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AGE AND GROWTH OF WHITE GRUNT (*HAEMULON PLUMIERI*): A COMPARISON OF TWO POPULATIONS ALONG THE WEST COAST OF FLORIDA

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ABSTRACT

Sex-specific age and growth were determined for white grunt, *Haemulon plumieri* (Lacepède, 1801), from their main fishing area on the Gulf coast of Florida. In total, 4043 fish were collected using hook-and-line or trap gear: 2617 from the central and 1426 from the north-central Gulf coast of Florida. White grunt were aged reliably using thin-sections of sagittal otoliths. Both marginal-increment analysis and chemical marking with oxytetracycline indicated that one annulus was deposited in a 12-mo period, with the opaque zone forming mainly during May. Ages of white grunt ranged from 0–18 yrs, and fish ranged in size from 7–41 cm total length. White grunt from the north-central region were larger at age than those from the central region, and males attained a larger size than females in both regions. Asymptotic lengths of males and females combined ranged from 296–343 mm total length. Comparatively, white grunt from the Gulf coast of Florida were of similar size-at-age as fish from southeastern (Atlantic) Florida but were smaller than white grunt from North and South Carolina. Regional growth differences of white grunt are problematic for any comprehensive fishery management plan on a Florida-wide, Gulf-wide, or southeastern U.S-wide basis.

Grunts of the family Haemulidae, and in particular white grunt, *Haemulon plumieri* (Lacepède, 1801), are important in recreational and commercial fisheries in the southeastern U.S. Most (>95%) of the total annual harvest of white grunt in the southeastern U.S. is landed in Florida. Approximately 85%–90% of the landings in Florida are from the west coast of Florida (inclusive of Monroe county, which includes most of the Florida Keys), with only 10%–15% from the east coast (Murphy et al., 1999). Total annual landings from the west coast of Florida peaked at 1040–1410 metric tons (mt) during 1989–1995, of which the recreational hook-and-line fishery was ~65%–70%, the headboat hook-and-line fishery was 20%–28%, and the commercial hook-and-line and trap harvest was 5%–20% in any one year (Murphy et al., 1999). From 1996–1998, total annual harvest of white grunt from the west coast of Florida decreased to ~850 mt per year (Murphy et al., 1999), but has since continued to increase to catch levels reported in the early 1990s (National Marine Fisheries Service Statistics, www.st.nmfs.gov).

Currently, white grunt is an unregulated species with respect to daily bag, size-limit, and total allowable catch on the west coast of Florida, both at the state level (Florida Fish and Wildlife Conservation Commission (FFWCC), Tallahassee) and the federal level (exclusive of Florida Keys) (Gulf of Mexico Fishery Management Council, Tampa). In 1998, the Florida Marine Fisheries Commission (FMFC, now the FFWCC) began public meetings to consider implementation of statewide regulations for white grunt (FMFC, 1998). The proposed regulations were to include a 305-mm (12 in) total length limit and a 20-fish aggregate daily bag limit. At the time, however, basic demographics of white grunt from the core area of the fishery, the Gulf coast of Florida, were unknown. Age and growth data were only available for white grunt

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from North and South Carolina (Manooch, 1976) and from North Carolina south to the northeastern coast of Florida (primarily north of 32°) (Padgett, 1997). However, age and growth data for white grunt from these two studies with overlapping areas were very different: white grunt from the Carolinas grew relatively larger and faster and were, on average, younger than white grunt observed in Padgett's (1997) study. More recently, age and growth have been determined for white grunt from southeastern Florida (Palm Beach through the Florida Keys), showing that fish from the southern area also grow slower and are smaller at age than white grunt from the Carolinas (Potts and Manooch, 2001). Given the large variation in age and growth observed in white grunt from the Carolinas south to the Florida Keys, it was essential to determine the age and growth of white grunt from the Gulf coast of Florida.

The goal of this study was to determine sex-specific age and growth parameters of white grunt from the Gulf coast of Florida. In addition, the ageing method for white grunt in the Gulf of Mexico was validated using both marginal-increment analysis and chemical marking with oxytetracycline. Finally, the age and growth parameters of white grunt from the Gulf coast of Florida were compared to the parameters of white grunt from North and South Carolina (Manooch, 1976; Potts and Manooch, 2001), from North Carolina to northeast Florida (i.e., the South Atlantic Bight) (Padgett, 1997), and from southeastern Florida (Potts and Manooch, 2001), to assess implications to management regimes.

Methods

Fish Collections and Biological Sampling

White grunts were collected from two general regions off the Gulf coast of Florida: a central region between St. Petersburg Beach (27°45′N, 82°45′W) and Port Richey (28°15′N, 82°45′W) and a north-central region between Crystal River (28°54′N, 82°35′W) and Steinhatchee (29°40′N, 83°25′W) (Fig. 1). Fish in the central region were collected by sampling the headboat fishery, which used hook-and-line fishing over natural live-bottom. Grunts in the north-central region were collected from natural live-bottom and artificial reefs, primarily using headboat, recreational, research, and commercial hook-and-line fishing or commercial trap gear. In addition, a small number of fish were also collected in the north-central region using spearfishing, inshore trawling, and sabiki (bait) rigs. All fish were collected in 2–24 m of water and 5–50 km offshore. Fish were either sampled where they were landed (i.e., for headboat fishery) or placed on ice for transport to the laboratory for processing.

All fish were uniquely numbered and measured for maximum total length (MTL), natural total length (NTL), fork length (FL) (Anderson and Neumann, 1996) (to the nearest mm), and total body weight to the nearest 0.1 g. For fish sampled at the dock from the headboat fishery, a subsample of whole white grunt was measured for either one or all of MTL, NTL, and FL, and weighed (to the nearest 1 g), depending on access to the fish before and/or after filleting. Prior to filleting, fish were measured for MTL and FL; after filleting fish were measured for filleted maximum total length (FMTL) and filleted fork length (FFL). All length measurements were then converted into one consistent length measurement, MTL, based on length-length conversion regressions (Murie and Parkyn, 1998); MTL is referred to as simply TL hereafter.

Both sagittal otoliths were removed, rinsed in water to remove all surrounding membranes, and stored dry for later processing. Fish were sexed by both macroscopic examination of whole gonads and microscopic squashes of fresh gonadal tissue samples following Murie and Parkyn (1999).

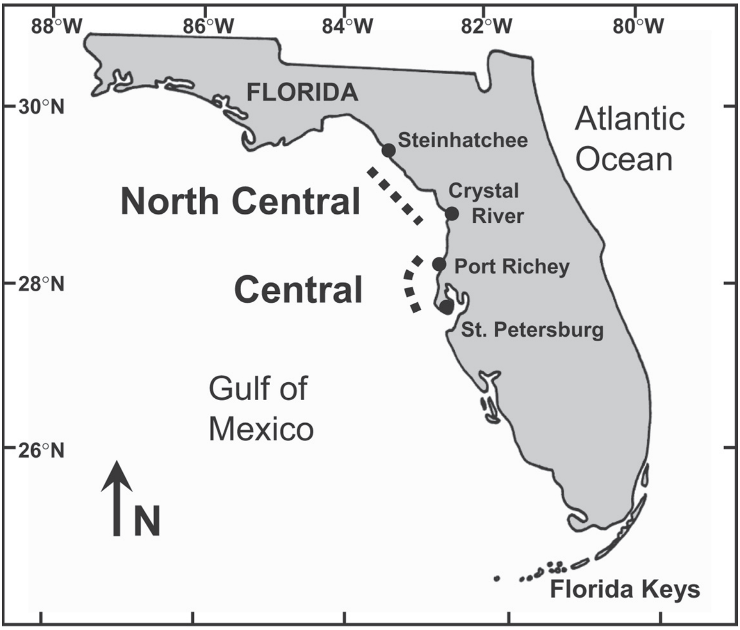

Figure 1. Location of north-central and central west coast of Florida collections of white grunt (heavy dashed lines).

Age Estimates

For ageing, the left sagittal otolith was mounted and cross-sectioned into 0.5-mm sections using a Buehler® Isomet 1000 digital sectioning saw. Sections were permanently mounted in Histomount® (National Diagnostics) and viewed using a stereomicroscope (20–45×) with transmitted light. Annuli in sections viewed under transmitted light appear as opaque brown rings (opaque zone) against an otherwise translucent background (translucent zone). Ages were assigned based on the number of opaque zones. All otoliths were aged by a primary reader (D.M.) and subsets were independently read by a second experienced reader (D.P.) and a third inexperienced (but trained) reader (C. Hanson). If ages between the experienced readers differed, both readers independently aged the otolith for a second time. An age was assigned only when three out of the four ages agreed (otoliths were discarded if ages did not agree). In addition, a random age-stratified sample of 100 sectioned otoliths was sent to an additional experienced reader of white grunt otoliths (J. Potts, NMFS, Beaufort laboratory) for an interagency ageing comparison.

All fish were assigned an age based on the international birth date of January 1st (Chilton and Beamish, 1982) for the specific purpose of estimating ageing precision between readers. This facilitated age comparisons between readers because white grunts collected throughout the year would be correctly assigned to the appropriate age class based on the year of their birth. For example, a white grunt caught in April with three complete opaque zones and a wide translucent zone (growth on the edge) would be assigned an age of four to be comparable to a white grunt also caught in April that had four opaque zones with the fourth on the edge of the structure. Both of these fish are considered to be from the same year-class, which should be reflected in their age estimates to facilitate comparison between readers and agencies. Ageing precision was estimated by calculating: 1) the percent agreement between two independent readers (number of fish aged by Reader 1 and Reader 2 that did not differ, expressed as a percentage of all fish aged); 2) the coefficient of variation (CV) (Kimura and Lyons, 1991); 3) the Index of Precision (D) (Chang, 1982); and 4) the concordance correlation (r_c) (Lin, 1989). Percent agreement is not "age independent" but rather it provides age-specific estimates and as such, while commonly used, it is not very valuable unless combined with another measure of precision such as CV (Kimura and Lyons, 1991). The CV and D methods are "age independent" and therefore provide precision estimates over the range of ages. The lower the CV or D value, the greater the precision. Although not in common use yet, we also included the concordance correlation because it was superior to comparison of coefficients of variation, to paired t-tests, and to regression, and hence was a more powerful and robust method of assessing reproducibility (precision) of ageing (Lin, 1989). As with a regression coefficient, the concordance correlation values range from 0 (no reproducibility) to 1.0 (perfect reproducibility).

Validation of Age Determination

The method of age determination for white grunt was validated using both marginal-increment analysis and an oxytetracycline (chemical) tagging method.

Marginal-Increment Analysis.—Timing and periodicity in the opaque zone formation in sagittal otoliths was examined by measuring the relative amount of marginal increment (translucent zone) on the edge of the otolith, calculated as the index of completion $C = W_n/W_{n-1}$ (Tanaka et al., 1981); where W_n is the width of the marginal increment and W_{n-1} is the width of the previously complete annulus. Thin-sections of otoliths for marginal-increment analysis were measured using a digital image-analysis system (IMAGE-1®, Universal Imaging Corp.). Otoliths were measured along an axis on the proximal (internal) medial surface, where the opaque zones were most distinct. A plot of the monthly mean index of completion over a 12-mo period was examined for the number and timing of minima present. To assess any difference in opaque zone deposition in relatively young versus older fish, an index of completion was determined for fish 1–4 yrs of age and fish ≥ 5 yrs of age.

Chemical (Oxytetracycline) Tagging.—White grunts were collected from live-bottom areas from the west coast of Florida and transported live to the University of Florida's Whitney Marine Laboratory, where they were kept in a flow-through seawater system. After allowing the grunts to recover from decompression and transport stress (2–3 d), each fish was individually anaesthetized using MS-222 (tricaine methanesulfonate), measured for length and weight, and then tagged in the left epaxial musculature with a Passive Integrated Transponder (PIT) tag to allow identification of individual fish. Each fish was then immediately injected interperitoneally with oxytetracycline (OTC) dissolved in sterile saline at a concentration of 50 mg kg^{-1} body weight (Beamish et al., 1983; Thomas et al., 1995). Fish were maintained in large (~6.7-m diameter and 1.5-m deep), outdoor tanks with flow-through seawater and fed Silver-Cup® fish pellets, whole shrimp, and squid at ~1%–2% body weight per day.

Two weeks after the injection of OTC, one white grunt was sacrificed to verify that the OTC had been incorporated into its otoliths. After 12 mo in captivity, the remaining fish were sacrificed to extract the otoliths. After removal, the left sagittal otolith was prepared for thin-sectioning as outlined previously except that exposure to white light was minimized to prevent fading of the fluorescent mark from the OTC (Beamish et al., 1983). Once sectioned, otoliths were exposed to both transmitted visible light to count and locate all opaque zones, and then to epi-fluorescence illumination to view the fluorescent mark of the OTC. Digital images from the visible and epi-fluorescent illumination were then superimposed using Adobe® Photoshop® to facilitate the comparison of the position and number of opaque zones in relation to the OTC mark. The number of opaque zones formed after the OTC-mark indicated the number of annuli formed in a 12-mo period.

Modeling Age and Growth

Age and growth data of male and female white grunt from the two sampling regions (central and north-central Gulf coast of Florida) were modeled by fitting the von Bertalanffy (Ricker, 1975) growth curve to back-calculated length-at-age data, for the most recent opaque zone, using non-linear regression with a Marquardt algorithm (PROC NLIN; SAS, 2000). The form of the von Bertalanffy growth curve for length-at-age was:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right]$$

where L_t = back-calculated length-at-time t (age); L_∞ = asymptotic length; k = Brody growth coefficient; and t_0 = theoretical age when length would be 0.

Back-calculated lengths-at-age used in the von Bertalanffy growth model were determined using the body proportional method (Francis, 1990):

$$L_A = \left[(a + bR_A)/(a + bR_C)\right]L_C$$

where L_A = back-calculated length to opaque zone A; a = intercept from the linear regression of total length as a function of otolith radius (i.e., $L_c = a + bR_c$); b = slope from the linear regression of total length as a function of otolith radius; R_A = otolith radius to opaque zone A; R_c = total otolith radius at time of capture; and L_c = total length at time of capture. Otolith radius was measured along an axis on the proximal (internal) medial surface along the sulcul groove, from the core to the external surface. It has been noted in other fish that there is greater differential growth in the dorsal plane of the otolith compared to the medial plane (Gauldie and Nelson, 1990), which can aid in improving r^2 values in the otolith radius to fish length regressions. With older white grunts, however, annuli are only formed on the medial surface and it is not possible to measure a complete radius as a linear distance along the dorsal plane of the otolith. Differences in the fish length-otolith radius regressions among areas, sexes, and gears (hook-and-line versus trap in the north region) were tested using analysis of covariance (ANCOVA) (Zar, 1996) and pooled when non-significantly different. Comparative ANCOVA analyses were restricted to data from fish over a similar size range.

Differences in growth curves between males and females, between regions, and between gears were determined using likelihood ratio tests (Kimura, 1980; Cerrato, 1990) to test for coincident curves. Growth curves were fit and compared only over a similar range of ages (Haddon, 2001). Sexes, areas, and/or gears were pooled for growth analyses only if the curves were found to be coincident. All tests of significance were at $\alpha \le 0.05$.

Age-length keys were constructed for white grunts from the central and north-central regions of the Gulf coast of Florida. Data for age-length keys were pooled without regard to sex for comparison with age-length keys given by Potts and Manooch (2001), since sex-specific data were not available to them. Age-length data were also pooled when there was not a significant difference between age and growth based on region or gear differences. Age-length data were grouped into 25-mm length classes.

In addition, the relationship between the length and weight (i.e., "plumpness") of white grunt was described by the relationship $\log_{10} W = \log_{10} a + b\log_{10} L$; where W = total wet weight in g; L = maximum total length in mm; a = the y-axis intercept of the regression; and b = the slope of the regression. This was then transformed into the power function, $W = aL^b$. Differences in the $\log_{10}$(weight) vs $\log_{10}$(length) relationships among areas, sexes, and gears were tested using analysis of covariance (Zar, 1996).

Results

Fish Collections and Length Frequencies

During 1998–2000, 4043 white grunts were sampled from the west coast of Florida: 1426 from the north-central area, and 2617 from the central area. White grunts collected in the north-central area were 16–41 cm TL, with the majority between 25 and 31 cm (Fig. 2A,B). The hook-and-line samples from the north-central region had a greater proportion of larger females and larger males than the samples obtained us-

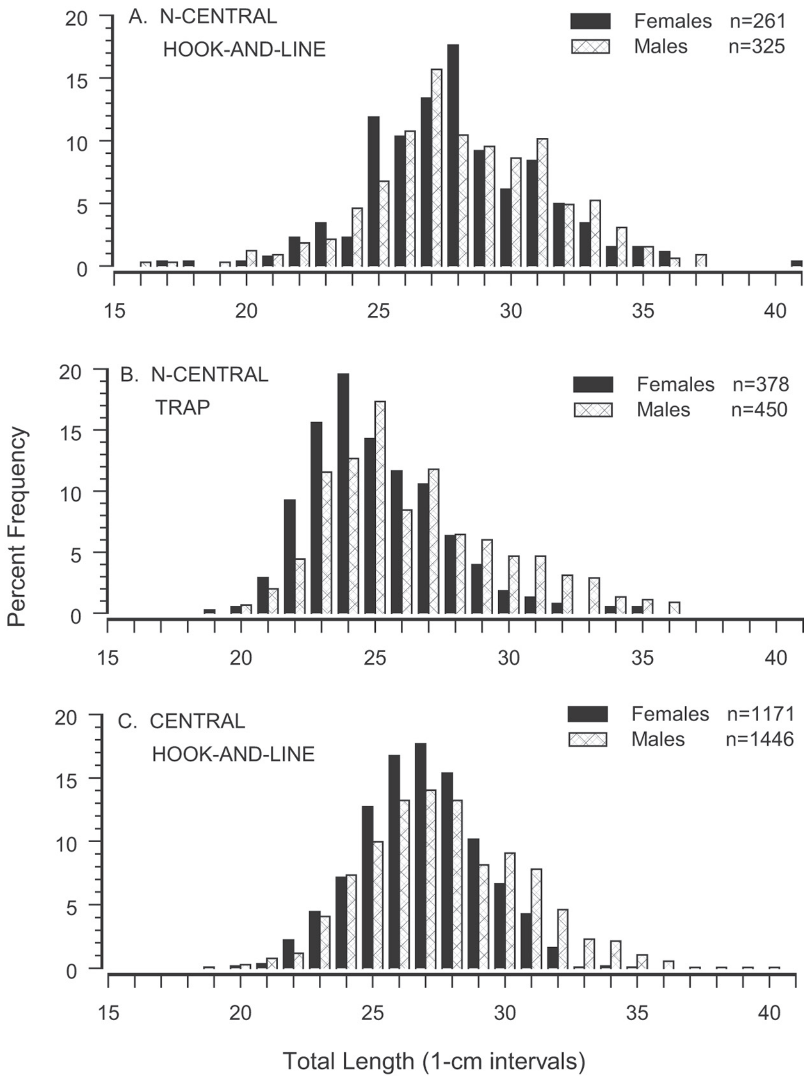

Figure 2. Size frequency distributions for male and female white grunt collected in the north-central region by (A) hook-and-line gear and (B) trap gear, and for white grunt collected in the central region by (C) hook-and-line gear. The north-central hook-and-line frequency distribution does not include 12 white grunts <12 cm TL collected by sabiki bait rigs or inshore trawls. Total lengths are in 1-cm intervals.

ing trap gear (Fig. 2B). Twelve 0-age fish, ranging from 4.0–11.5 cm TL, were caught in September in the north-central region by inshore trawls (n = 3) and sabiki rigs (n = 9). In the central region, white grunts collected using hook-and-line gear were 19–40 cm TL (Fig. 2C), with the majority between 24 and 31 cm. Males dominated size-classes >30 cm TL (Fig. 2C).

Age Determination

In total, 4029 white grunts were aged using thin-sections of sagittal otoliths: 1416 fish from the north-central region and 2613 fish from the central region. Thin-sec-

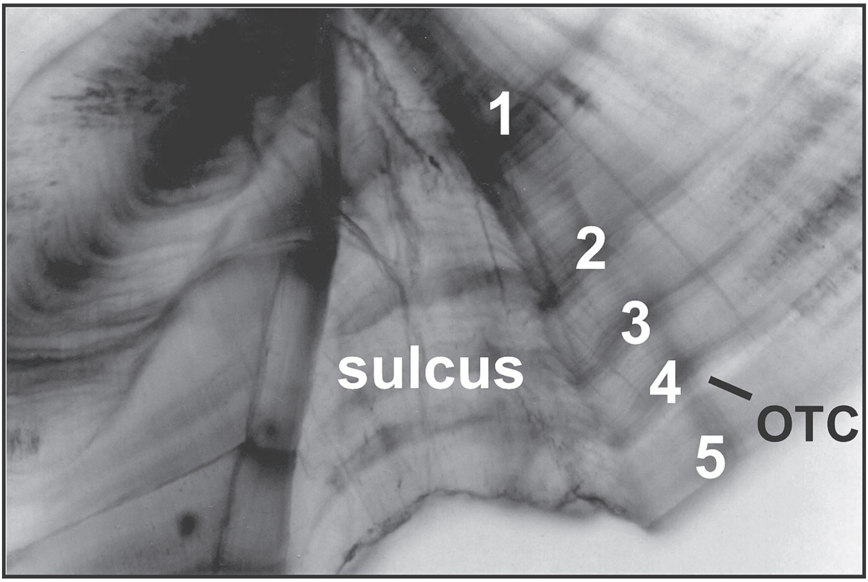

Figure 3. Thin-sectioned otolith from an oxytetracycline (OTC) -injected white grunt showing the core of the otolith, the OTC mark, and five annuli (opaque zones numbered). There is only one opaque zone between the OTC-mark and the edge of the otolith, validating that one annulus is deposited in a 12-mo period.

tions of sagittal otoliths were unambiguous to read using a zoom-stereomicroscope under transmitted light. Annuli were formed by thin opaque zones alternating with wider translucent zones. Opaque zones were enumerated along either the dorsal or ventral area of the sulcus (Fig. 3). Observed ages of white grunts ranged from 0–15 yrs in males and 0–18 yrs in females.

White grunts were aged with 98% (n = 2095) agreement between primary and secondary experienced readers. All ageing disagreements were ±1 yr difference. The CV between the experienced readers was 0.47%, with a D = 0.33 and an r_c = 0.998. Agreement between the primary experienced reader and the inexperienced, but trained, reader was also high at 97.5% (n =1587), with a CV = 0.42%, a D = 0.30, and an r_c = 0.996. As between experienced readers, all differences in age estimates were ±1 yr. In addition, agreement between the primary reader and an experienced reader from a NMFS laboratory (J. Potts) was 96% (n = 99 slides from an age-stratified, random sample, one reading of the original 100 was excluded because it could not be put into an age class due to lack of an edge reading), with a CV = 0.40% and D = 0.28. All differences between the primary reader and the NMFS reader were also ±1 yr, with two of the four reading differences involving 10–11 yr old fish. All ageing precision tests indicated that using thin-sections of sagittal otoliths was a precise method for ageing white grunt.

Validation of Age Determination

Marginal-Increment Analysis.—The index of completion plotted on a monthly basis over a 12-mo period was similar for white grunts aged 1–4 yrs and ≥5 yrs for both the central and north-central regions (Fig. 4A and B, respectively), thus all fish were pooled. The index of completion plot was unimodal (Fig. 4C), indicating that white

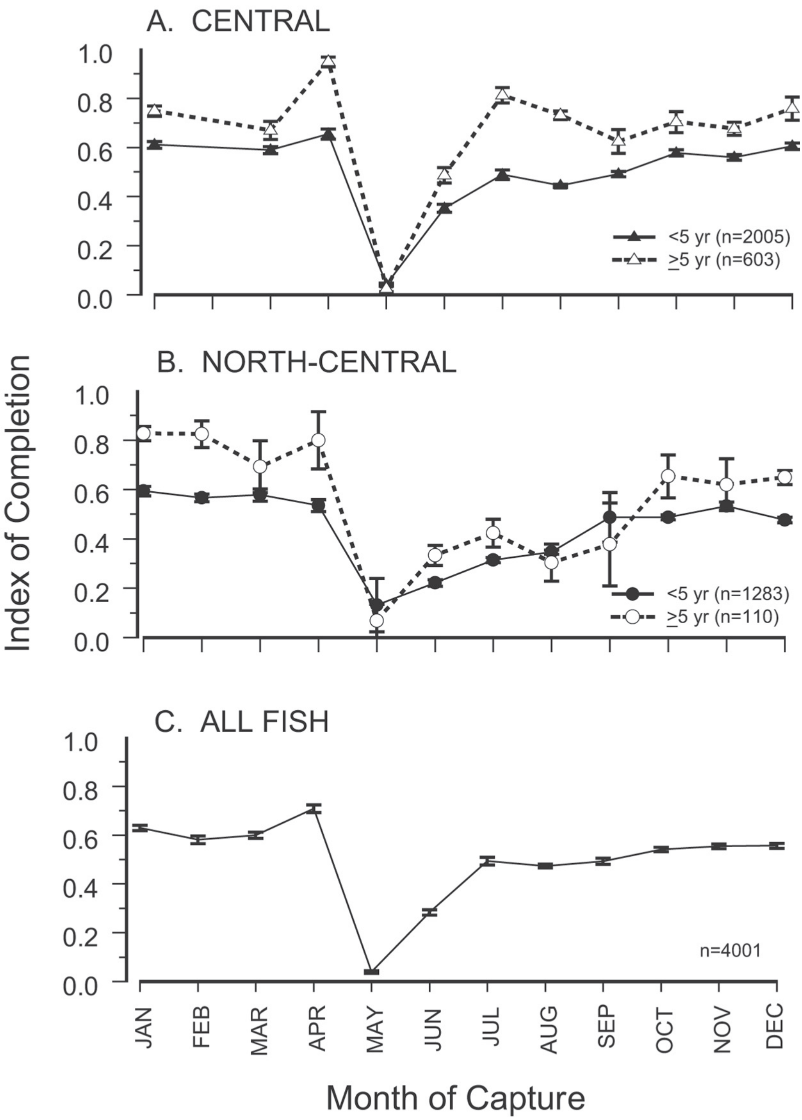

Figure 4. Mean index of completion (± 1SE) for white grunts 1–4 yrs of age and ≥5 yrs collected from either (A) the central Gulf coast of Florida or (B) the north-central Gulf coast, and for (C) all white grunt pooled. Only one minimum was observed, validating the deposition of one annulus in a 12-mo period.

grunt in the Gulf of Mexico deposit only one annulus each year. In addition, the index of completion was at a minimum in May, indicating deposition of the opaque zone during this time.

Oxytetracycline Tagging.—Fourteen white grunts of varying sizes (125–339 mm TL; 1–5 yrs old) retained their PIT tags during 12 mo in captivity for the validation study. One fish was initially sacrificed to do a preliminary check of the OTC injection concentration, which indicated that the OTC injection rate was adequate to provide a distinct mark in the otoliths.

Of the 13 white grunts maintained in captivity, nine that had been injected with OTC in May or June of 1998 were sacrificed 12 mo later in May or June 1999, respectively. Four white grunts injected with OTC in early July of 1998 were sacrificed in early July of 1999. When examined internally, all of these fish showed reproductive synchrony with fish captured in the wild (Murie and Parkyn, 1999).

Otoliths from the 13 OTC-injected white grunts showed the presence of one opaque zone and one translucent zone between the time each fish was injected with OTC and the time they were sacrificed one year later (Fig. 3). This confirmed that white grunts between the ages of 1 and 5 yrs-old deposit one annulus per year. Deposition of the opaque zone around May was also supported by evidence in the OTC-marked fish that had been injected in June because the fish appeared to have formed an opaque zone just prior to their injection date (Fig. 3).

Back-Calculated Length-At-Age

There were significant differences in the relationships of fish length and otolith radius for grunts between areas (central versus north-central), sexes, and gears (hook-and-line versus trap for north-central fish) (all ANCOVAs with $P < 0.0001$). Separate regressions for each combination of area, sex, and gear were therefore used in back-calculating length-at-age (Table 1).

Growth curves for male white grunts sampled in the north-central area by traps versus hook-and-line were coincident (Likelihood Ratio Test (LRT): $\chi^2 = 4.06$, df = 3, P = 0.26, for ages 1–6), and were therefore pooled. Similarly, female white grunts sampled in the north-central area by traps or hook-and-line also had coincident growth curves (LRT: $\chi^2 = 3.72$, df = 3, P = 0.29, for ages 1–10), and were therefore pooled. However, growth curves for female versus male white grunts from the north-central area were not coincident (LRT: $\chi^2 = 69.52$, df = 3, $P < 0.001$, for ages 1–10, hook-and-line and trap pooled) and sex-specific growth curves were retained (Fig. 5). Similarly, sex-specific growth curves were retained for white grunts sampled from the central area as well because of non-coincident curves (LRT: $\chi^2 = 404.18$, df = 3, $P < 0.001$, ages 1–15). In addition, the growth curve of males from the north-central area was significantly different than the curve for males from the central area (LRT: $\chi^2 = 46.62$, df = 3, $P < 0.001$, for ages 1–10), as were the growth curves between females from each area (LRT: $\chi^2 = 102.64$, df = 3, $P < 0.001$, for ages 1–10). Separate growth curves were therefore retained for males and females from both north-central and central areas sampled by hook-and-line gear, with trap-caught males and females pooled with north-central hook-and-line caught males and females respectively. These dif-

Table 1. Parameter estimates for otolith radius (*OR*) as a function of total length (*TL*) for male and female white grunts from central and north-central (N-central) areas of the Gulf coast of Florida, collected using hook-and-line (HL) and trap (TR) gears. All regressions were significant ($P < 0.0001$).

Area	Sex	Gear	Regression	r^2	n
N-central	Female	HL	$TL = 164.45 + 81.51*OR$	0.43	260
N-central	Male	HL	$TL = 146.16 + 108.13*OR$	0.46	321
N-central	Female	TR	$TL = 147.37 + 89.97*OR$	0.43	368
N-central	Male	TR	$TL = 93.88 + 151.28*OR$	0.51	441
Central	Female	HL	$TL = 194.26 + 49.97*OR$	0.50	1169
Central	Male	HL	$TL = 165.96 + 82.06*OR$	0.48	1442

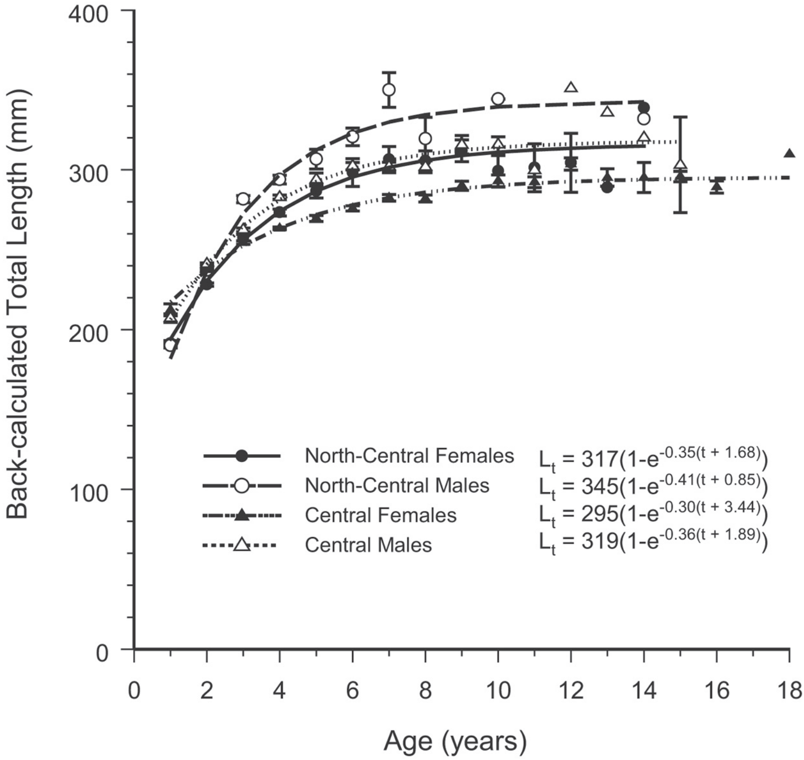

Figure 5. Back-calculated mean total length (± 1SE) as a function of age for male and female white grunt from the north-central and central Gulf coast of Florida. Lines represent sex-specific and area-specific von Bertalanffy growth curves. Specific parameter estimates for the curves are given in Table 2.

ferences in growth with respect to area and sex were evident from the von Bertalanffy growth curves based on individual back-calculated lengths-at-age (Fig. 5; Table 2).

White grunts in both the north-central and central areas showed rapid growth for the first 3–4 yrs, with a subsequent reduced growth rate and little growth occurring beyond age 7–8 (Fig. 5). In both the north-central and central areas, male white grunts were on average larger than females beyond age 3–4. In addition, both male and female white grunts from the north-central area were larger on average than the same sex from the central area.

Age-length keys for white grunts from both the central and north-central regions showed a wide range in ages for fish by length category, especially for fish in size categories from 275–400 mm TL (Tables 3,4). In addition, these age-length keys demonstrate that for white grunt from the Gulf coast of Florida, the largest fish sampled (i.e., categories ≥ 350-mm TL) were not the oldest fish (i.e., most were <7 yrs of age).

Weight-Length Relationships

The relationship between total body weight (*W*) and total length (*TL*) was not significantly different for male and female grunts collected in the north-central area using either hook-and-line or trap gear (ANCOVA: slopes P = 0.13, elevations P = 0.13), and a pooled regression by sex and gear was therefore used to relate length to weight for north-central fish (Fig. 6): $W = 2.83 \times 10^{-5}\, TL^{2.88}$ ($r^2 = 0.97$, n = 1207, P < 0.0001).

Table 2. Von Bertalanffy parameters (± 1SE) fitted to back-calculated total length (TL)-at-age for white grunts from central and north-central (N-central) regions on the Gulf coast of Florida (this study), from the Carolinas and from southeast Florida (Potts and Manooch, 2001), and from the Carolinas to northeast Florida (Padgett, 1997). Padgett's (1997) study included data from MARMAP (Marine Resources Monitoring Assessment and Prediction program) sampling, as well as commercial fisheries samples.

Source	Area	Sex	L_∞ (mm)		k		t_0 (yrs)		n	Range of ages (yrs)
This study	Florida Gulf coast									
	N-central	Male	345	(6.65)	0.41	(0.03)	–0.85	(0.11)	762	1–14
	N-central	Female	317	(4.54)	0.35	(0.03)	–1.68	(0.18)	628	1–14
	Central	Male	319	(3.13)	0.36	(0.03)	–1.89	(0.20)	1,442	1–15
	Central	Female	295	(2.18)	0.30	(0.02)	–3.44	(0.33)	1,169	1–18
Potts and Manooch (2001)	Carolinas	Both	591	(38.39)	0.08	(0.02)	–4.21	(0.80)	720	1–13
	Southeast Florida	Both	327	(3.12)	0.19	(0.02)	–4.21	(0.67)	618	2–15
Padgett (1997): MARMAP	Carolinas to northeast Florida	Male	370		0.32		–0.36		628	1–17
		Female	334		0.35		–0.70		730	1–22
Padgett (1997): Commercial	Carolinas to northeast Florida	Male	514		0.11		–4.99		226	2–17
		Female	353		0.29		–3.79		294	2–27

Table 3. Age-length key of white grunt from the central Gulf coast of Florida. Percentage of fish in 25-mm length (TL) categories as a function of age. Sexes are combined.

		Age (yrs)																
TL (mm)	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	18
150–174	0																	
175–199	7	42.9	57.1															
200–224	108	19.4	75.0	3.7	0.9			0.9										
225–249	541	5.0	71.5	15.2	7.4	0.2	0.7											
250–274	995	0.7	37.8	24.5	27.6	2.6	3.1	1.9	1.4	0.1	0.2							
275–299	619	0.2	10.2	18.4	35.4	5.2	9.5	9.7	4.8	2.4	1.1	1.4	0.2	0.2	0.3	0.5	0.5	0.0
300–324	269		1.9	7.8	29.7	5.2	16.4	13.0	7.1	4.5	5.9	2.6	2.6	0.4	0.7	1.5	0.4	0.4
325–349	62		4.8	4.8	30.6	4.8	25.8	12.9	3.2	3.2	4.8			1.6	1.6	1.6		
350–374	10		10.0		30.0		20.0	10.0		10.0	10.0		10.0					
375–399	2			50.0		50.0												
n	2,613																	

Table 4. Age-length key of white grunt from the north-central Gulf coast of Florida. Percentage of fish in 25-mm length (TL) categories as a function of age. Sexes are combined. Age-length key does not include 12 white grunts that were <12 cm TL and age 0.

		Age (yrs)													
TL (mm)	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14
150–174	4	75.0	25.0												
175–199	12	50.0	50.0												
200–224	140	56.4	42.9		0.7										
225–249	406	24.1	69.5	5.7	0.5	0.2									
250–274	390	7.2	62.6	14.9	13.1	1.5	0.8								
275–299	227		39.2	22.9	26.4	4.8	2.2	1.3	0.4	0.4	0.4	0.9	0.4	0.4	
300–324	144		13.9	34.7	28.5	9.0	4.9	2.1	4.2	2.1	0.7				
325–349	59		5.1	27.1	25.4	10.2	13.6	3.4	3.4	3.4	1.7	1.7	1.7		3.4
350–374	12				41.7	8.3	16.7	25.0			8.3				
375–399	0														
400–424	1						100								
n	1,395														

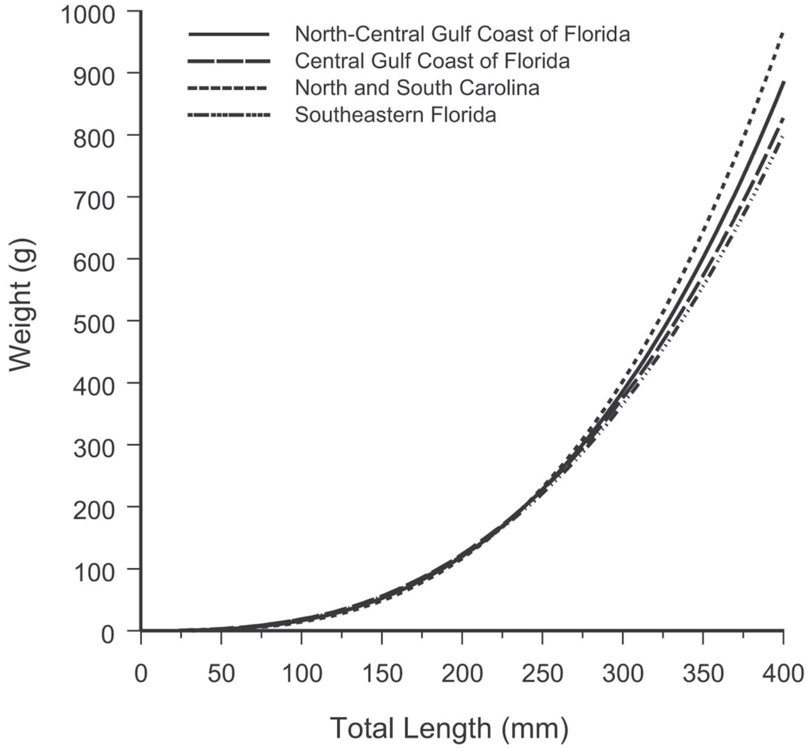

Figure 6. Total body weight as a function of total length for white grunt from the north-central and central regions of the Gulf coast of Florida, southeastern Florida (Potts and Manooch, 2001), and North and South Carolina (Potts and Manooch, 2001). Males and females were pooled for each area.

Male and female white grunts collected in the central area were also not different with respect to their weight-length relationship (ANCOVA: slopes $P = 0.33$, elevations $P = 0.30$) and were therefore pooled: $W = 5.78 \times 10^{-5}\ TL^{2.75}$ ($r^2 = 0.95$, $n = 1078$, $P < 0.0001$).

However, the relationship between weight and total length was different for white grunts from the north-central area compared to fish from the central area (ANCOVA: slopes $P < 0.0001$, elevations $P < 0.0001$). Based on the allometric relationship, the body weight of white grunts from the north-central area increased at a faster rate in relation to their total length compared to white grunts from the central region (Fig. 6).

Discussion

Sex-specific and area-specific differences in growth were evident for white grunts from the Gulf coast of Florida. Male and female white grunt in both the central and north-central areas of the Gulf coast grew rapidly during their first 4 yrs, followed by slower growth after age 5–6. Male white grunts were, however, consistently larger than females from the same geographical area. This trend of males being larger than females of the same age has been previously noted in white grunts from North Carolina and South Carolina (Manooch, 1976), although they were not statistically

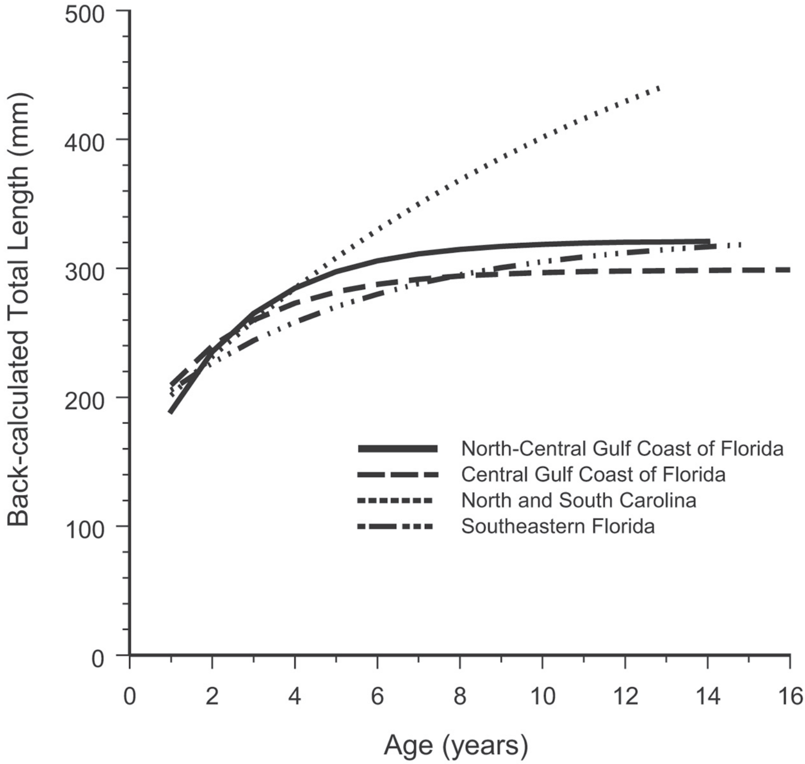

Figure 7. Von Bertalanffy growth curves for back-calculated total length as a function of age for white grunt from the north-central and central Gulf coast of Florida (this study), North and South Carolina (Potts and Manooch, 2001), and southeastern Florida (Potts and Manooch, 2001).

analyzed due to small sample size. Padgett (1997) analyzed sexes separately for white grunt collected off the southeastern seaboard, primarily from South Carolina, and also noticed that males were consistently larger than females. Little of what is known of white grunt spawning behavior would indicate sexual selection for increased male size, unless territoriality is involved in securing females or spawning sites. This may be a possibility since mouth-to-mouth pushing is observed in many grunt species (Böhlke and Chaplin, 1993). However, because of a lack of sexual dimorphism in body shape or color (Billings and Munro, 1974), it is currently unknown whether the fish involved are female-male pairs engaged in ritualized courtship behavior or male-male pairs engaged in agonistic behavior.

Growth of white grunt may be modulated on a relatively small-scale or regional level. This was suggested by the observation that white grunts in the north-central area were consistently larger than grunts from the central area, despite the distance between these two sampling regions being only ~70 km. White grunts may be particularly susceptible to regionalized growth differences because of their propensity to remain near a “home” reef throughout their life with low rates of large-scale movement (Springer and McErlean, 1962; Moe, 1966; Beaumariage, 1969; Tulevech and Recksiek, 1994).

These regional-specific differences in the growth of white grunt could be problematic for a comprehensive fishery management plan on a Florida-wide, Gulf-wide, or southeastern U.S. basis because growth plasticity appears to occur throughout their range in the southeastern U.S (Fig. 7). Growth of white grunts from southeast Florida (Potts and Manooch, 2001) was more continuous with age compared to the rapid increase in growth followed by little growth (almost asymptotic) for white grunts from the Gulf coast of Florida (Fig. 7). However, white grunts from southeast Florida show similar size-at-age for fish older than 6–7 yrs and their estimated asymptotic length of 327 mm TL (Potts and Manooch, 2001) was comparable to asymptotic lengths for white grunts from the Gulf coast (Table 2).

Observed differences in the age and growth of white grunt among the Carolinas, southeastern Florida, and the Gulf coast of Florida cannot be attributed to differences in ageing methods. Although this was a possibility with Manooch's (1976) earlier work because he used primarily scales to age white grunt, which can underestimate the age of older fish (Chilton and Beamish, 1982), the additional data and reanalysis by Potts and Manooch (2001) using sectioned otoliths supported the growth differences observed previously in Carolinian fish. In addition, white grunt were aged with more precision within our ageing laboratory (98% agreement and CV=0.47% between two independent readers), as well as between agencies (96% agreement between our laboratory and J. Potts at the NMFS Beaufort laboratory), than many other fishes (Kimura and Lyons, 1991).

It is also unlikely that differences in the methods of analysis used in this and the Potts and Manooch (2001) study to model white grunt growth are responsible for the observed growth differences among regions. Although Potts and Manooch (2001) used a weighted (inverse of sample size at each age) von Bertalanffy growth curve, we did not see any difference between an unweighted- and a weighted-growth curve when we applied an inverse-weighting scheme to our data. This was probably because both the unweighted and weighted curves reach a plateau of much reduced growth by 6 yrs of age or ~300–310 mm TL, with the reduced growth continuing for another 10 yrs of ageing data, versus the more continual growth observed by Potts and Manooch (2001). In addition, low r^2 values for regressions of white grunt length as a function of otolith radius occurred in this study (r^2 = 0.43–0.51), in southeastern Florida (Potts and Manooch, 2001; r^2 = 0.51), and in commercial fish samples from South Carolina to northeast Florida (Padgett, 1997; r^2 = 0.18–0.29). This suggests that growth in fish length is uncoupled to some degree with the growth in the radius of the otolith, which may present a bias when back-calculating fish length based on otolith radius measurements. To graphically assess whether this was a specific problem in our study, we assigned white grunt actual ages expressed as the number of opaque zones plus the decimal portion that the capture day represented in a year that began on May 1st. This birth date corresponded to the midpoint of spawning of white grunts on the west coast of Florida based on a high proportion of hydrated females and a maximum gonadosomatic index (Murie and Parkyn, 1999). For fish that exhibited the beginning of an opaque zone earlier in April, the number of opaque zones was adjusted down by 1 yr to avoid over-ageing (e.g., a fish caught on 3 April with a third opaque zone on the edge would be assigned an absolute age of 2.92 yr). Conversely, fish that exhibited a wide translucent zone at the edge of their otolith after May 1st, indicating a delay in the opaque zone deposition, had 1 yr added to their opaque zone count. The resulting growth curves based on observed (measured) length as a function of actual age were entirely coincident with back-calculated length-at-age growth curves over comparable age ranges. Differences in the two approaches to modeling growth may have been ameliorated in white grunt specifically because the timing in the deposition of their opaque zone (May) is coincident with their spawning birth date (~May 1st).

Growth curves of white grunt collected from North Carolina to northeast Florida (Padgett, 1997) cannot be compared directly without reanalysis because Padgett used mean back-calculated lengths-at-age based on back-calculating to all previous annuli (opaque zones) (Padgett, 1997), whereas Potts and Manooch (2001) and our study used back-calculated length to only the most recently formed opaque zone. However, Padgett (1997) also documented growth differences between males and females, and between fish caught using commercial gear versus the fishery-independent gear used in the Marine Resources Monitoring Assessment and Prediction program (MARMAP). In addition, although Padgett sampled a similar geographic area as Manooch (1976), the latter having recently been supplemented and reanalyzed by Potts and Manooch (2001), the two different studies describe different patterns of growth with Padgett's (1997) study recording smaller size-at-age and an older maximum age of 27 yrs compared to Potts and Manooch's (2001) study (maximum age of 13 yrs). The differences in age and growth of white grunt between these two studies remains unresolved (Potts and Manooch, 2001).

In contrast to white grunt from the Gulf coast, the growth curve estimated by Potts and Manooch (2001) for white grunt in the Carolinas was fundamentally different, both in its basic shape (no evident growth plateau), growth coefficient (very low, k = 0.08), and estimated asymptotic length (L_∞ = 591 mm). Back-calculated total length to last opaque zone formation was similar to Gulf coast white grunt for the first 4 yrs but by age 10 the fish from the Carolinas were ~8.5 cm larger than grunts from the Gulf coast. Potts and Manooch (2001) observed a similar difference between white grunt from the Carolinas and from southeastern Florida but did not observe a growth "plateau" in white grunt from southeastern Florida at an early age. This qualitative comparison was also supported by the growth coefficients, with k = 0.19 for white grunt from southeastern Florida (Potts and Manooch, 2001) and k = 0.30–0.41 for white grunt from the Gulf coast. The greater k-values for Gulf coast fish indicate a faster rate of de-acceleration to an average asymptotic length (Ricker, 1975).

Effective management of white grunt using regulations of minimum size limit should consider absolute differences in body sizes from different regions. For example, implementation of a 305-mm (12 in) size limit may be possible for white grunt in the Carolinas, but is probably not economically feasible for the white grunt fishery from the Gulf coast of Florida because >95% of the fish currently landed in the recreational fishery are below this length (Murphy et al., 1999). Additionally, any minimum size limit imposed would need to take into account that the growth of white grunt in the Gulf becomes asymptotic, indicative of almost determinate growth. In contrast, growth of white grunt in southeastern Florida, and especially in the Carolinas, exhibits a more typical indeterminate growth pattern with fish size increasing with age at a decelerated rate. One effect of the virtually determinate growth in white grunt in the Gulf is that an age-length key becomes relatively ineffective after 2–3 yrs of age. For example, a 305-mm fish can range from 2–18 yrs old, with ~70% of 305-mm fish being 3–7 yrs old. This is in contrast to white grunt from the Carolinas where a 305-mm fish can range from 3–8 yrs old, with ~85% either 4 or 5 yrs old (96 out of 113 fish; Potts and Manooch, 2001). For white grunt from the west coast of Florida, it would therefore not be advisable to project an age-length key based on sampling fish in one or two specific years to other years where only lengths were reported because there would be reduced confidence that a shift in age frequencies could be detected in their length frequencies (Hilborn and Walters, 1992).

Growth of fish, in general, can be influenced by a variety of factors, including environmental variables (e.g., water temperature, food supply), human-induced variables (e.g., fishing mortality), and genetics (e.g., stocks). These factors are generally confounding in natural systems and experimental protocols are needed to separate the specific effect of each on the growth of white grunts. For example, an increase in water temperature, within the physiological range of a fish, is correlated with an increase in growth if increased food consumption is adequate to sustain the growth along with simultaneous increases in metabolism and activity (Lagler et al., 1962; Jennings et al., 2001). Whereas temperature may be relatively easily quantified in the field, food availability is more difficult to assess. Currently, comparative food availability and consumption rates of white grunt from the Carolinas and the Gulf coast of Florida are lacking. Elucidating the role of either temperature or food consumption, and their interaction, on growth in white grunts requires concurrent field measurements of both variables or research using controlled feeding experiments.

Fishing pressure may also affect growth by reducing intraspecific competition and therefore alleviating food limitations, which may result in increased growth rates and larger size-at-age and/or early maturation (Toresen, 1990). In contrast, heavy fishing pressure may affect growth by the selective removal of the larger, faster-growing individuals over time, leaving individuals predisposed towards relatively slower growth to reproduce. For example, in red porgy, *Pagrus pagrus* (Linnaeus, 1758), there is evidence that over-exploitation over decades (20 yrs) has led to an overall decrease in their mean size-at-age along the Atlantic coast (Harris and McGovern, 1997). Fishing grounds for white grunt off the central sampling area are closer to shore and more readily accessible compared to the north-central sampling area. In addition, human population density in the central sampling area is >35 times that of the north-central area (Census 2000: Florida Profile, U.S. Census Bureau, U.S. Department of Commerce, Economics and Statistics Administration, <www.census.gov>). Both of these factors could contribute to greater levels of fishing pressure in the central sampling area (e.g., Tampa and St. Petersburg) compared to the north-central area (e.g., Cedar Keys and Suwannee) and may, in part, explain why white grunt in the central area are smaller at age than in the north-central area.

Growth may also be regulated directly by the genetic composition of the stock irrespective of fishing mortality effects. Recently, three distinct lineages of white grunt have been identified through mitochondrial DNA analysis: 1) a northern or "Carolinian" type found from the Carolinas south to the Florida Keys, and off Panama City, Gulf of Mexico; 2) a southern or "Caribbean" form found in the Florida Keys, Yucatán, Belize, and Puerto Rico; and 3) a third form found exclusively in Trinidad (Chapman, 1998). The Carolinian and Caribbean forms mix in the Florida Keys, with the Caribbean form dominant. Therefore, the possibility exists that the growth rate and size differences among white grunt from southeastern Florida (Potts and Manooch, 2001), the Gulf of Mexico (this study), and the Carolinas (Manooch, 1976; Potts and Manooch, 2001) may, in part, have a genetic constraint.

Further exploration of the extent and causes of regional growth differences in white grunt populations will be necessary to delineate appropriate management units. Reef-associated species that have low rates of movement, such as white grunt, may be particularly susceptible to localized changes in fishing pressure, food limitation, and habitat enhancement or destruction, that ultimately affect their growth, reproduction, and mortality. As with white grunt populations in southeastern Florida (Potts and Manooch, 2001), white grunt from the Gulf coast of Florida need to be considered separately from white grunt populations in the Carolinas when regulations are considered and implemented. Differences in the age and growth of white grunt are not as pronounced between southeastern Florida and the Gulf coast of Florida as they are between Florida and the Carolinas. Similarly, differences have also been observed recently for mortality rates among regions (Murie and Parkyn, 2003). Within south Florida and the Gulf coast of Florida, it may therefore be possible to consider similar size regulations. Based on stock assessments (inclusive of mortality rates) for southeastern Florida (Potts, 2000) and the Gulf coast of Florida (Murphy et al., 1999; Murie and Parkyn, 2003), white grunt were not designated as being over-fished, nor was over-fishing occuring at current fishing mortality rates, and it was therefore unnecessary to implement any regulations. There is concern that this condition may change, however, as more desired species, such as groupers and snappers, have stricter regulations imposed and fishing pressure increases on alternate species, such as white grunt.

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