LIFE HISTORY, POPULATION DYNAMICS, AND FISHERY MANAGEMENT OF THE GOLDEN TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, FROM THE SOUTHEAST ATLANTIC AND GULF OF MEXICO

By

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To my Father

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There is a growing concern over the lack of life history information for many deepwater fisheries species, including golden tilefish, *Lopholatilus chamaeleonticeps.* Basic age and growth estimates are essential for proper stock assessment and management decisions. My first objective was to use lead-radium dating to validate the timing of growth increments. Radiometric ages closely agreed with age estimates from traditional age estimations (growth increment counts in thin sagittal otolith sections) for females and unknown sex fish. However, radiometric ages did not agree with traditional age estimates for males. This difference may be attributed to differing growth rates and increment formation by gender or the transition of gender. Golden tilefish longevity of 26 ± 6 yrs was confirmed using both methods.

My second objective was to describe the reproductive parameters and strategy for golden tilefish along the east coast of Florida and the northern Gulf of Mexico. Male golden tilefish reached maturity at a younger age (male, <1 yr; female, 2.5 yr) and smaller size (male, 150 fork length [FL] mm; female, 331 FL mm) than females. Golden tilefish gonads are described as being intersexual, identified as having non-functional (opposite) sex tissue (functional males

71% had multiple stages of atretic oocytes; functional females 26% had self-contained male tubules). Male gonads also contained a cavity that originated from ovarian lumen and sperm sinuses. Golden tilefish gonads exhibited intersexual tendencies, and I found evidence supporting a protogynous hermaphroditic reproductive strategy.

My third objective was to apply the resulting life history characteristics (objectives 1 and 2) to two statistical age structure stock assessment models. Each of these models represented the ends of the spectrum of model complexity. The available data for golden tilefish stock assessment was typical for many species with irregular sampling for length and age composition data and highly variable indices of abundance. I completed a stock assessment for golden tilefish using the simple Stochastic Stock Reduction Analysis model and the more complex Stock Synthesis model. The two models agreed in stock status of golden tilefish (not overfished and not undergoing overfishing), as well as, in historical annual biomass and exploitation rates.

CHAPTER 1
GENERAL INTRODUCTION

Golden tilefish, *Lopholatilus chamaeleonticeps* (Goode and Bean, 1880), is a deep-water demersal fish found in the Atlantic Ocean from Nova Scotia to the Gulf of Mexico (Dooley, 1978). Golden tilefish are managed by three fishery management councils (Northeast Atlantic, South Atlantic, and Gulf of Mexico). In 2004, the first fishery management regulation in the Gulf of Mexico was established as an annual quota for golden tilefish of 200 metric tons. This regulation was initiated as part of the red grouper *Epinephelus morio* rebuilding plan to guard against commercial long-liners shift to deep-water groupers and tilefish fisheries. The regulation was not based on any biological basis (NOAA, 2004). The lack of basic life history information and golden tilefish's unknown population status in the Gulf of Mexico motivated this research.

Age, growth, mortality, and reproduction are a few of the most valuable life history data necessary for stock assessment. Earlier research on golden tilefish from the waters of southern New England, South and North Carolina and Georgia concluded that golden tilefish are a long-lived fish reaching maximum ages of up to 40 yrs, have a slow growth rate, display sexual dimorphic growth and mature at least by age 5 (Turner et al., 1983; Harris and Grossman, 1985; Grimes et al., 1986; Palmer et al., 2004). These studies provided initial data as a foundation for my research.

In my first chapter, I validated the timing of band deposition in sagittal otoliths using the natural decay of ^{210}Pb and ^{226}Ra and establish an accurate age estimation criteria for golden tilefish. For some teleosts, establishing the timing of band deposition can be imprecise given the effect of environmental conditions on the rate of absorption of calcium carbonate and other trace elements into the otolith matrix. Golden tilefish reside in a very specific habitat preferring a soft, but malleable sediment along the continental shelf in water depths 80-400 m (Freeman and

Turner, 1977), inhabit burrows (Able et al., 1982), and within a specific thermal cline (9-14^{o}C; Grimes et al., 1986). My first chapter will be submitted to a journal that publishes original studies on the ecology of fishes and their relationship with the environment.

In the second chapter I describe the reproductive strategy of golden tilefish. Teleosts exhibit a large diversity of reproductive strategies from fish remaining the same sex throughout their life time (gonochoristic) to fish changing sex during their lifetime (hermaphroditic). This chapter will be submitted to a journal that focuses on general fish biology, in particular, reproductive studies involving the classification of reproductive phases based on histology.

Finally, in my third chapter, I used the age, growth, and reproductive information obtained in my research along with data collected from the golden tilefish fishery to determine the status of the stock in the Gulf of Mexico. Stock status was predicted using two statistical age structured stock assessment models. I plan to publish this chapter in a journal that features original research affecting marine fisheries.

My dissertation provides the first description of life history and stock status of golden tilefish from the northern Gulf of Mexico. My research describes the methods to appropriately assign age to golden tilefish in the Gulf of Mexico and south Atlantic through validating the timing of band deposition in sagittal otoliths. This work also disputes golden tilefish's gonochoristic reproductive strategy by providing a comprehensive description of the histological classification of the maturity phases of males and females, the occurrence of non-functional tissue in both mature, functional males and females, and histological evidence to describe golden tilefish as protogynous hermaphrodites. And finally, my discoveries of basic life history information of golden tilefish are applied to two age structure stock assessment models to

determine if the golden tilefish stock in the Gulf of Mexico is overfished or undergoing overfishing.

CHAPTER 2
AGE ESTIMATION AND LEAD-RADIUM DATING OF GOLDEN TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*[1]

Introduction

Age-structured stock assessment models that rely on accurate estimates of fish age can provide misleading results leading to erroneous management decisions if fish ageing is imprecise or invalidated. As an example, estimates of size-at-age are required for growth estimation, which is critical for diagnosing growth overfishing (Parma and Deriso, 1990), and estimates of longevity play an important role in calculating natural mortality (Hoenig, 1983) and lifetime fecundity (Rochet, 2000). Thus, accurate age and growth estimates and age estimation criteria are essential for a proper stock assessment.

Validating the timing of band deposition in otoliths is critical in determining longevity, as well as an accurate rate of growth. Otoliths form rings but proving whether or not the ring (or band) is laid down annually or bi-annually, due to some physiological or environmental factor can be difficult, especially for deep water species (Cailliet et al., 2001). There are several methods to validate the timing of band deposition such as marginal increment analysis, tag and recapture of known aged fish, chemically marking fish with recapture, and radiochemical dating (Campana, 2001).

The focus of my dissertation is the golden tilefish, *Lopholatilus chamaeleonticeps* which is a deep-water demersal fish found in the Atlantic from Nova Scotia to the Gulf of Mexico (Dooley, 1978). Previous research used both sagittal otoliths (Turner et al., 1983; Harris et al., 2001; Palmer et al., 2004) and anal fin rays (Harris and Grossman, 1985) to assign an annual age

[1]The research in this chapter was completed in collaboration with A. Andrews (NOAA Fisheries Service, Pacific Fisheries Science Center, Honolulu, HI). A. Andrews provided technical expertise on analytical methodology. I conceived the original project, aided in securing funding, drafted methods, assisted with sample collection, and interpretation of analytical results. Research was funded by NOAA Fisheries Service, Marine Initiative Research Program (Andrews, 2009a).

to golden tilefish caught in the Middle Atlantic-Southern New England region and the U.S. South Atlantic waters off the coasts of North and South Carolina and Georgia. These studies revealed golden tilefish had longevities of 40 years (Palmer et al., 2004) with females more prevalent in the older age classes (Turner et al., 1983; Harris et al., 2001). These longevities were based on the results of marginal increment analysis in thin sectioned sagittal otoliths (Turner et al., 1983) and thin sectioned anal fin rays (Harris and Grossman, 1985).

Marginal increment analysis (MIA) is used widely in age and growth studies and involves recording, either digitally or manually, multiple measurements from ageing structure (otoliths, fin ray) measurements (e.g., otolith core to otolith edge, otolith core to each growth increment). But to properly validate the timing of band deposition through MIA several criteria must be met, such as a random selection of fish collected over a long time period (e.g., including more than one deposition cycle), age structure measurements must be exact and not subjective given the instrumentation used to measure (manually or digitally), and results should be considered age-specific (Campana, 2001). Validating golden tilefish band deposition in sagittal otoliths using MIA was obscured by low sample sizes ($n < 5$) per month per age group (only 8 age groups; ages 1-3, 4, 5, 7, 8, 9, 10-17), and large confidence intervals among mean values (Turner et al., 1983). Nevertheless, it was still concluded that golden tilefish had an annuli band formation with most opaque zone of annulus formation completed by June, even though younger and older fish exhibited different timing of band formation (June versus March, respectively, Turner et al., 1983). The MIA study using golden tilefish anal fin rays also concluded an annuli band formation although the increment measurements were imprecise given skin still attached to the external ray, and in some ray sections the translucent bands along the margin may not have represented a completed increment (Harris and Grossman, 1985).

Due to the inconclusiveness of the MIA, radiochemical validation methods were applied to golden tilefish. One such method is bomb radiocarbon which relies on C^{14} levels emitted into the atmosphere during nuclear testing in the late 1950s (Campana, 1997). The increase in C^{14} levels in the ocean and subsequent C^{14} levels incorporated into carbonate structures (i.e., otoliths) can provide an independent estimate of age (Kalish, 1995). This method validated the timing of band deposition successfully for a variety of species inhabiting shallow water reefs red snapper, *Lutjanus campechanus* (Baker and Wilson, 2001), benthopelagic red fish *Centroberyx affinis* (Kalish, 1995), and continental shelf quillback rockfish *Sebastes maliger* (Kerr et al., 2005). However, radiocarbon dating is affected by the amount of C^{14} available in the water column, which decreases below depths of 100 m (Stuiver and Östlund, 1980).

Earlier efforts to validate golden tilefish band deposition using bomb radiocarbon resulted in lower amounts of radiocarbon in otolith cores compared to haddock (*Melanogrammus aeglefinus*) and red snapper (*Lutjanus campechanus)* delta C^{14} reference curves (Harris, 2005). One possible reason for the inconclusiveness of the radiocarbon study is the depth at which golden tilefish reside and the absorption of atmospheric C^{14} at these depths (Stuiver and Östlund, 1980). There is very little information regarding the golden tilefish early life history (larval and juvenile stages) but of the few larval golden tilefish that have been identified, these were collected at depths > 100 m (pers. comm., D. Drass, NOAA Fisheries Service, Pascagoula, MS) and most adult tilefish reside at a minimum of 100 m (SEDAR, 2011a). Similarly, lower radiocarbon levels detected in yellowedge grouper (*Epinephelus flavolimbatus*) compared to red snapper radiocarbon levels were contributed to the depths preferred by these fish (Cook et al., 2009). This suggests that use of C^{14} for golden tilefish may not be successful.

Therefore, in my dissertation a second method of radiochemical dating using the natural decay of lead (^{210}Pb) and radium (^{226}Ra) was applied. For fish, lead-radium dating depends on the incorporation of radium-226 from the environment, where it is locked into the otolith matrix and subsequently decays to lead-210. The lead-radium dating can be used to provide an independent estimate of age, as well as a form of age validation for traditional age estimation methodologies (Smith et al., 1991; Panfili et al., 2002).

Lead-radium dating is a geochronological technique that has been used to date recent geological formations, such as accretionary carbonates (e.g., Condomines and Rihs, 2006). Use of this system as a chronometer relies on the decay of the relatively long-lived radioisotope radium-226 (^{226}Ra) to the relatively short-lived granddaughter product lead-210 (^{210}Pb). Because the half-life of radium-226 is much greater (~1600 years) than lead-210 (22.26 years) the disequilibrium of the lead-radium system can function as a natural chronometer as lead-210 builds into equilibrium with radium-226. The otolith lead-radium system can be used to provide a radiometric estimate of age based on the disequilibrium within the first year or few years of growth (otolith core). This tool is unique because it is strictly regulated by the passage of time. Given a measured lead-radium activity ratio from otolith core material, an age can be estimated within the margin of uncertainty from the measured quantities occurring from the natural decay of radium-226 to lead-210 (Smith et al., 1991; Panfili et al., 2002). This approach is an improvement over radiocarbon because it is not dependent on atmospheric C^{14} deposition, which may not be reliable at the depths tilefish are found. This kind of information can serve as a form of age validation for other age estimation methods (e.g., traditional growth zone counts; Andrews et al., 2009).

My objectives were to establish an accurate traditional age estimation methodology using sagittal otoliths and to validate growth increments in golden tilefish sagittal otoliths using innovative radiochemical dating methods. It is expected that by validating the timing of band deposition in golden tilefish sagittal otoliths an accurate age assignment will provide new insight into golden tilefish life history such as age at maturity, fecundity, growth, and mortality. This is information necessary in the development of age based stock assessment models (as discussed in chapter 4) to make informed fishery management regulations. Errors in age estimation could lead to erroneous conclusions related to the stock status of golden tilefish that could have serious ecological or economical impacts.

Materials and Methods

Sample Collection

Federal port agents collected otoliths from golden tilefish harvested by commercial long-line gear in 2007 along the east coast of Florida (Fig. 2-1). Port agents targeted twenty fish (for both male and female) per 100 mm size bins (300 - 1000 mm, fork length). Port agents provided field measurements of fish lengths (fork or total length, to 1.0 mm), weights (whole or gutted, to 0.1 kg), and removed both sagittal otoliths and gonads. Port agents also gathered information describing catch location (latitude, longitude, depth, or NMFS statistical shrimp grid) during dockside interviews. Sex was assigned using macroscopic description of whole gonads (female – oval in shape, pinkish to red in color; male – thin, taper to a point, normally white in color).

Traditional Age Estimation

In order to compare the results of lead-radium dating, actual counts of pairs of opaque and translucent growth bands (referred to as traditional age) were interpreted from thin sectioned sagittal otoliths. One otolith from each pair of golden tilefish sagittal otoliths was sectioned by taking a transverse section (dorso-ventral plane) through the focus using a Hillquist petrographic-

type saw (Cowen et al., 1995). A secondary reader and I aged the sectioned otoliths using transmitted light with a stereo microscope. This method was similar to that of previous golden tilefish ageing studies (Fig. 2-2) (Turner et al., 1983; Palmer et al., 2004). Each reader made initial estimates of age by examining the otolith sections with a wide-ranging magnification to fully investigate the quantifiable pairs of opaque and translucent growth bands. The secondary reader and I discussed our initial readings to establish traditional age estimation criteria. The otolith sections were re-read by each reader using the established criteria. Indices of precision (average percent error and percent agreement ± 1 and ± 2 bands) (Campana, 2001) were calculated to determine the accuracy of the ageing criteria between readers. Both readers agreed on the final age estimates that determined the otoliths used for lead-radium dating. A third independent reader (experienced in ageing deep water grouper species) also aged the golden tilefish sections to determine if my ageing criteria were consistent and repeatable.

Otolith Growth Increment Deposition

Growth increments in thin-sectioned sagittal otoliths were described both qualitatively and quantitatively to determine sexual dimorphic patterns of growth. I qualitatively characterized growth increment deposition as either horizontal (increments deposited horizontally along the ventral sulcus) or vertical (increments deposited vertically along the ventral axis). Each thin sectioned sagittal otolith was captured digitally using a digital camera (Hitachi, Model KP-D50 color) connected to a desktop computer equipped with Image Tool software (University of Texas Health Science Center in San Antonio: UTHSCA, Version 3.0). The distance between the core and the mid-line of the completed growth increment (a pair of translucent and opaque bands) was measured along the ventral axis to quantitatively describe growth increment deposition.

Lead-radium Dating Age Groups

There are four major limitations of lead-radium dating that must be considered before forming age groups. These limitations are: 1) core size and potential age of juvenile otoliths; 2) individual and collective otolith sample mass availability for juvenile and cored adult otoliths; 3) potential radium-226 activity; and 4) total sample age (estimated age plus time since capture). The approach in this study was similar to most other studies performed in that initial sample masses were chosen to provide a good indication of lead-210 and radium-226 activity, given a best guess at the lowest case scenario. Typical radium-226 activity in otolith material is 0.03 to 0.05 $dpm \bullet g^{-1}$. Based on this estimate, a minimum of 0.5 grams of core material for each lead-radium age group was targeted to collect sufficient counts at the alpha (α)-spectrometer, with a more optimal target of more than 1.0 g for each age group.

Because of its rarity in collections, only one juvenile otolith was available as a reference for adult otolith coring. Readers agreed the juvenile tilefish was 2 years of age and based on the dimensions and whole otolith weight of this otolith, the target of core extractions was approximately 8 mm x 4 mm x 1 mm (length x width x thickness) and a weight of 0.05 grams (g). Hence, the number of otoliths required for an adequate sample size of 0.5 g was ~10, with more than 10 providing more optimal conditions for measuring lead-radium activities.

After otoliths were chosen for each of lead-radium age groups (based on traditional age estimation), each otolith was cored to the first 2 years of growth by: 1) grinding on a lapidary wheel; and 2) comparing the extracted core microscopically, as well as macroscopically, to the reference juvenile otolith mentioned above. It was necessary to core each otolith to isolate the lead-radium activity to the first few years of the otolith's growth. Alternate pairs of opaque and translucent growth bands visible in the otolith were used to verify the concentric structure of each core to the first few years of growth. Careful consideration to the shape of the juvenile

otolith was taken as the extraction took place. Due to the sensitivity of lead-radium dating to the amount of otolith material, otolith coring was completed under the supervision of A. Andrews at Moss Marine Laboratory (Moss Landing, CA). It was noted that the orientation of the otolith slowly rotated upward on the anterior end within the first few years of growth. In addition, the shape of the juvenile otolith was slightly concaved to the distal side (Fig. 2-3). Both of these morphological characteristics were approximated in the core extractions, where a combination of microscopic examination and measurements provided the best indication of when the core extraction was finished. Dry (room temperature) otolith core weights (similar to the reference juvenile tilefish otolith) were used as the final determination that core extraction was complete. In most cases, the cores needed fine-tuning with minor grinding and more microscopic and measurement observations. Finally, otolith cores were pooled into respective lead-radium age groups and prepared for lead-radium dating analysis.

Lead-radium Dating Analysis

Given the sophisticated laboratory equipment and specialized training needed to complete the lead-radium dating, this analysis was conducted by A. Andrews at Moss Marine Laboratory (Moss Landing, CA). A detailed protocol describing sample preparation, chromatographic separation of radium-226 from barium and calcium, and analysis of radium-226 using mass spectrometry is described elsewhere (Andrews et al., 1999). The procedures used in this study were an improvement of the established protocol: 1) by shifting the collection interval on the final chromatography column to begin at 200 μL (as opposed to 250 μL) to increase radium recovery; and 2) by using an improved ICP-MS (Inductively Coupled Plasma Mass Spectrometry) technique to purified radium samples. Other than these details, only an overview of the radium-226 procedures is provided with details on the determination of lead-210 activity. Standardized trace-metal clean procedures and equipment were used throughout sample

preparation, separation, and analysis, since the levels of radium-226 and lead-210 typically found in otoliths were extremely low (femtograms (10-15 g) for radium-226 and attograms (10-18 g) for lead-210). Also, ultra-pure, double distilled (GFS Chemicals®) acids and dilutions used in this study were made using Millipore® filtered Milli-Q water (18 MW cm^{-1}).

Dried and weighed samples were dissolved in TFE beakers on hot plates at 90°C by adding 8N HNO_3 in 1-2 mL aliquots. Alternation between 8N HNO_3 and 6N HCl, with an aqua regia transition, several times resulted in complete sample dissolution. The dried sample, after dissolution, formed yellowish precipitate. To reduce remaining organics (otolin), and to put the residue into the chloride form required for the lead-210 activity determination procedure, samples were redissolved in 1 mL 6N HCl and taken to dryness five times at 90-120°C. A sufficient amount of organics was removed once a whitish residue formed. It was these samples that were used to determine lead-210 activity prior to ICP-MS analysis.

The alpha decay of polonium-210 as a daughter proxy for lead-210 was used to determine lead-210 activity in the otolith samples. Since it takes two years for the alpha decay of polonium-210 and to ensure the activity of polonium-210 was due solely to the ingrowth from lead-210, only the cores of adult fish were used in analysis. Samples were prepared for polonium-210 analysis by spiking them with polonium-208 (a yield tracer). The amount of polonium-208 added was based on observed radium-226 levels in other studies of deepwater fishes (Andrews, 2009b). This amount was adjusted to about 5 times the expected polonium-210 activity in the otolith sample to reduce error in the lead-210 activity determination. These spiked samples were redissolved in approximately 50 mL of 0.5N HCl on a hot plate at 90°C covered with a watch glass. The polonium-210 and polonium-208-tracer was autodeposited for 4 hours onto a silver planchet. The activities of these isotopes were determined using a-spectrometry on

the plated samples. Additional procedural and system details are described elsewhere (Andrews et al., 1999). The remaining solution after polonium plating was dried and saved for radium-226 analyses on a Nu Plasma™ HR ICP-MS located in the Department of Geology at University of Illinois-Urbana, Champagne.

Radiometric Age Estimation

Radiometric age was determined from the measured lead-210 and radium-226 activities. Since the lead-radium activities were measured using the same sample, these calculations were independent of sample mass. Radiometric age was calculated using an equation derived from Smith et al. (1991) to compensate for the ingrowth gradient of lead-210-radium-226 in the otolith core,

$$t_{age} = \frac{\ln\left(\frac{1-\left(\frac{A^{210}Pb}{A^{226}Ra}\right)}{(1-R_0)\left(\frac{1-e^{-\lambda T}}{\lambda T}\right)}\right)}{-\lambda} + T,$$

where t_{age} = the radiometric age at the time of analysis,

$A^{210}Pb$ = the measured lead-210 activity at time of analysis and reported as $dpm \bullet g^{-1}$ (disintegrations per minute per gram),

$A^{226}Ra$ = the radium-226 activity measured using ICPMS (reported as $dpm \bullet g^{-1}$),

R_0 = the activity ratio of lead-210 and radium-226 initially incorporated,

λ = the decay constant for lead-210 ($\ln(2) \bullet 22.26 \bullet yr^{-1}$), and

T = the estimated core age based on the first few growth zones.

An initial uptake ratio of $R_0 = 0.0$ was used, based on the close agreement of the measured juvenile age group lead-radium ratio with the expected ingrowth curve; however, other studies have accounted for what appeared to be exogenous lead-210 with minor adjustments necessary

(e.g., Kastelle et al., 2000; Stransky et al., 2005). A radiometric age range was calculated, based on the analytical uncertainty, for each sample by using error propagation through to the final age determinations (2 SE, standard error). Calculated error included the standard sources of error (i.e., pipetting, spike and calibration uncertainties, etc.), alpha-counting statistics for lead-210, and the ICPMS analysis routine.

Radiometric versus Tradition Age Estimation

Traditional age estimation (determined from otoliths growth band counts) and radiometric age estimation (determined from lead-radium dating) were compared by lead-radium sample age groups. These estimations were also compared to the expected ^{210}Pb:^{226}Ra ingrowth curve. Age agreement, or disagreement, between the two methods in terms of potential ageing bias (95% confidence intervals, 2 SE) was given consideration.

Results

Sample Collection

Port agents collected a total of 223 golden tilefish (female, n = 95; male, n = 101; unknown sex, n = 27). The sex of tilefish was determined by examining whole gonads. The smallest fish was a male (389 mm FL) and the largest fish was of unknown sex (935 mm FL). Of the eight size bins, port agents sampled four size bins (400-799 mm FL; Fig. 2-4) sufficiently (sample size > 20 per size bin). There were difficulties in collecting small tilefish due to gear selectivity and a lack of larger fish (800+ mm FL) caught by the fishery.

Traditional Age Estimation

Readers determined golden tilefish thin-sectioned sagittal otoliths were difficult to interpret given several different shapes of otolith sections and diverse patterns of band deposition (Fig. 2-5). Readers interpreted otolith sections using a magnification of 10 – 20x with a stereo-microscope aided by transmitted light. Initial reader agreements resulted in 18% average percent

error (APE), 8% reader agreement, and reader agreement ± 1 band 22% and ± 2 bands 26%. The traditional age estimation criteria involved 1) counting alternating pairs of thin opaque and translucent bands that were present both along the ventral axis and ventral sulcus, 2) interpreting otolith sections at no more than 20x magnification, and 3) taking the shape (stocky or elongated) of the otolith section into consideration when interpreting the distance between bands. After the agreement of an ageing criteria, reader agreement increased to 28%, APE lowered to a more acceptable value of 6% (similar to other long-lived fish aged at the NOAA Fisheries Service, Panama City Laboratory, Panama City, FL), with percent agreements ± 1 band and ± 2 bands increased to 78% and 95%, respectively. Final age estimates used for further analysis were based on the agreed pattern of growth increment recognition between readers. Readers determined tilefish to be age 4 – 32 years old, with females occurring in most age groups (5 – 32 years; Fig. 2-6). Otolith interpretations were completed by an additional third reader and resulted in similar age estimates (female age 5 – 25, male age 4 – 12) and similar precision (APE 7.5%, percent agreement ± 1 band 25%, percent agreement ± 2 bands 63%).

Otolith Growth Increment Deposition

Golden tilefish otoliths showed sexual dimorphic differences in otolith morphology. Adult females tended to deposit growth increments in a manner that thickened the otolith horizontally on the proximal side (sulcus) (Fig. 2-5A). Males deposited growth bands in a more vertical, longitudinal manner (Fig. 2-5B). Golden tilefish also showed sexual dimorphic growth increment deposition. Average growth increments were similar between genders until age 8, thereafter males deposited increments at larger distances (Fig. 2-7). Additionally, some male sagittal otoliths showed an unusual pattern of growth increment deposition; the first four bands composed of several thinner, darker increments followed by fainter increments deposited in more even groupings (Fig. 2-8).

Lead-radium Dating Age Groups

Twelve age groups were formed for the lead-radium analysis of golden tilefish otoliths (Table 2-1). Estimated age for the series of groups ranged from 5-7 years to 22-28 years with sexes separated for the first two age groups. Within the separate-sex age groups, each was randomly split into sample replicates, resulting in 2 male and 2 female groups for both 5-7 year and 10-13 year age groups. Randomization led to age ranges that differed slightly in range (i.e., GTL 5-7 M1 = 6-7 years and GTL 10-13 M1 = 10-12 years); however, the average estimated age was relatively consistent at 6.2 to 6.4 years for the 5-7 yr groups, and 10.6 to 11.4 years for the 10-13 yr age groups. The older age groups could not be separated by sex because of a lack of reproductive tissue collected and the low sample availability. Two 15-19 year groups were separated by otolith weight into a low (A) and high (B) weight classification. A similar situation was the result for the oldest age groups, where randomization led to slightly different age ranges, the low weight age group range from 20-27 years and the higher otolith weight group ranged from 22-28 years.

Fish length was lowest on average for the 5-7 yr female age groups and range up to more than 750 mm FL on average for the oldest age groups (Table 2-1). In general, the length of fish increased with estimated age, but some age groups included some relatively large individuals (e.g., GTL 5-7 M1, maximum length = 860 mm FL; Table 2-1). Whole otolith weight was also lowest for the 5-7 yr female age groups at below 0.4 g on average. Otoliths for adults were massive and exceeded 1.7 g on average for the 22-28 yr age group. For the younger randomized age groups, average otolith weight was lower for females relative to males in all cases. Hence, relative to estimated age, females were typically smaller with lighter otoliths for the first two age groups (5-7 yr and 10-13 yr). For the two older age groups, the heaviest 15-19 yr group (GTL 15-19 B) was similar on average for both fish size and otolith weight to the 20-27 yr age group.

The oldest age group (GTL 22-28) exceeded almost all groups in terms of otolith weight both on average and in range; only GTL 15-19 B included otoliths that overlapped in weight.

Lead-radium Dating Analysis

Lead-radium determinations were made for all 12 age-group samples (Table 2-2). The number of otoliths that made up each age group ranged from 9 to 21 for total sample weights of just over 0.5 g to greater than 1.5 g. Mean core weight was slightly greater than the target weight of 0.05 g and ranged from approximately 0.063 g to 0.081 g per core. This was anticipated to an extent because the cleaning process usually removes ~5% of the external material, but in this study removed only 1-3%. To make a better approximation on the representation of core age in radiometric modeling, 3 years was used in lieu of 2 years as the core age since the juvenile otolith used for reference contained growth pass the end of the second annulus formation. Lead-210 activity increased as expected from the youngest to the oldest age groups by a factor of ~3 times. Samples ranged from 0.00419 ± 13.8% dpm•g^{-1} for GTL 5-7 F1 to 0.01359 ± 6.7% dpm•g^{-1} for GTL 22-28. Radium-226 activity was lower than expected for the region by a factor of about 2 to 5 times. The activity ranged from an average of 0.01413 ± 22.6% dpm•g^{-1} for the GTL 10-13 M1 groups to 0.02573 ± 16.1% dpm•g^{-1} for GTL 22-28. Radium-226 recovery was low for a few samples (the most massive samples may have overloaded the Sr column with barium causing radium recovery to suffer) and the runs were deemed unreliable (error greater than 30% and close to background counts on the ICP-MS). To recover the opportunity to age the samples, an average of all measured values with less than 25% error (13-23%) was used in place of the unreliable values (n = 6; 0.01989 ± 15.7% dpm•g^{-1}); this replacement occurred for GTL 5-7 M1, M2, and GTL 10-13 F2. For the other randomly split age groups an average of the measured values for the pair was used as the radium-226 activity for the groups. For the older age groups that were not randomly split, sample specific radium-226 activities were used.

Radiometric versus Tradition Age Estimation

Both the total sample age (estimated age plus time since collection) and age corrected for time since collection were calculated to compare radiometric age with traditional age estimated from growth zone counting (Table 2-3). Agreement of the total sample age with the ingrowth curve was good for some sample groups and markedly different from what was expected for other groups (Fig. 2-9). Sample measurements to the left of the ingrowth curve were underestimated for age using growth increment counting, which was most apparent with the male groups, especially GTL 10-13 M1 and M2. Young female and the older mixed age groups radiometric and traditional age estimates were largely in agreement, but the 15-19 yr groups age were slightly underestimated by a few years on average. No apparent trend related to otolith weight was discernible based on the similarity of radiometric age determinations for the oldest groups (GTL 15-19 A and B, GTL 20-27, and GTL 22-28).

Discussion

Longevity, the maximum number of years of life, is related to natural mortality. If a fish lives a very long time (longevities in terms of multiple decades), the overall stock will be less productive. This phenomenon has been best documented in very long-lived (centennial) fish such as orange roughy (*Hoplostethus atlanticus*) and numerous species of rockfish (Mace et al., 1990; Musick, 1999). I am very confident in my estimates of longevity for golden tilefish from the east coast of Florida, since lead-radium dating and traditional age estimations were in good agreement in estimating longevity (lead-radium 26 ± 6 yrs, traditional average age 25.2 ± 3 yrs). My estimates of longevity were very similar to those published for golden tilefish from other ageing studies (35 yr, Turner et al., 1983; 33 yr, Harris and Grossman, 1985; 34 yr, Harris et al., 2001; 40 yr, Palmer et al., 2004). Not only have I proven longevity using the natural decay of radium-206 to lead-210 but I have also provided a more precise method to interpret growth

bands in thin sectioned sagittal otoliths. Even though radiometric and traditional age estimation methods were in agreement in the oldest age groups, these methods did not agree in the male age groups, with ages differing by 5-15 years. The differences in traditional age versus lead-radium dating in male tilefish may be due to: 1) the uptake of ^{226}Ra differed from the mean values used, 2) growth rates or 3) the pattern of growth increment deposition differed by gender.

It is important to recall that lead-radium dating depends on the level of radium-226 uptake. Radium-226 levels in the otolith cores were lower than expected (typically 0.3 to 0.5 dpm•g^{-1}) and this was difficult to explain in the broader context of measured values from other lead-radium dating fish studies to date (Andrews, 2009b). The flux of radium-226 is typically greatest near continental margins and sea floors with low sedimentation rates (Broker and Peng, 1982), or from nearshore environments like the coastal waterways of Florida (Fanning et al., 1982). However, seasonal fluctuations of radium isotopes along the southeastern U.S. continental shelf (Moore, 2007) and the decrease of ^{226}Ra by depth and distance from shore (W. Moore pers. comm., University of South Carolina, Columbia, SC) could account for these lower radium levels. In addition, little or no information exist for the early life stages of golden tilefish and commercial fisheries typically catch tilefish > 400 mm FL even though there is no size limit (Freeman and Turner, 1977). The only exception on record was with the 210 mm FL juvenile that was recovered from the mouth of moray eel by an observer. Small fish may be avoiding the gear because most commercial long-liners use large circle hooks (15/0-13/0) or may inhabit a different area than where fishing occurs (depths > 200 m) (Freeman and Turner, 1977; Hale, 2011). It is assumed male and female juveniles settle in similar habitats and are exposed to similar levels of radium; therefore, the intake of radium should be the same regardless of sex.

Because of the low values, and in some cases poor radium recovery, the activity of radium-226 suffered for some samples. Counts at the ICP-MS were close to background making the end result unreliable. This led to the use of a mean activity value, in lieu of the unreliable measured values to recover radiometric age determinations for a few groups. While this could be considered a weak point in the findings, the overall determination of radiometric age from the mean values was consistent with the relatively accurate lead-210 and radium-226 activity values, both in terms of activity and group age. Historically, mean radium-226 values were used in successful lead-radium dating studies, typically providing lower precision and an additional assumption for radium-226 uptake (e.g., Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1991). While it is desirable to acquire much greater age estimation accuracy, the relatively low precision from radium-226 uncertainty in the golden tilefish otolith cores did not preclude an age determination within the reported margin of error. Hence, it is unlikely that the differences in age observed for the male age groups were not the result of analytical error and that there were actual differences in the age and growth of adult male fish.

Golden tilefish otoliths had structural differences in otolith morphology that suggest variations in band deposition and growth rate by gender. Male golden tilefish do grow faster and obtain much larger sizes than female golden tilefish (see chapter 3). In the following chapter, I provide evidence that golden tilefish are protogynous hermaphrodites. The differences in growth, differences in deposition of growth increments and morphology of sagittal otoliths between the genders may be due to some females transitioning into males. In each of the male sample groups used for lead-radium dating, at least 70% of the male gonads contained female gametes of varying degree of development (see chapter 3). This transition may also be the reason for different patterns of growth increment depositions in male sagittal. Nevertheless, I am

confident that the lead-radium analysis was not obscured by the differences in band deposition by gender since the extracted core material composed of the first three years of otolith growth, which was similar by gender.

The comparison of traditional age estimates and radiometric age estimates relies on the accuracy and precision of the traditional ageing methodology. Accuracy refers to the similarity of the traditional age estimate and actual age (based on a validation method) and precision is the repeatability (or consistency) of the method of growth band interpretation (Campana, 2001). Golden tilefish thin sectioned sagittal otoliths showed a variety of different patterns in growth increments that were difficult to interpret. My traditional ageing methodologies were based on previous published methods for ageing golden tilefish sagittal otoliths (Turner et al., 1983; Palmer et al., 2004), along with the integration of methods used for interpreting yelloweye rockfish (*Sebastes ruberrimus;* Andrews et al., 2002). The difficulty in the interpretation of growth increments in golden tilefish sagittal otoliths was also one of the reasons for the inconclusiveness of the radiocarbon validation study (Harris, 2005). Although my traditional age estimates were in good agreement for the female and unknown sex age groups, the disagreement in the male age groups is most likely due to the underageing and misinterpretation of the growth increments in male golden tilefish rather than the results of lead-radium analysis. My traditional age estimations may have been less accurate due to the different patterns of growth increments in primary (some males deriving from a male immature phase) and secondary (males transitioning from females) male golden tilefish (Sadovy and Shapiro, 1987; Walker and McCormick, 2009).

The application of lead-radium radiometric dating relies on several assumptions 1) the otolith is a closed system with no loss or gain of ^{226}Ra, 2) the update of exogenous ^{226}Ra is negligible, and 3) the update of ^{226}Ra is in constant proportion to the otolith mass growth rate

(Kimura and Kastelle, 1995). My study addressed each of those assumptions by using an improved technique (Andrews et al., 1999) that used otolith cores (as well as the first years of growth) so that any difference in ^{226}Ra intake given the changes in growth rate of the otoliths was eliminated. Also, the usage of advances in thermal ionization mass spectrometry (TIMS) were applied to reduce error and subsequently increasing analytical precision of small quantities of ^{226}Ra isotopes through the use of improved ICP-MS. And finally, in addition to these new techniques, precautions were made to minimize contamination during all sample processing (e.g., double distilled acids).

Conclusion

Determining sustainability in fish stocks relies on estimates of growth, age at maturity, longevity, natural mortality, and recruitment variability; all of which rely on an accurate estimate of age. In some fish, for example splitnose rockfish (*Sebastes diploproa*; Bennett et al., 1982) and Patogonian toothfish (*Dissostichus eleginoides*; Andrews, 2009b) traditional age estimations are difficult even with successful validation studies. In situations where age estimates are both imprecise and biased, an ageing error matrix can be incorporated into the modeling process (Punt et al., 2008; Gertseva and Cope, 2011; Candy et al., 2012). It is recommended that a reference collection of known ages be routinely read by multiple readers from multiple ageing facilities to fully capture the imprecision and bias associated with traditional ageing estimations into the ageing error matrix. The reference collection needs to include samples that fully represent the range of ages (especially the older fish) and with sufficient sample sizes per age class to enable appropriate statistical analysis (Campana, 2001; Punt et al., 2008). Therefore, given the inconclusiveness of validating each of the age and gender groups for golden tilefish, I recommend the use of an ageing error matrix in assessment models to incorporate the uncertainty in traditional age estimates (as is used in following chapter 4 in Stock Synthesis).

Table 2-1. Summary of estimated age with fish and otolith characteristics for golden tilefish age-groups from the east coast of Florida processed in this study. Estimated age composition, fork length (FL), and whole otolith weight are given. The sex composition for samples GTL 5-7 and 10-13 was signified by an M or F in the sample number. Sexes were mixed or unavailable for the older age groups.

Age group & sample number	Age range (yr)	Average age (yr)	Average FL (mm)	FL (mm) range (2 SE)	Average otolith wt. (g)	Otolith weight range (2 SE)
GTL 5-7 M1	6-7	6.4	549	436-860 (39)	0.470	0.348-0.596 (0.034)
GTL 5-7 M2	5-7	6.3	520	465-620 (17)	0.453	0.330-0.663 (0.030)
GTL 5-7 F1	5-7	6.4	483	402-535 (28)	0.391	0.277-0.504 (0.046)
GTL 5-7 F2	5-7	6.2	465	412-508 (18)	0.366	0.270-0.488 (0.039)
GTL 10-13 M1	10-12	10.6	683	494-796 (37)	0.889	0.681-1.198 (0.079)
GTL 10-13 M2	10-13	10.8	729	570-810 (40)	0.964	0.630-1.261 (0.095)
GTL 10-13 F1	10-13	11.1	613	524-660 (22)	0.776	0.592-0.964 (0.071)
GTL 10-13 F2	10-13	11.4	620	570-725 (24)	0.757	0.589-1.063 (0.073)
GTL 15-19 A	15-19	16.8	699	620-780 (31)	1.024	0.899-1.124 (0.037)
GTL 15-19 B	15-19	16.4	750	643-842 (36)	1.345	1.139-1.628 (0.095)
GTL 20-27	20-27	22.5	731	680-824 (28)	1.287	1.073-1.521 (0.086)
GTL 22-28	22-28	25.2	763	700-900 (43)	1.710	1.541-2.002 (0.096)

Table 2-2. Coring and radiometric results for golden tilefish age groups from the east coast of Florida processed in this study. The total number of otoliths (n), age group weight and the average core weight are listed with the measured ^{210}Pb and ^{226}Ra activities for the samples (± 2 SE). Calculated activity ratios and their corresponding margin of error were used to calculate sample age and uncertainty (Table 2-3).

Age group & sample number	n	Sample Weight (g)[1]	Average core weights (g)[2]	^{210}Pb (dpm g^{-1}) ± % error[3]	^{226}Ra (dpm g^{-1}) ± % error[3]	^{210}Pb:^{226}Ra (2 SE)
GTL 5-7 M1	20	1.52521	0.07626	0.00491 ± 7.8%	0.01989 ± 15.7%[4]	0.24686 (0.04319)
GTL 5-7 M2	21	1.57928	0.07520	0.00589 ± 6.1%	0.01989 ± 15.7%[4]	0.29613 (0.04972)
GTL 5-7 F1	9	0.57104	0.06345	0.00419 ± 13.8%	0.02478 ± 18.2%[5]	0.16922 (0.03187)
GTL 5-7 F2	10	0.70606	0.07061	0.00564 ± 9.9%	0.02478 ± 18.2%[5]	0.22758 (0.03690)
GTL 10-13 M1	15	1.02671	0.06845	0.00783 ± 6.6%	0.01413 ± 22.6%[5]	0.55385 (0.09596)
GTL 10-13 M2	14	1.03334	0.07381	0.00737 ± 6.8%	0.01413 ± 22.6%[5]	0.52166 (0.09078)
GTL 10-13 F1	11	0.75149	0.06832	0.00593 ± 8.9%	0.02083 ± 13.1%[6]	0.28465 (0.04507)
GTL 10-13 F2	11	0.89425	0.08130	0.00766 ± 7.0%	0.01989 ± 15.7%[6]	0.38518 (0.06599)
GTL 15-19 A	12	0.79502	0.06625	0.00866 ± 7.1%	0.01758 ± 23.2%[6]	0.49260 (0.04396)
GTL 15-19 B	10	0.67835	0.06167	0.00862 ± 8.2%	0.01917 ± 14.1%[6]	0.44981 (0.04785)
GTL 20-27	10	0.67733	0.06773	0.00886 ± 7.8%	0.01788 ± 20.1%[6]	0.49551 (0.10672)
GTL 22-28	10	0.68193	0.06819	0.01359 ± 6.7%	0.02573 ±16.1%[6]	0.52832 (0.09215)

[1] Cleaned and dried sample weight prior to processing.

[2] Extracted otolith cores after cleaning.

[3] Calculation based on propagation of 2 SE using the delta method (Knoll, 1989) and the ICPMS analysis routine (± 2 SE).

[4] Poor radium recover from original sample led to use of an average radium activity for all sample specific measurements below 25% error.

[5] Average radium-226 for sample replicates.

[6] Sample specific radium-226.

Table 2-3. Comparison of estimated age and radiometric age for golden tilefish from the east coast of Florida processed in this study. Total sample age is given as the average age plus the time since capture for direct comparison with radiometric age. Radiometric age was calculated from the measured ^{210}Pb:^{226}Ra activity ratios and age range was based on the analytical uncertainty and error propagation (± 2 SE). Corrected age for time since capture date was calculated for direct comparison with the estimated average age of the age group.

Age group & sample number	Average age (yr)	Time since capture (yr)	Total sample age (yr)	Radiometric age (range; yr)	Corrected age (range; yr)
GTL 5-7 M1	6.4	1.3	7.7	10.6 (8.8-12.5)	9.3 (7.6-11.2)
GTL 5-7 M2	6.3	1.3	7.6	12.8 (10.6-15.1)	11.5 (9.3-13.8)
GTL 5-7 F1	6.4	1.4	7.8	7.5 (6.3-8.7)	6.1 (4.9-7.4)
GTL 5-7 F2	6.2	1.2	7.4	9.8 (8.3-11.4)	8.6 (7.1-10.1)
GTL 10-13 M1	10.6	1.4	12.0	27.4 (21.2-35.2)	26.0 (19.8-33.8)
GTL 10-13 M2	10.8	1.4	12.2	25.2 (19.6-32.0)	23.8 (18.2-30.5)
GTL 10-13 F1	11.1	1.4	12.5	12.3 (10.3-14.4)	10.9 (8.9-13.0)
GTL 10-13 F2	11.4	1.4	12.8	17.1 (13.9-20.8)	15.7 (12.4-19.4)
GTL 15-19 A	16.8	1.5	18.3	23.3 (16.5-31.9)	21.8 (15.0-30.4)
GTL 15-19 B	16.4	1.5	17.9	20.7 (16.7-25.3)	19.2 (15.0-23.8)
GTL 20-27	22.5	1.5	24.0	23.5 (17.3-31.1)	22.0 (15.9-29.7)
GTL 22-28	25.2	1.4	26.6	25.6 (19.9-32.6)	24.2 (18.5-31.2)

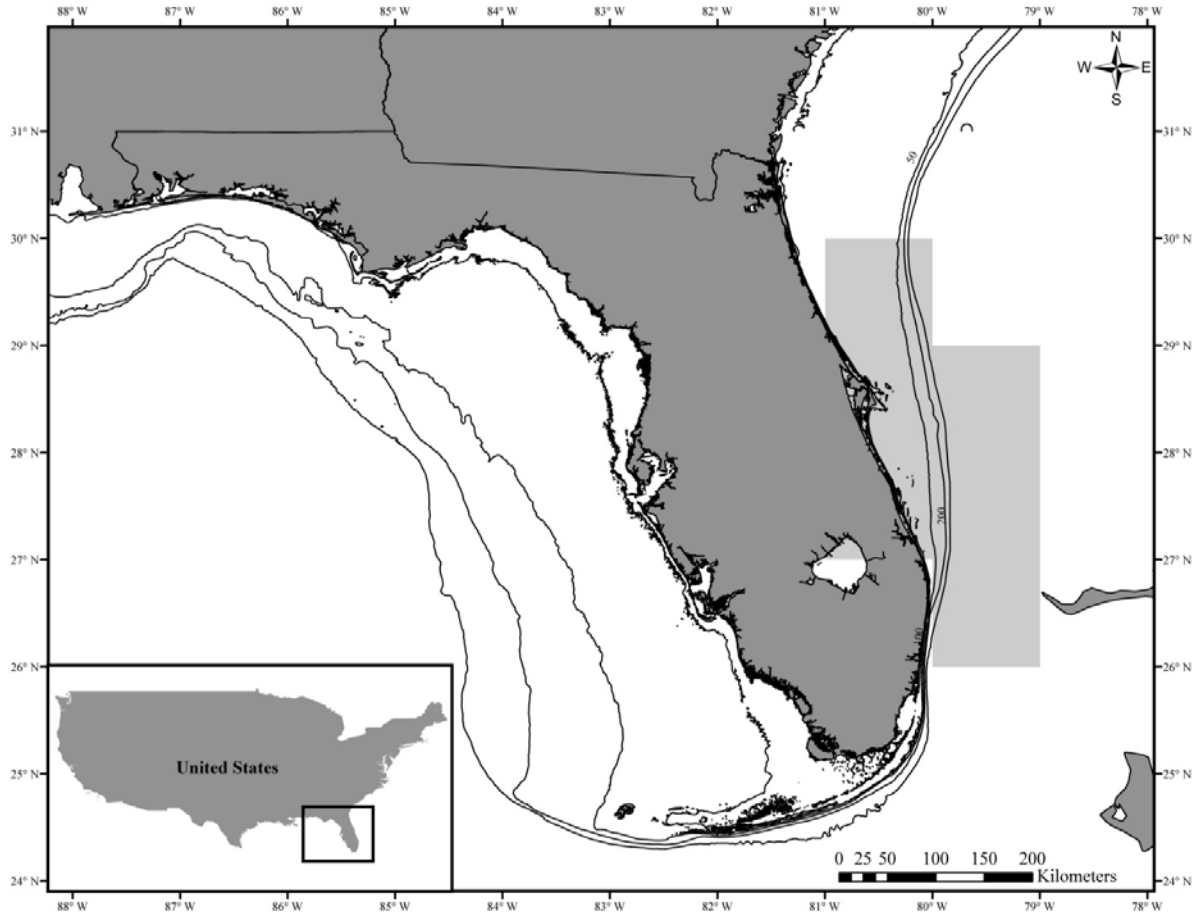
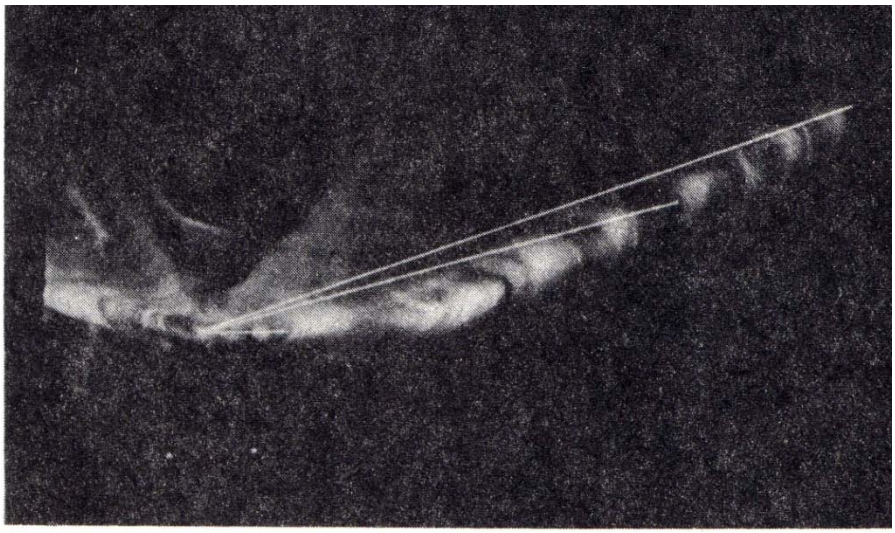


Figure 2-1. Map of collection area for golden tilefish. The shaded area indicates where golden tilefish otolith samples were collected and used in the lead-radium analyses. Golden tilefish were intercepted from commercial long-line vessels fishing along the 200 m contour off the east coast of Florida.

(**A**)



(**B**)

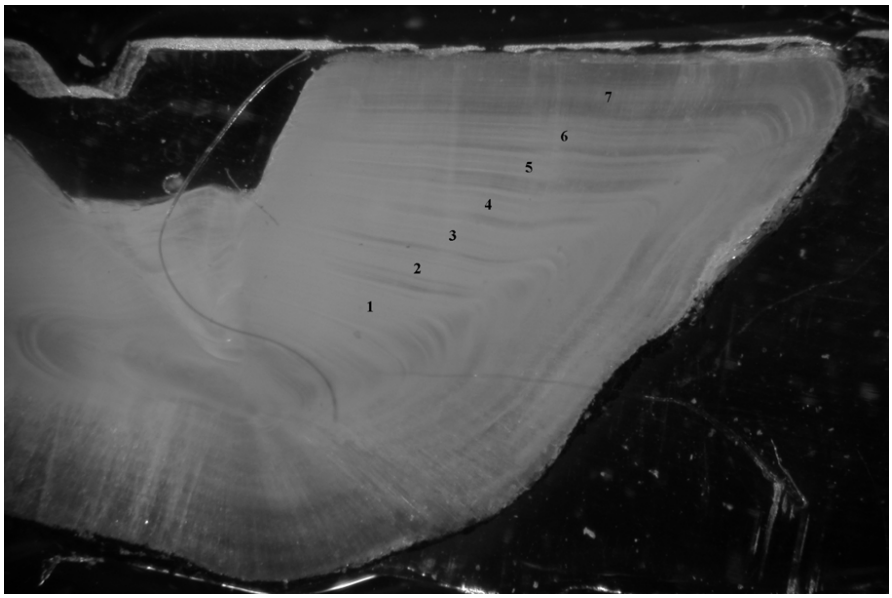


Figure 2-2. Images of thin sectioned golden tilefish sagittal otoliths from previous ageing studies. Displayed are the respective age estimations (**A**) 8 yr old male golden tilefish (77 cm fork length) (Turner et al., 1983) and (**B**) 7 yr old golden tilefish (Palmer et al., 2004). An increment consisted of one translucent and one opaque zone (reflected light, Turner et al., 1983; transmitted light, Palmer et al., 2004). Photographs copied from citations.

(**A**)

(**B**)

(**C**)

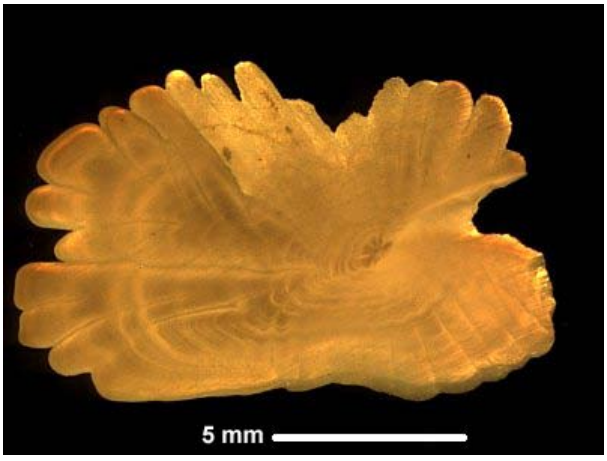


Figure 2-3. Image of the juvenile golden tilefish otolith. (**A**) whole, (**B**) thin sectioned (transmitted light), and (**C**) extracted core.

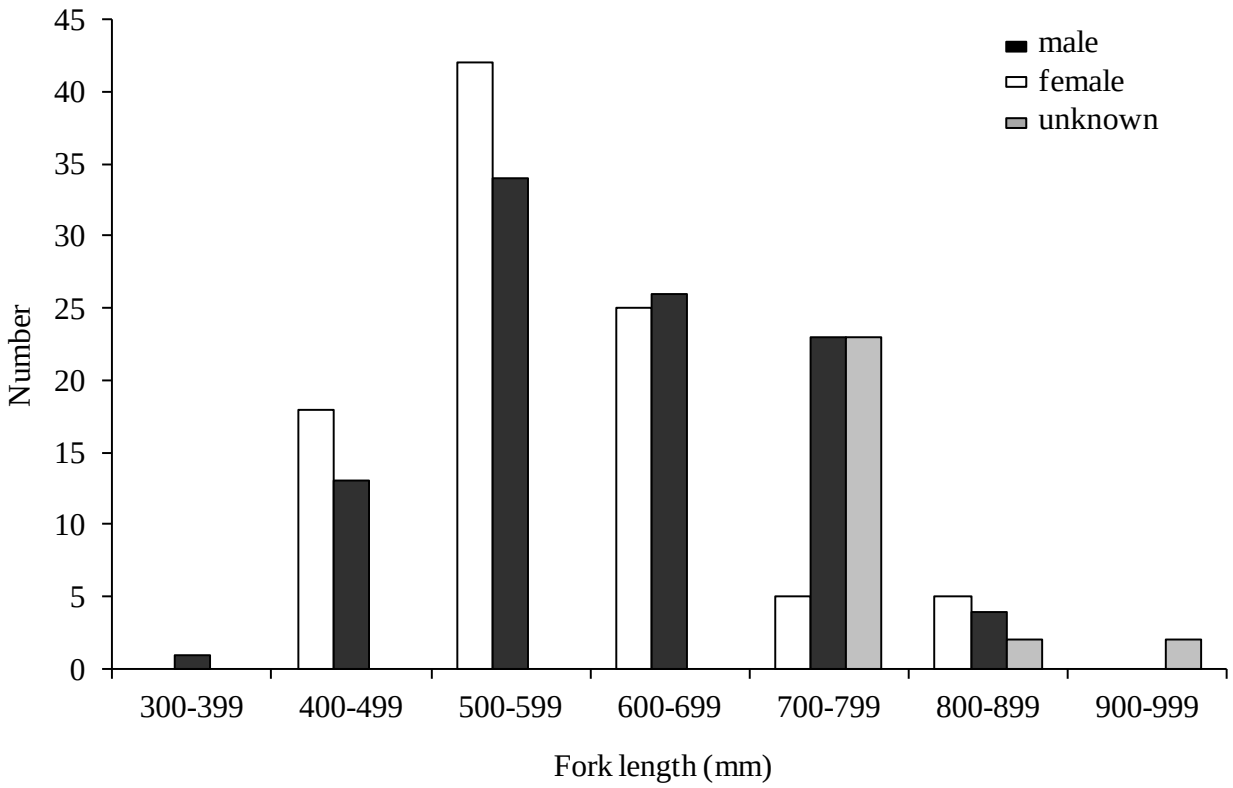


Figure 2-4. Length frequency of golden tilefish. Fish were collected from commercial long-line fishery in 2007 from the east coast of Florida (male, black bars; female, white bars; unknown sex, gray bars).

(**A**)

(**B**)

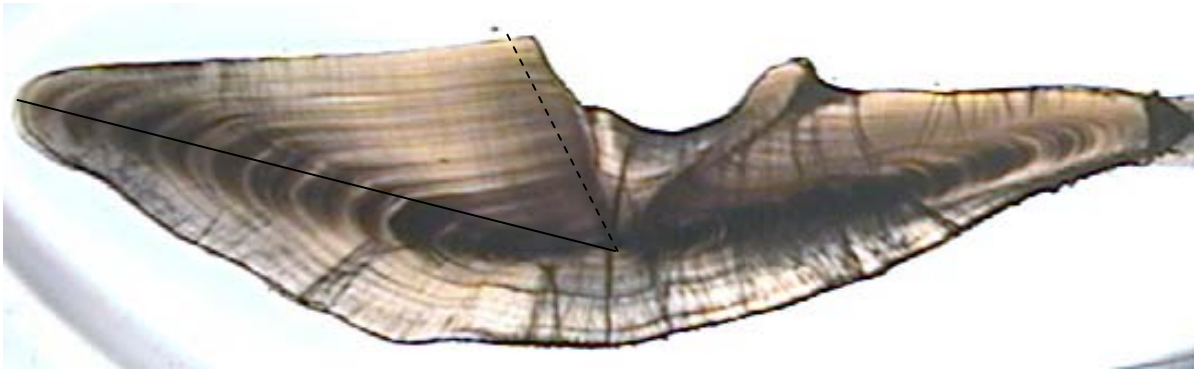


Figure 2-5. Thin-sectioned sagittal otoliths of golden tilefish. Otolith sections were viewed with transmitted light (15x) (**A**) female (age 26 yrs, 734 mm FL) and (**B**) male (age 10 yrs, 758 mm FL). Traditional age was determined by interpreting opaque increments along ventral axis (solid lines) and along ventral sulcus (dashed lines).

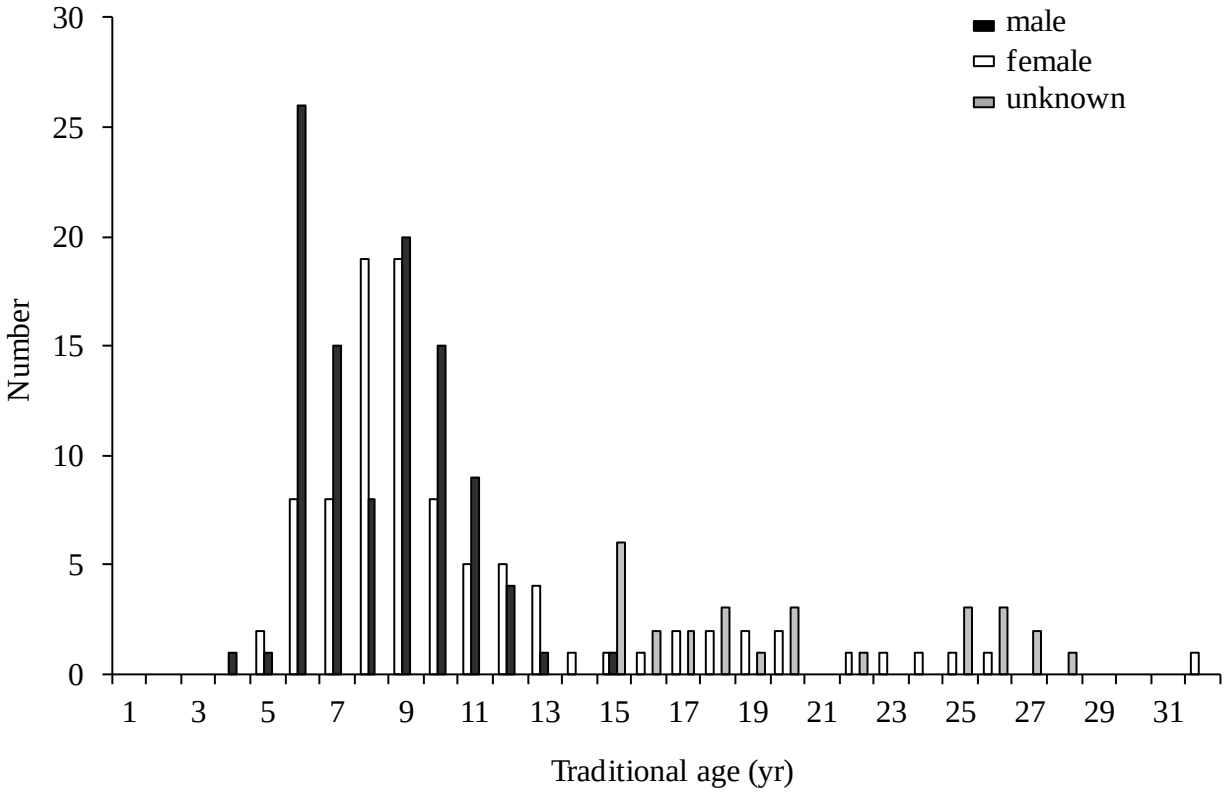


Figure 2-6. Age frequency of golden tilefish. Fish were collected from commercial long-line fishery in 2007 from the east coast of Florida. Traditional age estimation (counting otolith growth zones) for male (black bars), female (white bars) and unknown sex (gray bars).

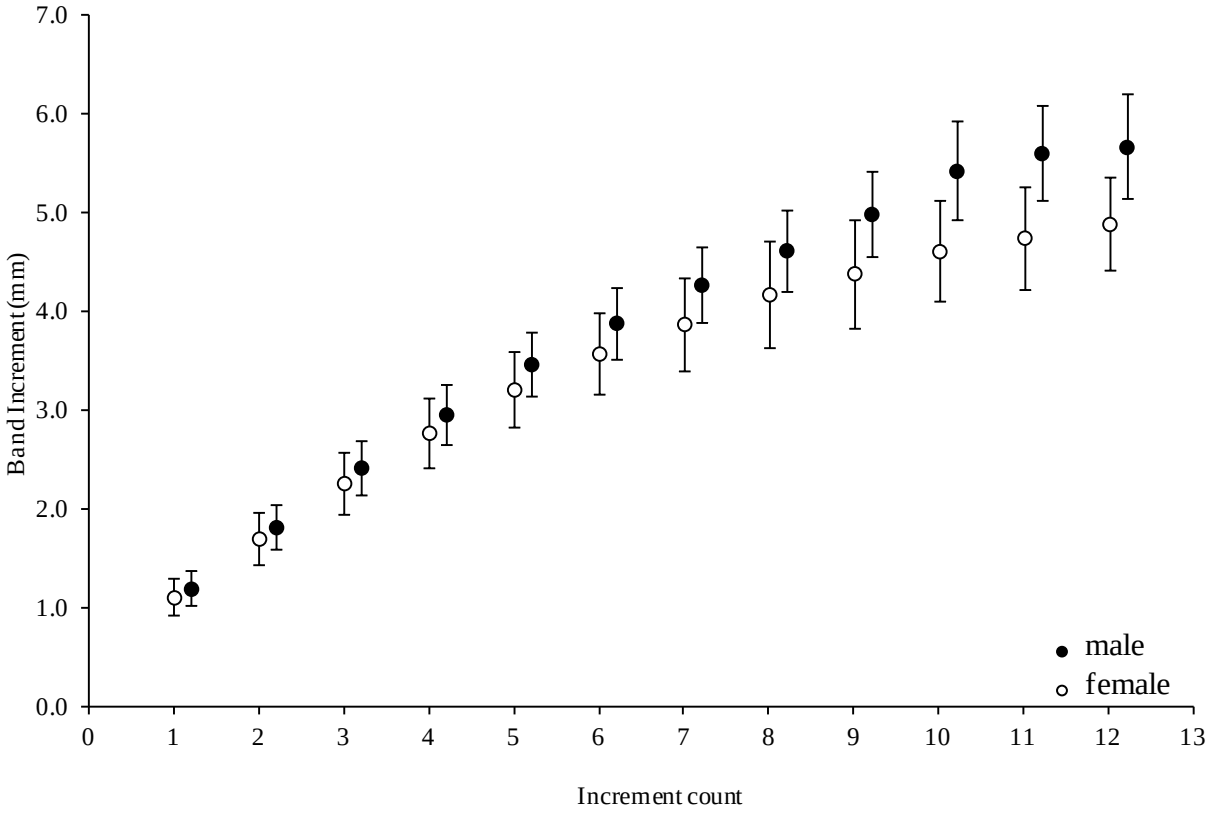


Figure 2-7 Otolith increment counts and band increment measurements by gender for golden tilefish from the east coast of Florida. Band increments were measured from the core to the mid-line of the increment for males (solid black circles) and females (solid white circles) and reported as mean ± standard deviation.

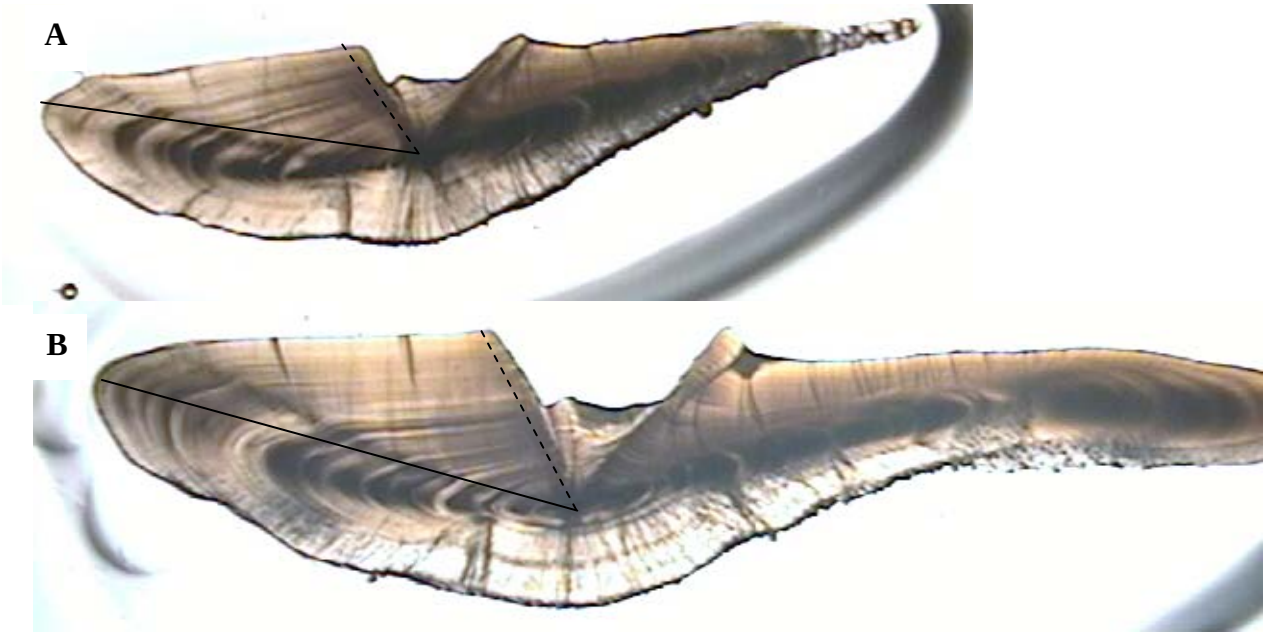


Figure 2-8. Examples of thin-sectioned male golden tilefish sagittal otoliths. (**A**) age 6 yr, 530 mm FL and (**B**) age 11 yr, 810 mm FL depicting changes in growth increment deposition possibly due to the transition of gender. Otolith sections were viewed using a stereo microscope with transmitted light (15x). Traditional age was determined by interpreting opaque increments along ventral axis (solid lines) and along ventral sulcus (dashed lines).

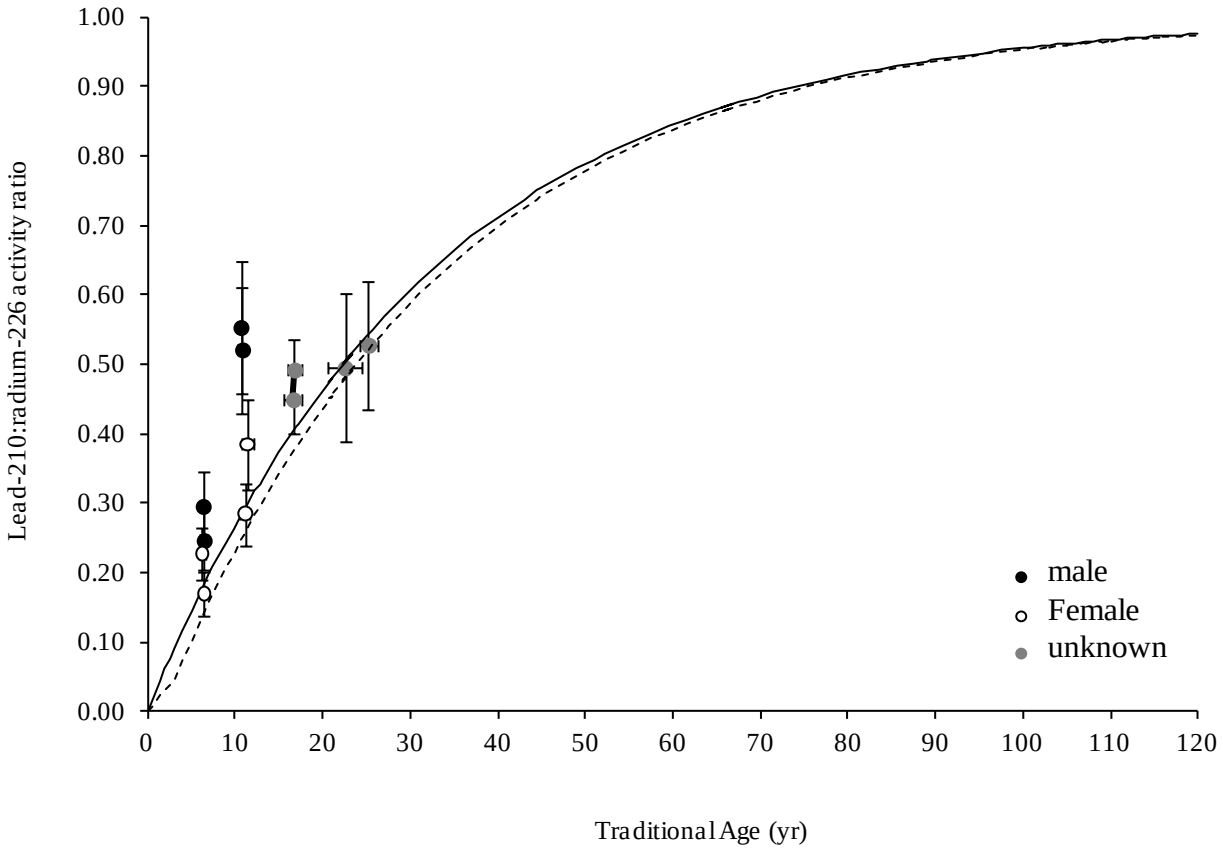


Figure 2-9. Measured ^{210}Pb:^{226}Ra ratios with respect to average traditional age for golden tilefish samples processed in this study. Males (solid black circles), females (solid white circles) and unknown sex (solid gray circles), plotted with the expected ^{210}Pb:^{226}R ingrowth curve (solid line) and 2 year ingrowth compensation (dotted line). Horizontal error bars represent 2 standard errors (SE) around the mean of the sample growth-zone age. The vertical error bars represent the analytical uncertainty associated with measuring the ^{210}Pb:^{226}Ra ratio (2 SE).

CHAPTER 3
EVIDENCE FOR HERMAPHRODITISM IN GOLDEN TILEFISH (*LOPHOLATILUS CHAMAELEONTICEPS*)

Introduction

Teleosts can be described as being gonochoristic or hermaphroditic (Sadovy de Mitcheson and Liu, 2008). Gonochores are individuals that remain the same sex their entire lives and hermaphrodites spend some proportion of their lives as either sex. Hermaphrodites can be further described as either simultaneous (contain both functional and mature ovarian and testicular tissue) or sequential. There are two types of sequential hermaphrodites, protogynous (functional female tissue replaced by functional male tissue) or protandrous (functional male tissue replaced by functional female tissue). All hermaphrodites can also be described as intersexual, having both male and female germinal tissue (Atz, 1964). However, just describing the presence of non-functional (opposite) sex tissue within an individual's gonad does not necessarily mean that individual is a functional hermaphrodite. It is necessary to prove, histologically, that the individual functioned as both sexes during its lifetime to determine a hermaphroditic reproductive strategy (Sadovy de Mitcheson and Liu, 2008; Lowerre-Barbieri et al., 2011).

The focus of this study is the golden tilefish, *Lopholatilus chamaeleonticeps* (Goode and Bean, 1880). Tilefishes are classified into two families (Branchiostegidae, Malacanthidae) and five genera (*Caulolatilus, Lopholatilus, Branchiostegus, Malacanthus, Hoplolatilus*) (Dooley, 1978). The tilefish families, like most teleosts (Atz, 1964), exhibit a large diversity of reproductive strategies. Tilefish families are described as being gonochoristic (*Caulolatilus priceps*; Elorduy-Garay and Ramirez-Luna, 1994) to having intersexual gonads (*Caulolatilus microps*, Ross and Merriner, 1983; *Branchiostegus japonicas*, Watanabe & Suzuki, 1996) and

protogynous hermaphrodites with polygyny mating systems (*Malacanthus plumieri*, Baird, 1988).

Previous reproductive studies have classified golden tilefish as gonochoristic but these studies also detected a small percentage of male gonads contained previtellogenic oocytes (1%, Erickson and Grossman, 1986; <0.1%, Grimes et al., 1988; < 0.01 %, Palmer et al., 2004). The presence of early developed oocytes in testes is not uncommon in fish with a gonochoristic reproductive strategy, especially if the species exhibits a bisexual (non-functioning) juvenile stage (Sadovy and Shapiro, 1987). Furthermore, golden tilefish male gonads did not contain oocytes in a more advanced stage (or atretic, degenerating oocytes) nor did male gonads contain an ovarian lumen, characteristics that suggest a male gonad originated from a female gonad (Erickson and Grossman, 1986; Grimes et al., 1988; Palmer et al., 2004).

There are several criteria to successfully prove a protogynous hermaphroditic reproductive strategy (Sadovy and Shapiro, 1987). These criteria rely on the histological analysis of gonadal tissue from functional males and females. Three criteria are specific to functional males: 1) a lumen (or membrane-lined cavity) remains unused in testes, 2) late stage (cortical alveolar, vitellogenic, hydrated) and atretic (or degenerating) oocytes are present in testes, and 3) sperm sinuses are present along the testes' wall. The final criterion is the identification of gonads in a transitional stage, which is a gonad containing degenerative tissue of one sex with developing functional tissue of the opposite sex. Hermaphroditism is difficult to prove and can be misdiagnosed. Therefore, it is necessary to not only follow the criteria above but also to collect fish from a large range of sizes and from throughout the year (Sadovy and Sharpiro, 1987; Sadovy and Domeier, 2005).

My objectives of this chapter are: 1) describe the reproductive phases by sex, 2) determine the reproductive seasonality, 3) estimate the age and size at maturity, and 4) apply the criteria described by Sadovy and Shapiro (1987) to classify the reproductive strategy of golden tilefish collected along the east coast of Florida and throughout the northern Gulf of Mexico. This is information necessary in the development of age based stock assessment models (as discussed in chapter 4) to make informed fishery management regulations (SEDAR, 2011a). Misidentifying the reproductive strategy of a species can be troublesome, especially if the measure of spawning stock biomass does not consider sperm limitation with the removal of the largest, typically male fish from the population (Alonzo and Mangel, 2004).

Materials and Methods

Sample Collection

Golden tilefish were collected by NOAA Fisheries Service, Southeast Fisheries Science Center (SEFSC) sampling programs throughout the northern Gulf of Mexico and east coast of Florida (2000-2009). Since most golden tilefish landed by the commercial fishery are thoroughly gutted at-sea, Trip Interview Program port agents made special requests to willing commercial captains to collect whole fish to obtain gonad tissue. At-sea observers on-board commercial long-line vessels also provided biological samples (otoliths and gonads). Two fishery independent surveys provided additional golden tilefish biological samples (NOAA/SEFSC Pascagoula, MS; Cooperative Research Project 08CRP009). Both of these long-line surveys used a standardized sampling design with sets chosen randomly based on depth (see Grace et al., 2004 for complete description).

Otolith Processing and Assigning Age

The sagittal otolith was used as the primary ageing structure (see chapter 2). Sagittal otoliths were sectioned using a Hillquist thin sectioning saw, and sections were viewed using a

stereomicroscope with reflected light. The traditional age estimation criterions, as described in chapter 2, were applied to the otoliths associated with fish collected with gonads. Two readers (myself, the primary reader and a secondary reader) interpreted the otoliths and indices of precision (Average Percent Error, Percent Agreement, Coefficient of Variation) were calculated (Campana 2001). All fish were assigned an annual age equal to the annulus count by convention.

Gonad Processing

Golden tilefish gonads were weighed to the nearest 0.1 g and fixed in 10% neutral buffered formalin for a minimum of two weeks. Preserved gonads were subsampled along the posterior-anterior axes of the gonad and a small subsample (1 cm^3) was removed and placed in a cassette for histological processing. Histological processing of golden tilefish gonads were prepared by the Louisiana State University School of Veterinary Medicine, Histopathology Laboratory in Baton Rouge, LA. Tissues were embedded in paraffin, sectioned to a thickness of 4-6 μm, mounted on glass slides and stained with hematoxylin-1 and eosin-Y following standard histological procedures.

Gonad Development

Golden tilefish histological slides were viewed using a compound microscope at 40 to 400x magnification to determine the functional sex, reproductive phase, and the reproductive strategy (gonochoristic or hermaphroditic)[1]. Functional sex is defined by the presence and prevalence of leading (most advanced) gamete stage identified in the gonad, following Sadovy de Mitcheson and Liu 2008 (Table 3-1 and 3-2). Male and female gonads were classified as immature or mature given the dominate stage of spermatogenesis or oocyte development,

[1] Histological slides were interpreted by H. Lyon (NOAA Fisheries Service, Panama City, FL), given her expertise in interpreting both gonochoristic and hermaphroditic gonads.

respectively (Table 3-3 and 3-4). The structural and germinal features of male and female gonads were described to meet the criteria, as described by Sadovy and Shapiro (1987), to determine whether or not golden tilefish exhibit characteristics of hermaphrodites.

Female gonads were staged using oocyte developmental characteristics (Wallace and Selman, 1981; Hunter and Macewicz, 1985; Tyler and Sumpter, 1996; McMillan, 2007) and assigned to a phase of reproduction (Table 3-4) based on the leading gamete stage, indicators of prior spawning and short-term atresia. Evidence of prior spawning is described by the number of brown bodies (macrophages), presence of old hydrated oocytes, stage of atresia, the condition of the muscle bundles, presence of connective tissue, appearance of lamellae in the gonad tissue, and thickness of gonad wall. Golden tilefish females with developing, active, spawning or resting gonads were considered sexually mature. Females that possessed cortical alveolar oocytes were considered mature only if indicators of prior spawning were present (Rideout et al., 2000; Rhodes and Sadovy, 2002). As with females, male maturation was based on the dominant gamete stage. Golden tilefish males with all stages of spermatogenesis were considered sexually mature (Table 3-3). Male and female reproductive phases were based on standardized terminology used in teleost reproductive literature (Brown-Peterson et al., 2011).

The criteria described by Sadovy and Shapiro (1987) were used to classify the reproductive strategy (gonochoristic, hermaphroditic) of golden tilefish. These criteria are based on the configuration of germinal tissue within functional male and female gonads: 1) determine the existence of a cavity within the germinal tissue and if the cavity is membrane-lined in both male and female gonads, 2) determine the existence of transitional individuals where gonads contain degenerative tissue of one sex and developing tissue of the opposite sex, 3) describe the present or absence and stage of development of non-functional (opposite) sex tissue and classify the

placement of the non-functional tissue (floater, embedded, attached, in duct, or a combination of placements), and 4) describe the presence or absence of sperm sinuses and their location within male germinal tissue.

Estimates of Maturity

Size and age at maturity were calculated using a logistic regression model: $Y_i = (\exp (a + (b * X_i)/(1 + \exp (a + (b * X_i))$, where Y_i = proportion mature at length or age (X_i), a = intercept, and b = slope of the logistic regression. The logistic regression model was fit to binomial maturity data (immature=0, mature=1) and was used to determine the size and age at which 50% of females or males in the population reached sexual maturity. The slope and intercept of the logistic regression were determined using a linear model with the binomial family and logistic option in R (R Development Core Team, 2011).

Spawning Seasonality

The timing of peak spawning was assigned using gonad-somatic indices (GSI) for males and females using the following formula: GSI = (GW/(TW-GW)) * 100; where GW = total gonad weight (g) and TW = total fish weight (g). Monthly mean GSI values were calculated to estimate seasonal reproductive patterns.

Other Criteria for Hermaphroditism

There are two population level life history traits which support the occurrence of hermaphroditism (Sadovy and Shapiro, 1987). Male and female length-at-age data was compared to determine if growth rates differed between the sexes and if one sex dominated the larger and subsequent older age classes. An unpaired Student's t-test with unequal variances was used to determine if mean length-at-age differed significantly between the sexes at each age. The comparison of size at age data was restricted to age classes with sample sizes ≥ 5. The sex ratio of golden tilefish was also calculated to determine if the sex ratio skewed from 1:1.

Breeding Strategy

Previous research documented the importance of the predorsal adipose flap in defining alternative breeding strategies for golden tilefish males (Grimes et al., 1988). The height of the adipose flap has also been used to classify golden tilefish as male or female. Therefore, the height of the adipose flap was measured from the base of the head to the maximum vertical height of the adipose flap. The relationship between the height of the adipose flap by gender and maturity stage was evaluated.

Results

Sample Collection

A total of 1,859 golden tilefish were provided by multiple NOAA Fisheries Service sampling programs throughout the Gulf of Mexico and east coast of Florida (Table 3-5). A majority of samples were collected in 2007-2009 (east coast of Florida, 93%; Gulf of Mexico, 73%). A decrease in the number of third and fourth quarter annual samples from the east coast of Florida occurred due to regional fishery closures. The golden tilefish fishery in the Gulf of Mexico also experienced seasonal time closures, but sampling through fishery independent surveys provided continuous monthly samples.

Otolith Processing and Assigning Age

Golden tilefish thin sectioned otoliths are difficult to interpret given several different shapes of otolith sections and diverse patterns of growth deposition (see chapter 2). Given the difficulty in determining accurate age estimates, I had the assistance of a secondary reader (D. Berrane, NOAA Fisheries Service, Beaufort, NC) to quantify the imprecision in age estimation. Indices of precision were calculated from those otoliths read by both readers (n = 200) with an average percent error of 7%, with percent agreement of 32% increasing to 95% ± 3 years.

Gonad Processing

In a majority (66%) of males the entire gonad was blocked, due to the small size of male gonads. Female gonads were much larger and were subsampled before blocking, germinal tissue was removed from the posterior portion (53%), both the posterior and anterior portions (14%), and in 12% of females the entire gonad was blocked.

Gonad Development

Of the 1825 gonads histologically classified (98% of gonads collected), 773 were functional females and 1052 were functional males. Although sampling was extensive and a large range of lengths of golden tilefish were collected (280 – 1040 mm FL), only 16 (12 males, 4 females) golden tilefish were classified as immature (Table 3-6). The immature males were collected in August, September, and December, with mature, spawning males capable of spawning collected in most months (Fig. 3-1A). The majority of mature female gonads were in spawning capable reproductive stage from January – June (Fig. 3-1B). In ten gonad samples maturity stage could not be determined due to inconsistencies in gonad preservation. Golden tilefish gonads contained both structural and germinal features to support hermaphroditism.

Sexual Maturity

It was difficult to determine the difference between an immature male and resting male during non-spawning season. Therefore, the classification of maturity in males was subjective to the interpretation of the stages of spermatogenesis. Fish with undetermined maturity stage were not used in this analysis (male, n = 4; female, n = 6). Immature males were evident from a larger distribution of lengths and ages compared to immature females (Table 3-6). Male golden tilefish were estimated to reach maturity at a younger age (male, < 1 yr; female, 2.5 yr) and smaller length (male, 150 mm FL; female 331 mm FL) than females (Table 3-7, Fig. 3-2). Only four

immature females were collected and these fish were less than 400 mm in length and six years of age. The smallest mature female was 338 mm FL and age 3 years.

Histological Evidence for Hermaphroditism

Both functional male and functional female gonads contained a membrane lined cavity (Fig. 3-3A): criterion 1) in approximately 15% of the males this cavity was qualified as originating from ovarian lumen and remained unused for sperm transportation (Fig. 3-3, B and C). Non-functional (opposite) sex tissue was present in both functional males and females: criterion 2) 26% of the functional females had tubules containing all stages of spermatogenesis and 71% of the functional males had multiple stages of oocyte development. The relative placement of non-functional tissue was a combination of locations: functional females had self-contained tubules of male tissue (consisting of several stages of spermatogenesis) scattered throughout the lumen (Fig. 3-4) and functional males contained oocytes attached, floating, embedded, in the ducts or a combination of locations within the germinal tissue (Fig. 3-5, A, B, C, and D). Functional male gonads contained oocytes of all stages in testes; criterion 3) primary growth was the dominate stage (88%), followed by vitellogenic (29%), cortical alveolar (28%), late hydrated (6%), and hydrated (4%) (Fig. 3-6). And the final criterion, male sperm sinuses were present and located within the gonad wall (Fig. 3-7).

Spawning Seasonality

Gonad-somatic index (GSI) suggests golden tilefish have a prolonged spawning season. Golden tilefish GSI values were elevated from January through June with the peak in April for both males and females (Fig. 3-8). Reproductive seasonality did not differ between the fish collected off the east coast of Florida and the northern Gulf of Mexico, therefore data was combined.

Other Criteria for Hermaphroditism

Golden tilefish exhibited sexually dimorphic growth. Male golden tilefish were more prevalent in the larger size classes (Fig. 3-9A). However, male and female golden tilefish occurred within the same range of ages (age 3 – 33 yrs, Fig. 3-9B). Males were significantly larger in all but one (age 4) of the age classes with sample sizes ≥ 5 (age 4 – 16, Fig. 3-9C). Finally, the overall sex ratio of golden tilefish was slightly skewed (1.3:1.0) with males dominating the population.

Breeding Strategy

Measurements of the height of the adipose flap proved to be sexual dimorphic. Large mature males had larger adipose flaps than females, especially for fish > 500 mm FL (Fig. 3-10). Most females' adipose flaps measured < 10 mm in height. It was difficult to distinguish an immature male and immature or mature female given just the height of the adipose flap.

Discussion

Through detailed histological photomicrographs I documented the simultaneous occurrence of mature testicular and ovarian tissues in golden tilefish from the U.S. South Atlantic waters off the east coast of Florida and the northern Gulf of Mexico. This is strong evidence that golden tilefish are hermaphroditic, not gonochoristic (Sadovy de Mitcheson and Liu, 2008). Golden tilefish gonads qualify as being protogynous hermaphrodites by satisfying each of the criteria of Sadovy and Shapiro (1987); male gonads contained a membrane lined cavity, originating from ovarian lumen, which remains unused for sperm transportation and female gonads also contained a similar membrane lined lumen, male gonads contained follicles of all stages in testes and sperm sinuses were present within the testes' wall.

The most difficult criterion to satisfy is identifying fish undergoing transition since not all sex changing fish exhibit the same structural changes in germinal tissue when undergoing

transition (Sadovy and Shapiro, 1987; Sadovy de Mitcheson and Liu, 2008). For example, in the Family Serranidae there are three types of configurations of the germinal tissue during transition: *Serranus*, has complete separation of ovarian and testicular tissue by connective tissue; *Ryiticus-Anthias*, has testicular tissue remains isolated along the ovarian wall with no connective tissue, and *Epinephelus*, has mixed ovarian and testicular tissue (Smith, 1965). In order to apply these configurations to other sex changing fish, Sadovy and Shapiro (1987) relabeled these as delimited, unlimited, and mixed. Given these definitions, I have classified golden tilefish with a mixed configuration of germinal tissue since the non-functional sex tissue was located throughout the gonad and was adjacent to functional sex tissue. In functional males, non-functional female oocytes were located in a variety of placements within the male germinal tissue (attached, embedded, floating, and in the ducts) and in functional females, non-functional male tubules were found scattered within the female germinal tissue and were self-contained within their own germinal epithelium. In comparison, the germinal configuration of golden tilefish females undergoing transition to male were different than that of protogynous hermaphrodites *Epinephelus morio* (red grouper; Moe, 1969) and *Mycteroperca phenax* (scamp; Lombardi-Carlson et al., 2012), given the non-proliferation (in terms of the amount) of male tissue throughout the female gonad. In both functional males and females golden tilefish, the non-functional (opposite sex) tissue amounted to only a small percentage (<1%) of the entire gonad.

A majority (49%) of the golden tilefish sampled had non-functional tissue. The functional males with newly developed oocytes (primary growth, cortical alveolar, and vitellogenic) were considered to have transitioned from mature, active females that had not recently spawned, whereas males with early or late hydrated oocytes transitioned from recently

spawned or spent females. These latter males would be considered 'truly' transitional fish since these functional male gonads contained degenerating female oocytes and were undergoing proliferating spermatogenesis (Shapiro and Sadovy, 1987). For functional females with male tubules, these females were considered to be preparing for sex change. Similar structural features have been documented in protogynous gobies (*Eviota* sp.; Cole, 1990) and coral sea trout (*Plectropomus* sp.; Adams, 2003), where testicular tissue remains dormant in functional females until sex change. Functional males and functional females with opposite sex tissue were collected mainly during the spawning season (males, 69%; females, 85%), alluding to a very highly social mating behavior (as first proposed by Grimes et al., 1988). Golden tilefish have likely minimized the cost of changing sex and increased their overall reproductive fitness by minimizing the time not reproducing given the occurrence of dormant testicular tissue in females and transitional fish during the spawning season (Hoffman et al., 1985; Adams, 2003).

It is possible that I have misconstrued fish in transition with golden tilefish exhibiting a juvenile bisexual phase. This phase is defined in terms of gonad morphology and not gonad function (Sadovy and Domeier, 2005). Typically a juvenile bisexual phase is temporary and restricted to a certain size, age, or gamete stage (Sadovy de Mitcheson and Liu, 2008), but golden tilefish males and females with opposite sex tissue were identified from the same distribution of lengths. In addition, there were not any differences in the lengths of functional male golden tilefish characterized as having primary oocytes to more developed (vitellogenic, hydrated) oocytes within the testes. Therefore, it is unlikely that golden tilefish exhibit a juvenile, bisexual phase.

After thorough examination of male histological slides, evidence supports that male golden tilefish have a diandric mode of maturation. Males with a diandric mode of maturation are

described as some males deriving from an immature phase (primary) and other males transitioning from females (secondary). This was evident given the collection of small, immature males, as well as the occurrence of remnant atretic oocytes in male testes. This greater flexibility in male development has been attributed to variations in social and environmental conditions (Adams, 2003). Further evidence to support diandry is that males were observed at similar ages as the female age at first maturity and there was a complete overlap of ages for males and females (Fennessy and Sadovy, 2002). Typically, gonadal investment differs between primary males (those derived from immature males) and secondary males (those derived from females) (Choat et al., 1996; Drillings and Grober, 2005) but there were not any difference in gonado-somatic index between primary and secondary males.

Previous reproductive research on golden tilefish also reported having two classes of males (spawning and non-spawning, Grimes et al., 1988). They based their conclusions on the differentiation of males by a secondary sexual characteristic (height of dorsal adipose flap), immature males at smaller sizes, and the maintenance of reproductive territories by males in habitat limited environments. Golden tilefish from the Gulf of Mexico and along the east coast of Florida have a secondary sexual characteristic that is sexually dimorphic, with large mature males having larger adipose flaps and females having smaller adipose flaps. However, the average height of the adipose flap did not vary between male types. Grimes et al. 1988 concluded that the larger percentage of small, immature males represented non-spawning males but this reproductive phase was based only on visual inspection of male gonads. In addition, it is not clear if these males were sampled during the spawning season, as it is difficult to distinguish immature from resting, mature males during non-spawning seasons. Golden tilefish do exist in a very specific habitat type of soft, but malleable sediment along the continental shelf in water

depths 80-400 m (Freeman and Turner, 1977), inhabit burrows (Able et al., 1982), and reside in a specific thermal cline (9-14^{o}C; Grimes et al., 1986). Previous submersible observations and still camera images of golden tilefish in and around their burrows have revealed great insight on the behavior of these elusive fish (Able et al., 1982; Grimes et al., 1986; Jones et al., 1989; Able et al., 1993) but until a combination of visual observations of tilefish in their natural environment along with histological confirmation of sex and maturity of those observed individuals can be conducted, any conclusions on the mating behavior and morphological development of males and females is speculative.

Theoretically, from a population ecological perspective, it can be advantageous to be hermaphroditic (Tomlinson, 1966). There is a higher chance of successful breeding if individuals can change sex when populations are at low densities. In addition, there is a 50/50 chance an individual will come into contact with the opposite sex especially if individuals exist in relative isolation given a limited habitat and are less mobile. Golden tilefish do exist in relative isolation within burrows and densities may fluctuate given exploitation rates and seasonal changes in water temperature, making it beneficial to be able to change sex.

Reproductive strategy can vary geographically, especially if sexual development is influenced by social factors and habitat availability (e.g., Teleost families: Pomacentridae [damselfishes]; Sadovy de Mitcheson and Liu, 2008). The anemonefish (*Amphiprion clarkii*) relies heavily on sea anemone for shelter and spawning and the distribution of anemones dictates the anemonefish reproductive strategy and mating behavior (Moyer, 1980; Ochi, 1989). In tropical areas with low density of sea anemones, female anemonefish are more likely to change sex (functional hermaphrodites) when the larger male anemonefish are removed (Moyer, 1980) but sex change is less likely (functional gonochores) in temperature areas with high densities of

anemone and subsequent higher densities of male anemonefish (Ochi, 1989). Similarly, in obligate coral dwelling damselfishes (*Dascyllus aruanus*) the area coverage and distance between coral colonies governs the need to change sex (Cole, 2002; Asoh, 2003). Therefore, it is plausible that the reproductive strategy of golden tilefish varies along its distribution given the availability of suitable habitat (see description above).

Teleosts can display a large diversity of reproductive strategies from remaining the same sex their entire lifetime (gonochores) to changing sex during their lifetime (hermaphrodites) to some fish gonads containing non-functional, opposite sex tissue (intersex) (Atz, 1964). It is not uncommon for gonochoristic teleosts to contain immature, oocyte stage (primary oocytes) in a male gonads (Lowerre-Barbieri et al., 2011), but it is uncommon for male gonads of a gonochoristic teleosts to contain mature, oocyte stages (cortical alveolar, vitellogenic, early hydrated, late hydrated) as detected in golden tilefish. Simultaneous hermaphroditic teleosts are characterized by a 1:1 sex ratio, an undelimited germinal tissue configuration (no mixing of opposite sex tissue), and both male and female germinal tissues are clearly functional (Sadovy and Shapiro, 1987). Functional male and female golden tilefish did contain opposite sex germinal tissue but this tissue amount to < 1% of the entire gonad and was assumed non-functional; therefore, lessening the possibility of simultaneous hermaphroditism. Intersex is mostly prevalent in freshwater teleosts and is typically associated with a hormonal imbalance in male teleosts due to endocrine disruptors in the environment (Hinck et al., 2009). Unlike the male gonads of golden tilefish, intersex gonads contain only early staged oocytes (previtellogenic and vitellogenic) and compose of a small proportion (< 3%) of the population (Bateman et al., 2004; Hinck et al., 2009). Protandrous hermaphroditism is difficult to prove since male tissue seldom remains in mature, female gonads. The best evidence for protandry is

the occurrence of degenerative male tissue in a gonad with developing female tissue (Sadovy and Shapiro, 1987). Female golden tilefish gonads did not contain degenerative male tissue but instead tubules containing several stages of spermatogenesis. Therefore, based on histological evidence supporting each of the above criteria and population level life history, golden tilefish from U.S. South Atlantic waters off the east coast of Florida and the northern Gulf of Mexico are most likely sequential protogynous hermaphrodites.

Previous literature on the reproductive strategy of golden tilefish concluded this fish is gonochoristic (Erickson and Grossman, 1986; Grimes et al., 1988; Palmer et al., 2004), not hermaphroditic as I have concluded. There are difficulties to scientifically prove the factors contributing to the occurrence of hermaphroditism in golden tilefish along the east coast of Florida and throughout the northern Gulf of Mexico. The best evidence could be obtained through controlled scientific experiments on golden tilefish in their natural environment using underwater remotely operated vehicles or manned submersibles. These experiments could help identify the triggering factors, environmental or social conditions, changes in densities, controls by the central nervous system or variations in hormones (Baroiller et al., 1999) or mating systems (St. Mary, 2000) that are contributing to this alternative reproductive strategy.

Conclusion

Given the premise that fishing is size selective (removing the larger, older fish), the reproductive strategy (gonochoristic or hermaphroditic) of the species can influence the response to overfishing (Bannerot et al., 1987; Armsworth, 2001). As in the case in protogynous hermaphrodites, the larger, older fish are predominately males and these populations are more likely to feel the effects of size-selective fishing through sperm limitation, shifts in behavior and skewed sex ratios (Bannerot et al., 1987; Armsworth, 2001; Alonzo and Mangel, 2004; Heppell et al., 2006). Since it is difficult to observe how a population compensates for sperm limitations,

especially for deep water fish, stock assessment models can attempt to incorporate the uncertainty of how a fish with a protogynous hermaphroditic reproductive strategy responds to the impact of fishing. In the next chapter, I explored how understanding and modeling the protogynous hermaphroditic life history can influence stock assessments, and compared those results to a simpler model that ignores hermaphroditism.

Table 3-1. Descriptions and photomicrographs of histological sections of male golden tilefish leading gamete stages. Hematoxylin-1 and eosin-Y stain, magnifications and scales on photomicrographs.

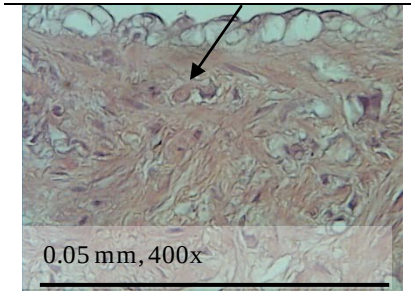
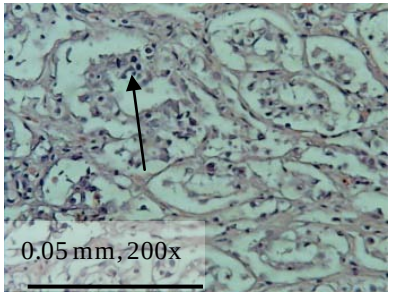
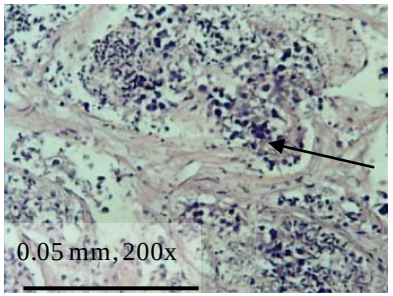
Photomicrographs	Leading Gamete Stage	Description of male leading gamete stage
	Spermatogonium (SG)	Stained light purple, fuzzy in appearance, large in diameter but not located in spermatocysts.
	Primary Spermatocyte (PS)	Darkly stained, mostly non-spherical in shape, relatively large diameter and present in spermatocysts.
	Secondary Spermatocyte (SS)	Cells more spherical and darker than primary spermatocytes, smaller in diameter and present in spermatocysts.

Table 3-1. Continued

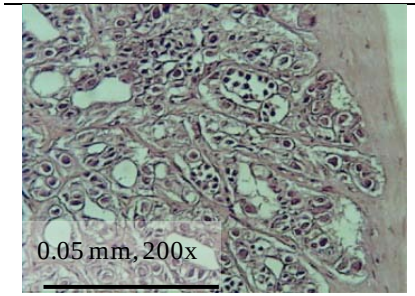
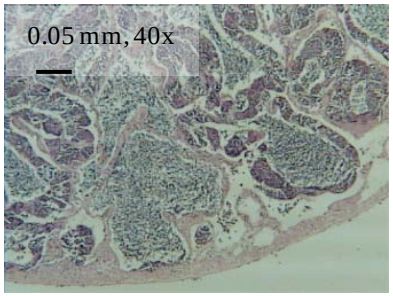
Photomicrographs	Leading Gamete Stage	Description of male leading gamete stage
	Spermatid (ST)	Black staining, spherical and smaller than previous stages, in spermatocysts. Tails not present.
	Spermatozoa (SZ)	Black staining, pink tails present, spherical and similar in size to spermatids. Spermatocysts appear to merge together (due to extensive discontinuous germinal epithelium) forming large pools.

Table 3-2. Descriptions and photomicrographs of histological sections of female golden tilefish leading gamete stages. Hematoxylin-1 and eosin-Y stain, magnifications and scales on photomicrographs.

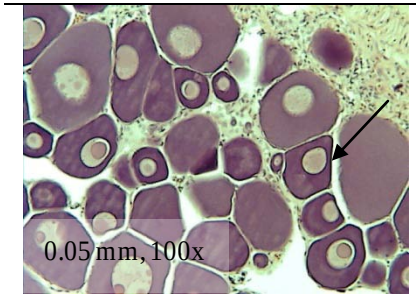
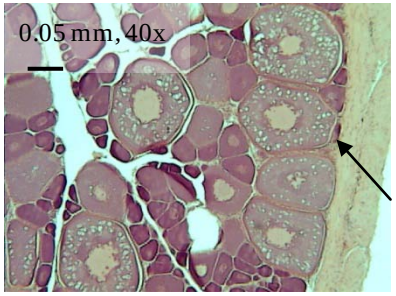
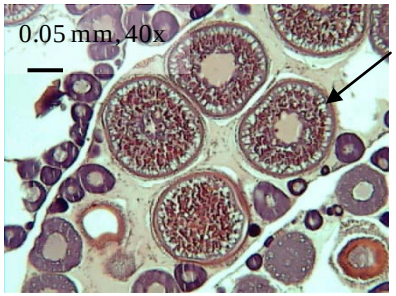
Photomicrographs	Leading Gamete Stage	Description of female leading gamete stage
	Primary Growth (PG)	Definitive follicle is formed, follicular epithelium envelopes oocyte, germinal vesicle present, large clear cytoplasmic area
	Cortical Alveolar (CA)	Three main components: cortical granules (appear white), thin band or zona radiate (appears as a red ring) surrounds the oocyte, and small droplets or lipids appear. Germinal vesicle present
	Vitellogenic (V)	Yolked oocytes are mostly spherical. Yolk is first seen as small, red, spherical granules around the germinal vesicle and cortical alveolar granules (appear white) move to the periphery of oocyte.

Table 3-2. Continued

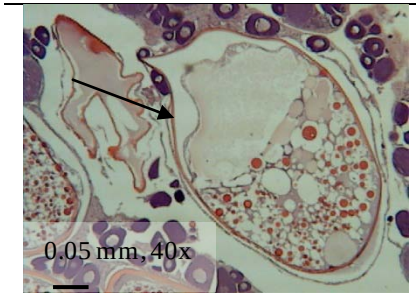
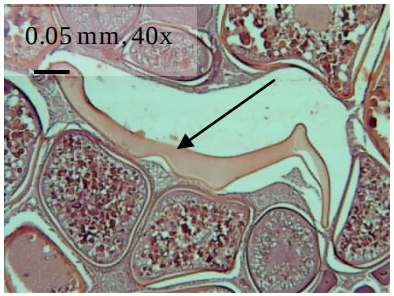
Photomicrographs	Leading Gamete Stage	Description of female leading gamete stage
	Early Hydrated (EH)	Yolked oocytes, less spherical in shape in conjunction with lipids coalescing into one or two clear spheres. Some attributes of the maturation stage may have begun including migration of the germinal vesicle. Start of final oocyte maturation.
	Late Hydrated (LH)	Oocytes reach their maximum volume through hydration and are amoeboid in shape. Oocyte becomes more translucent as lipid and protein yolk droplets coalesce, germinal vesicle disappeared

Table 3-3. Descriptions and photomicrographs of histological sections of male golden tilefish reproductive phases. The sample size (n) for each phase is provided. Hematoxylin-1 and eosin-Y stain, magnifications and scales on photomicrographs.

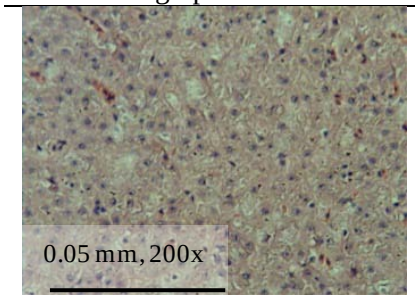
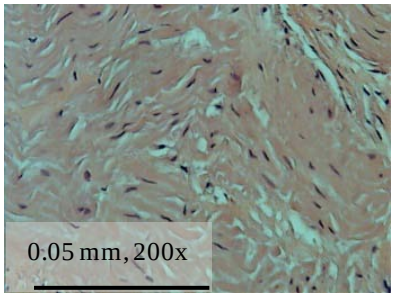
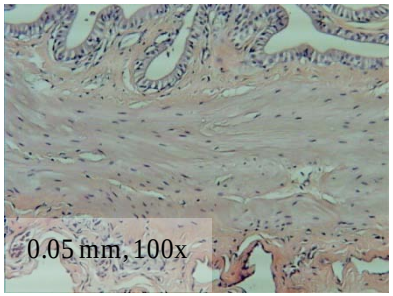
Photomicrographs	Reproductive Phase	n	Description of male reproductive phase
	Immature, inactive	8	Includes males with spermatogonia and no evidence of spermatogenesis.
	Inactive, uncertain	11	Difficult to distinguish from regressed, except for lack of developed tissue.
	Developing virgin	1	Spermatogenesis begins, spermatocytes present and no prior indicator of maturity.

Table 3-3. Continued

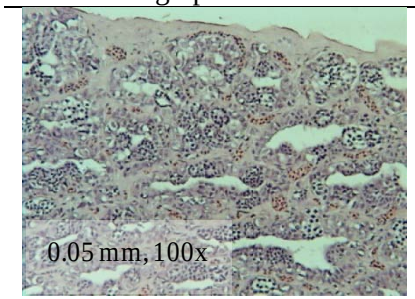
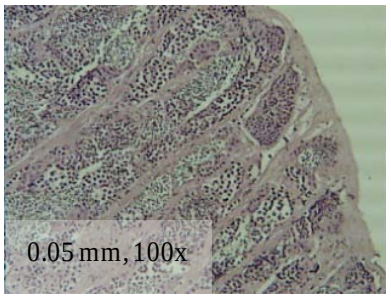
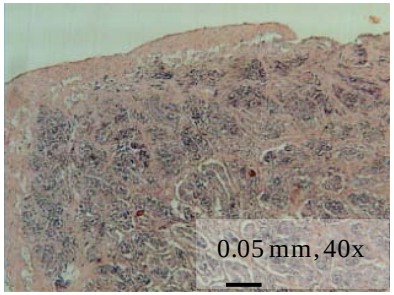
Photomicrographs	Reproductive Phase	n	Description of male reproductive phase
	Developing	203	Spermatogenesis and the formation of spermatocytes begins. Little or no spermatozoa.
	Active, mature	0	This class is not used for males, essential the same as developing
	Spawning, capable	591	All stages of spermatogenesis may be present. Spermatozoa evident and filling lobules and sperm ducts
	Spent, post spawn	2	Spermatogenesis ceasing, some residual spermatozoa present, spermatogonia proliferation common.

Table 3-3. Continued

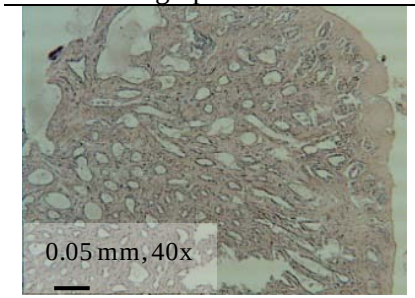
Photomicrographs	Reproductive Phase	n	Description of male reproductive phase
	Regressed, inactive, mature	234	Spermatogonia dominate, no active spermatogenesis, and some residual spermatozoa may be present.

Table 3-4. Descriptions and photomicrographs of histological sections of female golden tilefish reproductive phases. The sample size (n) for each phase is provided. Hematoxylin-1 and eosin-Y stain, magnification and scale on photomicrographs.

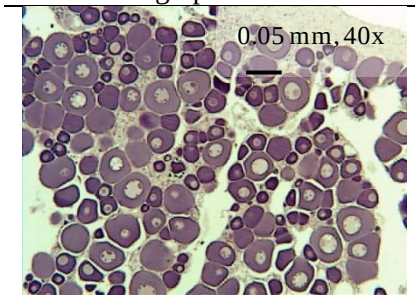
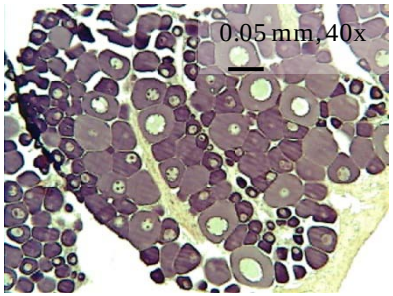
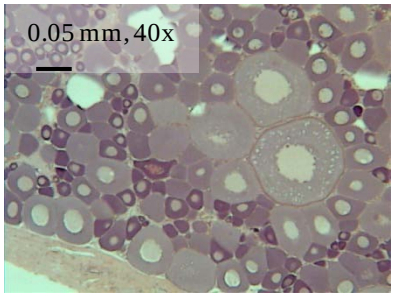
Photomicrographs	Reproductive Phase	n	Description of female reproductive phase
	Immature, inactive	1	Primary growth oocytes only, no evidence of prior spawning.
	Inactive, uncertain	4	Only primary growth oocytes present, not capable of spawning in distant future and no evidence of prior spawning.
	Developing virgin	0	Cortical alveolar oocytes dominate and no prior indicators of maturity No female tilefish were assigned this phase
	Developing	12	Cortical alveolar oocytes present. Prior spawning indicators confirm maturity.

Table 3-4. Continued

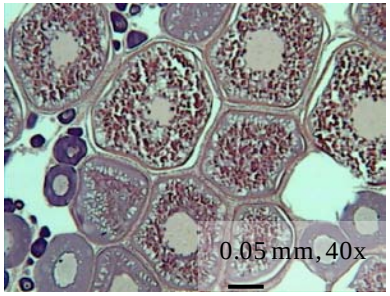
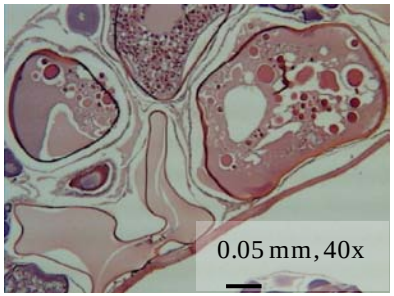
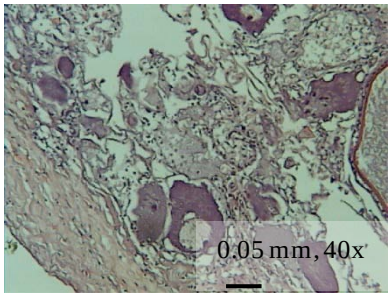
Photomicrographs	Reproductive Phase	n	Description of female reproductive phase
	Active, mature	100	Vitellogenic oocytes present and fish should spawn within days or weeks.
	Spawning, capable	327	Fish is reproductively active and capable of spawning. Early and late hydrated oocytes, as well as vitellogenic oocytes. Postovulatory follicles (old or new) may be present.
	Post-ovulatory, spent	7	All oocytes stages may be present, majority of oocytes (>50%) experiencing atresia.

Table 3-4. Continued

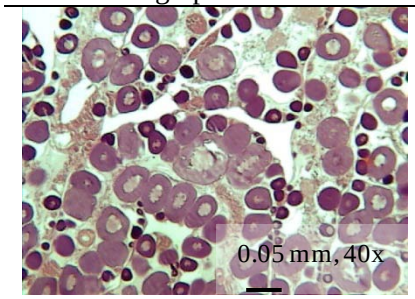
Photomicrographs	Reproductive Phase	n	Description of female reproductive phase
	Regressed, inactive, mature	321	Primary growth oocytes only, evidence of sexual maturity and recentl spawned.

Table 3-5. The number of golden tilefish collected by month. Fish were collected by multiple sources throughout the east coast of Florida and Gulf of Mexico (years combined: 2000-2009).

Month	east coast of Florida	Gulf of Mexico	Total
January	168	82	250
February	196	47	243
March	115	73	188
April	235	39	274
May	115	55	170
June	48	49	97
July	0	11	11
August	0	147	147
September	28	167	195
October	45	20	65
November	0	152	152
December	0	67	67
Total	950	909	1859

Table 3-6. Summary statistics by sex and maturity for golden tilefish. Data was combined for fish collected from the east coast of Florida and Gulf of Mexico. Functional sex (with and without opposite sex tissue), maturity stage (immature, mature (immature, mature) showing sample size (n), range of fork length and mean length ± standard error (SE). Fish where maturity stage could not be accurately determined were not included (male, n = 4; female, n = 6).

Functional sex	Maturity stage	Opposite sex tissue	n	Range	Mean ± SE
Male	immature	No	3	471-499	487 ± 8
		Yes	9	432-748	559 ± 37
Male	mature	No	341	375-1040	667 ± 6
		Yes	695	389-970	647 ± 5
Female	immature	No	3	290-394	357 ± 33
		Yes	1	336	na
Female	mature	No	562	338-824	531 ± 4
		Yes	201	390-800	565 ± 6

Table 3-7. Results of the logistic regressions for size and age at maturity for male and female golden tilefish. Data was combined for fish collected from the east coast of Florida and Gulf of Mexico. Parameters of the logistic regression (intercept, slope) were calculated using a general linear model with the binomial family and logistic option in R (R Development Core Team 2011).

	Intercept	Slope	Estimate
Male			
FL (mm)	-1.509	0.010	150
Age (yr)	0.864	0.442	> 1
Female			
FL (mm)	-18.175	0.055	331
Age (yr)	-3.087	1.256	2.46

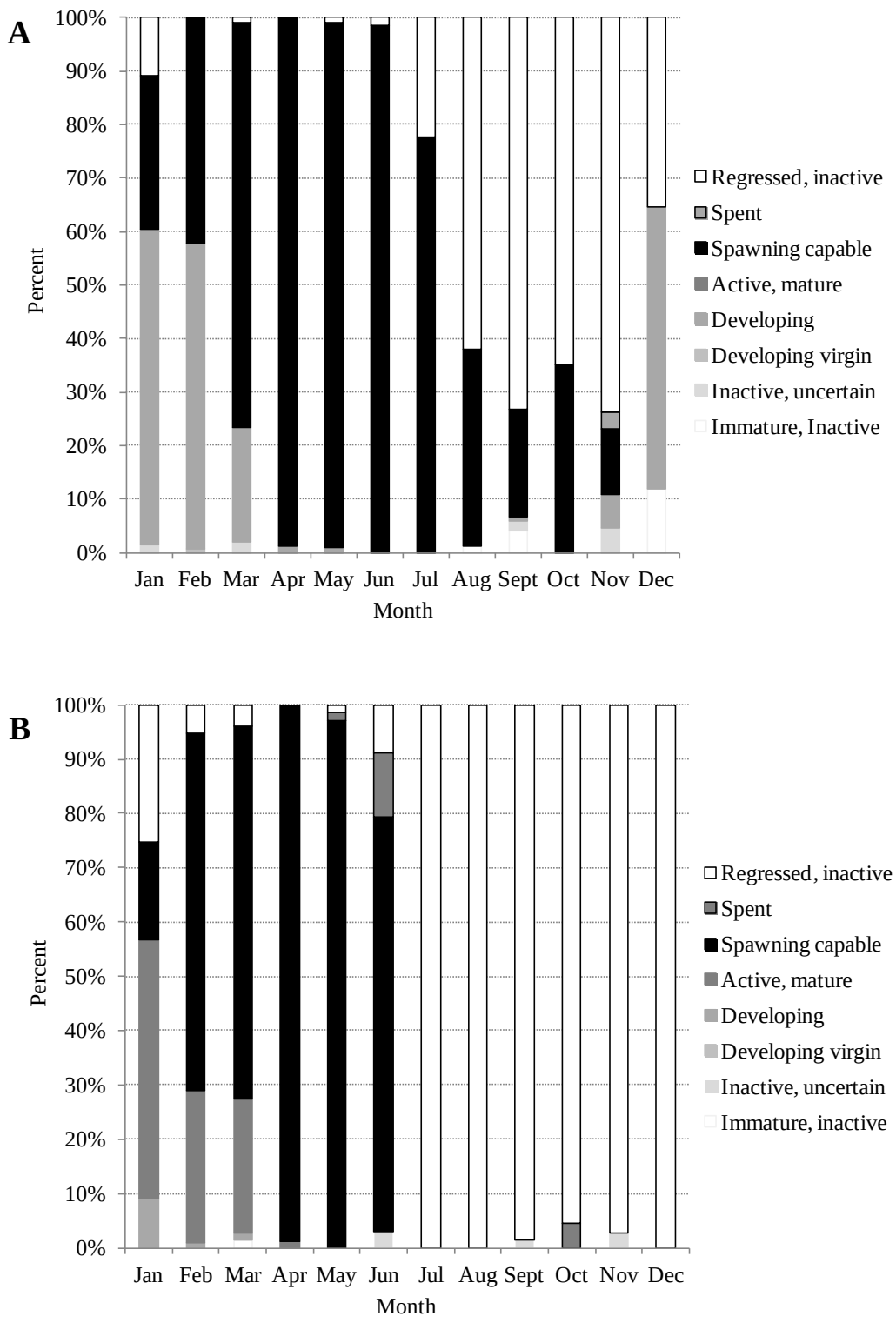


Figure 3-1. Golden tilefish proportion by reproductive stage by month and gender. See tables 3.3 and 3.4 for complete description of reproductive stages for (**A**) males and (**B**) females, respectively. Data was combined for fish collected from the east coast of Florida and Gulf of Mexico.

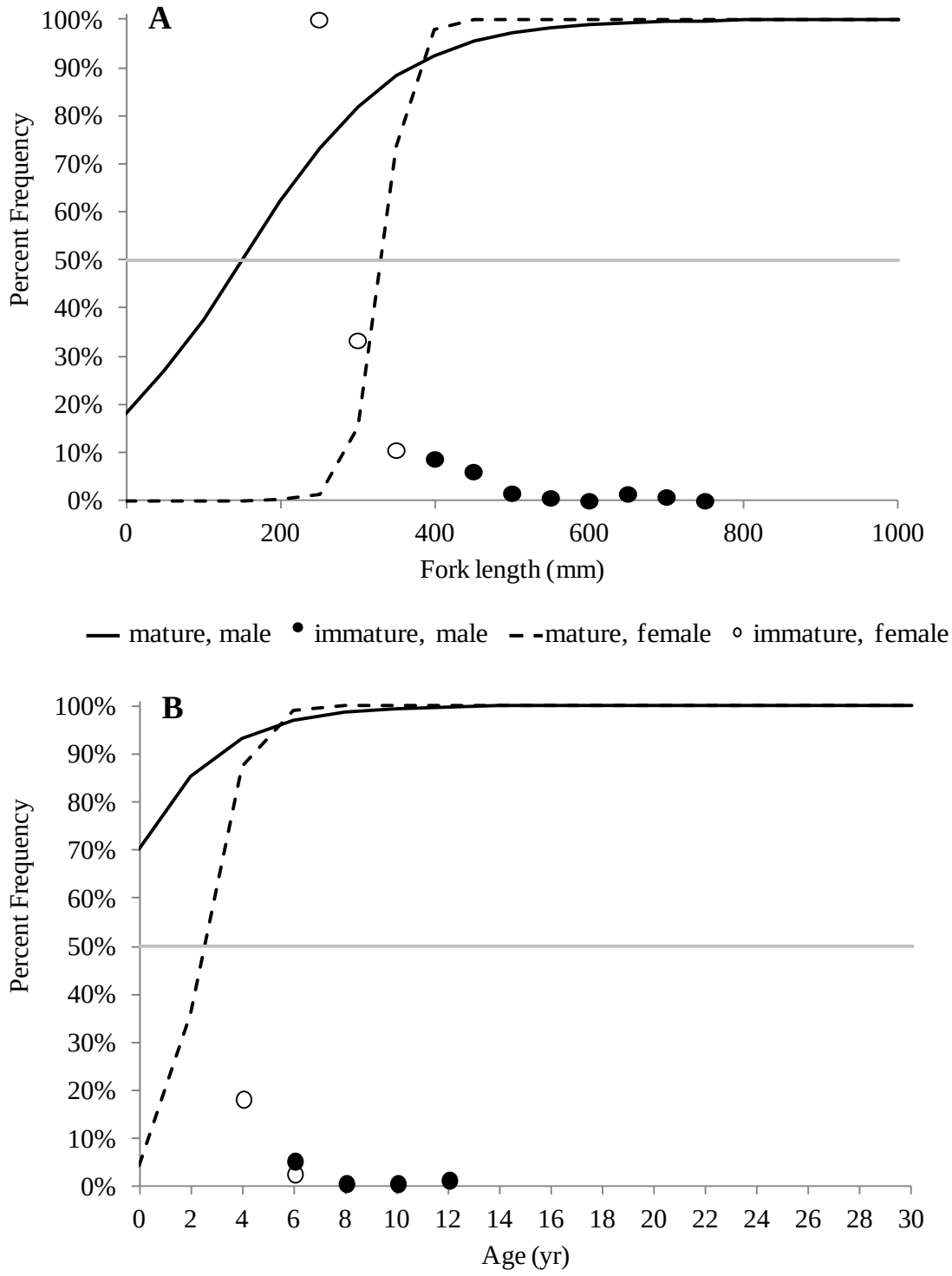


Figure 3-2. Golden tilefish proportion mature and immature by gender. Maturity estimates for males (mature: solid black line, immature: black circles) and females (mature: dotted black line, immature: white circles) by (**A**) length and (**B**) age. Data was combined for fish collected from the east coast of Florida and Gulf of Mexico. Proportion mature predicted by logistic regression. Proportion immature based on observed data at length and age. Solid gray line indicates 50% mature.

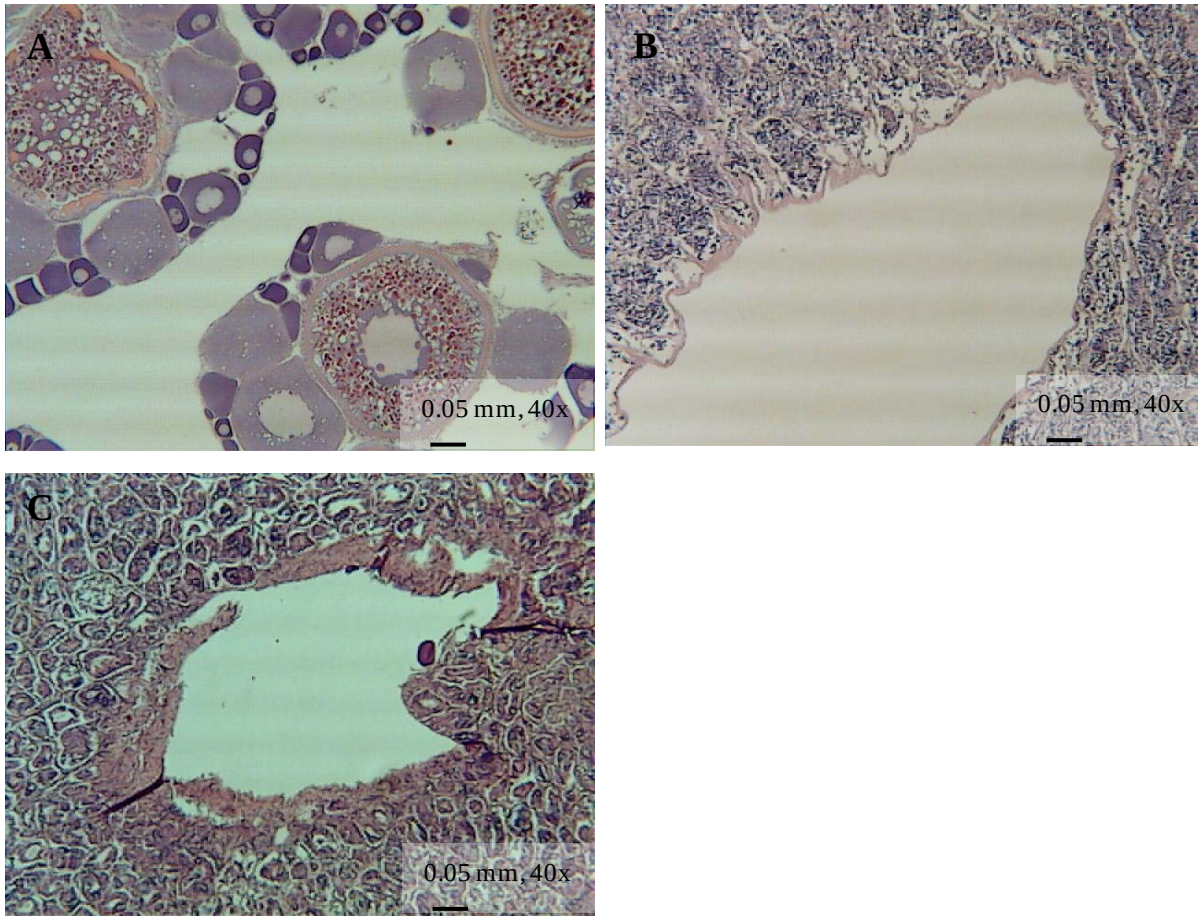


Figure 3-3. Photomicrographs of golden tilefish histological sections showing membrane lined cavity originating from ovarian lumen in both a female and male gonads. (**A**) Active, mature female (490 mm FL, age 9) collected in January 2007 in the Gulf of Mexico, showing primary growth, cortical alveolar and vitellogenic oocytes. This cavity remains unused in males for sperm transportation as shown in a (**B**) spawning male (570 mm FL, age 12) collected in March 2009 in the Gulf of Mexico, showing all stages of spermatogenesis, spermatozoa evident and filling lobules and sperm ducts and a (**C**) developing male (524 mm FL, age 10) collected in January 2008 off the east coast of Florida, showing formation of spermatocytes beginning. Hematoxylin-1 and eosin-Y stain, magnifications and scales on photomicrographs.

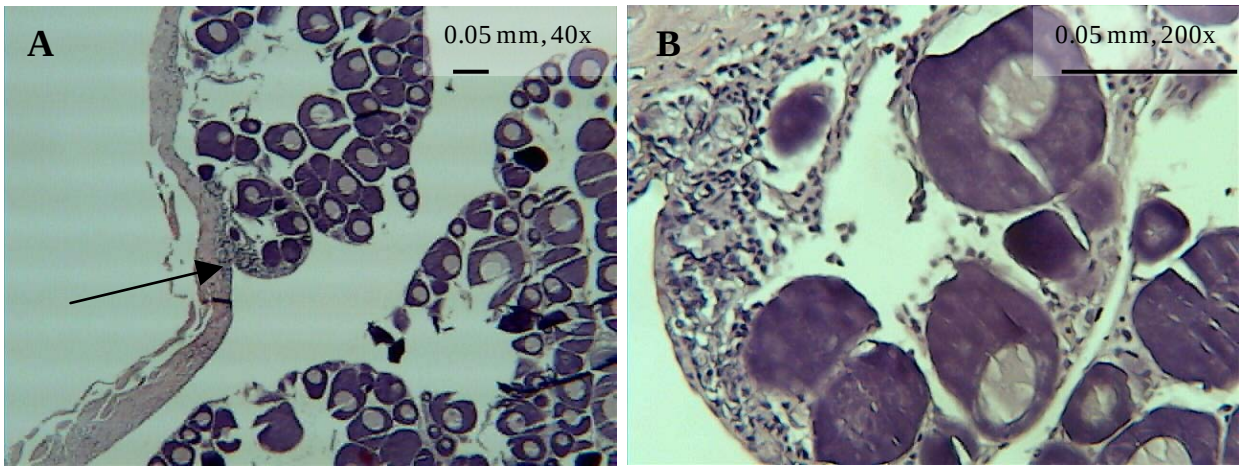


Figure 3-4. Photomicrograph of golden tilefish histological sections showing an immature female containing male tissue. The female (336 mm FL, age 4) collected in March 2009 in the Gulf of Mexico contained male tubules (several stages of spermatogenesis) at (**A**) 40x magnification and (**B**) 200x magnifications. Hematoxylin-1 and eosin-Y stain, magnifications and scales on photomicrographs.

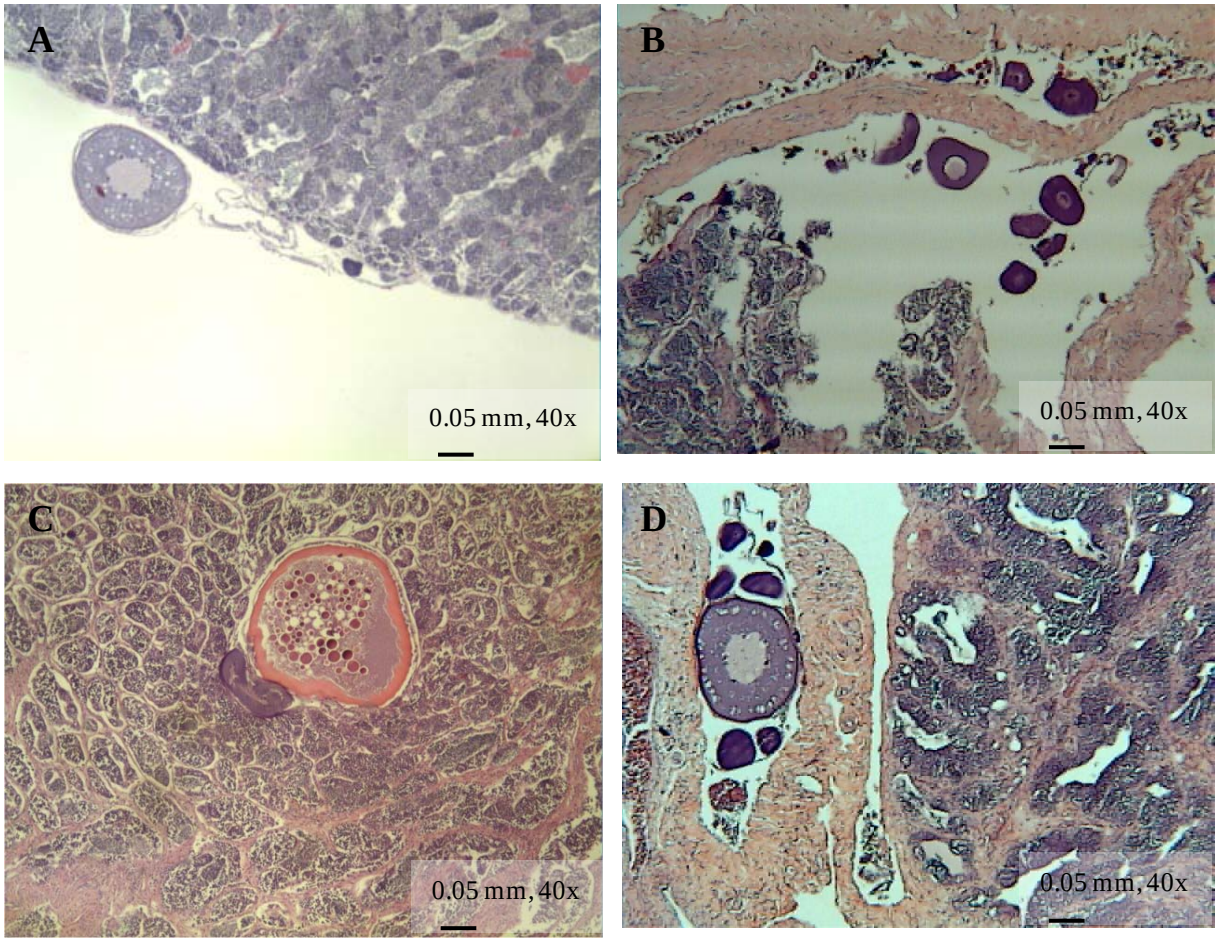


Figure 3-5. Photomicrographs of golden tilefish histological sections showing the placement of oocytes within functional male gonads. (**A**) Attached vitellogenic oocyte in a spawning male (620 mm FL, age 10) collected in June 2009 from the Gulf of Mexico, (**B**) floater cortical alveolar oocytes in a spawning male (507 mm FL, age 6) collected in February 2007 off the east coast of Florida, (**C**) embedded vitellogenic oocyte in a spawning male (484 mm FL, age 6) collected in April 2008 off the east coast of Florida and (**D**) primary growth, cortical alveolar, and vitellogenic oocytes in the ducts of a spawning male (670 mm FL, age 11) collected in February 2007 off the east coast of Florida. Hematoxylin-1 and eosin-Y stain, magnifications and scales on photomicrographs.

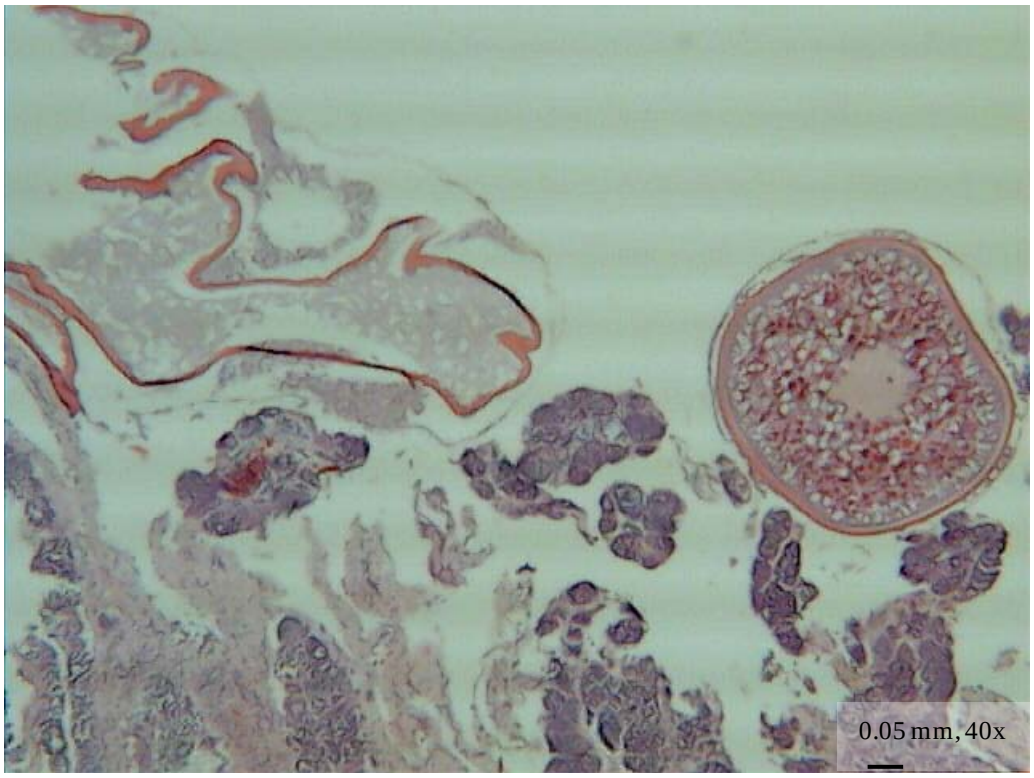


Figure 3-6. Photomicrograph of golden tilefish histological section showing a spawning male containing vitellogenic and late hydrated oocytes. The male (646 mm FL, age 8) collected in June 2006 in the northern Gulf of Mexico Hematoxylin-1 and eosin-Y stain, magnification and scale on photomicrograph.

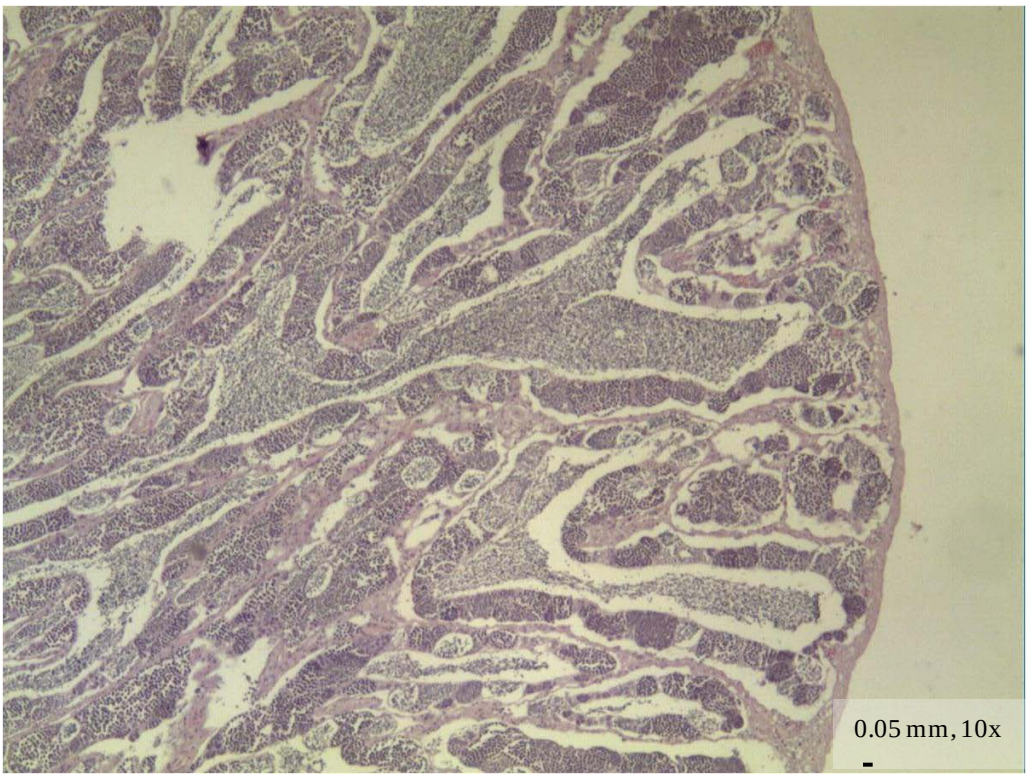


Figure 3-7. Photomicrograph of golden tilefish histological section showing sperm sinuses within the gonad wall of a spawning male. The male (748 mm FL, age 9) collected in April 2008 off the east coast of Florida. Hematoxylin-1 and eosin-Y stain, magnification and scale on photomicrograph.

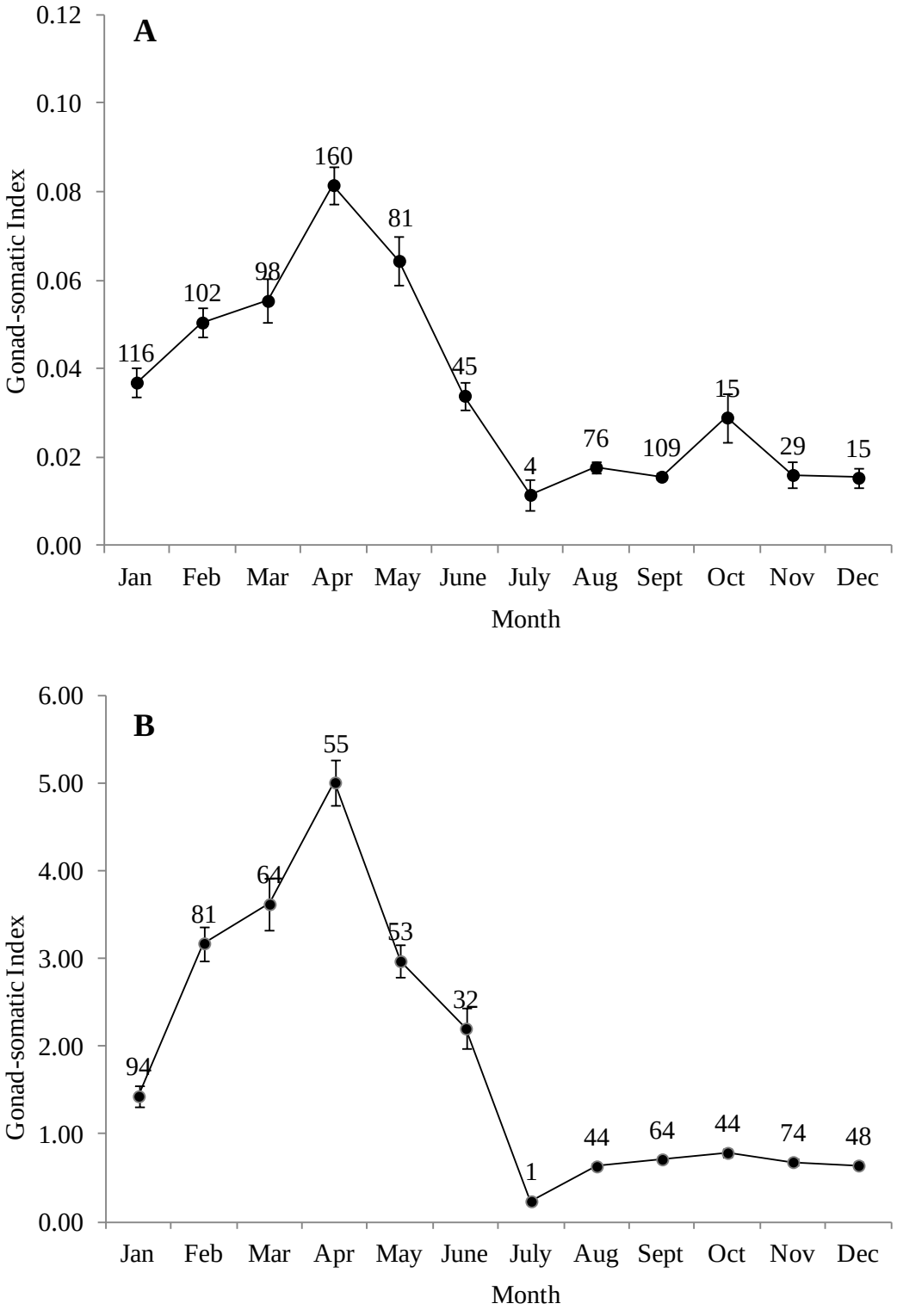


Figure 3-8. Golden tilefish gonad-somatic indices by month and by gender. (**A**) Male and (**B**) female golden tilefish. Gonad-somatic index reported as mean ± standard error. Reproductive seasonality did not differ between the fish collected off the east coast of Florida and the northern Gulf of Mexico, therefore data was combined. Sample sizes appear above error bars.

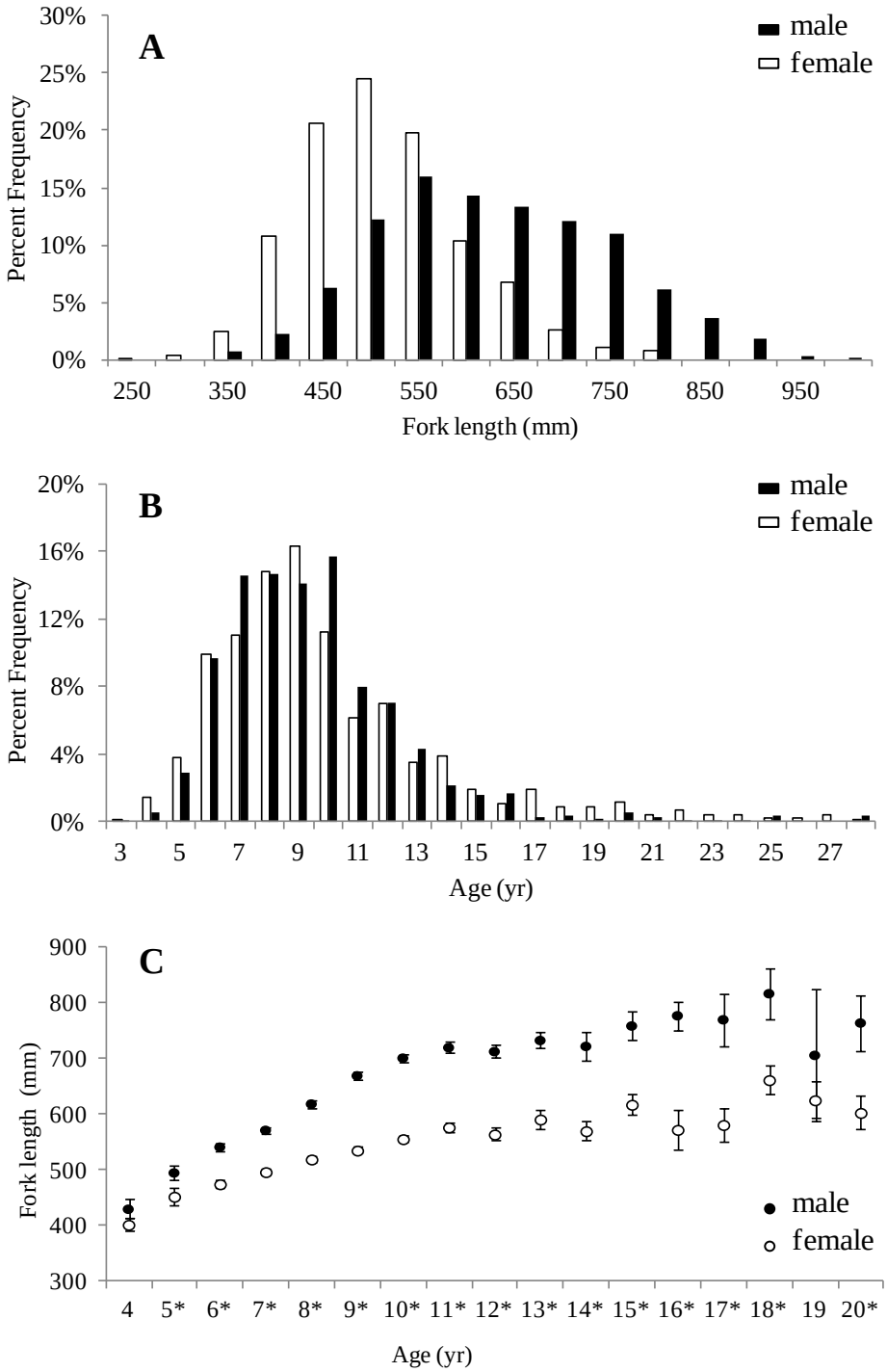


Figure 3-9. Golden tilefish age and length data by gender. (**A**) Fork length (mm) and (**B**) age distributions by sex males (black bars) and females (white bars) and (**C**) mean size ± standard error at age by sex (males, black circles; females, white circles). *indicates significant differences between the sexes determined through an unpaired Student's t-test with unequal variances, $p \leq 0.05$. Data was combined for fish collected from the east coast of Florida and Gulf of Mexico.

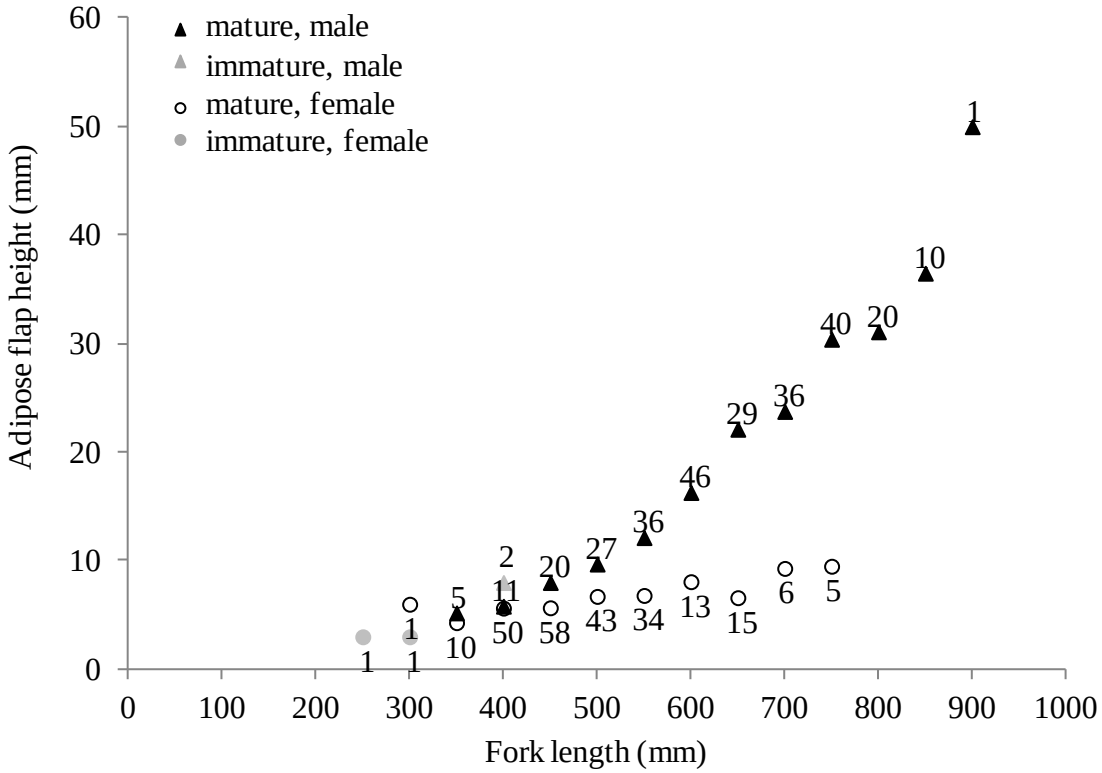


Figure 3-10. Golden tilefish adipose flap height by length, maturity stage and gender. Sample sizes are above the male data points (immature, n = 2, gray triangles; mature, n = 282, black triangles) and below the female data points (immature, n = 2, gray circles; mature, n = 235, white circles). Maturity determined through histology.

CHAPTER 4
MODEL CHOICE AND QUANTITY OF INFORMATIVE DATA: A CASE STUDY OF THE GOLDEN TILEFISH ASSESSMENT IN THE GULF OF MEXICO

Introduction

A stock assessment is an analysis in which the dynamics of a fish population are modeled, historical trends of harvest (biomass, exploitation rate) are estimated, and alternative management scenarios are tested (Hilborn and Walters, 1992). There are several choices of model types used in stock assessment analyses ranging from simple, surplus production models to complex, statistical catch-at-age models that incorporate auxiliary information (e.g., environmental and stock mixing parameters). The complexity of the model increases as the quantity of input data and the amount of observed data predicted increases. There are generally two schools of thought in regards to the use of simple versus complex assessment models 1) use a simple model and add complexity given the quantity of informative data (Richards and Schnute, 1998; Schnute and Richards, 2001; Walters and Martell, 2004) or 2) use a complex model and remove model detail until the observed data are sufficiently modeled (Methot, 2009a; Cope, *in press*). A compromise (and a recommendation) is to use multiple models in assessments (Hilborn and Walters, 1992; National Research Council, 1998; Walters and Martell, 2004).

Federal assessments for fish stocks in the Gulf of Mexico have included a multitude of model configurations, from simple, surplus production models, virtual population analysis, to complex statistical catch-at-age models. As an example, a surplus production which incorporates covariates (ASPIC; Prager, 1992, 1994) is a biomass dynamic model used by NOAA Fisheries Service and is based on the Graham-Schaeffer logistic production model. This model is easily modified by the user and eliminates the requirement of other assessment approaches to use catch per unit effort data but cannot make the use of any available age and length data, therefore

requires less data. Alternatively, statistical catch-at-age models can incorporate a larger quantity of data such as age- and size- specific information and are also used by NOAA Fisheries Service, for example, age-structured assessment program (ASAP; Legault and Restrepo, 1999), and numerous modified virtual population analysis (VPAs; Goodyear, 1997; Porch, 1999) (e.g., ADAPT; Conser and Powers, 1990; Powers and Restrepo, 1992). Most recently, fish stocks in the Gulf of Mexico are being modeled using Stock Synthesis (Methot, 2000, 2009b). This statistical catch-at-age model uses likelihood methods to determine the goodness of fit between the observed data and simulated population models and allows an even larger quantity of data to model size and age selectivities, spawner-recruitment functions, hermaphrodism, time-varying catchability, environmental variability, and even models the potential biases in the observation process. Stock Synthesis is likely the most highly parameterized model routinely used as part of the stock assessment process by US federal fisheries assessments.

Regardless of the simplicity or the complexity of the stock assessment model used to assess a fish population, most models have a similar overall structure (Walters and Martell, 2004). Assessment models consist of a state dynamic model (the submodel including historical disturbances and other unknown processes in the actual system) and an observation model (the submodel how observational quantities are related to the unobserved system state) (Walters, 1986). These models also include a model fitting criterion (e.g., maximum likelihood estimation) to find what combination of state dynamics and observation model best predicts the observed data. Similarly, stock assessment models have the same objective - to estimate the current state of the fished population.

Each type of model has different assumptions related to the parameters in the model and how these parameters interact to create the prediction model. These assumptions are often

unique to each type of model and ultimately are fundamental to creating the prediction model and in turn generating parameter estimates of interest such as fishing mortality rate used to define the stock status. Because these assumptions are fundamental to the model outcomes, and ultimately the management decisions based on these model outcomes, it is highly recommend that different types of models, with different assumptions, be used in assessing fish stocks (Hilborn and Walters, 1992; National Research Council, 1998; Walters and Martel, 2004). That way if two types of models give different predictions about stock status, then managers should explore the differences in model assumptions to determine why the results diverge and whether additional research on specific assumptions could resolve uncertainties about the stock status by improving the available data (Hilborn and Walters, 1992).

Therefore, my objective was to compare two age structure models that differ in complexity, a relatively simple stochastic Stock Reduction Analysis (SRA) age structure model and a more complex model Stock Synthesis (SS) using Gulf of Mexico golden tilefish as my case study[1]. Multiple model variations for SRA and SS will be presented. The comparison between models will be conducted on one of the SS model variation for golden tilefish (indices emphasized and age and length composition data deemphasized) and the Gulf wide stochastic Stock Reduction Analysis model (age selectivity fitted through SS and without age composition). These model formulations allow a straightforward comparison of the models' results.

Materials and Methods

Model Descriptions

Stochastic Stock Reduction Analysis (SRA) is a stochastic age structured population model with Beverton-Holt stock-recruitment function that simulates populations forward in time

[1] The research presented in this chapter incorporates data, model inputs, and results evaluated during the stock assessment of golden tilefish in the Gulf of Mexico (SEDAR, 2011a).

starting before fishing began (Walters et al., 2006). This model is parameterized by taking management objectives, annual exploitation rate (U) producing maximum sustainable yield at equilibrium (U_{MSY}) and maximum sustainable yield (MSY) as leading parameters, then calculates the Beverton-Holt stock-recruit parameters from these parameters and from per-recruit fished and unfished eggs and vulnerable biomasses (Forrest et al., 2008; Martell et al., 2008). In SRA, recruitment is assumed to have had log-normally distributed annual anomalies. The SRA model produces a distribution of trajectories of vulnerable biomass over time (due to recruitment anomalies), as well as, probability distributions of MSY, Umsy, $U_{year,}$ Goodyear's Compensation Ratio (recK), and stock status. There are four main assumptions in SRA: 1) the population is at virgin conditions the first year data are provided; 2) there is stochastic variation in recruitment for all years; 3) historical recruitment have arisen from variation around a single, stationary stock recruitment curve; and 4) survival rate is constant for all years. The main premise in stochastic SRA is to try to best explain the fluctuations in stock size given historical catches and recruitment (Walters et al., 2006). In order to model changes in the fishery, given changes in targeted species, gear used, and size and/or age regulations (i.e., size limits), age selectivities (or vulnerabilities) can vary over time. Stochastic SRA is written in visual basic, uses a Windows based interface for user inputs, and Bayes posterior distributions for biomass, exploitation rate, and leading parameters are calculated using Markov Chain Monte Carlo (MCMC) integration. The likelihood function used in the MCMC search algorithm can include terms for relative abundance indices that change over time, deviations of current exploitation rates, and multiple length and/or age composition. Stochastic Stock Reduction Analysis has been applied to several Gulf of Mexico species including red snapper (*Lutjanus campechanus*; SEDAR, 2005), red

grouper (*Epinephelus morio*; SEDAR, 2006), and yellowedge grouper (*Epinephelus flavolimbatus*; SEDAR, 2011b).

Stock Synthesis (SS) is a statistical catch-at-age model that incorporates a variety of biological, population level, and fisheries data (Methot, 2000). Stock Synthesis can simultaneously analyze age and length composition data, growth, mortality, age and length selectivities, catch histories, indices of abundance, fishery effort, recruitment deviations, etc., with each parameter having its own degree of uncertainty. Stock Synthesis has been termed an integrated analysis model because of its flexibility and its ability to handle missing or incomplete data series, multiple stock sub-areas, and time-varying parameters (Methot, 2009a). Stock synthesis can model recruitment using either a Beverton-Holt or Ricker stock-recruitment functions. Recruits are assumed to be age 0 fish and, just as in SRA, recruitment variation is modeled with a lognormal distribution. The premise of SS is to "bring the model to the data" and model the potential biases in the observed data (Methot, 2000). Stock Synthesis is compiled using ADMB (Auto Differentiation Model Builder). Stock Synthesis has mainly been applied to groundfish fisheries along the United States west coast (Pacific Fishery Management Council, 2000) but within the last few years, SS (version 3.03a; Method, 2009b) has been applied to fish stocks in the Gulf of Mexico assessments (SEDAR, 2011a, 2011b).

Gulf of Mexico Golden Tilefish Case Study

Golden tilefish, *Lopholatilus chamaeleonticeps*, is a deep-water demersal fish found in the Atlantic from Nova Scotia to the Gulf of Mexico (Dooley, 1978). Golden tilefish are managed by three fishery management councils (Northeast Atlantic, South Atlantic, and Gulf of Mexico). In the Gulf of Mexico, golden tilefish are managed by a total allowable catch of 200 metric tons which was implemented in 2004. This regulation was initiated as part of the red

grouper rebuilding plan to guard against commercial long-liners shifting to deep-water groupers and tilefish fisheries (NOAA, 2004).

As I reported in previous chapters, golden tilefish use very specific habitat types, commonly soft, but malleable sediment along the continental shelf in water depths 80-400 m (Freeman and Turner, 1977). Golden tilefish inhabit burrows (Able et al., 1982), reside in a specific thermal cline (9-14^{o}C; Grimes et al., 1986) and have limited movement (Grimes et al., 1983). Therefore, the golden tilefish stock in the Gulf of Mexico was modeled within regions of the northern Gulf of Mexico (east and west of the Mississippi drainage, Fig. 4-1). This separation accounted for spatial differences in fishing effort (Table 4-1), region specific growth (see below), and subsequent recruitment variability.

Golden tilefish age and length composition data were available for the fishery dependent and fishery independent sources. Data was delineated by region providing the capture location information (latitude, longitude, or NMFS statistical grid). A majority of the age and length composition data were obtained from the commercial long-line fishery in the eastern region (1984-2009; Table 4- 2 and 4-3, Fig. 4-3, 4-4, and 4-5). Given the difficulty in validating the age estimates of golden tilefish (chapter 2), an ageing error matrix was incorporated into Stock Synthesis. Sex-specific age and length composition data were also available for the last nine years of the time series (2001-2009, Table 4-3).

Golden tilefish ages and total lengths from the entire time series (1997-2009) were used to obtain gulf wide and region specific growth parameters. The data was fit to a von Bertalanffy growth model and growth parameters were estimated by non-linear regression (Solver, Microsoft Excel) (Table 4-4). I also determined golden tilefish to have sexually dimorphic growth (see chapter 3). Golden tilefish were also modeled (in SS only) with sexual dimorphic growth, with

males capable of obtaining larger sizes at faster rates than females (Table 4-4). Gender and region specific growth parameters were estimated within SS, due to the lack of observational data (Table 4-3). In addition, SS modeled golden tilefish as protogynous hermaphrodites (given the evidence in chapter 3), with only 57% of population remaining female and estimating size at transition through a logistic regression. Using a logistic regression I estimated that female tilefish reach maturity at a young age (2 yrs) and small size (344 mm TL) (see chapter 3 for details), even though golden tilefish are long-lived and reach lengths of over a meter.

Golden tilefish fecundity was not modeled directly but as a proxy, through a regression of body weight and gonad weight (Table 4-4). Only females with vitellogenic or hydrated oocytes collected during the spawning months (January through June) were used to estimate regressions. Each assessment model used a different regression as a proxy for fecundity. Stochastic SRA used a linear relationship between body weight and the average weight at maturity. There are three possible regressions to use as proxies for fecundity in Stock Synthesis (Methot, 2000) and given the data, I used a non-linear relationship between gonad weight and body weight.

Estimates for natural mortality for golden tilefish were calculated using numerous regressions. These regressions were applied to a variety of golden tilefish datasets (e.g., males, females, all data; von Bertalanffy growth model unconstrained, and with t_o constrained at zero), resulting in a distribution of natural mortality estimates (SEDAR, 2011a). After removing unrealistically high natural mortality values ($M > 0.25$), the mode of the distribution was 0.14. This estimate of natural mortality was the same as was estimated using Hoenig (1983) regression model for teleosts for all data based on longevity (30 yrs). Therefore, natural mortality was based on longevity for both models (Table 4-4), with SS also incorporating an age-specific mortality (reference age 4; Lorenzen, 2005).

Golden tilefish catch histories began in 1965 with the primary source of harvest the commercial hand-line fishery (Table 4-1). Commercial bottom long-line gear was introduced in the Gulf of Mexico in the late-1970s, and by the 1980s golden tilefish were primarily being harvest by this gear type. Since golden tilefish are not managed by a size limit and are caught at great depths, discards are minimal and any reported discards were added to the respective fishery landings (SEDAR, 2011a).

There were two sources of indices of abundance for golden tilefish: fishery dependent, commercial long-line fishery (CMLL) and fishery independent, NOAA/National Marine Fisheries Service (NMFS) bottom long-line survey (LL Survey) (SEDAR, 2011a). The fishery dependent index was based on NOAA Fisheries Service, Southeast Fisheries Science Center Coastal Fisheries Logbook Program for self-reported commercial bottom long-line catch per unit effort data (1992-2009). Since commercial long-line trips are not identifiable by the target fishery, the Stephens and MacCall 2004 method was used to restrict the logbook data to trips most likely to catch golden tilefish (e.g., NMFS Statistical Grids, species associations). The standardized index of abundance for commercial long-line fishery was constructed using a delta lognormal approach with three factors (subregion, days at sea, year) and three factor interactions (subregion*year, days at sea*year, subregion*days at seas). The same modeling approach was used for the fishery independent bottom long-line survey (factors: water depth, survey area, year). The fishery independent index began in 2000 and only used data from stations that fished in the depths golden tilefish inhabit (125-365 m). Both standardized indices were calculated by region and corresponding coefficients of variations (CV) were incorporated in both assessment models (Fig. 4-2, A, B, C, and D).

Age and size selectivities were constructed based on both fishery dependent and fishery independent age and size composition. There were multiple age and size selectivities used in Stock Synthesis (SS) for each specific combination of source (commercial hand-line, commercial long-line and bottom long-line survey), gender (female, male), and region (east and west). The best fit for both length and age data were through logistic regressions (SEDAR, 2011a). Size selectivities were fitted using a double logistic regression with normal distribution and constrained to be asymptotic (Fig. 4-6). Age selectivities (in SS) were fitted based on the logistic regression (Fig. 4-7A). In Stochastic Stock Reduction Analysis (SRA) selectivities are modeled as a matrix of age vulnerabilities by year. Initial age vulnerabilities in SRA were modeled using a virtual population analysis but final model runs (for comparison to SS) used the resulting average (across genders and regions) commercial long-line age selectivities fitted by SS (Fig. 4-7B).

Uncertainty in Stock Status

I evaluated the uncertainty in the parameters that determined the status of golden tilefish stock in the Gulf of Mexico. Stock assessments conducted by NOAA Fisheries Service follow regional fishery management and scientific guidelines when determining stock status. The probabilities of being overfished and/or undergoing overfishing to determine stock status were based on Spawning Stock Biomass (SSB) and Exploitation (U) at Maximum Sustainable Yield (MSY) for Stochastic SRA and based on Spawning Stock Biomass (SSB) and Fishing mortality (F) at a Spawning Potential Ratio (SPR) of 30% for the Stock Synthesis model. Therefore, the uncertainty in the ratios of SSB_{2009}/SSB_{MSY} and U_{2009}/U_{MSY} for Stochastic SRA and the ratios of $SSB_{2009}/SSB_{SPR30\%}$ and $F_{2009}/F_{SPR30\%}$ for Stock Synthesis were examined through the resulting MCMC chains. I tested the convergence of the MCMC chain for each parameter using two

diagnostic tests (Geweke and Hiedelberger and Welch convergence tests) and trace and correlation plots (coda and PBS modeling packages; R Development Core Team, 2011).

Results

Stochastic Stock Reduction Analysis (SRA)

In order to make predictions about the status of golden tilefish populations east and west of the Mississippi drainage, stochastic SRA model was executed separately by region and for the entire Gulf of Mexico stock. For each region specific model, I applied the default values for recruitment anomalies (1.0) and standard deviation of recruitment (0.5) and recruitment was modeled without autocorrelation. Next, I ran SRA using region specific life history parameters (Table 4-2), catch histories (Table 4-1), and commercial long-line indices with varying degrees of uncertainty (coefficient of variation) (Fig. 4-2). I compared the two age vulnerability schedules by running each model (gulf wide, East, West) twice, once using the age vulnerability back-calculated by virtual population analysis and again using the age vulnerabilities estimated by SS through a logistic regression (Fig. 4-7B). Finally, I incorporated the age composition data into the SRA model for the gulf wide and Eastern Gulf of Mexico model runs. Age composition data was not sufficient to model the Western Gulf of Mexico with age data.

Stochastic SRA model convergence is based on the acceptance rate of the Markov Chain Monte Carlo (MCMC) sampling procedure. Stochastic SRA experienced difficulties in fitting the eastern region and Gulf wide models for golden tilefish; therefore, the default parameters controlling the movement along parameter space for the MCMC were adjusted. All models were manually ceased after several million iterations (Gulf wide, 4.0×10^6, 16% acceptance rate; East, 4.2×10^6, 23% acceptance rate; West, 4.4×10^6, 30% acceptance rate). The eastern region was predicted to have a high probability that recent catches have been at or above MSY and in

the western region recent catches have been at MSY by SRA, given the sample distribution of maximum sustainable yield (MSY) and exploitation at MSY (Umsy) (Fig. 4-8).

Stock Synthesis (SS)

Stock synthesis was also applied to region specific data to predict whether or not the golden tilefish population in the Gulf of Mexico was overfished or undergoing overfishing. In SS only one model was compiled, recruitment was distributed evenly between the regions. A single Beverton-Holt stock-recruitment function was estimated in SS with recruitment deviations forced to sum to zero with a fixed value of 0.15 for the standard deviation of recruitment. Bias adjustments were applied to the calculation of recruitment (Methot and Taylor, 2011). The level of adjustment was based on the amount of data informing recruitment (1965-1983 no bias adjustment; 1984-1997 linear increase in bias adjustment; 1997-2006 full bias adjustment; 2007-2009 no bias adjustment). Stock Synthesis can process a larger capacity and complexity of data therefore, region- and gender-specific growth patterns and mortality functions (Table 4-2) were used. In addition, age-selectivities by gender and source (Fig. 4-6 and 4-7A) were applied in SS but due to the lack of sufficient gender data collected with length frequency data, size-selectivities were only constructed by source and region. Finally, golden tilefish in the Gulf of Mexico were modeled using region specific catch history by commercial gear type (Table 4-1) and commercial long-line indices and bottom long-line survey indices with varying degrees of uncertainty (coefficient of variation) (Fig. 4-2).

The fit of Stock Synthesis (SS) is measured in terms of the value of negative log-likelihood (NLL). The total negative log-likelihood in SS (for the models ran for golden tilefish) contained six major components (catch histories, indices of abundance, length composition, age composition, recruitment, and priors for estimated parameters). I chose to discuss two (model 1 and model 12) of the fifteen model variations (sensitivities), which were presented during the

Southeast Data, Review, and Assessment Workshops for golden tilefish from the Gulf of Mexico (SEDAR, 2011a) and are thus of greatest interest to fishery managers. These models (1 and 12) varied by the amount of uncertainty incorporated into the calculation of the total NLL. In Stock Synthesis, an emphasis factor (lambda, λ) is multiplied to the corresponding likelihood component to calculate the total NLL to incorporate uncertainty into the model (Methot, 2009b). In Model 1, no lambdas were applied to the data components and a large NLL was calculated with most of the NLL pertaining to the age and length compositions (Table 4.5). By evaluating (visually) the residuals of the age and length composition (Fig. 4.9 and 4.10), it was evident that SS had difficulties predicting the age and length composition especially in the western region. Therefore, to test the sensitivity of SS to the uncertainty of the age and length composition, model 12 was run. Model 12 emphasized the indices of abundance ($\lambda = 25$) and deemphasized the age and length composition data ($\lambda = 0.05$) (Table 4.5).

Model Comparison

Models were compared in terms of predicted biomass, exploitation rates, and stock status. Both SRA (gulf wide) and SS (model 12) predicted the eastern region of the Gulf of Mexico yielded a higher carrying capacity of golden tilefish compared to the western region given the historical catches (Fig. 4-11). In addition, both models predicted the same trend in historical biomass levels by region, SRA biomass trajectories appear lower than SS because SRA reports the vulnerable, not the total biomass as in SS. Gulf wide exploitation rates were nearly identical between the models until 1993, at which SRA predicted slightly higher exploitation (Fig. 4-12). Stochastic SRA used total egg production as a proxy for spawning stock biomass (SSB). The probability of being overfished is the resultant of unique MCMC iterations in which the ratio of SSB_{2009}/SSB_{MSY} is less than 1.0 and the probability of overfishing comes from the number of unique MCMC runs in which the ratio of U_{2009}/U_{MSY} is greater than 1.0. SRA predicted that

golden tilefish in the Gulf of Mexico are not experiencing overfishing (probability overfishing: 1.26%) and are not overfished (probability overfished: 0.11%). In SS, the probabilities of being overfished and/or undergoing overfishing are based on spawning potential ratio (SPR) and not MSY therefore, Gulf of Mexico golden tilefish stock status between the models cannot be compared directly. Nevertheless, the final model runs in SS determined tilefish was not undergoing overfishing (based on $SPR_{30\%}$) and was not overfished.

The comparison of SRA model runs using varying age vulnerability schedules resulted in similar stock status (not overfished and not undergoing overfishing) for each region and for the entire Gulf of Mexico golden tilefish stock. Predicted historical vulnerable biomass trajectories had similar trajectories but SRA model runs using the age vulnerability schedule back-calculated through virtual population analysis (VPA) resulted in lower initial (eastern region, 30%; western region, 8%) and final biomass (eastern region, 10%; western region, 6%), compared to SRA model runs using the age vulnerabilities estimated through SS (Fig. 4-11). SRA model runs with the VPA age vulnerabilities predicted 16-20% higher historical exploitation, during peak exploitation years (1988, 1995, and 2005) (Fig. 4-12). Age composition data were added to the eastern and Gulf wide models to help better inform the model for estimating mortality rates and recruitment. Stochastic SRA model runs with age composition data provided similar historical biomass trajectories (Fig. 4-11) and exploitation rates (Fig. 4-12), as well as decreased probabilities of overfishing (with age composition, 0.35%) and overfished (with age composition, 0.05%).

Uncertainty in Stock Status

For both models, original MCMC chains were thinned prior to tests of convergence. The MCMC chains tested for convergence from the Stochastic SRA (SRA) model consisted of 5,048 iterations that originated from the 4.0×10^6 MCMC iterations, the first 200 iterations were part of

the burn-in and removed, and the remaining chain was thinned every 800th iteration. The MCMC chains tested for convergence from the Stock Synthesis (SS) model consisted of 4,000 iterations. These chains were constructed from MCMCs ran for 1.0 x 10^6 iterations, the first 1,000 iterations were part of the burn-in and removed, with every 200th iteration saved. The resulting MCMC chains for the ratios of SSB_{2009}/SSB_{MSY} and U_{2009}/U_{MSY} for Stochastic SRA and the ratios of SSB_{2009}/SSB_{SPR} and F_{2009}/F_{SPR} for Stock Synthesis passed both tests of convergence (Table 4-6). The Geweke's test of convergence did not find any differences in the mean of the first 10% of the chain compared to the mean of the last 50% of the chain, concluding all chains resulted from a stationary distribution. Similarly, the Heidelberger and Welch's (stationary – compared samples along the entire chain and half width – compared half the width of the 95% confidence intervals of the mean with the mean) tests of convergence concluded the samples of each chain came from stationary distribution and from a chain of sufficient length. Trace plots for each ratio also provided evidence that MCMC sampling for each chain were from stationary distributions (Fig. 4-13 and 4-14). The stock status parameters from Stochastic SRA and Stock Synthesis had similar correlations (SRA, -68; SS, -62) and uncertainties (Fig. 4-15 and 4-16). By presenting the uncertainty in the MCMC chains for those parameters that determine stock status, better confidence in the models results can be concluded.

Discussion

These two age structure models provide an example of comparing a simple (stochastic Stock Reduction Analysis, SRA) and a complex (Stock Synthesis, SS) model structure. On one side of the spectrum, SRA, a simple age-structure model uses basic biological inputs and catch data (conditioned on catch removal process) to provide an estimate of the current stock size and status, based on the historical catch history. The complex age-structure model (SS) modeled region and gender specific growth, mortality, selectivities, indices of abundance, and estimated

62 parameters (e.g., von Bertalanffy growth parameters, virgin recruitment, stock-recruitment steepness parameter, recruitment deviations). Using similar data, but different model structure, the results of these models suggest similar conclusions concerning the stock status of golden tilefish in the northern Gulf of Mexico. Specifically this stock is not overfished and currently not undergoing overfishing.

A main aim of any stock assessment model is to determine the present abundance of fish given the historical removals. Since assessment scientists cannot simply count the number of fish present in a stock, a vector of removals is constructed, an index of abundance is calculated, and information describing the age, growth, reproduction, and mortality of a population are used to predict the present abundance (Schnute and Richards, 2001). In each of the main inputs of assessment models (removals, indices, life history), both process (error associated with unpredictability of biological processes) and measurement (error associated with observational data, e.g., data reporting) errors are present (Schnute and Richards, 2001). Assessment models also contain structural errors associated with programmed assumptions and constraints (Hilborn, 2003). Each of these errors make up the uncertainties associated with stock assessments. In complex models, like Stock Synthesis, as more functional components are incorporated into the model structure, basic parameter interactions are more difficult to interpret and the assessment process is less transparent to managers and stake holders (Walters, 1986; Hilborn, 2003). Although complex models can have less process and measurement error an increase in modeling structural error can be just as problematic (Mohn, 2009). Therefore, to conduct a successful stock assessment Schnute and Richards (2001) recommend the following: 1) use a suite of models because no model can fully capture all the intermingled processes of a fish stock; 2) do not only rely on the trends of the fishery (i.e., landings), 3) investigate other fields (e.g.,

economics, oceanography); 4) start with a simple model and add complexity given the observed data, and 5) use computer simulation to test management scenarios.

A quote attributed to the statistician George E.P. Box states that "Remember that all models are wrong; the practical question is how wrong they have to be to not be useful" and this certainly applies to fisheries assessment models. In the case of golden tilefish, my challenge was to develop and compare two types of population assessment models using the same data, knowing that the data on golden tilefish biology and the fishery landings were sparse. We can attempt to model the uncertainty in the observational model but a key question is can we truly model the biological and environmental complexity of fisheries (Schnute and Richards, 2001) and if not, does this impact our ability to develop sustainable management plans. In the example of golden tilefish from the northern Gulf of Mexico, there are three trends evident from the data inputs that have very large influences on my ability to determine stock status 1) there was a lack of consistency in sampling the fishery for age and length composition, 2) there was a lack of signal from either the fishery dependent or the fishery independent indices of abundance, and 3) there was a lack of duration (length of coverage for the time series) for the most of the data (except for catch).

The golden tilefish fishery in the Gulf of Mexico consists of a limited number of vessels with a low total allowable catch (TAC, 200 metric tons) in comparison to the larger reef fish fisheries (red snapper, TAC = 1,610 metric tons; red grouper, TAC = 2,610 metric tons; GMFMC, 2011). This small number of vessels creates opportunities and also adds complexity to filling the data gaps. Ideally with a small number of vessels, fewer port agents would be required to canvas the landings for biological samples. However, port agents are primarily dedicated to sampling much larger and more economically important fisheries such as those from

reef fish. Additional there is difficulty in obtaining biological samples from port agents since most golden tilefish are gutted at-sea and most fish are iced and boxed onboard fishing vessels, with delivery trucks waiting dockside to quickly ship the catch to fish markets in the northeastern United States (pers. comm., P. Antosh state of Alabama port agent). This requires biological samples to be taken from on-board observer programs, which are more expensive and dictated by vessel selection.

In the Gulf of Mexico, biological and landings data have been collected from the commercial sector since the early 1990s through a NOAA Fisheries Service dock side sampling program called the Trip Interview Program (TIP). This program has port agents stationed at major commercial ports along the shoreline of the entire Gulf of Mexico from Key West, FL to Brownsville, TX. Federal stock assessments are based on the data collected by these port agents, many of which have collected data since the inception of this program. In general, the goal of TIP is to conduct representative sampling (age and length data) across time, location, gears and trips (Hoenig, 2007). This type of on-site sampling is the most reliable but requires an appropriate statistical design to be maintained (National Research Council, 1998). These port agents are field statisticians, attempting to purposely sample landings of multiple species from one or many fishing vessels at one time. A recent independent review of TIP sampling design recommended that a systematic sampling scheme (sampling the j^{th} fish) could provide less bias in data collection then the current purposely sampling (Hoenig, 2007). As a result of these shortcomings from the sampling program, both stock assessment models were affected by the lack of biological samples, as well as, the limited number (<10 yr) of years of consecutive data that was available for modeling.

The data requirements for stock assessment models increase exponentially with model complexity (Hall, 2003). Regardless of the complexity of the model only quality, informative data should be used in models, otherwise noisy, insufficient data can lead to bad management decisions (Adkison, 2009). As in the case of golden tilefish, data inputs consisted of short time series of consecutive data, small annual sample sizes for age and length composition (especially by gender and region) and highly variable indices of abundance. The only long term time series data, which was considered collected with some confidence and both models assumed to be collected without error, was the historical catch data. The total catch history is one of the most vital fishery based data (Shepherd, 1984; Pope, 1988; Hall, 2003).

The next most important fishery based data is an unbiased estimate of abundance (Hilborn and Walters, 1992; Schnute and Richards 2001; Methot, 2009a). The two indices of abundance used to model golden tilefish were highly uncertain and did not provide much signal for either model. An index of abundance that does not truly reflect the changes in abundance or indices that are conflicting can result in misleading stock status (National Research Council, 1998), as was suggested in the case in the northern cod (Walters and Maguire, 1996). In my opinion, the data used to construct both the fishery dependent and independent indices were inadequate. The fishery dependent index was based on data sub-setting from commercial log book data using the Stephens and MacCall (2004) method. This method was first tested using species associated with the bocaccio rockfish recreational fishery off the coast of Northern California. This data sub-sampling relies on the accurate reporting by fishers of species associated with golden tilefish but if a co-species does not have a commercial value or a fisher does not have permit, than the co-species is discarded, not landed and most likely not recorded in the logbook. Yellowedge grouper and other deepwater groupers had the highest associations

with the golden tilefish from the analysis of commercial logbook data for both the sub-areas (SEDAR, 2011a). However, the species most associated with golden tilefish during fishery independent surveys were gulf hake (*Urophycis cirrata*) and Cuban dogfish (*Squalus cubensis*) neither species appeared in the species association list for data sub-setting nor are of much value commercially. Therefore, there needs to be a more appropriate manner to query the logbook database. My recommendation is to add a target species data field to the logbook database to allow for more direct sampling of positive trips by species.

Similarly, it is as important to have a fishery independent survey to estimate the trend in relative abundance. This survey should be conducted through a stratified random, sampling design to calculate a true independent estimate of abundance not just for the exploited stock but for the mature, spawning fish as well as recruits (Hall, 2003). An index of abundance is considered vital information for stock assessments (Shepherd, 1984). However, the data used to construct the fishery independent index of abundance is based on a bottom long-line survey that only spends 10% of the annual sampling in depths (183-366 m) associated with golden tilefish. This annual survey is conducted for eight weeks in the Gulf of Mexico covering depths of 9-366 m with most effort in the shallowest depths (SEDAR, 2011a). This bottom long-line survey provides the data for calculating indices of abundance for numerous shallow-water reef fish (groupers, snappers; SEDAR, 2005, 2006), as well as small coastal sharks (Highly Migratory Species, 2007). I propose that an annual survey, statistically designed for deep-water, demersal species be conducted throughout the Gulf of Mexico with efforts solely at the deeper depths (183-366 m). This survey would complement the current survey but be designed to provide better quality and quantity of informative data on abundance for numerous poorly known commercially harvested species (e.g., deep-water groupers).

Additionally, in developing a stock assessment it is as important to obtained length frequency data (Shepherd, 1984). Typically, length frequency data can provide insights into recruitment trends, growth, and mortality (Anderson and Neumann, 1996) assuming that length data has been collected systematically, in a randomized strategy that encompasses the entire range of lengths and at sufficient annual sample sizes (for length based assessment, sample size > 1000, Erzini, 1990; for age-based assessment, sample size > 100, Anderson and Neumann, 1996). However, golden tilefish length frequency and age samples were not collected consecutively throughout the time series of catch and were collected in insufficient sample sizes. The number of consecutive years of data and the sample size of the age composition data were determined to heavily influence the results of Stock Synthesis especially in terms of biomass and predictability of the catch (Yin and Sampson, 2004). Therefore, one must be as explicit and straightforward about the uncertainty of the data and the assumptions of the model, regardless of the model's complexity, during a stock assessment (Walters and Maguire, 1996).

The assessment for golden tilefish was heavily influenced by the lack of quality and especially the quantity of data and was judged to be a 'data-poor' species (SEDAR, 2011a). I have presented two assessment models that vary in complexity, a simple, age-structure depletion based model - stochastic Stock Reduction Analysis model and a complex, integrated analysis model – Stock Synthesis but both agreed in stock status, historical biomass and exploitation. Stock Synthesis had difficulty in predicting observational data (e.g., age and length frequencies, indices of abundance) and model performance increased as age and length data streams were deemphasized. In stochastic Stock Reduction Analysis, model results were not sensitive to the additional age composition data and the status of the golden tilefish stock, predicted historical biomass trajectories and exploitation were similar with and without the age composition data.

Although the stock status of golden tilefish in the northern Gulf of Mexico was determined to be in good standing, this species has characteristics that makes it highly susceptibility to capture and to overfishing (Grimes and Turner, 1999). Golden tilefish have a unique habitat preference and borrowing behavior that increases this species vulnerability to fishing, especially if fishers overharvest at one particular site. In addition, golden tilefish are long lived, slow growing, and have a complex breeding and reproductive strategy that is not completely understood. The previous assessments for golden tilefish from the Northeast Atlantic (NEFSC, 2005) and South Atlantic (SEDAR, 2004) management areas have resulted in overfished and overfishing conditions and providing stricter management regulations golden tilefish in both of these areas are now in rebuilding stages (NEFSC, 2009; SEDAR, 2011c). The assessments in these areas also suffered from insufficient life history data and unbiased estimates of abundance, same as the Gulf of Mexico assessment models presented here. Therefore, efforts need to continue to collect annual, biological samples from fishery dependent sources, as well as, developing species or at least complex level (e.g., deep water) fishery independent surveys.

Conclusion

Federal stock assessment scientists, as well as independent experts, agree that the quality and complexity of a particular assessment should be directly related to the quality and quantity of data available (Ludwig and Walters, 1985; Hilborn and Walters, 1992; Schnute and Richards, 2001; Mace et al., 2001; Walters and Martell, 2004). I recommend that data should be scored and ranked accordingly, and the complexity of the model should reflect the quality and quantity of informative data. Data should be ranked based on the number of consecutive years of data (e.g., 10 years; Yin and Sampson, 2004), the number of individual samples that generated the data (e.g., for length composition at least 10x the number of length bins; Gerritsen and McGrath, 2007), how the data were collected (e.g., randomly, fishery independent), and the spatial

coverage of the data (e.g., the number of vessels interviewed, the number of fish houses/docks). Additionally, I recommend meta-data on the behavior of the industry should be documented, since a majority of data used in stock assessment models rely on the cooperation of the fishers (Cotter et al., 2004). As it is recommended by many assessment scientists, data inputs should always incorporate some degree of uncertainty (such as standard deviations, probability distributions) and the assumptions of assessment models should be discussed openly for the assessment process to remain transparent to managers and stakeholders.

Table 4-1. Commercial landings for the northern Gulf of Mexico golden tilefish. Landings (gutted metric tons) are presented by commercial hand-line (CMHL) and long-line (CMLL) fishery by region, east (E) and west (W), delineated by the Mississippi River drainage.

Year	CMHL E	CMHL W	CMLL E	CMLL W	Total
1965	2.82	0.00	0.00	0.00	2.82
1966	0.81	0.00	0.00	0.00	0.81
1967	0.44	0.00	0.00	0.00	0.44
1968	0.60	0.00	0.00	0.00	0.60
1969	0.13	0.00	0.00	0.00	0.13
1970	0.00	0.00	0.00	0.00	0.00
1971	1.33	0.00	0.00	0.00	1.33
1972	0.45	0.00	0.00	0.00	0.45
1973	1.62	0.00	0.00	0.00	1.62
1974	1.70	0.00	0.00	0.00	1.70
1975	6.00	0.00	0.00	0.00	6.00
1976	9.98	0.00	0.00	0.00	9.98
1977	14.74	0.00	0.00	0.00	14.74
1978	9.57	0.24	0.00	0.00	9.81
1979	11.88	0.00	2.32	0.48	14.68
1980	7.79	0.00	2.79	0.73	11.31
1981	52.51	0.00	36.43	11.30	100.24
1982	24.68	0.00	56.14	41.51	122.33
1983	5.78	0.21	56.11	32.29	94.39
1984	5.32	0.85	74.53	41.62	122.32
1985	4.05	4.98	37.18	66.61	112.82
1986	19.69	3.98	59.82	51.22	134.72
1987	30.90	8.04	69.41	109.16	217.50
1988	35.88	19.16	104.74	225.05	384.82
1989	16.51	25.73	41.61	100.27	184.12
1990	27.01	1.37	50.71	65.01	144.11
1991	7.48	9.98	48.32	20.98	86.76
1992	5.43	5.98	38.82	35.73	85.96
1993	6.33	2.96	61.26	44.67	115.22
1994	5.09	0.66	107.99	43.56	157.30
1995	0.95	3.25	66.93	120.71	191.84
1996	0.59	1.20	48.99	34.50	85.28
1997	1.05	0.23	116.58	18.72	136.59
1998	0.55	0.65	90.93	28.21	120.34
1999	2.53	1.78	88.82	58.51	151.64
2000	1.72	2.24	109.25	80.96	194.17
2001	6.49	0.12	136.73	52.81	196.15
2002	3.92	0.64	99.93	114.59	219.08
2003	1.40	0.88	95.45	64.46	162.19
2004	1.24	0.25	114.88	72.88	189.25

Table 4-1. Continued.

Year	CMHL E	CMHL W	CMLL E	CMLL W	Total
2005	1.63	1.74	138.60	96.57	238.54
2006	2.37	0.08	100.18	23.41	126.04
2007	0.42	0.84	118.05	9.78	129.10
2008	0.05	0.13	117.47	23.52	141.18
2009	0.54	0.03	142.19	23.61	166.38
Total	341.95	98.23	2433.17	1713.45	4586.80

Table 4-2. Annual sample sizes of length composition data for golden tilefish from the northern Gulf of Mexico. Data reported by commercial gear (hand-line, CMHL; long-line, CMLL) and region (east, E; west, W) northern Gulf of Mexico divided by Mississippi River drainage. For those years with higher sampling effort, an effective sample size of 200 was applied. Numbers in parenthesis reflect the number of sex-specific length records which were modeled in Stock Synthesis.

Year	CMHL E	CMHL W	CMLL E	CMLL W
1984			106	100
1985				
1986			2	26
1987		1	25	126
1988		1	48	175
1989			2	82
1990		3	153	128
1991	14 (4)	15	35	415
1992	1	95	23	395
1993	22 (1)	12	14 (1)	162
1994	2	47	642 (6)	295
1995	2	7	245	185 (5)
1996	30 (1)	1 (2)	316	62
1997	20		655	20
1998	19		411	13
1999	34	5	560	
2000	24 (6)		795	35
2001	46 (108)	2	777	
2002	100 (3)		197	
2003	2	19	610 (7)	18
2004	10		1685	40
2005	174(2)	20	1559 (6)	34
2006		1 (2)	1,125	15 (2)
2007	(1)	9	905	93 (2)
2008	2 (2)	52	473 (18)	410
2009	11	38 (10)	580 (91)	577
Total	641	342	12,069	3415

Table 4-3. Annual sample sizes of age composition data for golden tilefish from the northern Gulf of Mexico. Data reported by fishery dependent (commercial hand-line, CMHL; commercial long-line, CMLL) and fishery independent (National Marine Fisheries Service bottom long-line survey, LL Survey) sources. Sex was determined through the histological examination of gonad tissue.

Year	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
CMHL													
Female													6
Male													10
Unknown				5		24	34	2	44	3	10	55	43
CMLL													
Female								3	8		8	58	171
Male								4	51	29	53	54	156
Unknown	43	4		11	44	74	273	500	491	208	276	580	996
LL													
Survey				3	19	7		6	8	11	15	5	13
Female				1	18	8		30	12	15	41	21	31
Male				2	10	30		1		5	2	2	
Unknown													
Total	43	4	0	22	91	143	307	578	614	271	405	775	1426

Table 4-4. Life history parameters for golden tilefish from the northern Gulf of Mexico by region and gender. Growth parameters were estimated through non-linear regression. Length at maturity was estimated using logistic regression. Proxies for fecundity were based on spawning female body weight and gonad weight regressions. Natural mortality was estimated using Hoenig (1983) regression model for teleosts for all data based on longevity (30 yrs). See text for further details. *these values represent the estimated parameters used in Stock Synthesis (total length (cm), weight (kg)).

Parameter	Applied to both regions	East Sexes combined	East Male*	East Female*	West Sexes combined	West Male*	West Female*
Von Bertalanffy							
asymptotic length	83	88	92	82	77	87	66
growth coefficient	0.14	0.11	0.13	0.11	0.17	0.16	0.19
Length at Maturity	34						
Fecundity	proxies						
Stochastic SRA	linear regression						
Stock Synthesis	non-linear regression						
Length-Weight							
alpha	7.52×10^{-6}						
beta	3.08						
Natural Mortality	0.137						

Table 4-5. Negative log-likelihoods for the major components of the stock synthesis model for golden tilefish from the northern Gulf of Mexico. Stock Synthesis (SS) model 1 was the base model and model 12 emphasized the indices of abundances ($\lambda = 25$) and deemphasized the age and length compositions ($\lambda = 0.05$). These values represent the Negative log-likelihoods (NLL) multiplied by the lambdas (λ) for all sources and regions combined.

Component	NLL: model 1	NLL: model 12
Catch	3.05×10^{-6}	3.26×10^{-6}
Indices	4.76	-494.64
Length composition	2397.15	141.82
Age composition	4966.29	303.12
Recruitment	175.21	140.94
Parameter priors	35.59	35.69
Total	7579.00	126.93

Table 4-6. Summary statistics and results of diagnostic tests for convergence for MCMC iterations for parameters from each model that determined stock status for golden tilefish from the northern Gulf of Mexico. Summary statistics for Stochastic Stock Reduction Analysis (SRA) and Stock Synthesis (SS) include sample size (n), median (2.5% and 97.5% quantiles), Geweke Z-score, Hiedelberger and Welch pass or fail stationary test (H and W, stationary), and Hiedelberger and Welch pass or fail half width test (H and W, half width). Parameters that determined stock status (SRA: Spawning Stock Biomass (SSB) in 2009/ Spawning Stock Biomass (SSB) at Maximum Sustainable Yield (MSY) and Exploitation (U) in 2009/ Exploitation (U) at Maximum Sustainable Yield (MSY); SS: Spawning Stock Biomass (SSB) in 2009/ Spawning Stock Biomass (SSB) at Spawning Potential Ratio (SPR) of 30% and (B) Fishing mortality (F) in 2009/Fishing mortality (F) at Spawning Potential Ratio (SPR) of 30%).

Model	Parameter	n	Median (2.5%, 97%)	Geweke Z-score	H and W Stationary	H and W Half-width
SRA	SSB_{2009}/SSB_{MSY}	5028	1.92 (1.46,2.35)	-4.12	pass	pass
	U_{2009}/U_{MSY}	5028	0.28 (0.16, 0.59)	-2.38	pass	pass
SS	SSB_{2009}/SSB_{SPR}	4000	1.99 (1.76, 2.26)	-1.39	pass	pass
	F_{2009}/F_{SPR}	4000	0.49 (0.39, 0.62)	1.78	pass	pass

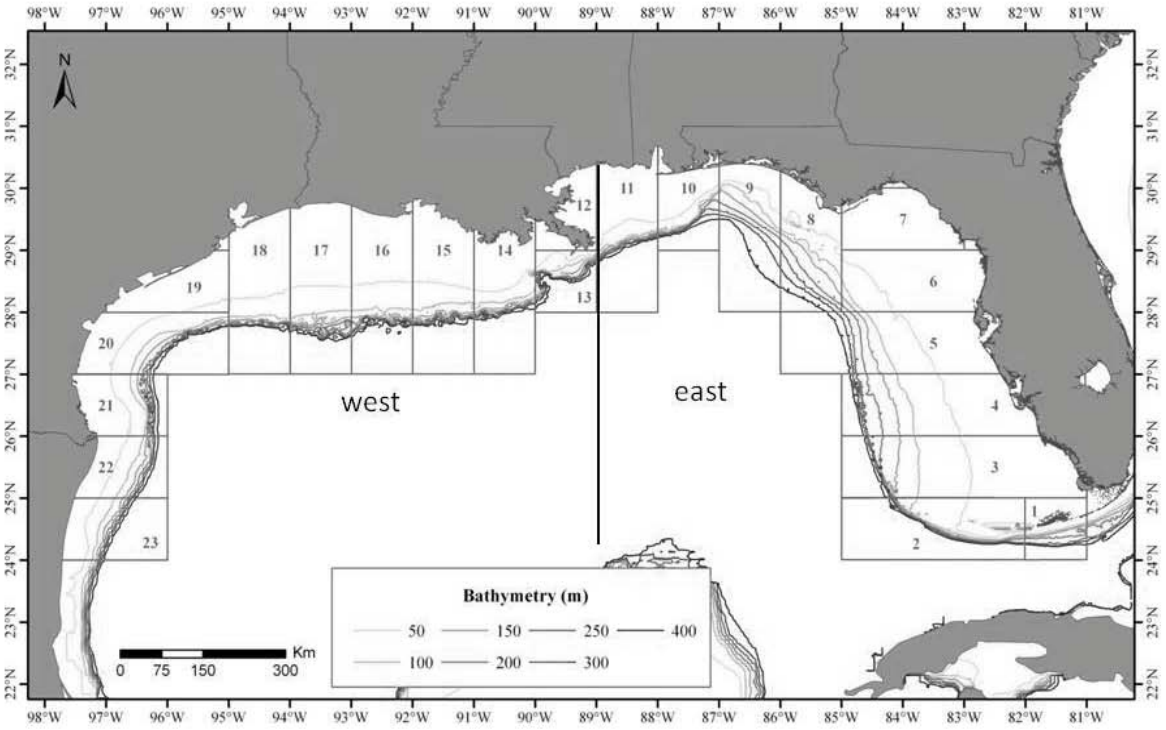


Figure 4-1. Northern Gulf of Mexico spatial map displaying the National Marine Fisheries Service (NMFS) statistical grids. Golden tilefish inhabit depths 100-400m. Golden tilefish were modeled with two sub-areas (east, west) of the Mississippi drainage (East: NMFS grids 1-11; West: NMFS grids 12-23). Depth contours in meters.

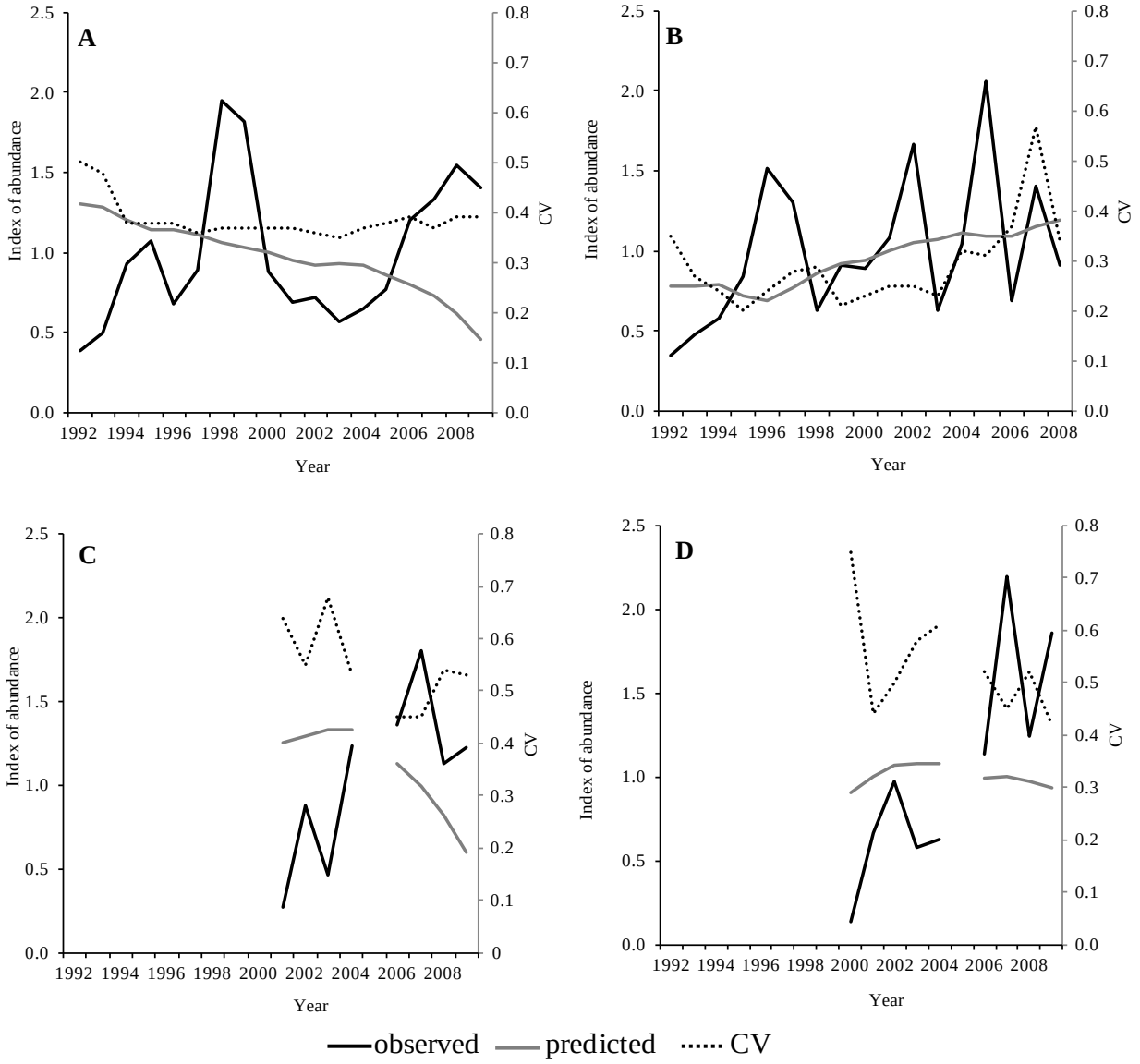


Figure 4-2. Standardized indices of abundance for golden tilefish from the northern Gulf of Mexico by region and by source. (**A**) Commercial long-line east, (**B**) commercial long-line west, (**C**) bottom long-line survey east, and (**D**) bottom long-line survey west. Indices of abundance (observed, solid black line; predicted in Stock Synthesis, solid gray line) and coefficient of variation (CV, dotted lines).

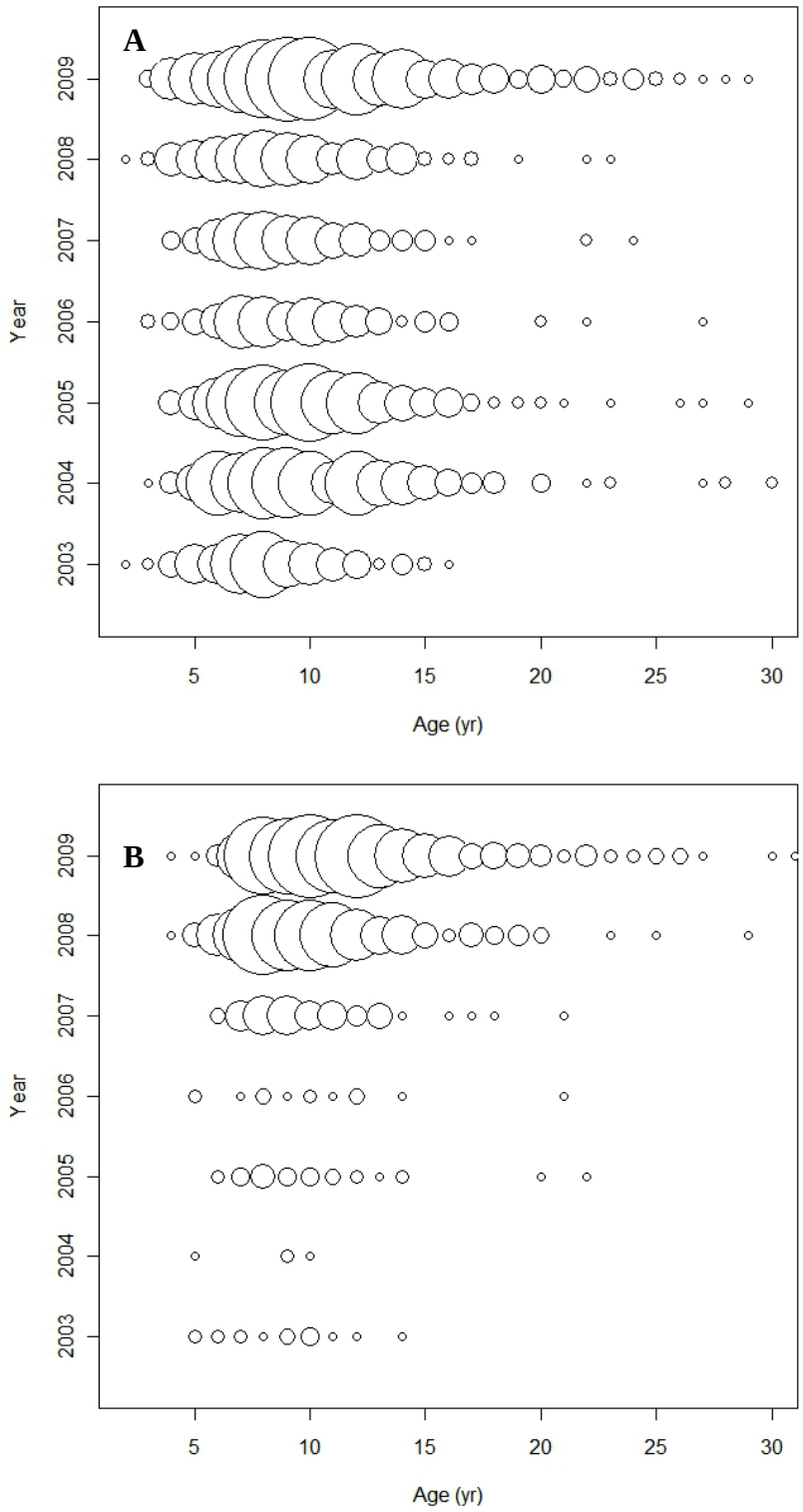


Figure 4-3. Annual age composition for golden tilefish from the northern Gulf of Mexico. Data reported from commercial long-line fishery by region (**A**) east and (**B**) west of the Mississippi River drainage. Each circle is proportion to the sample size at age in a given year. The largest circle size represents 96 fish and the smallest circle 1 fish.

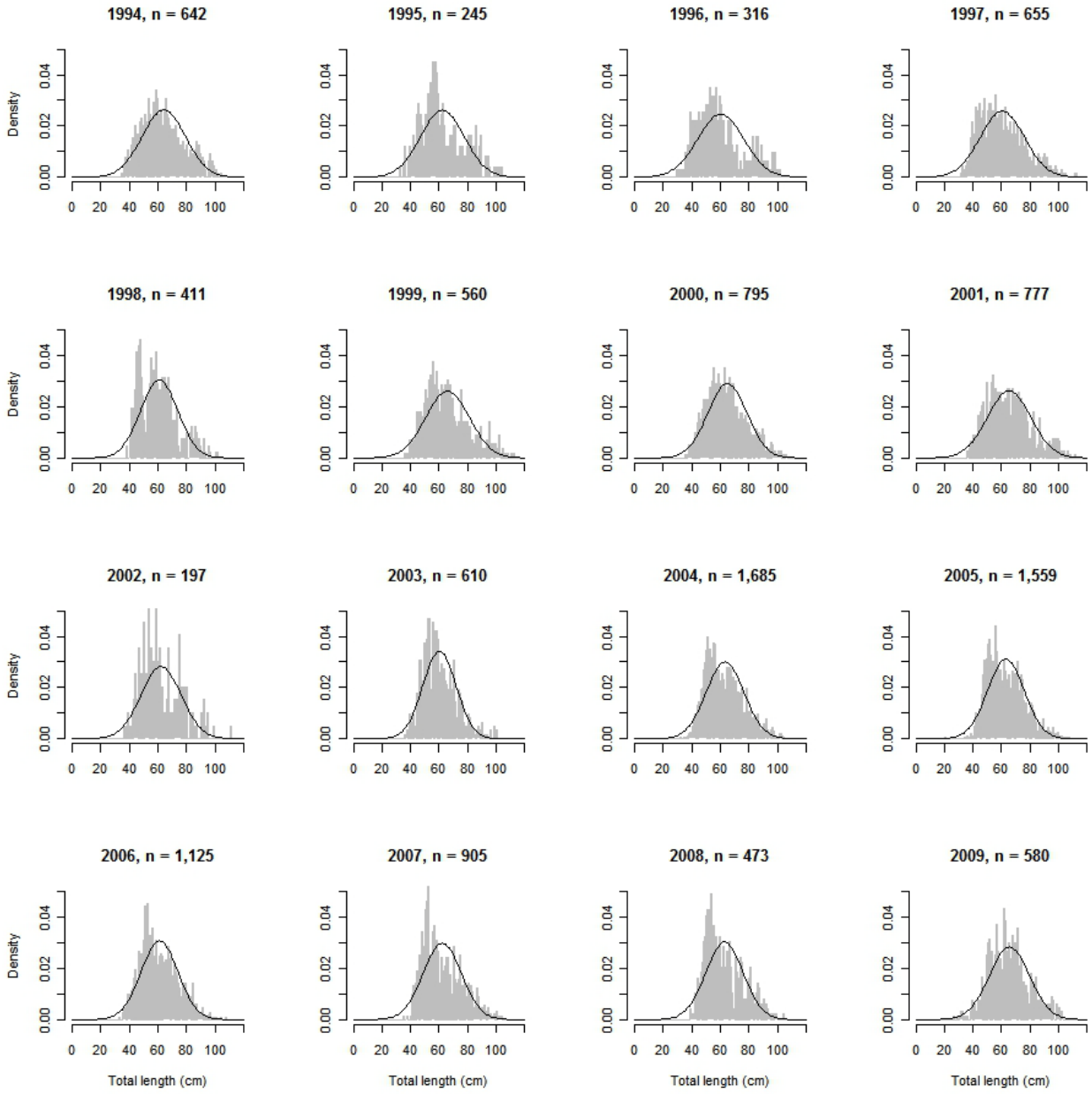


Figure 4-4. Observed annual length composition data for golden tilefish from the northeastern Gulf of Mexico. Data reported from commercial long-line fishery. The trend lines indicate the normal distribution.

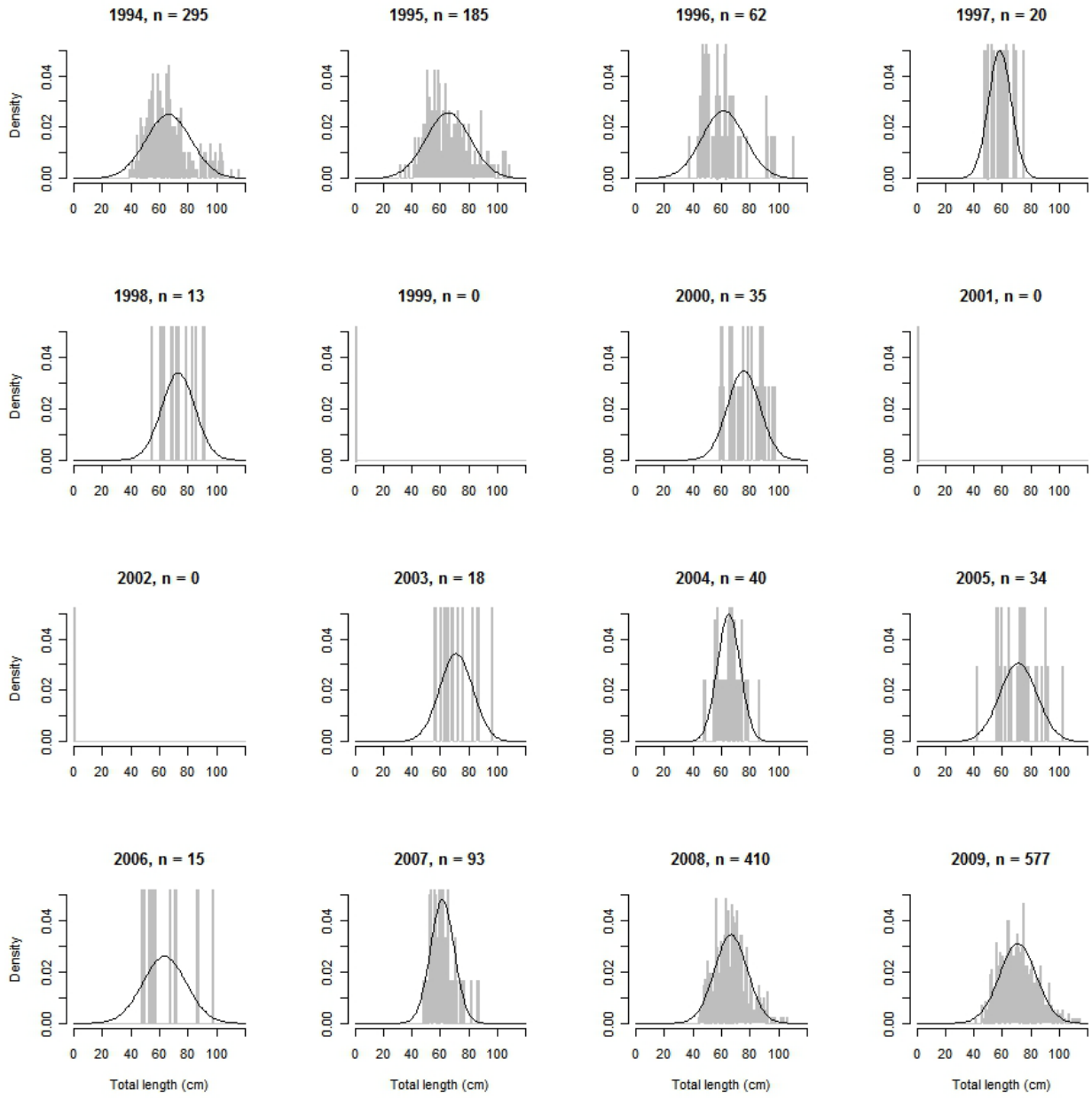


Figure 4-5. Observed annual length composition data for golden tilefish from the northwestern Gulf of Mexico. Data reported from commercial long-line fishery. The trend lines indicate the normal distribution.

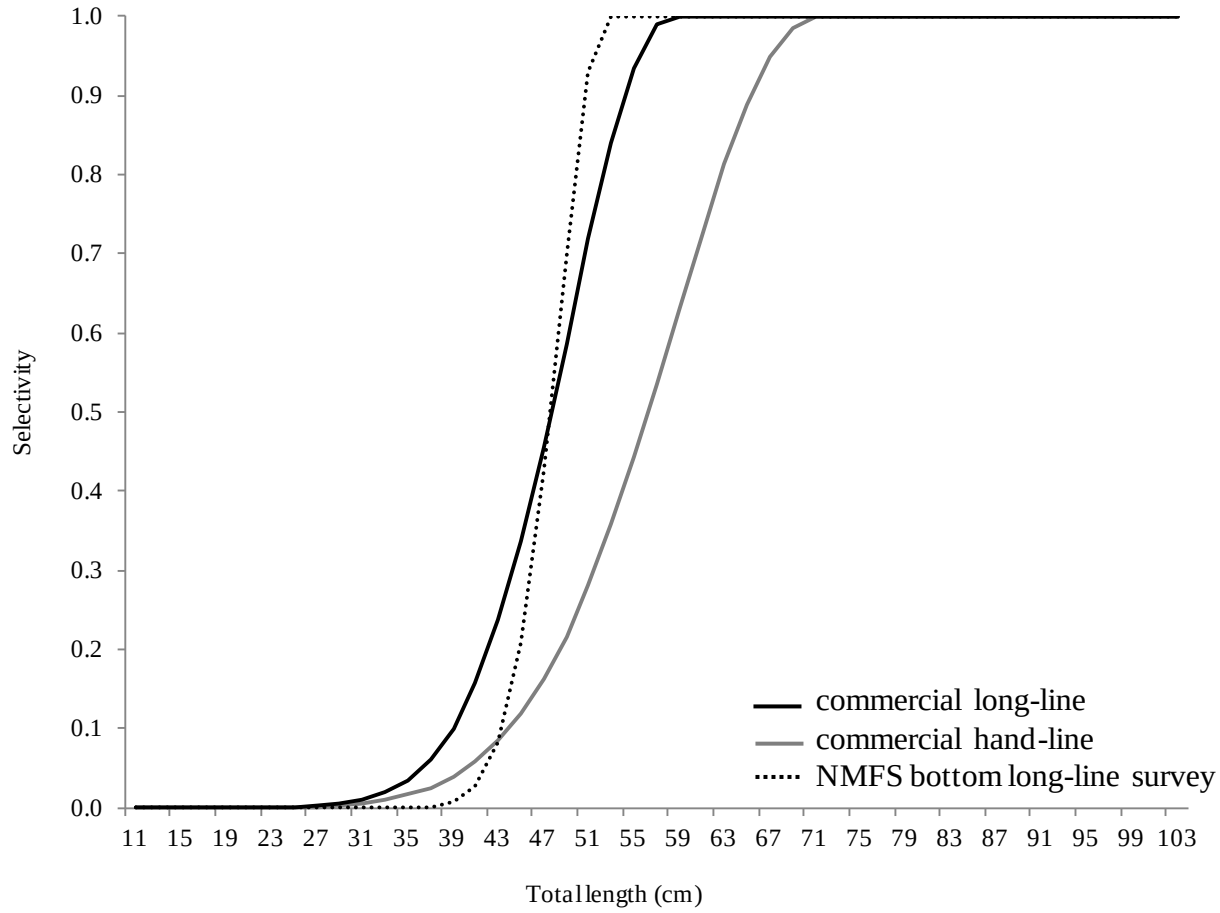


Figure 4-6. Stock synthesis size selectivities for golden tilefish from the northern Gulf of Mexico. Selectivities were fit in stock synthesis using a double logistic regression for commercial long-line (solid black line), commercial hand-line (solid gray line), and NMFS bottom long-line survey (dotted black line).

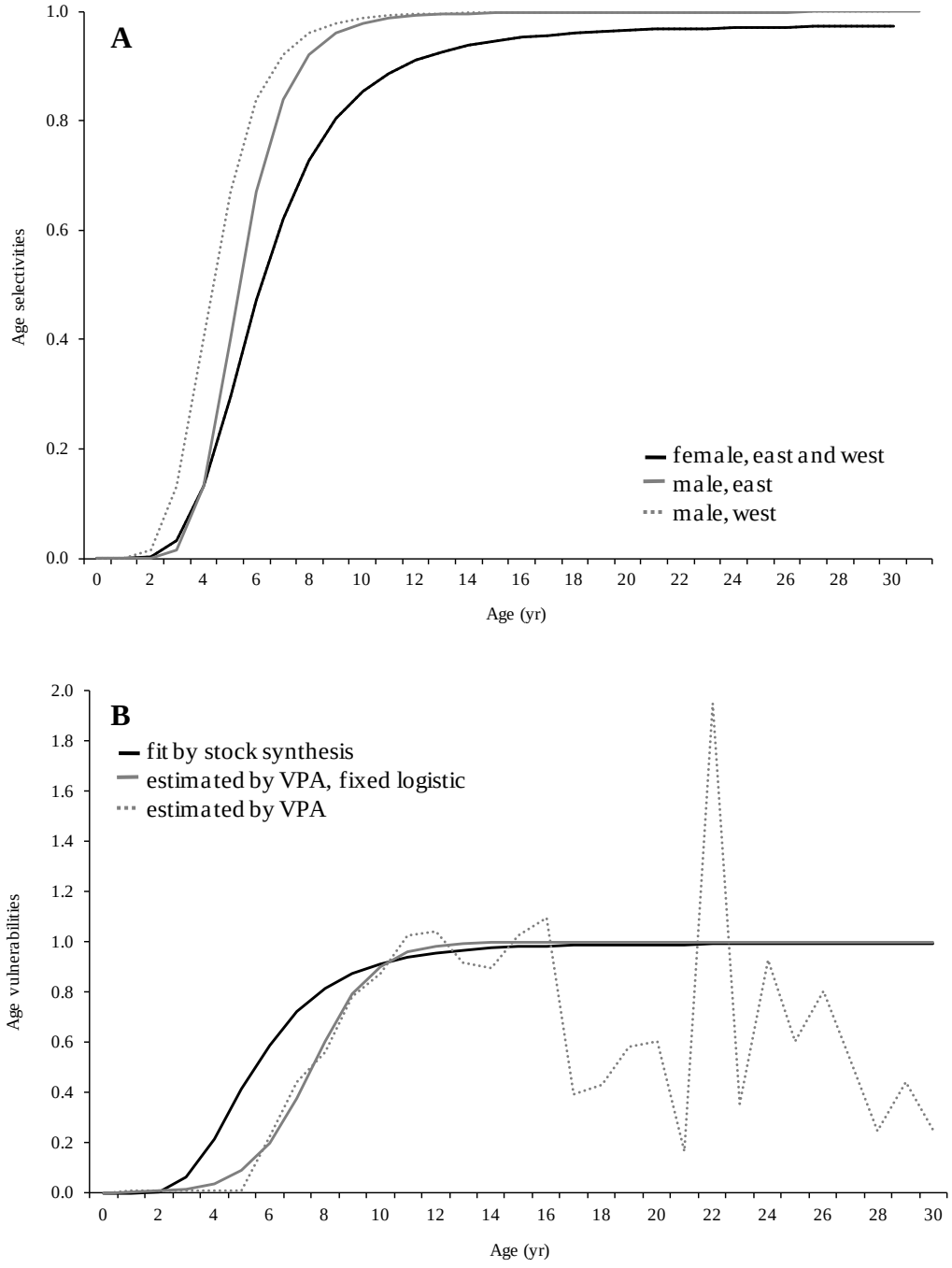


Figure 4-7. Age selectivities for each assessment model for golden tilefish from the northern Gulf of Mexico. (**A**) Stock synthesis selectivities based on logistic regression for commercial long-line fishery by region and gender (female age selectivity same for both regions, solid black line; male east, solid gray line; male west, dotted gray line) and (**B**) stochastic Stock Reduction Analysis vulnerabilities fit within stock synthesis (averaged across region and gender from commercial long-line, solid black line), calculated through VPA and fixed to logistic curve (solid gray line) and observed age vulnerabilities back-calculated through VPA (dotted gray line).

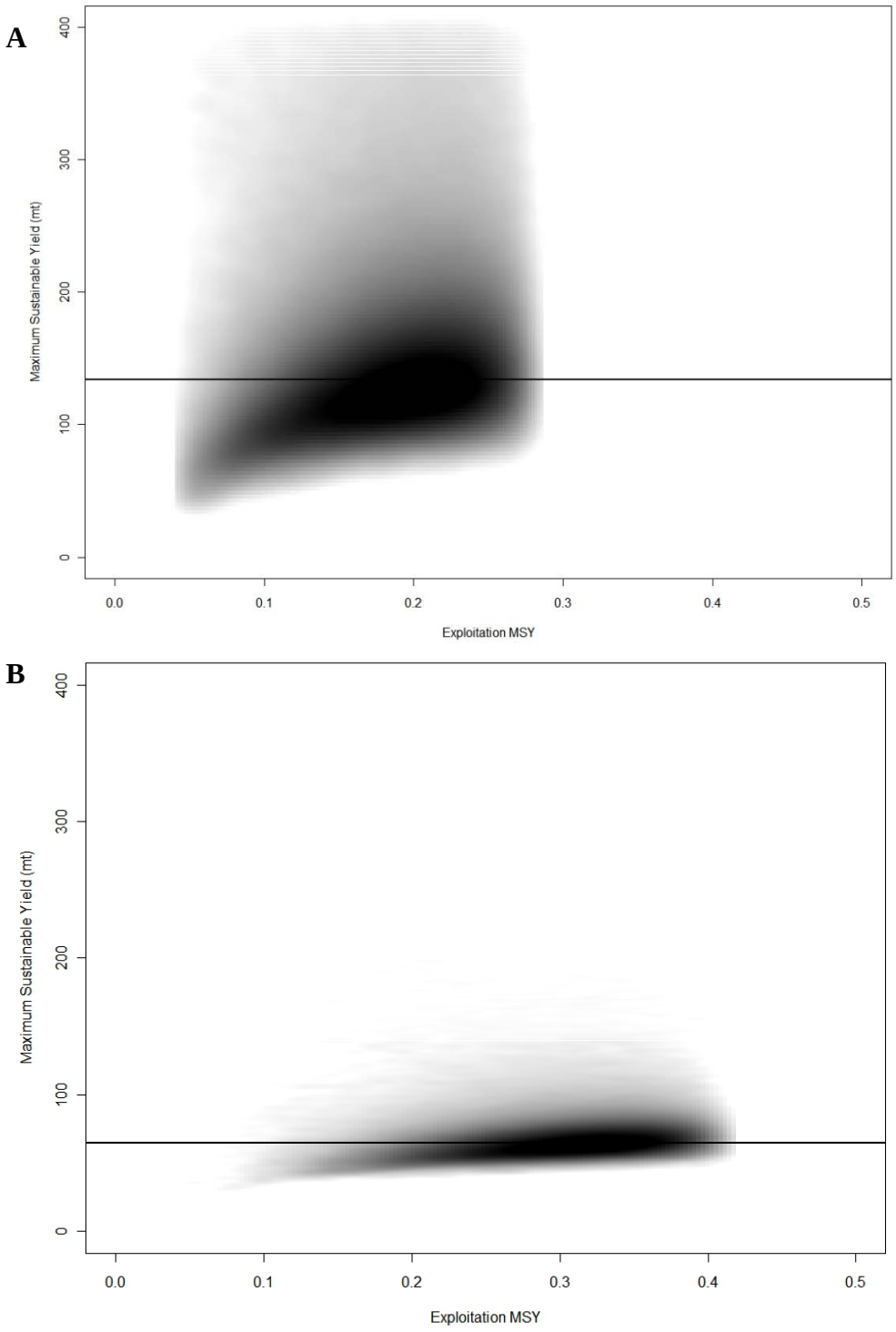


Figure 4-8. Distribution of maximum sustainable yield given the distribution of exploitation at maximum sustainable yield for golden tilefish from the northern Gulf of Mexico from Stochastic SRA. (**A**) East and (**B**) west of the Mississippi River drainage. The solid line indicates the average catch for the given time series for either region. Smooth scatter plot (R Development Core Team, 2011) color symbolizes density of points (grey is lowest and black is highest density).

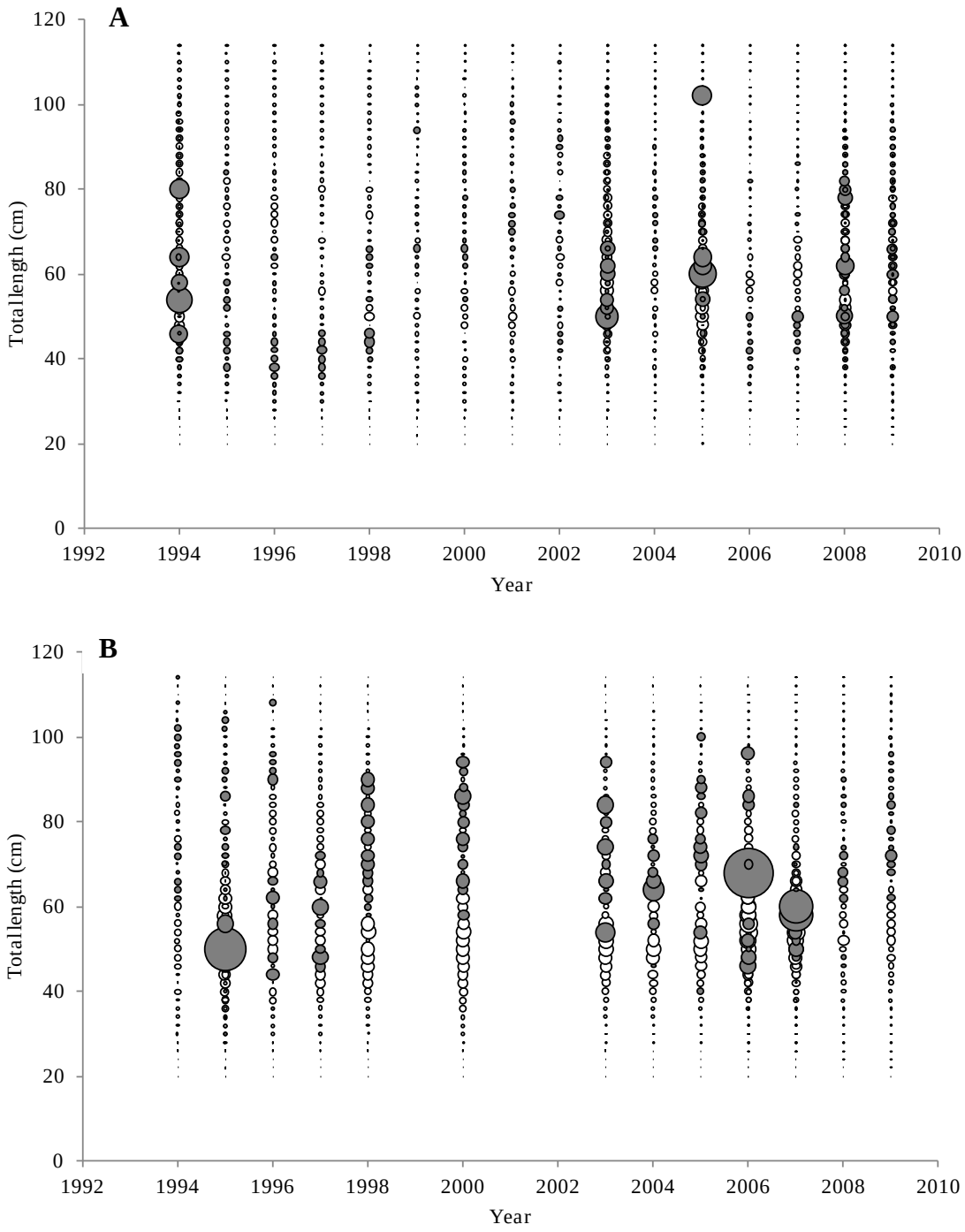


Figure 4-9. Residuals for fits of length composition for golden tilefish from the northern Gulf of Mexico of unknown gender. Data reported from the commercial long-line fishery (**A**) east and (**B**) west of the Mississippi River drainage from Stock Synthesis. Solid circles are positive residuals (i.e., observed greater than predicted) and open circles are negative residuals (i.e., predicted greater than observed). The size of the bubble indicates the sum of residuals at length bin by year (maximum residual sum; east = 0.27, west = 0.93).

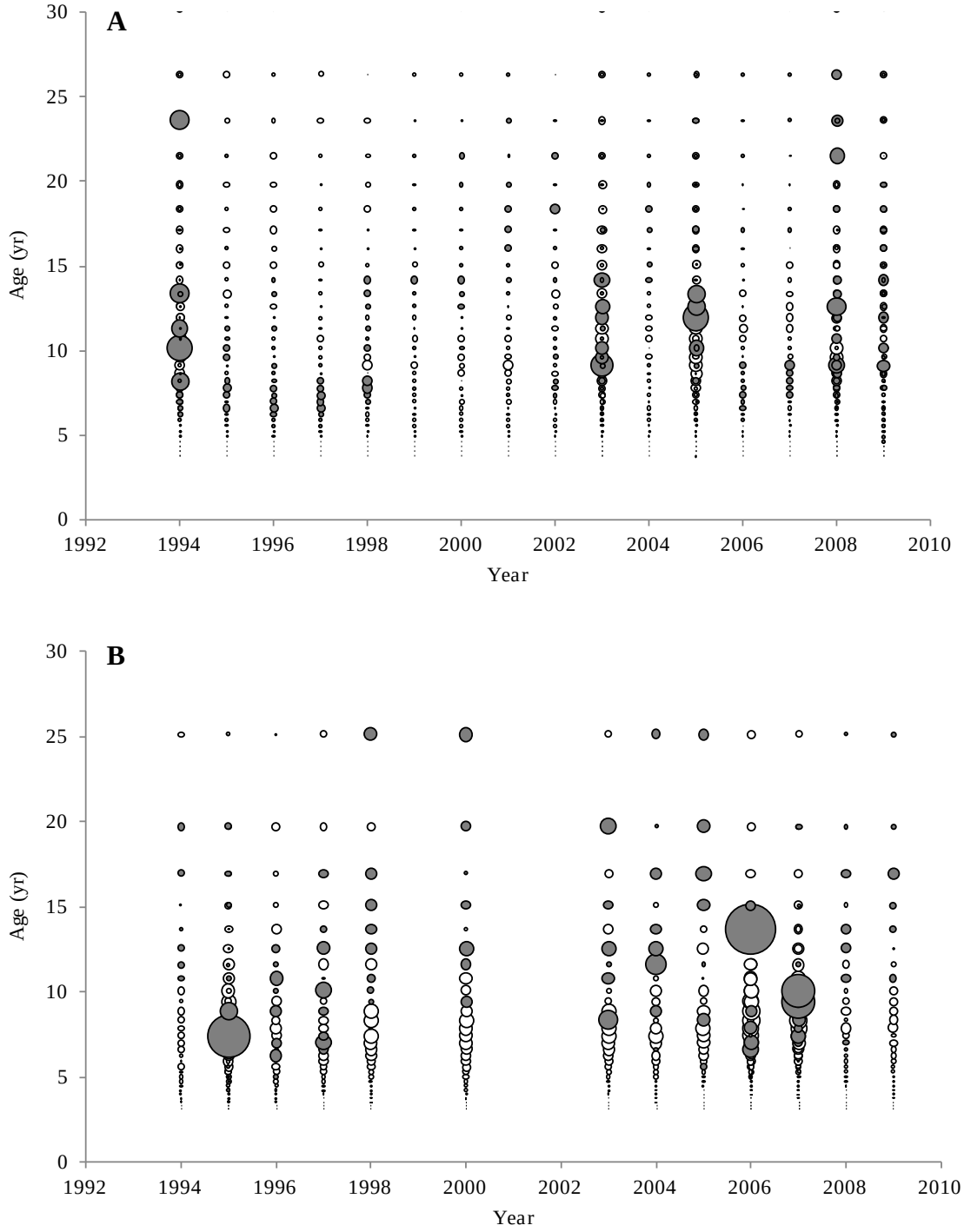


Figure 4-10. Residuals for fits of age composition for golden tilefish from the northern Gulf of Mexico of unknown gender. Data reported from the commercial long-line fishery (**A**) east and (**B**) west of the Mississippi River drainage from Stock Synthesis. Solid circles are positive residuals (i.e., observed greater than predicted) and open circles are negative residuals (i.e., predicted greater than observed). The size of the circle represents the sum of residuals at age by year (maximum residual sum; east = 0.27, west = 0.93).

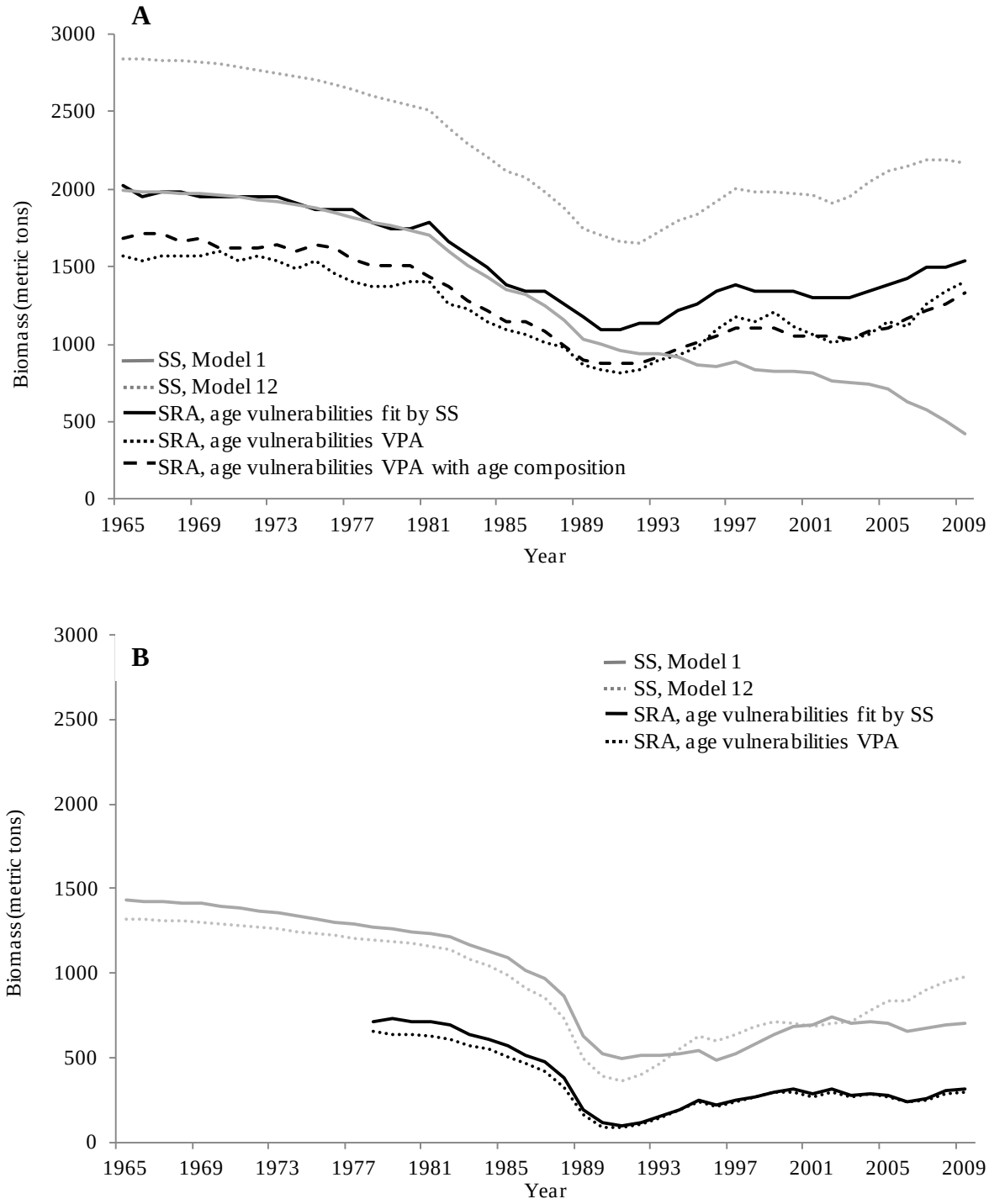


Figure 4-11. Predicted historical biomass from both assessment models for golden tilefish from the northern Gulf of Mexico. Biomass reported by region (**A**) east and (**B**) west of the Mississippi River drainage for stock synthesis (SS) (model 1, solid gray line and model 12, dotted gray line) and stochastic stock reduction analysis (SRA) model (age vulnerabilities fitted through SS, solid black line; age vulnerabilities calculated through VPA, dotted black lines; age composition data included, dashed black line). Biomass from SS is reported as total biomass. Biomass from SRA is reported as vulnerable biomass.

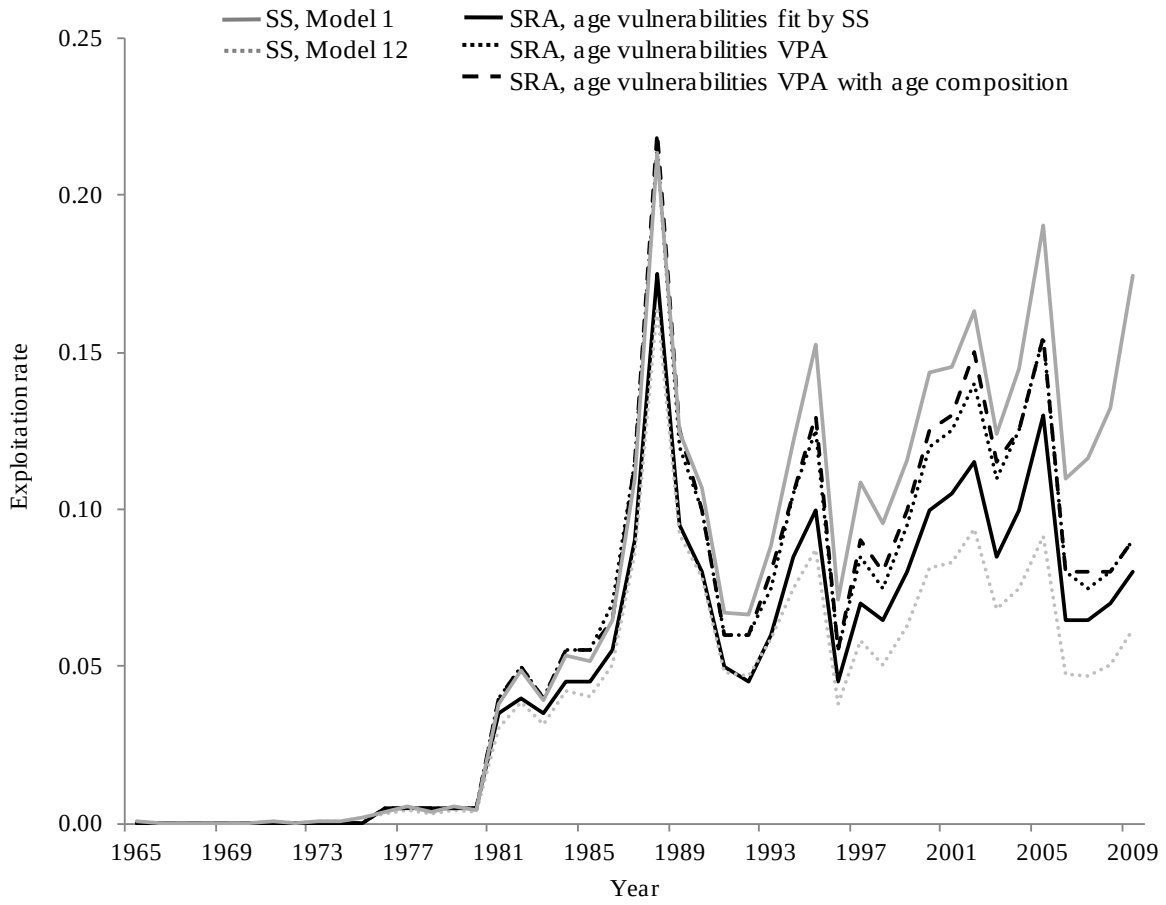


Figure 4-12. Predicted historical exploitation rates from both assessment models for golden tilefish from the northern Gulf of Mexico. Stock synthesis (SS) (model 1, solid gray line and model 12, dotted gray line) and stochastic stock reduction analysis (SRA) model (age vulnerabilities fitted through SS, solid black line; age vulnerabilities calculated through VPA, dotted black lines; age vulnerabilities calculated through VPA with age composition data, dashed black line).

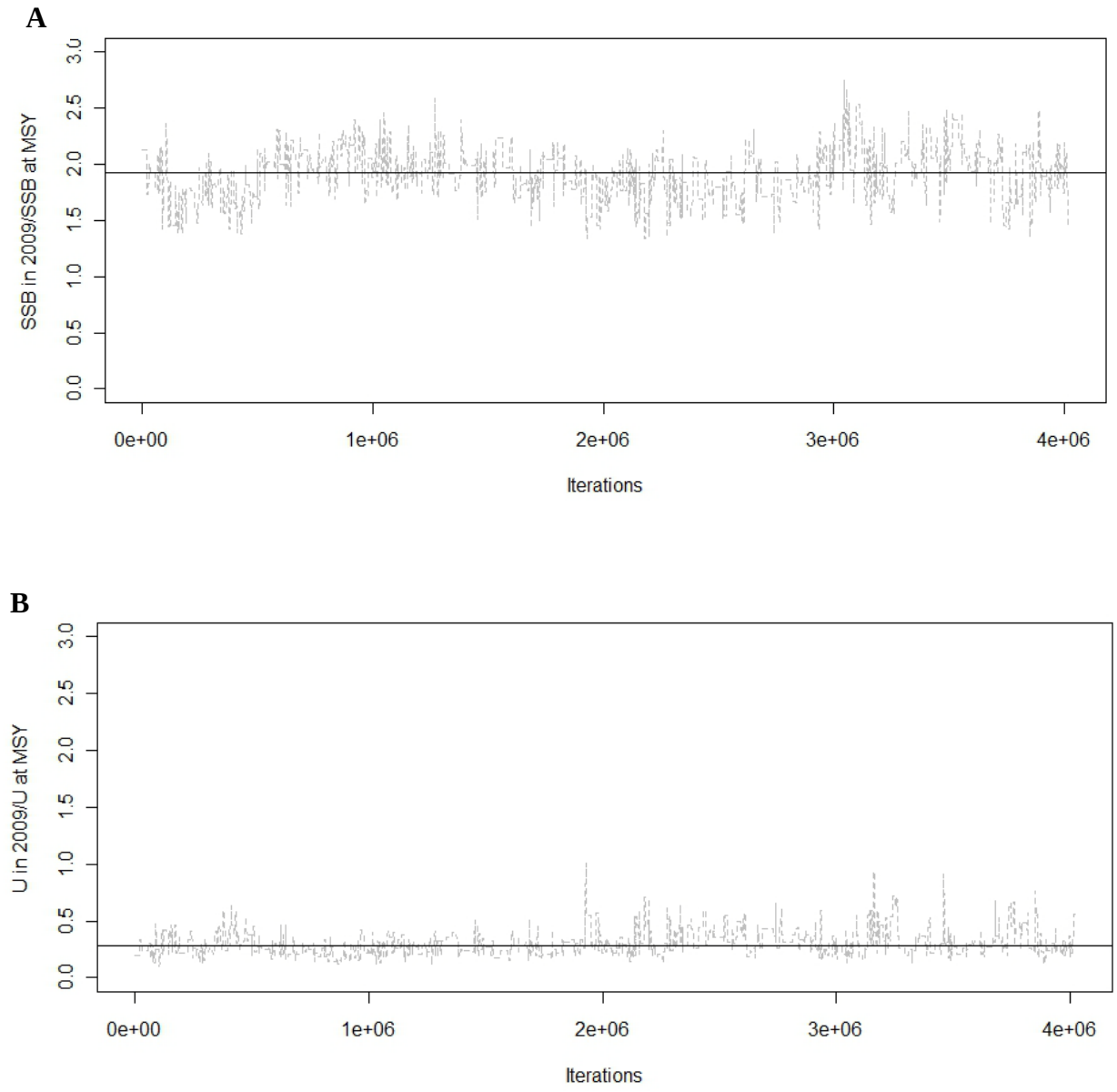


Figure 4-13. Trace plots of the parameters from Stochastic SRA assessment model that determined the stock status of golden tilefish from the northern Gulf of Mexico. (A) Spawning Stock Biomass (SSB) in 2009/ Spawning Stock Biomass (SSB) at Maximum Sustainable Yield (MSY) and (B) Exploitation (U) in 2009/ Exploitation (U) at Maximum Sustainable Yield (MSY) for values from resulting MCMC chains (coda package; R Development Core Team, 2011). Horizontal line represents the median value for each ratio.

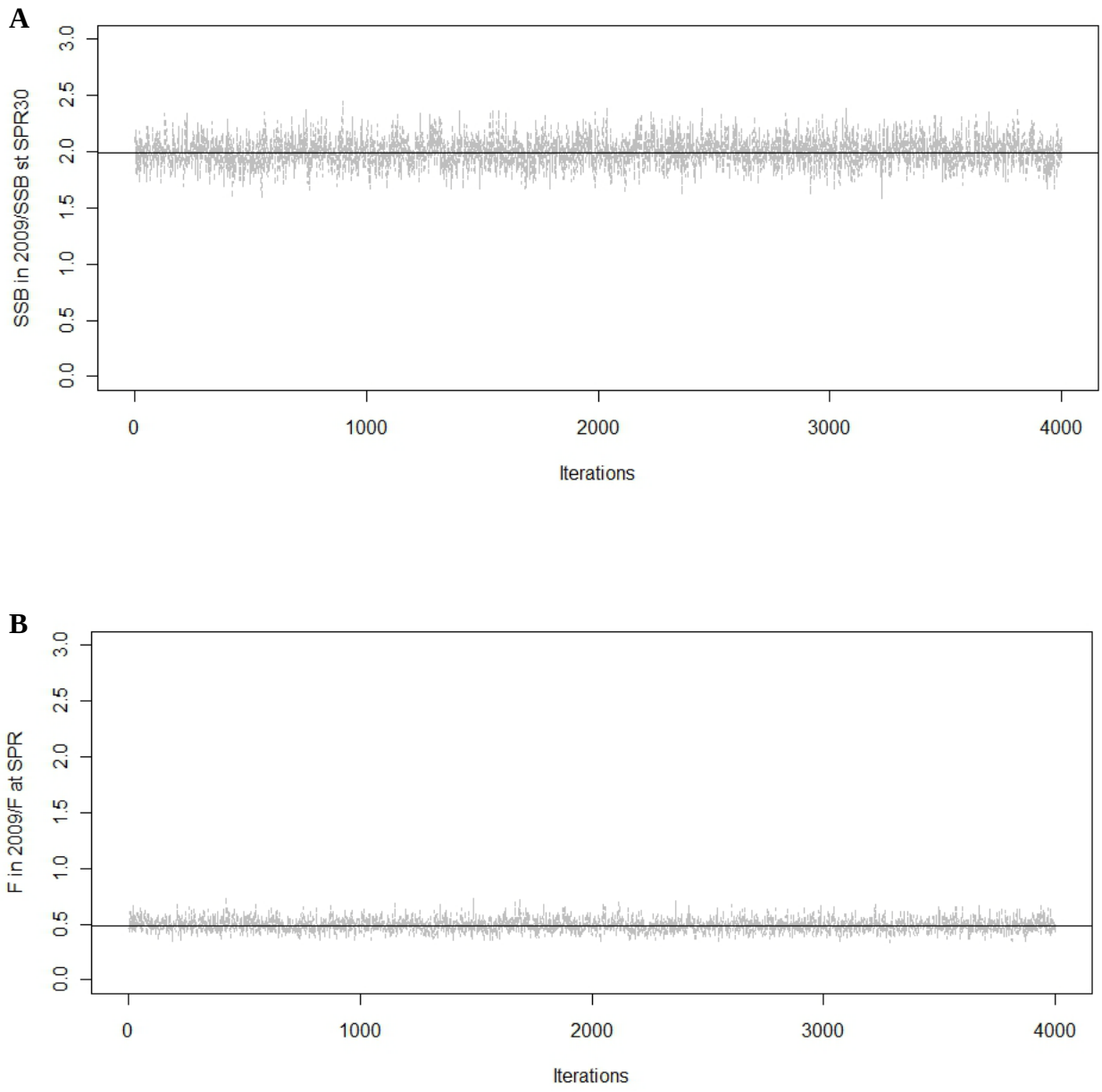


Figure 4-14. Trace plots of the parameters from Stock Synthesis assessment model that determined the stock status for golden tilefish from the northern Gulf of Mexico. (A) Spawning Stock Biomass (SSB) in 2009/ Spawning Stock Biomass (SSB) at Spawning Potential Ratio (SPR) of 30% and (B) Fishing mortality (F) in 2009/Fishing mortality (F) at Spawning Potential Ratio (SPR) of 30% for values from resulting MCMC chains (coda package; R Development Core Team, 2011). Horizontal line represents the median value for each ratio.

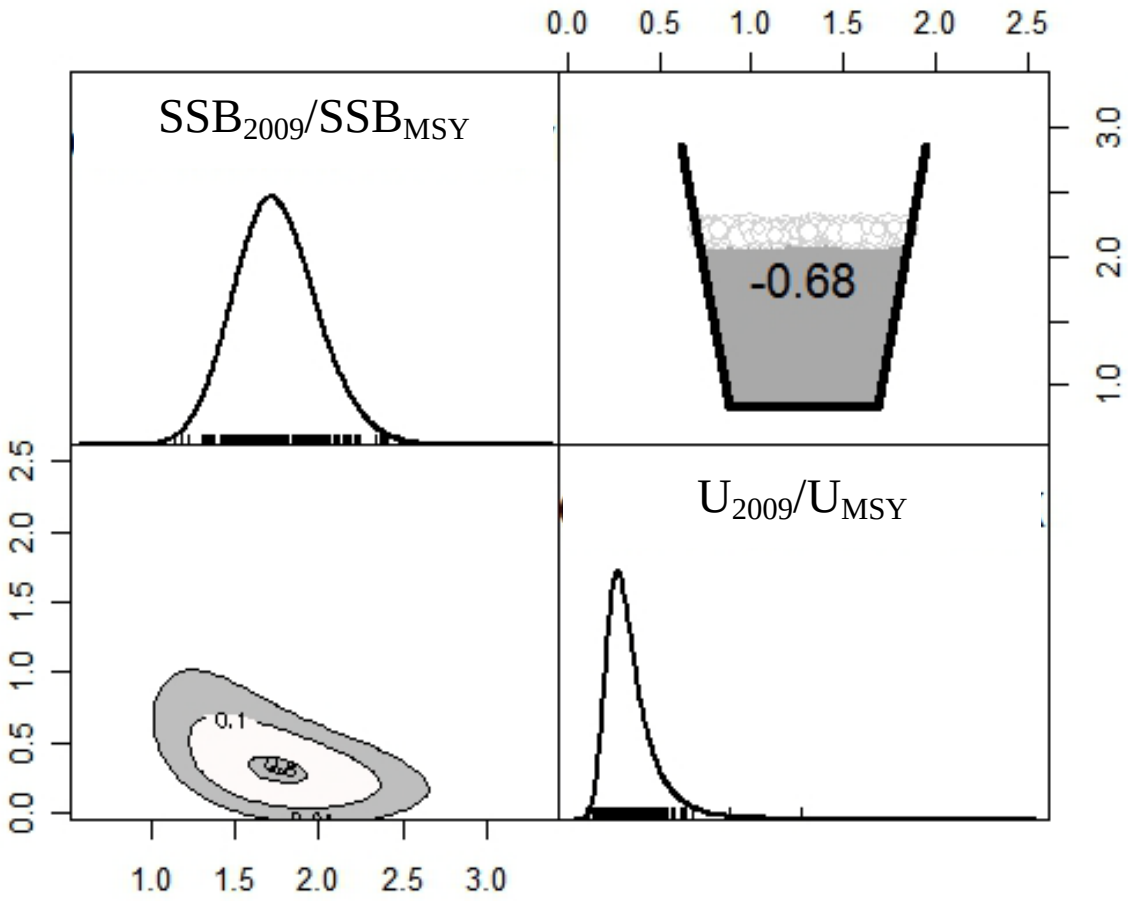


Figure 4-15. Fried egg and beer plot for the parameters from Stochastic SRA assessment model that determined the stock status for golden tilefish from the northern Gulf of Mexico. SSB_{2009}/SSB_{MSY} and U_{2009}/U_{MSY} values from resulting MCMC chains (PBS modelling package; R Development Core Team, 2011). The lower left half is the fried egg (density contours), the upper right half is the glass filled to the correlation point, and the diagonals show densities of the parameters.

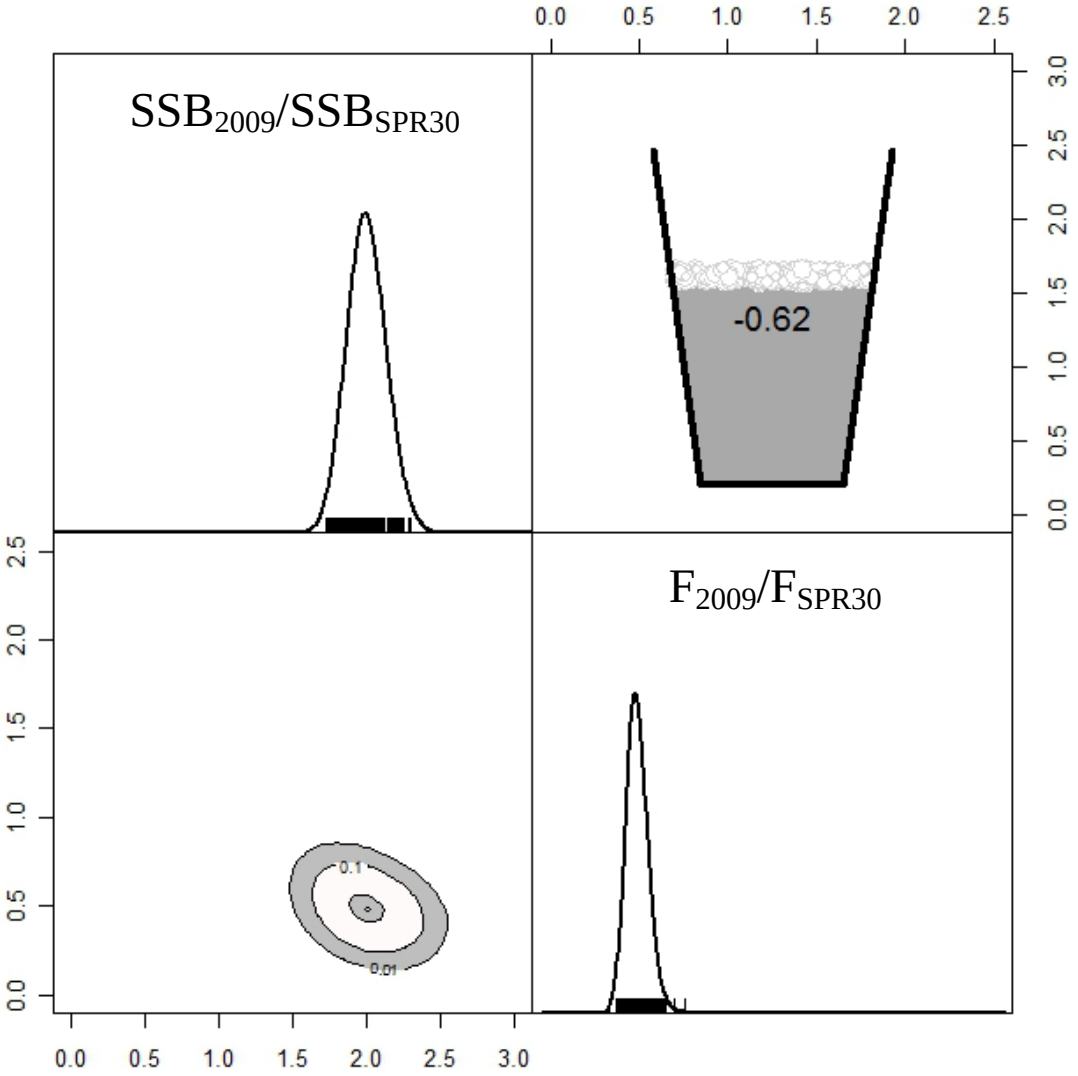


Figure 4-16. Fried egg and beer plot for the parameters from Stock Synthesis assessment model that determined the stock status for golden tilefish from the northern Gulf of Mexico. SSB2009/SSBSPR30 and F2009/FSPR30 values from resulting MCMC chains (PBS modelling package; R Development Core Team, 2011). The lower left half is the fried egg (density contours), the upper right half is the glass filled to the correlation point, and the diagonals show densities of the parameters.

CHAPTER5
CONCLUSION

Importance of Sampling

One of the key messages from this dissertation (and a reason for seeking my degree) is that for stock assessments to provide meaningful results to inform management policies, these stock assessments must use the best available data and assessment scientists should be knowledgeable on data limitations. It is very important to understand the methodologies of data collection. My doctoral research relied on federally funded long-term data collection and routine biological sampling. My dissertation included three main objectives: 1) the validation of the timing of band deposition in sagittal otoliths, 2) the description of the reproductive strategy, and 3) the prediction of the stock status of golden tilefish from the Gulf of Mexico. For each of these objectives, sampling from long-term fishery dependent monitoring programs for biological data (lengths) and samples (e.g., otoliths, gonads), along with effort and landings data and sampling from fishery independent surveys for biological samples and abundance data were critical to my research results. There are caveats in the collection of both fishery dependent and independent data that need to be understood to use these data sets appropriately.

Fishery dependent data can be advantageous in that it is more generally available for more species (all that have a management plan), inexpensive, and often routinely collected covering a broad geographic area (Begg, 2005). I relied on the long-term fishery-dependent program the NOAA Fisheries Service, Southeast Fisheries Science Center (SEFSC) Trip Interview Program (TIP) for collecting biological data and samples and the NOAA Fisheries Service, SEFSC Coastal Fisheries Logbook Program (CFLP), for relative abundance data. One caveat of these data is the size-selective nature of fisheries. A fishery can be size-selective due to a variety of fishery regulations of minimum size limit, an upper slot limit, gear restriction

(e.g., hook size, bait type), area closures, or depth restrictions. Another caveat of fishery dependent data is how TIP port agents collect biological samples from the landed catch. The TIP port agents' guidelines for biological sampling are to attempt to purposely sample landings of multiple species from one or many fishing vessels at one time, which has lead to some species being under sampled while other more economically important species are oversampled. A third caveat of fishery dependent data is the behavior of commercial fishers. The CFLP is a self-reporting program relying on the cooperation of fishers to accurately report where they fish (e.g., NMFS statistical shrimp grid), what they catch (e.g., type of fish landed, bycatch, discarded), and how they fish (e.g., number of days, number of hooks, length of mainline), and interpreting trends in abundance data may not be straightforward. Abundance data are highly influenced by fishers' behaviors. A fishers behavior can be affected by the current economics (i.e., cost per pound, fuel price, boat slip price), as well as technological advances (i.e., vessel electronics, changes in gear), which can alter the species being fished and the location of fishing.

I was able to address several of these limitations common in fishery dependent data through collaborating with TIP port agents. The TIP port agents are the primary contact for NOAA Fisheries Service with commercial fishers and are responsible for the collection of biological samples and in some Gulf of Mexico states monitor the reporting of landings data. My research objectives required specific biological sampling (e.g., both sagittal otoliths, gonads), but during routine TIP port agent biological sampling only one sagittal otolith is obtained and gonad tissue is not collected given that a majority of commercially harvested fish are gutted at-sea. I worked with TIP port agents by first explaining the necessity for specific biological samples and second by describing the type of biological information that would be gained from these samples. The TIP port agents then contacted willing commercial captains that agreed to

return to port with whole fish and allowed TIP port agents to have more time to process fish for both sagittal otoliths and gonad tissue. Through the efforts of both TIP port agents and cooperative commercial captains supplemental biological samples were collected and contributed to the sampling needs for my first two research objectives.

Fishery independent surveys provide an opportunity to collect data without the influences of the dynamics of a fishery (see caveats above). My research relied on two fishery independent surveys for biological samples and abundance data. However, abundance data collected during the long-term fishery independent survey was limited since only 10% of the survey's time is spent in depths associated with golden tilefish. I designed the second fishery independent survey with two objectives: 1) to estimate abundances of tilefish and deepwater grouper and 2) to characterize the spawning season of tilefish and deepwater grouper. This survey had two sampling methodologies to meet each objective, 1) randomized and stratified by depth (100 – 400 m) bottom long-line survey (2 nm mainline, 200 – 4 m gangions with #15 circle hooks) and 2) conduct site-specific monthly sampling using bottom long-line gear. This one year project also contributed to the monthly gonad samples necessary to describe the reproductive seasonality and strategy of golden tilefish. Although, this project was only conducted for one year, its abundance data can be used as a baseline for future long-term bottom long-line survey, specifically for tilefish and deepwater groupers.

Fishery Management

In the United States, fishery management is governed by the Magnuson-Stevens Act (NOAA, 2009). This act provides the framework to prevent overfishing by permitting fishing to occur within three levels of fishing (annual catch limit, acceptable biological catch, fishing at overfishing level). The status of a fish stock can be described as: 1) overfished if the current level of biomass has declined or 2) undergoing overfishing if the current level of fishing

mortality has declined below a level capable of producing a maximum sustainable yield NOAA, 2009). In 2004, a total allowable catch (TAC) of 200 metric tons for golden tilefish in the Gulf of was established to prevent overfishing. This regulation was based, not on biological information, but on the average of landings for the previous five years of fishing (prior to 2004).

My dissertation provided the much needed biological data to better inform management decisions for golden tilefish. In my first objective, I provided evidence for the longevity of golden tilefish, as well as, the uncertainty associated with traditional age estimates. This information is of particular importance, especially when predicting the productivity of a stock. I also provided evidence of golden tilefish to be classified as protogynous hermaphrodites. This type of reproductive strategy can have confounding affects to a population given the size-selective nature of fishing (removing the larger, older fish, predominately male). I applied this biological information to two assessment models that varied in complexity. These models agreed that golden tilefish stock in the Gulf of Mexico was not overfished nor was the stock undergoing overfishing. Thus, I conclude that the current fishery management regulation of total allowable catch of 200 metric tons is adequate in maintaining the golden tilefish population biomass at an optimal level.

LIST OF REFERENCES

Able, K. W., C. B. Grimes, R. A. Cooper, and J. R. Uzmann.
1982. Burrow construction and behavior of tilefish, *Lopholatilus chamaeleonticeps*, in the Hudson Submarine Canyon. Environ. Biol. Fishes 7:199-205.

Able, K. W., C. B. Grimes, R. S. Jones, and D. C. Twichell.
1993. Temporal and spatial variation in habitat characteristics of tilefish (*Lopholatilus chamaeleonticeps*) off the east coast of Florida. Bull. Mar. Sci. 53:1013-1026.

Adams, S.
2003. Morphological ontogeny of the gonad of three plectropomid species through sex differentiation and transition. J. Fish Biol. 63:22-36.

Adkison, M. D.
2009. Drawbacks of complex models in frequentist and Bayesian approaches to natural-resource management. Ecol. Appl. 19:198-205.

Alonzo, S. H., and M. Mangel.
2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. Fish. Bull. 102:1-13.

Anderson, R. O., and R. M. Neumann
1996. Length, weight, and associated structural indices. *In* Fisheries Techniques, 2nd edition. (B. R. Murphy, and D. W. Willis, eds.), p. 447-482. American Fisheries Society, Bethesda, Maryland.

Andrews, A. H.
2009a. Final Report. Lead-radium dating of golden tilefish (*Lopholatilus chamaeleonticeps*). MARFIN. 07MFIH007.
2009b. Lead-radium dating of two deep-water fishes from the southern hemisphere, Patagonian toothfish (*Dissostichus eleginoides*) and orange roughy (*Hoplostethus atlanticus*). Ph.D. Dissertation, 192 p. Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa.

Andrews, A. H., G. M. Caillet, K. H. Coale, K. M. Munk, M. M. Mahoney, and V. M. O'Connell.
2002. Radiometric age validation of the yelloweye rockfish (*Sebastes ruberrimus*) from southeastern Alaska. Aust. J. Mar. Freshw. Res. 53:139-146.

Andrews, A. H., K. H. Coale, J. L. Nowicki, C. Lundstrom, Z. Palacz, E. J. Burton, and G. M. Cailliet.
1999. Application of an ion-exchange separation technique and thermal ionization mass spectrometry to ^{226}Ra determination in otoliths for radiometric age determination of long-lived fishes. Can. J. Fish. Aquat. Sci. 56:1329-1338.

Andrews, A. H., D. M. Tracey, and M. R. Dunn.
2009. Lead-radium dating of orange roughy (*Hoplostethus atlanticus*): validation of a centenarian life span. Can. J. Fish. Aquat. Sci. 66:1130-1140.

Armsworth, P. R.
2001. Effects of fishing on a protogynous hermaphrodite. Can. J. Fish. Aquat. Sci. 58:568-578.

Asoh, K.
2003. Gonadal development and infrequent sex change in a population of the humbug damselfish, *Dascyllus aruanus*, in continuous coral-cover habitat. Mar. Biol. 142:1207-1218.

Atz, J. W.
1964. Intersexuality in fishes. *In* Intersexuality in Vertebrates Including Man (C. N. Armstrong, and A. J. Marshall, eds.), p. 145-232. Academic Press, London.

Baird, T. A.
1988. Female and male territoriality and mating system of the sand tilefish, *Malacanthus plumieri*. Environ. Biol. Fishes 22:101-116.

Baker, J., M. S., and C. A. Wilson.
2001. Use of bomb radiocarbon to validate otolith section ages of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico. Limnol. Oceanogr. 46:1819-1824.

Bannerot, S., W. F. Fox, and J. E. Powers
1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. *In* Tropical Snappers and Groupers: Biology and Fisheries Management (J. J. Polovina, and S. Ralston, eds.), p. 561-603. Westview Press, Boulder.

Baroiller, J. F., Y. Guiguen, and A. Fostier.
1999. Endocrine and environmental aspects of sex differentiation in fish. Cell. Mol. Life Sci. 55:910-931.

Bateman, K. S., G. D. Stentiford, and S. W. Feist.
2004. A ranking system for the evaluation of intersex condition in European flounder (*Platichthys flesus*). Environ. Toxicol. Chem. 23:2831-2836.

Begg, G. A.
2005. Life history parameters. *In* Stock Identification Methods, Applications in Fishery Science (S. X. Cadrin, K. D. Friedland, and J. R. Waldman, eds.), p. 119-150. Elsevier Academic Press, Amsterdam.

Bennett, J. T., G. W. Boehlert, and K. K. Turekian.
1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from 210 Pb/226Ra measurements in otoliths. Mar. Biol. 71:209-215.

Broker, W. S., and T. S. Peng.
1982. Tracers in the Sea, Lamont-Doherty Geological Observatory, Columbia University, Palisades, New York.

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri.
2011. A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish. 3:52-70.

Cailliet, G. M., A. H. Andrews, E. J. Burton, D. L. Watters, D. E. Kline, and L. A. Ferry-Graham.
2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? Experimental Gerontology 36:739-764.

Campana, S. E.
1997. Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock *Melanogrammus aeglefinus*. Mar. Ecol. Prog. Ser. 150:49-56.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59:197-242.

Campana, S. E., K. C. T. Zwanenburg, and J. N. Smith.
1990. $^{210}Pb/^{226}Ra$ determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47:163-165.

Candy, S. G., G. B. Nowara, D. C. Welsford, and J. P. McKinlay.
2012. Estimating an ageing error matrix for Patagonian toothfish (*Dissostichus eleginoides*) otoliths using between-reader integer errors, readability scores, and continuation ratio models. Fish. Res. 115-116:14-23.

Choat, J. H., L. M. Axe, and D. C. Lou.
1996. Growth and longevity in fishes of the Family Scaridae. Mar. Ecol. Prog. Ser. 145:33-41.

Cole, K. S.
1990. Patterns of gonad structure in hermaphroditic gobies (Teleostei Gobiidae). Environ. Biol. Fishes 28:125-142.
2002. Gonad morphology, sexual development, and colony composition in the obligate coral-dwelling damselfish *Dascyllus aruanus*. Mar. Biol. 140:151-163.

Condomines, M., and S. Rihs.
2006. First ^{226}Ra-^{210}Pb dating of a young speleothem. Earth Planet. Sc. Lett. 250:4-10.

Conser, R. J., and J. E. Powers.
1990. Extension of the ADAPT VPA tuning method designed to facilitate assessment work on tuna and swordfish stocks. ICCAT Collect. Vol. Sci. Pap. 32:461-468.

Cook, M., G. R. Fitzhugh, and J. S. Franks.
2009. Validation of yellowedge grouper, *Epinephelus flavolimbatus*, age using nuclear bomb-produced radiocarbon. Environ. Biol. Fishes 86:461-472.

Cope, J.M.
In press. Implementing a statistical catch-at-age model (Stock Synthesis) as a tool for deriving overfishing limits in data-limited situations. Fish. Res.

Cotter, A. J. R., L. Burt, C. G. M. Paxton, C. Fernandez, S. T. Buckland, and J. X. Pan.
2004. Are stock assessment methods too complicated? Fish Fish. 5:235-254.

Cowan, J., J. H., R. L. Shipp, I. Bailey, H. K., and D. W. Haywick.
1995. Procedure for rapid processing of large otoliths. Trans. Am. Fish. Soc. 124:280-282.

Dooley, J. K.
1978. Systematics and biology of the tilefishes (Perciformes: Branchiostegidae and Malacanthidae), with description of two new species. NOAA Tech. Rep. 411:1-78.

Drillings, C. C., and M. S. Grober.
2005. An initial description of alternative male reproductive phenotypes in the bluebanded goby, *Lythrypnus dalli* (Teleostei, Gobiidae). Environ. Biol. Fishes 72:361-372.

Elorduy-Garay, J. F., and S. Ramírez-Luna.
1994. Gonadal development and spawning of female ocean whitefish, *Caulolatilus princeps* (Pisces: Branchiostegidae) in the Bay of La Paz, B.C.S., Mexico. J. Fish Biol. 44:553-566.

Erickson, D. L., and G. D. Grossman.
1986. Reproductive demography of tilefish from the South Atlantic Bight with a test for the presence of protogynous hermaphroditism. Trans. Am. Fish. Soc. 115:279-285.

Erzini, K.
1990. Sample size and grouping of data for length-frequency analysis. Fish. Res. 9:355-366.

Fanning, K. A., J. A. Breland, and R. H. Byrne.
1982. Radium-226 and Radon-222 in the coastal waters of west Florida: high concentrations and atmospheric degassing. Science 215:667-670.

Fennessy, S. T., and Y. Sadovy.
2002. Reproductive biology of a diandric protogynous hermaphrodite, the serranid *Epinephelus andersoni*. Aust. J. Mar. Freshw. Res. 53:147-158.

Fenton, G. E., S. A. Short, and D. A. Ritz.
1991. Age-determination of orange roughy, *Hoplostethus atlanticus* (Pisces, Trachichthyidae) using ^{210}Pb:^{226}Ra disequilibria. Mar. Biol. 109:197-202.

Forrest, R. E., S. J. D. Martell, M. C. Melnychuk, and C. J. Walters.
2008. An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity. Can. J. Fish. Aquat. Sci. 65:286-296.

Freeman, B. L., and S. C. Turner.
1977. Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean. NOAA Tech. Ser. Rep. NMFS-NEFSC 5:1-41.

Gerritsen, H. D., and D. McGrath.
2007. Precision estimates and suggested sample sizes for length-frequency data. Fish. Bull. 105:116-120.

Gertseva, V. V., and J. M. Cope.
2011. Population dynamics of splitnose rockfish (*Sebastes diploproa*) in the Northeast Pacific Ocean. Ecol. Model. 222:973-981.

Goode, G. B., and T. H. Bean.
1880. Description of a new genius and species of fish, *Lopholatilus chamaeleonticeps*, from the south coast of New England Nineteenth Proceedings of the United States National Museum 2:205-209.

Goodyear, C. P.
1997. Fish age determined from length: an evaluation of three methods using simulated red snapper data. Fish. Bull. 95:39-46.

Grace, M., D. E. de Anda Fuentes, and J. L. Castillo-Géniz.
2004. Biological surveys to assess the relative abundance and distribution of coastal sharks and teleosts of the Mexican Gulf of Mexico; 1997, 1998, 2001, and 2002. Proc. Gulf Caribb. Fish. Inst. 55:271-279.

Grimes, C. B., K. W. Able, and R. S. Jones.
1986. Tilefish, *Lopholatilus chamaeleonticeps*, habitat, behavior and community structure in Mid-Atlantic and southern New England waters. Environ. Biol. Fishes 15:273-292.

Grimes, C. B., C. F. Idelberger, K. W. Able, and S. C. Turner.
1988. The reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, from the United States Mid-Atlantic Bight, and the effects of fishing on the breeding system. Fish. Bull. 86:745-762.

Grimes, C. B., S. C. Turner, and K. W. Able.
1983. A technique for tagging deep-water fish. Fish. Bull. 81:663-666.

Grimes, C. B., and S. C. Turner
1999. The complex life history of tilefish *Lopholatilus chamaeleonticeps* and vulnerability to exploitation. *In* Life in the Slow Lane, Ecology and Conservation of Long-Lived Marine Animals (J. A. Musick, ed.), p. 17-26. American Fisheries Society, Bethesda, MD.

GMFMC (Gulf of Mexico Fisheries Management Council).
2011. Commercial Fishing Regulations for Gulf of Mexico Federal Waters. Tampa, FL.

Hale, L.
2011. Bottom longline fishery bycatch of golden tilefish from observer data. 6 p. SEDAR25-DW11. Southeast, Data, Assessment, and Review, North Charleston, SC.

Hall, N. G.
2003. Data requirements of multispecies, spatial, and ecosystem models. Population dynamics for fisheries management 106-116 p. Australian Society for Fish Biology Proceedings.

Harris, M. J., and G. D. Grossman.
1985. Growth, mortality, and age composition of a lightly exploited tilefish substock off Georgia. Trans. Am. Fish. Soc. 114:837-846.

Harris, P. J.
2005. Validation of ages for species of the deepwater snapper/grouper complex off the southeastern coast of the United States. 12 p. MARFIN NA17FF2870.

Harris, P. J., S. M. Padgett, and P. T. Powers.
2001. Exploitation related changes in the growth and reproduction of tilefish and the implications for the management of deepwater fisheries. AFS Symposium 25:155-210.

Heppell, S. S., S. A. Heppell, F. C. Coleman, and C. C. Koenig.
2006. Models to compare management options for a protogynous fish. Ecol. Appl. 16:238-249.

Highly Migratory Species.
2007. Stock assessment report small coastal shark complex: Atlantic Sharpnose, Blacknose, Bonnethead, and Finetooth Shark. 395 p. NOAA/NMFS Highly Migratory Species Management Division, Silver Spring, MD.

Hilborn, R.
2003. The state of the art in stock assessment: where we are and where we are going. Sci. Mar. 67:15-20.

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty, Chapman and Hall, London.

Hinck, J. E., V. S. Blazer, C. J. Schmitt, D. M. Papoulias, and D. E. Tillitt.
2009. Widespread occurrence of intersex in black basses (*Micropterus* spp.) from US rivers, 1995–2004. Aquat. Toxicol. 95:60-70.

Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 81:898-903.
2007. Evaluation of TIP sampling design, field protocols, and data analysis procedures. 15 p. Semi-Annual Progress Report for the period 4/1/07 - 9/30/07 for NOAA/NMFS Grant # NA05NMF4741247 with NMFS-SERO.

Hoffman, S. G., M. P. Schildhauer, and R. R. Warner.
1985. The costs of changing sex and the ontogeny of males under contest competition for mates. Evolution 39:915-927.

Hunter, J. R., and B. J. Macewicz.
1985. Measurement of spawning frequency in multiple spawning fishes. NOAA Tech. Rep. 36:79-94.

Jones, R. S., E. J. Gutherz, W. R. Nelson, and G. C. Matlock.
1989. Burrow utilization by yellowedge grouper, *Epinephelus flavolimbatus*, in the northwestern Gulf of Mexico. Environ. Biol. Fishes 26:277-284.

Kalish, J. M.
1995. Application of the bomb radiocarbon chronometer to the validation of redfish *Centroberyx affinis* age. Can. J. Fish. Aquat. Sci. 52:1399-1405.

Kastelle, C. R., D. K. Kimura, and S. R. Jay.
2000. Using $^{210}Pb/^{226}Ra$ disequilibrium to validate conventional ages in Scorpaenids (genera *Sebastes* and *Sebastolobus*). Fish. Res. 46:299-312.

Kerr, L. A., A. H. Andrews, K. Munk, K. H. Coale, B. R. Frantz, G. M. Cailliet, and T. A. Brown.
2005. Age validation of quillback rockfish (*Sebastes maliger*) using bomb radiocarbon. Fish. Bull. 103:97-107.

Kimura, D. K., and C. R. Kastelle.
1995. Perspectives on the relationship between otolith growth and the conversion of isotope activity ratios to fish ages. Can. J. Fish. Aquat. Sci. 52:2296-2303.

Knoll, G. F.
1989. Radiation Detection and Measurement, Wiley, New York.

Legault, C. M., and V. R. Restrepo.
1999. A flexible forward age-structured assessment program. 49:246-253.

Lombardi-Carlson, L. A., M. Cook, H. Lyon, B. A. Barnett, and L. Bullock.
2012. A description of age, growth, and reproductive life history traits of scamp (*Mycteroperca phenax*) from the northern Gulf of Mexico. Mar. Coast. Fish. 4:129-144.

Lorenzen, K.
2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philos. Trans. R Soc. Lond. 360:171-189.

Lowerre-Barbieri, S. K., N. J. Brown-Peterson, H. Murua, J. Tomkiewicz, D. M. Wyanski, and F. Saborido-Rey.
2011. Emerging issues and methodological advances in fisheries reproductive biology. Mar. Coast. Fish. 3:32-51.

Ludwig, D., and C. J. Walters.
1985. Are age-structured models appropriate for catch-effort data? Can. J. Fish. Aquat. Sci. 42:1066-1072.

Mace, P. M., N. W. Bartoo, A. B. Hollowed, P. Kleiber, R. D. Methot, S. A. Murawski, J. E. Powers, and G. P. Scott.
2001. Marine fisheries stock assessment improvement plan. Report of the National Marine Fisheries Service National Task Force for Improving Fish Stock Assessments. 175 p. US Department of Commerce, National Oceanic and Atmospheric Administration.

Mace, P. M., J. M. Fenaughty, R. P. Coburn, and I. J. Doonan.
1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. N. Z. J. Mar. Freshwat. Res. 24:105-119.

Martell, S. J. D., I. Pine, W. E., and C. J. Walters.
2008. Parameterizing age-structured models from a fisheries management perspective. Can. J. Fish. Aquat. Sci. 65:1586-1600.

McMillan, D. B. 2007.
Fish Histology, Female Reproductive Systems. Springer, Netherlands.

Methot, R. D.
2000. Technical description of the Stock Synthesis assessment program. 56 p. NOAA Tech. Memo. NMFS-NWFSC-43.
2009a. Stock assessment: operational models in support of fisheries management. *In* The Future of Fisheries Science in North America (R. J. Beamish, and B. J. Rothschild, eds.), p. 137-165. Springer.
2009b. User manual for stock synthesis model version 3.03a. 143 p. NOAA Fisheries Service, Seattle, WA.

Methot, R.D. and I. G. Taylor
2011. Adjusting for bias due to variability of estimated recruitments in fishery assessment models. Can. J. Fish. Aquat. Sci. 68:1744-1760.

Moe, M. A.
1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. 95 p. Florida Department of Natural Resources, Marine Research Laboratory, St. Petersburg, FL.

Mohn, R.
2009. The uncertain future of assessment uncertainty. *In* The Future of Fisheries Science in North America (R. J. Beamish, and B. J. Rothschild, eds.), p. 495-504. Springer

Moore, W. S.
2007. Seasonal distribution and flux of radium isotopes on the southeastern U.S. continental shelf. J. Geophys. Res. Atmos. 112:1-16.

Moyer, J. T.
1980. Influence of temperate waters on the behavior of the tropical anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan. Bull. Mar. Sci. 30:261-272.

Musick, J. A.
1999. Criteria to define extinction risk in marine fishes: the American Fisheries Society initiative. Fisheries 24:6-14.

NOAA (National Oceanic and Atmospheric Administration).
2004. Fisheries of the Caribbean, Gulf of Mexico, and South Atlantic; Reef Fish Fishery of the Gulf of Mexico; Red Grouper Rebuilding Plan. Federal Register 69:7898-7903.
2009. Magnuson-Stevens Act Provisions; Annual Catch Limits; National Standard Guidelines; Final Rule. Federal Register 74: 3178-3213.

National Research Council.
1998. Improving fish stock assessments, National Academy Press, Washington, DC.

NEFSC (Northeast Fisheries Science Center).
2005. A Report of the 41th Northeast Regional Stock Assessment Workshop (41th SAW). 246 p. Northeast Fisheries Science Center Reference Document 05-14, Woods Hole, MA.
2009. A Report of the 48th Northeast Regional Stock Assessment Workshop (48th SAW). 842 p. Northeast Fisheries Science Center Reference Document 09-15, Woods Hole, MA.

Ochi, H.
1989. Mating behavior and sex change of the anemonefish, *Amphiprion clarkii*, in the temperate waters of southern Japan. Environ. Biol. Fishes 26:257-275.

Pacific Fisheries Management Council.
2000. Status of the Pacific Coast groundfish fishery through 2000 and recommended acceptable biological catches for 2001. Pacific Fishery Management Council, Portland, Oregon.

Palmer, S. M., P. J. Harris, and P. T. Powers.
2004. Age, growth and reproduction of tilefish, *Lopholatilus chamaeleonticeps*, along the southeast Atlantic coast of the United States, 1980-1987 and 1996-1998. 34 p. Southeast Data, Assessment, and Review. South Atlantic Fisheries Management Council, Charleston, SC.

Panfili, J., H. de Pontual, H. Troadec, and P. J. Wright.
2002. Manual of Fish Sclerochronology, Ifremer-IRD, Brest, France.

Parma, A. M., and R. B. Deriso.
1990. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. Can. J. Fish. Aquat. Sci. 47:274-289.

Pope, J. G.
1988. Collecting fisheries assessment data. *In* Fish Population Dynamics, 2nd edition (J. A. Gulland, ed.), p. 63-82. John Wily & Sons Ltd.

Porch, C. E.
1999. A Bayesian VPA with randomly walking parameters. ICCAT Collect. Vol. Sci. Pap. 49:314-326.

Powers, J. E., and V. R. Restrepo.
1992. Additional options for age-sequenced analysis. ICCAT Collect. Vol. Sci. Pap. 39:540-553.

Prager, M. H.
1992. ASPIC-A surplus-production model incorporating covariates. ICCAT Collect. Vol. Sci. Pap. 28:218-229.
1994. A suite of extensions to a nonequilibrium surplus-production model. ICCAT Collect. Vol. Sci. Pap. 92:374-389.

Punt, A. E., D. C. Smith, K. KrusicGolub, and S. Robertson.
2008. Quantifying age-reading error for use in fisheries stock assessments, with application to species in Australia's southern and eastern scalefish and shark fishery. Can. J. Fish. Aquat. Sci. 65:1991-2005.

R Development Core Team.
2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Rhodes, K. L., and Y. Sadovy.
2002. Reproduction in the camouflage grouper (Pisces : Serranidae) in Pohnpei, federated states of Micronesia. Bull. Mar. Sci. 70:851-869.

Richards, L. J., and J. T. Schnute.
1998. Model complexity and catch-age analysis. Can. J. Fish. Aquat. Sci. 55:949-957.

Rideout, R. M., M. P. M. Burton, and G. A. Rose.
2000. Observations on mass atresia and skipped spawning in northern Atlantic cod, from Smith Sound, Newfoundland. J. Fish Biol. 57:1429-1440.

Rochet, M. J.
2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. ICES J. Mar. Sci. 57:228-239.

Ross, J. L., and J. V. Merriner.
1983. Reproductive biology of the blueline tilefish, *Caulolatilus microps*, off North Carolina and South Carolina. Fish. Bull. 81:553-568.

Sadovy de Mitcheson, Y., and M. Liu.
2008. Functional hermaphroditism in teleosts. Fish Fish. 9:1-43.

Sadovy, Y., and M. L. Domeier.
2005. Perplexing problems of sexual patterns in the fish genus *Paralabrax* (Serranidae, Serraninae). J. Zool. 267:121-133.

Sadovy, Y., and D. Y. Shapiro.
1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia 136-156.

Schnute, J. T., and L. J. Richards.
2001. Use and abuse of fishery models. Can. J. Fish. Aquat. Sci. 58:10-17.

SEDAR (Southeast, Data, Assessment, and Review).
2004. SEDAR 4. Stock assessment of the deep-water snapper-grouper complex in the South Atlantic. 594 p,. Charleston, SC.
2005. SEDAR 7. Stock assessment report of Gulf of Mexico red snapper. 480 p., North Charleston, SC.
2006. SEDAR 12. Stock assessment report Gulf of Mexico red grouper. 358 p. North Charleston, SC.
2011a. SEDAR 22. Stock assessment report Gulf of Mexico tilefish. 467 p. North Charleston, SC.
2011b. SEDAR 22. Stock assessment report for yellowedge grouper from the Gulf of Mexico. 423 p., North Charleston, SC.
2011c. SEDAR 25. Stock assessment report South Atlantic tilefish. 330 p. North Charleston, SC.

Shepherd, J. G.
1984. The availability and information content of fisheries data. *In* Exploitation of Marine Communities (R. M. May, ed.), p. 95-109. Springer-Verlag, Berlin.

Smith, C. L.
1965. The patterns of sexuality and the classification of serranid fishes. American Museum Novitates 2207:1-20.

Smith, J. N., R. Nelson, and S. E. Campana
1991. The use of Pb-210/Ra-226 and Th 228/Ra-228 disequilibria in the ageing of otoliths of marine fish. *In* Radionuclides in the study of marine processes (P. J. Kershaw and D. S. Woodhead, eds.), p. 350-359. Elsevier, New York.

St. Mary, C. M.
2000. Sex allocation in *Lythrypnus* (Gobiidae): variations on a hermaphroditic theme. Environ. Biol. Fishes 58:321-333.

Stephens, A., and A. MacCall.
2004. A multispecies approach to subsetting logbook data for purposes of estimating CPUE. Fish. Res. 70:299-310.

Stransky, C., G. Kanisch, A. Kruger, and S. Purkl.
2005. Radiometric age validation of golden redfish (*Sebastes marinus*) and deep-sea redfish (*S. mentella*) in the Northeast Atlantic. Fish. Res. 74:186-197.

Stuiver, M. and H. G. Ostlund.
1980. GEOSECS Atlantic Radiocarbon. Radiocarbon 22: 1-24.

Tomlinson, J.
1966. The advantages of hermaphroditism and parthenogenesis. J. Theor. Biol. 11:54-58.

Turner, S. C., C. B. Grimes, and K. W. Able.
1983. Growth, mortality, and age size structure of the fisheries for tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic-Southern New England Region. Fish. Bull. 81:751-763.

Tyler, C. R., and J. P. Sumpter.
1996. Oocyte growth and development in teleosts. Rev. Fish Biol. Fish. 6:287-318.

Walker, S. P. W., and M. I. McCormick.
2009. Fish ears are sensitive to sex change. Biol. Lett. 5:73-76.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325-343.

Walters, C. J.
1986. Adaptive management of renewable natural resources, The Blackburn Press, Caldwell, New Jersey.

Walters, C., and J. J. Maguire.
1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. 6:125-137.

Walters, C. J., and S. J. D. Martell.
2004. Fisheries ecology and management, Princeton University Press, Princeton.

Walters, C. J., S. J. D. Martell, and J. Korman.
2006. A stochastic approach to stock reduction analysis. Can. J. Fish. Aquat. Sci. 63:212-223.

Watanabe, K., and N. Suzuki.
1996. Sex differentiation, sexual maturity and the spawning season of the red tilefish *Branchiostegus japonicus* on the Pacific coast of Tokushima prefecture. Nippon Suisan Gakkaishi 62:406-413.

Yin, Y., and D. B. Sampson.
2004. Bias and precision of estimates from an age-structured stock assessment program in relation to stock and data characteristics. N. Am. J. Fish. Manage. 24:865-879.

BIOGRAPHICAL SKETCH

Linda Anne Lombardi-Carlson was born in New Bern, North Carolina to Irene and to the late Fred Lombardi in 1974. Linda's father's employment with the U.S. Marine Corp permitted the family to move quite extensively during Linda's primary school years. Linda attended elementary schools in Kailua, Oahu, Hawaii and Stafford, Virginia. Linda's father was an avid fisher and although his catch per unit effort was extremely low, it was these experiences that enticed Linda's interest in the ocean. Linda spent her senior year of high school in Sydney, Australia. While in Australia, Linda completed a direct independent study with the University of Sydney. Linda returned to the states and graduated from North Stafford High School, Stafford, VA in 1993.

Linda began her collegiate education at Northern Virginia Community College in Woodbridge, Virginia, transferred to the University of North Carolina in Wilmington (UNCW), and graduated with a Bachelor of Science degree in Marine Biology in December 1996. Linda worked for the National Undersea Research Center in Wilmington, NC and completed a senior project under the direct of Dr. David Lindquist. During Linda's undergraduate school years, she also spent a summer abroad with the School for Field Studies in the Turks and Caicos Islands studying the resource management of coral reefs.

Following her graduation from the UNCW, Linda was an intern at Mote Marine Laboratory, Center for Shark Research. In 1998, Linda was employed by the NOAA Fisheries Service, Southeast Fisheries Science Center (SEFSC), Panama City Laboratory, Panama City, Florida and began to learn about Gulf of Mexico reef fish life history and the complexities reef fish fisheries management. In 1999, Linda began her Master of Science degree through a cooperative agreement between the National Marine Fisheries Service and the University of Mississippi, Department of Biology, under the direction of Dr. Glenn Parsons. Linda's graduate

research focused on the ecology and population dynamics of the bonnethead shark. Linda continued her employment as a fisheries biologist at NOAA/SEFSC Panama City after her graduation at the University of Mississippi in 2001.

Linda began taking graduate courses at the University of Florida, Fisheries and Aquatic Sciences in the Fall of 2006 to decide on continuing her education in quantitative fisheries. She officially began her PhD in the Fall of 2008 and defended in the summer of 2012. Linda is presently employed as a Research Fisheries Biologist at the NOAA/SEFSC laboratory in Panama City, Florida.