Age-size Structure of Gray Snapper from the Southeastern United States: A Comparison of Two Methods of Back-calculating Size at Age from Otolith Data

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Allyn G. Johnson, *National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32408*

L. Alan Collins, *National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32408*

Christopher P. Keim, *National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, FL 32408*

Abstract: The age-size structure of gray snapper (*Lutjanus griseus*) from Ft. Pierce, Florida, to Grand Isle, Louisiana, was examined. Otolith sections from 432 fish collected in 1991 to 1993 were used to compare 2 methods (direct proportion and regression) of back-calculation of size at age. The observed age range was 1 to 25 years and the size range was 236 to 764 mm total length. Differences were observed in back-calculated sizes at age between the 2 back-calculation methods, between sexes and geographic divisions. The back-calculated size at age was larger for ages 1 to 10 years from the direct proportion than from the regression method. Males were larger than females for ages 4 to 15 years using the direct proportion method, but only for ages 13 and 14 years using the regression method. Northern fish were larger at age than southern fish using both back-calculation methods.

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The gray snapper (*Lutjanus griseus*), also known as mangrove snapper, is a member of the reef fish complex occurring as adults along the Atlantic Coast from Massachusetts to Rio de Janeiro, Brazil, and in the Gulf of Mexico. They are associated with a broad range of habitats ranging from irregular substrates to smooth bottoms and seagrass beds. This species is important to both recreational and commercial fisheries (Manooch and Matheson 1981, Allen 1985).

Information on the age-size structure of gray snapper resources in U.S.

waters is scarce. Manooch and Matheson (1981) reported on Florida's Atlantic Coast resources in the late 1970s and indicated that sectioned otoliths were excellent for determining age and growth. They also reviewed earlier studies on this species. Rutherford et al. (1989) reported on catches from Everglades National Park, Florida, from 1958 to 1984 and found great fluctuations in the catch rate over the period. The fishery consisted of 1- to at least 7-year-olds with 3- to 4-year-olds making up 87% of the catch. Shipp (1991) determined the ages of 23 fish from the northern Gulf of Mexico using otolith sections (100% legibility) and the ages ranged from 1 to 27 years old (176 to 733 mm total length).

Outside U.S. waters, reports from Cuba (Claro and Pola 1977, Baez et al. 1980, Claro 1983) indicated the usefulness of otoliths for determining age and established that otolith growth marks (bands) are annuli.

This report conveys information on the age-size structure of gray snapper from southeastern U.S. waters for the period 1991–1993 and compares the results of 2 methods of back-calculation of size at age. This information is needed to evaluate the resource's present condition as the available data is a decade old. Additionally, there is a lack of information from the Gulf of Mexico.

Methods

Gray snapper were randomly sampled[1] from recreational (charter and head boats) and commercial (hook-and-line) fisheries from Fort Pierce, Florida, to Grand Isle, Louisiana, January 1991 to November 1993. We collected otoliths (sagittae-right or the pair) and measured body lengths [total (TL mm) and fork length (FL mm)] on each fish. When possible, sex and body weight (in kilograms) were recorded. All otoliths were stored dry. The otolith width (OW) across the core (focus) was measured in millimeters on 132 otoliths.

The otoliths were transversely sectioned following the method of Manooch and Matheson (1981). Sections (0.25 mm thick) were mounted with Flo-Texx[2] cement on glass slides and examined with transmitted light at 20X magnification. The opaque (dark) bands, which we assumed were annuli, were counted and the distance was measured from their distal edge to the core (focus). The total distance of core to distal edge of the section (R) was also recorded. The otolith sections were examined twice using two readers.

Back-calculations of size (length) at age (distal edge formation of the opaque band) were performed using 2 methods in order to provide values comparable to the reports in the literature. The methods were those of Manooch and Matheson (1981) and Lea (1910) hereafter referred to as Reg (regression) and DP (direct proportion), respectively. Theoretical growth parameters were derived using SAS PROC NLIN which is a non-linear curve fitting program.

[1] Randomly sampled means samples collected from the fisheries as available without regard to length, sex, time of year, etc.

[2] Reference to trade names does not imply endorsement of commercial products by the National Marine Fisheries Service.

SAS programs (procedures GLM, REG, TTEST) were used to analyze the data, to develop other relationships such as TL mm-weight (kg) and TL mm-FL mm conversions, and to make comparisons between the 2 methods of back-calculations, sexes, and geographic regions. Mortality estimates were made following the methods of Manooch and Matheson (1981), Nelson and Manooch (1982), and Hoenig (1983) under the assumption that the age structure of our collection represented the age structure of the resource.

Results and Discussion

Annuli on the otolith sections were clearly visible, as indicated by previous gray snapper studies (Manooch and Matheson 1981, Shipp 1991). We found 98.5% of the 461 otoliths examined to be readable, 95% (438) to be readable and measurable, and 93.7% (432) to be readable with all bands measurable. The agreement between 2 readers as to the number of bands was 94%. Beamish and Fournier's (1981) index of average error was 0.0087. The 432 fish (66 from Fort Pierce, Fla.; 30 from Key West, Fla.; 52 from St. Petersburg, Fla.; 180 from Panama City, Fla.; and 104 from Louisiana) were used for further analysis (Table 1).

The relationship between TL mm and otolith width (OW) before sectioning was TL mm = $-75.7305 + 7.1716$ (OW); $N = 132$; $r = 0.9506$. The relationship between TL mm and sectioned otolith radius (R) was closest using natural log (Ln) conversions. This relationship was TL mm = 4.8453 $R^{1.0717}$; $N = 438$; $r = 0.8876$. The higher correlation (r) for whole otolith widths suggests that some of the variation in the TL mm-R relationships was the result of sectioning

Table 1. Information on gray snapper collected from the Gulf of Mexico 1991–1993.

Year	Location	*N*	Total length range (mm)	Age range (years)
1991	Ft. Pierce, Fla.	3(3)	630–690	18–20
1992	Ft. Pierce, Fla.	49(45)	270–620	2–14
1993	Ft. Pierce, Fla.	19(18)	242–425	1–13
1991	Key West, Fla.	8(8)	236–480	2– 6
1992	Key West, Fla.	7(7)	291–500	4– 6
1993	Key West, Fla.	15(15)	342–635	3–11
1992	St. Petersburg, Fla.	19(19)	310–610	2–18
1993	St. Petersburg, Fla.	35(33)	240–600	2–11
1991	Panama City, Fla.	1(1)	441	4
1992	Panama City, Fla.	65(60)	349–764	3–20
1993	Panama City, Fla.	127(119)	298–729	2–23
1991	Grand Isle, La.	71(65)	325–730	3–21
1992	Grand Isle, La.	8(8)	370–740	3–20
1993	Grand Isle, La.	33(31)	282–740	2–25

N = number of fish collected and in parenthesis () is number with measurable bands which were used in study.

and the slightly scalloped margin of the otoliths. The relationship TL mm = 4.8453 $R^{1.0717}$ was used in back-calculation of size at age using the Reg method for all fish. The relationships for females only, TL mm = 6.5653 $R^{1.0020}$ and for males, TL mm = 4.5790 $R^{1.0895}$ were used in back-calculations of size-at-age by sex using the Reg method.

The age ranges of the fish were 1 to 25 years and 236 to 764 TL mm for females and 1 to 23 years and 245 to 735 TL mm for males.

A summary of TL mm at age at capture (observed) and back-calculated TL mm at age is presented in Tables 2 and 3 which provide values in the observed and back-calculated categories based on all fish in the study. Several items that can be ascertained from Tables 2 and 3 are:

1. The empirical length at age values found in this study generally were larger for younger fish (age 1–10 years) and were smaller for older fish (>10 years) than those reported by Manooch and Matheson (1981) for the east coast

Table 2. Summary of gray snapper total length (mm) at age values for the southeastern United States 1991–1993 (empirical values).

		Observed length at capture				
		Range				
Age	*N*	Min	Max	Mean	±SD[a]	I[b]
1	1	242	242	242.0		242.0
2	19	236	334	278.5	30.3	36.5
3	55	267	450	354.7	40.0	76.2
4	84	291	545	400.9	57.0	46.2
5	58	290	524	420.2	67.5	19.3
6	53	300	590	457.8	74.7	37.6
7	24	370	591	512.7	62.9	54.9
8	22	320	641	523.9	77.2	11.2
9	8	542	643	592.4	29.2	68.5
10	16	377	646	575.9	61.7	−16.5
11	10	520	640	577.9	45.0	2.0
12	12	425	702	608.4	75.2	30.5
13	7	422	648	572.1	78.2	−36.3
14	5	565	640	610.0	30.2	37.9
15	5	570	631	604.8	26.5	−5.2
16	5	580	710	665.0	61.0	60.2
17	7	550	655	621.4	34.2	−43.6
18	12	518	710	624.7	53.3	3.3
19	13	580	714	643.6	43.6	18.9
20	11	550	764	670.3	61.5	26.7
21	2	673	710	691.5	26.2	21.2
22	1	729	729	729.0		37.5
23	2	698	735	716.5	26.2	−12.5
24	0					
25	1	740	740	740		

[a]SD = 1 standard deviation.
[b]I = annual growth increment.

Table 3. Summary of gray snapper total length (mm) at age values for the southeastern United States 1991–1993 (back-calculated values).

	Mean back-calculated length at age[a]						
	Lea[a] (DP)			M&M[b] (Reg)			
Age	Mean	±SD[c]	I[d]	Mean	±SD	I	Probability[e]
1	145.7	41.1	145.7	133.6	36.8	133.6	0.0001*
2	263.8	48.2	118.1	252.3	42.6	118.7	0.0007*
3	334.1	49.6	70.3	323.5	42.7	71.2	0.0013*
4	379.3	54.5	45.2	365.1	43.2	41.6	0.0001*
5	417.9	59.3	38.6	401.6	47.9	36.5	0.0001*
6	452.5	58.9	34.6	433.2	50.1	31.6	0.0004*
7	481.5	55.3	29.0	462.1	52.8	28.9	0.0025*
8	501.5	55.4	20.0	483.6	52.7	21.5	0.0048*
9	520.6	53.1	19.1	504.8	53.6	21.2	0.0140*
10	534.5	52.7	13.9	521.5	56.1	16.7	0.0433*
11	548.3	51.6	13.8	542.9	57.0	21.4	0.3475
12	560.8	53.4	12.5	559.4	56.7	16.5	0.8324
13	569.9	47.8	9.1	578.0	60.7	18.6	0.2612
14	586.1	43.1	16.2	599.3	61.7	21.3	0.0959
15	598.7	44.3	12.6	612.2	65.7	12.9	0.0865
16	611.3	46.7	12.6	623.0	66.8	10.8	0.1664
17	618.7	44.5	7.4	632.7	68.0	9.7	0.0833
18	631.1	48.0	12.4	650.8	69.2	18.1	0.0262*
19	647.2	46.7	16.1	675.0	65.4	24.2	0.0739
20	667.9	49.7	20.7	696.9	76.6	21.9	0.2340
21	694.6	19.3	26.7	714.1	75.1	17.2	0.8888
22	707.6	18.8	13.0	737.8	94.2	23.7	0.8347
23	711.2	16.8	3.6	773.6	96.9	35.8	0.6901
24	725.5		14.3	674.1		−99.5	
25	732.7		7.2	641.3		−32.8	

[a]Lea = black-calculation method used followed Lea (1910).
[b]M&M = back-calculation method used followed Manooch and Matheson (1981).
[c]SD is 1 standard deviation.
[d]I is annual growth increment.
[e]Probability = the probability that the back-calculated length at age in Lea and M&M columns are different. TTEST with Cochran option. * = significantly different $p < 0.05$.

of Florida a decade earlier. Our empirical lengths at age values were similar to those reported by the contemporary study of Shipp (1991) for the northern Gulf of Mexico.

2. Our data showed the effect of truncation which may be caused by the minimum size limitations (10–12 inches (245–305 mm) + 1) placed on the fisheries by management (i.e., the low number of 1 and 2 year olds).

3. The back-calculated lengths at age from the 2 methods (Reg and DP) are significantly different for younger fish (1–10 year olds).

The differences in estimates between the 2 methods of back-calculations, ignoring the extreme ages (1 year old and >20 years old) where few samples were obtained, were not extreme. The maximum difference between mean back-calculated lengths at age was 29 mm and between annual growth increments was 23.8 mm using the 2 methods of back-calculation.

A sufficient number of gray snapper were collected from the Gulf of Mexico (Key West to Louisiana) to make comparisons of back-calculated length at age by sex (Table 4). The results from the 2 back-calculations are conflicting in that the DP method indicated significant differences (12 of 21 length at age comparisons differed) in back-calculated length at age between the sexes, while the Reg method indicated few significant differences (2 of 21 length at age comparisons differed). This conflict in results is probably caused by computational differences between the 2 methods. The DP method is a direct proportional approach, thus it retains individual fish variation with regard to otolith radial measurements. The Reg method uses a power curve of TL mm-R which is a least square fit, thus individual fish variations are averaged. Carlander (1981) pointed out additional considerations with regard to the traditional and regression methods of back-calculation that should be applied when interpreting the results of these methods.

Table 4. Comparison between back-calculated total length in mm at age by sex for gray snapper collected from Key West, Florida, to Grand Isle, Louisiana, 1991–1993.

	Lea (1910) method[a]					Manooch and Matheson (1981) method[b]						
	Males $N = 107$		Females $N = 164$			Males $N = 107$		Females $N = 164$			N of calc.[c]	
Age	Mean	±SD	Mean	±SD	P	Mean	±SD	Mean	±SD	P	Male	Female
1	155.7	43	149.8	41	0.27	138.8	42	147.2	34	0.09	107	164
2	280.7	48	273.9	42	0.23	263.2	46	270.8	37	0.15	107	164
3	354.7	46	345.5	38	0.09	337.5	45	342.3	36	0.37	103	163
4	403.5	51	390.2	41	0.04*	382.8	47	380.7	35	0.67	86	143
5	446.9	50	426.5	43	0.01*	422.6	54	415.5	37	0.35	68	114
6	482.6	402	458.0	46	0.00*	456.4	52	443.4	38	0.12	54	90
7	508.0	43	479.5	42	0.00*	482.8	62	468.1	39	0.19	37	78
8	527.8	42	500.4	44	0.01*	500.2	58	489.4	40	0.37	29	74
9	550.8	36	518.1	46	0.00*	520.5	64	508.7	42	0.42	23	65
10	564.7	37	532.2	45	0.00*	534.9	69	524.6	44	0.54	20	61
11	577.4	38	544.2	45	0.01*	556.1	65	543.0	45	0.45	17	52
12	595.1	37	557.1	46	0.00*	587.4	51	557.0	47	0.06	15	46
13	600.5	33	567.3	42	0.01*	615.4	48	573.4	49	0.11*	12	43
14	613.7	33	582.2	41	0.02*	630.4	52	591.9	51	0.04*	12	40
15	624.6	34	595.7	42	0.04*	644.4	59	606.1	54	0.09	10	36
16	636.5	37	608.7	45	0.08	649.1	57	616.9	54	0.16	9	35
17	640.0	32	618.2	44	0.15	671.9	55	626.5	58	0.07	32	8
18	653.7	35	632.6	47	0.25	688.0	68	647.2	53	0.22	6	28
19	664.6	36	640.5	56	0.26	700.6	70	663.3	62	0.29	6	18
20	675.4	38	672.5	69	0.93	727.7	86	683.4	78	0.44	4	8
21	704.5	2	709.0	8	0.56	771.4	124	642.7	—	0.38	2	2
22	717.6	—	716.3	8	—	874.2	—	649.3	—	—	1	2
23	723.4	—	718.2	—	—	881.9	—	656.0	—	—	1	1
24			725.5	—	—			662.6	—	—	0	1
25			732.7	—	—			669.2	—	—	0	1

[a]Back-calculations following the method of Lea (1910). SD is standard deviation, N is number of samples, — is no or insufficient data. P is the probability that total length at age is different between sexes; * = difference between sexes is significant $P < 0.05$ using T-TEST with Cochran option.

[b]Back-calculations following the method of Manooch and Matheson (1981). Using total length in mm = 6.5653 total radius$^{1.0020}$ for females ($N = 182$, $r = 0.8988$) and total length in mm = 4.5795 total radius $^{1.0895}$ for males ($N = 123$, $r = 0.8715$), developed from all females and males sampled.

[c]Number of calculations by sex used to compare weighted mean back-calculated total length at age.

Insufficient numbers of fish of each age from each area were collected to make geographic comparisons; however, comparisons can be made by combining areas. When the collections were combined into 2 arbitrary divisions (north ($N = 336$) and south ($N = 96$) of 27°N latitude) differences (SAS PROC T TEST with Cochran option and $P < 0.05$ for significant difference) were observed in the back-calculated lengths at age using both back-calculation methods. The DP method indicated that lengths at ages were significantly different between the 2 divisions for ages 1–6 years and 9 years. The Reg method indicated lengths at ages were significantly different between the 2 divisions for ages 2–6 years. The northern fish mean lengths at ages were larger than southern fish mean length at age for ages 1–13 years using both methods. Since northern fish predominated in this study, this finding should be considered preliminary. Table 5 presents a summary of von Bertalanffy growth parameters for the aforementioned comparisons.

In all comparisons the maximum lengths (L_∞) predicted were larger and their respective growth coefficients (K) were smaller using the Reg method than by using the DP method. Knight (1968) pointed out the close inverse correlation of L_∞ and K and expressed that caution should be taken in interpretation. This cautious viewpoint was reinforced by Vaughan and Kanciruk (1982).

Instantaneous total mortality (Z) estimates can be made using the regression method of plotting the Log_e of the age frequency on age. The slope of the

Table 5. Von Bertalanffy growth parameters of gray snapper, *Lutjanus griseus,* from the southeastern United States, 1991–1993.

	von Bertalanffy growth parameters[b]							
Comparison[a]	L_∞	K	t_o	SE of L_∞	SE of K	SE of t_o	Max. age	*N* fish
All samples								
Lea (DP)	673.3323	0.1552	−1.0655	12.4413	0.0119	0.2744	25	432
M&M (Reg)	792.2499	0.0783	−3.8971	34.0450	0.0989	0.5698	25	432
Gulf of Mexico								
by sex								
males[c]	852.6787	0.0691	−4.7817	96.8083	0.0210	1.4215	23	107
females[c]	818.3859	0.0638	−6.0580	68.0204	0.0155	1.3629	25	164
males[d]	687.9910	0.1695	−1.0088	21.8827	0.0222	0.4623	23	107
females[d]	662.2752	0.1665	−1.1986	12.7059	0.0178	0.4477	25	164
North vs south[e]								
Lea north (DP)	663.0304	0.1740	−1.0360	9.8161	0.0128	0.2809	25	336
Lea south (DP)	554.2275	0.1739	−0.9457	53.8234	0.0499	0.7872	14	96
M&M north (Reg)	811.2254	0.0716	−4.7090	44.0037	0.0112	0.7745	25	336
M&M south (Reg)	954.8228	0.1486	−1.7615	53.6146	0.0394	0.7551	14	96

[a]Comparison made using Lea (1910) method (Lea) and Manooch and Matheson (1981) method (M&M).

[b]$L_t = L_\infty(1-e^{-k(t-t_o)})$; where L_t = total length in mm at age t, L_∞ = maximum length, and K = growth coefficient, t_o = hypothetical age (in years) at which fish would have zero growth, SE = standard error, and N = number of fish.

[c]M&M using equations developed from each sex. Total length in mm = 6.5653 total radius$^{1.0020}$ for females ($N = 182$, $r = 0.8988$) and total length in mm = 4.57902 total radius$^{1.0895}$ for males ($N = 123$, $r = 0.8715$).

[d]Lea method.

[e]North vs south of 27°N latitude.

linear descending right limb of the curve after full recruitment (4 years) estimates Z. Z was estimated at 0.1669 for all fish (age range 4–25 years) and at 0.2645 for all fish when the age range was truncated at 14 years. Z estimated from maximum age was 0.1789 (Hoenig 1983). These estimates are less than previous estimates for the east coast of Florida (0.39 and 0.60) made by Manooch and Matheson (1981).

Natural mortality (M) was computed following the procedures of Nelson and Manooch (1982) with mean annual water temperature of 23 C. The estimates of M were 0.2046 and 0.1244 using values from von Bertalanffy equations from DP method and the Reg method, respectively. Estimates of M were also made using the functional regression of M on K method (Ralston 1987) which resulted in values of 0.3245 and 0.1307 for DP and Reg methods, respectively. The mortality estimates (Z and M) are summarized in Table 6.

The relationship between total length and fork length was described by:

$$\text{TL mm} = 11.92 + 1.0304 \text{ FL mm}; N = 276, r = 0.9951$$

The relationship between total weight in kilograms (W) and total length was described by:

$$W = 0.9723 \times 10^{-8} \text{ TL mm}^{3.0404}; N = 178, r = 0.9790$$

Additional study needs to be applied to gray snapper resources. Gray snapper live longer than previously reported (at least to 25 years), thus management needs information reflecting the Gulf of Mexico population structure. The results of this study suggest that back-calculation of length at age should use a direct proportional method for back-calculation (because of its retention of individual variation) rather than a regression method. Also, there is a need to

Table 6. Growth coefficients and mortality estimates for gray snapper.

Parameter[a]	Estimate	Method of back-calculation[b]	Method used to develop estimate[c]
K	0.1552	DP	VB
K	0.0783	Reg	VB
Z	0.1669	—	Reg 25
Z	0.2645	—	Reg 14
Z	0.1789	—	Hoenig
M	0.3245	DP	Ralston
M	0.1307	Reg	Ralston
M	0.2046	DP	N&M
M	0.1244	Reg	N&M

[a]K = growth coefficient, Z = instantaneous mortality rate, M = instantaneous natural mortality rate.

[b]DP = direct proportion method of Lea (1910).

[c]VB = von Bertalanffy growth equation. Reg = regression of $\log_e$ of age frequency average with 25 = maximum age of 25 years, 14 = maximum age of 14 years. Range truncated at 14 years. Hoenig = method of Hoenig (1983). Ralston = method of Ralston (1987). N&M = method by Nelson and Manooch (1982) with water temperature at 23C.

develop age-size structure information by geographic regions and for each sex as differences are indicated by this study.

Literature Cited

Allen, G. R. 1985. UN Food and Agricultural Organization (FAO) species catalogue. Vol. 6. Snappers of the world. FAO Fish. synopsis No. 125, Vol. 6. FAO, Rome. 208pp.

Baez, H., M., Alvarez-Lojonchere, L. S., and B. P. Tabio. 1980. Edad y crecimiento del caballerote, *Lutjanus griseus* (Linne), en Tunos de Zaza Cuba. Universidad de Habana, Centro de Investigaciones Maritimas, Revista de Investigacion Maritima, 1(2–3):135–159.

Beamish, R. J. and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Carlander, K. D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries 6(1):2–4.

Claro, M. R. 1983. Ecologia y ciclo de vida del caballerote, *Lutjanus griseus* (Linnaeus), en la plataforma Cubana. II Edad y crecimiento estructura de las poblaciones, pesquerias. Academia de Ciencias de Cuba, Reporte de Investigacia del Instituto Oceanologica. No. 8, 26 p.

——— and G. Bustamente Pola. 1977. Edad y crecimiento del caballerote, *Lutjanus griseus* (Linnaeus), en la plataforma suroccidental de Cuba. Academia de Ciencias de Cuba, Informe Cientifico-technologica No. 12:3–11.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bul. 81(4):898–903.

Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. J. Fish. Res. Bd. Can., 25(6):1303–1307.

Lea, E. 1910. On the methods used in herring investigations. Publications de Circonstance Conseil Permanente pour l'Exploration de la Mer 53:7–25.

Manooch, C. S., III and R. H. Matheson, III. 1981. Age, growth, and mortality of gray snapper collected from Florida waters. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 35:331–344.

Nelson, R. S. and C. S. Manooch III. 1982. Growth and mortality of red snappers in the west-central Atlantic Ocean and northern Gulf of Mexico. Trans. Am. Fish. Soc. 111:465–475.

Ralston, S. 1987. Mortality rates of snappers and groupers. Pages 375–404 *in* J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: Biology and fisheries management. Westview Press, Boulder, Colo. 659pp.

Rutherford, E. S., J. T. Tilmant, E. B. Thue, and T. W. Schmidt. 1989. Fishery harvest and population dynamics of gray snapper, *Litjanus griseus,* in Florida Bay and adjacent waters. Bul. Mar. Sci. 44(1):139–154.

Shipp, R. L. 1991. Investigation of life history parameters of species of secondarily targeted reef fish and dolphin in the northern Gulf of Mexico. Proc. Fourth Annu. MARFIN Conf., San Antonio, Texas. Pp. 80–85.

Vaughan, D. S. and P. Kanciruk. 1982. An empirical comparison of estimation procedures for the von Bertalanffy growth equation. J. Cons. Int. Explor. Mer. 40: 211–219.