A Tale of Two Timescales: Using Otolith Microchemistry to Improve Our Understanding of Alligator Gar Movement in the Lower Trinity River, Texas

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Abstract: Telemetry-based study of alligator gar (*Atractosteus spatula*) movement in the lower Trinity River, Texas, indicated that fish primarily remained within discrete home ranges less than 60 river kilometers (rkm), supporting the potential for local-scale management. However, the temporal scale of inference was limited (22 months), which may inadequately represent fish movements and home range size at the lifetime (i.e., ≥50 years) scale. Therefore, we used otolith microchemistry to examine the long-term movements of alligator gar ($n = 59$; total length range 1152 to 2420 mm, age range 4 to 60 years) between the lower Trinity River and Trinity-Galveston Bay system. Strontium:calcium (Sr:Ca) concentrations were measured along laser-ablated transects from the otolith core (i.e., time at hatch) to the edge (i.e., time at capture) for fish collected throughout the system, documenting movements between the river (freshwater) and bay (saltwater). We identified two residence contingents among fish in the lower Trinity River that differed in prevalence across the system. Multiple logistic regression indicated that river residence, in which fish remained in the river over their entire lifetimes, was most common at the upstream end of the study reach (63% of fish). In contrast, transience, in which fish moved between the river and bay, was prevalent nearest the river mouth (82% of fish). Although our inferences from the otolith data suggest a somewhat greater degree of homogenization across the system than was captured via telemetry, our results generally suggest localized management of alligator gar in the lower Trinity River could be appropriate.

Key words: Atractosteus spatula, residence, transience, management, scale

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Rising interest in the management and conservation of the alligator gar (*Atractosteus spatula*) has led to a growing body of work describing movement and home range of the species.

Sakaris et al. (2003) was the first to use telemetry to examine alligator gar movement and found that linear home ranges for six fish (TL range 970 to 1935 mm) varied from 3 to 12 km over 20 months in the Mobile-Tensaw Delta, Alabama, with movement positively related to fish size (TL). Similarly, Brinkman (2008) reported the mean linear home range of six adult fish (i.e., individuals >1100 mm TL) in Lake Texoma, Texas-Oklahoma, was 17 km over a 10-month period. Despite limited sample sizes and study durations, these initial efforts suggested that alligator gar may remain within relatively small home ranges within systems.

Buckmeier et al. (2013) built upon these early works, tracking the movements of 46 alligator gar collected throughout the 186 river kilometer (rkm) free-flowing reach of the Trinity River, Texas (hereafter referred to as the lower Trinity River). The authors reported that 83% of fish occupied discrete home ranges of less than 60 rkm over the 22-month study, with little overlap among fish tagged at the most upstream and downstream collection sites. Additionally, 79% of fish tagged within 10 rkm of the river mouth periodically emigrated into the Trinity-Galveston Bay system. Although home ranges of alligator gar in the lower Trinity River were substantially larger than those reported by the earlier works, the collective results of these studies indicated that alligator gar occupy discrete home ranges within systems. As a result, Buckmeier et al. (2013) suggested that management may be appropriate at local scales within systems, particularly if population abundance and dynamic rates vary.

These previous studies provided valuable insights on the movement and home range of alligator gar in a variety of systems. However, the information that can be obtained from an individual fish via telemetry is temporally limited because the operational life of transmitters is usually less than 3–4 years. Given alligator gar can exceed 50 years of age (Ferrara 2001, Buckmeier et al. 2012), such evaluations may represent less than 10% of an individual's lifetime. As noted by Buckmeier et al. (2013), longer-term data would confirm movement patterns and home range estimates, ultimately improving inferences used to define the appropriate scale for management.

Microchemistry has proven to be a useful tool for understanding movements and home range of fishes over long periods of time. The technique measures concentrations of trace elements that are continuously incorporated into the calcium-carbonate matrix of otoliths, scales or fin rays and are retained for the life of the fish (Pracheil et al. 2014). These elements can be useful indicators of movement if their concentrations in the environment are stable over time yet spatially varied, providing a natural marker across environmental gradients over the fish's lifetime at relatively fine temporal scales (e.g., weeks; Walther and Limburg 2012). The element strontium (^{88}Sr, hereafter referred to as Sr) is often informative in microchemical analyses because concentrations are typically stable over time and exhibit high spatial variability relative to other elements, including calcium (^{43}Ca; hereafter referred to as Ca), the primary element within the molecular structure of otoliths (Hedges et al. 2004, Pracheil et al. 2014). This is particularly the case between freshwater, estuarine, and marine habitats. Saltwater contains a significantly higher concentration of Sr relative to freshwater, resulting in a marked change in the Sr:Ca ratio in otoliths when fish transition between these habitats (Pracheil et al. 2014).

Microchemical analyses have been extensively applied in the Great Lakes, upper Mississippi River, and Colorado River ecoregions, but have seen limited use elsewhere (Pracheil et al. 2014). Daugherty et al. (2017) employed this technique to measure variations in otolith strontium:calcium (Sr:Ca) and quantify alligator gar use of the lower Guadalupe River (287 rkm in length) and San Antonio Bay, Texas, and found that the approach reliably identified multiple usage patterns that varied across the river-bay continuum. Lifetime river-residents predominated the upper river; whereas, the use of bay habitats was common among fish collected in the lower river. As a result, the authors recommended managing for two stocks in the system: a river-resident stock in the upper one-half (≈150 rkm) of the lower Guadalupe River, and a transient stock in the lower one-half of the river and bay.

What remains unclear is whether or not the results of Daugherty et al. (2017) are transferrable among populations and systems. If so, then river reaches up to about 150 rkm in length may be most appropriately managed as a single stock. Given that the lower Trinity River is of comparable length (186 rkm), we used the technique to gain further inferences on the movements of alligator gar in the lower Trinity River and Trinity-Galveston Bay system. Specifically, our objectives were to (1) utilize otolith Sr:Ca to infer movements between the river and bay among fish collected throughout the system and (2) identify factors that influence movement (e.g., capture location, fish age, sex, TL). Results of this study, along with those of previous works, will provide further guidance on the appropriate scale of management for alligator gar in the lower Trinity and other Gulf Coast river systems.

Methods

Study Site

The lower Trinity River begins in the tailrace below Lake Livingston, a 33,500-ha impoundment created by Lake Livingston Dam, which served as the upstream boundary of our study area. The river flows south-southeast before reaching the Trinity-Galveston Bay system (Figure 1). The watershed is dominated by forested and agricultural lands, although industry (primarily petrochemical)

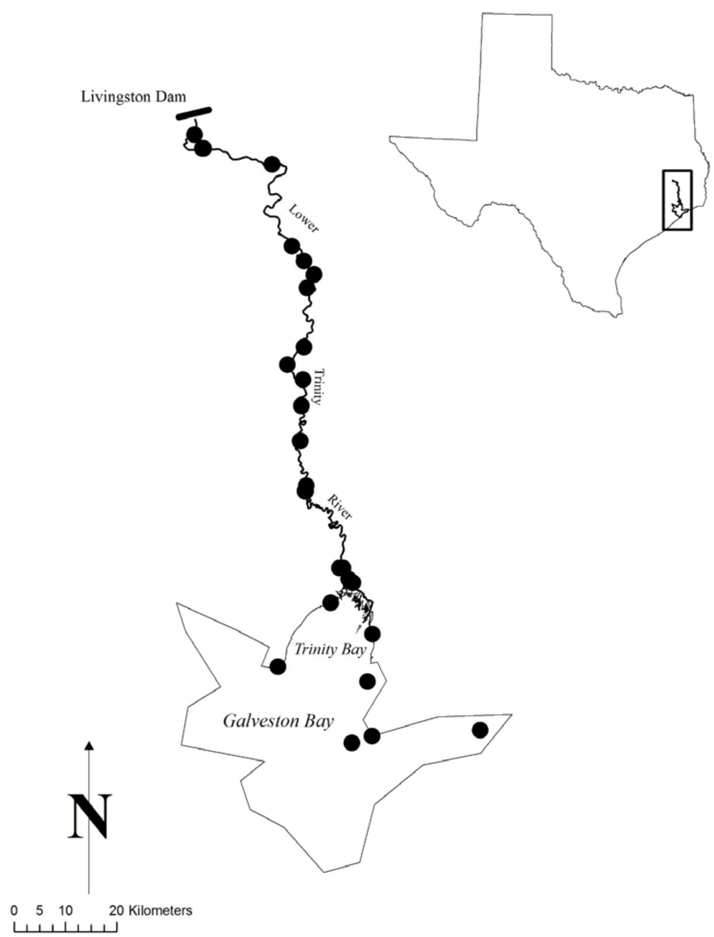

Figure 1. The lower Trinity River-Galveston Bay system. Filled circles denote catch locations of alligator gar.

is scattered throughout. The river is predominantly low gradient (range, 0.03–0.20 m km^{-1}), ranges from 70 to 120 m wide, and has a maximum depth of about 18 m, although much of the river is less than 2 m deep under normal flow conditions. Sand is the dominant substrate, with large woody debris present throughout the river, particularly in pool habitats (Buckmeier et al. 2013). The lower Trinity River empties into the Trinity-Galveston Bay system, which provides over 139,000 ha of estuarine habitat. Mean water depth in the bay is 2 m, and mean salinity is 17.4 ppt. Alligator gar are relatively common in the bay; the Coastal Fisheries Division of the Texas Parks and Wildlife Department (TPWD-CF) has recorded over 2500 catches of alligator gar in the system during annual community sampling from 1975 to 2017 (Daugherty et al. 2018).

Fish Collections

We used weighted-effort, multifilament experimental gill nets (61 m in length and 3 m in depth, #21 black-twine mesh, 89- to 140-mm bar measure mesh) to collect alligator gar throughout the lower Trinity River in 2015 and 2016 in low-velocity habitats (Figure 1) as described by Bodine et al. (2015). Gill nets were weighted by using various panel lengths of different mesh sizes relative to each other to minimize selectivity over the greatest size range of fish (Schlechte et al. 2016). We recorded the total length (TL), sex, and geographic coordinates of the catch location for each fish collected. Sex was determined using the procedure described by Ferrara and Irwin (2001). Fish were sacrificed and sagittal otoliths were extracted and stored in duplicate vials; one otolith was used for age estimation as described by Buckmeier et al. (2012) and the other was used for microchemical analysis. Otoliths were also obtained from an additional 14 alligator gar collected from the Trinity-Galveston Bay system by the TPWD-CF using experimental monofilament nets (184 m in length and 1.2 m in depth, 46-m panels of 76-, 102-, 127-, and 152-mm bar measure mesh). These fish were used to determine Sr:Ca levels in the otoliths that corresponded to known bay (i.e., saltwater) habitat use.

Otolith Analyses

Water chemistry can vary temporally (Elsdon et al. 2008), and ambient Sr:Ca concentrations in some freshwater systems can rival those of saltwater (Kraus and Secor 2004). Therefore, we first verified our assumption that Sr:Ca concentrations of freshwater environments in the lower Trinity River were consistent over time prior to microchemical analysis of the otoliths. Mean Sr:Ca in lower Trinity River water samples collected by the U.S. Geological Survey (1973 through 1994) was 3.37 (SD, 0.39) mmol mol^{-1}, which was similar to most freshwater systems (range, 2.1 to 4.5 mmol mol^{-1}; Kraus and Secor 2004, Farmer et al. 2013), and far less than those reported for saltwater habitats (> 8.5 mmol mol^{-1}; Volk et al. 2010, Walther and Limburg 2012).

We employed the same procedures to prepare, process, postprocess, and statistically analyze the microchemistry data as those described in Daugherty et al. (2017). Briefly, otoliths were embedded in Epofix cold-setting resin and sectioned along the transverse plane with an IsoMet low-speed saw (Buehler, Lake Bluff, Illinois). Sections were polished with lapping paper to expose the core, then affixed to a petrographic slide with cyanoacrylate glue, sonicated for 5 min, and rinsed with ultrapure water in triplicate. Laser ablation (LA) inductively coupled plasma mass spectrometry (ICP-MS) was then used to quantify Sr and Ca concentrations across each otolith from the core (time at hatch) to the edge (time at capture) along the axis that provided the longest possible transect and greatest data resolution. To correct for ablation yield differences among otoliths, Ca was used as an internal standard because it comprises a large, constant proportion otoliths (99% $CaCO_3$; Campana 1999). A glass reference standard was used to account for instrumental precision before and after every 10 samples. Strontium concentrations in the otoliths were consistently above the limit of detection (i.e., >0.003 mmol Sr mol Ca^{-1}).

We used quadratic discriminant function analysis (QDFA) in an intermediate analysis to assess our ability to classify fish to their catch location (i.e., river versus bay) and quantify the Sr:Ca (i.e., cutoff value) at the edge of otoliths that discriminated freshwater (river) and saltwater (bay) use. We limited the QDFA to fish collected at the most upstream sampling locations in the river (i.e., ≥159 RKM from the bay) and those collected from the bay by TPWD-CF. We did not include fish collected from the lower Trinity River near the bay due to increased potential of recent (i.e., within days) movement between habitats that may not be reflected in the chemistry data at the otolith edge. The jackknife (leave-one-out) technique with equal prior probabilities was used to assess our ability to classify these fish to their catch location (White and Ruttenberg 2007, Schaffler and Winkelman 2008, Schaffler et al. 2009, Schaffler et al. 2015). All statistical analyses of chemistry data were conducted using the MASS package in R (version 3.2.2; R Core Team [2015]).

We then created a scatterplot of the Sr:Ca data against the distance from the otolith core for each fish and used a Loess smoothing algorithm to create a fitted line plot of lifetime Sr:Ca (Daugherty et al. 2017). The cutoff value established by the QDFA was then superimposed on the plot to delineate lifetime movements of each fish. We classified individuals into two discrete movement contingents: fish exhibiting river residence (i.e., fish with Sr:Ca ratios less than the cutoff value across the otolith transect) and transience (i.e., fish with Sr:Ca ratios both less than and greater than the cutoff value across the otolith transect; Daugherty et al. 2017). To identify factors that explained significant proportions of the variation among contingents in the lower Trinity River, we used multiple logistic regression (MLR) to test for effects of fish age, sex, size, and catch location (expressed as rkm from the bay). We used a stepwise approach in SAS (SAS Institute 2017), with bidirectional elimination based on α levels ($\alpha_{enter} = 0.10$, $\alpha_{retain} = 0.05$) in which transience was the binary response variable.

Results

Due to analytical costs (≈US$64 per fish), we limited our sample to 59 individuals. Thus, we analyzed otoliths from 45 fish collected throughout the lower Trinity River (Figure 1) in 2015 ($n = 16$) and 2016 ($n = 29$) as well as the 14 fish collected from Trinity-Galveston Bay. Our sample from the river included 20 males, ranging from 1176- to 1743-mm TL and 3 to 27 years of age; the remaining 25 fish were female, ranging from 1152- to 2420-mm TL and 4 to 60 years old. Quadratic discriminant function analysis of fish collected from upper river sites ($n = 14$) and the 14 fish collected from the bay resulted in a classification success rate of 100%. Mean Sr:Ca (±SE) at the otolith edge was 0.85 mmol mol^{-1} (±0.037) for river fish and 2.096 mmol mol^{-1} (±0.069) for bay fish. A cutoff value of 1.47 mmol mol^{-1} Sr:Ca was derived from the QDFA to distinguish use of the lower Trinity River and Trinity-Galveston Bay (Figure 2). Among the 14 fish collected from the Trinity-Galveston Bay complex, four individuals exhibited exposure to freshwater earlier in life.

Lifetime Sr:Ca plots identified the existence of both river residence and transience (Figure 3). Eighteen fish (40% of fish sampled; 7 males and 11 females) exhibited lifetime river residence, with the remainder exhibiting transience (13 males and 14 females). The multiple logistic regression was significant ($P = 0.046$), and the distance of the catch location from the bay was the only factor retained in the model (Figure 4). The likelihood of transience was greatest near the bay (0.82), and least probable at the

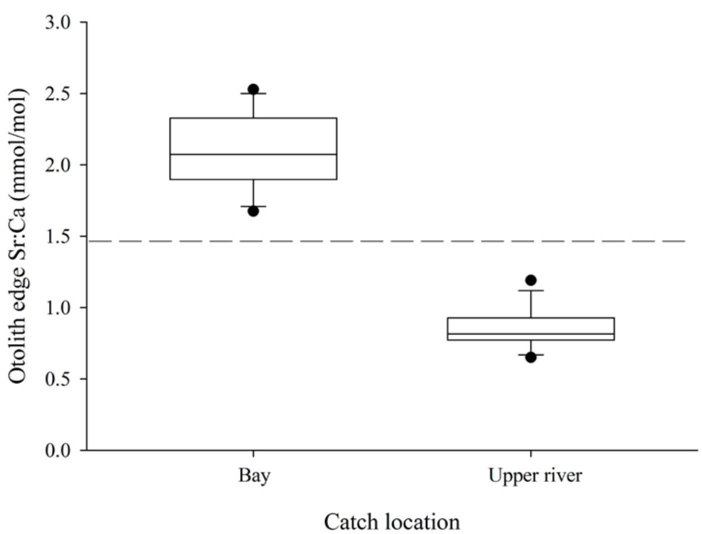

Figure 2. Box plots of otolith edge Sr:Ca ratios based on LA-ICP-MS for alligator gar collected from the lower Trinity River and Trinity-Galveston Bay system, Texas. The dashed line denotes the Sr:Ca ratio used to discriminate freshwater (river) and saltwater (bay) signatures in the otolith microchemistry data based on quadratic discriminant function analysis.

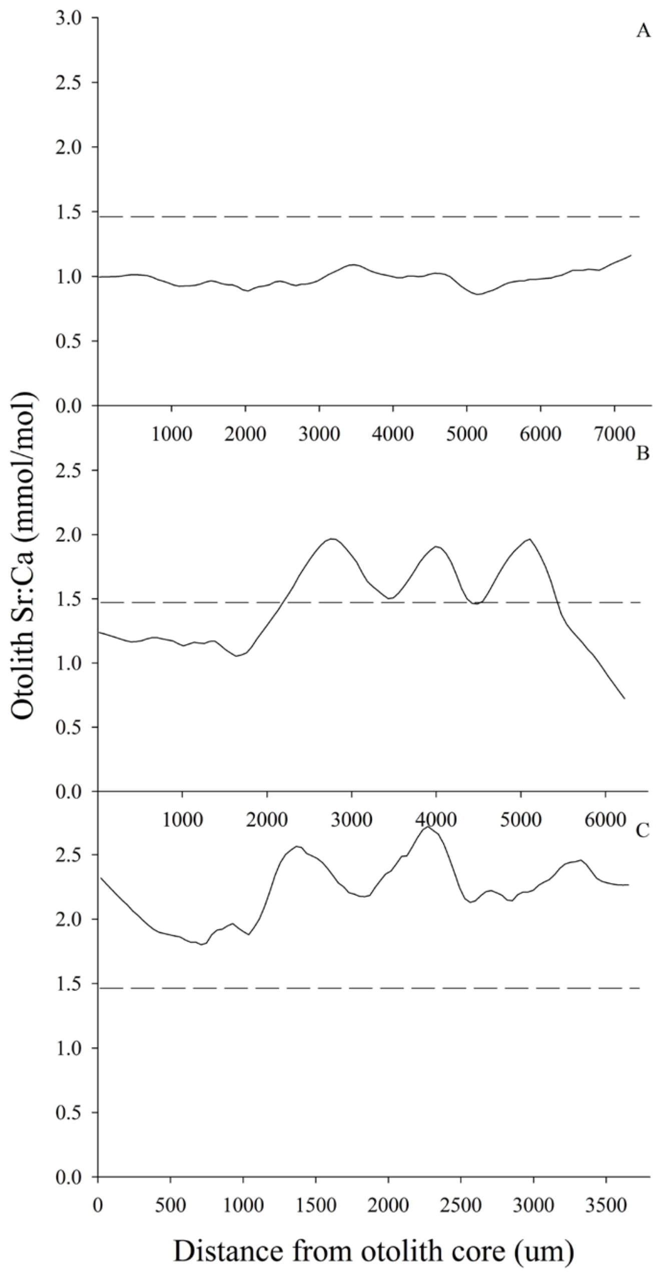

Figure 3. Selected otolith Sr:Ca profiles of alligator gar collected from the lower Trinity River and Trinity-Galveston Bay system, Texas. The dashed lines delineate movement between freshwater (i.e., the river; below line) and saltwater habitats (i.e., the bay; above line). Panel A illustrates lifetime river residence and panel B illustrates transience. Panel C illustrates the profile of a fish collected from Trinity-Galveston Bay.

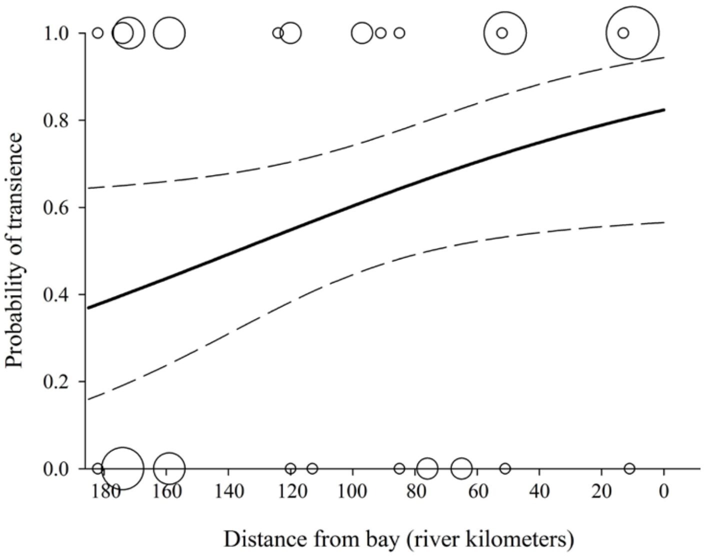

Figure 4. Relationship between the distance from the bay and the predicted probability of transience for alligator gar in the lower Trinity River-Galveston Bay system, Texas. Graduated, open circles (areas represent relative sample sizes) denote the observed distributions of river resident and transient fish; data were coded as a binary response variable (resident = 0, transient = 1). Dashed lines represent the 95% confidence bounds.

upstream end of the lower Trinity River (0.37). The likelihood of river residence or transience was equal (i.e., 0.5) about 138 rkm upstream of the bay (Figure 4).

Discussion

Many factors influence the movement and home range of fishes at varying temporal scales. For example, the diel pattern of daylight and darkness can change daily movements. Changes in water temperature and photoperiod can affect intra-annual movements, while differences in prey availability, ontogenetic shifts in diet or habitat needs, or random, large-scale environmental change can alter movement and home range at interannual and lifetime scales (Wootton 1998). Therefore, a comprehensive understanding of movement and home range can be best achieved using multiple approaches. Our use of otolith microchemistry provided a useful complement to the telemetry approach of Buckmeier et al. (2013) by extending the temporal dimension of information on the movement and home range of alligator gar in the lower Trinity River to the lifetime scale. Similar to the classification success reported by Daugherty et al. (2017) in the lower Guadalupe River (96%), our high classification success indicated that strontium provided a reliable natural tag for studying the long-term movement and home range of alligator gar in the lower Trinity River.

The distribution of movement contingents we observed in the lower Trinity River was highly comparable to those observed in the lower Guadalupe River-San Antonio Bay system by Daugherty et al. (2017). Multiple logistic regression analyses in both studies indicated that the distance of a fish's capture location from the respective bay in each system was the only significant predictor of movement between river and bay habitats (i.e., transience) over the lifetime of fish. In both systems, transience was most prevalent among fish collected nearest the river mouth, whereas river residence was most common at the upstream end of each study reach. In addition, the transition between movement contingents occurred at similar rates over the length of both rivers. In both systems, the probability of transience among fish collected near the mouth was 82%. In the lower Guadalupe River, the likelihood of transience 186 rkm upstream of the river mouth—the distance equal to the length of the lower Trinity River—was 32%, which is similar to that observed at the upstream end of the Lower Trinity River (37%). Thus, these similarities in fish movement, despite differences in system size, suggest that movement and home range of the alligator gar is largely behaviorally mediated and transferrable among systems.

Generally, our results corroborate the conclusions of Buckmeier et al. (2013); movements were significantly segregated over the longitudinal gradient of the lower Trinity River. However, inferences at the lifetime scale suggested a somewhat greater degree of homogenization across the system than was captured via telemetry. For example, Buckmeier et al. (2013) found that 20% (6 of 30) of the alligator gar fitted with telemetry tags in the upper one half (90 rkm) of the lower Trinity River entered the lower half of the reach during the study period. The authors further noted that these downstream movements were generally rare, temporary, and of short duration. In contrast, our microchemical analyses of fish collected from the upper half of the lower Trinity River ($n = 23$) indicated that about 52% of fish traversed the lower river and entered the bay at some point during their lifetimes. It remains unclear whether the downstream movements to the bay we detected in the Sr:Ca signatures were also infrequent and brief. Equilibration time—the time required for a change in environment (i.e., movement) to be reflected in the elemental composition in hard-part structures such as otoliths—is generally consider to occur on the order of from two weeks to one month (Walther and Limburg 2012). Therefore, the transitions between the river and bay habitats we detected were likely to be of similar or greater temporal magnitude. It is unlikely that our technique could detect shorter-term transitions between habitats (e.g, movements over a few days); however, the results of Buckmeier et al. (2013) suggest such short-term movements are localized, indicating such undetected movements would have little effect on our results at the lifetime scale. Although this was beyond the scope of our current study, future analyses that include the radial measurement of annuli, followed by superimposition of their respective positions over the Sr:Ca profile data, would allow us to characterize the timing and duration of movements for transient fish. If movement between the river and bay occurred relatively infrequently for a matter of months over the lifetimes of fish, followed by returns to their typical riverine habitats as suggested by the telemetry data, a greater degree of spatial segregation could be inferred.

In addition to understanding long-term movement of fishes, otolith microchemistry data is often used to determine natal origins. Although this was not the focus of our application, we observed Sr:Ca concentrations consistent with those found in Trinity-Galveston Bay in the otolith cores of 37% (22 of 59) fish we analyzed. This was common to 86% (12 of 14) fish collected from Trinity-Galveston Bay and 22% (10 of 45) of the individuals we collected from the lower Trinity River over half of which were collected within 50 rkm of the bay. Elevated Sr:Ca in the core material suggests that these individuals may have been spawned in estuarine habitats. Daugherty et al. (2017) found similar evidence in the lower Guadalupe River-San Antonio Bay system; however, it was limited to a small proportion of the sample (3 of 151 fish). Spawning has been observed in a Louisiana bay system at salinities less than 8‰ (A. Ferrara, Nicholls State University, personal communication), though the success of those efforts was not documented. Laboratory studies have reported alligator gar early life history stages can survive salinities up to 7‰ (Suchy 2009), suggesting the potential for successful reproduction in low-salinity habitats. Buckmeier et al. (2013) postulated that estuarine spawning may occur in shallow, vegetated areas of the lower Trinity River mouth and estuary. Future studies aimed at understanding alligator gar spawning habitat requirements and recruitment patterns in coastal river systems should consider the assessment of these habitat types in addition to riverine floodplains.

Collectively, the results of Buckmeier et al. (2013) and our current study suggest the movements of alligator gar in the lower Trinity River could be compatible with localized management. However, for river reaches shorter than the lower Trinity River, the degree of movement exhibited by alligator gar may favor management at the system scale. Physical characters of rivers change over their length, in turn affecting habitat characteristics and floodplain connectivity (Vannote et al. 1980). These changes influence the localized abundance and dynamics of fish populations. Thus, future work should focus on characterizing abundance, size and age structure, and dynamic rates across systems, which can be paired with movement and home range information to identify management boundaries (Daugherty et al. 2017). This information is particularly important in the free-flowing reaches of Gulf-coast tributaries like the lower Trinity River. These systems provide a diversity of habitats, including lowland river deltas and low-salinity estuaries that may support more frequent recruitment than upstream riverine areas (Buckmeier et al. 2013, Daugherty et al. 2017). A comprehensive understanding of movement at multiple temporal scales, coupled with information on how population demographics change across systems, will provide the information necessary to guide delineation of local management boundaries and objectives.

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Literature Cited

Bodine, K. B., D. J. Daugherty, J. W. Schlechte, and G. R. Binion. 2015. A strategy for increasing gill-net catch rates and minimizing sampling mortality of alligator gars. North American Journal of Fisheries Management 35:611–615.

Brinkman, E. L. 2008. Contributions to the life history of alligator gar *Atractosteus spatula*, in Oklahoma. Master's thesis. Oklahoma State University, Stillwater.

Buckmeier, D. L., N. S. Smith, and D. J. Daugherty. 2013. Alligator gar movement and macrohabitat use in the lower Trinity River, Texas. Transactions of the American Fisheries Society 142:1025–1035.

———, ———, and K. S. Reeves. 2012. Utility of alligator gar age estimates from otoliths, pectoral fin rays, and scales. Transactions of the American Fisheries Society 141:1510–1519.

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

Daugherty, D. J., K. L. Pangle, W. Karel, F. Baker, C. R. Robertson, D. L. Buckmeier, N. G. Smith, and N. Boyd. 2017. Population structure of alligator gar in a Gulf Coast river: insights from otolith microchemistry and genetic analyses. North American Journal of Fisheries Management 37:337–348.

———, J. W. Schlechte, and D. L. McDonald. 2018. Alligator gar in Texas coastal bays: long-term trends and environmental influences. Transactions of the American Fisheries Society.

Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology: an Annual Review 46:297–330.

Farmer, T. M., D. R. DeVries, R. A. Wright, and J. E. Gagnon. 2013. Using seasonal variation in otolith microchemical composition to indicate largemouth bass and southern flounder residency patterns across an estuarine salinity gradient. Transactions of the American Fisheries Society 142:1415–1429.

Ferrara, E. M. 2001. Life-history strategy of Lepisosteidae: implications for the conservation and management of alligator gar. Doctoral dissertation. Auburn University, Auburn, Alabama.

——— and E. R. Irwin. 2001. A standardized procedure for internal sex identification in Lepisosteidae. North American Journal of Fisheries Management 21:956–961.

Hedges, K. J., S. A. Ludsin, and B. J. Fryer. 2004. Effects of ethanol and preservation on otolith microchemistry. Journal of Fish Biology 64:923–937.

Kraus, R. T. and D. H. Secor. 2004. Incorporation of strontium into otoliths of an estuarine fish. Journal of Experimental Marine Biology and Ecology 302:85–106.

Pracheil, B. M., J. D. Hogan, J. Lyons, and P. B. McIntyre. 2014. Using hardpart microchemistry to advance conservation and management of North American freshwater fishes. Fisheries 39:451–465.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.rproject.org/>. Accessed October 2017.

Sakaris, P. C., A. M. Ferrara, K. J. Kleiner, and E. R. Irwin. 2003. Movements and home ranges of alligator gar in the Mobile-Tensaw Delta, Alabama. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 57:102–111.

Schaffler, J. J., C. S. Reiss, and C. M. Jones. 2009. Spatial variation in otolith chemistry of Atlantic croaker larvae in the Mid-Atlantic Bight. Marine Ecology Progress Series 382:185–195.

——— and D. L. Winkelman. 2008. Temporal and spatial variability in otolith trace-element signatures of juvenile striped bass from spawning locations in Lake Texoma, Oklahoma-Texas. Transactions of the American Fisheries Society 137:818–829.

———, S. P. Young, S. Herrington, T. Ingram, and J. Tannehill. 2015. Otolith microchemistry to determine within-river origins of Alabama shad in the Apalachicola-Chattahoochee-Flint River basin. Transactions of the American Fisheries Society 144:1–10.

Schlechte, J. W., K. A. Bodine, D. J. Daugherty, and G. R. Binion. 2016. Size selectivity of multifilament gill nets for sampling alligator gar: modeling the effects on population metrics. North American Journal of Fisheries Management 36:630–638.

SAS Institute. 2017. SAS user's guide: statistics, version 14.3 edition. SAS Institute, Inc. Cary, North Carolina.

Suchy, M. D. 2009. Effects of salinity on growth and survival of larval and juvenile alligator gar *Atractosteus spatula*, and on plasma osmolality of non-teleost Actinopterygiian fishes. Master's thesis. Nicholls State University, Thibodaux, Louisiana.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and S. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile chinook salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. Transactions of the American Fisheries Society 139:535–549.

Walther, B. D. and K. E. Limburg. 2012. The use of otolith chemistry to characterize diadromous migrations. Journal of Fish Biology 81:796–825.

White, J. W. and B. I. Ruttenberg. 2007. Discriminant function analysis in marine ecology: some oversights and their solutions. Marine Ecology Progress Series 329:301–305.

Wootton, R. J. 1998. Ecology of teleost fishes, second edition. Kluwer Academic Publishing, Dordrecht, the Netherlands.