Red Grouper (*Epinephelus morio*) age - length structure and description of growth from the eastern Gulf of Mexico: 1992-2001

Lombardi-Carlson, L. A., Fitzhugh, G. R., and Mikulas, J. J.

National Marine Fisheries Service
Southeastern Fisheries Science Center
3500 Delwood Beach Road
Panama City, FL 32408

Panama City Laboratory
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Abstract

Red grouper (*Epinephelus morio*) are classified as a shallow water grouper, distributed throughout the Gulf of Mexico but primarily harvest occurs along the West Florida Shelf. Red grouper were fully recruited to the fishery by age 5-7 and became rare by age 12. Three dominant year classes were identified (1989, 1990, and 1996), each of these year classes represented over 30% of the age structure for at least one year and was the most abundant age class for at least two years within the 10 year period: 1992-2001. Dominant year classes were apparent across the 10-year span due to good aging precision; overall APE was 3.4%, reflecting relatively low reader error. Commercial hand-line and long-line samples were harvested from similar depth distributions, however, a slight difference in growth rate was detected based on samples specific to these gears. The von Bertalanffy growth model was fitted to biological ages and lengths at capture and similar asymptotic lengths (L_∞ = 923 mm TL), but lower k (0.11), and lower t_o values (-3.21) compared to past studies in the eastern Gulf of Mexico and southeastern Atlantic. Because of problems with the distributions of data, an ad hoc fit was calculated for the von Bertalanffy function (L_∞= 920mm TL, k = 0.16, and t_o = zero) that may be useful as a simple representation of average growth.

Introduction

Red Grouper (*Epinephelus morio*) are widely distributed throughout the Gulf of Mexico, Caribbean, and U.S. South Atlantic. Adults are fished from North Carolina to Brazil (Moe 1969, Stiles and Burton 1994) and in U.S. Gulf waters, red grouper are classified as the major component (about 69%) of the shallow water grouper complex (Schirripa and Legault 1997, 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 fathoms), mainly inhabiting reefs and hard bottom areas (Moe 1969). Recognized as one the most valuable fishes from the Gulf of Mexico, red grouper are a highly sought target species and during the last stock assessment were classified as overfished and undergoing overfishing (Schirripa *et al*. 1999).

Because age and growth information is critical to stock assessment, our goal is to characterize age structure over time, by gear type and by depth/location based on a continuous decade of otolith samples from 1992-2001. This includes newer un-analyzed samples from 1997-2001 and re-aged samples from earlier collections archived at this laboratory (1992-1996; Johnson and Collins 1994, Johnson *et al*. 1997). We provide age-length keys, meristic conversion equations, updated growth curves, a comparison of the old and updated age estimates and compare results with previous studies.

Methods

Collection of Samples

Port agents from numerous federal and state funded sources (Trip Interview Program – TIP, Beaufort Head Boat Survey – HB, Marine Recreational Fishery Statistical Survey- MRFSS, scientific sampling surveys – SS) collected red grouper otoliths from the eastern Gulf of Mexico from 1992 to 2001. Measurements of fish lengths (total and/or fork), weights (whole or gutted), and removal of otoliths were completed in the field, and corresponding otolith weights were recorded per sample at the NMFS/SEFSC in Panama City, Florida. Information describing catch location (latitude, longitude, depth, or statistical reporting grid) was often reported with the samples. Trip Interview Program, Beaufort Head Boat Survey, and Marine Recreational Fisheries Statistical Survey port agents randomly collected red grouper from the landings of both recreational and commercial fisheries, reflecting all gear types (e.g. hand-line, bandit, power-lines, long-lines, trap).

Otolith preparation, sectioning, and aging technique

As described in Moe (1969), the sagittal otolith was used as the ageing structure. 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 the sulcus acousiticus. This area was consistently used to obtain and combine accurate readings from both whole and sectioned otoliths (Figure 1a and b). Only the collection number and fish number were available to the readers during reading of the otoliths.

Whole otoliths were submerged in water, placed concave side up in a black watch glass, and viewed through a stereomicroscope with the aid of reflected light from a fiber optic light source. Normally, whole otoliths were manipulated with the use of forceps to acquire a flat surface to age. This was helpful when bands were close together and in determining edge types. Each opaque band equated to one year of growth, an annulus (Moe 1969, Johnson and Collins 1994, Stiles and Burton 1994, Burgos 2001). Edge types were recorded as either translucent or opaque.

Otoliths that were difficult to interpret either due to otolith thickness or opaqueness 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. As otoliths were read the number of opaque bands plus the edge type was recorded. The decision to section was based on the primary readers judgment. By aging a considerable number of otoliths whole, processing time and costs were reduced.

Age and Growth Analysis

The 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 a year in age between the period of January 1st to June 30th if their edge-type was translucent. Typically, marine fish in the southeastern U.S. complete annulus formation (opaque zone formation) 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 3rd (opaque) annulus would have soon formed. Any fish caught before June 30th 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. There were a few instances when an opaque edge was detected from fish caught late in the year (November and December). We assumed these fish were depositing the next year's band early and one year was subtracted from their band count to calculate an annual age.

In addition to annual or cohort age, biological age was determined for use in growth curves. A fractional period of a year was determined as the difference from peak spawning and capture date (red grouper peak spawning = May 15th; Moe 1969, Collins *et al*. 2002). If capture date was later in the year than 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.

Two readers participated in aging the otoliths. The primary reader (L.L.C.) read all samples and the secondary reader (J.M.) read at least 20% of the samples from each year. Three indices of ageing error were calculated per year and for all samples combined for those otoliths read by both readers: (1) Average Percent Error (APE), (2) Coefficient of variation, and (3) Percent of Readings in Agreement within ±1 or ± 2 band counts (Beamish and Fournier 1981, Chang 1982). The secondary reader mean age ± 95 % confidence intervals were calculated given the primary reader's age to detect any age bias between readers (Campana *et al.* 1995). Although whole and sectioned ages were not explicitly compared for individual fish, reader precision estimates for both whole and sectioned ages were compared to investigate whether any differences were apparent between these two methods.

The samples previously aged, 1992 through 1996, by Johnson (1994, 1997) were re-read by the primary reader (1, 597 sections, 514 whole otoliths). As processing techniques and equipment have improved over time, the sections (n = 1597) were re-sanded, polished, and sealed with cyto-seal and re-read by the primary reader. The same 3 indices of ageing error were calculated for those otoliths read by the primary reader and Johnson (see above). Johnson's mean age ± 95% confidence intervals were determined given the primary reader's age to detect any age bias between readers (Campana *et al*. 1995).

Age-length frequencies were produced for each year with all modes and gears combined. This was performed in order to detect any apparent trends in age structure during the 10-year period. Annual age and observed length at capture were used to construct age-length keys. The age-at-length data were aggregated into 50 mm (~2 inch) intervals for all years combined and for each year separately (Bartoo and Parker 1983).

Meristic relationships were calculated for lengths, body weights, and otolith weights for all red grouper caught from 1992 to 2001. Conversions from fork length (mm) to total length (mm) and for age (years) to otolith weight (g) were calculated through a linear regression (S plus 2000, Math Soft, Inc). Conversions from total length (mm) to whole weight (kg) and gutted weight (kg) and from fork length (mm) to whole weight (kg) and gutted weight (kg) were calculated through a non-linear regression (S plus 2000, Math Soft, Inc).

Growth curves, based on biological ages were constructed using the von Bertalanffy growth function

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

where

L_t = length at time t,

L_∞ = asymptotic length,

k = growth coefficient,

t = time, and

t_o = age at time zero

and the Schnute and Richard's function

$$y_t = y_\infty (1 + \alpha e^{-at^c})^{-(1/b)}$$

where

y_t = size at time t,

y_∞= average maximum value of variable y,

t = age,

a, b, c, and α = fitted parameters (Haddon 2000).

Growth curve model fits were accomplished using the Solver routine in Microsoft Excel 2000. These parameters were estimated using a least square non-linear regression. Different fits of the von Bertalanffy growth function were compared for different gear types using a maximum likelihood ratio approach (Haddon 2000) and executed using SAS code. This method assigns a degree of freedom for each parameter (L_∞, k, t_o) and does not assume equal variances.

Results

Red groupers have been sampled and aged at the National Marine Fisheries Service-Southeastern Fisheries Science Center in Panama City, Florida, since 1979 (Johnson and Collins 1994). Although there have been periods of low sampling effort, there is a continuous decade of otolith samples from 1992 through 2001. A total of 6,438 red grouper otoliths were collected from commercial, recreational, and scientific survey landings during this period. A majority of the red grouper otoliths were collected by Trip Interview Program port agents at 87% (annual range: 60-95%), followed by Scientific Survey (NMFS-Panama City, FL and Pascagoula, MS laboratory personal) at 9% (annual range: 1-40%), 3% (annual range: 0-13%) from the Beaufort

Head Boat Survey, and 1% (annual range: 0-4%) from MRFSS port agents/contractors (Figure 2a). Seventy-eight percent of the samples were randomly selected from commercial landings, 16% of the samples were randomly selected from recreational landings, and 6% were collected by scientific survey with the use of hand-line, long-line or trap gear types (Figure 2b). The commercial samples comprised of 62% from long-line, 33% from hand-line, and 5% caught in traps (Figure 2c). A majority of the samples (60%) were sampled from the last 3 years of sampling (1999-2001: Table 1). In 2001, the greatest number of samples were received (n = 2008), representing about 0.1% of the total red grouper harvested by number.

Of the total otoliths collected, the primary reader aged 6,353 red grouper otoliths (3,081 sections and 3,272 whole). A total of 6,073 samples (96% of all samples) were used in this analysis and those eliminated included samples that could not be read, mostly due to problems associated with processing (off-angle sections and over polishing). The second reader read 57% (n = 3454) of the otolith collection. An overall APE of 3.4% was calculated between the readers with an annual range from 2.1 to 4.9%. A coefficient of variation was calculated at 4.8%. The overall percent of readings in agreement ±1 year was 87% (annual range: 81-99%) and ±2 years were 95% (annual range: 91-100%). No age bias was detected for fish aged 10 years or younger, however, after age 10 there was a slight difference between readers, the secondary reader tending to age low (Figure 3a). A comparison of reader precision for whole versus sectioned ages revealed that agreements were higher for whole otolith ages (APE = 2.4%) than for sectioned ages (APE = 4.3%).

The primary reader aged 1,627 (1,182 sections, 445 whole) red grouper otoliths previously aged by Johnson (1994, 1997). An overall APE of 4.7% was calculated between the readers with an annual range from 2.1 to 5.8% throughout the archive years (1992 – 1996). A coefficient of variation was calculated at 6.7%. The overall percent of readings in agreement ±1 year was 89% (annual range: 86-93%) and ±2 years were 98% (annual range: 98-100%). In addition, no age bias was estimated for fish aged 10 years or younger, however, after age 10 there was a slight difference with the primary reader and Johnson; the primary reader tending to age higher (Figure 3b).

Length frequencies throughout the 10-year period were affected by the 20-inch size limit (508 mm) established in 1990 (Figure 4). However, samples of undersized by-catch in 1994 and 1996 (Johnson *et al*. 1997) and increasing undersized scientific survey samples in 2000 and 2001 (Figure 4) increased the percentage of red grouper less than 500 mm, which was useful for growth analysis. We observed that the size structure changed slightly over the 10-year period apparently corresponding to changes in age structure. In general, the size structure from our otolith sampled fish, was similar in comparison to length frequencies (1992 – 1997) reported in the last assessment (Schirripa *et al*. 1999).

Red grouper fully recruited to the fishery by age 5 to 7 and became rare by age 12 to 14 (< 3% of the total annual age structure; Figure 5). Dominant age classes were apparent and exceeded 30% of the total age structure during at least one year and dominated the age structure for two years or more within the 10-year period. Three dominant year classes were present over the decade (Figure 5). The 1989 cohort dominated in 1994 and 1995 corresponding to the 5 and 6 year old fish. The 1990 cohort dominated in 1996 and 1997 as 6 and 7 year old fish. The only other year class to show age-structure domination for two successive years or more and exceed 30% of all the ages was the 1996 age cohort, observed as age 4 and 5 year old fish in 2000 and 2001.

The age-length keys reflected the annual age structure and further show the break down by size class (Table 2a – 2j). For example, the year 1999 has the oldest age structure of the 10-year period. This is the only year that fish in the 600-649 mm size class were predominately 8 years old (Table 2h).

Most regressions for converting units of length, whole body weights, otolith weights and age contained at least 1200 samples (Table 3). The equation converting from fork length (mm) to total length (mm) was calculated with an r^2 value of 0.98 with a sample size of 2066. The regression for age (years) and otolith weight was estimated with an r^2 value of 0.72.

The von Bertalanffy growth model was fitted to observed lengths and biological ages for combined data and for each mode and gear separately (Table 4, Figure 6). The highest asymptotic length (L_∞) was estimated from commercial long-line samples (L_∞ = 1026 mm), whereas the lowest asymptotic length was calculated from all the data combined (L_∞ = 923 mm). Similar growth coefficient (k) values were detected among all data combined (k = 0.11), commercial hand-line (k = 0.10), and recreational samples (k = 0.11). Size at time zero (t_o) values were different among the comparisons, however these values may be unreasonable due to the lack of smaller sized fish (less than 300mm TL) in the age data set (Figure 6). Maximum likelihood test ratios detected differences among all pairs of comparisons (Table 5).

Since the von Bertalanffy growth curve is limited in it's flexibility to mimic average fish growth through an entire life span, a Schnute and Richard's 5-parameter growth function (Craig 1999, Haddon 2000) and an ad-hoc "best estimate" growth curve were also fitted to the observed lengths and biological ages for all data combined. The Schnute and Richard's 5-parameter growth function projected a higher asymptotic length (1009mm TL) and a lower size at the origin, compared to the unconstrained von Bertalanffy growth function (Table 4, Figure 7). The ad-hoc growth curve was constructed by manipulating 2 of the 3 parameters from the von Bertalanffy growth function, L_∞ was set to 920mm (based on the original fit with all data), t_o was restricted to zero, and k was unconstrained in the curve fit. The result was that k was intermediate to values estimated in previous studies (k = 0.16; Table 6).

Discussion

Moe (1969) completed the first in-depth investigation on the biology, including age and growth estimates, of the red grouper. Continued efforts have been conducted in the southeastern Atlantic (Stiles and Burton 1994), northeastern Gulf of Mexico (Johnson and Collins 1994), and in the southwest Gulf of Mexico and in the Bay of Campeche (Doi *et al*. 1981). Our investigation both adds to the historical data and provides a comparison to results obtained over a period of 40 years (1960s – 1990s).

Dominant year classes were observed and identified from the age structure from the 10-years of continuous data (1992-2001). A dominant year class typically appeared early (age 4) in the age structure, composing at least 10% of the age structure at this early age (cohorts: 1989, 1990, 1996; Figure 5). It may be noteworthy that we observed (and arbitrarily defined) dominant red grouper age classes as those that exceeded 30% of annual age structure in a given year. Also, noteworthy is that two sequential year classes of red grouper (1989 and 1990) appeared to be distinguishable as dominant cohorts. But for gag, we observed dominant ages that exceeded 40% of annual age structure (Fitzhugh *et al*. in press). Both groupers were relatively easy to age and for both species, dominant year classes were apparent for several years among the age distributions. Our observation that “dominant” red grouper cohorts tended not to achieve as high an age proportion as “dominant” gag cohorts, may indicate that red grouper recruitment is less episodic.

Studies show that when otoliths appear easy to interpret and age, and reader precision is high (Morrison *et al*. 1998), year class patterns are often more evident across years (Campana 2001). This appears to be the case for red grouper compared to many species. An APE of 3.4% between the primary and secondary reader was below the median value of 5.5% determined from a review of 117 studies (Campana 2001). An APE of 4.7% was calculated in comparison to an earlier ager (A. Johnson) and was also below the median. Differences detected for the older samples (pre – 1997) could be due to differences in sectioning techniques. We also found that the APE from ages of whole otoliths (APE = 2.4%) were lower than the APE from sectioned otoliths (APE = 4.3%), which appears counter-intuitive given the problems that have resulted when aging programs were devoted to using whole otoliths (Campana 2001). Our finding that whole otoliths were easier to interpret with greater precision may be due to the fact that the youngest fish (majority less than 10 bands) were aged whole.

There is always concern that limited sampling of otoliths will not enable adequate representation of the catch. While our sample size (n > 6,000) far exceeds that of previous studies, annual representation is still rather low (about 0.1% harvest by number in 2001). There were fluctuations in the sample sizes over the years, but we noted consistent patterns in the age structure from 1992 to 2001. For example, common ages for red grouper consisted of fish from 4 to 8 years old every year. Annual sample size variations seem to affect the older age classes – late teens and twenties (Figure 8). During those years of increased sample sizes (greater than 800 individual fish; 1999, 2000, and 2001), at least 20% of the age structure was comprised of fish older than 10 years of age. But we have some confidence that the age-sampled red grouper are representative of the catch for the common sizes and ages. Our size structure was similar in comparison to the length frequencies (1992 – 1997) reported in the last stock assessment (Schirripa *et al*. 1999). We also have some confidence that red grouper are reasonably well sampled since the primary area of harvest is the West Florida shelf, which is relatively small in comparison to other fisheries that encompass larger geographical areas. However, commercial trap samples were under represented and may be an exception.

Since the otolith samples were obtained from several gear types, it is often of interest to examine if gear selectivity might result in different growth curves and independent reviewers have asked for these comparisons (Kenchington 2001). A maximum likelihood approach (Haddon 2000) was used to test for coincident curves comparing recreational hook and line, commercial hook and line, commercial long-line and commercial trap gears (Figure 6, Table 4). In every comparison, the curves were not coincident. Further examination of the parameters revealed the cause of the gear-based differences, which were usually either asymptotic length (L_∞) or t_o, relating back to the problems with rare observations at the extremes of the curves affecting the fit. Haddon (2000) cautions against drawing ill-reasoned conclusions in growth curve comparisons because of the nature of the data fitting problems.

Although gear-specific curves were not coincident, the differences may not reflect meaningful biological differences based on observations of how and where red grouper are harvested. In other fisheries, such as red snapper and gag, the differences in the size and age structure between hook and line and long-line gears are very notable and are probably related to the different depths and habitats where the gears are fished (Cass-Calay *et al*. 2001, Allman *et al*. in press, Fitzhugh *et al*. in press). But the gear-specific size and age differences are not as pronounced for red grouper. Commercial long-line and hook and line gears targeting red grouper overlap a great deal in the depth zones fished (Figure 9). Never-the-less, red grouper caught by recreational and commercial hook and lines in shallower water depths were slightly younger at size compared to fish caught by the commercial long-lines in deeper water depths (Figure 10). We feel that age/size characterization by depth and habitat is an area of work that requires further attention. But if the need is for a simple representation of average growth, then combining as much of the data as possible from the different gears, across years, to yield a single growth curve may be justified.

Two growth functions were produced using all of the data available: a von Bertalanffy function and an Schnute and Richard's function (Figure 7). These produced generally best fits for comparison to earlier results and for comparing the differences between the typical 3-parameter and higher-parameter curve fits. The original von Bertalanffy fit resulted in an estimate of t_0 of –3.21 years at zero size. This degree of difference from the origin has been criticized in a stock assessment review for gag because the curve would inflate the average size-at-age for the first two years, before the fish are recruited to the fishery (Kenchington 2001). Therefore, we again fit the von Bertalanffy function with a common constraint of t_o equal to zero. This in effect, forced the curve through the size-age origin, which in principal would better mimic the average growth trajectory for young fish. However, when the constraint of t_o equal to zero was applied to the complete red grouper data set, k increased to 0.23 and asymptotic length (L_∞) became unrealistically low (785 mm TL). Our final ad-hoc approach of constraining asymptotic length to 920mm TL based on the original fit, and t_o to zero resulted in a value of k of 0.16, which was intermediate to values from other studies (Table 6) and may be the most biologically reasonable result for our von Bertalanffy fit to our overall data set. Several red grouper otolith-based age studies, as well as these results, confirm that asymptotic length (L_∞) is about 900-1000 mm TL for the von Bertalanffy function since the 1980s (Table 6; Johnson and Collins 1994, Stiles and Burton 1994, Fuentes *et al*. cited in Contreras *et al*. 1994). This was also confirmed by tag and recapture estimates (Schirripa and Burns 1997) and makes sense when viewing size-at-age scattergrams (Figure 8).

Although the two different growth functions cannot be explicitly tested for coincident curves, the 5-parameter Schnute and Richards (SR) curve resulted in sum of squares error only slightly less than the von Bertalanffy growth function (VBGF) for the same data set (SR=27,587,227 versus VBGF=27,596,183). Also, as expected because of it's increased flexibility, the Schnute and Richard's curve approached a size-age origin closer to zero than did the original fit of the von Bertalanffy function (Figure 7). Although Schnute and Richard's function is more difficult to fit (5-parameter vs. 3), is less well known, less commonly used, and perhaps less biologically intuitive, it may be useful if it is important to model growth during the first few years as well as after recruitment to the fishery.

Two of the earlier Gulf of Mexico age studies are noteworthy in that few large red grouper (>800 mm TL) were captured, leading to speculation that growth and/or longevity has changed between the 1960s-1980s compared to the 1990s (Moe 1969, Johnson and Collins 1994). In both studies, red grouper from the earlier time period resulted in a low asymptotic length (L_∞; 789–792 mm TL) compared to studies in the 1990s. Both studies from the earlier time period sampled proportionally more young fish (Moe, 15% ≤ age-3; Johnson and Collins Time period 1, 14% ≤ age-3) compared to this study (0.09% ≤ age-3) and also resulted in a size-age origin much closer to zero than this study. Again this highlights the importance in data sources and distribution (Johnson and Collins 1994). That the growth difference over time is real is best supported by Moe's (1969) assertion that "although sampling was not completely random, no obvious bias for age or size of adult fish was apparent". Moe sampled the commercial hook and line fishery (1963-1964) similar to our samples taken from 1992 to 2001.

In general, our results differ from previous studies due to the distribution of the data as mentioned earlier. Because of the size limits and dependence on fishery-dependent sources, and increased sample size, our data is characterized by a low proportion of young red grouper (age-3 and less) and a much higher number of older individuals (ages in the teens and 20s). Previous studies rarely reported red grouper older than age-16 (Moe 1969, Johnson and Collins 1994, Stiles and Burton 1994, Schirripa and Burns 1997).

Future Research

We recommend that further in-depth investigations should be completed to increase our understanding of the life history of red grouper, *Epinephelus morio*, from the northeastern Gulf of Mexico. Habitat specific data, such as depth, location, and bottom topography, should be collected and correlated to the red grouper caught in those areas. An increase in annual otolith samples more representative of the harvest by fishing mode is recommended. Although, there was no reader bias for ages commonly harvested, (≤ age 10) and reader precision was relatively high, more effort concerning age corroboration and absolute age validation for the oldest ages (e.g., radiocarbon analysis) is also a priority.

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List of Table Captions

Table 1. Samples sizes of red grouper otoliths collected from the eastern Gulf of Mexico divided by mode and gear for each year.

Year	CM LL	CM HL	CM TR	CM other	CP	HB	PR	SS HL	SS LL	SS TR	Total
1992	132	40	14		24	32	1	5			248
1993	148	137	38		56	20	1	5			405
1994	40	203	1		59	26		12			341
1995	145	175	39		94	50		20		3	526
1996	96	83	8	6	132	43		62			430
1997	7	38	17	1	63	25	9				160
1998	103	58	32		72	22	4	1			292
1999	640	80	29		101	8	2	9			869
2000	390	221	38	6	59	12		68			794
2001	1210	559	39	3	45	1	2	68	78	3	2008
TOTALS	2911	1594	255	16	705	239	19	250	78	6	6073

Key to abbreviations:
CM LL – Commercial Long-line
CM HL – Commercial Hand-line
CM TR – Commercial Trap
CM other – Commercial other gear types: spear, ect.
CP – Charter boat
HB – Beaufort Head Boat
PR – Private
combined for Recreational Samples
SS HL – Scientific Survey Hand-line
SS LL – Scientific Survey Long-line
SS TR – Scientific Survey Trap

Table 2a - 2j. Age-length keys for red grouper from the eastern Gulf of Mexico for each year: 1992 to 2001, sample sizes are in parenthesis (size bins are in 50mm increments, for example 500mm includes 500 to 549mm in total length).

Table 2a. 1992, n = 248

Age		3	4	5	6	7	8	9	10	11	12	13	17	29
TL (mm)	n													
300	0													
350	0													
400	2			0.50 (1)	0.50 (1)									
450	2		0.50 (1)	0.50 (1)										
500	42	0.02 (1)	0.02 (1)	0.31 (13)	0.31 (13)	0.21 (9)	0.05 (2)	0.05 (2)			0.02 (1)			
550	44		0.02 (1)	0.18 (8)	0.39 (17)	0.20 (9)	0.18 (8)	0.02 (1)						
600	31			0.42 (13)	0.29 (9)	0.23 (7)	0.06 (2)							
650	39			0.10 (4)	0.18 (7)	0.38 (15)	0.18 (7)	0.15 (6)						
700	45				0.07 (3)	0.33 (15)	0.29 (13)	0.13 (6)	0.09 (4)	0.02 (1)	0.02 (1)	0.04 (2)		
750	25					0.12 (3)	0.28 (7)	0.12 (3)	0.20 (5)	0.12 (3)	0.16 (4)			
800	15					0.07 (1)	0.07 (1)	0.07 (1)	0.33 (5)	0.20 (3)	0.07 (1)	0.07 (1)	0.13 (2)	
850	1										1.00 (1)			
900	2			0.50 (1)										0.50 (1)
950	0													
1000	0													

Table 2b. 1993, n = 405

Age		3	4	5	6	7	8	9	10	11	12	13	15	18	24	25
TL (mm)	n															
300	1	1.00 (1)														
350	0															
400	4		1.00 (4)													
450	10	0.10 (1)	0.70 (7)		0.10 (1)		0.10 (1)									
500	65	0.02 (1)	0.32 (21)	0.28 (18)	0.25 (16)	0.11 (7)	0.03 (2)									
550	70		0.07 (5)	0.13 (9)	0.36 (25)	0.29 (20)	0.11 (8)	0.01 (1)	0.01 (1)	0.01 (1)						
600	73		0.07 (5)	0.16 (12)	0.40 (29)	0.25 (18)	0.10 (7)		0.03 (2)							
650	73			0.10 (7)	0.26 (19)	0.42 (31)	0.19 (14)	0.03 (2)								
700	55		0.02 (1)	0.04 (2)	0.11 (6)	0.36 (20)	0.31 (17)	0.11 (6)	0.04 (2)	0.02 (1)						
750	31				0.13 (4)	0.16 (5)	0.35 (11)	0.10 (3)	0.10 (3)	0.13 (4)		0.03 (1)				
800	18						0.11 (2)	0.39 (7)	0.11 (2)	0.11 (2)	0.06 (1)	0.11 (2)	0.06 (1)			0.06 (1)
850	4							0.50 (2)			0.25 (1)			0.25 (1)		
900	1														1.00 (1)	
950	0															
1000	0															

Table 2c. 1994, n = 341

Age TL (mm)	n	3	4	5	6	7	8	9	10	11	12	13	14	15	21	24	25	27
300	0																	
350	3	1.00 (3)																
400	3	0.33 (1)	0.67 (2)															
450	44	0.02 (1)	0.48 (21)	0.43 (19)	0.07 (3)													
500	101	0.03 (3)	0.33 (33)	0.50 (51)	0.07 (7)	0.04 (4)	0.01 (1)	0.01 (1)	0.01 (1)									
550	53		0.23 (12)	0.45 (24)	0.17 (9)	0.09 (5)	0.02 (1)		0.02 (1)	0.02 (1)								
600	42		0.07 (3)	0.10 (4)	0.57 (24)	0.24 (10)	0.02 (1)											
650	29			0.03 (1)	0.34 (10)	0.34 (10)	0.28 (8)											
700	33				0.09 (3)	0.15 (5)	0.45 (15)	0.09 (3)	0.12 (4)		0.06 (2)	0.03 (1)						
750	17					0.06 (1)	0.12 (2)	0.29 (5)	0.24 (4)	0.12 (2)			0.06 (1)	0.06 (1)	0.06 (1)			
800	11							0.27 (3)	0.18 (2)	0.27 (3)	0.09 (1)	0.18 (2)						
850	2																0.50 (1)	0.50 (1)
900	2											0.50 (1)				0.50 (1)		
950	1						1.00 (1)											
1000	0																	

Table 2d. 1995, n = 526

Age TL (mm)	n	3	4	5	6	7	8	9	10	11	12	13	14	16	21	22	23	25
300	0																	
350	5		0.40 (2)	0.40 (2)	0.20 (1)													
400	8			0.50 (4)	0.38 (3)	0.13 (1)												
450	22		0.14 (3)	0.32 (7)	0.32 (7)	0.23 (5)												
500	124		0.06 (7)	0.30 (37)	0.40 (50)	0.16 (20)	0.07 (9)	0.01 (1)										
550	102		0.03 (3)	0.17 (17)	0.48 (49)	0.22 (22)	0.08 (8)	0.01 (1)	0.01 (1)		0.01 (1)							
600	86		0.01 (1)	0.20 (17)	0.38 (33)	0.29 (25)	0.08 (7)	0.02 (2)			0.01 (1)							
650	69			0.06 (4)	0.19 (13)	0.29 (20)	0.26 (18)	0.14 (10)	0.06 (4)									
700	51			0.02 (1)	0.04 (2)	0.06 (3)	0.37 (19)	0.27 (14)	0.14 (7)	0.06 (3)	0.02 (1)		0.02 (1)					
750	32			0.03 (1)	0.03 (1)	0.03 (1)	0.09 (3)	0.34 (11)	0.25 (8)	0.16 (5)	0.03 (1)	0.03 (1)						
800	19						0.05 (1)	0.05 (1)	0.16 (3)	0.16 (3)	0.16 (3)	0.26 (5)		0.11 (2)	0.05 (1)			
850	5										0.20 (1)		0.60 (3)					0.20 (1)
900	3														0.33 (1)	0.33 (1)	0.33 (1)	
950	0																	
1000	0																	

Table 2e. 1996, n = 432

Age		3	4	5	6	7	8	9	10	11	12	13	15	17	24
TL (mm)	n														
300	0														
350	6	0.17 (1)	0.17 (1)	0.67 (4)											
400	28	0.04 (1)	0.11 (3)	0.68 (19)	0.14 (4)	0.04 (1)									
450	45			0.49 (22)	0.47 (21)	0.04 (2)									
500	97		0.03 (3)	0.28 (27)	0.49 (48)	0.20 (19)									
550	80		0.01 (1)	0.13 (10)	0.41 (33)	0.34 (27)	0.05 (4)	0.05 (4)	0.01 (1)						
600	48			0.06 (3)	0.44 (21)	0.35 (17)	0.10 (5)	0.02 (1)	0.02 (1)						
650	52			0.02 (1)	0.17 (9)	0.48 (25)	0.21 (11)	0.08 (4)	0.02 (1)				0.02 (1)		
700	44				0.05 (2)	0.11 (5)	0.23 (10)	0.43 (19)	0.14 (6)	0.02 (1)	0.02 (1)				
750	15						0.07 (1)	0.67 (10)	0.27 (4)						
800	15						0.07 (1)	0.27 (4)	0.33 (5)	0.13 (2)	0.07 (1)	0.07 (1)		0.07 (1)	
850	0														
900	2					0.50 (1)									0.50 (1)
950	0														
1000	0														

Table 2f. 1997, n = 160

Age		3	4	5	6	7	8	9	10	11	12	13	14	15	16
TL (mm)	n														
300	0														
350	0														
400	0														
450	13			0.15 (2)	0.38 (5)	0.38 (5)	0.08 (1)								
500	44	0.05 (2)	0.09 (4)	0.14 (6)	0.41 (18)	0.30 (13)	0.02 (1)								
550	32		0.16 (5)	0.25 (8)	0.25 (8)	0.28 (9)	0.06 (2)								
600	25			0.08 (2)	0.24 (6)	0.36 (9)	0.28 (7)	0.04 (1)							
650	14			0.07 (1)	0.14 (2)	0.43 (6)	0.29 (4)	0.07 (1)							
700	16				0.13 (2)	0.50 (8)	0.19 (3)		0.06 (1)	0.13 (2)					
750	10				0.10 (1)	0.10 (1)	0.30 (3)	0.10 (1)	0.10 (1)	0.10 (1)	0.10 (1)		0.10 (1)		
800	4											0.75 (3)		0.25 (1)	
850	2														1.00 (2)
900	0														
950	0														
1000	0														

Table 2g. 1998, n = 292

Age TL (mm)	n	3	4	5	6	7	8	9	10	11	12	13	14	15
300	0													
350	0													
400	0													
450	9		0.33 (3)	0.33 (3)	0.11 (1)	0.11 (1)	0.11 (1)							
500	65	0.03 (2)	0.12 (8)	0.28 (18)	0.20 (13)	0.18 (12)	0.11 (7)	0.05 (3)		0.03 (2)				
550	58		0.12 (7)	0.31 (18)	0.26 (15)	0.14 (8)	0.09 (5)	0.05 (3)	0.03 (2)					
600	62		0.03 (2)	0.05 (3)	0.27 (17)	0.40 (25)	0.11 (7)	0.08 (5)	0.03 (2)		0.02 (1)			
650	56			0.09 (5)	0.25 (14)	0.34 (19)	0.18 (10)	0.09 (5)	0.02 (1)	0.02 (1)		0.02 (1)		
700	18					0.11 (2)	0.44 (8)	0.33 (6)	0.06 (1)		0.06 (1)			
750	14			0.07 (1)	0.07 (1)	0.21 (3)		0.14 (2)	0.21 (3)	0.14 (2)	0.14 (2)			
800	9						0.11 (1)	0.11 (1)	0.11 (1)	0.22 (2)	0.11 (1)		0.11 (1)	0.22 (2)
850	1												1.00 (1)	
900	0													
950	0													
1000	0													

Table 2h. 1999, n = 869

Age TL (mm)	n	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	20	28
300	0																		
350	0																		
400	0																		
450	16		0.13 (2)	0.38 (6)	0.06 (1)	0.13 (2)	0.25 (4)	0.06 (1)											
500	165	0.01 (1)	0.02 (4)	0.27 (44)	0.23 (38)	0.21 (35)	0.13 (22)	0.08 (14)	0.02 (4)	0.02 (3)									
550	167		0.02 (3)	0.17 (28)	0.17 (28)	0.19 (32)	0.20 (34)	0.14 (24)	0.07 (11)	0.02 (3)	0.02 (3)	0.01 (1)							
600	165		0.01 (1)	0.04 (7)	0.15 (25)	0.13 (21)	0.32 (53)	0.22 (37)	0.06 (10)	0.04 (7)	0.01 (2)	0.01 (1)		0.01 (1)					
650	149			0.01 (1)	0.06 (9)	0.17 (25)	0.32 (48)	0.24 (36)	0.15 (22)	0.02 (3)	0.01 (2)	0.01 (1)	0.01 (1)	0.01 (1)					
700	126				0.01 (1)	0.10 (13)	0.36 (45)	0.28 (35)	0.13 (17)	0.06 (8)	0.03 (4)	0.01 (1)	0.02 (2)						
750	48					0.02 (1)	0.08 (4)	0.19 (9)	0.21 (10)	0.27 (13)	0.13 (6)	0.08 (4)	0.02 (1)						
800	25						0.04 (1)	0.12 (3)	0.08 (2)	0.20 (5)	0.20 (5)	0.20 (5)	0.04 (1)	0.04 (1)	0.04 (1)	0.04 (1)			
850	8									0.25 (2)	0.13 (1)		0.13 (1)		0.13 (1)		0.13 (1)	0.13 (1)	0.13 (1)
900	0																		
950	0																		
1000	0																		

Table 2i. 2000, n = 794

TL (mm)	n	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	23
300	0																				
350	8	0.63 (5)	0.13 (1)	0.25 (2)																	
400	11	0.18 (2)	0.73 (8)	0.09 (1)																	
450	39	0.03 (1)	0.69 (27)	0.15 (6)	0.10 (4)		0.03 (1)														
500	162		0.38 (62)	0.17 (28)	0.19 (31)	0.10 (17)	0.07 (12)	0.03 (5)	0.01 (2)	0.02 (3)	0.01 (1)	0.01 (1)									
550	146		0.23 (34)	0.14 (20)	0.22 (32)	0.14 (21)	0.10 (15)	0.08 (11)	0.05 (7)	0.03 (5)	0.01 (1)										
600	124		0.08 (10)	0.07 (9)	0.27 (34)	0.15 (18)	0.13 (16)	0.11 (14)	0.08 (10)	0.09 (11)	0.01 (1)	0.01 (1)									
650	115			0.01 (1)	0.26 (30)	0.17 (19)	0.14 (16)	0.14 (16)	0.14 (16)	0.09 (10)	0.05 (6)							0.01 (1)			
700	102				0.08 (8)	0.18 (18)	0.23 (23)	0.21 (21)	0.15 (15)	0.10 (10)	0.05 (5)	0.01 (1)	0.01 (1)								
750	51					0.04 (2)	0.14 (7)	0.31 (16)	0.14 (7)	0.14 (7)	0.08 (4)	0.06 (3)	0.04 (2)		0.06 (3)						
800	28							0.04 (1)	0.07 (2)	0.18 (5)	0.11 (3)	0.21 (6)	0.14 (4)	0.21 (6)							0.04 (1)
850	8									0.13 (1)		0.13 (1)				0.13 (1)	0.13 (1)	0.13 (1)	0.25 (2)	0.13 (1)	
900	0																				
950	0																				
1000	0																				

Table 2j. 2001, n = 2008

TL (mm)	n	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	24	27
300	6	0.83 (5)		0.17 (1)																			
350	12	0.17 (2)	0.08 (1)	0.50 (6)	0.25 (3)																		
400	25		0.16 (4)	0.48 (12)	0.28 (7)	0.04 (1)	0.04 (1)																
450	111		0.01 (1)	0.14 (15)	0.62 (69)	0.20 (22)	0.01 (1)	0.01 (1)			0.02 (2)												
500	487			0.05 (24)	0.63 (305)	0.17 (82)	0.09 (42)	0.03 (15)	0.02 (9)	0.01 (4)	0.01 (3)	0.00 (2)	0.00 (1)										
550	431			0.02 (9)	0.56 (242)	0.13 (55)	0.17 (74)	0.04 (19)	0.02 (10)	0.02 (8)	0.01 (6)	0.01 (6)	0.00 (1)	0.00 (1)									
600	271			0.00 (1)	0.32 (88)	0.19 (51)	0.25 (69)	0.11 (29)	0.03 (7)	0.04 (12)	0.04 (12)		0.01 (2)										
650	265				0.06 (15)	0.07 (19)	0.38 (101)	0.17 (45)	0.07 (19)	0.15 (40)	0.06 (16)	0.03 (8)	0.01 (2)										
700	206					0.00 (1)	0.21 (43)	0.23 (48)	0.12 (24)	0.22 (46)	0.12 (24)	0.04 (8)	0.02 (4)	0.02 (4)	0.01 (2)	0.01 (2)							
750	98				0.02 (2)		0.05 (5)	0.05 (5)	0.09 (9)	0.23 (23)	0.20 (20)	0.15 (15)	0.06 (6)	0.03 (3)	0.03 (3)	0.04 (4)	0.03 (3)						
800	67							0.01 (1)	0.03 (2)	0.01 (1)	0.10 (7)	0.18 (12)	0.12 (8)	0.19 (13)	0.09 (6)	0.09 (6)	0.07 (5)	0.01 (1)		0.03 (2)	0.01 (1)	0.03 (2)	
850	24										0.04 (1)	0.08 (2)	0.17 (4)	0.13 (3)	0.21 (5)	0.08 (2)		0.08 (2)	0.13 (3)		0.04 (1)		0.04 (1)
900	5				0.20 (1)										0.20 (1)		0.20 (1)			0.40 (2)			
950	0																						
1000	0																						

Table 3. Meristic regressions for red grouper from the eastern Gulf of Mexico: 1992 through 2001.

Conversion & Units	Equation	Sample Size	r^2 values	Data Ranges
from FL (mm) to TL (mm)	TL (mm) = 1.04 * FL (mm) + 3.47	2066	0.98	TL (mm): 299 to 954 FL (mm): 290 to 910
from TL (mm) to W. Wt (kg)	W. Wt (kg) = 5.32x10-9 * (TL ^3.16)	1877	0.92	TL (mm): 285 to 954 W. Wt (mm): 0.30 to 16.96
from FL (mm) to W. Wt (kg)	W. Wt (kg) = 5.48x10-9 * (FL ^3.18)	1434	0.95	FL: 290 to 910 W. Wt: 0.40 to 16.96
from TL (mm) to G. Wt (kg)	G. Wt (kg) = 5.71x 10-8 * (TL ^2.79)	473	0.89	TL (mm): 403 to 980 G. Wt (mm): 0.82 to 15.05
from FL (mm) to G. Wt (kg)	G. Wt (kg) = 2.32x 10-9 * (FL ^3.31)	392	0.92	FL (mm): 443 to 890 G. Wt (mm): 0.91 to 13.15
from TL (mm) to Otolith Wt (g)	Otolith Wt (g) = 6.32 x 10-7 * (TL ^ 2.03)	1215	0.86	TL (mm): 285 to 900 Otolith Wt (g): 0.06 to 1.01
from FL (mm) to Otolith Wt (g)	Otolith Wt (g) = 3.72 x 10-7 * (FL ^ 2.13)	3129	0.82	FL (mm): 290 to 890 Otolith Wt (g): 0.05 to 0.95
from Age (years) to Otolith Wt (g)	Otolith Wt (g) = 0.03 * Age (years) + 0.05	3644	0.72	Age (years): 2 to 29 Otolith Wt (g): 0.06 to 1.01

Table 4. Growth curve parameters for biological ages and lengths at capture for red grouper by different gear types and for different growth curves from the eastern Gulf of Mexico: 1992 – 2001 (scientific survey samples, n = 334, added to all data to calculate von Bertalanffy parameters).

Mode and Gear	Sample Size	L_∞	k	t_o
All data	6073	923	0.11	-3.21
Long-line	2911	1026	0.07	-6.44
Hand-line	1594	943	0.10	-3.51
Trap	271	944	0.07	-8.50
Recreational	963	960	0.11	-2.45
Ad-hoc	6073	920	0.16	0.00

Schnute and Richards: $y_\infty = 1009$, a = 1.52, b = 1.26, c = 0.34, $\alpha = 16.77$

Table 5. Maximum likelihood test ratios, chi-square values, and p values for comparisons of the von Bertalanffy growth curves between pairs of different modes and gears for red grouper from the eastern Gulf of Mexico: 1992-2001.

Comparison	Maximum Likelihood Ratio	Chi-Square Value	p value
Commercial long-line vs. hand-line	17.70	5.07×10^{-4}	$p < 0.0001$
Commercial hand-line vs trap	42.67	2.89×10^{-9}	$p < 0.0001$
Commercial Hand-line vs. Recreational	27.48	4.67×10^{-6}	$p < 0.0001$

Table 6. Growth parameters from the von Bertalanffy growth curve from previous studies on the red grouper.

Publication	Sample Years	Area	L_∞	k	t_o
Moe 1969	1963-1964	West Florida shelf	672	0.18	-0.45
Fuentes *et al*. 1989 cited in Contreras *et al*. 1994	1973-1987	southwest Gulf of Mexico Bay of Campeche	936	0.11	-0.23
Johnson and Collins 1994	1979-1981	eastern Gulf of Mexico	789	0.18	0.83
	1991-1992	West FL shelf	926	0.16	0.93
Stiles and Burton 1994	1972-1988	southeastern Atlantic	922	0.17	0.30
Schirripa and Burns 1997		eastern Gulf of Mexico West FL shelf	808	0.21	-0.30
Burgos 2001	1996-1999	southeastern Atlantic	853	0.21	-0.81

List of Figure Captions

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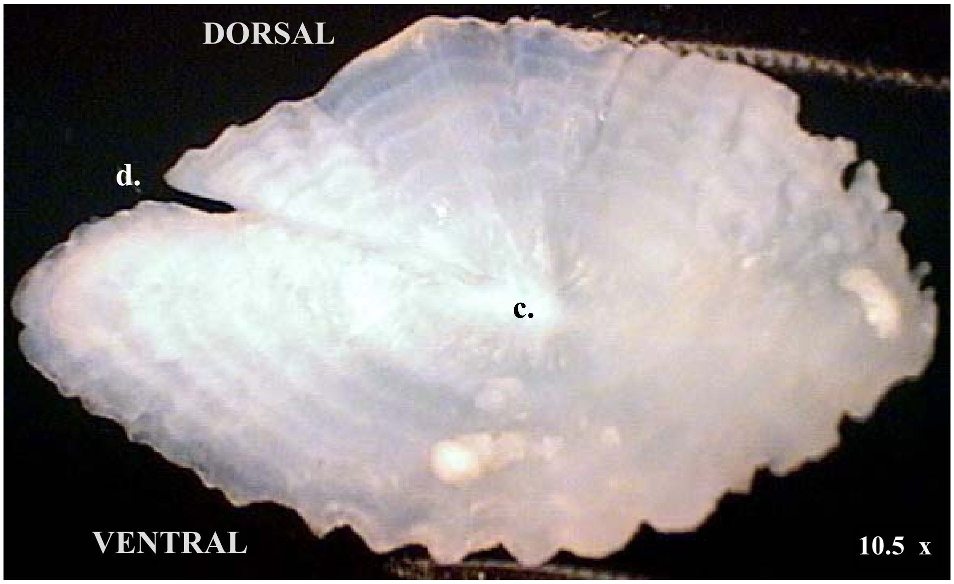
8 Size at age scattergrams by year for red grouper sampled for otoliths in the eastern Gulf of Mexico.

9 Comparison of depths fished by mode and gear for red grouper from the eastern Gulf of Mexico from 1992 to 2001: a. commercial long-line, n = 1851; b. commercial hand-line, n = 750; c. commercial trap, n = 97; and d. recreational, n = 37.

10 Mean biological age ± standard deviation (estimated only when more than 10 fish were present within a size category): commercial hand-line (n = 1594, gray circle), commercial long-line (n = 2911, black circle), commercial trap (n = 271, open circle), recreational samples, n = 962, black triangle).

Figure 1. Examples of the ageing structure from a red grouper (a) whole otolith and (b) sectioned otolith. The core (c), sulcus acousiticus (d), band counts, edge type, and age are identified for each example.

a. Band count = 8, edge type = T (translucent), Age = 9 years old



b. Band count = 10, edge type = T (translucent), Age = 11 years old

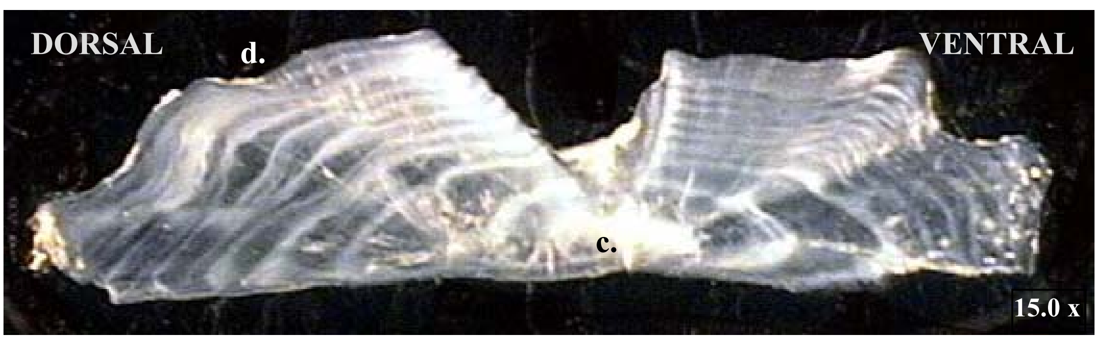
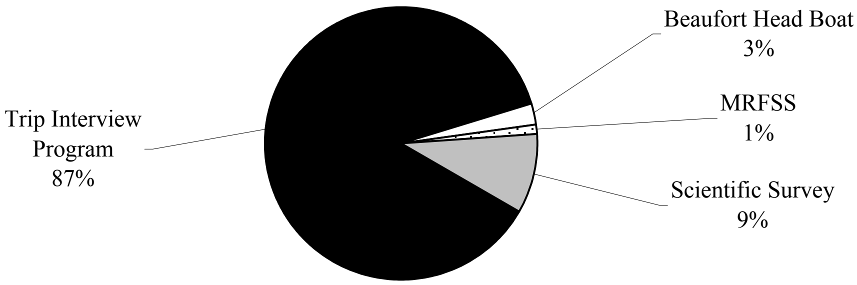
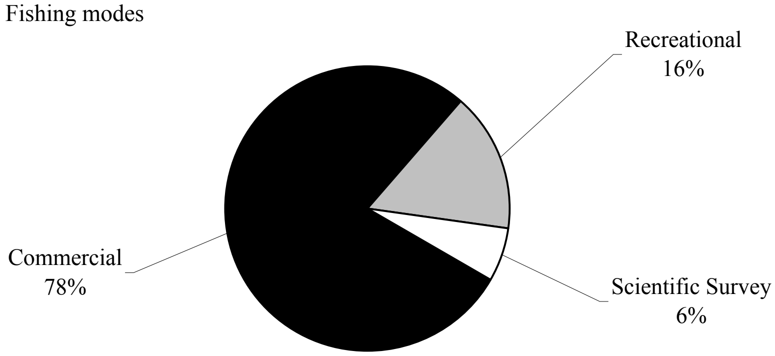


Figure 2. Percentages of red grouper otolith samples collected from 1992 to 2001 (n = 6075) by (a) sampling programs, (b) fishing modes, and (c) commercial fishing sector by gear type.

a. Sampling program



b. Fishing modes



c. Commercial mode by gear

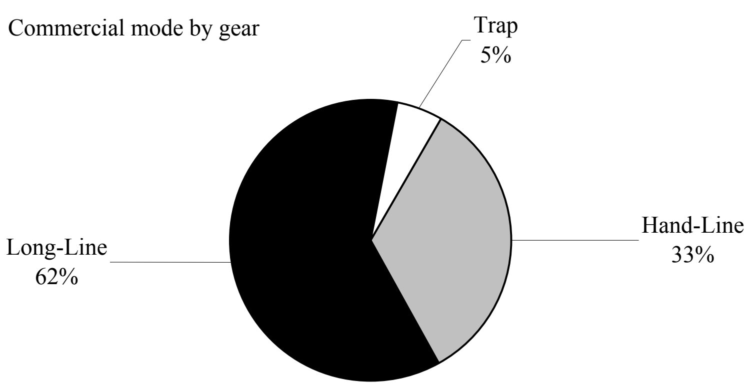


Figure 3. Age bias between primary and secondary reader for red grouper; a. 1992 to 2001, n = 3454, b. 1992-1996, n = 1627. Mean age of secondary reader given age of primary reader, error bars are ± 95 % Confidence Intervals.

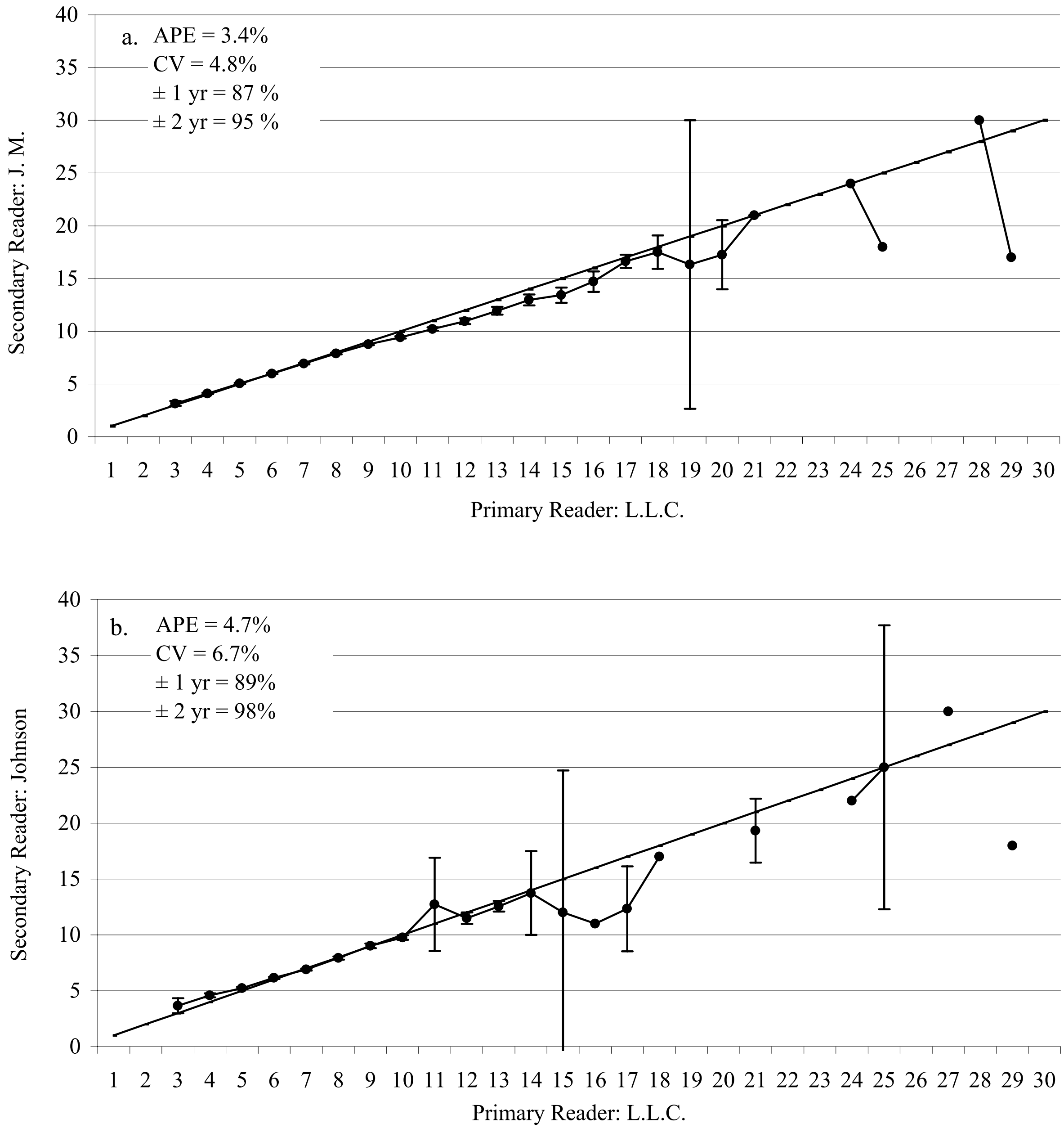


Figure 4. Length frequencies for red grouper sampled for otoliths from the eastern Gulf of Mexico: 1992 - 2001.

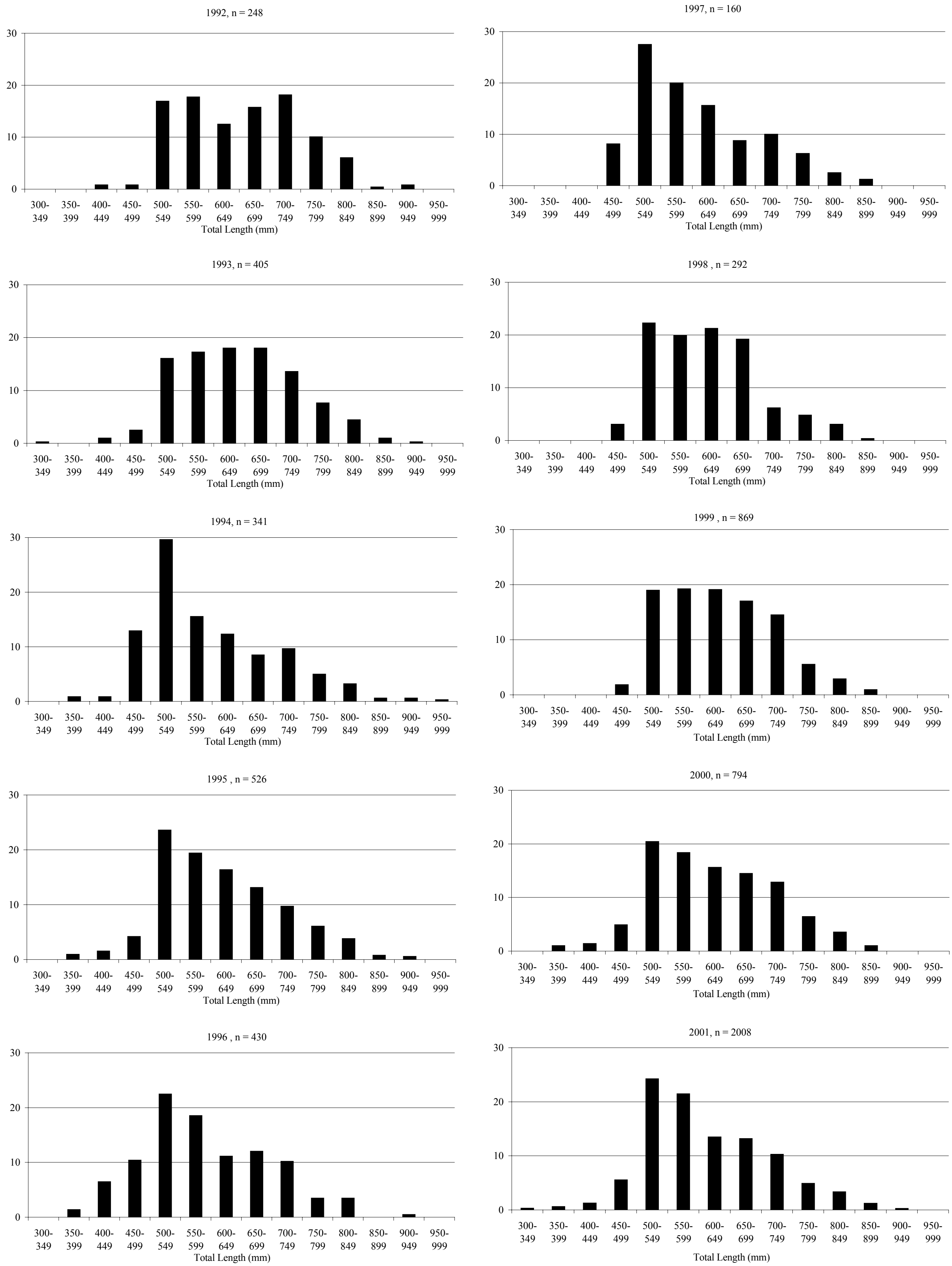


Figure 5. Age frequencies for red grouper from the eastern Gulf of Mexico: 1992 - 2001, lines indicate dominant year classes that exceed 30% of the age structure in at least one year and is the most abundant for at least two years.

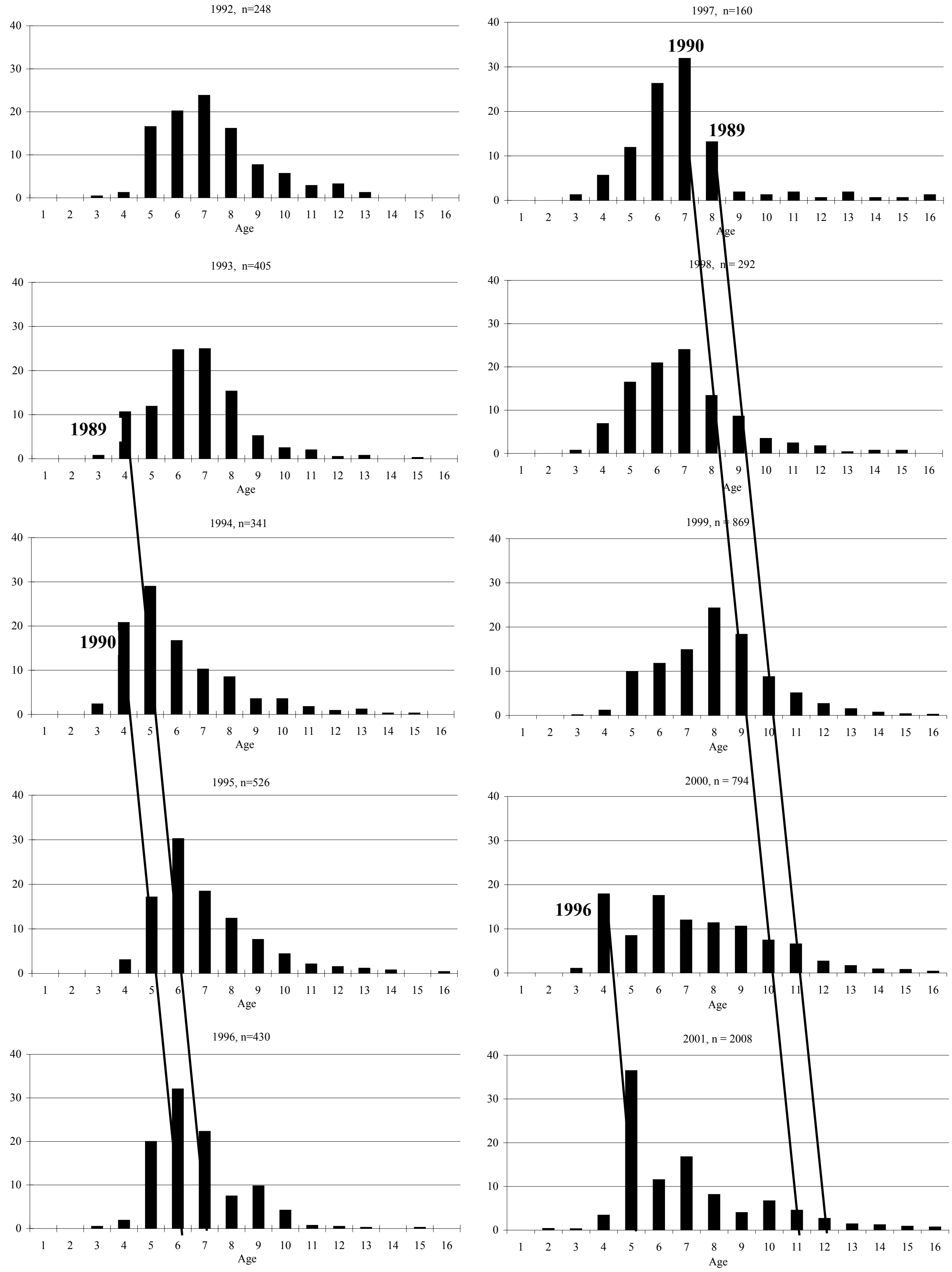


Figure 6. Comparisons of growth curves by mode and gear (commercial long-line, n = 2911; commercial hand-line, n = 1594; commercial trap, n = 271; recreational: n = 962) for red grouper sampled from the eastern Gulf of Mexico: 1992 - 2001.

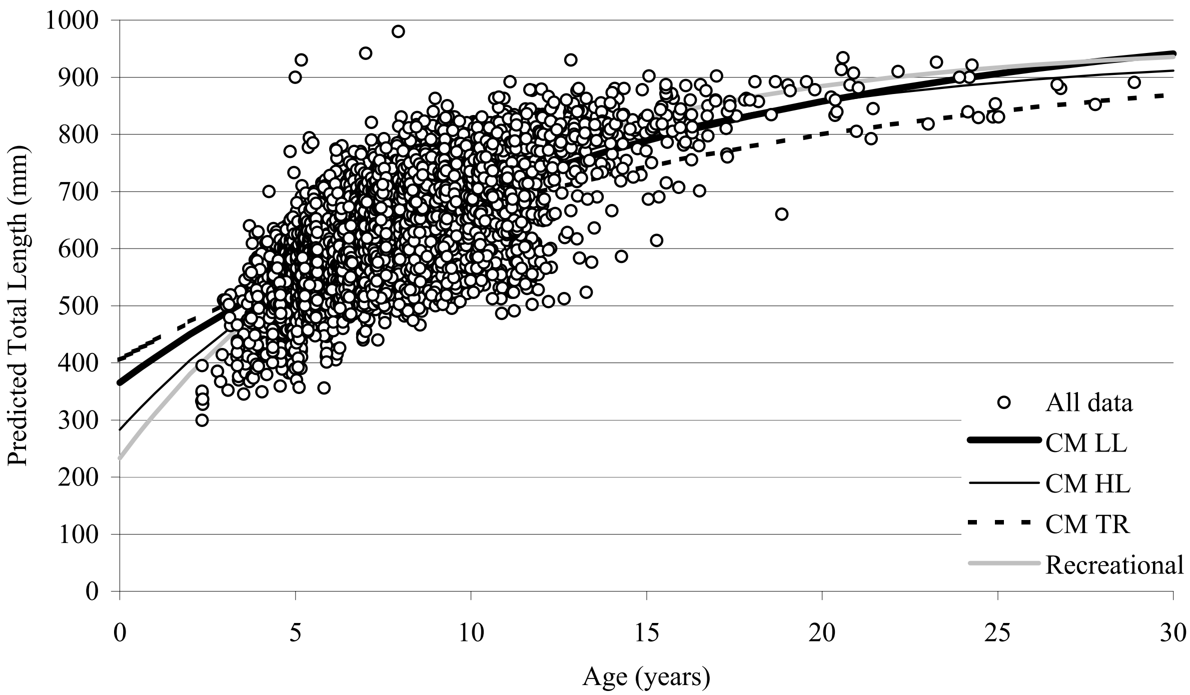


Figure 7. Comparison of growth curves: von Bertalanffy (unconstrained), ad hoc fit - von Bertalanffy (forced through origin), and Schnute and Richards for all red grouper samples from the eastern Gulf of Mexico: 1992-2001.

Figure 8. Size at age scattergrams by year for red grouper sampled for otoliths in the eastern Gulf of Mexico.

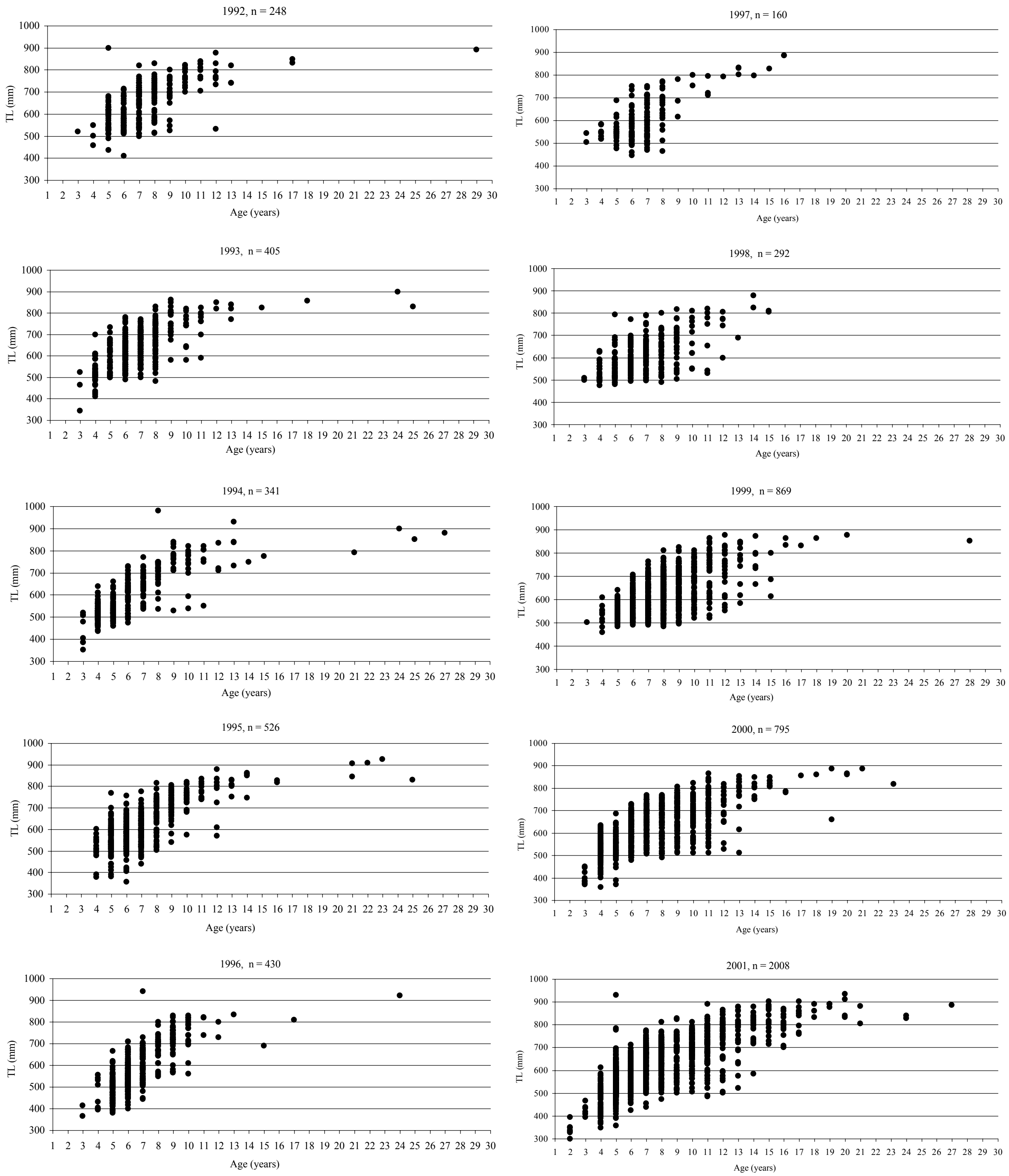


Figure 9. Comparison of depths fished by mode and gear for red grouper from the eastern Gulf of Mexico from 1992 to 2001: a. commercial long-line, b. commercial hand-line, c. commercial trap, and d. recreational.

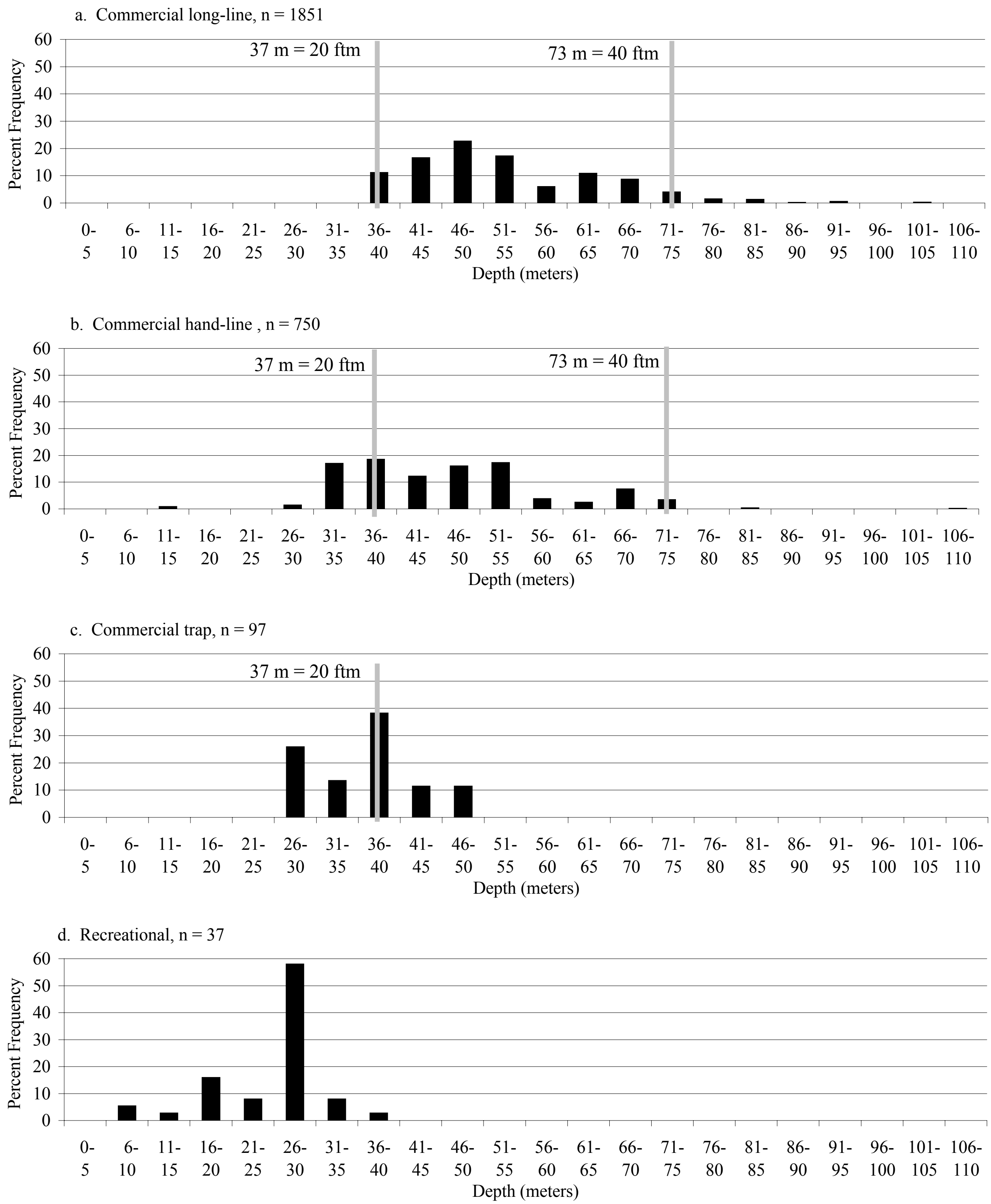


Figure 10. Mean biological age ± standard deviation (estimated only when more than 10 fish were present within a size category): commercial hand-line (n = 1594, gray circle), commercial long-line (n = 2911, black circle), commercial trap (n = 271, open circle), recreational samples, n = 962, black triangle).