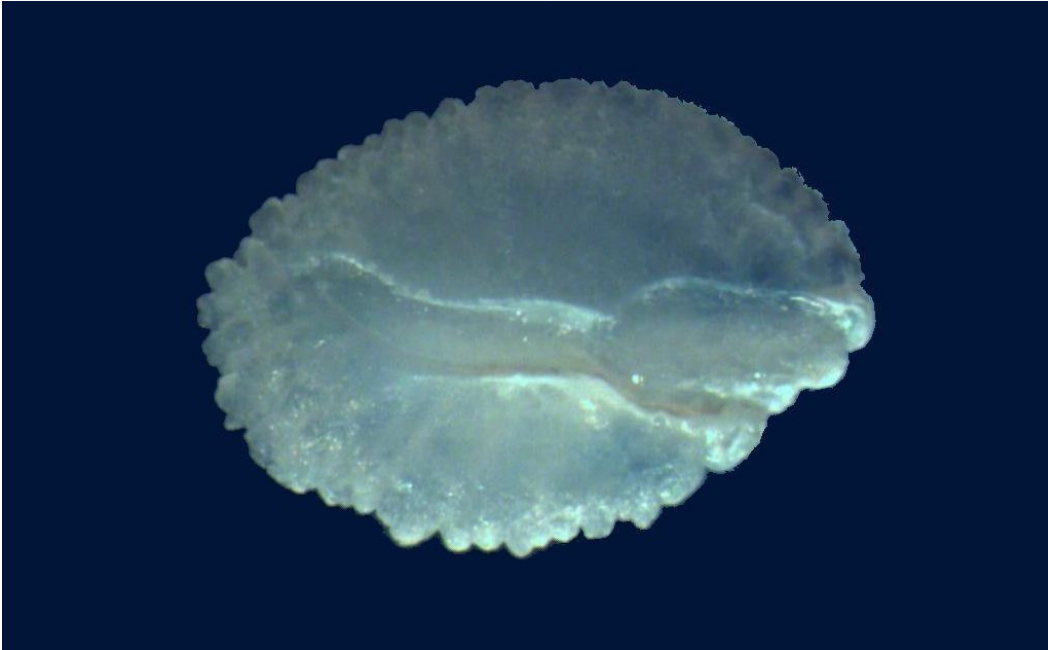


Figure 2.1. Proximal view of whole juvenile red snapper sagittal otolith.

As fish age they grow in size and often inhabit different habitat types during that process. Many fish have populations that are spatially distributed by size (Gust, Choat, & McCormick, 2001)(Mitchell, Henwood, Fitzhugh, & Allman, 2004). After spawning it is quite common for the larvae to settle in one area while juveniles are found in another and sub-adults and adults are found in a yet another area. The habitats will often have different bottom and sediment types, and possibly entirely different ecosystems. In red snapper, juvenile individuals are often found inshore in more sheltered, protected areas while older sub-adults and adults are found offshore in reef habitats. The primary reasons for the age and size distributions are that the younger groups have different prey requirements and they receive a greater degree of protection from larger predators prior to moving to the reef areas (Szedlmayer & Lee, 2004).

Understanding the ageing process and being able to estimate age from hard parts is an essential step in developing the data required to study the population dynamics of the red snapper. Furthermore, the study of such dynamics help fisheries management develop a thorough understanding of the specific life stage processes of fish if it is to be effective in predicting the long term fluctuations in abundance and biomass that are due to fishing and natural mortalities. For the red snapper, this means that it is necessary to be able to follow and quantify the effects of fishing mortality on the cohorts throughout their lifecycle. This includes the mortality effects on recruits due to the shrimp trawl industry from just after settlement (ages 0 and 1), through the impacts on the intermediate age and size classes caught in the recreational and commercial hook and line fisheries, to the commercial longline fishery which harvests the older and larger individuals.

2.2 Problem Identification

The red snapper in the Gulf of Mexico has a very long and intense history of exploitation. Porch et al. (2007) state that the fishery in the Gulf started in the early 1840s and the resource has been under intense fishing pressure ever since, except for a few short periods of social and economic unrest (C. E. Porch et al., 2007). Gallaway et al. (2009) state that the Gulf of Mexico red snapper population has been overfished since before 1994 to at least the 2004 assessment period (Gallaway et al., 2009). Due to this long period of heavy exploitation and stock depletion the size structure of the stock has become highly

stratified and relatively few individuals remaining are found to belong to the older age and larger size classes. The absence of the larger individuals in the older age classes affects the statistical determination of the expression of individual growth for the species. The result is that the determined growth function parameters tend to be shifted to a lower asymptotic length (L_{∞}) and a higher growth coefficient (K), therefore, the red snapper reaches a smaller maximum size-at-age at a faster growth rate than expected. Further, the selectivity patterns of the fishing gears result in the vast majority of commercial landings being comprised of individuals belonging to the 2 – 6 age classes (Nieland et al., 2007). Due to the ontogenic shift in habitat preference by red snappers, where older and larger individuals are found in deeper waters, growth parameter estimation for the stock is affected by the disproportionate landings of the handline gears which are mainly used in the shallower habitat ranges for the species. The impact of the gear selectivity, as well as the availability of the red snapper age classes in the areas of the gears' operation, may result in biased size-at-age distributions in the samples that are used to determine the life history parameters for stock assessments (McClanahan & Mangi, 2004; Taylor, Walters, & Martell, 2005).

An additional factor that may have increased the possibility of bias in the samples were the effects of the different minimum size limits enforced in the commercial and recreational fisheries over the more than two-and-a-half decades and their impacts on the distribution of size-at-age of the stock (Hood et al., 2007). Management of the Gulf of Mexico red snapper fishery began when the Magnuson-Stevens Fishery Management and Conservation Act went into effect

in 1976. This act empowered the Secretary of Commerce and the Gulf of Mexico Fisheries Management Council to make management decisions for fish stocks in federal waters. The red snapper was included in the Reef Fish Fishery Management Plan which was put into effect in 1981 after it was observed that the red snapper landings for both the commercial and recreational fisheries were declining. The Reef Fish Fishery Management Plan in 1984 established a 13 inch (330.2 mm) total length minimum size for both the commercial and recreational fisheries. Amendment 5 to the Reef Fish Fishery Management Plan was implemented in 1994 which was intended to increase the minimum size to 16 inches (406.4 mm) over a five-year period. The minimum size was increased to 14 inches (355.6 mm) in 1994, and then to 15 inches (381.0 mm) in 1995 for both the commercial and recreational fisheries. The minimum size was briefly set at 18 inches (457.2 mm) for the recreational fishery during the months June – August in 1999, after which the recreational fishery season was closed for the remainder of the year. In 2000 the minimum size in the recreational fishery was set at 16 inches (406.4 mm) and remains at that size to date. For the commercial fishery, the minimum size was reduced to from 15 inches (381.0 mm) to 13 inches (330.2 mm) in 2007 and currently remains at that size limit. Table 2.1 displays a summary of the changes in minimum size since management was introduced. Figures 2.2 and 2.3 shows the history of the main management regulations enforced on the recreational and commercial fishery respectively.

Table 2.1. Changes in the minimum size enforced in the red snapper fishery by year.

Commercial Fishery		Recreational Fishery	
Year	Size Limit (in)	Year	Size Limit (in)
1984	13	1984	13
1994	14	1994	14
1995	15	1995	15
2007	13	2000	16

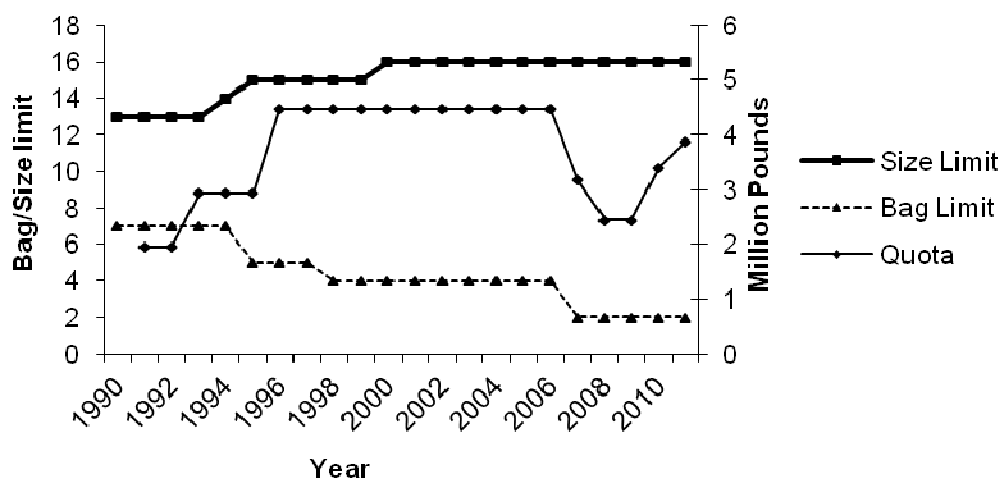


Figure 2.2 Graph showing management measures imposed on red snapper recreational fishery.

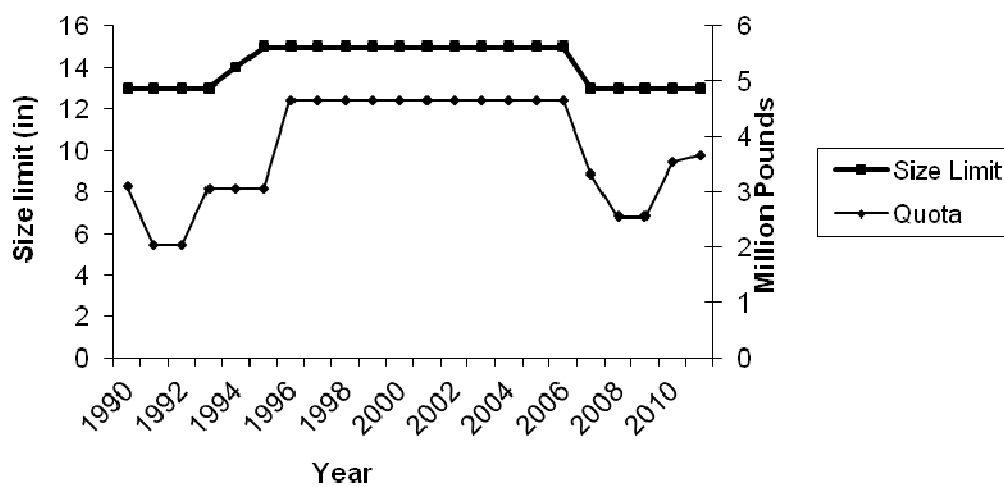


Figure 2.3 Graph showing management measures imposed on red snapper commercial fishery.

The minimum size for the commercial fishery was reduced from 15 inches (381.0 mm) to 13 inches (330.2 mm) in 2007. In order to test whether the change in the minimum size limit had an impact on the size distribution of the stock, a t-test for difference between the mean sizes of 1-year old red snappers in the years 2005 and 2008 was performed. The 1-year old snappers were selected because it would be expected that the faster growing individuals of this group would be affected by the lowered minimum size by mortalities from both landings and discards in 2008. These 1-year old snappers were collected by NOAA Fisheries scientific surveys and were therefore not subject to fishery dependent effects from the commercial or recreational fisheries. The mean sizes of the 1-year old red snapper for these years were 308.25 and 180.32 mm in 2005 (N = 20) and 2008 (N = 217), respectively. The test resulted in a t value of 14.8 and $p < 0.0001$, which indicated that there was a significant difference in the mean

sizes of 1-year old red snappers in 2005 and 2008. (Some factors that may play a role in the noted differences in the sizes of 1-year old snappers in the specific years include cohort strength, food availability and mean water temperature). A test for the difference between the variances (F-test) for the two samples resulted in an F value of 1.07 and $p = 0.4592$, indicating there was no significant difference between the variances of the 2005 and 2008 samples. These tests show conclusively that there are significant impacts on the stock size distribution by the minimum sizes imposed on the fisheries, which could lead to biased size-at-age distribution samples for use in growth function parameter determination.

Growth functions for red snapper were determined in studies by Wilson and Nieland (2001) and Patterson et al. (2001). However, the plots of the functions (Wilson and Nieland, fig. 2.4; Patterson et al., fig 2.5) both indicate that there is good fit only for the age range from which the majority of the data is drawn, i.e., between ages 2 to 6 years. The functions underestimate lengths-at-age for individuals between 7 to 12 years and overestimate lengths-at-age for individuals over age 15. The growth functions from these studies were based on data that was highly influenced by the absence of the larger sizes-at-age categories due to the extended history of overexploitation of the stock. In spite of the large database with information on individuals between age 0 to approximately 30 years, the majority of the data in the previous studies was generated from individuals within a restricted size and age range (2-6 years), with relatively very few data points coming from older individuals, despite the long life span of greater than 50 years for this species (Fischer et al., 2004;

Fischer et al., 2004; Patterson III et al., 2001; C. A. Wilson & Nieland, 2001). This was probably due to the above mentioned stratification that resulted from the high exploitation of the stock. However, this restricted size-at-age range led to the variance in size-at-age being decreased with increased mean size and age, which is contrary to normal biological expectations (Conover & Munch, 2002). Fischer (2007) indicated that more juveniles and older red snappers ought to be included in samples used for generating parameter estimates in order to ensure accuracy and to improve our knowledge of red snapper growth in the Gulf of Mexico.

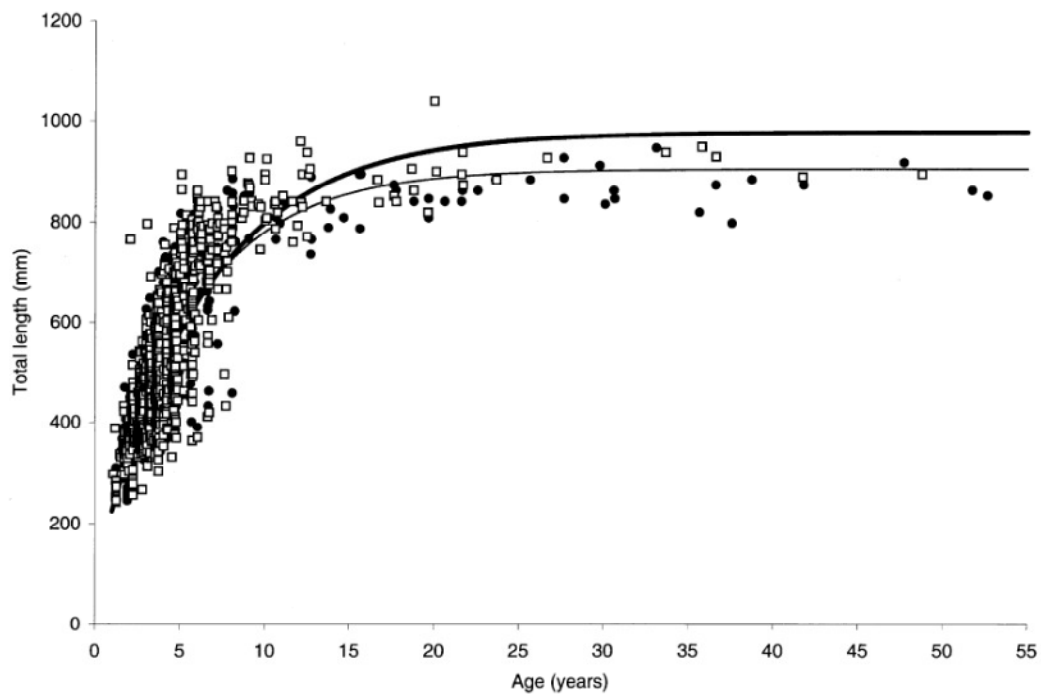


Figure 2.4. Figure from Wilson and Nieland (2001) showing observed data and von Bertalanffy growth models for male (closed circles, thin line) and female (open squares, thick line) red snapper from the Gulf of Mexico.

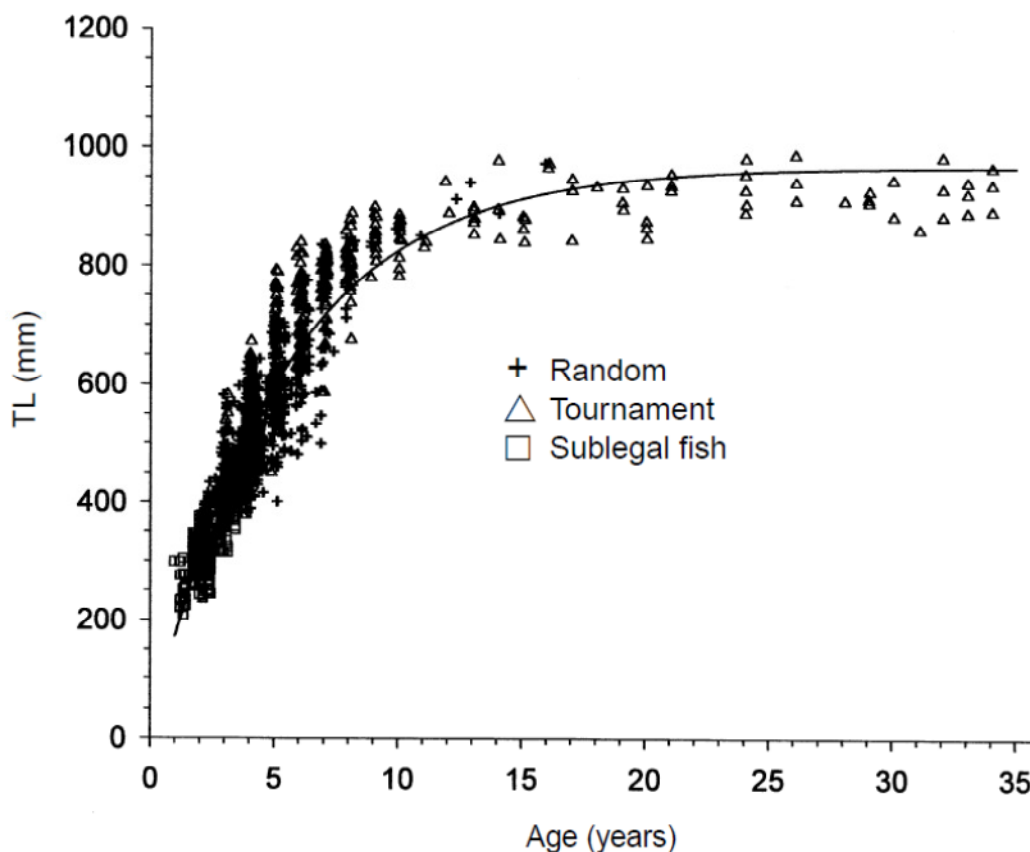


Figure 2.5. Figure from Patterson et al. (2001) showing observed data and von Bertalanffy growth model for red snapper from the Gulf of Mexico.

Growth parameters were also estimated for use in the SEDAR (2005) red snapper stock assessment (Table 2.4). These parameters were corrected for the minimum size sampling bias (SEDAR7-AW-01) (Diaz, Porch, & Ortiz, 2004), however like Wilson and Nieland (2001) and Patterson et al. (2001), the vast majority of the data (98.4%) was derived from fish less than 8 years old.

The goal of this chapter is to improve upon the available growth functions available for red snapper in the Gulf of Mexico. The previous growth functions were determined from biased fishery dependent samples that were stratified as a result of the very long history of heavy exploitation in a fishery that was

overfished, and therefore the larger and older individuals were not available to be sampled. Further, most of the samples for growth function parameter estimation were derived from the directed fisheries and were therefore subject to gear selectivity and resource availability issues that contributed to biased sampling. This work will therefore reanalyze and model the growth of red snappers by taking a new approach to back-calculate length-at-age to achieve an unbiased size-at-age distribution for growth function parameter estimation. This new approach seeks to resolve the significant issue of the lack of older and larger size-at-age individuals due to the effects of exploitation. This work will also develop the use of the otolith area as a more accurate measurement for back-calculation of lengths-at-age than use of otolith radius measurements.

2.3 Materials and Methods

2.3.1 Otolith samples

Two length-at-age data sets comprised of 110 and 260 individual records for red snapper from the Gulf of Mexico were initially provided at different times by the NMFS Panama City Laboratory in Panama City, Florida, USA. These data sets contained information on the individual fish identification from which the measurements were taken, date of capture, State where the fish was landed, total length, age determined from sagittal otolith annulus readings, and measurements to each otolith annulus taken along the dorsal side of the sulcus acousticus. These data sets were combined, hereafter referred to as database 1 (DB1), and contained data on fish between age 2 and age 17 years. In addition,

two sets of sagittal otolith transverse sections and one set of whole sagittal otoliths along with their corresponding fish data sets were also provided by NMFS Panama City Laboratory. The data sets contained, when available, the individual fish identification, date of capture, state where the fish was landed, total length measurements, sex, age determined from sagittal otolith annulus readings and capture information. One set of the otoliths transverse sections was a select group of 187 definitive, well cut and polished otoliths that were used for ageing training purposes by NMFS and contained data on fish between ages 2 and 8 years old. The other set of otolith sections were specifically comprised of 302 age 1 individuals, while the whole otoliths were collected from 30 age 0 (less than 4 months old) fish. Both the age 0 and age 1 fish were all collected during NMFS scientific surveys. The age 0 whole otoliths were all taken from the right side of the fish and its data set had no sex information. These last three data sets were combined, hereafter referred to as database 2 (DB2), to form a comprehensive data set in order to complement each other and expand the age and size range of data available for analyses. The otoliths and data for DB2 were taken from fish sampled between two major periods, the years 1998-2000 and 2007-2008. Any records in DB1 or DB2 that were deficient in the information needed for any of the analyses were excluded from the data set.

2.3.2 Preparation and measurement of otoliths and otolith annuli

Age information determined from otoliths for all of the data sets (except the age 0 individuals) was provided by the trained, experienced readers from the NMFS Panama City laboratory. The age 0 whole otoliths had to be sectioned to

count and measure the annuli in order to determine the age of these fish. Under a dissecting microscope, a line was marked along the transverse plane with pencil over the core of each otolith to indicate the locus where the section was to be taken. These otoliths were thereafter embedded in an epoxy encapsulating resin, sectioned to a thickness of 1.0 mm to include the core with a Buehler Isomet low speed saw and cut along the marked line in the transverse plane. The sections were then adhered to glass slides with Crystal bond (Crystal bond, SPI Supplies), abraded with wet Buehler Microcut P4000 and P2400 silicon carbide grinding papers and polished with Buehler Micropolish II alumina suspension on a Buehler Micropolishing cloth until the core was revealed (C. A. Wilson & Nieland, 2001). Images of all of the otoliths were captured at 10X magnification with an OptixCam 5 megapixel camera attached to a Bausch & Lomb StereoZoom 7 microscope and measurements were made with the camera system's built-in software. Additional high resolution images and measurements of selected age 0 otoliths were captured with a Leica DMLB Microscope at 25-100X magnification using an Infinity 2 (2 megapixel) camera and Image Pro Plus 7.0 software.

In the red snapper the growth of the otolith is greatest, when cut in the transverse plane, along the dorso-ventral axis. The opaque bands are more compressed and distinct along the proximal-distal axis. It is thus easier for the distinct opaque bands to be counted for ageing purposes on the dorsal side of the sulcus acousticus, where they are more defined and evident. Since growth is greatest along the dorso-ventral axis, otolith radius measurements made along

this axis may be a better predictor of somatic growth than along the proximal-distal axis where the ageing measurements are made. However, the opaque bands are wider and relatively less well-defined along the dorsal and ventral axes where the distance within and between the bands are larger (Rezende & Ferreira, 2004), therefore careful determination of annulus measurements are required. The otolith radius measurements from the core to each annulus along the dorsal side of the sulcus acousticus made by NMFS in the ageing process were confirmed, and then corresponding measurements were made from the core to each annulus along the axis of the ventral radius of each otolith. The annulus radius measurements along the ventral axis were defined by measuring the distance from the core to the midpoint of each annulus opaque band. The ventral radius was selected because the ventral axis was more uniform in shape and structure than the dorsal side of the otolith. In addition, the area on the ventral side of each otolith was also measured at the same time in order to develop a regression relationship for the total length to otolith ventral area which would be used in a new back-calculation method for red snapper length-at-age estimation.

In the particular case of the age 0 prepared otolith slides, measurements were made along the dorsal side of the sulcus acousticus, along the ventral axis as well as the otolith ventral area using the OptixCam camera and its software. In addition, under varying high magnification objectives, the Leica DMLB Microscope and Infinity 2 microscope camera was used to select and capture images (Fig. 2.6) of six well defined sections for ageing purposes. The Image Pro

Plus 7.0 software was used to carefully mark the daily growth increment rings on the selected captured images to determine the actual daily age of the selected individuals. These daily ages and the otolith ventral radius measurements were used to calculate a mean daily ventral radius growth rate which was then applied across the entire age 0 group to estimate the age in days for each member of the group.

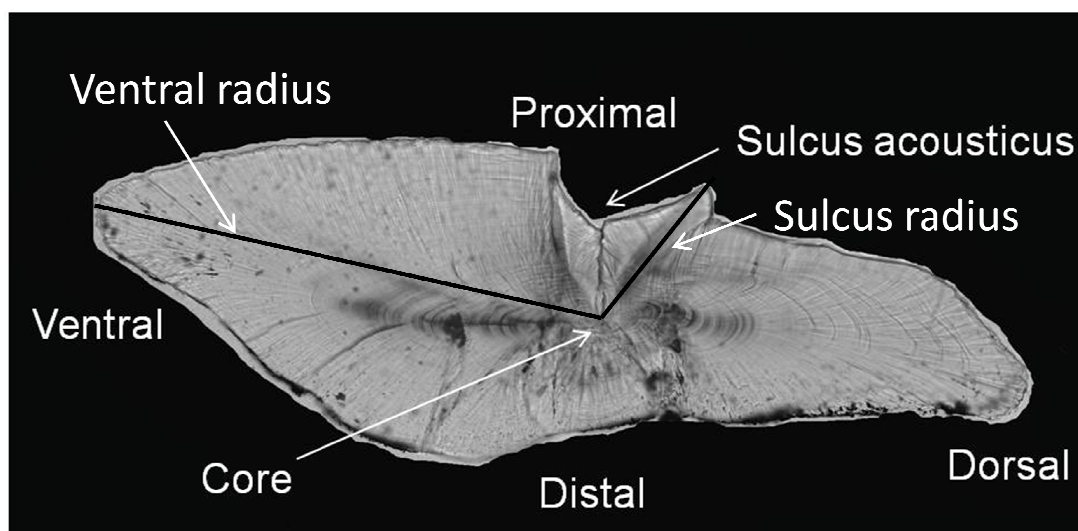


Figure 2.6. Image of a transverse sectioned age 0 red snapper sagittal otolith.

2.3.3 Back-calculation of growth histories

Otolith microstructure analysis has become a very important and essential tool in fish biology and fisheries management. It is recognized as being the most precise means of age determination, and therefore its importance in fisheries management cannot be understated. Age determination is involved in parameter estimation of the age structure of the stock, natural mortality, fishing mortality, age at first spawning, fecundity, and growth rates. The correlation between otolith size and somatic size allows the growth histories to be back-calculated

(Mosegaard, Svedäng, & Taberman, 1988; Takasuka et al., 2008; Vigliola & Meekan, 2009). Back-calculation methods use the measurements made on a hard part of a fish and its body length to infer lengths at previous ages to be estimated. These methods are commonly used when the sample sizes do not cover adequate ranges of ages and lengths so as to be representative of the life history of the species in question (Francis, 1990), (Vigliola & Meekan, 2009).

The sample size for the size at age data for DB2 can therefore be increased by use of back-calculation procedures on the morphometric characteristics of the red snapper otolith and body length.

Back-calculation methods have several basic requirements. First, the deposition rate of increment does not vary. Second, the increments are able to be read with accuracy and precision. And third, there is a relationship between the growth of the otolith and the somatic growth of the fish (Vigliola & Meekan, 2009). Importantly, back-calculations should be based on data where the length and hard part measurements are unbiased, and not drawn from collection samples that are stratified by gear, availability, exploitation patterns or habitats. However, despite the long and significant fishery impacts, many research efforts on the red snapper in the Gulf of Mexico have used such affected data to describe the growth history. (Szedlmayer, 1998), (Patterson III et al., 2001; C. A. Wilson & Nieland, 2001).

One of the earliest and simplest back-calculation models is the Dahl-Lea formulation, which is a direct ratio, i.e., proportional, model because it assumes a

constant linear relationship, passing through zero, between the growth of the hard part and body length. The formulation is expressed as:

$$L_i = \left(\frac{R_i}{R_c}\right) L_c \quad 2.1$$

where L_i = back-calculated fish body length at annulus i , L_c = fish body length at capture, R_i = otolith radius at annulus i , and R_c = total otolith radius at capture. However, since fish growth may vary over time, especially between ontogenetic stages, fish of the same size may have different sized otoliths (growth effects). In addition, age effects may occur where there is a consistent deposition of otolith material although the daily somatic growth rate may vary. These effects may cause the requirement of Dahl-Lea model linearity in the otolith-somatic growth relationship not to be met (Campana, 1990), (Secor & Dean, 1992).

This uncoupling of the relationship between the growth of the otolith and the somatic growth of the fish may generally occur under the two mentioned conditions: 1) growth effects - when the otoliths from slow-growing fish at a given particular size are larger than those of faster growing fish at the same size, and 2) age effects – when a constant or proportional amount of calcification occurs on the otolith despite variations in the somatic growth rate (Campana, 1990; Vigliola & Meekan, 2009) (Secor & Dean, 1992) (J. A. Wilson, Vigliola, & Meekan, 2009). Since growth is known to vary over different life stages, growth effects may also vary over time, causing growth rate changes in the otolith size-somatic size trajectories. Further, age effects and growth effects have been shown not to be mutually exclusive (Morita & Matsuishi, 2001). Both these growth effects and age effects result in fitted regressions that differ significantly from the mean of the

individual otolith radius-fish length slopes, which would be a source of bias in back-calculations based on these relationships.

Because of these issues and possible errors that may result from back-calculations made under these conditions, research has continued on different approaches to improve back-calculation methods. Some researchers have analyzed otolith radius at age, instead of back-calculated length at age, to generate growth rate data sets and thereby avoid the above mentioned errors. These researchers argued that since otolith radius is a proxy for fish length, the back-calculation was unnecessary. However, Vigliola and Meekan (2009) have shown that, depending on the age range being considered, otolith radius may be a poor proxy of fish length when comparing size-at-age.

Other researchers have sought to improve back-calculation procedures. These efforts have resulted in several additional methods being proposed. Campana (1990), noting the growth effect, added a biological intercept to the Fraser-Lee linear back-calculation model to reduce the impact of variable growth rates in the population. He found that the procedure “accurately predicted previous lengths in the presence of both stochastic error and time-varying growth rates.” However, the model was still found to be sensitive to non-linear time-varying growth effects (J. A. Wilson et al., 2009). Francis (1990) reviewed the back-calculation literature and recommended that procedures be based on one of the two proportional hypotheses proposed by Whitney and Carlander (1956). These hypotheses and definitions are as follows: The Scale Proportional

Hypothesis (SPH) – if an otolith was 10% larger when the fish was caught than the average scale for a fish of that size, then the scale would be 10% larger than normal throughout life; and the Body Proportional Hypothesis (BPH) – if a fish at the time of capture was 10% smaller than the average fish with an otolith of that size then the fish would be 10% smaller than the expected length throughout life (Wilson 2009, Vigliola 2009). A Time-Varying Growth model was put forward by Sirois in 1998 to address the issue of non-linear fish length-otolith radius relationships by incorporating a growth effect factor into a biological intercept model (Wilson 2009). However, Wilson (2009) reports that the model still assumes a linear length-otolith relationship and therefore may not be appropriate when the relationship is non-linear for reasons other than the growth effect.

The Modified-Fry model, which forced an allometric body length-otolith radius function to pass through a biological intercept, was developed by Vigliola et al. (2000) in taking another approach to non-linearity. Wilson (2009) reported that this model was robust to growth effects. Further, the Age Effects model developed by Morita and Matsuishi (2001) was designed to remove bias due to age effects by assuming that the otolith measurements were congruent with a linear multiple regression of otolith radius on body length and age and then applying the SPH condition.

2.3.4 Growth model

The von Bertalanffy growth function as expressed by Beverton and Holt (1957) was used to model growth of the Gulf of Mexico red snapper. This

function is commonly used to model the growth of fish, and has been used to estimate the growth parameters of the red snapper (Fischer et al., 2004; Patterson III et al., 2001; C. A. Wilson & Nieland, 2001). The function has the formulation:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) \quad 2.2$$

where L_∞ is the theoretical maximum asymptotic length a fish will reach in the population, k is a growth coefficient which describes the rate at which the asymptotic length is approached, and t_0 , the hypothetical age when the total length would be zero. The von Bertalanffy model has been widely used to express fish growth because it: 1) follows most of the growth characteristics of fish, 2) is simple in its parameters and 3) as more comprehensive and accurate data that is fully representative of the population being studied is collected the model fits are improved.

Four back-calculation models were selected to investigate the individual growth history from data on otolith radius measurements and fish length. The models selected included a multiple regression model, an age effects model, a power model and the Modified-Fry model.

The multiple regression model was initially suggested as a result of analysis of the orientation of the relationship of the total length to the otolith radius and age data from the available data sets. All of the data relationships were then linearized by use of a natural logarithm transformation. The multiple regression model was utilized to test three different data conditions. The first data condition was a 2-way regression model that used DB1, which only had

information on the total length, the age determined from the otolith annuli and the otolith radius measured along the dorsal side of the sulcus acousticus. The model formulation and linearized form were as follows:

$$L_i = a(R_i^b)(T_i^c) \quad 2.3$$

$$\ln(L_i) = \ln(a) + b\ln(R_i) + c\ln(T_i) \quad 2.4$$

where L_i = back-calculated fish body length at annulus i , a = intercept of the model, b = the coefficient for the log transformed sulcus acousticus radius, R_i = sulcus acousticus radius at annulus i , c = the coefficient for the log transformed age, and T_i = age at annulus i . The second data condition was identical to the first condition except that it was based on DB2 for which the otoliths sections had been available for supplementary measurements. The third data condition was a 3-way regression model that used the data from the second condition but the added the data of the otolith radius measured along the ventral axis as an additional independent variable. The model formulation and linearized form for this condition were:

$$L_i = a(VR_i^b)(SR_i^c)(T_i^d) \quad 2.5$$

$$\ln(L_i) = \ln(a) + b\ln(VR_i) + c\ln(SR_i) + d\ln(T_i) \quad 2.6$$

where L_i = back-calculated fish body length at annulus i , a = intercept of the model, b = the coefficient for the log transformed ventral radius, VR_i = ventral radius at annulus i , c = the coefficient for the log transformed sulcus acousticus radius, SR_i = sulcus acousticus radius at annulus i , d = the coefficient for the log transformed age, and T_i = age at annulus i .

The age effects model assumes that the otolith radius results from a

combination of the length and age of the fish and allows for continuous growth of the otolith, even during periods when somatic growth stops (Morita & Matsuishi, 2001). The model was designed to remove any bias due to age effects. This model uses the fit of a multiple regression model of otolith radius on the independent variables of length and age (Eq. 2.7) to generate the coefficients used in the equation 2.8:

$$R_i = a + bL_i + cT_i \quad 2.7$$

where R_i = ventral radius at annulus i , a = intercept of the regression model, b = the coefficient for the total length at capture, L_i = total length at annulus i , c = the coefficient for the age at capture, and T_i = age at annulus i .

$$L_i = -\frac{a}{b} + \left(L_{cpt} + \frac{a}{b} + \frac{c}{b} T_{cpt} \right) \frac{R_i}{R_{cpt}} - \frac{c}{b} T_i \quad 2.8$$

where L_i = back-calculated fish body length at age i , a = intercept of the regression model (Eq. 2.7), b = the coefficient for the total length at capture from the regression (Eq. 2.7), c = the coefficient for the age at capture from the regression (Eq. 2.7), L_{cpt} = total length at capture, T_{cpt} = age at capture, R_i ventral radius at annulus i , R_{cpt} = ventral radius at capture, and T_i = age at age i .

The log-transformed power model is based on the assumption that a power curve exists in the relationship between the otolith radius and the total length of the fish (Ehrhardt, 1992). The model requires as an input the intercept from the simple regression of the log transformed total length on otolith radius. The model formulation is:

$$\ln(L_i) = \frac{\ln(R_i)\ln(L_t - a)}{\ln(R_t)} + \ln(a) \quad 2.9$$

where L_i = back-calculated fish body length at annulus i , R_i = ventral radius at annulus i , L_t = total length at capture, a = intercept of the regression model, and R_t = ventral radius at capture.

The Modified-Fry model was found by studies to produce more precise estimates of size-at-age than several other models (Vigliola, Harmelin-Vivien, & Meekan, 2000), (Vigliola & Meekan, 2009). It includes the use of the biological intercept concept (total length and otolith ventral radius at hatching) with a statistically determined parameter of fish size at otolith formation. The formulation of the Modified-Fry model is as follows:

$$L_i = a + \exp\left(\ln(L_{op} - a) + \frac{[\ln(L_{cpt} - a) - \ln(L_{op} - a)][\ln(R_i) - \ln(R_{op})]}{[\ln(R_{cpt}) - \ln(R_{op})]}\right) \quad 2.10$$

where L_i = back-calculated fish body length at annulus i , a = length of fish at otolith formation, L_{op} = total length of fish at hatching, L_{cpt} = total length at capture, R_i = otolith ventral radius at annulus i , R_{op} = otolith ventral radius at hatching, and R_{cpt} = otolith ventral radius at capture.

In addition to the above four models, a new area model was derived from the Dahl-Lea back-calculation formulation based on the linear regression of the total length to the otolith ventral area. The linear regression model and the derived area model are respectively expressed as:

$$L_t = a + b(A_t) \quad 2.11$$

$$L_i = a + \left(\frac{L_t - a}{A_t}\right) A_i \quad 2.12$$

where L_t = total length at capture, a = intercept of the regression model, b = slope of the total length-total otolith ventral area regression model, A_t = otolith ventral

area at capture, L_i = back-calculated fish body length at annulus i , and A_i = otolith ventral area at annulus i . The otolith ventral area at capture was measured from the lowest point of the sulcus acousticus to lowest point of the anti-sulcus and along the ventral edge of the otolith (fig 2.7). The area of the annulus was similarly measured to the end of the opaque bands in accordance with the ventral radius ageing measurements. The intercept parameter (a) from the regression of total length to otolith ventral area ($N = 505$) was used in the new back-calculation model (eq. 2.12) for the oldest available red snapper otoliths ($N = 24$).

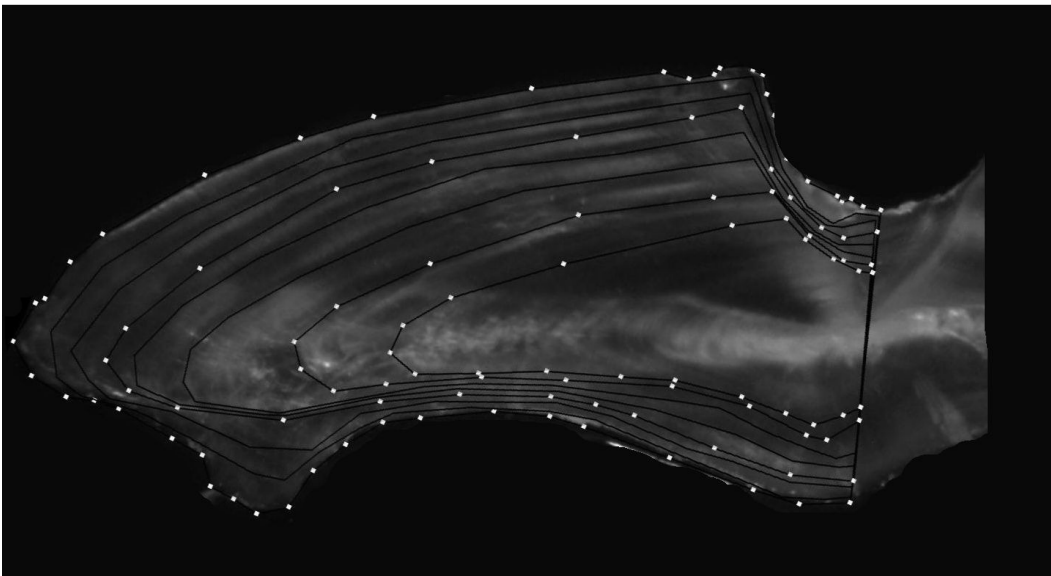


Figure 2.7. Image showing ventral areas measured for each annulus for the otolith ventral area based back-calculation model.

The actual otoliths for DB1 were not available for supplemental measurements (ventral radius and otolith ventral area) to complement the data needed for the back-calculation models so additional data sets and otoliths were requested from NMFS and DB2 was received and used.

2.4 Results

2.4.1 Otolith morphometric analyses

DB1 (N = 366) was found to have a overall trend of a decreasing standard deviation in mean length with increasing mean length-at-age, especially for mean lengths greater than 500 mm (Fig. 2.8). This indicated that the samples were biased in the size-at-age distributions and therefore likely to yield erroneous growth function parameters.

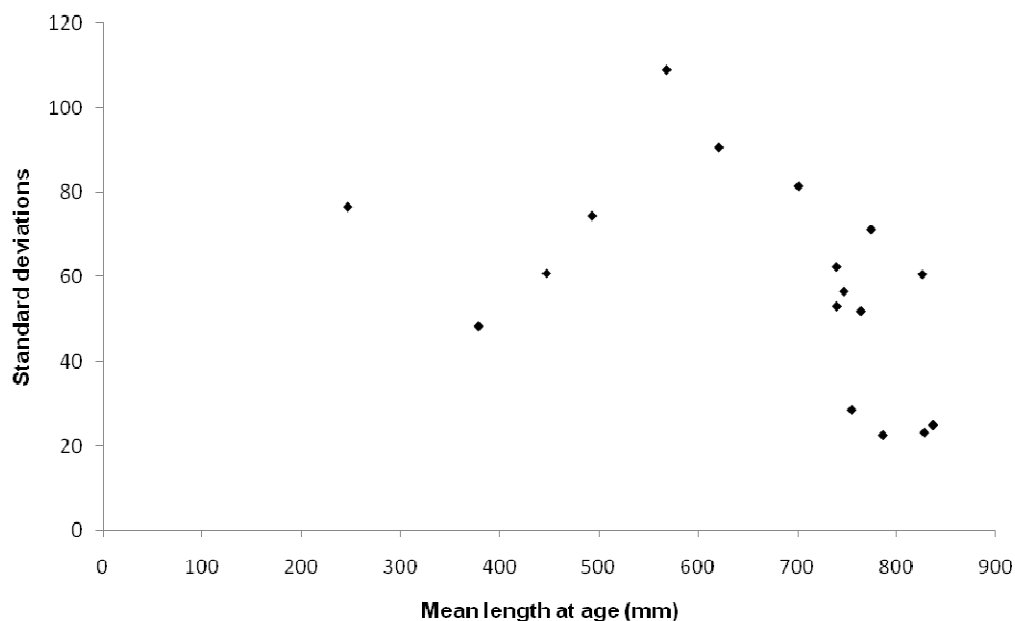


Figure 2.8. Standard deviation of mean length-at-age on mean length-at-age for DB1.

Analyses of the relationships between the total length and the otolith sulcus acusticus radius for individual age groups in DB1 found that when the otoliths of whole ages were considered (i.e., the otoliths where the edge beyond the last opaque band was very small or not present) uncoupling of the relationship between the total length and the otolith sulcus acusticus radius was

found (Fig. 2.9). The whole ages should show a consistent positive relationship within and between the different ages as they represent the continuous positive incremental growth of the otolith relative to the somatic growth at the same relative point in time. Some age classes indicated that the somatic length decreased with otolith radius increase while other age classes showed an increase in this trend or no response at all. The age classes with negative or no otolith radius-somatic length relationships are termed as uncoupled.

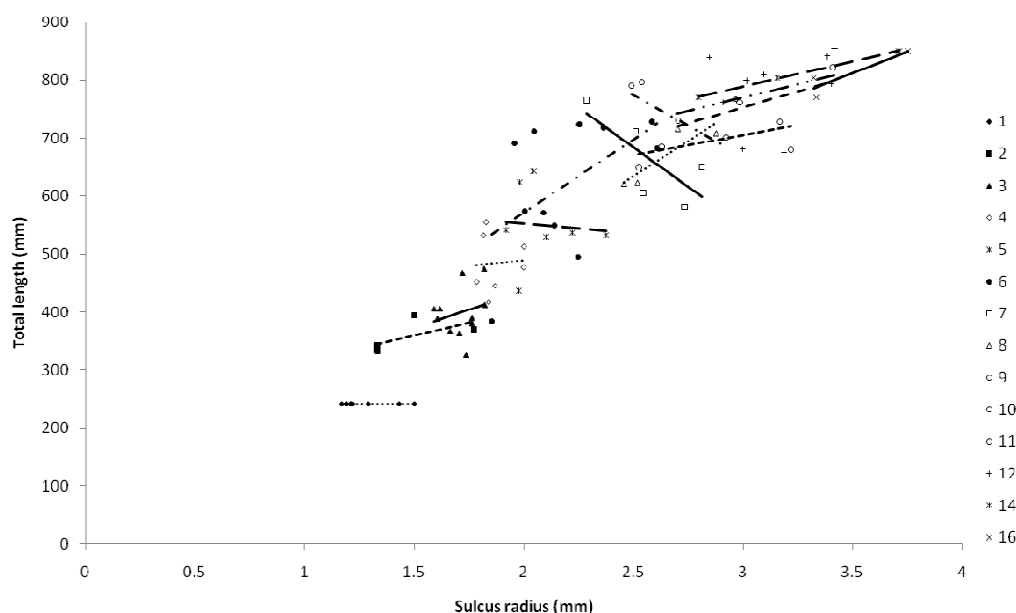


Figure 2.9. Relationship of total length to sulcus acoustic radius for individual whole age groups.

To resolve these uncoupling issues additional information on hard parts and size-at-age data sets, which included otoliths and data for juveniles and young-of-the-year red snapper, were requested from NMFS. After DB2 was received the supplementary data that was collected from the hard parts were the ventral radius measurements as well as the area of the ventral side of the otolith.

The results estimated that the age 0 individuals ranged from 60 to 90 days old, which is consistent with the recorded capture dates and the known prolonged spawning period for the red snapper. Unfortunately, there was no additional growth data or hard parts available from NMFS for individuals from age classes greater than 8 years old.

It was felt that the otolith ventral radius would be a more accurate and precise measure for growth correlation than the sulcus acousticus radius for two possible reasons. These are that when cut in the transverse plane: (i) the dorso-ventral axis of the otolith has a greater range of growth per year than the axis along the sulcus acousticus, and therefore may better reflect the somatic growth pattern; and (ii) there should be a proportionally smaller impact of measurement error due to its larger measurement distance when compared to the sulcus acousticus radius.

In comparing the relationships of the total length to the sulcus acousticus and to the ventral radii of DB2 it was found that a power model performed as an accurate descriptor for both of the relationships. The ventral radius (for DB2) did prove to be much more strongly associated with the total length ($r^2 = 0.960$) (Fig. 2.10), than did the sulcus acousticus radius ($r^2 = 0.716$ for DB1 and $r^2 = 0.888$ for DB2 (Fig 2.11)). These results supported the contention that the ventral radius would serve as a more accurate predictor for red snapper total length than the sulcus acousticus radius.

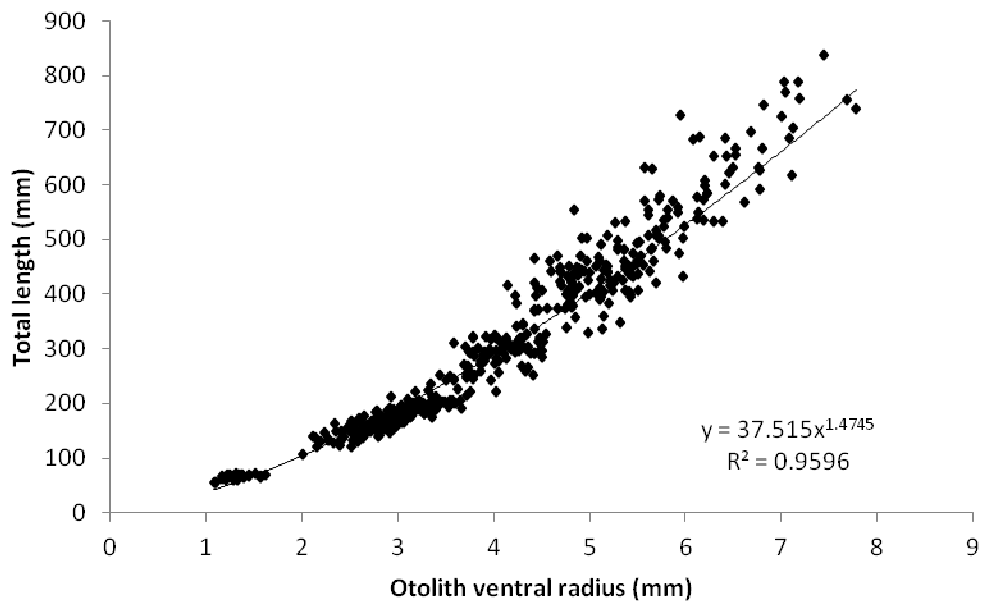


Figure 2.10. Relationship of total length to ventral radius for DB2.

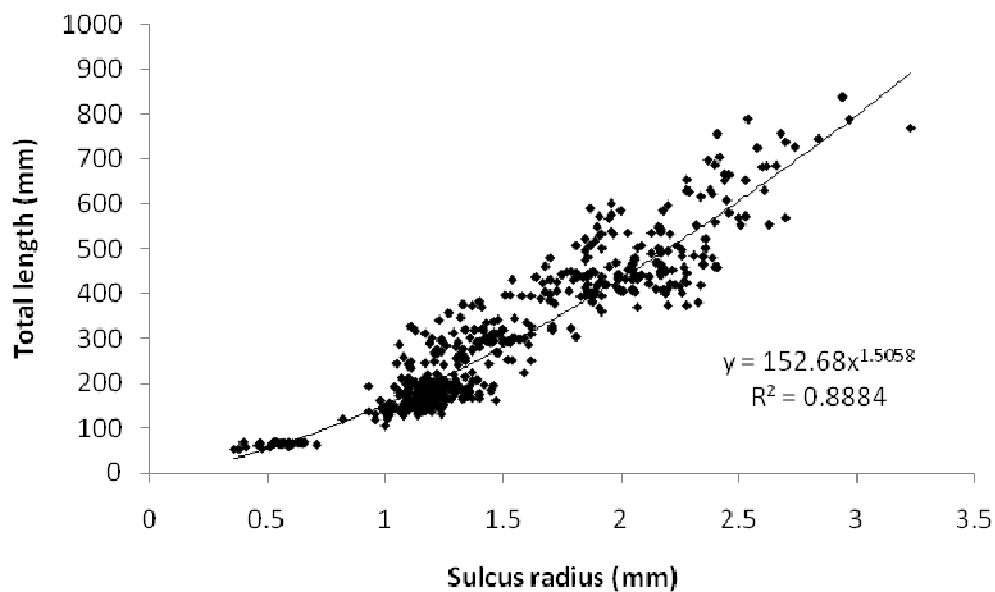


Figure 2.11. Relationship of total length to sulcus acousticus radius for DB2.

The remainder of these analyses was therefore done using DB2 in order to take advantage of the use of the ventral radius measurements. The analysis of total length to otolith radius by individual ages was repeated using the ventral radius measurements of DB2. The plot of total length on ventral radius by age showed that the issue of decoupling in the total length-otolith radius relationship that was found with DB1 had been resolved by use of the ventral radius measurements instead of the sulcus acusticus radius measurements (Fig 2.12).

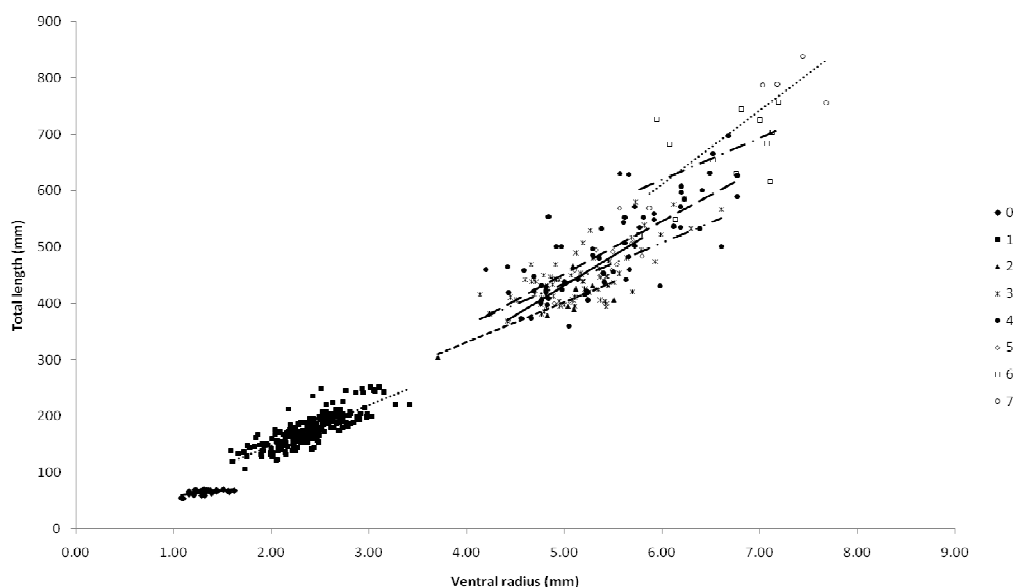


Figure 2.12. Relationship of total length to ventral radius by age class for DB2.

There was no statistically significant difference in the fitted relationships of log-transformed total length to log-transformed ventral radius by sex at the $\alpha = 0.05$ level (Fig. 2.13). A one-way ANCOVA test (Table 2.2) for differences in slopes and intercepts for males and females ($N = 160$ and $N = 127$, respectively) resulted in values of $P = 0.863$ for intercepts and $P = 0.223$ for slopes, both greater than the usually accepted statistical standard of $P = 0.05$.

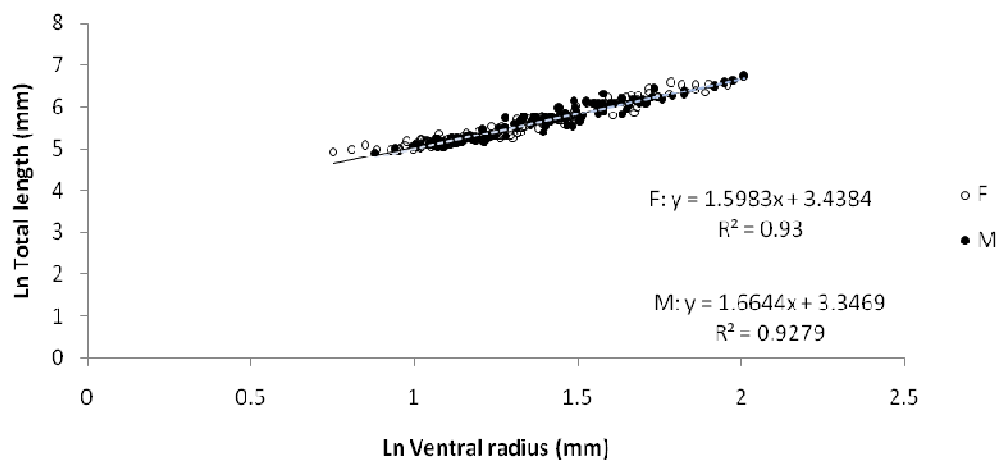


Figure 2.13. Relationship of log total length to log ventral radius by sex.

Table 2.2. Ancova table for relationship of log total length to log otolith ventral radius by sex.

ANCOVA SUMMARY - Intercepts

Source	SS	df	MS	F	P
adjusted means	0	1	0	0.03	0.8626
adjusted error	3.61	284	0.01		
adjusted total	3.61	285			

Test for homogeneity of regressions: Slopes

Source	SS	df	MS	F	P
between regressions	0.02	1	0.02	1.49	0.2232
remainder	3.59	283	0.01		
adjusted error	3.61	284			

The relationship between the sulcus acusticus radius and the ventral radius was found to be statistically significant with the linear regression producing a coefficient of determination of 0.811 (Fig. 2.14). When considered by sex this

relationship was not significantly different in slopes nor intercepts, indicating that the sexes maintain similar relationships between the two radii within the size and age range considered (Fig. 2.15). The one-way ANCOVA test (Table 2.3) for differences in slopes and intercepts for males and females ($N = 160$ and $N = 127$, respectively) resulted in values of $p = 0.158$ for intercepts and $p = 0.278$ for slopes, both larger than the $p = 0.05$ standard usually used in statistical inference.

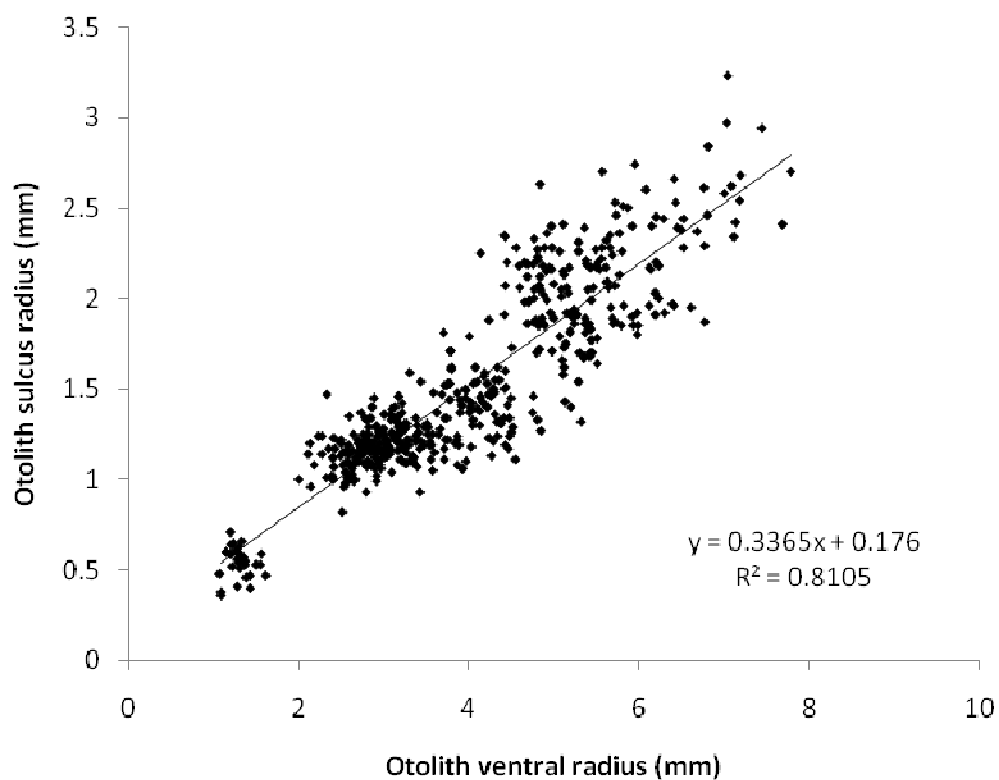


Figure 2.14. Relationship of otolith sulcus acoustic radius to ventral radius.

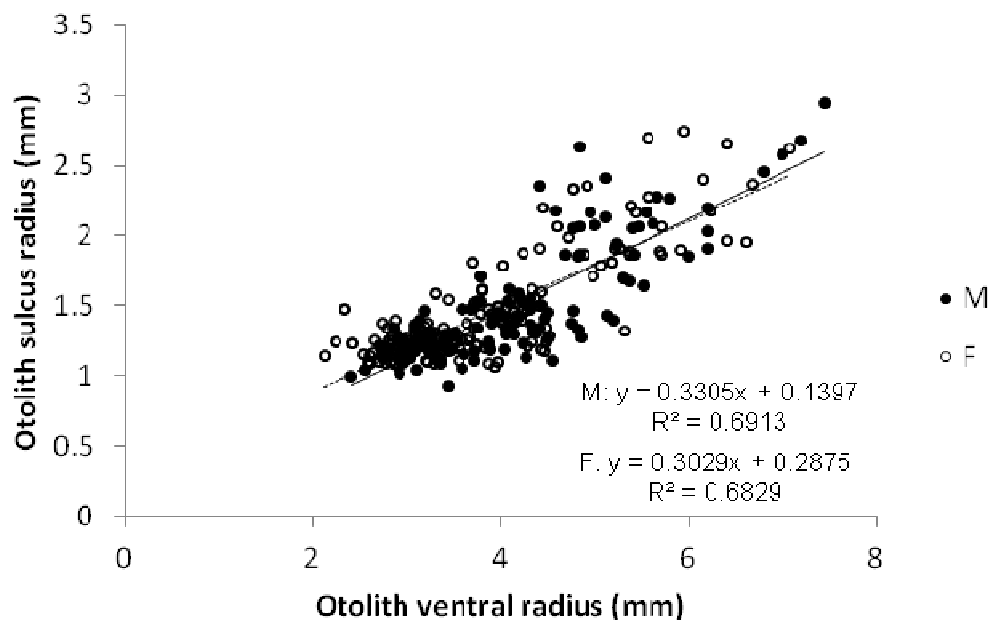


Figure 2.15. Relationship of otolith sulcus radius to ventral radius by sex.

Table 2.3. Ancova table for relationship of sulcus acousticus radius to otolith ventral radius by sex.

ANCOVA SUMMARY: Intercepts

Source	SS	df	MS	F	P
adjusted means	0.1	1	0.1	2	0.1584
adjusted error	14.04	284	0.05		
adjusted total	14.14	285			

Test for homogeneity of regressions: Slopes

Source	SS	df	MS	F	P
between regressions	0.06	1	0.06	1.18	0.27828
remainder	13.98	283	0.05		
adjusted error	14.04	284			

2.4.2. Back-calculations

The multiple regression methods used here were simple direct ratio models that tend to have an over-all averaging effect over the entire size and age range. The first two-way multiple regression model (Eq. 2.3) was based on the NMFS-provided measurements of lengths, ages and otolith radius measurements made along the dorsal side of the sulcus acousticus. These DB1 data, which were measured as a part of the age determination process, were log-transformed and used to back-calculate previous lengths-at-age. These back-calculated lengths-at-ages were then used to fit a von Bertalanffy growth function which resulted in the following parameter estimates: $L_{\infty} = 978.130$ mm, $k = 0.122$ yr⁻¹, and $t_0 = -1.399$ yr. Figure 2.16 shows these results. A t-test for whether the slope of the relationship of the model and observed data differed from 1 gave a value of $t = 1.400$, which was less than the critical $t_{(.05,15)}$ value of 2.131 so therefore the null hypothesis was not rejected.

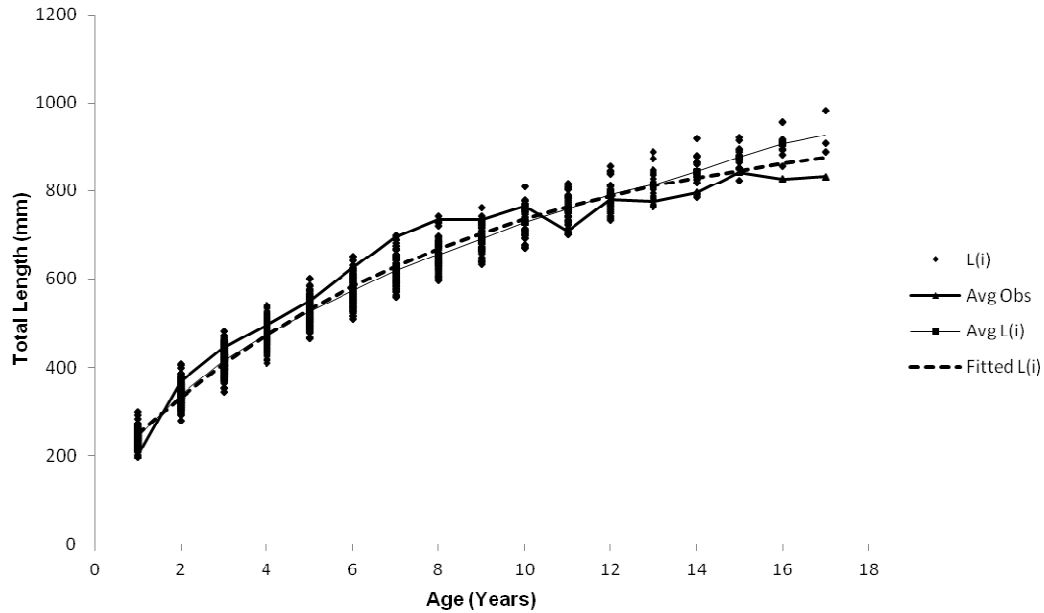


Figure 2.16. Plot of back-calculated lengths-at-age $L_{(i)}$, average back-calculated length-at-age $\text{Avg } L_{(i)}$, mean observed length-at-age Avg Obs and fitted length-at-age $\text{Fitted } L_{(i)}$ for the 2-Way Multiple Regression model based on DB1 sulcus acusticus radius measurements and age.

Using the otoliths received from NMFS that form DB2, similar measurements to those above were made and another two-way regression model was made for comparison purposes. The von Bertalanffy growth function parameters found were: $L_{\infty} = 1232.913$ mm, $k = 0.114 \text{ yr}^{-1}$, and $t_0 = -0.353$ yr. The results for this regression model are shown in figure 2.17. The t-test for whether the slope of relationship between the model and the observed mean lengths-at-age differing from 1 had a value of $t = 0.251$. This was less than the critical value of $t_{(.05,7)} = 2.365$, therefore the null hypothesis was accepted.

Using the additional morphometric data collected from the otoliths, a three-way multiple regression model (Eq. 5) was made based on the log-transformed data including the total length, age, sulcus acusticus radius and

ventral radius measurements. The von Bertalanffy growth function parameters for this model were: $L_{\infty} = 1081.697$ mm, $k = 0.128$ yr⁻¹, and $t_0 = -0.158$ yr. Figure 2.18 shows these results. The t-test for the relationship of the slope of the back-calculated mean length-at-age and the observed mean length-at-age to be different from 1 had a value of $t = 0.976$, less than the critical value of 2.365, therefore the null hypothesis was accepted.

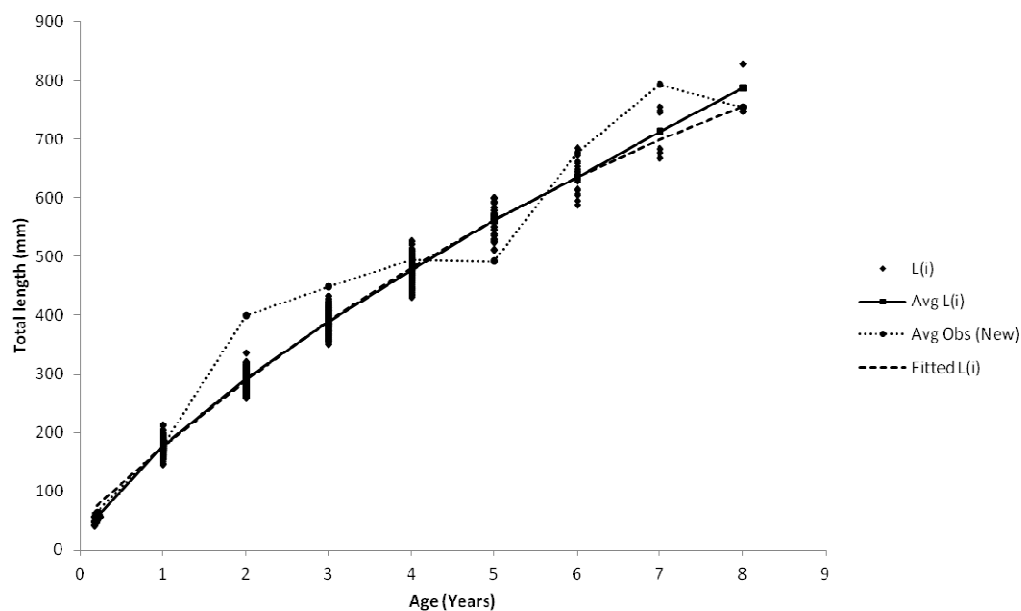


Figure 2.17. Plot of back-calculated lengths-at-age $L_{(i)}$, average back-calculated length-at-age Avg $L_{(i)}$, mean observed length-at-age Avg Obs (New) and fitted length-at-age Fitted $L_{(i)}$ for the 2-way Multiple Regression model based on DB2 sulcus acousticus radius measurements and age.

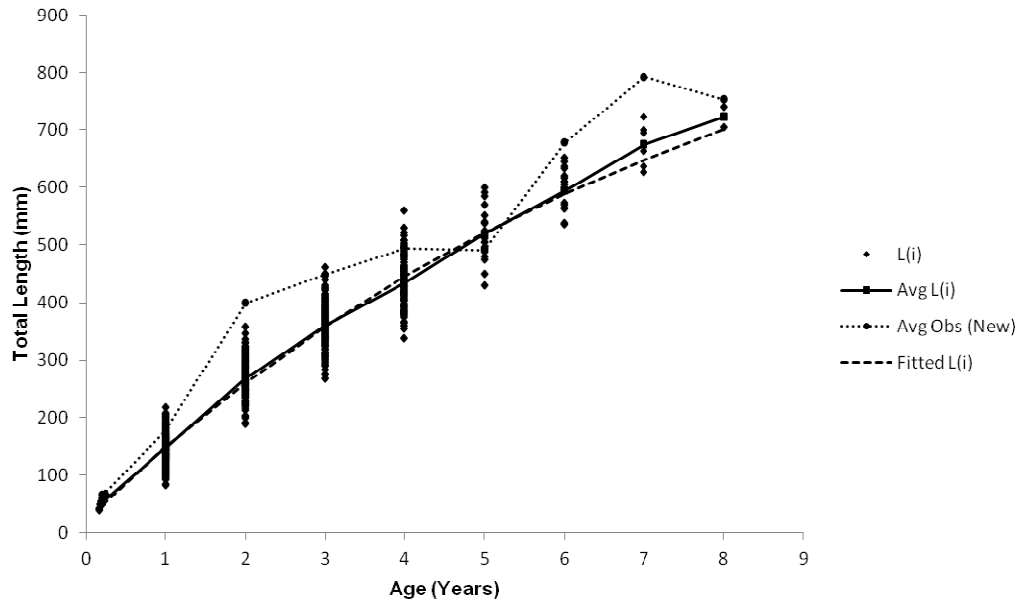


Figure 2.18. Plot of back-calculated lengths-at-age $L_{(i)}$, average back-calculated length-at-age $\text{Avg } L_{(i)}$, mean observed length-at-age Avg Obs (New) and fitted length-at-age $\text{Fitted } L_{(i)}$ for the 3-Way Multiple Regression model based on DB2 sulcus acousticus radius, ventral radius and age.

The age effects model (Eq. 2.8) of Morita and Matsuishi (2001) was also used to back-calculate lengths-at-age for the data collected from the supplied otoliths (Vigliola & Meekan, 2009). A von Bertalanffy growth function based on derived data from this model produced parameters of: $L_{\infty} = 1109.627$ mm, $k = 0.145 \text{ yr}^{-1}$, and $t_0 = -0.204$ yr. These results are given in figure 2.19 below. A t-test for the relationship of the slope of the back-calculated mean length-at-age and the observed mean length-at-age to be different from 1 had a value of $t = 0.349$ while the critical t value was $t_{(.05,7)} = 2.447$, so the null hypothesis was accepted.

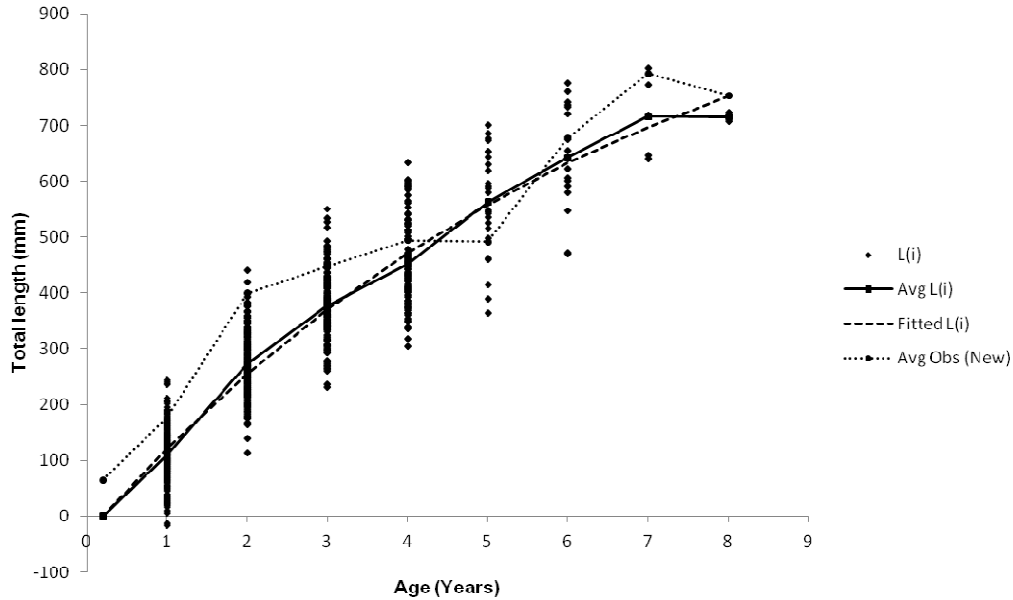


Figure 2.19. Plot of back-calculated lengths-at-age $L_{(i)}$, average back-calculated length-at-age $Avg L_{(i)}$, mean observed length-at-age $Avg Obs (New)$ and fitted length-at-age $Fitted L_{(i)}$ for the Age Effects model.

Back-calculation for lengths-at-age for the data was next done using a power model (Eq. 2.9) based on data measured from the radii of the otoliths. This model resulted in a von Bertalanffy growth function with parameters of: $L_{\infty} = 927.558$ mm, $k = 0.179 \text{ yr}^{-1}$, and $t_0 = 0.156$ yr. Figure 2.20 illustrates these results and a plot of the back-calculated data. The t-test for whether the relationship between the model and observed mean lengths-at-age differed from 1 had a value of $t = 0.073$, which was less than the critical value of $t_{(0.05,7)} = 2.365$ so the null hypothesis was accepted.

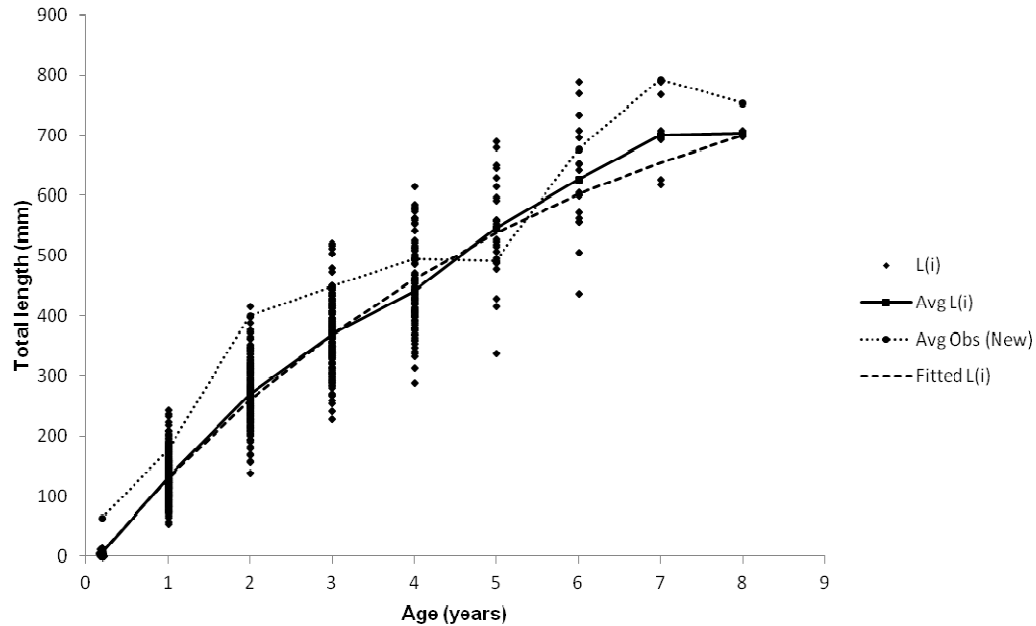


Figure 2.20. Plot of back-calculated lengths-at-age $L(i)$, average back-calculated length-at-age $Avg L(i)$, mean observed length-at-age $Avg Obs (New)$ and fitted length-at-age $Fitted L(i)$ for the Log Power model

The final model used to back-calculate the otolith data was the Modified-Fry model (Eq. 2.10). The von Bertalanffy growth function parameters for this model were: $L_{\infty} = 924.870$ mm, $k = 0.184$ yr^{-1} , and $t_0 = -0.087$ yr. Figure 2.21 shows these results. The relationship of the back-calculated lengths-at-age to the observed lengths-at-age for the Modified-Fry model is illustrated in figure 2.22. The figure indicated that the model fits the data quite well with a high coefficient of determination ($r^2 = 0.962$). A t-test was used to determine whether the slope or intercept of the relationship between the model and observed mean lengths-at-age differed from 1. The results for the slope indicated that the calculated t value (0.191) was less than the critical t value (2.365) ($\alpha = 0.05$, 7 df), therefore the null hypothesis of no significant difference between the slopes of the back-calculated length-at-age and the observed length-at-age was accepted.

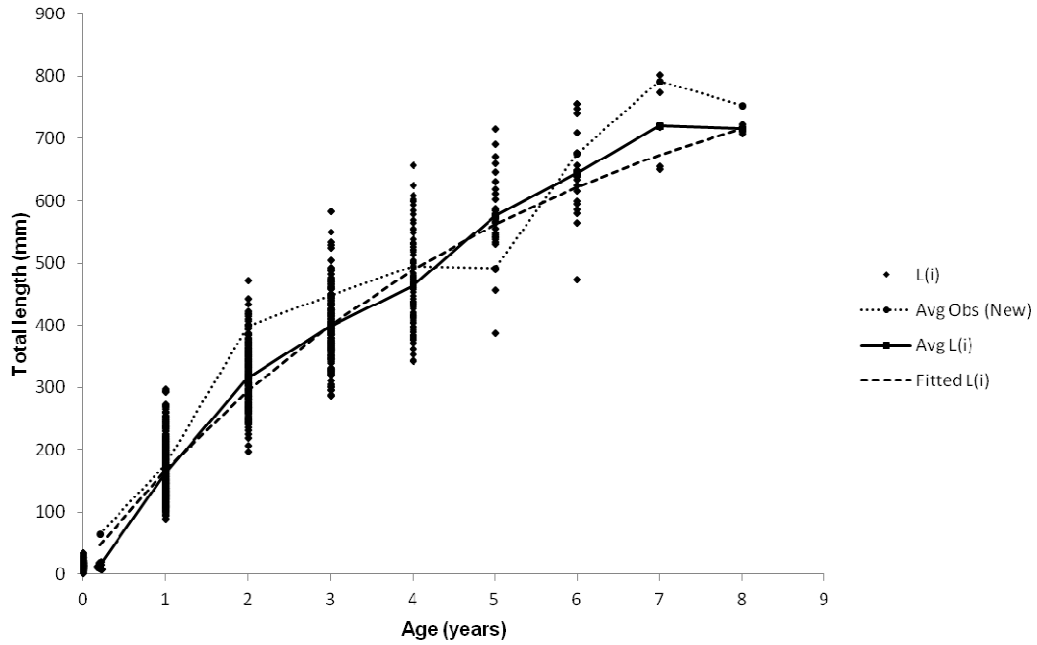


Figure 2.21. Plot of back-calculated lengths-at-age $L(i)$, average back-calculated length-at-age $Avg L(i)$, mean observed length-at-age $Avg Obs (New)$ and fitted length-at-age $Fitted L(i)$ for the Modified-Fry model

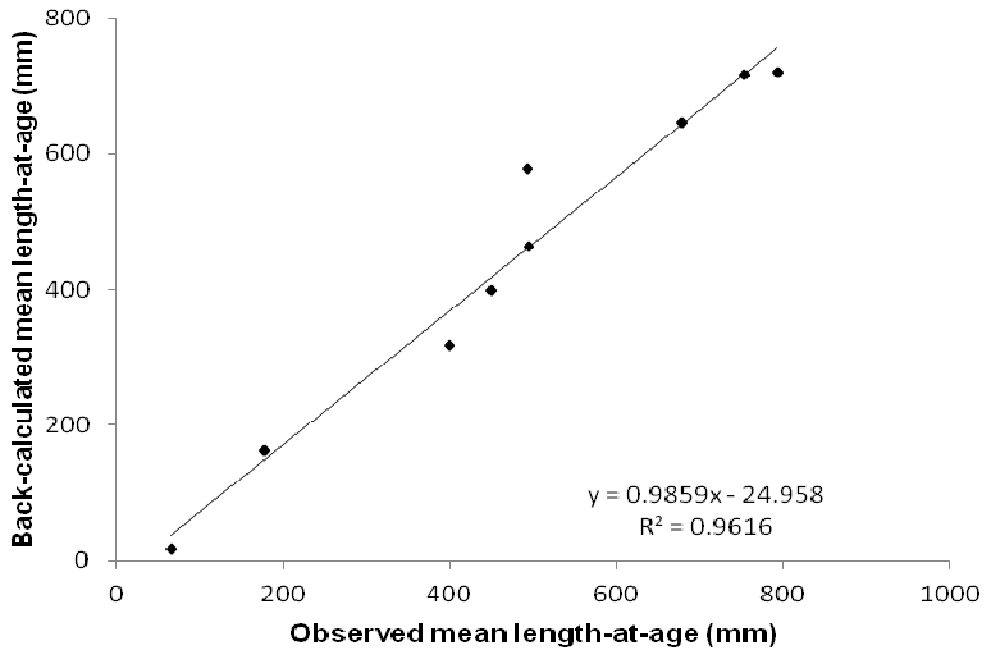


Figure 2.22. Relationship of back-calculated mean length-at-age to observed mean length-at-age for Modified-Fry Model.

The von Bertalanffy growth curves for each of the tested models (figure 2.23) appear to be grouped well together, especially in the early, fast growing age range for the species. A summary of the von Bertalanffy growth parameters as determined by the various models is given in table 2.4. This table also provides the results found by Wilson and Nieland (2001), Patterson et al. (2001) and by the SEDAR (2005) process for comparison purposes.

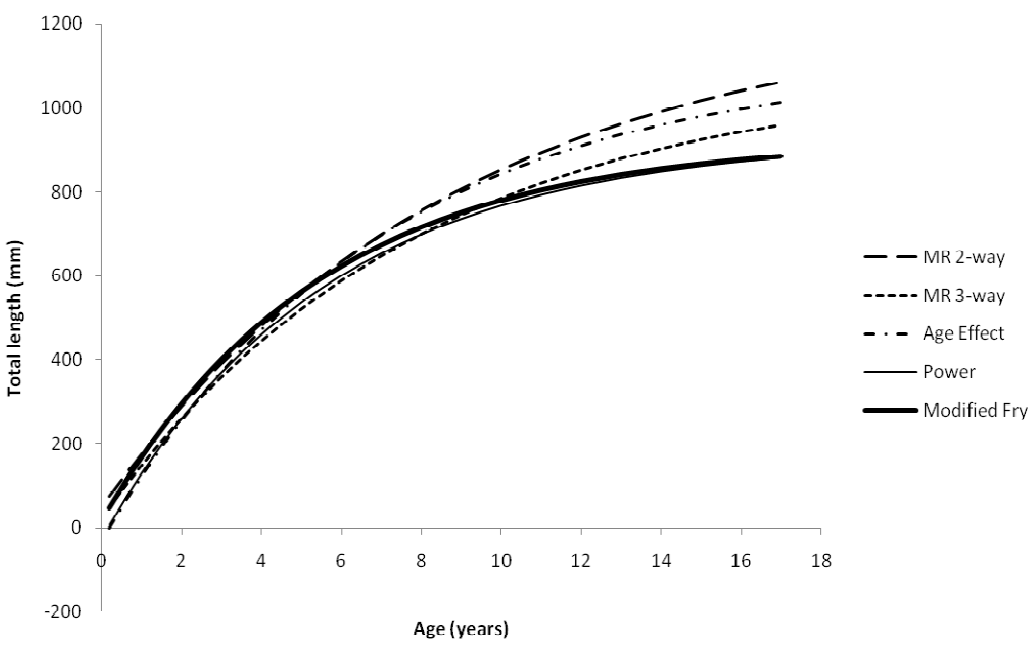


Figure 2.23. Growth curves resulting from the models.

Table 2.4. Summary of von Bertalanffy growth parameters from models.

Model	L_{∞}	k	t_0	N
2 way multiple regression – DB1	978.130	0.122	-1.399	366
2 way multiple regression – DB2	1232.913	0.114	-0.353	410
3 way multiple regression – DB2	1081.697	0.128	-0.158	410
Age Effects – DB2	1109.627	0.145	0.204	410
Log Transformed Power – DB2	927.558	0.179	0.156	410
Modified Fry – DB2	924.870	0.184	-0.087	410
Wilson and Nieland (2001)	941	0.18	-0.55	3791
Patterson et al. (2001) - all	969	0.192	0.020	1755
Patterson et al. (2001) – excluding tournament fish	1181	0.120	-0.652	1466
SEDAR (2005)	876.9	0.22	0.37	65,535

Figure 2.24 shows the standard deviations on mean length-at-age for the Modified-Fry back-calculated data. There is a very clear increasing trend in the standard deviation with increase in mean length-at-age, however, the rate of increase decreases with increasing mean length, as indicated by the natural logarithmic function that is fitted to the back-calculated data ($r^2 = 0.91$).

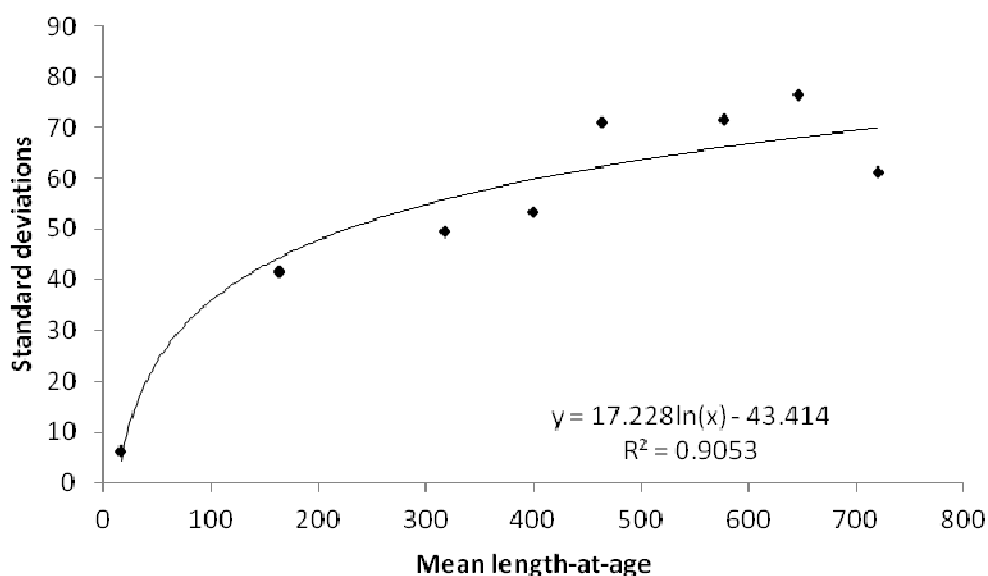


Figure 2.24. Standard deviations for mean length-at-age from back-calculated lengths-at-age based on the Modified-Fry model.

The growth parameters estimated for all of the models were impacted by both gear selectivity and minimum size effects over the long and intensive history of exploitation of the red snapper fishery. Therefore, it was necessary to address the above issues through the construction of a simulated growth database that was designed to reflect a realistic and unbiased distribution of the size-at-age categories, one in which the standard deviation of the size-at-age increased as mean size increased, as should be biologically expected (Conover & Munch, 2002). A Monte Carlo approach was used to generate experimental length-at-age

data from the Modified-Fry model which would be used to simulate an unbiased virgin red snapper length-at-age population structure. This was accomplished by using the mean and standard deviation for each age class from the back-calculated length-at-age data to generate a theoretical normal distribution (probability density function (pdf)) for the length classes within each age class. The expected frequencies for each length class were obtained by multiplying the pdf for that class by the number of survivors for that age class from the natural mortality function used in the stock assessment process for red snapper. This virgin length frequency distribution was then scaled down to 200 individuals per age class by assigning the appropriate proportional numbers to each length bin. This unbiased population structure was then used to re-generate the von Bertalanffy growth function parameters and the variance-covariance matrix. Table 2.5 displays the resulting unbiased growth function parameters and the variance-covariance matrix.

Table 2.5. Estimated von Bertalanffy growth parameters and variance-covariance estimates from normalized Modified-Fry Back-calculation method.

	L_{∞}	K	t_0
Estimates	1201.40	0.123694	-0.1771
Standard Errors	42.30	0.006658	0.027345
Variance-Covariance Matrix			
	L_{∞}	K	t_0
L_{∞}	0.178927E+04	-0.279363E+00	-0.689971E+00
K	-0.279363E+00	0.443275E-04	0.121824E-03
t_0	-0.689971E+00	0.121824E-03	0.747774E-03

Standard error of estimate 57.9019

2.4.3 Total length-otolith area relationship

The relationship between the total length and the otolith ventral area for the red snapper (N = 505) was highly significant (Fig. 2.25). The coefficient of determination had a value of 0.963, indicating the very strong prediction power for the regression model within the age range of the samples. Table 2.6 below gives the regression results. Figure 2.26 reveals the relationship between the total length and the otolith ventral area by sex. Both regressions had highly significant coefficients of determination, 0.956 and 0.940 (N = 127 and N = 160 for males and females, respectively). The one-way ANCOVA test, results given in table 2.7, indicated that, in this case, there was a statistically significant difference between the males and females for the slopes of this relationship (P = 0.002), indicating that females grew at a faster rate; however, there was no significant difference for the intercepts (P = 0.311) at the $\alpha = 0.05$ level.

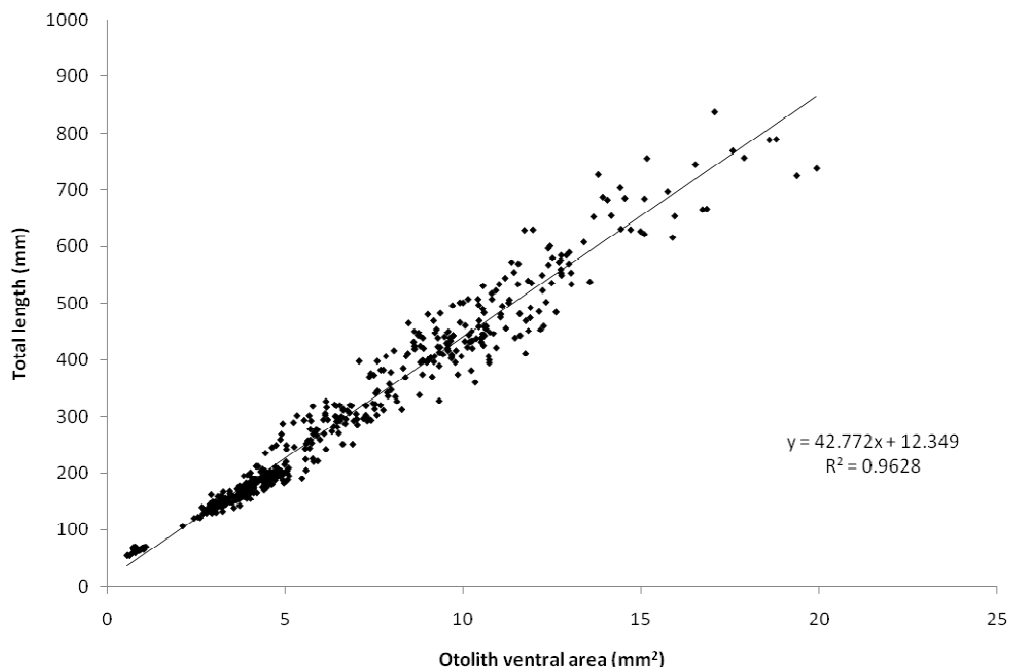


Figure 2.25. Relationship of total length to otolith ventral area for red snapper.

Table 2.6. Regression results for relationship of total length to otolith ventral area for red snapper.

<i>Regression Statistics</i>						
Multiple R	0.981199					
R Square	0.962752					
Adjusted R Square	0.962678					
Standard Error	32.27178					
Observations	505					

<i>ANOVA</i>						
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>Significance F</i>	
Regression	1	13540295	13540295	13001.17	0	
Residual	503	523858.2	1041.468			
Total	504	14064153				

	<i>Coefficients</i>	<i>Standard Error</i>	<i>t Stat</i>	<i>P-value</i>	<i>Lower 95%</i>	<i>Upper 95%</i>
Intercept	12.34899	2.940483	4.199648	3.16E-05	6.571852	18.12614
Area	42.77159	0.375115	114.0227	0	42.0346	43.50857

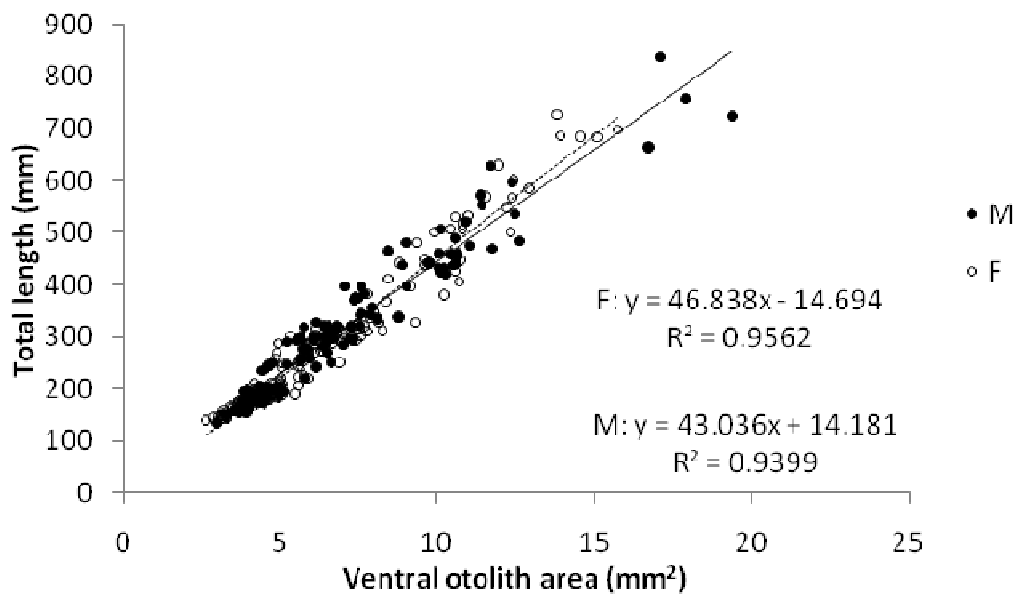


Figure 2.26. Relationship of total length to otolith ventral area by sex.

Table 2.7. Ancova table for relationship of total length to otolith ventral area by sex.

ANCOVA SUMMARY – Intercepts

Source	SS	df	MS	F	P
adjusted means	1052.14	1	1052.14	1.03	0.311022
adjusted error	288706.25	284	1016.57		
adjusted total	289758.39	285			

Test for homogeneity of regressions: Slopes

Source	SS	df	MS	F	P
between regressions	9236.08	1	9236.08	9.35	0.002443
remainder	279470.16	283	987.53		
adjusted error	288706.25	284			

The intercept coefficient, found in table 2.6, from the regression of the total length to otolith ventral area relationship was subsequently used in the area back-calculation model (eq. 2.12). The new otolith ventral area based back-calculation model did not exhibit the decrease in standard deviation with increasing size (fig. 2.27) that was seen in the case of DB1. The relationship between the back-calculated mean length-at-age from the area model and the observed mean-length-at-age did not differ significantly from a 1:1 ratio ($t = 1.443$, $t_{crit} = 2.447$) (fig. 2.29).

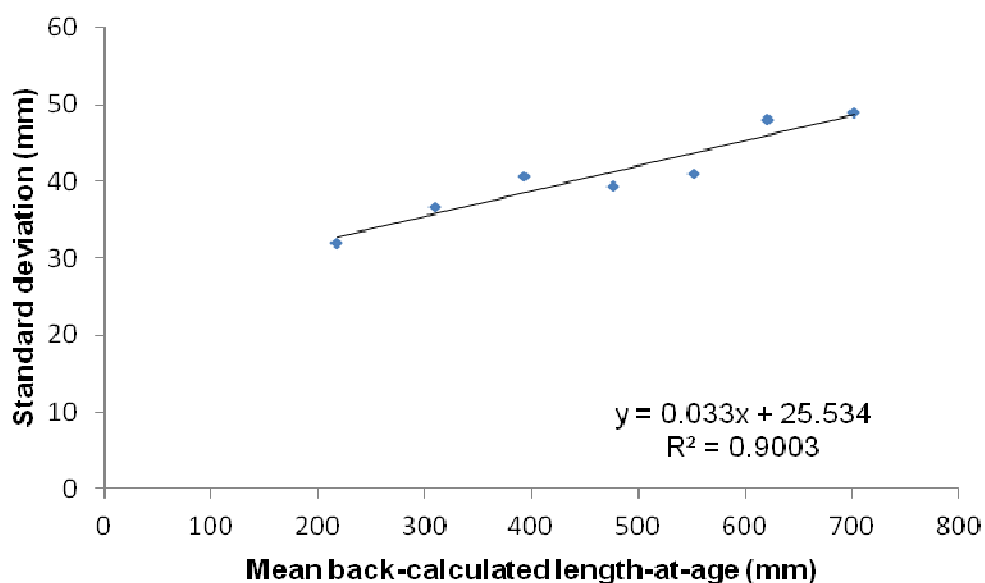


Figure 2.27. Relationship of standard deviation of back-calculated mean length-at-age to mean back-calculated length-at-age from otolith ventral area-total length model.

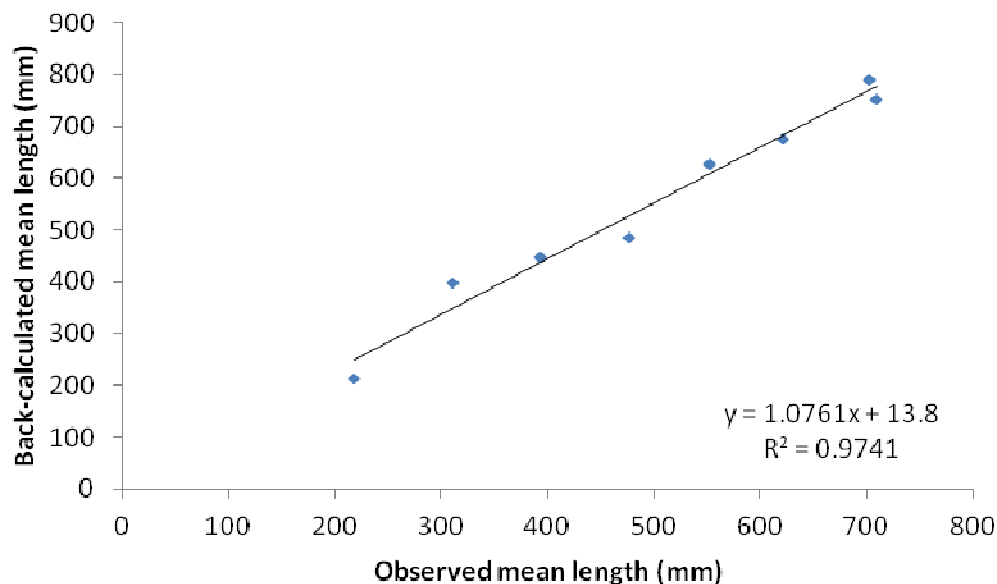


Figure 2.28. Relationship of back-calculated mean length-at-age to observed mean length-at-age from total length-otolith ventral area model.

2.5 Discussion

A major issue when using size-at-age data, especially fisheries dependent data, for fitting growth functions is that the data may be assumed to be representative of the entire population or stock being considered and important factors that affect the growth function such as migratory patterns and periods, nursery areas and feeding grounds may not be evaluated. Further, when using size-at age to compare growth rates it is important that the samples should be in the same growth phase based on environmental conditions (Weatherly & Gill, 1987). This assures that the variability in growth is reduced.

Similar to the research studies by Wilson and Nieland (2001) and Patterson et al. (2001), DB1 (N = 366 fish) also had the issue of a decreasing standard deviation with an increasing mean length-at-age (Fig. 2.8). This

analysis indicated the samples were biased in the size-at-age distributions and therefore likely to yield erroneous growth function parameters. Therefore it was necessary to resolve the issue of uncoupling found with the total length-otolith radius relationship before valid growth parameters could be generated. This uncoupling may have been caused by several factors, but probably was primarily due to the fact that the major axis of otolith growth, when cut in the transverse plane, is along the dorsal-ventral axis and not along the proximal-distal axis. The development and use of the ventral axis measurements of the otolith proved to be a significant contribution to the resolution of the uncoupling issue. These measurements proved to have a higher association and greater accuracy with the somatic growth than the sulcus acousticus measurements.

In the case using the original data sets (DB1) where the otoliths were not available, the two-way multiple regression model using age and the sulcus acousticus radius based back-calculated data (L_i) (Fig. 2.16) revealed a relatively poor fit to the average lengths-at-age for the observed data. The poor fit was apparent in spite of the adjusted r^2 for the multiple regression having a value of 0.7559. Figure 2.17 also revealed that neither the average of the back-calculated lengths-at-age nor the von Bertalanffy growth function fitted to the back-calculated data by least squares procedures provided a reasonable match to the observed average lengths-at-age. The model underestimated the lengths-at-age for individuals below ten years old and overestimated individuals over age eleven.

Similarly, the back-calculations based on the two-way multiple regression model using age and the sulcus acousticus measurements from DB2 (Fig. 2.18) also provided a poor fit to the observed mean lengths-at-age throughout the data range, except perhaps, for age four. The multiple regression had an adjusted r^2 that was very significant at 0.9427, but this did not translate into a good fit for the model. This model under this condition also severely underestimated the observed lengths-at-ages for most of the individuals in the data set. The three-way multiple regression model (Eq. 2.5) was based on the measurements derived from the ventral radius, the sulcus acousticus radius and age. Despite the additional parameter used in this regression case, the back-calculated data derived from this multiple regression model still provided a poor fit to the mean length-at-age of the observed data. The adjusted r^2 for the multiple regression was a very strong 0.9743, i.e., a very large proportion of the variation in length was explained by the independent regressors in the model, but this did not result in a strong fit for the (C. E. Porch et al., 2007) back-calculated data. The results, shown in figure 2.15, indicated that the trend for underestimation of the observed values by regression models continued.

The Age Effects model is perhaps best used for long-lived, slow-growing fish where otolith growth continues even when somatic growth is small and other models tend to overestimate past growth (Secor & Dean, 1992),(Morita & Matsuishi, 2001). The larger otoliths found in slower-growing fish can cause a bias in the otolith radius-fish length relationship upon which back-calculation procedures are based, however, the Age Effects model is designed to reduce or

remove this bias (Morita & Matsuishi, 2001)(Vigliola & Meekan, 2009). The Age Effects model formulation in Equation 8 utilizes the coefficients determined from the multiple regression given below in Equation 2.7. This regression had an adjusted r^2 value of 0.9408 which indicated that the model terms (age and total length) accounted for a very large portion of the variation in the ventral radius measurements. Despite the strong fit of the regression model parameters, the back-calculated data underestimated the mean length-at-age for the observed data, especially for the younger ages (Figure 2.20).

The power model assumes that the relationship between the total length and otolith radius follows a power curve function. The model formulation is given in Equation 2.9 and uses the intercept determined from the regression of the logarithmically transformed total length to otolith radius measurements. The back-calculated data are plotted in figure 2.21 along with the mean length-at-age for the observed data. The fitted von Bertalanffy growth function that is derived from the back-calculated data is also plotted. The linear regression had a coefficient of determination (r^2) value that was very significant at 0.9625, however this did not transform into a good fit of the back-calculated data to the mean observed length-at-age throughout the data range. The power model back-calculated data also underestimated the mean observed lengths-at-ages for most of the ages in the new data set. The fitted von Bertalanffy function under this model produced a L_∞ parameter of 927.56 mm.

The Modified-Fry model is a biological intercept model that assumes proportionality between the otolith and somatic growth rates and also uses the

fish size at otolith formation (parameter a) as an additional factor in its formulation. It has been found to be appropriate for use under conditions where there is allometry in the somatic length-otolith radius relationship (Vigliola & Meekan, 2009). Vigliola and Meekan (2009) recommended use of the model under these conditions and argued that it increases precision and reduces bias in the back-calculated size-at-age. The model formulation is found in Equation 2.10 and the back-calculated data are plotted in figure 2.22 along with the mean length-at-age for the observed data. This model generally had a slight underestimation of the mean length-at-age of the observed data but provided the best fit of any of the previous models attempted. Figure 2.23 indicates the very high coefficient of determination ($r^2 = 0.9616$) between the model's back-calculated and the observed length-at-age with a slope of 0.99. The fitted von Bertalanffy growth curve parameter had values of: $L_{\infty} = 924.87$, $K = 0.18$, $t_0 = 0.08$, which were quite similar to those of Patterson et al. (2001) being: $L_{\infty} = 969$, $K = 0.19$, $t_0 = 0.02$.

An important result from the Modified-Fry model is displayed in figure 2.25 where the relationship of the normalized standard deviation to total length (on a logarithmic scale) is shown. The relationship was very highly associated and had a coefficient of determination value of 0.957 indicating that there was steady proportional increase in the standard deviation with increasing length-at-age. The figure indicates that the Modified-Fry model behaved as expected and demonstrated an increasing trend in the standard deviation-at-age to length-at-age through the data range available. This is contrasted with figure 2.9 where the

standard deviation declined with increasing length-at-age. This indicated that the normalized results of the Modified-Fry model were successful in correcting the decline in the standard deviation in size-at-age with mean length increase.

It is important to note that all of the models, regardless of the theoretical differences in their structures, produced back-calculated mean length-at-age values that did not differ significantly from the mean length-at-age values of the observed data. This is indicative of the high variance in the growth of the red snapper.

A very strong relationship was found between the total length and the ventral area of the otolith for red snapper in the Gulf of Mexico. The Back-calculation method based on the relationship between the otolith ventral area and total length was quite robust within the data regression range as the results of the analysis indicated that there was a 1:1 ratio of the back-calculated mean length-at-age to the observed mean length-at-age. This back-calculation method using otolith ventral area may therefore be a better predictor of size-at-age for the red snapper than use of otolith radius. However, it is important to note that this method may be difficult and time consuming as it requires the careful and individual measurements of each annulus from many otoliths. The opaque bands may be visually difficult to discern precisely on the ventral axis, therefore the need for much care and attention when making measurements cannot be over-emphasized. Otolith shape can be an effective measure for the study of morphometrics.

2.6 Conclusions

Growth was very plastic in the red snapper and the current size-at-age distribution is highly impacted by the long and intense history of exploitation in the fisheries. Because of this exploitation history it may be very difficult to collect an unbiased age sample, especially of the adults, from the remaining population. The use of the otolith ventral radius proved to be a more robust measure for back-calculating the total length of the red snapper. It was more highly correlated with the total length than the measurement taken along the dorsal side of the sulcus acousticus. This is not unexpected as the degree of otolith growth in the red snapper is greater in the dorso-ventral axis than in the proximo-distal axis. Similarly, it may be expected that a 2-dimensional measure of otolith growth could provide a stronger relationship to somatic growth than a single axis measurement, while a 3-dimensional measurement (e.g. volume, density) could be even more robust than a 2-dimensional measure.

The fact that all of the models produced back-calculated mean lengths-at-age that had a 1:1 relationship with the observed mean lengths-at-age indicates that the models were all relatively robust and forgiving. It was felt, in light of the nature of the source of bias in the observed data, that the Modified-Fry model gave the best results and was therefore more representative of the growth for red snapper in the Gulf of Mexico. The relationship of the logarithm transformed standard deviation in length-at-age on length-at-age generated from the Modified-Fry model (fig. 2.22) indicates that the issue of the decrease in standard deviation with increasing size found in the original data was satisfactorily

resolved. However, since the data analyzed had a restricted maximum age of seven years this conclusion can only be safely used within the data regression range. This demonstrates the vital importance of ensuring a fully representative range of samples is available for analysis purposes.

The normalized unbiased Modified Fry model gave a large L_{∞} after the Monte-Carlo simulations. These results indicate that the current stock status is most likely very biased due to the removal of the larger individuals from the stock through heavy exploitation. This supports the suggestion that current growth models may underestimate the L_{∞} parameter due to the absence of the older and larger individuals in the stock.

The ventral area has thus far been shown to be a very accurate predictor of the somatic growth in the red snapper. Further research is required to extend the size-at-age range to the older and larger sized individuals in the population. Should additional research confirm that the otolith ventral area retains its relationship with somatic growth throughout the species size range this method would be a valuable contribution towards growth studies for this intensively managed and for the recovery of the fish population.

Chapter 3. Assessment of the Viability of Minimum Size Regulations to Recover Spawning Potential Ratio

3.1 Background

Mortality reference points are used in the Reef Fish Fishery Management Plan used to define management goals of the red snapper fishery in the Gulf of Mexico. One of these mortality reference points is the Spawning Potential Ratio (SPR), which expresses the spawning potential of the stock relative to the spawning potential of the virgin stock. This ratio is thus a measure of the relative decline in spawning potential due to fishing exploitation. In general, the greater the exploitation rate the lower the SPR. It is possible to define fishing mortality reference points that correspond to certain levels of SPR. Calculations of these reference points depend on several operational fishery characteristics such as selectivity of the gear, the spatial-temporal character of the fishing intensity and catchability, as well as biological characteristics such as maturity and fecundity at size, size-age relationships by sex and seasonal length-weight relationships. The red snapper stock in the Gulf of Mexico has been labeled as severely overfished and initial stock assessments had put the SPR at 1% (Goodyear 1995, 1996). Subsequent assessments estimated that SPR did not exceed 10% (Anon. 1997; Porch 2004). Following the recommendation of Mace et al. (1996), a recovery plan for red snapper was established so that a 20% SPR would have been attained by the year 2019, but this was subsequently revised to 2032 (Reef Fish Amendment 27, 2008). This controversial fishery management decision was designed to avoid the complete closures of the direct and indirect fisheries

impacting the stock. Some argue that this did not comply with the guidelines for recovery plans in the Magnuson Stevens Fishery conservation and Management Act (MSFCMA) and only delayed the inevitable pain associated with the need to severely reduce harvest rates (Cowan Jr. et al., 2010).

There are one indirect and two direct fisheries that target red snapper in the Gulf of Mexico. The indirect shrimp trawl fishery impacts the stock through its bycatch of ages 0 and 1 fish, resulting in profound consequences to the future reproductive capabilities of the stock. Of the two directed fisheries, the commercial fishery operates primarily in the spring, while the recreational fishery harvests the majority of its share of the quota in the summer and early fall. These two direct fisheries exploit different fractions (size structures) of the stock; hence, their impacts on the stock are dissimilar. Both fisheries are managed by a minimum size length and a total allowable catch (TAC). In 1984, the minimum size for all fisheries was set at 13" total length (TL), but because of continuous concerns about an increasing exploitation trend, the minimum size was raised to 14" TL in 1994 and 15" TL in 1995. In 2000 the minimum size was increased to 16" TL for the recreational fishery and in 2007 the minimum was reduced to 13" for the commercial fishery (Fig. 3.1) (Goodyear 1995, Schirripa and Legault 1999, Hood and Steele, 2004). Concurrently with minimum size regulations, quotas for the commercial fishery were being met at increasingly shorter time frames - in 95, 77, and 50 days for the years 1993, 1994, and 1995, respectively (SEDAR, 2005). In 1998, the recreational fishery had filled its quota by September, and the season was closed for the remainder of the year. Since that

time the recreational quota has been met within the allocated seasonal time frames with few changes to the declared period of the fishing seasons.

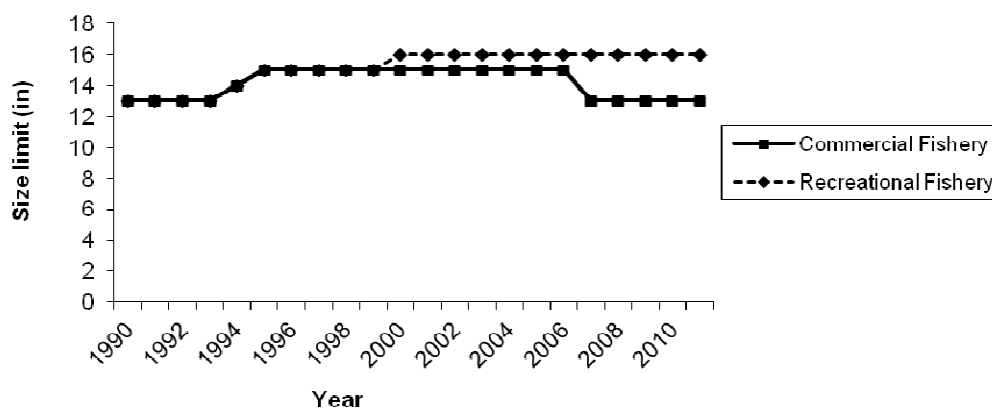


Figure 3.1 History of minimum size limits in the Gulf of Mexico red snapper commercial and recreational fishery

Changes in minimum size regulations reflect uncertainty associated with the assessments of stock status and with appropriate management measures to be imposed upon the directed fisheries. First, with regard to the minimum size, there is uncertainty about the amount of undersized fish caught, and what proportion of those that are released actually survive. Initially, it was suggested that release mortality was about 33% for the commercial fishery and 20% for the recreational fishery, though both could possibly be even higher (Goodyear, 1995). Several studies conducted during the 1990s found evidence that release mortality was depth related. Parker (1991) and Render and Wilson (1993) caught fish from depths around 20m, returned them to that depth in wire cages, and observed approximately 20% mortality. A field experiment of red snapper survival

rates found an increasing trend between release mortality and depth of capture, with a low of 1-10% for depths less than 30m, and a high of 44% for depths between 37 and 40m (based on releases at the surface) (Gitschlag & Renaud, 1994). Release mortality was also found to vary seasonally, with higher losses occurring in the fall after the quotas have been filled. Any additional red snapper caught incidentally in the directed fisheries for other species (e.g. red grouper, vermillion snapper) would have to be released, and those that perish in this process would increase the overall mortality of the species. The amount of the discards and the release mortality resulting from them are not known precisely, however, the percentage of discards by fleet and year are believed to be substantial. In 2007 an individual fishing quota was established for the commercial fishery and fishers without a quota are unable to land any red snapper. The recreational fishery is also prevented from landing any red snapper outside of its short season, thereby causing additional unrecorded discards and mortality.

Table 3.1 Table of discard percentages in the recreational and commercial fisheries (SEDAR7).

Recreational Percent Discards			
Year	Ages		
	1	2	3
1984	6	1	0
1985	21	9	1
1986	2	3	0
1987	12	3	1
1988	26	12	1
1989	34	19	3
1990	91	30	3
1991	85	42	1
1992	82	65	6
1993	96	54	4
1994	78	68	7
1995	87	82	9
1996	93	93	19
1997	87	89	20
1998	92	95	18

HL Percent Discards			Longline Percent Discards		
Year	Ages		Year	Ages	
	3	4		3	4
1984	0	0	1984	0	0
1985	8.5	0	1985	9	0
1986	8.5	0	1986	7	0
1987	9	0	1987	10	0
1988	9	0	1988	8	0
1989	8.5	0	1989	8	0
1990	9	0	1990	11	1
1991	12	1	1991	14	1
1992	14.5	1	1992	16	1
1993	15.5	1	1993	18	1
1994	35	3	1994	43	3
1995	27.5	4	1995	28	4
1996	33.5	3.5	1996	22	3
1997	31	3	1997	35	3
1998	32	3	1998	36	3

The Magnuson-Stevens Fishery Conservation and Management Act of 1996 required an independent evaluation of the scientific and management basis for the red snapper fishery in the Gulf of Mexico. This independent peer review of

the assessment work carried out in 1997 (Anon. 1997) highlighted the many uncertainties associated with the fishery. There was some concern that the projections for rebuilding the stock by 2019 were overly optimistic given the implemented regulations (which were considered to be insufficient) and the level of uncertainty associated with several key fishery components: bycatch estimates, possible underreporting of commercial catch statistics, and the accuracy and precision of recreational catch estimates. A review of the recovery period in 2001 led to a recommendation for this date to be changed to 2032 (Amendment 22, 2005). This was due to the fact that stock rebuilding forecasts and management regulations to achieve rebuilding were sensitive to many factors that were considered uncertain. Changes in the minimum size limit and/or more frequent seasonal closures exacerbate the uncertainty of the resulting release mortality. This stresses the need for quantifying the effectiveness of the minimum size changes on management of the red snapper stock.

The operation of the fisheries varies temporally, release mortality varies temporally and by depth, and the size distribution of the stock has spatial variability with older, larger individuals favoring hard limestone (deeper) bottoms (Moseley, 1966) while smaller juveniles are more frequently associated with structures over sandy or muddy (shallower) bottoms (Workman and Foster, 1994). Exploitation patterns of the different fleets affect stock abundance in ways that are not well understood. Because fishing mortality rates are uneven across size and age groups. This complexity in exploitation patterns highlights how the

consequences of establishing a minimum size are not simply to reduce or eliminate the catch of young immature fish. The effects upon the stock of minimum size regulations are therefore not well understood.

Three depth related factors are important when considering the effectiveness of minimum size regulations, the relative distribution of undersize fish, their relative survival upon release and their relative probability of capture (catchability). In shallower areas, where juveniles are more concentrated, the catch and release of the undersized fish is more significant than in deeper areas where there are fewer undersized fish. Moreover, 1) releases of undersized fish will have a differential release mortality due to differential survivorship as depth decompression effects on animals released at different depths are different, and 2) catchability differences among these depth-related groups are also different.

Age based dynamic pool models are traditionally used to evaluate potential yield-per-recruit (YPR) and spawning stock biomass-per-recruit (SSB/R) relative to fishing mortality and size at recruitment. Therefore, they can be used as a method to assess minimum size restrictions by estimating potential yield and the spawning biomass of a cohort through the summation across discrete age-increments under specified conditions of growth and natural mortality. The models assume equilibrium, therefore within each age-interval, growth and natural mortality are assumed to apply uniformly to all members of the cohort, and fishing mortality is constant among age classes. However, not all individuals follow the same growth trajectory. The susceptibility of individual fish to fishing and release mortality is a size rather than age-dependent event.

However, age-based YPR and SSB/R models are particularly inappropriate for species, such as red snapper, that are subject to complex and dynamically changing temporal exploitation patterns by fleets that target different size-age groups. Therefore, a length-age based and seasonally explicit YPR and SSB/R model that provides a more precise, accurate and realistic depiction of cohort dynamics is developed in this chapter. The model uses directly measurable variables that are linked to management measures such as minimum size restrictions and season closures.

3.2 Goals and Objectives

The goal is to contribute to the recuperation of overexploited red snapper fisheries in the Gulf of Mexico. This will be achieved by providing a better understanding of the effectiveness of minimum size regulations imposed on the fisheries as an instrument to control fishing mortality of the undersized, hence, immature fish.

To accomplish this goal the following objectives are:

1. To develop a theoretical size-age seasonal yield-per-recruit model to simulate the effect of minimum size options and closed seasons for the Gulf of Mexico red snapper.
2. To gather information regarding the temporal nature of red snapper population size structures in the Gulf of Mexico.
3. To determine if minimum size limits are an effective management tool for managing the recovery of the Gulf of Mexico red snapper stock.

3.3 Materials and methods

3.3.1 Growth

In this chapter a temporal size-age yield-per-recruit model was developed such that it could be used to assess the impact of different minimum size regulations imposed on the red snapper directed fisheries. For this purpose there is a need for characterizations of the population size and age structures in time such that seasonal fishing intensity could be used to create fishing exploitation patterns under the different minimum size policies. In order to accomplish this work it was necessary to analyze the temporal nature of the length and age structures in the existing databases, the statistical attributes of the length at age distributions of the stock and the associated reproductive biology, and the nature of the fishing mortality by the fleets that seasonally affect the population. The work performed under each of these items is explained below.

Temporal changes in the size and age distribution of red snapper in the Gulf of Mexico could be elucidated if size-age data were properly collected from random samples derived from an appropriate experimental sampling design that considers the natural temporal distributions of the population. A revision and analysis of the existing length frequency database provided by NMFS and extensively analyzed by Diaz, et al. (2004a) and Diaz (2004) were used for this purpose. Maturity and fecundity parameters are associated with the population length frequency distributions. A review of these data found that most of the available length frequency samples originated from landings that were highly affected by the prevailing minimum size at the time of sample collection (Diaz et

al. 2004a; Figs. 2 and 3) (Figure 3.2 and 3.3). Also, samples from commercial landings were not proportionally allocated among the gear types, while the samples from recreational landings usually represented all the fish that were caught and retained during a fishing trip. The statistical consequences of using unbalanced sampling designs that result from changes in the minimum size regulations may result in effects that cannot be measured with the existing data. This is especially true when such changes are done in periods that were less than the generation time of the species. Note that in the analysis in this chapter, the estimates of size-age YPR and equilibrium SPR are derived assuming a fixed minimum size.

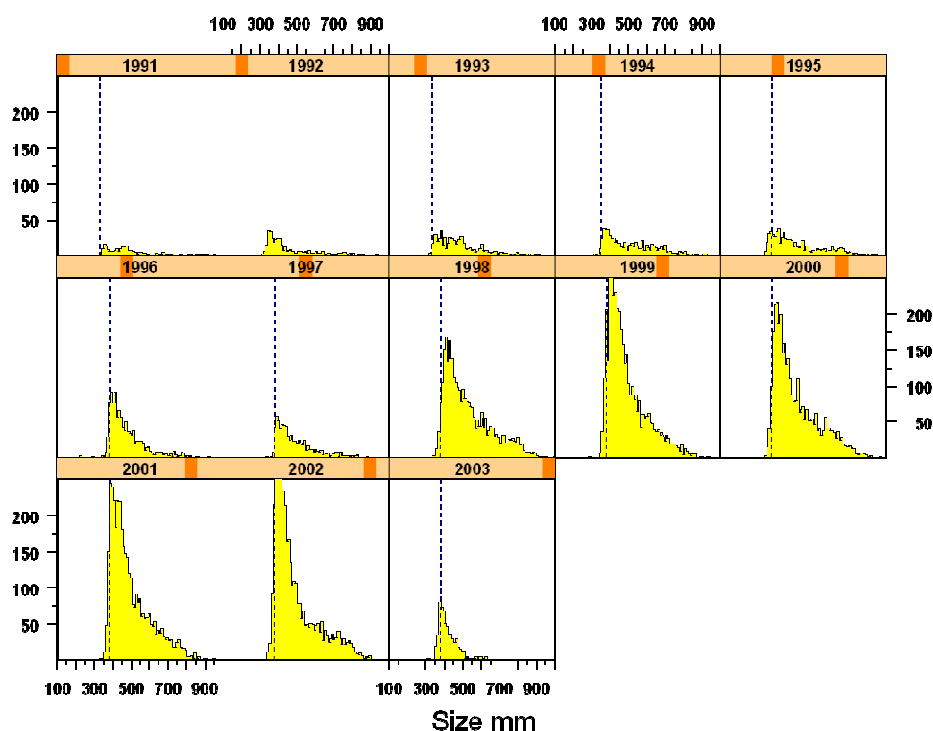


Figure 3.2 Seasonal size frequencies for commercial fisheries in the Gulf of Mexico indicating minimum size effects from Diaz et al., 2004.

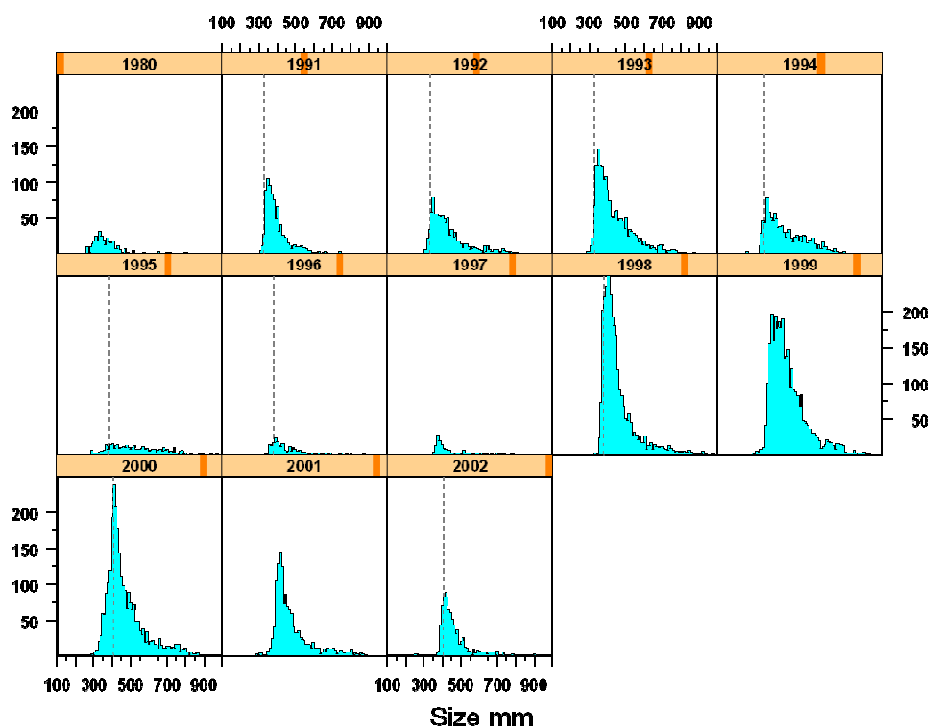


Figure 3.3 Seasonal size frequencies for recreational fisheries in the Gulf of Mexico indicating minimum size effects from Diaz et al., 2004.

On the other hand, as indicated in table 3.1, the persistent high level of undersize discards of red snapper in the different fisheries does not allow for simple statistical expansions of the observed size-age specification found in the landings to the total catch (i.e., landings plus discards). The lack of biological data and samples from the discarded undersized fish has been one of most difficult problems related to the study of red snapper growth (Diaz et al., 2004; Wilson and Nieland, 2001; Patterson et al., 2001).

The overfished status of the stock is reflected in the absence of the larger individuals-at-age in the biological samples among the older fish. This issue also statistically affects the growth parameters estimated from these databases.

Chapter 2 in of this dissertation focused on resolving these statistical issues related to the characteristics of the biological samples. In the minimum size assessment included in this chapter the growth functions and variance-covariance estimated in the previous chapter are used (Table 3.2).

Table 3.2. Red snapper von Bertalanffy growth parameters and variance-covariance estimates from Monte Carlo simulated data.

	L_{∞}	K	t_0
Estimates	1201.40	0.123694	-0.1771
Standard Errors	42.30	0.006658	0.027345
Variance-Covariance Matrix			
	L_{∞}	K	t_0
L_{∞}	0.178927E+04	-0.279363E+00	-0.689971E+00
K	-0.279363E+00	0.443275E-04	0.121824E-03
t_0	-0.689971E+00	0.121824E-03	0.747774E-03

Standard error of estimate – 57.9019

3.3.2 Fecundity and Maturity

The SPR is a reference point used in red snapper fishery management which requires knowledge of maturity schedules at size-age that define spawning seasons as well as the individual size-age fecundity. Schirripa and Legault (1999) provided a maturity-size relationship based on data from Wilson et al. (1994). Schirripa and Legault (1999) and Porch (2004a and b) reviewed the existing data on red snapper fecundity. The use of the models developed by these authors requires some careful consideration before they could be applied in minimum size assessment. The Schirripa and Legault (1999) fecundity model

was fitted to batch fecundity on total length in inches based on data from Collins et al. (1994) and then transformed into fecundity-age via a growth equation. The Porch (2004a and 2004b) model is a fecundity-age function fitted to the combined samples of fecundity at age data from Cowan et al. (2002) and Fitzhugh et al. (2004). The conceptual aspects of the models that are important in the minimum size assessment are as follows: 1) the Schripa-Legault model assumes that all individuals of the same length have the same average fecundity, despite any differences in their ages, and fecundity is only regulated by the maturity affecting smaller lengths across ages. 2) The Porch (2004) model assumes that all individuals of a given age will have an average fecundity despite the differences in sizes at age. In order to test the potential differences in the outcome generated by each fecundity model, the two conceptual approaches were implemented in the length-age yield per recruit model developed in this chapter.

The parameters of the Schripa-Legault fecundity model are given as $a = 0.1681$ and $b = 5.57$ for the power function

$$Fec = aL^b + \epsilon \quad 3.1$$

In the case of the maturity at length, the analysis in this chapter uses the same data from Wilson et al. (1994) which was used by Shirripa and Legault (1999) but fitted to a logistic model expressed as

$$Mat(\%) = \frac{100}{(1 + \alpha \exp(-\beta * TL))} \quad 3.2$$

where $\alpha = 55192595$ and $\beta = 1.1525$ and the is function plotted in figure 3.4. The product of maturity and batch fecundity (i.e., per-capita production) is presented

in figure 3.5 while the per-capita production in terms of age is presented in figure 3.6. These functions are used in the seasonal length-age YPR and equilibrium SPR model developed in this chapter.

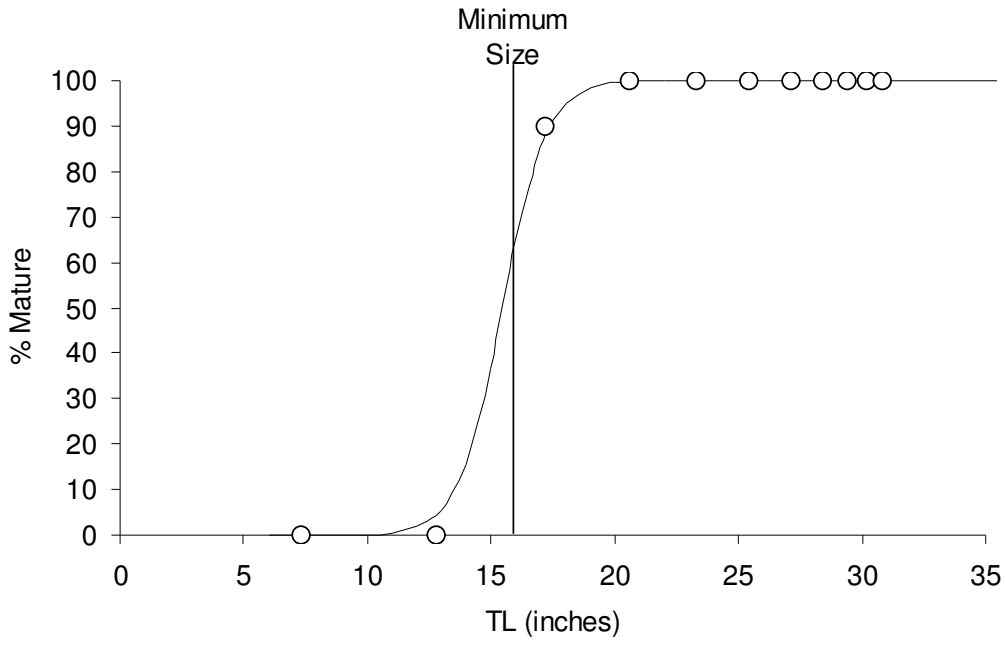


Figure 3.4. Percent of red snapper mature at size. The minimum size (16") for the recreational fishery is shown.

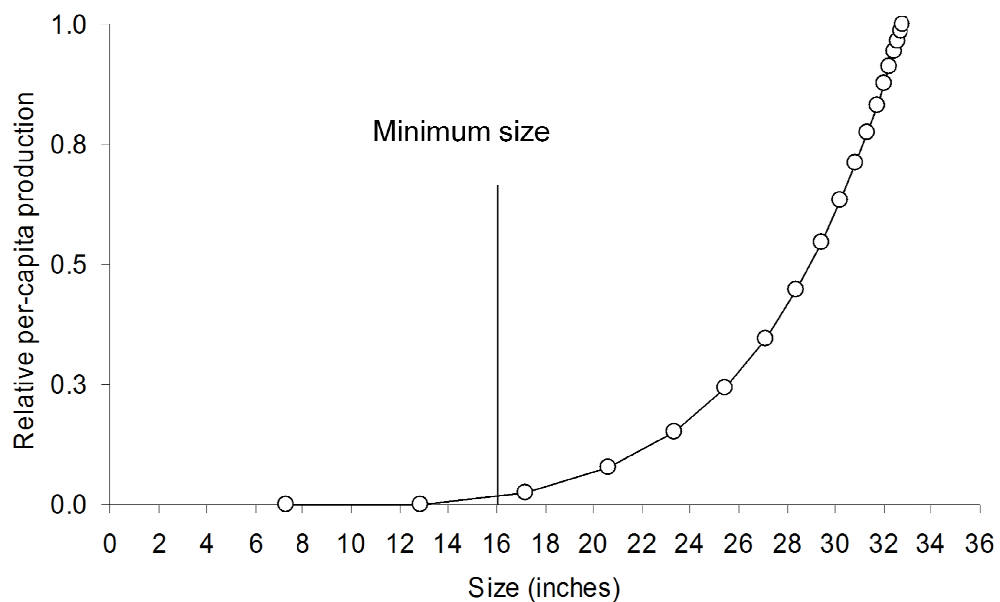


Figure 3.5. Relative per-capita production on total length. The minimum size (16") for the recreational fishery is shown.

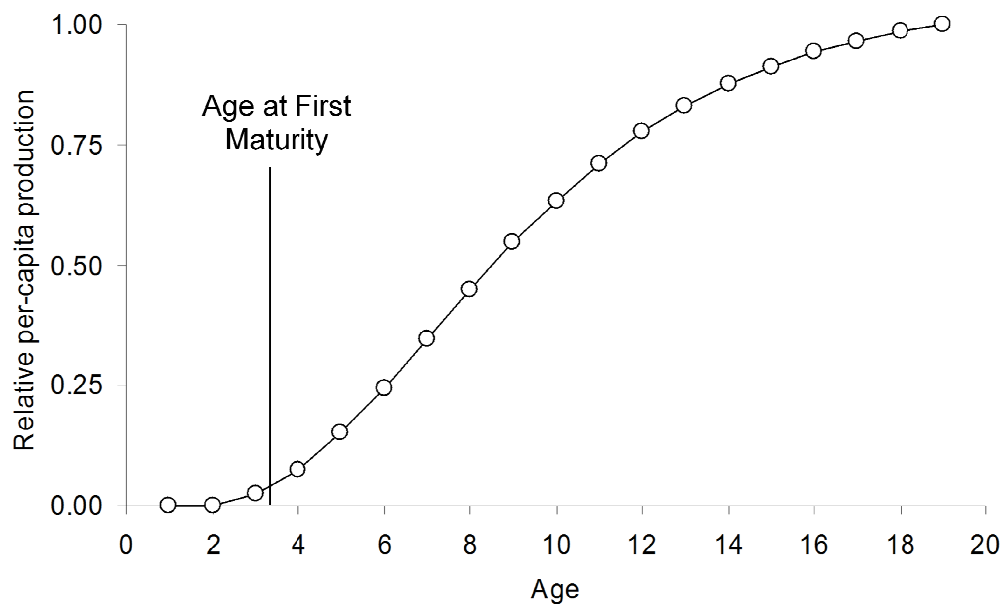


Figure 3.6. Relative per-capita production on age. The age of first maturity is shown.

Red snapper females mature mostly during the spring and early summer. Spawning takes place over an extended time frame, with a period of increased gonosomatic index from May to August (Collins et al., 1994) (Figure 3.7) and juveniles start appearing in trawl samples from June to October. Based on this seasonal maturity schedule the biological year for the seasonal size-age yield per recruit assessment is deemed to start on July 1 and growth, seasonal fishing and natural mortalities are scheduled accordingly in the model.

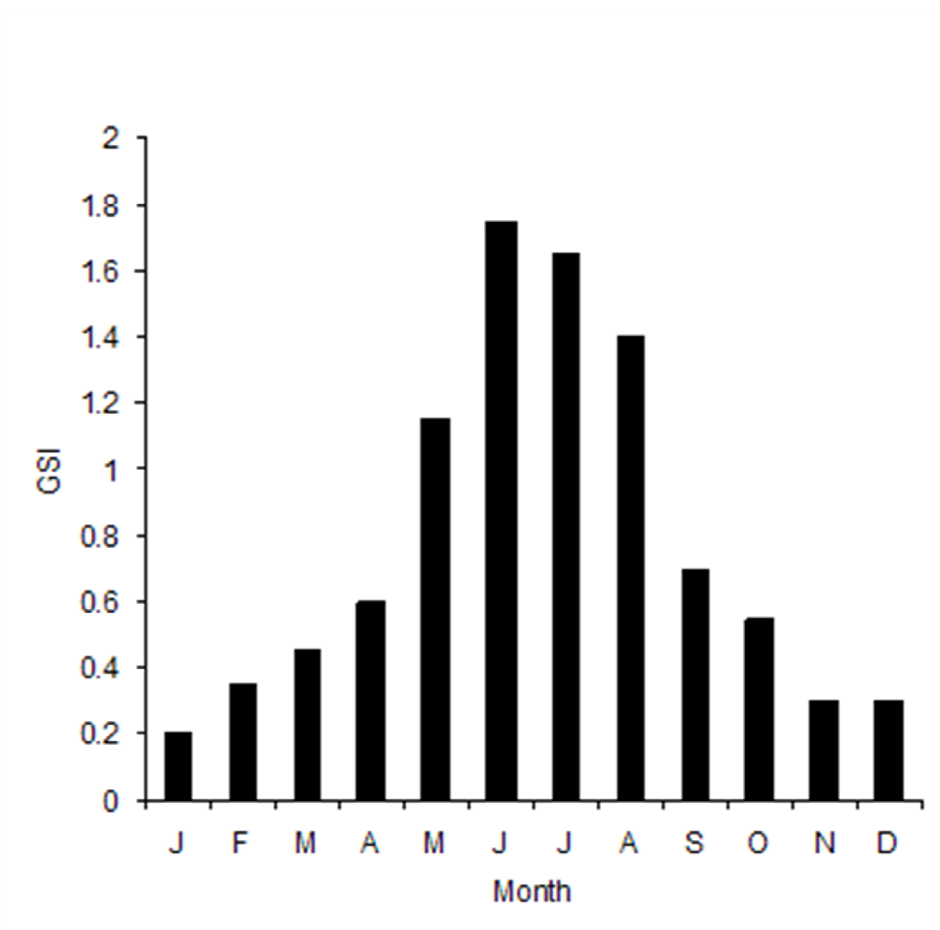


Figure 3.7. Seasonal maturity from gonosomatic index from Collins et al., 1994

3.3.3 Availability patterns, fishing mortality rates, natural mortality rates and release mortality.

The size-age yield per recruit model uses an availability term defined by the exploitation pattern at age and the fishing seasons (specific months) for each fishery. These availability vectors were calculated using fishing mortality at age estimated for each fishing gear (including the mortality due to the shrimp bycatch) corresponding to the time when the minimum size enforced in the fishery was the lowest (13" TL; 1984-1989) (Figure 3.8). This adoption allows the inclusion of the most likely age range liable to be caught in each gear type. The exploitation pattern is modified within the model by the minimum size adopted, which should be larger than 13" TL. If smaller minimum sizes are tested, then the exploitation patterns would need to be modified accordingly. The apical fishing mortality rates at age used were those for the actual fisheries selected for measuring the effects of minimum size assessment. The fishing mortality values for each fishery considering annual and seasonal aspects of each fishery are from the SEDAR 2005 full assessment of the fishery (an update to this assessment was conducted in 2009) are given in table 3.3.

Table 3.3. Fishing mortality rates for each fishery from SEDAR 7 (2005)

Fishery	Annual apical F	Monthly apical F
Shrimp bycatch	1.52	0.152
Long line	0.00266	0.000266
Recreational HL	0.226	0.037667
Commercial HL	0.157	0.157

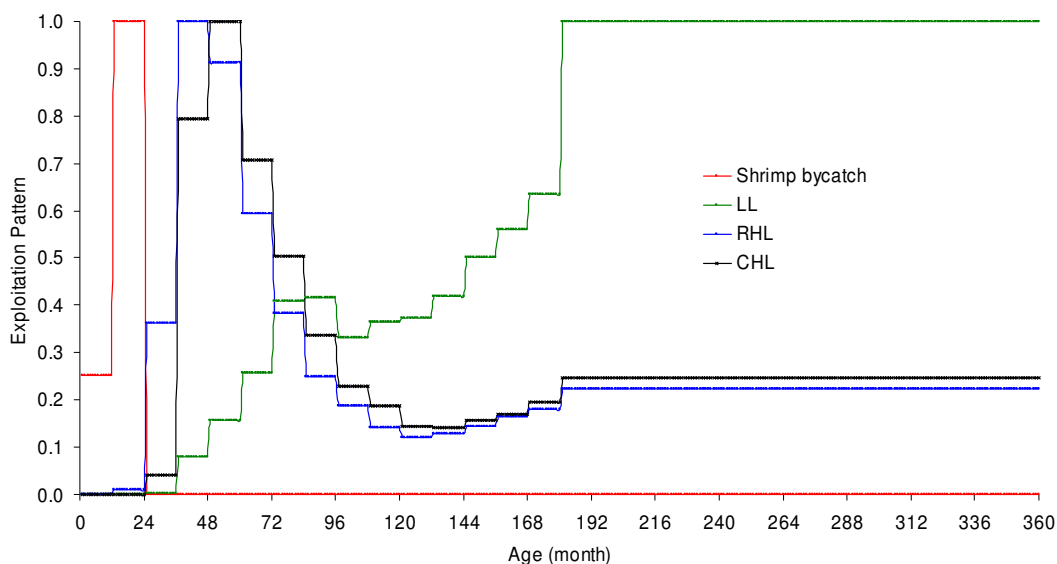


Figure 3.8. Exploitation patterns by gear (fishery) type for 13" TL minimum size.

The natural mortality rate of the red snapper is not well known. However, given the longevity of the species (over 53 years; Wilson and Nieland 2004; Patterson et al., 2004) the values discussed by Schirripa and Legault (1999) are adequate. For this purpose, $M = 0.5$ for age 0, $M = 0.3$ for age 1 and $M = 0.1$ for ages 2+ are adopted in this analysis.

Release mortality has been estimated by several authors, but in this analysis the release mortality schedule that was adopted by SEDAR 2005 is used: 1) no survival of red snapper caught by the shrimp trawl fishery, 2) 20% mortality in the recreational and commercial hook and line fisheries, and 3) 40% in the commercial longline fishery. Release percentages used in the estimations are those in Table 3.1, where an average was assumed for the East-West commercial HL fisheries.

3.3.4 Seasonal size-age yield per recruit model

In typical annual per-recruit calculations, yield accumulates and potential spawning production (relative stock fecundity) declines from the time a given number of fish recruit to the fishery at an age corresponding to given selectivity and availability patterns and they last until the oldest available age. These annual per-recruit items accumulate as the cohort is subjected to both age specific natural and fishing mortalities. The previous approach is too coarse and generic when more detailed aspects of the seasonal population dynamics (e.g., growth, natural mortality, maturity, fecundity, etc.) and fisheries (e.g., gear types, gear selectivities, fishing seasons, temporal availability, minimum size, etc.) need to be incorporated in the per-recruit calculations. In such cases a size-age yield per recruit is preferred. Because of the computational intricacies due to individual growth transfer rates in individually based models (Buijse et al., 1992; Shepherd and Idoine, 1993), Legault (1996) developed an effective way to deal with this situation when large and complex simulations of size-age population structures are required. However, the algorithm developed by Legault (1996) is not a true individually based model but one where either a cohort or an entire population of cohorts can be followed as a group through a growth transfer matrix that is independent of effects other than the individual's growth dynamics. A key element in this procedure is that the growth dynamics must be unbiased; that is, they should represent the variance of the natural population size-at-age; hence, the growth parameters and their variances and covariances should not be influenced by selectivity and availability patterns. In chapter 2 an analysis of

growth issues was completed and the variance-covariance matrix for the parameters (table 3.2) was used in the Legault growth transfer matrix algorithm.

Legault's (1996) computer intensive algorithm creates a growth transfer matrix using the simulated individual growth characteristics of the red snapper given in the chapter on growth and this matrix is then used in a size-age per-recruit model. The transfer matrix was designed to contain age-length bins that were dimensioned at 1 cm by 1 month boundaries (Figure 3.9). This allowed for the correct transition of individual growth through the size range and life span of the red snapper (1 through 100 cm in length and 1 through 360 months). The analysis in the previous chapter corrected potential selectivity-availability biases present in age at length data; therefore, the per-recruit simulations should be representative of the dynamics of a natural red snapper cohort. The adoption of the algorithm requires that: 1) a large number of individuals are introduced in the algorithm (such that all the transfer size-age bins are filled up with a growth transfer value, $G_{a,s,i}$, where a = age, s = size, i = growth increment). 2) For each individual entering (recruited) in the matrix at a given size-age, a couplet of the growth parameters L_{∞} and K is selected following a bivariate normal distribution with the statistical attributes (variances and covariances) corresponding to each parameter, and t_0 is estimated from a uniform distribution with a preset range. And 3) each individual will grow through size-age bins following the specifically randomly selected von Bertalanffy growth function in the previous step. An initial (recruitment) cohort abundance of 10 million fish were introduced in the algorithm and all size-age cells were used without trajectories falling outside of the

expected growth path. In this manner the transfer matrix is built only once outside the per-recruit computations and it is used in as many of seasonal fishing mortality and minimum size computations as desired. For this purpose, the algorithm estimates the abundance of each age-size group as:

$$N_{a,s} = \sum_i^n N_{a-1,s-i} G_{a-1,s-i,j} \quad 3.3$$

where $N_{a,s}$ is the cohort abundance of age a (in month) and size s (in cm). Therefore, the initial recruitment abundance is spread out in time and size as $N_{a,s}$ values and the sum of these values over s for any age a are all equal to the original recruitment abundance. This "mortality less" size-age population structure that grows according to statistically linked von Bertalanffy parameters can be modified according to natural and fishing mortality at age and size patterns and the resulting cohort size-age structure can be used to assess several biological responses, such as exploitation outcomes (yield-per-recruit) or reproductive dynamics effects of exploitation (spawning potential ratio).

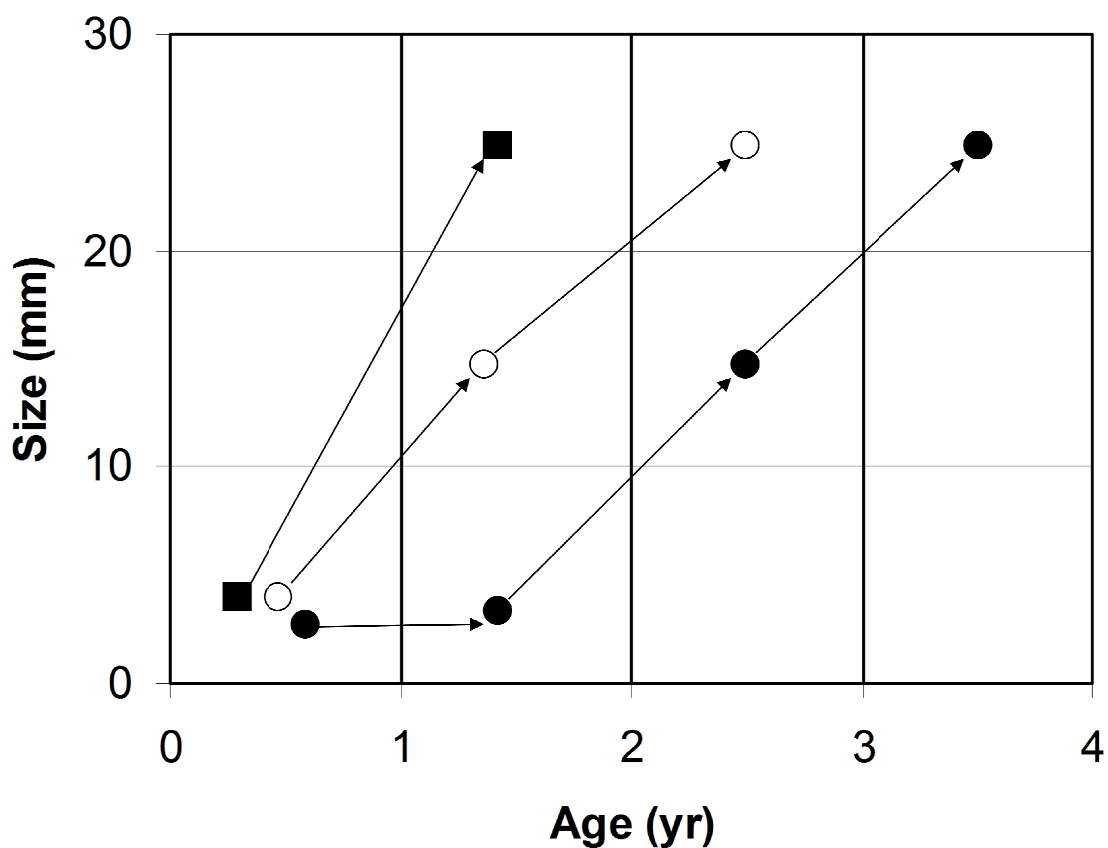


Figure 3.9. Growth transfer matrix used for red snapper.

The size-age yield per recruit analyses carried out in this way incorporates the four exploitation patterns corresponding to four fleets: 1) the shrimp trawl fisheries where red snapper is significantly caught as bycatch mainly at ages 0 and 1, 2) a recreational hook and line fishery where ages 3, 4, and 5 are predominant with significant discards of ages 1 and 2, 3) a commercial hook and line fishery where ages 3, 4, and 5 are mainly predominant, and 4) a commercial long line fishery that targets red snapper in deeper water, thus mostly targeting ages 4+ with discards of age 3 fish. Seasonal exploitation by each of these fisheries was modified by a matrix containing the months when each fishery is

open or closed to fishing. The resulting fish in the per-recruit simulations were subjected to a minimum size and the resulting under sized fish were subjected to release mortality. An accounting system controls all these mortality events and accumulates catches by size-age and estimates cohort reproductive potential using seasonal (month) maturity at age and fecundity at age or size depending on the desired procedure to measure this fecundity at the population level.

The fishing mortality equation is size-age specific affecting the length distribution starting with a specific minimum size:

$$F_{a,s,m} = \sum_{g=1}^4 EP_{a,g} * FS_{g,m} * AF_g \quad 3.4$$

where $EP_{a,g}$ is the exploitation pattern of age a and gear g ; $FS_{g,m}$ is the selectivity factor of gear g under a minimum size m ; and AF_g is the apical fishing mortality rate for gear g . While the release mortality for fish under the minimum size is defined as the product of the percentage of fish released (discarded) below the minimum size (table 3.1) times the release mortality rate adopted by gear type. The monthly natural mortality rate (M) and the fishing mortality rate by gear type under different minimum size condition is added to form the total monthly mortality rate ($Z_{a,s}$) that is applied to each size-age group represented by the $N_{a,s}$. These mortalities are accumulated throughout the exploited life span of the cohort. Catch, $C_{a,s}$, is obtained by the standard catch equation and yield at age is simply the product of catch at a given size within age multiplied by the weight-at-size power function adopted. The parameters for this weight-at-size power function are: a coefficient = .000009636 and the exponent $b = 3.0972$ (SEDAR 2005). Yield per recruit is the accumulated yield at age under the

minimum size and fishing mortality adopted in a given run. The fishing mortality reference point used for red snapper is one generating a desired SPR (i.e. compares the current spawning potential to that which would have been present if there was no fishing). In this analysis we evaluate how to achieve at least 20% SPR by the year 2032. The formulation used for calculating SPR is:

$$SPR = \frac{\sum_{a=0}^{Maxa} NE_{a,s} P_a e^{-Z_{a,s}}}{\sum NV_{a,s} P_a e^{-M_a}} \quad 3.5$$

where NE is the exploited abundance in numbers at age a and size s , P is the per capita fecundity at age a , NV is the unexploited or virgin abundance in numbers at age a .

The size-age structured per-recruit model thus formulated was run for three minimum sizes in the directed fisheries: 13" TL, 16" TL, and 20" TL. These three sizes cover the initial minimum size imposed on the fishery (13" TL), the current minimum size implemented in the recreational HL fishery (16" TL), and a hypothetical very large size (20" TL). The effects of minimum size were also analyzed by setting up different levels of shrimp bycatch mortality at: current level, 75%, 50%, 25% and 0% of current level.

3.4 Results

The results indicated that the three tested minimum sizes do not protect dramatically different age ranges due to the fact that early growth is fast and then after age 10 slows significantly (chapter 2). Under this condition, minimum size definitions between 13" TL and 16" TL that were imposed on the directed fisheries fall in the lowest range of the per capita production (fecundity),

therefore, it appears that both the size, as well as age, of first capture are inconsequential with the savings of spawning products in the depleted stock targeted by the directed fisheries. Also, discards below the selected minimum sizes are large in all fisheries and release mortality is also high. Furthermore, the directed fisheries continue to catch the species incidentally during the closed seasons, therefore adding to the overall discard mortality and reducing the opportunity to retain mature stock.

3.4.1 Effects of exploitation on size and age structure of the population

Figure 3.10 shows the abundance of size-at-age in the unexploited stock (left) and exploited stock (right).

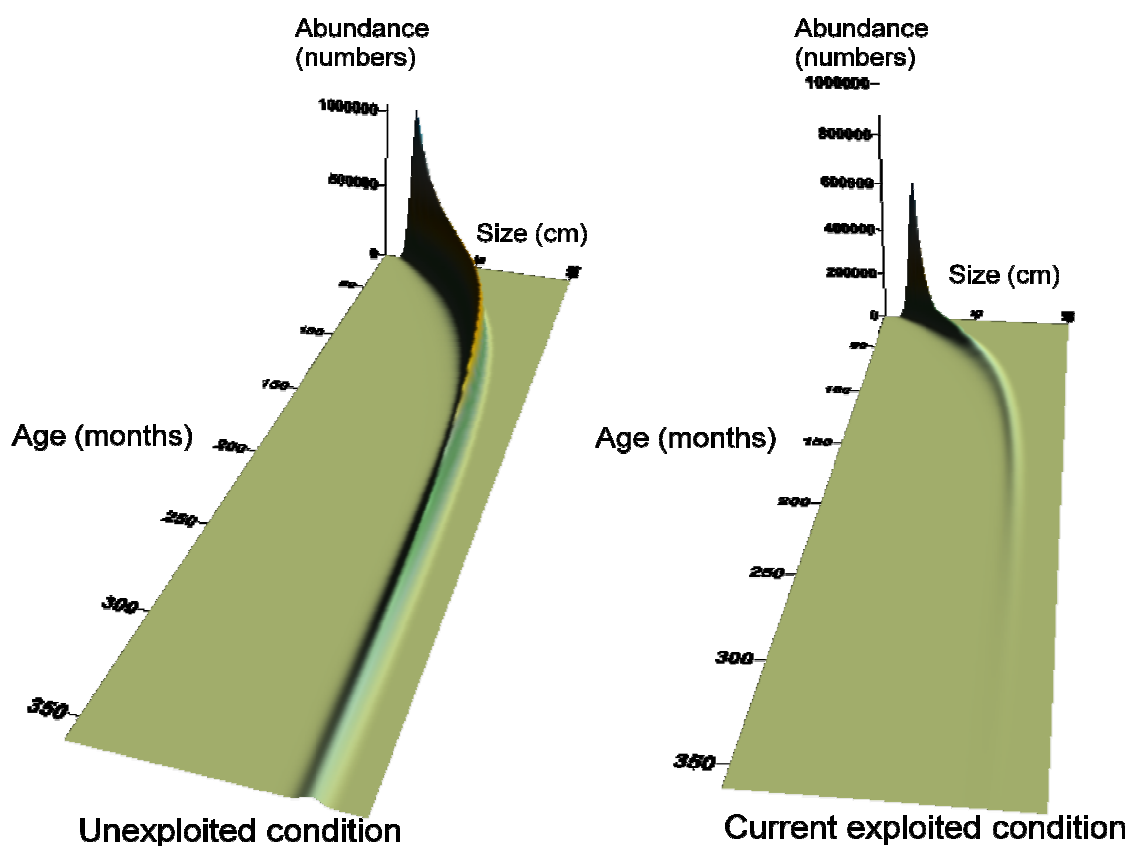


Figure 3.10. Simulated abundance of size-at-age in the Gulf of Mexico red snapper unexploited (left) and exploited (right) stock

3.4.2 SPR trends under indirect and direct fishing mortalities

The SPR trends are presented as two scenarios: (1) a hypothetical case where the shrimp bycatch is the only fishing mortality acting on the red snapper stock, and (2) where both the shrimp bycatch and directed fishing mortality are acting in the stock. Figure 3.11 indicates the trends depict the increment in SPR as the current level of shrimp bycatch mortality (100% in the figure) is reduced to 75%, 50%, 25%, and eliminated (0%). The shrimp bycatch greatly impacts the SPR when acting in absence of directed fishing mortality (closed circles); however, the reduction of the shrimp bycatch while keeping the current directed fisheries fishing mortality rate constant (open circles) does not improve the recuperation of the SPR as significantly. The reason for this condition is due to the fact that the current (SEDAR 2005) apical fishing mortality rates in each of the directed fisheries is high, and the recuperation of the stock spawning biomass through reductions in shrimp bycatch mortality results in very large catch by the directed fisheries, which therefore impacts the SPR. In fact, when shrimp bycatch is zero, the current (SEDAR 2005) combined apical fishing mortalities generate an 18.5% SPR. Consequently, any attempt to increase the SPR above the 18.5% mark under no shrimp bycatch effects may be futile without a considerable reduction in the fishing mortality from the directed fisheries. Furthermore, if the 50% mandated shrimp bycatch reduction is accomplished through better trawl designs and bycatch excluder devices, then the SPR increases only to 7.23% under the current fishing mortality in the directed fisheries.

The SPR estimated under the current (SEDAR 2005) apical mortality rates of the directed fisheries and under 100% of the current shrimp bycatch mortality (0.15/month) is only 2.83% (Fig 3.11). Figure 3.11 also shows that under the full shrimp bycatch mortality (100% of 0.15/month) and in the absence of directed fishing mortality the SPR is 15.29%. This is indicative that any fishery management efforts in the directed fisheries designed and implemented to recuperate the stock to levels above the 15.29% will be futile unless the shrimp bycatch mortality is reduced substantially.

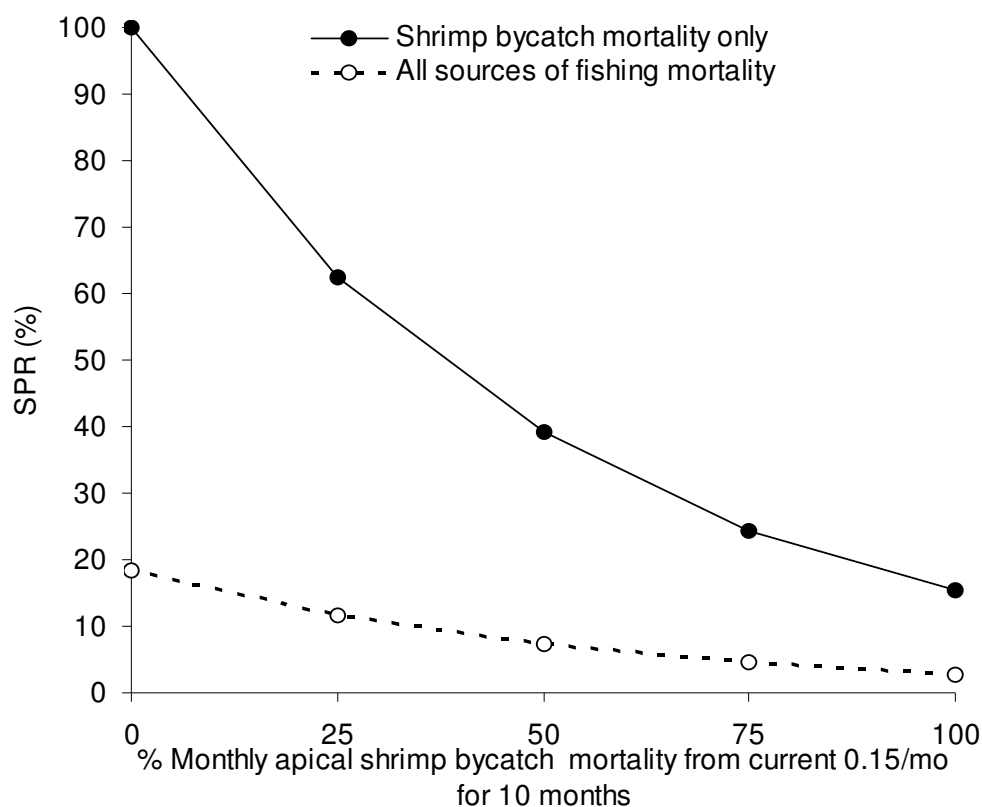


Figure 3.11. Spawning Potential Ratios (SPR) under current fishing mortality rates (incidental and directed) and under current shrimp bycatch mortality only, and for several reductions in shrimp bycatch mortality

The equilibrium SPR differences due to changes in minimum size between 13" TL, 16" TL and 20" TL are shown in table 3.4. In fact, for any level of shrimp bycatch reduction between 100% and 0% differences in SPR are minimal for the different minimum sizes. This is indicative of the ineffectiveness of minimum size regulations in the directed red snapper fisheries when most of the potential spawning capability is affected by the excessive fishing mortality on juveniles as bycatch in the shrimp fisheries.

Table 3.4. Spawning potential ratio under 3 different minimum sizes, different levels of shrimp bycatch mortality and in absence of directed fishing mortality (shrimp bycatch mortality only).

Minimum size	13 in.	15 in.	20 in.	
Shrimp Bycatch %	Total F SPR	Total F SPR	Total F SPR	Shrimp F SPR only
100	2.8286	2.8286	2.8302	15.29
75	4.5234	4.5235	4.5261	24.45
50	7.2338	7.2340	7.2381	39.10
25	11.5684	11.5686	11.5752	62.53
0	18.5001	18.5005	18.5110	100.00

The results of the yield-per-recruit (YPR) analyses are presented in figure 3.12. The trends in YPR are indicative that there are only slight differences between minimum sizes of 13" or 16" in TL, while the 20" TL generates a lower YPR due to the fact that maximum growth is almost over by the time Red snapper reaches such a large minimum size. However, the gains in YPR as the shrimp bycatch is reduced to zero from current levels (100%) are very significant. In fact, when the minimum size is 13" TL, YPR increases from 0.109 kg/R to 0.715 kg/R, while at 16" TL, YPR increases from 0.105 kg/R to about 0.688 kg/R.

These values imply that a reduction in shrimp bycatch generates very significant gains in YPR. These gains are about 5.7 times as large as the YPR under the current (SEDAR 2005) conditions. The implications of the above results are that the effect of red snapper mortality as juveniles in the shrimp fisheries creates a clear growth overfishing problem.

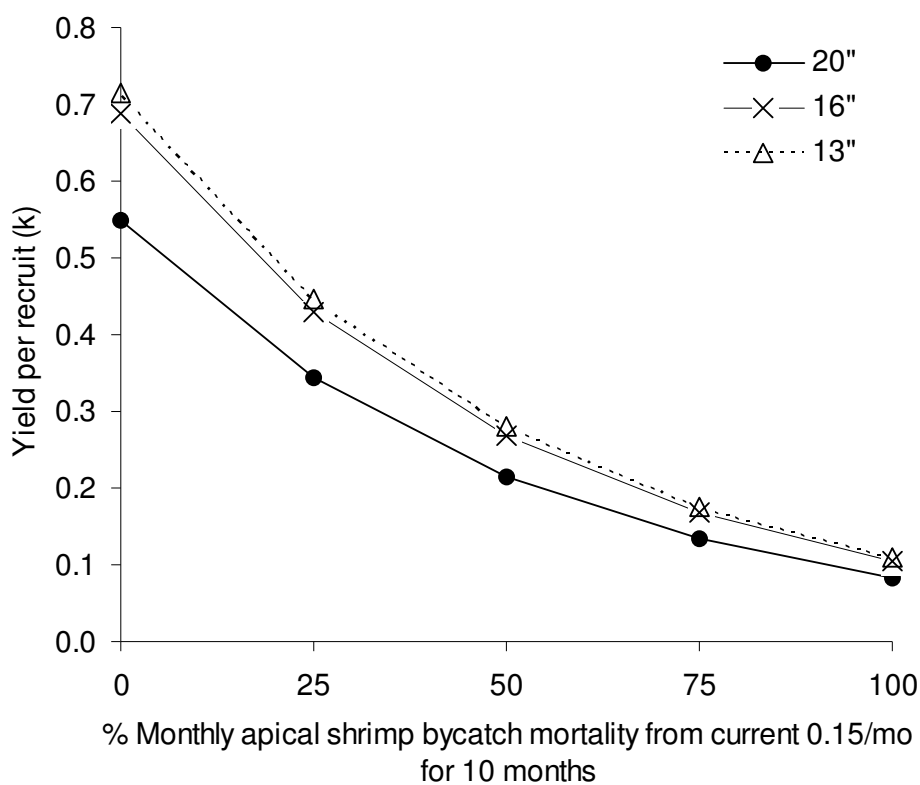


Figure 3.12 YPR for Red snapper in the Gulf of Mexico for 13" TL, 16" TL and 20" TL minimum sizes and for decreasing percentages of current shrimp bycatch mortality.

3.5 Conclusions

The results of the analyses show that the minimum size regulations will not contribute to the recuperation of the SPR to 20% while the shrimp bycatch mortality precedes the mature cohorts. Likewise, discards made due to the minimum size or during closed seasons do not appear to contribute to the stock recuperation. More importantly, even in the absence of shrimp bycatch, SPR under the current levels of apical fishing mortality rates in the directed fisheries (18.5%) appear well below the management objective of recuperating the stock to 20% SPR. Given that fishery management frames are set to reduce the bycatch in the shrimp fishery to 50%, it is not feasible that the stock would ever recover to the 20% SPR by managing minimum size in the directed fishery. This is due to several reasons: (a) the small differences in the average age of a 13 inch and 16 inch red snapper, (b) the small difference in fecundity between fish of these two sizes, (c) the survival of released fish is not ensured and discard levels are high, especially in shallow waters and under larger minimum sizes, and (d) natural mortality is low for these fish by the time they reach the minimum size for this fishery so there are few natural losses if they remain in the water. The significance of these results is that the spawning stock biomass is very much depleted under the current fishing mortality conditions and none of the management scenarios in the directed fishery appear to be effective to meet the fishery management objective of 20% SPR unless drastic and economically impacting reductions of red snapper landings are implemented.

Chapter 4. Summary and Conclusions.

4.1 Summary of growth analysis results

An analysis of the previous work on the age and growth of the red snapper in the Gulf of Mexico by other authors indicated that several age categories were underrepresented, most likely due to gear selectivity and minimum size effects. This therefore required that proportionality be assured between the somatic growth and that of the otoliths. The initial analysis of the growth of the red snapper indicated that there was a decoupling of relationship between somatic growth and otolith growth within several age classes, therefore a reliable description of somatic growth would not be realized using the otolith information for back-calculation purposes. This issue was resolved by use of a new otolith radius measurement, made along the primary axis of growth, instead of the previous measurements which were made primarily for ageing purposes. The new measurements, the ventral radii, had statistically superior relationships to the somatic growth than the previous measurements and resulted in the coupling between the otolith and somatic growth relationships. The analysis by sex also indicated no evidence of sexual dimorphism in relation to the otolith growth. This use of the ventral radius to provide more robust relationships between otolith and somatic growth was an important finding for the study of growth in the red snapper.

Four different types of models were investigated for individual growth history estimations for the red snapper. These included a multiple regression model, an age effects model, a power function model and the Modified-Fry

model. The outputs from the models showed that none of the models gave results that differed significantly from the observed mean lengths-at-age, indicating that each model could be used to adequately represent the observed data, despite the differences in the estimated parameter values. This gives a strong impression of the possible variance that can exist in the growth of this species. The method selected for further investigations of the growth parameters was the Modified-Fry method because it had the strongest relationship between the back-calculated and observed mean lengths-at-age and between the standard deviations and the mean length-at-age.

To account for the gear selectivity and minimum size effects on the population a simulated growth database was created using Monte Carlo methods and based on the Modified-Fry model results. The mean and standard deviation of each back-calculated length-at-age class were used to create theoretical normal distributions which were used to generate an unbiased virgin length-at-age population structure for red snapper in the Gulf of Mexico. This population structure was then used to estimate the new von Bertalanffy growth parameters found in table 2.5 where the asymptotic length is larger than most estimates from other authors. The parameters derived from the unbiased population structure may therefore support the contention that the larger individuals are missing or unavailable to the fishery due to the long history of heavy exploitation (Walter & Ingram, 2009).

An additional growth model based on the area of the otolith annular rings was also developed in this work. The model produced a very strong relationship

between the total length and the otolith annular area. The back-calculated mean length-at-age did not differ significantly from the observed mean lengths-at-age, indicating that this model could also be used to adequately represent the observed data. This model, however, was thought to be too unwieldy and time consuming for routine use for the red snapper as each annulus must be carefully and accurately measured. This would prove to be difficult when the annuli are not distinct and easily identified in the otolith sections. However, this method could be very easy and robust in species where the annuli are clear and distinct.

4.2 Summary of minimum size effects on SPR recovery

Despite multiple changes in the minimum size and other management measures over more than the last two decades the red snapper stock has not been evaluated as recovering. This is due to the overexploitation from the intense fishing pressure resulting from the more than 130 year old history of the fishery as well as the mortality of juveniles as bycatch in the shrimp fishery. This has resulted in the stock recovery date being continuously delayed. The minimum size plays a strong role in the discards made by the directed fisheries where in the past the discard rate has exceeded 90% of the fish caught in the recreational fishery. The mortality due to these discards is caused by barotrauma, hook damage and predation on the hooked and released fish.

An algorithm that created a growth transfer matrix, using the output of the growth function developed in chapter 2, was used to develop a cohort size-age structure that was subsequently modified by natural mortality and the fishing mortality effects of the various gears. The resulting cohort structure was then

used in the yield-per-recruit and spawning potential calculations to assess the impact of different minimum sizes used in the fishery. The management scenarios of different minimum sizes under several levels of shrimp bycatch reduction were then analyzed. The results indicated that the management target of 20% SPR was unattainable under the current directed fisheries mortality, even in the complete absence of the bycatch of the shrimp fishery (18.5%). Similarly, the SPR goal is not met under the current shrimp mortality, even in the absence of directed fisheries (15.29%). Both the directed fisheries mortality as well as the shrimp bycatch mortality would have to be reduced to meet the target SPR level. If the desired 50% reduction in shrimp bycatch mortality (from 2001-2003 levels) is met then the SPR would be about 7.23% under the current levels of directed fisheries mortality. These results are consistent under any of the minimum sizes established in this study, indicating that the minimum size regulations, due to the high mortality among the large number of discards, are not helpful to the recuperation of the spawning stock and to increase the SPR. The mortality on juveniles due to the bycatch of the shrimp fishery also adversely affects the future spawning capability of the stock.

4.3 Management recommendation

The use of a minimum size as a major management measure in the directed fisheries is contraindicated by the high mortality among the released undersized fish. This mortality affects the fish that are approaching the size of first maturity and affects the future spawning capacity of the stock. It is therefore recommended that the minimum sizes in the directed fisheries be eliminated so

that all fish caught, regardless of size, would be retained and counted towards the total allowable catch, so that when the quotas are filled the directed fisheries would cease their operations. This measure would be expected to reduce the total mortality and positively impact the spawning stock as fewer of the larger, more fecund, individuals would then be harvested and removed from the stock. The increased presence of these larger and more productive individuals would therefore improve the spawning capacity and SPR.

4.4 Additional research

In order to develop more robust estimates of the growth parameters more research is needed to capture information on the missing ages and sizes that are not collected due to the selectivity of the fishing gears. This requires the funding of scientific surveys and less dependence on fisheries dependent data for analysis. A comprehensive and properly designed sampling scheme is required to collect reliable data for analysis.

Additional research on the stock-recruitment relationship for the red snapper is needed due to the fact that recruitment appears to have been stable or even increased in spite of the large decline in stock abundance over its long history of exploitation.

Research is needed on the fishing areas, operations and fleet characteristics to provide a better analysis of the exploitation pattern effects on size –age groups. This information would assist in providing more robust data on red snapper cohorts, recruitment and spawning biomass.

A better understanding of the connection between the east and west stocks is needed. This can be researched through tagging studies and/or otolith chemistry investigations.

Increased sampling of the recreational fishery is needed to monitor and provide information on the effects of the increasing numbers of participants in the recreational fisheries over the last 50 years. This is important due to the very high number of discards due to the minimum size limits and closed season captures.

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