



Nova Southeastern University NSUWorks

HCNSO Student Theses and Dissertations

HCNSO Student Work

4-19-2018

Age and Growth of Hogfish (Lachnolaimus maximus) in Southeast Florida

Ian A. Towne it86@nova.edu

Follow this and additional works at: https://nsuworks.nova.edu/occ_stuetd Part of the <u>Marine Biology Commons</u>, and the <u>Oceanography and Atmospheric Sciences and</u> <u>Meteorology Commons</u>

Share Feedback About This Item

NSUWorks Citation

Ian A. Towne. 2018. Age and Growth of Hogfish (Lachnolaimus maximus) in Southeast Florida. Master's thesis. Nova Southeastern University. Retrieved from NSUWorks, . (465) https://nsuworks.nova.edu/occ_stuetd/465.

This Thesis is brought to you by the HCNSO Student Work at NSUWorks. It has been accepted for inclusion in HCNSO Student Theses and Dissertations by an authorized administrator of NSUWorks. For more information, please contact nsuworks@nova.edu.

Thesis of Ian A. Towne

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

M.S. Biological Sciences

Nova Southeastern University Halmos College of Natural Sciences and Oceanography

April 2018

Approved: Thesis Committee

Major Professor: Paul Arena

Committee Member: Dave Kerstetter

Committee Member: Angela B. Collins

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Age and Growth of Hogfish (Lachnolaimus maximus) in Southeast Florida

By

Ian A. Towne

Submitted to the Faculty of Halmos College of Natural Sciences and Oceanography in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Biology

Nova Southeastern University

2018

ABSTRACT

Hogfish (Lachnolaimus maximus; Walbaum 1792) from Southeast Florida were aged using sectioned otoliths and growth rates were calculated using the von Bertalanffy growth equation. The samples were collected from Broward County (n=209); other regions of Southeast Florida (n=18), the Florida Keys (n=35) and Bahamas (n=43). Growth rates were determined for each of these areas and were then compared to previously reported growth rates from other regions including the eastern Gulf of Mexico and Florida Keys. There was significant separation at the 95% confidence level between growth rates from each reagion. The average maximum fork length increased, from the Florida Keys (336mm) to Southeast Florida (414-mm) by 78-mm. However, the annual survival rate was the same (S=61%) between these two regions and the maximum age of Southeast Florida (age 12) was still half that of the previously reported eastern Gulf (age 23). Broward County was divided into three reef zones each at different depths (5-m, 10m, and 20-m) and growth rate and survival rate were compared between zones. Results showed a decrease in maximum fork length with reef depth (857-mm, 420-mm, 352mm), as well as an increase in mean age (age 3, 4, 5), maximum age (9, 10, 12), and survival (42%, 65%, 73%), respectively. The decrease in observed growth rate of an area as a whole (e.g. Florida Keys) may represent an example of Lee's phenomena caused by increased top-down selective fishing pressure. However, the growth rates of individual hogfish are most likely a result of differences in habitat and food resource availability. This study provides baseline age and growth information for hogfish in Southeast Florida prior to the recent changes to the fishery regulations, which will help fisheries management better understand the effects of alternative management strategies.

Keywords: Hogfish; Wrasse; Otolith; Growth Rate; Spearfishing; Lee's Phenomena

ii

ACKNOWLEDGEMENTS

I am truly grateful for the support of the South Florida spearfishing community and inspired by their passion for this unique species and the sport of spearfishing. A special thanks to all those who dedicated their time to this study, especially Spearfishers S. Ash, J. Posillico, R. Ferrira, A. Quincoses, and J. Fernandez. Fishery Independent specimens were collected with the help of Spearfishers J. Secord, O. Cinti, S.D. Eisen, J. Hornbeck, N. Kornder, and T. Weiser. Thanks to the Fish and Wildlife Research Institute (FWRI) age and growth lab for the extensive training in otolith ageing methodology and help in the conceptual development of this project. Thank you R. McBride for the discussions and advice regarding the findings of this study. Lastly, thank you to my Committee, P. Arena, D. Kerstetter, A. Collins, for their time and unrelenting support which ultimately made this study possible.

TABLE OF CONTENTS

ABSTRACT	II
ACKNOWLEDGEMENTS	III
INTRODUCTION	1
Study Species	1
The Hogfish Fishery	
Ageing	
Prior ageing studies	
Current Population status	5
MATERIALS AND METHODS	7
Study Area	8
Regional Comparison	8
Broward County Reef Comparison	9
Sampling	
Regional Samples	
Broward County Reef Samples	
Data collection	
Laboratory techniques	
Location data	17
Data Analysis	17
Annual Otolith Layer Deposition	17
Age Validation	17
Survival	
Growth Rate	19
RESULTS	19
Annual Otolith Layer Deposition	
Age validation	
Age Growth and Survival	23
Regional Comparison	
Broward County Reef Comparison	
DISCUSSION	
Regional Comparison	34
Broward County Reefs Comparison	
Dwarfism	
Management implications	40
CONCLUSION	41

LITERATURE CITED	42
Appendix A - Amendments affecting Hogfish	48
APPENDIX B - BIMONTHLY LENGTH-FREQUENCY HISTOGRAMS	50
APPENDIX C - LENGTH-WEIGHT SCATTER PLOT	51

List of Figures

Figure 1. Regional catch locations of hogfish	
Figure 2. Broward County catch locations of hogfish.	9
Figure 3. Photos show the method of accessing the otoliths	14
Figure 4. Cross section of three-year-old hogfish	16
Figure 5. Annual otolith deposition of hogfish	20
Figure 6. Age bias plots	22
Figure 7. Scatter plots of individual hogfish by region.	25
Figure 8. Length-frequency histograms of hogfish by region	27
Figure 9. Scatter plots of individual hogfish in Broward county by reef	29
Figure 10. Length-frequency histograms of hogfish in Broward county by reef	31
Figure 11. Relationship between the survival rate and L_{∞} of hogfish.	33

List of Tables

Table 1. Estimates of	growth and survival	l of hogfish by	geographic	region	. 24
	0				

INTRODUCTION

Study Species

The hogfish, *Lachnolaimus maximus*, is the largest wrasse species (Family Labridae) in the western Atlantic Ocean, reaching a total body weight of 16-kg (Colin 1982). Hogfish are the most ancestral species of the Labridae family, diverging from the Hypsigenyines group approximately 52 million years ago, and remains the only species in its group today (Cowman et al. 2009). Locally referred to as "hog snapper," hogfish are a shallow-water, reef-dwelling species (Davis 1976; Colin 1982). Adults are commonly found on gorgonian hard-bottom habitats and in association with hard vertical structures, such as ledges or artificial structures (Davis 1976; Collins and McBride 2011). Juveniles are typically found on seagrass beds (Davis 1976; Collin 1982), implying an ontogenetic habitat shift. While inactive at night, hogfish forage during the day in sediment for benthic invertebrates, such as crabs and mollusks (Randall and Warmke 1967; Munoz et al. 2010).

Similar to most other wrasses, hogfish are protogynous hermaphrodites, meaning that all individuals are born female and transition to males later in life (Davis 1976). The sexual transition from female to male is largely controlled by size of the individual and social dynamics (McBride & Johnson 2007; Munoz et al. 2010; Collins and McBride 2011). The earliest transition to male is at approximately 300 mm fork length, and all surviving hogfish individuals will transition to male eventually (Davis 1976). The oldest female recorded was 12 years old (64-cm-FL), and a transitional specimen was aged to 18 years; the oldest aged male was 23 years old (McBride and Richardson 2007).

Hogfish broadcast spawn, with spawning events occurring as individual pairs, although one male will reproduce with numerous females each day over the course of the spawning season (Colin 1982; McBride and Johnson 2007). Spawning does not appear to be correlated to any lunar cycle, tide, or water temperature change (Colin 1982). However, males exhibit a change in coloration and behavior during mating season, suggesting that spawning is initiated by social behavior (Colin 1982; Munoz et al. 2010). Spawning occurs mostly at dusk between the months of November and June reaching a peak between March and April (Davis 1976; Colin 1982; Claro et al. 2001; McBride &

1

Johnson 2007; Munoz et al. 2010; Collins and McBride 2011). Larvae disperse over the following 26 ± 3 days before settling on to suitable nursery habitat (e.g. seagrass beds) (Victor 1986).

Hogfish form social groups called harems, with one male and many females. One large male can typically maintain a harem of up to fifteen females, and studies have suggested harem size is determined by individual male size (Colin 1982; McBride & Johnson 2007; Muñoz et al. 2010; Collins and McBride 2011). In areas with high fishing effort, hogfish have been observed in smaller harems of two to three females (Munoz et al. 2010). Since the sex ratio of males to females decreased as the fishing pressure targeting males increased, hogfish may be sperm limited (McBride & Johnson 2007).

Previous studies suggest that females will not undergo a sex change if a male is present and instead will simply continue to increase in size (Colin 1982; Munoz et al. 2010). When a male is removed from the harem, and no available male quickly replaces it, one or more of the largest females will transition to male (Davis 1976). Munoz et al. (2010) suggested that if the male is removed from the harem just before or during the spawning season, the entire harem may not be able to reproduce that season. Spearfishers typically target the largest individuals (pers. obs.) and, in the case of hogfish, this individual would likely be the male in the harem. Therefore, increased fishing pressure will likely result in decreased reproductive output for hogfish, thus potentially leading to overfishing.

The Hogfish Fishery

Hogfish are targeted by both recreational and commercial fishers, although most of the landings are recreational. According to the most recent data from 2014, approximately 60% of the total annual catch of hogfish (by weight) was caught by recreational fishers (MRIP 2014; NMFS 2014). However, effort in the commercial sector has been rapidly increasing since the early 2000s, mainly from an increase in commercial spearfishing, which now makes up 90% of the commercial gear type used to target hogfish (Cooper et al. 2013).

There is little information available regarding recreational hogfish catch throughout its range, although the Marine Recreational Information Program (MRIP) provides catch statistics that may elucidate some general trends for the fishery. The majority of the recreational catch (92%) comes from Florida, which includes the West Coast of Florida (WFL) and East Coast of Florida (FLK/EFL) stocks, while 8% were caught in North and South Carolina (GA-NC stock) (MRIP 2014). Within Florida, 70% were caught in WFL and 30% in FLK/EFL. Additionally, 98% of recreational fishers use private/rental boats, while 1.9% swim from shore and only 0.1% use charter boats (MRIP, 2014). The average weight of hogfish landed in North Carolina was 5.4-kg, whereas in Florida it was approximately 0.9-kg. The main gear type used is spear, although both the West Coast of Florida and North Carolina have recently seen an increase in hook-and-line type recreational landings (Cooper et al. 2013).

The commercial fishery makes up 40% of the annual catch of hogfish with WFL, NC/GA and FLK/EFL stocks accounting for 37.8% (NC/GA), 18% (FLK) and 4.2% (EFL) of the catch, respectively (NMFS 2013). From a state-by-state perspective, 70% of the catch comes from Florida, approximately 16% from South Carolina, 14% from North Carolina, and 0.06% from Virginia. In the last 20 years, there has been a shift in gear types used from hook-and-line to spearfishing (NMFS 2014). In the early 1990s, 30-50% of the commercial harvest was by commercial hook and line fishers, but since the early 2000s, commercial spearfishing has become more dominant and today accounts for 90% of the commercial landings (Cooper et al. 2013).

Ageing

The most common way to age wild fishes involve examining layers within hard body parts, such as scales, fin spines, vertebrae, and otoliths (Devries and Frie 1996; Campana 2001). However, the type of hard-part used for ageing analysis is often species specific; for example, salmonid scales are too small and uninformative to be used for aging purposes. While scales can be removed non-lethally and used to accurately age a young fish, the accuracy of scale-based ageing decreases as the fish ages and is unreliable for many long-lived adult fishes due to scale reabsorption during stress periods ("Crichton effect", Simkiss 1974; Das 1994). In contrast, while otoliths require the fish to be lethally sampled, this structure is the most accurate for aging fish since annually deposited layers cannot be reabsorbed or destroyed over time (Marshall and Parker 1982; Campana 1983a 1983b; Green et al. 1985; Neilson and Green 1985).

Otoliths are calcified structures located in the posterioventral portion of the cranium within a pair of otic capsules (Das 1994; Doray et al. 2004). Otoliths are important for hearing and orientation, giving them the common name "ear bones" (Popper and Lu, 2000; Devries and Frie 1996). There are three types of otoliths in each capsule, named the lapillus, sagittus, and asteriscus (Devries and Frie 1996); since there are capsules on both sides of the cranium, there are thus three pairs of otoliths in most fishes. Sagittal otoliths are typically used in ageing studies since they are the largest and easiest to work with (Devries and Frie 1996).

Otoliths are formed by externally adding layers of minerals within a calcium carbonate matrix to the existing nucleus, similar to that of a molluscan pearl. Unlike dorsal or pectoral spines, otoliths are not vascularized, and thus internal layers cannot be resorbed with age or poor nutrition (Das, 1994).

Prior ageing studies

McBride and Richardson (2007) aged 1465 specimens of hogfish from 1995 to 2001 from the West Coast of Florida and the Florida Keys using sectioned otoliths (Fig. 1). This study was the first of its kind for hogfish and is currently the largest and most thorough life history assessment available. In particular, McBride and Richardson (2007) suggested that size-selective fishing mortality may be occurring in the Florida Keys, presumably as a result of overfishing the larger individuals. The authors highlighted changes in the growth curves amongst sub-regions in the Florida Keys (Key Largo-Key West, Marquesas Key, and Dry Tortugas). It was found that hogfish size increased as the sample location moved away from the densely populated Key West-Key Largo area towards the Dry Tortugas. Maximum length changed from 336-mm-FL to 397-mm-FL in Marquesas Key to 651-mm-FL in the Dry Tortugas (McBride and Richardson 2007). Similarly, Collins and McBride (2011) found that maximum length and age of hogfish in the eastern Gulf of Mexico increased with depth and distance from shore. The difference in growth rates indicate possible evidence of size-selective instantaneous mortality once the fish grow larger than 305mm FL, which corresponds with their legal-size limit from 1995-2017.

Current Population status

Over the last few decades, spearfishing has rapidly grown in popularity, likely contributing to an increase in the annual catch of hogfish (Sluka and Sullivan 1998; Cooper et al. 2013). A 60% decline in the hogfish population over the last three decades has been attributed to increasing fishing pressure combined with outdated fishing regulations (Choat et al. 2010; Cooper et al. 2013). Regardless of actual cause, the total fishing mortality for hogfish in 2001 has previously been estimated as high as four times greater than MSY (Ault et al. 2003).

In 2015, the National Marine Fisheries Service (NMFS) announced the first ever in-season closure for the recreational fishery of hogfish in federal waters because the annual recreational catch limit was reportedly exceeded by 267% (NMFS 2015). The recreational catch for that year was determined to be 103,292-kg, exceeding the quota by 64,575-kg (NMFS 2015). The most recent hogfish stock assessment by the Florida Fish and Wildlife Conservation Commission (FWC) specifically listed additional research needs for this species, which included focused life-history studies for the East Florida and Georgia/North Carolina stocks in order to test for differences in growth, maturity and fecundity relative to the West Florida stock, from which more detailed information was already available (Cooper et al. 2013).

The minimum size and recreational bag limit regulations for hogfish have not changed since their inception in 1994 (Current hogfish regulations are provided in Appendix A.). In the past 22 years, the human population of Florida has increased by 40% (U.S. Census Bureau 2015), likely a causative factor in the concomitant increase in fishing pressure (Bohnsack et al., 1994; McBride & Richardson, 2007)

Recently, Seyoum et al. (2015) genetically separated the hogfish population of the U.S. Atlantic and Gulf of Mexico waters into three different stocks (NC/GA, EFL/FLK, WFL), providing data that supported separate management of each stock. As a result, the South Atlantic Fishery Management Council (SAFMC) and the Gulf of Mexico Fishery Management Council (GMFMC) has developed the Snapper Grouper Amendment 37 (SAFMC) and Amendment 43 (GMFMC) creating specific management plan for each region. The most recent stock assessment (SEDAR 37, Cooper et al. 2013) assessed all three stocks; however, the assessment was unable to yield significant age-growth data for the EFL/FLK and NC/GA stocks off the U.S. South Atlantic coast. Only 114 and 104 samples were available from the East Coast of Florida and North Carolina, respectively (Cooper et al., 2013).

The primary objective of this study was to collect life history data of hogfish within a defined region of Southeast Florida's Atlantic coast (90% of samples collected within a reef tract area of approximately 50-km²), with a focus on age and growth via sagittal otolith ageing methods. The age and growth data from the Southeast Florida region were then compared to the populations of hogfish in the Florida Keys and Eastern Gulf previously sampled by Mcbride and Richardson (2007). Additionally, Broward County, Florida hogfish were also separated by catch location into three reef zones, each reef zone representing a different depth range and distance from shore, and compared for differences in age, growth, and survival.

MATERIALS AND METHODS

This study was broken up into two parts; a "regional comparison" of hogfish, and a "Broward County reef comparison" to address the primary (H_0^{1}) and secondary hypothesis (H_0^{2}) separately.

Study Area

Regional Comparison



Figure 1. Regional catch locations of hogfish, Lachnolaimus maximus, collected for this study. The black dots represent catch locations the red striped polygons define each region sampled in this study which include Southeast Florida, Florida Keys, and the Bahamas.



Figure 2. Broward County catch locations of hogfish, Lachnolaimus maximus, collected for this study. The black dots represent catch locations. The three reefs 1^{st} , 2^{nd} , and 3^{rd} are indicated by the three polygons of differing shades of blue. See Legend in top left corner. The defined hard bottom (dotted green area) was compiled by Walker (2012).

The Upper Florida reef tract largely consists of three reef tracts noted by the three major ridges which run parallel to the shore (Figure 2). The reefs are generally described as having the following common characteristics:

1st reef - The innermost reef is the shallowest of the three reefs ranging from 3-m to 6-m in the sand, with a prominent 1-m inner ledge, and flat shallow reef crest. This habitat is dominated by a combination of scleractinian and octocorals, *Palythoa* sp. anthozoans, macroalgae, and sponges (Walker 2012). It is commonly used by snorkelers, beach divers, and those looking for Caribbean spiny lobster *Panulirus argus*. This reef tract is also the most popular area for freedive spearfishers, likely due to its depth (pers. obs.).

 2^{nd} reef- The middle reef depth ranges from 6-m to 15-m with a complex inner structure with vertical relief up to 2-m in some areas dominated by scleractinian corals. The outer portion is flat hard bottom that gradually slopes to down to 15-m dominated by octocorals and large sponges (Walker 2012). This is a popular dive area for many SCUBA charter boats (pers. obs.).

3rd reef- The outer reef depth ranges from 15-m to approximately 25-m with an inner facing reef crest ledge (0.5-m) and an outer spur and groove formation. Large barrel sponges and octocorals dominate this reef along with some flattened scleractinian corals (Walker 2012).

Sampling

Hogfish were collected opportunistically from recreational fishers (e.g. fisherydependent), which included limited catch location and time data. Fishery-independent sampling was conducted by the primary author under the Special Activity License #SAL-16-1815-SR sanctioned by the Florida Fish and Wildlife Conservation Commission, which permitted the collection of any size hogfish, with waiver of seasonal fishery and area closures, size and bag limits. Hogfish were collected from January 2016 to August 2017. Specimens were collected via spearfishing using both SCUBA and snorkel equipment. A total of 325 hogfish specimens were aged from areas including Southeast Florida (n=227), Florida Keys (n=35), and Bahamas Islands (n=43) (Figure 1).

Regional Samples

The primary sampling location was Southeast Florida (SEFL), which included Palm Beach, Broward, and Miami-Dade counties. Southeast Florida sampling occurred year round from January 2016 to August 2017. Specimens were collected from every calendar month on each reef tract. In total, 243 specimens were collected from the Southeast Florida region, of those 227 specimens were aged, 53 of which were fisherydependent collection. Of the hogfish aged in the Southeast Florida region (n=227), 209 were caught primarily within Broward County waters (Figure 1).

The Bahamas region was later included in the analysis due to donations of hogfish samples from this area. There have been no prior studies of hogfish in the Bahamas, although this area is often visited by spearfishers from the U.S. who seek larger and more abundant hogfish compared to the East Coast of Florida (pers. obs.). Samples were collected from the Bahamas primarily during the spring and summer months, when the weather is more conducive for boating. Forty-three specimens were aged from the Bahamas region, all of which were fishery dependent due to the inability to collect undersized specimens in a foreign country without proper permitting.

The Florida Keys was opportunistically sampled and collected for comparison with previous work. Thirty-five specimens were aged from the Florida Keys region (Figure 1), 25 of which were fishery-dependent.

There were also 26 fishery-dependent specimens collected from Wilmington, North Carolina at a spearfishing tournament. However, because the sample was small, and the study lacked sufficient funding for further collection from this region, these data were added to an ongoing age, growth, and reproduction study of hogfish in the Carolinas region (S. Van Sant and D. Wyanski, pers. comm.). Weights and fork lengths from this region were only included in the weight length relationship analysis section of this study for comparative purposes.

Broward County Reef Samples

Specimens collected from Southeast Florida were separated by catch location into three reef tracts (Figure 2). All reefs were sampled year-round. Only individuals that had accurate catch locations were used. Collections from the three reef tracts were as follows: 107 specimens from the first reef (30 fishery dependent), and 96 were aged (11 were lost or damaged); 82 specimens from the second reef (10 fishery dependent), and 80 were aged; and 35 specimens from the third reef (three fishery dependent), and 33 were aged. The remaining 18 hogfish were caught outside of the defined reef zones and were therefore not included (Figure 1).

Data collection

Data collected from each specimen, when available, included date and time of capture, location (latitude, longitude), depth, total weight (TW), fork length (FL), age (via sagittal otolith), and a photograph of the individual.

Laboratory techniques

The total weight (TW) was collected to the nearest 0.1-kg. Fork length (FL) was measured to the nearest millimeter, from the end of the snout with the jaw completely closed to the fork of the tail.

The otolith was removed by making a horizontal cross section of the cranium that splits the canal containing the myelencephalon in half, using a sectioning axis just above the orbital (eye) passing through the skull (Figure 3). The brain was then removed, exposing both the left and right otoliths in the posteroventral cranium just below the myelencephalon canal, one in each pocket on either side of the cranium (Figure 3). Fine tweezers were used to carefully remove each sagittal otolith and place them in a labeled vial with 70% ethanol to sanitize and prevent decomposition, which may erode some of the otolith (Milton and Chenery 1998).



Figure 3. The photo to the left shows the method of accessing the otoliths used. The photo to the right shows the pair of sagittal otoliths located within the cranium below the myelencephalon canal once the brain tissue was removed.

To age each fish, the left otolith (or, when necessary, the otolith in the best condition) was marked on the concave/smooth side at the core using a pencil. A silicone mold was then half-filled with Araldite 502 epoxy resin. Once the epoxy had cured, the marked otolith was placed with the mark facing up in the mold and the mold was then filled with Araldite 502 epoxy resin again. Once the epoxy fully cured, the embedded otolith was removed from the mold and hot-glued to a piece of file folder cardboard, then secured to a low-speed diamond wheel saw (SBT Model 650; South Bay Technology Inc.). Three otolith core sections were cut by four high precision circular diamond saw blades spaced 0.3-0.5-mm apart. The sections were then placed onto a microscope slide and permanently fixed using Flo-Texx Mounting Medium/Liquid Coverslip (Thermo Scientific). Using a microscope, the yearly opaque layers and the remaining margin, estimated to the nearest 25%, were observed, counted, and recorded (Figure 4).



Figure 4. Cross section of three-year-old hogfish, Lachnolaimus maximus, otolith with 0% margin and three complete opaque layers..

Location data

Each specimen was separated by catch location. This was done using the opensource global information systems (GIS) software QGIS (Version 3.0.1) to first create polygons outlining each region/reef (Figure 1). Global positioning system (GPS) coordinates from geotagged photos (fishery-independent collections) and from recreational fishers who donated carcasses (fishery-dependent collections) were spatially joined with the polygons, thus creating a column which listed the name of the polygon (region/reef) that the catch location falls within (Figure 1; Figure 2). A spatial join is a GIS operation where the data of one map layer (e.g., polygon) is added to the data of another layer (e.g., specimen catch locations).

Data Analysis

Annual Otolith Layer Deposition

Annulus deposition as estimated through marginal increment analysis was plotted by month to demonstrate timing of annulus formation and the results herein agreed with previous work (McBride and Richardson 2007) (Figure 5). Results supported using the McBride and Richardson (2007) methodology to assign final age: for specimens caught from January-May, if the margin past the last opaque zone was >50% complete then the final age equaled the number of opaque zones plus one; for June – August this was only true if the margin was >75%; and for September – December the age was equal to the number of opaque zones regardless of margin.

Age Validation

If there was an age disagreement between the two readers, the otolith was re-read by each reader until there was a consensus. If readers could not reach consensus, the sample was omitted from the age results. The age bias plot method introduced by Campana et al. (1995) was used to identify systematic bias between the validated and estimated age read by a reader to assess the accuracy of each reader. This accuracy was calculated in R Studio (Version 1.1.383) using the 'ageBias' program from R package 'FSA' (Ogle 2017). Where the read age is compared to the true age, which is the age once total agreement is achieved between all readers. The precision of both readers was measured using the mean (average) coefficient of variation (ACV) introduced by Chang (1982).

Equation 1-ACV

$$ACV = 100 \times \frac{1}{N} \sum_{j=1}^{N} \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(Y_{ij} - \overline{Y}_{j}\right)^{2}}{R-1}}}{\overline{Y}_{j}}$$

where *N* is the number of fish aged, *R* is the number of replicated age estimates per fish, Y_{ij} is the *i*th age determination of the *j*th fish, and \overline{Y}_j is the average age for the *j*th fish. The ACV was calculated using the 'agePrecision' program in 'FSA'.

Lastly, the McNemar test, Evans-Hoenig test, and Bowker test (McNemar 1947; Bowker 1948; Evans and Hoenig 1998) were used to assess the symmetry of ageagreement. The formulas of these three tests are described in Evans and Hoenig (1998). These tests were calculations extracted from the results of the 'ageBias' program using the 'summary' program with the argument (what = "symmetry"). For a more detailed description of these programs and their implementation, refer to <u>https://cran.r-</u> <u>project.org/web/packages/FSA/FSA.pdf</u>.

Survival

To calculate the survival rate \hat{S} , we used the estimator from Robson and Chapman (1961):

$$\hat{S} = \frac{\sum_{x}^{k} x f_x}{\left(\sum_{x}^{k} f_x + \sum_{x}^{k} x f_x - 1\right)}$$

Where x is the youngest age (in years) fully vulnerable to fishing, f_x is the number of fish per age-class x, and k is the oldest age class. The term x in this case will equal age 3 and k will be the oldest fish sampled common to all areas, which was 9. This calculation was performed using 'agesury' from R package 'fishmethods' (Nelson 2017).

Growth Rate

Age and length data were fit to the growth model: Equation 3- von Bertalanffy growth equation

 $E[L|t] = L_{\infty} (1 - e^{(-K[t-t_0])})$

where E[L|t] is the mean fish length (L) at age (t) and t_0 (x-intercept), L_{∞} (maximum estimated length), K (rate of the curve) are parameters of the estimated growth rate. Using R's 'nls' program the data were fit to the von Bertalanffy growth function via the nonlinear least squares regression method. The resultant was then bootstrapped using 'nlsBoot' to calculate 95% confidence intervals for the parameters L_{∞} , K, and t_0 .

RESULTS

Ages for all regions were combined for the *Age validation* section with a total sample size of 325 aged fish. The following section, *Age Growth and Survival*, is split into two sections for the primary and secondary hypotheses. The primary hypothesis being the *Regional Comparison* (Southeast Florida vs. Bahamas vs. Florida Keys vs. Eastern Gulf of Mexico), and the secondary being the *Broward County Reef Comparison* (1st reef vs. 2nd reef vs. 3rd reef).

Annual Otolith Layer Deposition

Visually estimated marginal increment analysis (Figure 5) showed a peak in opaque layer deposition of hogfish between the months March-May which correlates with peak spawning season for this species (McBride and Johnson 2007, Collins and McBride 2015).



Figure 5. Annual otolith deposition of hogfish, Lachnolaimus maximus, determined using visual estimations from both Ager A and Ager B of the percent margin completion to future opaque zone. Where the red bar represents the mean % to margin, the box represents the upper and lower 25% inner quartiles and the whisker represent the outer 25% quartiles (n=325).

To confirm the assumption of annual opaque layer deposition of hogfish sagittal otoliths, a box and whisker plot was used to describe the average margin growth of hogfish for each month of collection. Because the percent margin was estimated by each reader independently, they were subject to varying individual interpretation. For this reason, margin estimations were plotted separately, to account for the individual variation of each reader. For example, when the last opaque layer was visible, but had no additional margin, reader B was more likely to record the otolith as three opaque layers and a #1/4 margin (e.g., 25%) rather than two opaque layers and a #4/4 margin (e.g., 100% or 0%) (Fig. 6). The minor difference in % margin interpretation does not affect the final age. However, when plotted, this resulted in greater variation during peak opaque layer deposition months, March through May for Reader B (Figure 5).





Figure 6. Age bias plots with mean (points) and range (intervals) of the differences between initial sectioned otolith age estimates of agers A - B (black points) and the final agreed age (dashed line). Histograms at the top and right of the plot represent the frequency distribution of the otolith age estimates (top), and differences in estimates of agers A - B and final agreed age (right)

There was 97.4% agreement between the readers, and the calculated ACV (Equation 1) was 0.26, which is far below 10, demonstrating high precision. A consensus was reached after the second read of each disagreement; therefore, no specimens were omitted. The age bias plot showed no significant deviation from the final age for both readers, except for age 11, where there was only one individual (Figure 6). Additionally, all three tests of symmetry (McNemar, Evan-Hoenig, Bowker) yielded p-values greater than 0.05 for both readers, the lowest being 0.3. This indicates a strong relationship between the final age and the initial age assigned by the reader.

Age Growth and Survival

Growth rate parameters and annual survival estimates were calculated for Southeast Florida and the Bahamas and compared to the eastern Gulf of Mexico and Key West-Key Largo parameter estimates from McBride and Richardson (2007) (Table 1). Parameters and survival estimates were also calculated for each reef zone in Broward County Florida (Table 1)

Annual Survival K L_{∞} t_0 Ŝ SE Region 97.5% 2.5% 97.5% 2.5% 97.5% 2.5% n FL Keys^a 288 355 336 317 0.697 0.562 0.427 0.007 -0.188 -0.383 61.6% 6.5% E Gulf^a 833 0.093 0.079 0.065 -1.461 -1.836 -2.211 3.4% 601 1001 917 70.5% Bahamas^b 0.052 0.066 43 1998 1005 487 0.566 0.02 -6.509 -10.223 66.0% 4.5% SEFL^b 227 414 393 0.577 0.411 0.27 -0.329 -1.213 -3.188 61.0% 2.3% 443 1st Reef^c 857 0.222 0.091 0.027 -1.208 -2.831 -4.7 42.0% 4.8% 96 1978 586 2^{nd} Reef^c 420 385 0.545 0.314 0.121 -0.456 -1.71 -4.973 65.0% 3.6% 80 529 3^{rd} Reef^c 33 942 331 1.898 -40.2 352 14.644 0.547 0.011 -0.881 73.0% 4.5%

Table 1. Estimates of growth and survival of hogfish, Lachnolaimus maximus, by geographic regions described in Figures 1 and 2. Number of fish aged = n. The predicted von Bertalanffy growth parameters (L_{∞} , K, t0) and 95% confidence limits (97.5%, 2.5%) were calculated from the von Bertalanffy growth equation (Equation 3). The Chapman-Robson annual survival rate (\hat{S}) and standard error (SE) were calculated from the Chapman-Robson growth equation (Equation 2). See Figure 9 and Figure 10 for plot of growth data. See age histograms from Figure 9 for data used to calculate survival rate.

^a FL Keys and East Gulf data from McBride and Richardson (2007).

^b Total age length data collected for this study by each region, described in Figure 1.

^c Total age length data collected for this study by each reef zone, described in Figure 2.

Regional Comparison



Figure 7. (A–C) Scatter plots of individual hogfish, Lachnolaimus maximus, size (fork length) and age (years), from (A) the Southeast Florida region, (B) the Bahamas region, and (C) Individual observations opportunistically collected from the Florida Keys Region overlaid with the von Bertalanffy curve (red line) from McBride and Richardson (2007) data (see Table 1 for parameters). (D) Solid line indicates von Bertalanffy growth curves for each data available region: eastern Gulf, Key Largo–Key West (McBride and Richardson 2007), Southeast Florida, and the Bahamas.

The data collected for this study from the Florida Keys could not be fit with a von Bertalanffy growth curve because data collection was limited and lacked 0-1 age classes (Figure 7-C). Thus, the parameters from McBride and Richardson (2007) were overlaid to demonstrate repeatability of their results. The data fit the curve well, especially at the older ages, suggesting that McBride and Richardson (2007) growth parameters are consistent with previous data collected 20 years ago (Figure 7-C).

There were significant differences found in the growth rates of hogfish between regions. L_{∞} (maximum length) was 414-mm fork length (FL) in the Southeast Florida region, which is a notable increase from the Florida Keys ($L_{\infty} = 336$ -mm-FL; McBride and Richardson 2007), however, it is still much smaller than the Eastern Gulf ($L_{\infty} = 917$ -mm-FL; McBride and Richardson 2007) (Table 1; Figure 7-D). The oldest individual caught in the Florida Keys both in this study and prior studies was 10 years old (314-mm-FL) (McBride and Richardson 2007). The two oldest Southeast Florida fish caught were age 12 (349-mm-FL; 321-mm-FL). There were six individuals equal to or greater than 10 years old, which ranged in size from 321-mm-FL to 381-mm-FL. Although there were six hogfish from Southeast Florida greater than nine-years old, these individuals were very small in size, similar to the older individuals caught in the Florida Keys (Figure 7-A;C). Moreover, there were 26 hogfish over 450-mm-FL, the largest being 574-mm-FL, caught in the Southeast Florida region. Comparatively, only one Florida Keys hogfish was greater than 450-mm-FL, which measured 560-mm-FL, collected by McBride and Richardson (2007) (Figure 7).



Figure 8. length-frequency histograms of hogfish, Lachnolaimus maximus by region. Total number of included = n. The y axis indicated the number of fish. The x-axis indicates size ranges (left) and age ranges (right).

The average fork length of hogfish sampled increased from 336-mm-FL in the Florida Keys, to 351-mm-FL in Southeast Florida, and to 438-mm-FL in the Bahamas. The Bahamas was significantly different in fork length from Southeast Florida (t-test; P=1.8e-08). There was no significant difference between Southeast Florida and the Florida Keys (t-test; P=0.06), although sample sizes were not equal (n=227 vs 35). The average age for all three regions was age four.

Compared to the 288 hogfish collected by McBride and Richardson (2007) in the Florida Keys (S=61.5%), the survival rate was not significantly different in Southeast Florida (S=61%) (Table 1). The survival rate increased to 66% in the Bahamas, although sampling was limited compared to Southeast Florida.



Figure 9. (A–C) Scatter plots of individual hogfish, Lachnolaimus maximus, size (fork length) and age (years), from Broward county reefs (A) First reef, (B) Second reef, and (C) Third reef. See Figure 2 for sub-region description. The solid line (VBGF) and dashed lines (95% C.l.) indicate the von Bertalanffy growth equation and 95% confidence limits (C.l.) (see Table 1 for parameters). (D) The solid line indicates von Bertalanffy growth curves for each Southeast Florida reef sub-region: First reef (blue), Second reef (black), and Third reef (red). Dashed lines indicate the 95% confidence limits of the von Bertalanffy growth curves.

Hogfish specimens collected from Southeast Florida which had accurate catch locations, were separated into three reef sub-regions defined in Figure 2. The oldest age class common to all three reefs was age nine. The first reef (depth 3-6-m) showed a significantly different growth rate in comparison to reefs two and three past age two (Figure 10-D). The growth rates of the second reef and third reef showed significant separation from each other past age four (Figure 10-D). The most significant difference was between the inner reef first reef, L_{∞} =857-mm-FL, and the outer third reef, L_{∞} =352-mm-FL (Table 1). At age nine, the von Bertalanffy predicted fork length of first reef hogfish was 38% longer (351-mm-FL vs 564-mm-FL; Figure 10) and four times the weight (Figure 8) of third reef hogfish. The oldest individual from the first reef was age nine (504-mm-FL) out of 96 individuals (1% over age 8) and the oldest from the second reef was age 10 (320-mm-FL) out of 80 individuals (4% over age 8). Whereas, the two oldest individuals from the third reef were age 12 out of 33 individuals collected, 18% over age eight all of which ranged in size from 318-mm-FL to 381-mm-FL.



Figure 10. length-frequency histograms of hogfish, Lachnolaimus maximus from Broward county reefs. Total number of included = n. The y axis indicated the number of fish. The x-axis indicates size ranges (left) and age ranges (right).

The average age of hogfish increased as depth increased, from age three (1^{st} reef), to age four (2^{nd} reef), to age five (3^{rd} reef). However, the average fork length decreased as depth increased, from 355-mm-FL (1^{st} reef), to 341-mm-FL (2^{nd} reef), to 334-mm-FL (3^{rd} reef). Moreover, the distribution of age classes widen with depth/reef, while the distribution of lengths narrow (Figure 10).

Furthermore, the survival rate increased with depth/reef (42% to 65% to 73%) and was inversely related to the change in growth rate between the three reefs. To demonstrate this relationship, the von Bertalanffy predicted hogfish fork length at age nine (oldest common age) (Figure 10-D) were plotted against the estimated percent survival on the three reefs (see Table 1).

Growth rate / % Survival



Figure 11. Relationship between the survival rate (s) (see Table 1) and L_{∞} of hogfish, Lachnolaimus maximus in Southeast Florida separated by reef. The estimated size at age nine was used because that was the maximum universal age. $R^2=1$.

The resulting plot showed a linear fit of $R^2=1.0$ between these two calculated values, which come from two unrelated equations, and the Robson Chapman equation has no length component. This demonstrated that as the fork length of hogfish at age 9 increased, survival rate simultaneously decreased.

DISCUSSION

Hogfish from all regions sampled in this study showed opaque layer deposition on an annual basis with a peak in deposition during the spring spawning season. The timing of otolith deposition is consistent with the previous findings of McBride and Richardson (2007).

Regional Comparison

There were regionally significant differences found in growth rate of hogfish. To compare growth rate by region the von Bertalanffy parameter L_{∞} was used to best describe this difference (Wang and Milton 2000). The growth rate of hogfish caught in the Southeast Florida region (Figure 1) increased significantly (P = 0.00) from Florida Keys region, located 75-km to the south ($L_{\infty} = 414$ -mm-FL vs 336-mm-FL). Hogfish caught in the Florida Keys region had an age/length relationship consistent with the growth rate of hogfish from the same region previously found by McBride and Richardson (2007). This further warrants the comparisons made between these two studies despite a significant temporal difference in data collection (~20 years). Moreover, despite the increase in growth rate, which McBride and Richardson (2007) correlated to fishing pressure, hogfish from Southeast Florida and the Florida Keys had the same survival rate, indicating there may be similar amounts of fishing pressure at these sites.

Furthermore, the Bahamas are approximately 90-170-km from the Southeast coast of Florida making it a popular spearfishing location for those in search of fishing grounds with less fishing pressure. This is similar to the Dry Tortugas (130-km) from Key West, where McBride and Richardson (2007) found an increase in L_{∞} and survival rate. Although the sample size for this study was limited, hogfish collected from the Bahamas were also found to have an L_{∞} of 1005-mm-FL, an increase of 59% from the Southeast Florida region, and a 5% increase in annual survival rate (S=66%). The growth rate of the Bahamas was very similar to the Eastern Gulf of Mexico region from McBride and Richardson (2007) and L_{∞} was slightly higher. Although hogfish individuals in the Bahamas region had a greater survival rate than those in Southeast Florida, it was still less than the Eastern Gulf (McBride and Richardson 2007). Despite collecting individuals up to 660-mm-FL from the Bahamas, which could have easily been 12+ years old according to the growth curve, the oldest aged fish was only nine, and all the larger fish caught had fast growth rates (Figure 7-B). Our inability to obtain older hogfish in the Bahamas region is a reason to be concerned, and a possible indication that overfishing is beginning to occur in the region. However, the sample size from the Bahamas region was small (n=43) and limited in age classes. Therefore, further investigation of the Bahamas region is needed to truly assess the hogfish fishery in that region.

Broward County Reefs Comparison

The three reef tracts sampled in Southeast Florida showed significantly different growth rates. Past age three, all three reefs showed separation of 95% confidence limits up to age twelve. Past age twelve the confidence limits of the third reef growth rate increase significantly due to a low sample size (n=33). Thus, the three reefs are most accurately compared by the estimated fork length of the oldest age common to all three reefs (age nine) rather than L_{∞} . The fastest growth rate was that of the first reef, where at age nine hogfish was on average 564-mm-FL. The growth rate then sharply decreased by 72%, to 405-mm-FL on the second reef, and 351-mm-FL on the third reef. The third reef in particular, largely displayed evidence of dwarfism in the population relative to the growth rates of the Broward County first reef, Bahamas, and offshore Eastern Gulf hogfish (Collins and McBride 2011).

The vast majority of the fish from the third reef were independently collected. Thus, reviewing the location data collected for these individuals, it was noted on more than four occasions that 2-8 dwarf individuals were collected at one time from a small area (\pm 50-m²) on the same day, suggesting that individuals were possibly of the same harem or where at least members of the same cohort. All individuals from the third reef over age six strongly displayed male coloration and morphological features, although gonads were not examined.

The annual survival rate also varied by reef, increasing with depth. However, the growth rate was inversely related to depth (Figure 11) implying a correlation between increased fishing pressure and higher growth rates. The most logical explanation for this correlation is likely due to human tendency to select the largest individuals when hunting/fishing (Darimont et al. 2015; Miranda et al. 1987). Spearfishing is highly selective compared to most other fishing methods since spearfishers can visually assess their area and target the most desirable fish, similar to terrestrial big game hunting. A hunter/fishers bias towards larger individuals can cause a top-down selective fishing pressure. The larger an individual hogfish grows, the higher fishing pressure becomes for that hogfish. Moreover, the faster an individual grows, the less likely that individuals who survive to an older age, resulting in proportionally fewer, fast-growing individuals who survive to older age classes (past age four), compared to slow-growing individuals (compare Figure 9-A to Figure 9-C) (Lee 1912). This effect is known as the Lee's Phenomena (see "Lee's Phenomena" per Lee 1912; Francis 1990).

When combining reef tract data (1st-3rd reefs) to assess growth rate of hogfish, the lack of older fish in fast-growing habitats (1st reef) combined with the higher abundance of fish in slower growing habitats (3rd reef) causes an overall reduction in growth rate in the area. Thus, increased size-selective fishing pressure, which disproportionately targets larger hogfish, is likely responsible for the observed decrease in growth rate of hogfish

from Southeast Florida relative to the less pressured eastern Gulf of Mexico (see Figure 9-D).

Furthermore, the mean age increased with increasing reef/depth range, suggesting an ontogenetic shift, consistent with Collins and McBride (2011). There was also a major decrease in maximum potential fork length (L_{∞}) of hogfish with increasing depth range. In fact, the difference in growth rates of individuals between the first and third reef (L_{∞} = 857 vs 352-mm-FL) indicate that there are likely at least two distinct cohorts of hogfish within this reef system. Further support for this suggestion is the lack of first-reef hogfish under 370-mm-FL, older than five, and the lack of third-reef hogfish older than five over 380-mm-FL with the exception of one individual (Figure 9). The expected initial juvenile (<1 yr old) recruitment of individuals from inshore to nearshore reef areas likely still occurs. However, a later ontogenetic shift to the deeper third reef seems unlikely, because this would imply hogfish were shrinking as the moved from the first to the third reef.

Recreational fishers have anecdotally described seeing large hogfish occasionally on the third reef and deep wrecks (20-40m) in Broward County (pers. comm.). Furthermore, Bryan et al. (2013) recorded hogfish at depths between 90-120 m during ROV transect dives in Broward County. Fourteen of the eighteen hogfish observed were associated with sunken vessel artificial reefs. The individuals observed were very large (~460-mm-FL) and document the existence of hogfish at far greater depths than those sampled in this study (pers. comm., Bryan et al. 2013). These deep-water hogfish may be larger due to a lack of fishing pressure or possibly suggest an ontogenetic shift to mesophotic habitats.

In addition to the differences of hogfish growth and survival between the three reefs, there were also notable differences in both harem density and foraging habitat. While there were no transects conducted in this study, 85% (177 of 209) of the hogfish were collected by the primary author. As a result, during collection the primary author was able to qualitatively observe the habitat and behavior of the hogfish. On the third reef and some of the second reef, hogfish were found in the greatest abundance where the

hard bottom reef intersected with sand bottom. All but six of the third reef hogfish were collected over sand, often 5-30-m away from the actual reef edge. Hogfish in this sand bottom environment were also observed in large harems from 5-15 individuals on more than four separate occasions, all of these contained at least one male, and two of those schools contained two males. Furthermore, the third reef hogfish were often found in closer proximity to each other. On two occasions, there were approximately 30 or more individuals within $50-m^2$ area.

In contrast, first reef hogfish were rarely seen in aggregations greater than three individuals, typically all females and were generally much more scattered. Hogfish on the first reef were generally found in association with vertical structures such as coral heads, ledges, and dense gorgonian communities rather than sand bottom. These first reef hogfish also appeared to be wary of divers compared to hogfish of the third reef, who often approached the spearfisher out of curiosity. Additionally, out of 21 fish collected from a first reef area within 2-km of Port Everglades, four individuals (20%) appeared to have prior spear injuries that had healed (pers. obs.).

Dwarfism

Hogfish are not the only wrasse species documented having dwarf cohorts. Dwarfism was reported in California's equivalent wrasse species, California sheephead *Semicossyphus pulcher*, at Guadalupe Island by Warner (1975), but the cause of this dwarfism was not known or discussed. In this study, several observations suggested a reason for the growth differences of hogfish in Southeast Florida. First off, Collins and McBride (2011) found a decrease in growth rate ($L_{\infty} = 381$ -mm-FL) nearshore, where the mean group density of hogfish was greatest (groups of 0–25 fish; mean=5.4 per 300-m²). Whereas offshore, the mean group density decreased (groups of 0–15 fish; mean=1.3 per 300-m²) and growth rate increased ($L_{\infty} = 896$ -mm-FL). Although density was not assessed in this study, anecdotal observations suggest a similar relationship between hogfish density and hogfish growth rate. Therefore, hogfish in high densities may have a relation to decreased individual hogfish growth.

Dwarfism in third reef hogfish is likely due to a lack of food resources. Supporting this assumption, Hornbeck (2017) found a significant decrease in δ^{15} nitrogen values for invertivores (including hogfish) between the first and second reef in Broward County, indicating a possible decrease in proteinaceous food sources between the first reef and the second/third reefs. Furthermore, schooling behavior is a common strategy used by foraging fishes to avoid predation (White and Warner 2007). Stenberg and Persson (2005) suggested that foraging in large groups increases the ability of individual members to find food resources in environments where food is sparse. Nunes et al. (2013) similarly showed that feeding frequency increased with group size in three invertivore wrasse (Labridae) species in the Western Atlantic (*Halichoeres poeyi, H. penrosei* and *H. brasiliensis*), indicating an increase in foraging efficiency. Thus, if food resources are in fact significantly more limited in the third reef zone, then these fish may be schooling to maximize foraging efficiency, which explains the higher densities observed by the primary author.

Furthermore, structurally complex habitats play a key role in providing shelter from predators for many fish species, including hogfish (Hixon and Beets 1993). Increased complexity also has a higher surface area, theoretically supporting a larger benthic community, that many reef fish rely on for food. Thus, differences in complexity can affect competitive interactions and survival behaviors among fishes (Jones 1988; Syms and Jones 2000). In this study, slow-growing hogfish on the third reef zone were commonly found feeding over a sand-bottom environment where there was no structural complexity. In contrast, the fast-growing first reef hogfish were found in structurally complex reef areas. If more structurally complex habitats are providing both increased protection from predation and more abundant food resources, then perhaps there is less need for large group sizes in those areas. Nevertheless, it appears that hogfish in Southeast Florida may be adapting different survival and feeding strategies to better exploit the resources of different habitats, which may explain some of the variations noted in this study.

Management implications

As of August 31, 2017, the newly proposed management changes to the U.S. hogfish fishery went into effect. Because the East Florida Stock was determined to be overfished, it is now under a ten-year stock recovery plan. The recreational regulations, which formerly allowed five fish per day year-round with a minimum size of 305-mm-FL, is now one fish per day with a minimum size of 405-mm-FL, and a limited season (closed October 31 to May 1). While these changes appear drastic to the fishing community, the results from this study support that there is heavy fishing pressure in Southeast Florida and this should be alleviated over time through these regulation changes.

This study examined a very limited geographic region but still pinpointed distinct spatial differences in growth rate and survival. The survival rate of the first reef population is a reason for concern as a high rate of mortality was revealed for these faster growing individuals. The increased size limit should effectively protect these fish from fishing pressure for twice as long, from ages 2-3 to age 4-6. Doubling the number of spawning seasons for larger individuals will allow additional spawning events and increased total fecundity (larger females produce significantly more eggs; Collins and McBride 2015). In addition, the closed season protects these fish during times of spawning when removal of large males can rapidly lead to sperm limitation. This also inevitably benefits the fishery stakeholders by increasing the abundance of larger hogfish for the fishers. Additionally, the weight of a minimally legal fish is now double that of the prior limit and the decreased bag limit will likely increase the abundance and size of legal hogfish (Weight-length relationship provided in Appendix C).

CONCLUSION

The results of this study indicate a decreased overall growth rate and low survival rate for Southeast Florida relative to the eastern Gulf of Mexico, which is similar to findings of previous work performed in other regions (McBride and Richardson 2007; Collins and McBride 2011). These data support recent stock assessments that have declared the Southeast Florida stock to be overfished. The decrease in growth rate could be due to highly selective top-down fishing pressure causing a downward shift in the size at age demographic of the remaining older hogfish individuals (i.e. Lee's Phenomena). With the recently implemented regulation changes that increased the minimum size to 406-mm fork length, we expect overall average size and age of hogfish within this region to increase, as well as average size at age and the abundance of faster growing hogfish. Lastly, this study provides a baseline measure of the hogfish population in a defined region off Southeast Florida prior to the implementation of the major changes in the management of hogfish. These data will contribute to future stock assessments of hogfish and assist with effective fisheries management of this economically valuable marine fish.

LITERATURE CITED

- Ault, J. S., S. G. Smith, G. A. Diaz, and E. Franklin. "Florida Hogfish Fishery Stock Assessment." 89, 2003.
- Bohnsack, J. A., D. E. Harper, D. B. McClellan, and M. Hulsbeck. "Effects of Reef Size on Colonization and Assemblage Structure of Fishes at Artificial Reefs Off Southeastern Florida, USA." *Bulletin of Marine Science* 55, no. 2-3 (1994): 796-823.
- Bowker, A. H. "A Test for Symmetry in Contingency Tables." *Journal of the American Statistical Association* 43, no. 244 (1948/12/01 1948): 572-74.
- Bryan, D. R., K. Kilfoyle, R G. Gilmore, and R. E. Spieler. "Characterization of the Mesophotic Reef Fish Community in South Florida, USA." *Journal of Applied Ichthyology* 29, no. 1 (2013): 108-17.
- Campana, S. E. "Calcium Deposition and Otolith Check Formation During Periods of Stress in Coho Salmon, Oncorhynchus Kisutch." Compartive Biochemistry and Physiology 75A (1983): 215-20.
- Campana, S. E., and S. R. Thorrold. "Otoliths, Increments, and Elements: Keys to a Comprehensive Understanding of Fish Populations?". *Canadian Journal of Fisheries and Aquatic Sciences* 58, no. 1 (2001): 30-38.
- Campana, S. E., M. C. Annand, and J. I. McMillan. "Graphical and Statistical Methods for Determining the Consistency of Age Determinations." *Transactions of the American Fisheries Society* 124, no. 1 (1995/01/01 1995): 131-38.
- Chang, W. Y. B. "A Statistical Method for Evaluating the Reproducibility of Age Determination." *Canadian Journal of Fisheries and Aquatic Sciences* 39, no. 8 (1982/08/01 1982): 1208-10.
- Choat, J. H., D. Pollard, and Y. J. Sadovy. "Lachnolaimus Maximus." In *The IUCN Red List of Threatened Species 2010*, 2010.

- Claro, R., and J. P. Garcia-Arteaga. "Growth Patterns of Fishes of the Cuban Shelf." *Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, DC* (2001): 149-78.
- Colin, P. L. "Spawning and Larval Development of the Hogfish, Lachnolaimus Maximus (Pisces: Labridae)." *Fishery bulletin-United States, National Marine Fisheries Service (USA)* (1982).
- Collins, A. B., and R. S. McBride. "Variations in Reproductive Potential between Nearshore and Offshore Spawning Contingents of Hogfish in the Eastern Gulf of Mexico." *Fisheries Management and Ecology* 22, no. 2 (2015): 113-24.
- Collins, A. B., and R. S. McBride. "Demographics by Depth: Spatially Explicit Life-History Dynamics of a Protogynous Reef Fish." *Fishery Bulletin* 109, no. 2 (2011): 232-42.
- Cooper, W., A. B. Collins, J. O'Hop, and D. Adis. "The 2013 Stock Assessment Report for Hogfish in the South Atlantic and Gulf of Mexico. Florida Fish and Wildlife Conservation Commission." *SEDAR* 37 (2013).
- Cowman, P. F., D. R. Bellwood, and L. Herwerden. "Dating the Evolutionary Origins of Wrasse Lineages (Labridae) and the Rise of Trophic Novelty on Coral Reefs." *Molecular Phylogenetics and Evolution* 52, no. 3 (2009): 621-31.
- Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. "The Unique Ecology of Human Predators." *Science* 349, no. 6250 (2015): 858-60.
- Das, M. "Age Determination and Longevity in Fishes." *Gerontology* 40, no. 2-4 (1994): 70-96.
- Davis, J. C. "Biology of the Hogfish, Lachnolaimus Maximus (Walbaum), in the Florida Keys." University of Miami, 1976.
- Devries, D. R., and R. V. Frie. *Determination of Age and Growth*. Fisheries Techniques. Edited by B. R. Murphy and D. W. Willis. 2nd ed. Bethesda, Marylard: American Fisheries Society 1996.

- Doray, M., B. Stéquert, and M. Taquet. "Age and Growth of Blackfin Tuna (Thunnus Atlanticus) Caught under Moored Fish Aggregating Devices, around Martinique Island." *Aquatic Living Resources* 17, no. 1 (2004): 13-18.
- Evans, G. T., and J. M. Hoenig. "Testing and Viewing Symmetry in Contingency Tables, with Application to Readers of Fish Ages." *Biometrics* 54, no. 2 (1998): 620-29.
- Francis, R. "Back-Calculation of Fish Length: A Critical Review." *Journal of Fish Biology* 36, no. 6 (1990): 883-902.
- Geen, G. H., J. D. Neilson, and M. Bradford. "Effects of Ph on the Early Development and Growth and Growth and Otolith Microstructure of Chinook Salmon, *Oncorhynchus Tshawytscha.*" *Canadian Journal of Zoology* 63 (1985): 22-27.
- Hixon, M. A., and J. P Beets. "Predation, Prey Refuges, and the Structure of Coral-Reef Fish Assemblages." *Ecological Monographs* 63, no. 1 (1993): 77-101.
- Hornbeck, J. R. "A Comparison of the Ichthyofaunal Trophic Ecology at Selected Limestone Artificial Reef Sites and Adjacent Natural Reef Sites." Nova Southeastern University, 2017.
- Jones, G. P. "Experimental Evaluation of the Effects of Habitat Structure and Competitive Interactions on the Juveniles of Two Coral Reef Fishes." *Journal of Experimental Marine Biology and Ecology* 123, no. 2 (1988): 115-26.
- Lee, R. M. "An Investigation into the Methods of Growth Determination in Fishes by Means of Scales." (1912).
- Marshall, S. L., and S. S. Parker. "Pattern Identification in the Microstructure of Sockeye Salmon (*Oncorhynchus Nerka*) Otoliths." *Canadian Journal of Fisheries and Aquatic Sciences* 39 (1982): 542-47.
- McBride, R. S., and A. K. Richardson. "Evidence of Size-Selective Fishing Mortality from an Age and Growth Study of Hogfish (Labridae: Lachnolaimus Maximus), a Hermaphroditic Reef Fish." *Bulletin of Marine Science* 80, no. 2 (2007): 401-17.
- McBride, R. S., and M.R. Johnson. "Sexual Development and Reproductive Seasonality of Hogfish (Labridae: Lachnolaimus Maximus), an Hermaphroditic Reef Fish." *Journal of Fish Biology* 71, no. 5 (2007): 1270-92.

- McNemar, Q. "Note on the Sampling Error of the Difference between Correlated Proportions or Percentages." *Psychometrika* 12, no. 2 (June 01 1947): 153-57.
- Milton, D. A., and S. R. Chenery[†]. "The Effect of Otolith Storage Methods on the Concentrations of Elements Detected by Laser-Ablation Icpms." *Journal of Fish Biology* 53, no. 4 (1998): 785-94.
- Miranda, L. E., W. M. Wingo, R. J. Muncy, and T.D. Bates. "Bias in Growth Estimates Derived from Fish Collected by Anglers." *Age and growth of fish. Iowa State University Press, Ames* (1987): 211-20.
- Muñoz, R. C., M. L. Burton, K. J. Brennan, and R. O. Parker. "Reproduction, Habitat Utilization, and Movements of Hogfish (Lachnolaimus Maximus) in the Florida Keys, USA: Comparisons from Fished Versus Unfished Habitats." *Bulletin of Marine Science* 86, no. 1 (2010): 93-116.
- Neilson, J. D., and G. H. Geen. "Effects of Feeding Regimes and Diel Temperature Cycles on Otolith Increment Formationin Juvenile Chinook Salmon (*Oncorhynchus Tshawytscha*)." *Fishery Bulletin* 83 (1985): 91-100.
- Nelson, G. A. "Fishery Science Methods and Models in R." CRAN, 2017.
- NMFS. "Commercial Catch Statistics." *NOAA*, Retrieved from http://www.st.nmfs.noaa.gov/st1/commercial/, 2014.
- NMFS."In-season Closure of Recreational Hogfish Harvest in the South Atlantic". *NOAA*, 2015.
- Nunes, J. C. C., C. L. S. Sampaio, and F. Barros. "How Wave Exposure, Group Size and Habitat Complexity Influence Foraging and Population Densities in Fishes of the Genus Halichoeres (Perciformes: Labridae) on Tropical Rocky Shores." *Marine Biology* 160, no. 9 (September 01 2013): 2383-94.
- Ogle, D. H. "Fsa: Fisheries Stock Analysis." In *R package version 0.8.17*, 2017.
- Popper, A. N., and Z. Lu. "Structure–Function Relationships in Fish Otolith Organs." *Fisheries research* 46, no. 1 (2000): 15-25.

- Randall, J. E., and G. L. Warmke. "The Food Habits of the Hogfish (Lachnolaimus Maximus), a Labrid Fish from the Western Atlantic." *Caribbean Journal of Science* 7, no. 3-4 (1967): 141-44.
- Robson, D. S., and D. G. Chapman. "Catch Curves and Mortality Rates." *Transactions of the American Fisheries Society* 90, no. 2 (1961/04/01 1961): 181-89.
- Seyoum, S, A. B. Collins, C. Puchulutegui, R. S. McBride, and M. D. Tringali. "Genetically Determined Population Structure of Hogfish (Labridae: Lachnolaimus Maximus) in the Southeastern United States." *Fishery Bulletin* 113, no. 4 (2015).
- Simkiss, K. *Calcium Metabolism of Fish in Relation to Ageing*. Ageing of Fish. Edited by T. B. Bagenal London: Unwin Brothers Limited, 1974.
- Sluka, R. D., and K. M. Sullivan. "The Influence of Spear Fishing on Species Composition and Size of Groupers on Patch Reefs in the Upper Florida Keys." *Fishery Bulletin* 96, no. 2 (1998): 388-92.
- Stenberg, M, and A Persson. "The Effects of Spatial Food Distribution and Group Size on Foraging Behaviour in a Benthic Fish." *Behavioural processes* 70, no. 1 (2005): 41-50.
- Syms, C., and G. P. Jones. "Disturbance, Habitat Structure, and the Dynamics of a Coral-Reef Fish Community." *Ecology* 81, no. 10 (2000): 2714-29.
- United States Census Bureau. Retrieved from: http://www.census.gov, 2015, July 25.
- Victor, B. C. "Duration of the Planktonic Larval Stage of One Hundred Species of Pacific and Atlantic Wrasses (Family Labridae)." *Marine Biology* 90, no. 3 (1986): 317-26.
- Walker, B. K. "Spatial Analyses of Benthic Habitats to Define Coral Reef Ecosystem Regions and Potential Biogeographic Boundaries Along a Latitudinal Gradient." *PloS one* 7, no. 1 (2012): e30466.
- Wang, Y. G., and D. A. Milton. "On Comparison of Growth Curves: How Do We Test Whether Growth Rates Differ?". *Fishery Bulletin* 98, no. 4 (2000): 874-80.

- Warner, R. R. "The Reproductive Biology of the Protogynous Hermaphrodite Pimelometopon Pulchrum (Pisces: Labridae)." *Fishery Bulletin* 73, no. 2 (1975): 262-83.
- White, J. W., and R. R. Warner. "Behavioral and Energetic Costs of Group Membership in a Coral Reef Fish." *Oecologia* 154, no. 2 (2007): 423-33.

APPENDIX A

Table. Amendments affecting Hogfish (Cooper et al. 2013)

Description of Action	Amendment affecting Hogfish	Date	Management Agency
4" trawl mesh; established minimum size limits for several species; limitations on harvest and gear	Snapper Grouper FMP	8/31/1983	SAFMC FMP
Established 12" FL minimum size for Hogfish from state waters	F.A.C. Chap 68-14	7/1/1985	State of Florida F.A.C.
Established a 5 Hogfish per day bag limit in state waters	F.A.C. Chap 68-14	12/1/1986	State of Florida F.A.C.
Trawls prohibited	Snapper Grouper Amend 1	1/12/1989	SAFMC FMP
Required permit to fish for, land or sell snapper grouper species	Snapper Grouper Amend 3	1/31/1991	SAFMC FMP
Fish traps prohibited, entanglement nets & longlines within 50 fathoms prohibited, aggregate bag limit of 10 snappers	Snapper Grouper Amend 4	1/1/1992	SAFMC FMP
Required the appropriate federal permit to exceed the recreational bag limit in state waters.	F.A.C. Chap 68-14	12/1/1992	State of Florida F.A.C.
Designates Hogfish as a "restricted species", establishes a minimum size limit of 12 inches fork length, and establishes a daily recreational bag limit of 5 Hogfish per person.	F.A.C. Chap 46-14	7/1/1994	State of Florida F.A.C.
Established a minimum size limit of 12" (305 mm) FL for Hogfish; specified allowable gear; required dealer, charter, and headboat federal permits	Snapper Grouper Amend 7	1/23/1995	SAFMC FMP
Implemented a Hogfish recreational bag limit of 5 per person within Florida EEZ	Snapper Grouper Regulatory Amend 6	5/1/1995	SAFMC FMP

MSY proxy for Hogfish is 30% static SPR; OY proxy is 40% static SPR	Snapper Grouper Amend 11B	12/2/1999	SAFMC FMP
Prohibited commercial fishermen from harvesting or possessing the recreational bag limit of reef fish species on commercial trips.	F.A.C. Chap 68-14	7/1/2007	State of Florida F.A.C.
Comprehensive ACL Amendment to meet MSA mandate to establish ACLs and AMs for species managed by the council that are not undergoing overfishing, including Hogfish. ACL for Hogfish in commercial sector: 48,772 lb (22,123 kg) round weight; ACL for Hogfish in recreational sector: 98,866 lb (44,845 kg) round weight	Snapper Grouper Amend 25	4/16/2012	SAFMC FMP
Action to revise the acceptable biological catch estimates, annual catch limits (ACL), and recreational annual catch targets for Hogfish; ACL for Hogfish in commercial sector: 49,469 lb (22,439 kg) round weight; ACL for Hogfish in recreational sector: 85,355 lb (38,716 kg) round weight	Snapper Grouper Regulatory Amend 13	7/17/2013	SAFMC FMP
Georgia to North Carolina federal and state waters- Minimum size limit increased to 17" FL and a recreational bag limit of 2 per day. East Florida federal and state waters- Minimum size limit increased to 16" FL and a recreational bag limit of 1 per day. Season closed from Oct. 31 st – Apr. 30 th .	Snapper Grouper Amendment 37	8/24/2017	SAFMC
Gulf of Mexico state and federal waters- Minimum size limit increased to 14" FL.	Snapper Grouper Amendment 43	8/24/2017	GMFMC

APPENDIX B



Figure. Bimonthly length-frequency histograms of hogfish, Lachnolaimus maximus. Total number of individuals collected = n

APPENDIX C



Hogfish Weight-Length (n=134)

Figure. Length-weight scatter plot fitted with predictive curve and 95% Confidence limits. Data incudes all regions including tournament data collected from North Carolina. Weights collected show a strong positive relationship between length and weight.

Weights and lengths from specimens from all regions were used to plot the relationship between weight and length. A predictive curve was fitted to the data along with 95% confidence limits Figure 8. All of the individuals over 600mm were from a fishing tournament in North Carolina, the largest of which was 10kg. The largest fish weighed from Southeast Florida was 3.3kg.