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SEDAR74-DW-34

20 May 2022

Please cite this document as:

Steven Garner, Steven, Robert Allman, Beverly Barnett and Naeem Willett. 2022. Description of age, growth, and natural mortality of Red Snapper from the northern Gulf of Mexico 1980 and 1986-2019. SEDAR74-DW-34. SEDAR, North Charleston, SC. 33 pp.

Description of age, growth, and natural mortality of Red Snapper from the northern Gulf of Mexico 1980 and 1986-2019

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INTRODUCTION

Quality age data (i.e., high accuracy and precision) are crucial for informing a variety of parameter estimates in stock assessments, such as size- and egg production-at-age, age-specific natural mortality, and tracking cohorts over time. Several studies have been conducted using sagittal otoliths to age red snapper and provide basic information on growth and annulus formation (Futch and Bruger, 1976; Bortone and Hollingsworth, 1980; Nelson and Manooch, 1982; Wilson and Nieland, 2001; Manooch and Potts, 1997; Patterson et al., 2001; Fischer et al. 2004). Recently, the maximum age of Gulf of Mexico red snapper has been validated to at least 45 years using otolith core $\Delta^{14}C$ analysis (Barnett et al. 2018; Andrews et al. 2019). Additionally, red snapper otolith reader interpretation and the repeatability of age estimates (i.e., precision) have been examined (Allman et al., 2005). The goal of this report is to characterize age data for Gulf of Mexico (GOM) red snapper collected in 1980 and from 1986-2019 as they pertain to length distributions, growth, natural mortality, and ageing error.

METHODS

Sample collection and processing

Red snapper were sampled from recreational landings from the Gulf of Mexico (GOM) between Texas and the west coast of Florida during the spring and summer of 1980 and then consistently from both recreational and commercial landings from January 1986 through December 2019. (Figure 1). Samples were collected intermittently from fishery independent sources through 2006 and then consistently through 2019. Throughout the time series, fish were measured to the nearest mm fork length and/or total length and weighed to the nearest g, and sex was determined macroscopically if landed whole. Sagittal otoliths were removed, cleaned with distilled water, dried and a subset weighed to the nearest 0.0001 g prior to sectioning. All otoliths were processed and aged with the exception of those from the commercial hand-line fishery, which were sub-sampled based on landings by NMFS fishing grid due to the magnitude of samples collected annually.

Otoliths were processed with a Hillquist high-speed thin sectioning machine utilizing the methods of Cowan et al. (1995) or on an Isomet low-speed saw. Two transverse cuts were made through the otolith core to a thickness of 0.5 mm. Ages were assigned based on the count of annuli (opaque zones observed on the dorsal side of the sulcus acousticus in the transverse plane with reflected and/or transmitted light at 40x, including any partially completed opaque zones on the otolith margin) and the degree of marginal edge completion. Red snapper off the Southeastern U.S. complete annulus formation by late spring to early summer (Patterson et al., 2001; Wilson and Nieland, 2001; White and Palmer, 2004; Allman et al., 2005). Therefore, age was advanced by one year if a large translucent zone was visible on the margin and capture date was after December 31st and before July 1st; after June 30th age was equal to opaque zone count. By this traditional method, an annual age cohort is based on a calendar year rather than time since spawning (Jearld, 1983; Vanderkooy et al., 2020). Biological (i.e., fractional) ages were estimated for fitting growth curves. Biological age accounts for the difference in time between peak spawning (defined as 1 July for red snapper) and capture date (difference in days divided by 365.25). This fraction is added to annual age if capture date is after July 1st and subtracted if capture date is before July 1st (Vanderkooy et al., 2020).

Reader precision and aging error

Reader precision among laboratories was estimated using an otolith reference set (n = 200) to ensure repeatability of ageing. Average percent error (APE; Beamish and Fournier, 1981) was used to estimate precision between readers. An APE ≤ 5% is considered acceptable for moderately long-lived species with relatively difficult to read otoliths (Morison et al., 1998; Campana, 2001). Once an APE of ≤ 5% was achieved without obvious bias, the reader was considered to be proficient and could begin ageing. Reader precision within the Panama City laboratory was measured using 20% overlap reading with another experienced ager.

Ageing error was estimated with several different scenarios to model bias and precision for the primary reader using the Northwest Fisheries Science Center's aging error (nwfscAgeingError) package in R (Punt et al. 2008). Bias models included options for no bias, linear bias, or curvilinear bias. Precision model scenarios included models for no error, constant coefficient of variation (CV), curvilinear standard deviation (SD), or curvilinear CV. Error models assumed that the overlap (expert) reader aged without bias or error. Akaike's corrected information criterion (AICc) along with diagnostic plots of expected values, expected CI's, and SD were used to select the best fit model to describe ageing error and select the appropriate aging error matrix for input in the assessment. Ageing error models were not estimated separately for each subregion because there is no evidence to suggest a difference in readability among regions.

Growth

Growth was modeled with size-modified von Bertalanffy growth functions fit to red snapper size (FL cm)-at-age (yr) data with AD Model Builder (Diaz et al., 2004; Fournier et al. 2012). Several models with different methods for estimating the variance component were considered including constant SD, constant CV, CV as a linear function of age and CV as a linear function of size-at-age. Growth models were applied to unweighted data as well as data weighted by the inverse of the count of each calendar age (i.e., 1 / # of observations in age class). Growth models were estimated for each subregion (West, Central, or East) in a 3-substock scenario as well as for a single stock scenario. Growth models were applied to all size-at-age data (population set of models) that included inputs of historical fork-length converted size limits for the commercial and recreational sectors for each length-limit-specific regulatory period. Growth models also were estimated for three time stanzas: 1) 1991 to 2008, 2) 2009-2015, or 3) 2016 to 2019 based on yearly trends in red snapper biomass levels that roughly correspond to depletion, rebuilding, and asymptotic recovery of the stock.

Natural mortality

Growth and longevity estimates were used to inform red snapper natural mortality with several different methods including those described in Hoenig (1983), Lorenzen (1996), Hewitt and Hoenig (2005), and Then et al. (2015). Specifically, based on a given set of VBGF parameters, weight (g)-at-length (FL mm) parameters, and longevity estimate, an average natural mortality estimate was estimated and then scaled to age-specific rates from the Lorenzen function (Lorenzen 1986).

RESULTS

Sample collection

A total of 239,409 ages were assigned to red snapper sampled from the GOM from 1980 and from 1986 to 2019, which consisted of 96,571 samples from the West, 118,228 from the Central, and 24,610 from

the East subregion (Figure 2). The number of age samples by year, subregion, and fishery (commercial, recreational, fishery independent, or unknown) are listed in Table 1.
The proportion of age samples by state landed and data provider are shown in Figure 3. The number of age samples by year, subregion, and gear type (vertical line [handline or hook-and-line], longline [bottom longline or vertical longline], other [trap, trawl, spear], or unknown) are listed in Table 2. The size distribution of red snapper lengths was different among subregions with differently intense right-skewed distributions for the West and Central and a normal distribution for the East (Figure 4). Mean (SE) fork length (cm) of red snapper was highest (52.7 ± 0.07) in the East and lowest (46.43 ± 0.03) in the Central subregion. Mean age (yr, fractional) of red snapper differed by only 0.6 yr among subregions with the West subregion having the highest (4.95 ± 0.01) and the Central having the lowest (4.30 ± 0.01) mean age. The distribution of ages among subregions was generally similar but the West subregion had more and a higher proportion of older fish (Figures 5-7). The oldest observed ages (calendar) were 57, 49, and 45 for the West, Central, and East subregions, respectively (Figure 6). Age distributions by subregion and year are shown in Figures 8-10. All three regions show evidence of a strong 2014 year-class. Fork lengths (cm) of red snapper captured by the commercial fishery were larger in the East, larger in the West for fish captured by the recreational fishery, and similar among regions for fishery independent samples (Figure 11). Red snapper ages from recreational and fishery independent samples were oldest in the West, while fish from commercial samples in the West and East were similarly older than the Central subregion (Figure 12). Frequency distributions of red snapper age samples by year from the commercial and recreational sectors are shown in Figures 13 and 14.

Reader precision and ageing error

Average percent error was calculated for age estimates of the red snapper reference set from NOAA/NMFS Panama City, the Florida Fish and Wildlife Research Institute (FWRI), Alabama Marine Resources Division (AMRD), Mississippi Department of Marine Resources (MSDMR), Louisiana Department of Wildlife and Fisheries (LWDF), and Texas Parks and Wildlife (TPW) (Table 3). For the data provided by NOAA/NMFS Panama City, a total of 4,792 red snapper otolith sections that were read by the primary reader also were read by an expert reader, which excluded samples deemed unreadable. Reader agreement was 66.9% with 94.1% of age estimates having a difference of ±1 year between reader ages estimates. Absolute standard deviation between PCLab agers was 0.30, absolute coefficient of variation was 5.34, and absolute percent error was 3.78. Ageing error model output (Table 4) indicated that a model with a linear bias and curvilinear SD had the lowest AIC, AICc, and BIC but a model with no bias and curvilinear SD was the second best fit (Figure 15). Age-specific pairwise comparisons indicated significant differences between expert and primary reader mean age estimates for ages 2, 3, 5-8, and 10 yrs, but mean ages between readers only differed by 0.02 to 0.31 yrs. Significant differences were likely due to large sample sizes within these age-classes.

Growth

Visual inspection of growth functions plotted against size-at-age data indicated that models fit to weighted data provided better fits to the older age classes (15+ yrs), which had disproportionately fewer samples than younger age classes (Figure 16). Population growth model parameters indicated that the parameter for mean size-at-maximum length (L_∞) had decreased by 3.54 cm since the data were last assessed in SEDAR52. Modeling the variance component of von Bertalanffy growth functions (VBGF) as a linear function of size-at-age produced the best fit to the weighted size-at-age data based on AICc values (Table 5). Different variance forms were best fit to each of the three subregions (Table 6) however, subregion-specific growth models with variance modeled as a linear function of size-at-age had a cumulative AICc value of only 5.5 points higher than the best fit models for the West and East subregions, respectively. Stock synthesis requires a single functional form for growth, thus, parameters estimated with VBGF models with variance as a linear function of size-at-age were used for the final analyses. Growth parameters estimated for L_∞ were lowest in the West compared to the other two regions, which had similar values; parameter estimates for k were highest in the East compared to the other two regions, which had similar values (Figure 17). Mean (±95%CI) size-at-age increased at similar rates among regions from 0-5 yrs, then diverged with fish from the East increasing fastest towards the mean maximum length (Figure 18). Mean size-at-age in the Central and West subregions began to diverge at approximately age-10 where fish from the Central began to approach the same mean maximum size as fish from the East whereas fish from the West remained smaller-at-age at older ages. For VBGF parameters estimated by time stanza, with ages from the Central and East combined due to lower sample sizes collected during the most recent time-period, strong divergence in size-at-age was not observed among stanzas within subregions (Figure 19). Fish from the most recent time stanza (2016-2019) did have smaller size-at-age for some age classes, but confidence intervals overlapped in most cases.

Natural mortality

Multiple studies have validated the longevity of different reef fishes using $\Delta^{14}C$ decay curves, with GOM red snapper longevity validated to at least 45 yrs (Barnett et al. 2018; Andrews et al. 2019). The method used to directly estimate observed age in bomb radiocarbon studies of red snapper otoliths (i.e., observed annuli counts) was the same method used to produce production age estimates as well as to produce the maximum age estimate of 57 yrs. The maximum age sample was evaluated by multiple experienced readers (Allman personal communication). Therefore, the maximum age estimate used in SEDAR52 was increased to 57 yrs for SEDAR74. Based on this longevity, the average natural mortality rate ($\bar{M}$) over the fishable lifespan of red snapper was estimated to be 0.0796 yr^{-1} based on the Hoenig method for fish (Hoenig 1983) and 0.0526 yr^{-1} based on the Hewitt and Hoenig method (Hewitt and Hoenig 2005). Based on the methods of Then et al. (2015), which recommend Hoenig's nonlinear estimates of M, average natural mortality for red snapper was estimated to be 0.1206 yr^{-1} based on estimates from all fishes (excluding the pygmy goby, *Eviota sigillata*, $M = 49.57$ yr^{-1}), 0.1207 yr^{-1} based on estimates from reef fishes, and 0.1040 yr^{-1} based on estimates from other Lutjanids. The Lutjanid-specific estimate of average *M* was recommended by the life-history group for use in SEDAR74. Following the methods described in SEDAR52, natural mortality for ages 0 and 1 were fixed to 2.0 and 1.2 yr^{-1}, respectively, with all other age-specific natural mortality estimates scaled using the Lorenzen function (Lorenzen 1996). Lorenzen-based age-specific natural mortality estimates were then scaled to the Then et al. (2015) function for all fishes, reef fishes, or Lutjanids (Figure 20) with the Lutjanid-scaled estimates recommended for use as the final vector of natural mortality-at-age for SEDAR74. Also following the methods of SEDAR52, age-2 was recommended as the first age fully selected by the directed fishery. This natural mortality vector resulted in a cumulative survival to the oldest age-class of only 0.1%. However, this estimate was deemed reasonable for a species like red snapper based on its life history (rapid growth, early maturity, long-lived, low natural mortality, and infrequent strong year classes), and considering that only a very small number of individuals have been observed to exceed 45 yrs of age despite having aged hundreds of thousands of individuals.

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Table 1. Number of red snapper age samples by fishery (commercial, recreational, fishery independent, or unknown), subregion (West, Central, or East), and year.

	COM			REC			FI			UNK		
Year	W	C	E	W	C	E	W	C	E	W	C	E
1980	0	0	0	0	325	0	0	0	0	0	2	0
1986	0	0	0	348	1	1	0	0	0	0	0	0
1987	0	0	0	146	0	0	0	0	0	0	0	0
1988	0	0	0	350	1	0	0	0	0	0	0	0
1989	0	0	0	82	0	1	0	0	0	0	0	0
1990	0	0	0	36	0	0	0	0	0	0	0	0
1991	25	178	12	629	272	2	0	0	0	0	2	0
1992	210	116	34	511	441	5	0	7	0	22	2	0
1993	341	136	43	1236	632	62	5	0	0	0	0	0
1994	500	121	36	540	593	53	0	2	0	0	0	0
1995	97	85	26	147	371	0	0	21	0	0	0	0
1996	0	9	6	0	195	0	1	1	0	0	0	0
1997	0	1	41	0	157	1	36	1	0	0	0	0
1998	1519	235	36	1306	1857	2	1	16	0	0	0	0
1999	1873	902	172	435	1590	14	0	10	0	38	96	0
2000	1037	1381	111	255	647	3	76	115	0	50	77	0
2001	1205	1247	140	74	595	12	83	3	1	9	43	0
2002	4418	1165	182	772	3034	15	73	127	0	0	0	0
2003	3456	1500	177	968	6445	40	58	12	4	0	0	0
2004	3350	989	347	1195	4075	4	47	16	5	0	0	0
2005	2999	1131	379	1442	5331	57	357	423	4	0	0	0
2006	3362	1146	378	1524	3743	88	147	133	3	0	0	0
2007	1931	1211	178	1072	651	22	229	400	24	0	0	0
2008	2020	1147	343	940	542	63	355	234	30	0	0	0
2009	2528	949	1275	1178	960	372	253	450	337	13	22	6
2010	2293	1149	1461	876	1563	375	396	1487	460	0	0	35
2011	1695	2896	1052	1203	1403	385	2118	1385	311	0	0	17
2012	3110	3581	869	1512	2194	141	1890	1134	132	1	206	16
2013	1614	2063	1225	2399	2765	183	2656	1119	221	2	0	0
2014	1203	1792	1876	1986	4039	196	1445	1380	102	0	1	0
2015	1750	2386	1373	1834	4794	344	466	1544	141	0	0	0
2016	1806	2769	1633	1632	2486	73	566	1806	184	0	1	0
2017	1372	3167	1696	2032	1865	491	2308	1739	225	0	0	18
2018	1802	4253	1267	2178	2756	483	409	1828	307	0	0	0
2019	1801	4430	1730	1981	2750	410	331	1174	28	0	0	0

Table 2. Number of red snapper age samples by fishing mode (vertical line, longline, other, or unknown), subregion (West, Central, or East) and year (1980-2019).

	VL			LL			OT			UNK		
Year	W	C	E	W	C	E	W	C	E	W	C	E
1980	0	325	0	0	0	0	0	2	0	0	0	0
1986	348	1	1	0	0	0	0	0	0	0	0	0
1987	146	0	0	0	0	0	0	0	0	0	0	0
1988	350	1	0	0	0	0	0	0	0	0	0	0
1989	82	0	1	0	0	0	0	0	0	0	0	0
1990	36	0	0	0	0	0	0	0	0	0	0	0
1991	654	450	2	0	0	12	0	2	0	0	0	0
1992	721	544	23	0	0	15	22	22	1	0	0	0
1993	1548	768	75	29	0	30	5	0	0	0	0	0
1994	1034	714	81	0	0	8	6	2	0	0	0	0
1995	236	476	7	0	0	19	8	1	0	0	0	0
1996	0	205	0	1	0	6	0	0	0	0	0	0
1997	0	159	32	0	0	10	36	0	0	0	0	0
1998	2479	2054	13	347	0	25	0	54	0	0	0	0
1999	2232	2496	84	76	6	102	38	96	0	0	0	0
2000	950	2137	32	418	1	82	50	82	0	0	0	0
2001	1100	1830	77	262	15	76	9	43	0	0	0	0
2002	3173	4228	29	413	98	168	1106	0	0	571	0	0
2003	2354	7918	49	314	39	172	1396	0	0	418	0	0
2004	3059	5044	117	687	34	239	375	2	0	471	0	0
2005	4094	6761	127	252	35	313	18	89	0	434	0	0
2006	4102	4889	238	586	1	204	138	132	27	207	0	0
2007	2637	2016	89	392	93	135	70	153	0	133	0	0
2008	2517	1538	96	352	182	315	345	203	25	101	0	0
2009	3294	2112	1109	333	22	684	211	247	197	134	0	0
2010	2914	3484	1193	158	665	1082	320	50	56	173	0	0
2011	4104	4584	1135	867	981	572	25	119	58	20	0	0
2012	4585	5948	849	1257	995	253	607	166	56	64	6	0
2013	4053	4939	901	2041	927	679	577	81	49	0	0	0
2014	3303	5853	962	1216	1122	1124	115	237	88	0	0	0
2015	3508	7136	916	538	1348	808	4	240	134	0	0	0
2016	3421	5353	983	576	1450	860	7	209	47	0	50	0
2017	5279	5253	1698	433	1325	566	0	193	166	0	0	0
2018	3900	7110	1418	489	1663	588	0	64	51	0	0	0
2019	3249	7083	1361	864	1194	778	0	77	22	0	0	7

Table 3. Ageing precision estimates for the number of ages (n), percent agreement (%Agree), average standard devitation (ASD), average coefficient of variation (ACV), average absolute difference (AAD), and average percent error (APE) for the red snapper reference set read by each data provider: NMFS Panama City (PC), Florida Fish and Wildlife Research Institute (FWRI), Alabama Marine Resources Division (AMRD), Mississippi Marine Resources Division (MSDMR), Louisiana Department of Wildlife and Fisheries (LDWF), Texas Parks and Wildlife (TPW).

Source	n	%Agree	ASD	ACV	AAD	APE
PC	196	78.1	0.238	4.48	0.168	3.17
FWRI	200	84.0	0.138	2.44	0.098	1.73
AMRD	197	84.3	0.126	2.52	0.089	1.78
MSDMR	191	48.2	0.444	10.25	0.314	7.25
LDWF	199	64.8	0.316	8.14	0.224	5.76
TPW	200	25.5	0.866	16.38	0.613	11.58

Table 4. Ageing error model fit statistics for primary reader bias (none, linear, or curvilinear bias) and standard deviation (SD) modeled with no parameter, constant coefficient of variation (CV), curvilinear SD, or curvilinear CV. Best-fit model parameters are indicated with bold text.

Model	Bias model	SD model	AIC	AICc	BIC	ΔAIC	ΔAICc	ΔBIC
1	None	None	743168.5	743171.8	743246.4	710446.6	710445.2	710431.7
2	None	Constant CV	35606.6	35610.2	35688.2	2884.7	2883.6	2873.6
3	None	Curvilinear SD	32775.1	32779.5	32864.2	53.2	52.8	49.5
4	None	Curvilinear CV	35610.6	35614.9	35699.6	2888.7	2888.3	2885.0
5	Linear	None	743170.5	743174.1	743252.1	710448.6	710447.5	710437.4
6	Linear	Constant CV	35608.6	35612.6	35693.9	2886.7	2886.0	2879.3
7	**Linear**	**Curvilinear SD**	**32721.9**	**32726.6**	**32814.7**	0.0	0.0	0.0
8	Linear	Curvilinear CV	35612.6	35617.3	35705.4	2890.7	2890.7	2890.7
9	Curvilinear	None	1626925.4	1626929.7	1627014.5	1594203.5	1594203.1	1594199.8
10	Curvilinear	Constant CV	40649.3	40654.0	40742.1	7927.4	7927.4	7927.4
11	Curvilinear	Curvilinear SD	33297.2	33302.8	33397.4	575.3	576.2	582.8
12	Curvilinear	Curvilinear CV	40653.3	40658.8	40753.5	7931.4	7932.2	7938.8

Table 5. Parameter estimates from von Bertalanffy growth models fit to red snapper length (FL cm)-at-age (fractional, yr) data for a single stock, one region (Gulf of Mexico) model. The population model runs include all observations with year-specific size limits input for commercial and recreational fisheries. The fishery model runs include only observations from commercial or recreational fisheries. Variance parameter(s) were modeled with constant sigma, constant coefficient of variation (CV), CV as a linear function of age, or CV as a linear function of size-at-age. Weighting was used for a subset of each population or fishery model by taking the inverse of the count for each age-class in the dataset.

Model	Variance parameter	Parameters	Weighting	Region	N	Objective function value	AICc	ΔAICc	L_∞	k	t_0	varpar[1]	varpar[2]	Max gradient component
Population	Constant sigma	4	--	GOM	229519	732323.0	1464650.0	6000.0	77.50	0.2066	-0.170	7.553	--	3.20E-02
	Constant CV	4	--	GOM	229519	730571.0	1461150.0	2500.0	80.52	0.1680	-0.913	0.157	--	5.96E-02
	CV as linear function of age	5	--	GOM	229519	729418.0	1458850.0	200.0	81.59	0.1649	-0.884	0.172	0.001	1.97E-01
	CV as linear function of size-at-age	5	--	GOM	229519	729318.0	1458650.0	0.0	80.63	0.1731	-0.728	0.208	0.115	3.50E-04
	Constant sigma	4	Inverse	GOM	229519	3377.3	6762.6	4.2	81.00	0.1544	-1.121	6.010	--	1.16E-03
	Constant CV	4	Inverse	GOM	229519	3391.2	6790.5	32.0	79.97	0.1739	-0.980	0.079	--	1.13E-03
	CV as linear function of age	5	Inverse	GOM	229519	3375.2	6760.4	2.0	81.59	0.1458	-1.275	0.115	0.011	9.36E-07
	CV as linear function of size-at-age	5	Inverse	GOM	229519	3374.2	6758.4	0.0	**82.10**	**0.1407**	**-1.062**	**0.395**	**0.057**	8.64E-09

Table 6. Parameter estimates from von Bertalanffy growth models fit to red snapper length (FL cm)-at-age (fractional, yr) data for a three subregion (West, Central, or East Gulf of Mexico) model. The population model runs include all observations with year-specific size limits input for commercial and recreational fisheries. Variance parameter(s) were modeled with constant sigma, constant coefficient of variation (CV), CV as a linear function of age, or CV as a linear function of size-at-age. Weighting was used for a subset of each population or fishery model by taking the inverse of the count for each age-class in the dataset.

Model	Variance parameter	Parameters	Weighting	Region	N	Objective function value	AICc	ΔAICc	L_∞	k	t_0	varpar[1]	varpar[2]	Max gradient component
Population	Constant sigma	4	--	West	92690	299932.0	599873.0	676.0	76.56	0.2103	-0.056	7.899	--	3.30E-05
	Constant CV	4	--	West	92690	302351.0	604710.0	5513.0	76.71	0.1841	-0.732	0.156	--	7.27E+04
	CV as linear function of age	5	--	West	92690	300730.0	601471.0	2274.0	79.49	0.1717	-0.759	0.185	0.005	5.53E-04
	CV as linear function of size-at-age	5	--	West	92690	299593.0	599197.0	0.0	78.58	0.1847	-0.450	0.283	0.087	1.21E-03
	Constant sigma	4	--	Central	112434	350543.0	701095.0	9064.0	80.66	0.1789	-0.429	7.379	--	2.36E-01
	Constant CV	4	--	Central	112434	346092.0	692190.0	159.0	87.46	0.1354	-1.300	0.150	--	1.01E-02
	CV as linear function of age	5	--	Central	112434	346057.0	692124.0	93.0	87.77	0.1336	-1.331	0.148	0.202	1.01E-02
	CV as linear function of size-at-age	5	--	Central	112434	346011.0	692031.0	0.0	87.85	0.1323	-1.381	0.138	0.172	3.69E-06
	Constant sigma	4	--	East	24490	77592.3	155193.0	0.0	80.28	0.2092	-0.541	6.084	--	2.00E-03
	Constant CV	4	--	East	24490	78731.7	157471.0	2278.0	76.41	0.2206	-0.757	0.136	--	2.30E+04
	CV as linear function of age	5	--	East	24490	78043.6	156097.0	904.0	83.01	0.1825	-0.938	0.131	0.006	6.39E-03
	CV as linear function of size-at-age	5	--	East	24490	77703.0	155416.0	223.0	80.91	0.2010	-0.674	0.192	0.068	9.95E-05
	Constant sigma	4	Inverse	West	92690	159.5	327.0	14.3	81.30	0.1496	-1.150	5.460	--	4.65E-09
	Constant CV	4	Inverse	West	92690	168.3	344.6	31.8	80.30	0.1667	-0.997	0.094	--	4.48E-06
	CV as linear function of age	5	Inverse	West	92690	151.4	312.8	0.0	82.26	0.1449	-1.144	0.150	0.001	2.47E-05
	CV as linear function of size-at-age	5	Inverse	West	92690	153.1	316.3	3.5	**81.88**	**0.1361**	**-1.092**	**0.394**	**0.041**	1.00E-05
	Constant sigma	4	Inverse	Central	112434	165.9	339.8	2.9	85.55	0.1443	-1.133	6.198	--	1.05E+00
	Constant CV	4	Inverse	Central	112434	175.8	359.6	22.6	84.63	0.1506	-1.255	0.103	--	6.86E-06
	CV as linear function of age	5	Inverse	Central	112434	169.0	347.9	11.0	84.67	0.1499	-1.221	0.137	0.039	9.15E-06
	CV as linear function of size-at-age	5	Inverse	Central	112434	163.5	337.0	0.0	**85.43**	**0.1471**	**-1.020**	**0.318**	**0.057**	4.28E-05
	Constant sigma	4	Inverse	East	24490	104.8	217.6	0.0	85.77	0.1678	-0.794	6.054	--	1.38E-06
	Constant CV	4	Inverse	East	24490	112.3	232.5	14.9	84.11	0.1862	-0.694	0.113	--	1.34E-06
	CV as linear function of age	5	Inverse	East	24490	106.9	223.7	6.1	85.55	0.1726	-0.757	0.147	0.028	2.26E-06
	CV as linear function of size-at-age	5	Inverse	East	24490	104.8	219.6	2.0	**85.99**	**0.1659**	**-0.736**	**0.252**	**0.063**	2.64E-07

Figure 1. Number and proportion of red snapper age samples by commercial (COM), recreational (REC), fishery independent (FI), or unknown (UNK) collected from the Gulf of Mexico from 1980 and from 1986 to 2019.

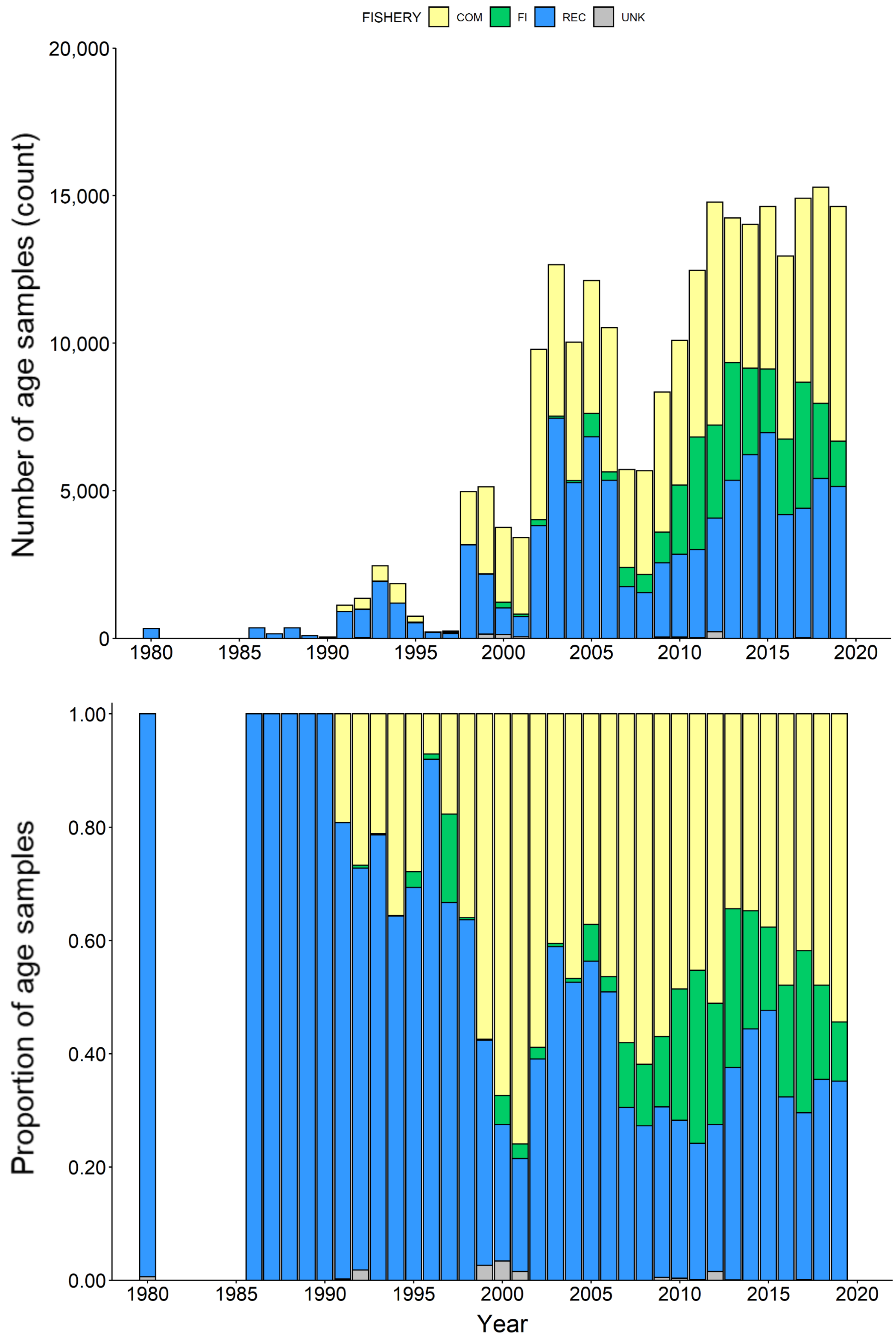


Figure 2. Number of age samples by West (W), Central (C), or East (E) subregion collected from the Gulf of Mexico from 1980 and from 1986 to 2019.

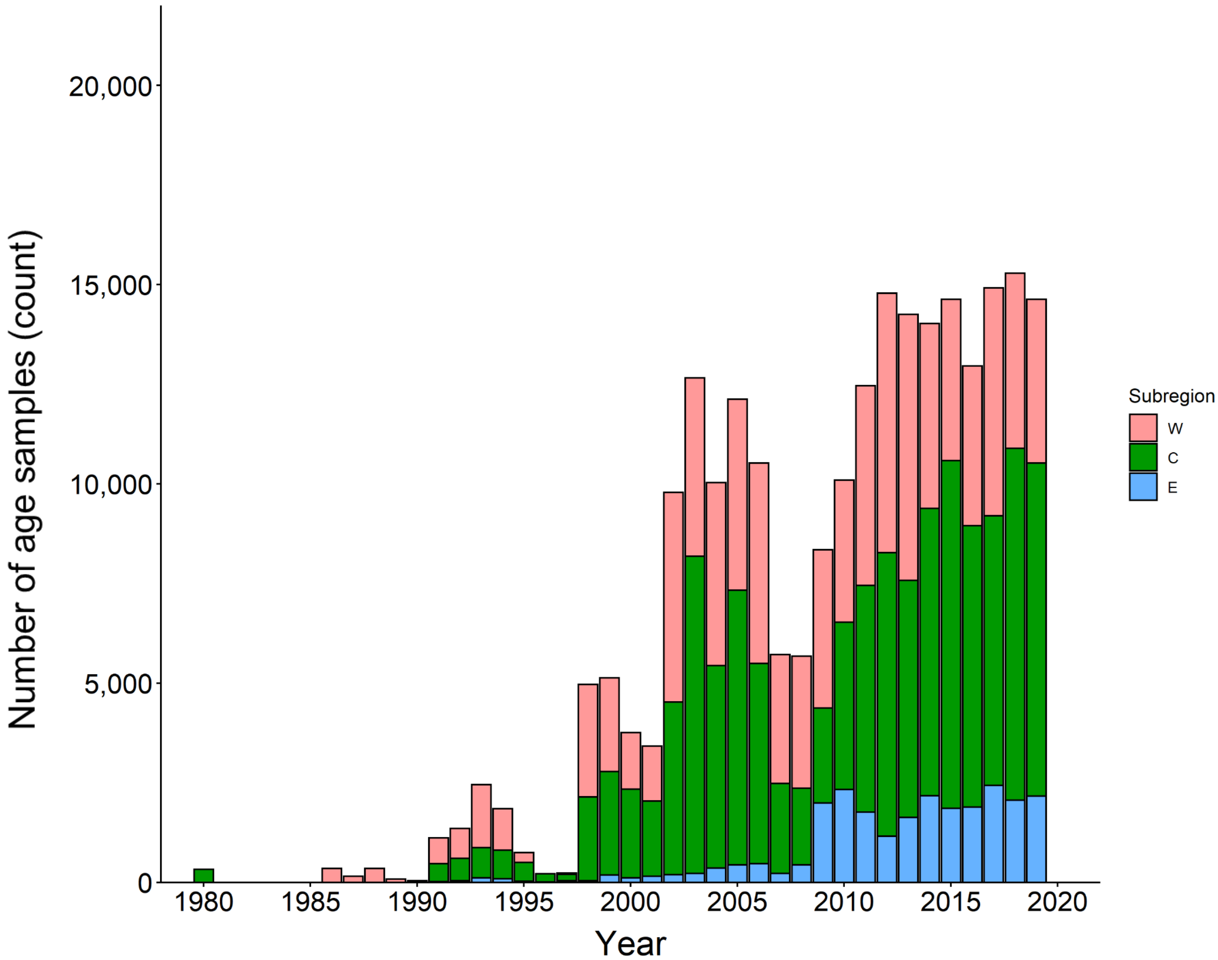


Figure 3. Proportion of red snapper age samples by state and data provider collected from the Gulf of Mexico from 1980 and from 1986 to 2019. Multiple labels from the same source indicate separate studies.

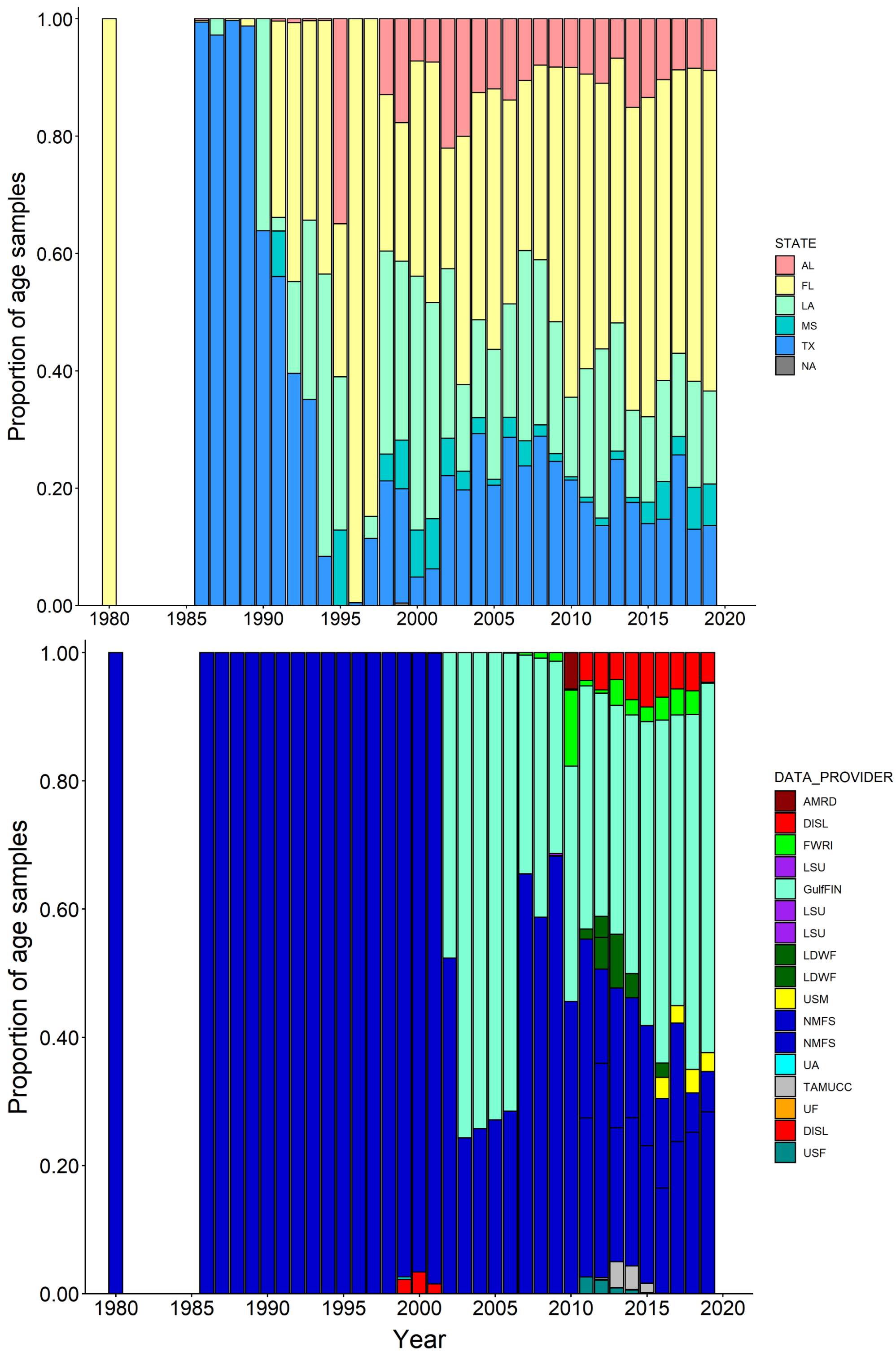


Figure 4. Frequency (%) histograms of final fork length (cm) by subregion (West, Central, or East) for red snapper age samples collected in the Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 2 cm.

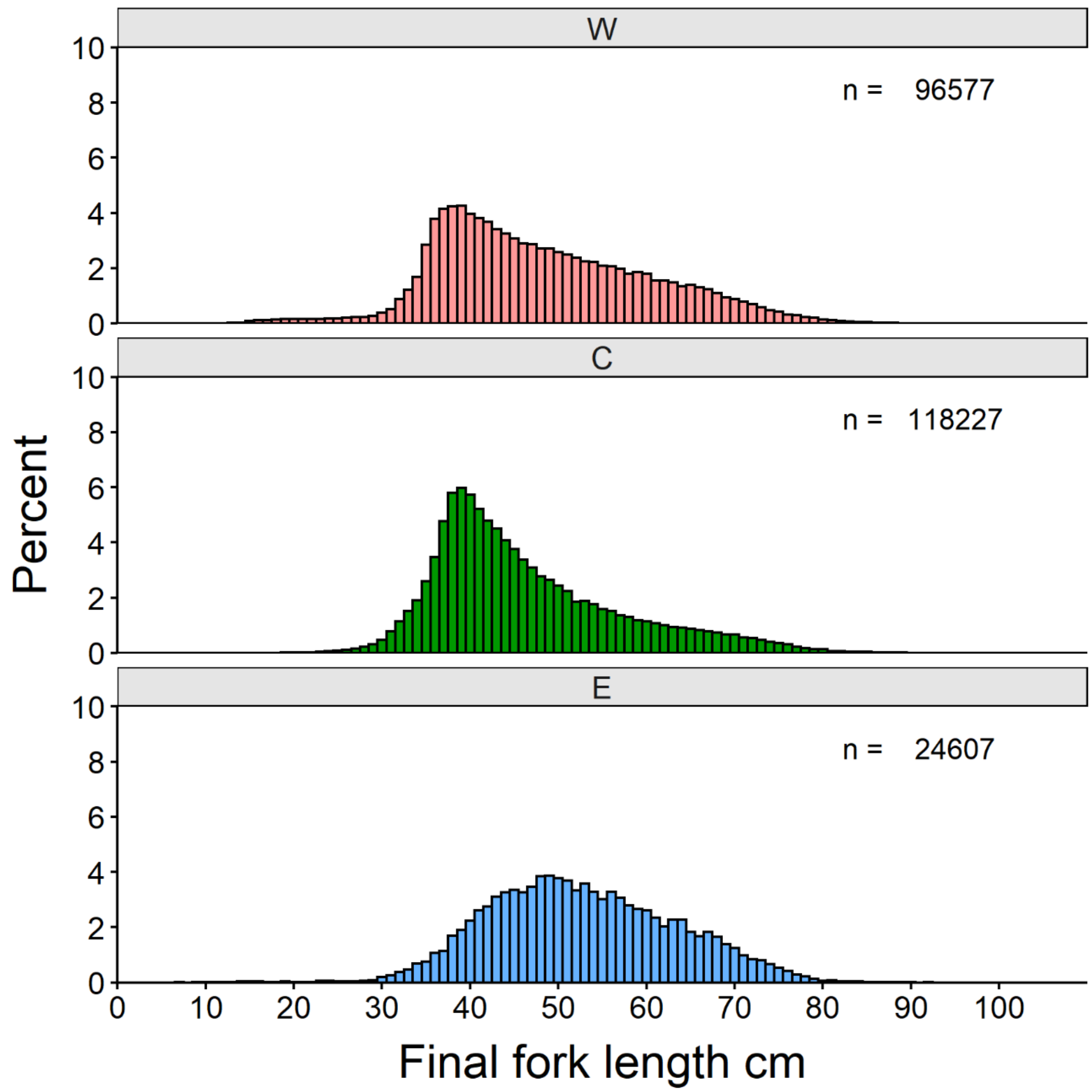


Figure 5. Boxplots of fractional age (yr) by subregion (West, Central, or East) for red snapper age samples collected in the Gulf of Mexico from 1980 and from 1986 to 2019. Upper and lower hinges indicate the first and third quartiles and whiskers extend to 1.5*IQR. Outliers are indicated by filled circles.

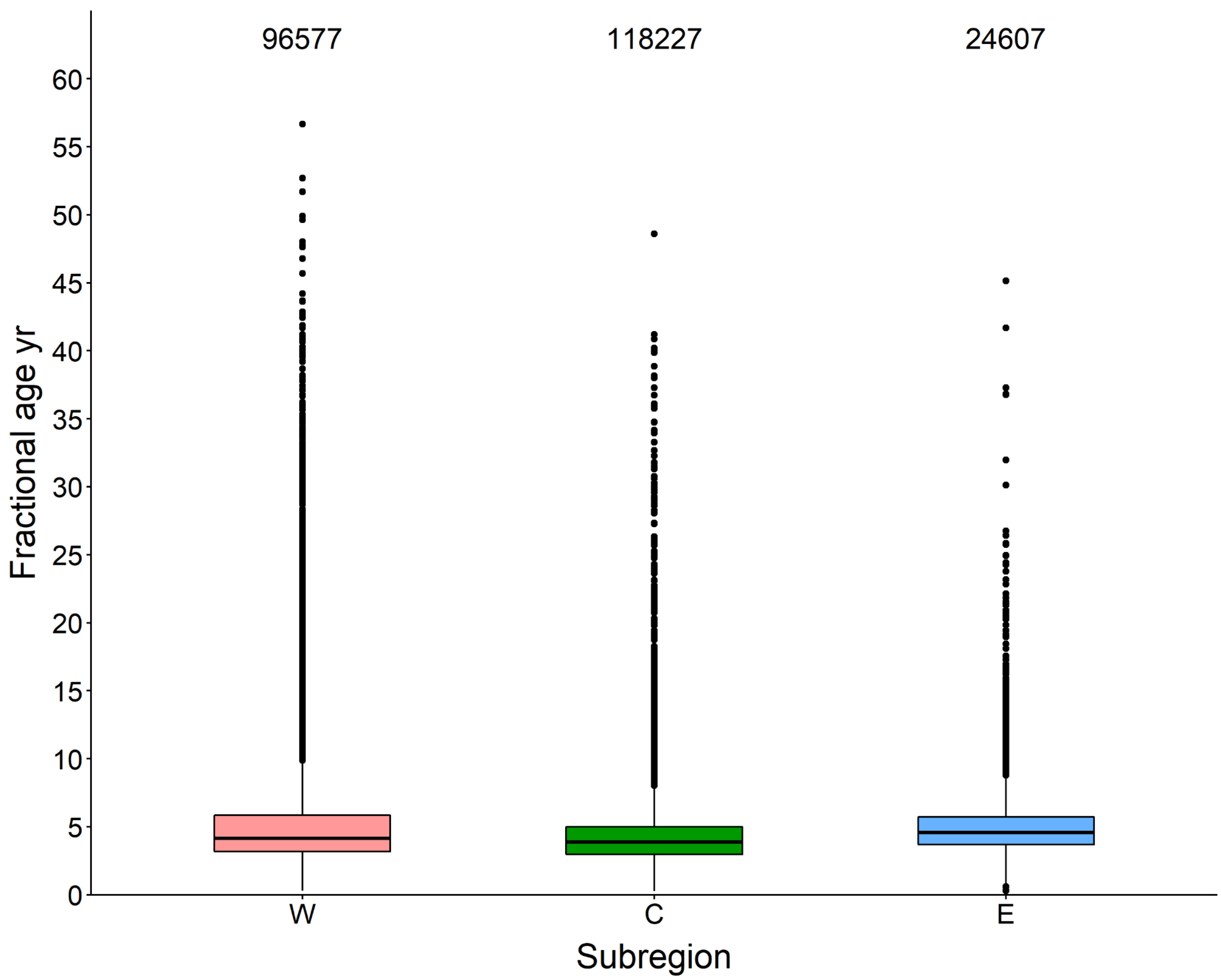


Figure 6. Frequency (%) histograms of calendar age (yr) by subregion (West, Central, or East) for red snapper age samples collected in the Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 1 yr. Arrows represent maximum age observed in the West (57 yr), Central (49 yr), or East (45 yr) subregion.

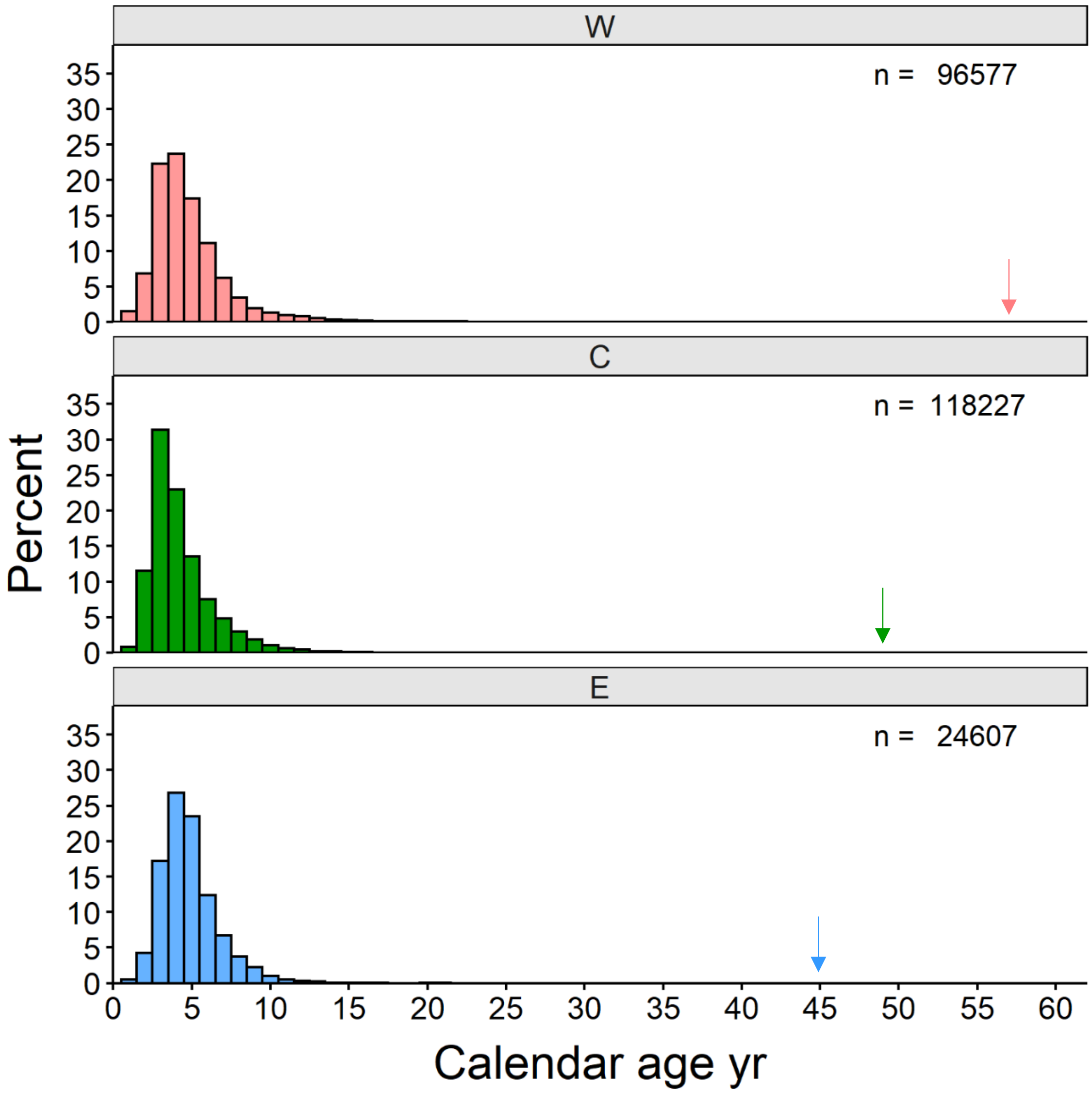


Figure 7. Bar plots of age-specific counts for red snapper age samples collected from 1980 and from 1986 to 2019 from the West, Central, or East subregion of the Gulf of Mexico. The number of observations for each age is shown to the left of each panel.

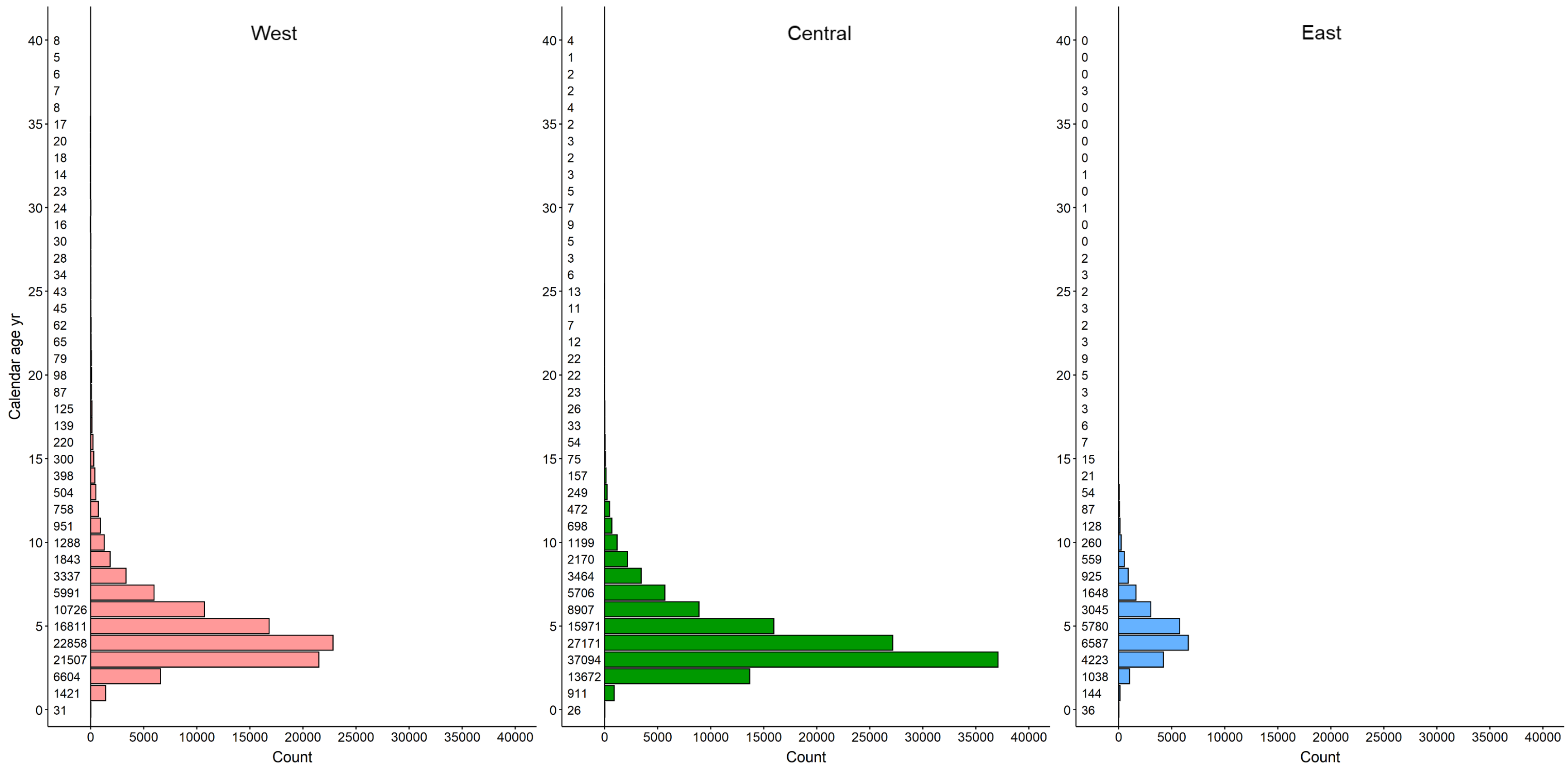


Figure 8. Frequency (%) histograms of calendar age (0 to 20 yrs) for red snapper age samples collected from the West subregion Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 1 yr. Years with <5 observations (1996) are not shown.

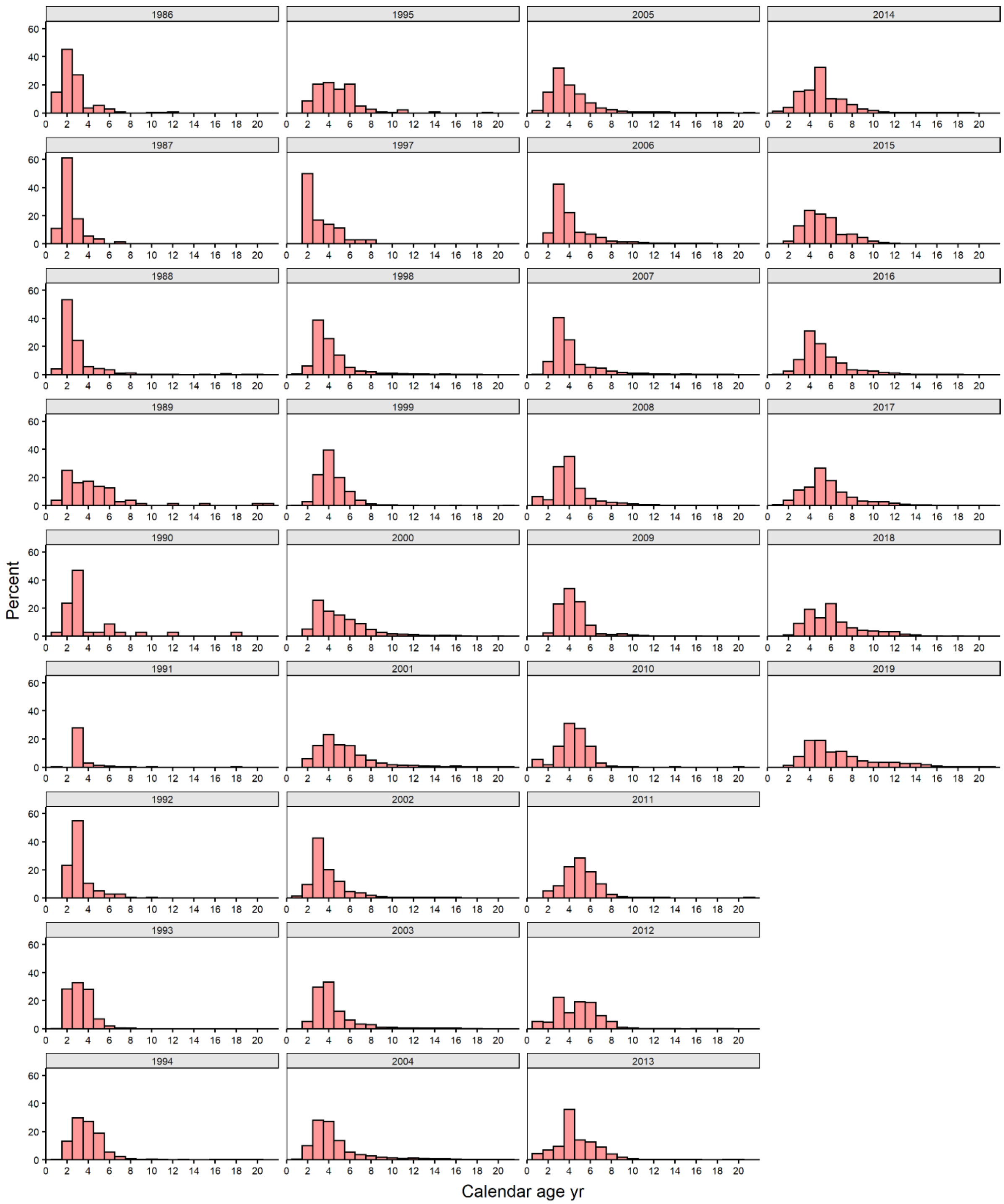


Figure 9. Frequency (%) histograms of calendar age (0 to 20 yrs) for red snapper age samples collected from the Central subregion Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 1 yr. Years with <5 observations (1986 and 1988) are not shown.

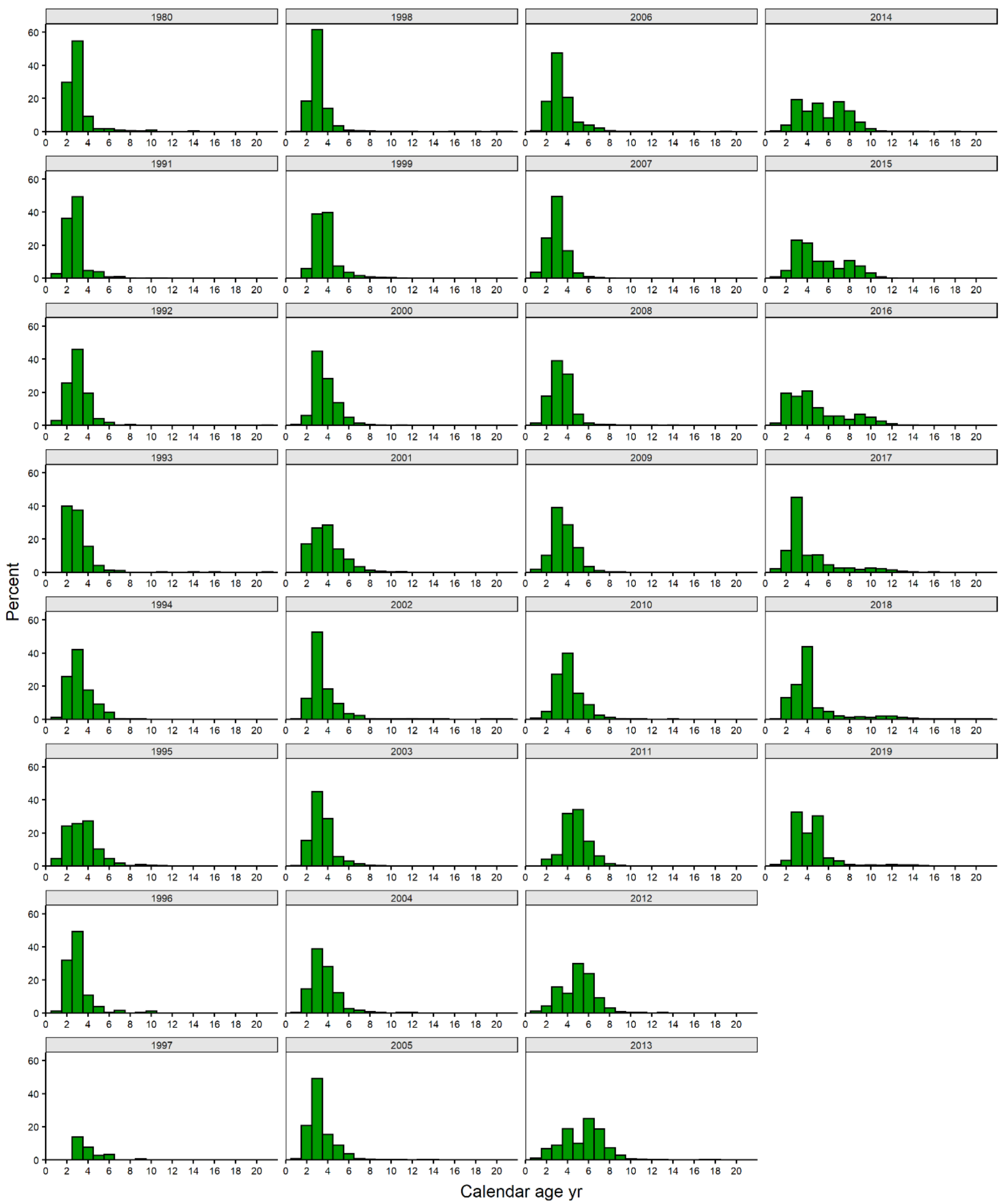


Figure 10. Frequency (%) histograms of calendar age (0 to 20 yrs) for red snapper age samples collected from the East subregion Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 1 yr. Years with <5 observations (1986 and 1989) are not shown.

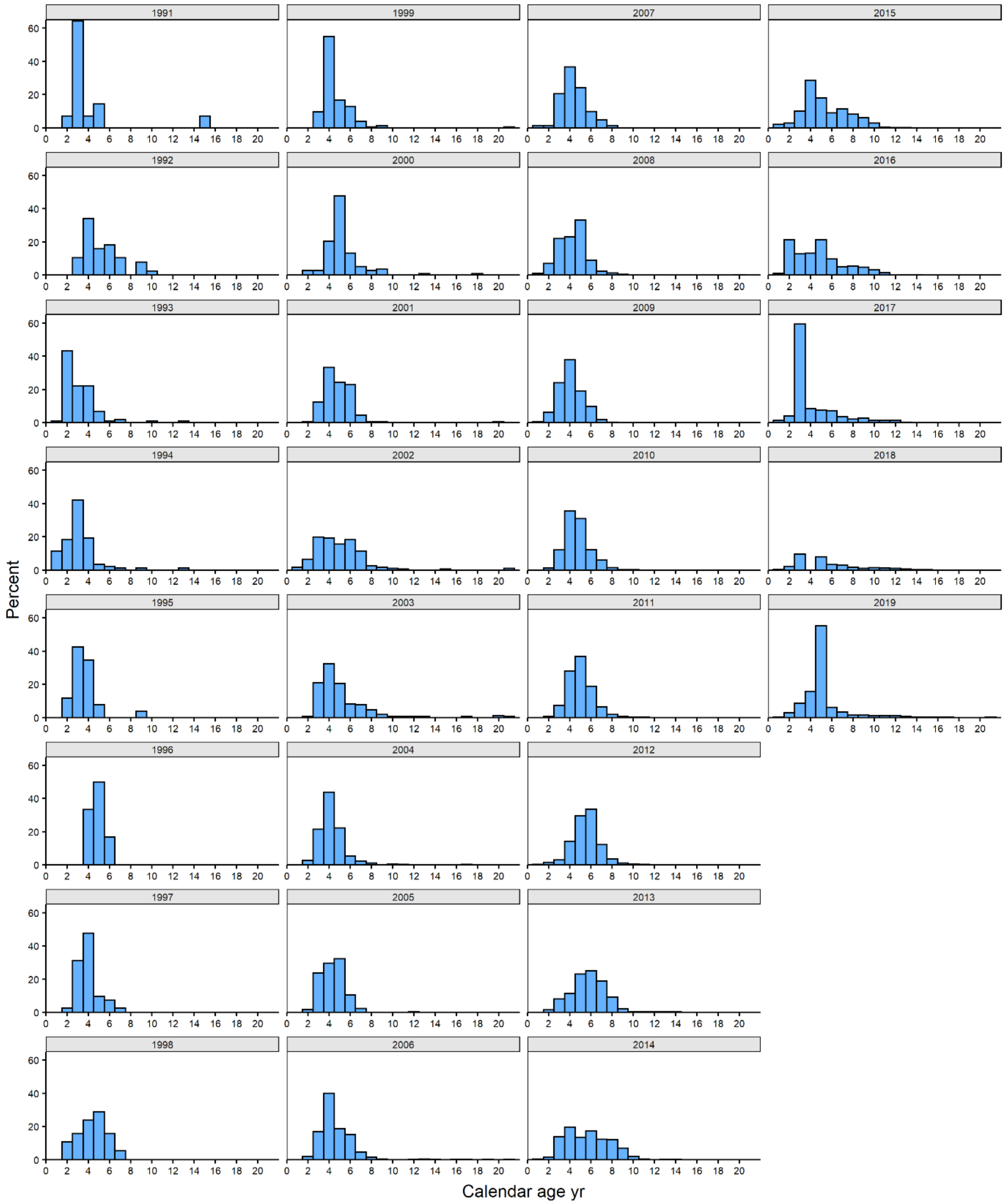


Figure 11. Boxplots of final fork length (cm) by subregion (West, Central, or East) and fishery (commercial, fishery independent, recreational, or unknown) for red snapper age samples collected in the Gulf of Mexico from 1980 and from 1986 to 2019. Upper and lower hinges indicate the first and third quartiles and whiskers extend to 1.5*IQR. Outliers are indicated by filled circles.

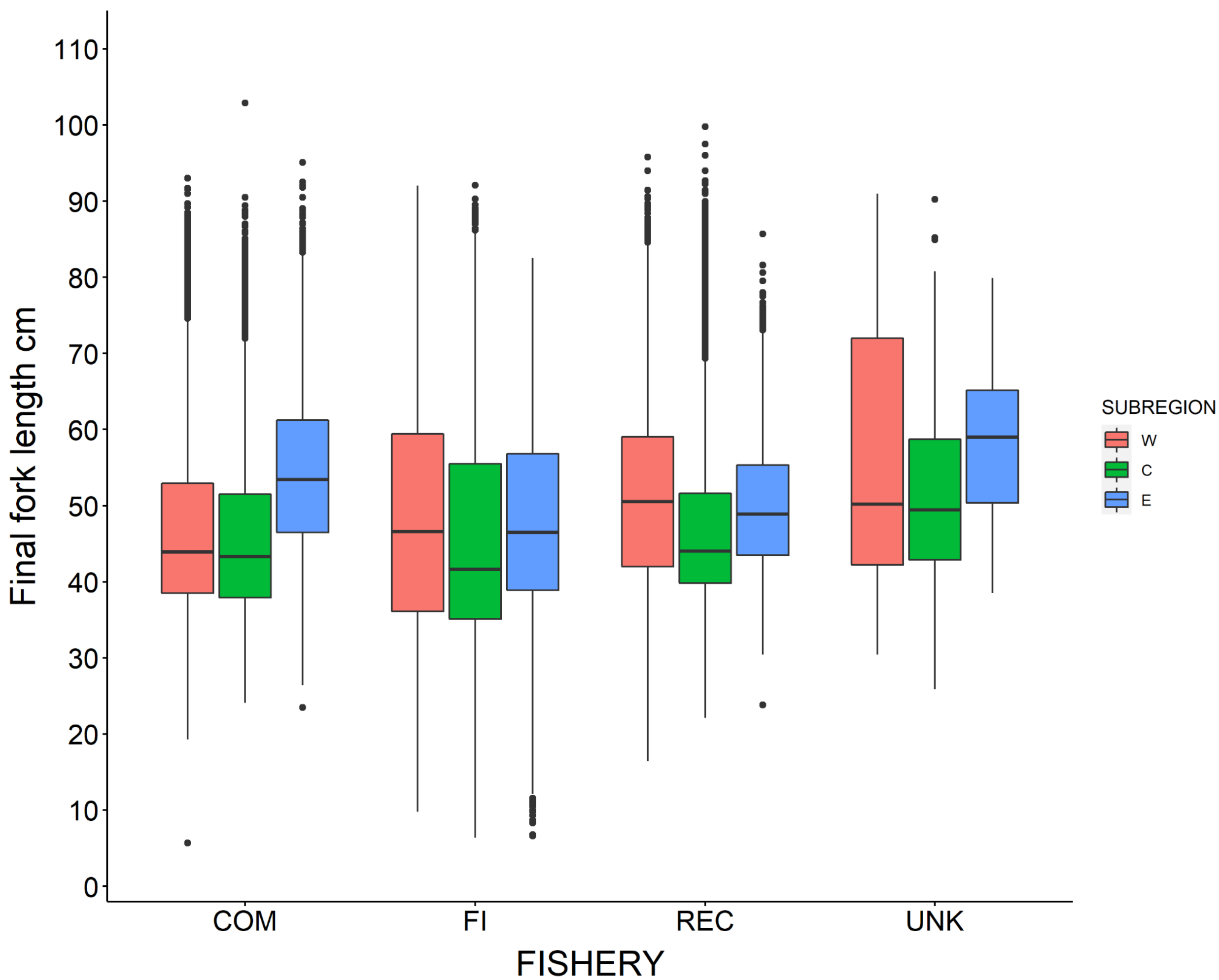


Figure 12. Boxplots of fractional age (yr) by subregion (West, Central, or East) and fishery (commercial, fishery independent, recreational, or unknown) for red snapper age samples collected in the Gulf of Mexico from 1980 and from 1986 to 2019. Upper and lower hinges indicate the first and third quartiles and whiskers extend to 1.5*IQR. Outliers are indicated by filled circles.

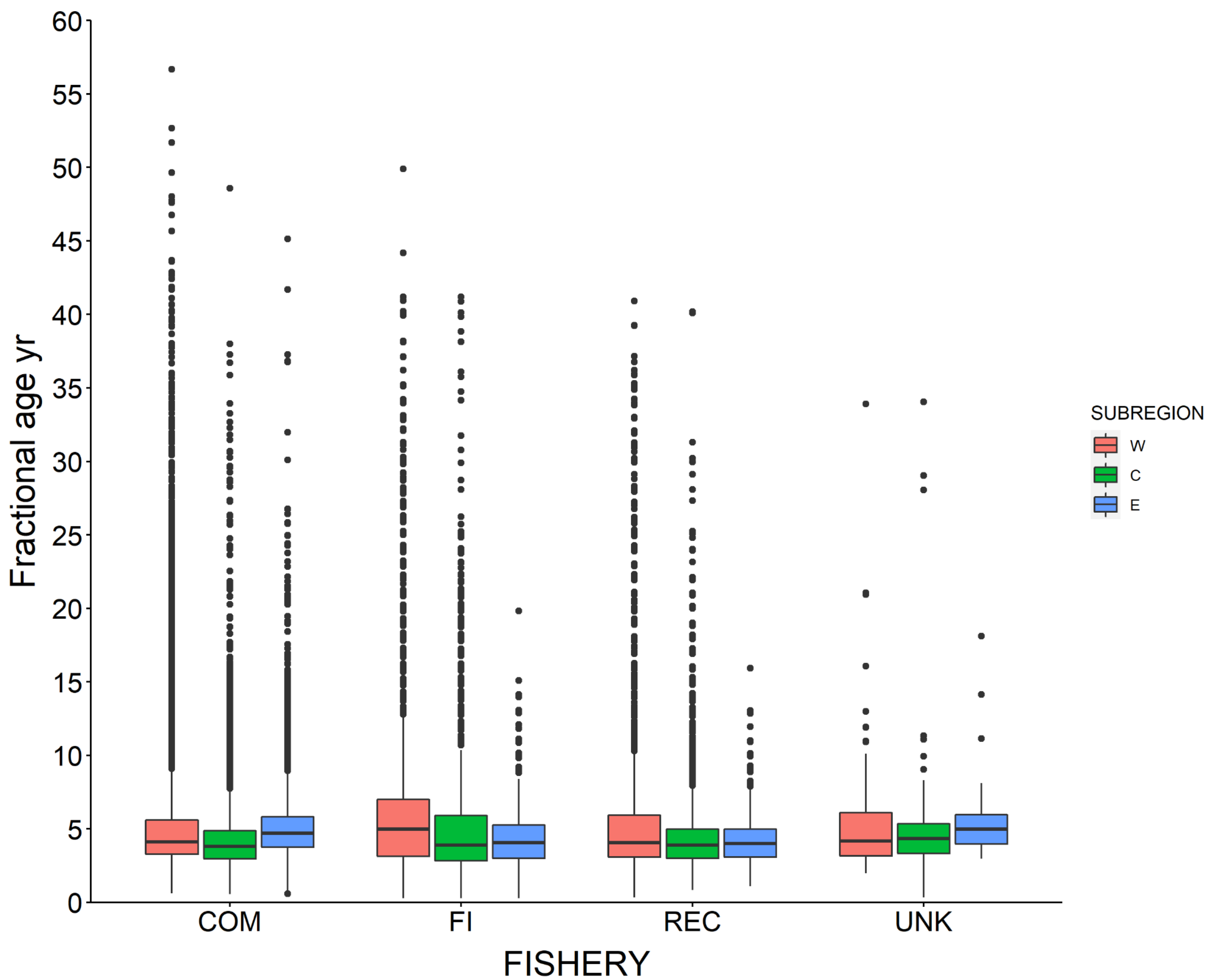


Figure 13. Frequency (%) histograms of calendar age (yr) for red snapper age samples collected from the commercial fishery in Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 1 yr.

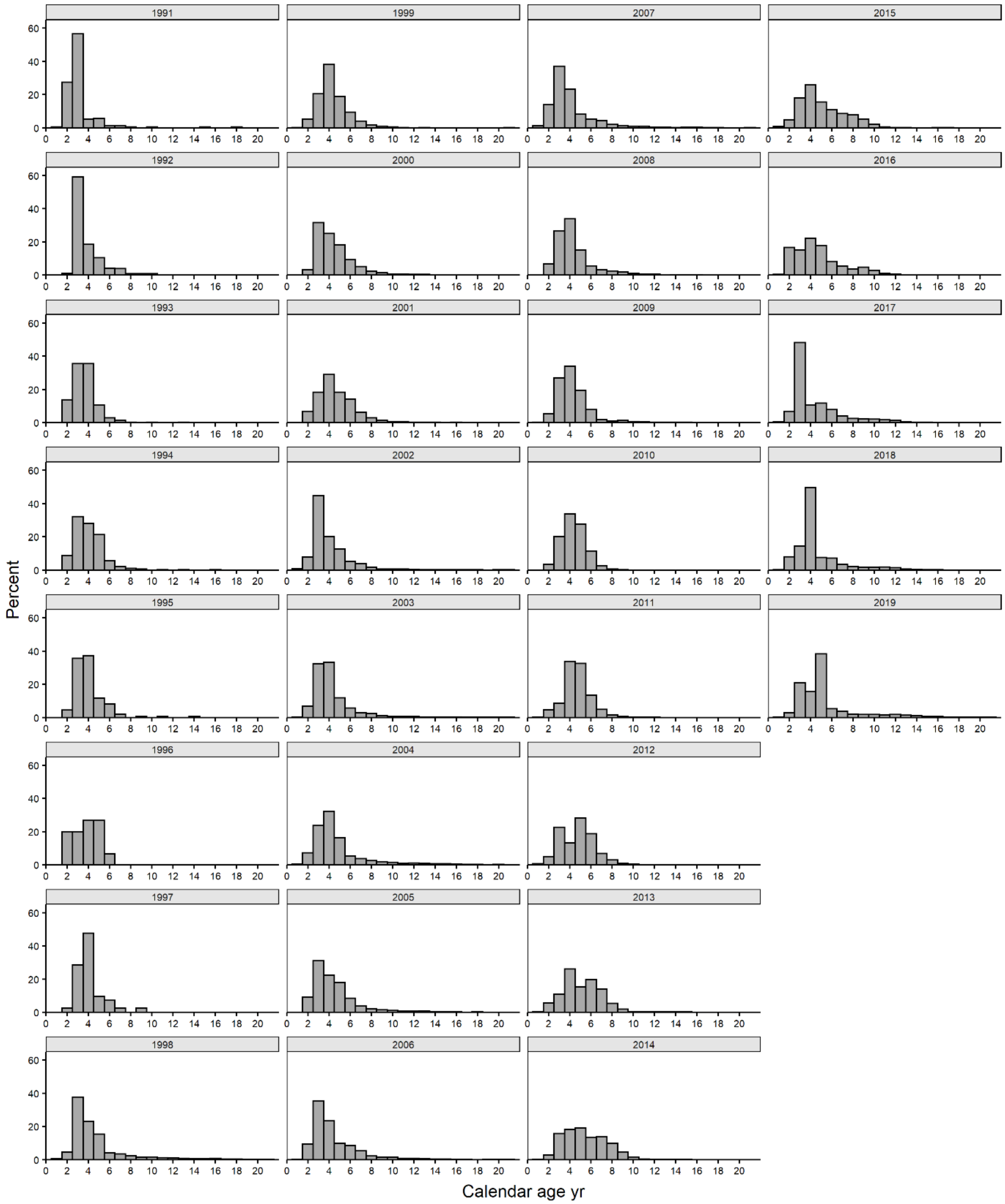


Figure 14. Frequency (%) histograms of calendar age (yr) for red snapper age samples collected from the recreational fishery in Gulf of Mexico from 1980 and from 1986 to 2019. Bin increments are equal to 1 yr.

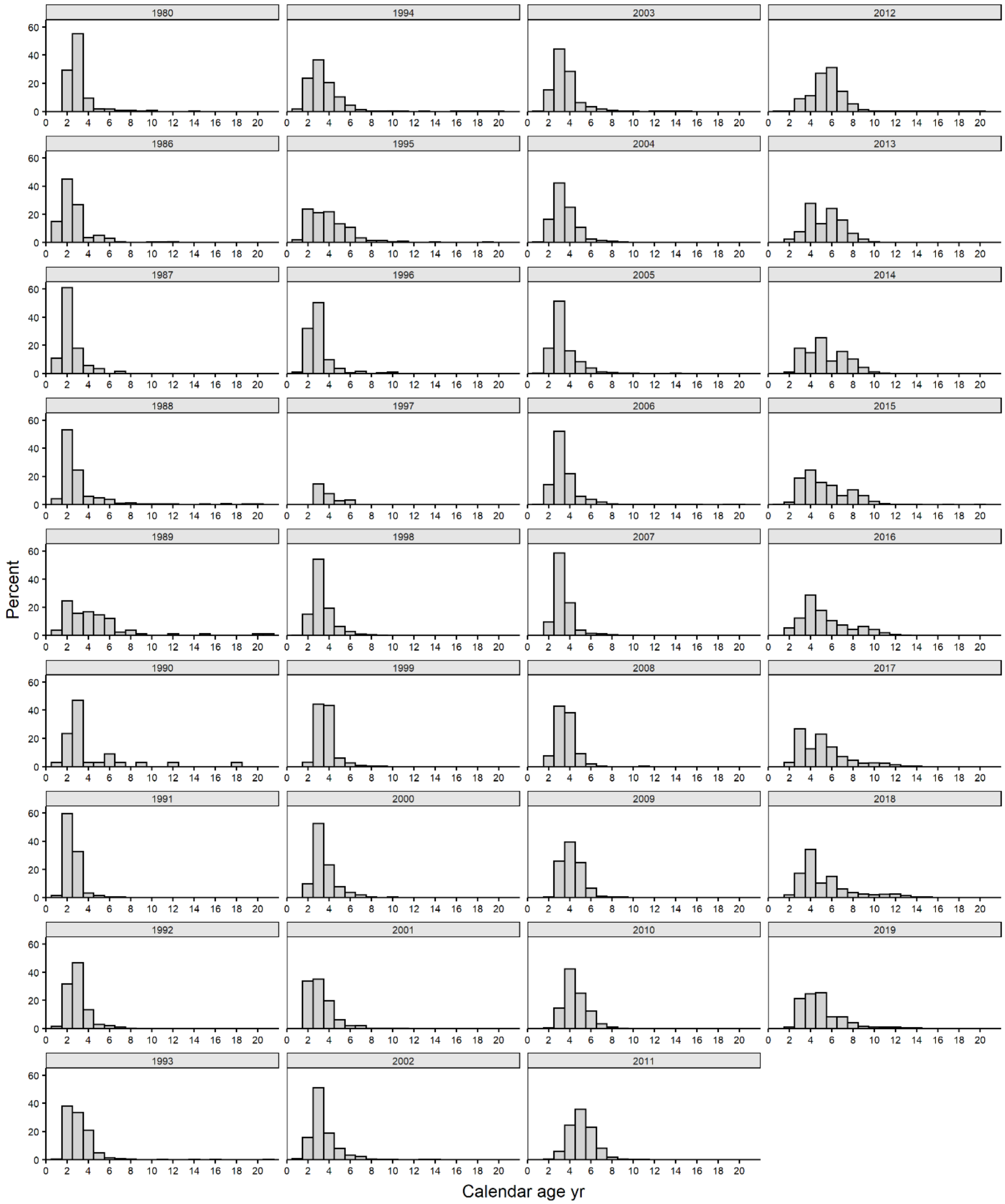
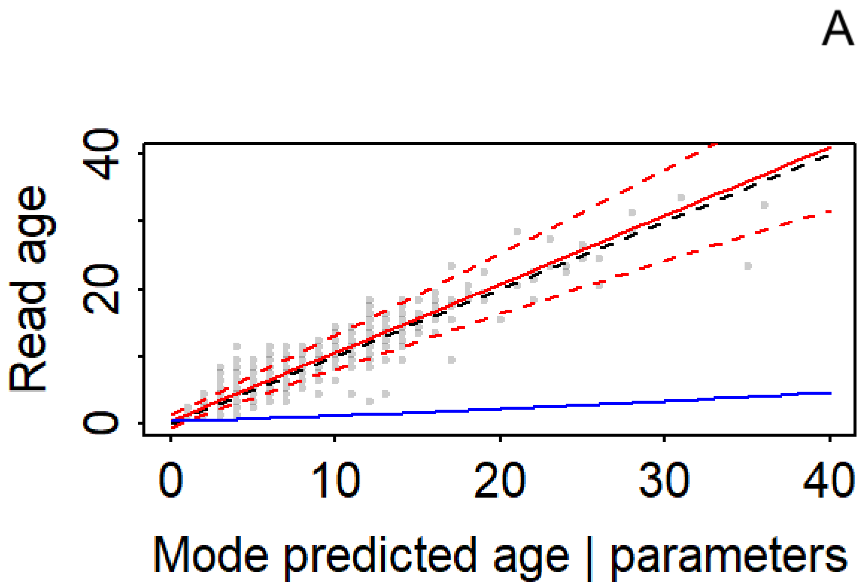


Figure 15. Error models fit to age data showing A) a linear bias with curvilinear SD and B) no bias with curvilinear SD. Points indicate mode predicted vs age estimated by reader 1 (primary reader), solid red lines indicate the expected values, dashed red lines indicating the CI of the expected values, and the solid blue line indicates the SD. The second reader was assumed to age without error.



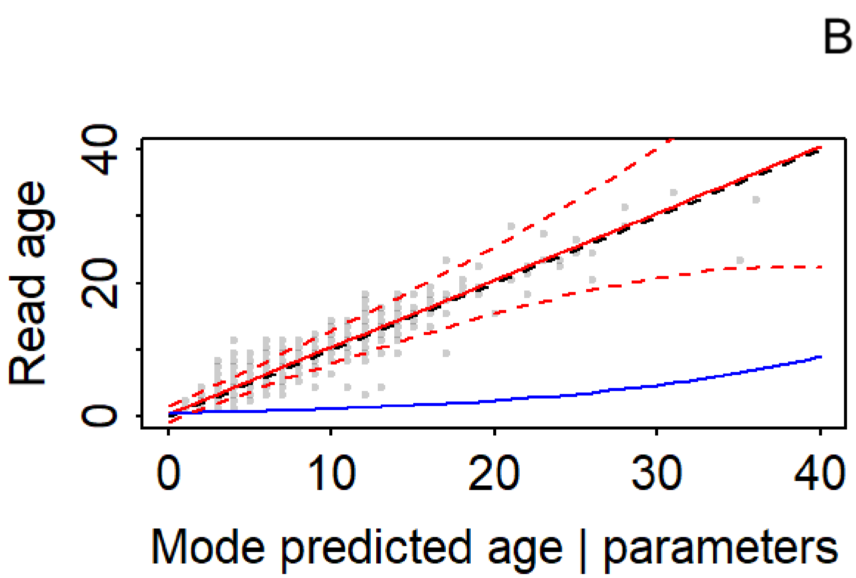


Figure 16. Scatter plot of fractional age (yr) versus final fork length (cm) for red snapper age samples collected from 1980 and from 1986 to 2019 from the Gulf of Mexico. Lines indicate best fit parameters from size- modified von Bertalanffy growth models. Parameter values are listed in Table 5.

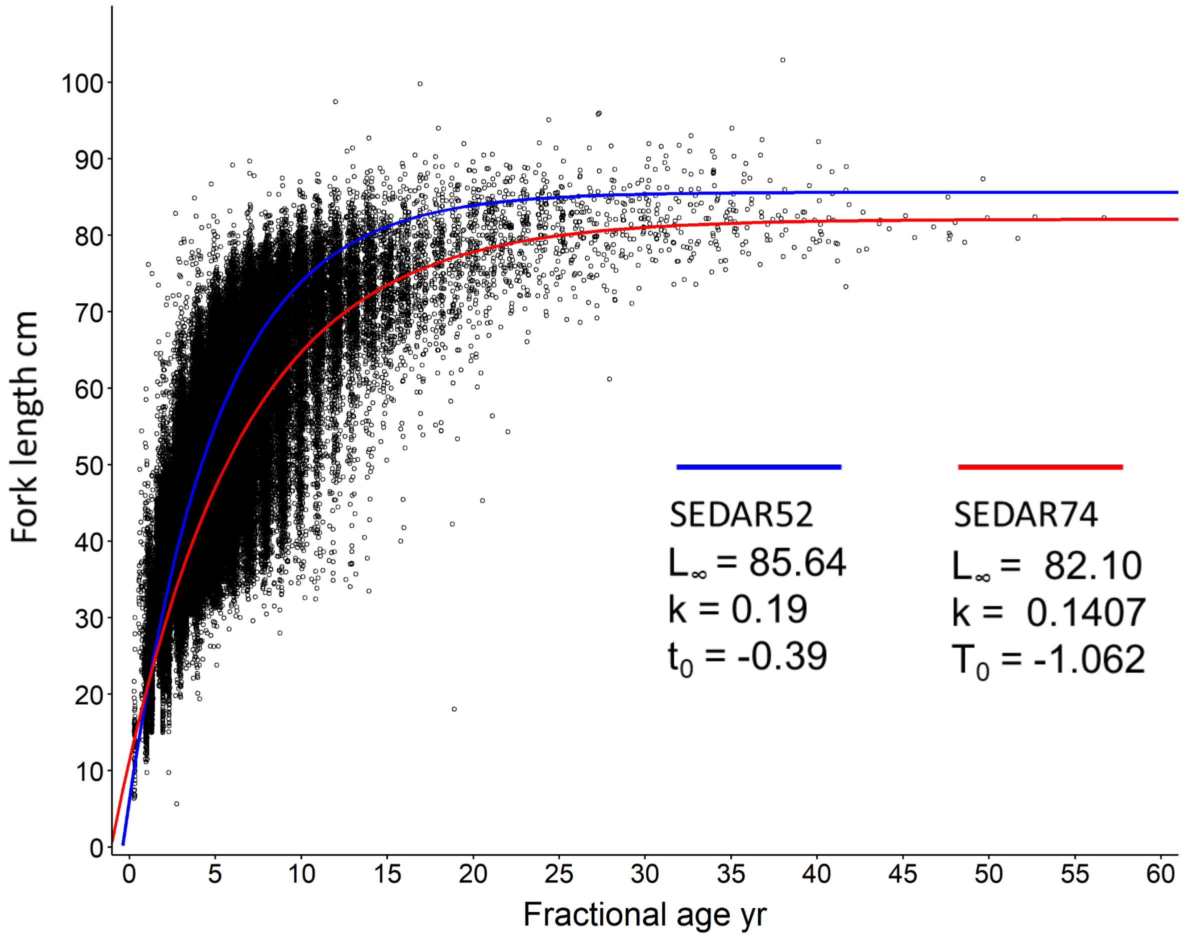


Figure 17. Scatter plot of fractional age (yr) versus fork length (cm) for red snapper age samples collected from 1980 and from 1986 to 2019 from the West, Central, or East subregion of the Gulf of Mexico. Lines indicate best fit parameters from size-modified von Bertalanffy growth models with inverse weighting of age data. Parameter values are shown on the plot and listed in Table 6.

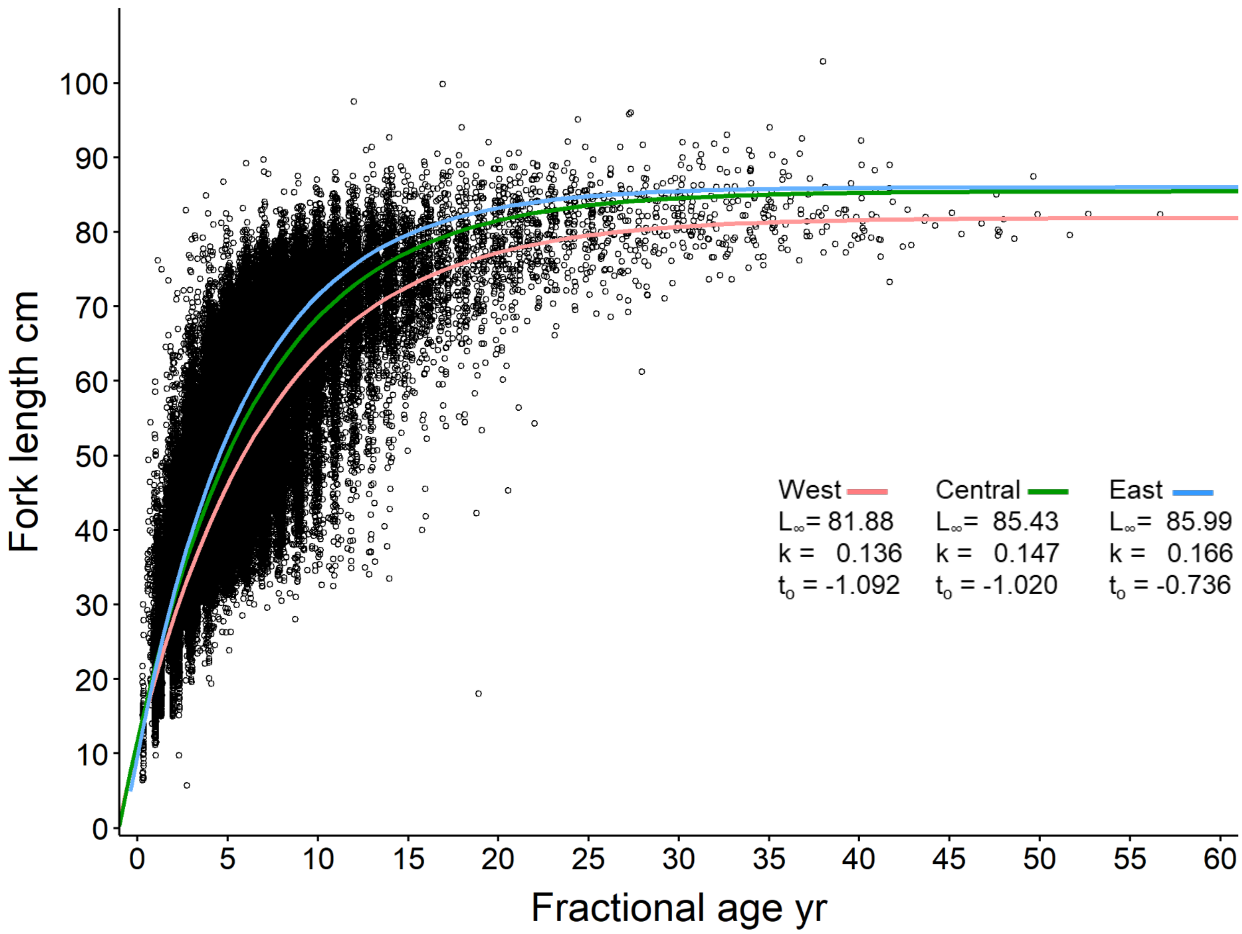


Figure 18. Mean size (FL, cm) at age (calendar, yr) of red snapper by subregion (West, Central, or East) for age samples collected from 1980 and from 1986 to 2019 from the Gulf of Mexico. Error bars indicate 95% CIs.

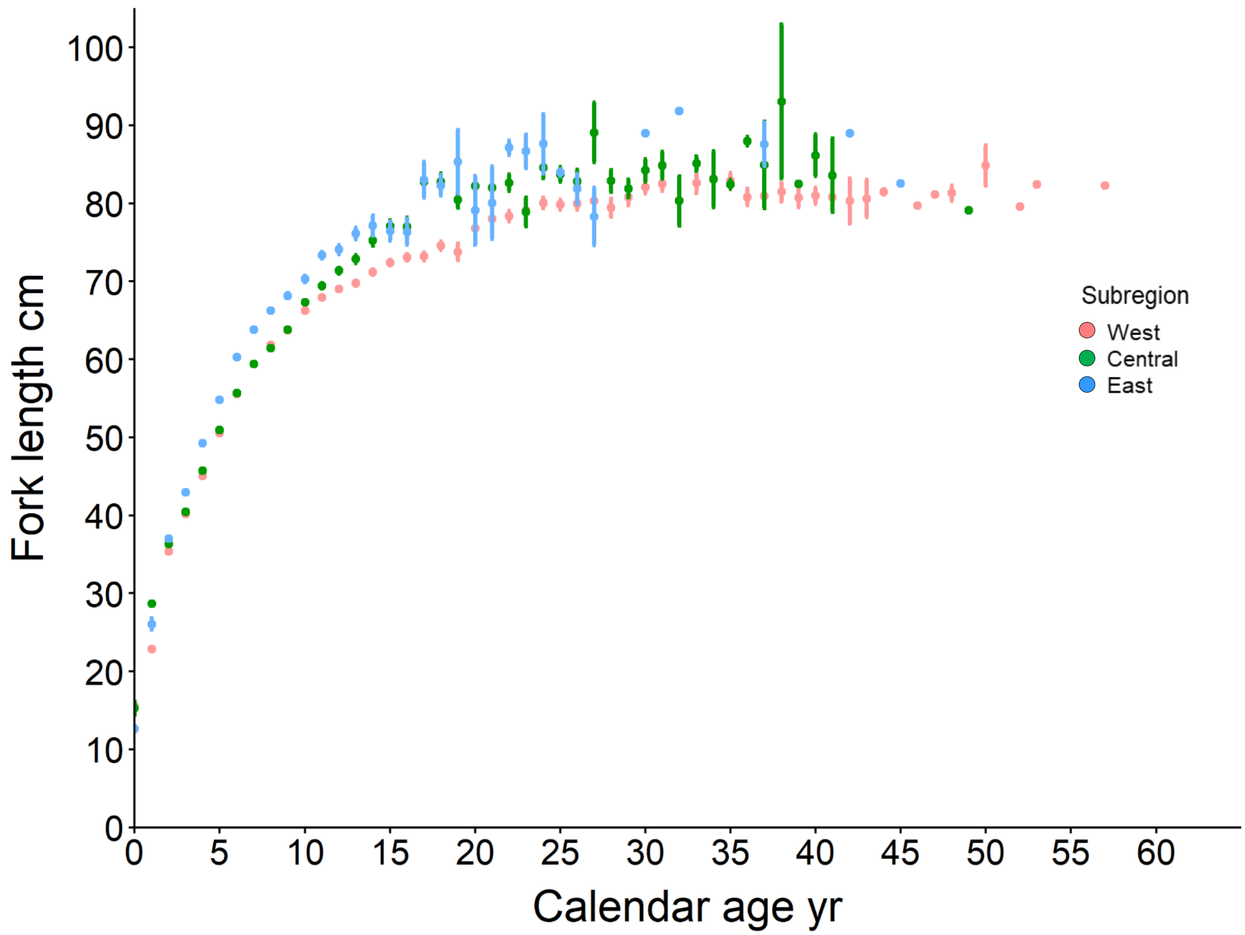


Figure 19. Mean size (FL, cm) at age (calendar, yr) of red snapper age samples collected from each stanza from the West or East (Central and East) subregion of the Gulf of Mexico. Error bars are 95% CI.

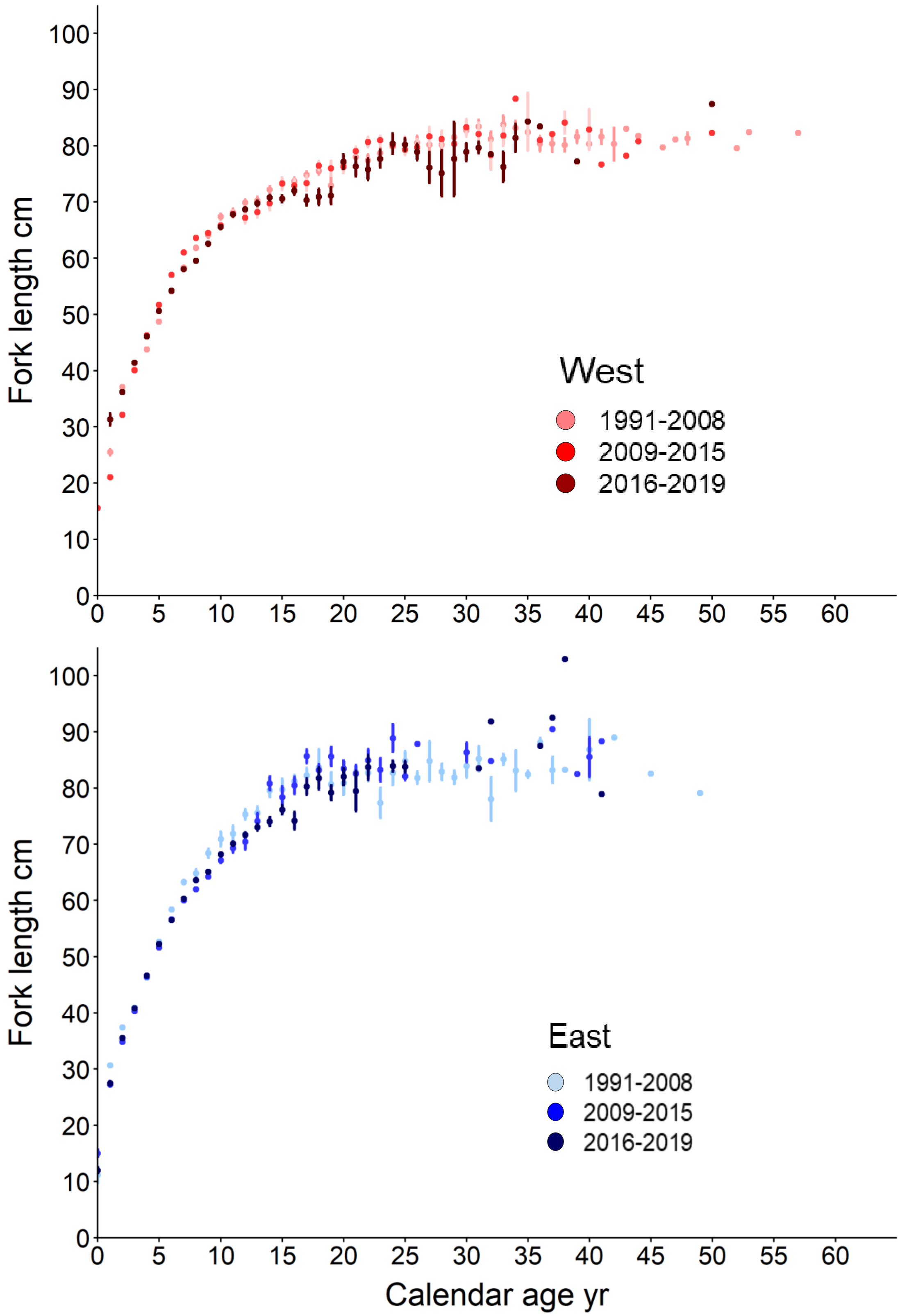


Figure 20. Age-specific natural mortality estimates for Gulf of Mexico red snapper. Lorenzen (L) natural mortality curves are shown scaled to the average natural mortality rate yr^{-1} based on longevity from Hoenig (H) or Then (T) for all fishes, reef fishes, or Lutjanids. Ages 0 and 1 were assigned fixed values of 2.0 and 1.2 yr^{-1}, respectively in all cases. Note that age-specific estimates for L to T reef fishes (blue) visually overlap estimates for L to T all fishes (green).