



Abstract—The Atlantic croaker (*Micropogonias undulatus*) is an important commercial species in the Gulf of Mexico, but this stock has been reduced historically as bycatch in other fisheries. Sagittal otoliths ($N=190$) were removed from larval and early juvenile Atlantic croaker collected within a Louisiana tidal pass over a 2-year period, from October 2006 through March 2007 and from September 2007 through March 2008. Standard length (SL) at age in days after hatching (dah), over both years, was fitted with a Laird-Gompertz growth model, and similar models were fitted separately to year and season to determine whether different spawning subgroups existed. In both years, the maximum growth rate occurred 20 days earlier in spring than in fall. Otolith microstructure measurements were used to determine the age (~40 dph) at which larvae encountered differing water mass characteristics of the coastal boundary zone (the offshore to inshore recruitment corridor). Growth rates increased after fish encountered lower-salinity (<20) waters of the coastal boundary zone and estuary of Bayou Tartellan, LA. Temporal variability in spawning of Atlantic croaker, determined with age-length keys, revealed that the highest frequency of hatch dates occurred during November in 2006 and 2007.

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Age, growth, and recruitment of larval and early juvenile Atlantic croaker (*Micropogonias undulatus*), determined from analysis of otolith microstructure

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The Atlantic croaker (*Micropogonias undulatus*) in the western Atlantic range from the Gulf of Maine to the northern Gulf of Mexico (GOM). That range potentially may extend into the southern GOM, the Lesser Antilles, and southern Caribbean and from Brazil through southern Argentina (Smith, 1997). The status of the Atlantic croaker stock is unknown (NMFS, 2009), although it is expected to be below maximum sustainable yield. The amount of Atlantic croaker harvested commercially has been cyclic, ranging from 1100 metric tons (t) per year to more than 15,000 t per year; annual levels recently were estimated at approximately 9000 t, with a value of approximately \$8 million (NMFS, 2012). These fluctuations reflect the high variability in recruitment patterns driven by both small and large spatial and temporal scales of environmental conditions, such as wind field patterns, storm frequency, salinity, temperature, hypoxic zones, and local hydrographic features (Norcross, 1983; Norcross and Austin, 1988; Able, 2005; Eby et al., 2005; Montane and Austin, 2005).

The commercial stock is further affected by the amount of Atlantic croaker that is caught as bycatch, principally through shrimp trawling—an amount that is calculated to be 60–80% of the catch by weight (NMFS, 2012). The amount of Atlantic croaker caught annually as bycatch can total from 100,000 to 400,000 t, and data from the 1990s indicated that Atlantic croaker may have made up almost 73% of the total bycatch of short-lived demersal species (NMFS, 2009, 2012). The results of analysis of samples collected during 1986–2006 by Southeast Area Monitoring and Assessment Program crews show that the Atlantic croaker, which was classified as a bycatch species, to be the dominant species by weight at depths less than 30 m off the Louisiana coast (Helies and Jamison¹). At depths

¹ Helies, F. C., and J. L. Jamison. 2009. Reduction rates, species composition, and effort: assessing bycatch within the Gulf of Mexico shrimp trawl fishery. NOAA/NMFS Cooperative Agreement Number NA07NMF4330125 (#101). Final Report, 182 p. Gulf and South Atlantic Fisheries Foundation Inc., Tampa, FL. [Available at [website](#).]

greater than 30 m, the Atlantic croaker was either the second or third bycatch taxon by weight, depending on sampling period (Helies and Jamison¹). This high level of bycatch and directed fishing-induced mortality may increase the importance of minor variations in mortality rates of the early life history stages to overall stock success, variations that greatly affect recruitment rates (Norcross, 1983; Diamond et al., 2000).

A peak in spawning occurs from July through December and in larval estuarine recruitment during October–November (Cowan, 1988; Ditty et al., 1988; Warlen and Burke, 1990; Barbieri et al., 1994a). Atlantic croaker spawn over a wide range of inner continental shelf depths (i.e., 54 m or shallower), and a portion of the population moves inshore toward estuaries to complete spawning during the winter and early spring months (Barbieri et al., 1994a, 1994b). Hydrologic variability at large and small spatial and temporal scales can greatly affect the numbers of Atlantic croaker larvae able to successfully recruit to estuarine nursery grounds (Norcross, 1983; Shaw et al., 1988; Raynie, 1991; Raynie and Shaw, 1994). Once larvae are in the estuary, lower water temperatures in the first winter increase their mortality rate as verified in both the field (Norcross and Austin, 1988; Hare and Able, 2007) and laboratory (Lankford and Targett, 2001a, 2001b).

Previous studies on age and growth of Atlantic croaker generally have focused on the Mid-Atlantic Bight (MAB) and South Atlantic Bight (SAB), however, limited studies have occurred in the GOM. For these studies, linear growth rate models have been created from counts of daily rings within otoliths and paired readers have found growth rates between 0.16 and 0.27 mm/d (Warlen, 1982; Thorrold et al., 1997); in the GOM, the growth rate for this species has been determined to be 0.19 mm/d (Cowan, 1988). The occurrences of higher growth rates for larval Atlantic croaker during the spawning and estuarine recruitment peak in the late summer and early fall and of lower larval growth rates during the overwinter period and into the spring have led to the notion that different spawning subgroups may exist (Warlen, 1982). This hypothesis is further supported by differences in growth rates and recruitment dynamics that are based on latitude along the estuaries of the MAB and SAB (Barbieri et al., 1994b; Thorrold et al., 1997).

Daily formation of otolith increments have been confirmed in *Micropogonias* (Campana, 1984; Cowan, 1988; Albuquerque et al., 2009), making such increments a reliable proxy for age. Otolith rings for larval fish, formed daily, not only can provide information on growth rates but can also be used to estimate approximate times of larval estuarine ingress (i.e., transport time from offshore spawning grounds to estuarine nurseries) (Hoover et al., 2012). The approximate timing of larval and early juvenile ingress of Atlantic croaker to estuarine nurseries from offshore spawning grounds in the MAB and SAB has been estimated to vary between 30 and 60 d after hatching. (Warlen, 1980; Warlen and Burke, 1990; Hettler and Hare, 1998; Hoskin, 2002; Hoover et al.,

2012). Daily otolith rings have been also used to examine environmental parameters that affect growth and survivorship (Campana, 1999; Campana and Thorrold, 2001) and to determine within-season cohorts for Atlantic herring (*Clupea harengus*), on the basis of variable growth between seasons in the same year (Brophy and Danilowicz, 2002). Larval otolith growth rings and microstructure were initially examined through direct observation by paired readers using light microscopy; however, video and digital methods have become prevalent with the increase in image resolution from high-megapixel digital imaging sensors (Ralston and Williams, 1989; Campana, 1992; Morales-Nin et al., 1998).

For this study, we had 5 primary objectives. The first objective was to define and determine an iterative digital filtering mechanism that can provide a more accurate and automated determination of daily increments in otoliths of larval Atlantic croaker. The second objective was to determine the length at age of Atlantic croaker larvae collected in a tidal pass in the northern GOM from fall through spring over a 2-year recruitment period. The third objective was to compare observed larval growth rates determined from linear and nonlinear growth models with those determined from previous studies. The fourth objective was to estimate, on the basis of ring counts corrected for hatching date and time at first ring formation, times for estuarine ingress through the tidal pass from the coastal boundary zone. Finally, the fifth objective was to determine the effect of hydrodynamic patterns associated with differences between continental shelf and estuarine waters on growth of larval and early juvenile Atlantic croaker.

Materials and methods

Sampling location

Ichthyoplankton sampling was conducted in Bayou Tartellan, near Port Fourchon, Belle Pass, Louisiana (Fig. 1A). Bayou Tartellan and Bayou LaFourche are the first major inland channel bifurcations from the connection with the GOM at Belle Pass (29°5' 53.9"N, 90°13'17.8"W). The location of sampling was within a seasonally well-mixed tidal pass (i.e., tidal pass with little stratification in temperature, salinity or dissolved oxygen) that has high turbidity and a relatively small drainage basin that contributes a very low volume of freshwater input. The site (Fig. 1B; 29°6.82'N, 90°11.07'W) where passive sampling was conducted with a plankton net was located at the end of a dock that extended 3.7 m into the tidal pass from the northern bank of Bayou Tartellan, and the site had a water depth of approximately 10 m.

Field sampling method

Ichthyoplankton sampling was conducted with a fixed davit placed at the end of the dock and from which

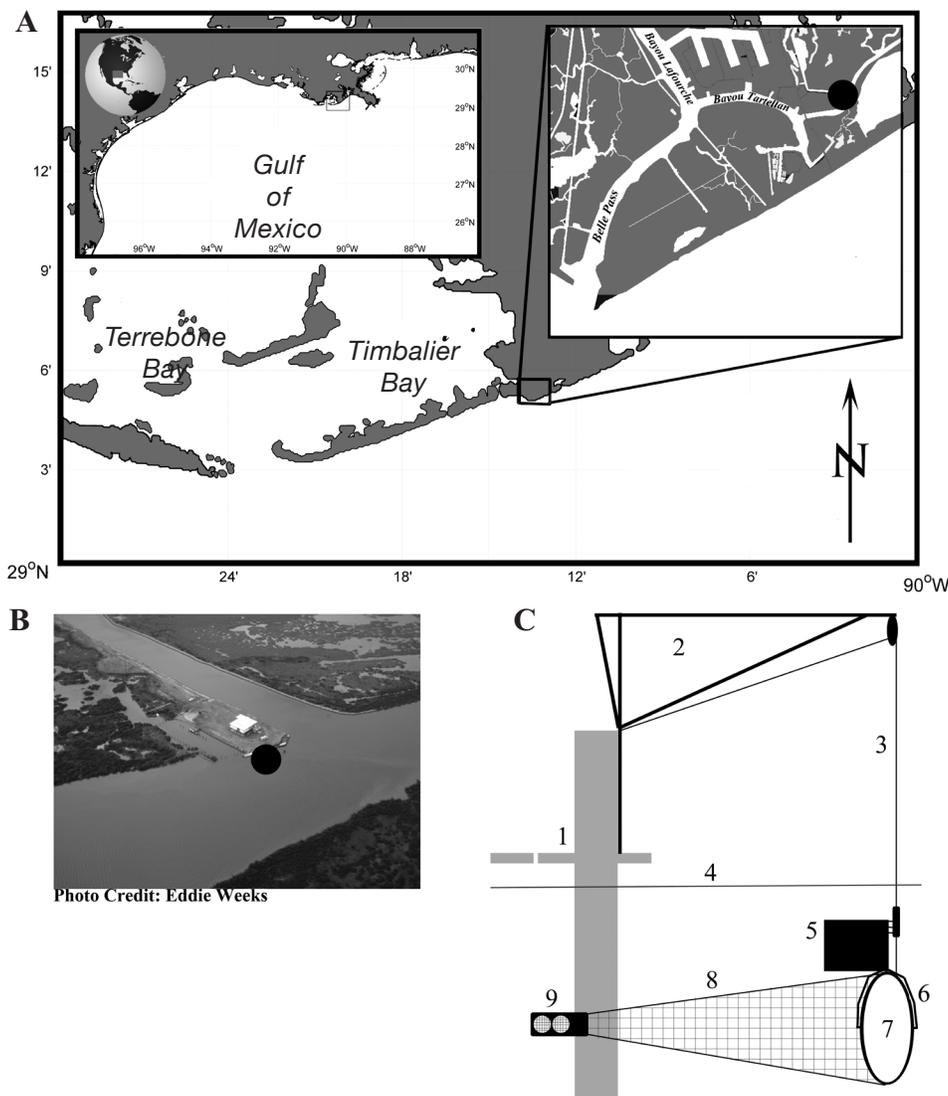


Figure 1

(A) Map of the sampling location for this study in relation to the Gulf of Mexico and coastal Louisiana. The upper right inset represents the area around Port Fourchon, Belle Pass, Louisiana, and the sampling site in Bayou Tartellan identified by a black circle on the map. Sampling for larval and juvenile Atlantic croaker (*Micropogonias undulatus*) was conducted from October 2006 through April 2007 and then from September 2007 through April 2008. (B) Aerial photograph of the sampling site on Bayou Tartellan; the black circle again identifies the sampling site. (C) Diagram of the sampling system: 1) fixed dock where the sampling system was attached, 2) davit that was used to extend the net farther into the channel, 3) cable system by which the net was raised and lowered, 4) water surface, 5) orientation vane for the net system, 6) 60-cm metal ring that held open the net mouth, 7) pivoting gimbal, 8) 333- μ m mesh net, dyed dark green, and 9) plastic, vinyl-coated codend with 333- μ m drainage ports.

a stainless steel cable was suspended from above the sampling deck to the channel bottom (Fig. 1C). Ichthyoplankton were sampled passively with a 60-cm ring net (333- μ m mesh, 2-m length) that was dyed dark green to minimize visibility, and hence avoidance, and that was attached to a gimbal with a vane for orientation into the current. A plastic, vinyl-coated codend with

333- μ m mesh drainage ports was attached to the end of the net to facilitate sample collection. A flowmeter (model no. 2030; General Oceanics², Miami, FL) with a

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

slow-velocity rotor was positioned just off center of the ring to determine volume of filtered water.

Ichthyoplankton samples were collected every 4 h over a 72-h period, twice monthly from early October through April over a 2-year period (2006–2008), except December and January, when samples were taken only on a monthly basis. In addition, there were 2 sampling efforts made in September 2007. The sampling season was chosen to coincide with wind-dominant meteorological events (i.e., atmospheric cold front passages) from late fall to early spring and to increase the probability of collecting larvae and small juveniles (Hernandez et al., 2010). Individual sampling dates were chosen to match the largest astronomical tidal ranges. During passive sampling, one ichthyoplankton collection was taken at the surface and another near the bottom. They were taken in random order for each sampling effort. Surface collections were 6 min long, and near-bottom collections were 10 min long to compensate for vertical differences in current speed and, ultimately, for volume of filtered water (i.e., sampling effort). For near-bottom collections, the net mouth was closed during deployment until the net was in position, was opened for sampling, and was closed for retrieval to prevent vertical contamination of the sample during transit through the water column. Surface collections had a mean filtered volume of 13.3 m³ (standard deviation [SD] 16.8), and near bottom collections had a mean filtered volume of 16.6 m³ (SD 22.4). Nets were washed down with a freshwater source to avoid biological contamination from marine taxa.

Ichthyoplankton samples were fixed initially for approximately 3.5 h in freshly made, buffered (sodium phosphate, dibasic NaH₂PO₄·H₂O, and monobasic Na₂HPO₄) 10% formalin. Samples were then rinsed, thoroughly drained, and switched into a 70% ethanol solution. This procedure parallels methods described by Butler (1992). Although some studies have shown that formalin may damage otoliths of small specimens (Brothers, 1984), sagittal otoliths in other species have not shown evidence of dissolving (Ré, 1983; Landaeta et al., 2014), especially during very short exposures.

During each collection of ichthyoplankton samples, estuarine hydrographic parameters were measured dockside with a portable YSI 85 instrument (YSI Inc., Yellow Springs, CO). A continuously sampling YSI 600R multiparameter water-quality sonde (YSI Inc.), moored on the bottom of the channel floor offshore of the dock, also measured the same parameters. Hydrographic data were downloaded periodically as necessary and archived. Predicted diurnal tides were obtained from NOAA's Center for Operational Oceanographic Products and Services ([website](#)) for a nearby tide gauge station at Port Fourchon (station ID: 8762075; 29°6.8 N, 90°11.9 W). Tide height data and the difference between the predicted and measured tidal prism were downloaded for that station.

A bottom-mounted, upward-looking acoustic Doppler current profiler (ADCP), a 1200-kHz broadband Workhorse H-ADCP (Teledyne RD Instruments, Pow-

ay, CA), was placed in the center of Bayou Tartellan (offshore of the dock), for the duration of the study, to measure the vertical profile of current velocity and direction. Boat surveys were also conducted along Bayou Tartellan and Bayou LaFourche out to Belle Pass through the use of downward-looking ADCPs to provide a channel-wide correction factor for the mid-channel, stationary upward-facing ADCP. A volume transport was calculated in cubic meters per second for Bayou Tartellan from these data. To remove the effects of tide and inertia, a sixth-order 40-h Butterworth low-pass filter (Roberts and Roberts, 1978) was applied to the raw volume transport to produce a net water transport (NWT). These net transport data effectively show the lower-frequency subtidal oscillations associated with atmospheric cold front events and other wind-forcing factors, and these data filter out the higher-frequency diurnal tidal oscillations (Li et al., 2009).

Laboratory methods

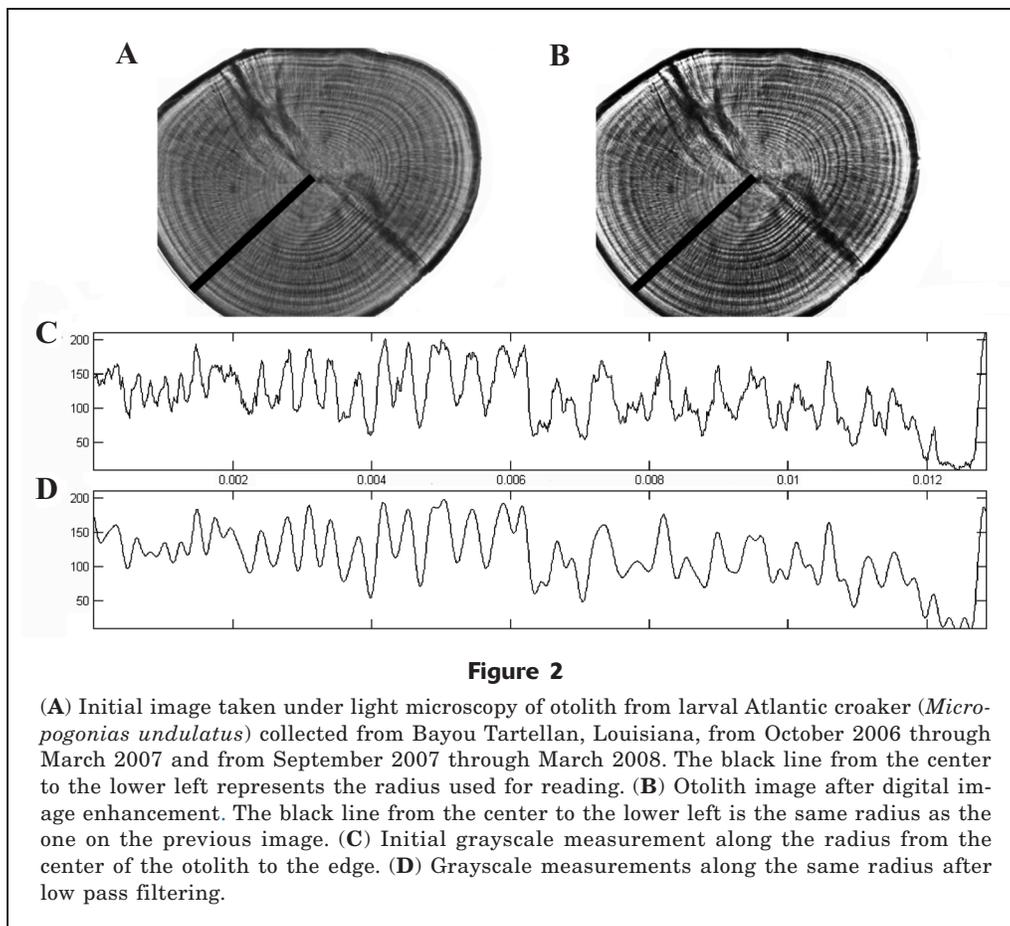
In the laboratory, ichthyoplankton collections with a volume of material greater than 200 mL were divided in half with a Motodo plankton splitter (Motodo Plankton Splitter, Aquatic Research Instruments, Hope, ID 83836), and those collections with a volume greater than 400 mL were split into quarters. Samples were sorted under a dissecting stereoscope, and all ichthyoplankton were removed. A subset of sorted samples was checked for completeness of ichthyoplankton removal by a second party and sorted again if necessary.

Ichthyoplankton were identified to the lowest taxonomic level possible, depending on size and physical condition of each organism. Some larval fishes that were difficult to identify were stained with Alizarin blue and Alizarin red to facilitate meristic counts. Atlantic croaker larvae and early juveniles (hereafter referred to as larvae for brevity) were separated and stored for otolith analysis. Identifications were based on literature from Fahay (1983), and Richards (2006).

Atlantic croaker larvae were subsampled for otolith analysis on the basis of a normal distribution of standard length (SL) of all specimens collected. Measurement of SL to the nearest 0.1 mm was conducted with a Leica MZ6 stereoscope (Leica Microsystems Inc., Buffalo Grove, IL) calibrated against a stage micrometer. Atlantic croaker larvae were sampled from every collection that contained this target species. For samples in which 3 or less Atlantic croaker larvae were collected, all larvae of this species were scheduled for otolith removal. For samples that contained more than 3 larvae of Atlantic croaker, 3 larvae, specifically the shortest and longest specimens, along with one that was closest to the mean SL for all Atlantic croaker in the sample, were selected and scheduled for otolith removal.

Otolith removal, preparation, and age interpretation

Removal and preparation of sagittal otoliths from Atlantic croaker larvae selected for dissection followed



the method described by Barbieri et al. (1994a, 1994b). All dissections were conducted with an Olympus SZX12 stereoscope (Olympus Corp., Tokyo) with a 1× objective lens. Both left and right sagittal otoliths were removed and placed on a slide with Permount mounting medium (Thermo Fisher Scientific, Waltham, MA), the left otolith concave side up and the right otolith concave side down. Otoliths were polished with 0.3- μm alumina paste and a microcloth to reveal the core. Otoliths were etched with 0.1-N hydrochloric acid for between 10 and 20 s to facilitate readability under a compound stereoscope. Digital images were taken at a magnification from 500× to 1250× with an Olympus BX41 compound stereoscope equipped with a phase contrast filter to highlight light- and dark-ring discontinuity zones of otoliths with oil immersion (Fig. 2A).

Adobe Photoshop CS4, vers. 11.0 (Adobe Systems Inc., San Jose, CA) was used to convert the image from color to grayscale and to enhance differences between light and dark rings by increasing contrast and brightness (Fig. 2B). Measurements of otolith radii lengths, the distance from the otolith nucleus to the distal edge, and of grayscale values for each radius were conducted with ImageJ image analysis software, vers. 1.44p, (National Institutes of Health, Bethesda, MD). Measurement of each radius produced a calibrated length

and corresponding grayscale values that ranged from 0 (black) to 255 (white) along that radius. A central radius and 2 radii to the left and right of the central radii, offset by a single pixel each, were measured. All 5 radii were averaged to produce the grayscale values later used for filter analysis, to avoid the bias that could be introduced by choice of the radius for reading (Morales-Nin et al., 1998). Radius length and grayscale data were collected for each otolith that was imaged (Fig. 2C).

Image data were imported into MATLAB, vers. 7.6.0.324 R2008a (The MathWorks Inc., Natick, MA) for filtering and nominal age determination. Low pass filter structure was determined with a fast Fourier transform (FFT) to transform the initial radii measurements into frequencies to identify and exclude high-frequency subdaily discontinuities from the otolith radius. The low-pass filter was fitted iteratively to the individual otoliths, on the basis of the understanding that the Nyquist frequency is the daily otolith increment accreted by the larvae. As noted by Morales-Nin et al. (1998), this iterative fitting is done for each otolith because of increments of varying radius length between otoliths, differences in magnification, and variable growth rates for individuals. An inverse FFT was then performed to transform the signal from the frequency domain back

into the distance measurements for location of the sinusoidal peaks and, therefore, of the position and width of the respective rings along the radius used for reading (Fig. 2D).

Ten otoliths were selected at random to be analyzed by using the traditional paired-reader method. These results were then used to compare them against 2 new, independently run FFT-generated ring counts. The same number of rings were observed for all 10 otoliths through the independently run FFT method, and only 1 otolith had a difference of 1 ring between the FFT method and the paired-reader method.

Otolith aging and larval hatching dates

Larval age, estimated as days after hatching (dah), was determined from the increment counts for each otolith radius with the methods previously described. Daily formation of increments has been validated and deposition has been confirmed to have a positive relationship to growth of larval Atlantic croaker (Searcy, 2005). Moreover, daily increment formation has been confirmed and validated for other species in the family Sciaenidae that live in similar environments, such as red drum (*Sciaenops ocellatus*; Wilson et al., 1987) and spot (*Leiostomus xanthurus*; Warlen and Chester, 1985). For the purposes of our analysis, we, therefore, assumed that increment deposition occurs daily. Following the methods used by Cowan (1988) and on the basis of laboratory work (Arnold³), we applied a 4-d lag for first increment formation after hatching for larvae of Atlantic croaker, (Warlen and Chester, 1985). This application resulted in a calculation of total age by adding 4 to the otolith count. Estimated ages were calculated for specimens for which otolith radii were measured. Ages were estimated for all other larvae and early juveniles not selected for dissection by using age-length keys and the FSA package for R software, vers. 2.13.0 (R Development Core Team, 2011). The hatching date was determined by subtracting the age (dah) from the date of collection.

Growth and timing of estuarine ingress

A linear model was run to allow direct comparison of our results with those of previous studies where a linear model was used. Larval growth of Atlantic croaker is slowest near the hatching date, increases thereafter, and slows again as larvae settle and begin further organ and sensory development; therefore, a derivative of the Gompertz model was selected as the nonlinear model for our study because it highlights this specific pattern of growth (Gompertz, 1825). Somatic growth of larval Atlantic croaker was modeled with only the directly analyzed otolith data by using a Laird-Gompertz growth model (Laird et al., 1965; Zweifel and Lasker,

1976; Lozano et al., 2012). This model had a set intercept of $L_{\text{null}}=1.5$ mm in notochord length (NL) to accurately represent the hatching length (dah=0; Warlen, 1980; Cowan, 1988; Barbieri et al., 1994a, 1994b). We used the following equation for the Laird-Gompertz growth model:

$$L_t = L_{\text{null}}e^{k(1-e^{-at})}, \quad (1)$$

where L_t = the SL, measured in millimeters, at an age (dah);

L_{null} = the SL at hatching for Atlantic croaker;

a = the rate of exponential decay; and

k = a dimensionless parameter so that ka represents the instantaneous growth rate at hatching.

Hindcasting was used to estimate growth rates with the Laird-Gompertz growth model (Lozano et al., 2012) for ages of larvae that were not sampled, because larvae were located offshore at these early ages,

Instantaneous growth rates (i.e., the rate of growth at a particular time in dah) were estimated with the maximum growth rates calculated both from the equation for the first derivative of the Laird-Gompertz model and from the mean growth rates calculated on 10-d intervals. We used the following equation to determine the first derivative of the Laird-Gompertz model:

$$G_{\text{DI}} = L_{\text{null}}e^{k(1-e^{-at})} * (kae^{-at}), \quad (2)$$

where G_{DI} = the instantaneous daily growth rate by means of the first derivative of the Laird-Gompertz model.

Mean growth rates for the 10-d interval were calculated with the following equation:

$$G_{\overline{10}} = \frac{(L_{t_2} - L_{t_1})}{\Delta t}, \quad \text{where } t_2 > t_1 \quad (3)$$

and where $G_{\overline{10}}$ = the average growth rate for that 10-d interval;

L_{t_1} = the modeled SL at an initial time; and

L_{t_2} = the modeled SL at time .

Instantaneous growth rates then were determined from the natural log of the lengths in the mean growth equation described above.

The estuarine recruitment date for larvae was determined from the difference in the width of the daily increments and variation in distance of the ring from the otolith core. The recruitment date for the pretransformation larvae (<10 mm) was determined as the day after hatching at which there was an increase in the ring width and an increase in the distance between 2 adjacent rings. Movement by the larvae into the estuary, where there is lower salinity, increased nutrient loads, and higher primary production, has been shown to cause a rapid increase in growth for larvae and young-of-the-year juveniles (Hoss et al., 1988; Moser and Gerry, 1989).

A multivariate analysis of variance (MANOVA) was performed to test for differences in length and

³ Arnold, C. R. 1983. Univ. of Texas Mariculture Project 1982–1983, 36 p. Marine Science Institute, Univ. Texas, Port Aransas, TX.

age between seasons, nested within years. A significant result from a MANOVA model would indicate that there were differences in the composition of length and ages in the larvae and early juveniles of Atlantic croaker that were collected. Growth rates were tested with an F -test to compare the residual sums of squares for the pooled Laird-Gompertz growth model with those of the Laird-Gompertz growth models that were fitted by season and sampling year (Chen et al., 1992).

Distributions of lengths and calculated ages that were based on readings of otoliths were tested for normality with a Shapiro-Wilk's test. A mixed model was applied by using R software (vers. 2.13.0) to look at growth rates of individual larvae with respect to salinity, temperature, and NWT within the tidal pass:

$$y_{ij} = \beta_0 + \beta_1 \text{Salinity}_{ij} + \beta_2 \text{WaterTemp}_{ij} + \beta_3 \text{NWT}_{ij} + \beta_4 \text{Tide}_{ij} + \tau_i + \varepsilon_{ij}, \quad (4)$$

where y_{ij} = the response variable of growth rate for the random group i and individual j ;

β_0 = the intercept term;

β parameters = the effects for each of the variables (i.e., salinity, water temperature, and NWT), with tide being a binary dummy variable for each of the tide states (i.e., flood or ebb);

τ_i = the random effect of sampling month when the larvae were collected; and

ε_{ij} = the random error term for the model.

Results

Hydrology

There were no statistical differences in water temperature by sampling depth. This result is consistent with a seasonally, vertically well-mixed tidal pass, such as Bayou Tartellan. Generally, water temperatures followed the normal seasonal trends, in which water was warmer during the early fall (i.e., September and October) and cooler during the winter before rising again during March and April. There was a noticeable drop in temperature during November 2006, and median water temperature remained below 15°C through early February 2007. During the winter months, colder temperatures and greater temperature fluctuations were recorded than those recorded during fall or spring months. In particular, for the December 2007 sampling effort, there was a fluctuation range of 10.2°C during the 72-h sampling period. Although water temperature also decreased in November 2007, the median water temperature did not fall below 17°C during all remaining sampling efforts, resulting in higher water temperatures during year 2 of sampling.

No statistically significant differences were found between surface or near-bottom salinities, once again supporting a seasonally, vertically well-mixed estu-

ary. In general, 95% of all measured practical salinity values fell between 21.5 and 31.4 within a total range of 14.5–33.2 and with a mean of 27.32. Median salinity values dropped by more than 5 between December 2006 and January 2007. In early February 2007, the median value was similar to that of January 2007 but ranged from as high as 32 to a low of nearly 20 over a 4-d period. Aside from median salinities of approximately 28 in late February 2007, the median salinity in Bayou Tartellan remained below 25 until early April 2007. Salinities during late 2007 and early 2008, with the exception of early March, showed less variation and were generally higher than those of the previous sampling year.

Catches of larval Atlantic croaker

There were 3118 larval and early juvenile Atlantic croaker collected from October 2006 through March 2007, and 425 larvae were collected from September 2007 through March 2008. Sampling continued through April in both 2007 and 2008; however, no Atlantic croaker were collected during that period. Catches in November 2006 accounted for 53.5% of the total number of Atlantic croaker larvae collected over both sampling periods. As in 2006, collections made in November 2007 had the greatest number of larvae caught in the second sampling period, but a second peak was observed in March 2008.

Table 1

Hatching dates for larval and early juvenile Atlantic croaker (*Micropogonias undulatus*) collected in Bayou Tartellan, Louisiana during 2006–2008. Hatching dates are based on back-calculated otolith ages and collection dates after application of age-length keys. Percentages of the total number of larvae collected in that sampling year and cumulative percentages are based on half-month intervals.

Interval	2006–2007		2007–2008	
	%	Cumulative %	%	Cumulative %
08/15–08/31	0.26	0.26	0.00	0.00
09/01–09/15	8.97	9.23	4.65	4.65
09/16–09/30	29.74	38.97	21.71	26.36
10/01–10/15	32.56	71.54	17.83	44.19
10/16–10/31	10.51	82.05	18.60	62.79
11/01–11/15	2.05	84.10	3.88	66.67
11/16–11/30	4.10	88.21	5.43	72.09
12/01–12/15	6.15	94.36	1.55	73.64
12/16–12/31	0.26	94.62	3.10	76.74
01/01–01/15	1.28	95.90	6.98	83.72
01/16–01/31	3.08	98.97	10.85	94.57
02/01–02/15	1.03	100.00	5.43	100.00
02/16–02/28	0.00	100.00	0.00	100.00

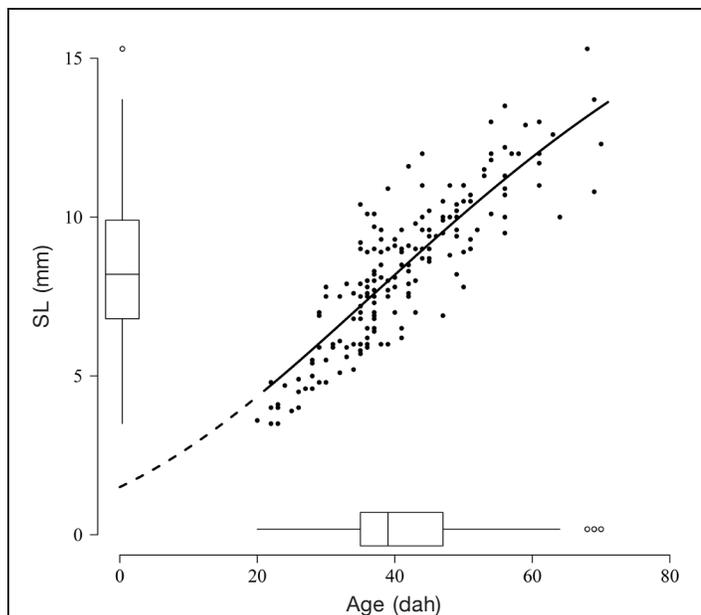


Figure 3

Relationships of estimates of standard length (SL) versus age in days after hatching (dah) determined with a Laird-Gompertz growth model, for larval Atlantic croaker (*Micropogonias undulatus*) collected from Bayou Tartellan, Louisiana, from October 2006 through March 2007 and from September 2007 through March 2008. This model was forced through the intercept at the estimated 1.5-mm notochord length at hatching to accurately reflect length at hatching. Boxplots show the median, 25% and 75% quantiles, and 95% confidence intervals, and outliers are provided for each axis. The Laird-Gompertz model was parameterized with the following equation: $SL = 1.5 \cdot e^{2.613272(1 - e^{-0.026186 \cdot \text{Age}})}$.

Length, age, and hatching dates determined from counts of otolith increments

Sagittal otoliths were removed from 203 larvae and early juveniles of Atlantic croaker. Of those removed, 13 otoliths were not readable and were excluded from analysis. The length frequency plot of all larval Atlantic croaker that were aged ($N=190$) followed a normal distribution (Shapiro-Wilk: $P=0.43$), with a mean of 8.3 mm SL (SD 5.4) and range from 3.5 to 15.3 mm SL). However, the distribution of lengths was flatter in year 1 (SD=2.5 mm SL) than in year 2 (SD=2.0 mm SL). All ages of larval Atlantic croaker, from both direct measurement and estimation, also followed a normal distribution (Shapiro-Wilk: $P=0.11$) with a mean age of 41 dph (SD 10.1), a median of 39 dah, and a range of 20–70 dah.

In general, SL increased as the spawning and recruitment season progressed. Smaller larvae (<7 mm SL) were most prevalent in October for sampling year 1 and in September and October for sampling year 2. For both sampling periods, the median SL of larvae sampled began to stabilize in late November and early Decem-

ber and remained relatively constant through the spring. In both sampling years, the highest numbers of hatching dates occurred between 16 September and 31 October (Table 1). In year 1, cumulatively, more than 95% of all calculated hatching dates had occurred before 15 January 2007, but, during year 2, the 95% cumulative distribution was not reached until early February 2008, after a small, secondary peak in late January.

Modeled growth rates and dates of estuarine ingress

There was a significant linear relationship between measured lengths and estimated ages for larval Atlantic croaker ($P<0.001$; coefficient of determination [r^2]=0.76). The linear model indicated that the average growth rate was 0.20 mm/d, and it underestimated the hatching length (at 0.97 mm NL). The Laird-Gompertz growth model for the entirety of the data set, forced through the 1.5-mm-NL hatching length, provided a model fit that accounted for changes in growth rate due to sensory and organ development better than the fit of the linear model, which had nonstatistically independent and nonhomoscedastic errors that indicated a nonlinear relationship of growth rates that were variable through time. However, it only partially accounted for a slower initial growth rate at ages less than 20 dah (Fig. 3).

The sum of squared residuals was significantly reduced when models were fitted by season and sampling year than when a model was fitted with data pooled from both sampling years ($P=0.007$). Length, age, and growth were significantly different for seasons within years ($P<0.001$). Larvae collected during the peak spawning and recruitment season from September through December of 2006 and 2007 were shorter and younger than those collected from January through March of 2007 and 2008 (Fig. 4A; Chambers et al., 1983). Initial growth rates in the fall (September–December) of 2006 and 2007 were lower than those in the spring (January–March) of 2007 and 2008, but they steadily increased and did not level off at older ages. In contrast, larvae collected in the spring of 2007 and 2008 had higher initial growth than those collected in the previous fall seasons, but rates in both spring seasons leveled off quickly and resulted in shorter fish at ages greater than 50 dah and 60 dah, respectively (Fig. 4B). Compared with patterns observed in year 1, the difference in patterns of larval growth rates in fall compared with those in spring was more pronounced in year 2, when there were generally warmer water temperatures and higher salinities.

The ages and magnitudes of maximum growth rates for larval Atlantic croaker differed significantly within sampling year by season in the Laird-Gompertz models ($P<0.001$). Overall, the Laird-Gompertz models fitted by year and season showed that the maximum growth

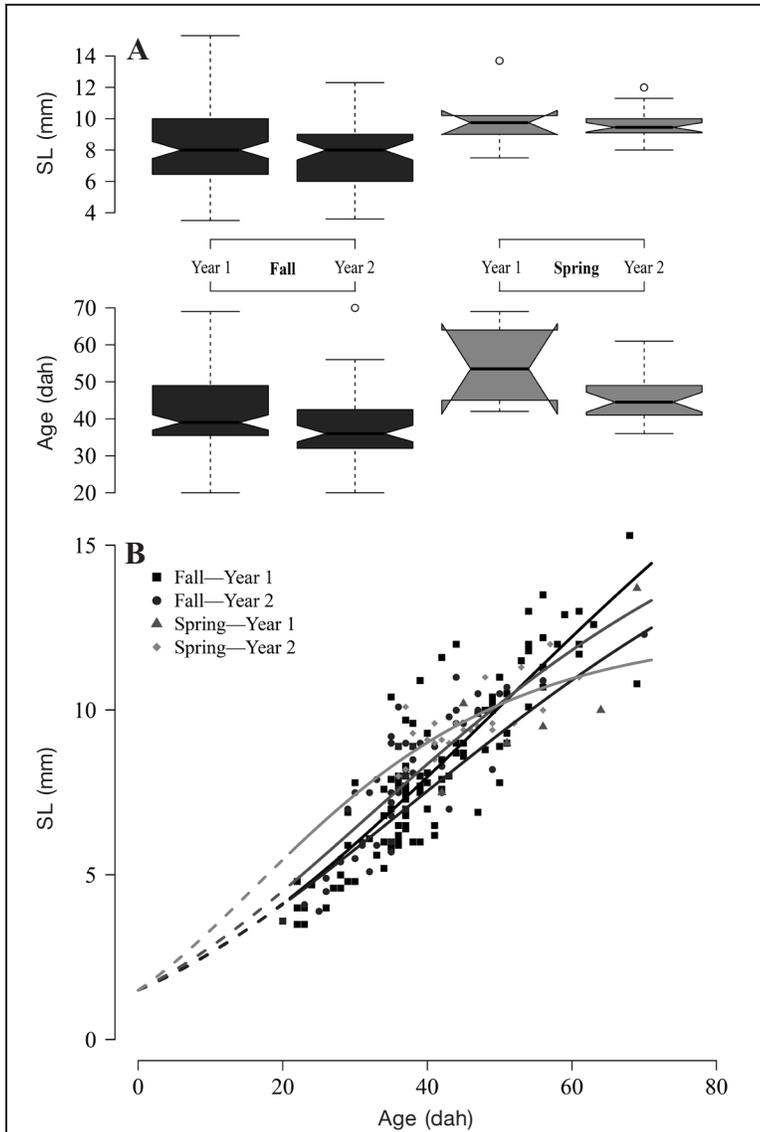


Figure 4

(A) Boxplots from a comparison of estimates of standard lengths (SL) and ages in days after hatching (dah), by season, for otoliths of larval Atlantic croaker (*Micropogonias undulatus*) collected from October 2006 through March 2007 (year 1) and from September 2007 through March 2008 (year 2). Fall sampling was conducted during September–December and spring sampling occurred during January–March. Nonoverlapping notches between any 2 boxplots represent “strong evidence” of statistically different median values, as described by Chambers et al. 1983. (B) Relationships of SL versus age determined with the Laird-Gompertz growth models for otoliths of larval Atlantic croaker, by season and sampling year. All models are forced through the intercept at the estimated 1.5-mm notochord length at hatching to accurately reflect growth rates at ages in dah less than the minimum otolith determined age. Model parameterizations were calculated as follows:

$$\text{Fall of year 1: } SL = 1.5 \cdot e^{2.89159(1 - e^{-0.02155 \cdot \text{Age}})},$$

$$\text{Fall of year 2: } SL = 1.5 \cdot e^{2.50594(1 - e^{-0.02893 \cdot \text{Age}})},$$

$$\text{Spring of year 1: } SL = 1.5 \cdot e^{2.54838(1 - e^{-0.02152 \cdot \text{Age}})},$$

$$\text{Spring of year 2: } SL = 1.5 \cdot e^{2.11260(1 - e^{-0.04726 \cdot \text{Age}})},$$

rates in the fall occurred when larvae were approximately 20 dah younger than larvae whose maximum growth rates occurred in spring. The maximum instantaneous growth rate was higher in fall 2006 (0.214 mm/d; 49 dah) than in fall 2007 (0.177 mm/d; 37 dah), but larvae in the fall of each year had the same minimum growth rate of 0.093 mm/d (Fig. 5). A greater initial instantaneous growth rate was observed in spring 2008 (0.150 mm/d) than in spring 2007 (0.113 mm/d). Although, the maximum instantaneous growth rate in spring 2008 (0.216 mm/d) was greater than the maximum rate in spring 2007 (0.196 mm/d), it occurred at an earlier age (16 dah versus 32 dah) and decreased rapidly thereafter. The 10-d averages for the 2 sampling years were slightly different. The highest average growth rate in year 1 was 0.203 mm/d at ages between 40 and 50 dah (Table 2), correlating with a peak at 49 dah in the fall of sampling year 1 (Fig. 5). In year 2, the highest average growth rate of 0.193 mm/d occurred at ages between 20 and 30 dah (Table 2)—a rate that was consistent with the peak in instantaneous growth rates that occurred at 16 dah during the spring of year 2 (Fig. 5).

The estimated average date of estuarine ingress after hatching was similar for both fall and spring seasons in both sampling years, but there were differences between seasons in the mean distance of the ring from the otolith core. Regardless of season or year, rapid changes in distance of the ring from the core and ring width happened around 40 dah, before the ontogenetic shift from late larvae to early juvenile has been reported to occur at approximately 10 mm SL (Barbieri et al., 1994a, 1994b). Mean distance of the otolith ring from the core, as a proxy for growth, was fairly stable before 40 dah and increased more rapidly and became more variable after that point (Fig. 6A). In particular, in spring 2007 and 2008, distances from the core were greater than the distances for the same age in the fall of 2006 and 2007. Mean otolith ring width was somewhat constant at approximately 0.5 μm for the fall of both sampling years and 1.1 μm for the spring of both years until 40 dah, when mean ring width became much more variable and generally increased with ring count thereafter (Fig. 6B).

Statistical analysis

The mixed model fitted for water temperature, salinity, and NWT, by tide, to the estimated growth rate of all individuals col-

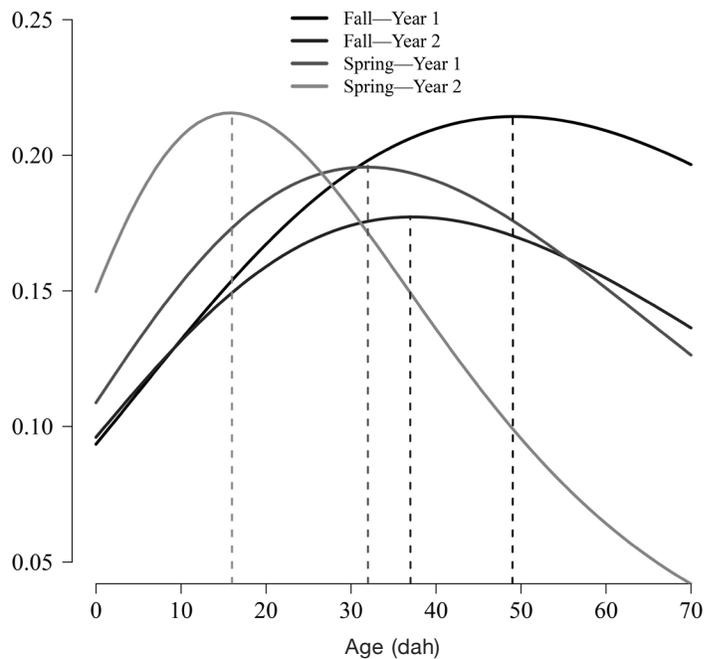


Figure 5

Maximum growth rates for Atlantic croaker (*Micropogonias undulatus*) larvae and early juveniles collected in Bayou Tartellan, Louisiana, from October 2006 through March 2007 and from September 2007 through March 2008, based on the first derivative of the Laird-Gompertz growth model for otoliths of larval Atlantic croaker. Solid lines indicate daily growth rates (mm/d) as the slopes of the estimates from the Laird-Gompertz models at any age in days after hatching (dah). Dashed lines indicate the maximum growth rates for fall of year 1 (2006), fall of year 2 (2007), spring of year 1 (2007), and spring of year 2 (2008).

lected during both sampling years, having significant model terms for all continuous variables. The only model terms that were not significant at the a priori alpha level of 0.05 were tidal stage and salinity as a function of tidal stage. The nonsignificance of the tidal stage term is likely a function of masking due to higher order interaction terms.

The individual model terms generally showed a trend of increased growth rate with ingress through the tidal pass, supporting the notion that otolith ring width and growth rate both increase at ingress, regardless of sampling year or season. The interaction of ebb tides with water temperature showed higher growth associated with colder temperatures that are indicative of shallow estuarine waters during late fall and winter (October–March) ($P=0.040$; Fig. 7A). The flood tide interaction with water temperature showed a similar trend, although more muted, likely a result of higher temperatures of waters from the inner continental shelf to the coast. Increased growth was also associated with decreasing salinity, regardless of tidal stage, resulting in a nonsignificant interaction ($P=0.901$), al-

though the 95% confidence interval was much larger at lower salinities during flood tides (Fig. 7B). As with interactions with water temperature, modeled growth rates associated with salinities that were more consistent with estuarine conditions were significantly greater ($P=0.046$) than growth rates associated with higher salinities. Higher growth rates also were associated with large negative NWT on ebb tides, indicative of lower-salinity waters further up the estuary ($P=0.001$; Fig. 7C). However, during flood tides, no relationship was apparent statistically.

Discussion

Successful estuarine recruitment of Atlantic croaker larvae through tidal passes along the northern GOM depends on a highly variable spawning regime, on advantageous environmental conditions such as hydrographic, tidal, and wind-forcing factors, and ultimately on larval growth (Norcross and Austin, 1988; Eby et al., 2005; Montane and Austin, 2005). Hindcasting of the Laird-Gompertz growth model to 0 dah allowed us to infer growth rates of larvae along the recruitment corridor across the continental shelf and coastal zone. The bottleneck nature and the highly variable hydrodynamic environment of a seasonally well-mixed tidal pass at Bayou Tartellan, as well as the associated increase of larval growth with ingress into the estuarine nursery ground (Searcy et al., 2007), presented the challenges and rewards of successful estuarine recruitment for larval Atlantic croaker that were spawned offshore.

The highest frequency of hatching dates occurred between late September and early October for both sampling years, but hatching continued through the late winter and early spring (Fig. 5), indicating an overwinter spawning and recruitment period. The peak hatching dates corresponded well with the previously described period of July through December for peak spawning and recruitment (Warlen and Burke, 1990; Barbieri et al., 1994b) and with an overall spawning and recruitment period from August through May (Hettler and Chester, 1990). Differences in the distribution of hatching dates between year 1 and year 2 of the study highlight the variability in yearly spawning of Atlantic croaker that was due to factors on various spatial (Miller and Able, 2002) and temporal (Norcross, 1983) scales. For example, year 2 distribution of hatching dates peaked less than that of year 1. In addition, a higher percentage of larvae were recruited in the months after December 2007 than in other periods,

Table 2

Average growth rates (mm/d) and instantaneous growth rates (G) for larval and early juvenile Atlantic croaker (*Micropogonias undulatus*) collected in Bayou Tartellan, Louisiana, based on otolith data grouped by age blocks of 10 days after hatching (dah). Rates are provided for 2 sampling years—October 2006 through March 2007 and September 2007 through March 2008—and for the overall combined data.

Blocks (dah)	2006–2007		2007–2008		Overall	
	(mm/d)	G	(mm/d)	G	(mm/d)	G
0–10	0.115	0.057	0.138	0.065	0.124	0.060
10–20	0.152	0.045	0.175	0.048	0.161	0.046
20–30	0.181	0.036	0.193	0.035	0.187	0.036
30–40	0.198	0.029	0.190	0.025	0.196	0.027
40–50	0.203	0.023	0.173	0.019	0.192	0.021
50–60	0.198	0.018	0.149	0.014	0.178	0.016
60–70	0.185	0.014	0.122	0.010	0.158	0.013

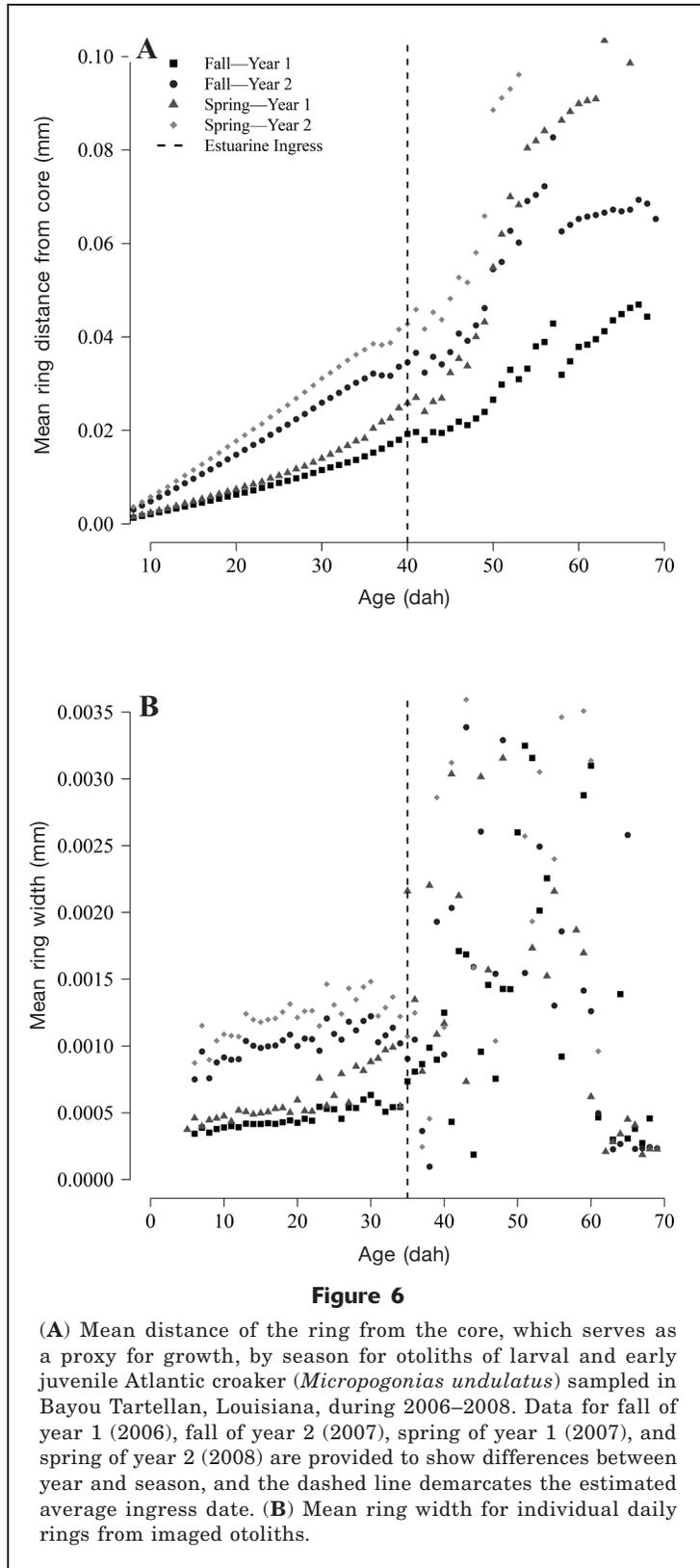
indicating a more protracted spawning season (Barbieri et al., 1994a). The second peak in hatching dates in late January and early February for both sampling years indicates a possible second spawning subgroup (Fig. 6; Warlen, 1980; Thorrold et al., 1997). Warmer water temperatures during winter sampling efforts in year 2 were very similar to temperatures during the fall months in sampling year 1, potentially explaining the protracted spawning season in 2007–2008 (Lankford and Targett, 2001a, 2001b; Hare and Able, 2007).

Growth rates of larval and early juvenile Atlantic croaker collected in Bayou Tartellan increased and became variable after larvae encountered lower-salinity (<20) coastal boundary and estuarine waters, as did growth rates for Atlantic croaker when entering estuarine waters along the MAB (Nixon and Jones, 1997). The growth rate of 0.20 mm/d from the linear model in our study compares favorably with the growth rate of 0.19 mm/d documented from larvae collected from inner continental shelf waters offshore of Sabine Pass, Texas, and the Mermentau River, Louisiana (Cowan, 1988). The instantaneous maximum growth rates from the Laird-Gompertz model for the fall and spring of both sampling years fell within the range of growth rates reported for coastal waters off North Carolina: 0.16–0.27 mm/d (Warlen, 1980). The differences in seasonal growth rates within the Laird-Gompertz models provide evidence of spawning and recruitment subgroups with maximum growth rates occurring 20 dah later in the fall than in the spring—a finding indicating that the larvae spend a longer time period in a more productive and potentially more suitable essential fish habitat during the spring (Searcy et al., 2007; Sponaugle, 2010). Similar subgroups also have been observed in North Carolina waters (Warlen, 1980) and the MAB (Thorrold et al., 1997), where seasonal differences in growth rates were a result of food availability and variation in salinity.

The differences in seasonal growth rates observed in our study, however, may also be partially explained by the movement of spawning fish farther inshore as the season progressed (Barbieri et al., 1994a, 1994b), thereby shortening their time within the recruitment corridor when transiting to estuarine nursery grounds and more favorable growth conditions. Lower salinities (<15) indicative of estuarine waters have been shown to increase somatic growth rates of larval Atlantic croaker (Peterson et al., 1999). Although all analyses of growth in our study revealed similar growth rates, the use of the Laird-Gompertz model allowed more accurate hindcasting of the low growth rates of larvae in the recruitment corridor on the continental shelf because we used model true estimates of hatching length, and the linear models failed to accurately reflect or account for length at hatching.

The mean age of larval Atlantic croaker that transgressed the lower-salinity (<20) waters of the coastal boundary layer and entered the estuary was estimated to be approximately 40 dah, on the basis of changes in otolith ring width and distance of the ring from the core (Fig. 6, A and B). Ontogenetic change in otolith shape did not affect ring width or distance from the core because all otoliths in our study were roughly circular. Studies of ingress into Chesapeake Bay, Delaware Bay, and Pamlico Sound have shown ages at time of ingress to be between 30 and 60 dah (Warlen, 1980; Miller et al., 2003; Schaffler et al., 2009a, 2009b), a range that compares favorably with the results from direct aging of larvae collected for our study in the Bayou Tartellan tidal pass: between 22 and 70 dah.

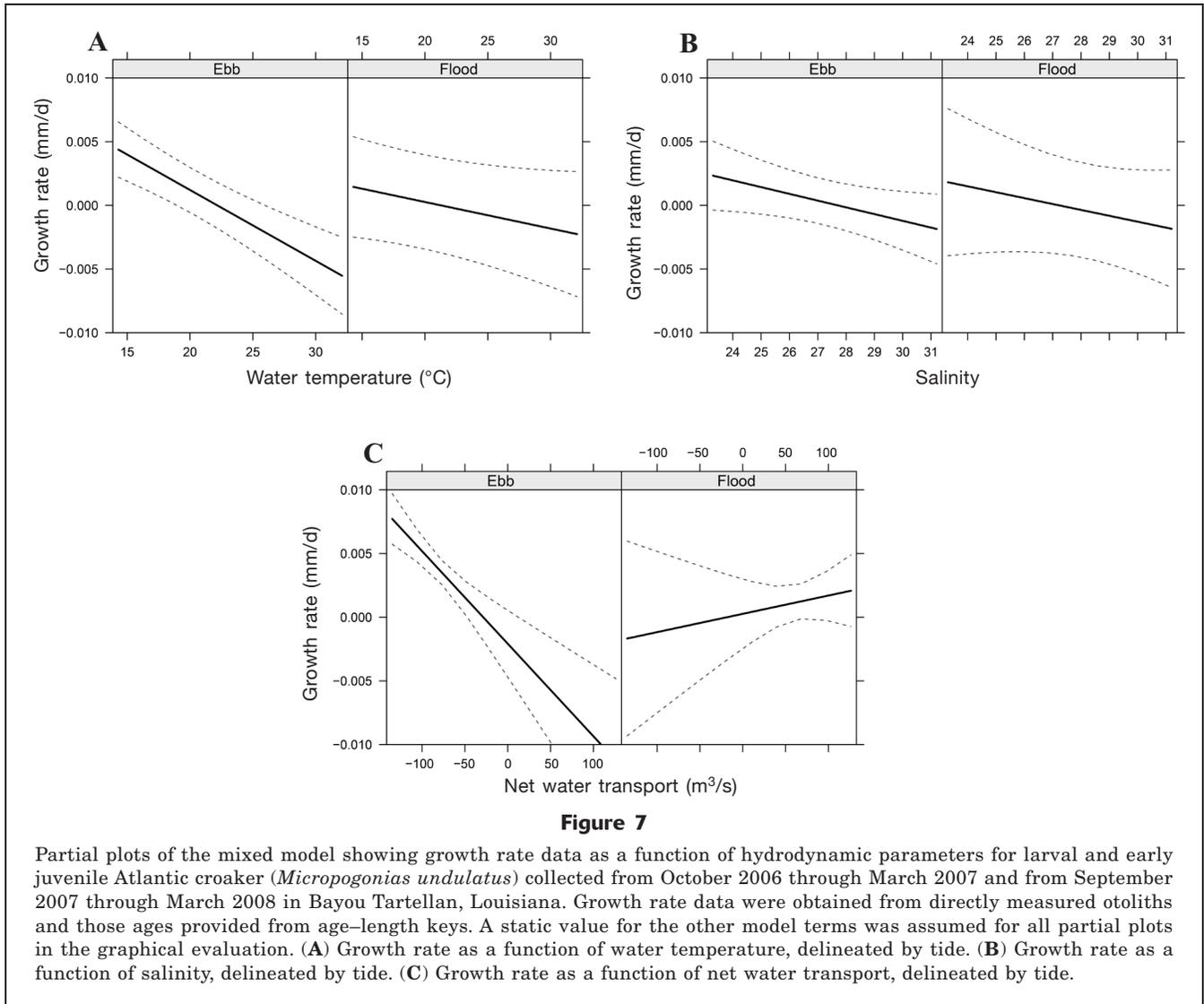
The role of periodic atmospheric winter frontal passages on densities of larval Atlantic croaker has been shown to be significant in this system (Kupchik, 2014), indicating that patterns such as inlet geomorphology and wind-forcing factors can play a large role in the timing of ingress for Atlantic croaker (Raynie



and Shaw, 1994; Joyeaux, 1998; Wood, 2000). Larval ingress can be driven by active mechanisms like selective tidal stream transport, but the vertically well-mixed nature of tidal passes in the northern GOM and particularly in our sampling site of Bayou Tartellan indicates that the driving forces are passive mechanisms of recruitment and retention, such as residual bottom flow (Joyeux, 1999; Schultz et al., 2003), wind-driven transport (Shaw et al., 1985; Joyeaux, 1999; Hare et al., 1999; Hare and Govoni, 2005), or flow differentials across channels due to boundary conditions and marsh edge effects (Lyczkowski-Shultz et al., 1990; Raynie, 1991; Raynie and Shaw, 1994; Kupchik, 2014).

Growth rates for Atlantic croaker larvae collected in water masses with salinities and temperatures consistent with continental shelf waters were lower than growth rates for larvae collected in water masses with characteristics associated with estuarine or coastal boundary waters. The effect of salinity on growth rate is further exemplified by the steep increase in growth rate during ebb tides, which bring low salinities indicative of waters from the upper estuarine nursery ground. Increased growth associated with lower salinities has been documented previously for larval Atlantic croaker in other estuaries (Peterson et al., 1999). Growth rate as a function of water temperature showed no difference associated with tide. Higher growth rates were associated with lower water temperatures, and those rates probably reflected the increased productivity of estuaries, which, during late fall and winter, have cooler temperatures and lower salinities than the warmer, more saline waters of the GOM. The notable exception to this pattern was the increase in growth rate that occurred during positive NWTs associated with flood tides, and this increase in growth rate may be a function of interim or prefrontal conditions associated with southerly winds and higher coastal sea level in relation to the reestablishment of the tidal prism after flushing from northerly winds of the postfrontal phase. Results from the mixed model confirmed the importance of salinity for growth of larval and juvenile Atlantic croaker that has been noted in previous studies (Sogard, 1992; Rooker and Holt, 1997; Lankford and Targett, 2001a) and the temporal and spatial variability that has been associated with differences between estuarine and continental shelf waters (Searcy et al., 2007).

Analysis of digital images of daily rings in saccular otoliths of larval Atlantic croaker, collected in Bayou Tartellan from October 2006 through March 2007 and from September 2007 through March 2008, provided a fast, reliable method for analyzing otolith rings, growth rate,



and estuarine ingress. The digital image filters reduced the need for human interpretation and allowed direct measurement and averaging of multiple readings to avoid aliasing from subdaily increments or other small scale microfeatures that could confound accurate age determination. Furthermore, the digital analysis allowed us to obtain exact measurement of otolith ring widths and distances from the core to confirm the estimated estuarine ingress date determined from changes in growth rates. Analyses of digital images of otoliths from Atlantic croaker allowed a more confident estimation of the age at which larval Atlantic croaker transition from the continental shelf to the more hydrodynamically variable and potentially more productive coastal boundary zone and lower-salinity estuarine waters.

The linear growth model was useful for comparison with results from previous studies but less effective than the Laird-Gompertz growth curves in detailing

accurate growth rates of Atlantic croaker larvae. The Laird-Gompertz growth models allowed hindcasting to accurately include the NL at hatching and rate of growth more effectively in the dah before sampling. They provided more detail about the timing of ingress of Atlantic croaker into estuaries, where growth rates were expected to increase. The models revealed the limited somatic growth of larvae before recruitment into the lower-salinity estuarine system of Bayou Tartellan. Moreover, they allowed us to calculate instantaneous growth rates that reflect small-scale, daily changes affected by spatial location within the recruitment corridor without the bias introduced from overall averages expressed in a linear relationship with a singular rate of 0.20 mm/d or without the bias introduced from groupings of larvae in dah.

With the Laird-Gompertz models we estimated maximum growth rates, showing the difference of maximum growth rates that occurred later (with respect to dah)

in the fall than in the spring. The observed differences in growth rates between the fall spawning and recruitment season and the spring recruitment season provide evidence of spawning subgroups for the first time in the northern GOM—a finding that is similar to growth rates of the subgroups that have been found in North Carolina waters and in the MAB. This result was confirmed by the differences in otolith microstructure between the fall and spring for both sampling years, and the microstructure analysis was able to show within-year variability in batch spawning—a variability that would produce different cohorts with variable distances from offshore spawning grounds to inshore recruitment corridors. The highly significant salinity component in the mixed model that revealed a relationship between growth rate and the hydrodynamics in Bayou Tartel-lan gave evidence of the importance of the low salinity and high productivity of estuarine waters for maximizing growth for larval and, ultimately, juvenile Atlantic croaker.

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