Regional variation in the population structure of gray snapper, *Lutjanus griseus,* along the West Florida shelf

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REGIONAL VARIATION IN THE POPULATION STRUCTURE OF GRAY SNAPPER, *LUTJANUS GRISEUS*, ALONG THE WEST FLORIDA SHELF

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ABSTRACT

We examined variation in life history traits of gray snapper [*Lutjanus griseus* (Linnaeus, 1758)] from three regions along the west Florida shelf with varying levels of fishing pressure. A total of 1132 gray snapper 254–724 mm TL were sampled from recreational and commercial fisheries. Overall the ratio of females to males was not significantly different from 1:1. Mean size decreased from north to middle to south (commercial 489–441 mm TL; recreational 501–345 mm TL). Gray snapper ages ranged from 2 to 26 yrs. Mean age decreased from north to middle to south (8.4 to 6.1 to 4.6 yrs) for the recreational fishery, while mean age in the commercial fishery was greatest in the middle region (9.4 yrs) and similar in the north (7.9 yrs) and south (7.6 yrs). Mean size-at-age for the most common ages (5–12 yrs) decreased from north to south. Von Bertalanffy growth curves differed between sexes with a greater L_∞ for males. Instantaneous mortality increased from north to south with the largest difference in the recreational fishery (Z = 0.14–0.55). Instantaneous natural mortality (M) estimates varied greatly by the method used (0.17–0.36): Hoenig's estimate of M using a maximum age of 26 yrs was 0.17; the Ralston estimate was 0.36 and the Pauly estimate was 0.24. Observed regional differences in size and age distributions as well as in growth and mortality rates are likely due to differences in exploitation rate.

Ecologically important patterns and processes occur at differing, but explicit, scales, thus spatial scales at which a system is explored will determine which patterns and processes are detected and which are missed (Sale, 1998). For reef fish, scale is of particular importance due to their patchy distribution. Fisheries science has traditionally applied a large-scale perspective to the study of marine systems due in part to the large geographic areas that fisheries management agencies are tasked with overseeing (Kritzer and Sale, 2006). Accurate estimates of life history parameters such as growth and mortality are crucial for stock assessments, therefore an understanding of the scale at which these parameters vary is essential for effective management decisions. Latitudinal variation in life history traits has been noted on a large scale (e.g., East coast of North America) and has been linked to differences in growing season (Conover, 1990). Variation also has been noted on a smaller scale for white grunt [*Haemulon plumieri* (Lacépède, 1801)], red porgy [*Pagrus pagrus* (Linnaeus, 1754)] and red grouper [*Epinephelus morio* (Valenciennes, 1828)] from the west Florida shelf (WFS) (Murie and Parkyn, 2005; DeVries, 2006; Lombardi-Carlson et al., 2008), for gray triggerfish [*Balistes capriscus* (Gmelin, 1789)] off Alabama (Ingram, 2001), and for yellowtail snapper [*Ocyurus chrysurus* (Bloch, 1791)] (Allman et al., 2005) and gray snapper [*Lutjanus griseus* (Linnaeus, 1758)] (Manooch and Matheson, 1981; Burton, 2001) from the Atlantic coast of Florida. This small-scale variation has been attributed to regional differences in exploitation rate.

Gray snapper, also known as mangrove snapper, are found in the western Atlantic from North Carolina and Bermuda south to Brazil as well as in the Gulf of Mexico. Rarely, individuals are recorded as far north as New England (Hoese and Moore,

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1977). Adults generally occur offshore and are associated with coral reefs or other hard bottom substrate. Available tagging information suggests that adult movement is limited: of 13 gray snapper tagged and recovered, only two had moved more than 9 km in 4 yrs (Bortone and Williams, 1986). Spawning of gray snapper off Florida is thought to occur June through September with individuals probably spawning more than once during the spawning season (Starck, 1971; Domeier et al., 1996; Allman and Grimes, 2002). Juvenile gray snapper are associated with inshore seagrass beds and mangrove thickets (Manooch and Matheson, 1981; Chester and Thayer, 1990; Allman and Grimes, 2002). Young snapper remain in seagrass beds until ~80 mm standard length (SL) when they begin to congregate around debris and channel edges and then move farther offshore. Size at first maturity occurs at 175–198 mm total length (TL) or 3 yrs of age (Starck, 1971; Domeier et al., 1996). Gray snapper support important commercial and recreational fisheries in the Gulf of Mexico. Commercial landings of gray snapper along the WFS ranged from a high of 423 mt in 1983 to 108 mt in 2006 and recreational landings ranged from 1644 mt in 1984 to 403 mt in 2006 (pers. comm. from National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, MD). There is evidence that many exploited reef fishes including gray snapper are undergoing overfishing off the Florida Keys (Ault et al., 1998). At present, gray snapper are managed in the U.S. Gulf of Mexico as a single stock, and the Gulf of Mexico Reef Fish Stock Assessment Panel has recommended that gray snapper be considered for future stock assessment (RFSAP, 1999).

Previous studies have examined the age and growth of gray snapper from the southeast U.S. using scales (Croker, 1962; Starck, 1971; Rutherford et al., 1983) and otoliths (Manooch and Matheson, 1981; Johnson et al., 1994; Burton, 2001; Fischer et al., 2005). The only study in which gray snapper from the WFS were aged (Johnson et al., 1994) had insufficient sample size for geographic comparisons. The goal of this study was to examine latitudinal variation in sex ratios, size and age distributions, and growth and mortality rates of gray snapper along the WFS in three regions with varying levels of fishing pressure.

Methods

Gray snapper were sampled from commercial and recreational hook and line fisheries along the WFS from January 2001 to December 2005. To examine potential regional differences within each fishery, the WFS was divided into three regions: (1) Northwest, comprising Escambia County, east to Wakulla County, (2) Middle, comprising Pinellas County south to Charlotte County and (3) South, comprising Lee County south to Monroe County (Fig. 1). All fish were weighed whole (W) to the nearest gram (g) and measured to the nearest millimeter TL or if fork length (FL) was measured, TL was estimated from FL using the equation: TL (mm) = 1.06*FL (mm) − 7.22 (unpubl. data, N = 963, $r^2 = 0.99$, FL = 180–698 mm). Sagittal otoliths (hereafter referred to as otoliths) were collected, and sex was determined macroscopically if the fish was landed with an intact gonad. The relationship between W and TL was expressed using the power equation $W = a(\mathrm{TL})^b$. For comparison between sexes and regions, length-weight relationships were made linear using $\log_e$ transformations. Analysis of covariance (ANCOVA) was used to test for differences between sexes and regions.

Otolith Processing and Aging.—Otoliths were weighed to the nearest milligram and then processed with a high-speed thin sectioning machine utilizing the methods of Cowan et al. (1995). Two transverse cuts were made through the otolith core to a thickness of 0.5 mm. Ages were assigned based on counts of opaque zones observed on the dorsal side of the sulcus acusticus in the transverse plane with reflected light at 40×, including any partially completed

Figure 1. Map of gray snapper (*Lutjanus griseus*) sampling locations along the West Florida Shelf. Dashed lines denoted boundaries for Northwest, Middle, and South regions.

opaque zones on the otolith margin and the degree of marginal edge completion. Otoliths were classified into one of three marginal edge categories: (1) opaque zone just forming to fully complete, (2) translucent zone just forming to two-thirds complete, and (3) translucent zone greater than two-thirds to fully complete. Typically, marine fishes in the southeastern U.S. complete opaque zone formation by late spring to early summer (Patterson et al., 2001; Wilson and Nieland, 2001; Garcia et al., 2003; Allman et al., 2005). Therefore, age was advanced by 1 yr if a large translucent zone (i.e., greater than two-thirds to fully complete) was visible on the margin and capture date was from 1 January to 30 June; after 30 June, age was equal to opaque zone count. By this traditional method, an annual age cohort is based on a calendar year rather than time since spawning (Jearld, 1983; Vanderkooy and Guindon-Tisdel, 2003). The percentage of otoliths with opaque margins was calculated by month to estimate the timing of annulus formation.

An experienced primary otolith reader aged all otolith sections and an experienced secondary reader independently aged a random sample of 20% of the sections with no prior knowledge of fish length. Average percent error (APE; Beamish and Fournier, 1981) was used to estimate precision between readers.

Length and Age Distributions.—Analysis of variance (ANOVA) was used to compare mean TL and age between sexes and regions. An interaction term was included in each model to establish if there were confounding differences between region and sex. Total length and age were first $\log_e$ transformed to meet the assumptions of normality and homogeneity of variance. Tukey's test was used for pair-wise comparison of means. Size and age distributions were compared by sex and pair-wise by region with the Kolmogorov-Smirnov two-sample test (KS). A χ^2 test was used to determine if sex ratios differed from a 1:1 ratio overall or among regions.

Growth.—To examine growth differences between fisheries and among regions, we chose to compare size-at-age for the most common ages (3–12 yrs) using ANOVA. Those age classes in which there was not a significantly difference between fisheries were combined for analysis to obtain a larger sample size. To avoid potential size bias using smaller recreationally-caught fish, only fish above the commercial size limit (305 mm TL) were used.

The von Bertalanffy model was fitted to TL at biological age using the solver function in Microsoft Excel 2000 (Haddon, 2001):

$$L_t = L_\infty\,(1 - e^{-k(t - t_0)})$$

where L_t = length at age t, L_∞ = asymptotic length, k = growth coefficient, t = age, and t_0 = theoretical age when length = zero. To estimate biological age, a fractional year was calculated using the equation: absolute value [(capture date – spawning date)/365]. August 1 was selected as the peak spawning date based on gray snapper gonadosomatic indices (Domeier et al., 1996). Fractional year was added to annual age if capture date was after 1 August or subtracted if capture date was earlier. Von Bertalanffy growth curves were calculated for all fish combined, separately by fishery, and by sex for the recreational fishery. Growth curves were not calculated by sex for commercial fish since most were landed gutted. Since our samples were fishery-dependent and subject to size limits, they contained no small young fish; therefore, growth curves were also calculated with t_0 restricted to zero. Growth curves were compared between sexes using a likelihood ratio test (Cerrato, 1990).

Mortality Rate.—Instantaneous total mortality rates (Z) were calculated with age-based catch curves (Ricker, 1975) for each fishery and within each fishery by region. The $\log_e$ of fish frequency in each age class, from the first fully recruited age through the oldest age, was regressed on age and Z was estimated from the descending slope, b. Only age classes with at least five observations were included in the analysis (Chapman and Robson, 1960). A homogeneity of slopes test and analysis of covariance (ANCOVA) were used to compare Z between fisheries and among regions. The assumptions of normality and homogeneity of variance were met prior to analysis. Instantaneous natural mortality (M) was estimated using three methods: Hoenig (1983), using the oldest observed age; Pauly (1980), using mean annual Gulf of Mexico sea surface temperature (25.08 °C Locarnini et al., 2006) and von Bertalanffy growth parameters L_∞ and k; and finally, Ralston (1987) which used only k. Hoenig's (1983) M was subtracted from Z to estimate fishing mortality (F) since previous studies suggested that Hoenig's method was probably the most suitable estimate of M (Burton, 2001; Fischer et al., 2005). The other methods for calculating M were used to examine the variability between methods and to compare to earlier studies.

Results

In total, 1132 gray snapper 254–724 mm TL were sampled from the recreational (65%) and commercial (35%) fisheries. Sex was recorded for 639 individuals, mainly from the recreational fishery (93%) since commercially caught fish were most often gutted at sea.

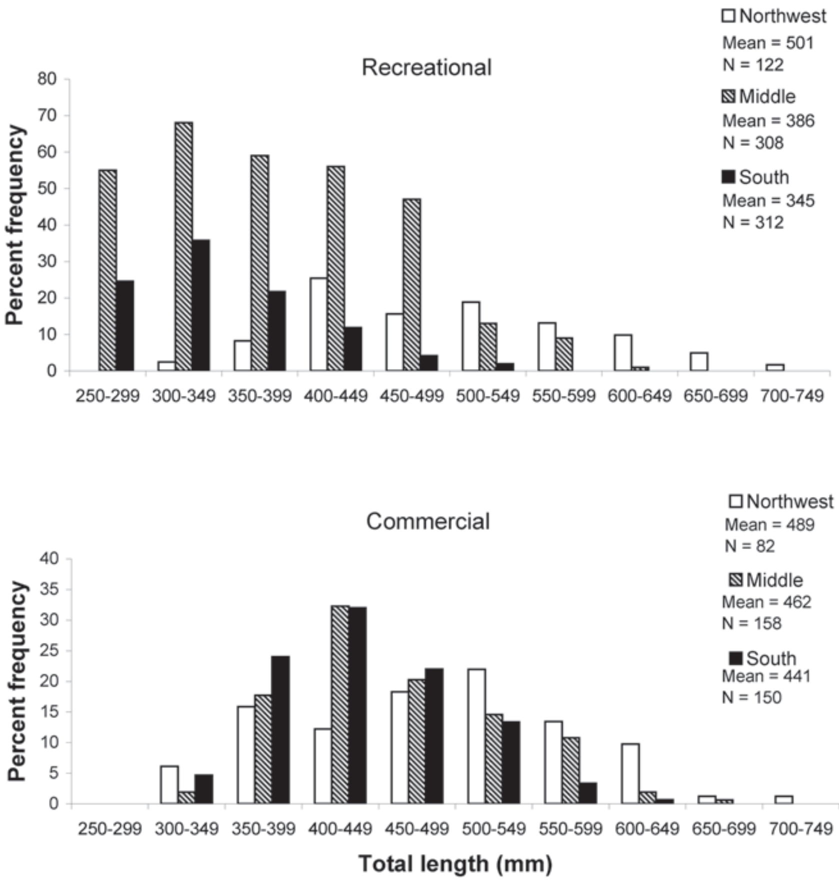

Figure 2. Length frequency distribution of gray snapper (*Lutjanus griseus*) from the recreational and commercial fisheries along the west coast of Florida by region.

Differences were noted in size distributions between fisheries and regions. Commercially-caught gray snapper were larger on average than recreational fish (459 vs 387 mm TL) (Fig. 2). Regional differences in TL were significant in both recreational and commercial fisheries [ANOVA: recreational: $F_{2,589} = 158.17$, $P < 0.001$, means (SE): middle = 386 (4.54), north = 501 (8.07), south = 345 (3.30); commercial: $F_{2,387} = 10.66$, $P < 0.001$, means (SE): middle = 462 (5.52), north = 489 (9.98), south = 441 (4.93)] with average TL increasing from south to north in both fisheries. For fish caught in the recreational fishery, there was no significant interaction between region and sex in their TL ($F_{2,589} = 0.95$, $P = 0.39$), nor an effect due to sex alone ($F_{1,589} = 0.08$, $P = 0.78$). Too few sexes were recorded from the commercial fishery (n < 50) for comparison. Pair-wise comparisons of mean lengths were significantly different for each region (Tukey's test: $P < 0.05$) and length distributions within each fishery were significantly different for all regions (KS: $P < 0.05$) except middle and north in the commercial fishery (KS: $P = 0.52$).

The length-weight relationship was expressed by the equation $W = 4.0 \times 10^{-8}\ \mathrm{TL}^{2.81}$, and the relationship did not differ between sexes ($F_{1, 281} = 0.49$, $P = 0.48$) or among

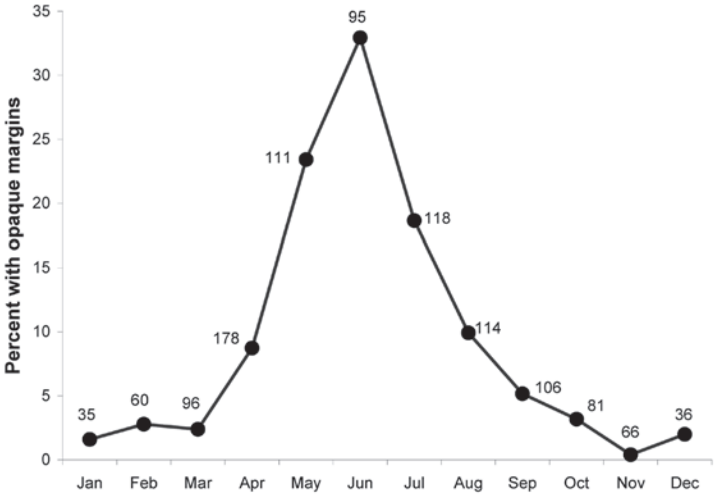

Figure 3. Percentage of gray snapper (*Lutjanus griseus*) otoliths with an opaque margin by month. N = number of otoliths examined.

regions ($F_{2,335}$ = 1.33, P = 0.27). The overall ratio of females to males (1:0.99) was not significantly different from 1:1 (χ^2 = 0.01, P = 0.92) and regionally was not different from 1:1 for the middle and south (χ^2 = 0.002, P = 0.97; χ^2 = 2.16, P = 0.14 respectively); however, there was a slightly higher ratio of males in the north (χ^2 = 4.3, P = 0.04). Size distributions did not differ significantly between sexes for the recreational fishery (KS: P = 0.13).

Ageing.—We were able to assign ages to 97% of all gray snapper sampled with a high degree of precision. Agreement between readers was 98%, with an APE of 1.64% (CV = 2.16%). Examination of otolith margins indicated that opaque increments were formed once annually, during the spring to early summer peaking in June (33%) and began to decline by July (19%) (Fig. 3).

Age Distributions.—Ages of gray snapper ranged from 2 to 26 yrs for the recreational fishery and from 2 to 22 yrs for the commercial fishery (Fig. 4). On average, fish from the commercial fishery were older (8.4 yrs) than those from the recreational fishery (5.8 yrs). Age distributions did not differ between sexes for the recreational fishery (KS: P = 0.93). Gray snapper recruited to the commercial fishery at age 5 for the north and middle regions and age 6 in the south, compared to age 4 for the middle and south and age 5 for the north in the recreational fishery. Average age in the recreational fishery decreased from north to south (8.4 to 6.1 to 4.6 yrs) (Fig. 4). In the commercial fishery average age was greatest in the middle region (9.4 yrs) followed by 7.9 yrs in the north and 7.6 yrs in the south. The percentage of older fish (≥ 10 yrs) also decreased in the recreational fishery from north to south (35% to 17% to < 1%); however, in the commercial fishery the middle region had the highest percentage of older individuals (44%) followed by the north (37%) and the south (22%). Not surprisingly, average age differed significantly among regions for both fisheries [ANOVA: recreational: $F_{2,578}$ = 66.73, P < 0.001, means (SE): middle = 6.1 (0.23), north = 8.4 (0.37), south = 4.6 (0.10); commercial: $F_{2,369}$ = 9.84, P < 0.001, means (SE): middle = 9.4 (0.31), north = 7.9 (0.43), south = 7.6 (0.28)], however there was no difference by

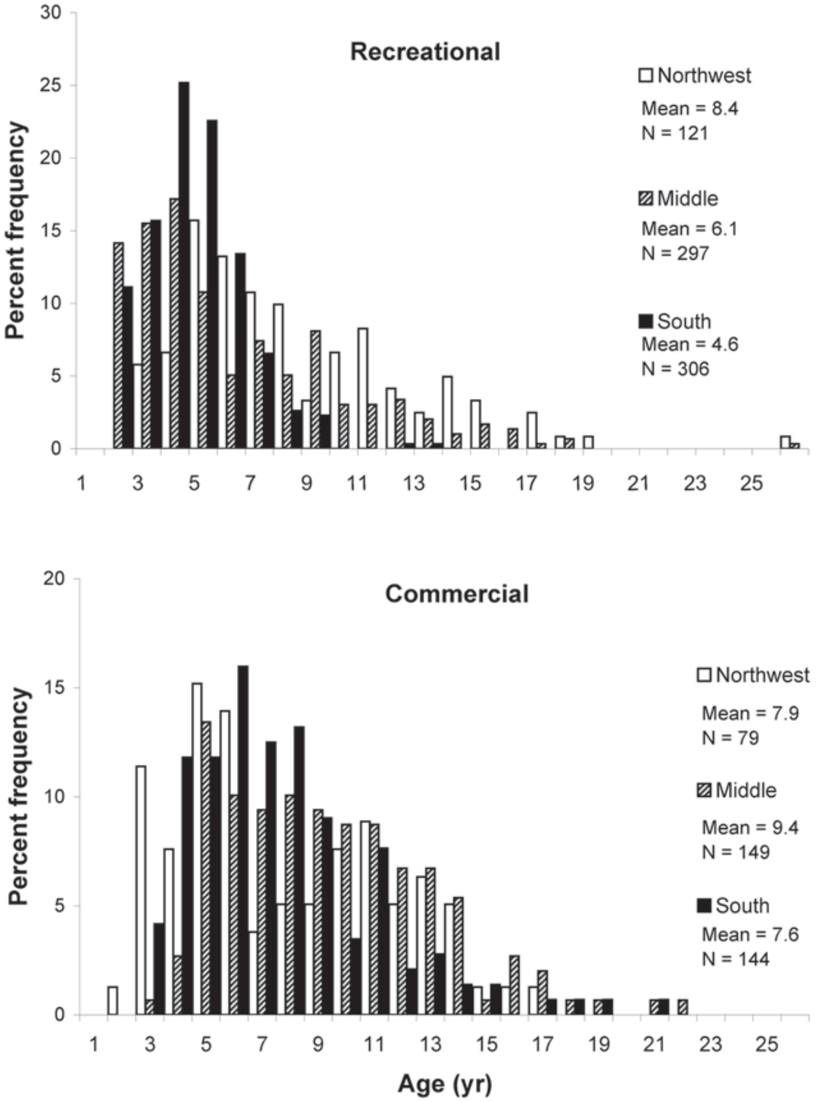

Figure 4. Age frequency distribution of gray snapper (*Lutjanus griseus*) collected from the recreational and commercial fisheries along the west coast of Florida by region.

sex (P = 0.23) and no region and sex interaction (P = 0.98). A Tukey's test revealed differences in mean age for the recreational and commercial fisheries by region for all regions with the exception of north and south in the commercial fishery. A KS test indicated significant differences in age distributions among regions for all comparisons except middle vs north in the commercial fishery (P = 0.74).

Growth.—Differences in size-at-age were noted by fishery and by region. Commercially caught red snapper were on average significantly larger at age than recreationally caught fish for ages 3–6 (ANOVA: age 3: $F_{1,115} = 38.69$, $P < 0.001$, age 4: $F_{1,160} = 42.08$, $P < 0.001$, age 5: $F_{1,166} = 24.48$, $P < 0.001$, age 6: $F_{1,119} = 7.25$, $P < 0.001$). Size-at-age was marginally different by region for age 5 ($F_{2,46} = 3.63$, $P = 0.034$) in the com-

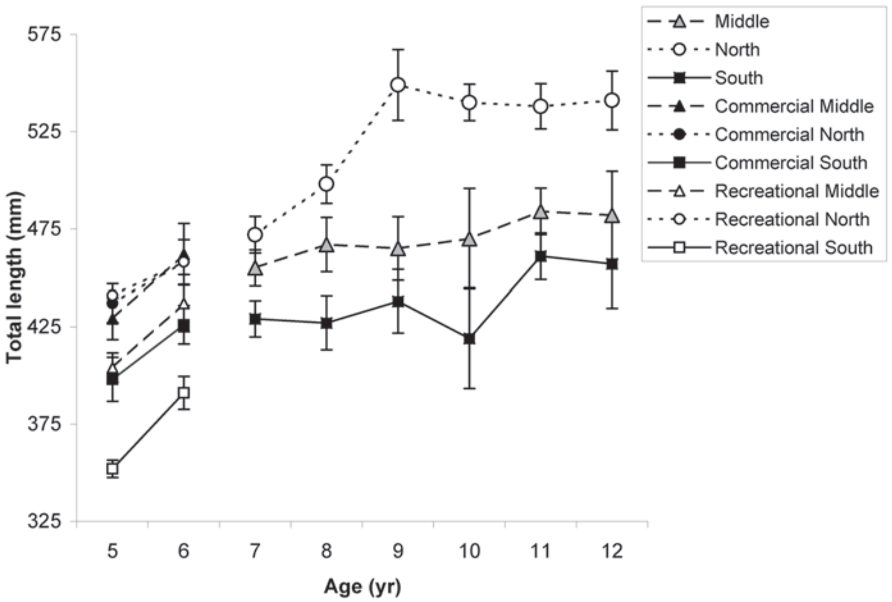

Figure 5. Mean size-at-age for common age classes of gray snapper (*Lutjanus griseus*) by fishery and region along the west coast of Florida. Fisheries were combined for ages 7–12. Bars are standard error of the mean (SE). All age classes had significantly different sizes by region with the exception of age 5 for the commercial fishery.

mercial fishery and different for ages 5 ($F_{2,116} = 47.42$, $P < 0.001$) and 6 ($F_{2,69} = 10.71$, $P < 0.001$) in the recreational fishery (Fig. 5). Regional comparisons within each fishery were not possible for ages less than 5 due to insufficient sample size. Since there was no difference in recreational and commercial samples for ages 7–12, these ages were combined to increase sample size. Mean size-at-age for the combined fisheries by age class (ages 7–12) were significantly different and decreased from north to south (ANOVA: age 7: $F_{2,128} = 4.60$, $P = 0.01$, age 8: $F_{2,106} = 9.29$, $P < 0.001$, age 9: $F_{2,109} = 12.01$, $P < 0.001$, age 10: $F_{2,69} = 10.95$, $P < 0.001$, age 11: $F_{2,85} = 10.30$, $P < 0.001$, age 12: $F_{2,66} = 4.82$, $P = 0.01$). Size differences increased with age and exceeded 100 mm between regions for some age classes (Fig. 5). Von Bertalanffy growth models for gray snapper from the WFS showed an increase in variation of size-at-age with age and there were few fish aged beyond 15 (Fig. 6). Von Bertalanffy growth parameters, both for models in which t_0 was unconstrained and in which it was constrained to 0, are shown in Table 1 by fishery, for both fisheries pooled, by sex for the recreational fishery and for sexes pooled. Too few observations were available to provide meaningful growth estimates within each fishery by region. Growth curves differed significantly between sexes, with a greater L_∞ for males ($\chi^2 = 402$, < 0.001).

Mortality.—The instantaneous total mortality rate (Z) for both fisheries combined was 0.22 (ages 5–22) and was 0.20 (ages 5–17) and 0.26 (ages 4–15) for commercial and recreational fisheries, respectively (Table 2). Mortality rates (Z) were not significantly different between fisheries (ANCOVA: $F_{1,20} = 0.06$, $P = 0.81$), however there were regional differences. Mortality (Z) increased from north to south and was significantly different between regions (Homogeneity of slopes test: $F_{2,27} = 13.22$, P

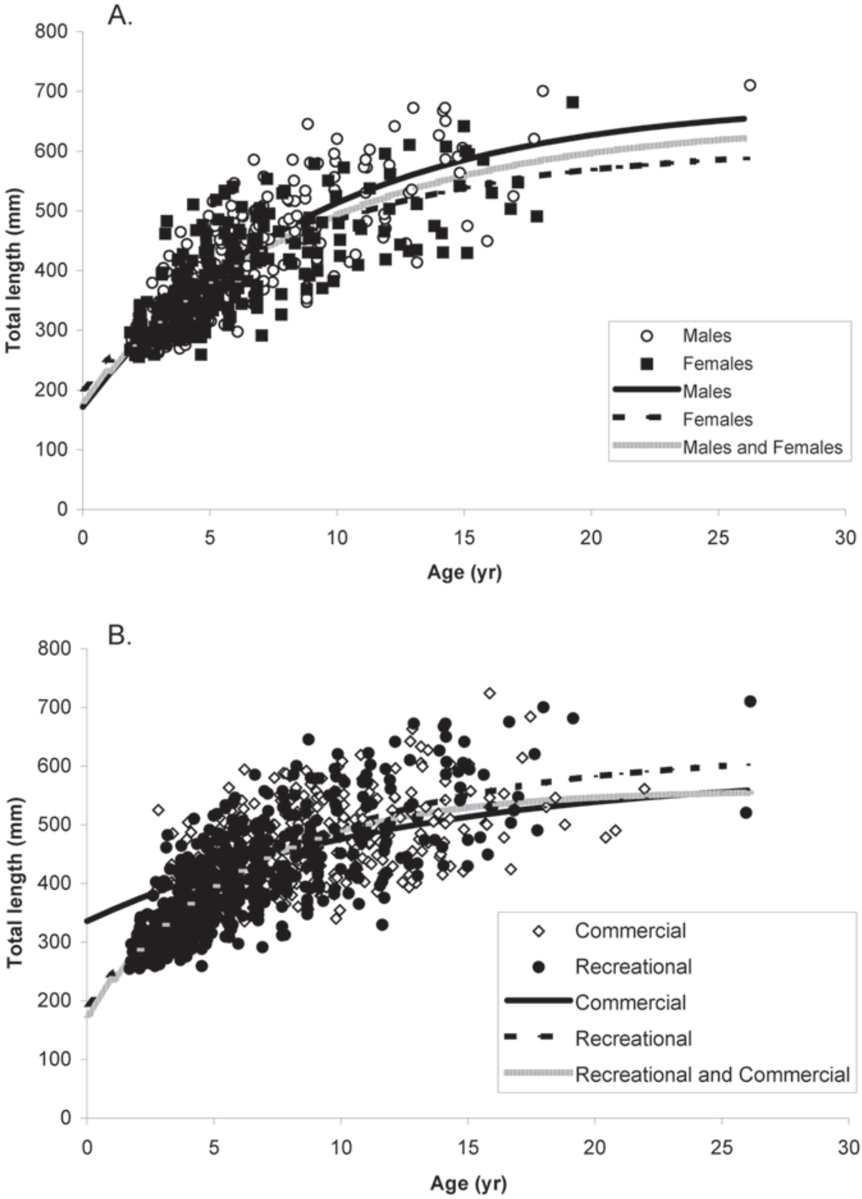

Figure 6. Observed total length (mm) at age and von Bertalanffy growth functions fitted to Florida west coast gray snapper (*Lutjanus griseus*) data for (A) the recreational fishery, by sex and for sexes combined, and (B) the recreational and commercial fisheries and both fisheries combined.

< 0.001; Middle and North $F_{1,20} = 5.27$, $P = 0.03$; Middle and South $F_{1,18} = 13.04$, $P = 0.002$; North and South= $F_{1,16} = 20.33$, $P < 0.001$) .

Instantaneous natural mortality (M) estimates varied greatly by the method used. Hoenig's (1983) estimate of M using a maximum age of 26 yrs was (0.17). The Ralston (1987) estimate was highest at 0.36 and the Pauly (1980) estimate intermediate at 0.24. Using Hoenig's (1983) M, our overall estimate of fishing mortality (F) was 0.05.

Table 1. Von Bertalanffy growth equation parameters for gray snapper (*Lutjanus griseus*) with t_0 unconstrained and constrained to 0 from this study and results from other studies.

Study and location	N	Maximum age (yrs)	L_∞ (mm)	k	t_0
1. Current: WFS					
Recreational (males, females and unknown)	724	26	621	0.12	–3.14
			509	0.31	0
Commercial (males, females and unknown)	372	22	590	0.08	–10.51
			493	0.41	0
Pooled (recreational and commercial)	1,096	26	559	0.17	–2.23
			506	0.33	0
Recreational (males)	286	26	683	0.11	–2.63
			557	0.26	0
Recreational (females)	297	19	605	0.12	–3.40
			497	0.31	0
Recreational (males and females)	583	26	648	0.11	–3.00
			528	0.28	0
2. Fischer et al. (2005): Louisiana					
Recreational (males and females)	833	28	656	0.22	0
Males	441	28	655	0.23	0
Females	387	28	657	0.21	0
3. Burton (2001): Florida east coast					
Recreational and commercial north Florida	528	24	717	0.17	–0.03
Recreational and commercial south Florida	729	13	625	0.13	–1.33
4. Johnson et al. (1994): Atlantic and Gulf of Mexico					
Recreational and commercial	432	25	792	0.08	–3.90
5. Claro (1983): SW Cuba					
Commercial	88	6	548	0.23	–1.06
6. Baez et al. (1980): Cuba					
Commercial	467	7	513	0.24	–0.62

Discussion

The maximum ages of 26 yrs from the recreational fishery and 22 yrs from the commercial fishery, fall within the range of those reported by Fischer et al. (2005) (28 yrs) and Johnson et al. (1994) (25 yrs) from the northern Gulf of Mexico and Burton (2001) (24 yrs) and Manooch and Matheson (1981) (21 yrs) from the northwestern Atlantic. Overall, average length and age were greater in the commercial fishery than in the recreational fishery, probably a result of differences in size limits (255 mm TL recreational vs 305 mm TL commercial), gear type used, and depths exploited by each fishery. The recreational fishery typically targets areas closer to shore than the commercial fishery. The similarity in size and age structure between recreational and commercial fisheries in the north was probably due to the nature of the recreational fishery, which, unlike in the middle and south regions, tends to be concentrated on offshore reefs. Overall, sex ratios were not significantly different from 1:1, consistent with the results of Fischer et al. (2005) from Louisiana.

Otolith-based ages have been validated in gray snapper using bomb radiocarbon analysis (Fischer et al., 2005), and the timing of opaque zone formation has been

Table 2. Total instantaneous mortality rates (*Z*) for gray snapper (*Lutjanus griseus*) by region along the west Florida Shelf.

Fishery	*Z*
Commercial	
North	0.11
Middle	0.08
South	0.14
All regions	0.20
Recreational	
North	0.14
Middle	0.23
South	0.55
All regions	0.26
Total	
North	0.14
Middle	0.23
South	0.36
All regions	0.22

reported using otolith margin analysis (Burton, 2001; Fischer et al., 2005, this study). Reader agreement was high (APE = 1.64%) and we considered an APE ≤ 5% acceptable for moderately long-lived species with relatively difficult to read otoliths (Morison et al., 1998; Campana, 2001). Examination of the percentage of otoliths with opaque margins from our study indicated that opaque increments were formed once annually during May to July. These results differed from those of Fischer et al. (2005) who suggested that increments were formed in the winter months. Possible reasons for this discrepancy could be geographic differences in the timing of opaque zone formation, or differences in reader interpretation of the otolith margin. In addition, Fischer et al. (2005) had few observations during January to March. Burton (2001) reported that annulus formation occurred during June or July for Atlantic gray snapper, similar to our findings.

We observed a decrease in mean size and age from north to south in the recreational fishery. Previous studies noted similar latitudinal differences. Gray snapper from northeast Florida were larger and older compared to southeast Florida; differences were attributed to greater fishing pressure in southeast Florida (Manooch and Matheson, 1981; Burton, 2001). Differences were not as obvious in the commercial fishery. Mean size decreased from north to south, but there was no difference in length distributions between middle and north regions and mean age was greatest in the middle region.

In recreational landings from Louisiana, 77% of male and 80% of female gray snapper were ≤ 10 yrs (Fischer et al., 2005), values similar to those we found in the north and middle regions of the WFS (72% and 86% ≤ 10 yrs, respectively). In contrast over 9% of gray snapper from the southern region were < 10 yrs. The commercial fishery was composed of slightly older fish than the recreational fishery in the middle and south regions: 71% in the north, 65% in the middle, and 84% in the south were ≤ 10 yrs. An earlier study from the Florida east coast recorded the youngest age structure (commercial and recreational combined) with 95% of fish ≤ 10 yrs (Burton, 2001).

In our study, gray snapper collected in the northern region were larger at age than those from the south. A similar geographic trend was noted off the east coast of Florida. Burton (2001) found that mean observed and back-calculated sizes-at-age were largest for gray snapper from north of 27.8°N latitude and found, as we did, that differences in size-at-age increased with age. Similarly, Johnson et al. (1994) found back-calculated size-at-age for ages 1–13 were larger from north than south of 27°N latitude (Gulf of Mexico and Atlantic combined). Increased fishing can enhance growth rates by decreasing intra-specific competition for food resources and can increase mortality and selectively remove the largest fish, thereby influencing growth patterns (Kritzer, 2002). Reduction in size-at-age has been attributed to increased fishing pressure in several other reef fish species (Buxton, 1993; Harris and McGovern, 1997; Zhao et al., 1997).

For t_0 restricted to 0, our L_∞ for the recreational fishery (509 mm) was smaller than that reported by Fischer et al. (2005) (656 mm) and k was larger (0.31 and 0.22, respectively). Overall, Fischer et al. (2005) sampled slightly larger, older individuals and this may explain the difference in the growth coefficients between the studies, given that k is strongly correlated with L_∞. Burton's (2001) growth curves using back-calculated lengths at age had higher L_∞ estimates for northeast and southeast Florida (717 and 625 mm, respectively), but growth coefficients similar to our combined recreational and commercial growth curve (0.17 and 0.13, respectively). Johnson et al. (1994) used back-calculated ages to estimate von Bertalanffy growth curves and estimated an L_∞ of 792 mm and reported the smallest k (0.08) which was the same as the k in our study for the commercial fishery. Báez et al. (1980) also used back-calculated ages to estimate an L_∞ of 513 and a k of 0.24 for commercial fish collected off Cuba compared to our L_∞ of 590 and k of 0.08 for the commercial fish and similar to the values recorded by Claro (1983) for gray snapper off SW Cuba (L_∞ = 548, k = 0.23). A likelihood ratio test indicated von Bertalanffy growth curves differed between sexes in our study as did growth curves for gray snapper off Louisiana (Fischer et al., 2005), but were not different for fish caught off Cuba (Báez et al., 1980).

Instantaneous mortality (Z) increased from north to south with the largest differences in the recreational fishery (0.14–0.55). This same latitudinal trend was noted off the east coast of Florida and was attributed to higher fishing pressure off southern Florida (Manooch and Matheson, 1981; Burton, 2001). Our estimate of Z for the recreational fishery on the norther WFS (0.14) was close to those reported by Fischer et al. (2005) for Louisiana (0.17–0.18). Our estimate of Z for all regions and fisheries combined (0.22) was slightly higher than the 0.18 reported by Johnson et al. (1994) for fish collected in the Gulf of Mexico and Atlantic, possibly reflecting increasing fishing pressure since the Johnson et al. (1994) study. In addition, estimates of Z from the Atlantic (Manooch and Matheson, 1981, Z = 0.39–0.60; Burton, 2001, Z = 0.34–0.95) were considerably higher than our overall estimates, suggesting greater fishing pressure on the east coast of Florida than on the west coast. Estimates of Z for the commercial fishery (0.08–0.14) were relatively low compared to those for the recreational fishery (0.14–0.55) and were fairly similar across regions despite greater landings in the south. In 2005, 52% of WFS gray snapper commercial landings were from the south, 29% from the middle and 19% from the north (Florida Fish and Wildlife Commission), suggesting that the commercial offshore population of gray snapper is less susceptible to overfishing than the more nearshore recreational fishery.

Our estimate of M using the Hoenig (1983) method (0.17) was similar to Fischer et al.'s (2005) for Louisiana (0.15) and Burton's (2001) for northeast Florida (0.18). The Ralston (1987) method yielded an M of 0.36, over two times that of the Hoenig (1983) estimate, and similar to the values reported by Fischer et al. (2005) for Louisiana (0.40) and Burton (2001) for northeast Florida (0.37). Our Pauly (1980) estimate (M = 0.24), however, was much lower than Fischer et al.'s (2005) (M = 0.51) and Burton's (2001) (M = 0.43 and 0.38). These differences were probably due to large differences in L_∞, a required parameter in the Pauly (1980) model. Hoenig's (1983) method appears to have provided the most realistic estimates of M for gray snapper. This value did not exceed any of the combined regional values of Z, our most robust measure of mortality, and Fischer et al. (2005) also concluded that Hoenig's (1983) estimate of M was probably the most appropriate for gray snapper collected off Louisiana. Our overall estimate of fishing mortality was higher (0.05) than that of Fischer et al. (2005) (0.02). Fischer et al. (2005) concluded that gray snapper were lightly fished off Louisiana. Regionally, Z was similar to M in the north also suggesting a low exploitation rate (Hoenig, 1983).

In summary, observed differences among regions in size and age distributions and in growth and mortality rates can probably be attributed to differences in exploitation rate. Gray snapper typically are not targeted in the northern region but are "by-catch" for fishers targeting other reef fish such as red snapper [*Lutjanus campechanus*, (Poey, 1860)]. In the more populous south Florida, gray snapper are a prized and often targeted recreational species (Manooch and Matheson, 1981; Burton, 2001). Additionally, sub-adult and young adult gray snapper are commonly associated with mangroves (Starck, 1971; Faunce et al., 2002; Faunce and Serafy, 2007), which occur only in the middle and southern regions of the WFS (Zieman and Zieman, 1989). Fishers targeting this inshore habitat would tend to land the youngest, smallest individuals which may partially account for regional differences in size and age distributions in the recreational fishery.

Gray snapper are managed as a single stock in the U.S. Gulf of Mexico by the Gulf of Mexico Fishery Management Council. Preliminary genetic evidence (Wallace et al., 2003) appeared to support this management strategy, although recent genetic work suggests three distinct groups (northwestern Gulf, north central and northeastern Gulf, and the east coast of Florida) (J. Gold, Texas A&M University, pers. comm.). The regional demographic differences we found suggest that gray snapper in the southwest Florida region have been undergoing heavier fishing pressure compared to areas to the north. Increased restrictions on dominant reef fish species in the north, such as red snapper, may also increase exploitation rates of gray snapper and put them at risk of overfishing.

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