

## Gulf of Mexico Science

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Volume 34  
Number 1 Number 1/2 (Combined Issue)

Article 3

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2018

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DOI: 10.18785/goms.3401.03

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### Recommended Citation

Anderson, J., D. McDonald, B. Bumguardner, Z. Olsen and J. W. Ferguson. 2018. Patterns of Maturity, Seasonal Migration, and Spawning of Atlantic Croaker in the Western Gulf of Mexico. *Gulf of Mexico Science* 34 (1). Retrieved from <https://aquila.usm.edu/goms/vol34/iss1/3>

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# Patterns of Maturity, Seasonal Migration, and Spawning of Atlantic Croaker in the Western Gulf of Mexico

JOEL ANDERSON, DUSTY McDONALD, BRITT BUMGUARDNER, ZACHARY OLSEN, AND JASON W. FERGUSON

Atlantic croaker (*Micropogonias undulatus*) are one of the more common finfishes in the Gulf of Mexico. They are a significant component of Gulf bait fisheries and an important midtrophic component of nearshore food webs. In this study, life-history parameters associated with growth, maturity, and seasonal migration were estimated for Atlantic croaker in Texas and integrated into previously described data throughout the rest of the species range. The major findings of this work were the following: (1) a majority (> 76%) of age-1 female Atlantic croaker were sexually mature; (2) egress of adults from inshore habitats took place in late fall (Oct./Nov.) in consecutive years (2002 and 2003); (3) egress of adults was predictably coincident with declining growth after age-1 and the onset of sexual maturity; and (4) ingress of juvenile Atlantic croaker into inshore nursery grounds began in early winter and progressed through early summer, but a majority of recruits appeared in a short span between Feb. and April. Seasonal patterns of migration of both adult and juvenile Atlantic croaker are consistent with those described in other parts of the species' range and imply offshore spawning in the fall and winter followed by year-round inshore development of postlarvae and juveniles. Given the importance of inshore residency of juvenile Atlantic croaker, abundance estimates from fishery-independent sampling were scaled up to system-wide estimates of juvenile abundance in two prominent Texas estuaries and used to qualitatively assess the potential impacts of the commercial fishery on the inshore segment of the population.

## INTRODUCTION

Atlantic croaker *Micropogonias undulatus* are members of the family Sciaenidae with a vast geographical range, having been found as far north as Maine and as far south as Argentina. Though they are found throughout the Gulf of Mexico (hereafter "Gulf"), they are most abundant off Louisiana and Mississippi (Lassuy, 1983). On the U.S. Atlantic coast they are seldom found south of Indian River Lagoon (McRae, 1997), suggesting a range discontinuity between Gulf and Atlantic populations (Lankford et al., 1999). Atlantic croaker are utilized as a food fish and as bait and as such are harvested both recreationally and commercially. Although the overall Gulf landings historically have been small in comparison to landings in the rest of the United States, there has been an increase in commercial landings for some Gulf states since the mid-1990s. This increase has been driven primarily by the live bait industry, which targets the inshore juvenile life stage. Increasing catch has been realized in Texas in particular, where the use of Atlantic croaker to catch large sport fish has become very popular. Since 1994 in Texas, the vast majority of total Atlantic croaker landings are sold as live bait, and these landings

are approaching 50,000 kg annually. Perhaps more importantly, Atlantic croaker make up a large portion of commercial shrimp trawl discards, with an estimated 61% of shrimp trawl tows in the Gulf encountering Atlantic croaker as bycatch (Ortiz et al., 2000). Among other factors, this has resulted in a decline in the catch rate of this species since at least the mid-1970s (Ortiz et al., 2000).

Adult Atlantic croaker are known to undergo a seasonal migration from inshore habitats to offshore areas prior to spawning. This seasonal migration is fairly consistent throughout the observed range of the species, although the timing of this migration may differ based on latitude. Ross (1988) observed differences in the spawning season between Atlantic croaker north and south of Cape Hatteras in North Carolina, with northern individuals spawning in late summer/fall and southern individuals spawning mainly in fall/winter. White and Chittenden (1977) similarly suggested that the spawning season of Atlantic croaker inhabiting areas north of Cape Hatteras may begin and end earlier than in areas south of Cape Hatteras. Barbieri et al. (1994b) observed reproductively mature females July–Dec. in Chesapeake Bay, suggesting a protracted spawning season overlapping summer

months. In the Gulf, Cowan (1988) suggested peak spawning was Oct.–Nov., implying that sexual maturity may occur later in the year in Gulf populations, and also found that spawning was rare after Jan. Spawning was observed from at least Sep.–March in the Gulf by White and Chittenden (1977). Consistent throughout all previous studies was a general trend of offshore migration prior to spawning, which has been observed in both the Atlantic and Gulf (Haven, 1959; White and Chittenden, 1977; Miller and Able, 2002; Miller et al., 2003).

Following spawning, Atlantic croaker larvae first go through a coastal planktonic phase, followed by an estuarine demersal stage as they grow (Norcross, 1991). Atlantic croaker larvae in Chesapeake Bay were found in Sep. (Norcross, 1991), and larvae in Delaware Bay were observed Sep.–Oct. by Miller et al. (2003). Across their range, larvae ingress back into estuaries via passive transport (Norcross, 1991) and spend a large part of their first year of development in estuarine nursery habitats (Haven, 1959; White and Chittenden, 1977; Barbieri et al., 1994a; Miller and Able, 2002; Miller et al., 2003). Although these general patterns of maturity, migration, and spawning have been described throughout much of the species' range, the timing of life-history events in Atlantic croaker from the western Gulf have received minimal attention in the literature. The vast majority of bait landings in Texas target inshore juveniles, indicating that the timing and demographics of inshore residency could be beneficial for informing decisions regarding the commercial fishery for the species. The objective of the current study was to elicit basic biological parameters associated with inshore Atlantic croaker, and the findings were used to estimate the impact on Atlantic croaker populations of commercial trawl operations operating in inshore waters.

#### METHODS

*Migration and recruitment of Atlantic croaker in Texas inshore areas.*—Fishery-independent sampling data were used to examine the migratory patterns of adult and juvenile Atlantic croaker in Texas in 2002 and 2003. These years were chosen so that they would coincide with life-history data collection (see below). Three types of gears were used for this analysis; all three gears are employed routinely by the Texas Parks and Wildlife Department, Coastal Fisheries Division (TPWD-CF). Gillnets were used to sample the

adult population of Atlantic croaker. Bag seines and otter trawls were used to sample the juvenile and young adult population (generally < 150 mm). All gears were deployed inshore (in bays, usually bounded by barrier islands).

Gillnets were constructed with four 45.7-m panels of 76-mm, 102-mm, 127-mm, and 152-mm mesh sizes and set overnight perpendicular to the shoreline at randomly selected stations. Gillnet samples were collected for 10 consecutive weeks in the spring (April–June) and fall (Sep.–Nov.) of each year. The bay areas sampled and quantity of nets set per system, per season were as follows: Sabine Lake (SL) 45, Galveston Bay (GB) 45, Cedar Lakes (CL) 10, East Matagorda Bay (EMB) 20, Matagorda Bay (MB) 45, San Antonio Bay (SAB) 45, Aransas Bay (AB) 45, Corpus Christi Bay (CCB) 45, Upper Laguna Madre (ULM) 45, and Lower Laguna Madre (LLM) 45 (Fig. 1). The catch-per-unit effort (CPUE) of Atlantic croaker was calculated as the number of individuals caught divided by the soak time in hours. Mean values of CPUE by month were used to estimate the relative abundance of adult Atlantic croaker in inshore areas in the two sampled seasons. It was assumed that a decline in relative adult abundance during the fall months should circumstantially support offshore migration of adults in late fall.

Bag seines were 18.3 m long and 1.8 m deep, with 19-mm stretched nylon mesh in the wings and 13-mm stretched nylon mesh in the bag. Bag seines were pulled along shorelines for 15.2 m in randomized 1 × 1-foot stations twice per month in each month. The number of bag seine samples per month in each inshore area were as follows: SL = 20, GB = 20, CL = 10, EMB = 10, MB = 20, SAB = 20, AB = 20, CCB = 20, ULM = 20, and LLM = 20. The relative abundance of Atlantic croaker in bag seines was estimated by dividing the total catch by the area sampled in hectares. Relative abundance was estimated coast-wide, by month, in each successive year. Relatively high abundance of juvenile Atlantic croaker in bag seines is assumed to relate directly to the recruitment of young-of-the-year (YOY) individuals to inshore nursery habitats.

Trawls were 6.1-m-wide otter trawls with 38-mm stretched nylon multifilament mesh throughout and doors that were 1.2 m long and 0.5 m wide. Trawls were pulled for 10 min at 3 mph in circular fashion at randomly selected 1 × 1-foot stations. The number of trawl samples per month in each system is as follows: SL = 10, GB = 20, CL = 0, EMB = 10, MB = 20, SAB = 20, AB =

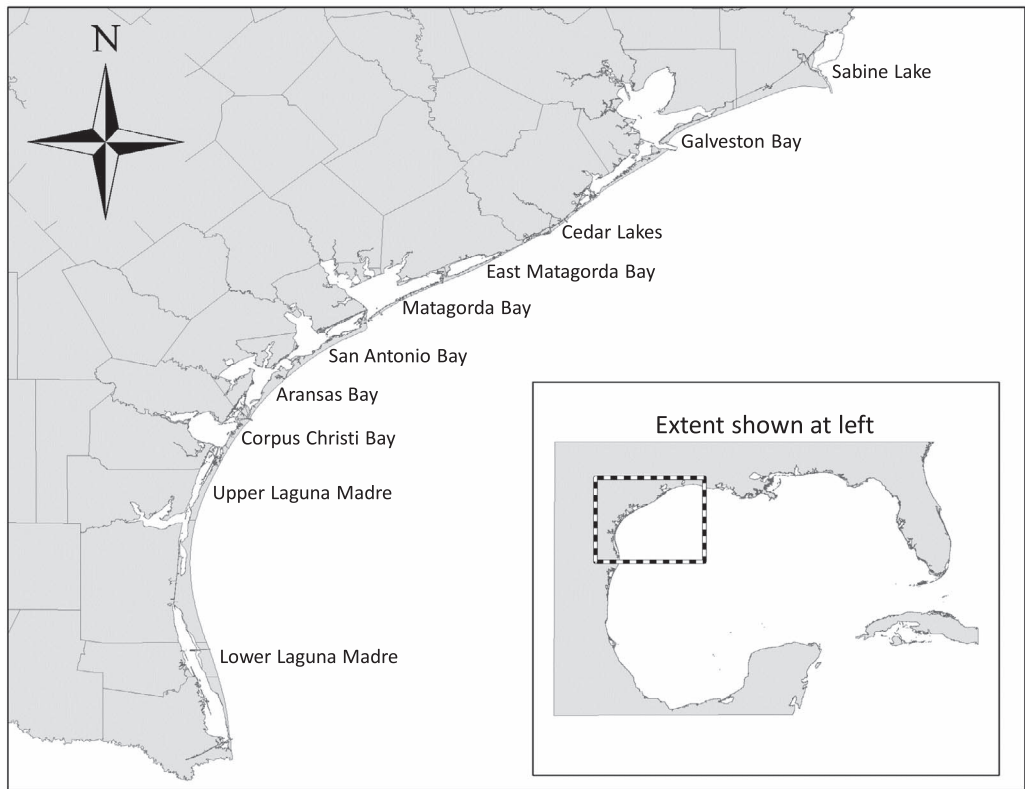


Fig. 1. A map of the inshore bay systems of Texas, from which Atlantic croaker samples were taken in 2002–03. The inset shows the sampling geography relative to the entire Gulf of Mexico.

20, CCB = 20, ULM = 10, and LLM = 10. In the event of a positive catch of Atlantic croaker in a bag seine or a trawl, up to 19 individuals were measured to the nearest millimeter in total length (TL) to estimate a mean length of the catch. These estimates were used to generate monthly length–frequency histograms of inshore juvenile Atlantic croaker using combined bag seine and trawl data. It was anticipated that both bag seine and trawl gears target primarily juveniles (TL < 150 mm). However, it was also expected that trawls might select for larger individuals. This assumption was tested using a t-test assuming unequal variances, with gear predicting TL.

*Growth, maturation, and spawning of Atlantic croaker in Texas.*—Atlantic croaker specimens were collected from each of the 10 previously described Texas inshore areas using gillnets (described above) in the spring and fall of 2002 and 2003. Emphasis for collection was placed on fall nets, but limited additional adult specimens were

collected in gillnet and trawl samples in Jan., March, April, May, June, and Aug. in order to compare months in which it was expected that spawning was not occurring. All specimens were kept on ice after capture, followed by transport to the Perry R. Bass Marine Fisheries Research Station in Palacios, Texas (hereafter “PRB”). At PRB, TL of each fish was measured to the nearest millimeter; if TL was not available, standard length (SL) was measured and then converted to TL using the following equation:

$$TL = 6.51 + 1.18 \times SL.$$

This equation was devised using linear regression of TL versus SL of all specimens for which both measurements were made. Fish body weight (BW) was assessed to the nearest 0.5 g. The relationship between growth in length and weight was examined using a linear regression function fit to a plot of log (TL) against log (BW).

For all specimens, both sagittal otoliths were removed, cleaned, and stored dry in paper

envelopes. The left sagittal otolith was prepared for processing by embedding it in epoxy resin. If the left otolith was missing or broken, the right otolith was used. Sequential 0.3-mm sections were made from the otolith with a Buehler high-speed saw until the otolith core was sectioned. The section containing the otolith core was mounted on a glass slide and examined using Optimas image analysis and data acquisition software version 6.51 (Bioscan, Inc., Edmonds, WA). Ages were assigned based on the number of annuli present, an arbitrary assumed birthdate of Oct. 15 was chosen based on the data of White and Chittenden (1977), and the beginning of annulus formation was assumed to take place on March 15, based on monthly analyses of marginal increment lengths here (data not shown) and elsewhere (Barbieri et al., 1994a). Age in months was rounded to the nearest whole year for length-at-age analysis. Based on an initial examination of differences in growth between sexes, and supported by the finding of Barbieri et al. (1994a), a single von Bertalanffy growth model was constructed using the length and age data for males and females combined and 95% confidence intervals calculated on length at age. All plotting and analyses related to the logistic regression and von Bertalanffy growth models were conducted in R version 3.1.1 (R Core Team, 2014) using the 'FSA' package for routines related to growth curves (Ogle, 2016) and R base packages for the remaining analyses.

Gonads were removed for all specimens, when possible, weighed to the nearest 0.1 g, and eggs of five randomly selected females from each collection date for each bay were examined for maturation stage using the criteria and methods of Brown-Peterson et al. (1988). An ovarian sample was placed in clearing solution (Brown-Peterson et al., 1988) and assigned to one of five maturation stages based on egg size and appearance (1 = primary oocytes, 2 = cortical alveoli, 3 = advancing, 4 = vitellogenic, and 5 = hydrated). In the event that multiple stages were present, multiple stages were noted and the highest stage was recorded. Gonadosomatic indices (GSI) were calculated for all specimens using the following equation:

$$\text{GSI} = \left( \frac{\text{GWT}}{\text{BW} - \text{GWT}} \right) \times 100,$$

where GWT was gonad weight and BW was the total weight of the fish (both expressed in grams).

Classification (mature vs immature) of individual fish was based on both GSI and assigned maturation stages, in the event that both data points were available. Maturity was assumed if eggs were observed at any stage beyond primary oocytes. Preliminary examination suggested that GSI values of  $> 0.65\%$  were associated with advanced stage ova; therefore, classification of females for which eggs were not examined was based on a conservative threshold value for which maturity was assumed when  $\text{GSI} > 1\%$ .

*Estimates of juvenile harvest by the commercial fishery.*—Fishery-independent (FIN) trawl catches conducted by TPWD (described above) were converted to spatial CPUE (catch/ha), and these values were scaled up to estuary-wide abundance for two prominent Texas estuaries, Matagorda Bay (approximately 109,300 ha) and Galveston Bay (approximately 160,061 ha). Monthly mean values of TL of individuals observed in FIN samples were converted to BW, and the total available monthly bay-wide biomass was then calculated by multiplying monthly mean abundance by mean BW. Biomass estimates were compared to monthly harvest estimates (in pounds) in both estuaries, using the harvest data from Culbertson et al. (2004), in order to estimate the impact of harvest on inshore juvenile Atlantic croaker. Trawls are the main gear used for harvest of Atlantic croaker both for bait and for bycatch landings in commercial shrimp operations. It was assumed that the harvest data of Culbertson et al. (2004) encompassed both of these catch elements.

## RESULTS

*Migration and recruitment of Atlantic croaker in Texas inshore areas.*—Gillnet sampling of adults in inshore areas in Texas resulted in observation of 4,848 individuals (size range, 125–600 mm TL). The analysis of variance model including bay and season as predictors of catch was significant ( $R^2 = 0.11$ ,  $P < 0.0001$ ), and the parameter estimate for season indicated elevated catch in the fall ( $P < 0.0001$ ). Catch was highest in Galveston Bay and Corpus Christi Bay and lowest in the upper and lower reaches of the Laguna Madre (Fig. 2a). Qualitative post hoc assessment of catch by month indicated that Sep. and Oct. had the highest overall catch of adult croaker in both years (Fig. 2b).

Atlantic croaker ( $n = 15,065$ ) ranged between 16 and 205 mm TL in shoreline bag seines. A

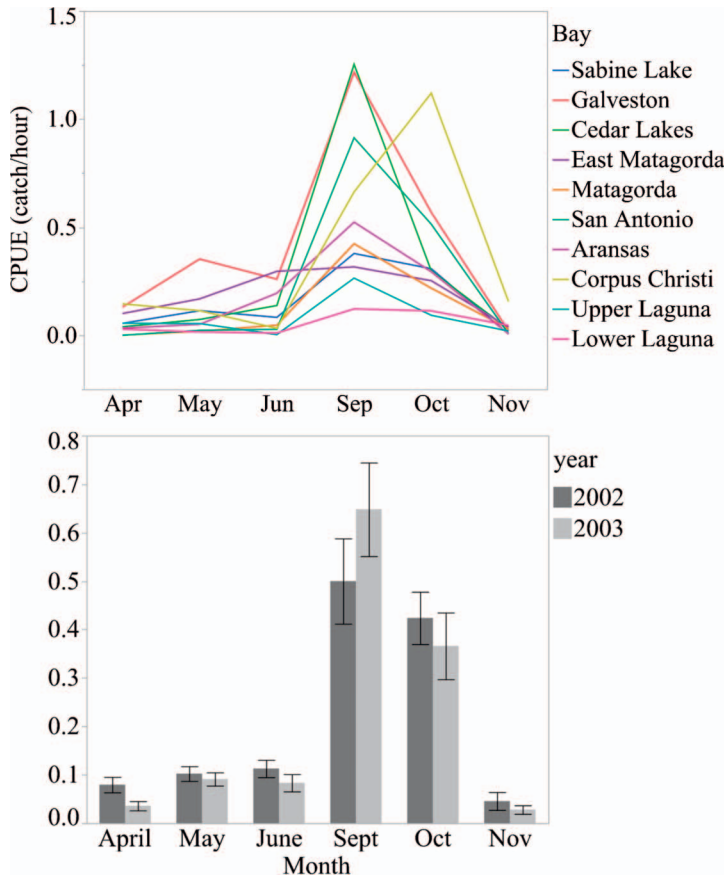


Fig. 2. Monthly fishery-independent gillnet catch-per-unit effort (CPUE) of Atlantic croaker in spring (April–June) and fall (Sep.–Oct.) in consecutive years in Texas inshore waters. Mean CPUE was calculated as the number of individuals caught per hour of soak time. The data are represented here in two ways: (a) the per-bay CPUE (both years combined), with bays organized north to south in the legend, and (b) annual coast-wide CPUE (all bays combined) in consecutive years. Whiskers around the tops of bars represent the 95% confidence interval around the estimated mean CPUE.

majority (90%) of individuals in bag seine samples were < 100 mm TL, suggesting that this gear primarily targets juveniles (mean TL = 62 mm, median = 53 mm). In both years, bag seine samples indicated an increasing presence of juvenile Atlantic croaker in the winter and spring, particularly in Feb. through April (Fig. 3). This was followed by declining abundance in summer and fall. It was assumed that juvenile Atlantic croaker began to size out of the bag seine gear at this time, although in both years they were sampled in all months.

There was a significant difference in size selectivity between seines and trawls ( $t = 148$ ,  $P < 0.0001$ ), with trawls selecting for larger individuals (mean TL = 118 mm, median = 140 mm). Similar to bag seines, trawls had a unimodal distribution, although in the case of

trawls catch was highest in April–Aug. and peaked in May/June (Fig. 4). When bag seine and trawl gears were combined, there was an observed wide range in TL occurring in the spring as individuals transition from shoreline bag seines to open-water trawls (Fig. 5).

*Growth, maturation, and spawning of Atlantic croaker in Texas.*—Across 2 yr of data collection, 729 adult Atlantic croaker captured in gillnets were assayed for length, weight, gonad weight, and age (2002:  $n = 357$ ; 2003:  $n = 372$ ). These collections included 146 males and 583 females. The relationship between TL and BW was highly predictive ( $R^2 = 0.975$ ,  $P < 0.001$ ) and was consistent across both years with both sexes combined (Fig. 6). The range of ages observed in these specimens was 1–6 yr, with a median and

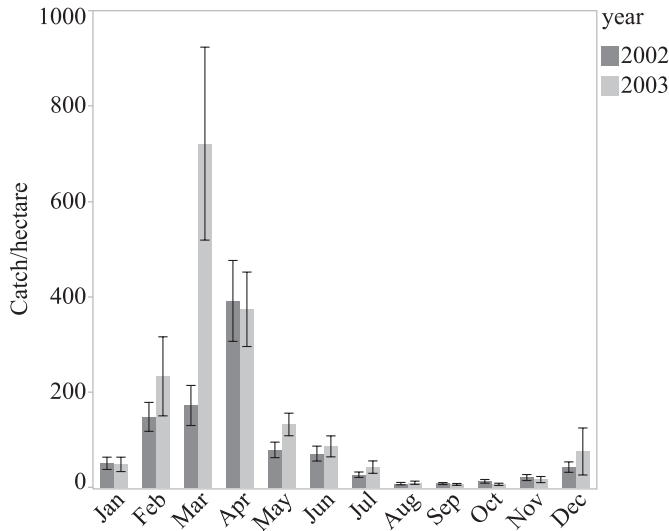


Fig. 3. Mean monthly catch/ha of juvenile Atlantic croaker in two consecutive years, calculated from fishery-independent bag seine samples taken in Texas inshore waters. Whiskers on each bar represent the 95% confidence interval around mean monthly estimates (replicated among samples within inshore areas, as well as among different areas).

mean of 1.9 yr (SD =  $\pm 0.55$  yr; Table 1). The fitted von Bertalanffy growth curve suggests fast growth up to age 1, followed by slowed growth to age 2 and thereafter (Table 2; Fig. 7). Similar to what was observed by Barbieri et al. (1994a), size at age was highly variable, making model fit difficult for the small number of older individuals ( $> 3$  yr) sampled.

A subset ( $n = 324$ ) of assayed females was used to examine maturity via egg staging. In the months of Jan. through Aug., 76 females were examined, all of which were in the primary oocyte stage (Fig. 8a). In the fall months, Sep.–Nov., 248 females were examined, with 95% being found in advanced stages (stages 2–4). Multiple egg stages were noted within some

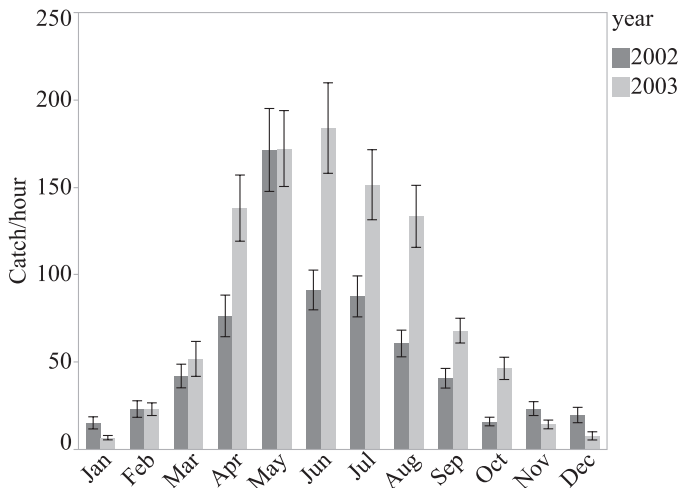


Fig. 4. Mean monthly catch/hr of juvenile Atlantic croaker in two consecutive years, calculated from fishery-independent open-water trawl samples taken in Texas inshore waters. Whiskers on each bar represent the 95% confidence interval around mean monthly estimates (replicated among samples within inshore areas, as well as among different areas).

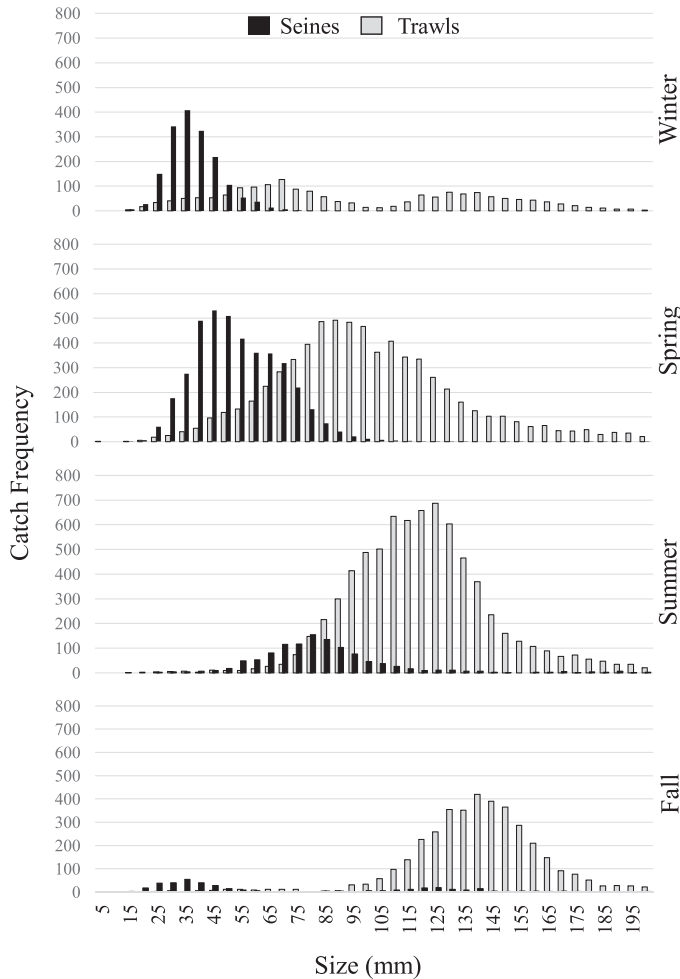


Fig. 5. Length–frequency histograms of Atlantic croaker encountered in fishery-independent bag seines (black bars) and trawls (gray bars) in four seasons in Texas inshore areas. The X-axis is 5-mm length classes observed in both gears. The Y-axis represents combined counts of each length class over 2 yr of observation (2002–03) in four seasons: winter (Dec.–Feb.), spring (March–May), summer (June–Aug.), and fall (Sep.–Nov.).

individuals, implying batch spawning in Atlantic croaker. Coincident with egg maturation, the GSI of females increased dramatically as maturation progressed, with vitellogenic females allocating (on average) over 5% of their body mass to gonad development (Fig. 8b). Based on a conservative maturation threshold of  $GSI > 1.0\%$ , no females showed gonad development (maturity) in the months Jan. through Aug. In contrast, 421 females out of 481 (88%) examined in the fall had GSI values representative of maturity. This included 76% maturation of age-1 females and 93% maturation of age-2 females in the months Sep.–Nov. Gonad maturation as measured by GSI was conservative; it is likely that most individuals are sexually mature by age-

1. Of the age-1 females explicitly examined for egg stage in fall months (Sep.–Nov.), 133/137 (97%) had egg stages that indicated maturity (beyond primary oocytes).

*Estimates of juvenile harvest by the commercial fishery.*—Culbertson et al. (2004) reported that 61,800 pounds of Atlantic croaker landed in the Texas inshore fishery in 2001. Of this number, approximately 25,827 pounds were landed in Matagorda and Galveston bays combined. Commercial catch in both systems peaked in the months of June–Sep., with an overall peak in July (Table 3). Estimates of abundance and biomass of Atlantic croaker in FIN trawl samples peaked in the late spring and early summer. In both



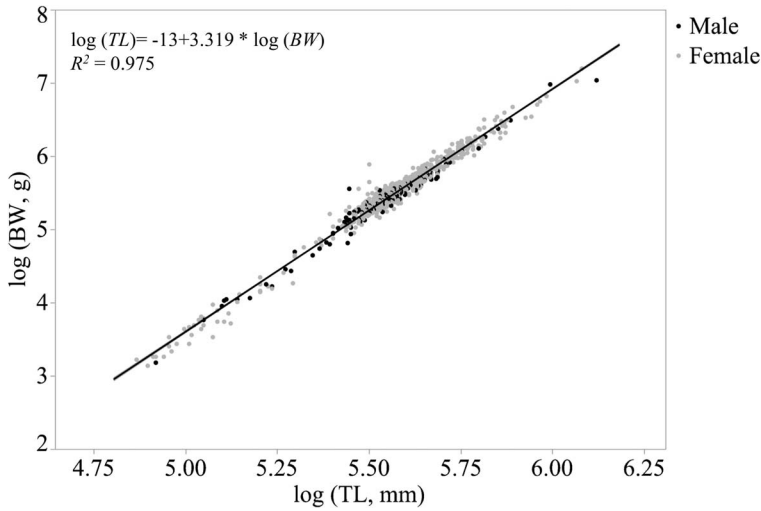


Fig. 6. The lengthweight (mm and g, respectively) relationship of male (n = 146; black points) and female (n = 583; gray points) Atlantic croaker observed in inshore fishery-independent gillnet samples in Texas in 2002 and 2003. The line of fit is a standard least squares regression curve fit to the log-transformed data; the regression function and coefficient of determination ( $R^2$ ) are inset.

estuaries, the reported commercial harvest of Atlantic croaker never exceeded 5% of the estimated available biomass in any month (Fig. 9).

DISCUSSION

In this study, two general migratory periods were observed, based upon the relative abundance of Atlantic croaker in the sampling gears employed. These migratory periods generally followed those reported by Haven (1959), with an inshore migration of postlarvae and juveniles in the spring, followed by offshore migration of large juveniles and mature adults in the fall. With regard to the latter, we observed a dramatic egress of adult Atlantic croaker from inshore areas in the fall between Oct. and Nov. In both years, and in all bay systems examined, relative

abundance of adult Atlantic croaker in gillnet sampling was significantly lower in Nov. compared to Sep. and Oct. The pattern of offshore movement of adults and older juveniles prior to spawning has been reported by numerous previous studies (Haven, 1959; White and Chittenden, 1977; Yakupzack et al., 1977; Ross, 1988; Miller and Able, 2002; Miller et al., 2003).

The second migratory pattern observed was a consistent ingress of juveniles into inshore areas that began in late winter and peaked in early spring (Feb.–April) in both years. The relative catch of juveniles (50–150 mm) increased through winter, was highest in spring, and declined steadily from the bag seine and trawl gears by fall. This disappearance coincided with high abundance of individuals in the gillnet gear in late summer/early fall. A similar shift in gear selectivity was described by Yakupzack et al. (1977), who demonstrated a transition in abundance in trawl samples from spring (generally targeted inshore-directed YOY) to trap samples

TABLE 1. A summary of the length at age data for Atlantic croaker in samples taken from fishery-independent gillnet samples in inshore areas in Texas.

Age	N	Mean length (mm)	Length range (mm)
1	124	216	130–289
2	508	272	143–387
3	91	270	199–397
4	2	388	375–401
5	3	427	390–455
6	1	431	NA

<sup>a</sup> NA = Not Applicable.

TABLE 2. Outputs from the von Bertalanffy growth model on Atlantic croaker length at age. Parameter estimates are given with standard error (SE) and 95% confidence intervals (CIs).

Parameter	Estimate (SE)	95% CI	t-Value	P-value
$L_{inf}$	286.08 (5.81)	276.48–299.97	49.21	<0.0001
K	1.55 (0.35)	0.99–2.59	4.45	<0.0001
$t_0$	0.09 (0.18)	–0.33–0.41	0.52	0.604

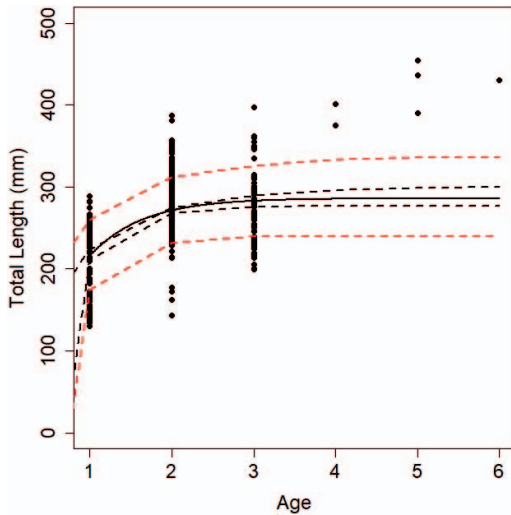


Fig. 7. Plotted length and age data for Atlantic croaker. A fitted von Bertalanffy growth curve is given (solid black), along with 95% confidence intervals (dashed black) and 95% prediction intervals (dashed red).

in late summer (generally targeted offshore-directed adults). In the current study, the transition in selectivity from smaller-meshed active gears (seines and trawls) to the large-mesh passive gear (gillnets) generally was coincident with a transition in size from juvenile to adult fish and preceded the fall decline in abundance from all gears. These migratory patterns imply annual inshore-resident growth of juveniles in the spring, followed by offshore movement of adults for spawning in the fall, and finally inshore transport of larvae in late winter and early spring.

Recruitment of YOY Atlantic croaker into estuaries occurred year-round and was highest Dec.–June. However, 73% of YOY individuals observed in seine samples occurred in the 3-mo period between Feb. and April. This short peak in recruitment implies a concurrently short spawning period. Previous studies have described the spawning period for Atlantic croaker as protracted, spanning as long as Sep. through March, with mid-season peaks around Oct. (White and Chittenden, 1977; Barbieri et al., 1994b). However, Cowan (1988) observed spawning in a relatively short window (Nov.–Jan.) in the northern Gulf and suggested that spawning after Jan. is rare. The current data seem to support the conclusion of Cowan (1988), as the majority of recruits observed in inshore samples occurred over a 3-mo window. This pattern was

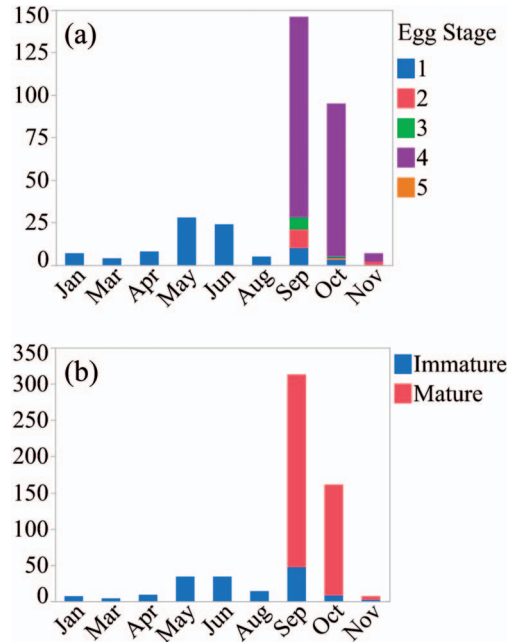


Fig. 8. Atlantic croaker female sexual maturity by month. Maturity was observed in two ways: (a) the threshold gonadosomatic index (GSI) of  $> 1\%$  was used to determine maturity based on a comparison of advanced egg stages and GSI in a subset of individuals ( $n = 583$  GSI method), and (b) egg stage itself was diagnosed in a subset of individuals ( $n = 324$  staging method). Egg stages were as follows: 1 = primary oocytes, 2 = cortical alveoli, 3 = advancing, 4 = vitellogenic, and 5 = hydrated.

repeated over two consecutive years. Despite a short recruitment period, there was a wide distribution of individual lengths in spring months (March–May) in combined bag seine and trawl samples. Juvenile croaker were found in both gears at this time and ranged in size from  $\sim 50$  to 150 mm in TL in significant numbers. Significant individual variation in growth has been demonstrated elsewhere (Barbieri et al., 1994a), and Cowan (1988) suggested that growth rates vary seasonally based on water temperature and food availability. In fact, significant variation in size within cohorts was confirmed by age analysis in the current study, and this finding suggests that estimation of recruitment timing based on length/frequency analysis might be biased by individual variation in growth rates.

The small number of age-4+ fish observed in the length–age data set is expected given that these data were collected exclusively inshore. Similar to the findings of Barbieri et al. (1994a), size at age is highly variable, making model fit

TABLE 3. Commercial harvest data from Matagorda and Galveston bays in 2001. Landings were from commercial harvest reports summarized by Culbertson et al. (2004). Abundance and total biomass were estimated by scaling up the observed CPUE from FIN samples to estuary-wide estimates in both areas. The proportion of the available biomass that was harvested was determined by dividing monthly commercial landings by the total available biomass in that month. Since biomass was estimated from a single gear (inshore trawls), it is expected that biomass in this instance reflects only that segment of the population susceptible to commercial trawling operations in Texas.

Month	Commercial landings (pounds)		Abundance (No. of individuals)		Total biomass (pounds)		Proportion harvested (%)	
	Matagorda	Galveston	Matagorda	Galveston	Matagorda	Galveston	Matagorda	Galveston
Jan.	0	6	520,997	182,736	20,943	7,346	0.000	0.001
Feb.	0	8	838,878	364,139	33,389	14,494	0.000	0.001
March	0	20	1,986,528	837,653	83,471	35,197	0.000	0.001
April	152	128	2,655,990	3,307,927	124,163	154,640	0.001	0.001
May	1,006	1,568	2,790,793	4,054,879	142,741	207,395	0.007	0.008
June	2,120	2,487	1,895,444	5,382,051	101,185	287,310	0.021	0.009
July	2,677	5,340	1,307,046	3,447,981	74,877	197,524	0.036	0.027
Aug.	2,072	4,077	1,007,382	2,909,109	59,861	172,867	0.035	0.024
Sep.	759	2,497	878,043	1,263,148	55,577	79,953	0.014	0.031
Oct.	254	415	674,928	713,605	45,020	47,600	0.006	0.009
Nov.	99	131	521,908	324,124	32,113	19,944	0.003	0.007
Dec.	7	4	398,945	169,398	20,848	8,852	0.000	0.000

difficult for these older fish, and the small sample of older fish ( $n = 6$  individuals age-4+) makes performance of the model for these ages unreliable. Thus, biological interpretation of the  $L_{inf}$  parameter is cautioned. Regardless, the model performs well for younger, inshore fish, and the limited data for older fish suggest that growth for most individuals has already started to slow by the time they migrate offshore to spawn. The size-at-age function estimated here results in predictive values of size-at-age that are similar to

those generated previously using a variety of methods (White and Chittenden, 1977; Barger, 1985; Ross, 1988; Barbieri et al., 1994b) and is strikingly consistent with estimates of age-1 and age-2 individuals generated from scale markings (White and Chittenden, 1977). In each case, growth of Atlantic croaker is rapid up until age-1, at which point it slows considerably. We interpret this deceleration in growth rate as coinciding with a presumed shift of metabolic energies from somatic to reproductive.

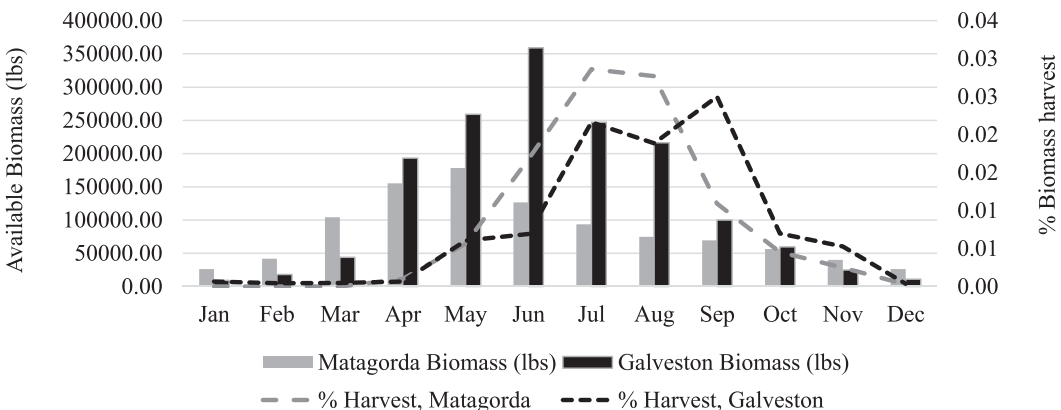


Fig. 9. The harvest of Atlantic croaker as a percentage of overall available biomass for the year 2001. Biomass estimates were made by scaling-up CPUE data from monthly FIN trawls to estimate estuary-wide biomass in Matagorda and Galveston bays. The % harvest was then estimated by comparing the fishery-dependent commercial landings data from Culbertson et al. (2004) to overall biomass. In this case, estimates of available biomass reflect merely the segment of the population that is susceptible to standard shrimp trawls as they are deployed in Texas waters. Thus, % harvested is a reflection of only that segment of the population that is available to the trawl gear, broken down by month.

With regard to shifting metabolic energies, the slowing of growth and declining abundance of adult individuals in inshore samples in the fall coincides with advanced stage ova and developing gonadal tissue for both males and females. Out of 481 females examined from Sep. through Nov., 421 (88%) had GSI values representative of maturity. This included 76% maturation of age-1 females and 93% maturation of age-2 females in the months of Sep. and Nov. combined. Developing gonadal tissue for both males and females occur in Sep. and continue through Nov., at which point inshore abundance declines dramatically. A final note about maturation: none of the mature females examined here from inshore gillnet samples had eggs that were hydrated. When paired with the finding of Barbieri et al. (1994b) that hydration indicates imminent spawning, this result suggests that Atlantic croaker may spawn offshore almost exclusively in the western Gulf.

#### MANAGEMENT IMPLICATIONS

The results from this study lead to some general conclusions about the biology of Atlantic croaker in the western Gulf. First, based on the absence of hydrated females in this study, spawning in Texas likely occurs exclusively offshore. Second, spawning occurs over a relatively short season in the late fall/early winter in Texas. Juveniles were observed in inshore bag seine samples year-round, but there was a distinctive 3-mo peak abundance from Feb. through April, suggesting a concurrently long spawning season stretching presumably from Oct. through Dec. Third, larvae recruit to estuarine nursery areas over an extended period; in Texas, juveniles (< 150 mm TL) were observed year-round but peaked in spring and summer. And fourth, YOY Atlantic croaker typically mature in estuaries and become sexually mature by age-1.

With regard to the first point above, in its most recent biological species profile, the Gulf States Marine Fisheries Commission suggested that data were needed pertaining to the location and habitat characteristics of Atlantic croaker spawning grounds (GSMFC, 2017). In previous studies, spawning habitat has been described as primarily offshore (Cowan, 1988), but some evidence also suggests occasional inshore spawning (Barbieri et al., 1994b). The current data suggest that spawning of Atlantic croaker in Texas occurs entirely offshore, a finding that is supported by two lines of

evidence. First, adults are in high abundance during the late summer and early fall inshore in all bays, but inshore abundance declines sharply in Oct./Nov. Sampling by TPWD gillnets is conducted in a randomized design and includes areas adjacent to Gulf passes. It is unlikely that spawning aggregations are residing in unsampled inshore areas; instead, it is more likely that observed declines in abundance are driven by offshore migration. Second, advancing maturity stages were observed coincident with declines in abundance in the fall. However, egg hydration was not observed in any individuals. Barbieri et al. (1994b) demonstrated cyclical spawning activity in Atlantic croaker involving hydration followed by ovulation and spawning; thus, the absence of hydrated females inshore can be taken as evidence of offshore spawning. Offshore samples were not collected in the course of this study, but these findings imply that future studies regarding the location and habitat of spawning Atlantic croaker in Texas should necessarily be focused on offshore habitats.

Finally, with regard to commercial landings of Atlantic croaker, the mean % harvest of individuals in the inshore fishery never exceeded 5% of the estimated overall abundance in either Matagorda or Galveston bays over all months. While this finding implies a minimal impact of the inshore fishery on overall population growth, some caveats apply. First, bycatch discard is a significant mortality factor in many organisms, including Atlantic croaker, and discard mortality is a source of uncertainty in estimates of overall fishing mortality (Davis, 2002). Commercial landing reporting in Texas is dependent upon a mandatory reporting structure, but it is unclear how the landings estimates reported in Culbertson et al. (2004) may be biased downward as a result of unreported bycatch discard mortality. Second, landings of inshore Atlantic croaker are highly variable across the species range (Hare and Able, 2007), particularly in Texas (Culbertson et al., 2004). Estimates derived from the narrow time reported here (2001) may not be consistently applied across years, and, thus, the harvest impacts reported here may not be entirely applicable in subsequent time frames. With those caveats in mind, it is interesting to note that the finding of a relatively low impact of the commercial inshore fishery on Atlantic croaker populations in Texas seems to support the interpretation of Diamond et al. (2010),

who reported that larval and juvenile mortality of Atlantic croaker had relatively small impacts on population growth relative to postspawned egg stages and adult mortality in both the Gulf and Atlantic. This indirectly implies a measure of sustainability for the inshore commercial Atlantic croaker fishery in Texas, given that the underlying assumptions of the analysis presented here might be consistently met.

## ACKNOWLEDGMENTS

Fishery-independent sampling of Atlantic croaker in Texas was accomplished by the resource management personnel of Texas Parks and Wildlife Department (TPWD), and sampling was funded in part by a grant from the Federal Aid in Sportfish Restoration program (USFWS). R. Weixelman, C. Mayes, D. Westbrook, and E. Young assisted with laboratory methods. Mark Fisher coordinated the internal review of the manuscript and provided helpful comments. Work was funded in part by a grant through the Federal Aid in Sportfish Restoration fund (USFWS-WSFR).

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