

Gulf and Caribbean Research

Volume 27 | Issue 1

2016

Age, Growth and Natural Mortality of Blackfin Snapper *Lutjanus buccanella* from the Southeastern United States and U. S. Caribbean

Michael L. Burton

NOAA Southeast Fisheries Science Center, Beaufort Laboratory, michael.burton@noaa.gov

Jennifer C. Potts

NOAA Southeast Fisheries Science Center, Beaufort Laboratory, jennifer.potts@noaa.gov

Daniel R. Carr

Independent Affiliation

DOI: 10.18785/gcr.2701.10

Follow this and additional works at: <http://aquila.usm.edu/gcr>

 Part of the [Aquaculture and Fisheries Commons](#), and the [Marine Biology Commons](#)

Recommended Citation

see attached

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Gulf and Caribbean Research by an authorized editor of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

GULF AND CARIBBEAN

R E S E A R C H

Volume 27
2016
ISSN: 1528-0470



Published by

**THE UNIVERSITY OF
SOUTHERN MISSISSIPPI**

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

AGE, GROWTH AND NATURAL MORTALITY OF BLACKFIN SNAPPER, *LUTJANUS BUCCANELLA*, FROM THE SOUTHEASTERN UNITED STATES AND U.S. CARIBBEAN.

Michael L. Burton¹, Jennifer C. Potts¹, and Daniel R. Carr²

¹National Marine Fisheries Service, Southeast Fisheries Science Center, 101 Pivers Island Rd., Beaufort NC 28516-9722; ² 3103 Country Club Rd., Morehead City, NC 28557-3016; Corresponding author, email: michael.burton@noaa.gov

ABSTRACT: We determined ages of Blackfin Snapper (*Lutjanus buccanella* Cuvier 1828; $n = 622$) collected from the southeastern United States coast and U.S. Caribbean from 1979–2015 using sectioned sagittal otoliths. Opaque zones were determined to be annular, forming March – July (peaking in April–June). Blackfin Snapper ranged from 1–27 years and from 180–609 mm total length (TL). Body size relationships for Blackfin Snapper were: $TL = 1.09 FL + 0.81$ ($n = 203$, $r^2 = 0.99$); $FL = 0.91 TL + 3.38$ ($n = 203$, $r^2 = 0.99$); $TL = 1.23 SL + 14.27$ ($n = 83$, $r^2 = 0.97$); $FL = 1.14 SL + 10.84$ ($n = 83$, $r^2 = 0.99$); $W = 7.79 \times 10^{-9} TL^{3.09}$ ($n = 216$); and $W = 9.54 \times 10^{-9} FL^{3.11}$ ($n = 228$). The von Bertalanffy growth equation was: $L_t = 549 (1 - e^{-0.20(t+1.51)})$ ($n = 622$). Point estimate of natural mortality was $M = 0.16$, while age-specific estimates of M ranged from 0.65–0.21/y for ages 1–27. This study presents the first findings of life history parameters for Blackfin Snapper from the Atlantic waters off the southeastern United States and U.S. Caribbean.

KEYWORDS: Lutjanidae, Life history parameters, Fisheries management, Caribbean reef fish, data-limited species.

INTRODUCTION

Blackfin Snapper (*Lutjanus buccanella* Cuvier 1828, Family Lutjanidae) are found in the tropical western Atlantic and are capable of attaining weights of up to 14 kg but usually average < 4 kg (Grimes et al. 1977). The species is found from North Carolina throughout Bermuda and the Caribbean, including the Gulf of Mexico, and as far south as northeast Brazil (Cervigon 1966). Adults typically inhabit the continental shelf edge or live-bottom areas in depths from 9–219 m. Blackfin Snapper are of minor importance to the southeastern United States (SEUS, North Carolina to Florida Keys, including the Dry Tortugas) reef fish fishery but are more important to anglers in the U.S. Caribbean (Puerto Rico and the U.S. Virgin Islands). Estimated recreational landings of Blackfin Snapper in the SEUS averaged 1,006 kg from 1981–2014, while landings from the private/charter sector in Puerto Rico averaged 5,178 fish annually from 2000–2012 (T. Sminkey, unpublished data, NMFS, Silver Spring, MD). Commercial landings for the SEUS averaged 386 kg from 1982–2014 but were 22,750 kg annually from 2000–2014 for the U.S. Caribbean (D. Gloeckner, unpublished data, NMFS Southeast Fisheries Science Center (SEFSC), Miami, FL). Sylvester et al. (1980) reported that Blackfin Snapper was the second most commonly landed deepwater Snapper in the U.S. Virgin Islands, behind Silk Snapper (*Lutjanus vivanus*).

Blackfin Snapper is currently managed in the SEUS by the South Atlantic Fishery Management Council's Snapper–Grouper Fishery Management Plan (FMP; SAFMC 2015) with a 305 mm total length (TL, 12 inches) minimum size limit in both commercial and recreational fisheries and

includes a 10 snapper per person per day bag limit (excluding Red Snapper, *Lutjanus campechanus*, and Vermilion Snapper, *Rhomboplites aurorubens*) in the recreational fishery. The species is managed in the U.S. Caribbean by the Caribbean Fishery Management Council's Reef Fish FMP with annual catch limits. The Magnuson–Stevens Fishery Conservation and Management Act requires that annual catch limits be set for all managed species (or species groups) in both the SEUS and U.S. Caribbean territories, despite the fact that many of these species may be data-poor (SERO 2015). Data-limited assessment methods currently in use require basic inputs such as natural mortality or growth parameters which, when combined with catch histories or size distributions, can be used to estimate fishery targets or limits. Even this rudimentary data is sparse or non-existent for many reef fish species in the SEUS and U.S. Caribbean, however.

We studied Blackfin Snapper from the SEUS in order to fill in data gaps in their life history in SEUS or U.S. Caribbean waters. While Claro and Lindeman (2008) published a thorough review of the biology of the family Lutjanidae from the tropical western Atlantic region, previous estimates of age–growth parameters or mortality rates of the species came from stocks outside the SEUS or U.S. Caribbean and were derived used methods other than sectioned sagittal otoliths (Thompson and Munro 1983: Jamaica, length frequency data; Espinosa and Pozo 1982: Cuba, urohyal bones). This study uses archived sagittal otolith samples collected over decades of sampling to provide the first estimates of life history parameters for Blackfin Snapper from the SEUS and U.S. Caribbean region, thereby filling in a significant data

gap and contributing to the proactive management of data-limited reef fish resources in the regions.

MATERIALS AND METHODS

Age determination and timing of opaque zone formation

Blackfin Snapper ($n = 505$) were opportunistically obtained from fisheries landings by NMFS and state agencies' port agents sampling the recreational headboat and commercial fisheries along the SEUS coast from 1981–2015. Additional samples were collected by NMFS fishery-independent surveys from the waters of Puerto Rico and the U.S. Virgin Islands in 1979 and 2009 ($n = 131$). All fishery-dependent specimens were captured by conventional vertical hook and line or longline gear. Fishery-independent specimens were captured using vertical hook and line, bottom longline, or fish traps. Fork length (FL, mm) and/or TL (mm) of specimens were recorded from fishery-dependent and fishery-independent samples, and standard length (SL, mm) from fishery-independent samples. Whole weight (W, kg) was recorded for fish landed in the headboat fishery and from fishery-independent samples. Fish landed by commercial fisheries were eviscerated at sea, thus whole weights were not available. Sagittal otoliths were removed and stored dry in coin envelopes. Otoliths were mounted on glass microscope slides and sectioned using a diamond-edged wafering blade on a Buehler Isomet low speed saw following the methods of Potts and Manooch (1995). Three 0.5 mm sections were taken near the otolith core. The sections were mounted on microscope slides with thermal cement and covered with mounting medium before analysis. The sections were viewed under a dissecting microscope at 12.5X using reflected light. Each sample was assigned an opaque zone count by an experienced reader with extensive experience interpreting otolith sections (Burton 2001, 2002; Burton et al. 2012). Sections were read with no knowledge of date of capture or fish size. A randomly chosen subset of otoliths ($n = 142$; 23% of all otoliths) was then read by a second experienced reader and an index of average percent error (APE) was calculated following Beamish and Fournier (1981).

Timing of opaque zone formation was assessed using edge analysis. The edge type of the otolith was noted: 1 = opaque zone forming on the edge of the otolith section; 2 = narrow translucent zone on the edge, generally < 30% of the width of the previous translucent zone; 3 = moderate translucent zone on the edge, generally 30% – 60% of the width of the previous translucent zone; 4 = wide translucent zone on the edge, generally > 60% of the width of the previous translucent zone (Harris et al. 2007). Based upon edge frequency analysis, all samples were assigned a calendar age, obtained by increasing the opaque zone count by one if the fish was caught before that year's opaque zone was formed

and had an edge which was a moderate to wide translucent zone (type 3 or 4). Fish caught during the time of year of opaque zone formation with an edge type of 1 or 2, as well as fish caught after opaque zone formation, were assigned a calendar age equivalent to the opaque zone count. This adjustment to opaque zone counts functionally put each fish into its correct annual cohort. Finally, while Munro et al. (1973) suggested that peak spawning of Blackfin Snapper occurred in April in Jamaica, Erdman (1976) and Boardman and Weiler (1980) reported that Blackfin Snapper spawned year-round in Puerto Rico. Therefore, we decided not to adjust the age of the fish for the time of year caught (fractional age) due to the lack of a specific discrete birth month.

Growth

Von Bertalanffy (1938) growth parameters were estimated from the observed length at calendar age data using SAS PROC NLIN, a nonlinear regression procedure using the Marquardt iterative algorithm (SAS Institute, Inc. 1987). We anticipated there would be few fish of the youngest age classes available to us, as hook-and-line gear or fishers generally selected for larger fish, and because the SAFMC size limit since January 1992 of 305 mm TL may have excluded smaller fish from the landings. Consequently, the model would be unable to depict initial growth of the youngest fish, leading to difficulty in accurately estimating size at the youngest ages. We therefore re-ran the growth model using the method of McGarvey and Fowler (2002), which adjusts for the bias imposed by minimum size limits by assuming zero probability of capture below the minimum size limit. Size-at-age data were examined using analysis of variance (ANOVA) to determine if there were differences in total length-at-age by region (SEUS vs. U.S. Caribbean) and if pooling of data for estimation of growth curves was appropriate.

Body-Size Relationships

We examined the relationships between TL-W and FL-W for Blackfin Snapper for fish collected from the headboat fishery and the fishery-independent samples with non-linear regression and examining the residuals to determine if a ln-ln transformation of the data was appropriate. Samples from commercial fisheries were eviscerated at sea and thus weights were not available. We also examined the linear relationships between FL-TL and TL-FL ($n = 203$) and FL-SL and TL-SL ($n = 83$).

Natural Mortality

We estimated the instantaneous rate of natural mortality (M) using two methods:

(1) Hewitt and Hoenig's (2005) longevity mortality relationship, $M = 4.22/t_{max}$, where t_{max} is the maximum age of the fish in the sample, and

(2) Charnov et al.'s (2013) method using life history

parameters, $M_A = (L_A/L_\infty)^{-1.5} \times K$, where M_A is natural mortality at age A , L_∞ and K are the von Bertalanffy growth equation parameters and L_A is fish length at age A . We used the midpoint between integer ages (e.g., 0.5, 1.5, 2.5, etc.) to calculate age-specific M , because the Charnov et al. (2013) method cannot mathematically calculate M for age=0. Additionally, for stock assessment purposes where the integer age is used to describe the entire year of the fish's life, the mid-point gives the median value of M for that age.

The equation of Hewitt and Hoenig (2005) uses maximum age to generate a single point estimate of mortality. The Charnov et al. (2013) method, which incorporates life history information via the growth parameters, is based upon evidence suggesting that M decreases as a power function of body size. This method generates age-specific rates of M and has recently been used in the Southeast Data Assessment and Review (SEDAR) stock assessments (E. Williams, pers. comm., NMFS Beaufort Laboratory, Beaufort, NC).

There are many methods available with which to estimate natural mortality. We choose to use Charnov et al.'s M estimator function because the equation takes into account many aspects of life history strategies of many marine fish. We feel that Charnov's equation is the more appropriate model to use versus the equation of Lorenzen (1996) for 2 reasons. First, Lorenzen's method was developed using fish species from temperate regions almost exclusively and included lake, riverine and oceanic species and focused on body weight, but not other life history strategies. The fish in our study come primarily from a subtropical regime. Secondly, the Lorenzen equation used mean weight-at-age. Because many of our samples were from the commercial fishery where the weight of the fish was not available, there would have been more uncertainty in the mean weight-at-age compared to the mean length-at-age. Given the high correlation of weight to length, the using of mean length-at-age should not be any different than using the mean weight-at-age.

FIGURE 1. Monthly percentages of all otolith edge types for Blackfin Snapper (*Lutjanus buccanella*) collected from the southeastern United States and U.S. Caribbean from 1979–2015. Edge type codes: 1=opaque zone on edge, indicating annulus formation; 2=small translucent zone, <30% of previous increment; 3=moderate translucent zone, 30–60% of previous increment; 4=wide translucent zone, >60% of previous increment.

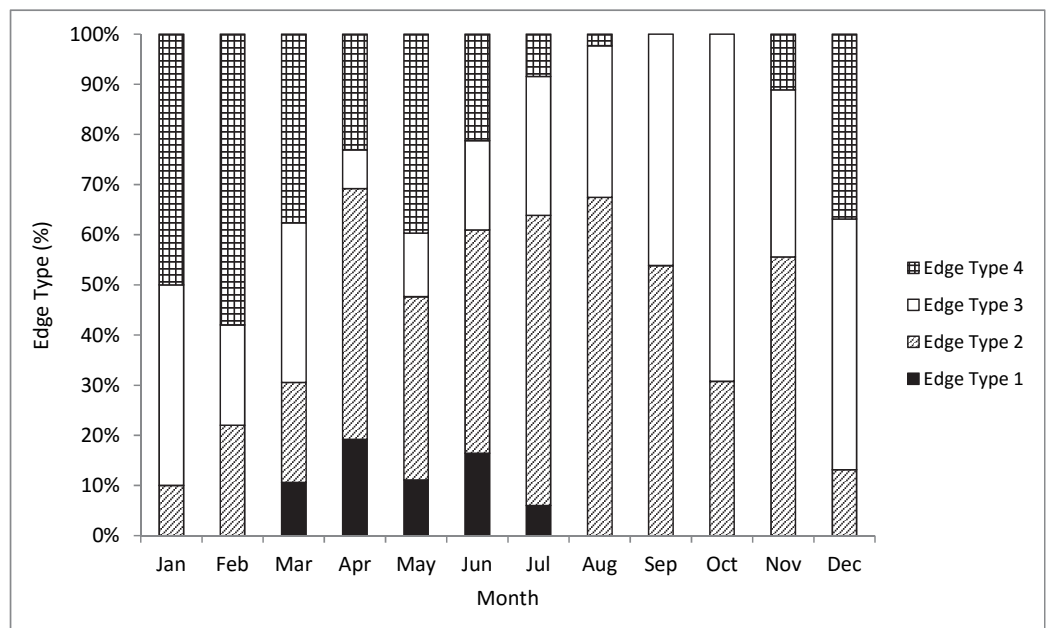


TABLE 1. Number of samples of sagittal otoliths that were used for age and growth study of Blackfin Snapper (*Lutjanus buccanella*) collected from 1979–2015 from fisheries landings and fishery-independent sampling along the coast of the southeastern United States and the U.S. Caribbean. Samples were collected in the following states: North Carolina (NC), South Carolina (SC), and Florida (FL), Puerto Rico, and the U.S. Virgin Islands (Caribbean).

State	Commercial	Recreational	Fishery-Independent
NC	230	1	0
SC	93	5	0
FL	45	117	0
Caribbean	0	2	129
TOTAL	368	125	129

RESULTS

Age determination and timing of opaque zone formation

A total of 636 otoliths from Blackfin Snapper were sectioned (Table 1); the majority came from the North Carolina and South Carolina commercial fisheries (39% and 15%, respectively). Twenty-seven percent of Blackfin Snapper sampled were from Florida, with the majority of these coming from the recreational sector. Fishery-independent samples from the Caribbean accounted for 22% of all samples. Opaque zones were counted on 622 (98%) of Blackfin Snapper sections, as 14 samples were unreadable and excluded from the analysis.

We were able to assign an edge type to all samples for our analysis of opaque zone periodicity. Blackfin Snapper otoliths exhibited opaque zones on the margin from March–July, with peaks in April and June (Figure 1). A shift to a



FIGURE 2. Sections from sagittal otoliths of Blackfin Snapper (*Lutjanus buccanella*). A. 415 mm TL, age 3, edge-type 3; B. 425 mm, age 6, edge-type 2. Age was determined by counting opaque increments (indicated by arrows) along the ventral axis and sulcus using transmitted light at 12.5 X magnification. Brackets indicate marginal increment.

narrow translucent edge was observed during July–September and November. Blackfin Snapper otoliths were without an opaque zone on the edge from August through February. Moderate to wide translucent edge was found December–March, and the widest translucent edge was found in February, prior to opaque zone formation beginning in March. We concluded that opaque zones in Blackfin Snapper otoliths formed annually. Finally, calendar ages were assigned as follows: for fish caught January through July and having an edge type of 3 or 4, the annuli count was increased by one; for fish caught in that same time period with an edge type of 1 or 2 and for fish caught from August to December, the calendar age was equivalent to the annuli count.

Blackfin Snapper sagittae (Figure 2) were clear and easy to interpret, resulting in an APE of 6.9% ($n = 142$) for opaque zone count agreement between the two readers. Di-

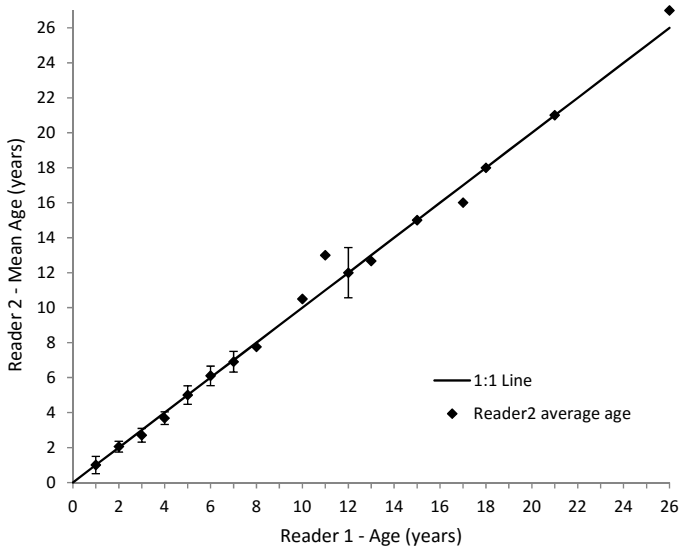


FIGURE 3. Age bias plot for 143 Blackfin Snapper sampled from the southeastern United States from 1979–2015 and aged by 2 primary readers. The first reader's age estimates (X-axis) are plotted against the second reader's mean age estimates for the same-aged fish (Y-axis). Error bars are 95% confidence intervals.

rect agreement between readings was 55%, and this agreement increased to 97% when ± 1 year was used. An age bias plot indicates good agreement between readers for ages 1–15, with no apparent systematic tendency for the second reader to under- or overestimate ages in comparison with the first reader (Figure 3). The mean difference between readers for ages 1–27 was only 0.34 years. The largest difference between readers was 2 years.

Growth

Blackfin Snapper in this study ranged from 180–609 mm TL and ages 1–27 but only 8 fish were estimated to be >15 years old (Table 2). ANOVA results show that mean TL-at-age was not significantly different by geographic re-

TABLE 2. Observed and predicted mean total length (TL, mm) from the freely estimated growth model and natural mortality at age (M , Charnov et al. 2013) for Blackfin Snapper (*Lutjanus buccanella*) collected from 1979–2015 along the coast of the southeastern United States and U.S. Caribbean. Standard errors of the mean (SE) are provided in parentheses.

Age	n	TL (mean \pm SE)	Predicted		
			TL range	TL	M/y
1	1	237	–	217	0.65
2	70	285 (5)	180 - 389	277	0.49
3	152	326 (4)	211 - 448	327	0.40
4	113	372 (5)	249 - 492	367	0.34
5	85	405 (7)	245 - 497	400	0.31
6	69	439 (6)	292 - 524	427	0.28
7	33	473 (10)	335 - 609	449	0.27
8	44	460 (8)	293 - 568	467	0.25
9	15	455 (16)	304 - 565	482	0.24
10	9	478 (37)	296 - 600	494	0.23
11	9	518 (17)	398 - 561	504	0.23
12	5	538 (20)	465 - 577	512	0.22
13	4	475 (39)	382 - 565	519	0.22
14	2	485 (27)	459 - 512	524	0.22
15	3	553 (35)	483 - 595	529	0.21
16	3	553 (11)	540 - 574	532	0.21
17	2	579 (14)	565 - 593	535	0.21
18	–	–	–	538	0.21
19	1	582	–	540	0.21
20	1	580	–	542	0.21
21	–	–	–	543	0.21
22	–	–	–	544	0.21
23	–	–	–	545	0.21
24	–	–	–	546	0.21
25	–	–	–	546	0.21
26	–	–	–	547	0.21
27	1	512	–	547	0.21

TABLE 3. von Bertalanffy growth parameters and standard errors (SE) from Blackfin Snapper (*Lutjanus buccanella*) from the southeastern United States and the U.S. Caribbean based on various model runs. Size-at-age was not significantly different by sex or by region (ANOVA: $F_{(2,620)} = 1.61$, $p = 0.11$). All lengths are TL (mm). All model runs were unweighted and not corrected for size-limit bias unless stated otherwise.

Model Run	n	L_{∞} (SE)	K (SE)	t_0 (SE)
Unweighted, freely estimated, all data combined	622	549 (15)	0.20 (0.02)	-1.51 (0.33)
Bias-corrected, all data combined	587	532 (9)	0.28 (0.01)	-0.04 (1.90)
Florida-Caribbean region	293	579 (23)	0.16 (0.02)	-1.60 (0.43)
North Carolina-South Carolina region	329	526 (21)	0.27 (0.05)	-0.99 (0.46)
Females	91	584 (62)	0.12 (0.04)	-2.26 (1.03)
Males	85	579 (37)	0.17 (0.04)	-1.17 (0.72)

gion (Florida–Caribbean: $n = 293$; Carolinas: $n = 329$; $F_{(2,620)} = 1.61$, $p = 0.11$). We then pooled all data and the resulting estimated von Bertalanffy equation was: $L_t = 549 (1 - e^{-0.20(t+1.51)})$ ($n = 622$; Figure 4, Table 3).

There were few fish < age=2 available to us, no doubt because hook-and-line gear or fishers generally select for larger fish. Also, in 1992 the SAFMC enacted a 305 mm TL (12 inch) minimum size limit on the species in the South Atlantic jurisdiction. Consequently, the model was unable

to depict initial growth of the youngest fish, thus explaining the slightly negative estimate of t_0 . We therefore re-ran the growth model using the method of McGarvey and Fowler (2002), which adjusts for the bias imposed by minimum size limits by assuming zero probability of capture below the minimum size limit. The resulting von Bertalanffy growth equation was: $L_t = 532 (1 - e^{-0.28(t+0.00)})$ ($n = 587$; Figure 4).

While the bias-corrected von Bertalanffy model better estimated size at the youngest ages than the uncorrected

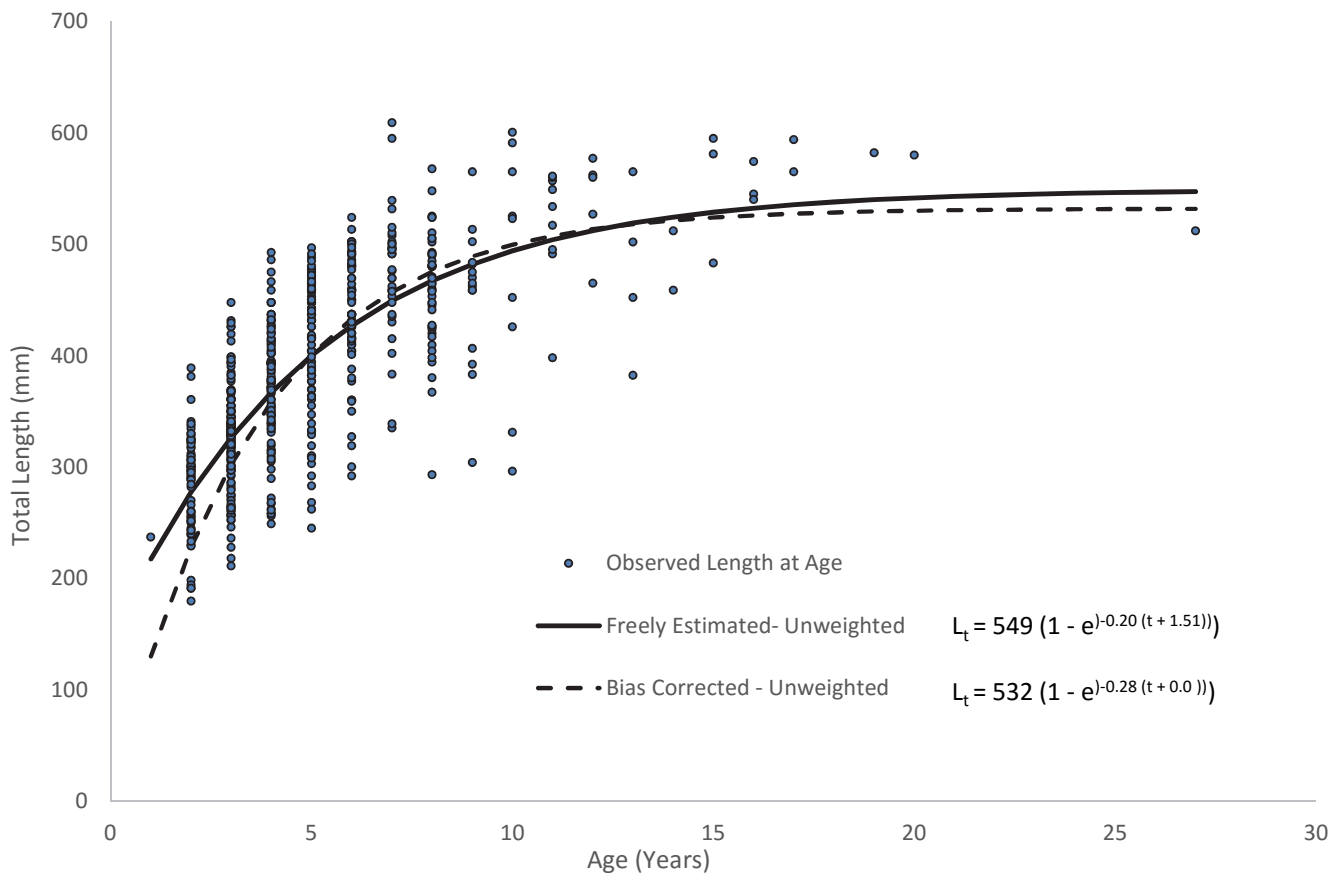


FIGURE 4. Comparison of southeastern United States - U.S. Caribbean Blackfin Snapper observed size at age to von Bertalanffy growth curves for freely estimated (unweighted) and size limit bias-corrected model runs (models follow McGarvey and Fowler 2002).

model (e.g., 130 mm TL vs. 217 mm TL for age=1), there was negligible difference in predicted sizes for most ages. By age=8 the curves converge and were nearly identical, with there being only 15 mm difference in predicted size at age=27, the oldest age in our sample (Figure 4). Our freely estimated growth curve fit the observed data very well, given the moderate range in length-at-age.

Body-size relationships

Body size relationships for Blackfin Snapper are shown in Table 4. The W-TL and W-FL relationships both exhibited additive variance in the residuals (variance not increasing with size), therefore we concluded that the direct non-linear fit was appropriate.

Natural mortality

Natural mortality (M) was estimated to be 0.15/y for

TABLE 4. Body-size relationships and associated statistics for Blackfin Snapper (*Lutjanus buccanella*) collected from 1979-2015 from the southeastern United States and the U.S. Caribbean.

Relationship	n	r ²	a (SE)	b (SE)
TL = bFL + a	203	0.99	0.81 (3.00)	1.09 (0.01)
FL = bTL + a	203	0.99	3.38 (2.74)	0.91 (0.01)
TL = bSL + a	83	0.97	14.27 (6.24)	1.23 (0.02)
FL = bSL + a	89	0.99	10.84 (2.84)	1.14 (0.01)
W = aTL ^b	216	–	7.79 × 10 ⁹ (4.47 × 10 ⁹)	3.09 (0.09)
W = aFL ^b	228	–	9.54 × 10 ⁹ (4.95 × 10 ⁹)	3.11 (0.08)

Blackfin Snapper when integrating all ages into a single point estimate and using the maximum age from our study of 27 years. Age-specific estimates of M ranged from 0.65 to 0.21/y for ages 1–27 (Table 2).

When considering the cumulative estimate of survivorship to the oldest age, the Hewitt and Hoenig method estimates 2.3% survivorship, while the Charnov estimate is 0.3%. Few of the fish in our samples were older than 12 years (17 of 622) and only 2 were 20 years or older (0.3%). Our age frequency suggests that the chance of survivorship to the oldest age may be as low as 0.3%. There is no evidence that the selectivity function of hook and line gear is dome shaped, thus our study had a chance of collecting the largest and oldest fish in the population. These observations give weight to the argument to use Charnov's estimate of M at age.

DISCUSSION

This study fills important gaps in basic life history information for Blackfin Snapper in the SEUS and U.S. Caribbean. We have shown that sagittal otoliths are a suitable structure for ageing, with agreement between readers close

to Campana's (2001) acceptable standard of 5% APE between readers for species of moderate longevity and reading complexity. One opaque zone was deposited per year from March–July. These results are similar to timing of annulus formation for other members of the family Lutjanidae in the SEUS (June for Gray Snapper (*Lutjanus griseus*), Burton 2001; May for Mutton Snapper (*Lutjanus analis*), Burton 2002). We present the first description of growth of Blackfin Snapper in SEUS waters. The species grows fast, attaining a mean observed length of 372 mm TL by age=4. Growth of fish in our study slowed after reaching a mean observed length of 473 mm TL at age=7. Mean observed size-at-age fluctuated for older ages, probably due to a combination of small sample sizes at the oldest ages as well as variability in size-at-age. Our study contained 17 fish older than age=12, ranging from 382–595 mm TL, but our largest fish was a 609 mm TL individual that was only age=7.

The maximum age of Blackfin Snapper in this study, 27 years, is substantially larger than Espinozo and Pozo's (1982) finding of a maximum age of nine years for Blackfin Snapper from the southeastern coast of Cuba, using urohyal bones, but is comparable to other *Lutjanus* spp. from the SEUS. The observed maximum age of Gray Snapper, a close congener, is 25 years (Burton 2001). Other large snappers have observed maximum ages recorded in the 40s (Mutton Snapper, SEDAR 2015) and 50s (Red Snapper, McInerney 2007; Cubera Snapper (*Lutjanus cyanopterus*), ML Burton unpublished data). Smaller lutjanids such as Lane Snapper (*Lutjanus synagris*) and Mahogany Snapper (*Lutjanus mahogoni*), have maximum ages of just 11 to 18 years, respectively (Brennan 2004; ML Burton, unpublished data). Schoolmaster (*Lutjanus apodus*), a small to medium snapper found in coastal habitats in the Florida Keys, was found to have a maximum age of 42 years (Potts et al. 2016). The maximum age of Blackfin Snapper from this study should be not be considered a true maximum age since, with increased sampling, a new maximum could be encountered.

The fact that there were no significant differences in mean TL-at-age between the northern sampled area (North Carolina–South Carolina) and the southern sampled area (Florida–U.S. Caribbean) allowed us to pool our data to generate a combined growth curve. This result may be useful to managers in areas with less resources available to conduct studies to generate life history information. These vital life history data could be combined with catch data using data-limited assessment methodologies to generate annual catch limits.

Natural mortality (M) of wild populations of fish is difficult to estimate but is an important input variable into stock assessments. A point estimate of M , such as that obtained using the method of Hewitt and Hoenig (2005), for the entire life span of a fish seems relatively uninformative, because as fish grow they become less vulnerable to preda-

tion. The estimate of M derived from the maximum age was a reasonable estimate for the fully recruited ages in our study but is an insufficient estimate of M for all ages. The age-varying M calculated using Charnov et al. (2013) is a more appropriate estimator for the younger ages. The initial Charnov estimates of M starting with the fully recruited age of 4 are slightly more than double the Hewitt and Hoenig estimate, reflecting higher natural mortality at younger ages. The age-specific estimates of M for the older ages continue to decrease until stabilizing at 0.21 at age-15.

When we compare estimates of M from this study with estimates from other lutjanids, we need to be cognizant of differences in both maximum size and longevity, two factors that influence estimates of M . Potts et al. (2016) estimated $M = 0.47-0.12$ for Schoolmaster for ages 1-42. Schoolmaster is a slightly smaller-sized fish than Blackfin Snapper but it has a higher maximum age (42 years vs. 27 years). Cubera Snapper, the largest lutjanid in the SEUS, is both larger and longer-lived than Blackfin Snapper (maximum size 1422 mm TL, maximum age 55 years; ML Burton, unpublished data), but the range of estimated values for M was similar, 0.50-0.05 for ages 1-55. Survivorship to the oldest age is similar between these three lutjanids, with Schoolmaster survivorship estimated at 0.3% (Potts et al. 2016) and Cubera Snapper survivorship estimated at 0.2% (ML Burton, unpublished data).

One limitation of many age-growth studies is the lack

of fish in smaller size classes, due to the fishery-dependent nature of the samples as well as the selectivity of fishing gear. We included fishery-independent samples to help overcome this problem, but only 11% of our samples were age-2 or younger, no doubt because the majority of our fishery-independent samples were still collected with gear (hook-and-line) that was selective for larger fish. One potential way to address this problem in future studies would be to structure fishery-independent sampling to include gear types that did not select only for larger fish (e.g., trawl, spear).

The data in this study were collected over a protracted period of time (36 years). While one could argue that this approach would be beneficial in capturing natural variability, it is true that population parameters can vary inter-annually for various reasons (e. g., variable recruitment, environmental variability, changes in fishing pressure), and it is likely that parameter estimates based on samples collected over a long time period would have increased variability. Reducing this variability may be possible by increasing the sample sizes or adding consistency to the temporal spread of samples. Species such as Blackfin Snapper are harvested frequently enough from SEUS waters that obtaining adequate biological samples for age and reproduction studies should not be problematic. With a minimal increase in resources, more gaps in information for data-poor and data-limited species, in both the SEUS and U.S. Caribbean, should be eliminated.

ACKNOWLEDGMENTS

We gratefully acknowledge the many NMFS headboat and commercial port samplers and the scientific personnel of the NOAA R/V Oregon II whose efforts made this study possible. Rob Cheshire, D. Meyer, T. Kellison, E. Williams and two anonymous reviewers provided reviews which greatly improved the manuscript. Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

LITERATURE CITED

- Beamish, R.J. and D.A. Fournier. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Science* 38:982-983.
- Boardman, C. and D. Weiler. 1980. Aspects of the life history of three deep water snappers around Puerto Rico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 32:158-172.
- Brennan, K.J. 2004. Age, growth and mortality of lane snapper, *Lutjanus synagris*, from the east coast of Florida. M.S. Thesis. East Carolina University, Greenville, NC, USA, 59 p.
- Burton, M.L. 2001. Age, growth, and mortality of gray snapper from the east coast of Florida. *Fishery Bulletin* 99:245-256.
- Burton, M.L. 2002. Age, growth and mortality of mutton snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. *Fisheries Research* 59:31-41.
- Burton, M.L., J.C. Potts, and D.R. Carr. 2012. Age, growth and natural mortality of rock hind, *Epinephelus adscensionis*, from the Gulf of Mexico. *Bulletin of Marine Science* 88:903-917. doi: 10.5343/bms.2011.1102

- Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59:197–242. doi: 10.1111/j.1095–8649.2001.tb00127.x
- Cervigon, F. 1966. Los peces marinos de Venezuela. Estación de Investigaciones Marinas de Margarita. Fundación La Salle de Ciencias Naturales, Caracas, Venezuela. 951 p.
- Charnov, E.L., H. Gislason, and J.G. Pope. 2013. Evolutionary assembly rules for fish life histories. *Fish and Fisheries* 14:212–224. doi: 10.1111/j.1467–2979.2012.00467.x/epdf
- Claro, R. and K.C. Lindeman. 2008. Biología y manejo de los pargos (Lutjanidae) en el Atlántico occidental. Instituto de Oceanología, CITMA, La Habana, Cuba, 472 p.
- Erdman, D.S. 1976. Spawning patterns of fishes from the northeastern Caribbean. Puerto Rico Department of Agriculture, Commonwealth of Puerto Rico, Area of Special Services, Commercial Fisheries Laboratory, Agricultural and Fisheries Contributions, Official Publication in the Area of Special Services 8:1–36.
- Espinoso, L. and E. Pozo. 1982. Edad y crecimiento del sesi (*Lutjanus buccanella* Cuvier 1828) en la plataforma suroriental de Cuba. *Revista Cubana de Investigaciones Pesqueras* 7:80–100.
- Grimes, C.B., C.S. Manooch III, G.R. Huntsman, and R.L. Dixon. 1977. Red snappers of the Carolina coast. *Marine Fisheries Review* 39:12–15.
- Harris, P.J., D.M. Wyanski, D.B. White, P.P. Mikell, and P.B. Eyo. 2007. Age, growth, and reproduction of greater amberjack off the southeastern U.S. Atlantic coast. *Transactions of the American Fisheries Society* 136:1534–1545. doi: 10.1577/T06–113.1
- Hewitt, D.A. and J.M. Hoenig. 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fishery Bulletin* 103:433–437.
- Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology* 49:627–647.
- McGarvey, R. and A.J. Fowler. 2002. Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest. *Fishery Bulletin* 100:545–558.
- McInerney, S.A. 2007. Age and growth of Red Snapper, *Lutjanus campechanus*, from the southeastern United States. M.S. Thesis, University of North Carolina–Wilmington, Wilmington, N.C. 96 p.
- Munro, J.L., V.C. Gaut, R. Thompson, and P.H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology* 5:69–84.
- Potts, J.C. and C.S. Manooch III. 1995. Age and growth of red hind and rock hind collected from North Carolina through the Dry Tortugas, Florida. *Bulletin of Marine Science* 56:784–794.
- Potts, J.C., M.L. Burton, and A.R. Myers. 2016. Age, growth, and natural mortality of schoolmaster, (*Lutjanus apodus*) from the southeastern United States. *PeerJ* 4:e2543. doi: 10.7717/peerj.2543
- South Atlantic Fisheries Management Council (SAFMC). 2015. Blackfin Snapper: Fish ID and Regs: Regulations by Species. Available: <http://safmc.net/regulations/regulations-by-species/blackfin-snapper/>. (viewed on 11/30/2016).
- SAS Institute, Inc. 1987. SAS/STAT guide for personal computers, version 6 edition. SAS Institute, Cary, NC, USA 1028 p.
- SEDAR. 2015. SEDAR 15A DW 15. Life History of *Lutjanus analis* inhabiting Florida waters. <http://sedarweb.org/sedar-15a-dw15-life-history-lutjanus-analis-inhabiting-florida-waters> (viewed on 11/30/2016).
- SERO. 2015. Summary of commercial and recreational fishing regulations for the U.S. Caribbean Exclusive Economic Zone for species managed by the Caribbean Fishery Management Council. http://sero.nmfs.noaa.gov/sustainable_fisheries/caribbean/documents/pdfs/regs_booklet.pdf. (viewed on 11/30/2016).
- Sylvester, J.R., D.W. Drew, and A.E. Damann. 1980. Selective life history of silk and blackfin snapper from the Virgin Islands. *Caribbean Journal of Science* 15:41–48.
- Thompson, R. and J.L. Munro. 1983. The biology, ecology and bionomics of the snappers, Lutjanidae. In: J. L. Munro., ed. Caribbean Coral Reef Fishery Resources Volume 17. ICLARM Studies and Reviews Manila, Phillipines, p. 94–109.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Human Biology* 10:181–243.