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Temporal and spatial trends in red grouper (*Epinephelus morio*) age and growth from the northeastern Gulf of Mexico: 1979-2005

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Introduction

Red grouper (*Epinephelus morio,* Family Serranidae), are widely distributed throughout the Gulf of Mexico, Caribbean, and U.S. South Atlantic and are classified as an important component (~70 %) of the shallow-water grouper landings (Schirripa et al. 1999, NMFS 2002). Red grouper are a highly sought target species and during the last stock assessment were classified as overfished and undergoing overfishing (NMFS 2002).

Because age and growth information is critical to stock assessment, the goal of this report is to characterize age-length structure temporally and spatially using 15 years (1991-2005) of data collected from the northeastern Gulf of Mexico. This analysis is an extension of an earlier report (Lombardi-Carlson et al. 2002), with additional years of data before (1979-1989) and after fishery regulations were established in 1990. The following are discussed: annual age and length distributions, temporal patterns of length and age between sectors and commercial gears, spatial patterns of commercial age and length data by depth, NMFS statistical grids, and regions, description of pre-regulatory data, and results of a size-modified von Bertalanffy growth model.

Methods

Data Collection

Otoliths were collected (1991-2005) by numerous federal and state sources representing both the commercial and recreational fisheries (Trip Interview Program – TIP, Beaufort Head Boat Survey – HB, Marine Fisheries Recreational Statistical Survey – MRFSS, Florida Fish and Wildlife Research Institute – FWRI, and Recreational Fisheries Information Network – RECFIN). Red grouper otoliths were collected from federally funded fishery independent surveys (NMFS Panama City, FL – PCLAB, and NMFS Pascagoula, MS – MSLAB). The Cooperative Research Program (CRP) also provided otoliths and site specific detailed capture locations. Prior to the establishment of these sampling programs, red grouper otoliths and length data were collected (1979-1989) from commercial and recreational fish houses (Saloman and Fable 1981). Measurements of fish lengths (total and/or fork), weights (whole or gutted), and removal of otoliths were completed in the field.

Information describing catch location (latitude, longitude, depth, or NMFS statistical sub-areas, further referred as grids; Patella 1975) was often reported with commercial samples. The west Florida shelf, where most red grouper were caught, encompasses the area from Cape Sable to Cape San Blas within the northeastern Gulf of Mexico (Smith 1976) and was divided into two regions: north and south of 28^{o}N latitude (just north of Tampa Bay). If detailed information on capture location was not available from port collections, fish could clearly be identified as being harvested north or south of 28^{o}N latitude based on port agent interviews of fishers. Depth data were either reported as a mean depth or a range of depths for the entire interview. If the range of depth was $\leq$ 5-fathoms (fm), then an average depth was calculated, otherwise both a start and an end depth were recorded.

Data Quality Control

Each of the data collection sources has separate but similar sampling procedures, data protocols, and reporting methodologies. Our facility uses data quality control guidelines in the interpretation of source-specific datasheets as described by the Procedure Manual for Age, Growth, and Reproduction (AGR) Lab (NMFS 2004). First, each species-specific collection is assigned an annual collection (or tracking) number and all collection-specific data (i.e. source, source number, state, sector, and gear) are proofed and entered in our Annual AGR Access Databases from the original datasheets. If such data are not provided, then the collector (port agent and/or survey leader) is contacted to track down the missing data. Our Annual AGR Access Databases were constructed with field-specific lists of suitable values (e.g. source, state, sector, and gear), validation rules, and user-specific security for data accessibility to enhance our data quality control procedures. Additionally, the source number (or interview number) is a source-specific number (or combination of intercept specific numbers) that permits the cross-referencing of data between databases (original source and Annual AGR Database). Next, after all the individual fish data are entered, proofing sheets are reviewed against the original datasheets and any corrections are made to the Annual AGR Database. Finally, all proofing sheets are initialed, dated and filed for further reference. Prior to 1998, no manual existed to implement these procedures. Therefore, to insure these standards of quality control, all 1991-1997 data were proofed using the TIP original datasheets (archived in Panama City, FL) and any missing data were resolved by accessing the TIP database (DELPHI, SEFHOST).

Sub-Sampling

Due to a substantial increase of port agent otolith sampling commencing in 2002, red grouper otoliths collected in 2002-2005 from commercial long-line intercepts were sub-sampled prior to estimating age. Records (n = 1,000) from each year were randomly sub-sampled based on the percentage of commercial long-line landings by NMFS grids. Landings were obtained from NMFS logbook 2001-2004 (S. Turner, SEFSC Miami). Red grouper otoliths collected in 2002-2005 from commercial hand-line, recreational, scientific survey, and Cooperative Research Projects were not sub-sampled; age was estimated for all samples.

Age Determination

The sagittal otolith was used as the primary ageing structure (Moe 1969). Red grouper ages were successfully interpreted from both whole and sectioned otoliths (Johnson and Collins 1994, Lombardi-Carlson et al. 2002). Four readers read red grouper otoliths and indices of precision (Average Percent Error, Percent Agreement, CV, D) were calculated, see Palmer et al. 2006 for further discussion. Annual ages were used for further analysis and fractional ages were also calculated to obtain decimal age to use in the growth model.

Annual ages, based on a calendar year, were calculated using the reader's annulus count, edge type and capture date (Jearld 1983). Annulus counts were advanced a year if the fish was captured between January 1 to June 30 and the edge type was determined to be fully translucent (edge type 6). Typically, marine fish in the southeastern U.S. complete annulus formation, an opaque zone, by late spring to early summer. Therefore, an otolith with two completed annuli and a large translucent zone would be classified as age 3 if the fish was caught during spring in expectation that a third (opaque zone) annulus would have formed soon. Any fish caught before June 30 with an opaque edge (type 2), the annual age was equal to the annulus count. After June 30, when opaque zone formation is underway or complete for red grouper in the Gulf of Mexico (Moe 1969), all fish were assigned an annual age equal to the annulus count by convention. There were a few instances when an opaque edge was detected from fish caught late in the year (November and December). It was assumed these fish were depositing the next year's band early and one year was subtracted from the annulus count to calculate an annual age.

In addition to annual or cohort age, biological age was calculated and used in the growth model. A fractional period of a year was determined as the difference from peak spawning date (May 15; Moe 1969, Collins et al. 2002) and capture date. If capture date was after the peak spawning date, the fractional period was added to annual age. If capture date was before the peak spawning date, the fractional period was subtracted from annual age to yield an estimate of biological age.

Temporal Trends

Age and length frequencies were produced for each year with all sectors and gears combined to examine annual trends in age structure during 1991-2005. Age and length distributions were compared annually by sectors (commercial, recreation) and by commercial gears (hand-line, long-line). The recreational sector composed of otoliths intercepted from charter boats (CP), head boats (HB), and private vessels (PR).

Length and age data were also compared temporally. Annual patterns of length and age data were compared by year using a one-factor analysis of variance (ANOVA) to test for any changes within the time series by sector (Zar 1999). Graphical representation of least significant difference (LSD) and Tukey post hoc test are also provided. Separate analyses were conducted for recreational and commercial samples, and by commercial gears.

Pre-Regulatory Dataset

Red grouper otoliths and length data collected in 1979-1989 (prior to regulations) were recovered from NMFS Panama City otolith archive. All otoliths recovered were re-aged according to the methods described above. Temporal changes in size-at-age were investigated between pre-regulatory (1979-1989) and post-regulatory (1991-1994) datasets by sectors and gears.

Description of Growth

Observed mean size-at-age data were compared by sectors. Commercial data were further analyzed by gear (hand-line and long-line) and region (north and south). Observed mean size-at-age data were compared within the above groups for selected age classes by an unpaired Welch two sample t-test with unequal variances (Zar 1999). The comparisons of size-at-age data were restricted to age classes within groups with sample sizes $\geq$ 10.

A growth curve, based on fractional ages and observed total lengths at capture, was modeled using the von Bertalanffy growth function and was fit by non-linear regression (Solver, Microsoft Excel). Since the majority of the data derives from commercial and recreational samples, a size-modified von Bertalanffy model was used to model growth parameters that take into account the non-random sampling due to minimum size restrictions (Diaz et al. 2004). This model assumes a constant standard deviation of size-at-age and uses a restrictive maximum likelihood estimation procedure with minimum size (20 in or 508 mm) as the left truncation limit for fisheries dependent observations. Fishery independent data were used to aid the model to predict growth at smaller sizes not collected in fishery dependent sampling.

Spatial Patterns

Commercial data were analyzed by depth to detect any differences between gear types and/or years. Commercial age data were grouped into 10-fm depth bins by gear. Commercial data were also compared by NMFS grid and region (north and south) to identify any patterns of length, age, or size-at-age among the capture locations. Patterns of length and age data were compared among NMFS grids using a one-factor ANOVA to test for any similarities among grids (Zar 1999). Size-at-age data were compared using an unpaired Welch two sample t-test with unequal variances for sample sizes of $n > 10$.

Results and Discussion

Data Collection

A total of 21,906 otoliths were collected from fishery dependent and independent sampling (1979-2005). Red grouper otoliths were obtained primarily from Florida's state and federal waters (99.7%) with very few samples collected elsewhere ($n = 71$, Table 1). Trip Interview Program's port agents collected a majority of the otoliths (81.5%, Table 2). The commercial industry was heavily sampled by port agents (84.3%, Table 3), followed by recreational vessels (9.5%). The percentage of commercial long-line intercepts increased to 72% of all commercial sampling, compared to previous sampling of only 61% (Lombardi-Carlson et al. 2002). Numerous fishery independent surveys collected red grouper throughout the years (5.2%, $n = 1,142$) using multiple gear types (long-line, hand-line, trap, and trawl). Seventy-seven percent of the red grouper otoliths were collected during the more recent years (2001-2005, Table 4).

Sub-Sampling

An average percentage of commercial long-line landings per NMFS grid during 2001-2004 was calculated to determine sub-sampling procedures (Table 5). For example, Grid 5 (Latitude 27°N, Longitude 82-84°W) accounted for 45% of red grouper commercial long-line landings; therefore about 45% of the otoliths available each year were randomly sub-sampled per year from Grid 5. If minimum number of otoliths was not available from a particular grid to be exactly representative (e.g. Grid 5 in 2002), than more otoliths were sub-sampled from adjacent grids. Grids 1, 7, 10, 11 and 13 accounted for < 4% of red grouper commercial long-line landings and no otoliths were collected in these grids. A total of 4,282 otoliths were randomly sub-sampled from reported commercial long-line samples collected in 2002-2005.

Age Determination

Previous age determinations reported in Lombardi-Carlson et al. 2002 were used in this report (n = 6,073), and an additional 10,611 otoliths were aged (1979-2005). A total of 16,684 otoliths were interpreted, of which 2% (n = 308) were indicated as unreadable, yielding 16,367 ages for further analysis (Table 4). Indices of precision were calculated among each pair of readers and all readers combined from a reference collection (240 otoliths), indicating high levels of precision and accuracy (APE = 3.5%, CV = 4.3%, percent agreement = 68%, percent agreement +/- 1 band = 91%, and percent agreement +/- 2 bands = 96%; Palmer et al. 2006).

Temporal Trends

Similar ranges of lengths and ages were sampled each year throughout the time series. Red grouper sampled by commercial, recreational, and scientific surveys had an average length of 613 ± 1 mm TL (mean ± se, range 117-1007 mm, median 596 mm; Figure 1a). Mean lengths were significantly different among years (single factor ANOVA, $F = 18.71$, $df = 14$, $p < 0.0001$, $r^2 = 0.02$) with fish collected in 1991 significantly larger than other years. Red grouper collected by all sectors reached a mean age of 7.53 ± 0.02 yrs (range = 1-29 yrs, median = 7 yrs; Figure 1b). Mean ages were also significantly different among years (ANOVA, $F = 26.27$, $df = 14$, $p < 0.0001$, $r^2 = 0.02$), with fish from 1991, 1999, 2002, and 2003 being significantly older (Figure 1b).

While central tendencies in length varied, annual length distributions of fish sampled for age were similar; a majority (82%, range = 61%-89%) of the fish collected were 500-750 mm in length (Figure 2). Annual red grouper length frequencies were negatively skewed (right shift) due to the 20 in (508 mm) size limit established in 1990 in the Gulf of Mexico commercial fishery and the Florida inshore recreational fishery. Undersized red grouper (n = 746) continued to be sampled through fishery independent surveys (1994-1996, 2002-2005; Table 3, Figure 2).

An additional 332 otoliths were recovered from a period previously reported (1992-2001, Lombardi-Carlson et al. 2002). These samples were mainly from 1994 and 1995. Age frequency distributions were slightly modified with this additional data, however no apparent differences were observed in the representation of the strong year classes previously identified (1989, 1990, and 1996; Figure 3). A strong year class was defined as exceeding at least 20%-25% of the age frequency for one year and remained dominant for at least two years. The 1991 year class had not been identified previously as being dominant, but it dominated the age structure in 1998 and 1999, as ages 7 and 8, respectively (Figure 3). In 2004, a new strong year class (the1999 cohort) dominated the 2004 and 2005 age structure, as ages 5 and 6, respectively (Figure 3). The 1999 cohort comprised 35% of the 2005 age structure, the largest contribution of any one cohort throughout the time series.

Annual age and length frequencies by sector revealed similarly sized and aged fish caught within each sector by year. Red grouper collected through intercepts of the commercial fishery had annual mean lengths of 604 -708 mm TL, with an overall mean size of 627 ± 1 (se) mm TL (range = 320-980 mm, median = 609 mm; Figure 4a). Mean lengths were significantly different among years (ANOVA, $F = 13.41$, $df = 14$, $p < 0.0001$, $r^2 = 0.01$), with commercial data collected in 1991 significantly larger than other years (Figure 4a). Red grouper collected by the commercial sectors reached an average age of 7.89 ± 0.03 yrs (range = 3-27 yrs, median = 7 yrs; Figure 4b). Mean ages determined from commercial samples were also significantly different among years (ANOVA, $F = 34.67$, $df = 14$, $p < 0.0001$, $r^2 = 0.04$), with fish collected from the years 1991, 1999, 2001, 2002, and 2003 significantly older (Figure 4b).

Annual box plots of lengths and ages revealed further similarities in the fish collected from the recreational sector (i.e. similar median values) across the time series. Recreational samples had a overall mean length of 597 ± 2 (se) mm TL and a overall mean age of 6.46 ± 0.06 yrs. Significant differences in mean lengths and mean ages were determined through ANOVA among years (length ANOVA, $F = 17.09$, $df = 14$, $p < 0.0001$, $r^2 = 0.11$; age ANOVA, $F = 9.34$, $df = 14$, $p < 0.0001$, $r^2 = 0.06$), but post-hoc tests revealed comparable lengths among the years (Figures 5a).

Commercial data were further divided by gear types: long-line (LL) and hand-line (HL). Fewer than 200 otolith samples were collected annually through intercepts of commercial long-line vessels from 1991-1998 (Table 3) thus limiting any conclusive results, however there were significant differences in mean lengths and ages among years from the long-line fishery (single-factor ANOVA lengths: $F = 9.51$, $df = 14$, $p < 0.0001$, $r^2 = 0.02$; age: $F = 28.79$, $df = 14$, $p < 0.0001$, $r^2 = 0.05$). Commercial long-line samples had an overall mean length of 638 ± 1 mm TL (range = 372-956 mm, median = 623 mm; Figure 6a) and mean age 8.26 ± 0.03 years (range = 3-27 yrs, median = 8 yrs; Figure 6b). Similarly, commercial hand-line samples were not consistently sampled until 2000 (Table 3). The results are not conclusive, but there were significant difference in length and age among years (single-factor ANOVA lengths: $F = 8.63$, $df = 14$, $p < 0.0001$, $r^2 = 0.02$; age: $F = 14.59$, $df = 14$, $p < 0.0001$, $r^2 = 0.04$). In general, commercial hand-line samples were smaller (608 ± 1 mm, range = 320-980 mm, median = 586 mm; Figure 7a) and younger (7.23 ± 0.04 yrs, range = 3-27, median = 6; Figure 7b) than commercial long-line samples, even though both gears caught similar size ranges of red grouper.

Pre-Regulatory

A total of 1,378 red grouper records collected in 1979-1989 were recovered from NMFS Panama City Laboratory otolith archive and data from several sampling programs. Only 441 records had otoliths, of which 423 were aged. The otoliths were collected from all sectors: 53% commercial, 28% recreational and 19% scientific survey. Commercial hand-line samples (n = 230, 1980-1981) were collected from three main regions of Florida: northwest, central, and south (categories as reported on datasheets). Recreational samples were obtained from dock-side sampling of recreational ports located in Panama City (n = 83, 1979-1980; Saloman and Fable 1981) and from Beaufort Head Boat Survey sampling from Naples and throughout the panhandle of Florida (n = 42, 1985-1989). In 1981, a scientific survey (R/V Oregon II) collected red grouper from the Florida Middle Grounds mainly with traps (n = 81; Russell 1982).

In 1990, the first federal regulatory amendments were enacted on the shallow-water grouper fishery by the Gulf of Mexico Fishery Management Council. These amendments established a minimal size limit (20 in), a recreational bag limit (5 grouper), a commercial quota (9.2 million LB for shallow-water groupers), and a commercial long line vessel fishing boundary (east of Cape San Blas, outside 20 fm). Pre-regulatory fishery dependent length and age data (1978-1989) were compared to post-regulatory data (1991-1994; Figure 8a-b). Post-regulatory red grouper were significantly larger in size-at-age for 9 of the 12 age classes for sample sizes ≥ 5 (Figure 8c, Table 6). Further analysis revealed significant differences in size-at-age were primarily collected from commercial intercepts (ages 4-10; Figure 9a, Table 7). Recreationally sampled fish were similar in size-at-age between the two time periods (Figures 9b-c). The fishery independent survey caught red grouper that were majority (85%) smaller then 450 mm TL and almost all (93%) were younger then age 6 yr (mean ± se; length 334 ± 10 mm, range 215-725 mm, median 324 mm; age 2.5 ± 0.20 yr, range 1-13 yr, median age 2 yr).

Description of Growth

Observed size-at-age data were compared between the main fishery dependent sectors: commercial (CM) and recreational (REC). Even though commercially caught red grouper were overall (all data combined, 1991-2005) significantly larger (CM: 627 ± 1 mm, REC: 597 ± 2 mm; t-statistic = 13.12, df = 2569, $p < 0.001$; Figure 10a) and older (CM: 7.89 ± 0.03 yr, REC: 6.47 ± 0.06 yr; t-statistic = 22.60, df = 2755, $p < 0.001$; Figure 10b). Recreationally caught red grouper were significantly larger at age (ages 5, 7-12, 14-15) compared to commercially caught fish (Figure 10c, Table 8).

Comparisons of data collected from commercial hand-line and long-line vessels were restricted to the more recent years (2000-2005) when sampling became more uniform for each of these gears. Red grouper caught by the two main commercial gear types long-line (LL) and hand-line (HL) were determined to be similar in length, age, and size-at-age (Figure 11). Long-line caught red grouper were slightly larger (LL: 636 ± 1 mm, HL: 609 ± 2 mm; t-statistic = -14.06, df = 8018, $p < 0.001$; Figure 11a) and older (LL: 8.35 ± 0.04 yr, HL: 7.37 ± 0.05 yr; t-statistic = -15.60, df = 8129, $p < 0.001$; Figure 11b) compared to hand-line caught fish. Significant differences in size-at-ages (ages 5, 6, and 8) were determined, however, mean values differed only by 8-12 mm (Figure 11c, Table 9).

Red grouper fractional ages and total lengths from the entire time series (1991-2005) were fit to a modified von Bertalanffy growth model to obtain population growth parameters

(Figure 12). One of the assumptions of the size-modified growth model is that there is a constant deviance in size-at-age; however, red grouper showed a variable deviance in length among ages (Figure 12a). The model predicted the following parameters: L_∞ = 854 mm, k = 0.16, t_o = -0.19 (Figure 12b). The modified von Bertalanffy predictions are below the observed mean size-at-age (ages < 5 yr) because of the truncation of sampling due to the minimum size restrictions (Figure 12c). The model showed large positive and negative residuals, and the residual distribution was slightly skewed to the positive (Figure 13a-b). Plots of residuals by categories age, sector, gear and year did show some bias, in particular that most median residuals were centered above zero (Figure 13c).

Previous growth curves constructed for red grouper in the Gulf of Mexico did not predict growth at the younger ages very well, possibly due to the size selection of samples at the lower tail of the age-length dataset and to the limited number of undersize fish in the dataset (1992-2001, n = 656; L_∞ = 923 mm, k = 0.11, t_o = -3.21; Lombardi-Carlson et al. 2002). The current dataset includes many more undersized red grouper (n = 1,161). The result of the size-modified von Bertalanffy fit suggests a better fit to the population growth (Figure 14). Asymptotic length is slightly less than previous calculations (current model, L_∞ = 854 mm; 2002 model, L_∞ = 923 mm), growth coefficient is slightly higher (current model, k = 0.16; 2002 model, k = 0.11), and size-at-time zero approaches the zero-intercept (current model, t_o = -0.91; 2002 model, t_o = -3.21).

Depth Patterns

Location data reported with otoliths indicates commercial long-line and hand-line vessels were fishing at broadly overlapping depths but long-line vessels tending to harvest more red grouper at depths > 20 fm (mean depth ± se, LL: 31.4 ± 0.1 fm, HL: 26.3 ± 0.2 fm; Figure 15a). While depth data were sparse in the early part of the dataset (1991-1998), overall depths fished were consistent across years (Figure 15b-c). Based on increased reporting of capture information in 2000-2005, a majority (95%) of the commercial fish sampled by both gear types were collected within 15-40 fm, with no direct relationship of age and length to depth fished, regardless of gear (Figure 16a-d).

No long-line samples were reported from the shallowest depth bin (0-19 fm; Figure 17a), which was expected since the use of long-line gear is restricted to waters deeper than 20 fm east of Cape San Blas, FL (encompassing the entire west Florida shelf). Age proportions were dominated by long-line gear in the other depth bins (20-29 fm, 30-39 fm, >40 fm; Figure 17a-d); however, commercial long-line and hand-line gears caught similarly aged fish. Since red grouper of similar age and length were caught readily by both gears regardless of depth fished, gear selectivity (for size-at-age) may be similar for these gears where vessels overlap spatially (Figures 16 and 17). A fuller examination of this possibility would be enabled by fishery independent observations of discards in these respective fisheries.

Latitude Patterns

Age and length of red grouper from commercial intercepts, with sufficient capture location (latitude, longitude, or NMFS grid) were compared by NMFS grid. Mean lengths were significantly different among grids (single factor ANOVA, $F = 108.60$, $df = 8$, $p < 0.0001$, $r^2 = 0.08$), with red grouper collected in grids 2-5 significantly larger than fish in grids 6-10 (Figure 18a). Mean ages were also significantly different among grids (ANOVA, $F = 180.10$, $df = 8$, $p < 0.0001$, $r^2 = 0.13$), with older fish collected from grids 2-5 (Figure 18b). Red grouper caught in grid 2 were among the largest (660 ± 4 mm, mean ± se) and oldest (9.07 ± 0.16 yr) fish collected and fish caught in grid 10 were the smallest (558 ± 3 mm) and youngest (5.54 ± 0.08 yr).

Red grouper were further compared at a regional spatial scale. The west Florida shelf was divided into two regions: north and south of 28^{o}N latitude (just north of Tampa Bay). These two regions encompass the majority of the grids red grouper were reported captured (north, grids 6-10; south, grids 1-5). Overall samples, red grouper caught in the southern region were significantly larger (south, 646 ± 1 mm; north, 599 ± 1 mm; t-test, $t = -24.99$, $df = 9839$, $p < 0.0001$) and older (south 8.91 ± 0.04 yr; north, 6.76 ± 0.04 yr; $t = -37.77$, $df = 9886$, $p < 0.0001$; Figure 19a-b). However, red grouper from the south were significantly larger only at the ages 4 and 6; by age 7 northern red grouper grew faster at older ages (Figure 19c, Table 10).

There are several factors related to harvest, recruitment, and latitudinal growth that could explain why red grouper displayed different lengths, ages, and sizes-at-age between these two regions. A majority of the red grouper commercial landings are reported from NMFS grid 5 (35%), with the southern region (grids 1-5) accounting for 64% of the landings (NMFS Logbook, Schirripa et al. 1999). If harvesting levels have affected the demographics of red grouper, then the southern region should be characterized by a truncated size and age structure. The fishery dependent data do not support this trend across the broad aggregated spatial scale available for examination.

In terms of recruitment, based on fishery dependent data, it is evident that a larger proportion of younger fish are caught in the northern region (Figure 20). There are two strong year classes present in the years compared between regions (1996 and 1999; Figure 20). Both of these strong year classes appear in larger proportions in the northern age distributions. In 2001, the 1996 cohort (age 5 yrs) composed of 49% of the northern age structure but only 9% of the southern age structure. Furthermore, the 1999 cohort showed a similar pattern of occurrence 46% and 66% of the northern age structure in 2004 and 2005, respectively (Figure 20).

Conclusions

This report summarizes over 25 years of fishery dependent sampling from commercial and recreational fisheries. Data were used to characterize the demographics of the landed catch and to estimate growth within the population. It is especially important to note the remarkable progression of strong year classes (1989, 1990, 1991, 1996, and 1999). Ageing of additional otoliths from earlier decades allowed insight into size-at-age patterns prior to the establishment of fishery regulations in 1990. Since the analysis of the red grouper population is primarily relying on the efforts of fishery dependent port agents, it is important that sampling regiment and protocols are maintained and reviewed. In particular, an increase in age-structure sampling in the recreational industry would be beneficial.

There are limits to the fishery dependent results particularly in that the data are geographically imprecise and only allowed the examination of demographic data at no smaller than a regional scale. These results require additional evidence of geographic differences in red grouper, for example from fishery independent recruitment surveys of juvenile fish and by identifying recruitment source locations of adults using such methods as otolith microchemistry (Patterson et al. 2004) and otolith shape analysis (DeVries et al. 2002).

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Table 1. Summary of the number of red grouper otoliths collected by state landed (FL – west coast Florida, AL – Alabama, MS – Mississippi, LA – Louisiana).

Year	FL	AL	MS	LA	Total
1979-89	435			1	436
1991	134				134
1992	285		5		290
1993	495				495
1994	526				526
1995	560		21		581
1996	470				470
1997	174				174
1998	306				306
1999	905				905
2000	809				809
2001	2,066				2,066
2002	2,871	2	5		2,878
2003	3,350	8	2	7	3,367
2004	4,061	14	1		4,076
2005	4,388	3		2	4,393
Total	21,835	27	34	10	21,906
Percent	99.7	0.1	0.2	0.0	

Table 2. Summary of the number of red grouper otoliths collected by source (TIP - Trip Interview Program, HB - Beaufort Head Boat Survey, FWRI - Florida Fish and Wildlife Research Institute, MRFSS - Marine Recreational Fisheries Statistical Survey, RECFIN - Recreational Fisheries Information Network, CO-OP - Cooperative Research Proposals, MSLAB -NMFS Pascagoula MS; PCLAB - NMFS Panama City, FL; Other - US Geological Survey, Unknown).

Year	TIP	HB	FWRI	MRFSS	RECFIN	CO-OP	MSLAB	PCLAB	Other	Total
1979-89		42					81	75	238	436
1991	102	32								134
1992	252	31					5		2	290
1993	477	18								495
1994	490	23						13		526
1995	522	34						25		581
1996	436	34								470
1997	163	10					1			174
1998	179		13				7	107		306
1999	850	2		33			11	9		905
2000	697	11		12			1	88		809
2001	1,852			31		2	82	98	1	2,066
2002	2,189	1	18	69	44	310	30	216	1	2,878
2003	3,026	29	28	121		54	61	48		3,367
2004	2,983	41	63	68	87	479	169	186		4,076
2005	3,624	29	20	18	67	458	50	127		4,393
Total	17,842	337	142	352	198	1,303	498	992	242	21,906
Percent	81.5	1.5	0.7	1.6	0.9	6.0	2.3	4.5	1.1	

Table 3. Summary of the number of red grouper otoliths collected by sector (CM - Commercial, CP - Charter Party, HB – Headboat, PR - Private, SS - Scientific Survey, TRN – Tournament, OBS- Observer on board commercial vessel, Unk – unknown) and gear (LL - Long-Line, HL - Hand-Line, SP - Spear, TR - Trap, TRW - Trawl). The recreational sector composed of otoliths intercepted from charter boats (CP), head boats (HB), and private vessels (PR).

Year	CM LL	CM HL	CM TR	CM SP	CP HL	HB HL	PR HL	SS HL	SS LL	SS TR	SS TRW	TRN	OBS	Unk	Total
1979-89		230			83	42		13	4	64					436
1991	48	46	2		1	37									134
1992	154	44	16		27	33	1	5				8		2	290
1993	201	93	84		61	21	2			4		29			495
1994	88	242	29		75	29		7		6		50			526
1995	151	202	41		99	61		21		4		1		1	581
1996	103	95	9	6	151	44		5					57		470
1997	8	41	17	1	67	30	9	1							174
1998	124	42	33		74	21	4	8							306
1999	662	77	31		104	9	2	18		2					905
2000	412	213	38	6	59	12		68		1					809
2001	1,237	584	40	3	48	1	2	69	79	3					2,066
2002	1,809	572	89	1	288	50	7	9	16	18		19			2,878
2003	2,422	567	65	4	96	30	67	25	61	14	9	7			3,367
2004	2,300	1,063	36	2	131	43	40	140	167	52	52		50		4,076
2005	3,443	630		4	62	52		73	32	88	4	5			4,393
Total	13,162	4,741	530	27	1,426	515	134	461	359	257	65	119	107	3	21,906
Percent	60.1	21.6	2.4	0.1	6.5	2.4	0.6	2.1	1.6	1.2	0.3	0.5	0.5	0.0	

Table 4. Summary of the number of red grouper otoliths collected, read, and determined unreadable (1979-1989, 1991-2001) or sub-sampled to be aged (2002-2005).

Year	Otoliths collected	Otoliths sub-sampled	Otoliths read	Otoliths not readable	Otoliths not readable (%)
1979-89	436		423	13	3
1991	134		119	15	11
1992	290		272	18	6
1993	495		492	3	1
1994	526		519	7	1
1995	581		528	53	9
1996	470		431	39	8
1997	174		159	15	9
1998	306		299	7	2
1999	905		885	20	2
2000	809		794	15	2
2001	2,066		2,026	40	2
2002	2,878	2,144	2,135	9	0
2003	3,367	2,030	2,016	14	1
2004	4,076	2,897	2,876	21	1
2005	4,393	2,421	2,402	19	1
Total	21,906	9,492	16,376	308	2

Table 5. Summary of the red grouper commercial long-line otoliths randomly sub-sampled for age determination (2002-2005) based on the percentage of red grouper commercial long-line landings within corresponding NMFS grid in 2001-2004 (S.Turner, SEFSC Miami). The NMFS grid associated with otolith samples was reported to port agents during intercepts.

NMFS Shrimp Grid	Percent Landed	Theoretical Sample Size	2002 # otoliths	2002 sub-sampled	2003 # otoliths	2003 sub-sampled	2004 # otoliths	2004 sub-sampled	2005 # otoliths	2005 sub-sampled	Total	Total sub-sampled
1	0.00	2									0	0
2	0.04	42	56	56	97	95	113	43	97	82	363	276
3	0.07	68	33	27	70	68	95	87	93	95	291	277
4	0.22	221	163	145	621	218	619	235	475	221	1,878	819
5	0.45	448	215	210	551	450	583	456	822	445	2,171	1,561
6	0.16	156	1,158	544	842	160	586	150	1,274	157	3,860	1,011
7	0.03	31		1							0	1
8	0.02	20	120	51	154	50	192	51	201	113	667	265
9	0.01	5	18	18	24	24					42	42
10	0.00	4									0	0
11	0.00	0									0	0
13	0.00	1									0	0
unknown	0.00	1	46	24	44	1	16	3	125	2	231	30
Total	1.00	1,000	1,809	1,076	2,403	1,066	2,204	1,025	3,087	1,115	9,503	4,282

Table 6. Pre- (1979-1989) and post- (1991-1994) regulatory comparisons of red grouper mean ± se size-at-age data and results of unpaired Welch two sample t-test. Significant levels for pair-wise comparisons: ^{NS} – not significant; *, $P < 0.05$; ** $P < 0.01$, ***, $P < 0.001$.

Age class	Time	TL (mm)	*t*	df
3	PRE	375 ± 9	4.62^{***}	154
	POST	479 ± 20		
4	PRE	467 ± 12	3.54^{***}	51
	POST	512 ± 5		
5	PRE	505 ± 14	3.00^{***}	41
	POST	550 ± 4		
6	PRE	547 ± 9	5.05^{***}	133
	POST	605 ± 7		
7	PRE	556 ± 13	6.68^{***}	64
	POST	655 ± 7		
8	PRE	614 ± 16	5.84^{***}	46
	POST	719 ± 8		
9	PRE	682 ± 13	3.80^{***}	39
	POST	741 ± 9		
10	PRE	679 ± 27	2.23^{*}	10
	POST	743 ± 9		
11	PRE	750 ± 16	1.14^{NS}	13
	POST	777 ± 11		
12	PRE	766 ± 14	-0.07^{NS}	26
	POST	765 ± 11		
13	PRE	722 ± 17	2.35^{*}	14
	POST	783 ± 19		

Table 7. Pre- (1979-1989) and post- (1991-1994) regulatory comparisons of commercially caught red grouper mean ± se size-at-age data and results of unpaired Welch two sample t-test. Significant levels for pair-wise comparisons: ^{NS} – not significant; *, $P < 0.05$; ** $P < 0.01$, ***, $P < 0.001$.

Age class	Sector	TL (mm)	*t*	df
4	PRE	469 ± 13	2.37^{*}	53
	POST	504 ± 6		
5	PRE	501 ± 15	2.75^{**}	37
	POST	545 ± 5		
6	PRE	522 ± 11	6.08^{***}	89
	POST	607 ± 8		
7	PRE	535 ± 13	7.27^{***}	61
	POST	645 ± 8		
8	PRE	566 ± 15	9.18^{***}	37
	POST	733 ± 10		
9	PRE	655 ± 12	5.03^{***}	23
	POST	742 ± 12		
10	PRE	632 ± 32	3.36^{*}	5
	POST	743 ± 10		

Table 8. Sector specific, commercial (CM) and recreational (REC), comparisons of red grouper mean ± se size-at-age data and results of unpaired Welch two sample t-test. Significant levels for pair-wise comparisons: ^{NS} – not significant; *, $P < 0.05$; ** $P < 0.01$, ***, $P < 0.001$.

Age class	Sector	TL (mm)	*t*	df
3	CM	508 ± 9	1.75^{NS}	30
	REC	483 ± 12		
4	CM	525 ± 2	1.54^{NS}	499
	REC	521 ± 2		
5	CM	554 ± 1	3.46^{***}	766
	REC	546 ± 2		
6	CM	578 ± 1	-0.97^{NS}	763
	REC	581 ± 2		
7	CM	614 ± 2	-2.53^{**}	364
	REC	625 ± 4		
8	CM	646 ± 2	-2.74^{**}	178
	REC	663 ± 6		
9	CM	660 ± 2	-5.12^{***}	89
	REC	705 ± 9		
10	CM	681 ± 3	-4.06^{***}	49
	REC	724 ± 10		
11	CM	698 ± 4	-3.98^{***}	34
	REC	755 ± 14		
12	CM	713 ± 5	-3.10^{**}	26
	REC	762 ± 15		
13	CM	740 ± 6	-1.87^{NS}	25
	REC	768 ± 14		
14	CM	750 ± 8	-3.12^{**}	13
	REC	811 ± 18		
15	CM	784 ± 8	-2.46^{*}	7
	REC	820 ± 13		

Table 9. Commercial gear, hand-line and long-line, specific comparisons of red grouper mean ± se size-at-age data and results of unpaired Welch two sample t-tests. Significant levels for pair-wise comparisons: ^{NS} – not significant; *, *P* < 0.05; ** *P* <0.01, ***, *P* < 0.001.

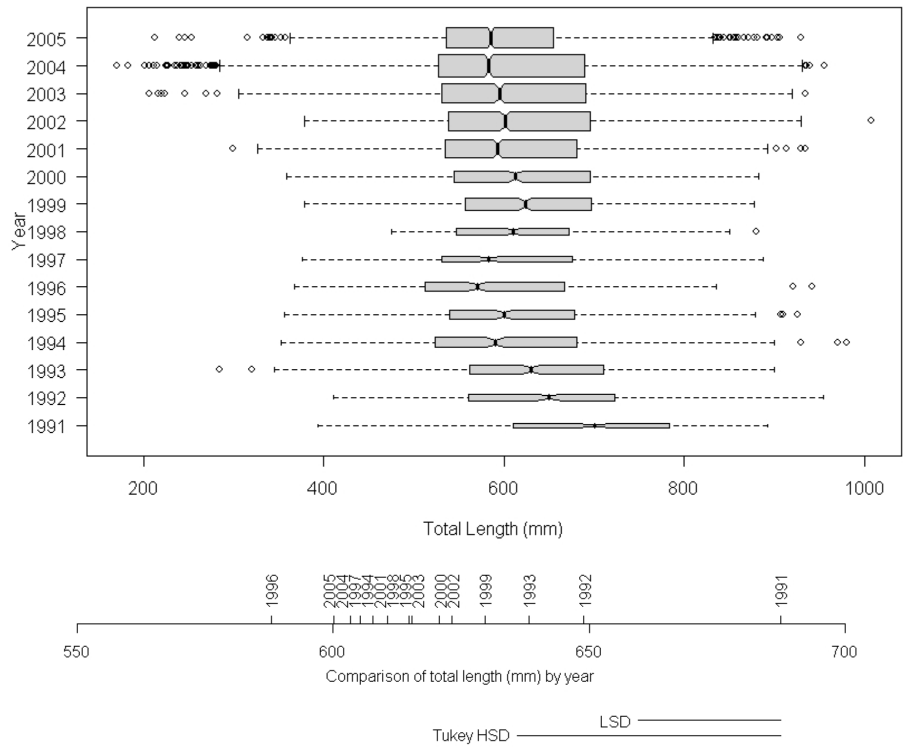
Age class	Sector	TL (mm)	*t*	df
4	hand-line	526 ± 14	-0.89^{NS}	166
	long-line	530 ± 9		
5	hand-line	549 ± 3	-3.44^{***}	1585
	long-line	557 ± 4		
6	hand-line	570 ± 2	-4.13^{***}	1789
	long-line	580 ± 2		
7	hand-line	609 ± 2	-1.16^{NS}	1245
	long-line	613 ± 2		
8	hand-line	636 ± 3	-2.55^{**}	877
	long-line	648 ± 2		
9	hand-line	652 ± 4	-0.64^{NS}	459
	long-line	656 ± 3		
10	hand-line	684 ± 5	1.67^{NS}	374
	long-line	673 ± 3		
11	hand-line	694 ± 6	0.02^{NS}	213
	long-line	693 ± 4		
12	hand-line	720 ± 8	1.13^{NS}	166
	long-line	707 ± 5		
13	hand-line	732 ± 9	-0.47^{NS}	121
	long-line	738 ± 6		
14	hand-line	764 ± 12	1.40^{NS}	90
	long-line	743 ± 7		
15	hand-line	797 ± 12	0.69^{NS}	52
	long-line	784 ± 10		
16	hand-line	784 ± 15	-0.93^{NS}	48
	long-line	801 ± 11		
17	hand-line	792 ± 28	-0.43^{NS}	22
	long-line	805 ± 12		
18	hand-line	765 ± 38	-1.75^{NS}	10
	long-line	834 ± 12		
19	hand-line	853 ± 9	1.40^{NS}	31
	long-line	827 ± 16		

Table 10. Regional specific, north (grids 6-10) south (grids 1-5), comparisons of commercial red grouper mean ± se size-at-age data and results of unpaired Welch two sample t-test. Significant levels for pair-wise comparisons: ^{NS} – not significant; *, $P < 0.05$; ** $P < 0.01$, ***, $P < 0.001$.

Age class	Sector	TL (mm)	*t*	df
4	North	523 ± 3	-3.19^{***}	144
	South	538 ± 4		
5	North	552 ± 1	-1.23^{NS}	786
	South	555 ± 2		
6	North	571 ± 2	-4.42^{***}	1946
	South	582 ± 2		
7	North	618 ± 3	2.95^{**}	1405
	South	607 ± 2		
8	North	650 ± 4	1.76^{NS}	713
	South	641 ± 3		
9	North	667 ± 5	2.59^{**}	428
	South	651 ± 3		
10	North	694 ± 5	3.79^{***}	408
	South	670 ± 4		
11	North	710 ± 7	2.73^{**}	293
	South	688 ± 5		
12	North	718 ± 11	0.72^{NS}	97
	South	709 ± 6		
13	North	755 ± 11	1.73^{NS}	80
	South	732 ± 7		
14	North	776 ± 13	2.19^{*}	50
	South	742 ± 9		
15	North	807 ± 18	1.05^{NS}	14
	South	786 ± 9		
16	North	766 ± 27	-1.24^{NS}	12
	South	800 ± 9		

Figure 1. Results of (a) length and (b) age single-factor ANOVA for all red grouper: 1991-2005. Box plots include the median, upper and lower quartiles (boxes: drawn in proportion to the square root of the sample size by year, if notches do not overlap then this indicates significant differences in median values, upper and lower range (dashed line), and outliers (open circles); Graphical representation of post-hoc tests: Least Square Differences (LSD) and Tukey Honest Significant Difference (Tukey HSD).

a.



b.

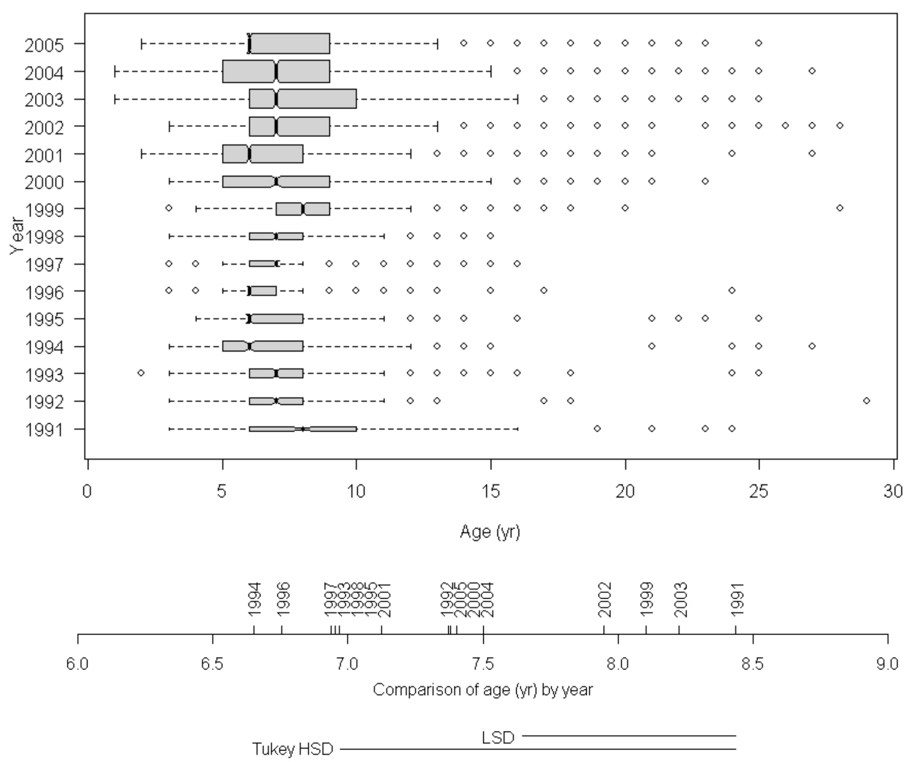


Figure 2. Length distribution (mm TL) of red grouper by year for all otoliths aged.

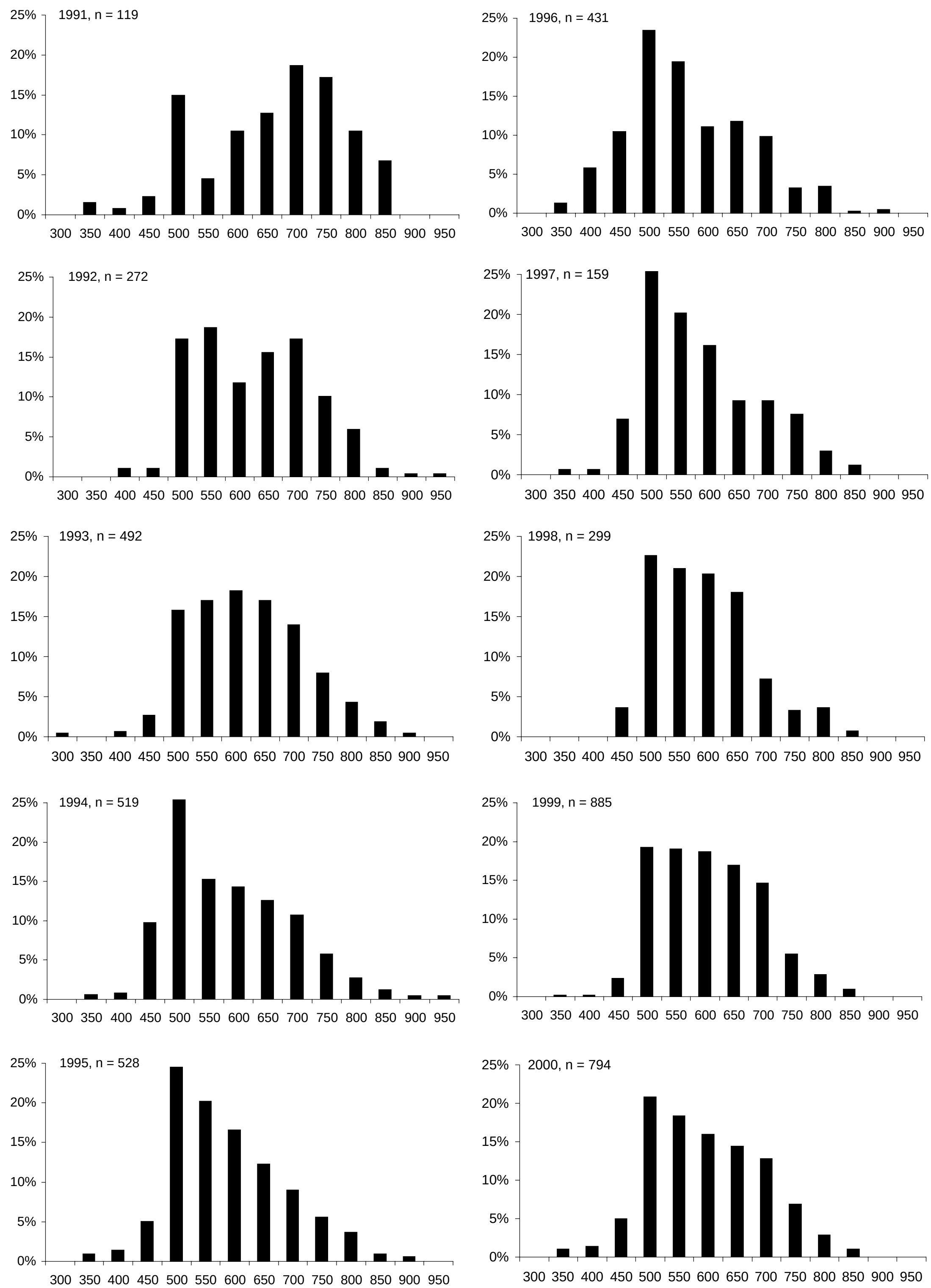


Figure 2. continued

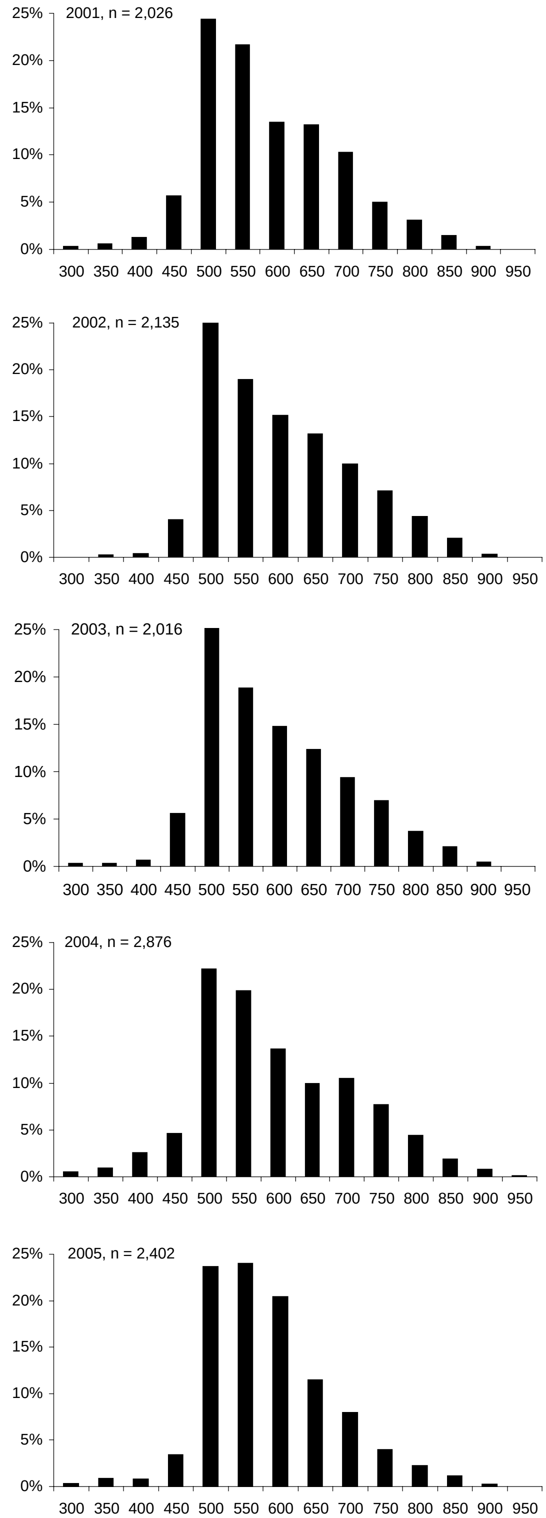


Figure 3. Age distribution (yr) of red grouper by year .

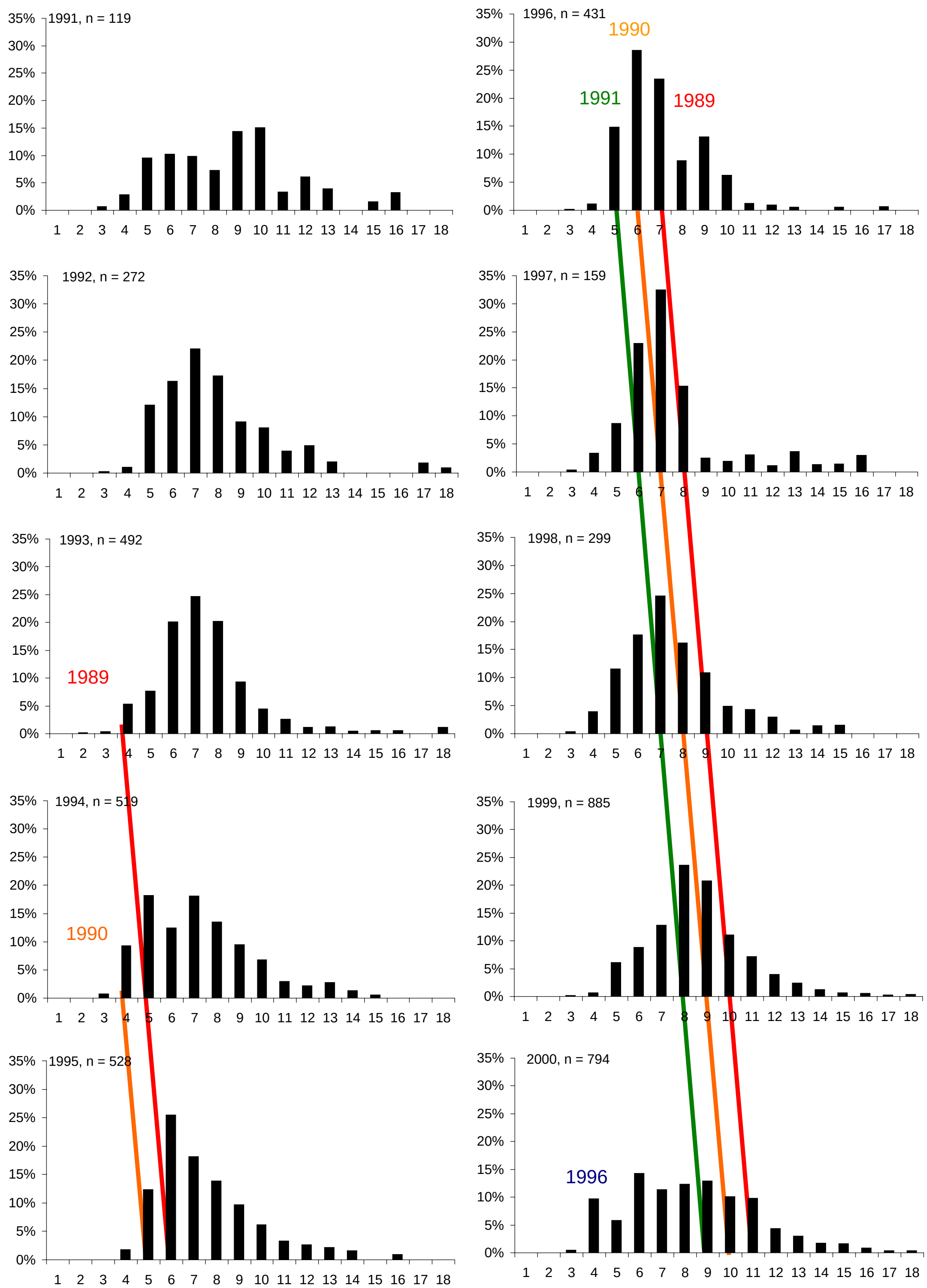


Figure 3. continued

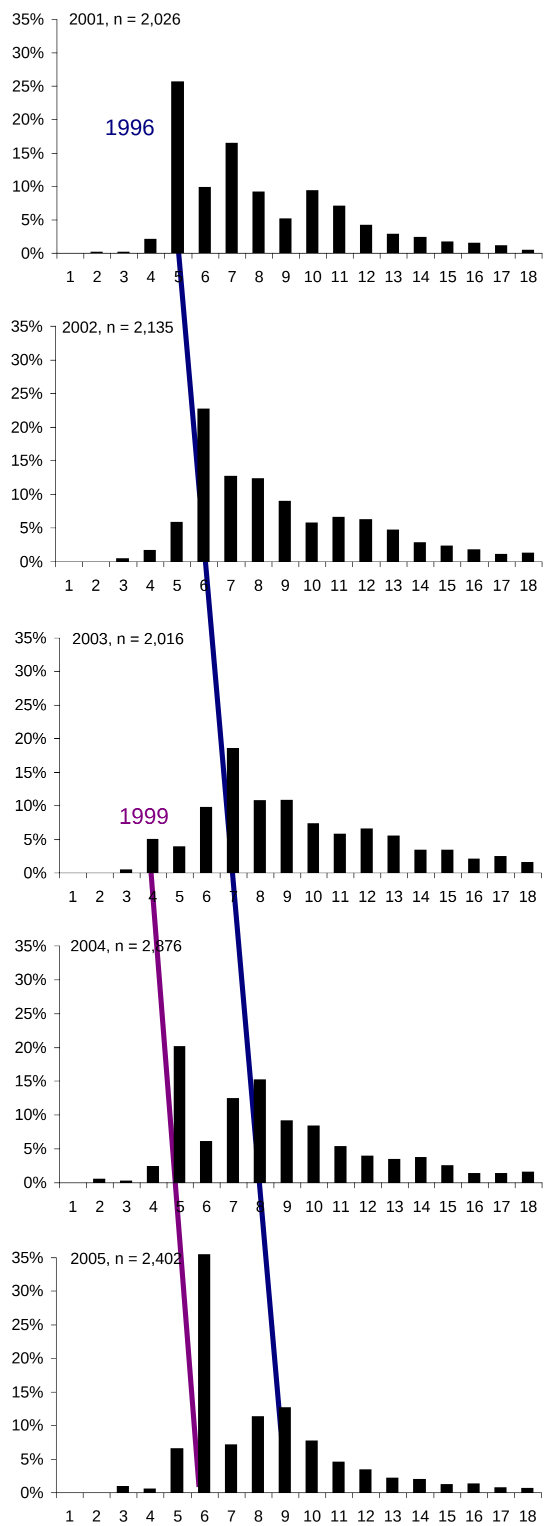
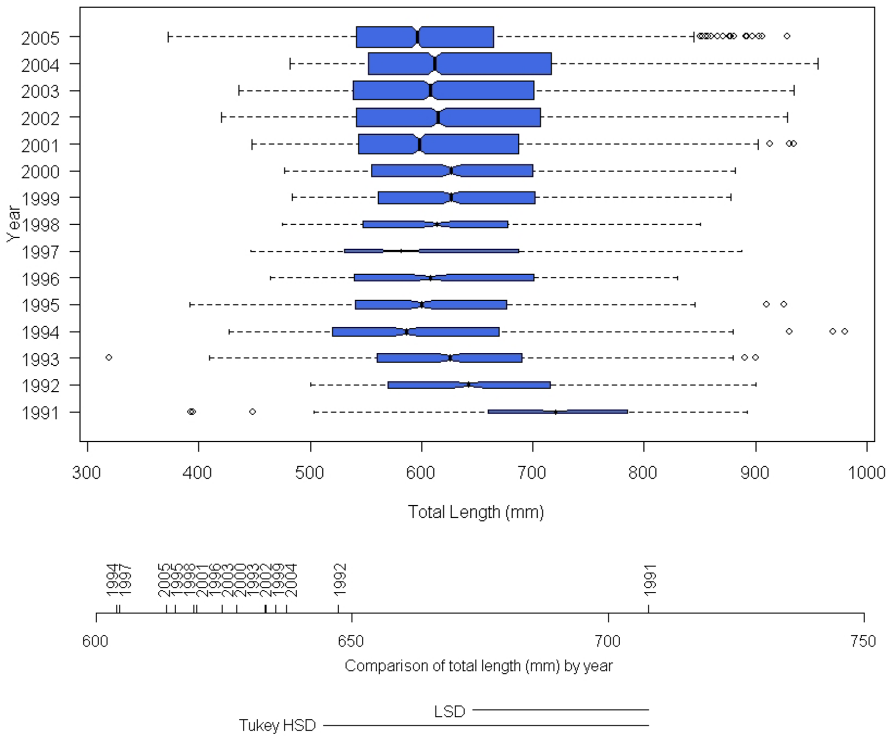


Figure 4. Results of (a) length and (b) age single-factor ANOVA for all commercially caught red grouper: 1991-2005. See Figure 1 for detailed explanation of box plots and post-hoc tests.

a.



b.

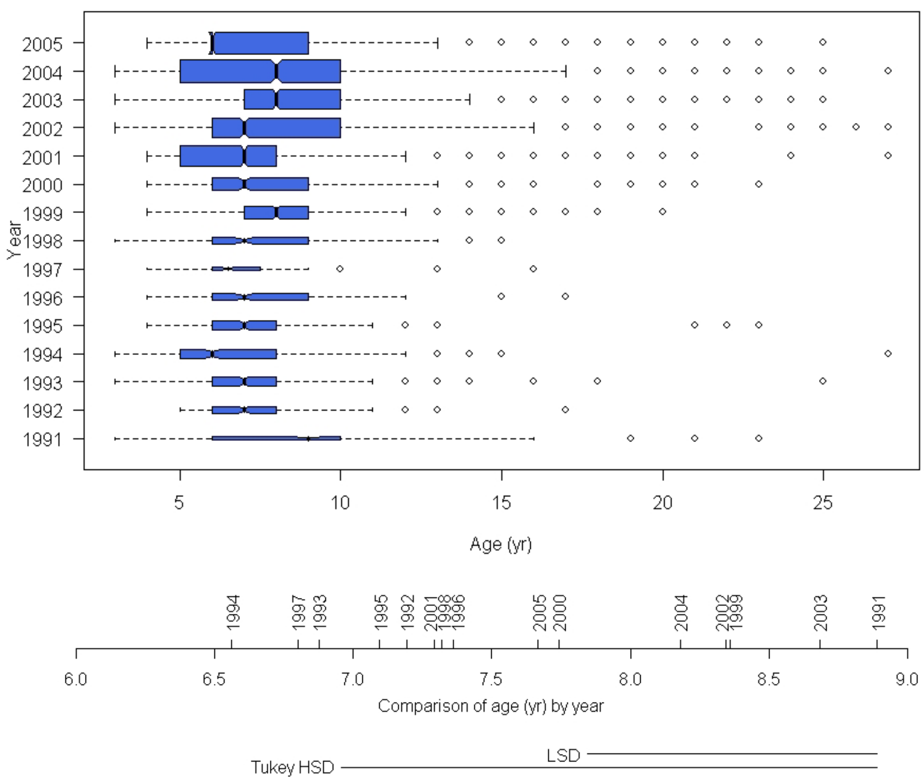
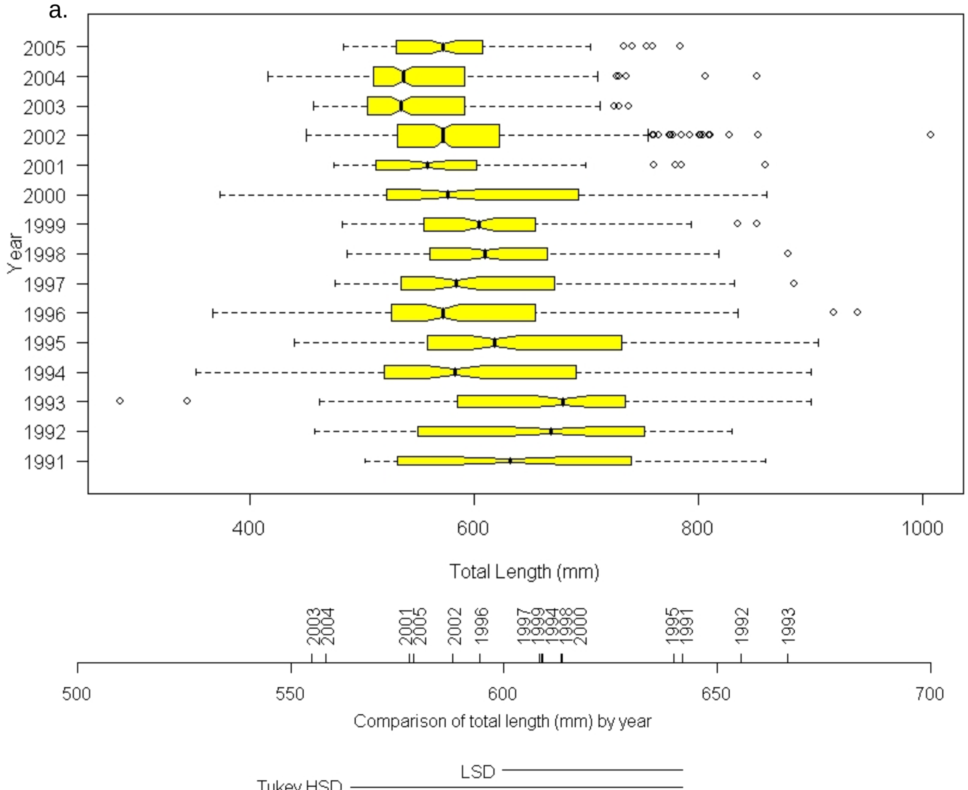


Figure 5. Results of (a) length and (b) age single-factor ANOVA for all recreationally caught red grouper: 1991-2005. See Figure 1 for detailed explanation of box plots and post-hoc tests.

a.



b.

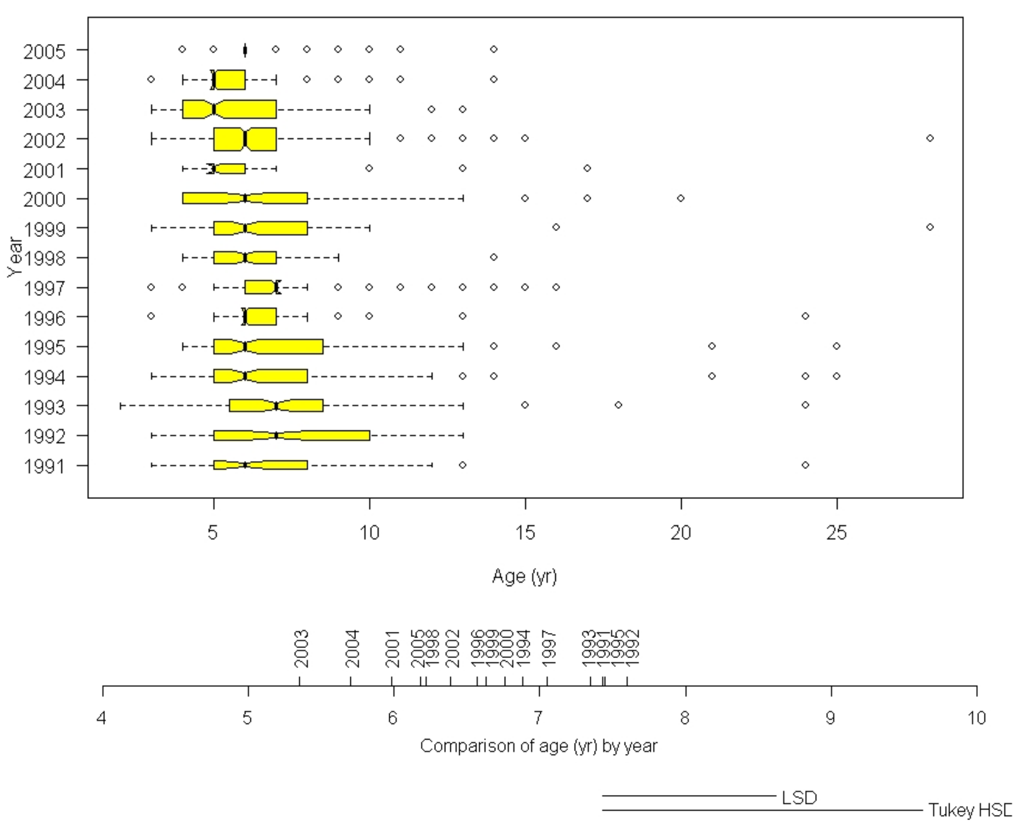
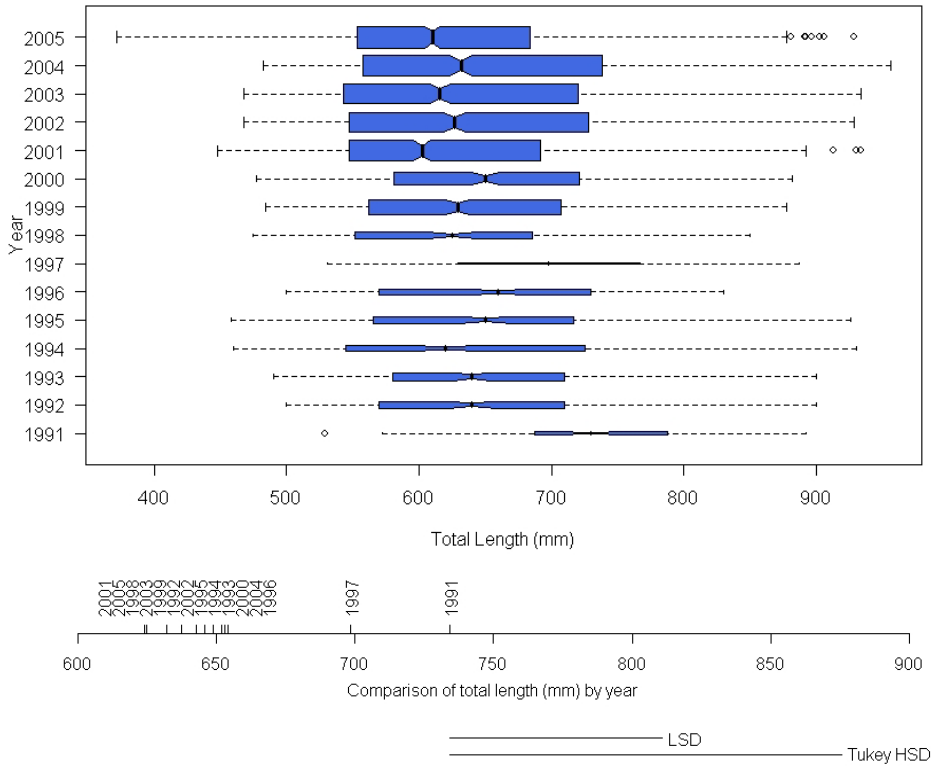


Figure 6. Results of (a) length and (b) age single-factor ANOVA for all commercial red grouper caught by long-lines: 1991-2005. See Figure 1 for detailed explanation of box plots and post-hoc tests.

a.



b.

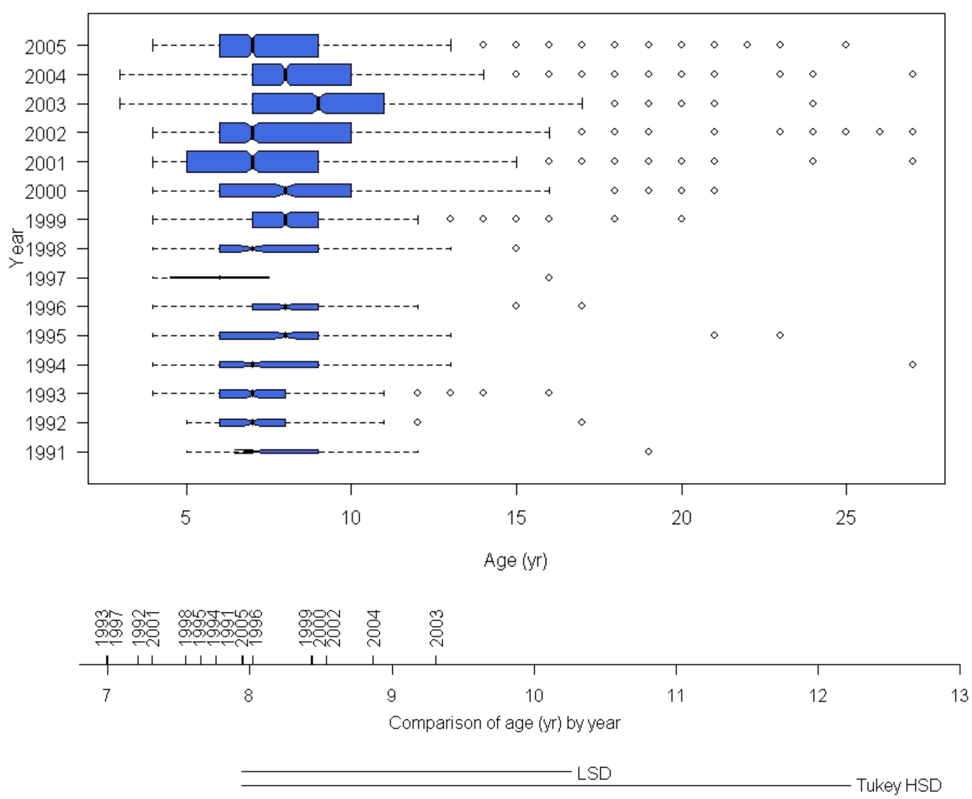
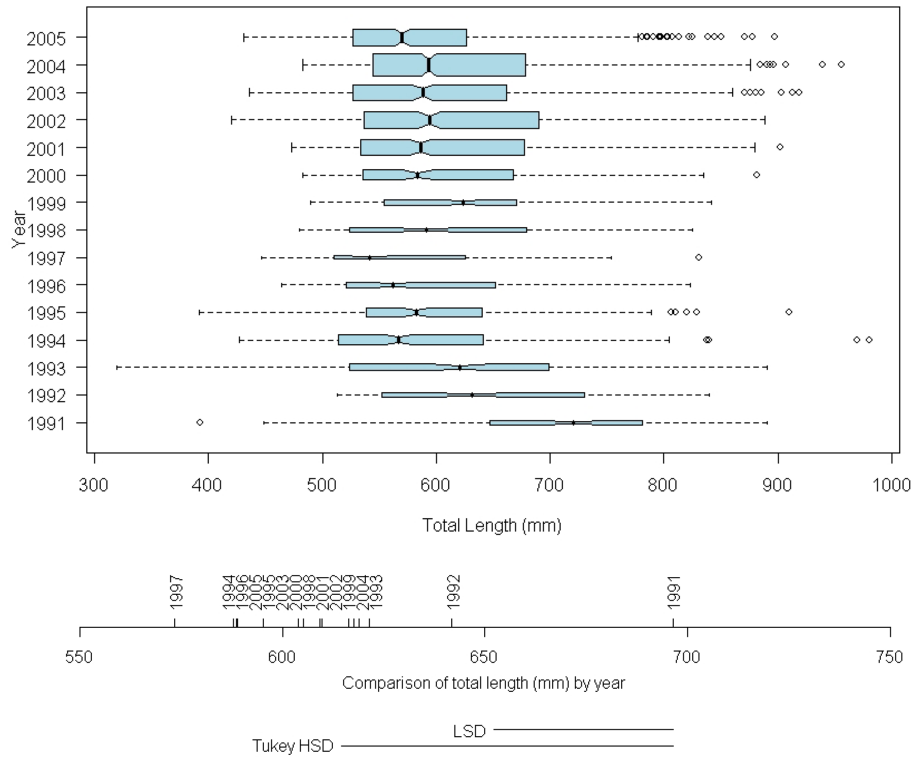


Figure 7. Results of (a) length and (b) age single-factor ANOVA for all commercial red grouper caught by hand-lines: 1991-2005. See Figure 1 for detailed explanation of box plots and post-hoc tests.

a.



b.

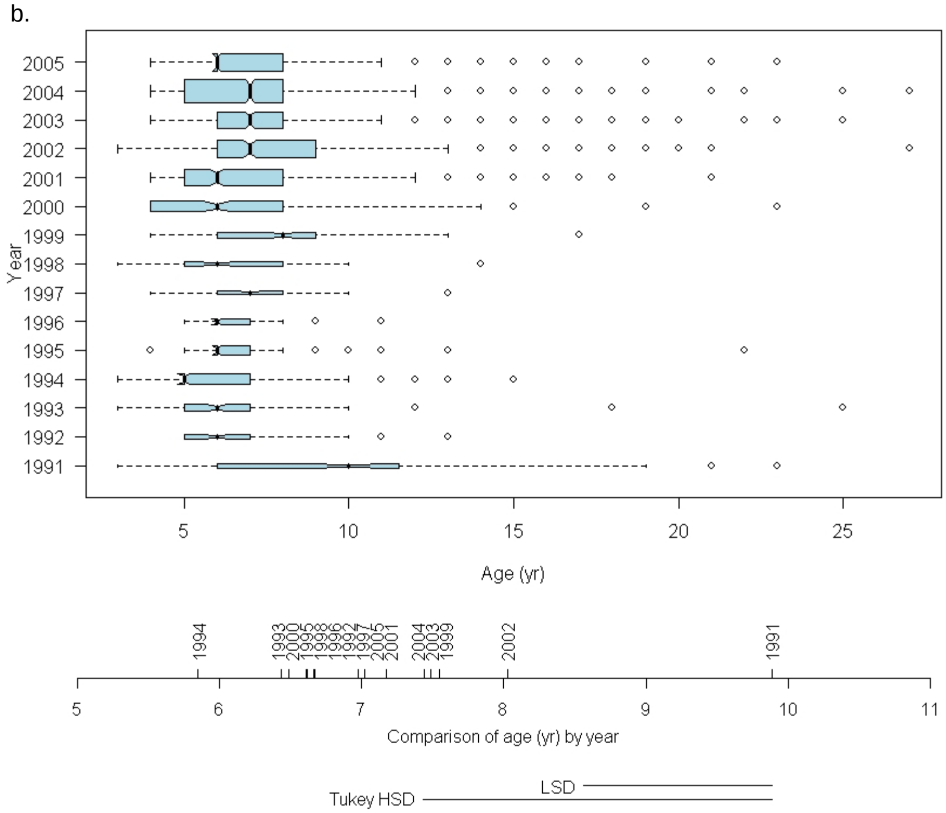


Figure 8. Comparison of red grouper (a) length distribution, (b) age distribution and (c) size-at-age (± se) data between two time periods PRE (1978-1989) and POST(1991-1994). Size-at-age comparisons only for those age groups with n ≥ 5, * Indicates significant differences.

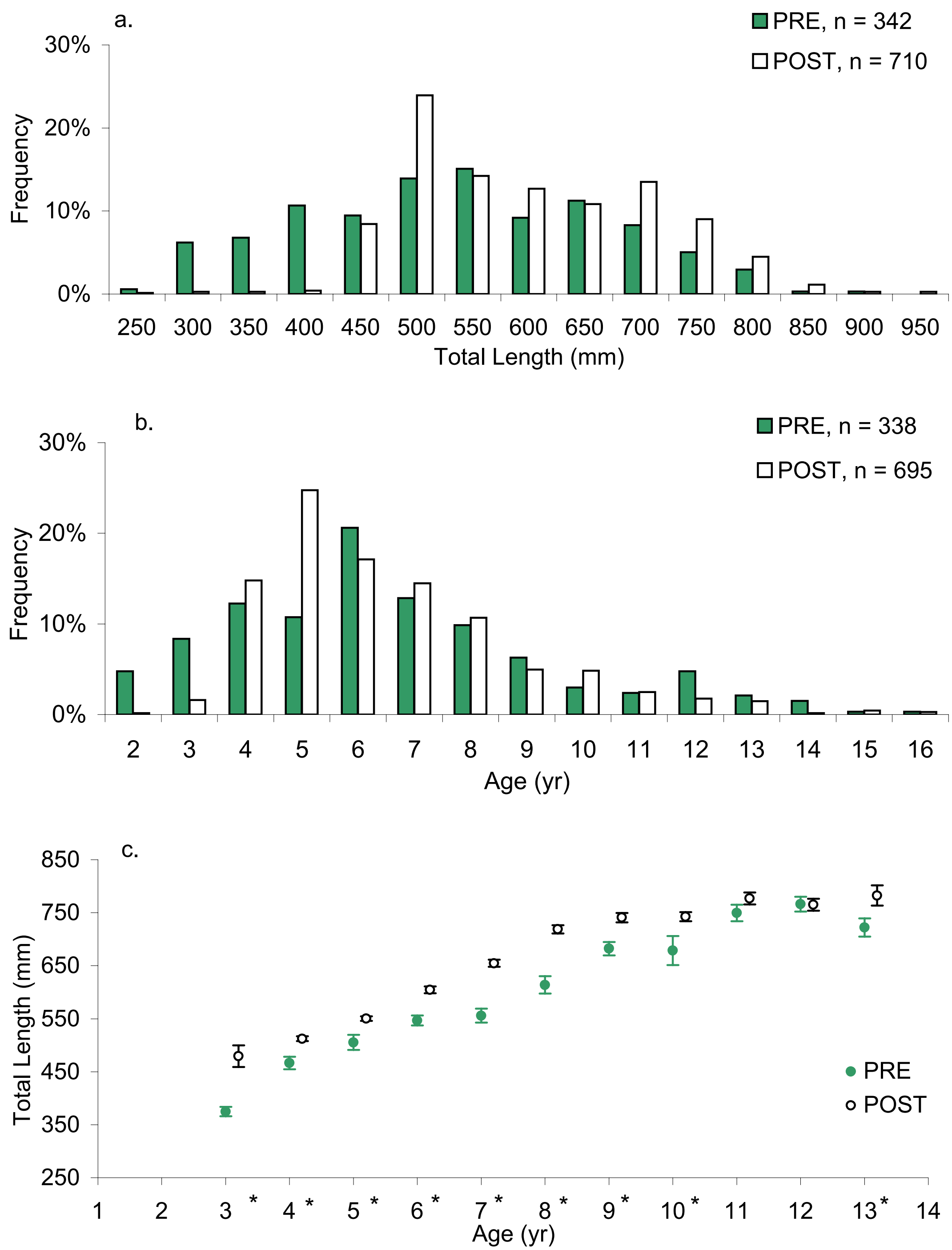


Figure 9. Comparison of red grouper (a) commercial, (b) recreational and (c) Head Boat Survey size-at-age (± se) data between two time periods PRE (1978-1989) and POST(1991-1994) by sector. Size-at-age comparisons only for those age groups with n ≥ 5, * Indicates significant differences.

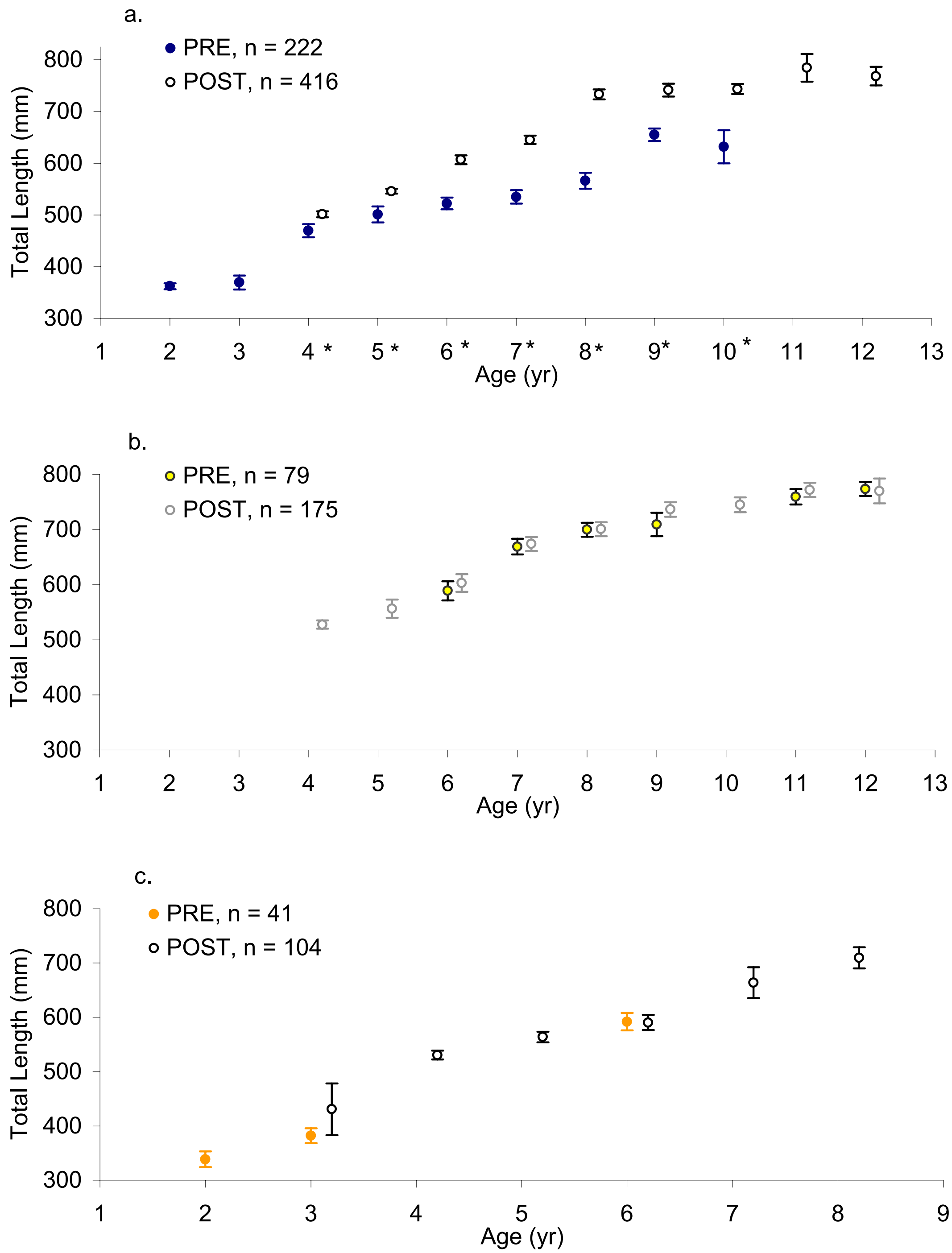


Figure 10. Comparisons of (a) length distribution, (b) age distribution and (c) size-at-age ± se data of red grouper by sector: commercial (CM) and recreational (REC). Size-at-age comparisons only for those age groups with n ≥ 5, * Indicates significant differences.

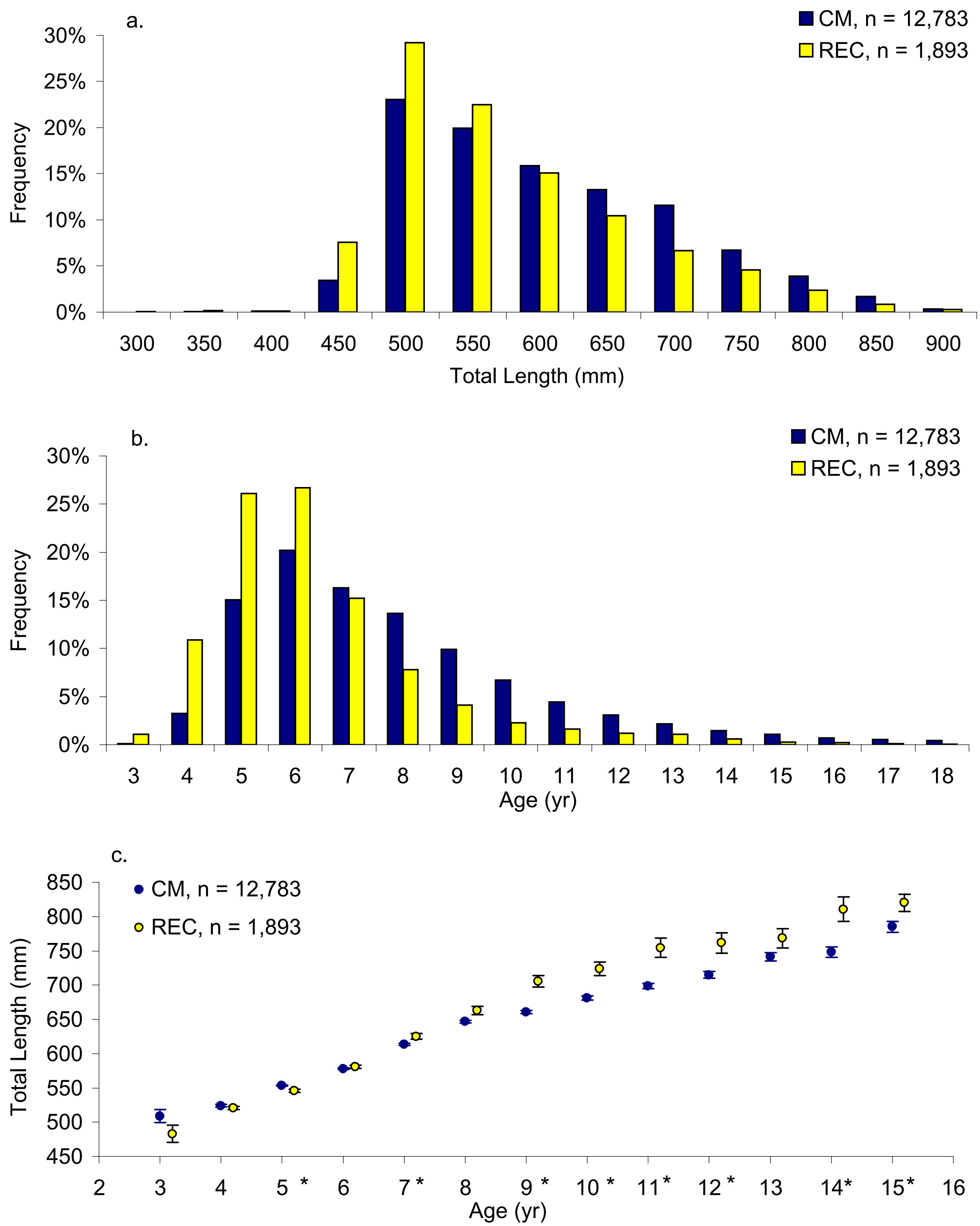


Figure 11. Comparisons of (a) length distribution, (b) age distribution and (c) size-at-age ± se data for commercially caught red grouper by gear, only includes data collected in 2000-2005 due to low sample sizes by gears in earlier years. Size-at-age comparisons only for those age groups with n ≥ 10, * Indicates significant differences.

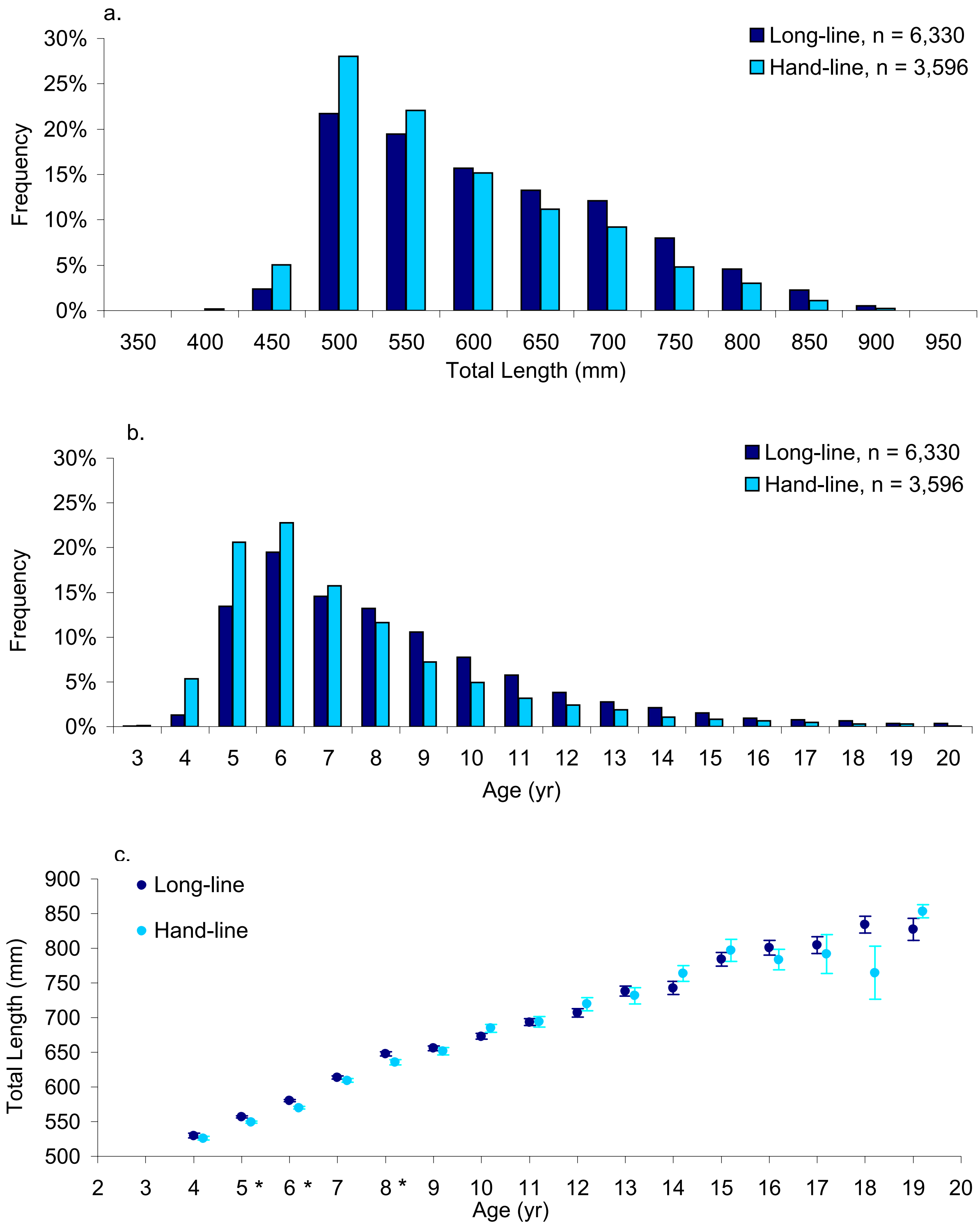


Figure 12. Results of size-modified von Bertalanffy growth curve (a) variance of length by age, (b) for mean fractional ages 0-30 and (c) for mean fractional ages 0-5. Observed mean size-at-age (black circles), estimated size-at-age (red line), and estimated 95% confidence intervals (red dashed line).

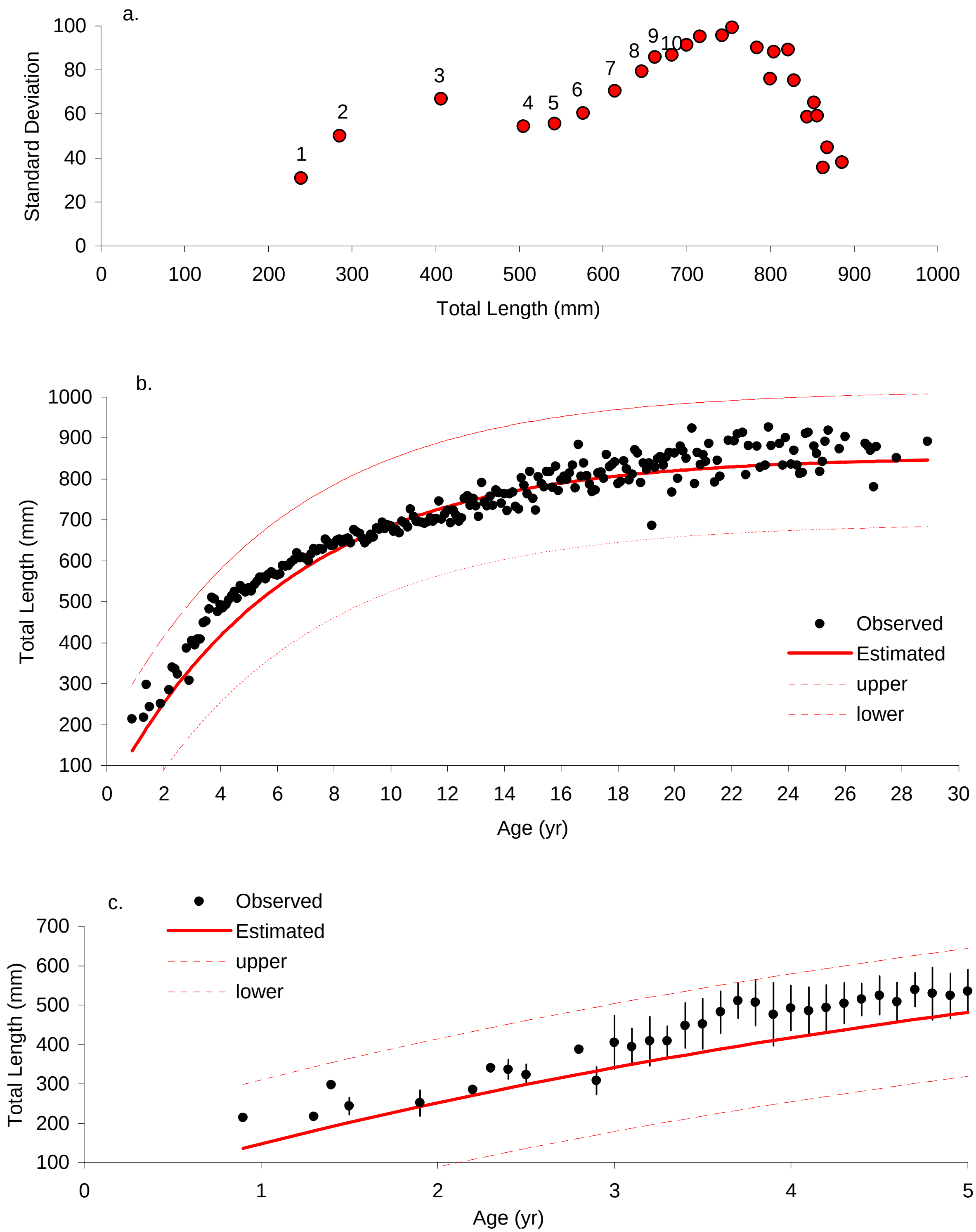


Figure 13. Residual plots for size-modified von Bertalanffy growth model (a) raw residuals, (b) cumulative normalized plot, and (c) residuals by age class, sector, gear, and year.

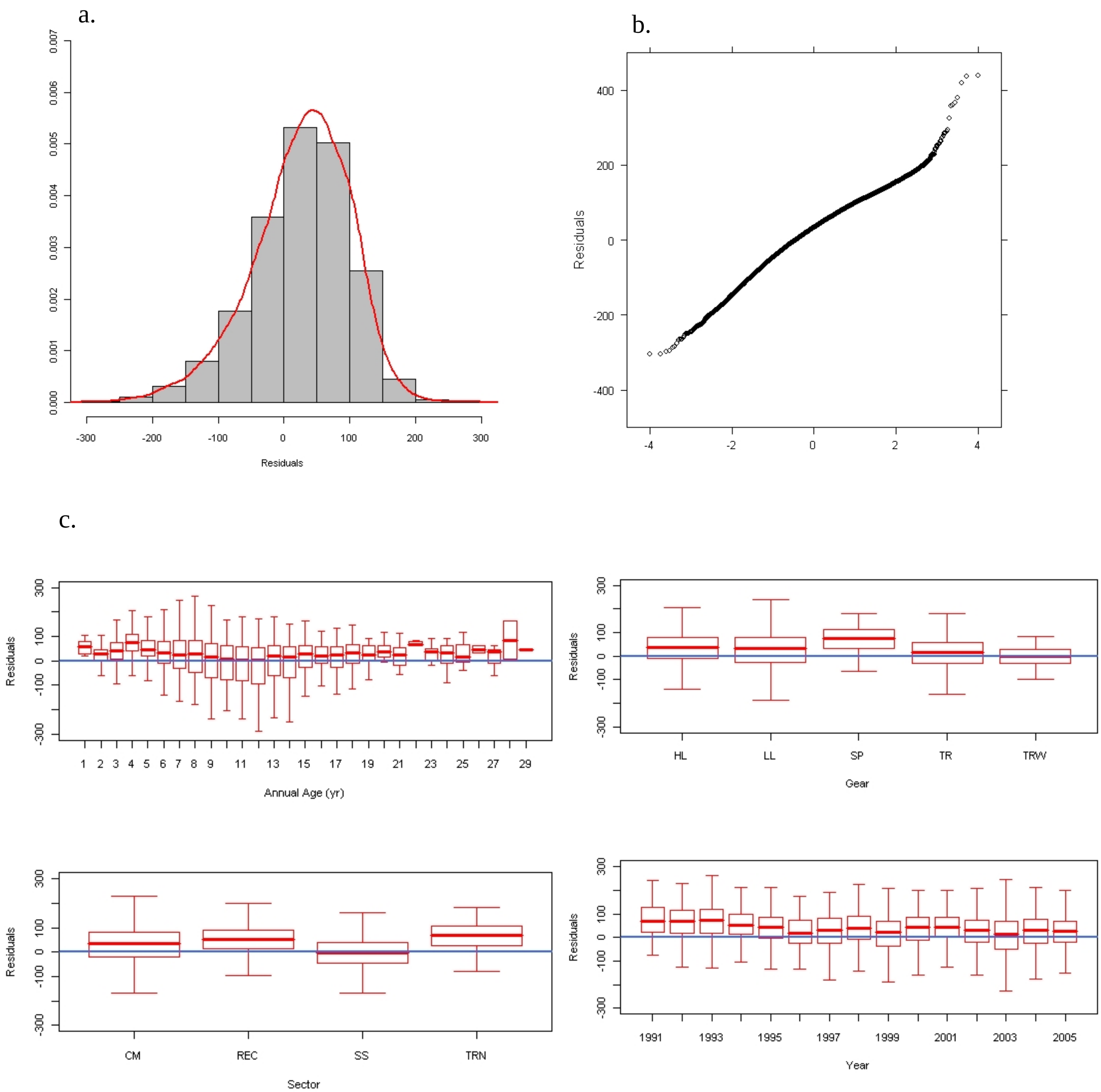


Figure 14. Scatterplot of red grouper observed length and fractional ages (1991-2005, n=15,953), resulting growth curves with size limit selectivity, and previous growth curve with no constraints (Lombardi-Carlson et al. 2002).

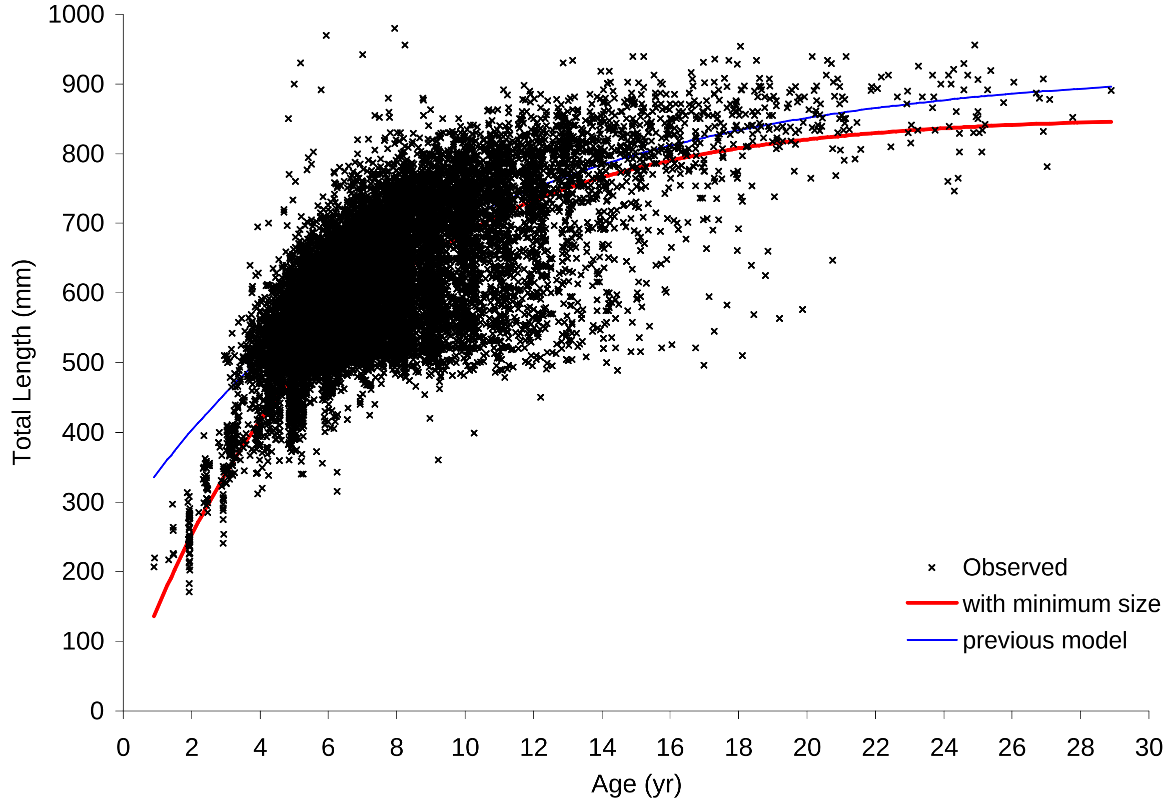


Figure 15. Characterization of commercial gears by depth fished (a) distribution, (b) long-line, and (c) hand-line, sample sizes appear for those years when n < 100.

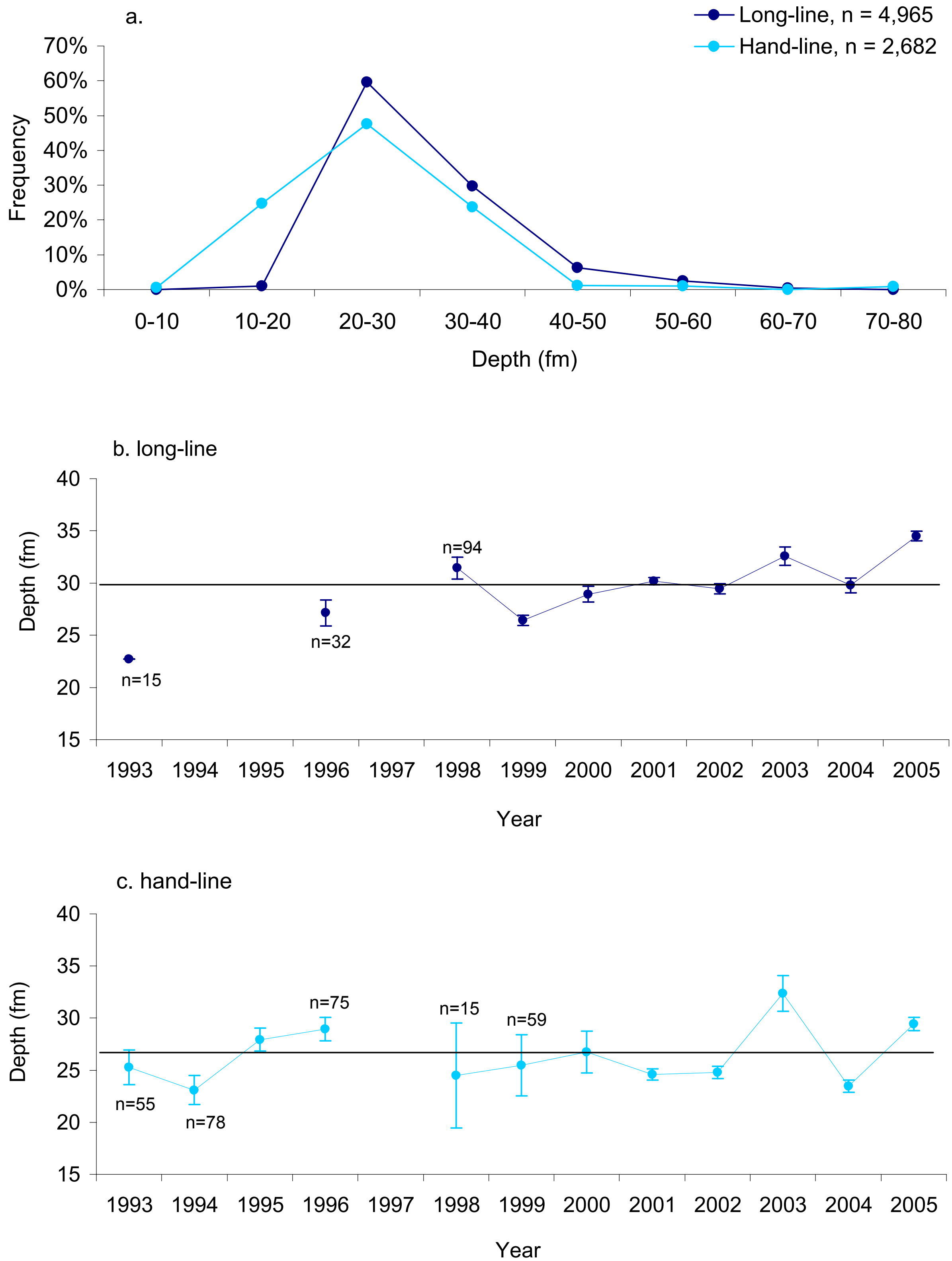


Figure 16. Characterization of (a) total length versus depth, (b) mean total length ± std by 5 fm depth bin, (c) age versus depth, and (d) mean age ± std by 5 fm depth bins for commercially sampled red grouper by gear (2000-2005).

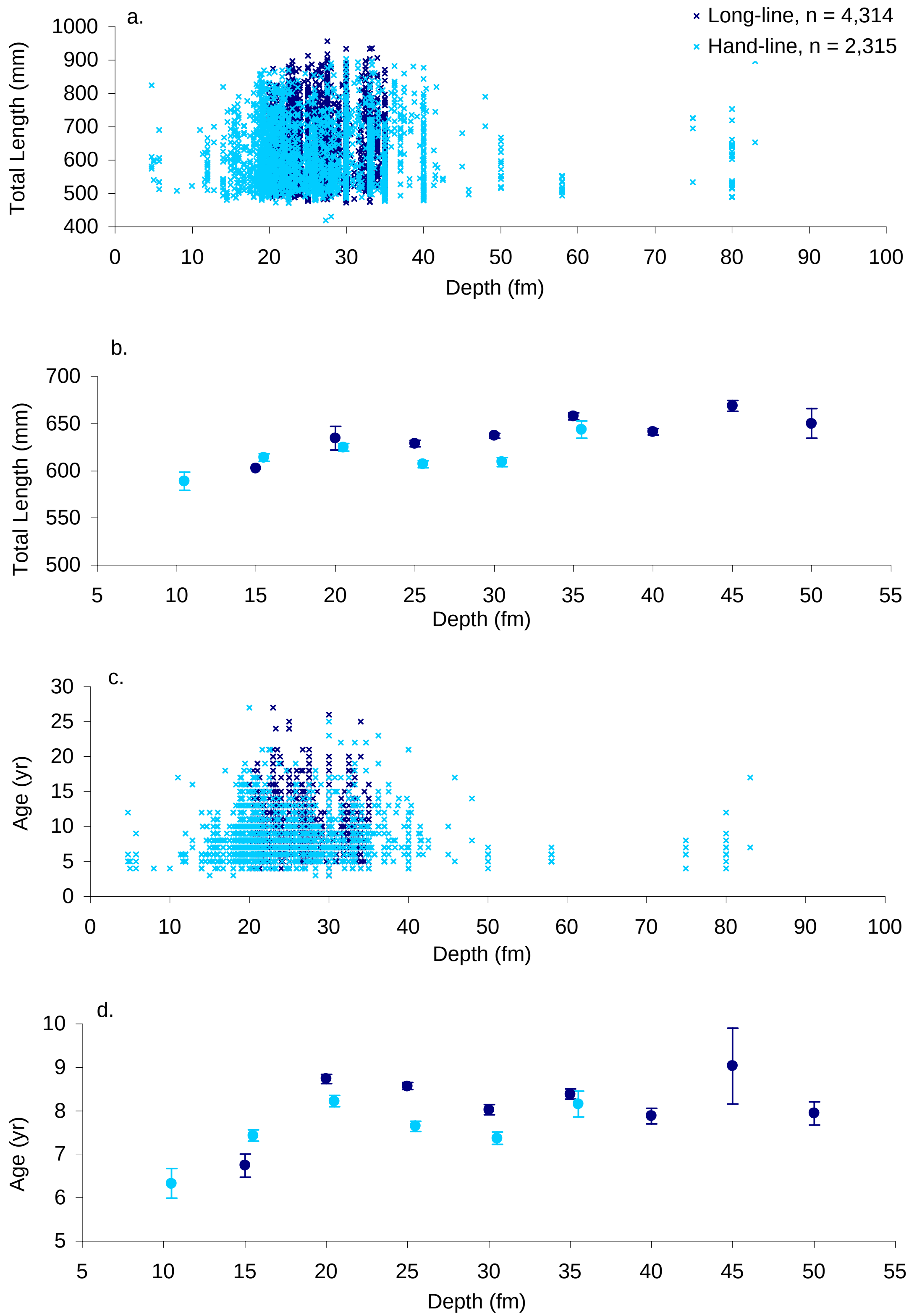


Figure 17. Age proportion data by depth bin (a) 0-19 fm, (b) 20-29 fm, (c) 30-39 fm, (d) >40 fm for commercial data by gear.

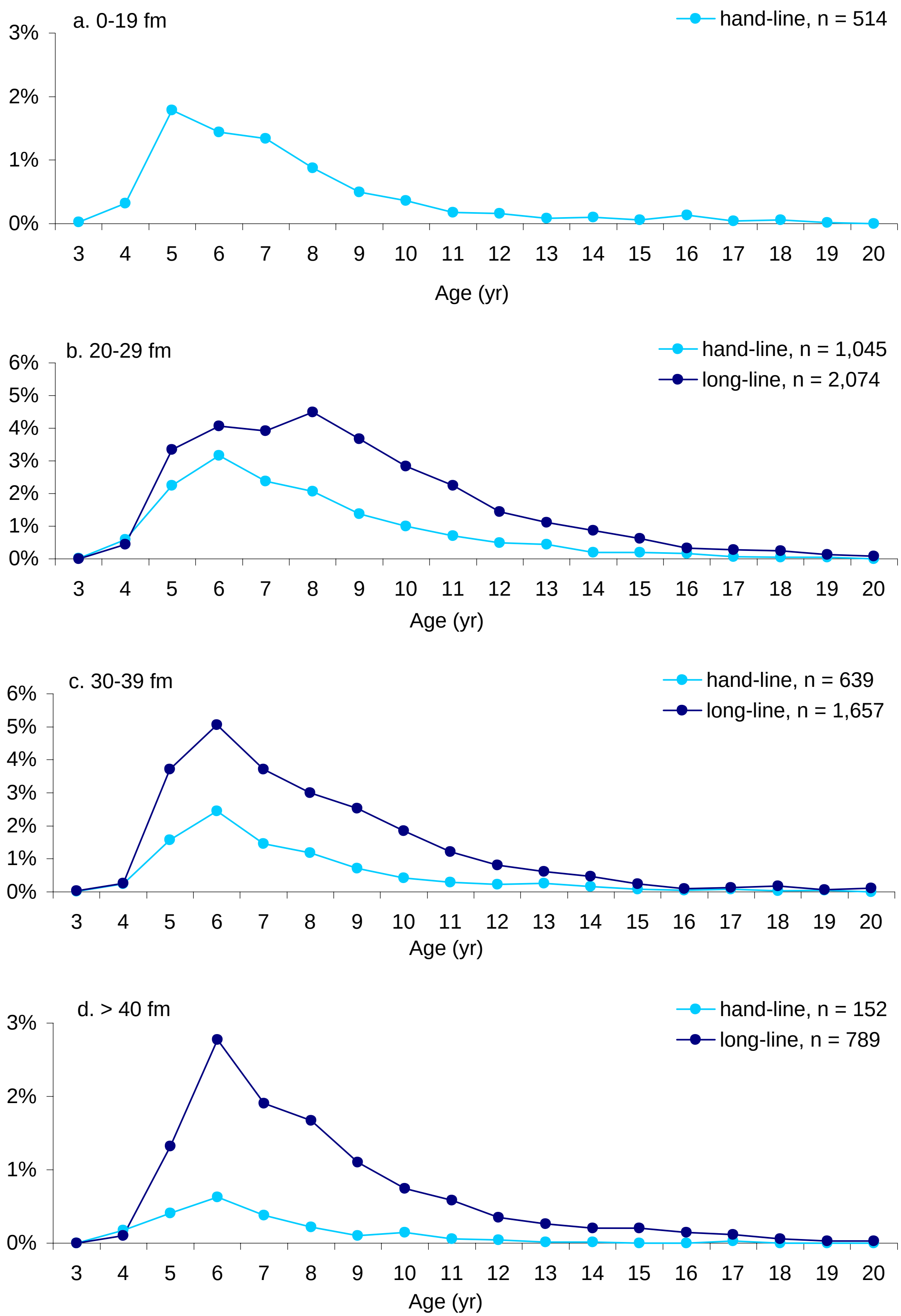


Figure 18. Results of (a) length and (b) age single-factor ANOVA for commercially caught red grouper (2000-2005) by NMFS Statistical Grid. See Figure 1 for detailed explanation of box plots and post-hoc tests.

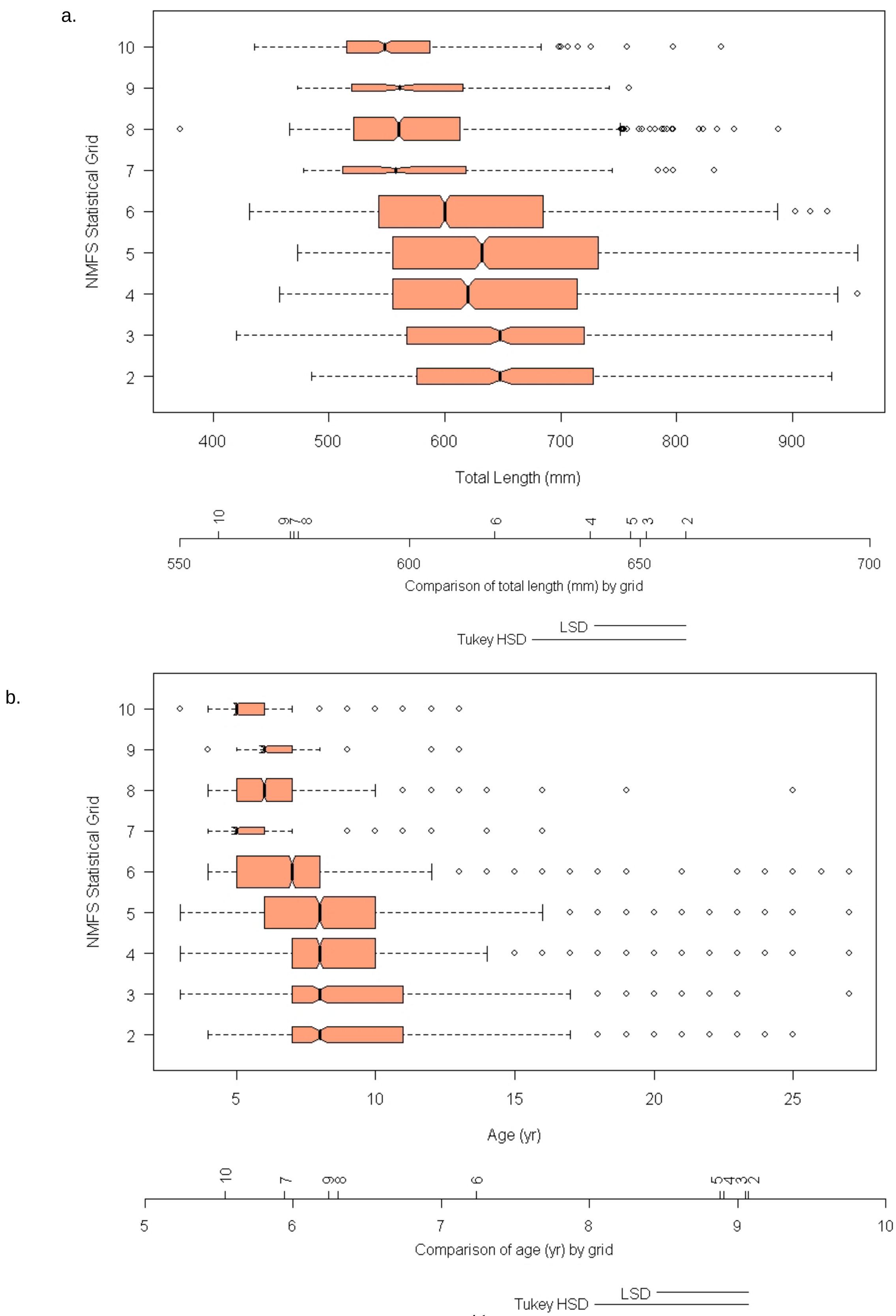


Figure 19. Comparison of red grouper (a) length distribution, (b) age distribution and (c) size-at-age (± se) commercial data (gears combined) by region (2000-2005) Size-at-age comparisons only for those age groups with n ≥ 10, * indicates significant differences.

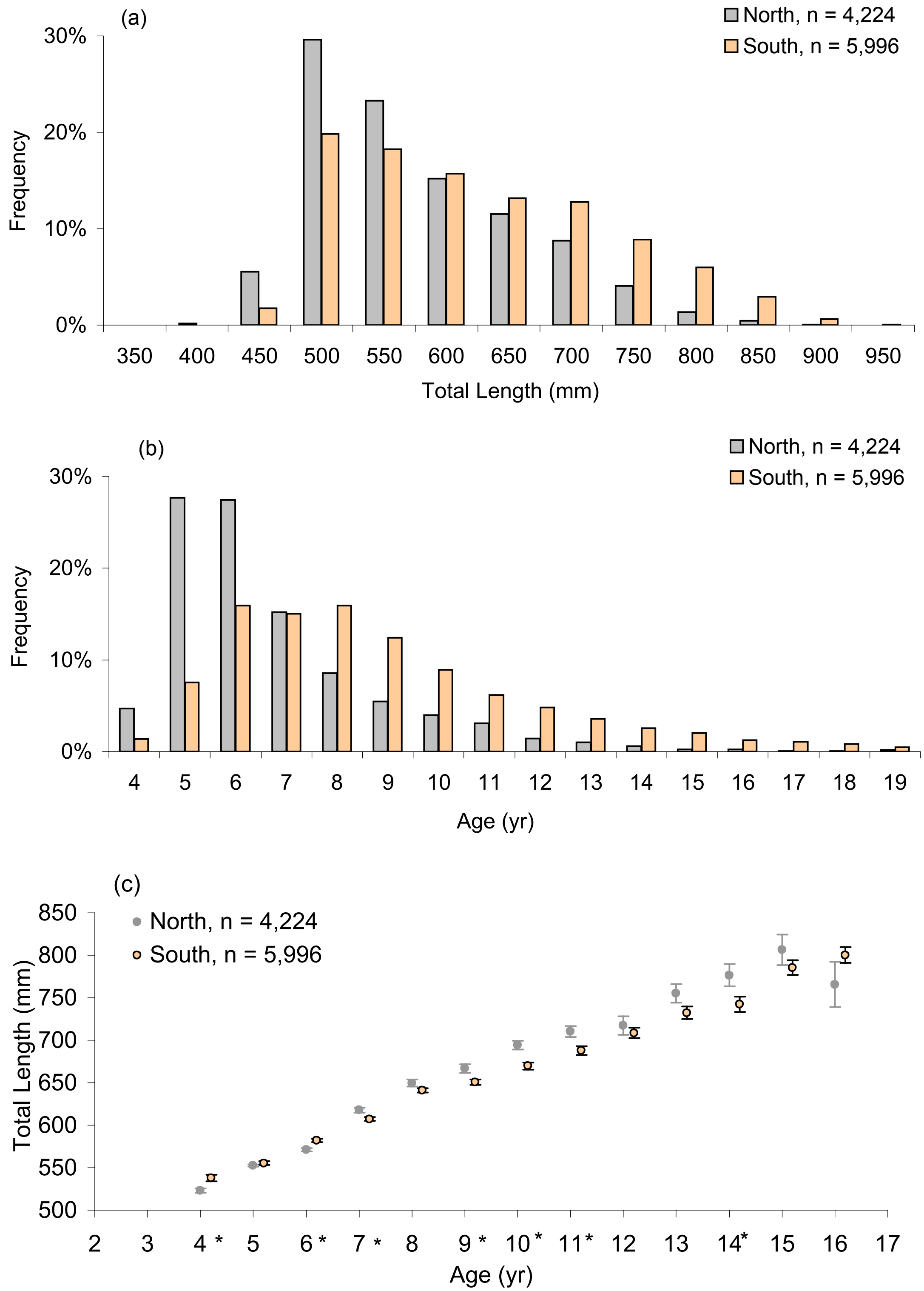


Figure 20. Age distribution (yr) of commercial (gears combined) red grouper (2000-2005) by region. Solid lines depict strong year classes 1996 (navy) and 1999 (purple).