Tributary streams provide migratory fish with access to floodplain habitats in a regulated river: evidence from alligator gar, *Atractosteus spatula*

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Abstract

Migratory fishes with periodic life history strategies are sensitive to river regulation. Populations of these fishes may persist in highly regulated rivers by using tributaries that provide access to intermittently connected spawning and early life stage habitat in floodplains. We analyzed system hydrology and associated movement of a long-lived periodic strategist, the alligator gar (*Atractosteus spatula*), in the Brazos River, Texas. We hypothesized that (1) flow regulation on the mainstem has resulted in the reduction of flood pulses, but tributaries have been less altered and (2) alligator gar migrate into tributaries during high flows and temperatures. Our analysis revealed that flood pulses were reduced in the mainstem but not in an adjacent, less regulated tributary where floodplain-inundating pulses now outnumber those in the mainstem. Using data from tagged fish, we derived statistical models predicting greater occurrence of alligator gar in tributaries when water temperature exceeded 25 °C and mainstem discharge exceeded 400 cubic meters per second. These results emphasize that movement into less regulated tributaries can mitigate impacts of river regulation on mainstem river populations of alligator gar.

Key words: flow regime, movement ecology, periodic life history, river network, telemetry

Introduction

Humans rely on rivers for water supplies, transportation, power generation, and fisheries (Karr and Chu 2000; Grill et al. 2019). Consequently, nearly all the world's rivers have been modified, often extensively. Lehner et al. (2011) estimated that there are >50 000 large dams (>15 m height) storing approximately one-sixth of annual global discharge. The combination of water consumption and impoundments has left only 23% of the world's longest rivers (>1000 km) flowing unimpeded (Grill et al. 2019). Furthermore, the number of dams and subsequent water storage is predicted to increase (Zarfl et al. 2015). Surface freshwater habitats constitute approximately 0.01% of the world's water by volume but contain nearly one-third of all vertebrate species (Dudgeon et al. 2006). Ultimately, conservation of the world's rivers is critical to maintaining both human water security and global biodiversity (Vörösmarty et al. 2010).

Among freshwater ecosystems, river floodplains (hereafter "riverscapes") exhibit exceptionally high biodiversity (Thomaz et al. 2007). However, river regulation alters the dynamics of riverscape ecosystems resulting in biodiversity loss (Dynesius and Nilsson 1994). Floodplain connectivity is essential for population persistence of many freshwater organisms (Ward 1998; Lewis et al. 2001). The flood pulse concept stresses the importance of periodic floodplain inundation for the productivity and biodiversity of rivers (Junk et al. 1989). Floodplains accessible to fishes during higher flows provide a wide range of benefits, including habitat for spawning, recruitment, foraging, and refuge (Junk et al. 1989). Consequently, fishes have emerged as model organisms and ecological indicators for riverscape connectivity, yet there is still limited understanding of fish migration into floodplains (Lasne et al. 2007; Castello 2008; Walker et al. 2022). This information is critical as fish species that rely on floodplains are among the most imperiled (Tockner and Standford 2002).

Among freshwater fishes, migration for reproduction is strongly associated with life history. Winemiller and Rose (1992) defined three life history strategies (i.e., periodic, opportunistic, and equilibrium) defined by trade-offs in demographic traits (i.e., age of maturity, fecundity, and juvenile survivorship) and gradients of environmental variation at various scales that select for these strategies. Periodic strategists, characterized by late maturation, large size, and high fecundity, can exploit large-scale spatiotemporal variation in environmental conditions. Migration is common among periodic strategists, presumably because movement into favor-

able habitats during appropriate periods has fitness benefits in terms of spawning success and subsequent early life stage survival (Winemiller and Rose 1992; Baras and Lucas 2001). Unfortunately, river fragmentation and regulation negatively affect both longitudinal (upstream–downstream) and lateral (river–floodplain) fish migrations. This is problematic because migratory fishes with periodic life history strategies (hereafter "migratory fishes") play critical ecological and economical roles, as they are often keystone species, subsidize biogeochemical cycles, and support popular recreational and commercial fisheries (Dugan et al. 2010; Flecker et al. 2010; Hildebrand et al. 2016). Unfortunately, there is high spatial overlap between the distribution of migratory fishes and regulated rivers, leading to an emerging conservation crisis for these species (Grill et al. 2019; He et al. 2019; Alò et al. 2021).

Despite global river regulation and habitat fragmentation, some migratory fish populations persist in regulated rivers (Agostino et al. 2004; Esguícero and Arcifa 2010). One reason for this may be the existence of unobstructed or less regulated tributaries that provide functional connectivity (e.g., floodplain access) ultimately promoting population persistence (Pracheil et al. 2013). Migratory fishes are known to use unregulated stretches of tributaries for important aspects of their life history such as reproduction and recruitment (Pracheil et al. 2009). Additionally, tributary migrations can fulfill population processes that no longer occur in highly regulated mainstem rivers, such as tributary movements by threatened humpback chub, *Gila cypha*, and Colorado pikeminnow, *Ptychocheilus lucius*, in the Colorado River Basin (Gorman and Stone 1999; Irving and Modde 2000). Thus, tributaries may be essential for the conservation of migratory fishes inhabiting large mainstem rivers (Starcevich et al. 2012).

In North America, the alligator gar, *Atractosteus spatula*, is a long-lived, periodic life history strategist known to migrate between mainstem and tributary reaches where spawning in tributaries has been documented (Inebit 2009; Kluender et al. 2017). Alligator gar are considered apex predators, and trophy angling for this species has increased in popularity in recent decades (Smith et al. 2020b). Alligator gar rely on seasonal connectivity to inundated floodplains and backwater habitats for reproduction and recruitment (Fig. 1a; Buckmeier et al. 2017; Smith et al. 2020a). Due to loss of floodplain connectivity (Fig. 1b), historical eradication efforts, and overharvest, populations of alligator gar have declined in the Mississippi River basin and many coastal rivers draining into the Gulf of Mexico (Kluender et al. 2017; Lochmann et al. 2021).

There is a general lack of knowledge regarding movements and habitat use by alligator gar across the range of the species (Buckmeier et al. 2013; Smith et al. 2020b). Recent studies have investigated the movements of alligator gar in lotic systems (Buckmeier et al. 2013; Smith et al. 2020b). However, these studies have generally focused on longitudinal movement of alligator gar in mainstem rivers with minimal consideration of lateral movement (Buckmeier et al. 2013; Wegener et al. 2017; Lochmann et al. 2021). Current populations of alligator gar are considered stable in Texas and Louisiana, yet mainstem rivers in these regions are just as fragmented as areas within their distribution where declines

have occurred (Smith et al. 2020b). Therefore, understanding the persistence of remaining alligator gar populations may be related to the use of less regulated tributaries that still provide floodplain habitat for reproduction (Fig. 1b). This strategy highlights the importance of using tributaries and their floodplains during flood pulses where mainstem connections no longer exist. Thus, understanding the extent, duration, and predictors of movement of alligator gar into tributaries is essential for the species conservation and management.

The goal of this study was to test the prediction that alligator gar use less altered tributaries to access floodplain habitat during elevated temperatures and high flows. First, we characterized flood pulse frequencies of the lower Brazos River and a tributary to test our hypothesis that hydrology of the mainstem has been more heavily altered compared with pre-impoundment conditions and a larger tributary. We predicted that a large tributary would flood more frequently than the mainstem that could be used for spawning when floodplain inundation in the mainstem was lacking. Second, using a combination of stationary and mobile telemetry, we assessed predictors of alligator gar occurrence in mainstem and tributary reaches and hypothesized that tributary occurrence would be strongest during higher flows that connect adjacent floodplains coinciding with optimal temperature conditions (i.e., 20–30 °C; see Buckmeier et al. 2017). Investigating these predictions could provide valuable information on the abiotic conditions eliciting significant movements into tributaries and how connectivity in regulated rivers might be managed to benefit alligator gar populations throughout their range, and by extension, declining populations of other migratory fishes in regulated river systems elsewhere.

Methods

Study area

The Brazos River is 2060 kilometers (km) long and originates near the border of New Mexico and Texas, flowing southeast to the western Gulf of Mexico (Kammerer 1987). The basin is highly regulated, including three large reservoirs in the central and upper subbasins (Supplementary Fig. S1) with surface areas over 30 km^2 capable of storing over 200% of annual Brazos River discharge (Lehner et al. 2011). Downstream, the lower 800 km is a meandering lowland river that primarily drains nutrient-rich forested and agricultural land (Winemiller et al. 2000). We tracked movements of alligator gar along 200 km of the Brazos River centered around College Station, TX (Fig. 2). We also tracked movements in 147 km of the lower sections of three major tributaries, including 58 km of the Little River, 56 km of the Navasota River, and 33 km of Yegua Creek upstream to the dam at Somerville Lake (Fig. 2). Minor tributaries (e.g., Beason creek; Fig. 2) were also tracked opportunistically during higher flows. The surrounding landscape around tributaries is generally less modified than the Brazos River, with significant patches of hardwood forest and open herbaceous vegetation with minimal road crossings preventing fish migrations. Tributaries typically flood annually with rises of over 3 m above me-

Fig. 1. Conceptual diagram demonstrating (*a*) high pulse flows and resulting lateral connectivity providing migration pathways (double arrows) into floodplains from unregulated mainstem and tributary rivers; and (*b*) high pulse flows in a regulated mainstem river where the effects of dams and levees prevent mainstem–floodplain connectivity, but tributaries still provide connectivity corridors to floodplains for migratory fishes such as alligator gar. Created with BioRender.com (https://biorender. com) using alligator gar image by Rick Hill (with permission).
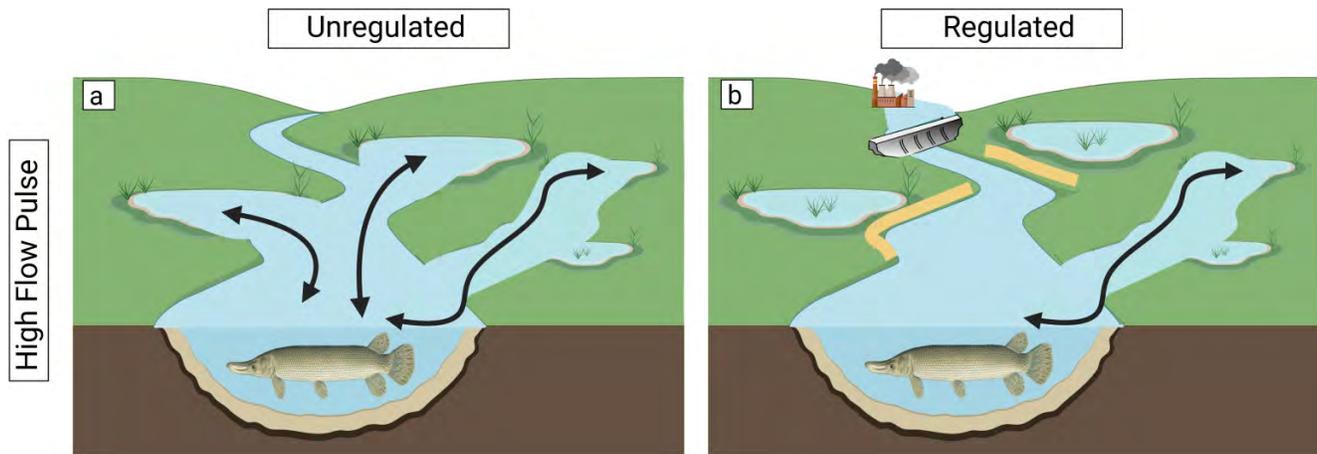
dian flows creating extensive floodplains (>5 km wide on the Navasota River), while Brazos River overbank events are rare and require significantly higher flows for floodplain connectivity. Average stream width was 70 m in the mainstem and 24 m in major tributaries during base flows and contained predominantly sand substrate with intermittent limestone outcroppings and gravel bars.

Fish collection and tagging

Alligator gar were captured primarily from three collection areas (Fig. 2) across five tagging events from April 2020 to March 2021 (Table 1). Tagging was distributed throughout the study area in low-velocity pool habitats within the mainstem, tributaries, and tributary confluences. We used large mesh experimental gill nets (76–127 mm mesh size, 61 m net length, 3 m net depth) as described by Bodine et al. (2015) and Schlechte et al. (2016). This included short-term net sets (typically ≤1 h) in areas with alligator gar surfacing activity or by locating fish using side scan sonar (Humminbird Helix 10 Chirp GPS G2N sonar unit) as described by Fleming et al. (2018). Upon capture, we collected morphological variables to predict sex as described by McDonald et al. (2018). We triple-tagged each captured fish using a passive integrated transponder tag, a T-bar anchor tag inserted in soft tissue directly posterior to the dorsal fin, and one of two transmitter types inserted into the peritoneal cavity. Transmitters were either an ultrasonic transmitter with a 14-month battery life span (model CT-82-2-I; Sonotronics, Tucson, Arizona) or a combined acoustic and radio-transmitter (CART) with a 26-month acoustic and 13-month radio battery life span (model MM-RC-16-25; Lotek, Ontario, Canada). Transmitters were surgically inserted with a single incision along the soft tissue directly posterior to the right pelvic fin following methods developed by the U.S. Fish and Wildlife Service, Baton Rouge Fish and Wildlife Conservation Office (K. Kimmel (personal communication)). Fish were kept in a plexiglass cradle

with an aluminum frame to reduce thrashing and increase stability during surgeries. Following tagging and recovery, fish were released within 100 m of the capture location. All capture and tagging protocols were reviewed and approved by the Texas A&M University Institutional Animal Care and Use Committee (permit IACUC 2018-0392 to JSP).

Telemetry

We monitored alligator gar movement using both stationary and mobile telemetry. For stationary telemetry, a total of 16 submersible ultrasonic receivers (SURs; Sonotronics SUR-3BT) were deployed (Fig. 2). We continuously monitored movement and exchange of fish across mainstem–tributary ecotones using a three-grid array of SURs deployed at each of the three major tributaries. This included an SUR directly upstream and downstream of each major tributary confluence along the mainstem, and an SUR within each major tributary upstream of its confluence. We separated SURs within the tributary confluence arrays by a minimum of 1200 m to ensure no overlap in detections was possible and that detections represented fish locations firmly within either the mainstem or tributaries. Additional SURs were deployed well within each of the major tributaries (≥6000 m) and throughout the Brazos River (Fig. 2). We attached temperature loggers (Onset HOBO® UTBI-001 TidbiT, Onset Computer Corp., Bourne, Massachusetts) to the SURs in the confluence of each major tributary and to the SURs directly downstream of these confluences along the mainstem to record hourly water temperatures. SURs were maintained such that they continuously listened for transmitters. However, three SURs were lost during a high-water event in May 2021, resulting in an approximately 90-day gap in mainstem receiver coverage directly upstream and downstream of the Little River confluence and downstream of Yegua Creek on the Brazos River. However, given the limited data collected on these SURs prior to their loss and that the receivers were lost toward the end of the

Fig. 2. Study area along the lower Brazos River subbasin centralized around College Station, TX, projected to NAD 1983 UTM zone 14N. Dark gray lines are the extent of the study area; black lines are standardized tracking regions conducted during each tracking event. Gray circles are submersible ultrasonic receiver (SUR) locations without temperature loggers, gray and black circles are SUR locations with a temperature logger, white diamonds are locations of USGS gages, and boxes are general regions where alligator gar were collected and tagged. River layers are from the medium resolution National Hydrography Dataset (version two; McKay et al. 2013); reservoir layer is from the existing reservoir database from the Texas Water Development Board (TWDB 2014). The College Station city, state, national, and international boundary layers were all gathered from the ArcGIS Hub (Esri 2014).
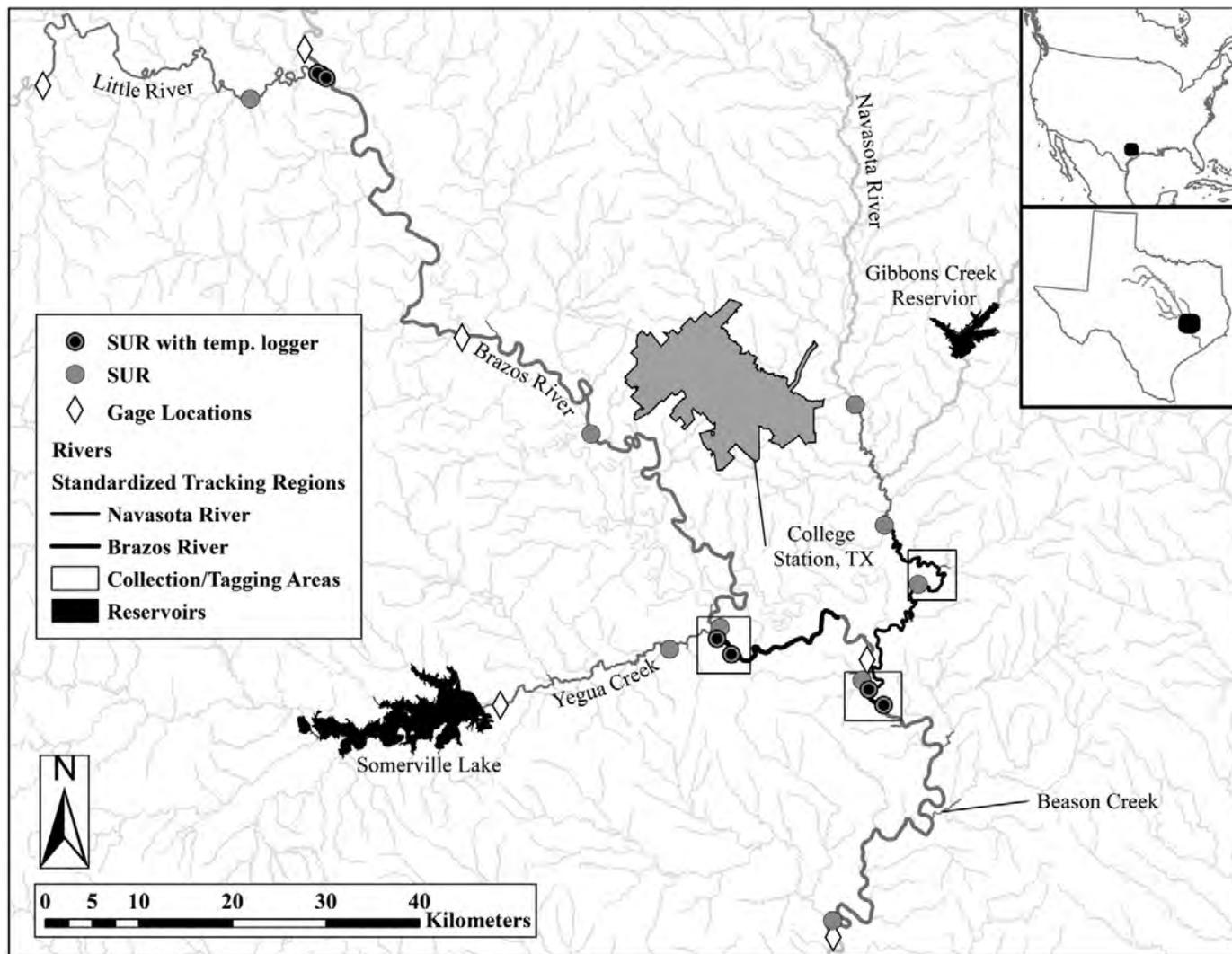
Table 1. Summary of the five tagging events including the date the tagging event begun, ended, and the number of alligator gar collected.

Tagging event	Date (start)	Date (end)	Number tagged
1	4/14/2020	4/30/2020	15
2	5/19/2020	5/27/2020	8
3	7/20/2020	7/23/2020	4
4	12/16/2020	12/17/2020	5
5	3/15/2021	3/17/2021	13

study period, we consider this insignificant for our analyses. Because of the dynamic nature of flows and stream widths, it is unlikely that SURs maintained total coverage of stream channels during high-water events (Casto-Yerty and Bettoli 2009). However, we emphasize that the SUR arrays generally acted as a series of grids to detect large-scale movements (e.g., migrations into tributaries).

We used mobile telemetry to determine whether alligator gar occupied mainstem versus tributary habitats in regions outside of the fixed ranges of the SURs, including minor tributaries where we had no coverage of stationary receivers. Thirteen tracking events were conducted from May 2020 to August 2021 at primarily monthly intervals (Table 2) by driving a boat downstream (≤ 8 km h^{-1}) using a Sonotronics

Table 2. Total count of tagged alligator gar, alligator gar available for detection, and proportion of relocated alligator gar across each mobile tracking event.

Tracking event	Date (start)	Date (end)	Total tagged	Tags available	Proportion relocated
1	5/11/2020	5/14/2020	15	15	0.73
2	6/2/2020	6/12/2020	23	22	0.91
3	9/10/2020	9/26/2020	27	18	1.00
4	10/7/2020	10/16/2020	27	18	0.89
5	11/4/2020	11/12/2020	27	18	0.89
6	1/13/2021	1/20/2021	32	19	1.00
7	2/22/2021	3/3/2021	32	19	0.84
8	3/24/2021	4/2/2021	45	31	0.97
9	4/21/2021	5/3/2021	45	31	0.87
10	5/26/2021	6/3/2021	45	29	0.48
11	6/23/2021	7/2/2021	45	27	0.85
12	7/22/2021	7/24/2021	45	24	0.92
13	8/23/2021	8/26/2021	45	21	0.81

Note: Numbers of tagged fish varied due to suspected mortality, tag failure, and emigration. Beginning and end of each tracking event are defined as the first and last days we searched for alligator gar.

USR-14 ultrasonic tracking receiver and a towable Sonotronics TH-2 omnidirectional hydrophone towed just below the water surface (<10 cm). Once a transmitter was detected, a Sonotronics DH-4 directional hydrophone was used to determine fish location and georeferenced using a global positioning system (GPS) device (Garmin GPSMAP 64st). The size and navigability of the study area made it impractical to completely survey for any given tracking event. Therefore, standardized tracking reaches (Fig. 2) were searched and these generally encompassed most tagged fish. Additional tracking was conducted outside of the standardized tracking regions when (1) detections were low in the standardized reaches, (2) flow stages were high, or (3) both situations occurred.

Data processing and subsetting

Stationary detections from SURs were processed using Sonotronics SURsoft data processing software (SURsoft version 1.0.6) as described by Buckmeier et al. (2013). Only high-confidence detections were analyzed to avoid uncertainty regarding background noise versus fish detection. Occurrence was modeled only on days when at least one alligator gar was detected by at least one SUR, while other days were excluded from this analysis. Daily detection data were then transformed to binary values where detections on tributary SURs were assigned a "1" and detections among mainstem SURs were assigned a "0" (see the Supplementary Material, Data Processing, for more details). Fish available for detection varied by tracking event due to suspected tag loss, harvest, emigration, or tag failure (Table 2). We considered a fish undetectable from its time of last detection if it was not detected on any of the SURs or relocated with mobile telemetry for two consecutive tracking events.

To account for variation in the number of fish available for detection, both stationary and mobile telemetry datasets were subsetted using a two-step data filtering process. The initial duration filter retained individuals if they were (1) still detectable through either mobile or stationary telemetry during the last two tracking events or (2) monitored until the transmitter battery failed. Battery failure was estimated at 14 months for acoustic transmitters and validated with a fish that was relocated in June 2021 approximately 14 months after capture where we observed a low battery signal from the transmitter. We included a 1-month buffer period to account for battery life variation where fish monitored for at least 13 months that became undetectable were likely from battery failure and were still retained for further analysis. Therefore, fish undetectable below this threshold were not analyzed as the fate of their transmitters was unknown. This allowed us to look at individuals with the highest amount of seasonal variation in environmental conditions (i.e., temperatures and flows) to best represent our sample of alligator gar tributary use (see Supplementary Table S1 for more information). Of the individuals retained for duration, we only modeled fish that made at least one transition from the mainstem into major tributaries (stationary telemetry) or major and minor tributaries (mobile telemetry).

Statistical analysis

Flow pulses

We performed hydrological analyses using U.S. Geological Survey (USGS) gages to test our hypotheses regarding flow pulses in mainstem and tributary water bodies (Table 3). Gages within the mainstem and tributaries were selected based on their (1) availability of hydrology data prior to river regulation; (2) remaining in operation; and (3) having no significant gaps (>20 years) in flow data. A combination of these criteria and regionally low resolution of gages limited our inferences to one mainstem gage and one tributary gage. We employed flow data from the Brazos River gage in Waco, TX (USGS Gage ID 08096500), and the Navasota River Gage (USGS Gage ID 08110800) near Easterly, TX (Supplementary Fig. S1). We quantified the annual frequency of flow pulse magnitudes with ecological relevance as determined by the Brazos River

Table 3. Summary of the variables being tested, their expected hypothesized effect, and the models used to investigate each explanatory variable.

Variable	Variable description	Hypothesized effect	Models used
Flood frequency	Annual frequency of 1-year, 2-year, 5-year flood recurrence intervals from Brazos and Navasota River USGS gages	More frequent flooding in tributaries, tributary flooding unchanged over time	GAM
Discharge	Brazos River discharge (c·m·s) measured from USGS gage near Bryan, TX	Higher discharge magnitude, higher tributary occurrence	GLMER, MLR
Temperature	Brazos River temperature (°C) measured from temperature logger on Brazos River	Higher temperature, higher tributary occurrence	GLMER, MLR
Discharge × temperature	Interactive parameter of Brazos River discharge and temperature	Higher discharge magnitude and temperature, higher tributary occurrence	GLMER, MLR
Sex	Predicted sex using morphological measurements from McDonald et al. (2018)	No influence on tributary occurrence	GLMER, MLR
Total length	Measured total length of each alligator gar (cm)	No influence on tributary occurrence	GLMER, MLR

Note: The variables were included in either generalized additive models (GAM) for our hydrological analysis, generalized linear mixed effects regression (GLMER) models for our stationary telemetry analysis, or multinomial logistic regression (MLR) models for our mobile telemetry analysis.

Basin and Bay Expert Science Team (Gooch et al. 2012). Specifically, the frequency of high-flow pulses (1-year recurrence interval) and overbank events (2- and 5-year recurrence intervals) were estimated (hereafter "1-year", "2-year", and "5-year" pulses). The discharge thresholds (i.e., 1-year, 2-year, 5-year) for these recommended pulses included 971, 1206, and 1583 cubic meters per second (c·m·s) in the Brazos River, and 345, 453, and 852 c·m·s in the Navasota River (Gooch et al. 2012).

We analyzed a continuous time series of flows including unregulated (pre-impact) and regulated (post-impact) time periods and noted the timing of impoundment construction along each river modeled. We developed generalized additive models (GAMs) using flow pulse counts (response variable) fitted as a function of time (explanatory variable) for each recurrence interval independently. We elected to use a generalized model structure with a negative-binomial error distribution, because the response variable was bound by zero, variance was greater than the mean, and used an additive model structure because the relationship between pulses and time was nonlinear (Wood 2006). We fit smoothing functions to time (years) that varied by our factor variable, gage identity (Brazos versus Navasota Rivers) to look at the interaction between this factor and time. Models were fit and summary statistics and parameter estimates were obtained using the "mgvc" package (Wood 2006) in R.

Stationary telemetry

For stationary telemetry, we used generalized linear mixed effects regression (GLMER) to model probability of fish occurrence in tributaries. This generalized model structure allowed us to use logistic regression and a binomial error distribution to encompass the binary structure of our response variable. Using mixed effects allowed us to account for nonindependence of repeated observations of the same fish

by using fish identification as a random term in the model. We allowed the intercept and slope of the relationships to vary by the random terms specific to each model (Harrison et al. 2018). We included four explanatory variables to test our hypotheses (Table 3) in this analysis: mean daily Brazos River discharge (c·m·s) measured at the Highway 21 crossing near Bryan, TX (USGS Gage ID 08108700); mean daily Brazos River temperature (°C) using a TidbiT deployed immediately downstream of the Navasota River confluence (Fig. 2); fish total length (cm); and predicted fish sex.

We considered all possible subsets and combinations of explanatory variables as well as univariate models (e.g., discharge only) and used Akaike Information Criterion corrected for small sample size (AICc) to compare candidate models, including an interaction term for discharge and temperature, and considered models competing when ΔAICc < 2. After model selection, we plotted the marginal effects of our top model. Prior to modeling, discharge, temperature, and fish total length were transformed using the "BestNormalize" package in R to best approximate Gaussian distributions and aid in model convergence (Peterson 2021). An ordered quantile normalization transformation was used on the explanatory variables and is notated by $Z_{parameter}$, where Z is the standard normal distribution with a mean of 0 and standard deviation (SD) of 1. For example, $Z_{Discharge} = 1$ would be a discharge datum that was ranked at 1 SD above the mean of transformed data, $Z_{Discharge} = 0$ (see the Supplementary Material, Data Transformation, for more details). For clarity, we plotted both transformed and untransformed explanatory variables and interpreted the untransformed predictors. Model fit was assessed using adjusted McFadden's pseudo-R^2 values for logistic regression. The scale of these pseudo-R^2 values is considerably lower than R^2 values using ordinary least-squares regression, where pseudo-R^2 values ranging from 0.2 to 0.4 are considered excellent fit (McFadden

1978). We fit GLMER models using the "lme4" package and developed and assessed candidate models from the "MuMIn" package in R (Barton 2009; Bates et al. 2014).

Mobile telemetry

We further modeled alligator gar detections across mainstem and tributary locations using mobile telemetry as an additional method for testing our hypotheses of tributary occurrence (Table 3). For this analysis, we used the same procedures as described for the stationary telemetry analysis. We classified the "state" of fish location for each tracking event using GPS coordinates. This resulted in three mutually exclusive states, where each fish was located in either the mainstem, a tributary, or not detected. We then used multinomial logistic regression (MLR) to model the relationship between fish state and the explanatory variables. After determining our top model through AICc, we used cross-validation to assess model accuracy. Accuracy of the top model was conducted by splitting the original dataset into testing and training sets (i.e., 40% testing, 60% training) and used as input for a confusion matrix to determine its degree of misclassification (Supplementary Table S2). The MLR output gives the probability of alligator gar being observed in each state where marginal effect plots from our top model were interpreted as with the GLMER results. MLR models were developed using the "nnet" package in R (Venables and Ripley 2002). All analyses were conducted in R version 4.1.2 (R Core Team 2021).

Results

Flow pulses

Flow data from the Brazos River gage were available for the period 1900–2018, and available data for the Navasota River ranged 1925–2018. For the Brazos River, there were significant reductions in pulse frequencies at the 1-year, 2-year, and 5-year pulse thresholds, but no significant temporal changes in the Navasota River (Table 4). Pulse frequencies at all thresholds declined the most in the mainstem Brazos River between approximately 1940 and 1980 during the period of impoundment construction (Fig. 3). Pulse frequencies in the mainstem dropped below frequencies in the Navasota after 1980 for the 1-year (Fig. 3a) and 2-year (Fig. 3b) thresholds. The decline of 5-year pulses in the Brazos River resulted in flow pulse frequencies that matched the Navasota River after 1980 (Fig. 3c).

Telemetry summary

Forty-five alligator gar (118–238 cm TL) were tagged during the study. Two individuals were not tracked due to one sedentary tag and one confirmed death. The remaining 43 individuals were relocated at least once and monitored between 1 and 16 months ($\bar{x} = 8.6$ months, SD = 4.6), resulting in 132 546 stationary receiver detections (Supplementary Table S3) and 259 mobile relocations that varied across individuals (range = 1–12 relocations, $\bar{x} = 6$, SD = 3.12). Twenty-nine of the 43 individuals met our duration criteria. However, five individuals were only detected through mobile telemetry, leaving 24 individuals for further analysis of stationary telemetry

data (Fig. 4a). Of these 24, we analyzed 14 individuals that made mainstem–tributary transitions, and these fish comprised 79% of the observations from the original dataset. The remaining 10 individuals were only detected in tributaries and not further analyzed. Of the 29 fish retained for duration (Fig. 4b), we analyzed 18 individuals that made mainstem–tributary transitions detected through mobile telemetry, and these fish comprised 54% of the observations from the original dataset. Ten of the 11 remaining individuals were only found in tributaries, while 1 individual was detected exclusively in the mainstem and was not analyzed (see Supplementary Table S4 for more information). Based on these data, mean displacement between relocations was approximately 6 km. However, several movements above 20 km into tributaries were observed during a high-water event from May to July 2021. Although spawning was not directly observed, several age-0 alligator gar were collected while conducting mobile telemetry during this high-water event in the Navasota River.

Stationary telemetry

Of the candidate GLMER models we assessed, the top model consisted of a two-way interaction term for discharge and temperature (i.e., Brazos River discharge and temperature). Support for this model was strong as it contained the lowest AICc value, the highest relative likelihood, had a high adjusted McFadden's R^2 of 28%, and no competing models (Table 5). The marginal effect plot of discharge showed an increase in the probability of alligator gar occurrence in tributary streams as discharge increased (Fig. 5a). When discharge values exceeded 400 c·m·s, the probability of alligator gar in tributaries was above 90% (Fig. 6a). There was strong agreement among individual fish observations at the random individual level, except for one individual that was predicted to be present in tributaries regardless of discharge (Fig. 5b). The marginal effect of temperature displayed a slight increase in tributary occurrence (Fig. 5c) with the highest probabilities occurring above mean temperatures of 25 °C (Fig. 6b). However, several individuals showed an opposing trend of declining probability of occurrence in tributaries as water temperature increased (Fig. 5d).

Mobile telemetry

Using the same candidate models for mobile telemetry, the top model consisted of a two-way interaction term for temperature and discharge (i.e., Brazos River discharge and temperature), along with the main effect of fish total length. This model also had the lowest AICc value, highest relative likelihood, moderate adjusted McFadden's R^2 of 19%, and no competing models (Table 5). Partitioning of the data and subsequent cross-validation revealed that the model had a misclassification rate of 39%. The parameter estimate for discharge was positive, revealing that the probability a fish was undetected increased with discharge. For the interactive parameter, the marginal effects plot for discharge at a temperature 1 SD below mean values (16 °C) showed a reversal of high probabilities between mainstem and not detected states with increases in discharge, while tributary probabil-

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Table 4. Summary of parameter estimates and smoothing functions for generalized additive models fit to the relationship between time and frequency of 1-year, 2-year, and 5-year flood pulses in the Brazos and Navasota rivers.

Flood frequency	Parameter estimates					Smoothing functions				
	Parameter	Estimate	SE	Z	p value	Parameter	edf	df	χ^2	p value
1-Year	Intercept	−0.72	0.18	−4.00	<0.01	GageBrazos	3.09	3.86	35.8	<0.01
	GageNavasota	0.51	0.23	2.26	0.02	GageNavasota	1.06	1.12	0.39	0.54
2-Year	Intercept	−1.69	0.34	−5.00	<0.01	GageBrazos	2.25	2.84	24.23	<0.01
	GageNavasota	1.03	0.38	2.75	<0.01	GageNavasota	1.00	1.00	2.26	0.13
5-Year	Intercept	−4.00	1.87	−2.14	0.03	GageBrazos	3.92	4.78	10.96	0.04
	GageNavasota	1.86	1.90	0.98	0.33	GageNavasota	1.00	1.00	0.01	0.92

Note: Parameter estimates represent the coefficients for intercept, standard error (SE), test statistic (Z), and the p value for each term in the model. Smoothing functions represent the effective degrees of freedom (edf), reference degrees of freedom (df), test statistic (χ^2), and p values for the smoothing functions derived from the gage locations.

ity simultaneously decreased under these "cool" conditions (Fig. 7a). At mean temperature of 23 °C, the probability of mainstem and not detected states followed a similar pattern to their response under "cool" conditions; however, tributary state probability increased and approached a 50% probability at values above mean discharge (Fig. 7b). At 1 SD above the mean temperature (29 °C), fish transitioned from mainstem to tributary states along a gradient of discharge magnitudes (Fig. 7c). Under these "warm" conditions, there was a reversal in states such that fish were predominantly in the mainstem at lower discharges, but above 500 c·m·s alligator gar occurrence exceeded a 75% probability for the tributary state (Fig. 6c). As temperature values increased, there was a decrease in the probability of fish being in the mainstem state and a concordant increase in probability of being undetected or detected in a tributary (Fig. 7d). However, tributary state probability remained below 50% across all temperatures (Fig. 6d). For fish total length, there was an increase in tributary occurrence and decline in the mainstem occurrence with increases in fish size (Fig. 7e), where the largest fish tagged (>200 cm) were most likely to be detected in tributaries (Fig. 6e).

Discussion

This study provides insight into the use of tributary habitats by a migratory fish inhabiting a regulated river. The Brazos River provides a microcosm for the global changes occurring in regulated rivers (Lehner et al. 2011), generally characterized by the removal of large flood pulses that historically provided mainstem river–floodplain connectivity. We found a clear reduction in the 1-year, 2-year, and 5-year flood frequencies along the Brazos River, but no detectable changes occurring in the Navasota River. These changes collectively created a reversal of pulse conditions such that the tributary now has greater pulse frequencies. Similar patterns in regulated rivers have led to the realization that tributary streams are essential in buffering the effects of riverscape alteration on large river biota in general, and fishes in particular (Pracheil et al. 2009; 2013).

The movements of alligator gar into and out of tributary streams suggest that transitions across the mainstem–tributary ecotone are predictable based on combined conditions of discharge magnitude and water temperature. This finding is similar to increased mainstem–tributary transition rates of alligator gar observed by Kluender et al. (2017) during elevated flows and temperatures. Previous studies suggested that inundation of floodplain habitat characterized by high-flow pulses during elevated seasonal temperatures is critical for successful recruitment of alligator gar (Robertson et al. 2018; Smith et al. 2020a). However, the inundation of mainstem floodplains requires higher pulse magnitudes compared with tributary streams, and these magnitudes might not be possible in some mainstem rivers under regulated and nonstationary hydrologic conditions (Poff 2018). Our work provides empirical evidence that high-flow pulses elicit a movement response among alligator gar, particularly when pulses occur during warmer water temperatures. These results provide quantitative guidance on management of flows that provide connectivity pathways for alligator gar in the Brazos River (Gooch et al. 2012), but more broadly, we elucidate ecological patterns that might be critical for the conservation of other migratory fishes inhabiting regulated rivers.

Previous research has established ecological links between flow pulses and occurrence or recruitment of small-bodied, opportunistic strategist fishes, such as the shoal chub (*Macrhybopsis hyostoma*), plains minnow (*Hybognathus placitus*), smalleye shiner (*Notropis buccula*), and sharpnose shiner (*Notropis oxythrynchus*) (Rodger et al. 2016; Nguyen et al. 2021). Our work broadens the understanding of flow–ecology relationships in the Brazos River by analyzing responses of a periodic life history strategist. We found that movement of alligator gar into tributary habitats was strongest when temperatures were above 25 °C and mainstem discharge exceeded 400 c·m·s, equivalent to a three-pulse-per-season recurrence interval (Gooch et al. 2012). This provides critical information pertaining to the ecological benefits of larger, rarer flow events less likely to occur within the life span of the average opportunistic species (Stewart-Koster et al. 2014). Konrad et al. (2011) suggested that reservoir releases might be timed with natural high-flow periods to achieve larger magnitude releases in regulated rivers. Given the rise of large-scale flow experiments, our study provides information that

Fig. 3. Generalized additive model fits from an analysis of mainstem versus tributary flood pulse frequencies for the (*a*) 1-year; (*b*) 2-year; and (*c*) 5-year recurrence intervals. Dark blue lines represent the smoothing function for the Brazos River models (dark blue circles) and light blue lines represent the smoothing function for the Navasota River models (light blue triangles) across time (years) for the flood count at each recurrence interval. Light grey shading areas are the 95% confidence intervals. Dashed lines represent the period of reservoir impoundment (approximately 1940–1980).
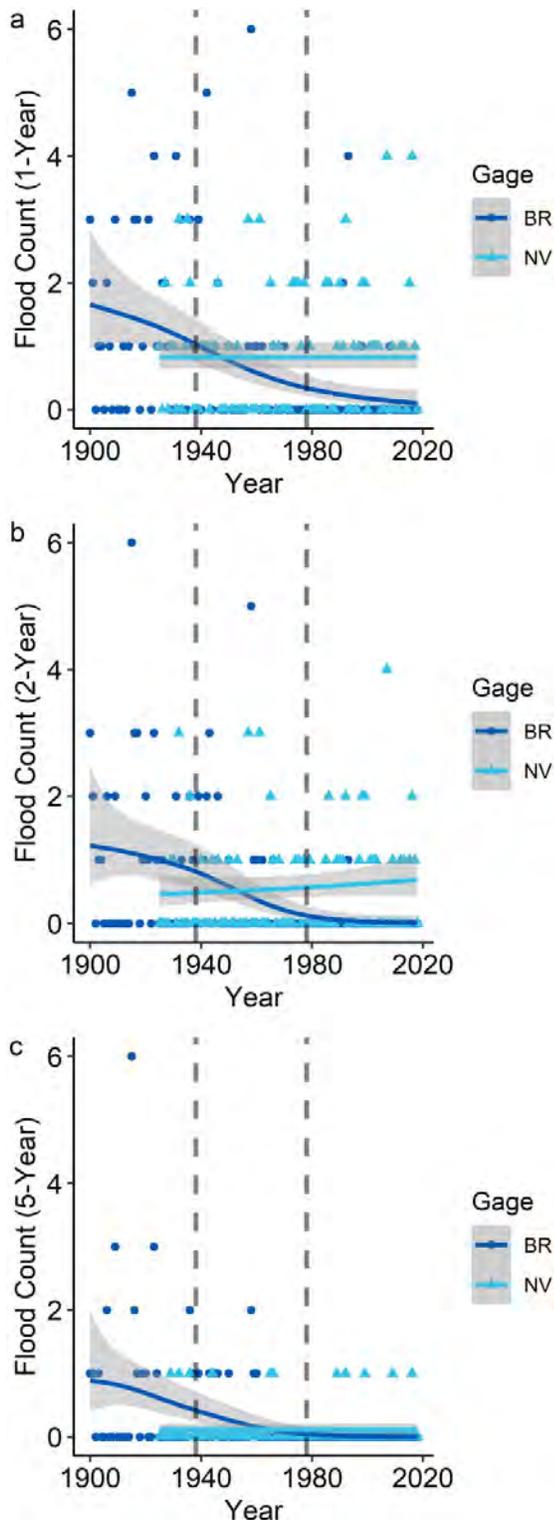
might be used to generate new hypotheses to be tested during these experiments, such as identifying discharge thresholds that elicit movement into tributaries and using flood inundation modeling techniques to validate floodplain connectivity and quantify spawning habitat during relevant flows (Olden et al. 2014). The broad spatial overlap between regulated rivers and distributions of migratory fishes reinforces that migratory fishes can serve as useful indicators to assess environmental flows for regulated rivers worldwide (Grill et al. 2019; Alò et al. 2021).

The coupled effects of habitat fragmentation and flow alteration broadly affect stream fish assemblages, but these effects might be offset by tributary connections. Within freshwater ecosystems, the importance of suitable river temperature and discharge conditions for fish migrations is well documented (Albanese et al. 2004; Taylor and Cook 2012). The migratory behaviors of fishes are often considered an adaptation to the dynamism in the environmental conditions under the natural flow regime (NFR) within lotic systems (Poff et al. 1997). We found that the historical frequency of floods in the lower Brazos River was much higher than under current conditions, and this pattern is widely reported among regulated rivers (Magillian et al. 2003). Previous studies have documented the consequences of fragmentation and flow alteration among fishes with different migratory adaptations (Haro et al. 2000; Pelicice et al. 2015). However, persistence of migratory fishes within regulated rivers may be explained by their plasticity and use of alternative migratory routes, such as tributaries, in the presence of impoundments on mainstem rivers (Antonio et al. 2007). Historically, flooding likely occurred in mainstem rivers and tributaries alike, leading to an adaptation to multiple migratory reproductive routes among migratory fishes (Koster et al. 2021). However, given many large mainstem rivers are fragmented today, selection toward migratory routes in tributaries that are more prone to flooding would be more advantageous for migratory fishes when mainstem–floodplain connectivity is more limited (Dunn et al. 2018). Tributaries can also provide biogeochemical inputs, such as organic matter, nutrients, and sediment, that can be limiting in fragmented mainstem rivers with disrupted energy flows (Sabo et al. 2018). These processes are known to positively influence the growth and survival of migratory fishes across various life history stages (Ebersole et al. 2006; Spurgeon et al. 2015). Therefore, tributaries that maintain certain aspects of the NFR provide a fitness advantage for migratory fishes that use these habitats for reproduction and early life stages (Pracheil et al. 2009, 2013). Our work extends the known benefits of tributaries to migratory fishes such as alligator gar by revealing common use of these habitats during higher temperatures indicative of the spawning season in a highly regulated river.

Although this study has elucidated predictors of tributary use for alligator gar, there are caveats and limitations that need to be acknowledged. Our study investigated just one migratory species in one system. However, given the extent of river regulation globally, other migratory fishes are likely challenged to respond to altered environments within fluvial networks (e.g., Koster et al. 2021). Further research in-

Fig. 4. Proportion of (*a*) stationary detections and (*b*) mobile detections sorted by water body for alligator gar retained by the duration filter. Water bodies represent detections in either the mainstem Brazos River (BR), or tributaries including the Little River (LR), minor tributaries (MT), Yegua Creek (YE), and the Navasota River (NV). Individuals that made mainstem–tributary transitions detected from stationary (*n* = 14) and mobile telemetry (*n* = 18) methods were used for further analyses and highlighted with dashed boxes.
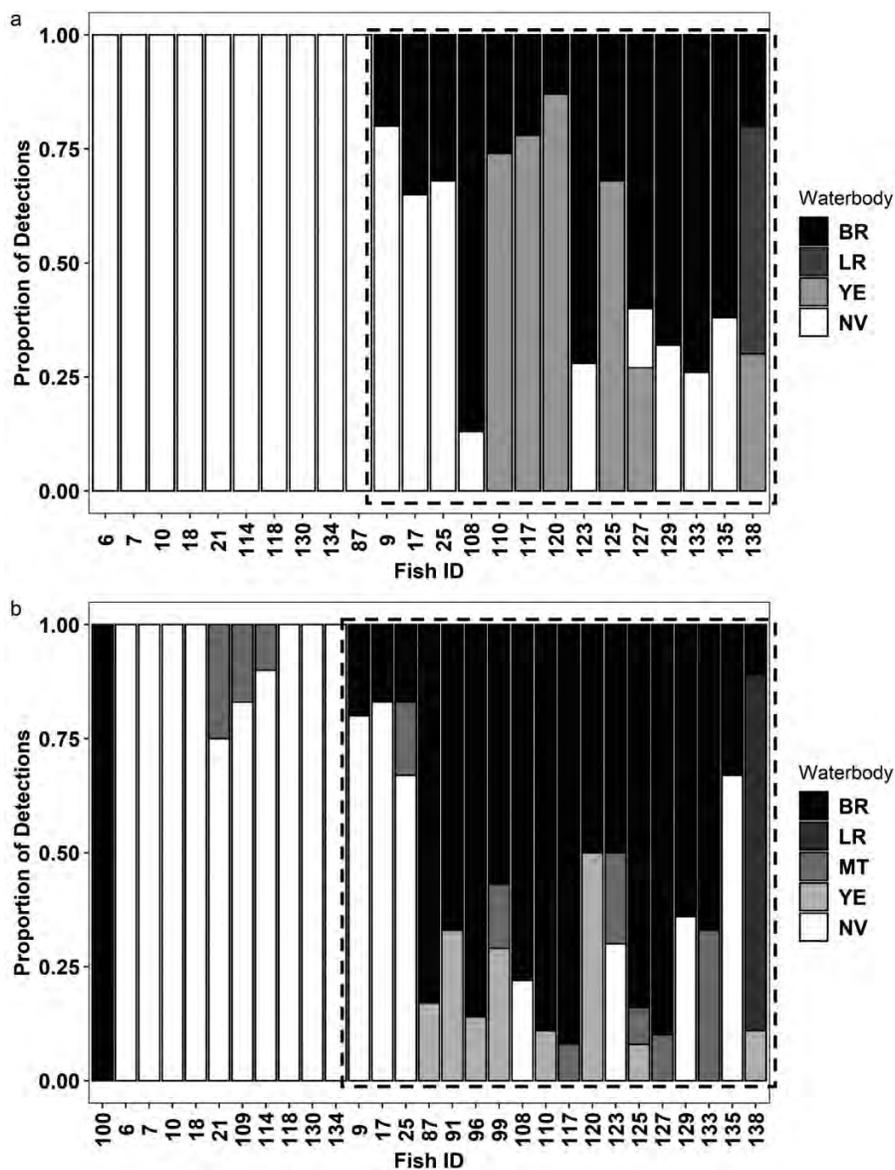
vestigating tributary use of migratory fishes inhabiting regulated rivers elsewhere could address the generality of this paradigm. Furthermore, we were unable to relocate every tagged fish during every tracking session, likely due to signal attenuation and the exponential increase in search area during higher flows. Signal attenuation caused by increased water depth and high conductivity is well known for radio-transmitters, and therefore we relied on ultrasonic transmitters or CART tags in our study design. However, interference from high velocities during higher flows cannot be ruled out as contributing to our inability to find some individuals (Cooke et al. 2013). This might explain why the probability of fish assigned to mainstem state in our MLR model suddenly transitioned to the undetected state as discharge increased during cooler temperatures (i.e., 16 °C). As modeled water temperature increased to 23 °C, increased discharge correlated with a greater number of undetected fish. We hypothesize this was related to fish moving into expansive floodplains where logistics prevented comprehensive searches and shallower water likely reduced ranges of ultrasonic transmitters (Kluender et al. 2017). Furthermore, there were differences in fish retained for our analyses across stationary and mobile telemetry techniques, due to differences in our ability to quantify tributary use between both methods. We observed less mainstem–tributary transitioning fish using stationary telemetry because the fixed locations of these receivers could

Table 5. Akaike information criterion for small sample size (AICc) ranking the top five GLMER models predicting tributary probability (TP) for the stationary telemetry dataset (top-half) and top five MLR models for predicting state probability (SP) for the mobile telemetry dataset (bottom-half).

Dataset	Model structure	k	AICc	ΔAICc	ω	Adjusted psuedo-R^2
Stationary	TP(D∗T)	4	945.5	0	0.58	0.28
	TP(D + S + T)	4	948.3	2.8	0.14	0.28
	TP(D∗T + S)	5	949.0	3.5	0.10	0.29
	TP(D + T)	3	949.5	4.0	0.08	0.27
	TP(D + T + TL)	4	950.2	4.7	0.05	0.28
Mobile	SP(D∗T + TL)	5	264.1	0	0.73	0.18
	SP(D∗T + S + TL)	6	267.4	3.3	0.14	0.18
	SP(D∗T)	4	267.9	3.9	0.11	0.13
	SP(D∗T + S)	5	271.4	7.3	0.02	0.11
	SP(D + T + TL)	4	273.9	9.8	<0.01	0.13

Note: Candidate model structure includes predictions as a function of discharge (D), water temperature (T), fish total length (TL), predicted fish sex (S), and various subsets and combinations of the parameters with additive (+) or interactive (∗) terms. For each model, we report the number of parameters (k), AICc score, ΔAICc, relative likelihood (ω), and McFadden's R^2. Note that the pseudo-R^2 value demonstrates model fit but not on the same scale as the traditional coefficient of determination.

Fig. 5. Marginal responses from the top GLMER model out of our candidate models in the stationary telemetry dataset including (*a*) the population-level response to mainstem discharge ($Z_{Discharge}$); (*b*) the random individual-level response to mainstem discharge; (*c*) the population-level response to temperature ($Z_{Temperature}$); and (*d*) the random individual response to temperature. Dark lines are the fitted response for each parameter at the population (single-line) and individual (line for each fish modeled) levels. Shaded grey regions are the 95% confidence intervals for the population-level models.
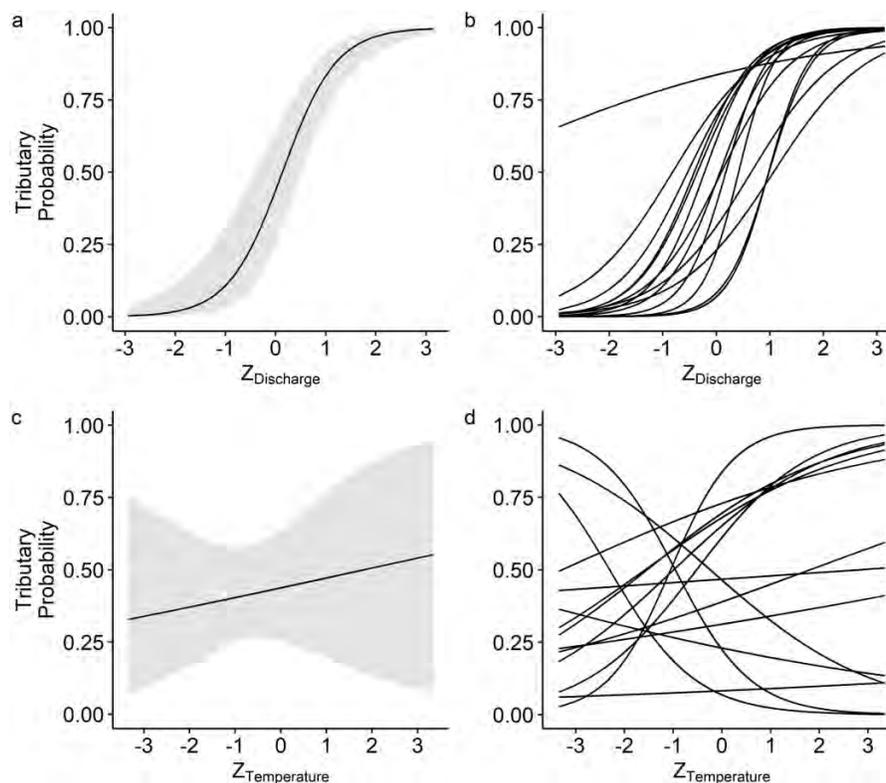
not account for the network of additional tributary streams within the study area. However, manual telemetry allowed us to determine additional tributaries alligator gar were using during high flows that our stationary grid was unable to detect. Therefore, we suspect that our analyses represent a conservative estimate of transitions and that a greater number of transitioning individuals likely occurred. Both stationary and mobile telemetry methods have advantages and disadvantages (Cook et al. 2013). Yet, the analysis of both techniques as others have done (e.g., Acolas et al. 2004; Buckmeier et al. 2013) gave consistent inferences regarding alligator gar tributary use.

Fig. 6. Marginal effect plots with untransformed data for predicting tributary occurrence of the top models in the stationary (*a*, *b*) and mobile (*c*–*e*) analyses, where (*a*) is the effect of discharge (c·m·s); (*b*) is the effect of temperature (°C); (*c*) is the interactive effect of discharge held at "warm" temperature conditions (i.e., 29 °C); (*d*) is the effect of temperature (°C); and (*e*) is the effect of fish total length (cm).
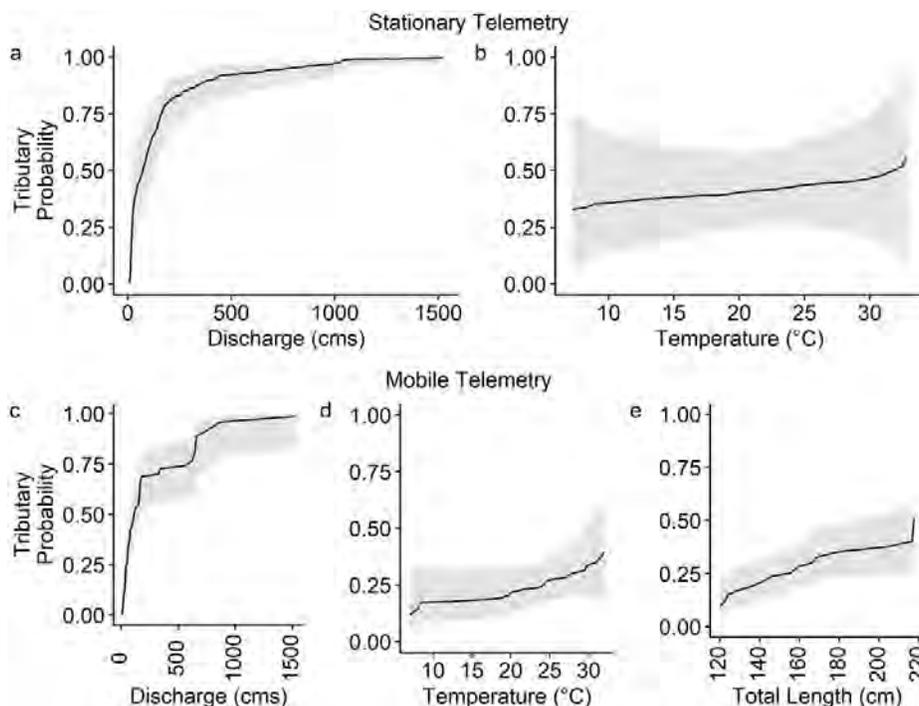
Fig. 7. Marginal responses from the top MLR model out of our candidate models in the mobile telemetry dataset including (*a*–*c*) the interaction between discharge ($Z_{Discharge}$) and temperature; (*d*) the main effect of temperature ($Z_{Temperature}$); and (*e*) the main effect of fish total length (Z_{TL}) for predicting state probability of occurrence (SP) in the three mutually exclusive states: mainstem (dark blue line), not detected (light blue line), and tributary (red line). Shaded areas represent the 95% confidence intervals for each state prediction. For (*a*–*c*), the effect of discharge (c·m·s) is shown to be held at (*a*) "cool" conditions 1 SD below mean temperature (16 °C); (*b*) "average" conditions at mean temperature (23 °C) conditions; and (*c*) "warm" conditions 1 SD above mean temperature (29 °C).
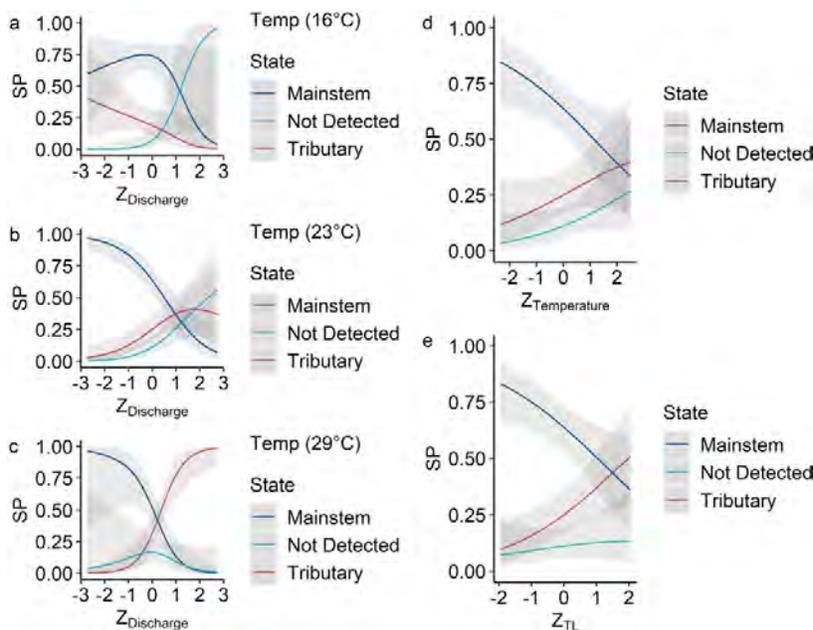
Conclusions

Large rivers are regulated on a global scale (Grill et al. 2019) and declines among riverine fishes are commonly attributed to this alteration (Haro et al. 2000; Pelicie et al. 2015). Migratory fishes in particular are sensitive to effects of flow alteration and fragmented lateral connectivity (Pracheil et al. 2009). Despite this sensitivity, migratory fishes persist in regulated riverscapes, perhaps because tributary inflows and access corridors to floodplain habitats mitigate impacts of environmental changes in river mainstems. We studied movements of alligator gar in the Brazos River to test the emerging paradigm that tributaries provide essential corridors and access to floodplains in rivers with reduced flow pulses and lateral connectivity in the mainstem. We showed that (1) flood pulses in the mainstem are infrequent in contemporary flows and a tributary continues to provide more frequent overbank pulses; (2) alligator gar migrate from mainstem to tributary habitats; and (3) these movements are driven primarily by discharge and water temperature. These findings can be used to develop more optimal management of alligator gar, further refine environmental flow standards, and act as a baseline for future studies investigating tributary use of migratory fishes inhabiting regulated rivers elsewhere.

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