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Temporal Age Progressions and Relative Year-Class Strength of Gulf of Mexico Red Snapper

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Abstract.—Red snapper *Lutjanus campechanus* sagittal otoliths were sampled from U.S. Gulf of Mexico commercial vertical hook and line, longline and recreational landings over a twelve year period (1991–2002). Our objectives were to examine the empirical age structure of red snapper through space and time, to gauge the relative year-class strength over time, and to compare the impact of strong year-classes upon annual age structure by fishing sector. The recreational fishery selected the youngest fish with a mode at 3 years and a mean age of 3.2 years. The commercial vertical hook and line fishery selected for slightly older fish with a mode of 3 years and a mean age of 4.1 year. The commercial longline fishery selected the oldest individuals with fish first fully recruited to the fishery by age 5 and, a mean age of 7.8 years. Only the commercial longline fishery age distributions were significantly different between the eastern and western Gulf of Mexico. Based on age progressions, strong 1989 and 1995 year-classes were dominant in the landings of the recreational and commercial vertical hook and line fisheries and the 1995 year-class was dominant in the commercial longline landings. A relative year-class index further highlighted these results, and we noted a significant correlation in year-class strength between recreational and commercial vertical hook and line sectors. The year-class index for combined sectors was also significantly correlated between eastern and western Gulf of Mexico with 1989 and 1995 year-classes similarly dominating both regions. An empirical age progression year-class index could be valuable in correlation with early life abundance indices of red snapper and serve to provide inference about the relative error of recruitment data.

Introduction

The economic and management importance of Gulf of Mexico red snapper *Lutjanus campechanus* has driven many life history studies including a recent focus on growth, demographics, and age structure (Patterson 1999; Nieland and Wilson 2000; Wilson and Nieland 2001; Allman et al. 2002; Fischer et al. 2004; Mitchell et al. 2004). Much of this work has highlighted spatial differences in growth and demographics in eastern versus western Gulf of Mexico. Examining spatial trends is particularly important for reef fish which can show affinities for patchy habitats and often exhibit high degrees of site fidelity

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during some phase of their life history. It is increasingly being realized that matching the relevant spatial scale to population attributes is an important prerequisite for meeting fishery management objectives (Sale 1998; Gust 2004).

While an improved understanding of spatial differences in life history and demographics is much needed, it is no less important to understand the degree to which life history and demographic attributes can change on temporal scales. Differences in recruitment patterns (i.e., year-class strength) can have a dramatic effect on the demographics of reef fish populations (Sissenwine 1984). Fluctuations in stock size have been attributed to changes in the age structure through the recruitment of strong year-classes (Laevastu and Favorite 1988). To date, studies of red snapper growth and age structure have been conducted within one year or using data sets aggregated over a few years. The degree that spatial and temporal differences in age structure may occur has not been fully examined.

Because of the importance of red snapper and controversies over its management, sampling and aging of the catch has increased since the early 1990s and this has allowed us to develop a time series of age structure from the landed catch. Our objectives were to examine the age structure of red snapper through space and time, to compare empirical age structure patterns by fishing sector and gauge the relative year-class strength over a 12 year time series. To do so, we employed the use of a relative year-class index (YCI) to estimate and compare year-class strength for the principal fishing sectors and for the east and west regions of the U.S. Gulf of Mexico.

Methods

Red snapper were randomly sampled by port agents from Texas to the west coast of Florida from February 1991 through December 2002 mainly through the trip interview program (www.sefsc.noaa.gov/tip.jsp). Fish were sampled from recreational and commercial landings. All fish were measured to total length (TL) or were converted to TL from fork length (FL) using the equation: TL (mm) = 1.061x FL (mm) + 2.601, $r^2 = 0.99$ (Allman et al. 2002). Sagittal otoliths (hereafter referred to as otoliths) were collected with corresponding fishery data. The left otolith was weighed to the nearest 0.0001 g. If the left otolith was not whole, the right otolith was weighed. A paired *t*-test found no significant difference between right and left otolith weights ($p = 0.20$).

Otolith processing and aging

Otoliths were processed with a high-speed thin sectioning machine utilizing the methods of Cowan et al. (1995). Two transverse cuts were made through the otolith core to a thickness of 0.5 mm. Due to recent advances in otolith preparation techniques, red snapper otoliths which were sectioned and aged during the early 1990s were ground, polished and re-aged. Otolith sections were assigned an age based on the count of annuli (opaque zones observed with reflected light at 40x counted along the dorsal side of the sucal groove in the transverse plane), including any partially completed opaque zones on the otolith margin) and the degree of marginal edge completion. For example, otoliths collected after 1 January were advanced a year in age if their edge type was a nearly complete translucent zone. Typically, marine fishes in the southeastern U.S. complete annulus formation by late spring to early summer (Patterson et al. 2001; Wilson and Nieland 2001; Garcia et al. 2003; Allman et al. 2005a). 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 annulus would have soon formed. For otoliths collected after 30 June all fish were assigned an age equal to the annulus count since opaque zone formation is typically complete. By this traditional method, an annual age-cohort is based on a calendar year rather than time since spawning (Jearld 1983; Vanderkooy and Guindon-Tisdel 2003). Red snapper otolith based ages have been validated (Baker and Wilson 2001) and the timing of annulus formation determined (Allman et al. 2005b).

Three otolith readers within our laboratory aged red snapper otoliths. To establish an estimate of reader precision (i.e., repeatability of age estimates), we prepared a reference collection of 300 red snapper otolith sections representing the ranges of age classes, seasons, sexes, years, preparation quality and collection locations (Campana 2001). Average percent error (APE; Beamish and Fournier 1981) was used to compare age estimates among readers for the reference collection. We considered an APE ≤ 5% acceptable for moderately long-lived species with relatively difficult to read otoliths (Morison et al. 1998; Campana 2001). The two most common sources of reader variation in red snapper otoliths were found to be interpretation of the first annulus and edge type. Criteria for identification and interpretation of both first annulus and edge type in red snapper were established in a previous study (Allman et al. 2005b). We examined the linear relationship between otolith weight and estimated age to identify possible systematic bias in age determinations (Morison et al. 1998). We added or subtracted one year from the estimated ages. If estimated ages were biased in either direction, the x-intercept would be closer to the origin by adding or subtracting one year. We restricted the regression to ages 1 through 10 where an overall, significant linear relationship between otolith weight and age was apparent ($F_{1,3128} = 6254$; $p < 0.001$).

Data analysis

To examine potential regional differences within fishing sector, red snapper which were sampled randomly from Florida, Alabama and Mississippi were classified as eastern Gulf of Mexico (hereafter eastern gulf) and those collected from Louisiana and Texas as western gulf. Age distributions were compared regionally with the Kolmogorov-Smirnov two-sample test (KS). A time series of age data were used to calculate a relative year-class index. Only the most common age classes that were well represented in the catches (2–6 years) with at least three consecutive years of data were used to construct the index. Year-class strength was estimated stepwise beginning with the calculation of the percentage age distributions in the annual age samples. Thereafter the mean percentage age distribution for the whole period was established. In the next step the different year-classes in different years were expressed as percentages of this distribution (Böhling et al. 1991). The index assumes total mortality does not affect any one year-class differently from another. Year-class indices were compared by fishing sector and region with Pearson correlation (Minitab, Inc. 1997).

Results

A total of 29,312 red snapper otoliths were randomly selected and aged for the period 1991 to 2002. Collections were fairly evenly divided between the commercial sector (54%) and the recreational sector (46%). Likewise, collections were almost evenly distributed between the eastern gulf (51%) and western gulf (49%). Due to increased funding for sampling of red snapper, the majority of otoliths were collected after 1997 (Table 1). Ages were successfully assigned to 96.5% (28,302) of otoliths read.

The red snapper reference collection APE for the three otolith readers was below the 5% benchmark (APE = 4.8%), so we assumed reader age interpretations were consistent. In addition, aging results from a red snapper otolith reference collection exchange indicated good agreement between Gulf of Mexico laboratories (Allman et al. 2005b). The regression of otolith weight on age was estimated separately with age, age + 1 and age – 1 to test whether the first increment was correctly assigned. There was no indication that otoliths were consistently biased. The intercept for the original ages was closer to the origin (0.006) than the age + 1 data (–0.146) or the age – 1 data (0.158) (Figure 1). In addition, the 95% confidence intervals for the original age data included zero (–0.012 to 0.024), while the age + 1 and age – 1 data did not (–0.168 to –0.124 and 0.143 to 0.173, respectively), however the relationship between otolith weight and age was not strongly related ($r^2 = 0.67$).

Red snapper ranged in age from 1 to 57 years. A comparison of age distributions indicated differences by fishing sector, region and sampling year. The commercial long-line fishery selected the oldest individuals with fish fully recruited to the fishery by age 5, mean age was 7.8 years, and 22% of individuals were greater than or equal to 10 years (Figure 2A). The com-

Table 1. Numbers of U.S. Gulf of Mexico red snapper aged by fishing sector within region. CHL = commercial vertical hook and line, CLL = commercial longline and REC = recreational.

	East			West		
Year	CHL	CLL	REC	CHL	CLL	REC
1991	210	13	273	25		631
1992	141	15	474	214		514
1993	169	31	725	355	31	1,180
1994	199	9	754	505		429
1995	157	21	380	48		10
1996	10	6	221			
1997	33	16	156			
1998	239	27	1,670	1,099	358	932
1999	770	111	1,692	2,061	76	457
2000	1,041	135	663	1,171	316	260
2001	1,185	92	638	1,133	191	74
2002	1,217	186	1,239	1,841	360	125

mercial vertical hook and line fishery selected for younger fish with a mode of 3 years, mean age was 4.1 years, and 1% of fish greater than or equal to 10 years (Figure 2B). The recreational fishery selected the youngest fish with fish fully recruited to the fishery at 3 years, with 90% of individuals 2, 3 and 4 (mean age = 3.2 years) and only 0.3% of fish were greater than or equal to 10 years (Figure 2C). Only the commercial long-line fishery age distributions were significantly different between eastern and western gulf (KS = 0.33, $P < 0.001$) (Figure 3A). Recruitment to the commercial long-line fishery was by age 4 in the east and age 5 in the west with a mean age of 7 years for the east and 8.2 years for the west. The age distribution from the commercial vertical hook and line fishery was similar between east and west with recruitment at age 3 for both regions and mean ages of 4.1 and 4.2 years, respectively (Figure 3B). Similarly, the recreational fishery suggested little difference between east and west with recruitment at age 3 and mean ages of 3.1 and 3.4 years, respectively (Figure 3C).

Age frequency distribution by sampling year revealed potential changes in the age at recruitment through time. The annual recruitment pattern of red snapper from the recreational fishery indicated recruitment alternated between age 2 or 3 prior to 1998 but only age 3 was noted during and after 1998 (Figure 4). Recruitment to the commercial vertical hook and line fishery alternated between age 3 or 4 all years (Figure 5). Recruitment to the commercial long-line fishery for the few years with large sample size was from age 4 to 6 (Figure 6).

There was evidence for strong 1989 and 1995 year-classes in the age structure of the recreational and commercial vertical hook and line fisheries and for 1995 in the commercial longline fishery. Generally these strong year-classes could be followed for 2–3 consecutive years (Figures 4–6). Strong year-classes followed a progression through the different fishing sectors, first appearing in the recreational fishery, then a year later appearing in the commercial vertical hook and line and then the commercial longline fishery the following year. For example, evidence for the dominance

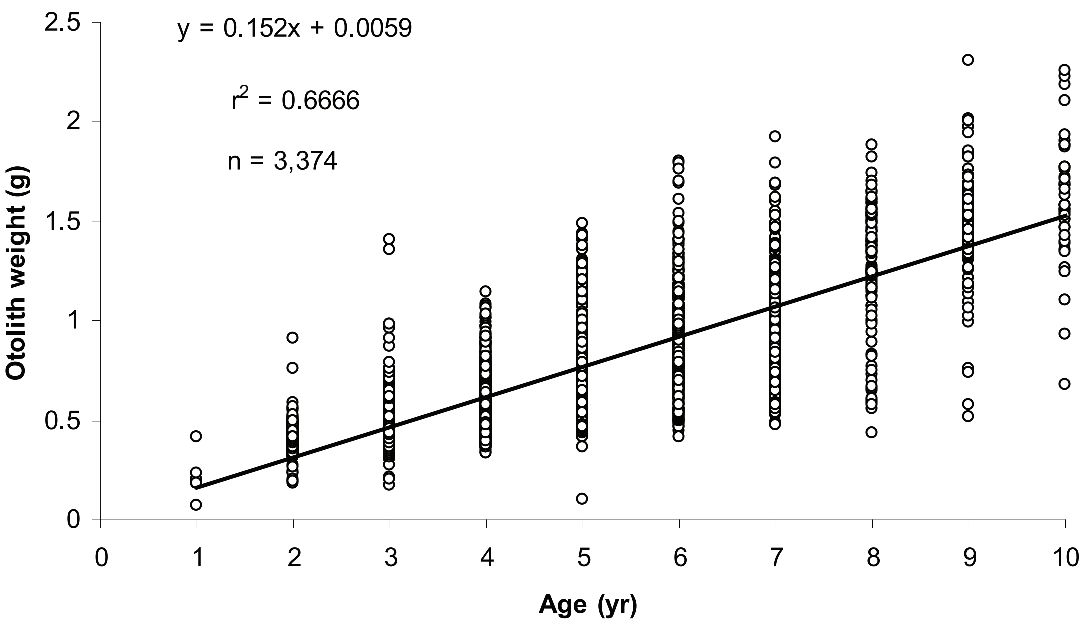


Figure 1. Red snapper otolith weight by estimated age with the fitted regression equation.

of the 1995 year-class first emerged with a large proportion of 2 year olds (>70%) in the recreational fishery in 1997, a year later this year-class was dominant in the commercial vertical hook and line fishery as 3 year olds, and in 1999 in the commercial longline fishery as 4 year olds (Figure 7 A–C). The 1989 year-class first was dominant in the recreational fishery as two year olds in 1991 and then in the commercial vertical hook and line fishery as three year olds in 1992 (Figure 7 D&E). We did not have commercial longline samples in large enough numbers prior to 1998 to resolve the 1989 year-class.

A relative year-class index (YCI) more clearly revealed the two dominant year-classes, with peaks in index values for the recreational and commercial vertical hook and line fisheries during 1989 and 1995 (Figure 8). Additionally, there was a significant correlation in year-class strength between these two fishing sectors (Pearson correlation = 0.924, $P <$ 0.001). The YCI for combined sectors was also significantly correlated between regions (Pearson correlation = 0.674, P = 0.032) with 1989 and 1995 year-classes similarly dominating in both regions (Figure 9).

Discussion

An annual aging program based on port sampling of red snapper otoliths enabled us to track multiple year age progressions among the principal gulf red snapper fishing sectors. It was apparent that consistent patterns in year-class strength were detectable over a period of several years. During 1991 to 2002, examination of annual age structure revealed that 1989 and 1995 year-classes were evident as relatively strong year-classes for recreational and commercial vertical hook and line as was 1995 for the longline sector. We noted differences in the age progression patterns among the three fishing sectors which suggest some differences in age selectivity. In the recreational and commercial vertical hook and line fisheries, 1989 and 1995 year-class dominance was evident in the progression of age 2 to age 4 red snapper in 1991 to 1993 and 1997 to 1999. In the longline fishery, the dominance of the 1995 year-class was observed in the progression of age 4 to age 6 in 1999–2001.

This shift in age tracking of younger fish in the vertical hook and line fisheries versus older fish in the long-line sector has been noted before and may reflect differences in gear, locations,

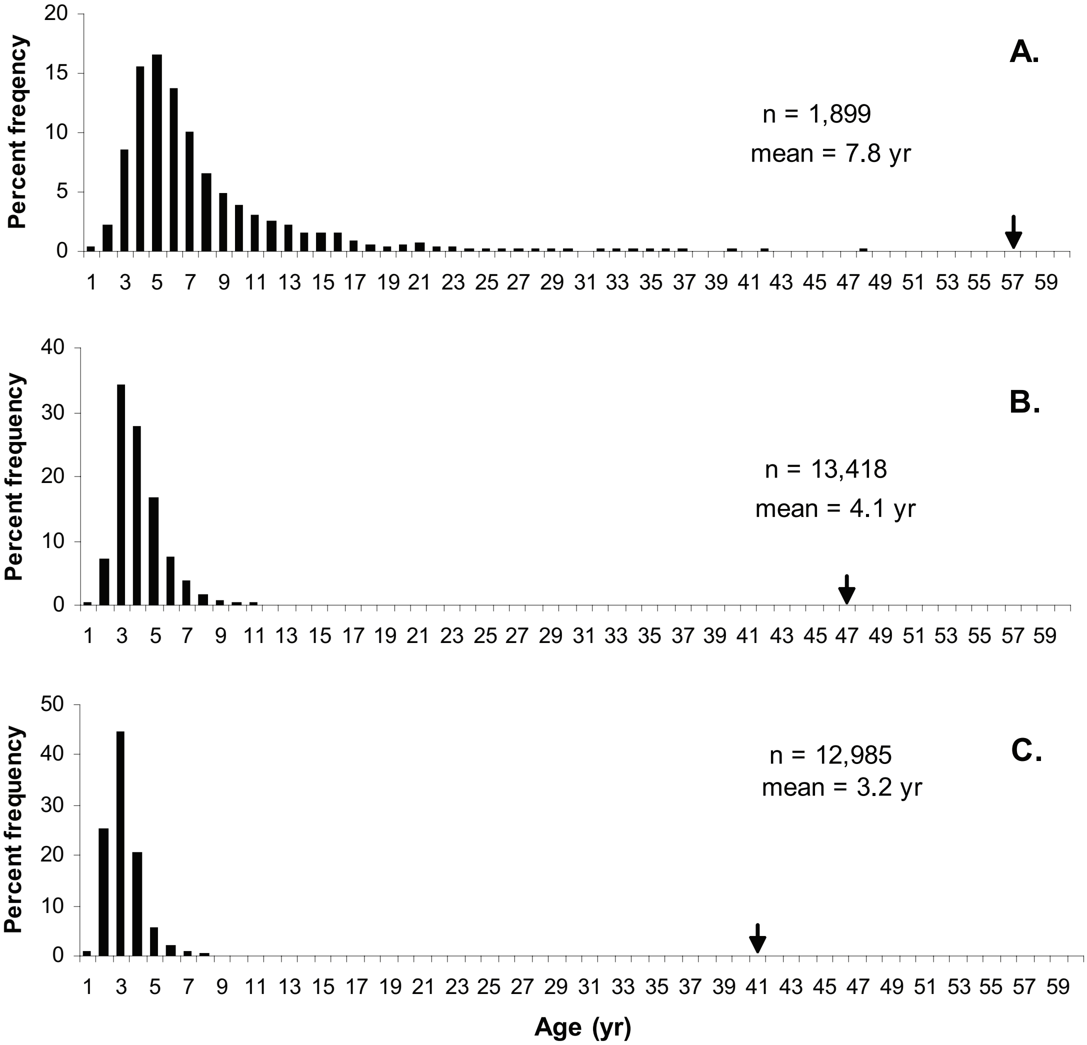


Figure 2. Age frequency distributions for red snapper (1991–2002): (A) commercial longline, (B) commercial vertical hook and line and (C) recreational. Arrows indicate maximum age.

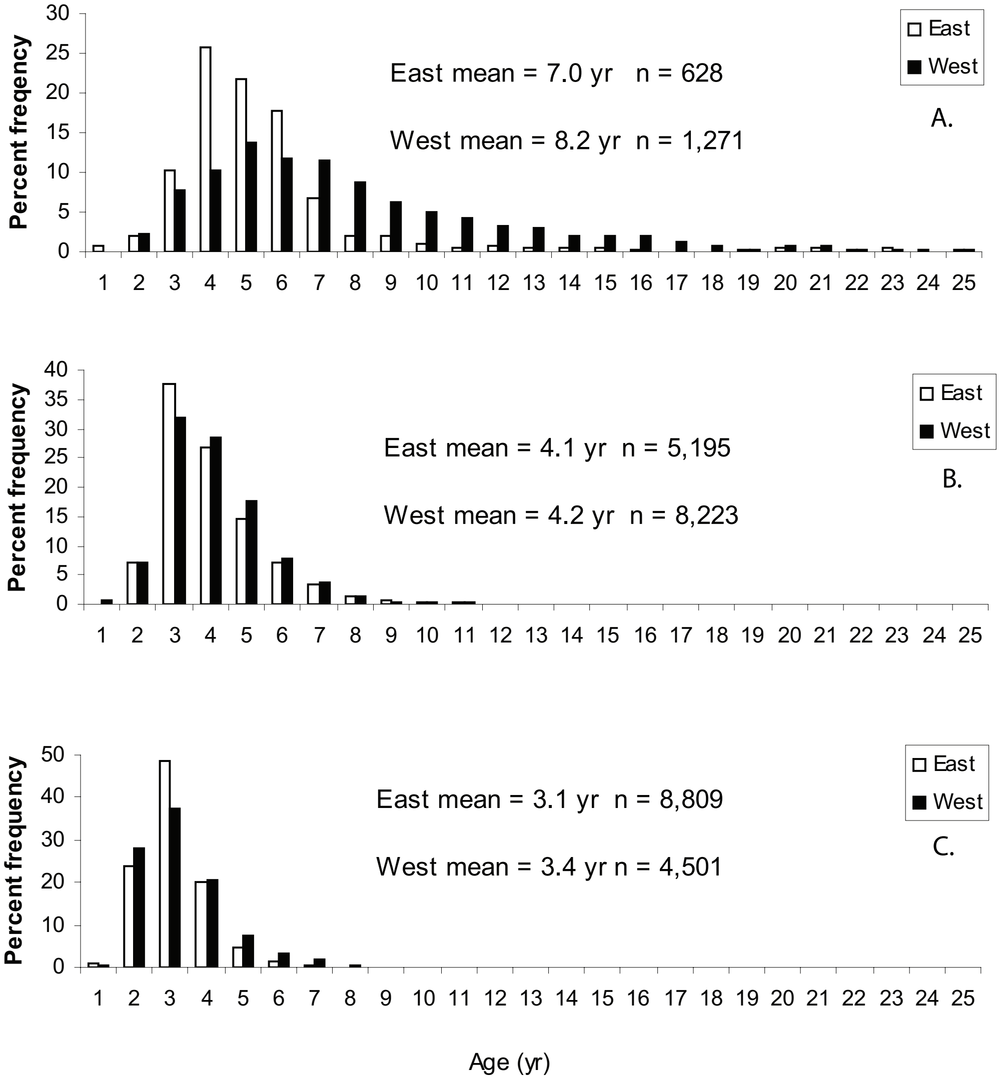


Figure 3. Age frequency of red snapper by sampling region (1991–2002): (A) commercial longline, (B) commercial vertical hook and line, and (C) recreational.

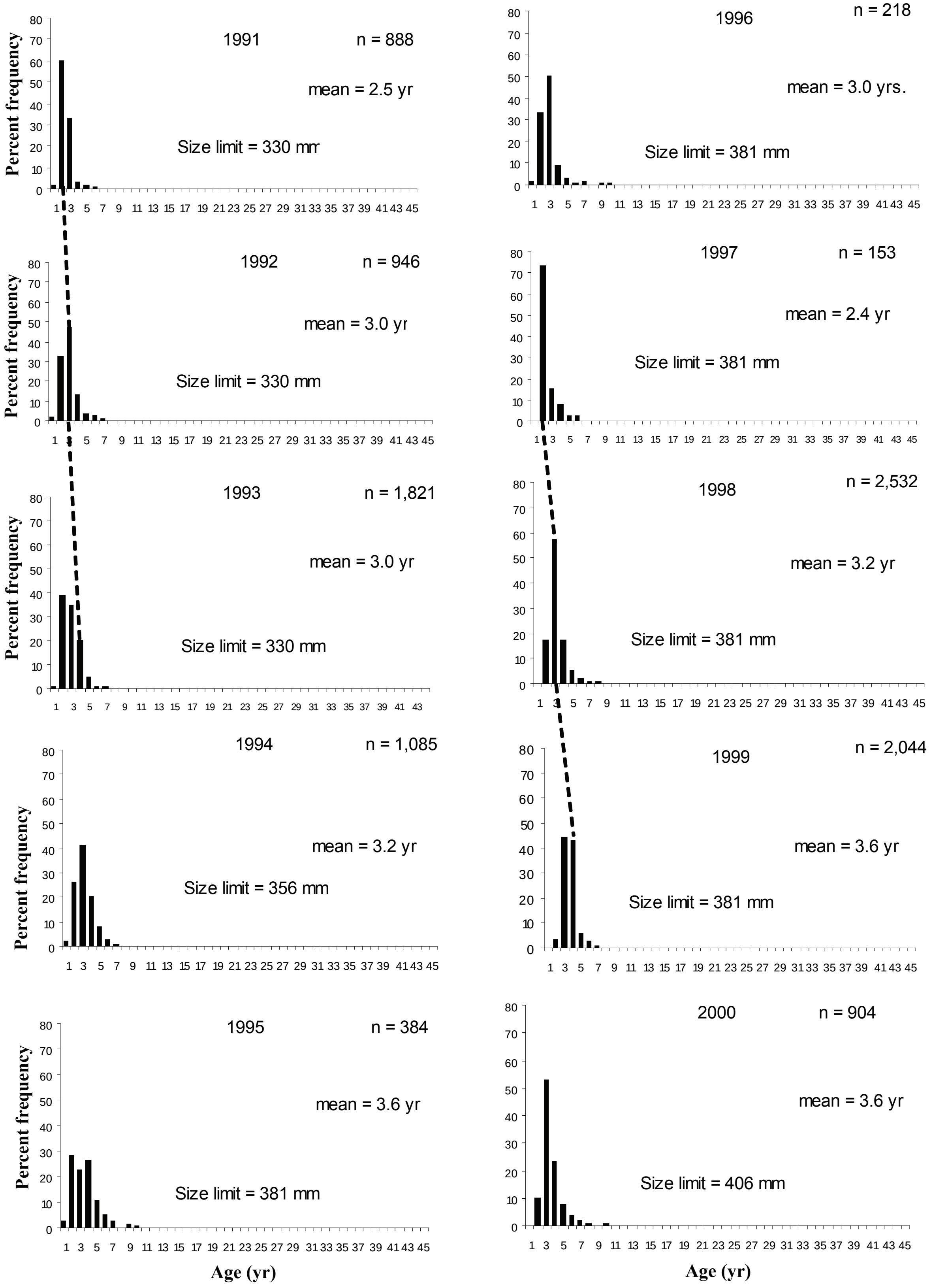
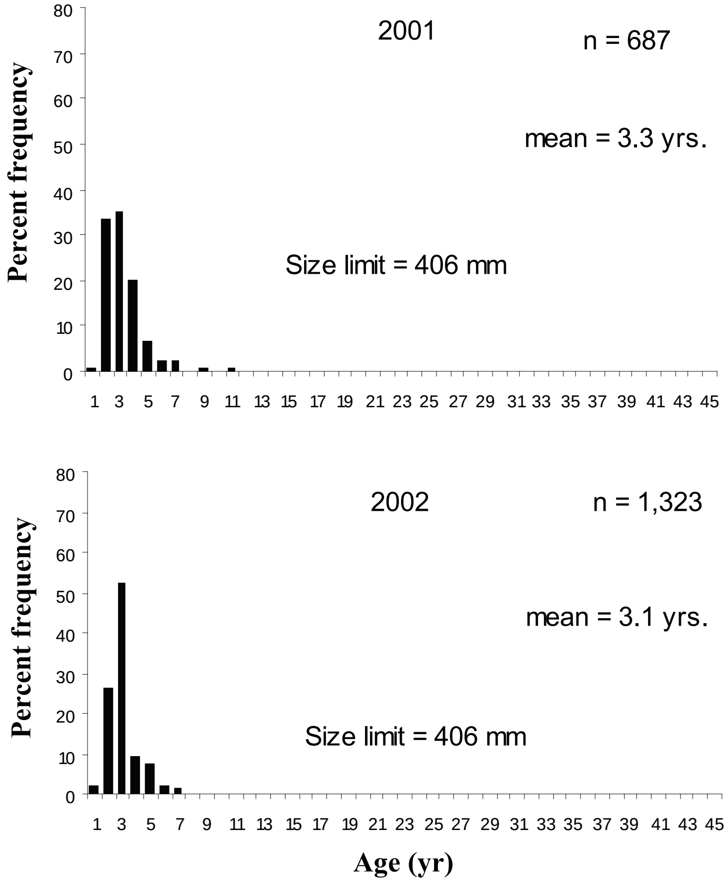


Figure 4. Age distribution of the recreational fishery by year. Dashed lines indicate year-class progression.

Figure 4. (Continued)



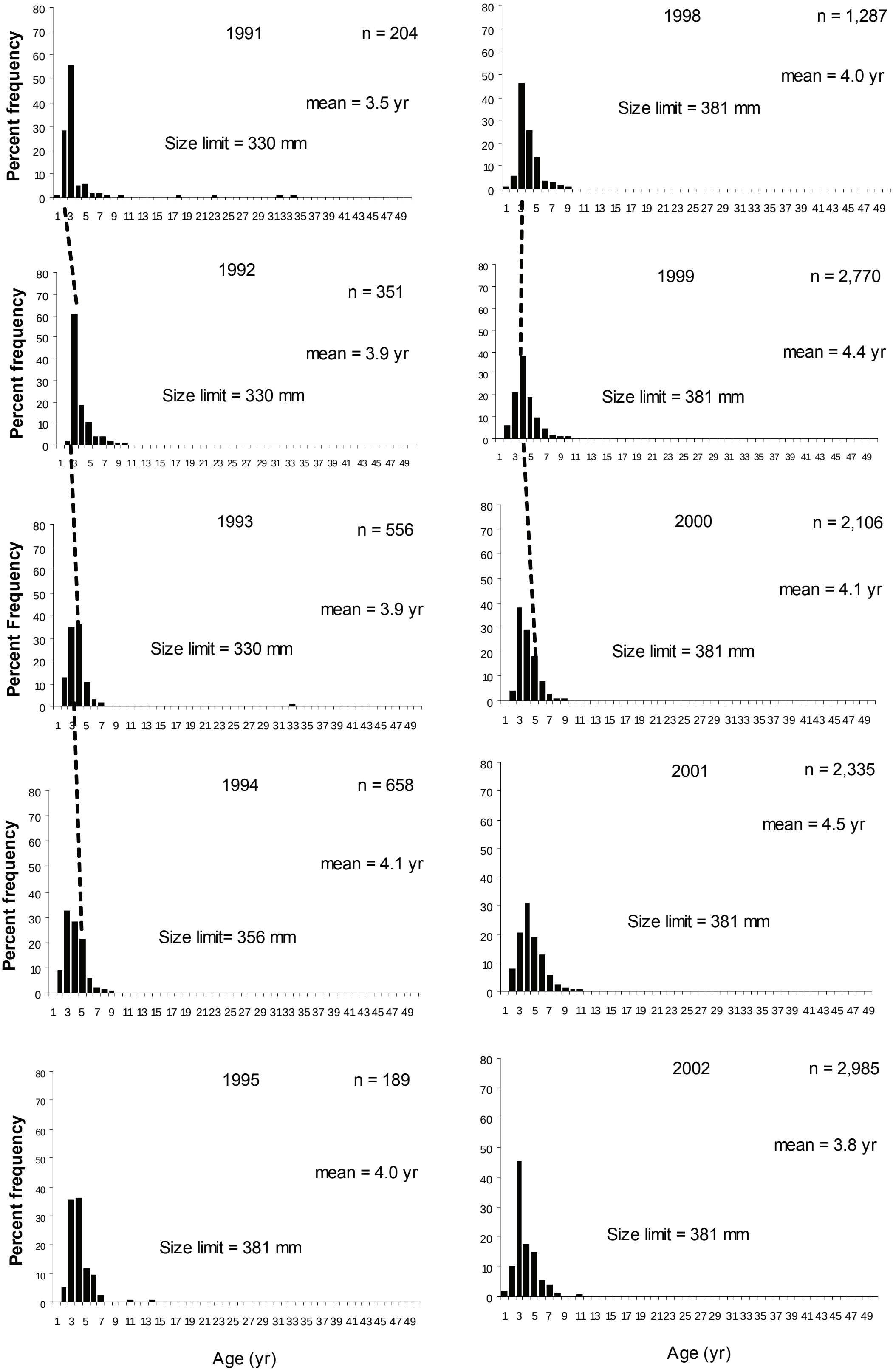


Figure 5. Age distribution of the commercial vertical hook and line fishery by year. Dashed lines indicate year-class progression.

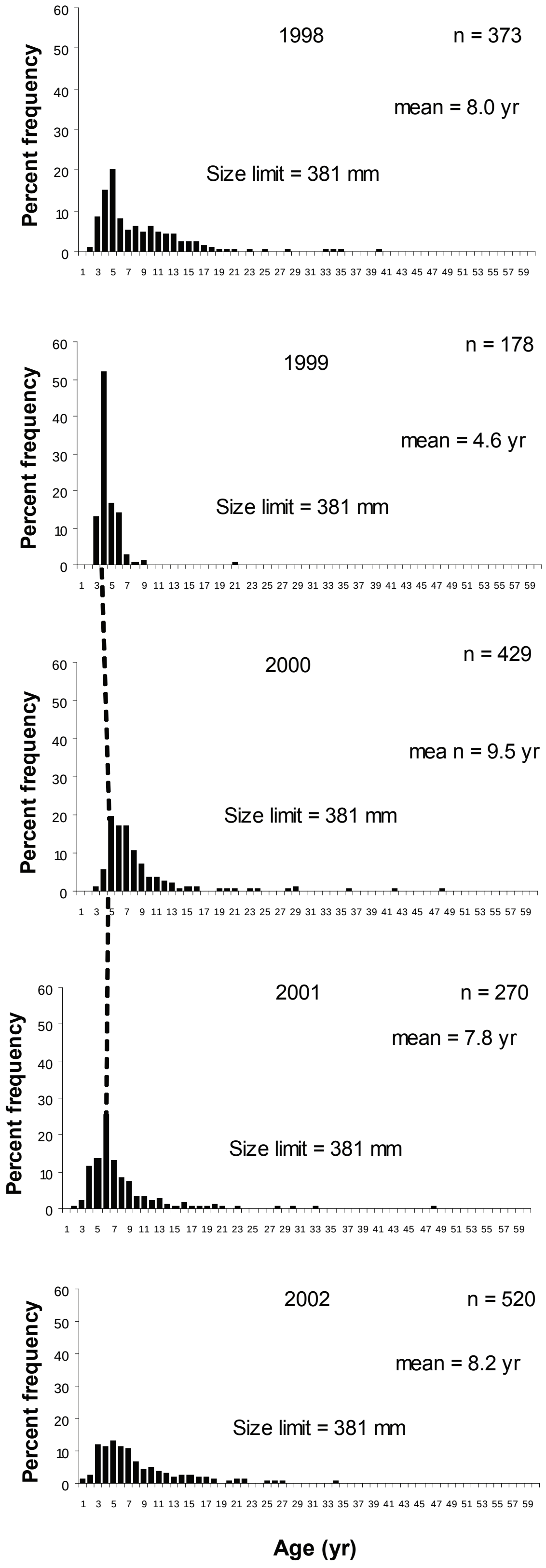


Figure 6. Age distribution for the commercial longline fishery by year. Dashed lines indicate year-class progression.

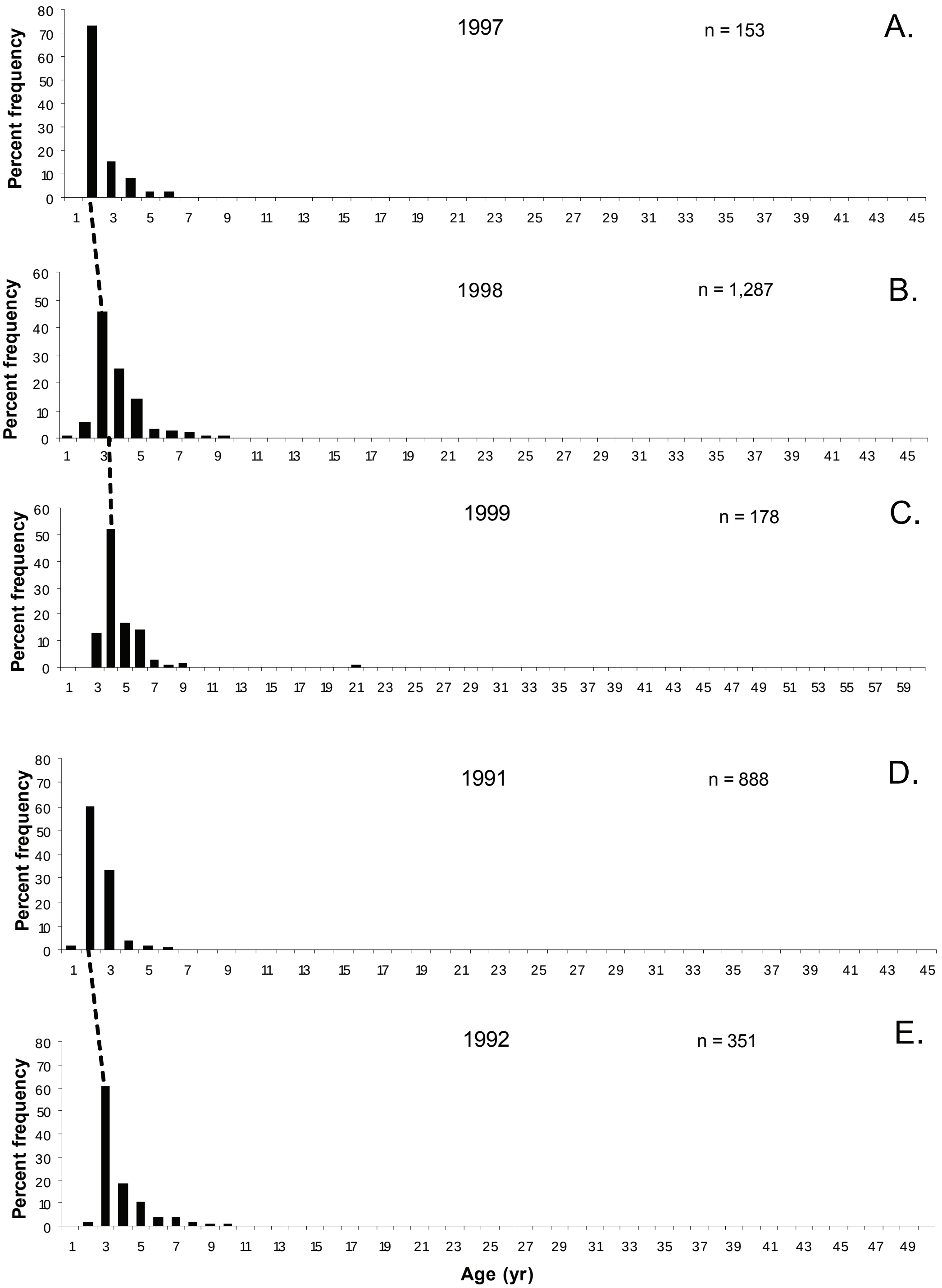


Figure 7. Progression of 1995 year-class (dashed line) through recreational (A), commercial vertical hook and line (B) and commercial longline (C) and 1989 year-class through the recreational (D) and commercial vertical hook and line (E).

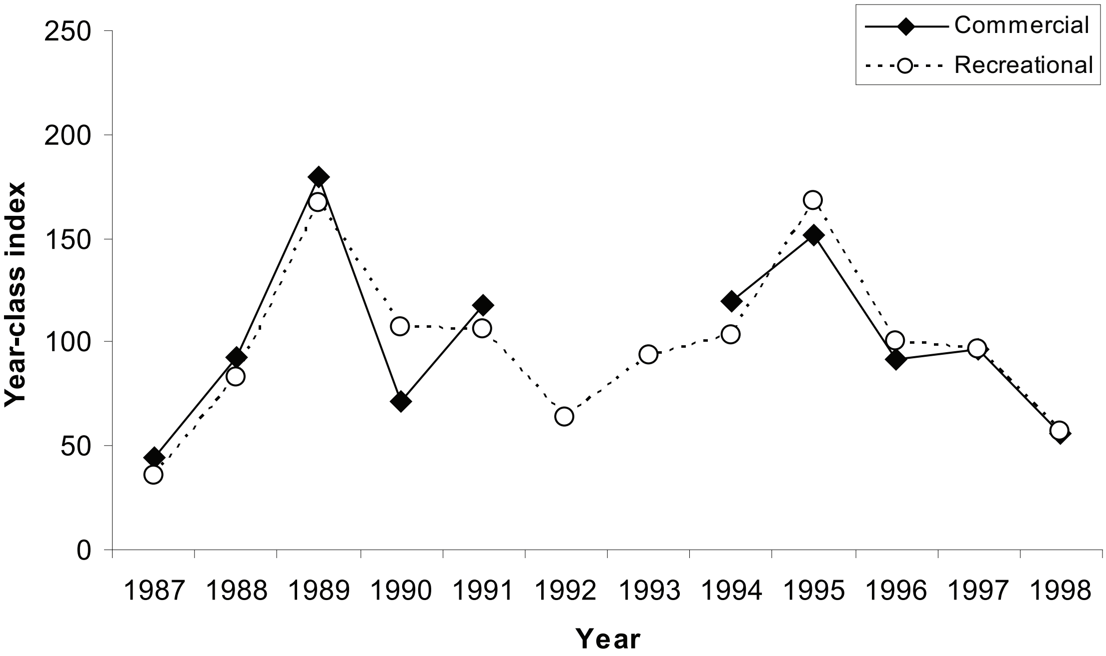


Figure 8. Red snapper year-class index calculated from Gulf of Mexico vertical hook and line sectors (eastern and western gulf combined).

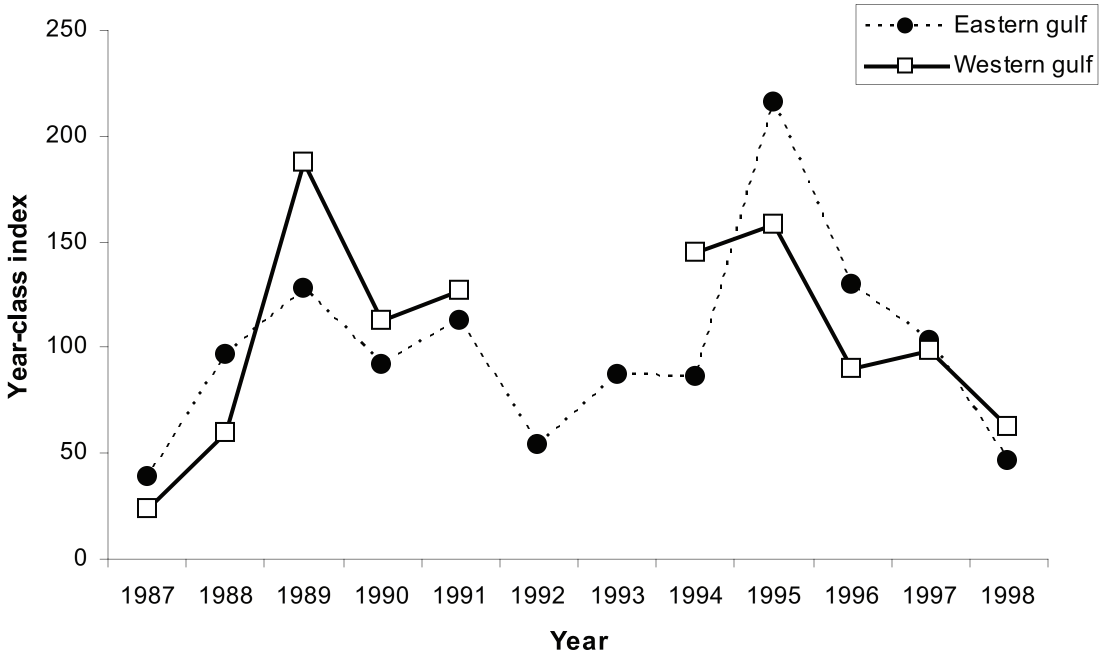


Figure 9. Red snapper year-class index calculated for the eastern and western Gulf of Mexico (commercial and recreational vertical hook and line sectors combined).

depths fished, fish behavior or habitat selection (Allman et al. 2002; Mitchell et al. 2004). Our observations reveal increased complexity in making gear selectivity comparisons because age structure is not static from year to year and dominant ages caught by different gears can overlap. For example, fish as old as age 4 year dominated in the vertical hook and line fisheries (1993, 1999, and 2001) while fish as young as age 4 dominated in the longline sector (1999 only; a shorter record to compare). But the overall pattern appeared to be an age progression over time with a year-class moving through a "gauntlet" of the respective fisheries. These empirical observations support the modeled assessment results showing vulnerability peaking at younger ages in the vertical hook and line sector compared to vulnerability of older fish taken in the longline sector (Porch 2007, this volume).

Size limits increased over the period of study for recreational and commercial vertical hook and line sectors (Hood and Steele 2004). We thus expected a shift to an older age structure over time, but changes were not readily apparent. The recreational size limit increased from 330 mm TL (13 in) in 1991 to 356 mm TL (14 in) in 1994, 381 mm TL (15 in) in 1995, and 406 mm TL (16 in) in 2000. Commercial vertical hook and line size limits increased similarly, except that the commercial size limit remained at 381 mm TL (15 in) after 1995. During the period of record for longline samples (1998–2002), the size limit also remained at 381 mm TL (15 in). These size limit changes basically split the middle of the size range for age 2 red snapper (compare raw size-at-age data in Nieland and Wilson 2000; Wilson and Nieland 2001; Allman et al. 2002). For example, age 2 dominated the recreational age structure in 1991 when the size limit was 330 mm TL, dominated again when the size limit increased to 381 mm TL (1997), and even exceeded 30% of the age structure when the size limit increased to 406 mm TL (2001). So the effect of size limit changes to age structure in the recreational sector seemed minimal. However, 2 year olds were not as frequent in the commercial vertical hook and line fishery and were virtually absent from the longline sector. They became even less frequent over the period of our age record, and after the size limit increased to 356 mm TL and then 381 mm TL, 2 year olds were never more than about 10% of the commercial vertical hook and line landings. This influence of size limits upon the age structure in the commercial fishery, as opposed to the recreational sector, suggests greater selection for larger and faster growing 2 year olds from a species exhibiting broad variation in size-at-age. The contrast between recreational and commercial vertical hook and line age structure also indicated differences in selectivity, albeit, more subtle than differences exhibited by the longline sector.

Our observations about age differences among gears are consistent with other studies showing that red snapper undergo a general ontogenetic shift in habitat and depth. Nieland and Wilson (2000) reported that age 1 and younger fish dominated benthic habitats sampled by survey trawls, whereas age 2 and age 3 fish dominated the samples obtained from explosive removal of an oil platform. Nieland and Wilson (2000) further indicated that commercial vertical hook and line collections of red snapper in Louisiana waters revealed few age 2 fish, and in a follow-up paper, they speculated that fish older than about age 6 become rare in the vertical hook and line catches due to mortality and emigration away from the oil platforms (Wilson and Nieland 2001). Mitchell et al. (2004) also suggested older red snapper may be less reef obligate, based on research longline catches.

The progression of strong year-classes in aging data has been used to corroborate the method of aging (Morison et al. 1998; Campana 2001). Our finding of age progressions independently observed among fishery sectors, as well as good precision among readers, provides strong support that our method of aging is consistent for the age range commonly observed (ages 2–6). To address concerns about bias in age assignment possibly due to first annulus interpretation (Allman et al. 2005b), we examined the otolith weight versus age relationship. By adding or subtracting one year to our original ages and re-estimating regression parameters, we mimicked the effect of being consistently biased in our assignment of the first annulus. As the regression of otolith weight with our original ages was closest to a zero intercept and was the only regression to have zero occur within the 95% confidence interval, the analysis provides evidence that our method of aging was not biased.

Our conclusions concerning age frequencies and year-class dominance in the catch are also based upon the assumptions that otolith samples collected by the various fishery-dependent programs are of sufficient sample size and represent simple random samples of the catch. Regarding sample sizes, Thompson (1987) showed that about 510 fish ages is a conservative and sufficient sample size such that all age-class proportions (viewed as multinomial proportions) should be within 5% of the statistical population proportions with 95% confidence. Otolith sample sizes for the principal stratification levels in our study, for example, fishing sector within a given year, sometimes fell below 510 samples. Regarding simple random sampling of age structures, it is known that the approach in theory may be the simplest (Quinn and Deriso 1999) but the practice can be difficult to impossible to achieve (Pope 1988; Aanes and Pennington 2003), thus even a quasi-random approach can be useful (Pope 1988). Therefore, the assumptions of sufficient sample size and simple random sampling were likely not always met in our estimates of age frequencies. However, consistent age progression observed in different fishery sectors suggests that the year-class signal determined from empirical age estimates may be robust to degrees of nonrandom sampling and low sample size. This does not eliminate concern over other possible nonrandom sampling effects, and thus every effort should be made to develop strategies for random sampling and to establish adequate stratification levels.

We generated an index of year-class strength by tracking progressions of the most common ages; thus a relative year-class index (YCI) based upon empirical age frequencies (Böhling et al. 1991). The 1989 and 1995 year-classes stood out over the 12 year record examined. Empirical tracking of dominant age classes in some fish populations has enabled inferences about recruitment processes in earlier life history stages (Böhling et al. 1991, McFarlane and Beamish 1992; Doherty and Fowler 1994; Russ et al. 1996). Our temporal comparison of year-class progressions and development of the YCI for separate gulf regions contributes to the understanding of spatial differences in stock dynamics and recruitment. Red snapper in the gulf traditionally have been managed as a single unit stock but development of a two stock, two region model was undertaken recently (Southeast data, assessment, and review 2005). This new management approach, viewing gulf red snapper as either one or two stocks, underscores how our understanding of stock structure and spatial dynamics is evolving. There were several lines of investigation that led to a two stock management approach. A recent study found variation in red snapper growth rates from east to west (Fischer et al. 2004). We detected differences in the age structure for the commercial longline fishery with older fish occurring more frequently in the western gulf, as did a research longline survey (Mitchell et al. 2004). However, our observed age progressions and the YCI indicated that year-class patterns were consistent between the eastern and western Gulf of Mexico. While we cannot discount that there may be differences in the stock structure between the eastern and western gulf, our results support a hypothesis that recruitment processes influencing year-class strength operate at large spatial scales.

Inference of recruitment trends from age structure has been common in fisheries but the approach requires simplifying assumptions. Hjort and Lea (1914) were the first to infer recruitment pulses from year-class trends. Subsequent development of indices have been based on samples measured in one year (common in freshwater systems assuming equal vulnerabilities across ages and years, e.g., Maceina 1997; Isermann et al. 2002; Cowx and Frear 2004) and from age progressions over time (assuming total mortalities experienced among year-classes are similar; e.g., Böhling et al. 1991, McFarlane and Beamish 1992; King et al. 2000; McGlennon et al. 2000). Age structured assessment models in theory can separate recruitment effects from cumulative mortality, vulnerability by age and yearly exploitation; but in practice, clear distinctions are difficult to make (Walters and Martell 2004). An age-progression approach may have utility for inference contrasts with other approaches if it is a reasonable assumption that exploitation rates have been relatively constant over the period of record (McFarlane and Beamish 1992). For example, comparison of multiple year-class indices, determined from different ontogenetic stages has commonly been conducted to determine the period when year-class strength is established (Helle et al. 2000). But, these correlations often reveal more about the relative error inherent in the various indices (Mukhina et al. 2003). Our empirical YCI is integrated over five years (the common ages), rather than measured in one year, and has traits of consistency and minimal age assignment bias in its estimation. We pose that our YCI could be valuable as a measurement standard for other indices of red snapper year-class strength and could specifically serve as the oldest stage year-class estimate. Currently three other red snapper indices are being developed, including a larval index based upon a plankton survey and age 0 and age 1 indices based upon length categories of red snapper captured in a trawl survey. Soon all red snapper indices will have a common record exceeding 15 years, and it is our hope that a correlation analysis can be conducted. We would expect closest correlation of the empirical YCI with the age 1 index, followed by the age-0 index, and then by the larval index. Deviations from this pattern, observed from a matrix of the index correlations, could then be useful to gauge the relative error inherent in any particular index.

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