# Regional size, age and growth differences of red grouper (*Epinephelus morio*) along the west coast of Florida

Linda Lombardi-Carlson [a,*], Gary Fitzhugh [a], Chris Palmer [a],
Chris Gardner [a], Robert Farsky [a], Mauricio Ortiz [b]

[a] *NOAA Fisheries Service, Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, FL 32408, USA*
[b] *NOAA Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149, USA*

## Abstract

Red grouper (*Epinephelus morio*) were collected from the west coast of Florida, the central area of fishery harvest in U.S. waters, by fishery-dependent sources during 2000–2005. The west Florida shelf was divided into two regions: north (capture locations $\geq 28°$N latitude) and south (capture locations $<28°$N latitude). Significant differences were found for age, length, and size-at-age by region and by gear; red grouper from the north were significantly younger and smaller on average than those from the south. Regional differences were also noted with respect to age progression; year class trends were only detected in the north. The 1996 year class dominated the landings in 2000–2001 (ages 4 and 5) and the 1999 year class dominated in 2004–2005 (ages 5 and 6). Regional data were fit to a size-modified von Bertalanffy growth model indicating smaller asymptotic length ($L_\infty$) and faster growth rate ($k$) in the north (north: $L_\infty = 800$ mm, $k = 0.23$ mm year$^{-1}$, $t_0 = 1.12$; south: $L_\infty = 863$ mm, $k = 0.15$ mm year$^{-1}$, $t_0 = 0.05$). Mortality estimates derived from catch curves resulted in higher total and fishing mortality in the north for both gears. Alternative explanations of regional differences likely depend on nursery delineation and correlation to periodic environmental events such as red tides and hurricanes; all possibly important factors based upon anecdotal information. Nevertheless, our finding of regional demographic differences in red grouper from the west coast of Florida suggests a more complex population spatial structure for red grouper.
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*Keywords:* Red grouper; *Epinephelus morio*; Stock; Life history; Spatial and temporal scales

## 1. Introduction

Red grouper (*Epinephelus morio*) are widely distributed throughout the Gulf of Mexico, Caribbean, and U.S. South Atlantic waters. Recognized as one of the most valuable fishes, red grouper are a highly sought target species and adults have been fished from North Carolina to Brazil (Moe, 1969; Stiles and Burton, 1994). In U.S. Gulf waters, red grouper are classified as the major component (about 69%) of the shallow water grouper commercial fishery and are predominately harvested from the west Florida shelf in the northeastern Gulf (Schirripa et al., 1999). Although primarily fished along the inner to mid-continental shelf, the species ranges in depth from 2 to over 120 m (65 fm), mainly inhabiting reefs and hard bottom areas (Moe, 1969).

Because of red grouper's importance, it has received considerable research attention and basic information on life history and biology has been reported (Moe, 1969; Johnson and Collins, 1994; Burgos et al., 2007). However, the spatial scales relevant to the population dynamics of red grouper have not been explored. It is increasingly being realized that matching spatial scale to population attributes is important for understanding the underlying ecological processes that give rise to those attributes (Ray and Hastings, 1996; Sale, 1998). This change in focus, to more spatially structured information is especially needed for reef fishes that have affinities for patchy habitats and often show high degrees of site fidelity during some phase of their life span (Sale, 1998; Gust, 2004). However, if life history and demographic information, assumed to be homogenous over large "basin-wide" spatial scales, vary at smaller spatial scales, management objectives may be difficult to achieve (McIntyre and Hutchings, 2003; Gust, 2004).

To date, red grouper have been treated as a single stock in U.S. Gulf of Mexico waters for assessment and management

* Corresponding author. Tel.: +1 850 234 6541x213; fax: +1 850 235 3559.
*E-mail address:* Linda.Lombardi@noaa.gov (L. Lombardi-Carlson).

purposes (NMFS, 2002; SEDAR, 2006). Genetic studies have not revealed any separate population structure or reproductive isolation among Gulf collections of red grouper based upon mitochondrial DNA (Richardson and Gold, 1997) or microsatellite genetic markers (Zatcoff et al., 2004). Genetic homogeneity alone may not be adequate to ascribe red grouper to a single Gulf stock. Despite the lack of genetic differentiation, Zatcoff et al. (2004) suggested that red grouper might have distinct stock structures due to possible separated distributions and evidence of little movement (Moe, 1966, 1972). Spatial distribution, demography and life history differences can often be an indication of stock structure even when evidence for genetic discrimination is lacking (Begg and Waldman, 1999; Dudgeon et al., 2000), as shown for red snapper (*Lutjanus campechanus*) in the Gulf of Mexico (Fischer et al., 2004).

The concept of managing separate stocks within a geographical area is new for fisheries in southeastern United States, but differentiation of stocks by statistical areas are and have been conducted in the Northwest Atlantic since the 1930s for multiple species (National American Council on Fishery Investigations currently the Northwest Atlantic Fisheries Organization). However, the rationalization of said areas were based on multiple factors; biological, stock structure, species distribution, oceanographic, submarine topography, administrative boundaries, the practicalities of data collection and the ability to regulate the fisheries (Halliday and Pinhorn, 1990). Ultimately for management regulation, it would be necessary to provide evidence that stocks from separate areas were insufficiently mixing and differences in age, growth, and maturity were consistent over time (e.g., Atlantic cod from the Gulf of St. Lawrence to the Georges Bank; McIntyre and Hutchings, 2003).

Accordingly, it was our objective to examine region-specific size, age and growth information for red grouper sampled from the west Florida shelf. We specifically desired to test whether demographic traits in size and age were uniform across the U.S. Gulf fishery for red grouper during the study period.

## 2. Materials and methods

### 2.1. Region identification and data collection

The present analysis is based on red grouper otoliths collected from commercial catches from the two primary gears (hand-line and long-line) used along the west Florida fishery during 2000–2005. These years were selected because they provide an increased and better balanced sample representation among gears and regions although, our records of red grouper age-structure sampling extend as far back as 1991 (Lombardi-Carlson et al., 2006). Measurements of fish lengths (fork or total length, to 1.0 mm), weights (whole or gutted, to 0.1 kg), and removal of otoliths were completed in the field. Information describing catch location (latitude, longitude, depth, or NMFS statistical shrimp grid) was reported with the otolith samples during routine Trip Interview Program (TIP) intercepts of commercial vessels and/or fish houses.

The west Florida shelf encompasses the area from Cape Sable to Cape San Blas within the eastern Gulf of Mexico (Smith,

1976) and was divided into two regions: north and south of 28°N latitude (just north of Tampa Bay, Fig. 1). The coastline of the west Florida shelf represents a shift from southern semi-tropical to northern temperate climate. The shelf is broad with the largest distance from the shoreline to the outer margins occurring below the 28° latitude. North of 28° the shelf has a low gradient with high density seagrass beds within 50 km and sparse seagrass beds extending as far as 100 km offshore (Moe, 1963; Zieman and Zieman, 1989). Furthermore, the northern offshore waters of the west Florida shelf are influenced by different levels of temperature, salinity, and sediment due to the climate, river discharge, and circulation patterns compared to the southern region (Zieman and Zieman, 1989; Wiseman and Sturges, 1999). Detailed information on capture locations was rarely available from port collections, but fish could clearly be identified as being harvested north or south of 28°N latitude based on port agent interviews of fishers. Fishers were more likely to divulge the direction, number of hours and/or number of nautical miles from port than specific capture locations of the catch. In addition to providing a north–south delineation along an environmental gradient, this latitude also offers a practical grouping of our data as it divides the spatial range of the west Florida fishery nearly in half (Schirripa et al., 1999; G. Davenport, personal communication, NMFS/SEFSC Miami).

### 2.2. Determining age

The sagittal otolith was used as the ageing structure (Moe, 1969). Red grouper ages were successfully read from both whole and sectioned otoliths (Johnson and Collins, 1994). Opaque bands were counted from the area just dorsal to a ridge formed by the sulcus acousticus; an area consistently used to obtain and combine accurate readings from both whole and sectioned otoliths. No meristic information was available to the readers during age estimation from otoliths.

Whole otoliths were submerged in water in a black watch glass, placed concave side up, and viewed through a stereomicroscope with the aid of reflected light from a fiber optic light source. Whole otoliths were manipulated with forceps to acquire a flat surface to age. This was helpful when bands were close together and in determining edge type. Each opaque band equated to one year of growth (annulus; Moe, 1969; Johnson and Collins, 1994; Stiles and Burton, 1994; Burgos et al., 2007). Edge types were recorded as opaque or translucent. If the otolith edge type was opaque, then the partially completed band was also counted as an annulus.

Whole otoliths that were judged by the readers to be difficult to interpret, either due to otolith thickness or to opacity, were sectioned using a Hillquist diamond-cutting saw (Cowan et al., 1995). Otolith sections were 0.7 mm in width. The sections were polished, sanded, and mounted on a slide. The number of opaque bands and the edge type were recorded.

Band count, edge type, and capture date were used to calculate the annual age of a fish based on a calendar year (Jearld, 1983). Otoliths were advanced one year in age if the outer translucent zone was complete by January 1 to June 30. For example, an otolith with two completed annuli and a large
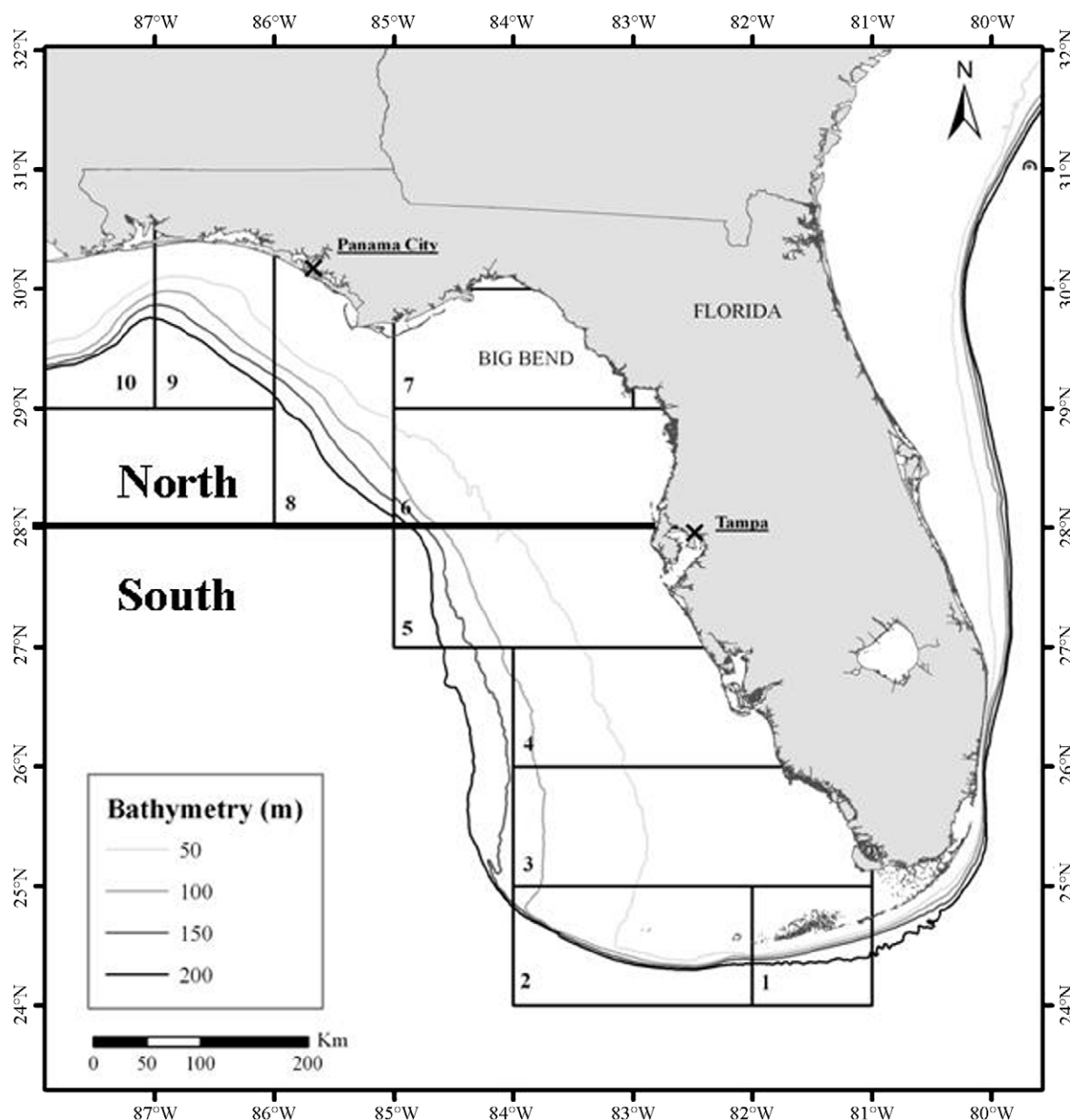
Fig. 1. Map of northeastern Gulf of Mexico, regions along the west Florida shelf separated at 28°N latitude, showing 50 m depth contours and NMFS statistical shrimp grids.

translucent zone would be classified as age 3 if the fish was caught during January–June in expectation that a 3rd annulus would have soon formed. For any fish caught during January–June with an opaque edge type, the calculated annual age was equal to the band count. After June 30, when opaque zone formation is underway or complete for red grouper in the Gulf of Mexico (Moe, 1969; Johnson et al., 1993), all fish were assigned an age equal to the band count by convention.

Four readers participated in ageing otoliths. A reference collection of red grouper otoliths was interpreted by each reader to calculate indices of precision. The reference collection consisted of otoliths ($n = 240$) collected throughout the year, incorporating a large range of lengths (354–863 mm total length), and representing a combination of easy and difficult otoliths (whole and sectioned) for interpretation (Campana, 2001). Three indices of ageing error were calculated for all otoliths read by all readers: (1) Average Percent Error (APE), (2) coefficient of variation, and (3) percent of readings in agreement within $\pm 1$ or $\pm 2$ band counts (Beamish and Fournier, 1981; Chang, 1982).

In addition to annual or cohort age, fractional age was determined for use in growth analysis. A fractional period of a year was determined as the difference between the peak spawning date and capture date (red grouper peak spawning is defined as May 15; Moe, 1969; Collins et al., 2002). If capture date was later in the year than peak spawning date, the fractional period was added to annual age. If capture date preceded the peak spawning date, then the fractional period was subtracted from annual age.

## 2.3. Age and growth contrast

Observed size and age data from fishery-dependent sources were compared using a single-factor, analysis of variance to test for the effect of regional and/or gear (Zar, 1999). If significant differences were determined through the single-factor-ANOVA of region and gear, then two-factor, fixed-effects analysis of variance (ANOVA) was used to test for the interactions of region and gear. Age and length frequencies were compared among gears (years combined) and among years (gears combined) to detect any apparent trends in age structure for the sampling period.
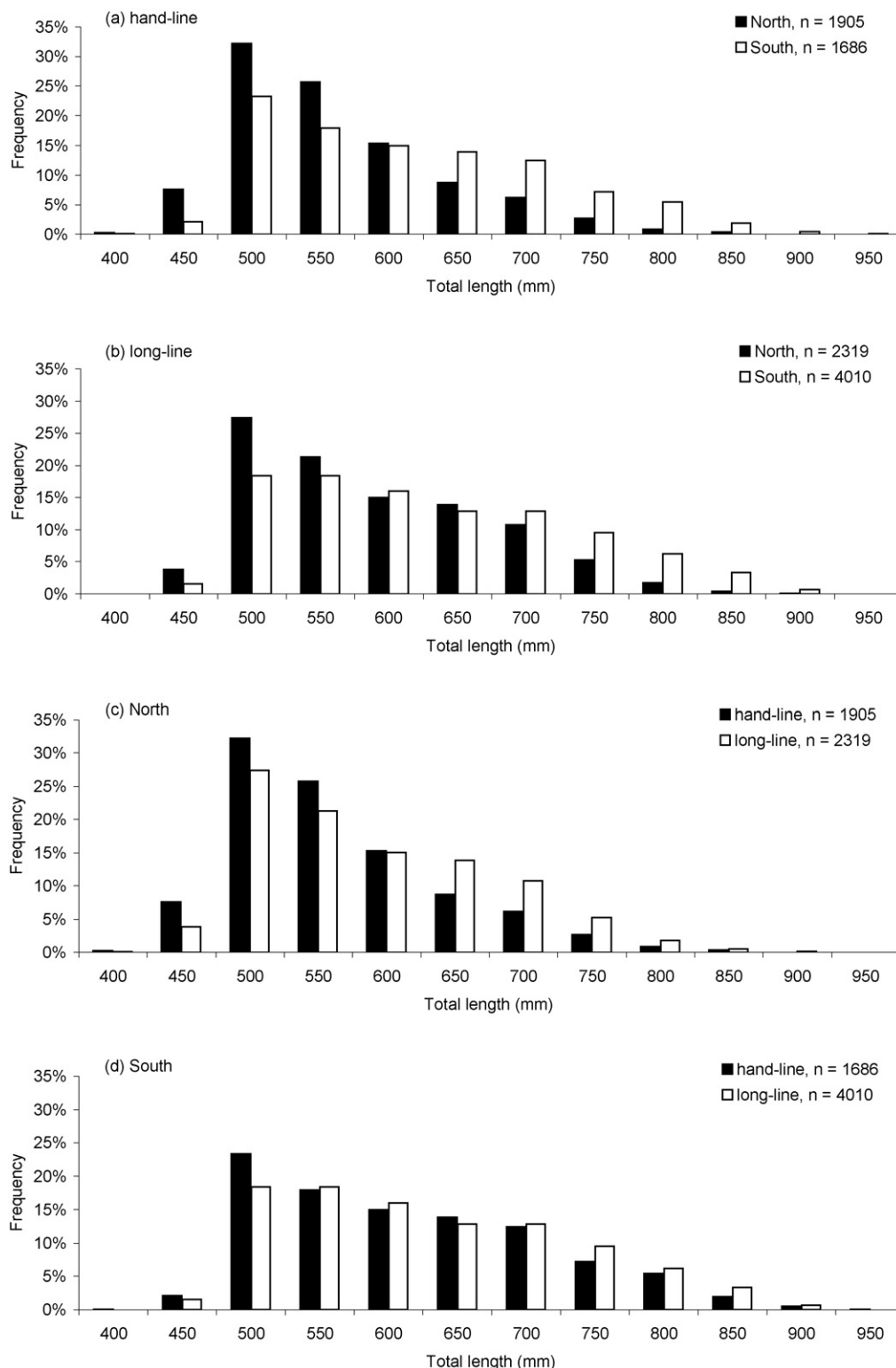


Fig. 2. Length–frequency histograms of red grouper by (a) hand-line and (b) long-line by region, (c) north and (d) south by gear.

Table 1

Results of two-way ANOVA comparing red grouper (*Epinephelus morio*) total length and age data by region (north and south of 28° latitude along the west Florida shelf) and gear (hand-line and long-line)

| Source | Total length | | | | | Age | | | |
|---|---|---|---|---|---|---|---|---|---|
| | d.f. | SS | MS | $F$ | $P$ | SS | MS | $F$ | $P$ |
| Gear | 1 | 963,997 | 963,997 | 107.43 | <0.0001 | 923 | 923 | 107.13 | <0.0001 |
| Region | 1 | 5,332,531 | 5,332,531 | 594.27 | <0.0001 | 11,219 | 11,219 | 1302.57 | <0.0001 |
| Gear × region | 1 | 63,228 | 63,228 | 7.05 | 0.008 | 0.021 | 0.021 | 0.0024 | 0.96 |
| Residuals | 9916 | 88,978,204 | 8,973 | | | 9916 | 85,407 | 9 | |

Growth curves, based on fractional ages and observed total lengths at capture, were modeled through two growth models, a size-modified von Bertalanffy growth function (Diaz et al., 2004) and a standard von Bertalanffy growth function (Haddon, 2001). Both models were fit by minimizing the least squares and by minimizing the log-likelihood with a global variable for standard deviation using the Solver routine in Microsoft Excel. The size-modified growth model was additionally fit by taking into consideration the non-random sampling due to minimum size restrictions (Diaz et al., 2004). This model uses a maximum likelihood estimation (MLE) procedure that assumes constant standard deviations of size-at-age and a left-normal truncated error distribution (as the minimum size limit, 508 mm TL). Regional size-modified growth curves were compared using a likelihood ratio test for coincident curves (Kimura, 1980; Haddon, 2001).

Observed mean lengths at age data were also compared by gear for selected age classes between regions using an unpaired Student's *t*-test with unequal variances. The region by gear comparisons of size at age data were restricted to age classes with sample sizes ≥10.

### 2.4. Mortality

Natural mortality (*M*) was estimated by region and by gear using Hoenig (1983) regression model for teleosts:

$$\ln(M) = 1.46 - 1.01 \ln(t_{max})$$

where $t_{max}$ refers to the maximum aged fish. This regression is the recommended model for estimating natural mortality over the rule-of-thumb approach (Hewitt and Hoenig, 2005). Esti-mates of instantaneous total mortality (*Z*) were calculated using catch curve analysis by region and by gear.

### 3. Results

Port agents collected 10,025 otolith samples directly from the commercially landed catch (hand-line 3625, long-line 6400); 4275 samples from the north and 5750 from the south. A major-ity (85%) of the otoliths were read whole (whole, $n = 8560$; sectioned, $n = 1465$). The decision of whether or not to sec-tion an otolith depends on the individual clarity of the otolith surface not a particular fish length or otolith weight, whole and sectioned otoliths were from similar size fish (whole, size range: 372–956 mm, mean ± S.E., 613 ± 7 mm; sectioned, size range: 475–956 mm, 702 ± 18 mm). Otoliths judged unreadable ($n = 105$) were removed from further analysis. The APE among readers was 3.5%, the coefficient of variation was 4.28%, and the percentage of readings in agreement within ±1 band count was 82%, increasing to 89% within ±2 band counts.

Ages and total lengths differed significantly among regions and gears. Hand-line caught red grouper were signifi-cantly smaller (north, $F_{1,4222} = 107.28$, $P < 0.0001$; south, $F_{1,5694} = 27.97$, $P < 0.0001$) and younger (north, $F_{1,4222} = 80.00$, $P < 0.0001$; south, $F_{1,5694} = 44.85$, $P < 0.0001$) compared to long-line caught fish from each region. In the principal con-trast between regions, southern red grouper were significantly larger and older regardless of gear (Figs. 2 and 3). Mean lengths (±S.E.) were 635 ± 2.4 mm, 651 ± 1.6 mm for fish from the south and 585 ± 1.8 mm, 611 ± 1.8 mm for fish from the north, hand-line and long-line, respectively. Mean ages (±S.E.) were 8.5 ± 0.1 years, 9.1 ± 0.1 years for fish from the south and

Table 2

Growth curve parameters and associated residuals for fractional ages and observed total lengths at capture provided for a size-modified growth curve and a standard growth curve for red grouper from the west Florida shelf: 2000–2005

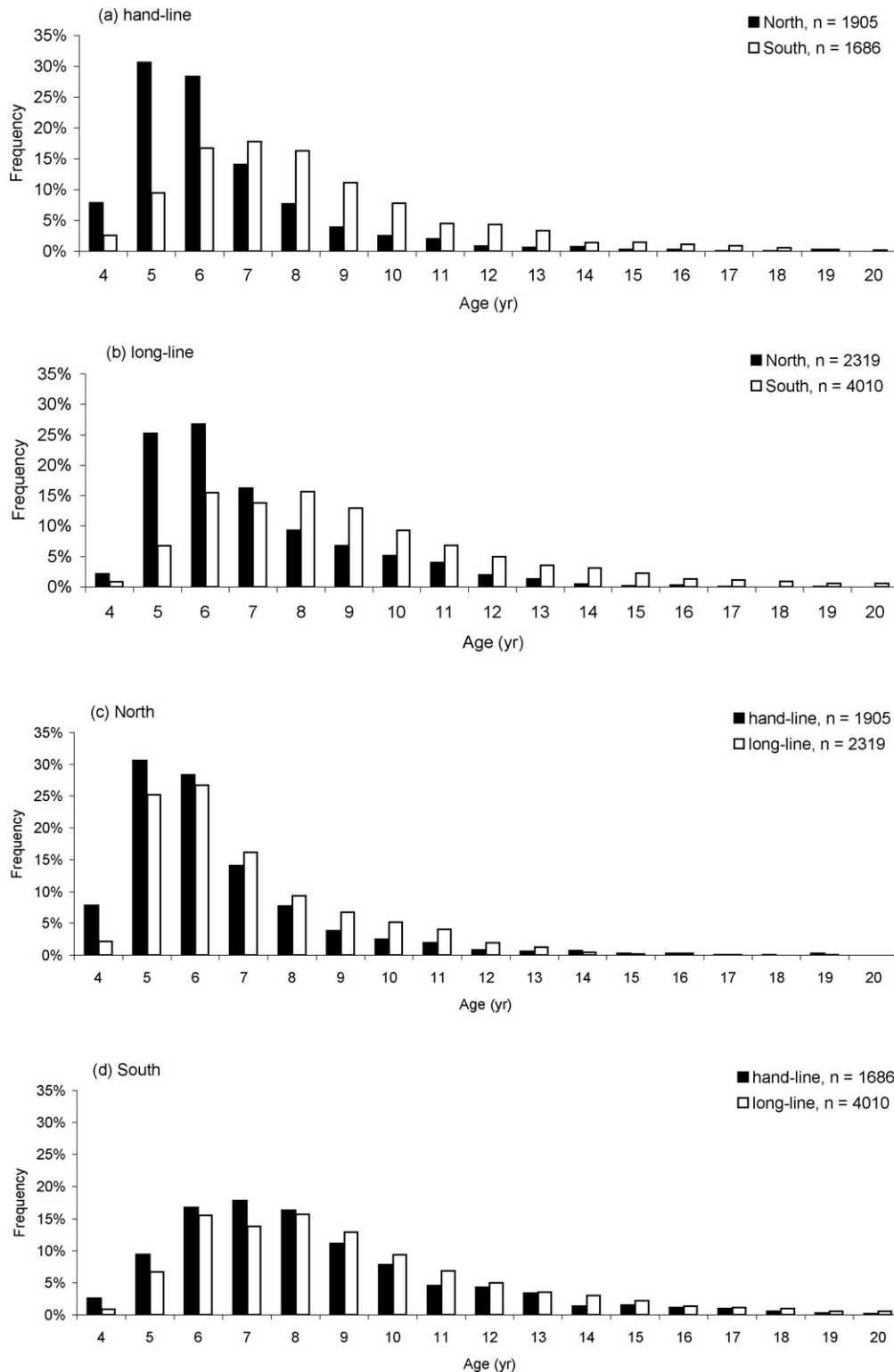| Model | $n$ | $L_\infty$ | $k$ | $t_0$ | Sum of squares | Standard deviation | Log-likelihood |
|---|---|---|---|---|---|---|---|
| All data | | | | | | | |
| Size-modified | 9920 | 848 | 0.17 | 0.32 | $5.1 \times 10^7$ | 88.09 | $5.1 \times 10^4$ |
| Standard | 9920 | 960 | 0.08 | −6.09 | $5.2 \times 10^7$ | 71.28 | $5.7 \times 10^4$ |
| North | | | | | | | |
| Size-modified | 4224 | 800 | 0.23 | 1.12 | $1.5 \times 10^7$ | 74.67 | $2.0 \times 10^4$ |
| Standard | 4224 | 916 | 0.10 | −4.07 | $1.5 \times 10^7$ | 59.40 | $2.3 \times 10^4$ |
| South | | | | | | | |
| Size-modified | 5696 | 863 | 0.15 | 0.05 | $3.5 \times 10^7$ | 94.61 | $3.2 \times 10^4$ |
| Standard | 5696 | 1097 | 0.05 | −9.40 | $3.5 \times 10^7$ | 78.94 | $3.3 \times 10^4$ |

Fig. 3. Age–frequency histograms of red grouper by (a) hand-line and (b) long-line by region, (c) north and (d) south by gear.

$6.4 \pm 0.1$ years, $7.1 \pm 0.1$ years for fish from the north, hand-line and long-line, respectively. There was also a significant interaction in lengths between gears and regions (Table 1) indicating that differences in lengths by gear were not independent of the region effect.

Age-structure differences were also evident between regions and gear types. The 1996 year class dominated the 2000–2002 catches as ages 4, 5, and 6, respectively, only in the northern age structure in both gears (Figs. 4 and 5). In 2001, the 1996 year class comprised half the northern hand-line (53%) and long-
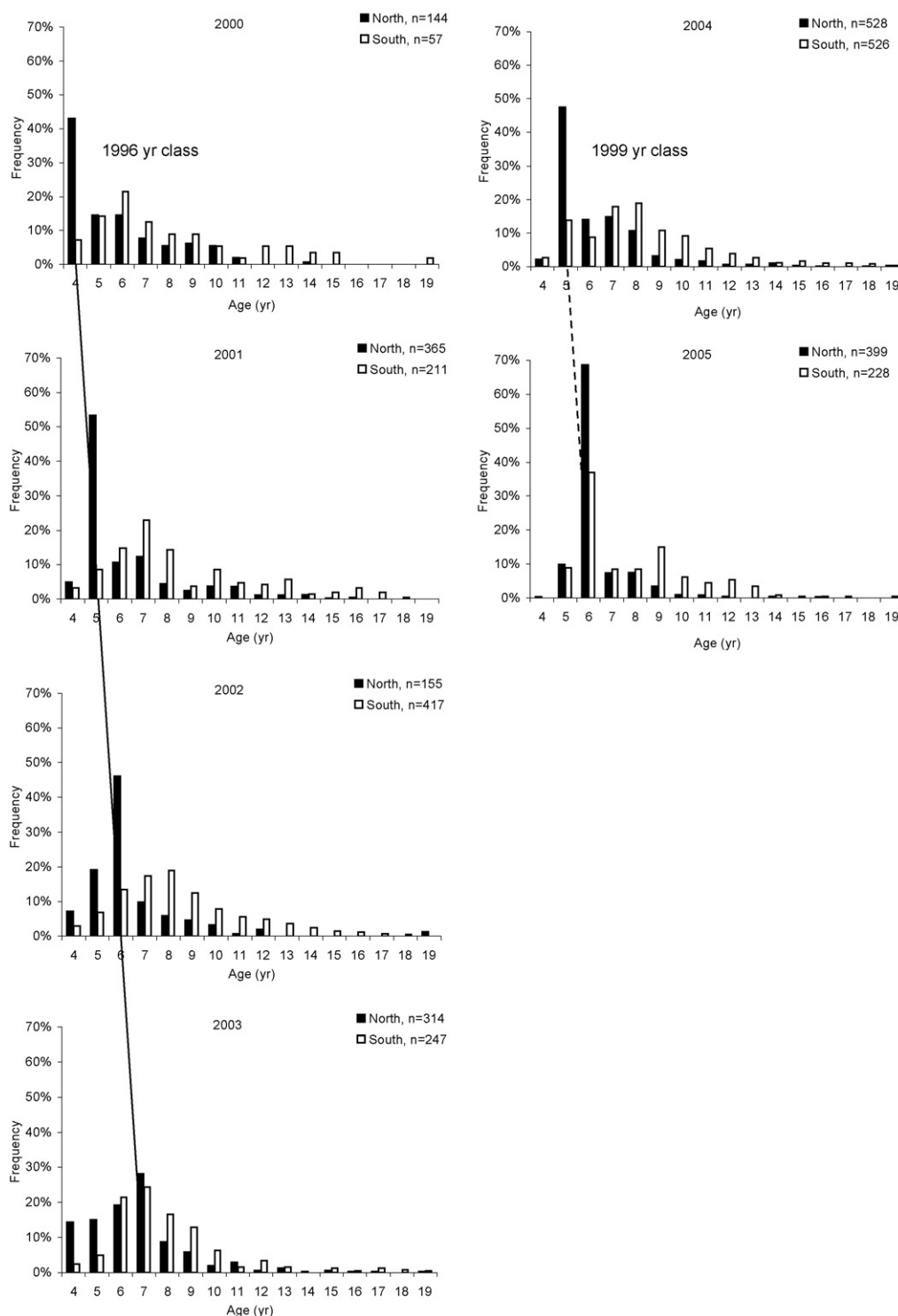
Fig. 4. Age distribution for commercial hand-line red grouper (2000–2005) by region. Lines depict strong year classes 1996 (solid) and 1999 (dashed).

line (47%) age structure, compared to only 9% of the southern age structure. The 1999 year class also dominated the northern age structure in 2004 and 2005 as ages 5 and 6, respectively, in both gears (Figs. 4 and 5). During 2005, the 1999 year class completely dominated the northern age structure, again in both gears (hand-line 69%, long-line 63%), with only 35% of the southern age structure (hand-line 37%, long-line 32%).

Red grouper fractional ages and observed total lengths (2000–2005) were fit to a size-modified von Bertalanffy growth model and a standard von Bertalanffy growth model to obtain population growth parameters (Table 2). The size-modified growth model and standard growth model were fit to all data combined and separate for each region. Red grouper showed similar standard deviation in size-at-age between the regions
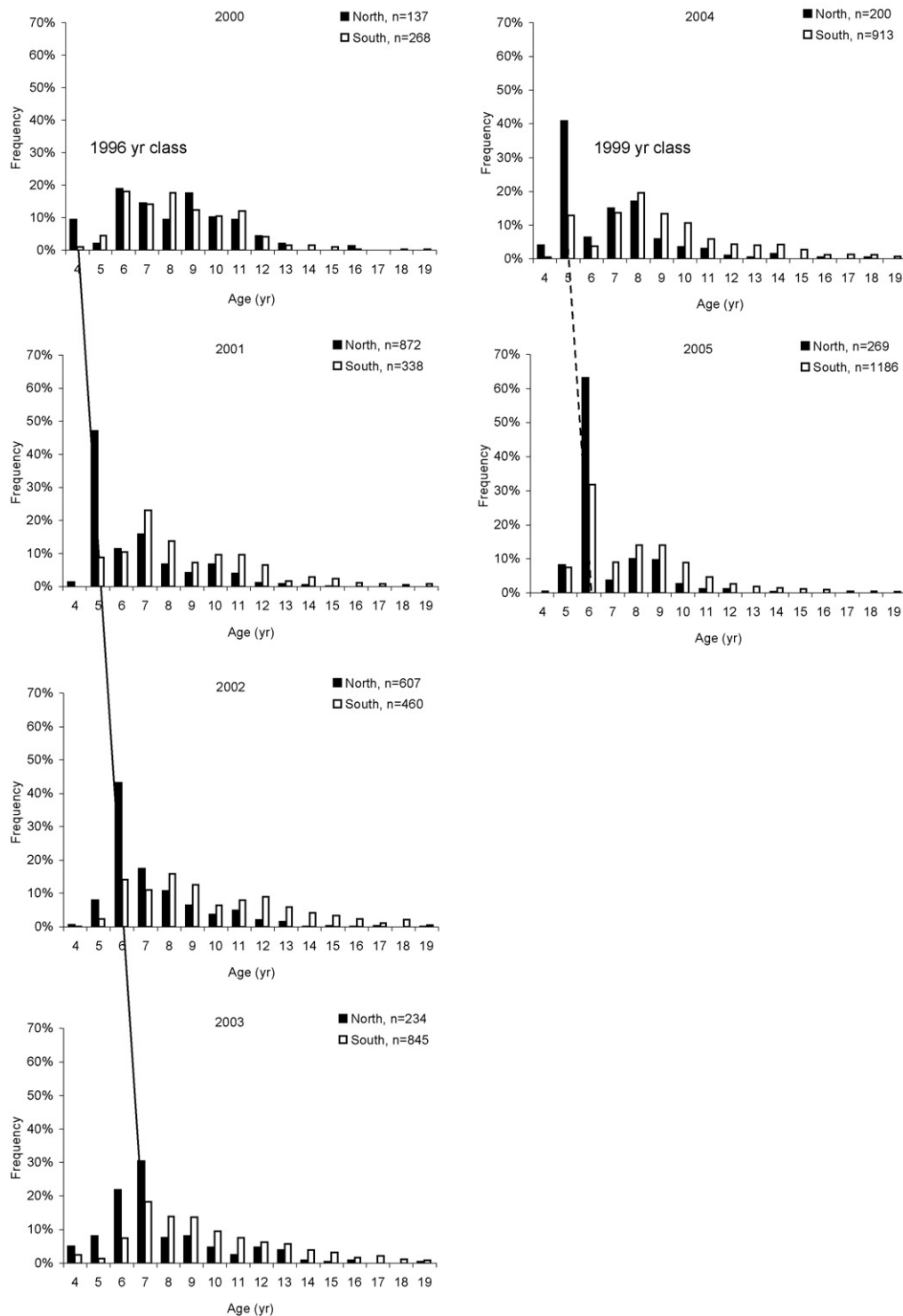
Fig. 5. Age distribution for commercial long-line red grouper (2000–2005) by region. Lines depict strong year classes 1996 (solid) and 1999 (dashed).

until age 9 (Fig. 6). Region-specific size-modified growth models revealed smaller log-likelihoods compared to the model fit to all data (Table 2). The size-modified growth model predicted faster growth in the north (north: $k = 0.23$ mm year$^{-1}$, south: $k = 0.15$ mm year$^{-1}$) but larger asymptotic size in the south (north: $L_\infty = 800$ mm, south: $L_\infty = 863$ mm; Table 2; Fig. 7). The size-modified von Bertalanffy growth parameters were deter-

mined to be significantly different between regions (likelihood ratio test $= 2.0 \times 10^3$, $P < 0.001$). The model showed large positive and negative residuals, with the residual distribution slightly skewed to the positive and plots of residuals by age did show some bias for all data combined and for each region, more than likely the affect of fishery-dependent data. The standard von Bertalanffy growth model fits were biased and unrealistic,
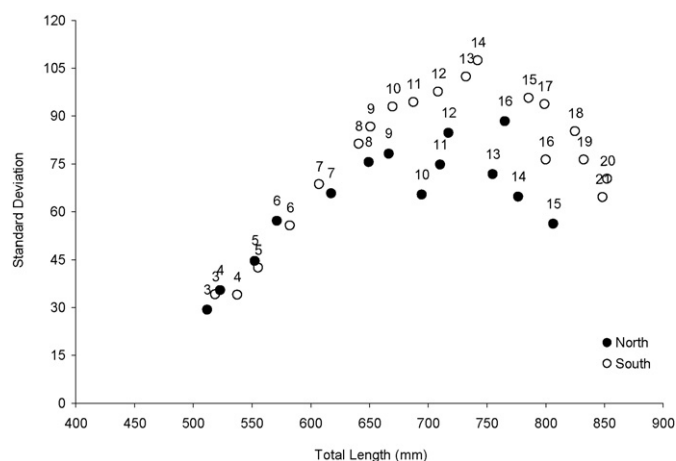
Fig. 6. Standard deviation of lengths at age by region (north, solid circle; south, open circle) for red grouper caught in the commercial fisheries: 2000–2005. Data points labeled by age.
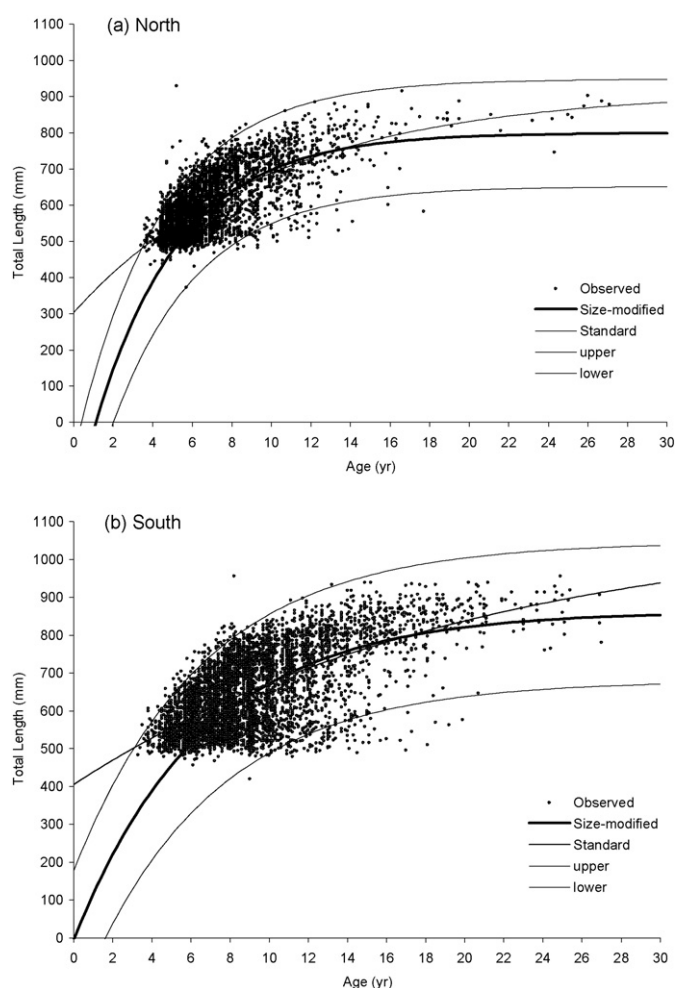


Fig. 7. von Bertalanffy growth curves for mean fractional ages 3–27 by region (a) north and (b) south for red grouper caught in the commercial fisheries: 2000–2005. Observed size-at-age (circles), size-modified estimated size-at-age (bold line), size-modified estimated 95% confidence intervals (dotted lines), and standard estimated size-at-age (thin line).

Table 3
Regional comparisons (north to south) of long-line caught red grouper observed size- at-age data and results of paired *t*-tests

| Age class | Region | $n$ | Mean ± S.E. | $t$ | d.f. |
|---|---|---|---|---|---|
| 4 | N | 49 | 526 ± 5 | −1.34[NS] | 77.04 |
|  | S | 34 | 536 ± 5 |  |  |
| 5 | N | 583 | 555 ± 2 | −1.22[NS] | 539.44 |
|  | S | 267 | 559 ± 3 |  |  |
| 6 | N | 618 | 574 ± 2 | 3.89 | 1222.09 |
|  | S | 616 | 587 ± 2 |  |  |
| 7 | N | 374 | 622 ± 4 | 3.00 | 818.66 |
|  | S | 548 | 608 ± 3 |  |  |
| 8 | N | 215 | 656 ± 5 | 1.75[NS] | 398.24 |
|  | S | 622 | 645 ± 3 |  |  |
| 9 | N | 156 | 676 ± 6 | 3.77[***] | 288.62 |
|  | S | 514 | 650 ± 4 |  |  |
| 10 | N | 120 | 695 ± 6 | 3.75[***] | 289.83 |
|  | S | 370 | 666 ± 5 |  |  |
| 11 | N | 93 | 720 ± 7 | 3.76[***] | 224.26 |
|  | S | 271 | 685 ± 6 |  |  |
| 12 | N | 45 | 715 ± 13 | 0.68[NS] | 73.79 |
|  | S | 198 | 705 ± 7 |  |  |
| 13 | N | 30 | 761 ± 13 | 1.80[NS] | 56.73 |
|  | S | 143 | 733 ± 9 |  |  |
| 14 | N | 11 | 780 ± 25 | 1.53[NS] | 13.49 |
|  | S | 122 | 739 ± 10 |  |  |

Significant levels for pair-wise comparisons as determined by *t*-test, [NS]not significant; [*]$P<0.05$, [**]$P<0.01$, [***]$P<0.001$.

predicting an overestimated asymptotic lengths, underestimated growth coefficients and large negative lengths at time zero for all data combined and by region separately (Table 2; Fig. 7).

Size-at-age plots for commercial samples revealed larger mean size-at-age for red grouper from the north caught by long-line gear (Table 3; Fig. 8). Red grouper were significantly larger beginning at age 6 and remained larger until age 11 in the long-line fishery. Similar size-at-age red grouper were caught by the hand-line fishery in both regions, except for size-at-age 4 (Table 4; Fig. 8). In the south, few young (ages 1–4) red grouper were caught by either gear type (<10% of the age structure, Figs. 4 and 5).

Maximum longevity was equivalent between the regions with a red grouper of 27 years caught in both regions. Since natural mortality was based on the maximum aged fish, a value of $M = 0.15$ was applied to both regions. Total mortality estimates ($Z$) assuming full selection to the fishery by age 6 and extending to age 19 (excluding 7 ages groups; north, $n = 11$; south, $n = 75$) indicated higher total mortality in the north (north $Z = 0.47$; south, $Z = 0.28$; Table 5). Gear specific catch curves (also based on ages 6–19 years) determined higher total mortality in the north for both gears (hand-line, $Z = 0.39$; long-line, $Z = 0.48$; Table 5; Fig. 9). Fishing mortality was estimated to be higher in the north ($F = 0.32$) compared to the south ($F = 0.13$) for all data combined and by gear (hand-line, $F = 0.22$; long-line, $F = 0.33$) (Fig. 9).
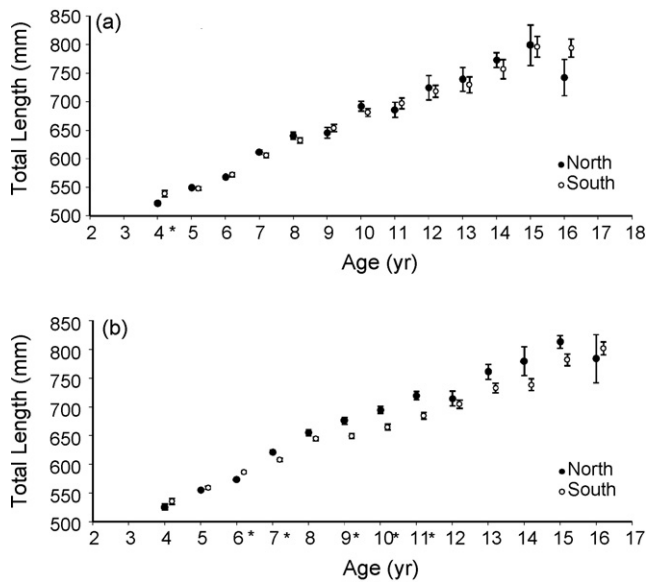
Fig. 8. Mean size-at-age plots of (a) hand-line and (b) long-line red grouper from two regions along the west Florida shelf. Only represents age classes with $n \geq 10$. The south data are slightly offset on the $x$-axis. Error bars reflect $\pm$ mean standard errors. *Significant differences in size-at-age as determined through $t$-test.

Table 4
Regional comparisons (north to south) of hand-line caught red grouper observed size-at-age data and results of paired $t$-tests

| Age class | Region | $n$ | Mean $\pm$ S.E. | $t$ | d.f. |
|---|---|---|---|---|---|
| 4 | N | 149 | 522 $\pm$ 3 | $-2.74$** | 66.51 |
|  | S | 43 | 539 $\pm$ 6 |  |  |
| 5 | N | 582 | 549 $\pm$ 2 | 0.27[NS] | 269.97 |
|  | S | 158 | 548 $\pm$ 3 |  |  |
| 6 | N | 538 | 568 $\pm$ 2 | $-1.12$[NS] | 534.61 |
|  | S | 279 | 572 $\pm$ 3 |  |  |
| 7 | N | 267 | 612 $\pm$ 4 | 1.07[NS] | 560.45 |
|  | S | 297 | 606 $\pm$ 4 |  |  |
| 8 | N | 146 | 641 $\pm$ 6 | 1.06[NS] | 313.02 |
|  | S | 271 | 633 $\pm$ 5 |  |  |
| 9 | N | 74 | 646 $\pm$ 9 | $-0.72$[NS] | 146.83 |
|  | S | 185 | 654 $\pm$ 7 |  |  |
| 10 | N | 48 | 693 $\pm$ 9 | 0.97[NS] | 110.82 |
|  | S | 130 | 682 $\pm$ 7 |  |  |
| 11 | N | 38 | 686 $\pm$ 13 | $-0.70$[NS] | 72.90 |
|  | S | 76 | 697 $\pm$ 9 |  |  |
| 12 | N | 15 | 725 $\pm$ 21 | 0.29[NS] | 21.45 |
|  | S | 72 | 719 $\pm$ 11 |  |  |
| 13 | N | 12 | 739 $\pm$ 21 | 0.38[NS] | 22.06 |
|  | S | 56 | 730 $\pm$ 14 |  |  |

Significant levels for pair-wise comparisons as determined by $t$-test, [NS] not significant; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

## 4. Discussion

Fishery-dependent analyses of size and age samples of red grouper revealed distinct regional differences within the U.S. fishery of the west Florida shelf. Smaller and younger fish
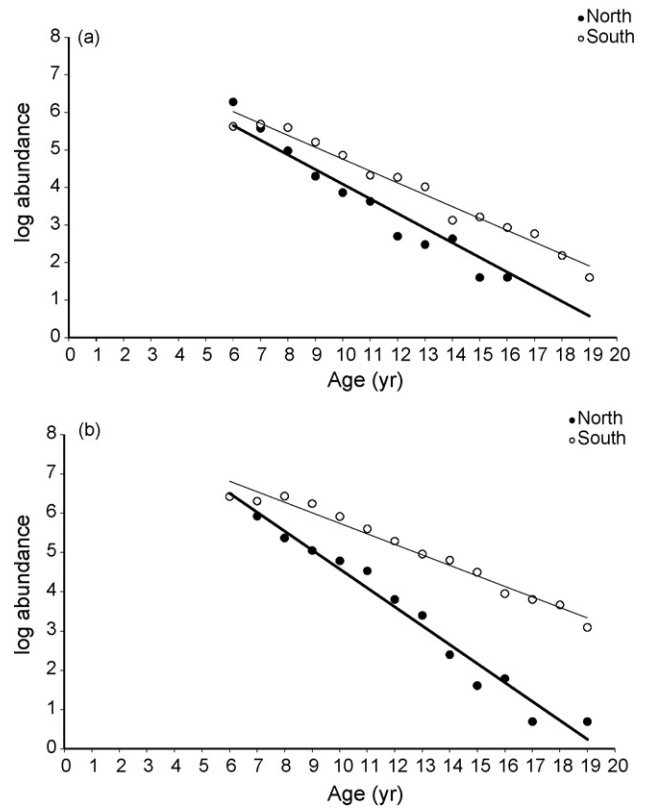


Fig. 9. Catch curves of (a) hand-line and (b) long-line commercially caught red grouper by region (2000–2005).

were more prevalent in the catch north of 28°N latitude during 2000–2005. Age-structure distributions were also different between regions with the 1996 and 1999 year classes being notably dominant in the north but not in the south. In addition, we found that regional growth curves were not similar and that growth rates among red grouper were significantly greater in the north. While it was beyond the scope of this study to test stock structuring mechanisms, there are several possible factors that may explain these regional differences. Fishery effects (amount of effort and/or gear selectivity), environmental effects, and particularly for reef fish, differential recruitment coupled with some degree of site fidelity, could all account for demographic differences arising across varied spatial scales (Begg, 2005).

Table 5
Estimates of mortality (natural, fishing, and total) by region and by gear

| Region | Gear | $M$ | $F$ | $Z$ |
|---|---|---|---|---|
| North | All data | 0.15 (27 years) | 0.32 | 0.47 |
|  | Hand-line | 0.17 (25 years) | 0.22 | 0.39 |
|  | Long-line | 0.15 (27 years) | 0.33 | 0.48 |
| South | All data | 0.15 (27 years) | 0.13 | 0.28 |
|  | Hand-line | 0.15 (27 years) | 0.17 | 0.32 |
|  | Long-line | 0.15 (27 years) | 0.11 | 0.27 |

Natural mortality ($M$) was calculated using Hoenig (1983) regression for teleosts based on the maximum aged fish (in parentheses). Total mortality ($Z$) was calculated using catch curves.
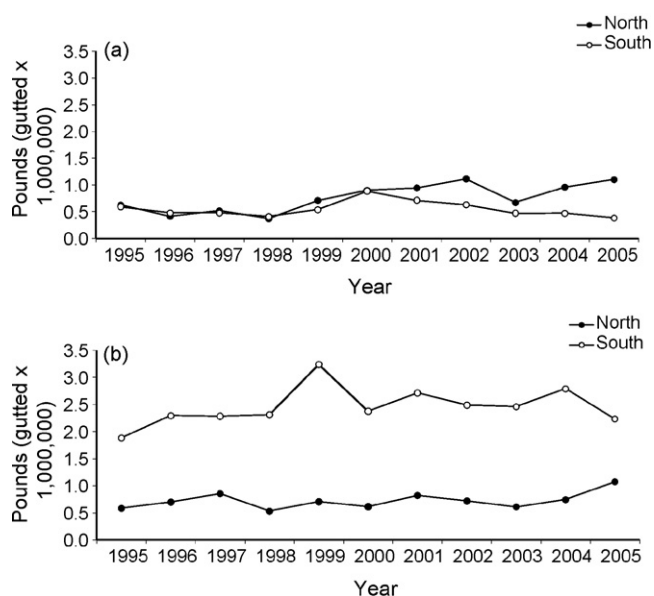
Fig. 10. Commercial landings (1995–2005) of red grouper from two regions (north and south) along the west Florida shelf by gear (a) hand-line and (b) long-line. Landings from SEDAR 12: Stock Assessment Report. Table 3 Section II (2006).

On initial examination, the demographic pattern described above suggests a region-specific fishery effect. Localized fishery effects have lead to differences in stock structure and life history traits among fish species over time (McIntyre and Hutchings, 2003). For example, it has been found that larger and older individuals can be selectively harvested leading to localized size truncation and compensatory responses among younger ages (Trippel, 1995; Law, 2000).

We expected the south to exhibit greater demographic effects due to fishing as we understand the southern region to experience higher fishing pressure. Early observations denoted the overall spatial extent of the northeastern Gulf "grouper grounds" (Adams and Kendall, 1889), and general trends such as increasing catch and effort occurred in the 1960s followed by catch declines in the 1970s and rough stabilization thereafter (Schirripa et al., 1999). Since 1986, more spatial catch information has become available as aggregated grouper landings became delineated by species. A majority of the U.S. red grouper have been harvested by the commercial industry west and south of Tampa, with the highest landings reported by longliners south of 28°N latitude (Fig. 10; SEDAR, 2006). Similar results were also reported for the recreational sector (SEDAR, 2006). Thus, if harvesting levels have affected the demographics of red grouper, then the southern region, accounting for larger percentage of landings, should be characterized by a more truncated size and age structure, unless the population size is much greater in the southern region.

The finding of faster growth in the north is consistent with the hypothesis of a countergradient variation in growth across the different regional temperature regimes. Countergradient variation is an adaptation to grow faster in areas characterized by colder temperatures and shorter growing seasons (Conover, 1990). Countergradient growth was also inferred from evidence

for grouper and shark species harvested along the west Florida shelf (Lombardi-Carlson et al., 2003; Strelcheck et al., 2003; Fitzhugh et al., 2003). However, countergradient variation in growth would not account for regional differences in age structure and size truncation and thus does not appear to be a sufficient explanation.

We considered whether our reliance on fishery-dependent data could be misleading us. Fishery-dependent data can be advantageous in that it is more generally available, inexpensive, and often routinely collected covering a broad geographic area (Begg, 2005), but there are a few caveats to its interpretation. First, fishery effects and gear selectivity challenge the assumption that samples are representative of the population (e.g., Begg, 1998) and we detected some size/age differences between hand-line and long-line gears that reflect differences in gear selection. Additionally, growth curve interpretation based upon fishery-dependent data bears caution due to size limits and rare observations at extremes of the size distribution (Haddon, 2001). To ameliorate our growth comparisons, we fit curves using a size-modified von Bertalanffy that accounts for the effect of the size limit. The model fits by region using a standard von Bertalanffy growth model fits were biased and unrealistic. Our use of a likelihood ratio test approach to compare growth curves also minimizes the tendency to misinterpret growth results (Cerrato, 1990). We also sought to minimize the possibility of misconstruing a temporal growth and age-structure pattern with a spatial pattern by drawing samples from 2000 to 2005 from both regions. There was a practical consideration for choosing samples from these six years because sufficient observations ($n > 100$) by gear and region were only available in this period. Thus, our interpretations are robust in reflecting regional demographic differences that existed during this time period.

To come up with satisfactory explanations of regional differences in recruitment, we needed to know more about red grouper nursery trends (recruitment sources) and the effects of ephemeral environmental influences; both may be important for structuring red grouper populations. If fishery and natural mortality effects can be excluded from consideration, age-structure differences are likely to arise from spatial differences in recruitment patterns. To detect these recruitment differences over the time required for red grouper to recruit to the fishery (a minimum of 3–5 years), regional or smaller scale site fidelity would have to be maintained. However, for red grouper, there is little information about either recruitment or age/size-specific site fidelity. What little is known from tagging studies is that red grouper probably maintain high site fidelity during their first few years and can make movements on the order of tens of miles upon reaching the age of maturity (~4–5 years). There is a general ontogenetic movement to deeper water over the life span (Moe, 1966, 1967, 1972; K. Burns, Mote Marine Laboratory, Sarasota, FL, USA, unpublished results). So at least during young ages, the information available suggests that movements may be restricted enough to maintain the spatial integrity of region-specific age structure if the age differences arise due to regional differences in recruitment. Red grouper are widely distributed over the west Florida shelf and many reef tracts and

hardbottom areas have been identified as productive for fishing (see Moe, 1963) however, little is known about the spatial location and extent of red grouper nursery areas (DeVries et al., 2006).

A number of reports indicate that red grouper are affected by ephemeral environmental events such as hurricanes and red tides within the eastern Gulf (Smith, 1976; Franks, 2003). Several distinct such events occurred during our six year time series. One common anecdote is that red grouper can be displaced in great numbers and catch rates can be quite high in the period following hurricanes (SEDAR, 2006). Such a displacement was documented; after Hurricane Lili passed through the north central Gulf in October, 2002, juvenile and adult red grouper appeared for the first time off Mississippi and were common in recreational catches (Franks, 2003). Their numbers have since dwindled (J. Franks, personal communication, Gulf Coast Research Laboratory, MS, USA). Anecdotal reports of periodic but massive fish die offs and particularly of grouper kills, presumably due to red tides, exist since the early 1900s (Edic, 1996). During and after a 1971 red tide, red grouper was noted to be a particularly susceptible species that was eliminated from reefs spanning a broad region of the west Florida shelf (Smith, 1976). More recently, a red tide episode during 2005–2006 resulted in observations of depleted reefs within coastal waters from the Big Bend to south Florida (26–29°N latitude; Hu et al., 2006; D. DeVries and B. Mamoudi, personal communication, NOAA Fisheries Service, Panama City, FL, USA and Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute, St. Petersburg, FL, USA, respectively). Some evidence exists that red tides are linked to hurricanes via submarine groundwater discharge (Hu et al., 2006) and thus both types of events could combine to affect movements and mortality of reef species; particularly red grouper.

## 5. Conclusions

We acknowledge the limits of fishery-dependent results particularly in that they are geographically imprecise and only allowed us to examine demographic data at no smaller than a regional scale (100 s of miles). We view our findings of demographic differences to be a first indication of possible stock delineation for red grouper from the northeastern Gulf of Mexico. Our results compel us to look for additional evidence of geographic differences in red grouper, using such methods as otolith microchemistry (Patterson et al., 2004), otolith shape analysis (DeVries et al., 2002), recruitment and population size estimates via nursery surveys and better correlation to environmental events. Additionally, further findings of regional differences with longer time series of recruitment will strengthen our inference of spatially demographic differences in red grouper population along the west Florida shelf.

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