Dispersive Behaviors of Black Drum and Red Drum: Is Otolith Sr:Ca a Reliable Indicator of Salinity History?

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ABSTRACT: We tested the hypothesis that strontium:calcium (Sr:Ca) in otoliths are reflective of environmental salinity experienced by two estuarine fishes during early life. Laboratory and field experiments were performed to examine the effects of salinity and temperature on Sr:Ca in otoliths of black drum (*Pogonias cromis*) and red drum (*Sciaenops ocellatus*). Otolith Sr:Ca of juveniles reared at four salinities (5‰, 15‰, 25‰, 35‰) differed significantly for *P. cromis* while no salinity effect was observed for *S. ocellatus*. Otolith Sr:Ca of both species were not affected by temperature (23°C and 30°C), suggesting that partitioning of Sr in otoliths of these taxa is constant over the temperature range examined. A field verification trial was conducted for *P. cromis* and a positive relationship between otolith Sr:Ca and ambient salinity was observed, even though the percent variability explained was modest. A series of Sr:Ca point measurements were taken from the core to the edge of the otoliths of wild *P. cromis* and *S. ocellatus*, and otolith Sr:Ca chronologies of both species showed conspicuous declines during the first few months of life. While Sr:Ca chronologies of both species suggest that ingress is associated with a reduction in otolith Sr:Ca, inconsistencies in laboratory and field experiments intimate that Sr uptake in the otolith may be insensitive to salinity and regulated by other factors (aqueous chemistry, ontogenetic shifts in habitat, or physiology). Results from early life history transects of otolith Sr:Ca conform to expected patterns of estuarine ingress-egress during early life and indicate that the approach may be useful for detecting large-scale habitat transitions (marine to estuarine habitats).

Introduction

Physicochemical gradients within estuaries vary over spatiotemporal scales creating a mosaic of environmental conditions (Alongi 1998; Ley et al. 1999; Able et al. 2001). Salinity is often regarded as the primary chemical scalar within estuaries since these systems are characterized by pronounced spatial and temporal fluctuations in marine and freshwater input. Estuarine-dependent fishes are regulated to some degree by salinity since this parameter affects metabolic costs, physiological performance, and growth (Aristizabal 1992; Lankford and Targett 1994; Swanson 1998). Predators and prey often segregate along salinity gradients within an estuary, leading to spatial changes in behaviors of associated taxa (Baltz et al. 1998; Peterson et al. 2000), so salinity is often used to delineate habitats and may directly or indirectly influence patterns of dispersal and recruitment success of fishes inhabiting estuaries (e.g., Lankford and Targett 1994; Kimura et al. 2000; Gelwick et al. 2001).

Recent advances in the microanalysis of otolith strontium (Sr) have afforded researchers a useful method for tracing salinity history and reconstructing dispersive behaviors of estuarine-dependent fishes (Limburg 1995; Kimura et al. 2000; Secor and Rooker 2000). The technique is based on the premise that otolith Sr, measured as strontium:calcium (Sr:Ca), varies as a function of ambient salinity. The underlying mechanism is that aqueous Sr:Ca is directly proportional to that in the otolith (Bath et al. 2000), and in estuaries, changes in aqueous Sr:Ca can be substantial and are typically described by a power function with a minimum value in freshwater (Surge and Lohmann 2002). Estimates of otolith Sr:Ca within and among daily or seasonal (annular) increments can be used to reconstruct salinity history of individual fish. While the use of otolith Sr for reconstructing environmental histories is well recognized and reported (Secor and Rooker 2000), the fundamental question of whether fish otoliths can function as reliable indicators of salinity history remains largely untested.

The response of otolith Sr:Ca over a range of known environmental conditions is rarely measured empirically (Secor and Rooker 2000). Of the validation studies conducted, only a few have attempted to contrast both laboratory-based and field-based estimates of salinity and temperature ef-

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fects (Secor et al. 1995; Townsend et al. 1995). Substantial inconsistencies have been reported in the literature regarding the effects of both salinity and temperature, and there has been disagreement over the influence of each factor in modifying otolith Sr:Ca (Campana 1999). The purpose of this study was to examine the capability of otolith Sr:Ca for measuring spatial-temporal patterns of estuarine dispersal during the early ontogeny of two estuarine-dependent fishes. Our primary objective was to experimentally assess the importance of salinity (independent of water chemistry or aqueous Sr:Ca) and temperature on Sr integration in otoliths of black drum (*Pogonias cromis*) and red drum (*Sciaenops ocellatus*) in both laboratory and field trials. We also investigated otolith Sr:Ca chronologies of wild *P. cromis* and *S. ocellatus.*

Materials and Methods

Due to differences in the timing of estuarine residency, it was not possible to run laboratory trials on *P. cromis* and *S. ocellatus* concurrently. Juvenile *P. cromis* used for laboratory trials were collected from Galveston Bay, Texas. Juveniles were seined from known nursery areas and individuals ranged in size from 75 to 129 mm standard length (SL). Insufficient numbers of *S. ocellatus* were collected in 2000 for the experimental trial and, as a result, juveniles (range: 28–54 mm SL) were obtained from the Sea Center Texas hatchery (Texas Parks and Wildlife Department) located in Lake Jackson, Texas. Both species were held in large holding tanks for approximately 10–15 d prior to experimentation. Individuals used for constructing otolith Sr:Ca life history chronologies were collected from three estuaries in Texas. Polyhaline to euhaline conditions characterized all three estuaries and annual means from daily estimates of salinity showed the Christmas Bay (31°4′E) and Aransas Bay (29°2′E) maintained higher salinity than Galveston Bay (23°6′E). *P. cromis* (BD 91, 93, 96, 98, 99, 102) were collected in September 1999 from Christmas Bay (29°04′N, 95°12′W), while *S. ocellatus* were collected in February 2000 from either Galveston Bay (RD 20, 21, 23; 29°16′N, 94°57′W) or Aransas Bay (RD 76, 88, 79; 28°53′N, 97°08′W). Wild-caught individuals ranged in age from approximately 4–5 and 6–8 mo for *S. ocellatus* and *P. cromis,* respectively.

Lab Validation Trials

Experiments using controlled levels of salinity and temperature were conducted separately for each species. At the beginning of an experiment, similar-sized individuals were marked using alizarin complexone (100 mg l^{-1} for 2 h), producing a discernible mark on the otolith. Randomly selected juveniles were acclimated over a 24-h period and stocked (5 per 40-l tank) at four salinities (5‰, 15‰, 25‰, 35‰) and two temperatures (23°C and 30°C). Salinity and temperature treatment levels were selected to represent conditions typically experienced by *P. cromis* and *S. ocellatus* in Texas estuaries during the first year of life. Only the 15‰ and 25‰ salinity treatments were investigated at the higher temperature (30°C). Salinity and temperature were monitored daily during laboratory validation trials and mean values for each treatment were within 1‰ or 1°C of target value; standard deviation of observed values within salinity and temperature treatments ranged 0.7–1.3‰ and 0.2–1.0°C, respectively. Three replicate tanks were established for each treatment level (total = 18 tanks). Experimental salinities were established by diluting seawater (35‰) with filtered water (2 MΩ cm^{-1}) at the Texas A&M University at Galveston/National Oceanic and Atmospheric Administration-National Marine Fisheries Service rearing facility. Aqueous Sr:Ca was assumed to be equivalent across treatments. Temperature differences were created by lowering ambient temperature in the rearing facility to 23°C and increasing temperatures in designated tanks to 30°C using heaters. Both species were reared in experimental conditions for 14 d. All captive fishes were fed ad libitum an artificial diet (Rangen, Inc).

Field Validation Trials

Juvenile *P. cromis* were collected from natural habitats, marked with alizarin complexone, and placed in 1.2-m^3 cages constructed of a PVC frame and covered with 1.25-cm nylon mesh. Individuals were randomly assigned to cages in three locations in Galveston, Texas: the mouth of Trinity River in Trinity Bay (29°45′N, 94°42′W), Kemah Cove, Galveston Bay (29°33′N, 95°02′W), and 6 miles offshore from the Galveston Ship Channel on production platform GA-150L (29°13′N, 94°38′W). Sites were selected to represent mesohaline (mean: 8.8‰), polyhaline (mean: 22.0‰), and euhaline (mean: 32.0‰) conditions, respectively. While this experiment contained a wide range of salinities, variation in water chemistry (Sr:Ca) was expected to be small, on the order of 2–3 mmol mol^{-1} (based on observed Sr:Ca in water at 8‰ and 32‰; Surge and Lohmann 2002). Individuals were held in cages for 2 wk, and temperature and salinity were recorded at each site every 3–4 d during the trial. Due to the lack of significant findings for *S. ocellatus* in the laboratory trial, a field validation experiment was not conducted.

Otolith Sr:Ca Analysis

Three (*P. cromis*) or four (*S. ocellatus*) fish were used from each tank for otolith Sr:Ca analysis. Oto-

liths were removed, cleaned, and set in epoxy resin. Transverse sections containing the core were cut from each otolith using a low-speed diamond blade saw. Thin sections were mounted to a slide with thermoplastic cement and polished using wet-dry sandpaper and a polishing cloth with 0.3 μm alumina polishing compound. Polished thin sections were carbon coated prior to elemental analysis to reduce charging. Elemental concentrations of Sr and Ca in otoliths were determined by Wavelength Dispersive X-ray Spectrometry (WDS) using a JEOL JXA-8900 electron probe micro-analyzer at the Central Facility for Microanalysis, University of Maryland, College Park, Maryland. Calcite and strontianite standards were used during each session. An area of 100 μm^2 (approximately 10 μm diam) constituted one microprobe sample and points were scanned using nominal beam diameter with an accelerating voltage of 25 kV and current of 20 nA. Peak Sr count time was 30 s, and peak Ca count time was 10 s. Mean detection limits of calcium oxide and strontium oxide were 70 (range: 50–94) and 93 (range: 68–106) ppm, respectively. In transverse otolith sections, analysis of the marginal growth increment was conducted by analyzing 4–5 points (approximately 10 μm diam) between the alizarin mark and otolith margin along the edge of the section from the sulcus to the ventral tip. Otolith Sr:Ca was estimated for each individual by taking the mean of all points assayed. Points were later identified with light microscopy as burn marks in the carbon coating that could be referenced to the alizarin mark. In the analysis of life history chronologies of otolith Sr and Ca, point measures from the core to the edge along the ventral axis of the section were analyzed. It was observed that with a minimum spacing of 16 microns there was no apparent overlap in burn marks between adjacent points; this minimum spacing was used for all analyses. Number of points analyzed for life history chronologies of otolith Sr:Ca ranged from 70 to 100 and were evenly spaced. Since individuals ranged in age approximately 4–8 mo, successive probe points corresponded to periods of roughly 2–4 d (assuming constant linear growth of the otolith).

DATA ANALYSIS

For laboratory trials, individual fish were used to assess the effects of salinity and temperature on otolith Sr:Ca. Individual fish in each tank were not independent, but treated as experimental units for statistical testing. Repeated measures analysis of variance (ANOVA) was used to model the effects of temperature and salinity, and independence of experimental units was not assumed with this analysis (Underwood 1999). The repeated measures approach allowed us to model correlation between fish within a given experimental tank. Regression analysis was used to model the effects of salinity on otolith Sr:Ca for pooled laboratory and field data of *P. cromis*. Before statistical testing, residuals were examined for normality and homogeneity among factor levels. Within group distribution and variance were examined and natural log transformations were used when necessary to meet parametric assumptions. A significance level (α value) of 0.05 was used for all trials.

Sr:Ca life history chronologies of wild specimens were examined by plotting Sr:Ca of point measures taken from the core to margin of the otolith. Locally weighted scatterplot smoothing (LOWESS regression analysis) was then used to evaluate functional relationships between otolith Sr:Ca and otolith radius (Trexler and Travis 1993). Smoothing weight or tension used for time series data was set at two levels (0.1 and 0.5). Tension determined the stiffness of the smoothing function and ranges from 0 to 1 (Wilkinson et al. 1996).

Results

VALIDATION TRIALS

In laboratory trials, otolith Sr:Ca varied significantly across salinity treatment levels for *P. cromis* ($p < 0.001$). Otolith Sr:Ca of *P. cromis* were positively associated with salinity (Fig. 1a, Table 1). Ratios ranged from 2.34 mmol mol^{-1} at 5‰ to 3.06 mmol mol^{-1} at 35‰. Ratios were lower (1.53–2.55 mmol mol^{-1}) for *S. ocellatus,* and no effect of salinity on otolith Sr:Ca was observed ($p = 0.068$; Fig. 1b, Table 1). Otolith Sr:Ca ratios of both species were not affected by temperature: *P. cromis* $p = 0.156$ and *S. ocellatus* $p = 0.210$ (Fig. 2).

Findings from the field enclosure experiment concurred with results from controlled experiments. Otolith Sr:Ca of *P. cromis* were positively related to ambient salinity ($p = 0.045$, Fig. 3). Sr:Ca in the otoliths of *P. cromis* were lowest at the mesohaline site (8.8‰) and highest for individuals caged at the euhaline site (32.0‰). Sr:Ca increased by approximately 0.014 mmol mol^{-1} per ‰ increase in ambient salinity. ANCOVA results indicated that the response of otolith Sr:Ca to salinity was similar for laboratory and field trials ($p = 0.564$). Regression analysis of pooled laboratory and cage data showed that otolith Sr:Ca of *P. cromis* increased at a rate of approximately 0.020 mmol mol^{-1} per ‰ increase in salinity (Fig. 3). Based on inspection of 95% confidence intervals, changes in salinity greater than 10‰ were required to produce a significant change in mean otolith Sr:Ca.

OTOLITH SR:CA LIFE HISTORY CHRONOLOGIES

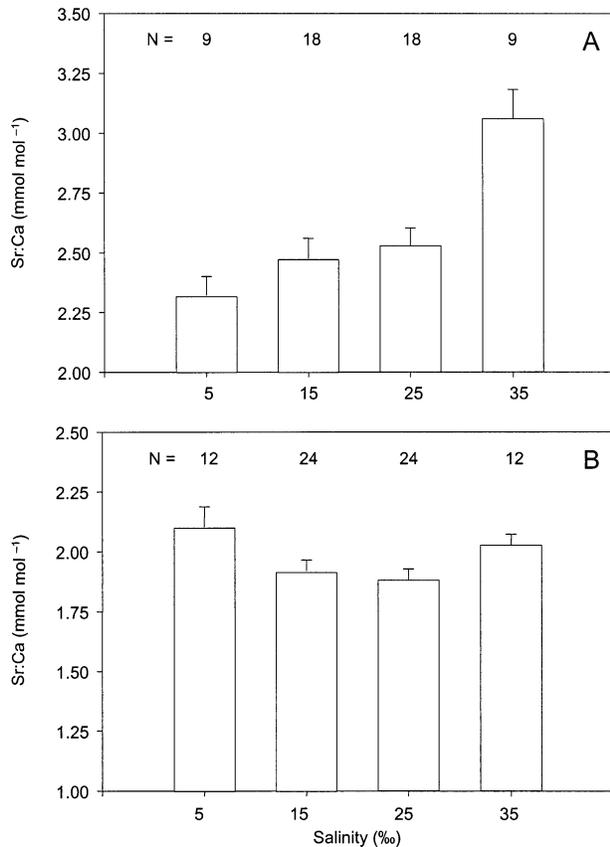Otolith Sr:Ca of wild *P. cromis* ranged in amplitude from approximately 2.0 to 2.5 mmol mol^{-1}

Fig. 1.   Mean Sr:Ca (±SE) of otoliths from A) black drum (*Pogonias cromis*) and B) red drum (*Sciaenops ocellatus*) reared at four salinities (5‰, 15‰, 25‰, 35‰) in the laboratory.

TABLE 1.   Repeated measures ANOVA results for main effects of salinity and temperature for black drum (*Pogonias cromis*) and red drum (*Sciaenops ocellatus*) reared at four salinities (5‰, 15‰, 25‰, 35‰) and two temperatures (23°C and 30°C) in the laboratory.

Source	SS	df	MS	F	p
Pogonias cromis					
Between subjects					
Salinity	3.188	3	1.063	13.010	0.000
Temperature	0.185	1	0.185	2.263	0.156
Error	1.062	13	0.082		
Within subjects					
Tank	0.365	2	0.183	1.889	0.171
Tank × salinity	0.764	6	0.127	1.317	0.285
Tank × temperature	0.746	2	0.373	3.858	0.034
Error	2.513	26	0.097		
Sciaenops ocellatus					
Between subjects					
Salinity	0.674	3	0.225	3.032	0.068
Temperature	0.129	1	0.129	1.741	0.210
Error	0.964	13	0.074		
Within subjects					
Tank	0.062	3	0.021	0.338	0.798
Tank × salinity	0.154	9	0.017	0.283	0.976
Tank × temperature	0.023	3	0.008	0.126	0.944
Error	2.363	39	0.061		

for four of six individuals (BD 91, 93, 96, 102; Fig. 4). Otolith Sr:Ca of *P. cromis* initially declined and ratios were lowest in the middle section of the otolith transect (0.2–0.4 mm) for several individuals (BD 91, 93, 96, 102); BD 98 showed significantly lower otolith Sr:Ca (1.5–2.2 mmol mol^{-1}). Otolith Sr:Ca of *P. cromis* in most individuals showed a slightly increasing trend from the middle section to the margin of the otolith, except for BD 99, which showed a sharply decreasing trend. Using the regression from the laboratory and field validation trials, lifetime salinity (mean of all salinity from Sr:Ca) of wild *P. cromis* was estimated to range from 8.0 to 19.6 (SD = 6.1–8.3).

More consistent patterns of otolith Sr:Ca were evident for wild *S. ocellatus* with a conspicuous drop in ratios during early life for all individuals (Fig. 5). Otolith Sr:Ca peaked near the core of the otolith for all individuals assayed and ratios near the core ranged from 2.3 to 2.8 mmol mol^{-1} with the highest values observed for individuals from Aransas Bay (RD 76, 77, 79). Interestingly, otolith Sr:Ca for the latter half of the life history chronology

were substantially lower than levels observed in laboratory reared *S. ocellatus*. Otolith Sr:Ca near the margin approached 1.0 mmol mol^{-1} for RD 23, 76, and 79.

Discussion

Otolith Sr:Ca are commonly used to infer past environments in which a fish lived, even though there is continuing disagreement over the validity of the approach (Campana 1999). Our response of otolith Sr:Ca to changing salinity in the laboratory was not consistent between the two sciaenids tested. We observed a positive relationship between otolith Sr:Ca and salinity for *P. cromis* in empirical and field trials but no difference in otolith Sr:Ca among salinity treatments was observed for *S. ocellatus*. While variable results from empirical trials seems to indicate that Sr uptake in otolith may not be linked strongly to salinity, otolith Sr:Ca chronologies of wild *P. cromis* and *S. ocellatus* showed patterns that agree with expected patterns of estuarine ingress or egress during early life.

In earlier work by Hoff and Fuiman (1995), the effect of salinity on otolith Sr:Ca of juvenile *S. ocellatus* was examined over a 10–40‰ range. Similar to Hoff and Fuiman (1995), we diluted seawater with deionized water to create salinity treatments and no effect of salinity on otolith Sr:Ca was observed in either study. While dilution lowers the concentrations of Ca and Sr, the Sr:Ca would be
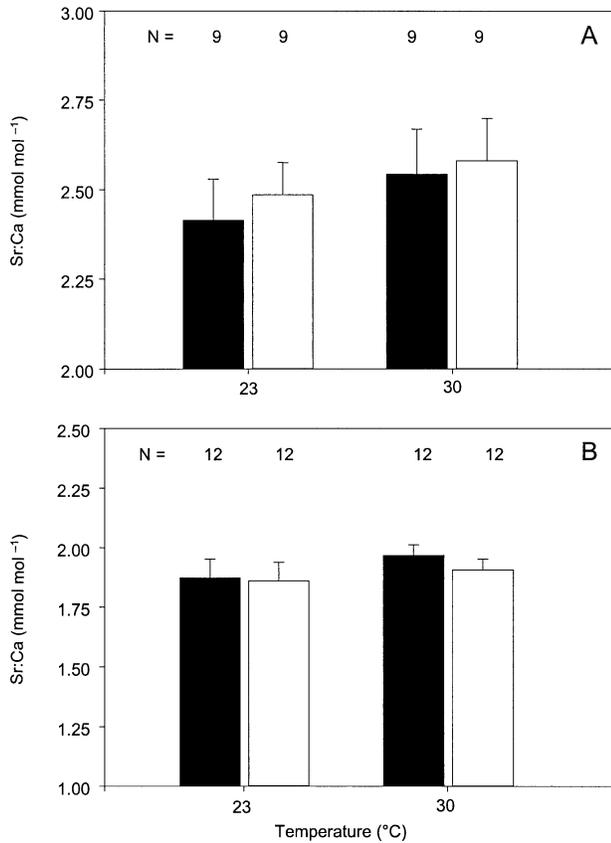
Fig. 2. Mean Sr:Ca (± SE) of A) of otoliths from black drum (*Pogonias cromis*) and B) red drum (*Sciaenops ocellatus*) reared at two temperatures (23°C and 30°C) in the laboratory. Temperature trials were conducted at two salinities: 15‰ (black bars) and 25‰ (open bars).
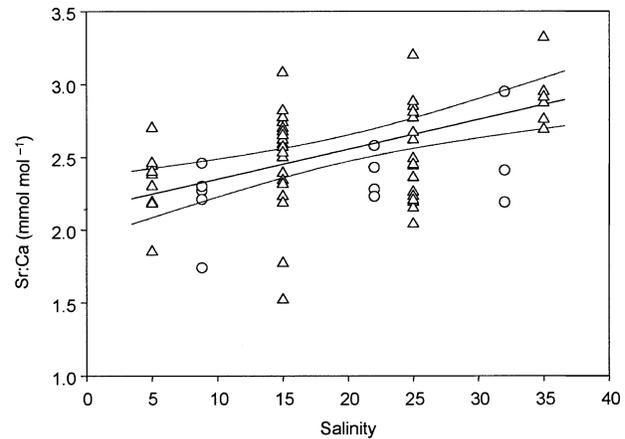

Fig. 3. Otolith Sr:Ca of black drum (*Pogonias cromis*) from laboratory (triangle) and field (circle) trials as a function of salinity. Simple linear regression plot with 95% confidence interval is shown. Linear equation: otolith Sr:Ca = 2.134 + 0.019 salinity; $r^2 = 0.24$.

the same in all treatments which is similar to levels experienced by these taxa in polyhaline to euhaline regions of the estuary where aqueous Sr:Ca changes gradually with salinity. The results of no treatment effect may be expected based upon recent findings that demonstrate that otolith Sr:Ca are linked directly to aqueous Sr:Ca (Bath et al. 2000; Milton and Chenery 2001).

As with *S. ocellatus,* we expected that aqueous Sr:Ca was constant across salinity treatments for *P. cromis* in the laboratory. The significant salinity treatment effect in both the laboratory and field trials suggests that salinity (independent of water chemistry) or some other factor that is correlated with salinity (e.g., osmoregulation or other metabolic process) modifies the partitioning of Sr into otoliths of *P. cromis*. Our results appear to contradict research from geochemical studies on biogenic calcium carbonates (corals, bivalves; e.g., de Villiers et al. 1994; Lea et al. 1999) that suggest aqueous Sr:Ca will be the primary determinant of otolith Sr:Ca. The finding of a salinity effect

independent of water chemistry (i.e., aqueous Sr:Ca) must be interpreted cautiously. Although significant, natural variation in otolith Sr:Ca explained by salinity through regression analysis was relatively low for both laboratory and field trials (25% and 23%, respectively). Salinity or some correlate of salinity may have influenced otolith Sr:Ca of *P. cromis* but this observation does not indicate that salinity is the primary determinant of otolith Sr:Ca.

Apart from salinity, Sr deposition in biogenic calcium carbonate is dependent upon temperature (de Villiers et al. 1995; Townsend et al. 1995; Klein et al. 1996). Temperature sensitivity of otolith Sr:Ca has been observed for many taxa, most notably for species inhabiting colder water (Radtke 1989; Townsend et al. 1992, 1995). Townsend et al. (1992) postulated that physiological discrimination of Sr in otoliths relaxes at low temperatures. Campana (1999) tested this hypothesis using meta-analysis by regressing slopes of published values from Sr:Ca versus temperature relationships against mean experimental temperature. A significant relationship was observed suggesting that Sr:Ca ratios decrease with increasing temperatures at low temperatures ($\leq 10°C$), and increase with temperature at high temperatures. Only experiments conducted in colder waters (10°C) produced slopes significantly different from zero. Uncoupling of the otolith Sr:Ca temperature relationship at higher temperatures appears to be relatively common in the literature and this may be due to integrated effects of matrix formation and calcification rate (Campana 1999). Bath et al. (2000) observed a significant positive association between temperature (20°C and 25°C) and otolith Sr:Ca in another
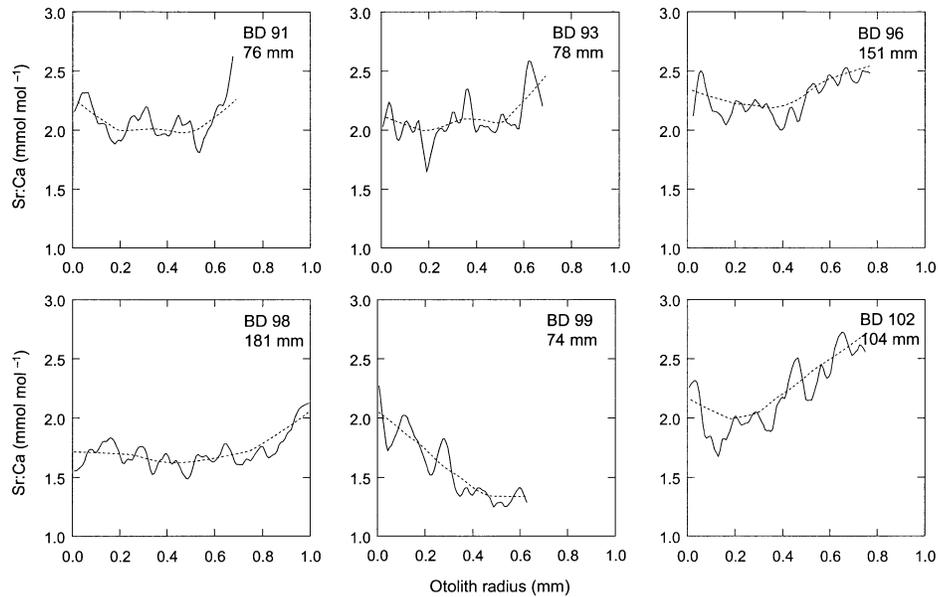
Fig. 4.   Otolith Sr:Ca life history chronologies of black drum (*Pogonias cromis*) from Christmas Bay, Texas. Sr:Ca were scanned along a transect from the core (otolith radius = 0) to the margin of the otolith. Two levels of tension for scatterplot smoothing (LOWESS regression) were used: 0.1 (solid line) and 0.5 (dashed line). Standard length (mm) provided for each individual.

sciaenid, spot (*Leiostomus xanthurus*). Experiments reported here for two sympatric sciaenids failed to show a significant temperature effect across a similar range of temperatures and support the idea that the otolith Sr:Ca-temperature relationship may decouple at higher temperatures. Still, conspicuous declines in otolith Sr:Ca chronologies of

wild *S. ocellatus* were observed and possibly linked to temperature shifts since these fall settlers may experience low temperatures (<20°C) during the winter and these conditions were not assessed empirically in this study.

Although findings from the empirical trials differed, otolith Sr:Ca chronologies of both species
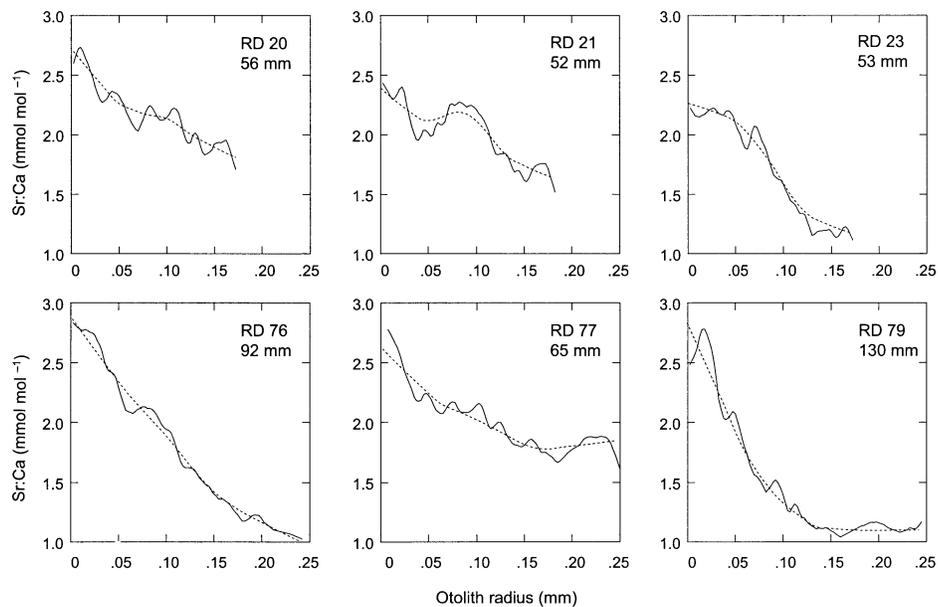

Fig. 5.   Otolith Sr:Ca life history chronologies of red drum (*Sciaenops ocellatus*) from Galveston Bay and Aransas Bay, Texas. Sr:Ca were scanned along a transect from the core (otolith radius = 0) to the margin of the otolith. Two levels of tension for scatterplot smoothing (LOWESS regression) were used: 0.1 (solid line) and 0.5 (dashed line). Standard length (mm) provided for each individual.

agree with expected patterns of movement during early life. Studies conducted in the Gulf of Mexico and eastern coast of the U.S. indicate that young *P. cromis* move into low salinity regions of the estuary (e.g., tidal creeks, rivers, secondary bays) during the winter as post-larvae or juveniles and spend several month in these habitats before migrating to higher salinity zones (Price and Schlueter 1985; Peters and McMichael 1990). In Florida, juvenile *P. cromis* moved from tidal creeks and secondary bays to passes and nearshore waters of the Gulf of Mexico at approximately 100–200 mm (Peters and McMichael 1990). This pattern of ingress followed by egress would take the form of a hyperbola with elevated Sr:Ca at each end (i.e., core and margin of otolith). Otolith Sr:Ca life history chronologies of several *P. cromis* followed this pattern (BD 91, 93, 96, 102), suggesting patterns of ingress followed by egress occur for *P. cromis* inhabiting estuaries in Texas. Conspicuous shifts in otolith Sr:Ca chronologies were also evident for wild *S. ocellatus,* indicative of a major shift in environmental conditions during early life. Larval *S. ocellatus* often spend the first month of life (August–October) in nearshore waters or areas near tidal passes before entering primary and secondary bays (Peters and McMichael 1987; Comyns et al. 1989). Once in the estuary, juveniles remain in these nursery grounds for several months (Rooker and Holt 1997; Rooker et al. 1998; Geary et al. 2001). Otolith Sr:Ca chronologies of all *S. ocellatus* examined showed a conspicuous decline during early life, corresponding with spatial life history patterns and expected gradients (albeit minor) in aqueous Sr:Ca. Whether the otolith Sr:Ca patterns occur due to water chemistry, salinity (independent of water chemistry), temperature, or a combination of factors, our results on both taxa support the interpretation of broad-scale movements between coastal and estuarine habitats.

In addition to physicochemical parameters, habitat-induced or developmentally-induced variation may be responsible for observed Sr:Ca patterns of wild *P. cromis* and *S. ocellatus.* Spatial shifts (coastal habitat to estuary) may influence environmental exposure to prey type and food availability that may influence Sr uptake (Farrell and Campana 1996; Kennedy et al. 2000). Ontogenetic shifts in growth rate, metabolic rate, or condition also occur during early life and these physiological changes have been shown to alter deposition of elements in otoliths by way of changes in metal binding capacity or protein mediated discrimination (Kalish 1989; Friedland et al. 1998; Arai et al. 2000). As a result, observed patterns of otolith Sr:Ca from the core to the margin of the otolith may be affected by ontogenetic shifts in habitat or physiology, and may not be linked simply to changes in salinity or Sr:Ca gradients.

Significant differences across salinity treatments in laboratory and field trials for *P. cromis* appear to indicate that salinity or some factor correlated with salinity may be an important determinant of otolith Sr:Ca. Otolith Sr:Ca in experimental trials on *S. ocellatus* also support the assertion that otolith Sr:Ca is linked to water chemistry (Sr:Ca water). These results demonstrate that mechanisms for modifying otolith Sr:Ca patterns may vary between closely related species, and precaution must be exercised when inferring environmental histories without further laboratory validation studies. While mechanisms responsible for Sr uptake in these taxa were not resolved in this study, otolith Sr:Ca chronologies of wild individuals were associated with patterns of estuarine ingress or egress during early life, suggesting the approach has promise for detecting large-scale habitat transitions (e.g., marine to estuarine habitats). Interactions among aqueous Sr:Ca, salinity (independent of water chemistry), temperature, and ontogeny must be examined comprehensively before the utility of the approach for detecting movement within the estuary or across major salinity gradients can be effectively applied.

Literature Cited

Able, K. W., D. M. Nemerson, R. Bush, and P. Light. 2001. Spatial variation in Delaware Bay (USA) marsh creek fish assemblages. *Estuaries* 24:441–452.

Alongi, D. M. 1998. Coastal Ecosystem Processes. CRC Press, LLC, New York.

Arai, T., T. Otake, and K. Tsukamoto. 2000. Timing of metamorphosis and larval segregation of the Atlantic eels *Anguilla rostrata* and *A. anguilla,* as revealed by otolith microstructure and microchemistry. *Marine Biology* 137:39–45.

Aristizabal, A. E. O. 1992. Effects of salinity and weight on routine metabolism in the juvenile croaker, *Micropogonias furnieri* (Desmarest 1823). *Journal of Fish Biology* 40:471–472.

Baltz, D. M., J. W. Fleeger, C. F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: Factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environmental Biology of Fishes* 53:89–103.

Bath, G. E., S. R. Thorrold, C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 2000. Strontium and barium uptake in aragonitic otoliths of marine fishes. *Geochimica et Cosmochimica Acta* 64:1705–1714.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. *Marine Ecology Progress Series* 188:263–297.

Comyns, B. H., J. Lyczkowski-Shultz, C. F. Rakocinski, and J.

P. STEEN, JR. 1989. Age and growth of red drum larvae in the northcentral Gulf of Mexico. *Transactions of the American Fisheries Society* 118:159–167.

DE VILLIERS, S., B. K. NELSON, AND A. R. CHIVAS. 1995. Biological controls on coral Sr:Ca and $\delta^{18}O$ reconstructions of sea surface temperatures. *Science* 269:1247–1249.

DE VILLIERS, S., G. T. SHEN, AND B. K. NELSON. 1994. The Sr:Ca-temperature relationship in coralline aragonite: Influence of variability in (Sr:Ca) seawater and skeletal growth parameters. *Geochimica et Cosmochimica Acta* 58:197–208.

FARRELL, J. AND S. E. CAMPANA. 1996. Regulation of calcium and strontium deposition on the otoliths of juvenile tilapia, *Oreochromis niloticus*. *Comparative Biochemistry and Physiology* 115:103–109.

FRIEDLAND, K. D., D. G. REDDIN, N. SHIMIZU, R. E. HAAS, AND A. F. YOUNGSON. 1998. Strontium:calcium ratios in Atlantic salmon (*Salmo salar*) otoliths and observations on growth and maturation. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1158–1168.

GEARY, B. W., J. R. ROOKER, AND J. W. WEBB. 2001. Utilization of saltmarsh shorelines by newly settled sciaenids in a Texas estuary. *Gulf and Caribbean Research* 13:37–49.

GELWICK, F. P., S. AKIN, D. A. ARRINGTON, AND K. O. WINEMILLER. 2001. Fish assemblage structure in relation to environmental variation in a Texas Gulf coastal wetland. *Estuaries* 24:285–296.

HOFF, G. R. AND L. A. FUIMAN. 1995. Environmentally induced variation in elemental composition of red drum (*Sciaenops ocellatus*) otoliths. *Bulletin of Marine Science* 56:578–591.

KALISH, J. M. 1989. Otolith microchemistry: Validation of the effects of physiology, age and environment on otolith composition. *Journal of Experimental Marine Biology and Ecology* 132:151–178.

KENNEDY, B. P., J. D. BLUM, C. L. FOLT, AND K. H. NISLOW. 2000. Using natural strontium isotopic signatures as fish markers: Methodology and application. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2280–2292.

KIMURA, R., D. H. SECOR, E. D. HOUDE, AND P. M. PICCOLI. 2000. Up-estuary dispersal of young-of-the-year bay anchovy *Anchoa mitchilli* in the Chesapeake Bay: Inferences from microprobe analysis of strontium in otoliths. *Marine Ecology Progress Series* 208:217–227.

KLEIN, R. T., K. C. LOHMANN, AND C. W. THAYER. 1996. Sr/Ca and C-13/C-12 ratios in skeletal calcite of *Mytilus trossulus*: Covariation with metabolic rate, salinity, and carbon isotopic composition of seawater. *Geochimica et Cosmochimica Acta* 60:4207–4221.

LANKFORD, T. E. AND T. E. TARGETT. 1994. Suitability of estuarine nursery zones for juvenile weakfish (*Cynoscion regalis*): Effects of temperature and salinity on feeding, growth and survival. *Marine Biology* 119:611–620.

LEA, D. W., T. A. MASHIOTTA, AND H. J. SPERO. 1999. Controls on magnesium and strontium uptake in planktonic foraminifera determined by live culturing. *Geochimica et Cosmochimica Acta* 63:2369–2379.

LEY, J. A., C. C. MCIVOR, AND C. L. MONTAGUE. 1999. Fishes in mangrove prop-root habitats of northeastern Florida Bay: Distinct assemblages across an estuarine gradient. *Estuarine, Coastal and Shelf Science* 48:701–723.

LIMBURG, K. E. 1995. Otolith strontium traces environmental history of subyearling American shad *Alosa sapidissima*. *Marine Ecology Progress Series* 119:25–35.

MILTON, D. A. AND S. R. CHENERY. 2001. Sources and uptake of trace metals in otoliths of juvenile barramundi (*Lates calcarifer*). *Journal of Experimental Marine Biology and Ecology* 264:47–65.

PETERS, K. M. AND R. H. MCMICHAEL, JR. 1987. Early life history of red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries* 10:92–107.

PETERS, K. M. AND R. H. MCMICHAEL, JR. 1990. Early life history of black drum *Pogonias cromis* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Northeast Gulf Science* 11:39–58.

PETERSON, M. S., B. H. COMYNS, J. R. HENDON, P. J. BOND, AND G. A. DUFF. 2000. Habitat use by early life history stages of fishes and crustaceans along a changing estuarine landscape: Differences between natural and altered shoreline sites. *Wetland Ecology* 8:209–219.

PRICE, W. W. AND R. A. SCHLUETER. 1985. Fishes of the littoral zone of McKay Bay, Tampa Bay System, Florida. *Florida Scientist* 48:83–96.

RADTKE, R. L. 1989. Strontium-calcium concentration ratios in fish otoliths as environmental indicators. *Comparative Biochemistry and Physiology* 92:189–193.

ROOKER, J. R. AND S. A. HOLT. 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: Patterns of distribution and growth. *Marine Ecology Progress Series* 158:139–149.

ROOKER, J. R., S. A. HOLT, M. A. SOTO, AND G. J. HOLT. 1998. Post-settlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21:318–327.

SECOR, D. H., A. HENDERSON-ARZAPALO, AND P. M. PICCOLI. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *Journal of Experimental Marine Biology and Ecology* 192:15–23.

SECOR, D. H. AND J. R. ROOKER. 2000. Is otolith strontium a useful scalar of life cycles in estuarine fishes? *Fisheries Research* 46:359–371.

SURGE, D. M. AND K. C. LOHMANN. 2002. Temporal and spatial differences in salinity and water chemistry in SW Florida estuaries: Effects of human impacted watershed. *Estuaries* 25:393–408.

SWANSON, C. 1998. Interactive effects of salinity on metabolic rate, activity, growth, and osmoregulation in the euryhaline milkfish (*Chanos chanos*). *Journal of Experimental Biology* 201:3355–3366.

TOWNSEND, D. W., R. L. RADTKE, S. CORWIN, AND D. A. LIBBY. 1992. Strontium:calcium ratios in juvenile Atlantic herring *Clupea harengus* L. otoliths as a function of water temperature. *Journal of Experimental Marine Biology and Ecology* 160:131–140.

TOWNSEND, D. W., R. L. RADTKE, D. P. MALONE, AND J. P. WALLINGA. 1995. Use of otolith strontium:calcium ratios for hindcasting larval cod *Gadus morhua* distributions relative to water masses on Georges Bank. *Marine Ecology Progress Series* 119:37–44.

TREXLER, J. C. AND J. TRAVIS. 1993. Nontraditional regression analyses. *Ecology* 74:1629–1637.

UNDERWOOD, A. J. 1999. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge, U.K.

WILKINSON, L., G. BLANK, AND C. GRUBER. 1996. Desktop Data Analysis with SYSTAT. Prentice Hall, Englewood Cliffs, New Jersey.