



Population connectivity of red drum in the northern Gulf of Mexico

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ABSTRACT: Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope ratios in otoliths were used to assess the degree of connectivity between early life and adult habitats of red drum *Sciaenops ocellatus* in the northern Gulf of Mexico. Young-of-the-year (YOY) red drum were sampled over a 3 yr period from major estuaries along the Texas coast, and otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were quantified to determine whether chemical tags in otoliths were region specific. North to south gradients were pronounced for otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, with values being higher (enriched in the heavier isotope) for YOY red drum from southern estuaries relative to those in the north. Four distinct regional groups of YOY red drum were identified using otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$: North (N), Sabine Lake and East Galveston Bay; North-Central (NC), Christmas Bay and Matagorda Bay; South-Central (SC), Aransas Bay and Redfish Bay; and South (S), Laguna Madre. Overall classification success to these regional nurseries was high for each year examined: 2001 (92%), 2002 (82%) and 2003 (90%). Mixed-stock analysis performed with age-2+ red drum collected in 2003 matched to the 2001 YOY baseline indicated that most of the sub-adult and adult red drum sampled in the S and SC regions were produced from the same areas (82 to 91%), with limited exchange between these regions. Mixing was more pronounced in the northern regions (N, NC), with a large percentage (35 to 42%) of individuals originating from the adjacent region to the south. Overall, the majority of sub-adult and adult red drum was collected within or near the same region occupied during the YOY period, suggestive of natal homing, retention within specific estuarine corridors, or lower survivability of recruits migrating from distant regions.

KEY WORDS: Otolith chemistry · Site fidelity · Natal homing · Residency · Stable isotopes · Stock identification · Estuarine contribution · Nursery origin · Red drum

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INTRODUCTION

Many fishes use estuaries to complete their life cycles and often spend months to years in these environments before migrating to coastal waters (Able et al. 2007). The degree of connectivity between estuarine and coastal environments is increasingly implicated as a key factor regulating population dynamics (Able 2005, Gillanders 2005). In response, a variety of approaches have been employed in recent years to assess movement and connectivity within and across

estuaries, including numerical transport models (Brown et al. 2004), tagging (Bottom et al. 2005), genetics (Bradbury et al. 2008) and otolith chemistry (Gillanders 2002, Rooker et al. 2004, Fodrie & Herzka 2008). Despite the fact that information on movement and mixing is considered fundamental to managing estuarine-associated fishes (Levin & Stunz 2005) and assessing estuarine nursery value (Beck et al. 2001), the degree of connectivity at local and regional scales is still poorly understood for many taxa (Secor & Rooker 2005).

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Chemical markers in otoliths are often used to assess population connectivity because otolith material deposited during the first year of life serves as a nursery tag (Campana 1999). To date, both trace elements and stable isotopes have been used to successfully discriminate fishes from different estuarine, coastal and marine environments, and to determine whether recruits originated from local or distant nurseries (Thorrold et al. 2001, Elsdon et al. 2008, Rooker et al. 2008a). Although trace elements serve as viable chemical tags for evaluating connectivity between estuarine and coastal habitats, strong interannual variability in these chemical signatures is relatively common, often requiring age-class matching of baseline samples to those of unknown origin (Thorrold et al. 1997, Gillanders 2005). Recent studies using carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope ratios indicate a high degree of accuracy in classifying individuals to nurseries coupled with lower interannual variability (Kerr et al. 2007, Rooker et al. 2008b), suggesting stable isotope ratios may serve as useful nursery tags.

Red drum *Sciaenops ocellatus* support a valuable sport fishery in estuarine and coastal waters of the Gulf of Mexico, and an improved understanding of regional production and connectivity of Gulf populations of red drum and other estuarine-dependent species is needed to develop efficacious conservation strategies. It is well established that red drum move between

early life (estuarine) and adult (estuarine/coastal) habitats; however, the degree of mixing by red drum produced in different nurseries and the level of site fidelity and/or natal homing displayed by individuals remains unresolved. The purpose of the present study was to characterize otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in red drum from regional nurseries and then use region-specific tags to predict the nursery origin of sub-adults and adults, and to assess the degree of mixing and population connectivity.

MATERIALS AND METHODS

Young-of-the-year (YOY) red drum (mean \pm SD total length = 27.7 ± 7.1 cm) were collected by hook-and-line over a 3 yr period (2001–2003) from bays and estuaries along the Texas Gulf Coast (from north to south): Sabine Lake, East Bay, Galveston Bay, Christmas Bay, Matagorda Bay, Aransas Bay, Redfish Bay and Upper/Lower Laguna Madre (Fig. 1). Sub-adult and adult red drum (age-at-maturity ca. age-1 to age-2 for males and age-3 to age-4 for females, Murphy & Taylor 1990) were collected by hook-and-line in 2003 near tidal passes or in coastal environments from several regions during the fall spawning event (September to November): Galveston Bay, Matagorda Bay, Corpus Christi Bay (includes Aransas Bay and Redfish

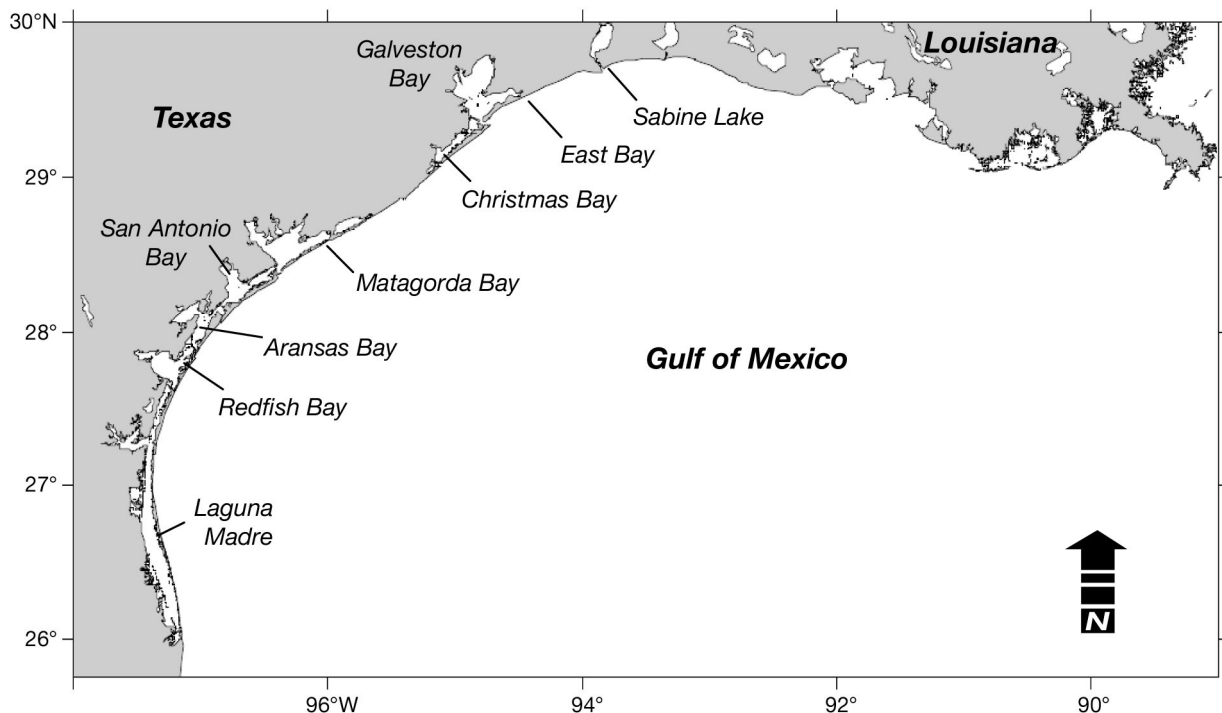


Fig. 1. Study area in the northern Gulf of Mexico with major bay systems shown

Table 1. *Sciaenops ocellatus*. Collection information for young-of-the-year (YOY) and sub-adult/adult red drum collected from 4 regions in the northern Gulf of Mexico: North (N), North Central (NC), South Central (SC) and South (S). n: sample size. Location codes: Aransas Bay (AB), Christmas Bay (CB), East Bay (EB), Galveston Bay (GB), Lower Laguna Madre (LL), Matagorda Bay (MB), Redfish Bay (RB), San Antonio Bay (SA), Sabine Lake (SL) and Upper Laguna Madre (UL)

Year	Region	Collection site (n)	Total length (cm)	
			Mean	Range
YOY				
2001	N	EB (12), GB (9), SL (13)	29.7	24.9–35.2
	NC	CB (14), MB (12)	23.9	19.1–29.5
	SC	AB (16), RB (9)	21.3	16.0–28.7
	S	LL (11), UL (10)	22.2	17.4–34.2
2002	N	EB (5), SL (11)	28.5	15.0–33.5
	NC	CB (12), MB (11)	25.8	18.3–33.0
	SC	AB (12), RB (10)	22.3	17.5–32.0
	S	LL (7), UL (13)	22.8	16.0–30.5
2003	N	EB (8), SL (10)	30.8	27.0–33.5
	NC			
	SC	AB (5)	25.4	22.5–31.9
	S	LL (6), UL (13)	25.3	20.0–30.7
Sub-adult/adult				
2003	N	GB (21), SL (11)	74.9	62.6–106.0
	NC	MB (25)	66.3	62.2–77.0
	SC	AB (32), RB (12), SA (9)	77.3	63.0–100.7
	S	LL (23), UL (18)	68.3	62.0–80.0

Bay) and Laguna Madre (Table 1). In addition, a smaller number of sub-adults or adults were sampled from these regions in May to August. For the purpose of the present study, age-2+ red drum is used to designate individuals collected in the summer or fall of the year approaching or slightly past their third birthday or the transition from age-2 to age-3 (lengths converted to age based on Murphy & Taylor 1990), suggesting that our sample of age-2+ or older red drum was likely comprised predominantly of young adults.

Sagittal otoliths of YOY and adult red drum were extracted, cleaned and rinsed with deionized water (DIH₂O). Whole otoliths of YOY red drum were powdered with an acid-washed mortar and pestle. For age-2+ and older red drum, sagittal otoliths were embedded in Struers epoxy resin and sectioned using a low-speed Buehler IsoMet® saw to obtain a 2.0 mm transverse section containing the core. Otolith sections were attached to a sample plate on a New Wave MicroMill System (New Ware Research), and the portion of the otolith corresponding to the YOY period was milled and removed. The drill path for the YOY section was a standard template with measurements derived from a series of sectioned otoliths from red drum 20 to 22 cm in total length (mean age ca. 7 to 8 mo; Fig. 2). Approximately 30 passes were made at a depth of 60 µm to isolate core material from the otolith. Surface

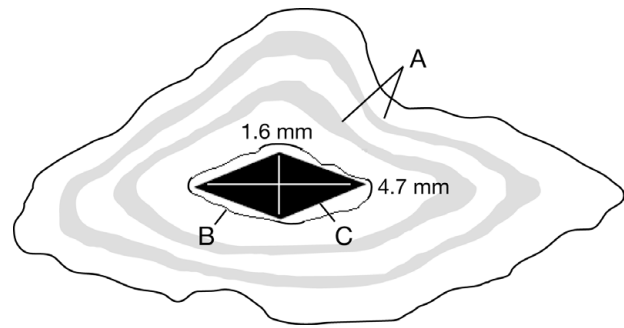


Fig. 2. *Sciaenops ocellatus*. Diagram of transverse section of otolith showing (A) annuli, (B) cross-section of sagittal otolith of young-of-the-year red drum, and (C) core material removed from transverse section (2.0 mm thick) of adult. Resulting prism was 1.6 mm (height) × 4.7 mm (width)

profiling was performed on each otolith to correct for bevelling in the section. Cored material was displaced as an intact diamond-shaped prism from the section and rinsed with DIH₂O before being powdered. Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were measured on a stable isotope mass spectrometer maintained at the Isotope Geochemistry Laboratory, Department of Geology, University of Maryland, USA. Stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope ratios reported here are based on isotopic ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ relative to an in-house standard calibrated to Pee Dee Belemnite.

Hierarchical cluster analysis based on otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of YOY red drum was used to partition bays and estuaries sampled into regional groups for statistical testing. Cluster analysis was performed using normalized Euclidean distance (root mean square distances) and average linkage. A 2-way mixed model ANOVA was performed with Year (random factor) nested within Region (fixed factor) to examine regional and interannual variability in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of YOY red drum. One-way ANOVAs were also used to examine the effect of Region (fixed factor) on otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ separately for each of the 3 years. Quadratic discriminant function analysis (QDFA) was used to classify YOY red drum because the variance-covariance matrix of predictor variables was dissimilar among samples from different regions (Rooker et al. 2008b). Otolith weights and fish lengths were slightly different among regions and years, but no size effect was detected for otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Consequently, we did not adjust for differences in otolith weight among YOY red drum in our baseline sample.

A maximum likelihood based mixed-stock analysis program HISEA developed by Millar (1990) was used to predict the nursery origin of sub-adult and adult red drum. The baseline data set used for mixed-stock analysis was comprised of whole otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

values of YOY red drum, while estimates of origin for sub-adults and adults collected in 2003 (age-2+) were based on isotopic values of otolith cores milled from transverse sections (corresponding to the YOY period). Age-2+ red drum collected in 2003 were matched with the 2001 baseline of YOY red drum, and direct matching was possible for over 60% of our unknown samples (Fig. 3). For the remaining age-3+ or older red drum with YOY periods before 2001, the 2001 baseline was used for predictions of nursery origin. Standard deviations around estimated proportions for sub-adult and adult red drum of unknown origin were generated in HISEA by bootstrapping with 500 resamplings of the baseline. Our sampling of nurseries along the coast of Texas was comprehensive; however, baseline (YOY) and unknown (sub-adults and adults) samples were plotted in ordination space to further evaluate whether all potential source populations were sampled. Only 2.6% of our unknown sample ($n = 4$) fell outside the 95% confidence ellipse of the baseline, suggesting that our baseline likely included all possible nurseries. Nevertheless, these 4 individuals were removed from the data set to assure that contribution estimates were not biased by nurseries not sampled (Hamer et al. 2005, Chittaro et al. 2009).

Ontogenetic variability in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can occur during the first year of life in marine fishes (Schloesser 2009), and thus the otolith isotopic composition of YOY red drum may not be homogenous throughout the carbonate matrix. In response, paired comparisons were run on whole otoliths and milled otolith cores from YOY red drum to determine whether the 2 approaches provided comparable measurements of otolith isotopic composition. No differences were

detected in paired comparisons of $\delta^{13}\text{C}$ in whole otoliths and cores from any of the regions investigated (paired t -test, $p > 0.05$). However, otolith core $\delta^{18}\text{O}$ was higher than whole otolith $\delta^{18}\text{O}$ for YOY red drum in the central and northern regions, being most pronounced in the north ($p < 0.05$). Otolith core $\delta^{18}\text{O}$ values for sub-adult and adult red drum were adjusted (NC, SC: $\delta^{18}\text{O} = 1.1$; N: $\delta^{18}\text{O} = 1.7$) using the mean difference between whole otolith and core from paired comparisons to properly adjust the unknown sample prior to mixed-stock analysis.

RESULTS

North to south gradients in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of YOY red drum were observed among bays and estuaries sampled, and 4 distinct regional groups were identified using natural variability in otolith isotopic composition (Fig. 4): North (N), Sabine Lake and East Galveston Bay; North-Central (NC), Christmas Bay and Matagorda Bay; South-Central (SC), Aransas Bay and Redfish Bay; and South (S), Laguna Madre (Table 1). Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of YOY red drum varied significantly among the 4 regions (ANOVA, $p < 0.01$), and univariate contrasts indicated that a region effect was present for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in 2001, 2002 and 2003 when year classes were analyzed separately (ANOVA, $p < 0.01$). Otolith $\delta^{13}\text{C}$ values increased along a north to south gradient, with values over 5.0‰ higher (enriched in ^{13}C) in the S than the N region. Mean otolith $\delta^{13}\text{C}$ values (all years pooled) by region

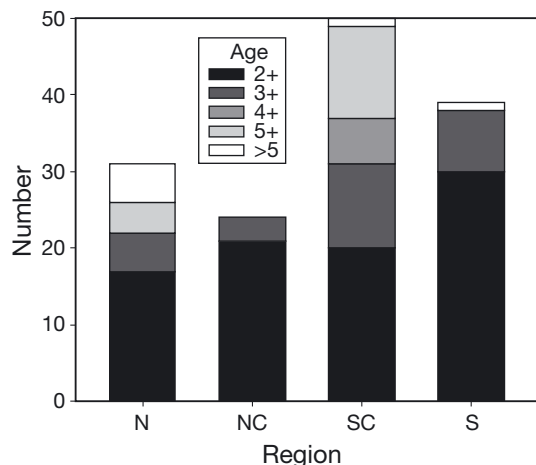


Fig. 3. *Sciaenops ocellatus*. Age-frequency distribution of sub-adult and adult red drum collected in 2003 from 4 sampling regions. Lengths converted to age based on Murphy & Taylor (1990). Age-2+ red drum represent individuals matched to 2001 baseline sample

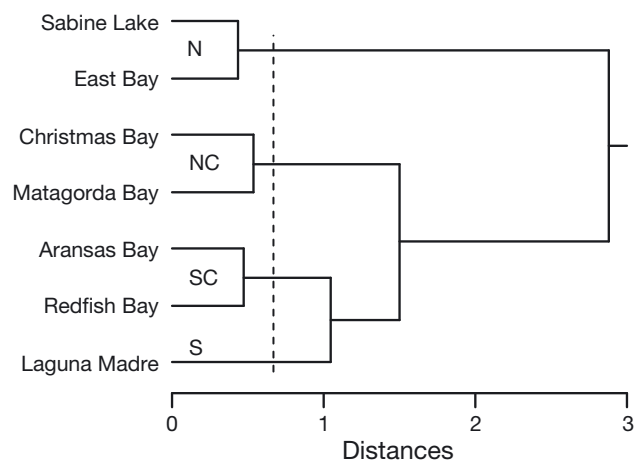


Fig. 4. *Sciaenops ocellatus*. Tree from hierarchical cluster analysis based on otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of young-of-the-year red drum collected from different regions in the northern Gulf of Mexico (year classes pooled). Results based on average linkage and normalized Euclidean distance. Four regional groupings were identified: North (N), North-Central (NC), South-Central (SC) and South (S)

were: N = $-5.9 \pm 1.9\%$, NC = $-3.3 \pm 1.7\%$, SC = $-2.3 \pm 1.5\%$ and S = $-0.6 \pm 1.9\%$. Similarly, a significant north to south trend was observed for otolith $\delta^{18}\text{O}$ and values were nearly 3.0% higher (enriched in ^{18}O) in the S relative to the N region. Mean otolith $\delta^{18}\text{O}$ values (all years pooled) by region were: N = $-3.2 \pm 1.2\%$, NC = $-1.8 \pm 0.5\%$, SC = $-1.0 \pm 0.4\%$ and S = $-0.5 \pm 0.8\%$.

Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of YOY red drum varied significantly among years within regions (ANOVA, $p < 0.01$; Fig. 5, Table 2), suggesting that water $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values within each region varied from year to year. Significant interannual variation in otolith $\delta^{13}\text{C}$ was detected in paired comparisons of YOY baseline samples in all 4 regions (Tukey's HSD, $p < 0.05$), while a significant difference in otolith $\delta^{18}\text{O}$ was observed between years in 3 (N, SC and S) of the 4 regions (Tukey's HSD, $p < 0.05$).

Cross-validated classification success from QDFA to the 4 regions was high for each year class of YOY red drum examined. Classification success was higher for YOY red drum collected in 2001 (92%) than either 2002 (82%) or 2003 (90%). Classification success for QDFA models based entirely on otolith $\delta^{18}\text{O}$ was higher (range across years = 76 to 88%) than models including only otolith $\delta^{13}\text{C}$ as a predictor variable (range across years = 57 to 76%), indicating that individually the resolving power of otolith $\delta^{18}\text{O}$ for discriminating regions was greater. However, classification success was highest for models including both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, indicating that both markers were useful for discriminating YOY red drum to regional nurseries. Although baseline values varied across years, overall cross-validated classification success to the 4 regions remained relatively high (77%) when the 3 year

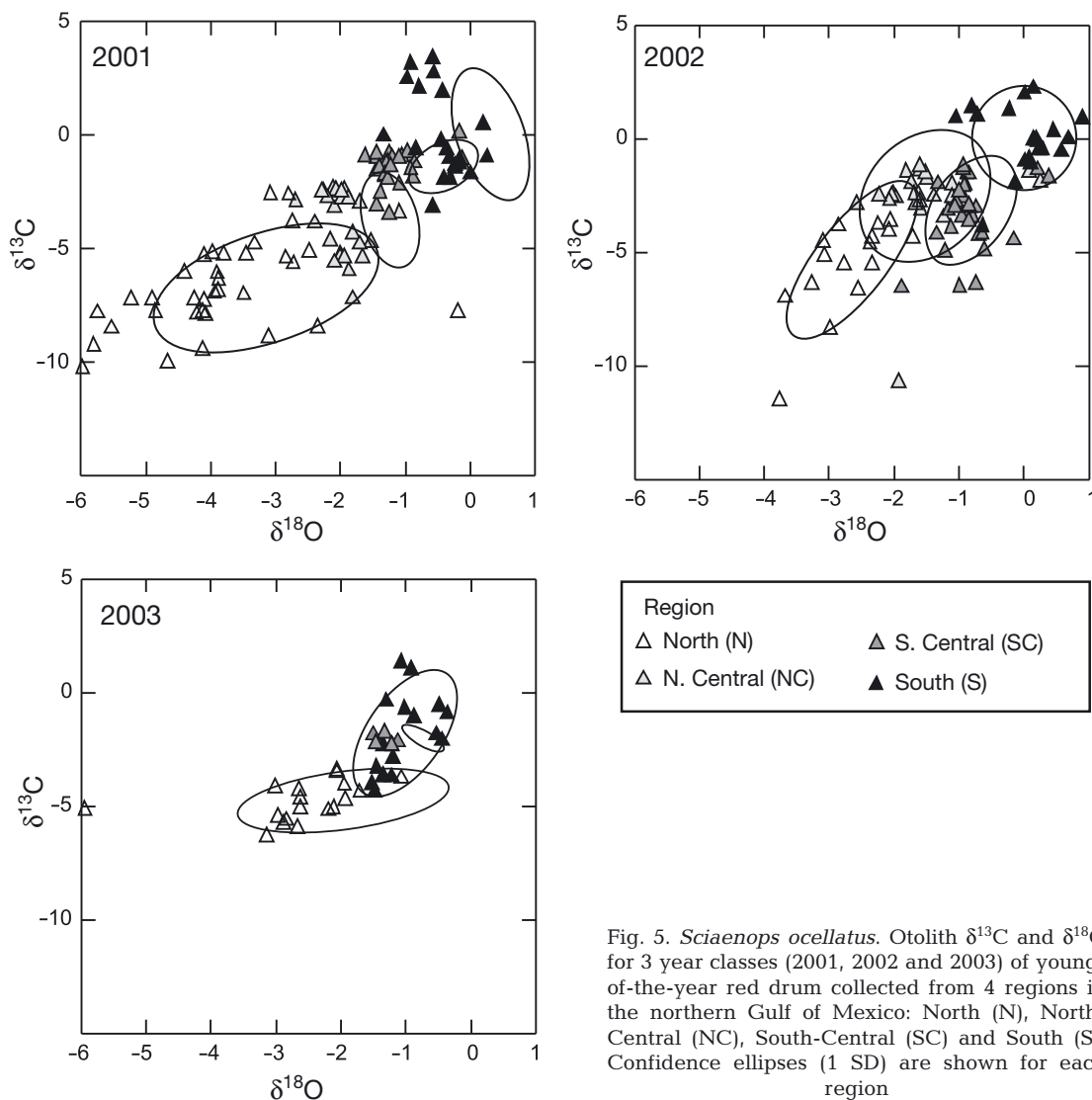


Fig. 5. *Sciaenops ocellatus*. Otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for 3 year classes (2001, 2002 and 2003) of young-of-the-year red drum collected from 4 regions in the northern Gulf of Mexico: North (N), North-Central (NC), South-Central (SC) and South (S). Confidence ellipses (1 SD) are shown for each region

Table 2. *Sciaenops ocellatus*. Mean \pm SD otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of young-of-the-year red drum by region (North [N], North-Central [NC], South-Central [SC] and South [S]) and year (2001, 2002 and 2003). nd: no data

Region	Year		
	2001	2002	2003
$\delta^{13}\text{C}$			
N	-6.7 \pm 1.9	-5.4 \pm 2.1	-4.8 \pm 0.8
NC	-3.8 \pm 1.4	-2.5 \pm 1.8	nd
SC	-1.4 \pm 0.8	-3.1 \pm 1.5	-2.0 \pm 0.2
S	0.0 \pm 1.9	0.0 \pm 1.4	-1.9 \pm 1.7
$\delta^{18}\text{O}$			
N	-3.9 \pm 1.1	-2.6 \pm 0.6	-2.6 \pm 1.0
NC	-2.0 \pm 0.3	-1.5 \pm 0.6	nd
SC	-1.2 \pm 0.4	-0.8 \pm 0.5	-1.3 \pm 0.1
S	-0.4 \pm 0.4	-0.1 \pm 0.5	-1.1 \pm 0.8

classes were pooled, indicating the baseline was relatively robust and likely suitable for predicting the origin of sub-adult and adult red drum whose first year of life was within a few years of the baseline period.

Otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of age-2+ red drum collected in 2003 from all 4 regions were matched to the 2001 baseline to determine their nursery origin (Fig. 6). Similar to YOY red drum, mean otolith core $\delta^{13}\text{C}$ of age-2+ red drum varied by region with values becoming higher with decreasing latitude: N = -4.3 \pm 1.8‰, NC = -2.9 \pm 1.1‰, SC = -1.7 \pm 1.2‰ and S = -1.1 \pm 1.5‰. Otolith core $\delta^{18}\text{O}$ values for age-2+ red drum were also highest and lowest in the S and N regions, respectively: N = -3.0 \pm 1.0‰, NC = -0.9 \pm 1.0‰, SC = -0.7 \pm 0.9‰ and S = -0.1 \pm 0.7‰. The general trend of increasing otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from northern to southern regions was also observed for older red drum with YOY periods outside our baseline (age-3+ or older, n = 59).

Direct maximum likelihood estimates of age-2+ red drum collected in 2003 and matched to the 2001 baseline (n = 89) indicated that the majority of sub-adult and adult red drum sampled in the SC and S regions were produced from the same areas (82 and 91 %, respectively), with limited exchange between these regions (Table 3). In the N and NC regions, percentages were lower of age-class matched red drum present in the same region occupied during the YOY period (54 and 47 %, respectively), and most of the remaining age-2+ red drum in both regions were produced from the next contiguous nursery to the south. In fact, the remaining age-2+ red drum in the N region were almost entirely of NC origin (42%), while in the

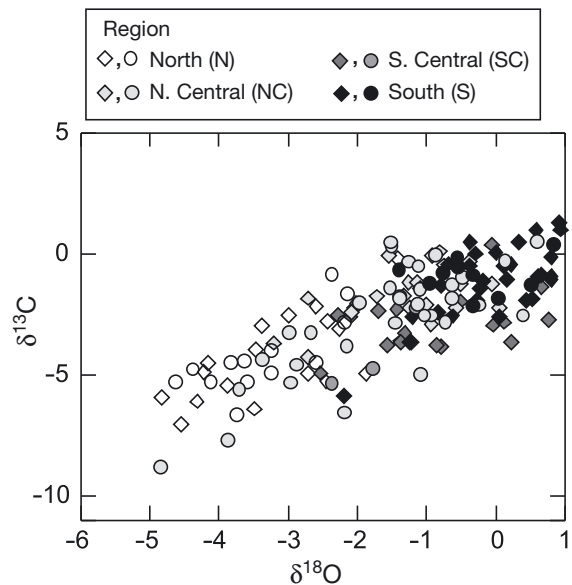


Fig. 6. *Sciaenops ocellatus*. Otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from sub-adult and adult red drum collected from 4 regions in 2003 in the northern Gulf of Mexico: North (N), North-Central (NC), South-Central (SC) and South (S). Otolith cores that fell outside the 95% confidence ellipse of the baseline (n = 4) were omitted from the plot. Age-2+ red drum matched to baseline are denoted by diamonds; circles represent individuals that could not be age-class matched

NC region the contribution from the SC region was 35%. Mixed-stock analysis was also performed on a group of age-3+ or older red drum (n = 59), with YOY periods outside the 2001 baseline period. In all 4 regions, the majority of sub-adult and adult red drum

Table 3. *Sciaenops ocellatus*. Estimates of natal origin (percent composition, \pm SD) of sub-adult and adult red drum collected from 4 regions (North [N], North-Central [NC], South-Central [SC] and South [S]) in the northern Gulf of Mexico. Otolith core $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of young-of-the-year (YOY) red drum from 2001 were used as the baseline to estimate the origin of age-2+ red drum with YOY periods that matched 2001 baseline (N = 89) and age-3+ or older red drum with YOY period outside baseline (N = 59). N: sample size. Percent values in **bold** denote sub-adult or adult red drum that originated from the same nursery as collection location

Region collected	N	Predicted origin			
		N	NC	SC	S
Age-class matched (age-2+)					
N	17	54.0 \pm 15.9	42.2 \pm 15.5	3.8 \pm 5.4	0.0 \pm 0.0
NC	21	0.0 \pm 0.0	47.1 \pm 21.2	34.9 \pm 30.4	18.0 \pm 15.4
SC	20	0.0 \pm 0.0	14.7 \pm 11.0	82.0 \pm 13.0	3.1 \pm 8.0
S	31	0.0 \pm 0.0	4.6 \pm 4.7	4.4 \pm 8.6	91.0 \pm 8.8
Outside baseline (age-3+ or older)					
N	14	58.9 \pm 15.6	31.2 \pm 19.5	9.9 \pm 11.6	0.0 \pm 0.0
NC	3	0.0 \pm 0.0	77.3 \pm 25.2	22.7 \pm 25.2	0.0 \pm 0.0
SC	32	11.5 \pm 6.5	21.0 \pm 9.0	50.7 \pm 16.9	16.9 \pm 13.9
S	10	0.0 \pm 0.0	0.0 \pm 0.0	1.5 \pm 10.5	98.6 \pm 10.5

were produced from the same region (range: 51 to 99 %) and, similar to the age-class matched individuals, the contribution of other nurseries was lowest in the S region (Table 3).

DISCUSSION

Spatial variation in otolith $\delta^{13}\text{C}$ was evident for YOY red drum with values increasing from north to south. Otolith $\delta^{13}\text{C}$ was highest for red drum collected in hypersaline waters of the S region (Laguna Madre), and positive relationships between salinity and measures of otolith $\delta^{13}\text{C}$ have been reported in other estuaries (Harrod et al. 2005, Kerr et al. 2007), supporting the observed pattern in our baseline values for YOY red drum. The relationship between salinity and otolith $\delta^{13}\text{C}$ observed along the Texas coast is likely regulated by freshwater inflow (precipitation), with more southerly locations (higher salinity) receiving less freshwater inflow, and thus less terrestrial carbon which lowers the $\delta^{13}\text{C}$ in the dissolved inorganic carbon (DIC) pool (Michener and Schell 1994). Differences in diet have also been shown to affect otolith $\delta^{13}\text{C}$ (Thorrold et al. 1997, Høie et al. 2004), and thus diet may be partly responsible for observed differences. In Texas, the areal coverage of seagrass increases from north to south, and its role as a primary source of organic matter is substantially higher in the south (Adair et al. 1994). Carbon isotope values in sediments and tissues of consumers in areas with significant seagrass coverage (e.g. Laguna Madre) reflect the inputs of these ^{13}C -enriched producers ($\delta^{13}\text{C} = -10$ to -12‰) relative to the north, where a large fraction of organic matter is derived from phytoplankton ($\delta^{13}\text{C} = -19$ to -21‰) or other sources of primary production such as salt marsh or benthic algae (Benedict et al. 1980, Herzka et al. 2001, Fry 2006, Fry et al. 2008). Therefore, it is possible that higher $\delta^{13}\text{C}$ values in the otoliths of YOY red drum from the south (seagrass dominated) compared to the north (seagrass limited) are related to the isotopic values of the dominant producers, albeit the direct effect of seagrass is likely minor because seagrass carbon is relatively refractory and most of the otolith carbon is expected to come from DIC in the water (Campana 1999). Although changes in $\delta^{13}\text{C}$ of the DIC pool related to freshwater inflow and, to a lesser extent, in $\delta^{13}\text{C}$ of the diet appear responsible for the observed gradient in otolith $\delta^{13}\text{C}$, changes in metabolism due to temperature or feeding related shifts (Thorrold et al. 1997, Høie et al. 2003) may also account for some of the observed variability.

Similar to otolith $\delta^{13}\text{C}$, a north–south gradient was observed for otolith $\delta^{18}\text{O}$ in YOY red drum, with higher values present in the hypersaline waters of the S

region and, to a lesser extent, the SC region relative to regions of high freshwater inflow in the north (N, NC). The observed pattern of increasing otolith $\delta^{18}\text{O}$ with increasing salinity has been reported in other studies, and results from the combined effects of evaporation (water enriched in ^{18}O) and freshwater inflow (rainwater depleted in ^{18}O) (Campana 1999). In previous studies, otolith $\delta^{18}\text{O}$ has been shown to increase by approximately 0.1 to 1.4 ‰ with salinity increasing by a practical salinity of 1 (e.g. Dufour et al. 1998, Bastow et al. 2002). Mean salinity in the S region of Laguna Madre (practical salinity ~35 to 40) is often 25 higher than sites in the N region (e.g. Sabine Lake, practical salinity ~10; Longley et al. 1994), which would translate to a difference in otolith $\delta^{18}\text{O}$ of 2.5 to 4.2 ‰ between the N and S regions using the $\delta^{18}\text{O}$ –salinity relationships described above. Mean otolith $\delta^{18}\text{O}$ was 2.7 ‰ higher in the S than N region for YOY red drum and falls within the predicted range, suggesting that processes influencing salinity may be largely responsible for spatial variation in otolith $\delta^{18}\text{O}$ values. Variability in otolith $\delta^{18}\text{O}$ of YOY red drum also may be linked to temperature-dependent fractionation, but an inverse relationship between otolith $\delta^{18}\text{O}$ and temperature is expected (Høie et al. 2004). For YOY red drum, a positive otolith $\delta^{18}\text{O}$ –temperature relationship was observed, with higher values for individuals from the warmer waters of the S region. Similar to the findings of Kerr et al. (2007), it appears that salinity was the dominant factor accounting for observed differences in otolith $\delta^{18}\text{O}$. The influence of temperature was likely negligible in the present study for the simple fact that temperature differences between the N and S regions are small (ca. 2 to 3 °C, Simons & Smith 2009; <http://co-ops.nos.noaa.gov>) relative to large (≥ 25) salinity differences (Orlando et al. 1991), which again are linked to regional differences in freshwater inflow (higher in the N region) and evaporation (higher in the S region).

Temporal variability in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was assessed by examining 3 cohorts of YOY red drum, and differences were detected among years for both stable isotopes. Interannual variability in the chemical composition of otoliths is well documented for trace elements and stable isotopes (Elsdon et al. 2008, Schloesser et al. 2009). Temporal shifts in baseline values often necessitate the matching of sub-adults or adults to juveniles from specific year classes (Gillanders 2005). In the present study, we observed that classification success to the 4 regions investigated was high when maximum likelihood estimates of origin were run separately by year. Moreover, discrimination of YOY red drum from the 4 regions in 2001, which served as the baseline for age-class matching of age-2+ red drum collected in 2003, was the highest of all

years examined (92%). Classification success declined when all 3 year classes were pooled (77%), suggesting that changes in environmental factors known to affect $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of water (e.g. rainfall, evaporation and temperature) varied among years. Of the 4 regions examined, interannual variability in otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of YOY red drum was most pronounced in the N region, which is consistent with the greater and more variable input of freshwater here relative to more southerly regions. In fact, the lowest otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the N region were observed in 2001 when freshwater inflow out of the main tributary (Sabine) in this region was highest of the 3 years examined (Texas Water Development Board 2007). The size and frequency of pulsed freshwater events in the N region were markedly higher than all other regions, with annual inflows (Sabine) being an order of magnitude higher than the S region (Laguna Madre) (ca. 12.0 and <1.0 million acre-ft [~ 14.8 to 1.2×10^9 m³], respectively; Texas Water Development Board 2007). This trend in freshwater input is consistent with the high degree of interannual variability observed for otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for YOY red drum from this region.

Milled otolith cores of sub-adult and adult red drum were matched to the baseline sample using a mixed-stock algorithm, and results clearly showed that a large fraction of age-2+ red drum from each of the 4 regions were produced from nurseries in the same region, suggestive of limited movement. Observed fidelity of sub-adult and adult red drum to natal sites may be due to localized retention or limited inter-estuary movement, which is common for species in the family Sciaenidae, including red drum (Baker & Matlock 1993, Murphy et al. 1998, Adams & Tremain 2000). Mark-recapture studies on red drum in the Gulf of Mexico and along the eastern seaboard of the US have shown that the majority of individuals originated from nurseries within the same estuary or region as the capture location (Osborn et al. 1982, Overstreet 1983, Nicholson & Jordan 1994). Moreover, Tremain et al. (2004) observed high site fidelity of red drum from a no-take zone in Florida, with over 95% of the recaptures occurring at the tagging location within the reserve. Genetic divergence of red drum across estuaries in the northern Gulf of Mexico has also been detected, but gene flow and stock mixing among regional estuaries is still assumed to be limited (Gold et al. 2001, Gold & Turner 2002). As a result, inter-estuary movements or straying behavior may be less common or on a smaller scale, particularly for young adults (~age-2+) that have only recently moved out of estuarine nursery areas.

An alternative explanation for the apparent fidelity of sub-adult and adult red drum to natal sites may be due to homing behavior. Evidence for natal homing is well established for anadromous species, including

certain clupeids (Walther et al. 2008), moronids (Waldman et al. 1996, Wingate & Secor 2007) and salmonids (Quinn 1993, Lohmann et al. 2008); nevertheless, few documented cases of homing exist for sciaenids and other estuarine-dependent taxa. Using otolith chemistry, Thorrold et al. (2001) reported natal homing rates of weakfish *Cynoscion regalis* to estuaries along the eastern seaboard to be from 60 to 81%, with the majority of mixing limited to adjacent estuaries. Similarly, Patterson et al. (2004) examined a small number of adult red drum (n=20) from a single bay in Florida and estimated that 75% originated from nurseries in the same bay. In the present study, estimates of potential homing to specific estuaries on the lower coast of Texas (S, SC regions) were relatively high and within or above the aforementioned range. More mixing occurred in the northern regions, with the majority of the migrants in each region originating from the adjacent region to the south, suggesting that most of the age-2+ or older red drum examined stayed within or in close proximity (<100 km) to their nursery sites. Alternatively, lower survival of migrants originating from outside nurseries may also explain the lower contribution rates and/or mixing of individuals from other regions. Although the dispersal potential of adult red drum is assumed to be high (Overstreet 1983), additional information on movement away from estuarine nurseries is needed to confirm that homing, rather than retention, was the primary behavior responsible for red drum being in tidal passes or coastal environments nearest to their putative nursery. The combined effects of localized retention and natal homing explain findings from tagging, genetics and otolith chemistry, but the degree to which each behavior is responsible for observed patterns remains unresolved. Moreover, red drum is long lived (>25 yr; Beckman et al. 1988, Murphy & Taylor 1990, Murphy & Crabtree 2001); therefore, our assessment was limited to the early adult phase. Homing behavior of marine fishes often varies as a function of age (e.g. Rooper et al. 2008a), suggesting that a wide range of adult age classes may be required to accurately depict the dispersive behaviors of red drum.

The relative value of presumed nurseries is commonly based on indirect measures of recruitment potential (Houde 2002), although such measures do not provide a means of determining actual contribution rates nor do they quantify levels of connectivity among estuarine ecosystems. Results presented here clearly demonstrate that otolith $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ represent viable markers of nursery origin that can be used to assess contribution rates of different nurseries to adult populations of red drum and possibly other estuarine-dependent fishes. Our findings suggest that mixing occurs among regional estuaries in the Gulf of Mexico,

but the majority of sub-adult and adult red drum appear to either remain in close proximity to their estuarine nurseries or return to natal areas to spawn following a dispersive phase. Either way, fishery yields of red drum appear directly linked to local production, with supplementary contributions from adjacent estuaries. Local-scale effects (e.g. pollution, fishing pressure and freshwater inflow) will therefore influence population dynamics of red drum within a specific region, signifying that spatially explicit management may be needed at smaller scales (i.e. bays or estuaries) to facilitate desired levels of production throughout the geographic range of this species.

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