Abstract—Gray snapper, *Lutjanus griseus*, were sampled from recreational headboat and commercial landings along the east coast of Florida, 1994–97. Fish were weighed (g) and measured (total length, TL, in mm), and sagittal otoliths were removed for aging. Marginal increment analysis on sectioned otoliths (n=1243) confirmed annulus formation in June and July. The oldest fish examined was 24 years old and measured 760 mm TL. Weight-length relations were not significantly different by sex. Weight-length relations were significantly different (F=39.198, P<0.001, df=10,705) for fish measured from the headboat survey from 1982–97 between north Florida ($W=8.4 \cdot 10^{-9} \cdot TL^{3.08}$, n=4034) and south Florida ($W=5.45 \cdot 10^{-9} \cdot TL^{3.15}$, n=6670), where W = total weight (kg). The TL-otolith radius (OR) relationships were described by the following equations: $TL = (10.02 \cdot \text{OR}) - 52.98$ (r^2=0.90, n=519, north Florida), and $TL = (9.90 \cdot \text{OR}) - 91.68$ (r^2=0.78, n=724, south Florida). Mean lengths at age from back-calculations to the last annulus ranged from 121 mm at the end of age 1 to 740 mm at age 24 for north Florida, and 227 mm at age 2 to 495 mm at age 15 for south Florida. The von Bertalanffy growth equations were $L_t = 717 \cdot (1-e^{(-0.17\,(t\,+\,0.025))})$ for north Florida and $L_t=625 \cdot (1-e^{(-0.13\,(t\,+\,1.33))})$ for south Florida. Estimates of M ranged from 0.14 to 0.43 for north Florida and from 0.29 to 0.38 for south Florida. Estimates of Z averaged 0.34 for north Florida and 0.95 for south Florida. Recruitment to the fisheries occurred between ages 5 and 8 for north Florida and ages 4 and 5 for south Florida. Estimates of F for gray snapper by area were 0.16 for north Florida and 0.66 for south Florida.

Manuscript accepted 16 November 2000.
Fish. Bull. 99:254–265 (2001).

Age, growth, and mortality of gray snapper, *Lutjanus griseus*, from the east coast of Florida

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The gray snapper, *Lutjanus griseus*, is a moderate-size (to 8 kg) snapper (Lutjanidae) widely distributed in the western Atlantic from Florida through Brazil, including Bermuda, the Caribbean and the northern Gulf of Mexico (Robins et al., 1986). Juveniles have been reported from as far north as Massachusetts (Sumner et al., 1911), and transforming gray snapper larvae have been caught in ichthyoplankton samples collected at Ocracoke and Oregon Inlets, North Carolina (Hettler and Barker, 1993). Adults are rarely caught in the fisheries of North Carolina; the larvae appear to be Gulf Stream exports and do not survive winter temperatures. Gray snapper occupy a variety of habitats during their life cycle. Adults are found near irregular, complex habitats, such as coral reefs, shipwrecks, rocky outcroppings and ledges, and other natural livebottom areas (Miller and Richards, 1980). Spawning occurs offshore, and eggs and larvae are transported into estuarine, shallow seagrass, and mangrove nursery areas by favorable currents. Larvae, juveniles, and smaller adults are found inshore in seagrass beds and around mangrove thickets, pilings, seawalls, and jetties. While they inhabit inshore areas, these younger fish are subject to fishing pressure from recreational fishermen. After moving offshore between the ages of 3 and 4 (Rutherford et al., 1983), gray snapper are caught by headboat[1] and commercial fisheries. The primary gear used in all fisheries for gray snapper is vertical hook-and-line gear.

Several investigators have conducted age-growth studies of gray snapper, but most have been restricted by limited geographic samples or gear types. Croker (1962), Starck and Schroeder (1970), and Rutherford et al. (1983) conducted age-growth studies on gray snapper using scales from limited areas in the Florida Keys and Florida Bay; all validated their aging techniques with marginal increment analysis. Manooch and Matheson (1981) aged otolith sections of gray snapper from headboat landings along the entire east coast of Florida but did not validate their aging method. Johnson et al. (1994) described age and growth with fish collected from recreational and commercial landings from Ft. Pierce, Florida, through Louisiana but failed to validate their aging method.

The bulk of gray snapper landings in the U. S. South Atlantic (North Carolina–Florida Keys) occurs in Florida. Combined landings of gray snapper from headboat,[2] private recreational and charterboat[3] and commercial[4] fisheries of Florida's east coast averaged 493,895 kg annually between 1986 and 1997. Average annual landings from the south Florida area (Ft. Pierce through the Dry Tortugas; 412,279 kg) were five times greater than those from north Florida (Fernandina Beach through Sebastian; 81,616 kg). The species is highly

[1] A vessel for hire which charges each angler on a per-person, or "per-head" basis.
[2] South Atlantic Headboat Survey. 1998. Unpubl. data. Administered by National Marine Fisheries Service (NMFS), 101 Pivers Island Rd., Beaufort NC 28516-9722.
[3] Marine Recreational Fisheries Statistics Survey (MRFSS). 1998. Unpubl. data. Administered by NMFS, 1315 East-West Highway, Silver Spring, MD 20910.
[4] General Canvass Landings Survey. 1998. Unpubl. data. Administered by NMFS, Southeast Fisheries Science Center (SEFSC), 75 Virginia Beach Dr., Miami, FL 33149.

valued by anglers for its fighting ability at all sizes (Manooch, 1984). Recreational landings averaged 60,685 kg for north Florida compared with 290,266 kg for south Florida annually between 1986 and 1997. Commercial landings averaged 20,931 kg for north Florida and 122,013 kg for south Florida for the years 1986–97.

In this study I describe the growth of gray snapper landed from the headboat and commercial fisheries of the east coast of Florida, including the Atlantic waters of Monroe County, FL. I attempt 1) to describe the age and growth of gray snapper from the east coast of Florida, 2) to validate growth increments on otoliths as annuli, 3) to estimate natural mortality (M), and 4) to estimate total mortality (Z) from catch curve analysis. I also compare size at age, growth rates, and mortality rates between the fish in the northern (Indian River County northward) and southern portions of Florida. I undertook this study to provide fishery managers with a current, validated age-growth study, not restricted in either fishery or geographic scope, to use in current stock assessments.

Materials and methods

Gray snapper were sampled from the landings of headboats and commercial fishing vessels from St. Augustine, Florida, through the Florida Keys by National Marine Fisheries Service (NMFS) port samplers from 1994 to 1997. Samples were not available from the Marine Recreational Fisheries Statistics Survey (MRFSS) owing to logistical and contractual problems. Fish samples were taken as available, independent of size, sex, or season. The left sagittal otolith was removed from each fish, rinsed with water, and stored dry. Otoliths were sectioned according to the methods of Potts and Manooch (1995).

I sorted the sectioned otoliths by 50-mm-TL intervals and read them in ascending order, as an aid in determining size at first annulus formation. Reflected light revealed alternating opaque and translucent rings. Opaque rings were presumed to be annuli and ages (in years) were assigned to specimens equal to the number of opaque rings. I measured the distance from the focus to the edge (otolith radius), the focus to successive opaque rings (annular measurements), and the distance between the distal edge of the last opaque zone and the otolith edge (marginal increment).

I analyzed marginal increments to validate the annual periodicity of ring deposition. Monthly mean marginal increments were calculated by age and for all ages combined. Means were plotted against month of capture, the minima indicating the month of annulus formation.

I regressed fish total weight (W) on fish total length (TL), by area, using all gray snapper sampled by the headboat survey from 1982 to 1997 (n=10,705). I examined both a direct nonlinear fit by using nonlinear least squares estimation (SAS Institute, Inc., 1987) and a linearized fit of the log-transformed data, examining the residuals to determine which regression was appropriate. Fish sampled from commercial fisheries were excluded from these analyses because they were eviscerated.

The relation of total length to otolith radius was estimated by regression:

$$L = a + b\,(R),$$

where L = total length in mm; and
R = otolith radius in ocular micrometer units.

Linear regression equations were developed for all data pooled as well as for north Florida and south Florida. Back-calculated size of each fish at the time of formation of each annulus was determined by substituting the measurement to each annulus into a body-proportional equation (Francis, 1990):

$$L_i = \{(a + bS_i) / (a + bR)\} L,$$

where L_i = fish total length (mm) at annulus i;
R = otolith radius;
a = intercept from the L-R regression;
b = slope from the L-R regression; and
S_i = measurement to the i^{th} annular ring.

Back-calculated size at time of formation of the last annulus was used in order to provide length-at-age data unbiased by differences in time of year of sampling. Area-specific data were developed by substituting coefficients from the area-specific L-R regressions into Francis's (1990) body-proportional equation. Use of a single back-calculation per fish avoids the violation of assumption of independence among sample elements (Vaughan and Burton, 1994), but this method does not necessarily provide all available information about the growth of all cohorts.

Theoretical growth parameters were estimated by fitting the back-calculated lengths at age to the von Bertalanffy (1938) growth equation:

$$L_t = L_\infty\left[1 - \exp\left(-K(t - t_0)\right)\right],$$

where L_t = total length at age t;
L_∞ = theoretical asymptotic length;
K = Brody growth coefficient; and
t_0 = theoretical age when fish length = 0.

Parameter estimates were obtained by using nonlinear regression analysis (SAS Institute, Inc., 1987). Theoretical lengths at age were derived for back-calculated lengths at age by using the last annulus (Vaughan and Burton, 1994).

I estimated the instantaneous rate of natural mortality (M), by area, using several methods. I used Hoenig's (1983) longevity-mortality relationship,

$$\ln(Z) = 1.709 - 1.084 \cdot \ln(t_{max}),$$

where t_{max} = the maximum age encountered; and estimates of M are for relatively unexploited stocks.

I used a second equation which adjusts for sample size in Hoenig (1983), who reasoned that with a larger sample

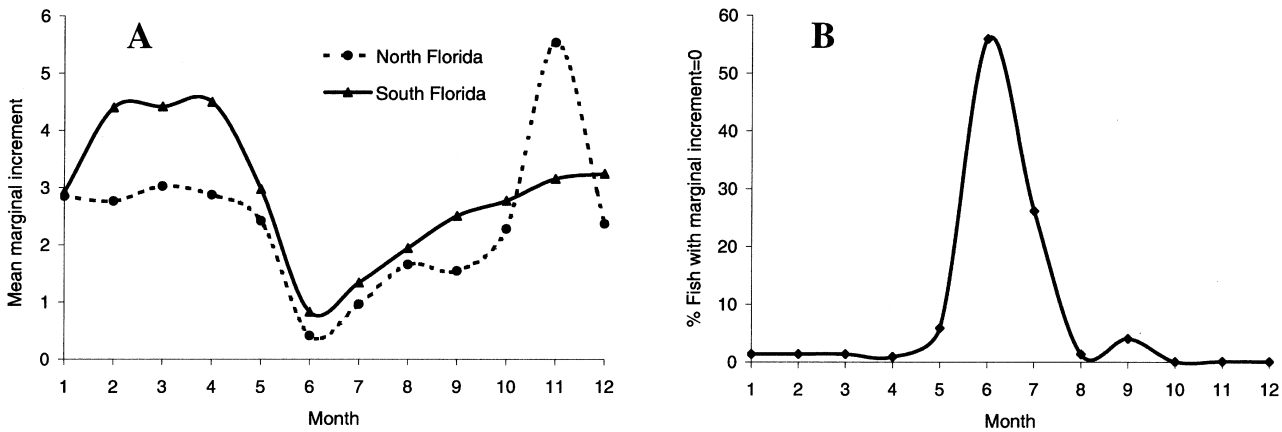

Figure 1

(**A**) Mean monthly marginal increment by area for gray snapper, all ages combined; (**B**) monthly percentage of fish with a marginal increment = 0.

size there is a greater probability of encountering the true maximum age of the fish:

$$Z = \ln(2n + 1)/(t_{max} - t_c),$$

where n = the sample size; and
t_c = the first age fully represented in the catches.

I used the Pauly (1980) method

$$\log_{10}M = 0.0066 - 0.279 \cdot \log_{10}L_\infty + 0.6543 \cdot \log_{10}K + 0.4634 \cdot \log_{10}T,$$

where L_∞ = the asymptotic length;
K = the Brody growth coefficient from the von Bertalanffy (1938) growth equation; and
T = the mean annual seawater temperature (°C).

I derived the latter from sea surface temperature readings from buoys operated by NOAA's National Oceanographic Data Center during 1998. Finally, I estimated M by using the regression of Ralston (1987):

$$M = 0.0189 + 2.06 \cdot K,$$

where K = the Brody growth coefficient.

Observed ages at length for all years combined were used to develop age-length keys (ALK) for each area (Ricker, 1975). I assigned aged fish (my samples) to 25-mm-TL intervals and calculated age distribution (as a percentage) for each size interval. Area-specific age-length keys were used to convert length frequencies from each area and fishery, weighted by the corresponding annual landings, into age frequencies by assigning ages to unaged fish from the length frequencies. Length-frequency data and annual landings data were acquired from the South Atlantic headboat survey, the MRFSS, and the Trip Interview Program (TIP)[5] survey. Total instantaneous mortality rate, Z, was estimated by the absolute value of the slope of the descending right limb of the plot of $\log_e$ *age frequency* on *age* (catch curves) (Beverton and Holt, 1957). Only fully recruited ages (age groups to the right of the top of the dome of the curve) were used to estimate Z because the age group at the top of the catch dome may not be fully vulnerable to the fishing gear (Everhart et al., 1975).

Results

Age determination and validation of annuli

A total of 98% (1243 of 1260) of gray snapper sampled had legible cross-sectioned otoliths. Opaque rings were distinct and easily counted. Otolith radius was correlated with fish length across all ages:

North Florida:
$$TL = (10.02 \cdot \text{OR}) - 52.98 \qquad (r^2=0.90, n=519),$$
South Florida:
$$TL = (9.90 \cdot \text{OR}) - 91.68 \qquad (r^2=0.78, n=724),$$
Areas combined:
$$TL = (11.05 \cdot OR) - 130.32 \qquad (r^2=0.89, n=1243).$$

Marginal increment analyses showed one minimum per year in June, validating the annual periodicity of otolith increments (Fig. 1A). The monthly percentage of fish with a marginal increment equal to zero (Fig. 1B) showed a single maximum and provided further evidence that annulus formation occurred yearly in June or July. To satisfy Beamish and McFarlane's (1983) assertion that individual ages need to be validated, I analyzed marginal increments by age for

[5] Trip Interview Program. 1998. Administered by Southeast Fisheries Science Center, NMFS, NOAA, 75 Virginia Beach Dr., Miami, FL 33149.

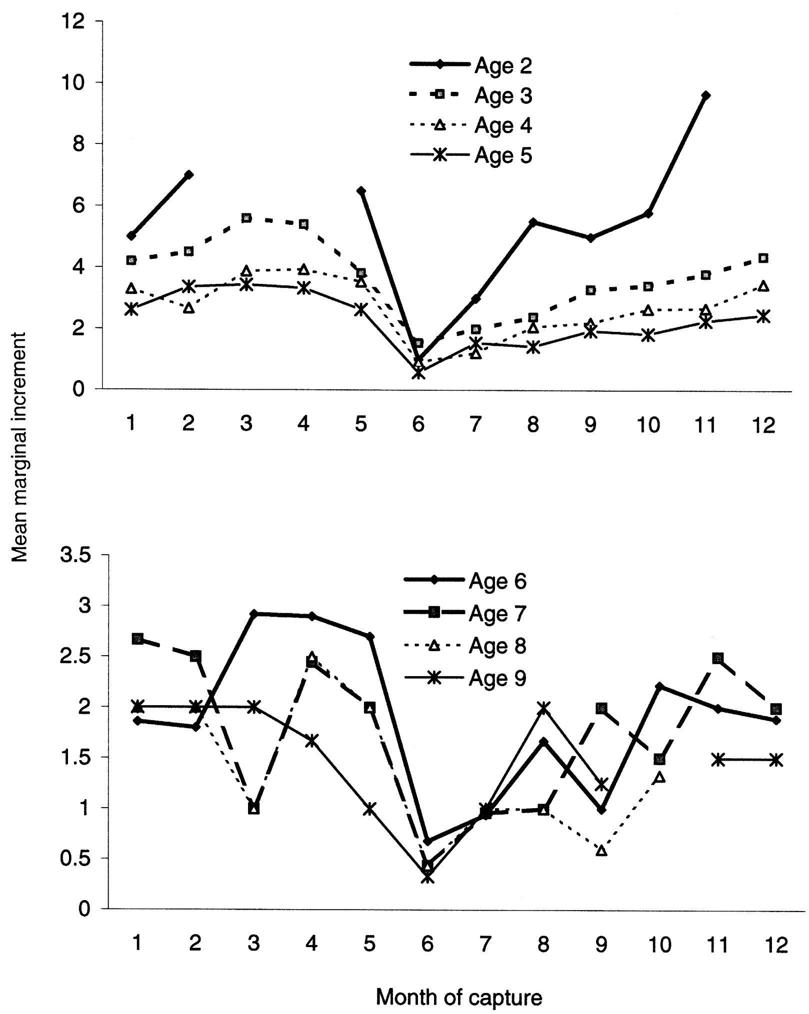

Figure 2
Mean monthly marginal increments of gray snapper otoliths by age, areas pooled.

all areas pooled. Annulus formation occurred in the summer months, with minima in June, for ages 2–9 (Fig. 2). Sample size was inadequate for analyses of older age classes.

Weight-length relationship

The relationship between W (kg) and TL (mm) for all gray snapper measured by the headboat survey from 1982 to 1997 was estimated by using a direct nonlinear fit with SAS PROC NLIN and the Marquardt algorithm software (SAS Institute, Inc., 1987). Examination of the residuals indicated an additive error term, and I concluded that the nonlinear fit was more appropriate than a linearized log-transform fit of the data. Area-specific regressions (see Table 1 for parameters and statistics) were

North Florida: $W = 8.4 \cdot 10^{-9}\, TL^{3.08}$,
South Florida: $W = 5.4 \cdot 10^{-9}\, TL^{3.15}$, and
Pooled areas: $W = 7.22 \cdot 10^{-9}\, TL^{3.11}$.

In addition, nonlinear regressions by sex, derived from the subset of aging samples for which I had sex information, were

Males: $W = 7.13 \cdot 10^{-9}\, TL^{3.11}$, and
Females: $W = 6.95 \cdot 10^{-9}\, TL^{3.10}$.

Although regression coefficients were significantly different by area (t=–8.024, P<0.001, df=10,704, and t=8.159, P<0.001, df=10,704 for intercept and slope, respectively), predicted weights for gray snapper at 300 mm, 400 mm, and 500 mm TL from north and south Florida for the respective length-weight regressions were similar: 0.35 vs. 0.34, 0.87 vs. 0.85, and 1.73 vs. 1.71 (kg). This result is likely due to the ability to detect statistically significant differences with an extremely large sample size when the actual differences may be very small and mean little biologically. Regression coefficients by sex were not significantly different, as indicated by overlapping 95% confidence intervals.

Table 1

Parameters and associated statistics for weight-length relationships of gray snapper by area and sex. SE = standard error; MSE = mean squared error.

Parameter (SE)	North Florida	South Florida	Areas pooled	Males	Females
a	$8.4 \cdot 10^{-9}$	$5.45 \cdot 10^{--9}$	$7.22 \cdot 10^{-9}$	$7.13 \cdot 10^{-9}$	$6.95 \cdot 10^{-9}$
(SE)	$(6.25 \cdot 10^{-10})$	$(2.76 \cdot 10^{-10})$	$(2.8 \cdot 10^{\pm 10})$	$(1.26 \cdot 10^{-9})$	$(1.88 \cdot 10^{-9})$
b	3.08	3.15	3.11	3.106	3.097
(SE)	(0.012)	(0.008)	(0.006)	(0.029)	(0.041)
n	4034	6670	10,704	262	212
MSE	0.078	0.020	0.042	0.019	0.034

Table 2

Mean observed total lengths at age of gray snapper by area.

	North Florida			South Florida		
Age (yr)	*n*	Mean Tl ±SE (mm)	Range (mm)	*n*	Mean TL ±SE (mm)	Range (mm)
1	13	218 ±24	181–255	—		
2	7	220 ±24	185–257	20	284 ±36	167–327
3	17	347 ±43	212-415	138	302 ±33	182–397
4	69	388 ±42	307–505	260	325 ±29	231–447
5	138	432 ±42	332–555	177	358 ±45	265–525
6	75	467 ±46	347–565	81	397 ±60	300–644
7	71	525 ±43	370–615	32	474 ±46	390–578
8	26	549 ±40	480–615	11	468 ±60	342–542
9	36	589 ±42	525–702	3	417 ±141	330–581
10	23	595 ±31	537–657	3	414 ±86	317–481
11	14	608 ±32	545–645	1	452	
12	9	623 ±30	580–685	—		
13	8	660 ±35	600–705	2	501 ±166	383–618
14	7	652 ±43	600–725	—		
15	3	682 ±34	660–722	1	504	504–504
16	1	677				
17	1	635				
18	2	649 ±68	600–697			
19	1	707				
20	1	630				
21	2	710 ±25	692–727			
22	—					
23	2	748 ±18	735–760			
24	2	740 ±28	720–760			

Growth

Mean observed lengths at age were larger for fish from north Florida than those for fish from south Florida for all ages except age 2 (Table 2), but sample size may have affected estimates for age-2 fish. North Florida fish ranged from 181 mm at age 1 to 760 mm at age 24. South Florida fish ranged from 167 mm TL at age 2 to 618 mm at age 13. The oldest fish from south Florida was age 15 and measured 504 mm. Age-1 fish were difficult to acquire in south Florida because of minimum-size catch regulations (305 mm TL in federal waters, and 250 mm TL in Florida waters). All age-1 fish from north Florida were collected through fishery-independent hook-and-line sampling. In both areas, most fish attain the federal minimum size limit (305 mm TL) by age 3.

Back-calculated sizes at age of gray snapper by area are shown in Tables 3 and 4. The mean total back-calculated lengths for gray snapper from north Florida, back-calculated to the last annulus, were larger than those for fish from south Florida for all ages except age 2. Given the obvious differences in size at age between the two areas, it seemed inappropriate to pool the data for the purposes of analyzing growth.

The linear regressions of the measurements to the first and second annuli on age for headboat and commercial specimens from north Florida were significantly different from zero (n=519, P=0.0001, r^2=0.04; and n=506, P=0.0012, r^2=0.02). Although this result indicates the presence of Lee's phenomenon for samples from these fisheries (Potts et al., 1998), the model explains very little of the variation, so that Lee's phenomenon was weak and likely masked by other environmental variables. The linear regressions of the measurements to the first and second annuli on age for headboat and commercial specimens from south Florida were not significantly different from zero (n=720, P= 0.23, r^2=0.002 and n=720, P=0.81, r^2=0.0001), indicating that size-selective mortality was not detected.

The von Bertalanffy (1938) growth equations, fitted to back-calculated lengths at age for the last annulus (Fig. 3A), were

North Florida:
$$L_t = 717\ (1 - e^{-0.17\ (t\ +\ 0.025)}),\text{ and}$$

South Florida:
$$L_t = 625\ (1 - e^{-0.13\ (t\ +\ 1.33)}).$$

Parameters and associated statistics for these equations as well as for equations fitted to the subset of data by sex, are listed in Table 5. Estimates of growth parameters were not significantly different between sexes [Hotelling's T^2 test, $F_{(0.025,\,3,\infty)}$= 1.0 (Bernard, 1981)] (Fig. 3B). However, estimates of growth parameters were significantly different between areas ($F_{(0.025,3,\infty)}$=84.1).

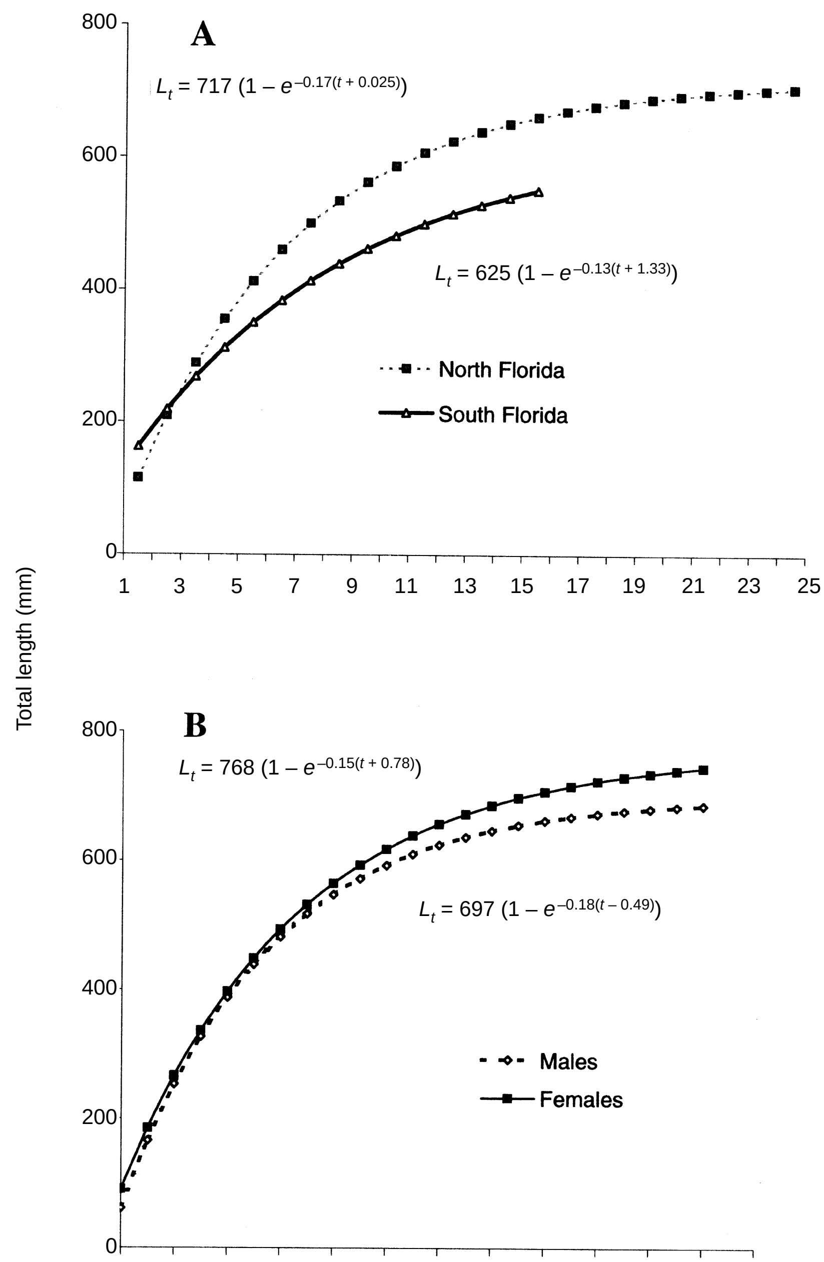

Figure 3

Theoretical growth curves for gray snapper by (**A**) area and (**B**) sex, areas pooled.

Mortality

Estimates of the instantaneous rate of natural mortality (M) varied considerably by method but were similar across areas for a given method. Estimates of M assume a constant natural mortality and so apply to all ages of fish. Hoenig's (1983) longevity-mortality relation returned the lowest estimates, 0.18 and 0.29 (north and south Florida), and his equation adjusted for sample size returned similar values between areas, 0.33 and 0.35. Pauly's (1980) equation, with growth parameters and mean seawater temper-

Table 3

Back-calculated total lengths (mm) of gray snapper aged by sectioned otoliths for North Florida. Obs. age = observed age.

		Annulus number																							
Obs. age	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	13	121																							
2	7	82	166																						
3	17	109	225	307																					
4	69	119	228	304	357																				
5	137	126	247	320	371	412																			
6	74	134	250	318	371	413	450																		
7	68	139	262	336	391	435	474	509																	
8	25	139	2652	335	389	432	468	504	536																
9	36	142	260	337	393	437	477	515	546	576															
10	22	133	244	321	375	422	462	497	527	556	581														
11	14	134	243	324	379	422	461	497	528	555	579	600													
12	9	129	247	324	377	418	457	490	519	547	574	595	614												
13	8	138	267	335	386	429	464	498	531	563	588	609	630	650											
14	7	126	250	325374356		418	452	484	511	539	563	582	604	6243	643										
15	3	114	227	300	356	406	456	493	530	559	583	603	623	643	659	676									
16	1	106	264	326	361	387	414	449	493	528	554	572	589	616	633	6514	668								
17	1	105	253	322	374	409	444	470	505	531	548	565	583	592	600	609	618	626							
18	2	164	262	322	364	392	425	453	476	499	523	541	560	579	597	616	625	635	644						
19	1	85	208	302	368	406	443	472	500	538	575	594	613	632	651	660	669	679	688	698					
20	1	115	201	296	344	382	411	439	468	487	506	525	544	554	563	582	592	601	611	620	630				
21	2	143	240	309	355	392	424	456	489	516	539	562	585	608	627	636	645	654	663	673	691	700			
22																									
23	1	120	219	308	388	437	477	507	537	556	576	596	616	636	646	656	666	675	685	695	705	715	725	735	
24	2	125	236	313	380	433	466	500	529	553	572	596	615	630	639	649	658	668	678	687	697	706	716	730	740
No. of calculations		520	507	500	483	414	277	203	135	110	74	52	38	29	21	14	11	10	9	7	6	5	3	3	2
Weighted means		129	246	322	375	421	463	503	531	558	574	591	609	626	633	642	643	650	662	676	685	706	719	732	740
Annual mean growth increment		129	117	76	53	46	42	40	28	27	16	17	18	17	7	9	1	7	12	14	9	21	13	13	8

atures of 25.0°C and 26.1°C for north and south Florida, estimated M at 0.43 and 0.38 for the two areas. The regression method of Ralston (1987) estimated M = 0.37 and M = 0.29 for north Florida and south Florida, respectively. I used a variety of estimation methods to give the reader a sense of the variation associated with estimating M, a parameter we often know little about but which is a very important variable in stock assessments.

Estimates of total mortality derived from catch curves differed substantially by area (Fig. 4). Estimates of Z for gray snapper from north Florida averaged 0.35 during 1986–97 for all fisheries combined. Gray snapper were fully recruited to the headboat fishery between ages 5 and 6, to the commercial fishery between ages 7 and 8, and to the private recreational fishery between ages 4 and 5. The average value of Z for 1986–97 for gray snapper from south Florida was 0.94, almost three times that of north Florida. Full recruitment occurs between ages 4 and 5 in all fisheries in south Florida.

Discussion

Differences in growth rates and size at age between areas were great enough to argue against pooling the data for growth analysis. However, the pooled data set does provide the opportunity for comparing my results against a previous similar study for the purpose of validating my aging estimates. Back-calculated lengths at age were in close agreement with lengths estimated previously by Manooch and Matheson (1981). Estimated lengths (mm) for ages 1, 5, 10, and 15 with measurements to the last annulus, were 87 vs. 89, 370 vs. 370, 559 vs. 556, and 630 vs 680 (present study vs. previous study). The close agreement in size

Table 4

Back-calculated total lengths (mm) of gray snapper aged by sectioned otoliths for South Florida.

		Annulus number														
Obs. age	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	—															
2	20	100	227													
3	136	89	195	272												
4	258	90	184	253	305											
5	174	94	190	254	303	341										
6	81	97	192	256	305	346	383									
7	32	96	212	283	337	382	424	461								
8	10	99	203	262	313	355	391	422	451							
9	3	71	179	248	286	317	342	367	392	414						
10	3	77	164	210	253	281	311	336	358	380	404					
11	1	70	152	197	243	279	316	343	370	397	425	443				
12	—															
13	2	84	198	244	280	307	335	358	385	408	431	454	473	491		
14	—															
15	1	73	138	213	260	288	307	335	354	382	401	420	438	457	475	495
No. of calculations		721	721	701	565	307	133	52	20	10	7	4	3	3	1	1
Weighted means		92	191	258	306	346	389	432	412	398	414	443	461	480	475	495
Annual mean growth increment		92	99	67	48	40	43	43	(20)	(14)	16	29	18	19	(5)	20

Table 5

Von Bertalanffy growth parameters and associated statistics for gray snapper by area and sex, 1994–1997.

Data set	L_∞	SE (L_∞)	95% CI	K	SE (K)	95% CI	t_0	SE (t_0)	95% CI	n
North Florida	716	11.33	693–738	0.17	0.01	0.16–0.19	–0.001	0.11	–0.22–0.22	520
South Florida	625	56.33	515–736	0.13	0.02	0.08–0.18	–1.33	0.41	–2.12–0.53	721
Males	697	22.93	652–742	0.18	0.017	0.15–0.21	0.49	0.21	0.08–0.89	339
Females	768	35.7	697–838	0.15	0.017	0.1 –0.18	0.16	0.26	–0.36–0.67	272

at age from these two studies, both of which used otoliths and comprised samples from the same geographic area, validates the aging of gray snapper determined in the present study. Back-calculated lengths at age of gray snapper determined from scales by Starck and Schroeder (1970) were generally smaller than those determined from otolith sections, reasons for which are unclear. My samples, as well as those of Manooch and Matheson (1981), were from Florida's east coast, whereas Starck and Schroeder (1970) used fish from only one location in the Florida Keys. A geographic bias may account for the difference in ages between the two studies.

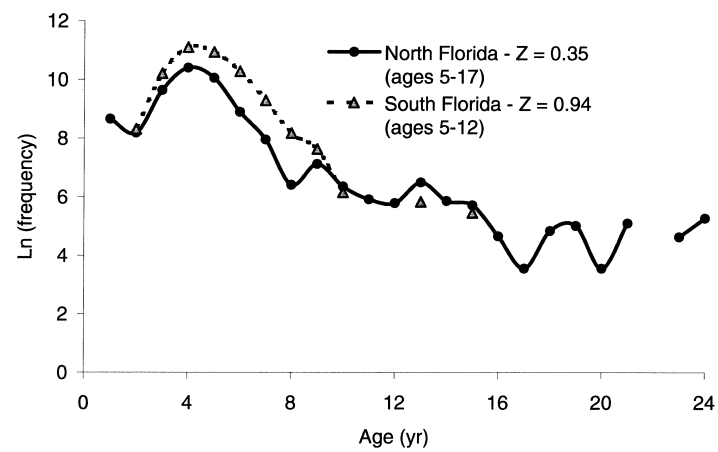

Figure 4

Catch curves for gray snapper, all fisheries combined, 1986–97.

Marginal increment analysis demonstrated that gray snapper ages 2–9 deposit one annulus per year, in June. These ages account for the majority of age classes in the fishery; thus I posit that the critical evaluations stressed by van Oosten (1929) and Beamish and McFarlane (1983) were met. Annual deposition of growth increments on otoliths of gray snapper was not validated by previous investigators and thus was an essential part of my study.

I constructed area-specific age-length keys using Sebastian Inlet, FL (27.8°N latitude), as the north–south dividing line. In addition to being the traditional division point for sample coverage for the south Atlantic headboat survey, it also approximates the nearshore–offshore break in distribution of reef habitat. I did not have enough data to construct annual ALKs as recommended by Ricker (1975) and Westrheim and Ricker (1978), and my decision to produce area-specific ALKs was based on *a priori* information gained as a port agent in Florida from 1982 to 1987. Gray snapper from headboats in north Florida were larger than gray snapper from headboats in south Florida. Moreover, Manooch and Matheson (1981) found differences in length-frequency distributions and estimates of total mortality by area (smaller fish and higher mortality, Z, in south Florida).

The difference in growth of gray snapper between north and south Florida is readily apparent. Mean observed and back-calculated sizes at age were largest for fish from north Florida, and these fish achieved a much greater maximum size and age than did their south Florida counterparts; significant differences in theoretical maximum size between areas were observed (Fig. 3A). Johnson et al. (1994) found similar results for gray snapper collected from the east coast of Florida and the Gulf of Mexico. They compared back-calculated size at age for fish captured from north and south of 27°N latitude and concluded that fish from the northern region were significantly larger than fish from the southern region for ages 1–13. Their latitude was proximal to the headboat survey divisional line used in the present study.

The differences observed in size at age become greater in older ages of gray snapper, although estimates for south Florida are affected by small sample sizes (few fish >age 8). The small sample size of older fish in south Florida probably reflect a lack of abundance rather than sampling deficiencies. Commercial and headboat data (Fig. 5) showed larger and presumably older fish taken from north Florida than from south Florida. The headboat fishery modal length intervals were 400–424 mm TL for north Florida and 300–324 mm TL for south Florida. Modal values of commercial length frequencies showed a greater difference between areas: 550–574 mm TL for north Florida compared with 325–349 TL mm for south Florida. Given the efficiency of modern fishing fleets (all using hook-and-line gear), this finding is strong evidence that the south Florida population of gray snapper has a truncated size distribution. Manooch and Matheson (1981) found a similar disparity in size distribution of gray snapper from headboats from north and south Florida, with respective modes at 450–499 mm TL versus 300–349 mm TL.

One possible explanation for the lack of older, larger fish in south Florida is the much greater fishing pressure there. Manooch and Matheson (1981) estimated the instantaneous rate of fishing mortality (F) to be 0.17 and 0.38 for north and south Florida, respectively. I estimated $F = 0.16$ and $F = 0.66$ for the respective areas for all fisheries combined, using Hoenig's (1983) estimates of $M = 0.18$ and $M = 0.29$ and the area-specific estimates of Z ($F=Z–M$).

The demography and geography of the Florida peninsula probably affect fishing pressure on gray snapper. South Florida is more densely populated than north Florida and thus has many more potential anglers. Specifically, anglers fished an average total of 186,687 days from south Florida headboats annually from 1982 to 1997, compared with an annual average total of 82,325 days from north Florida headboats. Shorter distance to the fishing grounds in south Florida (5–8 km) than to those in north Florida (40–50 km) also leads to increased exploitation. Increased pressure on younger inshore fish could lead to growth overfishing, whereas easier access to the mature adults offshore may contribute to recruitment overfishing. The latter scenario would be aggravated by the suspected tendency of gray snapper to undertake spawning migrations to offshore reefs (Domeier et al., 1997). This behavior, resulting in higher fish densities on these reefs, would increase their vulnerability to fishery harvest during summer months, a time of maximum fishing effort due to favorable weather conditions.

Another effect of long-term heavy fishing pressure could be a genetic shift in growth characteristics of the fish. Size-selective mortality could result in slower growing individuals in the population. Buxton (1993) found growth rates for *Chrysolephus cristiceps* (Sparidae) to be significantly lower in exploited than in protected populations. Zhao et al. (1997) found that mean back-calculated lengths at age for vermilion snapper, *Rhomboplites aurorubens*, declined from 1979 to 1987, concluding that this result was a true change in growth, posssibly caused by overfishing. Harris and McGovern (1997) attributed decreases in growth and maturity rates of red porgy (*Pagrus pagrus*), over time, to sustained heavy fishing pressure. Zhao and McGovern (1997) found similar decreases in size and age at maturity for vermilion snapper over time, attributing the declines to increasing fishing pressure. Other investigators, however, have hypothesized that these results were caused by size selectivity characteristics of different gears used during different sampling periods (e.g. Potts et al., 1998).

An alternate explanation for the lack of larger, older gray snapper in south Florida is emigration. An argument might be made that the inshore to offshore spawning migrations (Domeier et al., 1997) previously mentioned might take them beyond the range of the fisheries and make gray snapper less vulnerable to fishing gear in the south Florida area. This hypothesis seems highly unlikely given the range and technology of modern fisheries. Moreover, most reef fishes are thought to exhibit a sedentary lifestyle as adults, staying close to the same general reef area (Ehrlich, 1975; Heemstra and Randall, 1993; Samoilys, 1997). However, Moe (1969) found that red grouper (*Epinephelus morio*) showed some migratory behavior—22 individuals moved 29 km in 50 days, and another individual moved 76 km. Most of these movements were from inshore to offshore. A comprehensive tagging study could be designed to address the question of whether significant numbers of gray snapper migrate out of the south Florida area.

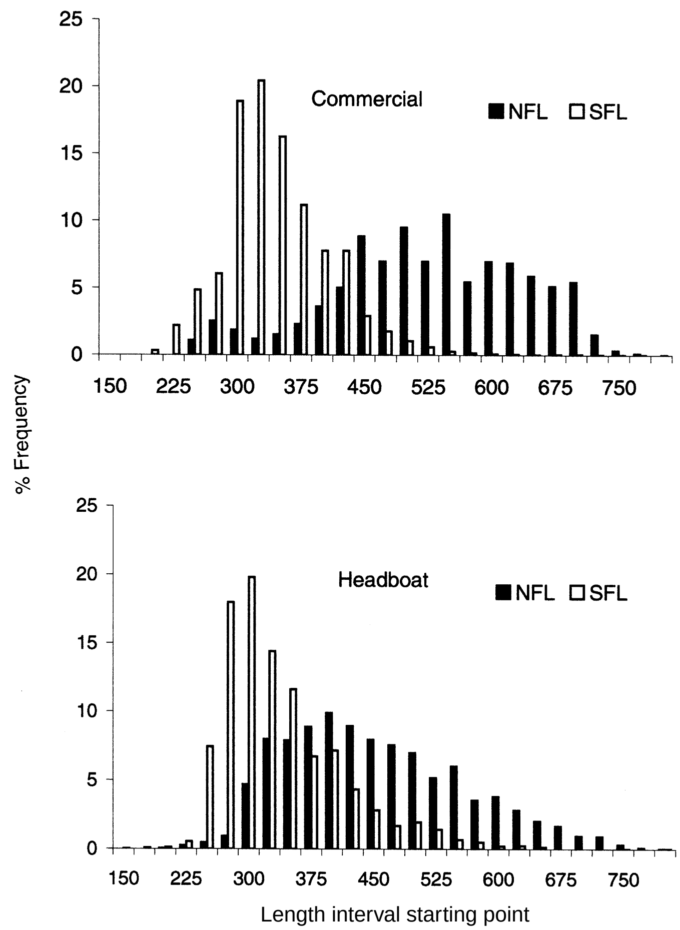

Figure 5

Length frequencies for gray snapper measured by fishery and area, 1986–97.

Management of gray snapper is the responsibility of the South Atlantic Fishery Management Council (SAFMC), whose current strategy is to manage this species, and most others in the snapper-grouper complex, as a single stock throughout their management area. It is very unlikely that gray snapper in north and south Florida are genetically distinct because of the northward flow of the Gulf Stream and the resulting widespread distribution of progeny. However, this study in conjunction with that of Manooch and Matheson (1981) strongly suggests that gray snapper have been exploited at higher rates of F in south Florida than in north Florida for at least two decades. As a result, gray snapper reach a smaller maximum size and younger maximum age in the population, as well as smaller sizes at most ages. These biological features carry implications for overall population health because fecundity is usually proportional to size or age, or to both. Fishery managers attempting to assess stocks of gray snapper should perform area-specific analyses in order to manage this species in the most effective manner. Given the results of this study, it seems that managing gray snapper as a stock unit could worsen overfishing conditions in south Florida.

Acknowledgments

I gratefully acknowledge the many port samplers whose efforts made this study possible: headboat samplers Dan Theisen, Pamela Washnock, and Peggy Kirwin, NMFS

Beaufort Laboratory; and commercial port samplers Charles Schaefer, Tim Brandt, Claudia Dennis, and Renee Roman, NMFS Miami Laboratory. Charles S. Manooch III and Jennifer Potts, NMFS Beaufort, provided guidance in the techniques of aging otolith sections. Doug Vaughan and Jim Waters, NMFS Beaufort, and Potts provided valuable advice on statistical analyses, and. C.S. Manooch, J. Potts, and Joseph Smith, NMFS Beaufort, as well as three anonymous reviewers, provided constructive critical reviews of the manuscript.

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